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ORIGINAL ARTICLE

Liana communities exhibit different species composition, diversity and community structure across forest types in the Congo Basin

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Abstract

Lianas are poorly characterized for central African forests. We quantify variation in liana composition, diversity and community structure in different forest types in the Yangambi Man and Biosphere Reserve, Democratic Republic of Congo. These attributes of liana assemblages were examined in 12 1-ha plots, randomly demarcated within regrowth forest, old growth monodominant forest, old growth mixed forest and old growth edge forest. Using a combination of multivariate and univariate community analyses, we visualize the patterns of these liana assemblage attributes and/or test for their significant differences across forest types. The combined 12 1-ha area contains 2,638 lianas (≥ 2 cm diameter) representing 105 species, 49 genera and 22 families. Liana species composition differed significantly across forest types. Taxonomic diversity was higher in old growth mixed forests compared to old growth monodominant and regrowth forests. Trait diversity was higher than expected in the regrowth forest as opposed to the rest of forest types. Similarly, the regrowth forest differed from the rest of forest types in the pattern of liana species ecological traits and diameter frequency distribution. The regrowth forest was also less densely populated in lianas and had lower liana total basal area than the rest of forest types. We speculate that the mechanism of liana competitive exclusion by dominant tree species is mainly responsible for the lower liana species diversity in monodominant compared to mixed forests. We attribute variation in liana community structure between regrowth and old growth forests mostly to short development time of size hierarchies.

KEYWORDS

ecological traits, liana assemblage attributes, old growth edge forest, old growth mixed forest, old growth monodominant forest, regrowth forest, Yangambi

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1 | INTRODUCTION

The Congo basin contains about 70% of Africa's rain forests. These forests constitute the second largest block of tropical forests in the world after the Amazon (Trefon, 2017). They can broadly be categorized into old growth monodominant forests, old growth mixed forests and regrowth forests. Patches of old growth monodominant forests, dominated by *Gilbertiodendron dewevrei* (De Wild.) J. Leonard, are commonly encountered alongside those of old growth mixed semi-deciduous forests with *Scorodophleus zenkeri* Harms. These persistent old growth monodominant forests are reported to have relatively low tree diversity as compared to the adjacent old growth mixed forests (Connell & Lowman, 1989; Hart, Hart, & Murphy, 1989; Sonké, 2005; Djuikouo, Sonké, Doucet, & Lewis, 2010). With increasing human activities, especially small-scale agriculture, these old growth forests are becoming fragmented in some parts of the region (Tyukavina et al., 2018; Zhuravleva et al., 2013). As a result, anthropogenic forest edges are being induced and old growth forests are quickly being converted into regrowth forests. This is the case of the non-persistent monodominant regrowth forest of *Musanga cecropiodes* R. Br. Unlike persistent monodominant forests, non-persistent monodominant forests have no inherent ability to regenerate under their own canopy. Because of that they only last for a few generations (Torti, Coley, & Kursar, 2001). Understanding how the presence of these different forest types (monodominant vs. mixed forests/regrowth vs. old growth forests) in the Congo basin impacts the overall plant communities, species composition and diversity is of paramount importance for biodiversity conservation. Most studies seeking to answer this question are often limited to tree communities (Djuikouo, Peh, Nguembou, Doucet, & Sonké, 2014; Hart et al., 1989; Makana, Terese, Hibbs, & Condit, 2004; Peh et al., 2014) while neglecting communities of other plant growth forms such as lianas.

Lianas are an essential component of tropical forests where they account for nearly 25%–35% of the woody species (Chave, Bernard, & Dubois, 2001; Schnitzer et al., 2012) and 10%–40% of all woody stems (Chave et al., 2001; Gentry, 1991). They take a non-negligible part in the overall carbon budget of tropical forests by encompassing approximately 10% of the fresh aboveground biomass (Chave et al., 2001; Gehring, Park, & Denich, 2004). Not only are they very diverse taxonomically, lianas also do differ in their functional and ecological traits. Among the key ecological traits that structure liana communities, we can mention climbing specialization (Ewers, Fisher, & Chiu, 1990; Naidu & Kumar, 2014), light requirement (Schnitzer, Kuzee, & Bongers, 2005) and seed dispersal mode (Bullock, 1995; Gentry, 1991).

Liana species density, diversity and distribution can significantly vary from continent to continent, forest type to forest type and even site to site within the same forest type. These variations are due to divergent evolutionary paths among biogeographical regions, or to differences in biotic and abiotic conditions prevailing along precipitation, fertility, altitudinal, successional or disturbance regime gradients (see DeWalt et al., 2015). For instance, Bary, Schnitzer, van

Breugel, and Hall (2015) showed that liana density rapidly increases early in succession, peaks in late secondary forest and eventually decreases in old growth forests. In general, liana species have high light and nutritional demands. They tend to be more abundant and diverse in secondary forests (DeWalt, Schnitzer, & Denslow, 2000) and disturbed areas of forests where sunlight can easily reach the floor such as treefall gaps (Babweteera, Plumtre, & Obua, 2000; Schnitzer & Carson, 2010) or edges of forest fragments (Addo-Fordjour & Owusi-Boadi, 2016; Zhu, Xu, Wang, & Li, 2004). They also proliferate in water- and nutrient-rich environments such as those existing in forest stands near streams (Schnitzler, 1995) or located in valleys (Putz & Chai, 1987).

Apart from their positive and direct contribution to tropical forest diversity, lianas have also the potential to adversely impact the structure and dynamics of tropical forests. Indeed, after infesting host trees, lianas can subject the latter to intense below- and aboveground competition and inflict severe mechanical damage (Schnitzer & Carson, 2010; Schnitzer et al., 2005). This may result in reduced growth and/or increased mortality of trees (Ingwell, Joseph, Becklund, Hubbel, & Schnitzer, 2010; Schnitzer & Carson, 2010) with consequences for the global carbon balance (Bugmann & Bigler, 2011; van der Heijden, Powers, & Schnitzer, 2015).

Despite the recognition of the increasing importance of lianas as a key component in tropical forest dynamics and functioning, they are poorly characterized in the tropical forest of the Congo basin in terms of their biology, ecology and functions. Only few studies have been published that explicitly take into account the structure and composition of liana assemblages in this region (see Ewango, Bongers, Makana, Poorter, & Sosef, 2015; Makana, Hart, & Hart, 1998; Thomas, Burnham, Chuyong, Kenfack, & Sainge, 2015). With this study, we try to close this gap in our understanding of liana ecology in the Congo basin. Using new inventory data from 12 1-ha forest plots, we assess the relative difference in liana communities across forest types in the Yangambi Man and Biosphere (MAB) Reserve, Democratic Republic of Congo. These different forest types include regrowth forest, old growth monodominant forest and old growth mixed forest. Given the potential influence of edges on plant communities, we distinguished old growth mixed forest found on the edge of agricultural fields (hereafter old growth edge forest) from that in the core of the forest.

Specifically, we address the following questions: (a) To what extent do liana species composition and diversity (taxonomic and functional) vary among the four different forest types? (b) Do liana communities adopt different ecological strategies – based on climbing mechanisms, leaf sizes, regeneration light requirements, diaspore types and dispersal syndromes as traits – as a function of the forest type in which they develop? (c) Are there differences in liana structural variables – density, diameter frequency distribution and basal area – across the four forest types? To answer these questions, we formally test the statistical hypotheses of no differences across the four forest types in terms of liana species in composition, diversity (taxonomic and functional), ecological trait distribution, diameter frequency distribution, density and basal area.

We predict that: (a) Differences in microhabitats will lead to a shift in liana species composition and ecological traits across forest types. (b) More light-rich environments will prevail in regrowth forest and old growth edge forest. Thus, these forest types will be more abundant and diverse in lianas compared to old growth mixed and monodominant forests. (c) The dominant tree species will hamper the development and establishment of other woody species in old growth monodominant forest. Therefore, lianas will be less abundant and diverse in old growth monodominant forest as compared to old growth mixed forest. (d) Short development time of size hierarchies will result in lianas with smaller diameters and lower basal areas in the regrowth forest in comparison to old growth forests.

2 | METHODS

2.1 | Study area, field inventory and data collection

The study was conducted in the UNESCO MAB Reserve of Yangambi (00°38' and 1°10' N, 24°16' and 25°08' E; 470 m of altitude). The reserve is located within the Congo River basin, about 100 km west of the city of Kisangani in the Democratic Republic of the Congo (Figure S1). It covers an area estimated at 6,297 km², and most of the study sites are confined in its southwestern part (00°48' N; 24°29' E). This region is characterized by the presence of a humid tropical forest and has a climate of type Af (following Köppen-Geiger; Peel, Finlayson, & McMahon, 2007). Mean annual precipitation is estimated at 1,762 ± 295 mm (1961–2012). The region has an average dry season length of 3.3 ± 1.3 months occurring between December and February, months during which monthly precipitation is lower than 100 mm. Another smaller dry period occurs between June and August with monthly precipitation lower than 150 mm. Temperatures are elevated but relatively constant throughout the year, ranging from 24.2 ± 0.4°C to 25.5 ± 0.6°C. The minimum temperature occurs in March and the maximum temperature in July. Soils in the Yangambi Plateau consist mainly of weathered Xanthic Ferralsols (WRB2014). These soils derived primarily from fluvioeolian sediments made principally of quartz sand, kaolinite clay and hydrates iron oxides (Van Ranst, Baert, Ngongo, & Mafuka, 2010).

