

Article

Diversity and structure of an arid woodland in southwest Angola, with comparison to the wider miombo ecoregion

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Abstract: Seasonally dry woodlands are the dominant land cover across southern Africa. They are biodiverse, structurally complex and important for ecosystem service provision. Species composition and structure vary across the region producing a diverse array of woodland types. The woodlands of the Huíla plateau in southwest Angola represent the extreme southwestern extent of the miombo ecoregion and are markedly drier than other woodlands within this ecoregion. They remain understudied however, compared to woodlands further east in the miombo ecoregion. We aimed to elucidate further the tree diversity found within southwestern Angolan woodlands by conducting a plot-based study in Bicuar National Park, comparing tree species composition and woodland structure with similar plots in Tanzania, Mozambique, and the Democratic Republic of Congo. We found Bicuar National Park had comparatively low tree species diversity, but contained 27 tree species not found in other plots. Plots in Bicuar had low basal area, excepting plots dominated by *Baikiaea plurijuga*. In a comparison of plots in intact vegetation with areas previously disturbed by shifting-cultivation agriculture, we found species diversity was marginally higher in disturbed plots. Bicuar National Park remains an important woodland refuge in Angola, with an uncommon mosaic of woodland types within a small area. While we highlight wide variation in species composition and woodland structure across the miombo ecoregion, plot-based studies with more dense sampling across the ecoregion are clearly needed to more broadly understand regional variation in vegetation diversity, composition and structure.

Keywords: Woodland, Miombo, Savanna, Diversity, Disturbance, Baikiaea

1. Introduction

Tropical woodlands extend over 12 countries in central and southern Africa, with an estimated area of ~3.7 million km² [1–3]. Within this, miombo woodlands are the dominant vegetation type, characterised by trees of the *Brachystegia*, *Julbernardia* and *Isoberlinia* genera, all within the Fabaceae family, subfamily Detarioideae [4–6]. These genera are seldom found as dominant species outside miombo woodlands, and while their contribution to the biomass of miombo woodlands is substantial, it varies throughout the region [5]. Across the range of southern African woodlands, variation in climate, edaphic factors, disturbance regimes and biogeography maintain a diverse array of woodland

types in terms of both species composition and physiognomy [7–9]. Many of these woodlands have a flammable grassy understory and thus are also considered as a form of savanna [10].

The miombo ecoregion extends across the continent in a wide 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 of a grassy herbaceous understorey with an often sparse tree canopy. In archetypical miombo woodlands, species of the genera *Brachystegia*, *Julbernardia* and *Isoberlinia* generally hold the most biomass, forming a mostly open woodland canopy. Distinct from dry tropical forests, miombo woodlands generally maintain a grassy understorey dominated by grass species utilizing the C₄ carbon fixation pathway [11]. Miombo woodlands are heavily structured by seasonal fire and herbivory, with fire particularly often preventing the creation of a closed tree canopy which would naturally occur in the absence of these disturbances [12,13]. Within the miombo ecoregion, other woodland types exist, notably, woodlands dominated by *Baikiaea plurijuga* or *Colophospermum mopane* [5].

Southern African woodlands are structurally complex but species poor in the tree layer compared to dry tropical forests which exist at similar latitudes [14,15]. These woodlands contain many endemic tree species however, and support a highly diverse woodland understorey, with an estimated 8500 species of vascular plants [16]. Miombo woodlands provide ecosystem service provision for an estimated 150 million people [17]. 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) [18]. As woodland resource extraction and conversion to agricultural land accelerates due to growing human populations, the conservation of miombo woodlands as a biodiverse and unique ecosystem has become a growing concern. Despite their importance however, dry tropical woodlands remain understudied compared to wet forests across the globe [19].

Over the previous two decades, the limited ecological research in southern African woodlands has been concentrated in the central and eastern parts of the miombo region, notably in southern Tanzania, Mozambique, Malawi, Zimbabwe and Zambia. The southwestern extent of miombo woodlands, which is found entirely within Angola has received considerably less attention [20]. Partly this is due to diminished research capacity during the Angolan civil war following the country's independence, which took place officially between 1975 and 2002, but with sporadic localised periods of civil unrest until around 2012 [21]. While botanical surveys of woodlands in this region are more plentiful [20,22], joint studies of woodland species composition and physical structure remain scarce. This is despite the value of these studies in helping to estimate woodland net primary productivity, carbon sequestration potential, and studies of community assembly. To properly understand spatial variation in woodland species composition and physical structure across the miombo ecoregion, it is necessary to fill understudied gaps. In this study we aim to address one such gap in southwest Angola, and place it in context with other woodlands across the miombo ecoregion.

