

**CONSTITUENTS AND DRIVERS OF COMPOSITION, DIVERSITY
AND STRUCTURE OF A CONGOLESE FOREST**

By

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Executive Summary

Tropical forest systems occupy 2% of the earth's land surface but host nearly 50% of the world's forests and support unique flora and fauna and ecological processes. They also provide a multitude of ecosystem services ranging from the provision of food and water to supporting livelihoods and climate change mitigation. However, tropical forests are under immense anthropogenic pressures, including conversion of forestland for agricultural purposes, logging and extraction of timber, and exploitation via hunting and poaching. These pressures fragment forests and alter ecological processes that are linked to the many ecosystem services they provide.

The Congolese forest of Central Africa is an important tropical forest belt of the world with a unique history of anthropogenic pressures, particularly logging and hunting activities. In this study, I examine the forests of the northern Republic of the Congo to understand the role of logging and hunting on forest diversity, composition, and structure. Specifically, I identify forest tree communities and determine the extent to which environmental drivers versus anthropogenic disturbance dictate forest composition, diversity and structure. To do so, I use a range of statistical techniques, including non-metric multidimensional scaling, classification and multi-level pattern analysis and multiple regression approaches.

The results of my study reveal that variation in species composition is explained by disturbance type (combination of logging and hunting, logging only, and no disturbance), distance to Kabo village (proxy for disturbance), and logging. I determined five tree species groups across the study area that largely represents a gradient of disturbance. Areas having combined pressures of hunting and selective logging included the highest number of species groups, while pristine areas included the lowest number of species groups. In addition, the indicator tree species characterizing the species groups also reflected the level of disturbance, with highly disturbed plots containing more characteristic secondary tree species and pristine areas containing primary tree species.

For drivers of tree species diversity, I concluded that edaphic factors including pH and phosphorous explain variation in diversity. Lastly, I determined there to be no significant driver of basal area across the plots, but variation in wood density was driven by total nitrogen and soil texture.

My study highlights the effects of disturbance on species composition across this forested landscape; whereas soil characteristics seemed to have a stronger role in controlling forest diversity and structure, although additional research is needed to fully elucidate the observed results. More studies are needed to decouple the effects of anthropogenic pressures and environmental factors on forest composition, diversity and structure, thereby providing more insight about these forests.

Introduction

Hosting at least two-thirds of the Earth's terrestrial biodiversity, tropical forests support unique flora and fauna and ecological processes (Myers et al., 2000). Tropical forest systems occupy 2% of the Earth's land surface and account for approximately 50% of the world's forests (Myers et al., 2000). From provision of food and water, carbon storage and sequestration to climate change mitigation; tropical forests provide crucial ecosystem services and economic goods (Lewis et al., 2009; Lewis, 2006). They are also known to have high diversity within communities (alpha diversity) and between communities (beta diversity) (Swenson et al., 2011), with plant systems being the major focus of many studies in the tropics (Pitman et al., 2001; Condit et al., 2002). As these diverse plant communities maintain a wide variety of ecosystem functioning and services, they must be prioritized for conservation and management (Gardner et al., 2009; Isbell et al., 2011).

As we move into the Anthropocene (Steffen et al., 2007), large parts of the world are undergoing extensive loss of forest habitats (Cardinale et al., 2012). The tropics, in particular, are facing severe pressures at both local (e.g. deforestation) and global scales, resulting in threats to the survival of the multiple biotas they host (Kareiva et al., 2007). Some of these growing pressures include conversion of land to agriculture, timber and wood extraction activities, and large-scale bushmeat hunting and poaching. These disturbances can cascade through the forest ecosystem to alter ecological processes and plant-animal interactions at multiple scales (Malhi et al., 2014; Poulsen et al., 2009).

In particular, logging activities and hunting and poaching have heavily modified patterns of floral and faunal composition, structure and diversity in the Congo basin (Malhi et al., 2014). Renowned for its wildlife, this region hosts the Sangha River Tri-National Protected Area that includes three national parks of the region - the Dzanga-Sangha Special Reserve (Central African Republic), the Nouabalé-Ndoki National Park (Republic of Congo) and the Lobéké National Park (Cameroon).

The Congo basin has a unique history in terms of logging and hunting pressures in comparison to the South East Asian and Amazonian tropical forest belts (John Poulsen,

personal communication). Selective logging practices are the main means of harvesting wood in these areas, which result in lower extraction rates, and thereby have a distinct effect on forest structure and biotic interactions (Malhi et al., 2014). This type of harvest involves extraction of a limited number of trees of recognized timber species per unit area and usually retains a major portion of the surrounding biodiversity (Koh and Wilcove, 2008). On the other hand, the “bushmeat crisis” across Africa has led to unsustainable rates of hunting for mammal meat that has negatively impacted faunal composition and diversity, and as a consequence, plant-animal interactions (Peres and Palacios, 2007; Poulsen et al., 2009).

