


# Diversity and structure of an arid miombo woodland in southwest Angola

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**Abstract:** Seasonally dry miombo woodlands are the dominant land cover across southern Africa. They are biodiverse, structurally complex and important for ecosystem service provision. Species composition and structure varies across the region producing a diverse array of woodland types. Woodlands of the Huíla plateau in southwest Angola represent the extreme southwestern extent of the miombo eco-region and are markedly drier than woodlands found elsewhere. They remain understudied however, compared to woodlands further east. We conducted a plot-based study of woodlands in Bicuar National Park, southwest Angola, comparing tree species composition and woodland structure with plots in Tanzania, Mozambique, and the Democratic Republic of Congo. We found that plots in Bicuar National Park had low tree species diversity, but contained 28 tree species not found in other plots. Plots in Bicuar had low basal area with notable exceptions in plots dominated by *Baikiaea plurijuga*. In a comparison of plots situated in areas degraded and not degraded by shifting cultivation, we found that species diversity was marginally higher in degraded plots. This study lends support that the woodlands of the Huíla plateau should be a conservation priority, representing a unique miombo woodland mosaic with regionally rare species.

**Keywords:** Miombo, Savanna, Woodland, Diversity, Degradation

## 1. Introduction

Tropical woodlands extend over 12 countries in central and southern Africa, with an estimated area of ~3.7 million km<sup>2</sup> [1–3]. Within this, miombo woodlands are the dominant vegetation type, characterised by trees of the *Brachystegia* and *Julbernardia* genera, both within the Fabaceae family, subfamily Detarioideae [4–6]. These genera are seldom found outside miombo woodlands, while their contribution to the biomass of miombo woodlands varies throughout the region [5]. Across the range of miombo woodlands, variation in climate, edaphic factors, disturbance regimes and biogeography maintain a diverse array of miombo woodland types in terms of both species composition and physical woodland structure [7–9].

Miombo woodlands are structurally complex but species poor in the tree layer compared to dry tropical forests which exist at similar latitudes [10,11]. Miombo woodlands contain many endemic tree species however, and support a highly diverse woodland understorey, with an estimated 8500 species of vascular plants [12]. Miombo woodlands are a conservation priority, especially considering their importance for ecosystem service provision for an estimated 150 million people [13]. Additionally

miombo woodlands hold ~18-24 Pg C in woody biomass and soil organic carbon, which is comparable to that held in the rainforests of the Congo basin (~30 Pg C) [14]. Despite their importance, miombo woodlands remain understudied compared to wet forests across the globe [15].

Over the previous two decades, the limited ecological research in miombo woodlands has been concentrated in the central and eastern parts of the miombo region, notably in southern Tanzania, Mozambique, Malawi, and Zambia. The south-western extent of miombo woodlands, which is found entirely within Angola has received considerably less attention [16]. Partly this is due to diminished research capacity during the Angolan civil war following independence, which took place officially between 1975 and 2002, but with sporadic localised periods of civil unrest until around 2012 [17]. While botanical surveys of miombo woodlands in this region are more plentiful [16,18], joint studies of miombo woodland species composition and physical structure remain scarce. This is despite the importance of these studies in helping to estimate woodland net primary productivity and thus carbon sequestration potential. To properly understand spatial variation in woodland species composition and physical structure across the region, it is necessary to fill understudied gaps in the miombo eco-region such as those in south-west Angola.

The miombo woodlands of southwest Angola are found in their most intact form in Bicular National Park and to a lesser extent in the adjacent Mupa National Park, on the Huíla plateau. Both of these national parks have been protected to varying extents since 1938 [16]. These woodlands exist in much drier conditions than other miombo woodlands, precipitation diminishes rapidly within the Huíla plateau towards the Angolan coast and the Namib desert (Figure 1a). The vegetation of the Huíla plateau holds many endemic species, around 83 endemic Fabaceae species [19] and the most endemic plant species of any part of Angola [20]. Linder [21] and Droissart *et al.* [22] both identify the western portion of the Huila plateau as a centre of tropical African endemism.

Much of the historic miombo woodland area in southwest Angola surrounding the Bicular and Mupa National Parks has been deforested in recent years, with a clear increase in deforestation activity since the end of the civil war owing to an increase in rural population and agricultural activity [16,23]. The western extent of southern African miombo woodlands found within the Huíla plateau region are therefore of great importance for conservation.

It is important to focus not only on areas of intact woodland areas in this area, but also that of degraded land in order to properly assess the biodiversity and woodland structure of the Park. Woodland degradation through grazing and shifting cultivation practices produce novel habitats which are not necessarily of lower conservation value [24,25]. Since Bicular National Park's rejuvenation following the reinforcement of park boundaries after the civil war, many areas of woodland that were previously heavily grazed, farmed, and used for timber extraction have been allowed to re-establish. This presents a unique opportunity to compare the species composition of these degraded areas with areas of nearby intact woodland that have not been farmed in living memory.

In this study we present results of the tree diversity and woodland structure of miombo woodlands found at the far western extent of miombo woodlands in Bicular National Park, Huíla province, Angola. Our study utilised permanent biodiversity monitoring plots set up within the park in 2018 and 2019. We compare the tree diversity and woodland structure of Bicular National Park with other areas of miombo woodland across the miombo eco-region using a common plot biodiversity census methodology. In addition, we take advantage of a unique opportunity to compare the tree species composition of areas of abandoned and now protected farmland that have begun to re-establish as woodland.

## 2. Materials and Methods

### 2.1. Study area

The miombo eco-region spans 10 countries in sub-Saharan Africa, extending across the continent in a band that reaches north into Kenya and the Democratic Republic of Congo (DRC) and south into the northeast of South Africa (Figure 1a). Miombo woodlands are defined both by their tree diversity

and by their structure. In true miombo woodlands species of the *Brachystegia* and *Julbernardia* generally hold the most biomass, forming a sparse woodland canopy. Distinct from dry tropical forests, miombo woodlands generally maintain a grassy understorey dominated by C4 grasses. Miombo woodlands are heavily structured by seasonal fire and herbivory, which often prevent the creation of a closed tree canopy which would naturally occur in the absence of these disturbances [26,27].

We chose three areas of miombo woodland across the region to compare with those in Bicuar National Park, Angola (S15.1°, E14.8°). The three sites were around Gorongosa National Park in central Mozambique (S19.0°, E34.2°), Kilwa District in southern Tanzania (S9.0°, E39.0°), and the Mikembo Natural Reserve in Katanga, southern Democratic Republic of Congo (DRC) (S11.5°, E27.7°). Within each of these woodland sites, multiple one hectare square plots had been installed previously to monitor biodiversity and biomass dynamics. We used these previous censuses, collected between 2012 and 2019, to estimate tree biodiversity and woodland structure. Sites range in Mean Annual Precipitation (MAP) from 864 mm y<sup>-1</sup> in Angola to 1115 mm y<sup>-1</sup> in the DRC. Mean Annual Temperature ranges from ~20.5 °C in Angola and DRC to ~25.8 °C in Tanzania (Figure 1b).

Bicuar National Park covers an area of ~7900 km<sup>2</sup>, established as a hunting reserve in 1938, and later as a national park in 1964. While fauna populations of the Park were severely damaged by the Angolan civil war, the interior of the Park remains as a largely intact mosaic of miombo woodland, mopane woodland, shrub/thicket vegetation and seasonally flooded grassland. Encroachment of agriculture and grazing, particularly along the northwest and western boundaries of the park, has led to a fragmented park boundary with patches of diminished thicket and woodland in areas of previously farmed land that have since been protected since park boundaries were re-established following the end of the civil war.

## 2.2. Plot data collection

A total of 64 one hectare square plots were sampled across the miombo region, from four localities including the 15 plots in Bicuar National Park. Figure 1a and Table 1 show the locations and general description of each group of plots, respectively.

Within each plot, every tree stem >5 cm stem diameter was recorded. For each tree stem the species and stem diameter were recorded. Taxonomy was checked against Global Biodiversity Information Facility (GBIF) records using the `taxize` package in R [28]. Tree coppicing due to fire, herbivory, and human actions is common in miombo woodlands. For trees with multiple stems, the identity of the parent tree was recorded.