From February to May 2017, we carried out a liana census in 3 1-ha plots per forest type (regrowth forest, old growth monodominant forest, old growth mixed forest and old growth edge forest). These 12 1-ha forest plots (Table S1 & Figure S1) were randomly selected within an existing network of permanent inventory plots established in the Yangambi MAB Reserve. The regrowth forest plots (age since disturbance from 12 to 25 years), dominated by the tree species *M. cecropioides*, were characterized by an open canopy. The old growth monodominant forest plots were dominated by the tree species, *G. dewevrei*. They were characterized by a closed canopy and a sparse understorey. In regrowth forest and old growth monodominant forest plots, ≥60% of the basal area consisted of one species (i.e., the dominant tree species). The old growth mixed forest plots were constituted of a semi-deciduous forest with a relatively

closed canopy and a very dense undergrowth. The old growth edge forest plots were formed of mixed semi-deciduous forests, but adjacent to agricultural land. They included forested area found within the first 200 m into the old growth mixed forest from the disturbance related to slash-and-burn agricultural activities. Topography in each of the delineated forest plots was very gentle with almost no elevational differences. One regrowth forest plot and all old growth monodominant forest plots were found near forest streams, which was not the case for old growth mixed and old growth edge forest plots. For a more detailed description of the study area and plot establishment, see Kearsley et al. (2013).

In each forest plot, we identified, measured and mapped all liana individuals with diameter ≥ 2 cm following the protocol established by Gerwing et al. (2006), and amended by Schnitzer, Rutishauser, and Aguilar (2008). We measured liana diameter at 1.3 m distance along the stem from the rooting position and marked the point of measurement with red paint in order to ensure repeatability of measurement. Only individuals of true liana species were included in the census, defined as a woody climbing plant that germinates on the ground but loses its capacity to support itself while growing. It consequently has to resort to an external support to ascend into the canopy (Gerwing et al., 2006).

In situ species identification of lianas was not possible for most of the individuals. Instead, we allocated liana individuals to morphospecies based on a combination of both reproductive (flowers or fruits) and vegetative (leaves, bark and trunk) features with the help a field botanist. We made herbarium collections for each morphospecies for further taxonomic identification. We collected multiple voucher specimens per morphotype, and identification was made by botanists at the University of Kinshasa (UNIKIN) and verified by collections at the herbarium of National Institute for Agronomic Study and Research (INERA). Family nomenclature is based on the Angiosperm Phylogeny Group classification (AGP IV et al., 2016) whereas that of species follows Lebrun and Stork (1991–1997).

We searched taxonomic literature for ecological traits of the identified liana species (Évrard, 1968; Ewango et al., 2015; Gerard, 1960; Jardin botanique Meise, 2013). These traits included climbing mechanism, leaf size, regeneration light requirement, diaspore type and primary dispersal syndrome. We grouped climbing mechanisms for all liana species into four categories following the classification proposed by Putz (1984a) as stem twiner, hook climber, root climber and tendril climber. Following Raunkiaer (1934), we classified species in terms of leaf size as lepto- (<0.2 cm²), nano- (0.2–2 cm²), micro- (2–20 cm²), meso- (20–200 cm²) and macro-phyllous (200–20,000 cm²). We derived regeneration light requirements from Évrard (1968) and categorized liana species as shade tolerant, partially shade tolerant, partially light demanding and light demanding. Diaspore types included sclerochore (diaspore with no appendage), pogonochore (diaspore with long hairs), ballochore (sling diaspore), pterochore (winged diaspore) and sarcochore (fleshy diaspore) as proposed by Dansereau and Lems (1957). We grouped species into three primary dispersal syndromes, namely anemochory, zoochory and barochory as suggested by Ewango et al. (2015).

2.2 | Data analysis

In the analyses of species composition and diversity, we considered only individuals (97.6% of all individuals) assigned to a morphospecies that represented a clear distinct species. Identifications were made at three taxonomic ranks including species (with all subspecific taxa grouped under the parent species), genus and family. For community structure analyses, however, we took into consideration all enumerated individuals.

In order to visualize the patterns of liana species composition and diameter frequency distribution, we used non-metric multi-dimensional scaling analyses (NMDS) (Kruskal, 1964). To test the null hypotheses that forest types did not differ in both of the above attributes of liana assemblages, we used one-way permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2017). We checked the assumption of multivariate homogeneity of dispersion among forest types for these attributes by means of the permutational analysis of multivariate dispersions (PERMDISP) (Anderson, 2006). For liana species composition, we used liana species abundance in each plot and Bray–Curtis distance as dissimilarity measure. The choice of this commonly used abundance dissimilarity measure was motivated by its ability to properly handle the presence of large proportion of zeros (species absences) in data sets. Indeed, Bray–Curtis dissimilarity metric does not consider shared species absences as being similar unlike many other distance measures (Clarke, Somerfield, & Chapman, 2006). For liana diameter frequency distribution, we grouped all liana stems into 13 different size classes using an interval of 2 cm, ranging from 2 to 28 cm. For each of these classes, we determined class frequencies in each plot. We used class sizes as independent variables and Bray–Curtis as dissimilarity measure. We computed the significance of the pseudo-*F* statistic in PERMANOVA using 9,999 permutations of the residuals under reduced models. Owing to the low number of unique permutations, we opted for Monte Carlo asymptotic *P*-values (PMC) (Anderson & Robinson, 2003) to conduct post hoc pairwise comparisons. These analyses were conducted by means of the PERMANOVA + add-on for PRIMER v.6 software (Anderson, Gorley, & Clarke, 2008).

Two approaches were taken to assess differences across forest types in terms of liana ecological traits. The first approach consisted in determining differences in functional diversity and the second involved differences in the pattern of ecological trait distribution. To achieve that, we used the matrix of 105 identified species across the four forest types and 5 ecological traits assigned to each species (see Table S2). For functional diversity, we adopted the method described by Webb, Ackery, and Kembel (2008). Within each forest type, we explored the ecological trait-based structure of the liana assemblage by calculating the trait dispersion. As measure of dispersion, we used the mean pairwise trait distance (MPD). Because we were dealing with composite qualitative data (nominal and ordinal), we obtained the distance matrix by means of the Gower metric. We subsequently computed standardized effect sizes (SES) of functional trait diversity

by measuring trait dissimilarity among co-occurring liana species. We finally compared the observed trait diversity patterns to those expected under the null model of species richness randomized 999 times. Positive SES values (SES MPD > 0) indicate ecological trait evenness, while negative SES values (SES MPD < 0) indicate ecological trait clustering, relative to the null model. This analysis was carried out by means of the R software package *picante* (Kembel et al., 2010). For ecological trait distributions, we performed a NMDS analysis using mean nearest neighbor trait distance (MNTD) weighted by species abundance. Then, we carried out a one-way PERMANOVA and a PERMDISP using the R software package *vegan* (Oksanen et al., 2019).

The taxonomic diversity of lianas in different communities was described by means of the non-parametric species richness estimator, Chao1 (Chao, Colwell, Lin, & Gotelli, 2009) and effective numbers of diversity (Daly, Baetens, & De Baets, 2018) also referred to as Hill numbers (Hill, 1973). We used Chao1 to determine sampling completeness, that is, accounting for missing identification of individuals and potential species not determined (Walther & Morand, 1998). This estimator was preferred because it is known to be valid under all types of species abundance distribution. It is therefore considered as a universal species richness estimator (Chao et al., 2009). We computed this diversity index using the R software package *biodiversityR* (Kindt & Coe, 2005). Hill numbers are a mathematically unified family of diversity indices differing among themselves only by an exponent *q* that determines the measure's sensitivity to species relative abundances (Hill, 1973; Jost, 2006; MacArthur, 1965). We used Hill numbers ($H_{SR}^{(q)}$) of orders $q = 0$, $q = 1$ and $q = 2$ to respectively approximate species richness (H_{SR}), the exponential of the Shannon index $\exp(H_{SR})$ and the reciprocal of the Simpson index $(H_{SR})^{-1}$ according to transformations proposed by Jost (2006). Following the method described by Chao et al. (2014), we subsequently conducted an individual-based rarefaction–extrapolation analysis on these effective diversity measures. First, we employed a standardized number of stems to estimate the effectiveness of liana sampling for each forest type. Using 50 bootstrap replicates, we then constructed 95% confidence intervals around effective diversity rarefaction–extrapolation curves for each forest type and compared them. Effective diversity measures were considered significantly different among forest types when the confidence intervals of the curves were non-overlapping. We conducted this analysis using the R software package *iNEXT* (Hsieh, Ma, & Chao, 2019).

Due to the limited number of replicates, we determined differences in liana abundance and basal area across forest types using one-way Bayesian analysis of variance (ANOVA) with the Gaussian family. We computed total liana abundance and total liana basal area for each plot by summing the values for all individuals present in the plot. For both structural attributes, we specified mildly informative priors in the Bayesian ANOVA to improve convergence and guard against overfitting, and constructed 95% confidence intervals using Markov Chain Monte Carlo (MCMC). Both Bayesian models were created in the Stan computational framework (Stan Development team, 2012) accessed with *brms* package (Bürkner, 2017).

