



Rate of forest recovery after fire exclusion on anthropogenic savannas in the Democratic Republic of Congo

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ABSTRACT

Deforestation in the tropics is often followed by the creation of anthropogenic savannas used for animal husbandry. By discontinuing burning regimes, forests may recolonize the savanna and carbon stocks may recover. However, little is known about the success and speed of tropical forest recovery, while such information is vital for a better quantification of efforts to reduce emissions from deforestation and forest degradation (REDD+) as well as supporting Forest Landscape Restoration (FLR) practices. Therefore, we designed a forest regeneration experiment within a savanna patch in the Mayombe hills (Democratic Republic of Congo), by discontinuing the annual burning regime in an 88 ha exclosure since 2005. 101 permanent inventory plots (40.4 ha) were installed in 2010 and remeasured in 2014. Tree species were classified as savanna or forest specialists. We estimate a forest specialist encroachment rate of 9 stems $\text{ha}^{-1} \text{yr}^{-1}$ and a savanna specialist disappearance rate of 16 stems $\text{ha}^{-1} \text{yr}^{-1}$. Average diameter of forest specialists did not change due to an increasing influx of recruits, while average diameter of savanna trees increased due to decreasing recruitment. Carbon stored by forest specialists increased from 3.12 to 5.60 Mg C ha^{-1} , suggesting a forest carbon recovery rate of 0.62 $\text{Mg C ha}^{-1} \text{yr}^{-1}$. Using the average carbon stock of 19 nearby mature rainforest plots as a reference, we estimate a total forest carbon recovery time of at least 150 years. The Manzonzi exclosure may potentially become an important reference experiment to quantify REDD+ schemes in Central Africa. Furthermore, this natural regeneration experiment demonstrates how carbon sequestration and biodiversity conservation can go hand-in-hand. However, more censuses are needed to better quantify the long-term carbon recovery trajectory within the protected area.

1. Introduction

Tropical intact forests account for about half of the terrestrial sink in established forests (Brienen et al., 2015; Lewis et al., 2009), storing about 55% of terrestrial carbon (Pan et al., 2011), yet covering only 7 to 10% of the global land area (Lewis et al., 2009). However, deforestation increasingly accounts for forest and carbon loss (Baccini et al., 2017). Gross tropical deforestation emissions ($2.9 \pm 0.5 \text{ Pg C year}^{-1}$) are only partly compensated by tropical forest regrowth ($1.6 \pm 0.5 \text{ Pg C year}^{-1}$), thus the tropics account for a net carbon source of $1.3 \pm 0.7 \text{ Pg C year}^{-1}$ due to land-use change (Pan et al., 2011).

Deforestation in the tropics contributes 3–17% to global anthropogenic CO_2 emissions (Baccini et al., 2012; van der Werf et al., 2009;

Harris et al., 2012). Causes for this deforestation are increasing land demands for urbanization, agriculture (through permanent or shifting cultivation) and industrial timber exploitation. In Central Africa, intentional burning is a widespread technique to clear dense vegetation covers and prepare the land for cultivation of crops or animal husbandry. This potentially results in substantial reduction of plant biomass (Bond et al., 2002), with large areas becoming savannas in terms of species composition and nutrient levels (Silva et al., 2013). Moreover, artificial tropical savannas are often maintained by intense fire regimes (Walker, 1981).

However, anthropogenic savannas can be converted back into forests. Bond et al. (2002) stated that some fire-prone ecosystems maintained by humans might be far from the physiological limits

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determined by climate. Accatino et al. (2011) showed that fire exclusion from savannas can result in increasing tree cover quickly (also shown by Shackleton and Scholes, 2000; Trapnell, 1959), eventually leading to larger carbon stocks. Carbon sequestration is nowadays regarded as one of the most important forest ecosystem services and in recent years there has been an increase in reforestation and afforestation projects throughout the tropics (The World Bank, 2018; WWF, 2017). These projects not only ensure continuing provision of ecosystem services and biodiversity conservation, but they also create the opportunity to receive funds through carbon credits. These funds can then be used for the development of local communities through REDD+ and payment for ecosystem services (PES) schemes. Precise and detailed carbon stock and sequestration estimates are vital towards creating carbon maps (for example the National Forest Carbon Map of the DRC), which can be used towards support for REDD+ programs, monitoring of forest cover and facilitating the assessment of carbon emissions (Saatchi et al., 2017; WWF, 2017). As stated by Ziegler et al. (2012) there is a need for experiments that demonstrate which transitions result in long-term, verifiable gains in sequestered carbon. Their meta-analysis from over 250 studies in SE Asia concluded that the abandonment of any agricultural system for permanent forest regeneration resulted in a certain positive carbon outcome. Another important aspect, besides carbon stock enhancement, is the potential of REDD+ schemes to deliver additional biodiversity benefits, through protection, managing and enhancing forests (Phelps et al., 2012). In this way, REDD+ schemes allow to integrate community development, carbon stock enhancement and biodiversity conservation. Although certain trade-offs exist and should be recognized (see Sullivan et al., 2017), the Congo Basin represents a prospective win-win outcome due to the carbon and biodiversity priority overlap (Phelps et al., 2012). The conversion from anthropogenic savannas to forests through fire exclusion has the potential to facilitate both the increase in carbon stock and conservation of biodiversity.

Certain conditions need to be met to successfully convert savanna into forest. Recruitment distance, or the distance from a mature forest is key in that aspect. Swaine et al. (1992) stated that fire exclusion patches develop faster if they are closer to mature forest. Rainfall is essential as well, as Sankaran et al. (2005) indicated that savannas with annual rainfall lower than 650 mm (dry savannas) are stable ecosystems (see also Favie et al. (2012)). Moist savannas with an annual rainfall regime exceeding 650 mm are mostly unstable ecosystems, and they might undergo a transition to a woodland system under optimal conditions (e.g. no disturbance by humans). However, the density of the tree cover does not always increase continuously with rainfall (Stayer et al., 2011).

Successful fire exclusion experiments have been conducted and reported on in South America and Africa. San Jose et al. (1998) assessed the changes in carbon stock and tree density in a 3 ha permanent plot, protected against fire and grazing, in the Biological Reserve Calabozo (Orinoco Llanos plains, Venezuela). They noticed an increase in carbon stock in the woody vegetation from 0.21 to 4.64 Mg C ha⁻¹ over a 25 year period. Moreira (2000) discussed the effect of fire exclusion on vegetation structure and composition of Cerrado savannas in Brazil, reporting an increase in woody plants, especially in open physiognomies. Swaine et al. (1992) inventoried a plot of 50 × 35 m in 1989 protected from fire and grazing since 1957 in Ghana. They noticed the appearance of forest canopy species and even important timber species like *Milicia excelsa* (Welw.) C.C.Berg. The success of this experiment was probably due to its proximity to a forested zone (Kpong, Ghana). Higgins et al. (2007) studied the effect of four decades of fire manipulation on woody vegetation in Kruger National Park (South Africa) and concluded that although the exclusion of fire influenced the size structure and biomass of certain tree populations, overall average stem density was not influenced by fire frequency, fire season or total fire exclusion. King et al. (1997) discuss the conversion of an anthropogenic savanna to forest in Gabon by protecting the savanna-forest edge from

fire. After three years, there was a rapid colonization by 45 species of tree seedlings in less-degraded savannas. The colonization of higher-degraded savannas happened at a much lower rate.

The examples of fire exclusion experiments described in the literature are mostly confined to the forest-savanna ecotone. Few fire exclusion experiments have been reported in Central Africa, an area that is under increasing deforestation pressure but with a great potential for successful forest regeneration due to favourable moist climatic conditions and the abundance of remaining forest patches. Therefore, the main objectives of this research are (1) to determine whether fire exclusion can lead to natural forest recovery in the Congo Basin by evaluating the species composition transition, (2) an estimation of the rate of forest recovery (in terms of stem density and carbon stocks), (3) an estimation of the time needed for full recovery of mature rainforest and (4) assessing the conservation potential of regenerating forest from a savanna patch. We selected a patch of savanna at the southernmost boundary of the Mayombe hills in the Lower Congo Province of the Democratic Republic of the Congo. This savanna patch is located in an area experiencing favourable conditions for rainforest, and the surrounding rainforest patches provide an influx of seeds. In order to monitor the success of forest recovery, a part of the savanna patch was excluded from burning and grazing since 2005 and tree species composition was monitored in two different inventory campaigns.

2. Methods and materials

2.1. Study area

This research was conducted in a 200 ha savanna patch near the villages of Manzonzi and Mao (S 5°43'45" – E 13°15'0"), a few km south of the UNESCO Man and Biosphere Reserve of Luki and approximately 30 km north of the city of Boma (Lower Congo province, Democratic Republic of the Congo, hereafter referred to as DRC) (Fig. 1). The savanna patch is located at the southernmost edge of the Mayombe hills, which are covered with semi-deciduous rainforests. The southern Mayombe hills experience a tropical climate with two distinct seasons. According to the Köppen Classification, the Mayombe is part of an Aw system (tropical savanna or tropical wet and dry climate), with a distinct dry season from June to September. Mean annual rainfall is 1180 mm yr⁻¹ and mean annual temperature is 24.6 °C. First rains start in September–October and end in May.

