Structure and Diversity of Lianas in a Tropical Forest Chronosequence in the Yoko Forest Reserve (Tshopo Province, DR Congo)

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ABSTRACT

A study was conducted on the structure and diversity of lianas in a chronosequence of Congolese tropical forests in the Yoko Forest Reserve (Tshopo Province, DR Congo). The main objective was to study the dynamics of lianas after the abandonment of agriculture at our site. A chronosequence approach was used to carry out this study. Four forests were considered on the basis of their age: 5-year old forest, 12-year old forest, 20-year old forest and 60-year old forest. The mixed primary forest of unknown age was also retained for comparison. Inventories of lianas with a diameter at breast height (dbh) ≥ 1 cm on supports were carried out in three 40 m $\times$ 40 m plots (totalling 0.48 ha) set up in each of these five forests. The functional traits of the lianas were observed in the field and supplemented by the basic literature.The following results were obtained: the number of species varied from the 5-year-old forest (i.e. 28 species/0.48ha) to a peak in the 60-year-old forest (i.e. 35 species/0.48ha). As for floristic diversity, the 12-year-old forest had the highest Fisher index value ($\alpha = 10.66$) and the 20-year-old forest for the Shannon (H= 2.92) and Simpson (D= 0.923) indices. The most abundant families are Dilleniaceae (in the 5-year-old forest), Euphorbiaceae (in the 12-year-old forest and in the 60-year-old forest), Fabaceae (in the 20-year-old forest) and Dichapetalaceae (for the primary mixed forest). And the families with the highest importance value indices are Passifloraceae (5-year forest), Euphorbiaceae (12-year and 60-year forests) and Fabaceae (20-year forest and primary mixed forest). The density of lianas was positively related to the age of the forest up to around 60 years, after which an older forest was associated with a decrease in the density of liana stems. Furthermore, the density and basal area of the lianas peaked at the age of 60, before beginning to decline. Most lianas were voluble (49.88%), zoochorous (63.73%) and hemi-heliophilous (47.51%). This pattern emerged in all 5 chronosequence forests in this study. The relative dominance of functional traits changed with forest age, and functional diversity was higher than predicted by the null model framework of species richness (SES MPD>0) in the 20-year-old forest and the mixed primary forest.

Introduction

Creepers are an important structural and functional component of tropical forests (Homeier *et al*., 2010; Anbarashan *et al*., 2013; Vivek *et al*., 2015). They play a significant role in the functioning processes of the entire forest, such as transpiration (Restom *et al*., 2001; Meinzer *et al*., 1999), net primary leaf productivity (Putz, 1983) and carbon sequestration (Chave *et a*l., 2001; Schnitzer *et al*., 2002). However, the abundance of lianas also has negative effects in tropical forests. The literature tells us that the abundance of lianas can limit the sequestration capacity of tropical forests and therefore carbon storage (Duran *et al*., 2013; Schnitzer *et al*., 2014; Van der Heijden *et a*l., 2015; Tymen *et al*., 2016; Maia *et al*., 2021), they also inhibit tree growth and density (Magrach *et al*., 2016; Garcıa *et al*., 2018; Visser *et al*., 2018) thus modifying the process of forest succession after disturbance (Schnitzer *et al*., 2002). The

physical presence of lianas sometimes inflicts damage on trees and reduces their value as timber and cause increased mortality of host trees (Sanchez-Azofeifa *et al*., 2017).

Studies on lianas thus allow us to obtain essential insight into the ecology and functioning of the entire forest ecosystem (Schnitzer, 2018) for a sustained understanding of the formulation of sustainable forest management practices (Schnitzer *et al*., 2004).

Chronosequence studies also provide important information on plant succession patterns and mechanisms (Pickett, 1989; Olff *et al*., 1997). During secondary succession, the forest evolves directionally towards a pre-disturbance condition in terms of composition, structure, diversity and biomass following a disturbance event (Chazdon *et al*., 2007). The abundance and diversity of lianas can vary considerably from one forest type to another and even between individual sites (Schnitzer *et al*., 2002). These

variations are due to divergent evolutionary pathways between biogeographic regions, or to differences between the biotic and abiotic conditions that prevail along rainfall, fertility gradients, succession or disturbance regimes (DeWalt *et al*., 2015), For example, the density of lianas (woody climbers) is increasing in most forests in the neotropics (Wright *et al*., 2004; Ingwell *et al*., 2010; Schnitzer *et al*., 2011; Campanello *et al*., 2012; Yorke *et al*., 2013; Schnitzer, 2015; Hogan *et al*, 2017; Geralomo *et al*., 2018), while it is declining in African tropical forests (Caballé *et al*., 2001; Ewango, 2010; Bongers *et al*., 2015; Thomas *et al*., 2015; Bongers *et al*., 2020), and a relatively stable liana population is found in Asia (Wright *et al*., 2015). Similarly, some studies have shown that liana density increases rapidly at the beginning of succession, peaks at the end of secondary forest and decreases in old-growth forests (Clark *et al*., 1990; Zahawi *et al*., 1999; DeWalt *et al*., 2000; Letcher *et al*., 2009; Barry *et al*., 2015). Similarly, there are studies that argue that lianas are much more abundant and diverse in young forests than in old forests (Zahawi *et al*., 1999; Dewalt *et al*., 2000). However, Mumbanza *et al.* (2020) found that young forests had fewer liana stems than old forests in the Congo Basin.