As a result of these disturbances, multiple studies have documented changes in tropical forests, including disruptions in ecological processes such as seed dispersal and forest regeneration (Abernathy et al., 2013; Malcolm and Ray 2008). In addition to the changes caused by these disturbances, environmental factors including nutrient content and fertility of soils have been shown to drive patterns of forest composition, diversity and structure (Pena-Carlos et al., 2012). Hence, the combination of disturbances and environmental factors need to be examined simultaneously to quantify the drivers of composition, diversity and structure of tropical forest systems.

In this study, I examine the role of logging and hunting on forest diversity, composition, and structure in the forests of the northern Republic of the Congo using data collected previously in 2013. Specifically, I (a) identify forest communities and determined the extent to which environmental drivers dictate forest composition; and (b) examine the effects of disturbance and environmental drivers on forest diversity and stand structure. I hypothesize that areas with similar disturbances will have similar forest composition. I also expect that abiotic variables, including edaphic factors, will control tree species diversity across the forest landscape. Lastly, I hypothesize that disturbance type and abiotic factors, such as light availability, will control variation in stand structure.

Materials and Methods

Study Site Description

This study was conducted between 2005-2013 in the Noubalé Ndoki National Park (NNNP; 4000 km²) and the Kabo Logging Concession (KLC; 2670 km²) in the northern region of the Republic of the Congo (Clark et al., 2009; Poulsen et al., 2009; Poulsen et al., 2011). With annual rainfall of 1600 mm and annual temperature of 25°C, the predominant dry season receives less than 100 mm rainfall per month (December to February), while the rainy season lasts around three months (September to November; MINEF, 2004). The topography of this region is relatively flat with an altitudinal range of 350-450 meters above sea level. The study area includes a gradient of disturbance created by hunting and logging near Kabo village that decreases with intensity with distance away, with no known hunting or logging within the national park (see below).

NNNP is characterized by rich tropical lowland *terra firme* forests covering approximately 70% of the landscape (Clark et al., 2013; Harris, 2002). NNNP hosts a variety of megafauna including the African forest elephant (*Loxodonta cyclotis*), the lowland western gorilla (*Gorilla gorilla gorilla*) and the bongo antelope (*Tragelaphus euryceros*) (Stokes et al., 2010). The park has not been logged, but studies have shown evidence of human populations in these areas for the last 40,000 years, which include presence of iron smelting sites that can affect forested areas (Zangato ME 1999; Lanfranchi et al., 1998).

KLC borders NNNP to the south where selective logging has been carried out since the early 1960s. Initially, 2.5 trees/ha were extracted with a focus on *Entandophragma utile*, *Entandophragma cylindricum* and *Micilicia excelsa* (Congolaise Industrielle des Bois 2006). With the end of the civil war in 1997, selective logging practices increased dramatically with the creation of new concessions and involvement of commercial operators (Laporte et al., 2007).

Approximately 3000 people reside in KLC, most of who live in the village of Kabo. The surrounding areas of the Kabo village have combined pressures of commercial

hunting and logging (since it is inside KLC), as evident by the variety of mammal meat recorded in the village markets at the time of data collection (Poulsen et al., 2009)

Data Description

In 2005, a total of 30 1-ha plots were delineated in NNNP, KLC and the area around the Kabo village (spanning an area greater than 3000 km²), to cover the entire disturbance gradient.

(i) Forest inventory data

Of the 30 plots, 20 plots were located inside KLC, with 10 plots within 5-12 km from the Kabo village, characterized by both hunting and logging pressures, and 10 plots situated 12-20 km from Kabo village where only selective logging was carried out. Ten plots were also established in NNNP where no disturbance was recorded (Poulsen, Clark & Palmer, 2013). All forest plots were randomly located using Distance (v4.1; Thomas et al., 2002) within the above strata, with a distance of at least 2.5 km between plots to ensure independent sampling (Clark et al., 2012).

In each plot, all trees greater than 10 cm diameter at breast height were measured and identified to species level (Clark et al., 2013). All tree surveys were conducted using standardized plot methodologies (Peacock et al., 2007) and three voucher samples were taken for each tree for tree identification (Clark et al. 2012). In total, 12532 stems were measured and 372 unique tree species were identified across all the plots in 2013.

(ii) Environmental variables data

To evaluate the determinants of forest composition, diversity and structure, I used eight environmental variables that were measured previously by Clark et al., (2012). Light availability was estimated in each of the plots using canopy photographs (Gap Light Analyzer v2.0; Frazer et al., 2001; *see* Clark et al., 2012). I used ArcMap to measure the distance of each plots from Kabo as a proxy for human disturbance (v10.3; McCoy et al., 2001). I also used logging as a proxy for disturbance in addition to the location of each site (KLC, NNNP, or near Kabo village). I then estimated distance of

each plot to the closest water network (2nd & 3rd order streams) using ArcMap (v10.3) to account for water requirements of forest systems.