The Mayombe region consists of a chain of forested hills stretching along the Atlantic Ocean from Gabon down to the Luki reserve (Hubau et al., 2012, 2013). It is part of the lower Guinean forest complex which is, together with the Congolian forest, part of the Central African forest complex (Hubau et al., 2012). The vegetation in the Mayombe hills is very fragmented (Hubau et al., 2015). Semi-deciduous forest patches are abundant in the north of the Congolese Mayombe hills (border with Congo-Brazzaville), while woodland savannas and grasslands are more abundant towards the Angolan border in the south (Fig. 1). The inhabitants of the region (and in particular the Manzonzi and Mao savannas) depend on savannas and grasslands for agriculture and cattle grazing and on woodlands and forests for hunting and gathering of fuelwood. Intensification of these activities has been an increasing threat to the forest ecosystem and forest fragmentation is an ongoing process. Hence, forest restoration programs are much needed to secure future forest ecosystem services in the area.

2.2. Plot enclosure and establishment

Within the 200 ha Manzonzi savanna patch, a contiguous 88 ha fire enclosure area was installed in 2005 with the logistic and financial support of WWF-DRC and WWF-Belgium. No cattle gates were installed, but an agreement was made with the local community to prevent burning and grazing. Within this enclosure, 101 separate tree inventory plots of 50 m by 80 m were put in place in 2010, each plot with an area

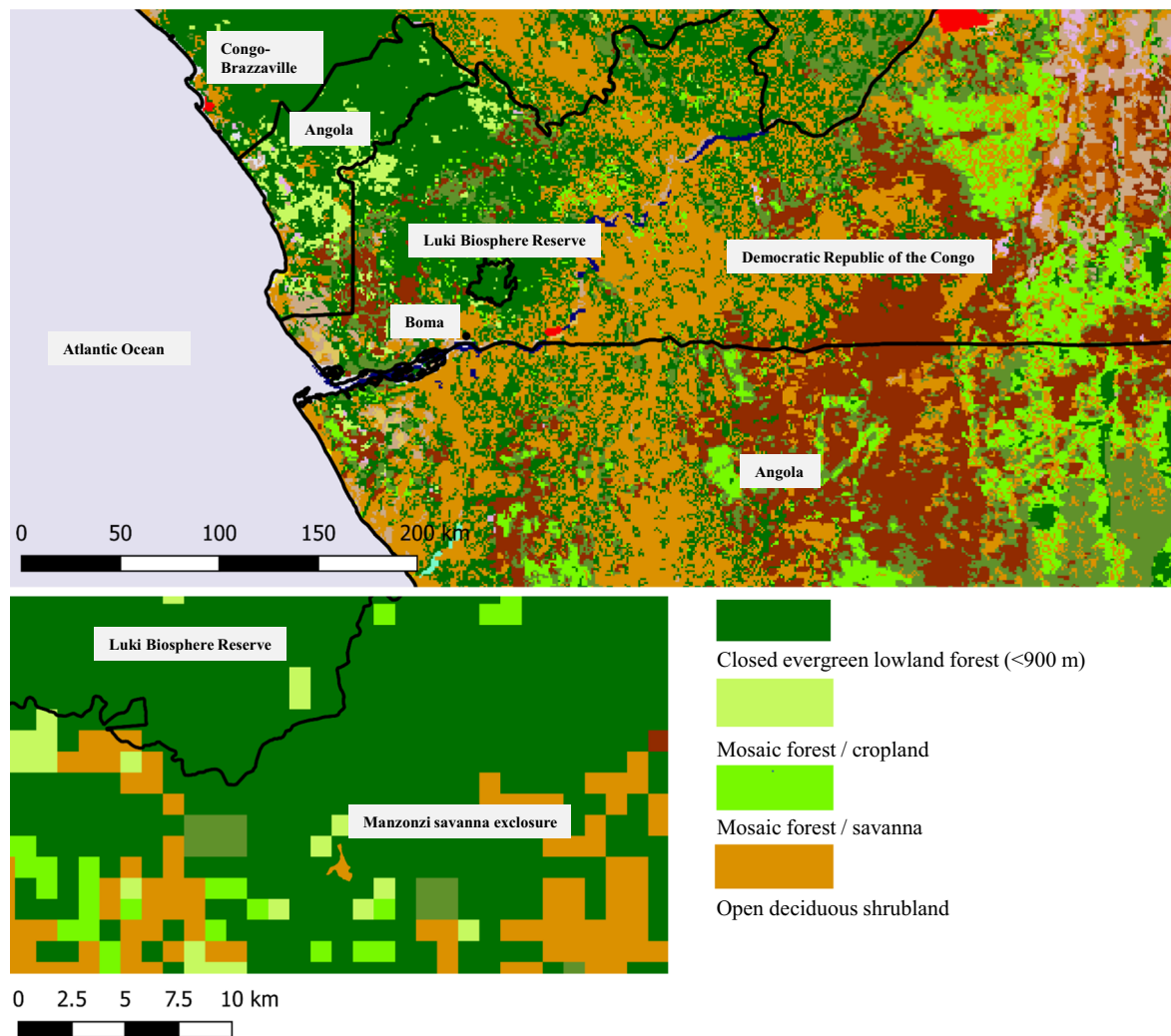


Fig. 1. Location of the Manzonzi enclosure in the Democratic Republic of the Congo.

of 0.4 ha, resulting in a total monitoring area of 40.4 ha. The plots are arranged in ten parallel North-South transects spread over the width of the enclosure. Since the start of the experiment, eight plots were transformed back to agricultural land. Therefore only the 93 undisturbed plots (comprising 37.2 ha) were used in the analysis.

The first inventory of the plots was done in 2010. Standard forest inventory protocols commonly use a 10 cm DBH threshold for tree diameter measurements (Phillips and Baker, 2009). However, as forests in an early stage of regeneration are characterised by an increasing abundance of small trees, we measured every tree with a DBH larger than or equal to 6.37 cm (circumference = 20 cm). Trees were tagged, measured at breast height (1.3 m) with a tape measure and determined to species level. In 2014 the same plots were inventoried again using the same protocol. Small trees that grew larger than 20 cm circumference during the monitoring period were recorded as recruits, tagged and measured.

2.3. Reference data

In order to compare Manzonzi stem metrics (density, diameter, carbon stock) with those of plots established according to standard procedures, both the 2010 and 2014 datasets were divided in two parts: the 'small trees dataset' ($6.37 \text{ cm} \leq \text{DBH} < 10 \text{ cm}$) and the 'large trees dataset' ($\text{DBH} \geq 10 \text{ cm}$). As such, we can compare the big trees dataset with a reference dataset of 19 permanent forest inventory plots that are located in the core area of the nearby Luki Biosphere reserve (Fig. 1).

These plots were established in 2009 using standard methods (Phillips and Baker, 2009). Each plot is 100 m by 100 m (1 ha) and all trees with $\text{DBH} \geq 10 \text{ cm}$ were tagged and measured. The rainforest plots in the Luki reserve serve as a reference dataset for the mature rainforest steady-state that is assumed to be the end-point of the Manzonzi savanna-to-forest recovery process.

2.4. Species classification

Each species in the Manzonzi enclosure dataset was classified according to its light preference, habitat preference and growth speed based on literature sources providing details on species-specific ecology and ecosystem preference. Most information was found in detailed vegetation descriptions of the Mayombe (Donis, 1948), the Bas-Congo (Compère, 1970), the Lower Guinea (Meunier et al., 2015), DRC (Lebrun and Gilbert, 1954) and Central Africa (Vandeweghe, 2004). Additional information was found in online databases (African Plants Database, 2016; Wageningen University and ICRAF, 2016).

Short-lived pioneers (SLP's) and long-lived pioneers (LLP's) are fast-growing species that can quickly colonize small or large clearings in a forest environment. They can form a closed canopy within 10 to 25 years after gap formation (Chazdon, 2008). SLP's grow fast but they don't live long, while LLP's grow slower compared to SLP's but they live relatively long and they can reach large dimensions. Non-pioneer light demanders (NPLD's) need a moderate amount of sunlight but they don't quickly colonize clearings. In a forest environment, they can germinate

and survive as seedlings under a semi-closed canopy (e.g. a pioneer forest), then grow steadily (Meunier et al., 2015). Finally, shade-tolerant species can grow under the canopy and reach mature dimensions without direct sunlight. They are abundant in the mature forest understory but they can also occupy large parts of old-growth forest canopy.