It should be noted that there is little information on the structure and diversity of lianas in most African tropical forests (Kuzee *et al*., 2005; Thomas *et al*., 2015; Mumbanza *et al*., 2020; Mumbanza, 2021), and relatively little information on the chronosequence of African secondary tropical rainforests, and Congolese forests in particular, which have progressed beyond the pioneer stages of succession, or on the recovery of their woody biodiversity. To this end, a better characterisation of the structure and diversity of lianas in a chronosequence of tropical forests is necessary in order to understand the ecology and management strategies of these forests.

Thus, the main objective of this work is to assess the dynamics of lianas along a tropical forest chronosequence in the Yoko Forest Reserve. It will enable us to understand how the structure, composition and diversity of the liana plant community recovers after slash-and-burn events in this region in order to improve our knowledge of the resilience of African forests to anthropogenic disturbance and to complement information from other tropical regions.

Materials and Methods

Study site

The study is being conducted around the Yoko forest reserve (N 00° 19′12″; E 25° 17′43″), located in the Ubundu territory, Tshopo province, DRC.

The Yoko forest reserve is bounded to the north by the town of Kisangani and disturbed forests, to the south and east by the Biaro river, and to the west by priority road 410 (Kisangani-Ubundu road), along which it extends from kilometre points 21 to 38. It is irrigated by the Yoko river, which divides it into two blocks: the northern block with 3,370 ha and the southern block with 3,605 ha, giving a total surface area of 6,975 ha at an average altitude of 400 m. The figure below shows the location of the study area in relation to the town of Kisangani.

Climatological data for the years 2013-2022 (Bangboka station) show average annual rainfall of 1,731 mm and an average annual air temperature of 25.18°C, with little seasonal variability. In our study area, it rains throughout the year, and the month with the highest water deficit is January, followed by February, March and July, while the rainiest months are, in order of importance: October, September and November. The region's climate is therefore described as an Af-type tropical rainforest climate according to the revised Köppen-Geiger classification (Peel *et al*., 2007).

In addition, the Yoko Forest Reserve has a ferralitic soil, mainly composed of quartz sand mixed with a little kaolinitic clay and hydrated iron oxides (Van Ranst *et al*., 2010).

Plant formations

Two main types of vegetation cover the Kisangani forest region: dense moist forests on dry land, which include evergreen forests and semi-deciduous forests, and forests on hydromorphic soils (Lebrun *et al*., 1954). Within these forests and as a result of human activities such as slash-and-burn agriculture, logging, cutting and charcoal-making, gathering, hunting, fishing and livestock rearing, there are secondary or reconstituting formations and agricultural complexes (Boyemba, 2011).

Methods

Sampling

In and around the reserve's forests, we used machetes and compasses to establish permanent 40 m x 40 m square sampling plots in triplicate along a chronosequence of forests dating from 5, 12, 20 and 60 years after the abandonment of agriculture. Plots of mixed primary forest of unknown age were added for comparison. We collected information on the age of each plot (n=15) through consultations with landowners and the expert judgement of reserve managers. We ensured that the plots had the same land-use history.

Data collection

We carried out the liana inventory according to the protocol established by Gerwing *et al.* (2006) and completed by Schnitzer *et al.* (2008). All liana stems (woody lianas on supports) with a diameter $\geq$ 1 cm were identified and measured using callipers and circumferential tape, generally at a distance of 1.3 m along the stem from the last rooting position. Herbaceous lianas, hemi-epiphytes, rattans and climbing Poaceae, Araceae, Arecaceae and Cyclanthaceae were excluded from the sampling. The family nomenclature used is based on the Angiosperm Phylogeny Group (APG III, 2009), while the species nomenclature follows Lebrun et al, (1991-1997).

For more detailed taxonomic identification, with the systematic collection of leaves, flowers or fruit where possible, we compiled a herbarium. The herbarium was collected in such a way that each (morpho-) species identified in a plot was collected at least once, and the identification for the second time was made by a botanist at the Faculty of Management of Renewable Natural Resources (UNIKIS) and verified from collections on the Internet (African Plants Database : https://www.villa.ge.ch/musinfo/bd/cjb/africa/ ; Tropicos :https://www.tropicos.org/).

The functional characteristics of lianas (climbing mechanism, regeneration light requirements, and primary dispersal syndrome) were assessed in the field and also using the available literature. We derived regeneration light requirements from Evrard (1968) and Ewango (2010) and classified liana species as shade tolerant, partially shade tolerant, partially light demanding and light demanding. We grouped the species into four main dispersal syndromes, as suggested by Ewango *et al.* (2015) and Jongkind (2005), namely anemochory (fruits or seeds dispersed by wind or air, generally with small, light wings or numerous long hairs adapted to aerial distribution), zoochory (generally brightly coloured fruits or seeds dispersed by animals with soft, fleshy outer layers), hydrochory (fruits or seeds dispersed in water, often with abundant corky tissues or floating air pockets) and ballochory (seeds or fruits/parts of fruits are ejected

mechanically from the plant). The climbing mechanism of all liana species has been classified into the following categories: (1) sarmentose lianas (attach themselves by the arrangement of their lateral branches or by sudden bends in their stems), (2) hook lianas (the stems are supported by short, curved and/or thickened branches), (3) vines with adhesive roots (they are anchored by adventitious roots applied to the support), (4) vines with tendrils (they are wrapped around the support by tendrils), (5) voluble vines (they wrap themselves around the branches of the support). In each 40×40 m2 plot, lianas were classified as small stems ($1cm \geq$ Dhp ≤ 3 cm), medium stems (3 cm $>$ Dhp ≤ 6 cm) or large stems (Dhp > 6 cm) (Vivek *et al*., 2015).