3 | RESULTS

A total of 2,638 liana stems were recorded across the four forest types in the 12 1-ha plots, of which 2,576 were identified to the species level. They represented 105 species (see Table S2 for complete list) stemming from 49 genera and 22 families. The most speciose families included Celastraceae-Hippocrateoideae (13 species), Fabaceae-Faboideae (11 species), Apocynaceae-Apocynioideae (10 species) and Connaraceae (10 species).

NMDS analysis based on species composition revealed that plots in the regrowth forest were separated from those in the other forest types in the first dimension whereas in the second dimension, plots in the old growth monodominant forest were separated from those present in the three other forest types (Figure 1a). One-way PERMANOVA showed that liana species composition differed significantly across forest types (F -ratio = 2.97, p = .001). The pairwise comparisons more or less corroborated the pattern shown in the NMDS analysis. Liana species composition in the old growth monodominant forest significantly differed from that in regrowth forest (p = .04), in old growth mixed forest (p = .04) and in old growth edge forest (p = .04). Liana composition in regrowth forest only marginally differed from that in old growth mixed forest (p = .06) and in old growth edge forest (p = .07). There was, however, no significant difference between old growth mixed forest and old growth edge forest (p = .459). The PERMDISP test revealed that liana species composition dispersion did not differ significantly across forest types (F = 3.03, p = .30).

Regarding taxonomic diversity, mean number of species (observed and estimated) were highest in old growth edge forest and lowest in regrowth forest (Table 1). There were no significant differences in rarefied-extrapolated H_{SR} among different forest types (Figure 2a). However, diversity extrapolation curves revealed that $\exp(H_{SH})$ and $(H_{SI})^{-1}$ were significantly lower in regrowth and old growth monodominant forests as compared to old growth mixed and old growth edge forests (Figure 2b,c).

The ecological trait-based structure of the liana assemblage showed that functional diversity was lower than expected under the null model of species richness (SES MPD < 0) in old growth mixed and old growth edge forests as well as in old growth monodominant forest for at least two communities out of three. However, it was higher than expected under the same null model in the regrowth forest (SES MPD > 0) for all three communities (Figure 3).

One-way PERMANOVA showed a significant difference in liana ecological trait distribution among forest types (F -ratio = 6.19, p = .015). This was confirmed by NMDS ordination which depicted a clear separation in the plane between old growth forests (constituted of old growth mixed forest, old growth edge forest and old growth monodominant forest) and the regrowth forest (Figure 1b). PERMDISP did not reveal any significant dispersion of ecological traits among forest types (F -ratio = 1.36, p = .39).

Liana community structure was characterized by a significantly variable diameter frequency distribution across forest types as revealed by one-way PERMANOVA (F -ratio = 4.44, p = .01). The largest difference in diameter frequency distribution was between

regrowth forest versus old growth monodominant forest (p = .02). Liana diameter frequency distribution in regrowth forest also significantly differed from old growth mixed forest (p = .03) and old growth edge forest (p = .03), and that in old growth monodominant forest marginally differed from old growth mixed forest (p = .06). However, liana diameter frequency distribution in old growth edge forest did not significantly differ from that in old growth mixed forest (p = .43) and in old growth monodominant forest (p = .57). The PERMANOVA analysis was visually supported by the NMDS ordination (Figure 1c). Forest types tended to separate one from another, and plots in each forest type tended to group together except for those in old growth edge forest and old growth monodominant forest. PERMDISP did not reveal any significant dispersion in diameter frequency distribution among forest types (F -ratio = 0.31, p = .81).

The output of one-way Bayesian ANOVA indicated that the old growth monodominant forest was the most densely populated forest type in terms of lianas with an average posterior distribution of 299 (95% CI [218, 371]) stems/ha, followed by old growth edge forest with 245 (95% CI [169, 315]) stem/ha. The regrowth forest was the least abundant of all forest types with only a mean posterior distribution of 144 (95% CI [68, 219]) stems/ha (Figure 4a).

It is plausible that 155 (95% CI [41, 259]) more liana stems/ha occurred in old growth monodominant forest than in regrowth forest. There is a possibility that the old growth monodominant forest also harbored marginally more liana stems/ha (113, 95% CI [-2, 219]) than the mixed old growth forest, but this difference was not statistically robust. However, it is fairly unlikely that more liana stems/ha were encountered in old growth monodominant forest compared to old growth edge forest (54, 95% CI [-50, 156]), and in old growth edge forest as compared to old growth mixed forest (58, 95% CI [-47, 159]). Taken together, old growth forests were likely to harbor 99 (95% CI [9, 184]) more liana stems/ha than the regrowth forest.

Total basal area was highest in old growth edge forest with an average posterior distribution of 0.57 m² ha⁻¹ (95% CI [0.33, 0.78]) and lowest in regrowth forest with a mean posterior distribution of 0.16 m² ha⁻¹ (95% CI [-0.08, 0.39]) (Figure 4b). It is likely that total basal area in regrowth forest was respectively 0.41 m²/ha (-0.41, 95% CI [-0.71, -0.08]), 0.35 m²/ha (-0.35, 95% CI [-0.69, -0.01]) and 0.37 m²/ha (-0.37, 95% CI [-0.70, -0.02]) lower as compared to old growth edge forest, old growth mixed forest and old growth monodominant forest. Compared to all these old growth forests lumped together, it is likely that total basal area in regrowth forest was lower by 0.38 m²/ha (-0.38, 95% CI [-0.65, -0.09]).

4 | DISCUSSION

Within the Yangambi MAB Reserve, we revealed some interesting differences in liana community attributes across different forest types. First, we observed a shift in liana species composition between, on the one hand, the regrowth forest and old growth forests and, on the other hand, the old growth monodominant forest and old growth mixed forest types. Second, we noticed that both monodominant forest types

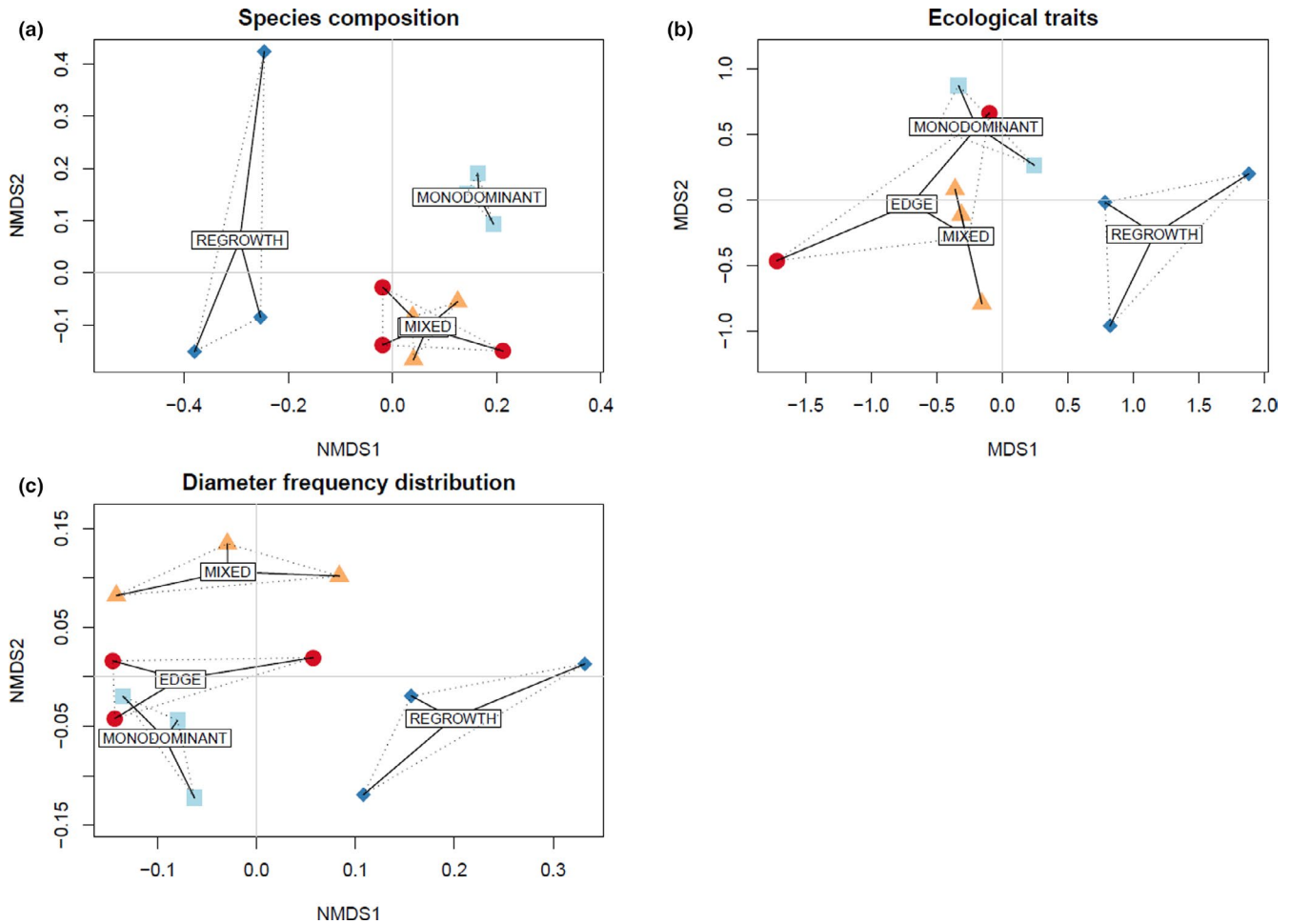


FIGURE 1 Results of non-metric multidimensional scaling (NMDS) ordinations for 12 liana communities in the Yangambi MAB Reserve based on species composition (a), ecological traits (b) and diameter frequency distribution (c). Filled symbols indicate the forest type of individual communities