Subsequently, each species was assigned to one of the following four habitat classes: savanna specialists, transition specialists, forest specialists and non-specialists. The ‘savanna specialist’ class contains non-pioneer light-demanding species typically occurring in open and dry woodland formations, or tree savannas. Examples are *Hymenocardia acida* Tul., *Crossopteryx febrifuga* (Afzel. ex G.Don) Benth., *Bridelia ferruginea* Benth. and *Maprounea africana* Müll.Arg. The ‘transition specialist’ class contains typical short-lived, fast-growing forest pioneers (SLP’s) such as *Macaranga spinosa* Müll.Arg. and *Musanga cecropioides* R.Br. ex Tedlie. The ‘forest specialist’ class contains long-lived pioneers (LLP’s) and non-pioneer light demanders (NPLD’s) that typically occur in old regenerating forests. Examples are *Albizia adianthifolia* (Schum.) W.Wight and *Lannea welwitschii* (Hiern) Engl. This class also contains some shade-tolerant species that typically occur in old-growth mature forests, such as *Aidia ochroleuca* (K.Schum.) E.M.A.Petit and *Trichilia gilgiana* Harms. The ‘non-specialist’ class contains species with a wide ecological amplitude, occurring in both forest and savanna ecosystems. Finally, for some species, ecological information is very scarce or non-existent so they could not be classified. In the following analysis only trees classified as forest, savanna or transition specialists are used (99.6% of the trees in the experiment). Appendix A presents a list of the species occurring in the experiment and their habitat classification.

2.5. Static forest metrics

For each tree and each census, Aboveground Biomass at the tree level (AGB, Mg stem⁻¹) was estimated using a published allometric equation for moist forests. This equation includes terms for diameter (DBH, mm), wood specific gravity (ρ , g cm⁻³) and total tree height (H, m) (Chave et al., 2014): $AGB_{est}(Mg) = 0.0673 \times (\rho(D/10)^2 H)^{0.976} / 1000$. Wood density values were derived from the dryad database (www.datadryad.org). Stems were matched to species-specific wood density values or the mean values for the genus or family, following standard methods (Lewis et al., 2009; Lopez-Gonzalez et al., 2011). Individual total tree height (H, m) was calculated using the Central African height-diameter allometry presented by Feldpausch et al. (2011): $H = 50.4531 \times (1 - \exp(-0.0471 \times D^{0.81197}))$. Aboveground Biomass-Carbon (hereafter referred to as AGC) is considered as 47% of the AGB following IPCC recommendations (Aalde et al., 2006). AGC at the plot-level (Mg C ha⁻¹) is then calculated as the sum of AGC of all trees in the plot, divided by the plot area (ha). The AGC and amount of stems per hectare were determined for every dataset (large and small) and for each habitat preference class and compared between 2010 and 2014 using the Welch two sample *t*-test. Boxplots were constructed using RStudio (RStudio Team, 2015) based on plot-level calculations. Average values and 95% bootstrapped confidence intervals (package boot in RStudio, Canty and Ripley, 2017) for AGC (Mg C ha⁻¹), amount of stems (N, trees ha⁻¹) and DBH (mm tree⁻¹) were determined for the forest, savanna and transition class, for both the 2010 and the 2014 datasets and for both the small trees and large trees datasets. The same procedure was applied on the reference dataset of 19 forest plots in the Luki reserve. All results are given in Table 1.

2.6. Dynamic forest metrics

In our dataset, all species classified as ‘forest specialists’ are long-lived forest pioneers and all species classified as ‘transition specialists’ are short-lived forest pioneers (Appendix A). Both classes were considered as forest species for analysis of forest recovery rates. Calculations of dynamic forest metrics are based on the large trees dataset only.

We calculated a ‘forest stem encroachment rate’ (stems ha⁻¹ yr⁻¹) as the difference between the 2010 and 2014 forest and transition specialist stem density (stems ha⁻¹), divided by the total monitoring interval length (four years). Similarly, we calculated a ‘forest carbon recovery rate’ (Mg C ha⁻¹ yr⁻¹) as the difference between the 2010 and 2014 AGC (Mg C ha⁻¹) in forest and transition specialists, divided by the interval length. A ‘savanna stem disappearance rate’ (stems ha⁻¹ yr⁻¹) and a ‘savanna carbon loss rate’ (Mg C ha⁻¹ yr⁻¹) were calculated in similar ways, using the savanna specialist dataset.

The time needed for savanna carbon disappearance and savanna stem disappearance was determined by dividing the amount of carbon stored or stems present in savanna specialists in 2014 by the savanna carbon loss rate or savanna stem disappearance rate respectively.

Finally, we predicted a long-term forest carbon recovery trajectory using the 2010 and 2014 AGC estimates, and assuming an end-point equal to the average AGC in the reference rainforest plots. We chose the form of the trajectory using a savanna protection experiment of the Orinoco Llanos plains as a reference (San Jose et al., 1998). The Llanos savanna protection plot was inventoried 4 times over a monitoring period of 25 years after savanna protection, hence offers much needed insights in long-term carbon recovery trajectories. The data shows that the initial phase of carbon recovery is not a linear process, but follows an exponential trajectory (San Jose et al., 1998). However, it is most likely that carbon recovery will level off at a later stage of the recovery period, due to canopy closure and a saturation of stem recruitment, followed by a natural stem thinning phase (Chazdon, 2008). Hence, the long-term recovery trajectory will likely follow a sigmoidal pattern, which we describe here using a Gompertz model: $AGC = agc1 + ((agc2 - agc1) \times \exp(-1 \times \exp(-k \times (t - t_{inf}))))$; where AGC is the forest Aboveground Biomass-Carbon (in Mg C ha⁻¹) at a given time after savanna protection (*t*, in yr); *agc1* is the minimum AGC at the start of the trajectory (*agc1* = 0); *agc2* is the asymptotic maximum AGC (*agc2* = the average AGC in the reference rainforest plots); *k* represents the slope of the recovery curve at the point of inflection defined by *t_{inf}*. The Gompertz model shows an initial exponential increase in AGC, until the increase starts to decline at the point of inflection. The *k* and *t_{inf}* parameters of the Gompertz model were parameterized using nonlinear least squares regression (command *nls* from the stats package in R) (Bates and Chambers, 1992).

3. Results

The total amount of carbon (from 9.91 to 10.87 Mg C ha⁻¹) and the total number of stems in the full dataset did not change significantly (from 9574 to 10,842 individuals) (Table 1). However, there are significant differences among the species classes and there are significant differences among the large and small trees datasets.

Aboveground carbon (AGC) in the forest specialist class increased from 1.85 to 3.29 Mg C ha⁻¹ yr⁻¹ stored in the large trees (*p* = 0.025) (Table 1, Fig. 2A). This partly offsets a significant decrease in carbon stored in savanna specialists (from 5.60 to 3.36 Mg C ha⁻¹ yr⁻¹; *p* < 0.001). These trends are especially due to a significant change in stem density in both classes (Table 1, Fig. 2B): an increase in forest specialist stem density (*p* = 0.003) partly compensates a decrease in savanna specialist stem density (*p* < 0.001). For the small trees dataset, the increase in AGC is significant for both the forest and transition specialist class (*p* < 0.001) (Table 1, Fig. 3A), while the decrease in AGC in the savanna specialist class is non-significant (*p* = 0.389). This results from a large increase in forest specialist stems (*p* < 0.001) (Table 1, Fig. 3B) and transition specialist stems (*p* < 0.001), which surpasses a small decrease in savanna specialists (*p* = 0.041).

The total number of individuals in the large tree dataset decreased from 150 to 124 stems ha⁻¹ (Table 1), which is mainly because of a decrease in the savanna specialist *Maprounea africana* (from a total number of 3560 to 1699 individuals on 37.2 ha) (Appendix A). However, the average stem density in the small tree dataset significantly

Table 1

Plot-level mean static metrics of 93 plots (each 0.4 ha) within the Manzonzi savanna enclosure, compared with mean metrics of 19 mature rainforest plots in the Luki reserve. Metrics are aboveground biomass-carbon (AGC), stem density (N) and diameter at breast height (DBH). 95% bootstrapped confidence intervals are shown between brackets. Metrics are averaged over all plots for the 2010 and the 2014 censuses separately, for the large trees (DBH ≥ 10 cm) and small trees (6.37 cm < DBH < 10 cm) datasets separately and for each species class separately. The 'all' species class indicates that trees that could not be classified are included as well.