Data analysis methods

Floristic characterisation index

Importance values were determined for each species recorded on the subplot based on a formula from Curtis *et al.* (1951) and Cottam *et al.* (1956) using the summation of density, dominance and relative frequency.

Diversity indices

There are several diversity indices, and the choice of which index is preferable in a given case depends on the research questions and the type of data available. However, at least some of the indices are known to depend on sample size (Williams, 1949; Mountford, 1962; Morisita, 1959).

Fisher's Alpha index (Fisher *et al*., 1943), Shannon's H index (Magurran, 2004), Simpson's D index (Simpson, 1949) were calculated as measures of liana diversity in this study using Past software. Fisher's α index is fairly easy to calculate as it only requires the number of individuals in the community whose diversity is being assessed. It takes into account rare species and is stable as a function of the number of individuals. Fisher's α index therefore only takes into account species richness and the total number of individuals observed (Magurran, 2004). This index is relatively insensitive to sampling effort and provides good estimates of the overall diversity of tropical forests, even in the case of small samples.

$$S = \alpha \ln\left(1 + \frac{N}{\alpha}\right)$$

S: species richness; N: number of individuals and α: Fisher index

At the same density and species richness, two stands can have very unequal structures. To take this into account, we have used the Simpson (D) and Shannon (H) indices, which can be obtained using the following relationships:

$$D = \frac{1}{\sum_{i=1}^{S} pi^2} \text{ and } H = -\sum_{i=1}^{S} pi \ln pi \quad \text{with } pi = \frac{n_i}{N}$$

Let be the density of species i in the sample, ni = number of individuals of species i, N = total number of individuals for all species and S = number of species.

Simpson's index measures the probability that two randomly selected individuals belong to the same species. This index has a zero value to indicate minimum diversity (when the probability is low that two randomly selected individuals belong to the same species) and a value of 1 to indicate maximum diversity (when the probability is high that all the individuals belong to the same species). It is also important to note that this index gives more weight to abundant species than to rare species. The Shannon index is minimal (H=0) when all the individuals in the stand belong to the same species. It is also minimal if, in a stand, each species is represented by a single individual, except for one species which accounts for all the other individuals in the stand.

Conversely, the index is maximum when all the individuals are equally distributed between all the species present.

Coefficient of similarity

Similarity coefficients can be calculated to quantify the degree of association between species, or the level of similarity between two sites (Nshimba, 2008). When specific abundance data are available, the Bray-Curtis, Morisita-Horn, etc. indices can be used. The similarity index calculated for this study is the Morisita-Horn index using Past software. Morisita - Horn corresponds to the ratio of the probability that 2 individuals drawn at random from 2 samples belong to the same species. This index has the advantage of comparing samples of the same size and essentially takes into account abundant species. The other advantage is that it is not very sensitive to species richness or sample size (Morisita, 1959).

$$\text{Morisita similarity index } C_{MH} = \frac{2 \sum (an_i \times bn_i)}{(da + db)aN \times bN}$$

aN = number of individuals in site a; bN = number of individuals in site b; an_i = number of individuals of species i in site a; bn_i = number of individuals of species i in site b; da: number of species specific to site a; db = number of species specific to site b (Magurran, 2004).

Density

This corresponds to the number of individuals per given surface area. It is therefore not particularly difficult to measure. However, a minimum pre-count diameter must be set. Above all, it is necessary to ensure that the sampling is sufficient, i.e. that the area considered is large enough for the average density to be stabilised (Pascal, 2003).

Basal area

Basal area is defined as the area occupied by the trunk at breast height or 1.30 m above the ground. It was calculated for each species by summing the basal area of all the individuals of that species.

$$G = \sum_{i=1}^{n} \frac{\frac{\pi * (DBH_i)^2}{4}}{\text{Superficie consideree}} \left(\frac{m^2}{ha}\right)$$

G = basal area of a stand, DBHi= diameter at breast height, n = total number of trees of each species per hectare

The total basal area and density of vines in each category were scaled per hectare.

Statistical processing of the data

Analysis of variance (ANOVA), which is a parametric test, was used to compare the means, in particular densities and basal areas, between the five chronosequence forests in this study. Where the analysis of variance was significant, Tukey's posthoc multiple comparison test was used to detect these differences.

We visualised the liana species composition pattern using the non-metric multidimensional positioning (NMDS) technique (Kruskal, 1964). Permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2017) was used to explore the difference in liana composition between forests in chronosequences. To do this, we used liana abundance in each plot and Bray-curtis distance as a measure of dissimilarity. Where the difference was significant, due to the low number of unique permutations, we opted for the asymptotic Monte Carlo method to conduct post hoc pairwise comparisons. Similarly, we used the non-metric multidimensional positioning (NMDS) technique to visualise the distribution of functional traits, using the average distance to the nearest neighbour of the trait, weighted by liana abundance, as a measure of dissimilarity. We then performed a PERMANOVA using the R package vegan software

(Oksanen *et al.*, 2019) to assess the difference in terms of functional traits between the different forests in chronosequences. Thus, our matrix was composed of 57 identified liana species and 3 functional traits. With regard to functional diversity and the assessment of the difference in functional diversity along the forest chronosequence, we used the method described by Webb *et al.* (2008) and Kembel *et al.* (2010). To this end, for each phase of forest development, we calculated the dispersion of traits using the mean pairwise distance (MPD) of traits. We then calculated the standardised effect sizes (SES) of functional trait diversity by measuring the dissimilarity of cohabiting liana species. Finally, we compared the observed trait diversities with those expected under the null hypothesis model of varietal richness, randomised 999 times. Positive SES values indicate regularity of functional traits while negative SES values indicate clustering of functional traits. We used Permanova+ Primer 6 and R to carry out these analyses. In addition, to make comparisons of proportions, particularly between diameter classes, we used the chi-square conformity test (Ibanda, 2012). We used R 4.0.3 (R core Team, 2020) to carry out all these analyses.