Stem diameter was recorded at 1.3 m from the ground along the stem as per convention using a diameter tape measure, except where stem abnormalities were present, then the stem diameter was recorded at the nearest 10 cm increment above 1.3 m without significant stem abnormalities [29]. To ensure consistency among stem diameter values recorded at different heights above the ground, the stem diameter at 1.3 m was estimated from the recorded stem diameter using a cubic polynomial allometric equation which adjusts for tree stem taper, calibrated on 100 stems measured at multiple heights in Niassa Province, Mozambique (Appendix A). Stems below 10 cm stem diameter were not measured in the DRC plots. We therefore estimated the number of 5-10 cm stems from the average proportion of 5-10 cm stems in all other plots. We gathered first that there was not a significant difference between groups of plots in the proportion of 5-10 cm stems using an ANOVA ( $F(2,49) = 2.07$ ,  $p = 0.14$ ).

In addition to the one hectare plots across the miombo ecoregion, we compared the tree biodiversity of intact areas of miombo woodland in Bicuar National Park with areas of woodland around the edge of the park that had been previously farmed or heavily grazed and had since been abandoned and reclaimed within the Park boundaries. We conducted 20 plot surveys of woodland diversity and structure around the edge of the Park in degraded woodland in 20x50 m (0.1 hectare) plots and compared those with 20x50 m subsamples of the 15 one hectare plots within the Park interior.

Like the one hectare plots, within these smaller 20x50 m plots we recorded the species and stem diameter of every tree stem >5 cm stem diameter.

### 2.3. Climatic data

The WorldClim dataset [30] was used to gather data on plot-level climatic conditions. We estimated Mean Annual Precipitation (MAP) as the mean of total annual precipitation values between 1970 and 2000, and Mean Annual Temperature (MAT) as the mean of mean annual temperatures between 1970 and 2000. The standard deviation of monthly precipitation and temperature were calculated to provide an estimate of the seasonality of these variables. We estimated Climatic Water Deficit (CWD) for each plot according to [31], as the sum of the difference between monthly rainfall and monthly evapotranspiration when the difference is negative, using the dataset available at [http://ups-tlse.fr/pantropical\\_allometry.htm](http://ups-tlse.fr/pantropical_allometry.htm).

### 2.4. Data analysis

We calculated the basal area (BA) of each stem using:

$$BA = \pi \times (D/2)^2 \quad (1)$$

Where  $D$  is the estimated stem diameter at 1.3 m having accounted for tree taper. We then calculated the total basal area of each plot as the sum of each stem's basal area.

All diversity measures were calculated on tree-level data, rather than stem-level data, to avoid artificial inflation of abundance for those species which readily coppice. We calculated the alpha diversity of each plot using the Shannon-Wiener index ( $H'$ ) (Equation 2), using the vegan package in R [32].

$$H' = - \sum_{i=1}^s p_i \ln p_i \quad (2)$$

We calculated the pairwise beta diversity among plot groups using the Sørensen coefficient ( $S_S$ ) (Equation 3) [33].

$$S_S = \frac{2a}{2a + b + c} \quad (3)$$

Where  $a$  is the number of species shared between two plots,  $b$  is the number of species unique to plot 1 and  $c$  is the number of species unique to plot 2.  $S_S$  multiplies the value of  $a$  by 2 in order to give greater weight to those species shared between plot groups. We calculated  $S_S$  for each pairwise combination of plots between pairwise groups of plots, then took the mean of these values of  $S_S$ , producing a single value of  $S_S$  for each pairwise combination of plot groups [34]. The value of  $S_S$ , which ranges between zero and one, was multiplied by 100 to give a "percentage similarity" between communities in species composition.

We estimated abundance evenness for each plot using Shannon equitability index ( $E_{H'}$ ) [35] (Equation 4), where  $H'$  is the Shannon-Wiener index  $S$  is tree species richness.

$$E_{H'} = \frac{H'}{\ln S} \quad (4)$$

We used Non-metric Multidimensional Scaling (NMDS) to assess the variation in species composition within and between groups of one hectare plots, and also between degraded and intact 20x50 m plots within Bicuar National Park, using the vegan R package. The number of dimensions for NMDS was minimised while ensuring the stress value of the NMDS fit was <0.1. NMDS analyses were run with 500 random restarts to ensure a global solution was reached. We used the Bray-Curtis distance measure in order to robustly deal with instances of species not being shared between plots [36]. We fit plot-level estimates of MAP, MAT and the seasonality of MAP and MAT to the resultant ordination to

investigate how these environmental factors influenced the grouping of species composition among plots. We calculated MAP and MAT seasonality as the mean of the standard deviation of monthly MAT and MAP, respectively, for each of the 18 years of available data. All analyses were conducted in R version 3.6.1 [37].

### 3. Results

#### 3.1. Alpha diversity

In Bicuar National Park we measured a total of 6565 trees within the one hectare plots, and a total of 30530 trees across all plot groups. Trees in Bicuar National Park belonged to 48 species within 18 families. Across all plots we recorded 213 species from 43 families. The most diverse family within each group of plots and among all plots was Fabaceae with 56 species. 28 tree species were found in Bicuar National Park which were not found in the other miombo woodland plots (Table 3). The most common of these unique species were *Brachystegia glaucescens* ( $n = 576$ ), *Baikiaea plurijuga* ( $n = 331$ ) and *Baphia massaiensis* ( $n = 303$ ). Four species unique to Bicuar National Park only had one individual recorded: *Elachyptera parvifolia*, *Entandrophragma spicatum*, *Oldfieldia dactylophylla*, *Peltophorum africanum*.

The range of alpha diversity in Bicuar National Park was similar to that in other plot groups (Figure 2). An ANOVA showed a significant difference in  $H'$  between plot groups ( $F(3,60) = 7.67$ ,  $p < 0.01$ ), and a post-hoc Tukey's test showed that  $H'$  in plots in Bicuar National Park was significantly different from those in DRC ( $p < 0.01$ ) but not significantly different from those in Mozambique ( $p = 0.47$ ) or Tanzania ( $p = 0.43$ ). Mean  $H'$  across plots in Bicuar National Park was  $1.62 \pm 0.522$ , the lowest of the four plot groups. Variation in  $H'$  is large within Bicuar National Park compared to that within other plot groups.  $H'$  ranged from 0.85 in ABG-015 to 2.56 in ABG-001.

#### 3.2. Beta diversity

The NMDS of plot species composition among one hectare plots was run with four dimensions. The stress value was 0.10. Plot diversity in Bicuar National Park formed three distinct groups. Plots ANG-9, -13, -15 were dominated by *Baikiaea plurijuga*, *Baphia massaiensis* and *Croton gratissimus* according to species scores from the NMDS. Plots ANG-4, -11, -12 were dominated by *Brachystegia glaucescens*, *Ochna pulchra* and *Hippocratea parvifolia*. The third group consisting of the remaining plots surprisingly had a species composition most similar to that of plots in the DRC group. This group is dominated by *Pterocarpus lucens*, *Strychnos pungens* and *Bridelia mollis*. All environmental factors fitted to the NMDS ordination significantly influenced the grouping of plots (Figure 3). MAT explained the most variation in plot position on the first two NMDS axes ( $R^2 = 0.74$ ,  $p < 0.01$ ), followed by the seasonality of MAP ( $R^2 = 0.67$ ,  $p < 0.01$ ). Variation in MAP drove much of the difference between plots in Bicuar National Park and those in Tanzania and Mozambique.

The pairwise Sørensen coefficient of percentage similarity showed that the species composition of plots in Bicuar National Park had low similarity with other plot groups in the study (Table 2). Similar to the NMDS, these results show that plots in Bicuar National Park are most similar to those found in DRC.