The miombo woodlands of southwest Angola are found in their most intact form in Bicuar National Park and to a lesser extent in the adjacent Mupa National Park, on the Huíla plateau [23]. Both of these national parks have been protected to varying extents since 1938 [20]. 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 [24] and the most endemic plant species of any part of Angola [25]. Linder [26] and Droissart *et al.* [27] both identify the western portion of the Huíla plateau as a centre of tropical African endemism.

Much of the historic miombo woodland area in southwest Angola surrounding the Bicuar 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 [20,28]. The western extent of miombo woodlands found within Bicuar National Park plateau are therefore of great importance for conservation as a refuge for wildlife and endemic plant species [20].

77 It is important to focus not only on the biodiversity of undisturbed woodland areas but also
78 previously disturbed land in order to properly assess the biodiversity and woodland structure of the
79 Park. Woodland disturbance through shifting cultivation practices produces novel habitats which
80 are not necessarily of lower conservation value [29,30]. Since Bicuar National Park's rejuvenation
81 following the reinforcement of park boundaries after the civil war, many areas of woodland that were
82 previously heavily grazed, farmed via shifting cultivation techniques, and used for timber extraction
83 have been allowed to re-establish and are now protected from further human resource extraction. This
84 presents a unique opportunity to compare the species composition of these disturbed areas with areas
85 of nearby woodland that have not been farmed in living memory.

86 In this study we present results of the tree diversity and woodland structure of miombo woodlands
87 found at the far western extent of miombo woodlands in Bicuar National Park, Huíla province, Angola.
88 Our study utilised recently installed biodiversity monitoring plots set up within the Park in 2018 and
89 2019. We compare the tree diversity and woodland structure of Bicuar National Park with biodiversity
90 monitoring plots previously established in other areas of miombo woodland across the miombo
91 ecoregion which use a common plot biodiversity census methodology. In addition, we take advantage
92 of a unique opportunity to compare the tree species composition of areas of abandoned and now
93 protected farmland that have begun to re-establish as woodland.

94 2. Materials and Methods

95 2.1. Study area

96 We chose three areas of miombo woodland across the miombo ecoregion to compare with those
97 in Bicuar National Park, Angola ($S15.1^\circ$, $E14.8^\circ$). The three sites were Gorongosa District in central
98 Mozambique ($S19.0^\circ$, $E34.2^\circ$) [31], Kilwa District in southern Tanzania ($S9.0^\circ$, $E39.0^\circ$) [32], and the
99 Mikembo Natural Reserve in Katanga, southern Democratic Republic of Congo (DRC) ($S11.5^\circ$, $E27.7^\circ$)
100 [33]. Within each of these woodland sites, multiple one hectare square plots had been installed
101 previously to monitor biodiversity and biomass dynamics. In Katanga, a larger 10 ha plot was
102 subdivided into ten 1 ha plots for this study. We used these previous censuses, collected between
103 2010 and 2019, to estimate tree biodiversity and woodland structure. Sites range in Mean Annual
104 Precipitation (MAP) from 864 mm y^{-1} in Bicuar to 1115 mm y^{-1} in Katanga. Mean Annual Temperature
105 ranges from ~20.5 °C in Bicuar and Katanga to ~25.8 °C in Kilwa (Figure 1b, Table 1).