TABLE 1 Taxonomic attributes of lianas in different forest types of the Yangambi MAB Reserve

Forest type	EDGE 1 ha N = 3	MIXED 1 ha N = 3	MONODOMINANT 1 ha N = 3	REGROWTH 1 ha N = 3
Taxonomic characteristics (mean \pm SD)				
Number of species	42.3 \pm 8.9	37.0 \pm 4.4	36.7 \pm 2.1	26.0 \pm 2.0
Number of genera	27.3 \pm 4.0	24.0 \pm 1.7	24.3 \pm 1.5	19.3 \pm 0.6
Number of families	16.7 \pm 2.9	16.7 \pm 0.6	14.7 \pm 1.2	12.3 \pm 0.6
Species richness non-parametric estimators (mean \pm SD)				
Chao1	58.1 \pm 15.4	52.2 \pm 11.3	49.2 \pm 8.17	31.7 \pm 3.2
Hill numbers (estimates and 95% CI) ^a				
q = 0	96.0 [79.4, 145.5]	65.0 [59.1, 86.8]	79.1 [62.3, 133.9]	65.1 [49.5, 125.2]
q = 1	32.9 [30.7, 36.2]	30.9 [28.9, 33.7]	24.4 [23.3, 26.4]	24.4 [22.5, 27.3]
q = 2	19.8 [19.3, 21.8]	19.4 [18.8, 21.9]	13.7 [13.5, 15.3]	15.1 [14.6, 17.5]

^aChao and Jost (2015).

had a lower taxonomic diversity than mixed forest types. Third, we found that functional diversity was higher in the regrowth forest compared to old growth forests. Finally, we noted that liana total basal area was lower in the regrowth forest compared to old growth forest as

anticipated. However, contrary to our expectation, the regrowth forest harbored fewer liana stems than old growth forests.

Regarding liana species composition, individuals of *Alchornea cordifolia* (Euphorbiaceae) abounded in the regrowth forest. This

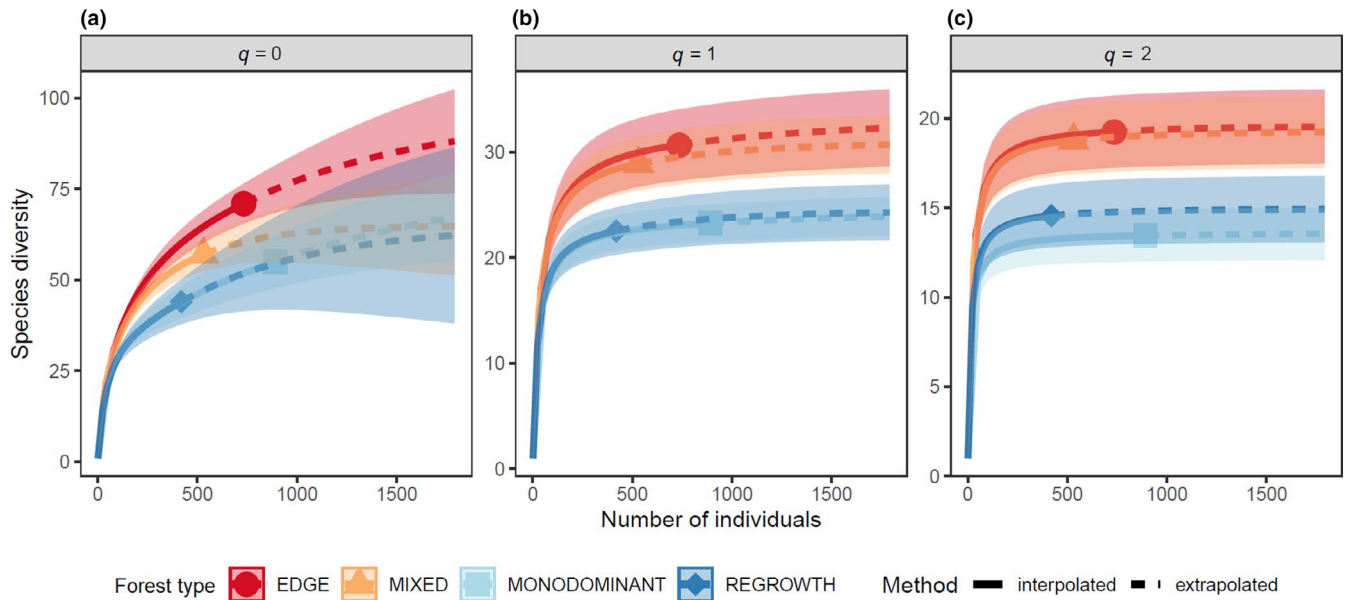


FIGURE 2 Individual-based rarefaction-extrapolation curves (with 95% CI) for lianas in different forest types in the Yangambi MAB Reserve: (a) $q = 0$ for richness (H_{SR}), (b) $q = 1$ for Shannon ($\exp(H_{Sh})$) and (c) $q = 2$ for Simpson ($(H_{Si})^{-1}$). The solid lines indicate rarefaction curves from the reference sample, and the dashed lines show the extrapolation curve. Each symbol represents the observed cumulative number of individuals within 3 1-ha plots of each forest type

FIGURE 3 Measures of standardized effect size (SES) of ecological trait community structure calculated for liana communities present in each forest type in the Yangambi MAB Reserve using Mean Pairwise Trait Distance (MPD) and the null model of species richness. Positive SES values (SES MPD > 0) indicate ecological trait evenness, while negative SES values (SES MPD < 0) indicate ecological trait clustering, relative to a null model of species richness. Violin plots show the distribution shape of the data

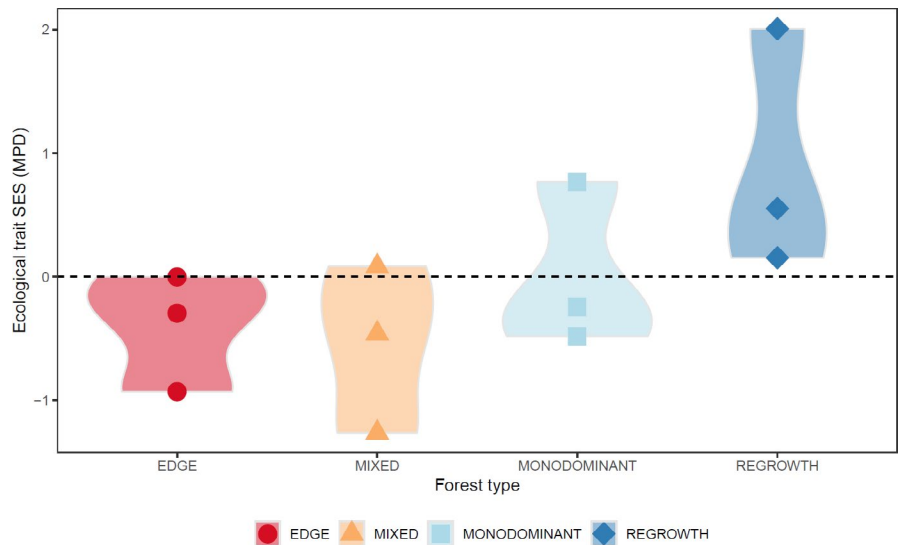
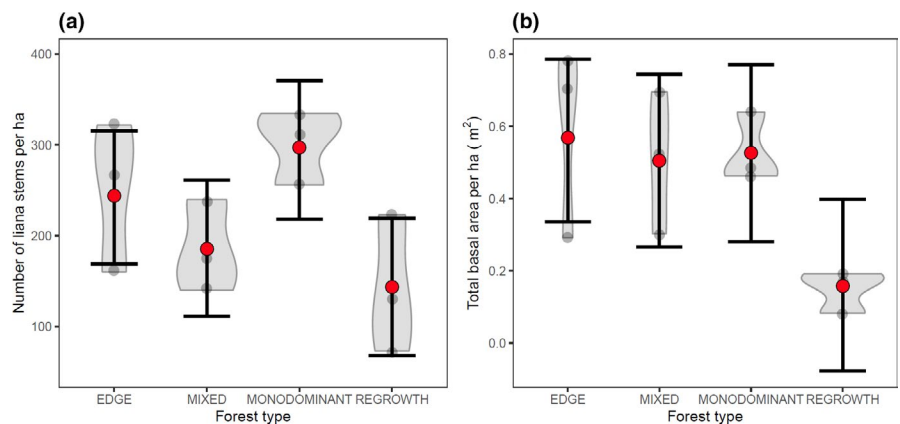


FIGURE 4 Liana stem abundance per ha (a) and total basal area per ha (b) in the Yangambi MAB Reserve. Small dots in gray show the observed values for each plot while the large circles in red with error bars show the mean of the posterior distributions and 95% CI. Violin plots show the distribution shape of the data



particular liana species is known to be widespread in secondary and riverine forests (Mavar-Manga, Lejoly, Quetin-Leclercq, & Schmelzer, 2008). It is often associated with anthropogenic disturbance and is an early colonizer of deforested areas (Agwu, 2001). As such, it requires light (canopy opening) for seed germination and growth of its seedlings. In the old growth mixed forests, both on the edge of agricultural fields and in core forest, the species *Mannionphyton fulvum* (Euphorbiaceae) was the most abundant. Ewango et al. (2015) also reported the dominance of this species in the Ituri old growth mixed forest. According to these authors, *M. fulvum* is a generalist species that is capable of thriving well in both light-rich and shady environments (Ewango et al., 2015). *Strychnos longicaudata* (Strychnaceae), which was the most abundant species in the old growth monodominant forest, is a light-demanding species often encountered along river banks in rain forests (de Ruijter, 2008).