#### 3.3. Woodland structure

An ANOVA showed a significant difference in basal area among plot groups ( $F(3,60) = 17.96$ ,  $p < 0.01$ ), and a post-hoc Tukey's test showed that basal area in Bicuar National Park was significantly lower than plots in DRC ( $p < 0.01$ ) but there was no significant difference between Bicuar and Mozambique ( $p = 0.53$ ) or Tanzania ( $p = 0.88$ ) (Figure 2). All plots in Bicuar National Park had a total basal area lower than  $3.3 \text{ m}^2 \text{ ha}^{-1}$ . Additionally, Bicuar plots had less variation in basal area between plots than other plot groups. Plots in Bicuar with the highest basal area were dominated by *Baikiaea plurijuga* and *Baphia massaiensis* (ANG-9, ANG-13, ANG-15).

### 3.4. Effect of degradation on diversity within Bicuar National Park

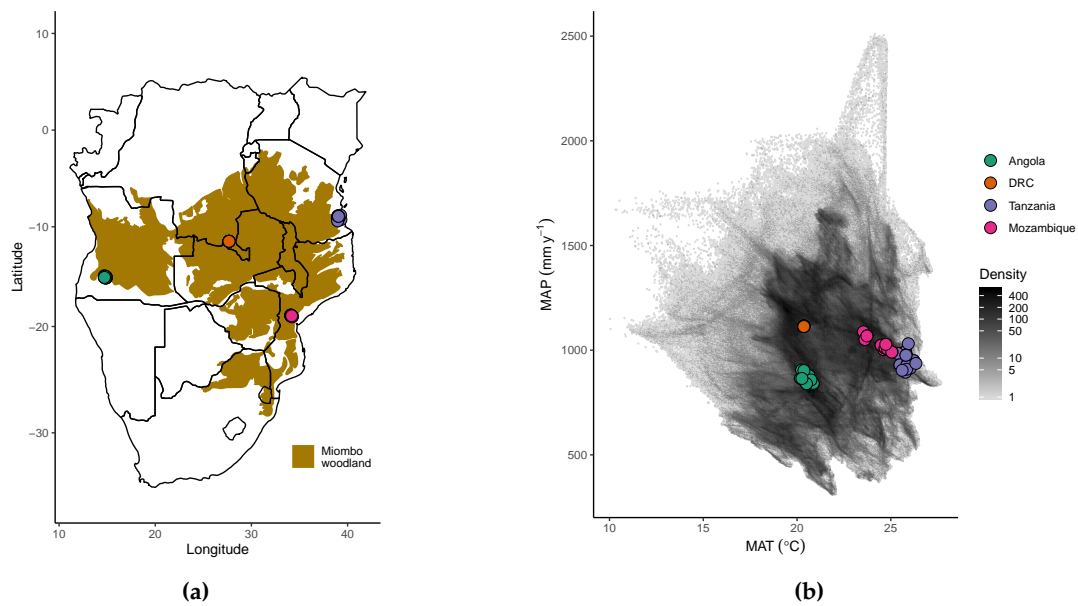
There was a marginal difference in the species composition of previously farmed degraded woodland plots and intact woodland plots, but with some overlap (Figure 6). Notably, Plots 4 and 7 in non-degraded woodland have a species composition more resembling degraded plots. The non-degraded plots 15, 13, and 9 represent distinct outliers in the NMDS. These three plots were dominated by *Baikiaea plurijuga* and *Baphia massaiensis* which were not encountered in the degraded plots. The most common species in the degraded plots was *Baphia massaiensis* ( $n = 158$ ), while in the intact plots the most common species was *Julbernardia paniculata* ( $n = 182$ ). Mean alpha diversity was marginally higher in degraded plots ( $H' = 1.68 \pm 0.367$ ) than in intact plots ( $H' = 1.31 \pm 0.462$ ) and an ANOVA showed that there was a significant difference in  $H'$  between the two groups of plots ( $F(1,33) = 7.04$ ,  $p < 0.05$ ). Species richness was also lower in non-degraded plots. Basal area was higher in non-degraded plots. There was no significant difference between degraded and intact plots in terms of abundance evenness, measured by Shannon equitability ( $E_{H'}$ ) ( $F(1,33) = 0.62$ ,  $p = 0.44$ ). Mean  $E_{H'}$  was  $0.79 \pm 0.122$  in degraded plots and  $0.76 \pm 0.142$  in non-degraded plots. 13 species were found only in the degraded plots and not in the non-degraded plots. The most common of these were *Combretum celastroides* ( $n = 30$ ), *Vachellia reficiens* ( $n = 14$ ), and *Gardenia ternifolia* ( $n = 11$ ).

### 3.5. Figures, Tables and Schemes

**Table 1.** Description of each group of plots used in the analysis.

Plot group	MAT (°C)	MAP (mm y <sup>-1</sup> )	CWD (mm y <sup>-1</sup> )	Latitude (DD)	Longitude (DD)	N plots	N species
Angola	20.5	864	-815	-15.12	14.81	15	49
DRC	20.4	1115	-762	-11.49	27.67	12	88
Mozambique	24.4	1029	-662	-18.95	34.16	15	78
Tanzania	25.8	956	-754	-9.05	39.05	22	76

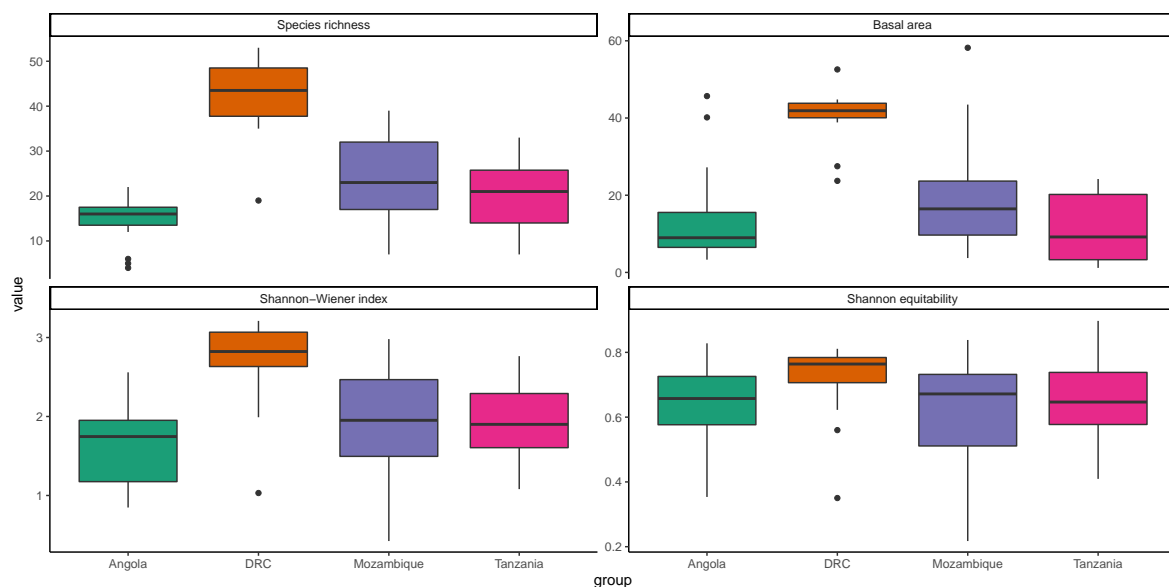




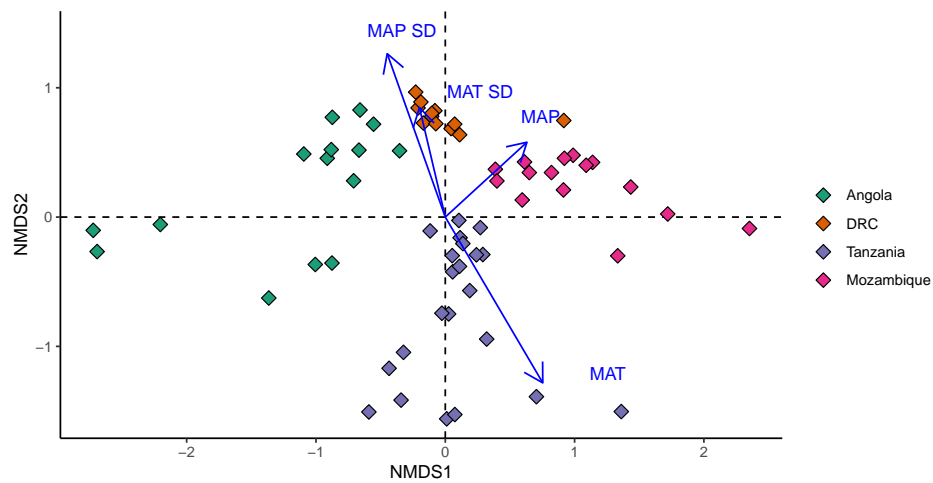
**Figure 1.** Locations of plots used in this study, by (a) geographic location with respect to the distribution of miombo woodland vegetation (shaded brown) [1], and (b) showing the plot locations compared to the climate space of the miombo eco-region estimated using the WorldClim dataset over the Miombo woodland vegetation extent with a pixel size of 30 arc seconds ( $0.86 \text{ km}^2$  at the equator) [30]. Note that the density colour scale is log-transformed.