Results

A total of 58 morpho-species were inventoried in the 2.4 ha covering the five vegetation categories under study, of which 4 were determined at the genus level (6.89%), and 1 remained undetermined (1.72%).

Floristic characteristics

Table 1 below shows the richness and diversity of flora in the five forests under study.

NMDS analysis based on liana composition revealed that plots in 5-year-old forest were separated from those in 60-year-old and mixed primary forest in the first dimension, while in the second dimension, plots in mixed primary forest were separated from those in other forests (Figure 2).

One-way PERMANOVA showed that liana composition differed significantly between forests in chronosequences (F ratio = 2.56; ddl= 4; p-value = 0.001**). Pairwise comparisons corroborated the pattern presented in the NMDS analysis. Thus, the composition of lianas in the 5-year-old forest differed significantly from those in the 60-year-old forest (p = 0.04*) and the mixed primary forest (p = 0.04*), and the composition of lianas in the 12-year-old forest differed significantly from that in the mixed primary forest (p = 0.04*). However, there was no significant difference between the 5-year-old forest and the 12- and 20-year-old forests.

The two diversity indices, Simpson's index and Shannon's index, indicate that the differences between the forests are significant (for example, for Simpson's index: F = 8.89; ddl = 4; p-value= 1.17e-06 ***) particularly between the 5-year-old forest and the rest of the forests (Thus, the Simpson index in the 5-year-old forest differs significantly from those in the 12-year-old (p = 0.007**), 20-year-old (p <1e-04***), 60-year-old (p <1e-04***) and mixed primary forest (p <1e-04***).

Floristic structure

Table 2 below shows the species importance value indices (IVI) for each forest.

Floristic similarity between the five forests studied

The five forests studied do not constitute the same plant community in terms of similarity. Considering the similarity index used in this study, namely the Morisita index (which takes into account the abundant species in the stands), analysis of the results of the Morisita similarity index

between these forests indicates that the 12-year-old and 20-year-old forests are very close floristically (MHC = 0.87 > 0.50), as are the 12-year-old and 60-year-old forests (MHC = 0.68 > 0.50), and the 20-year-old and 60-year-old forests (MHC = 0.59). However, the 5-year forest and the rest of the forests (12-year, 20-year, 60-year and FPM) as well as the mixed primary forest with the rest of the forests (12-year, 20-year and 60-year) constitute distinct plant communities (MHC < 0.50). These results demonstrate a similar evolution of the vegetation in terms of species composition from the 12-year forest to the 60-year forest.

Structural characteristics

The figure 3 shows the density and basal area of lianas according to their DBH classes in the 5 forests in our study.

It can be seen that the 60-year-old forest has the highest density and basal area values. However, the 5-year-old forest had the lowest density and basal area values. The Chi-square conformity test applied to compare the structures indicates that there is a highly significant difference between the three structural classes of these five forests (X2 = 52.09; df = 8; p-value = 1.613e-08). The analysis of variance shows that the difference in density between these five forests is statistically significant at the 5% threshold, as is the basal area (Figure 4).

Creeper functional traits

Of the three functional traits retained in this study, namely attachment mechanisms, dispersal modes and liana temperament, most lianas are voluble, zoochorous and hemi-heliophilous. This trend emerged in all 5 chronosequence forests in this study. Considering the pooled data, voluble lianas are represented by 49.88%, zoochores (63.73%) and hemi-heliophiles (47.51%). The one-way PERMANOVA showed a highly significant difference in the functional traits of lianas between the forests studied (F = 5.31; ddl= 4; p-value = 0.004**). This was confirmed by the NMDS ordination, which showed a clear separation in the plan between the youngest forests (made up of the 5, 12 and 20-year-old forests) and the oldest forests (made up of the 60-year-old forest and the primary mixed forest) (Figure 5 below).

It can be seen from the figure above that the oldest forests (60-year-old forest and mixed primary forest) tended to separate from each other and the patches within each forest tended to group together, except for the youngest forests (made up of 5-, 12- and 20-year-old forests). In addition, the structure of the liana assemblage based on functional characteristics showed that functional diversity was higher than predicted by the null model of species richness (SES MPD > 0) in the 20-year-old forest and the primary mixed forest (Figure 6).

Discussions

Floristic richness and diversity

This study reveals that the number of species varied from the 5-year-old forest (i.e. 28 species/0.48ha) to the peak in the 60-year-old forest (i.e. 35 species/0.48ha). However, there was no significant difference between the 60-year-old forest and the primary mixed forest in terms of floristic richness. In addition, the 12- and 20-year-old forests were more diverse than the other forests in our research site. The same trend was found by DeWalt *et al*, (2000) where they found that lianas were much more diverse in young forests (20 and 40 year old forests) than in forests over 70 years old and old growth forests. The reasons for these variations in our results are said to lie in the availability of light and suitable host trees in the different forests under study. Thus, the higher number of species found in the 60-year-old forest is due to the fact that it