Metric	Dataset	Species class	large trees dataset (DBH ≥ 10 cm)		small trees dataset (6.37 cm < DBH < 10 cm)	
			2010	2014	2010	2014
AGC (MgC ha ⁻¹)	Manzonzi savanna	Forest specialists	1.85 (1.17–2.85)	3.29 (2.32–4.29)	0.12 (0.09–0.16)	0.49 (0.41–0.58)
AGC (MgC ha ⁻¹)	Manzonzi savanna	Transition specialists	1.27 (0.55–2.28)	2.31 (1.56–3.15)	0.05 (0.03–0.07)	0.44 (0.36–0.53)
AGC (MgC ha ⁻¹)	Manzonzi savanna	Savanna specialists	5.60 (4.84–6.46)	3.36 (2.87–3.83)	0.87 (0.74–1.00)	0.79 (0.65–0.92)
AGC (MgC ha ⁻¹)	Manzonzi savanna	All	8.86 (7.73–10.22)	9.14 (7.64–10.86)	1.05 (0.94–1.17)	1.73 (1.54–1.91)
AGC (MgC ha ⁻¹)	Luki mature forest	All	197.92 (171.71–228.00)	–	–	–
N (trees ha ⁻¹)	Manzonzi savanna	Forest specialists	21.80 (14.95–29.14)	39.01 (31.13–47.37)	4.85 (3.71–6.17)	18.03 (15.30–20.89)
N (trees ha ⁻¹)	Manzonzi savanna	Transition specialists	13.50 (8.00–19.54)	31.66 (25.11–38.74)	2.52 (1.52–3.80)	21.12 (17.12–25.60)
N (trees ha ⁻¹)	Manzonzi savanna	Savanna specialists	114.48 (98.05–131.57)	51.69 (44.68–59.06)	34.90 (29.16–40.53)	27.04 (22.13–32.54)
N (trees ha ⁻¹)	Manzonzi savanna	All	149.96 (134.41–165.18)	123.78 (111.46–136.32)	42.58 (37.91–47.31)	66.75 (59.45–75.23)
N (trees ha ⁻¹)	Luki mature forest	All	490.00 (452.74–525.00)	–	–	–
DBH (mm tree ⁻¹)	Manzonzi savanna	Forest specialists	153.46 (145.25–162.54)	150.92 (144.52–157.61)	–	–
DBH (mm tree ⁻¹)	Manzonzi savanna	Transition specialists	163.63 (146.82–181.66)	147.04 (138.70–156.74)	–	–
DBH (mm tree ⁻¹)	Manzonzi savanna	Savanna specialists	132.39 (129.69–135.19)	142.42 (138.62–146.76)	–	–
DBH (mm tree ⁻¹)	Manzonzi savanna	All	138.58 (135.30–142.08)	144.90 (140.95–148.98)	–	–
DBH (mm tree ⁻¹)	Luki mature forest	All	232.23 (221.20–246.01)	–	–	–

increased from 43 to 67 stems ha⁻¹, which is mainly because of an increase in the number of forest and transition specialists.

The species-specific change in number of individuals is shown in Fig. 4. 71% of the forest specialist species (for example *Albizia lebbek* (L.) Benth.) show an increase in stem density from 2010 to 2014, while 78% of the savanna species (for example *Hymenocardia acida* and *Macarouea africana*) show a clear decrease in stem density (Appendix A). *Macaranga spinosa*, a forest pioneer species typically occurring during the transition of savanna to forest, shows a remarkable increase in the four-year time period (from 449 stems to 1955 stems; Fig. 4). *Macaranga monandra* Müll.Arg. is another forest pioneer species that shows a clear increase (from 0 stems to 543 stems; Fig. 4).

In contrast to a significant change in stem density, average DBH did not change significantly in the forest specialist and the transition specialist classes (Table 1, Fig. 2C). This is due to a large influx of recruits. However, average DBH in the savanna specialist class increased significantly (from 132 mm to 142 mm; $p < 0.001$), along with a significant decrease in stem density ($p < 0.001$). This illustrates the lack of recruitment in the savanna class, which leads to lower stem density and larger average diameter.

Species composition in the forest specialist class is dominated by long-lived pioneers and non-pioneer light demanders (Appendix A). 22 stems belong to shade-tolerant species, which is only 0.7% of the individuals classified as forest specialists. Furthermore, 62% of the individuals in the forest specialist class belong to species that are also occurring in the mature forest in the Luki reserve. However, most of these species are not dominant in the mature rainforest. Only five of these species occupy a basal area of at least 5 m² ha⁻¹ in the Luki reserve (about 15% of the basal area).

We estimate a forest and transition stem encroachment rate of about 9 stems ha⁻¹ yr⁻¹. Assuming that this stem encroachment rate will follow a linear trajectory, we estimate that it will take about 56 years to reach a stem density comparable to a mature rainforest (490 stems ha⁻¹, Table 1). However, at the end of this recovery period, most trees will be small, so recruitment will probably continue, followed by a self-thinning phase (Fig. 5a). In addition, we find that savanna specialists are disappearing very fast, at a rate of 16 stems ha⁻¹ yr⁻¹. We estimate that most savanna specialist stems disappeared within three years after the last census.

The carbon stored in the forest specialist class shows an increase, but there is still a long way to go before a mature forest carbon stock will be reached. In 2014, the average carbon stored by the forest

(3.29 Mg C ha⁻¹) and transition specialists (2.31 Mg C ha⁻¹) together (5.30 Mg C ha⁻¹) was only 2.83% of the average carbon stock in the reference forest plots (197.92 Mg C ha⁻¹, Table 1). Over the four-year monitoring period, the carbon recovery rate of the forest and transition specialists was 0.62 Mg C ha⁻¹ yr⁻¹. Assuming that long-term carbon recovery will not follow a linear but rather a sigmoid (Gompertz) trajectory, we estimate that at least 150 years will be needed to establish a carbon stock comparable to mature rainforest (Fig. 5B). This carbon recovery period is remarkably similar to the period needed to establish a carbon stock comparable to mature rainforest in the Orinoco Llanos plains (Venezuela), even though final carbon stocks (80 Mg C ha⁻¹) and carbon recovery rates (0.44 Mg C ha⁻¹ yr⁻¹) are smaller than those in our research area (San Jose et al., 1998).

4. Discussion

4.1. Favourable climatic conditions for forest recovery

Rainfall, given that fire is now absent in the enclosure, could be an important limiting factor for successful forest recovery. The total annual rainfall in the enclosure is approximately 1180 mm with a distinct dry season from May to September. Sankaran et al. (2005) stated that an annual rainfall higher than 650 mm may give rise to an unstable state in the savanna, which is the case for the enclosure. However, rainfall thresholds should be considered with care. King et al. (1997) suggest that a humid forest is getting rainfall-limited when annual rainfall doesn't exceed 1500 mm and if most annual rainfall is concentrated in a short wet season.

During the long dry season, the Mayombe hills receive < 50 mm precipitation, which would impede the presence of a dense humid forest (Couralet, 2010; De Mil et al., 2017). However, as the climate is influenced by southeastern Passat winds carrying fogs from the nearby Atlantic Ocean, the dry seasons are characterised by a relatively high air humidity and a drizzle-like rainfall locally known as 'masala'. The high relative humidity throughout the year reduces water stress, allowing the presence of dense rainforests that would otherwise be absent in this region (Couralet, 2010; De Mil et al., 2017). This is illustrated by the presence of dense rainforest in the Luki reserve, which is located only 5 km North of the Manzonzi savanna. The permanent inventory plots in the Luki rainforest have an average AGC content of 197 Mg C ha⁻¹ (Table 1), which is comparable to the overall mean in Central African rainforests (201 Mg C ha⁻¹, Lewis et al., 2013). Therefore, we conclude that climatic conditions