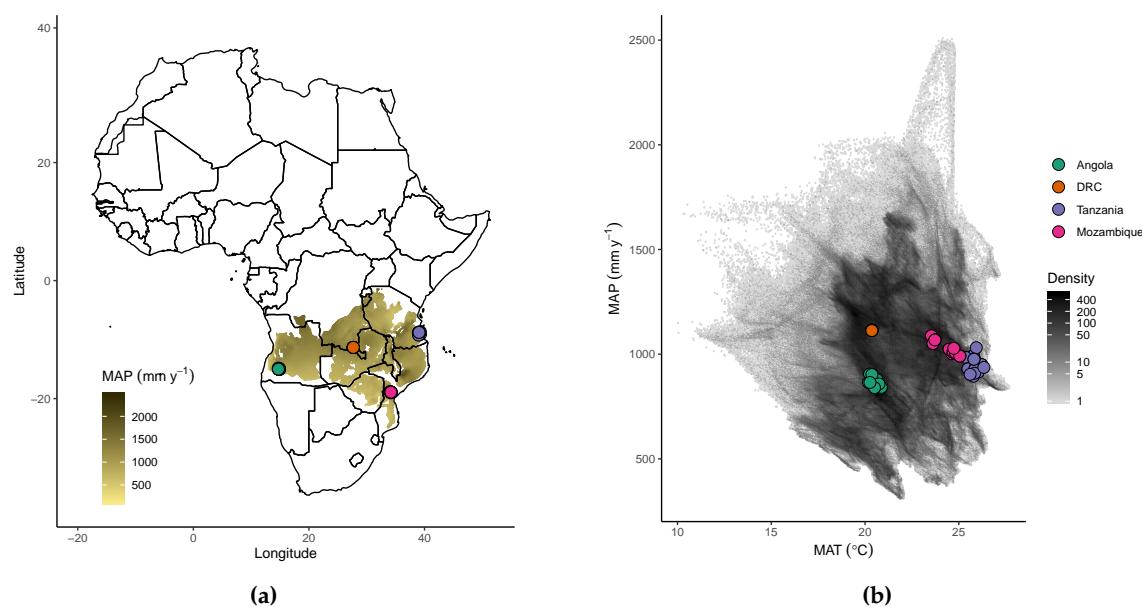


Figure 1. Locations of plots used in this study, by (a) geographic location with respect to the distribution of miombo woodland vegetation (shaded brown according to mean annual precipitation) [1], and (b) showing the plot locations compared to the climate space of the miombo ecoregion estimated using the WorldClim dataset over the Miombo woodland vegetation extent with a pixel size of 30 arc seconds (0.86 km² at the equator) [34]. Note that the density colour scale is log-transformed for visual clarity.

Table 1. Description of each group of plots used in the analysis. MAT = Mean Annual Temperature, MAP = Mean Annual Precipitation, CWD = Climatic Water Deficit, DD = Decimal Degrees.

Plot group	MAT (°C)	MAP (mm y ⁻¹)	CWD (mm y ⁻¹)	Latitude (DD)	Longitude (DD)	N plots	N species
Bicuar NP	20.5	864	-815	-15.12	14.81	15	49
DRC	20.4	1115	-762	-11.49	27.67	12	89
Mozambique	24.4	1029	-662	-18.95	34.16	15	162
Tanzania	25.8	956	-754	-9.05	39.05	22	248

106 Bicuar National Park covers an area of ~7900 km², established as a hunting reserve in 1938,
 107 and later as a national park in 1964 (Figure 2). While fauna populations in the Park were severely
 108 damaged by the Angolan civil war, the interior of the Park remains as a largely intact mosaic of miombo
 109 woodland, Baikiaea-Burkea woodland, shrub/thicket vegetation and seasonally flooded grassland.
 110 Encroachment of agriculture and grazing, particularly along the northwest and western boundaries of
 111 the Park, has led to a fragmented park boundary with patches of diminished thicket and woodland in
 112 areas of previously farmed land that have been protected since park boundaries were re-established
 113 following the end of the civil war.

114 2.2. Plot data collection

115 We sampled 15 one hectare plots in Bicuar National Park and collated data from a total of 64 one
 116 hectare plots across the miombo ecoregion within four sites. Figure 1a and Table 1 show the locations
 117 and general description of each site, respectively. Plots in Bicuar were situated at least 500 m from the
 118 edge of a woodland patch to prevent edge effects which may have altered tree species composition.