benefits from ecological conditions and stability that are relatively favourable to the maintenance of several groups of species. The other reason could be the dispersal methods and seed germination capacity of lianas (Ewango, 2010). From the 5-year-old forest to the primary mixed forest, passing through the 12-year-old, 20-year-old and 60-year-old forests, the appearance and disappearance of species is recorded at each stage. This means that the species richness of forests varies according to their age. It is therefore interesting to note that even after 20 years of forest disturbance, the floristic richness and diversity of lianas in the secondary forests (5-year, 12-year and 20-year forests) were still very different from those in the old-growth forest (60-year forest and mixed primary forest). This suggests that the recovery of liana floristic richness and diversity in disturbed forests could take many years, i.e. 60 years as shown in this study. This trend has also been found by other studies carried out in the Neotropics and South-East Asia, which have suggested that after around 60 years of abandonment of agriculture, the richness and diversity of secondary forests are comparable to those of the original forest (Addo-Fordjour *et al*., 2016; Rozendaal *et al*., 2019; Yirdaw *et al*., 2019). It should be noted that few quantitative data are available on the richness and diversity of lianas in chronosequence forests, and because the methodological approach of this study differs from those used by our predecessors, comparisons are difficult. However, we can say that the results of this study corroborate those found by Kuzée *et al*. (2005) in the Monogaga forest reserve in Côte d'Ivoire, where they found that out of a total of 48 species in their site, the 2-year-old forest contained fewer species per 0.1 ha (mean = 14) than the 20-year-old (mean = 21) and mature forests (mean = 16.5).

Floristic structure

This study shows that eight species (i.e. 14.03%) are the most frequent and are found in the five forests under study. These eight species include Artabotrys aurantiacus, whose density increases as the forest evolves. The opposite is true of Morinda morindoides. On the other hand, the density of Manniophyton fulvum, Dichapetalum mundense and Dalhousiea africana increases with forest age, peaking in the 60-year-old forest and then decreasing in the primary mixed forest. However, 19 species (i.e. 19.29%) were found only in one or other of the 5 chronosequence forests in this study.

The results of this study correctly reflect the true dynamics of the species in the 5 chronosequence forests. New species generally begin to colonise the forest and there is a gradual accumulation of liana species over time, as the forest develops (Chazdon *et al*., 2007). This development occurs in successive waves of colonisation. The species composition of each wave is predictable, as is the replacement sequence. Although some pioneer species of the first succession fail to recruit after the canopy closes, the legacy of the first species colonisations can persist for decades or even centuries, as some pioneer species can be very long-lived (Gemerden *et al*., 2003). We believe that shade-tolerant liana species colonise the site continuously during the successional phases when the canopy begins to close up in earnest. For example, certain short-lived, light-demanding liana species that, after being established under intense lighting, can persist for a very long time as shade-tolerant lianas, such as Manniophyton fulvum of the Euphorbiaceae family (Ewango, 2010). In this study, most of the liana species that dominated the primary mixed forest showed low dominance in the secondary forests and vice versa. This suggests that liana species, in addition to their demand or requirement, have probably responded differently to various environmental problems (Anbarashan *et al*., 2013).

The results of this study also show that although the floristic richness and diversity of lianas are recovered after about six decades after the abandonment of agriculture, this is not always the case with regard to liana species composition. The same trend has been found by previous studies which reported that liana species composition in some secondary forests (e.g. 60 year old forest) vary considerably compared to composition in primary forests (Addo-Fordjour *et al*., 2016).

Structural characteristics

The results obtained in this study show that liana density is positively related to forest age up to around 60 years, after which an older forest was associated with a decrease in liana stem density (see Mumbanza *et al*., 2022). Creeper density and basal area peaked at age 60, before beginning to decline (see similarly Letcher *et al*., 2009; Letcher, 2015). For example, Barry *et al*, (2015) also showed the same trend where liana density increases rapidly in early succession, peaks in late secondary forest and declines in old-growth forest. However, contrary to our expectations, the 5-year-old forest harbours fewer liana stems than the oldest forests. Similar results were found by Mumbanza *et al*. (2020) in the forests of the Yangambi Biosphere Reserve. We believe that our results are probably dictated by changes in light and support availability with succession and by the climbing methods used by lianas to climb their host tree (Hegarty, 1991, Putz *et al*., 1991). Gardette (1998) indicated that the main factors contributing to a high species richness or abundance of lianas include the presence of sufficient numbers of host trees of different size classes and the proximity of liana parents. The density of lianas in this study could be limited by the number of suitable supports in the early phases of succession and by the availability of light in the later phases of succession. However, the intermediate phases of the succession are characterised by an open canopy and the presence of a sufficient number of suitable supports, providing ideal conditions for liana proliferation (Balfour *et al*., 1993).

As with density, the changes in basal area observed during succession in this study would be influenced by the patterns of liana recruitment, growth and mortality in the 5 chronosequence forests (Mumbanza, 2021).

It is also important to note that other studies have shown that liana density increased up to 20 years after forest disturbance and then decreased (DeWalt *et al*., 2000; Kuzee *et al*., 2005; Letcher *et al*., 2009). In abandoned pastures in Ecuador, Zahawi *et al*. (1999) found that lianas were more abundant in plots with 2 to 5 years of succession.