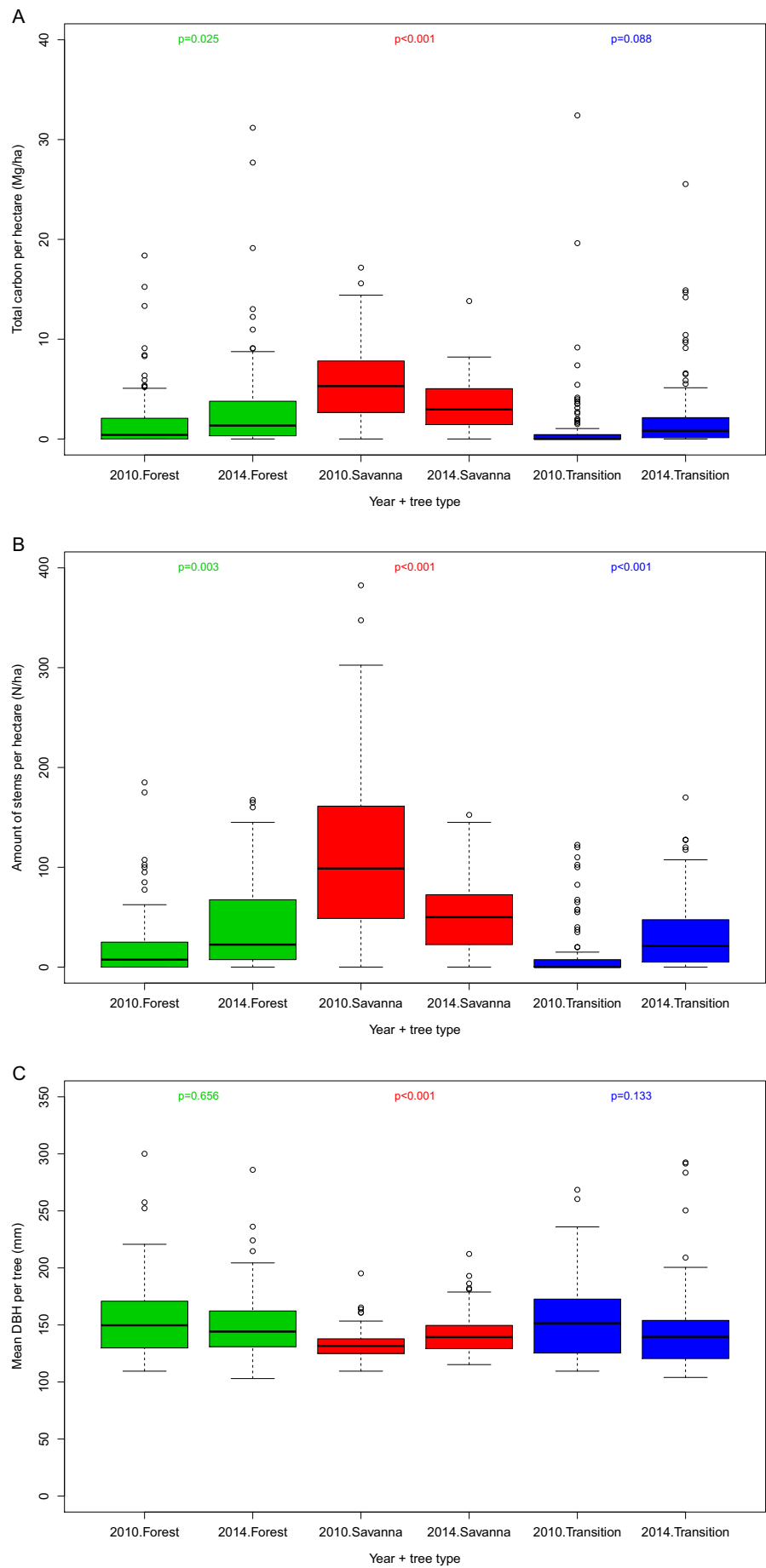


Fig. 2. Comparison of plot-level static metrics between 2010 and 2014, using the large tree dataset (DBH ≥ 10 cm). Boxplots in (A) show the distribution of plot-level aboveground biomass-carbon stocks (AGC), boxplots in (B) show the distribution of plot-level stem density and boxplots in (C) show the distribution of average plot-level DBH. Boxplots show the 25% quartile, the median value and the 75% quartile of the plot-level metrics. Outliers are marked with open circles. p-Values resulted from two-sided *t*-tests.

are favourable for rainforest regeneration in the Manzonzi savanna, while the fire regime probably prevented canopy closure before installation of the enclosure (Accatino and Michele, 2013; Anderson and Brown, 1986; Bond and Keeley, 2005).

Another limiting factor for forest recovery is proximity of seed trees belonging to forest specialist species. Research by Brookman-Amissah et al. (1980) and Chidumayo (1988) (as cited in Swaine et al., 1992) showed that zones that are more distant from a forest species source, had a larger proportion of savanna species. Since the enclosure in Manzonzi is not surrounded by a vast savanna landscape but by the Mayombe forest, there is a forest species recruitment potential. The Luki reserve is only 5 km away from the Manzonzi savanna, and

represents one of the southernmost large Mayombe rainforest patches, but smaller rainforest patches occur around the Manzonzi savanna. The forest recovery potential in the Mayombe was also mentioned by Schwartz et al. (1996) who claimed that small enclosed savanna patches in the Mayombe completely disappeared within centuries during a period of rainforest regeneration after a major rainforest collapse around 2000 cal yr BP. We conclude that the Manzonzi savanna is located close enough to forest patches to enable forest encroachment. The potential of forest specialists to recruit in regenerating savanna, is already illustrated by the presence of a few shade tolerant forest specialists in the inventory plots (Appendix A).

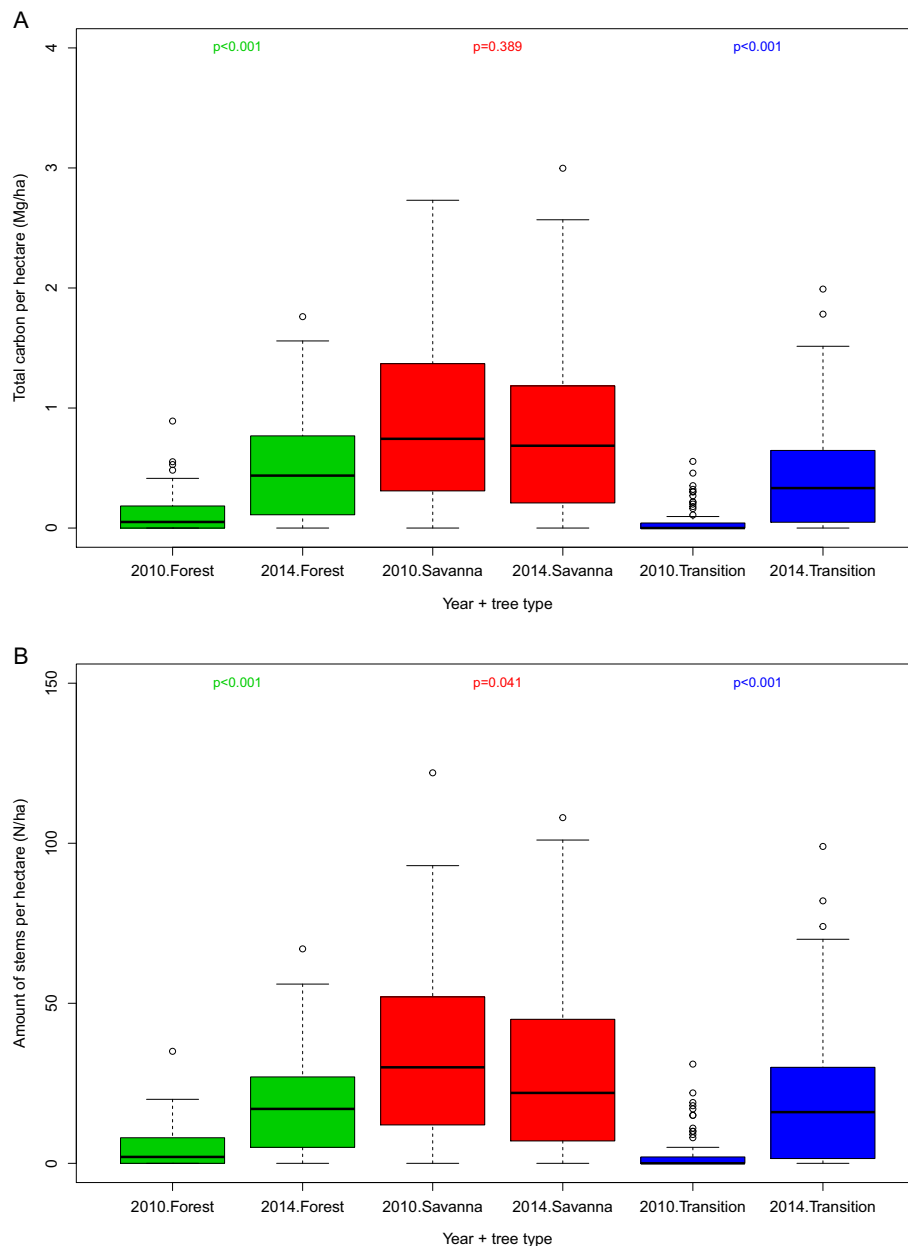


Fig. 3. Comparison of plot-level static metrics between 2010 and 2014, using the small tree dataset (DBH < 10 cm). Boxplots in (A) show the distribution of plot-level aboveground carbon stocks (AGC) and boxplots in (B) show the distribution of plot-level stem density. Boxplots show the 25% quartile, the median value and the 75% quartile of the plot-level metrics. Outliers are marked with open circles. p-Values resulted from two-sided *t*-tests.

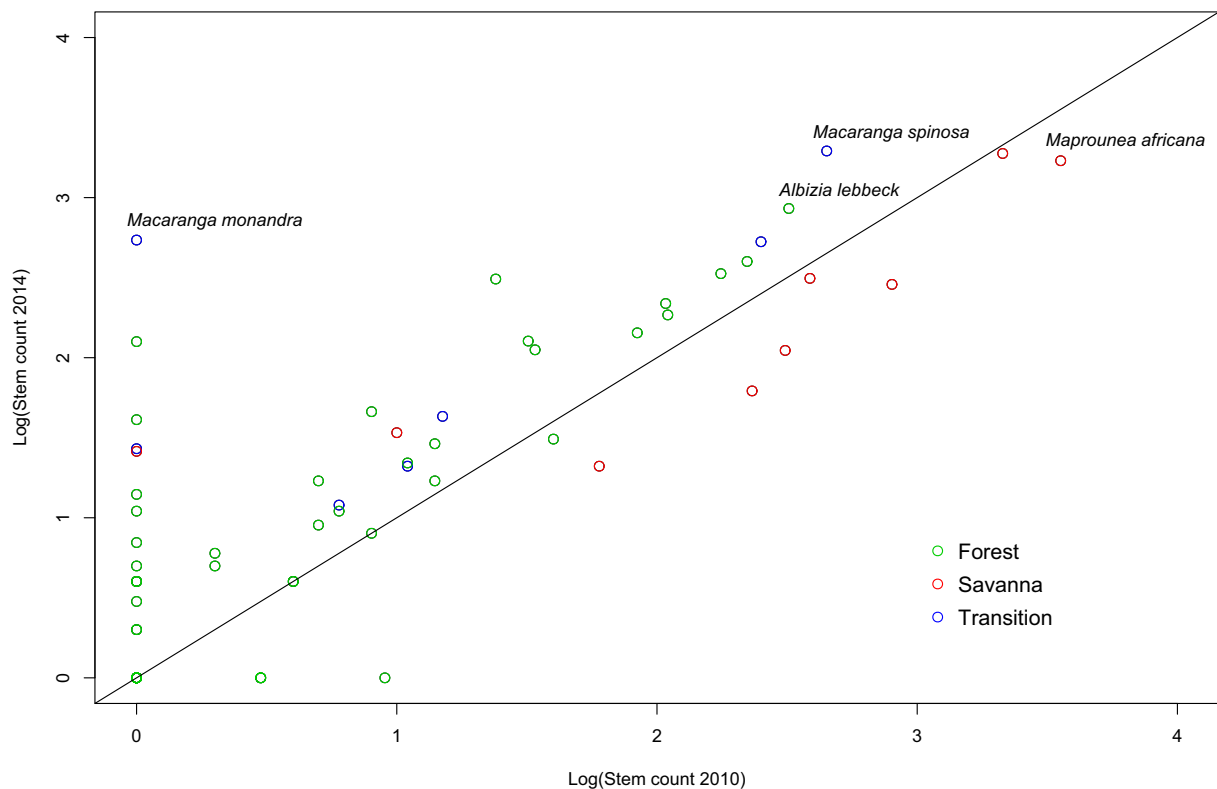


Fig. 4. Comparison of number of individuals (log-scale) per species between 2010 and 2014 in the large tree dataset (DBH ≥ 10 cm). Colours indicate to which vegetation type a certain species belongs. The black line indicates the 1:1 relation.