Based on ecological behaviors of these most abundant species, we can speculate that a gradient in light availability is mainly responsible for the difference in liana species composition noticed between the regrowth forest and old growth forests. Indeed, the lack of a full canopy in the regrowth forest makes it possible for light to reach the floor, supporting the development of more early-successional light-demanding liana species. The proximity of old growth monodominant forest plots to small streams on its part might have fostered the development of particular liana species, distinguishing them from old growth mixed forests. Although not exclusively, old growth monodominant forests in the Congo basin are often encountered along rivers (Fayolle et al., 2014). Indeed, the dominant tree species, *G. dewevrei* is believed to have limited drought resistance and water regulation potential. This possibly explains its establishment near forest streams where water tables are likely to be shallow (Kearsley et al., 2017). Differences in liana species composition between these two old growth forest types could also be explained by soil phosphorus (P) content, which, according to Kearsley et al. (2017), is marginally lower in monodominant forest compared to the mixed forest in the Yangambi MAB Reserve. Bauters et al. (2019) also suggested that differences in P cycling might be at the basis of *Gilbertiodendron* monodominance in tropical rain forest of the Congo basin, since no discernible differences were found in gross soil nitrogen (N) fluxes between the two forest types. Indeed, soil P concentration has been identified as one of the major environmental factors influencing liana species composition in subtropical and tropical forests (Addo-Fordjour & Rahmad, 2015; Malizia, Grau, & Lichstein, 2010).

As far as taxonomic diversity is concerned, forest types in the Yangambi MAB Reserve were characterized by relatively low mean liana species richness, driven mainly by noticeable numbers of rare species (singletons or doubletons). It ranged from 26 to 42 species/ha. These values are lower than what was reported in most liana censuses (≥ 2 cm diameter) conducted in lowland tropical forests. These include, among others, Putz (1984a) who reported 65 species/ha on average in Panama, Laurance et al. (2001) who recorded 70 species/ha on average in Brazilian Amazonia, Pérez-Salicrup, Sork, and Putz (2001) who

enumerated 51 species/ha in Bolivia or Ewango et al. (2015) in the Ituri forest in the Congo basin who found 64 species/ha on average.

Individual-based rarefaction curves did not detect any significant difference among forest types in terms of effective species richness. However, forest types did statistically differ in effective Shannon and Simpson indices, which were higher in both old growth mixed forest types compared to old growth monodominant and regrowth forests. Knowing that the regrowth forest was a non-persistent monodominant forest, it appears as though the same mechanisms shaping tree diversity also act for liana diversity in these forests. Indeed, forests with higher tree diversity seem also to harbor higher liana diversity and vice versa.

Because tropical forests are very complex systems, variations in liana species diversity among these forest types can be a result of many factors and processes. In the case of monodominant old growth forests in the Congo basin, the dominant tree species, *G. dewevrei* is known to be so efficient in regenerating under its own canopy at the expense of other tree species (Djuikouo et al., 2014). This species possesses a certain number of traits that can modify the understorey environment of the forest, giving it a strong competitive advantage in terms of regeneration over other tree species. These traits include, among others, low leaf litter decomposition rate, high seedling shade tolerance, large seed size and defense against herbivory (Hart et al., 1989; Torti et al., 2001). Furthermore, Hall et al. (2019) have recently argued that *G. dewevrei* exhibits efficient nutrient (both N and P) acquisition and use due to the association of its roots with ectomycorrhizal fungi. This association allows *G. dewevrei* to directly acquire N and P from soil organic matter while causing nutrient limitation to co-occurring species. We can speculate that the competitive exclusion exerted by *G. dewevrei* on other tree species is also extended on woody liana species, thus reducing their diversity in the old growth monodominant forest.

The regrowth forest in the Congo basin is generally characterized by the massive recruitment of the early-successional and fast-growing tree species, *M. cecropioides* (Aubréville, 1947) thanks to its large and persistent soil seed bank (Hall & Swaine, 1980). This dominant species can quickly preempt space and resources, thus outcompeting less fast-growing pioneer species in early stages of succession (Gourlet-Fleury et al., 2013). Besides its unique growth performance (Coombe & Hadfield, 1962; Leroy-Deval, 1967), *M. cecropioides* has large leaves and flexible trunks. Some tree species possessing these characteristics have the ability to avoid or shed lianas. This was particularly demonstrated for the species *Cecropia peltata* in Neotropical and Malaysian forests (Putz, 1984b; Putz & Holbrook, 1988). Because both *C. peltata* and *M. cecropioides* are closely related species of the Cecropiaceae family (Treiber, Gaglioti, Romaniuc-Neto, Madriñán, & Weiblen, 2016), the lower liana species diversity found in the regrowth forest in the Yangambi Reserve might be a consequence of competitive exclusion through liana avoidance and/or shedding imposed by the dominant species, *M. cecropioides*.

Moreover, we noticed that liana single species dominance was more pronounced in old growth monodominant and regrowth

forests than in both old growth mixed forest types. While *S. longicaudata* accounted for 20% of all stems and 14% of the basal area in the old growth monodominant forest, *A. cordifolia* accumulated 15% of all stems and 22% of the basal area in the regrowth forest. In old growth mixed forest and old growth edge forest, however, the most abundant species *M. fulvum* represented just over 10% of all counted stems and less than 10% of their basal area (see Table S2). This could be a further indication that conditions imposed by dominant tree species in these two distinct monodominant forests deter the development not only of a diverse tree community as it is known, but also that of a diverse liana community.

The higher liana diversity noticed in both old growth mixed forest types could be attributed to a more pronounced intra-species competition. This mechanism has been often mentioned as one of the underlying causes maintaining high diversity in mature tropical mixed forests (Alder et al., 2018; Pacala & Levin, 1997). The fact that liana diversity was highest in old growth edge forest than in any other forest type is not so surprising, and can be justified on two major counts. First, the latter forest type might have benefited from disturbance regimes in its vicinity. Because disturbed tropical forests offer ideal conditions for the proliferation of lianas (see Schnitzer & Bongers, 2011), their diversity is also expected to be higher there (see Laurance et al., 2001). Second, species diversity is generally reported to peak in forest margins and ecotones (Erdős, Gallé, Körmöczi, & Bátor, 2013). That is because forest margins and ecotones are considered as mixing zones where species from two or more bounded communities occur, making species diversity higher than in the centers of these communities (Risser, 1995).

In terms of ecological traits, the regrowth forest stood out from all the other forest types by having a higher functional diversity than it could be expected under the null model of species richness (Figure 3). Thus, the ecological attributes of liana species were over-dispersed in the regrowth forest whereas they were mainly clustered in old growth forests. The pattern of ecological trait clustering was, however, stronger in both old growth mixed forest types than in old growth monodominant forest. This finding signifies that co-occurring liana species in the regrowth forest had very dissimilar ecological traits, while the opposite was true for co-occurring liana species in the rest of old growth forests. Following research of Webb, Ackerly, McPeck, and Donoghue (2002) and Cavender-Bares, Ackerly, Baum, and Bazzaz (2004) on trait-based community assembly, we may deduce that the main ecological process driving liana community assembly in the regrowth forest was competitive exclusion whereas environmental filtering might have been predominantly acting in old growth forests.

Irrespective of the forest type, lianas in the Yangambi MAB Reserve were mainly light demanding, mesophyllous and stem twiners and had more animal dispersed seeds (see Figure S2a-e). This is in accordance with what was observed in others studies conducted in various tropical forests in Africa (Addo-Fordjour, Anning, Atakora, & Agyei, 2008; Ewango et al., 2015; Koffi, Kouamé, & Adou-Yao, 2016). Despite this general pattern, liana

communities in the regrowth forest harbored relatively more tendrill climber, wind-dispersed, nanophyll and light-demanding species compared to other forest types. This finding tends to suggest that liana species with these traits might have a higher success rate in the regrowth forest which is characterized by a more open canopy structure.