Soil samples from three random locations in each plot were collected, using a soil probe (2.85 x 83 cm) at 15 cm depth. The wet mass (weighed after collection) and dry mass (weighed after air-drying) were obtained for each of these samples. All three samples from each plot were pooled and mixed before laboratory analysis. Soil characteristics (including percent sand, clay or silt), nutrient availability and pH were analyzed at the IFAS Extension Soil Testing Laboratory, University of Florida (*see* Clark et al., 2012). Clark et al. (2012) performed principal component analysis to identify trends in the soil characteristics data and to reduce the number of soil variables for further analysis. The first principal component axis (PCA) explained 26.7% of the total variance and was correlated with soil texture (fractions of clay, sand, and silt in this study) and total nitrogen (N). PCA 2 explained 17.5% of the variance and was correlated with pH and phosphorous (P). PCA 3 explained 13.5% of the variance and was correlated with iron (Fe) and aluminum (Al). Together, the three principal components accounted for 57.5% of the variance in soil data.

Analysis

I calculated the abundance of each tree species in each plot as the sum of the basal areas of all trees per species -- basal area-weighted abundance (A_{BA}). I then calculated the Shannon's diversity index based on the abundance measured previously because it accounts for both the number of unique tree species and their relative abundance (Shannon and Weaver, 1949). Further, I calculated the number of trees measured in each plot and forest structure variables - median basal area and median wood density per plot. I chose these stand structure variables as they are commonly used in silviculture research and are easy to measure and interpret (del Río et al., 2016).

(i) Composition Analysis

To characterize species composition in the plots, I performed step down nonmetric multidimensional scaling analysis (NMDS) on the Bray Curtis dissimilarity distance (BC distance) matrix. The BC distance matrix was determined from the sum of the basal areas

of each tree species, i.e. A_{BA} . The BC distance is zero when two plots have the same species composition and one when plots do not share any species.

I used NMDS to reduce the 372 unique tree species data to two dimensional space to summarize species composition in each plot. NMDS makes no assumptions of linearity and is suitable when a species' response to underlying gradients is unknown (Dean Urban, personal communication). Lastly, I used a vector fitting approach to describe the NMDS axes in terms of the environmental gradients responsible for the plot composition. This approach fits environmental variables that are continuous or categorical onto ordination space. I performed this analysis using Vegan statistical package (Okasanen 2007).

I performed 20 iterations of NMDS and reduced the multidimensional tree species data to 2 dimensional ordination space that explained the most variation in species composition across the plots. I evaluated the performance of the NMDS analysis by examining the coefficient of determination, R^2 , and the goodness of fit of the model to the data. The NMDS was performed using the Ecodist statistical package (Goslee and Urban, 2007).

I estimated the unique tree species composition of each plot using a nonhierarchical agglomeration approach, partitioning around medoids, which is a classification approach to estimate unique groups in the data. This approach minimizes the average pairwise plot dissimilarities to form the unique groups based on species composition. This process involves two phases of "building" and "cleaning" groups around a representative plot called mediod. I chose this method because it is well suited for large datasets (Dean Urban, personal communication) and uses species dissimilarity distances such as the BC distance matrix calculated above. I estimated the number of unique compositional groups by maximizing the average silhouette width - a metric that compares the composition of a 1 ha plot against another 1 ha plot and groups them together based on the tree species composition. All classification analysis was performed using the Cluster statistical package (Maechler et al., 2012).

After having identified the presence of different species groups, I used multilevel pattern analysis to identify indicator tree species that are characteristic of each group. I

tested the statistical significance of the association between a tree species and a plot by using 999 random permutations. All multi-level pattern analysis was performed using the Indicspecies statistical package (De Cáceres et al., 2012).

(ii) *Diversity and Structure Analysis*

I fitted ordinary least squares multiple linear regression models to estimate environmental variables that explain the variation in diversity, wood density and basal area across the plots, with a stepwise backward elimination approach using the Akaike Information Criterion (AIC) to select the best model.

I performed all analysis using the various contributed packages in R v3.0.1 (R Development Core Team 2013).

Results

(i) *Plot description*

The number of trees within each plot ranged from 305 - 533 trees. Plots closest to Kabo village had the highest abundance of pioneer tree species characteristic of disturbed sites, including *Ceiba pentandra*, *Myriathus arboreus* and *Ricinodendron heudelotii*. All plots in the selectively logged KLC had abundant primary timber tree species such as *Celtis mildbraedii* and *Entandophragma cylindricum*. Lastly, *Entandophragma cylindricum*, *Greenwayodendron suaveolens* and *Entandophragma utile* were the most abundant tree species in the pristine plots in NNNP.

The Shannon's diversity index for the plots ranged from 3.11 to 3.94, with plots in the pristine areas of NNNP having the highest Shannon's diversity index and the selectively logged plots of KLC having the lowest diversity. There was no statistically significant difference in the Shannon's diversity index across the three disturbance types ($F_{2, 27} = 1.60$, $p = 0.2192$).