Functional traits of lianas

Of the three functional traits retained in this study, namely the attachment mechanisms, dispersal modes and temperament of lianas, most lianas are voluble, zoochorous and hemi-heliophilous. This trend emerged in all 5 chronosequence forests in this study. These trends have been found in several studies in Africa and elsewhere (Kuzee *et al*., 2005; Ewango, 2010; Thomas *et al*., 2015; Vivek *et al*., 2015; Wright *et al*., 2015). Zoochory dominance therefore indicates the extent to which lianas provide rewards for wildlife species. They play an important role in trophic relationships in these forests. In contrast, other studies have reported the dominance of wind-dispersed lianas (anemochores) in their sites (Parthasarathy *et al*., 2004; Cai *et al*., 2009). This can be

explained by the fact that in these forests with an open canopy in season, wind can disperse seeds more efficiently. However, for the pooled data, wind dispersal came third in our study with 2.67% of individuals. Our results report that the relative dominance of functional traits changed with forest age (see DeWait *et al*., 2000), and functional diversity is higher than predicted by the null model framework of species richness (SES MPD > 0) in 20-year old forest and primary mixed forest. This highlights the potential role played by environmental filtering in the formation of liana communities along this forest chronosequence (Mumbanza, 2021). Environmental filtering appears to become more pronounced at a late stage of succession for liana species, and strongly restricts the range of values of their functional traits (Cornwell *et al*., 2006). These results suggest that lianas rapidly colonise the forest after the abandonment of agriculture, and can maintain their competitive capacity by adjusting their functional strategies during succession.

Conclusion

This study focused on the structure and diversity of lianas in a tropical forest chronosequence in the Yoko Forest Reserve (Tshopo Province, DR Congo). The main objective was to assess the dynamics of lianas in our site. The results obtained indicate that:

- The floristic richness and diversity of lianas varies with age and the composition of lianas differs significantly between forests in chronosequences. The species that best characterise the 5-year-old forest at our site are Adenia cissampeloides (42.20%) and Tetracera alnifolia (30.78%). For the 12-year-old forest, we find Manniophyton fulvum (61.68%) and Adenia cissampeloides (28.96%). The 20-year-old forest is best characterised by Millettia duchesnei (58.43%), Manniophyton fulvum (25.00%) and Landolphia parvifolia (24.54%). The 60-year-old forest has Manniophyton fulvum (74.78%), Heinsia pulchella (26.33%) and Millettia duchesnei (26.27%). However, the species that best characterise the primary mixed forest are Strychnos camptoneura (39.29%), Agelaea paradoxa (28.98%), Dalhousiea africana (26.11%) and Dichapetalum mundense (23.03%).

- The density and basal area of lianas is positively related to the age of the forests. The five forests studied had an inverted J-shaped diametric structure and there was a highly significant difference between the structural classes in these five forests.