**Table 2.** Pairwise beta diversity comparison of plot groups measured by the Sørensen coefficient of percentage similarity. Values are the mean of pairwise comparisons of plots between each group of plots.

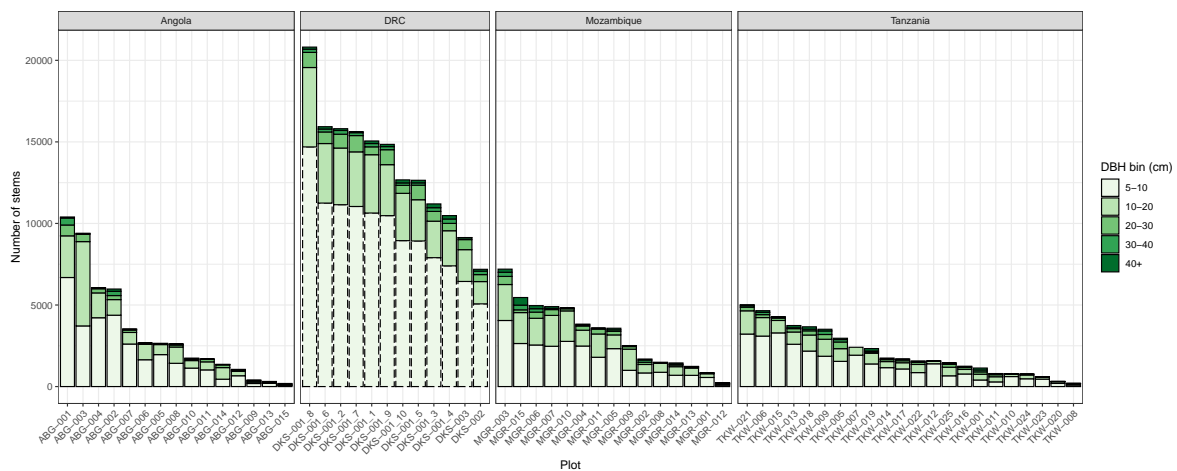
	Angola	DRC	Tanzania
DRC	16.3		
Tanzania	14.6	14.9	
Mozambique	11.3	14.7	15.8



**Figure 2.** Variation of alpha diversity estimates among plot groups.

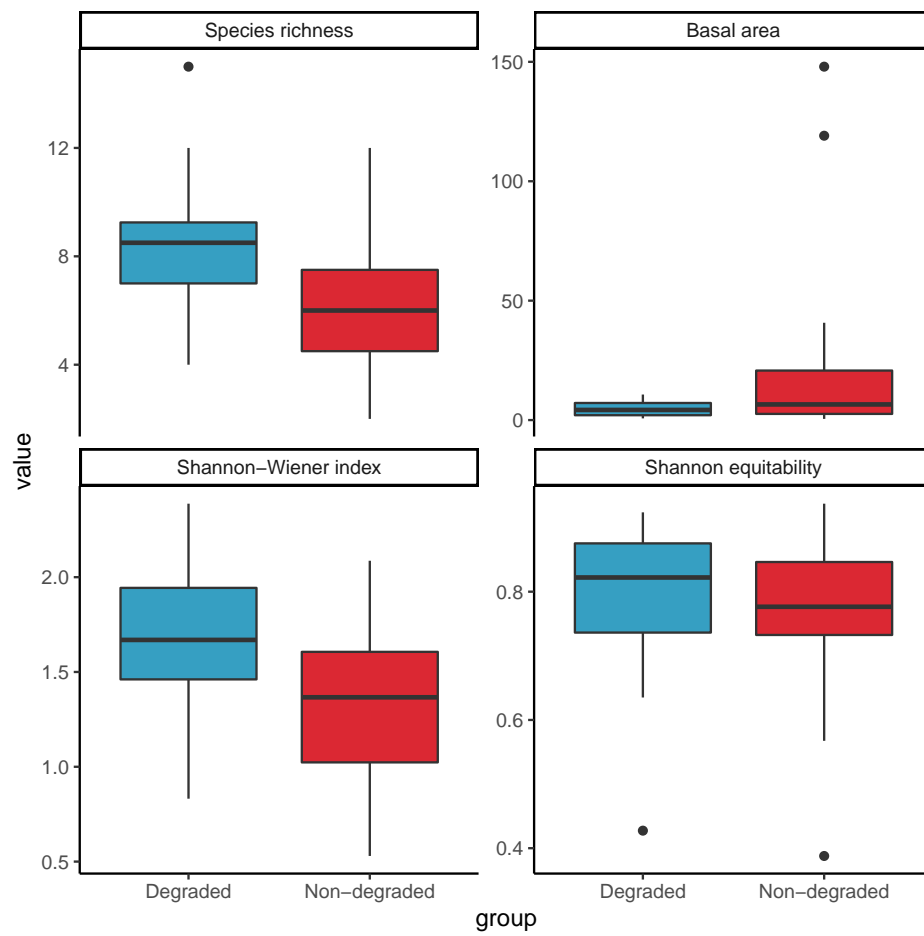


**Figure 3.** Environmental factors fitted to the NMDS ordination of species composition of one hectare plots. Diamonds are plot scores coloured by plot group. The lengths of arrows indicating environmental factor fits are scaled by  $R^2$ .

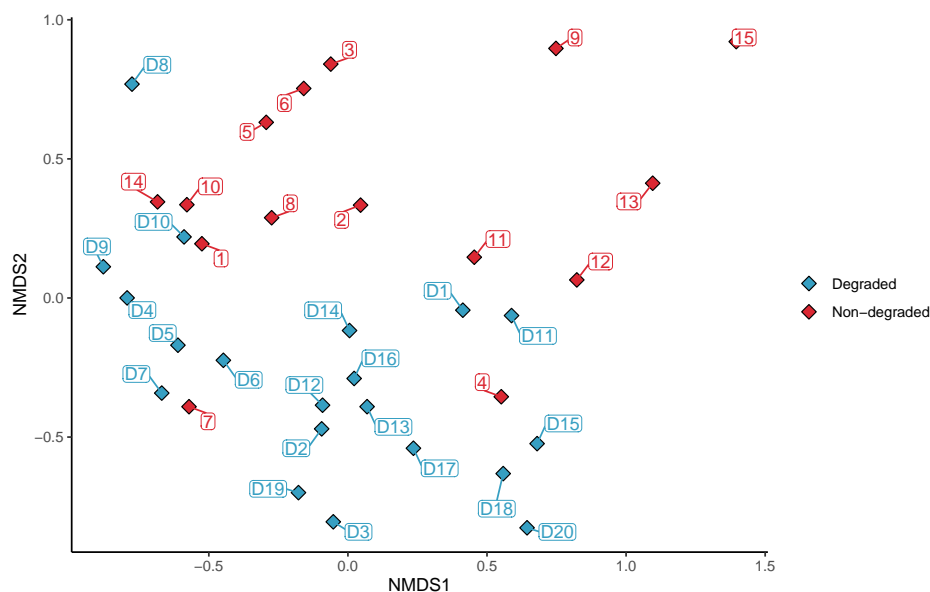


**Figure 4.** Ranked variation between plots in stem number within each group of plots, with bars stacked according to stem diameter class. Bars with a dashed outline for the 5-10 cm diameter stems in DRC plots indicate that these values were estimated from the mean proportional abundance of 5-10 cm stems in other all plots, as these measurements were not available for the DRC plots.