119 Within each plot, every tree stem ≥ 5 cm stem diameter was recorded, except in the DRC plots,
 120 where only stems ≥ 10 cm stem diameter were recorded. For each tree stem the species and stem
 121 diameter were recorded. Tree species were identified using local botanists at each site and taxonomy

122 was later checked against the African Plant Database [35]. In all sites Palgrave [36] and various other
123 texts were used as a guide for species identification in the field. Specimens that could not be identified
124 in the field, or subsequently at herbaria, were described as morphospecies. All tree species within the
125 Bicuar National Park plots were identified. Tree coppicing due to fire, herbivory, and human actions
126 is common in miombo woodlands, therefore, for trees with multiple stems, each stem ≥ 5 cm stem
127 diameter was recorded, while the parent tree was also recorded for diversity analyses described below.

128 Stem diameter was recorded at 1.3 m from the ground along the stem (diameter at breast height,
129 DBH) as per convention using a diameter tape measure [37]. Where stem abnormalities were present
130 at 1.3 m from the ground, which precluded the accurate estimation of stem diameter at 1.3 m, the
131 stem diameter was recorded at the nearest 10 cm increment above 1.3 m without significant stem
132 abnormalities [37]. To ensure consistency among stem diameter values recorded at different heights,
133 when the stem diameter was recorded at a height other than 1.3 m the stem diameter at 1.3 m was
134 estimated from the recorded stem diameter using a cubic polynomial equation which adjusts for tree
135 stem taper. This equation was calibrated on 100 stems measured at multiple heights in Niassa Province,
136 Mozambique ([Appendix A](#)). Stems below 10 cm stem diameter were not measured in the DRC plots.
137 We therefore estimated the number of 5-10 cm stems in each these plots by extrapolating a linear
138 regression of log stem abundance across the available stem diameter classes.

139 In addition to the one hectare plots across the miombo ecoregion, we compared the tree
140 biodiversity of undisturbed areas of miombo woodland in Bicuar National Park with areas of disturbed
141 woodland around the edge of the Park that had been previously farmed via shifting cultivation
142 methods, and had since been abandoned and reclaimed within the Park boundaries [Figure 2](#). We
143 identified areas previously farmed with the help of park rangers and local residents who identified
144 these areas from memory. We conducted 20 plot surveys of woodland diversity and structure in these
145 areas with 20x50 m (0.1 ha) plots, and compared their diversity and structure with 20x50 m subsamples
146 of the 15 one hectare plots within the Park interior. Like the one hectare plots, within these smaller
147 20x50 m plots we recorded the species and stem diameter of every tree stem ≥ 5 cm stem diameter.