The median basal areas varied from 122 cm to 171 cm, both in the selectively logged plots. Similarly, median wood density varied between 0.504 g/cm³ in plots closest to the Kabo settlement and 0.6707 g/cm³ in the pristine forest plots. The median basal area did

not differ significantly across the three disturbance types ($F_{2,27} = 0.115$, $p = 0.891$), but wood density did vary significantly across disturbance types ($F_{2,27} = 7.747$, $p = 0.0021$), with higher wood densities at the undisturbed sites ($t = 3.48$, $df = 17.652$, $p = 0.001$).

(ii) *Composition Analysis*

In this study, the NMDS axes represented the species composition across the plots and were a combination of the 372 tree species. The NMDS ordination analysis had a goodness of fit of 0.67 and explained 58.4% of the variation in the data. NMDS axis 1 explained 48.7% and NMDS axis 2 explained 9.7% of the variation. Disturbance type (i.e. varying pressures - hunted, selectively logged and pristine; $r = 0.264$, $p < 0.05$), distance to Kabo village ($r = 0.4998$, $p < 0.05$) and Fe and Al content ($r = 0.3125$, $p < 0.05$) were positively correlated to NMDS axis 1. Presence of logging ($r = 0.194$, $p < 0.05$) was negatively correlated to NMDS axis 1. pH and P were negatively correlated to NMDS axis 2 ($r = 0.312$, $p < 0.1$; Fig 1; Table 1).

The final classification model identified 5 species groups. The number of tree species in each of the species groups ranged from 66 to 97 species (Fig 2). The hunted and logged forest plots close to Kabo village included all five species composition groups. The selectively logged plots in KLC included three species groups and the pristine plots in the park included two species groups (Fig 3).

Of the 372 unique tree species, 26 indicator species were identified that best described the 5 species groups (Appendix - Table 2). The first set of indicator species, found in plots 1 & 2 (hunted and logged plots closest to Kabo village), included 10 indicator tree species composed primarily of *Myrianthus arboreous*, *Musanga cecropoides*, *Dialium tescmannii* and *Desplatsia chrysochlamys*. The second set of indicator species characterized plots 3, 8 & 7 (hunted and logged plots close to Kabo village) and included *Cola lateritia*, *Cola gigantea*, *Strombosia indet*, *Alstonia boonei* and *Ricinodendron heudelotii*. The third set of indicator species described plots 4, 5, 6 (hunted and logged plots close to Kabo village) and plots 18 & 19 (selectively logged plots in KLC). These included 4 indicator species: *Macaranga spinosa*, *Caloncoba welwitschii*, *Dichostemma glaucescens* and *Dictyandra arborescens*. The fourth and fifth

sets of indicator species described the remaining selectively logged and pristine plots. They were composed of 2 indicator species each, including *Pancovia pedicellaris* and *Dasylepis seretii* for the selectively logged plots, and *Celtis mildbraedii* and *Nesogordonia kabingaensis* for the pristine plots.

(iii) *Diversity and structure analysis*

pH and P explained the variation in diversity across all plots ($R^2= 0.382$, $F_{5,23}=2.843$, $p=0.016$). No environmental variable significantly explained the variation in basal area across all the plots, though total N, texture, Fe and Al, logging, disturbance type and leaf area index were retained in the final regression model ($R^2= 0.204$, $F_{6,22}=0.937$, $p=0.488$). Lastly, variation in median wood density across all plots was best explained by total N and soil texture ($R^2= 0.609$, $F_{5,23} = 7.15$, $p=0.001$).

Discussion

The results of my study reveal that the disturbance type, distance to Kabo village (proxy for disturbance) and logging explains variation in species composition. I determined five species groups that represent a gradient of disturbance evident by the indicator tree species characterizing each of these groups. Disturbance had the strongest effects on tree species composition and few detectable effects on species diversity or forest structure. Edaphic factors like pH and P had the strongest effects on species diversity. None of the environmental variables considered in this study strongly affected basal area, whereas median wood density of the plots was driven by total N and soil texture.

(i) *Composition analysis*

My study shows that disturbance type controls variation in species composition as hypothesized. Makana and Thomas (2005) stated that there is substantial change in the composition between secondary and primary forests, with dominant legume species characteristic of mature forests absent in secondary forests. Though several studies have concluded that selective logging practices retain tree species richness (Medjibe et al., 2011), variation in composition due to disturbances warrants further study to predict

long-term implications of changes in forest dynamics and cascading effects on plant-animal interactions and associated ecological processes.

The variation of the species composition based on the disturbance type is reflective of the spatially heterogeneous nature of disturbance in this landscape. Selective logging pressures can modify the forests at multiple scales and hence affect faunal assemblages. At the landscape scale, selective logging creates canopy gaps, especially during timber extraction (Asner et al., 2004). Construction of logging roads lead to fragmented forest patches and increased edge habitat (Poulsen et al., 2011). Also, hunting pressures across the disturbed plots are probably variable, with the greatest hunting intensity and frequency in the immediate surroundings of Kabo and decreasing pressures towards NNNP. Therefore, the spatially heterogeneous nature of disturbances in the landscape is contributing to the variation in species composition.