**Figure 5.** The variation in diversity and woodland structure between degraded and non-degraded 20x50 m (0.1 ha) plots in Bicular National Park.



**Figure 6.** NMDS ordination of species composition of 20x50 m plots located in degraded (D1-D20) and non-degraded (1-15) areas of woodland in Bicuar National Park. Coloured diamonds are plot scores.

## 4. Discussion

We compared the tree species diversity and woodland structure of miombo woodlands in Bicuar National Park in southwest Angola with three other groups of miombo woodlands across the miombo ecoregion. Our results show that Bicuar National Park is distinct in both woodland structure and species composition from these other woodlands. Notably, plots in Bicuar National Park contained 28 tree species which did not occur in other plots around the miombo eco-region. This lends support for the Huíla Plateau as an important area conservation of miombo woodland landscapes. The woodlands in Bicuar National Park were of low tree basal area, with few large trees except in plots dominated by *Baikiaea plurijuga*. Many other studies have drawn a relationship between water availability and basal area [38,39], and our study supports this, with Bicuar National Park being the most arid of the four sites considered in our study. The NMDS of species composition also showed that plots in Bicuar National Park are heavily influenced by aridity.

Within Bicuar National Park, three distinct woodland types were identified. The first, dominated by *Baikiaea plurijuga* and *Baphia massaiensis* represents the *Baikiaea* woodland type commonly found to the south of the miombo eco-region. While Timberlake *et al.* [40] refer to these woodlands as “undifferentiated woodlands”, they appear here as a distinct woodland type. *B. plurijuga* have been identified as an important species for conservation, being attractive to selective logging due to their large stature [41,42]. The woodlands created by *B. plurijuga* are also an important habitat for elephants (*Loxodonta africana*) [43,44], with Bicuar National Park and Mupa National Park being a key refugia. The second woodland type, dominated by *Brachystegia glaucescens* and *Ochna pulchra* represents a form of highly disturbed small stature woodland with a shrubby understorey and sparse canopy trees. The remaining plots resemble the more common true miombo woodland with *Julbernardia paniculata*, though with a number of species additions not seen in miombo woodlands found in the east of the miombo eco-region such as *Strychnos pungens*. This mosaic of woodland types makes Bicuar National Park a valuable habitat.

Degraded woodlands around the edge of Bicuar National Park were found to share some species with intact areas the Park but were largely different in their species composition. The species diversity

**Table 3.** Species found in one hectare plots in Bicuar National Park. Stem diameter and basal area are the mean of all stems with the standard deviation in brackets. Number of stems per hectare is mean of the number of stems in all one hectare plots where stems of that species are present. Species found only in Bicuar National Park are marked in bold text with an asterisk.

Family	Species	Stem diam. (cm)	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	N stems	N stems ha <sup>-1</sup>
Fabaceae	<i>Albizia antunesiana</i>	13.8(10.78)	0.23(0.290)	40	8
Fabaceae	* <b><i>Baikiaea plurijuga</i></b>	29.0(12.17)	1.72(1.390)	331	55.2
Fabaceae	* <b><i>Baphia bequaertii</i></b>	8.4(3.73)	0.27(0.420)	127	31.8
Fabaceae	* <b><i>Baphia massaiensis</i></b>	7.4(2.59)	0.12(0.120)	303	30.3
Fabaceae	<i>Bobgunnia madagascariensis</i>	9.0(4.91)	0.57(0.560)	32	10.7
Fabaceae	* <b><i>Brachystegia glaucescens</i></b>	15.4(10.71)	2.85(2.450)	576	115.2
Fabaceae	<i>Brachystegia spiciformis</i>	13.3(8.95)	2.96(3.450)	326	81.5
Phyllanthaceae	* <b><i>Bridelia mollis</i></b>	6.1(1.23)	0.05(NA)	23	23
Fabaceae	<i>Burkea africana</i>	12.1(8.50)	3.57(4.390)	863	71.9
Combretaceae	<i>Combretum apiculatum</i>	8.2(2.62)	0.14(0.070)	60	30
Combretaceae	<i>Combretum celastroides</i>	5.8(0.67)	<0.01(0.010)	7	3.5
Combretaceae	<i>Combretum collinum</i>	7.0(1.88)	0.96(1.380)	609	50.8
Combretaceae	* <b><i>Combretum hereroense</i></b>	6.9(1.79)	0.03(0.030)	73	12.2
Combretaceae	* <b><i>Combretum psidioides</i></b>	7.7(1.98)	0.04(0.070)	33	6.6
Combretaceae	<i>Combretum zeyheri</i>	7.1(2.02)	0.07(0.020)	61	10.2
Euphorbiaceae	* <b><i>Croton gratissimus</i></b>	7.5(2.61)	0.02(NA)	4	4
Ebenaceae	* <b><i>Diospyros batocana</i></b>	8.4(2.42)	<0.01(0.000)	2	1
Ebenaceae	* <b><i>Diospyros kirkii</i></b>	9.6(4.39)	0.13(NA)	11	11
Apocynaceae	<i>Diplorhynchus condylocarpon</i>	11.0(7.25)	1.51(3.970)	174	19.3
Malvaceae	* <b><i>Dombeya rotundifolia</i></b>	5.5(0.16)	<0.01(NA)	2	2
Celastraceae	* <b><i>Elachyptera parvifolia</i></b>	7.3(NA)	<0.01(NA)	1	1
Meliaceae	* <b><i>Entandrophragma spicatum</i></b>	14.6(NA)	<0.01(NA)	1	1
Fabaceae	<i>Erythrophleum africanum</i>	12.4(8.06)	0.51(0.790)	128	18.3
Rubiaceae	* <b><i>Gardenia volkensii</i></b>	6.6(2.05)	<0.01(0.000)	5	2.5
Fabaceae	* <b><i>Guibourtia coleosperma</i></b>	8.6(4.87)	0.02(0.020)	31	6.2
Phyllanthaceae	<i>Hymenocardia acida</i>	6.8(2.47)	0.08(NA)	6	6
Fabaceae	<i>Julbernardia paniculata</i>	12.3(6.89)	7.46(9.040)	1624	162.4
Fabaceae	* <b><i>Lonchocarpus nelsii</i></b>	16.3(9.25)	0.39(0.350)	165	15
Dipterocarpaceae	* <b><i>Monotes angolensis</i></b>	7.4(1.15)	<0.01(0.000)	2	1
Ochnaceae	* <b><i>Ochna pulchra</i></b>	7.2(3.37)	0.01(0.000)	26	8.7
Picrodendraceae	* <b><i>Oldfieldia dactylophylla</i></b>	8.5(NA)	<0.01(NA)	1	1
Fabaceae	* <b><i>Peltophorum africanum</i></b>	11.5(0.00)	<0.01(NA)	1	1
Fabaceae	<i>Pericopsis angolensis</i>	10.9(6.49)	0.34(0.400)	97	12.1
Phyllanthaceae	<i>Pseudolachnostylis maprouneifolia</i>	8.9(4.40)	0.26(0.460)	84	9.3
Combretaceae	* <b><i>Pteleopsis anisoptera</i></b>	8.1(4.15)	0.07(0.050)	81	20.2
Fabaceae	<i>Pterocarpus angolensis</i>	12.2(5.71)	1.50(1.260)	102	17
Fabaceae	* <b><i>Pterocarpus lucens</i></b>	7.3(1.39)	0.01(NA)	4	4
Rubiaceae	* <b><i>Rothmannia engleriana</i></b>	7.1(1.01)	<0.01(0.010)	5	1.7
Euphorbiaceae	* <b><i>Schinziophyton rautanenii</i></b>	9.7(3.49)	0.02(NA)	3	3
Polygalaceae	* <b><i>Securidaca longepedunculata</i></b>	8.4(2.69)	<0.01(0.010)	4	2
Loganiaceae	<i>Strychnos cocculoides</i>	11.3(4.77)	0.41(0.670)	19	6.3
Loganiaceae	* <b><i>Strychnos pungens</i></b>	6.7(1.58)	<0.01(0.000)	18	3.6
Loganiaceae	<i>Strychnos spinosa</i>	7.7(3.52)	0.20(0.480)	97	9.7
Combretaceae	* <b><i>Terminalia brachystemma</i></b>	7.3(2.29)	0.13(0.140)	174	29
Combretaceae	<i>Terminalia sericea</i>	8.1(3.90)	0.28(0.360)	214	23.8
Ximeniaceae	<i>Ximenia americana</i>	6.5(1.18)	<0.01(0.010)	7	1.8
Sapindaceae	<i>Zanha africana</i>	8.4(2.23)	0.05(NA)	6	6
Rhamnaceae	* <b><i>Ziziphus abyssinica</i></b>	5.9(1.27)	<0.01(NA)	2	2