Liana density was lowest in the regrowth forest as compared to other forest types. This result may at first sight appear surprising given the well-established assertion that lianas generally reach high densities early in forest succession after disturbance (Bary et al., 2015). A probable reason for this could be that many lianas in the regrowth forest were still seedlings, free-standing or had a diameter smaller than the cutoff of 2 cm, and hence were not inventoried. As the dominant tree *M. cecropioides* tends to avoid lianas, the lack of enough suitable supports could be yet another reason explaining the low liana density noticed in the regrowth forest. The higher number of liana stems observed in the monodominant old growth forest compared to adjacent mixed old growth forests may, for its part, be linked to its proximity to small streams. Dense forests along rivers are known to create suitable conditions for the proliferation of particular liana species (Schnitzler, 1995). The legacy of a more pronounced disturbance regime in the regrowth forest was, however, attested by its diameter structure distribution characterized by the scarcity of large lianas (≥ 10 cm) as opposed to old growth forests (Figure S3a-d). This means that development time of size hierarchies in the regrowth forest was shorter. As a consequence, liana total basal area and biomass were lower in the regrowth forest as compared to old growth forests.

5 | CONCLUSION

We found that liana community composition differed considerably across forest types in the Yangambi MAB Reserve, being probably influenced by differences in multiple local biotic and abiotic conditions. These conditions, especially the competition imposed by dominant tree species, might have been deterring the development of diverse liana communities in regrowth and old growth monodominant forests in contrast with old growth mixed forests (both on the edge and in core forest). The ecological trait diversity was higher than expected under the null model of species richness in the regrowth forest as opposed to old growth forests. The regrowth forest further differed from old growth forests by harboring a relatively higher proportion of liana species with ecological traits associated to a more open canopy structure. Structurally, we found fewer liana stems in the regrowth forest than in old growth forests contrary to what one could expect. We attributed the particular highest density of lianas in the old growth monodominant forest to its proximity to streams. The legacy of a more pronounced disturbance regime in the regrowth forest was witnessed by its near total absence of large liana stems and lower total basal area, distinguishing it from old growth forests. Overall, this work shows that liana assemblage attributes in the Congo Basin are redefined by forest types, with communities in the regrowth forest being the most distinct.

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CONFLICTS OF INTEREST

The corresponding author confirms on behalf of all authors that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3tx95x6c5> (Mumbanza et al., 2020).

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REFERENCES

- Addo-Fordjour, P., Anning, A. K., Atakora, E. A., & Agyei, P. S. (2008). Diversity and distribution of climbing plants in a semi-deciduous rain forest, KNUST botanic garden, Ghana. *International Journal of Botany*, 4, 186–195. <https://doi.org/10.3923/ijb.2008.186.195>
- Addo-Fordjour, P., & Owusu-Boadi, K. (2016). Linear edge effects on liana and tree communities in two tropical forest ecosystems in Ghana. *Ecological Research*, 31(5), 709–718. <https://doi.org/10.1007/s11284-016-1382-7>
- Addo-Fordjour, P., & Rahmad, Z. B. (2015). Environmental factor associated with liana community assemblages in a tropical forest reserve, Ghana. *Journal of Tropical Ecology*, 31, 69–79. <https://doi.org/10.1017/S0266467414000522>
- Adler, P. B., Smull, D., Beard, K. H., Choi, R. T., Furniss, T., Kulmatiski, A., ... Veblen, K. E. (2018). Competition and coexistence in plant communities: Intraspecific competition is stronger than interspecific competition. *Ecology Letters*, 21, 1319–1329. <https://doi.org/10.1111/ele.13098>
- Agwu, C. O. C. (2001). A study of Niger Delta environment through airborne palynomorphs, Port Harcourt, Nigeria. *Review of Paleogeology of Africa*, 27, 191–205.
- Anderson, M. J. (2006). Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*, 62, 245–253. <https://doi.org/10.1111/j.1541-0420.2005.00440.x>
- Anderson, M. J. (2017). *Permutational multivariate analysis of variance*. Wiley StatsRef: Statistics reference online. <https://doi.org/10.1002/9781118445112.stat07841>
- Anderson, M. J., Gorley, R. N., & Clarke, K. R. (2008). *PERMANOVA+ for PRIMER: Guide to software and statistical methods*. Plymouth, UK: PRIMER-E.
- Anderson, M. J., & Robinson, J. (2003). Generalized discriminant analysis based on distances. *Australian & New Zealand Journal of Statistics*, 45, 301–318. <https://doi.org/10.1111/1467-842x.00285>
- APG, Iv, Chase, M. W., Christenhusz, M. J. M., Fay, M. F., Byng, J. W., Judd, W. S., ... Stevens, P. F. (2016). An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society*, 181(1), 1–20. <https://doi.org/10.1111/boj.12385>
- Aubréville, A. (1947). Les brousses secondaires en Afrique Equatoriale. Côte d'Ivoire – Cameroun – AEF. *Bois Et Forêts Des Tropiques*, 2, 24–49.
- Babweteera, F., Plumptre, A., & Obua, J. (2000). Effect of gap size and age on climber abundance and diversity in Budongo Forest Reserve, Uganda. *African Journal of Ecology*, 38, 230–237. <https://doi.org/10.1046/j.1365-2028.2000.00245.x>
- Barry, K. E., Schnitzer, S. A., van Breugel, M., & Hall, J. S. (2015). Rapid liana colonization and community development along a secondary forest chronosequence. *Biotropica*, 47(6), 672–680. <https://doi.org/10.1111/btp.12259>
- Bauters, M., Verbeeck, H., Rütting, T., Barthel, M., Bazirake Mujinya, B., Bamba, F., ... Boeckx, P. (2019). Contrasting nitrogen fluxes in African tropical forests of the Congo Basin. *Ecological Monographs*, 89(1), e01342. <https://doi.org/10.1002/ecm.1342>
- Bugmann, H., & Bigler, C. (2011). Will the CO₂ fertilization effect in forests be offset by reduced tree longevity? *Oecologia*, 165, 533–544. <https://doi.org/10.1007/s00442-010-1837-4>
- Bullock, S. H. (1995). Plant reproduction in neotropical dry forests. In S. H. Bullock, H. A. Mooney & E. Medina (Eds.), *Seasonally dry tropical forests* (pp. 277–303). Cambridge, UK: Cambridge University Press. <https://doi.org/10.1017/CBO9780511753398.011>
- Bürkner, P. C. (2017). brms: An R Package for Bayesian Multilevel Models using Stan. *Journal of Statistical Software*, 80(1), 1–28. <https://doi.org/10.18637/jss.v080.i01>
- Cavender-Bares, J., Ackerly, D. D., Baum, D., & Bazzaz, F. (2004). Phylogenetic over dispersion in Floridian oak communities. *The American Naturalist*, 163, 823–843. <https://doi.org/10.1086/386375>
- Chao, A., Colwell, R. K., Lin, C. W., & Gotelli, N. J. (2009). Sufficient sampling for asymptotic minimum species richness estimators. *Ecology*, 90, 1125–1133. <https://doi.org/10.1890/07-2147.1>
- Chao, A., Gotelli, N. J., Hsieh, T., Sander, E. L., Ma, K., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84(1), 45–67. <https://doi.org/10.1890/13-0133.1>
- Chao, A., & Jost, L. (2015). Estimating diversity and entropy profiles via discovery rates of new species. *Methods in Ecology and Evolution*, 6(8), 873–882. <https://doi.org/10.1111/2041-210X.12349>
- Chave, J., Bernard, R., & Dubois, M.-A. (2001). Estimation of biomass in a neotropical forest of French Guiana: Spatial and temporal variability. *Journal of Tropical Ecology*, 17(1), 79–96. <https://doi.org/10.1017/S0266467401001055>
- Clarke, K. R., Somerfield, P. J., & Chapman, M. G. (2006). On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis measure for denuded assemblages. *Journal of Experimental Marine Biology and Ecology*, 330, 55–80. <https://doi.org/10.1016/j.jembe.2005.12.017>
- Connell, J. H., & Lowman, M. D. (1989). Low-diversity tropical rain forests: Some possible mechanisms for their existence. *The American Naturalist*, 134, 88–119. <https://doi.org/10.1086/284967>
- Coombe, D. E., & Hadfield, W. (1962). An analysis of the growth of *Musanga cecropioides*. *Journal of Ecology*, 50, 221–230. <https://doi.org/10.2307/2257206>
- Daly, A. J., Baetens, J. M., & De Baets, B. (2018). Ecological diversity: Measuring the unmeasurable. *Mathematics*, 6(7), 119. <https://doi.org/10.3390/math6070119>
- Dansereau, P., & Lems, K. (1957). The grading of dispersal types in plant communities and their ecological significance. *Contributions Institut Botanique De L'université De Montréal*, 71, 5–52.
- de Ruijter, A. (2008). *Strychnos longicauda* Gilg. In G. H. Schmelzer & A. Gurib-Fakim (Eds.), *Plant resources of tropical Africa 11(1)*. Medicinal