The species composition was characterized by five species groups. All five species groups were present in the plots having both hunting and selective logging pressures indicated by pioneer tree species *Myrianthus arboreous*, *Musanga cecropoides*, *Dialium tesmannii* and *Desplatsia chrysochlamys* (Meunier et al., 2015). But, plots further from Kabo village that had lesser pressures of hunting (probably due to the increased distance further from the village) and only selective logging pressures included species groups characterized by tree species that are transient between secondary and primary forests. Lastly, the species groups in NNNP are indicated by primary tree species- *Celtis mildbraedii* and *Nesogordonia kabingaensis*.

The species groups and their indicator species characteristic can be used to inform conservation and management (Lindenmayer et al., 2000). By monitoring these species, information regarding recruitment dynamics, especially for economically viable species, changing plant-environment relationships and development of pilot strategies can be done in a cost effective manner.

(ii) *Diversity and stand structure analysis*

There is no significant difference in tree species diversity across the disturbed landscape. Specifically, disturbance does not explain the variation in diversity across the

forested landscape in this study. This corroborates findings by Hall et al., (2003) who concluded that selective logging practices that involve low rates of timber extraction in Dzanga-Sangha Dense Forest Reserve had negligible impacts on tree species diversity. The low timber extraction rates in KLC might explain the similar diversity between the pristine and logged plots. As only a limited number of stands of a particular timber tree species are harvested during different harvest cycles, the number and abundances of various tree species are likely to be similar in pristine and logged plots. On the other hand, the non-significant difference in diversity between the plots near Kabo and the remaining plots, might be due to the slow replacement of primary tree species by successional species. Similar studies in the Bornean rainforests have also indicated no difference in diversity (Verburg and van Eijk-Bos, 2009).

With regards to stand structure analysis, there is no statistically significant difference in median basal area across the plots. A possible explanation for this might be the presence of large forest gaps within primary forests in the region, such that logged forest essentially replicates the structure of natural forest stands (Hall et al., 2003). On the other hand, low variation in basal area across all the plots may have made it difficult to detect the effects of any environmental drivers. Poulsen et al., (2013) found significant differences in aboveground biomass (AGB) across the plots, and hence AGB be a better measure of forest structure.

The effects of varying geological and edaphic factors on forest structure are poorly understood (Phillips et al., 2003); and hence, the role of soil characteristics in this study is unclear. However, in Dzanga-Sangha Dense Forest Reserve, tree species distributions were determined by variation in soil (Hall et al., 2004). The presence of timber trees *E. cylindricum* and *E. candollei* was related to the distribution of exchangeable cations Ca and Mg, whereas the abundance of *E. cylindricum* was strongly associated with Al. Similarly, Paoli et al., 2006 found that the abundance of *Dipterocarps*, in Southeast Asia, was significantly associated with nutrients such as P, K, Ca and Mg. Hence, soil nutrients can play an important role in micro-scale niche partitioning, and in turn, influence tree diversity and structure. To better understand the role of edaphic variables on the diversity and structure of central African forests may require more intensive field sampling focused on soil sampling (Paoli et al., 2006; Paoli et al., 2008).

An alternative explanation to the significant role of soil variables in this study could be that soil characteristics could be masking the effects of other abiotic environmental factors that were not accounted for in this study. For instance, Davidar et al., (2007) has stated that seasonality drives beta diversity among rainforests tree species. Similarly, climatic variables, primarily rainfall has been known to result in low recruitment of mammal-dispersed trees (Cordeiro and Howe, 2001). Large trees store most of the aboveground biomass, and the density and biomass of large trees are most associated with climatic variables that were not accounted for in my study (Slik et al., 2013).

Tropical forests across the world are under immense anthropogenic pressures due to the expanding extraction of natural resources (Cardinale et al., 2012). This study is a starting point to assist in decoupling the effects of anthropogenic pressures and changes in environmental factors in forest composition, diversity and structure in a poorly studied region of the tropics.