of these previously degraded patches was higher than was found in the intact plots. Other studies have shown a peak in species richness during woodland regrowth as pioneer species take advantage of a low competition environment, while some later stage woodland species remain from before the original disturbance [25,45]. The species most common in the degraded plots were *Combretum psidioides*, *Combretum collinum* and *Terminalia sericea*, all of which tend to remain as smaller highly coppiced trees rather than grow to larger canopy trees in disturbed woodlands [46]. There was a lack of species which tend to grow to large canopy trees in these degraded plots, possibly due to them being repeatedly felled for timber prior to reclamation by the Park, or due to them being unable to recruit into a more open, shrubby woodland.

In conclusion, the woodlands of Bicuar National Park represent an important miombo refugia at the far western extent of the miombo eco-region. These woodlands, both those degraded by previous farming activity and those which remain non-degraded, possess a number of species not found commonly in other miombo woodlands. Bicuar National Park should be considered a key conservation asset within the Huíla plateau.

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#### Abbreviations

The following abbreviations are used in this manuscript:

ANG	Angola
DRC	Democratic Republic of Congo
TZA	Tanzania
MOZ	Mozambique
MAP	Mean Annual Precipitation
MAT	Mean Annual Temperature
SD	Standard deviation
NMDS	Non-metric Multidimensional Scaling
DD	Decimal Degrees
ANOVA	Analysis of Variance

#### Appendix A. Estimation of stem diameter at 1.3 m via tree taper

```
##' @title Stem diameter Point Of Measurement (POM) adjustment
##' @description Function to estimate stem diameter at 1.3 given measurements
##'   at other POMs.
##' @author Casey M. Ryan
##' @return d130, the estimated diameter at a POM of 1.3 m (in cm).
##' @param d_in the diameter measured at the POM (in cm)
##' @param POM the height of the POM (in m)
##' @details The adjustment is based on a tree taper model developed as part of
##'   the ACES project (Abrupt Changes in Ecosystem Services
##'   https://miomboaces.wordpress.com/), using data from the miombo of Niassa.
##'   The model is a cubic polynomial, with three equations for different sized
##'   stems.
##' @section Warning: The model should not be used for POMs above 1.7 m.
##'   Extrapolating beyond the training data will give nonsense.
```

```

29615 ##' Thus, POMs >1.7 m are not adjusted.
29716 ##' @examples
29817 ##' POMadj(10, 0.3)
29918 ##' POMadj(1, 0.3) # d130 is negative, i.e. the stem probably wasn't 1.3 m tall
30019 ##' POMadj(50, 1.9) # generates warning, as outside calibration data range
30120 ##' \dontrun{
30221 ##' POMadj(50, 0) # zero or -ve POM is outside range, or nonsense
30322 ##' }
30423 POMadj <- function(d_in, POM) {
30524   stopifnot(is.numeric(d_in),
30625             is.numeric(POM),
30726             POM >= 0,
30827             sum(is.na(POM))==0,
30928             length(POM) == length(d_in))
31029   if (any(POM > 1.7))
31130     warning("POMs >1.7 m are outside the calibration data, no correction applied")
31231
31332   NAS <- is.na(d_in)
31433   d_in_clean <- d_in[!NAS]
31534   POM_clean <- POM[!NAS]
31635   # define the size class edges:
31736   edges <- c(5.0, 15.8, 26.6, 37.4)
31837   sm <- d_in_clean < edges[2]
31938   med <- d_in_clean >= edges[2] & d_in_clean < edges[3]
32039   lg <- d_in_clean >= edges[3]
32140
32241   # compute apredictions for delta_d, for all size classes
32342   delta_d <- data.frame(
32443     # if small:
32544     small = 3.4678+-5.2428 *
32645     POM_clean + 2.9401 *
32746     POM_clean^2+-0.7141 *
32847     POM_clean^3,
32948     # if med
33049     med = 4.918+-8.819 *
33150     POM_clean + 6.367 *
33251     POM_clean^2+-1.871 *
33352     POM_clean^3,
33453     # if large
33554     large = 9.474+-18.257 *
33655     POM_clean + 12.873 *
33756     POM_clean^2+-3.325 *
33857     POM_clean^3
33958   )
34059   # index into the right size class
34160   dd <- NA_real_
34261   dd[sm] <- delta_d$small[sm]
34362   dd[med] <- delta_d$med[med]
34463   dd[lg] <- delta_d$large[lg]
34564   dd[POM_clean > 1.7] <- 0 # to avoid extrapolation mess
34665
34766   # add NAs back in
34867   d130 <- NA
34968   d130[NAS] <- NA
35069   d130[!NAS] <- d_in_clean - dd
35170
35271   if (any(d130[!NAS] < 0))
35372     warning("Negative d130 estimated, repaced with NA")
35473   d130[d130 <= 0 & !is.na(d130)] <- NA
35574   return(d130)
35675 }
357