- Relative dominance of functional traits changed with forest age.
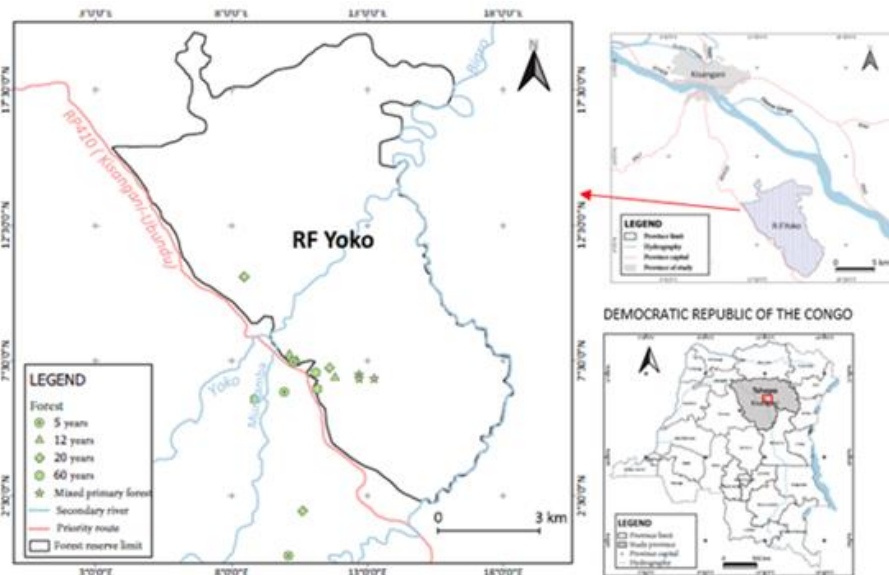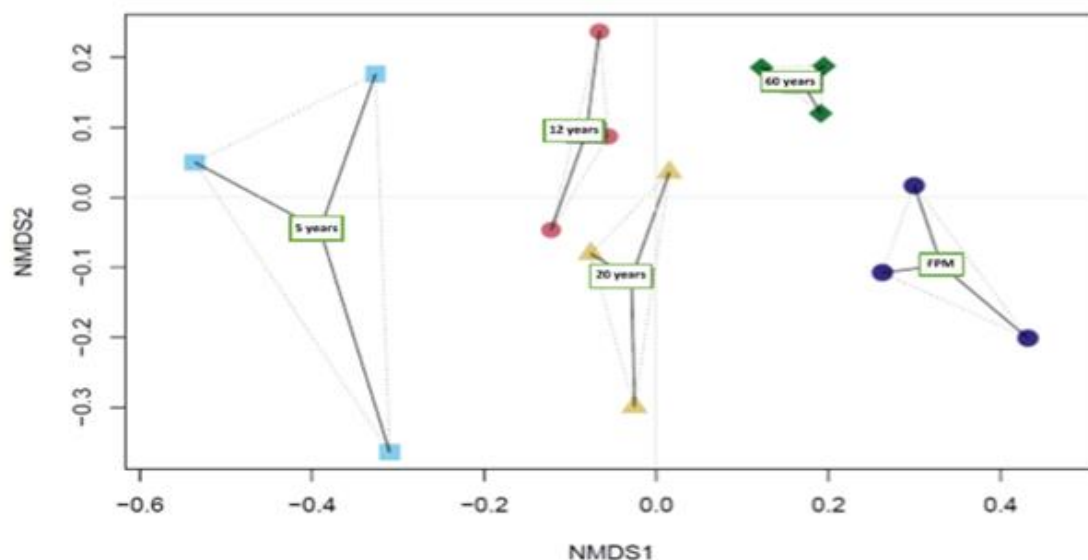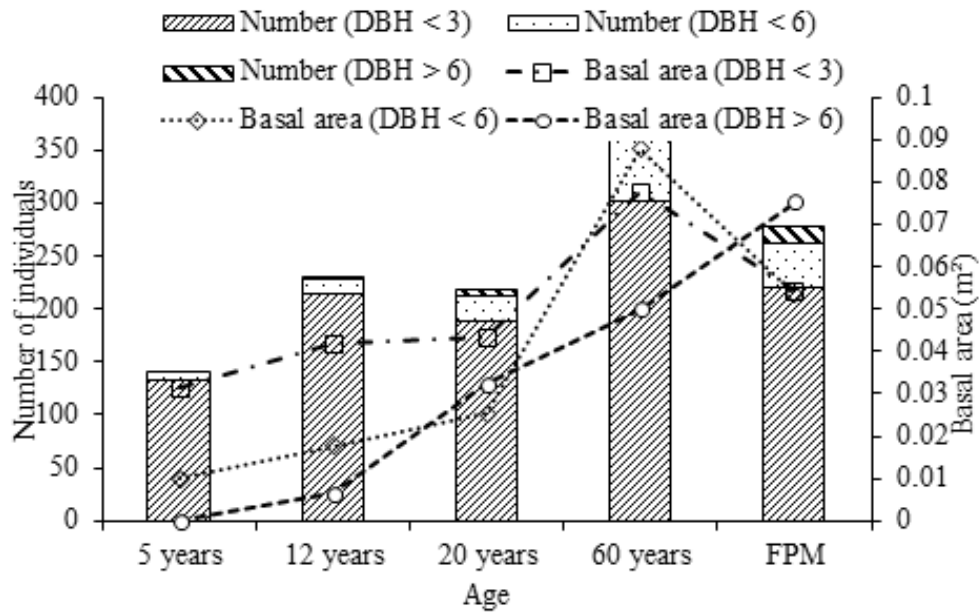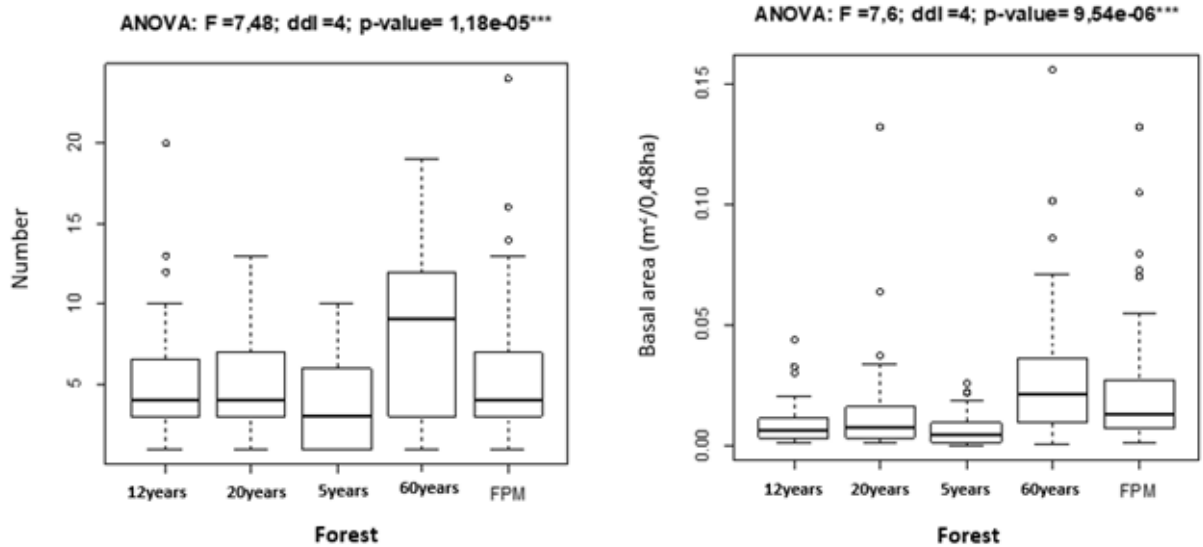

Figure 1. Location of the study area

Figure 2. Ordination results of the non-metric multidimensional scale (NMDS) of 15 liana communities according to their composition in the five forests studied

Figure 3. Density and basal area of lianas according to their DBH classes in the 5 forests studied

Figure 4. Dispersion of density (left) and basal area (right) values for the five forests surveyed. The box represents the interquartile range, i.e. the interval in which 50% of observations are grouped, and the thick bar inside the box indicates the median value; the low bar indicates the minimum value and the high bar the maximum value