4.2. Species turnover

Our dataset shows a remarkable shift in species dominance, even though the monitoring period is relatively short (four years). Savanna specialists in our experiment are disappearing at a fast rate. The dominant savanna specialists like *Maprounea africana* are being replaced by the fast-growing forest pioneer *Macaranga spinosa* (Fig. 4, Appendix A). Disappearance of the savanna specialists can be explained partly because their recruitment is hampered by the fast recruitment of forest pioneers (Table 1). Savanna trees that died over the monitoring period were not replaced by new savanna trees but by forest pioneers. This is also illustrated by the increasing average DBH of the savanna specialists (due to a lack of recruitment). Furthermore, savanna trees are light-demanding (Appendix A) but relatively small-statured. As such, they can't compete with the fast-growing forest pioneers and they are dying off as the canopy cover increases.

Forest specialists are becoming increasingly important in the Manzonzi enclosure. At this stage, these are mostly light-demanding species such as *Albizia lebbeck*. Long-lived light-demanders are typically abundant in young and old regenerating forests, during the stand initiation and stem exclusion phases and the early stages of canopy and understory transition (Chazdon, 2008; Chen and Popadiouk, 2002; Oliver and Larson, 1990). Most of these light-demanding species are not abundant in the reference plots in the mature forest of the Luki reserve (Appendix A), where long-lived light-demanders have been replaced by shade-tolerant and shade-bearing species (Oliver and Larson, 1990). However, a few shade-tolerant species typically occurring in the mature forest plots, are also becoming more abundant in the Manzonzi enclosure. Examples are *Maranthus glabra* (Oliv.) Prance and *Monodora myristica* (Gaertn.) Dunal. This illustrates how the Manzonzi enclosure is shifting towards a rainforest environment.

4.3. Forest stem encroachment

In the Manzonzi enclosure, there is an increase in forest specialist stems and a decline in savanna specialist stems, both of which are significant (forest specialists on the 95% level, savanna specialists on the 99% level, Fig. 2B). The estimated savanna stem disappearance rate is about 16 stems $\text{ha}^{-1} \text{yr}^{-1}$. If we assume a constant stem disappearance rate and consider 2014 as the starting position (with about 52 savanna specialist stems ha^{-1}), then it would take a little more than three years for the savanna specialists to disappear completely. However, there is no certainty that the stem disappearance rate will remain constant and there will possibly still be savanna species present after three years.

The estimated forest and transition stem encroachment rate is about 9 stems $\text{ha}^{-1} \text{yr}^{-1}$. If we assume a constant stem encroachment rate, then it would take around 56 years (after savanna protection) to reach an average stem count similar to the mature rainforest plots in the Luki reserve (490 stems ha^{-1}). In contrast, average forest specialist DBH did not increase significantly (Fig. 2C). This is due to a large influx of small trees, as illustrated by a large increase in forest and transition specialists in the small trees dataset ($p < 0.001$, Fig. 3B). This shows that the plots are in an active recruitment or stand initiation phase (Oliver and Larson, 1990; Chazdon, 2008). This phase typically takes only about 10 years in tropical rainforests (Chazdon, 2008) but in the case of savanna encroachment, the forest trees need to compete with tall grasses and with the savanna trees, which may delay the process (Chazdon, 2008).

Fig. 5A illustrates a hypothetical long-term pathway of the Manzonzi stem encroachment trajectory. Although we estimated that the plots will reach an average stem count of 490 stems after 56 years, the stems will be smaller than in mature rainforest due to a large share of young trees. As such, the stem density will probably continue to increase until a 'tipping point' will be reached. From that moment, we expect that the stem density will start to decline and average DBH will

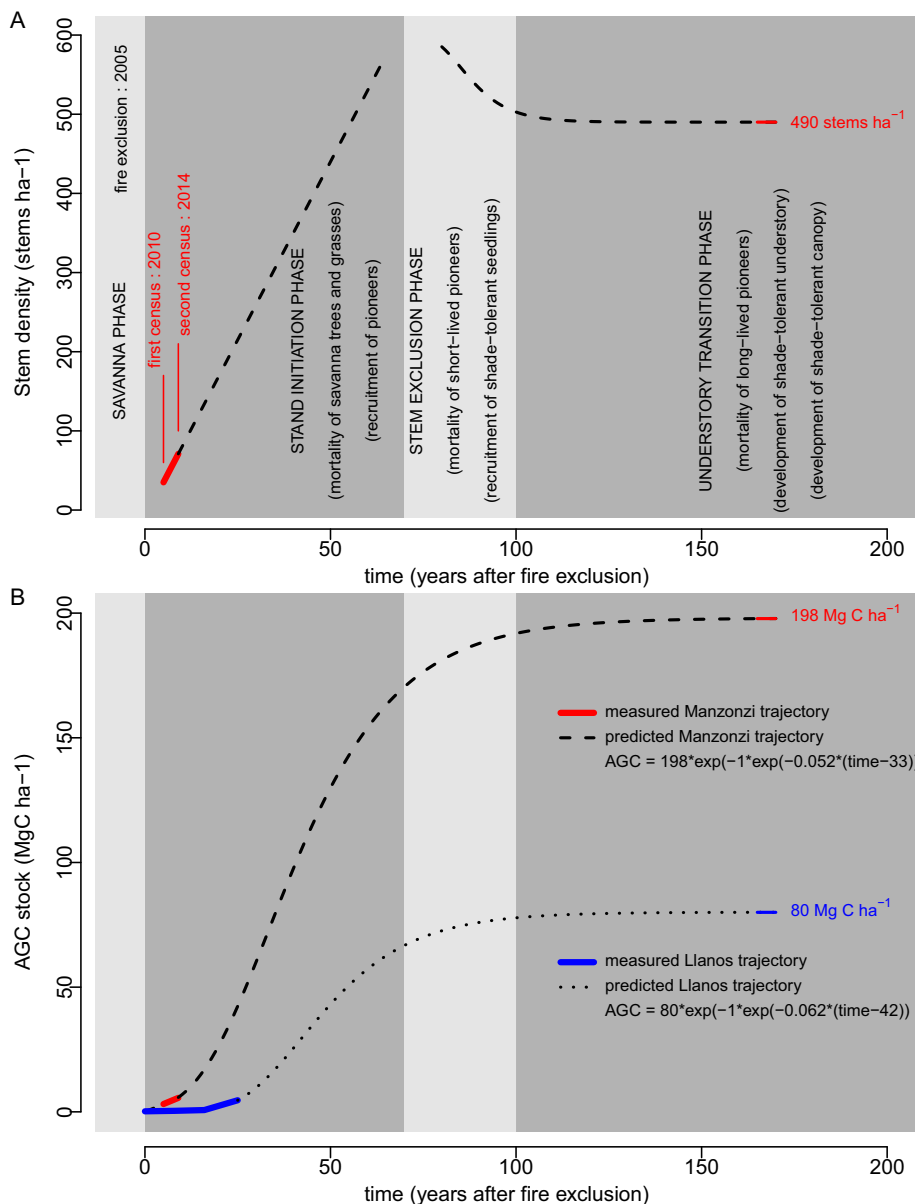


Fig. 5. Long-term trajectories of stem encroachment (A) and recovery of aboveground carbon stock (B). The red solid lines represent our observed monitoring period, while the black dashed lines are future predictions. In (A), stem density is assumed to be linearly increasing during the stand initiation phase (at the rate observed between 2010 and 2014); stem density is then expected to drop during a self-thinning phase (typically 25 years) until it will reach a stem density comparable to the average in the 19 reference plots in the nearby mature rainforest (Luki reserve; 490 stems ha⁻¹). In (B), forest carbon stocks are expected to increase exponentially at the start of the recovery period, but recovery rates will decline later on, resulting in a sigmoid trajectory, which is described here as a Gompertz model. The model was parameterised using the observed carbon stock at the 2010 and 2014 censuses, and assuming a final carbon stock of 198 Mg C ha⁻¹, which is the average stock in the reference plots. To compare, we also plotted the carbon recovery trajectory of a savanna protection experiment in the Orinoco Llanos plains (Venezuela; San Jose et al., 1998; monitoring period in blue). Parameterized models for both the Manzonzi and the Llanos trajectories are presented under their respective curves. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

increase. This self-thinning or stem exclusion phase typically takes about 10–25 years in the tropics (Capers et al., 2005; Chazdon, 2008; Oliver and Larson, 1990).