```

## References

1. Hopkins, B.; White, F. Vegetation Map of Africa. The Vegetation of Africa: A Descriptive Memoir to Accompany the UNESCO/AETFAT/UNSO Vegetation map of Africa. *The Journal of Ecology* **1987**, *75*. doi:http://dx.doi.org/10.2307/2260340.
2. Mayaux, P.; Bartholomé, E.; Fritz, S.; Belward, A. A new land-cover map of Africa for the year 2000. *Journal of Biogeography* **2004**, *31*, 861–877. doi:http://dx.doi.org/10.1111/j.1365-2699.2004.01073.x.
3. Arino, O.; Perez, J.R.; Kalogirou, V.; Defourny, P.; Achard, F. Globcover 2009. *ESA Living Planet Symposium 2010*, pp. 1–3.
4. Chidumayo, E. *Miombo ecology and management: an introduction*; Intermediate Technology Publications: London, UK, 1997.
5. Campbell, B.M.; Jeffrey, S.; Kozanayi, W.; Luckert, M.; Mutamba, M. *Household Livelihoods in Semi-Arid Regions: options and constraints*; Center for International Forestry Research: Bogor, Indonesia, 2002; p. 153.
6. LPWG, Azani, N.; Babineau, M.; Bailey, C.D.; Banks, H.; Barbosa, A.R.; Pinto, R.B.; Boatwright, J.S.; Borges, L.M.; Brown, G.K.; Bruneau, A.; Candido, E.; Cardoso, D.; Chung, K.; Clark, R.P.; Conceição, A.d.S.; Crisp, M.; Cubas, P.; Delgado-Salinas, A.; Dexter, K.G.; Doyle, J.J.; Duminil, J.; Egan, A.N.; de la Estrella, M.; Falcão, M.J.; Filatov, D.A.; Fortuna-Perez, A.P.; Fortunato, R.H.; Gagnon, E.; Gasson, P.; Rando, J.G.; de Azevedo Tozzi, A.M.G.; Gunn, B.; Harris, D.; Haston, E.; Hawkins, J.A.; Herendeen, P.S.; Hughes, C.E.; Iganci, J.R.; Javadi, F.; Kanu, S.A.; Kazempour-Osaloo, S.; Kite, G.C.; Klitgaard, B.B.; Kochanovski, F.J.; Koenen, E.J.; Kovar, L.; Lavin, M.; le Roux, M.; Lewis, G.P.; de Lima, H.C.; López-Roberts, M.C.; Mackinder, B.; Maia, V.H.; Malécot, V.; Mansano, V.; Marazzi, B.; Mattapha, S.; Miller, J.T.; Mitsuyuki, C.; Moura, T.; Murphy, D.J.; Nageswara-Rao, M.; Nevado, B.; Neves, D.; Ojeda, D.I.; Pennington, R.T.; Prado, D.E.; Prenner, G.; de Queiroz, L.P.; Ramos, G.; Filardi, F.L.R.; Ribeiro, P.G.; de Lourdes Rico-Arce, M.; Sanderson, M.J.; Santos-Silva, J.; São-Mateus, W.M.; Silva, M.J.; Simon, M.F.; Sinou, C.; Snak, C.; de Souza, É.R.; Sprent, J.; Steele, K.P.; Steier, J.E.; Steeves, R.; Stirton, C.H.; Tagane, S.; Torke, B.M.; Toyama, H.; da Cruz, D.T.; Vatanparast, M.; Wieringa, J.J.; Wink, M.; Wojciechowski, M.; Yahara, T.; Yi, T.; Zimmerman, E. A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny: The Legume Phylogeny Working Group (LPWG). *Taxon* **2017**, *66*, 44–77. doi:http://dx.doi.org/10.12705/661.3.
7. Privette, J.L.; Tian, Y.; Roberts, G.; Scholes, R.J.; Wang, Y.; Caylor, K.K.; Frost, P.; Mukelabai, M. Vegetation structure characteristics and relationships of Kalahari woodlands and savannas. *Global Change Biology* **2004**, *10*, 281–291. doi:http://dx.doi.org/10.1111/j.1529-8817.2003.00740.x.
8. Caylor, K.K.; Dowty, P.R.; Shugart, H.H.; Ringrose, S. Relationship between small-scale structural variability and simulated vegetation productivity across a regional moisture gradient in southern Africa. *Global Change Biology* **2004**, *10*, 374–382. doi:http://dx.doi.org/10.1046/j.1529-8817.2003.00704.x.
9. Chidumayo, E.N. Cahnges in miombo woodland structure under different land tenure and use systems in central Zambia. *Journal of Biogeography* **2002**, *29*, 1619–1626. doi:http://dx.doi.org/10.1046/j.1365-2699.2002.00794.x.
10. DRYFLOR, Banda-R, K.; Delgado-Salinas, A.; Dexter, K.G.; Linares-Palomino, R.; Oliveira-Filho, A.; Prado, D.; Pullan, M.; Quintana, C.; Riina, R.; Rodríguez, G.M.; Weintritt, J.; Acevedo-Rodríguez, P.; Adarve, J.; Álvarez, E.; Aranguren, A.; Arteaga, J.C.; Aymard, G.; Castaño, A.; Ceballos-Mago, N.; Cogollo, A.; Cuadros, H.; Delgado, F.; Devia, A.W.; Dueñas, H.; Fajardo, L.; Fernández, A.; Fernández, M.A.; Franklin, J.; Freid, E.H.; Galetti, L.A.; Gonto, R.; González-M., A.; Graveson, R.; Helmer, E.H.; Idárraga, A.; López, R.; Marciano-Vega, H.; Martínez, O.G.; Maturo, H.M.; McDonald, M.; McLaren, K.; Melo, O.; Mijares, F.; Moggi, V.; Molina, D.; Moreno, N.P.; Nassar, J.M.; Neves, D.M.; Oakley, L.J.; Oatham, M.; Olvera-Luna, A.R.; Pezzini, F.F.; Dominguez, O.J.R.; Ríos, M.E.; Rivera, O.; Rodríguez, N.; Rojas, A.; Sarkanen, T.; Sánchez, R.; Smith, M.; Vargas, C.; Villanueva, B.; Pennington, R.T. Plant diversity patterns in neotropical dry forests and their conservation implications. *Science* **2016**, *353*, 1383–1387. doi:http://dx.doi.org/10.1126/science.aaf5080.
11. Torello-Raventos, M.; Feldpausch, T.R.; Veenendaal, E.; Schrod, F.; Saiz, G.; Domingues, T.F.; Djabbletey, G.; Ford, A.; Kemp, J.; Marimon, B.S.; Marimon Jr, B.H.; Lenza, E.; Ratter, J.A.; Maracahipes, L.; Sasaki, D.; Sonké, B.; Zapfack, L.; Taedoumg, H.; Villarroel, D.; Schwarz, M.; Quesada, C.A.; Ishida, F.Y.; Nardoto, G.B.; Affum-Baffoe, K.; Arroyo, L.; Bowman, D.M.J.S.; Compore, H.; Davies, K.; Diallo, A.; Fyllas, N.M.; Gilpin, M.; Hien, F.; Johnson, M.; Killeen, T.J.; Metcalfe, D.; Miranda, H.S.; Steininger, M.; Thomson, J.; Sykora, K.