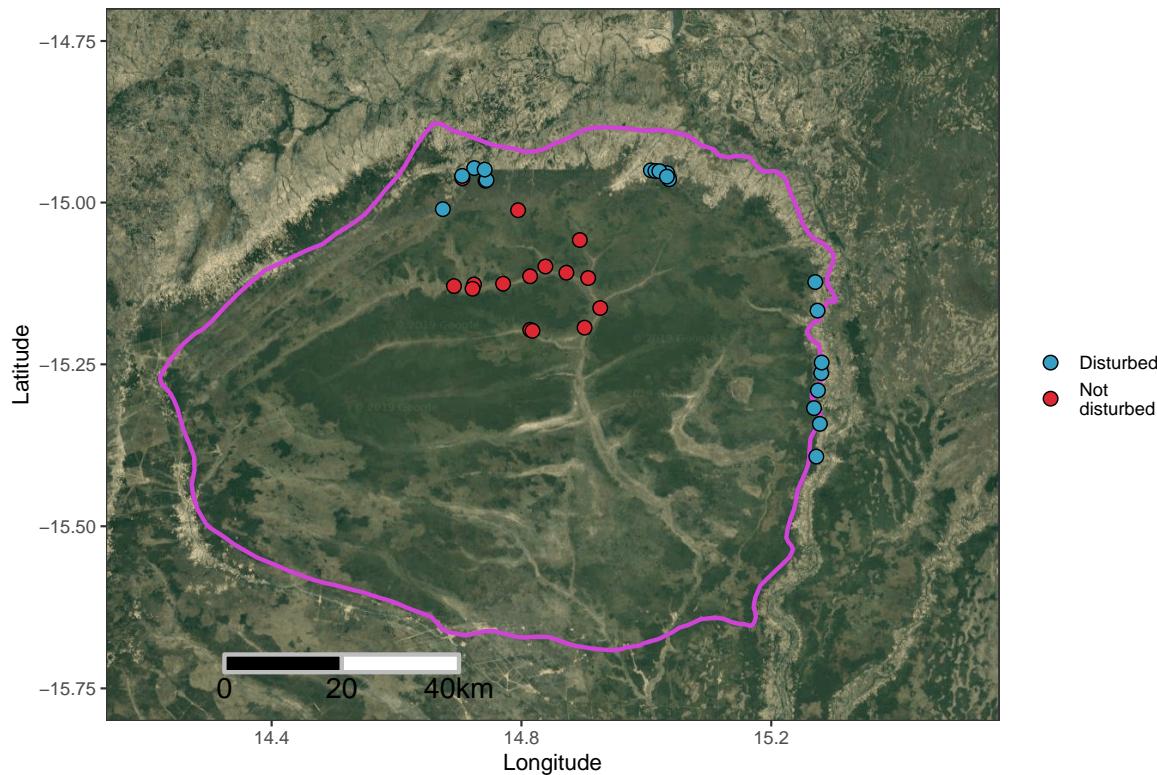


Figure 2. Location of plots in Bicuar National Park, southwest Angola. The Park boundary is shown as a pink outline, according to UNEP-WCMC and IUCN [38]. One hectare undisturbed plots are shown as red points, while disturbed 20x50 m (0.1 hectare) plots are shown as blue points. The map background is a true colour composite satellite image generated using the Google Maps Static Maps API in the `ggmap` R package [39].

148 2.3. Climatic data

149 The WorldClim dataset [34] was used to gather data on plot-level climatic conditions. We
 150 estimated Mean Annual Precipitation (MAP) as the mean of total annual precipitation values between
 151 1970 and 2000, and Mean Annual Temperature (MAT) as the mean of mean annual temperatures
 152 between 1970 and 2000. The seasonality of temperature (MAT SD) was calculated as the standard
 153 deviation of monthly temperature per year, respectively. We estimated Climatic Water Deficit (CWD)
 154 for each plot according to [40], as the sum of the difference between monthly rainfall and monthly
 155 evapotranspiration when the difference is negative, using the dataset available at http://ups-tlse.fr/pantropical_allometry.htm, which uses data from the WorldClim dataset 1970–2000.

157 2.4. Data analysis

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

$$g_i = \pi \times (d_i/2)^2 \quad (1)$$

159 Where d_i is the estimated stem diameter of stem i at 1.3 m having accounted for tree taper. We
 160 then calculated the total basal area of each plot as the sum of each stem's basal area. For the DRC plots
 161 which lacked 5–10 cm stems, we estimated basal area in this stem diameter class from our extrapolation
 162 of stem abundance in the 5–10 cm diameter class, assuming a mean stem diameter of 7.5 cm.

All diversity measures were calculated on individual 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') using the vegan package in R [41]. We calculated the pairwise beta diversity among sites using the Sørensen coefficient (S_S) [42]. We analysed the difference in alpha diversity measures and woodland structural variables among groups of plots using Analysis of Variance (ANOVA) statistical models, with a null hypothesis that there was no difference among the mean values of groups of plots. Post-hoc Tukey's HSD tests were used to investigate the degree to which pairwise combinations of plot groups differed in each case. We calculated S_S for each pairwise combination of sites using aggregated species composition data from all plots in each site. 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 ($E_{H'}$) [43] which is the ratio of H' to the log transformed species richness.

We used Non-metric Multidimensional Scaling (NMDS) to assess the variation in species composition among one hectare plots, and also between disturbed and undisturbed 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 Bray-Curtis dissimilarity as the optimal measure of ecological distance [44]. We fit plot-level estimates of MAP, MAT, the seasonality of MAT and CWD to the first two axes of the resulting ordination using the envfit function in the vegan R package to investigate how these environmental factors influenced the grouping of species composition among plots. All analyses were conducted in R version 3.6.1 [45].