The last stage of forest succession is the canopy and understory transition stage, which may take 100 to 200 years (Oliver and Larson, 1990; Chazdon, 2008, Fig. 5). During this stage, shade-intolerant long-lived pioneers (such as *Albizia lebeck*) are expected to gradually disappear and be replaced by more shade tolerant species typical for old-growth or mature forests (such as *Scorodophloeus zenkeri* Harms, *Greenwayodendron suaveolens* (Engl. & Diels) Verdc. or *Anonidium mannii* (Oliv.) Engl. & Diels). As such, the full process of forest regeneration, (including stand initiation, self-thinning and species transition stages) will last much longer than 56 years (Fig. 5).

4.4. Forest carbon evolution

Forest specialist carbon stocks in the Manzonzi exclosure increased from 3.12 to 5.6 Mg C ha⁻¹. This is still within the range of published savanna carbon stocks, which vary between 1.8 Mg C ha⁻¹ (trees are absent) and 30 Mg C ha⁻¹ (substantial tree cover) with an average stock of 7.2 Mg C ha⁻¹ yr⁻¹ (Grace et al., 2006). However, our

Gompertz model (Fig. 5B) suggests that the Manzonzi carbon stocks will exceed the savanna range by 2025 (20 years after exclosure).

We estimated a forest specialist carbon recovery rate of 0.62 Mg C ha⁻¹ yr⁻¹, and a total forest carbon recovery period of about 150 years, considering the average carbon stock in the mature forest plots as a reference (197.92 Mg C ha⁻¹ yr⁻¹, Fig. 5B). This carbon recovery period is remarkably similar to the period needed to establish a carbon stock comparable to mature rainforest in the Orinoco Llanos plains (Venezuela), even though final carbon stocks (80 Mg C ha⁻¹) and carbon recovery rates (0.44 Mg C ha⁻¹ yr⁻¹) are smaller in the Llanos experiment than those in our research area (San Jose et al., 1998).

Since the changes in forest specialist DBH (Fig. 2C) are non-significant, the carbon increase in the Manzonzi plots is driven by an increase in forest specialist stem density (Fig. 2B). Our estimate of carbon recovery time is comparable to the full stem turnover period described above (10 years for the recruitment phase, 25 years for the self-thinning phase, and about 100–200 years for the understory and canopy transition phase). As our Gompertz model illustrates (Fig. 5B), the carbon recovery rate will most likely not remain constant over the whole forest succession period. During the current regeneration phase, forest specialist species need to compete with savanna specialists and grasses. As

such, the carbon recovery rate may increase rapidly once the savanna trees disappeared. However, the carbon recovery rate is likely to decline again at the end of the stand initiation phase and during the self-thinning phase, when recruitment will drop to normal mature-forest levels and carbon recovery will be driven mainly by increasing DBH. The Gompertz model predicts that the decline in carbon recovery rate will start at about 33 years (point of inflection).

4.5. Future prospects of the enclosure

An enclosure experiment of this scale in the Congo Basin has never been described in scientific literature and we must continue monitoring the forest encroachment on this site. The future success of this experiment will depend on whether or not the forest trees will be able to ultimately out-compete the savanna trees and grasses (Baudena et al., 2014). When water supply is sufficient and anthropogenic fires are absent, forest trees are able to out-compete grasses and savanna trees. However, to succeed the forest trees need to rapidly form a closed canopy that will impede the development of a dense herbaceous layer, hence reduce the risk of a natural wildfire. Savanna trees will prevail if an intense fire regime will be maintained (Baudena et al., 2014). Bucini and Lambin (2002) state that fires maintain savanna ecosystems by preventing the invasion of woody species, especially in the savanna/forest transition zone. Accatino and Michele (2013) also indicated that canopy closure could be prevented by fire if the climate would not be favourable for forest establishment. The fire-regime in the Manzonzi enclosure was stopped in 2005 giving the vegetation time to recover after annual disturbances and paving the way for forest encroachment, as discussed above. This forest encroachment is already well on its way as can be seen by the increase in forest and transition individuals compared to the decline in savanna individuals. Based on the information obtained over a four-year period, we were now able to make first rough predictions of the pathway of forest succession in the Manzonzi savanna (Fig. 5). Continued monitoring of the plots will allow to test if the observed rates will be maintained in the future and further refine the forest succession pathway.

4.6. Implications for conservation

Our observed rates of forest recovery and our predicted long-term forest carbon recovery trajectory (Fig. 5B), are important figures to better quantify the carbon sequestration success of possible REDD + schemes in the tropics. Until now, the focus of ecologists has been on carbon sequestration rates in intact mature rainforests (Lewis et al., 2009; Brienen et al., 2015) and on quantifying carbon losses from land-use change (Baccini et al., 2017). However, with loss of forest area being an important component of global carbon emissions, investing in forest restoration in degraded forest areas will be a crucial element of future carbon sequestration efforts. More specifically, in the Democratic Republic of Congo, REDD + projects aiming at carbon recovery and biodiversity conservation are a top priority on the agenda of WWF-DRC. In the Mai-Ndombe province, a forest conservation effort was set-up using a participatory approach and over 60 PES contracts have been signed between the government and local communities (WWF-DRC, 2017). By 2018, a total of 4396 ha of savanna enclosures were protected from bush fires to allow natural reforestation (The World Bank, 2018). Such unique collaborations between ngo's, governments and local communities are rare in the tropics, but vital for conservation. Their success largely depends on adequate quantification and long-term prediction of recovery trajectories. However, scientific long-term tropical carbon restoration studies are extremely rare. Therefore, the Manzonzi savanna may potentially become an important reference experiment to quantify long-term carbon recovery rates and estimate the time needed for carbon recovery. This experiment is especially a reference to quantify future efforts within the DRC, but regarding the lack of such experiments, we argue that it may become an important

reference for savanna restoration efforts worldwide, if protection and monitoring efforts will continue.

Furthermore, the Manzonzi enclosure is a good example of a natural carbon restoration scheme, without the need of investing in plantations. Plantations of fast growing carbon-rich tree species are well-known examples of REDD + schemes minimizing the time needed for forest carbon restoration. However, monodominant plantations come at the cost of reduced biodiversity (Thomas et al., 2013, see also Díaz et al., 2009). Furthermore, some of the most widely used species (particularly *Eucalyptus* spp. and *Pinus* spp.) do not belong to the natural flora in Central Africa. This trade-off between carbon sequestration versus biodiversity conservation is a well-known issue when developing REDD + schemes (Hirsch et al., 2011; Phelps et al., 2012). Efforts based on plantations maximize carbon sequestration rates but they come at the cost of reduced biodiversity. This is especially a problem when native vegetation is cleared for plantations (Berkesy and Wintle, 2008; Noss, 2001). Our Manzonzi enclosure shows that carbon sequestration can go hand-in-hand with biodiversity conservation, by focusing on natural forest regeneration. This strategy corresponds to efforts to reconcile carbon and biodiversity conservation, as cited by Thomas et al. (2013): “You cannot maximize both biodiversity and carbon at the same time, but both can reach satisfactory levels when they are combined”.

Another important aspect of the Manzonzi enclosure, is the proximity of the Luki Man and Biosphere reserve (Fig. 1). The fire exclusion and forest recovery experiment represents a direct contribution to the major objective of UNESCO's Man and the Biosphere Programme (MAB). This Intergovernmental Scientific Programme aims at establishing a scientific basis for the improvement of relationships between people and their environments. According to UNESCO, “Biosphere reserves are ‘Science for Sustainability support sites’ – special places for testing interdisciplinary approaches to understanding and managing changes and interactions between social and ecological systems, including conflict prevention and management of biodiversity” (UNESCO, 2017). However, The Luki Biosphere Reserve is under heavy human pressure (Blaser et al., 2011). This may be tackled by (i) increasing national and international conservation efforts and (ii) integrating the community into conservation efforts through results-based return-on-investment. Forest recovery efforts improve ecosystem functioning, ecological and economical resilience, and ultimately human livelihood, but this does not get achieved immediately (Lamb et al., 2005). In order to fully integrate the Manzonzi fire exclusion experiment into the MAB efforts of the Luki Reserve, several steps need to be undertaken: (i) quantify the potential financial benefits of the observed and predicted carbon recovery rates to the local community, (ii) work out possibilities for community-level results-based payments (e.g. PES) through inclusion in an official REDD + system. These steps depend strongly on national and international policy. However, quantification of carbon sequestration rates has been a first and important step towards integrating fire enclosures like the Manzonzi experiment into national or international REDD + programmes.