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List of tables and figures

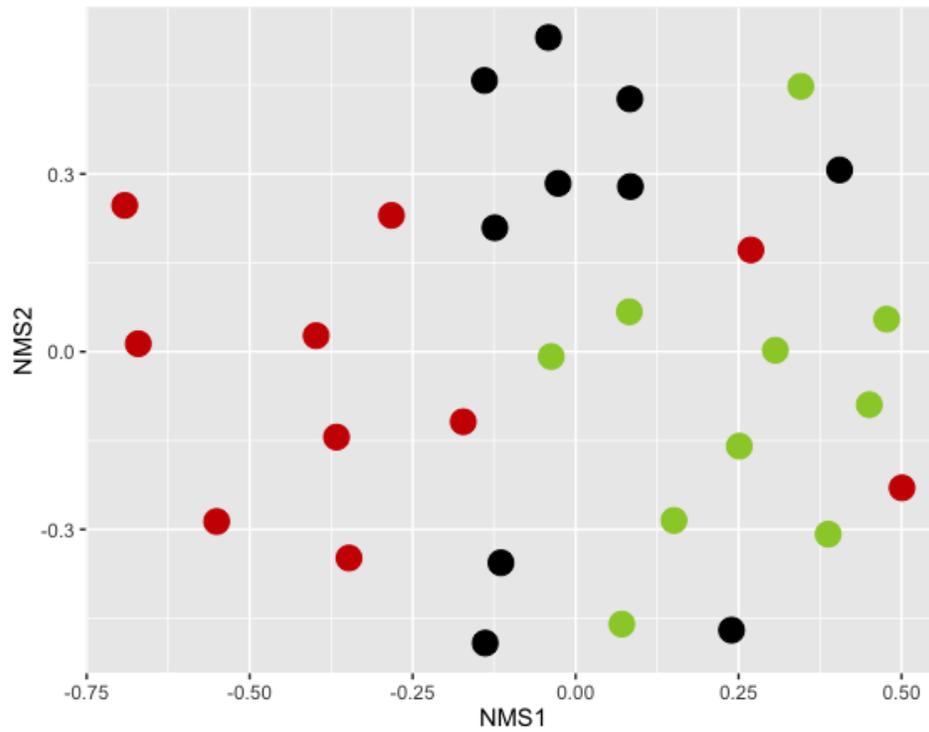


Figure 1 Species composition in two dimensional ordination space shows clear sorting based on disturbance type, presence of logging and distance to village. Plots with hunting and logging pressures are shown in red, selectively logged plots are shown in black, and pristine plots are indicated in green.

Table 1 Disturbance type (i.e. varying pressures - hunted, selectively logged and pristine), distance to Kobo village, and Fe and Al content are positively correlated to NMDS axis 1. Presence of logging is negatively correlated to NMDS axis 1. pH and P are negatively correlated NMDS axis 2 as indicated by the Pearson's correlation coefficient in columns NMDS 1 and NMDS 2. Only variables with a significance level <0.1 were selected.

Continuous variables				
Variables	NMDS 1	NMDS 2	R²	p
Soil PCA1	0.897	-0.443	0.151	0.115
Soil PCA2	0.489	0.873	0.179	0.074
Soil PCA3	0.996	0.087	0.312	0.011
Distance to village	0.952	0.305	0.499	0.002
Distance to stream	0.339	0.941	0.015	0.809
Leaf Area Index	-0.767	-0.642	0.033	0.646
Factors				
Variables	NMDS 1	NMDS 2	R²	p
Log-Log	-0.1818	-0.0751	0.1945	0.004
Log-Unlog	0.1659	0.1017		
Site-Log	0.1032	-0.0820	0.2641	0.005
Site-Pristine	0.1968	0.0864		
Site-Village	-0.2954	0.0349		

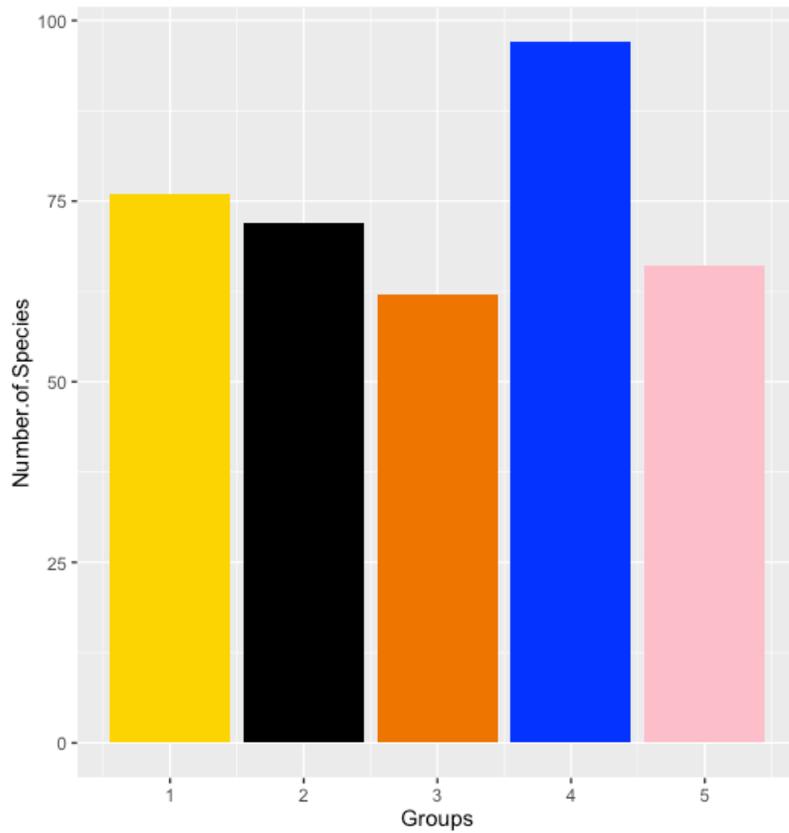


Figure 1 . The number of tree species in each group ranged from 66-97 trees. Hence, indicator tree species were estimated for each species group (see Appendix-Table1).