- plants, Vol. 1 (pp. 573–574). Wageningen, the Netherlands: PROTA Foundation.
- DeWalt, S. J., Schnitzer, S. A., Alves, L. F., Bongers, F., Burnham, R. J., Cai, Z., ... van Melis, J. (2015). Biogeographical patterns of liana abundance and diversity. In S. A. Schnitzer, F. Bongers, R. J. Burnham & F. E. Putz (Eds.), *Ecology of lianas* (pp. 131–146). New York, NY: John Wiley & Sons. <https://doi.org/10.1002/9781118392409.ch11>
- DeWalt, S. J., Schnitzer, S. A., & Denslow, J. S. (2000). Density and diversity of lianas along a chronosequence in a Central Panamanian lowland forest. *Journal of Tropical Ecology*, 16, 1–19. <https://doi.org/10.1017/S0266467400001231>
- Djuikouo, M. N. K., Peh, K. S. H., Nguembou, C. K., Doucet, J. L., & Sonké, B. (2014). Stand structure and species co-occurrence in mixed and monodominant Central African tropical forests. *Journal of Tropical Ecology*, 30, 447–455. <https://doi.org/10.1111/j.1365-2028.2010.01212.x>
- Djuikouo, M. N. K., Sonké, B., Doucet, J. L., Nguembou, C. K., & Lewis, S. L. (2010). Diversity and aboveground biomass in three tropical forest types in the Dja Biosphere reserve, Cameroon. *African Journal of Ecology*, 48, 1053–1063. <https://doi.org/10.1111/j.1365-2028.2010.01212.x>
- Erdős, L., Gallé, R., Körmöcz, L., & Bátor, Z. (2013). Species composition and diversity of natural forest edges: Edge responses and local edge species. *Community Ecology*, 14(1), 48–58. <https://doi.org/10.1556/ComEc.14.2013.1.6>
- Évrard, C. (1968). *Recherches écologiques sur le peuplement des sols hydromorphes de la cuvette centrale congolaise (Série scientifique 110)*. Bruxelles, Belgique: Ministère Belge de l'éducation nationale et culture, Publication INEAC.
- Ewango, C. E., Bongers, F., Makana, J. R., Poorter, L., & Sosef, M. S. (2015). Structure and composition of the liana assemblage of a mixed rain forest in the Congo Basin. *Plant Ecology and Evolution*, 148(1), 29–42. <https://doi.org/10.5091/plecevo.2015.984>
- Ewers, F. W., Fisher, J. B., & Chiu, S. T. (1990). A survey of vessel dimensions in stems of tropical lianas and other growth forms. *Oecologia*, 84, 544–552. <https://doi.org/10.1007/BF00328172>
- Fayolle, A., Picard, N., Doucet, J. L., Swaine, M., Bayol, N., Bénédet, F., & Gourlet-Fleury, S. (2014). A new insight in the structure, composition and functioning of central African moist forests. *Forest Ecology and Management*, 329, 195–205. <https://doi.org/10.1016/j.foreco.2014.06.014>
- Gehring, C., Park, S., & Denich, M. (2004). Liana allometric biomass equations for Amazonian primary and secondary forest. *Forest Ecology and Management*, 195, 69–83. <https://doi.org/10.1016/j.foreco.2004.02.054>
- Gentry, A. H. (1991). Breeding and dispersal systems of lianas. In F. E. Putz & A. H. Mooney (Eds.), *The biology of vines* (pp. 393–424). Cambridge, UK: Cambridge University Press. <https://doi.org/10.1017/CBO9780511897658.017>
- Gerard, P. (1960). *Etude écologique de la forêt dense à Gilbertiodendron dewevrei dans la région de l'Uélé (Série Scientifique 87)*. Bruxelles, Belgique: Ministère Belge de l'éducation nationale et culture, Publication INEAC.
- Gerwing, J. J., Schnitzer, S. A., Burnham, R. J., Bongers, F., Chave, J., Dewalt, S. J., ... Thomas, D. W. (2006). A standard protocol for liana censuses. *Biotropica*, 38, 256–261. <https://doi.org/10.1111/j.1744-7429.2006.00134.x>
- Gourlet-Fleury, S., Beina, D., Fayolle, A., Ouédraogo, D.-Y., Mortier, F., Bénédet, F., ... Decocq, G. (2013). Silvicultural disturbance has little impact on tree species diversity in a Central African moist forest. *Forest Ecology and Management*, 304, 322–332. <https://doi.org/10.1016/j.foreco.2013.05.021>
- Hall, J. B., & Swaine, M. D. (1980). Seed stocks in Ghanaian forest soils. *Biotropica*, 12, 256–263. <https://doi.org/10.2307/2387695>
- Hall, S. J., Harris, D. J., Saltonstall, K., Medjibe, V., Ashton, M. S., & Turner, B. L. (2019). Resource acquisition strategies facilitate *Gilbertiodendron dewevrei* monodominance in African lowland forests. *Journal of Ecology*, 00, 1–16. <https://doi.org/10.1111/1365-2745.13278>
- Hart, T. B., Hart, J. A., & Murphy, P. G. (1989). Monodominant and species-rich forests of the humid tropics: Causes for their co-occurrence. *The American Naturalist*, 133, 613–633. <https://doi.org/10.1086/284941>
- Hill, M. (1973). Diversity and evenness: A unifying notation and its consequences. *Ecology*, 54(2), 427–432. <https://doi.org/10.2307/1934352>
- Hsieh, T. C., Ma, K. H., & Chao, A. (2019). iNEXT: iNterpolation and EXTrapolation for species diversity. R Package Version, 2, 19. Retrieved from <http://chao.stat.nthu.edu.tw/blog/software-download/>.
- Ingwell, L. L., Joseph, W. S., Becklund, K. K., Hubbell, S. P., & Schnitzer, S. A. (2010). The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama. *The Journal of Ecology*, 98(4), 879–887. <https://doi.org/10.1111/j.1365-2745.2010.01676.x>
- Jardin botanique Meise (2013). *Flore numérique d'Afrique Centrale (République Démocratique du Congo, Rwanda et Burundi)*. Meise, Belgium. Retrieved from <http://www.br.fgov.be/RESEARCH/DATABASES/FOCA>.
- Jost, L. (2006). Entropy and diversity. *Oikos*, 113(2), 363–375. <https://doi.org/10.1111/j.2006.0030-1299.14714.x>
- Kearsley, E., de Haulleville, T., Hufkens, K., Kidimbu, A., Toirambe, B., Baert, G., ... Verbeeck, H. (2013). Conventional tree height-diameter relationships significantly overestimate aboveground carbon stocks in the Central Congo Basin. *Nature Communications*, 4, 2269. <https://doi.org/10.1038/ncomms3269>
- Kearsley, E., Verbeeck, H., Hufkens, K., Van de Perre, F., Doetterl, S., Baert, G., ... Huygens, D. (2017). Functional community structure of African monodominant *Gilbertiodendron dewevrei* forest influenced by local environmental filtering. *Ecology and Evolution*, 7, 295–304. <https://doi.org/10.1002/ece3.2589>
- Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., ... Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463–1464. <https://doi.org/10.1093/bioinformatics/btq1166>
- Kindt, R., & Coe, R. (2005). *Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies*. Nairobi, Kenya: World Agroforestry Centre (ICRAF).
- Koffi, B. A., Kouamé, D., & Adou-Yao, Y. C. (2016). Structure and composition of the liana assemblage of Azagny National Park in the Southern Côte d'Ivoire. *International Journal of Biodiversity and Conservation*, 8(8), 206–215. <https://doi.org/10.5897/IJBC2016.0969>
- Kruskal, J. B. (1964). Nonmetric multidimensional scaling: A numerical method. *Psychometrika*, 29, 115–129. <https://doi.org/10.1007/bf02289694>
- Laurance, W. F., Pérez-Saliciup, D., Delamônica, P., Fearnside, P. M., D'Angelo, S., Jerozolisnki, A., ... Lovejoy, T. E. (2001). Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology*, 82, 105–116. [https://doi.org/10.1890/0012-9658\(2001\)082\[0105:RFFATS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[0105:RFFATS]2.0.CO;2)
- Lebrun, J.-P., & Stork, A. L. (1991–1997). *Énumération des plantes à fleurs d'Afrique tropicale. Vols 1–4*. Genève, Suisse: Conservatoire et Jardin botaniques de la Ville de Genève.
- Leroy-Deval, J. (1967). Vie et mort des parasoliers (Musanga cecropioides). *Bois Forêts Tropiques*, 112, 31–38.
- MacArthur, R. H. (1965). Patterns of species diversity. *Biological Reviews*, 40(4), 510–533. <https://doi.org/10.1111/j.1469-185X.1965.tb00815.x>
- Makana, J. R., Hart, T. B., & Hart, J. A. (1998). Forest structure and diversity of lianas and understory treelets in monodominant and mixed stands in Ituri Forest, Democratic Republic of the Congo. In F. Dallmeier & J. A. Comiskey (Eds.), *biodiversity research, monitoring*