5. Conclusion

The Manzonzi enclosure is changing from a disturbed savanna structure towards a more forested state. The region is currently in a trade-off between emerging forest and a declining savanna with their accompanying species. The estimated savanna stem disappearance rate and forest encroachment rate are about 16 stems $\text{ha}^{-1} \text{yr}^{-1}$ and 9 stems $\text{ha}^{-1} \text{yr}^{-1}$ respectively. Future research should include further inventories to see if the evolution from savanna towards a more forested state is maintained. The current forest specialist carbon recovery rate is estimated at $0.62 \text{ Mg C ha}^{-1} \text{yr}^{-1}$, and a total forest carbon recovery period at 150 years. However, more censuses are needed to refine long-term trajectories. The case of the Manzonzi enclosure is a good example of how a REDD + scheme could enhance both carbon sequestration and biodiversity conservation. The ongoing support of the inhabitants of the

Manzonzi village will be vital for the success of the project. The authors want to stress that the continued follow-up of REDD+ -projects, both in implementation and support towards the inhabitants, will be crucial.

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Appendix A. Average stem density (N) per species within the Manzonzi enclosure for the 2010 and the 2014 censuses (full dataset = large and small trees together). Species are classified according to their light and habitat preference. Light preference classes are: short-lived pioneers (SLP), long-lived pioneers (LLP), non-pioneer light demanders (NPLD) or shade-tolerant species (ST)

Species name	Light preference ^a	Habitat preference	Manzonzi savanna plots (37.2 ha)		Luki rainforest plots (19 ha)
			N_2010	N_2014	N_2009
			Stems/ha	Stems/ha	Stems/ha
<i>Annona senegalensis</i>	NPLD-ST	Savanna	8.36	2.98	0.00
<i>Bridelia ferruginea</i>	NPLD	Savanna	21.51	7.72	0.00
<i>Crossopteryx febrifuga</i>	NPLD	Savanna	6.24	1.67	0.00
<i>Holarrhena floribunda</i>	NPLD	Savanna	0.27	0.91	0.00
<i>Hymenocardia acida</i>	NPLD	Savanna	57.28	50.73	0.00
<i>Maprounea africana</i>	NPLD	Savanna	95.70	45.70	0.00
<i>Psorospermum febrifugum</i>	NPLD	Savanna	0.00	0.70	0.00
<i>Sarcocephalus latifolius</i>	NPLD	Savanna	10.40	8.41	0.00
<i>Vitex madiensis</i>	NPLD	Savanna	1.61	0.56	0.00
<i>Albizia coriaria</i>	SLP	Transition	0.00	0.73	0.00
<i>Anthocleista vogelii</i>	SLP	Transition	6.75	14.25	0.00
<i>Harungana madagascariensis</i>	SLP	Transition	0.30	0.56	0.00
<i>Macaranga monandra</i>	SLP	Transition	0.00	14.60	0.00
<i>Macaranga spinosa</i>	SLP	Transition	12.07	52.58	0.11
<i>Musanga cecropioides</i>	SLP	Transition	0.16	0.32	1.00
<i>Vernonia conferta</i>	SLP	Transition	0.40	1.16	0.00
<i>Oncoba welwitschii</i>	SLP-LLP	Forest	2.90	5.86	1.89
<i>Tetrorchidium didymostemon</i>	SLP-LLP	Forest	2.26	3.84	0.21
<i>Xylopia aethiopica</i>	SLP-LLP	Forest	4.73	9.01	0.16
<i>Albizia ferruginea</i>	LLP	Forest	0.00	0.03	0.00
<i>Albizia gummiifera</i>	LLP	Forest	0.65	8.33	0.42
<i>Antiaris toxicaria</i>	LLP	Forest	0.13	0.24	2.21
<i>Barteria nigritana</i>	LLP	Forest	0.03	0.38	0.79
<i>Canarium schweinfurthii</i>	LLP	Forest	0.00	0.19	0.68
<i>Ficus mucoso</i>	LLP	Forest	0.00	0.03	0.00
<i>Hymenocardia ulmoides</i>	LLP	Forest	0.86	3.41	0.05
<i>Lannea welwitschii</i>	LLP	Forest	5.97	10.73	0.84
<i>Markhamia tomentosa</i>	LLP	Forest	1.08	0.83	0.00
<i>Milicia excelsa</i>	LLP	Forest	0.03	0.08	0.42
<i>Pteleopsis hyalodendron</i>	LLP	Forest	0.05	0.16	1.16
<i>Ricinodendron heudelotii</i>	LLP	Forest	0.00	0.03	2.00
<i>Xylopia hypolampra</i>	LLP	Forest	0.22	1.24	0.47
<i>Zanthoxylum gillettii</i>	LLP	Forest	0.38	0.78	5.74
<i>Albizia lebbek</i>	NPLD	Forest	8.63	22.98	0.00
<i>Dacryodes buettneri</i>	NPLD	Forest	0.13	0.46	4.37
<i>Entandrophragma utile</i>	NPLD	Forest	0.00	0.03	0.00
<i>Hyalodendron gabunense</i>	NPLD	Forest	0.38	0.46	12.11
<i>Millettia versicolor</i>	NPLD	Forest	2.96	4.97	0.16
<i>Myrianthus arboreus</i>	NPLD	Forest	0.03	0.03	0.00
<i>Piptadeniastrum africanum</i>	NPLD	Forest	0.00	0.11	2.21
<i>Pseudospondias microcarpa</i>	NPLD	Forest	0.16	0.30	0.11
<i>Pycnanthus angolensis</i>	NPLD	Forest	0.11	0.11	1.68
<i>Chrysophyllum africanum</i>	NPLD-ST	Forest	0.03	0.11	4.26
<i>Aidia ochroleuca</i>	ST	Forest	0.00	0.03	11.32
<i>Blighia unijugata</i>	ST	Forest	0.03	0.03	0.37
<i>Blighia welwitschii</i>	ST	Forest	0.03	0.03	1.32
<i>Corynanthe paniculata</i>	ST	Forest	0.00	0.03	10.74
<i>Dialium pachyphyllum</i>	ST	Forest	0.00	0.03	0.00

Dialium zenkeri	ST	Forest	0.08	0.00	0.00
Isolona dewevrei	ST	Forest	0.08	0.00	5.89
Maranthes glabra	ST	Forest	0.03	0.11	8.68
Microdesmis puberula	ST	Forest	0.03	0.00	0.32
Monodora myristica	ST	Forest	0.05	0.13	1.89
Sorindeia africana	ST	Forest	0.24	0.00	0.00
Treculia africana	ST	Forest	0.03	0.00	0.26
Trichilia gilgiana	ST	Forest	0.22	0.22	4.95
Alchornea cordifolia	?	Forest	0.03	1.10	0.00
Bridelia atroviridis	?	Forest	0.00	3.39	0.00
Deinbollia acuminata	?	Forest	0.03	0.00	2.16
Dracaena mannii	?	Forest	0.11	0.11	0.95
Empogona africana	?	Forest	0.03	0.03	0.00
Ficus recurvata	?	Forest	0.30	0.59	0.00
Garcinia sp	?	Forest	0.00	0.05	0.00
Psydrax palma	?	Forest	0.91	3.01	0.00
Quassia gabonensis	?	Forest	0.00	0.05	0.00
Sorindeia mayumbensis	?	Forest	0.00	0.30	3.37
Spondias mombin	?	Forest	0.03	0.03	0.37
Xylopia chrysophylla	?	Forest	0.00	0.13	0.95
Albizia adianthifolia	LLP	Non-specialists	0.86	1.24	0.16
Croton sylvaticus	?	Non-specialists	0.24	0.59	0.84
Dichrostachys cinerea	?	Non-specialists	0.00	0.59	0.00
Ficus sur	LLP	Non-specialists	0.08	0.13	0.00
Gardenia jovis-tonantiss	?	Non-specialists	0.08	0.00	0.00
Heinsia pulchella	?	Non-specialists	0.08	0.03	0.00
Maesopsis eminii	SLP	Non-specialists	0.22	0.19	0.21
Margaritaria discoidea	LLP	Non-specialists	0.00	0.11	0.00
Morinda lucida	LLP	Non-specialists	0.03	0.03	0.00
Ochna afzelii	NPLD	Non-specialists	0.19	0.22	0.00
Oxyanthus speciosus	?	Non-specialists	0.05	0.00	0.05
Steganotaenia araliacea	?	Non-specialists	0.43	0.46	0.00
Sterculia tragacantha	NPLD	Non-specialists	0.00	0.05	1.58
Unidentified	?	Unknown	0.03	0.19	0.00
Vismia affinis	?	Unknown	0.11	0.08	0.00

^a Short-lived pioneers (SLP), long-lived pioneers (LLP), non-pioneer light demanders (NPLD), shade-tolerant species (ST).

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Glossary

- AGB: Aboveground Biomass
 AGC: Aboveground Biomass-Carbon
 DBH: diameter at breast height
 LLP: long-lived pioneer
 MAB: man and biosphere
 NPLD: non-pioneer light demander
 PES: payment of ecosystem services
 REDD+: Reducing Emissions from Deforestation and Forest Degradation
 SLP: short-lived pioneer
 ST: shade tolerant