Figure 5. Ordination results of the non-metric multidimensional scale (NMDS) for 15 liana communities according to functional traits in the five forests under study
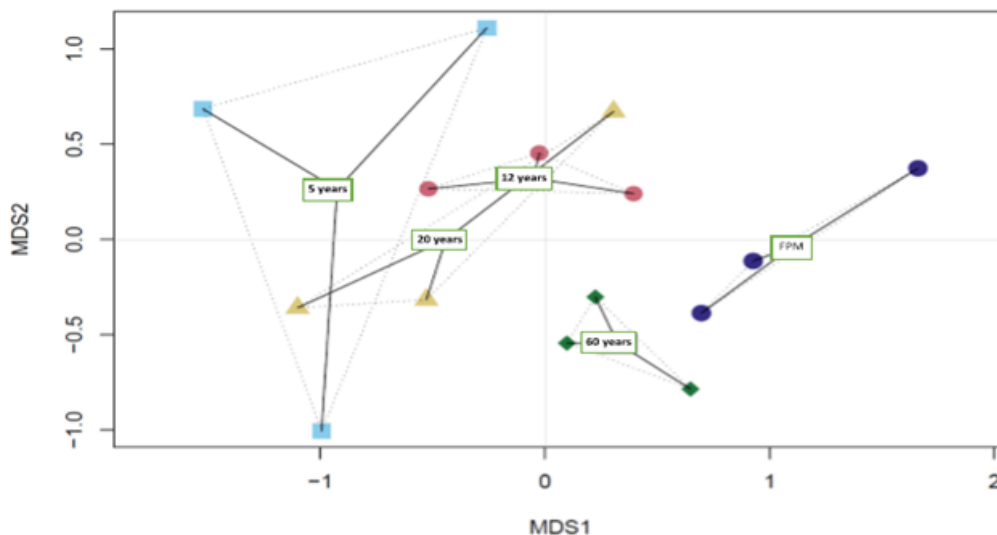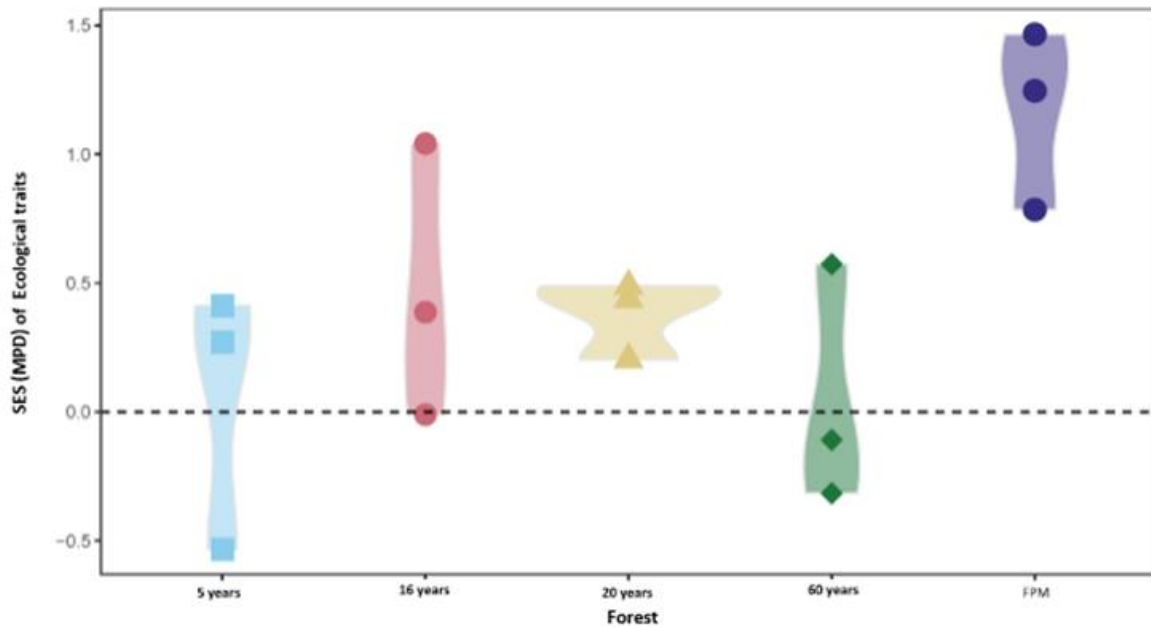
Legend. FPM : mixed primary forest

Figure 6. Measures of standardized effect sizes (SES) of ecological trait diversity of lianas present in each forest using mean trait peer distance (MPD) and the null model of species richness

Table 1. Floristic richness and diversity indices

Floristic characteristics	5years	12years	Forest 20years	60years	FPM	Site
Number of species	28	33	32	35	29	57
Number of genera	24	24	24	24	23	41
Number of families	16	14	15	16	16	23
Simpson Index	0,922	0,86	0,923	0,84	0,91	0,93
Shannon Index	2,87	2,67	2,92	2,48	2,77	3,2
Fisher alpha (α) diversity index	10,52	10,66	10,38	9,37	8,32	12,37

Table 2. The 5 most important species in the different forests under study

Species	Importance Value Indice (IVI)				
	5 years	12 years	20 years	60 years	FPM
Adenia cissampeloides	42,20	28,96	15,47	-	-
Tetracera alnifolia	30,78	-	-	-	-
Cnestis ferruginea	25,67	-	-	-	-
Morinda morindoides	24,46	17,16	-	-	-
Alchornea cordifolia	20,54	-	-	-	-
Manniophyton fulvum	-	61,68	25,00	74,78	-
Landolphia parvifolia	-	19,70	24,54	-	-
Parquetina nigrescens	-	15,76	-	-	-
Millettia duchesnei	-	-	58,43	26,27	-
Connarus griffonianus	-	-	15,33	-	-
Heinsia pulchella	-	-	-	26,33	
Dichapetalum mundense	-	-	-	19,41	23,03
Strychnos camptoneura	-	-	-	17,85	39,29
Agelaea paradoxa	-	-	-	-	28,98
Dalhousiea africana	-	-	-	-	26,11
Millettia macroura	-	-	-	-	17,28

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