3. Results

3.1. Alpha diversity

In Bicuar National Park we measured a total of 6565 trees within the one hectare plots, and across the four sites, a total of 25525 trees were sampled. Trees in Bicuar National Park belonged to 48 species within 18 families. Across all four sites we recorded 468 species from 43 families. The most diverse family within each site and among all plots was Fabaceae with 61 species. We encountered 27 tree species in Bicuar National Park which were not found in the other miombo woodland plots (Table 2). The most common of these unique species were *Brachystegia tamarindoides* ($n = 576$), *Baikiaea plurijuga* ($n = 331$) and *Baphia massaiensis* ($n = 303$). Four species unique to Bicuar National Park within this dataset only had one individual recorded: *Elachyptera parvifolia*, *Entandrophragma spicatum*, *Oldfieldia dactylophylla*, *Peltophorum africanum*.

Alpha diversity in Bicuar National Park was low compared to other sites (Figure 3). Mean H' across plots in Bicuar National Park was 1.6 ± 0.13 . An ANOVA showed a significant difference in H' among sites ($F(3,60) = 7.54$, $p < 0.01$), and a post-hoc Tukey's test showed that H' in plots in Bicuar National Park was significantly different from those in DRC ($H' = 2.7 \pm 0.19$, $p < 0.01$), Mozambique ($H' = 2.4 \pm 0.2$, $p < 0.01$) and Tanzania ($H' = 2.2 \pm 0.11$, $p < 0.05$). Variation in H' is large within Bicuar National Park, with H' ranging from 0.85 to 2.56, but this was a similar range to other sites. In contrast, the range of species richness within Bicuar National Park was much lower than other sites, suggesting that the wide range in H' was caused by variation in abundance evenness.

Table 2. Species found in one hectare plots in Bicuar National Park. Stem diameter and basal area are the mean of all stems with the standard error of the mean in parentheses. Number of stems per hectare is mean of the number of stems in all one hectare plots where stems of that species are present with the standard error of the mean in parentheses. Species found only in Bicuar National Park are marked in bold text with an asterisk.