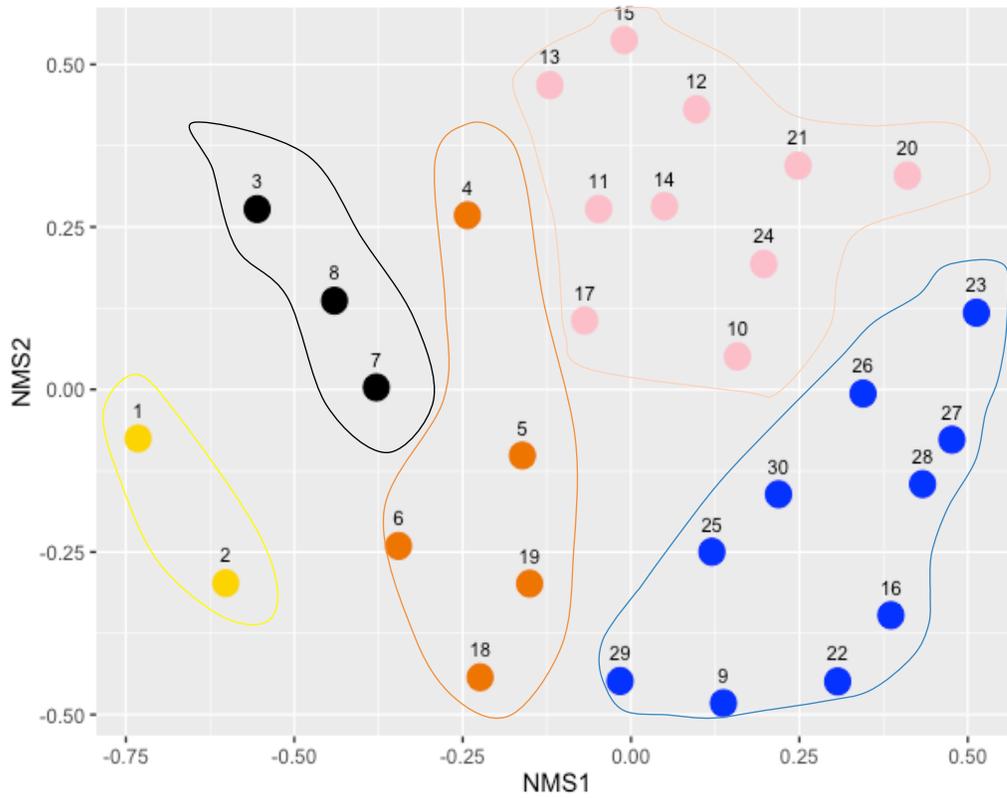


Figure 3 The five species groups resulting from the classification analysis represent varied levels of disturbance. All plots closest to Kabo (plots 1-10) with combined pressures of hunting and selective logging included all five species groups, while pristine plots (plots 21-30) included only two species groups.

Appendix

Table 1 List of abbreviations

NNNP	Noubalé Ndoki National Park
KLC	Kabo Logging Concession
PCA	Principal Component Analysis
P	Phosphorous
N	Nitrogen
Fe	Iron
Al	Aluminum
A_{BA}	Basal area-weighted abundance
NMDS	Nonmetric multidimensional scaling