- and modeling. *Conceptual background and Old World case studies* (pp. 429–446). London, UK: The Parthenon Publishing Group.
- Makana, J. R., Terese, B. H., Hibbs, D. E., & Condit, R. (2004). Stand structure and species diversity in the Ituri forest dynamics plots: A comparison of monodominant and mixed forest stands. In E. C. Losos & E. G. Leigh (Eds.), *Tropical forest diversity and dynamism: Findings from a large-scale plot network* (pp. 159–174). Chicago, IL: Chicago University Press.
- Malizia, A., Grau, H. R., & Lichstein, J. W. (2010). Soil phosphorus and disturbance influence liana communities in a subtropical montane forest. *Journal of Vegetation Science*, 21, 551–560. <https://doi.org/10.1111/j.1654-1103.2009.01162.x>
- Mavar-Manga, H., Lejoly, J., Quetin-Leclercq, J., & Schmelzer, G. H. (2008). *Alchornea cordifolia* (Schumacher & Thonn.) Müll. Arg. In G. H. Schmelzer & A. Gurib-Fakim (Eds.), *Plant resources of tropical Africa 11(1). Medicinal plants*, Vol. 1 (pp. 57–60). Wageningen, Netherlands: PROTA Foundation.
- Mumbanza, F. M., Bauters, M., Kearsley, E., Boeckx, P., Lubini, C. A., & Verbeeck, H. (2020). *Data from: Liana communities exhibit different species composition, diversity and community structure across forest types in the Congo Basin*. Dryad Digital Repository, <https://doi.org/10.5061/dryad.3tx95x6c5>
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., ... Wagner, H. (2019). *vegan: Community Ecology Package. R package version 2.5-6*. Retrieved from <https://cran.r-project.org/web/packages/vegan/index.html>.
- Pacala, S. W., & Levin, S. A. (1997). Biologically generated spatial pattern and the coexistence of competing species. In D. Tilman, & P. Kareiva (Eds.), *Spatial ecology: The role of space in population dynamics and interspecific interactions* (pp. 204–232). New York, NY: Princeton University Press. <https://doi.org/10.2307/j.ctv36zpz.16>.
- Peel, M. C., Finlayson, B. L., & McMahon, T. A. (2007). Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences*, 11, 1633–1644. <https://doi.org/10.5194/hess-11-1633-2007>
- Peh, K.-H., Sonké, B., Séné, O., Djuikouo, M.-N., Nguembou, C. K., Taedoum, H., ... Lewis, S. L. (2014). Mixed-forest species establishment in a monodominant forest in central Africa: Implications for tropical forest invasibility. *PLoS ONE*, 9(5), e97585. <https://doi.org/10.1371/journal.pone.0097585>
- Pérez-Salícru, D. R., Sork, V. L., & Putz, F. E. (2001). Lianas and trees in a liana forest of Amazonian Bolivia. *Biotropica*, 33(1), 34–47. <https://doi.org/10.1111/j.1744-7429.2001.tb00155.x>
- Putz, F. E. (1984a). The natural history of lianas on Barro Colorado Island, Panama. *Ecology*, 65, 1713–1724. <https://doi.org/10.2307/1937767>
- Putz, F. E. (1984b). How tree avoid and shed lianas. *Biotropica*, 16(1), 19–23. <https://doi.org/10.2307/2387889>
- Putz, F. E., & Chai, P. (1987). Ecological studies of lianas in Lambir National Park, Sarawak, Malaysia. *Journal of Ecology*, 75, 523–531. <https://doi.org/10.2307/2260431>
- Putz, F. E., & Holbrook, N. M. (1988). Further observation on the dissolution of mutualism between *Cecropia* and its ants: The Malaysian case. *Oikos*, 53, 121–125. <https://doi.org/10.2307/3565671>
- Raunkjær, C. (1934). *The life forms of plants and statistical plant geography*. Oxford, UK: Clarendon Press.
- Risser, P. R. (1995). The Status of the science examining ecotones - A dynamic aspect of landscape is the area of steep gradients between more homogeneous vegetation associations. *BioScience*, 45(5), 318–325. <https://doi.org/10.2307/1312492>
- Schnitzer, S. A., & Bongers, F. (2011). Increasing liana abundance and biomass in tropical forests: Emerging patterns and putative mechanisms. *Ecological Letters*, 14, 397–406. <https://doi.org/10.1111/j.1461-0248.2011.01590.x>
- Schnitzer, S. A., & Carson, W. P. (2010). Lianas suppress tree regeneration and diversity in treefall gaps. *Ecology Letters*, 13, 849–857. <https://doi.org/10.1111/j.1461-0248.2010.01480.x>
- Schnitzer, S. A., Kuzee, M. E., & Bongers, F. (2005). Disentangling above- and below-ground competition between lianas and trees in a tropical forest. *Journal of Ecology*, 93(6), 1115–1125. <https://doi.org/10.1111/j.1365-2745.2005.01056.x>
- Schnitzer, S. A., Mangan, S. A., Dalling, J. W., Baldeck, C. A., Hubbell, S. P., Ledo, A., ... Yorke, S. R. (2012). Liana abundance, diversity, and distribution on Barro Colorado Island. *Panama. PLoS ONE*, 7, e25114. <https://doi.org/10.1371/journal.pone.0052114>
- Schnitzer, S. A., Rutishauser, S., & Aguilar, S. (2008). Supplemental protocol for liana censuses. *Forest Ecology and Management*, 255(3), 1044–1049. <https://doi.org/10.1016/j.foreco.2007.10.012>
- Schnitzler, A. (1995). Community ecology of arboreal lianas in gallery forests of the Rhine valley, France. *Acta Oecologica*, 16, 219–236.
- Sonké, B. (2005). *Forêts de la Réserve du Dja (Cameroun): Etudes floristiques et structurales (Scripta Botanica Belgica, volume 32)*. Leuven, Belgique: Jardin botanique national de Belgique.
- Stan Development Team (2012). *Stan modeling language: User's guide and reference manual*. California, CA: CreateSpace Independent Publishing Platform. Retrieved from <http://mc-stan.org/users/documentation/>.
- Tarakeswara naidu, M., Aniel kumar, O., & Venkaiah, M. (2014). Taxonomic diversity of lianas in tropical forests of Northern Eastern Ghats of Andhra Pradesh. *India. Notulae Scientia Biologicae*, 6(1), 59–65. <https://doi.org/10.15835/nsb619193>
- Thomas, D., Burnham, R. J., Chuyong, G., Kenfack, D., & Sauge, M. N. (2015). Liana abundance and diversity in Cameroon's Korup National Park. In S. A. Schnitzer, F. Bongers, R. J. Burnham & F. E. Putz (Eds.), *Ecology of lianas* (pp. 11–22). New York, NY: John Wiley & Sons. <https://doi.org/10.1002/9781118392409.ch2>
- Torti, S. D., Coley, P. D., & Kursar, T. A. (2001). Causes and consequences of monodominance in tropical lowland forests. *The American Naturalist*, 157, 141–153. <https://doi.org/10.1086/318629>
- Trefon, T. (2017). Forest governance and international partnerships in the Congo Basin. *Science & Diplomacy*, 6(3). Retrieved from <http://www.sciencediplomacy.org/forest-governance-andinternational-partnerships-in-congo-basin>.
- Treiber, E. L., Gaglioti, A. L., Romaniuc-Neto, S., Madriñán, S., & Weiblen, G. D. (2016). Phylogeny of the Cecropieae (Urticaceae) and the evolution of an ant-plant mutualism. *Systematic Botany*, 41(1), 56–66. <https://doi.org/10.1600/036364416X690633>
- Tyukavina, A., Hansen, M. C., Potapov, P., Parker, D., Okpa, C., Stehman, S. V., ... Turubanova, S. (2018). Congo Basin forest loss dominated by increasing smallholder clearing. *Science Advances*, 4(11), eaat2993. <https://doi.org/10.1126/sciadv.aat2993>
- van der Heijden, G. M. F., Powers, J. S., & Schnitzer, S. A. (2015). Lianas reduce carbon accumulation and storage in tropical forest. *Proceedings of the National Academy of Science USA*, 112(43), 13267–13272. <https://doi.org/10.1073/pnas.1504869112>
- Van Ranst, E., Baert, G., Ngongo, M., & Mafuka, P. (2010). *Carte pédologique de Yangambi (planchette 2 : Yangambi, échelle 1 : 50.000)*. Ghent, Belgium: Ugent, Hogent.
- Walther, B. A., & Morans, S. (1998). Comparative performance of species richness estimation methods. *Parasitology*, 116, 395–405. <https://doi.org/10.1017/S0031182097002230>
- Webb, C. O., Ackerly, D. D., & Kembel, S. W. (2008). Phylocom: Software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, 24(18), 2098–2100. <https://doi.org/10.1093/bioinformatics/btn358>
- Webb, C. O., Ackerly, D. D., McPeck, M., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 33, 475–505. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150448>
- Zhu, H., Xu, Z. F., Wang, H., & Li, B. G. (2004). Tropical rain forest fragmentation and its ecological and species diversity changes in

southern Yunnan. *Biodiversity and Conservation*, 13, 1355–1372. <https://doi.org/10.1023/b:bioc.0000019397.98407.c3>

Zhuravleva, I., Turubanova, S., Potapov, P., Hansen, M., Tyukavina, A., Minnemeyer, S., ... Thies, C. (2013). Satellite-based primary forest degradation assessment in the Democratic Republic of the Congo, 2000–2010. *Environmental Research Letters*, 8(2), 024034. <https://doi.org/10.1088/1748-9326/8/2/024034>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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