- Mougin, E.; Hiernaux, P.; Bird, M.I.; Grace, J.; Lewis, S.L.; Phillips, O.L.; Lloyd, J. On the delineation of tropical vegetation types with an emphasis on forest/savanna transitions. *Plant Ecology & Diversity* **2013**, *6*, 101–137. doi:http://dx.doi.org/10.1080/17550874.2012.762812.
12. Frost, P. The Ecology of Miombo Woodlands. In *The miombo in transition: woodlands and welfare in Africa*; Campbell, B., Ed.; Center for International Forestry Research: Bogor, Indonesia, 1996; pp. 11–55.
  13. Ryan, C.M.; Pritchard, R.; McNicol, I.; Owen, M.; Fisher, J.A.; Lehmann, C. Ecosystem services from southern African woodlands and their future under global change. *Philosophical Transactions of the Royal Society B: Biological Sciences* **2016**, *371*, 1–16. doi:http://dx.doi.org/10.1098/rstb.2015.0312.
  14. Mayaux, P.; Eva, H.; Brink, A.; Achard, F.; Belward, A. Remote sensing of land-cover and land-use dynamics. In *Earth Observation of Global Change: The Role of Satellite Remote Sensing in Monitoring the Global Environment*; Springer-Verlag: Berlin, Germany, 2008; pp. 85–108. doi:http://dx.doi.org/10.1007/978-1-4020-6358-9\_5.
  15. Clarke, D.A.; York, P.H.; Rasheed, M.A.; Northfield, T.D. Does biodiversity - ecosystem function literature neglect tropical ecosystems. *Trends in Ecology & Evolution* **2017**, *32*, 320–323. doi:http://dx.doi.org/10.1016/j.tree.2017.02.012.
  16. Huntley, B.J.; Lages, F.; Russo, V.; Ferrand, N., Eds. *Biodiversity of Angola: science & conservation: a modern synthesis*; Springer: Cham, Switzerland, 2019. doi:http://dx.doi.org/10.1007/978-3-030-03083-4.
  17. Soares de Oliveira, R. *Magnificent and Beggar Land: Angola since the civil war*; Hurst Publishers: London, UK, 2015.
  18. Figueiredo, E.; Smith, G.F.; César, J. The flora of Angola: first record of diversity and endemism. *Taxon* **2009**, *58*, 233–236. doi:http://dx.doi.org/10.1002/tax.581022.
  19. Soares, M.; Abreu, J.; Nunes, H.; Silveira, P.; Schrire, B.; Figueiredo, E. The leguminosae of Angola: diversity and endemism. *Systematics and Geography of Plants* **2007**, *77*, 141–212. doi:http://dx.doi.org/10.2307/20649738.
  20. Figueiredo, E.; Smith, G.F. Plants of Angola/Plantas de Angola. *Strelitzia* **2008**, *22*, 1–279.
  21. Linder, H.P. Plant diversity and endemism in sub-Saharan tropical Africa. *Journal of Biogeography* **2001**, *28*, 169–182. doi:http://dx.doi.org/10.1046/j.1365-2699.2001.00527.x.
  22. Droissart, V.; Dauby, G.; Hardy, O.J.; Deblauwe, V.; Harris, D.J.; Janssens, S.; Mackinder, B.A.; Blach-Overgaard, A.; Sonké, B.; Sosef, M.S.M.; Stévant, T.; Svenning, J.; Wieringa, J.J.; Couvreur, T.L.P. Beyond trees: biogeographical regionalization of tropical Africa. *Journal of Biogeography* **2018**, *45*, 1153–1167. doi:http://dx.doi.org/10.1111/jbi.13190.
  23. Schneibel, A.; Stellmes, M.; Revermann, R.; Finckh, M.; Roder, A.; Hill, J. Agricultural expansion during the post-civil war period in southern Angola based on bi-temporal Landsat data. *Biodiversity and Ecology* **2013**, *5*, 311–319. doi:http://dx.doi.org/10.7809/b-e.00285.
  24. McNicol, I.M.; Ryan, C.M.; Williams, M. How resilient are African woodlands to disturbance from shifting cultivation? *Ecological Applications* **2015**, *25*, 2320–2336. doi:http://dx.doi.org/10.1890/14-2165.1.
  25. Gonçalves, F.M.P.; Revermann, R.; Gomes, A.L.; Aidar, M.P.M.; Finckh, M.; Juergens, N. Tree species diversity and composition of Miombo woodlands in South-Central Angola: a chronosequence of forest recovery after shifting cultivation. *International Journal of Forestry Research* **2017**, *2017*, 1–13. doi:http://dx.doi.org/10.1155/2017/6202093.
  26. Oliveras, I.; Malhi, Y. Many shades of green: the dynamic tropical forest-savannah transition zones. *Philosophical Transactions of the Royal Society B: Biological Sciences* **2016**, *371*, 1–15. doi:http://dx.doi.org/10.1098/rstb.2015.0308.
  27. Dantas, V.L.; Hirota, M.; Oliveira, R.S.; Pausas, J.G. Disturbance maintains alternative biome states. *Ecology Letters* **2016**, *19*, 12–19. doi:http://dx.doi.org/10.1111/ele.12537.
  28. Chamberlain, C.; Szocs, E. taxize - taxonomic search and retrieval in R. *F1000Research* **2013**.
  29. Kershaw, J.A.; Ducey, M.J.; Beers, T.W.; Husch, B. *Forest Mensuration*; John Wiley & Sons: Chichester, UK, 2017.
  30. Fick, S.E.; Hijmans, R.J. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* **2017**, *37*, 4302–4315. doi:http://dx.doi.org/10.1002/joc.5086.
  31. Chave, J.; Réjou-Méchain, M.; Búrquez, A.; Chidumayo, E.; Colgan, M.S.; Delitti, W.B.C.; Duque, A.; Eid, T.; Fearnside, P.M.; Goodman, R.C.; Henry, M.; Martínez-Yrizar, A.; Mugasha, W.A.; Muller-Landau, H.C.; Mencuccini, M.; Nelson, B.W.; Ngomanda, A.; Nogueira, E.M.; Ortiz-Malavassi, E.; Péliissier, R.; Ploton, P.; Ryan, C.M.; Saldarriaga, J.G.; Vieilledent, G. Improved allometric models

- to estimate the aboveground biomass of tropical trees. *Global Change Biology* **2014**, *20*, 3177–3190. doi:<http://dx.doi.org/10.1111/gcb.12629>.
32. Oksanen, J.; Blanchet, F.G.; Friendly, M.; Kindt, R.; Legendre, P.; McGlinn, D.; Minchin, P.R.; O'Hara, R.B.; Simpson, G.L.; Solymos, P.; Stevens, M.H.H.; Szoecs, E.; Wagner, H. *vegan: Community Ecology Package*, 2019. R package version 2.5-5.
  33. Koleff, P.; Gaston, K.J.; Lennon, J.J. Measuring beta diversity for presence-absence data. *Journal of Animal Ecology* **2003**, *72*, 367–382. doi:<http://dx.doi.org/10.1046/j.1365-2656.2003.00710.x>.
  34. Baselga, A. The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography* **2012**, *21*, 1223–1232. doi:<http://dx.doi.org/10.1111/j.1466-8238.2011.00756.x>.
  35. Smith, B.; Wilson, J.B. A consumer's guide to evenness indices. *Oikos* **1996**, *76*, 70–82. doi:<http://dx.doi.org/10.2307/3545749>.
  36. Legendre, P.; De Cáceres, M. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecology Letters* **2013**, *16*, 951–963. doi:<http://dx.doi.org/10.1111/ele.12141>.
  37. R Core Team. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria, 2019.
  38. Terra, M.C.N.S.; M., d.R.; Prado Júnior, J.A.; de Mello, J.M.; Scolforo, J.R.S.; Fontes, M.A.L.; ter Steege, H. Water availability drives gradients of tree diversity, structure and functional traits in the Atlantic-Cerrado-Caatinga transition, Brazil. *Journal of Plant Ecology* **2018**, *11*, 803–814. doi:<http://dx.doi.org/10.1093/jpe/rty017>.
  39. Strickland, C.; Liedloff, A.C.; Cook, G.D.; Dangelmayr, G.; Shipman, P.D. The role of water and fire in driving tree dynamics in Australian savannas. *Journal of Ecology* **2016**, *104*, 828–840. doi:<http://dx.doi.org/10.1111/1365-2745.12550>.
  40. Timberlake, J.; Chidumayo, E.; Sawadogo, L. Distribution and characteristics of African dry forests and woodlands. In *The Dry Forests and Woodlands of Africa: Managing for Products and Services*; EarthScan: London, United Kingdom, 2010; pp. 11–42. doi:<http://dx.doi.org/>.
  41. Ng'andwe, P.; Chungu, D.; Shakacite, O.; Vesa, L. Abundance and distribution of top five most valuable hardwood timber species in Zambia and their implications on sustainable supply. 6th International Conference on Hardwood Processing; Mottonen, V.; Heinonen, E., Eds.; Natural Resources Institute Finland: Natural Resources Institute Finland, Helsinki, 2017; pp. 18–27.
  42. Wallenfang, J.; Finckh, M.; Oldeland, J.; Revermann, R. Impact of shifting cultivation on dense tropical woodlands in southeast Angola. *Tropical Conservation Science* **2015**, *8*, 863–892. doi:<http://dx.doi.org/10.1177/194008291500800402>.
  43. Sianga, K.; Fynn, R. The vegetation and wildlife habitats of the Savuti-Mababe-Linyati ecosystem, northern Botswana. *KOEDOE* **2017**, *59*, 1–16. doi:<http://dx.doi.org/10.4102/koedoe.v59i2.1406>.
  44. Mukwashi, K.; Gandiwa, E.; Kativu, S. Impact of African elephants on *Baikiaea plurijuga* woodland around natural and artificial watering points in northern Hwange National Park, Zimbabwe. *International Journal of Environmental Sciences* **2012**, *2*, 1355–1368. doi:<http://dx.doi.org/10.6088/ijes.002020300022>.
  45. Kalaba, F.K.; Quinn, C.H.; Dougill, A.J.; Vinya, R. Floristic composition, species diversity and carbon storage in charcoal and agriculture fallows and management implications in Miombo woodlands of Zambia. *Forest Ecology and Management* **2013**, *304*, 99–109. doi:<http://dx.doi.org/10.1016/j.foreco.2013.04.024>.
  46. van Wyk, B.; van Wyk, P. *Field guide to trees of southern Africa*; Struik Nature: Cape Town, South Africa, 2014.