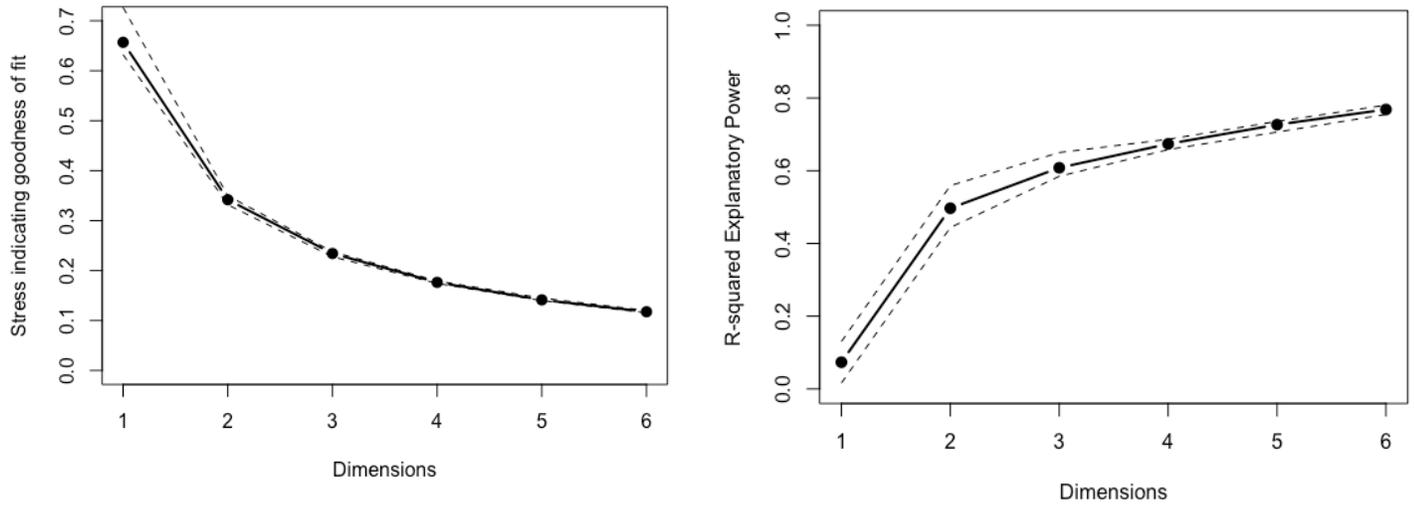


Figure 1 Two dimensions in ordination space were decided based on the natural break in the stress obtained after performing ordinations with 2-10 dimensions (left). The explanatory power of the ordination model was also the highest for 2 dimensions (right).

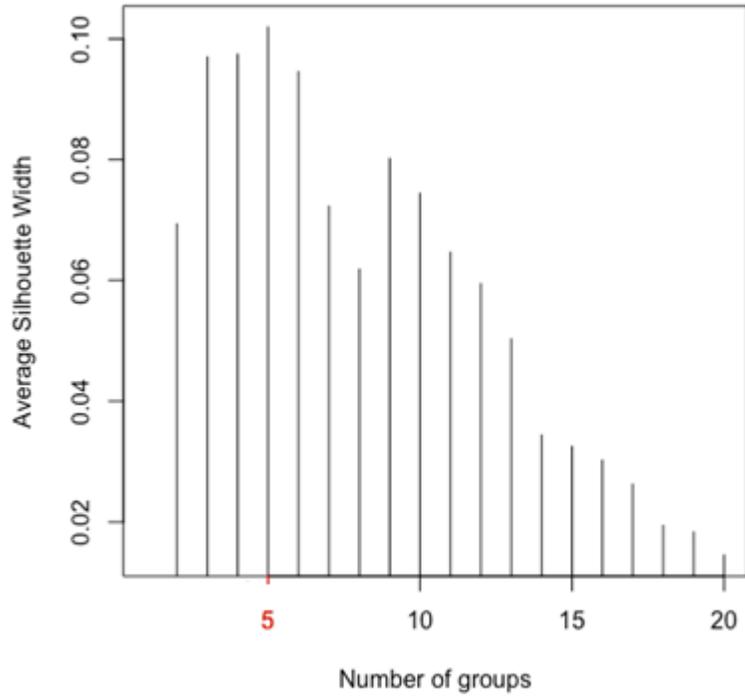


Figure 2 Classification analyses using PAM resulted in five species groups having the highest average silhouette width (in red)- a metric that compares the composition of a 1 ha plot against another 1 ha plot and groups them together based on similar tree species composition.

Table 2 All indicator tree species associated with each species group with a statistical significance ($p < 0.05$) are given below. An *Indicator Value* metric was used to measure the association between a tree species and a species group and the combination with the highest association statistic i.e. point biserial correlation coefficient* was selected. The statistical significance of this associative relationship between a tree species and a species group was tested using a permutation test (indicated by the p-value)

Group 1	Point biserial correlation coefficient*	<i>p</i>
<i>Schrebera arborea</i>	0.994	0.004
<i>Myrianthus arboreus</i>	0.933	0.004
<i>Musanga cercropioides</i>	0.759	0.012
<i>Desplatsia chrysochlamys</i>	0.749	0.010
<i>Mallotus oppositifolius</i>	0.748	0.004
<i>Desplatsia dewevrei</i>	0.713	0.022
<i>Dialium tessmannii</i>	0.654	0.027
<i>Zanthoxylum heitzii</i>	0.649	0.022
<i>Celtis philippensis</i>	0.635	0.037
<i>Diospyros indet</i>	0.627	0.027
Group 2		
<i>Cola lateritia</i>	0.830	0.005
<i>Cola gigantean</i>	0.780	0.016
<i>Strombosia indet</i>	0.694	0.014
<i>Duboscia macrocarpa</i>	0.672	0.022
<i>Alstonia boonei</i>	0.670	0.027
<i>Ricinnodendron heudelotii</i>	0.638	0.043
<i>Tricalysia crepiniana</i>	0.625	0.037
Group 3		
<i>Macaranga spinosa</i>	0.777	0.005
<i>Caloncoba welwitschii</i>	0.744	0.008
<i>Dichostemma glaucescens</i>	0.696	0.005
<i>Dictyandra arborescens</i>	0.637	0.025
Group 4		
<i>Pancovia pedicellaris</i>	0.690	0.019
<i>Santiria trimera</i>	0.596	0.025
Group 5		
<i>Celtis mildbraedii</i>	0.727	0.015
<i>Nesogordonia kabingaensis</i>	0.570	0.044

* The point biserial correlation is the abundance-based counterpart of the phi coefficient - a statistic commonly used to determine associations (Chytrý et al., 2002; see Indicspecies statistical package in R).