Family	Species	Stem diam. (cm)	Basal area (m ² ha ⁻¹)	N stems	N stems ha ⁻¹
Fabaceae	<i>Albizia antunesiana</i>	9.1(2.03)	0.07(0.040)	40	8(4.81)
Fabaceae	* <i>Baikiae plurijuga</i>	28.9(0.75)	1.72(0.570)	331	55.2(17.83)
Fabaceae	* <i>Baphia bequaertii</i>	7.4(0.36)	0.08(0.050)	127	31.8(18.14)
Fabaceae	* <i>Baphia massaiensis</i>	6.6(0.17)	0.05(0.020)	303	30.3(11.20)
Fabaceae	<i>Bobgunnia madagascariensis</i>	7.8(0.91)	0.04(0.020)	32	10.7(9.67)
Fabaceae	* <i>Brachystegia glaucescens</i>	12.9(0.48)	1.14(0.430)	576	115.2(72.67)
Fabaceae	<i>Brachystegia spiciformis</i>	11.4(0.52)	0.74(0.430)	326	81.5(46.56)
Phyllanthaceae	* <i>Bridelia mollis</i>	5.7(0.31)	0.02(NA)	23	23(NA)
Fabaceae	<i>Burkea africana</i>	8.5(0.33)	0.39(0.120)	863	71.9(19.11)
Combretaceae	<i>Combretum apiculatum</i>	7.6(0.45)	0.06(0.040)	60	30(15.00)
Combretaceae	<i>Combretum celastroides</i>	5.6(0.34)	<0.01(0.000)	7	3.5(2.50)
Combretaceae	<i>Combretum collinum</i>	6.3(0.09)	0.07(0.020)	609	50.8(20.48)
Combretaceae	* <i>Combretum hereroense</i>	6.7(0.26)	0.02(0.010)	73	12.2(5.69)
Combretaceae	* <i>Combretum psidioides</i>	7.4(0.43)	0.01(0.010)	33	6.6(4.17)
Combretaceae	<i>Combretum zeyheri</i>	6.3(0.35)	0.01(0.000)	61	10.2(3.03)
Euphorbiaceae	* <i>Croton gratissimus</i>	6.1(1.55)	<0.01(NA)	4	4(NA)
Ebenaceae	* <i>Diospyros batocana</i>	8.4(2.14)	<0.01(0.000)	2	1(0.00)
Ebenaceae	* <i>Diospyros kirkii</i>	9.3(1.64)	0.03(NA)	11	11(NA)
Apocynaceae	<i>Diplorhynchus condylocarpon</i>	8.2(0.52)	0.08(0.060)	174	19.3(7.57)
Malvaceae	* <i>Dombeya rotundifolia</i>	5.5(0.19)	<0.01(NA)	2	2(NA)
Celastraceae	* <i>Elachyptera parvifolia</i>	7.3(NA)	<0.01(NA)	1	1(NA)
Meliaceae	* <i>Entandrophragma spicatum</i>	14.6(NA)	<0.01(NA)	1	1(NA)
Fabaceae	<i>Erythrophleum africanum</i>	9.0(0.84)	0.10(0.040)	128	18.3(6.82)
Rubiaceae	* <i>Gardenia volkensii</i>	5.6(1.15)	<0.01(0.000)	5	2.5(1.50)
Fabaceae	* <i>Guibourtia coleosperma</i>	7.2(1.00)	0.02(0.010)	31	6.2(3.54)
Phyllanthaceae	<i>Hymenocardia acida</i>	5.9(1.25)	<0.01(NA)	6	6(NA)
Fabaceae	<i>Julbernardia paniculata</i>	10.1(0.21)	0.92(0.200)	1624	162.4(50.60)
Fabaceae	* <i>Lonchocarpus nelsii</i>	13.4(0.88)	0.15(0.030)	165	15(2.77)
Dipterocarpaceae	* <i>Monotes angolensis</i>	7.4(0.83)	<0.01(0.000)	2	1(0.00)
Ochnaceae	* <i>Ochna pulchra</i>	6.5(0.80)	0.01(0.000)	26	8.7(3.76)
Picrodendraceae	* <i>Oldfieldia dactylophylla</i>	8.5(NA)	<0.01(NA)	1	1(NA)
Fabaceae	* <i>Peltophorum africanum</i>	11.5(NA)	<0.01(NA)	1	1(NA)
Fabaceae	<i>Pericopsis angolensis</i>	8.4(0.61)	0.06(0.020)	97	12.1(5.08)
Phyllanthaceae	<i>Pseudolachnostylis maprouneifolia</i>	6.7(0.45)	0.03(0.010)	84	9.3(3.00)
Combretaceae	* <i>Pteleopsis anisoptera</i>	6.8(0.46)	0.07(0.020)	81	20.2(15.11)
Fabaceae	<i>Pterocarpus angolensis</i>	13.0(0.61)	0.15(0.100)	102	17(8.65)
Fabaceae	* <i>Pterocarpus lucens</i>	6.9(0.94)	<0.01(NA)	4	4(NA)
Rubiaceae	* <i>Rothmannia engleriana</i>	6.8(0.66)	<0.01(0.000)	5	1.7(0.67)
Euphorbiaceae	* <i>Schinziophyton rautanenii</i>	8.0(2.82)	<0.01(NA)	3	3(NA)
Polygalaceae	<i>Securidaca longepedunculata</i>	7.3(1.12)	<0.01(0.010)	4	2(1.00)
Loganiaceae	<i>Strychnos cocculoides</i>	10.4(1.17)	0.03(0.020)	19	6.3(3.53)
Loganiaceae	* <i>Strychnos pungens</i>	6.1(0.48)	<0.01(0.000)	18	3.6(0.93)
Loganiaceae	<i>Strychnos spinosa</i>	6.8(0.36)	0.02(0.010)	97	9.7(4.07)
Combretaceae	* <i>Terminalia brachystemma</i>	6.5(0.21)	0.04(0.020)	174	29(12.04)
Combretaceae	<i>Terminalia sericea</i>	7.1(0.28)	0.06(0.030)	214	23.8(12.18)
Ximeniaceae	<i>Ximenia americana</i>	6.1(0.53)	<0.01(0.000)	7	1.8(0.25)
Sapindaceae	<i>Zantha africana</i>	9.4(1.12)	0.01(NA)	6	6(NA)
Rhamnaceae	* <i>Ziziphus abyssinica</i>	5.9(1.13)	<0.01(NA)	2	2(NA)

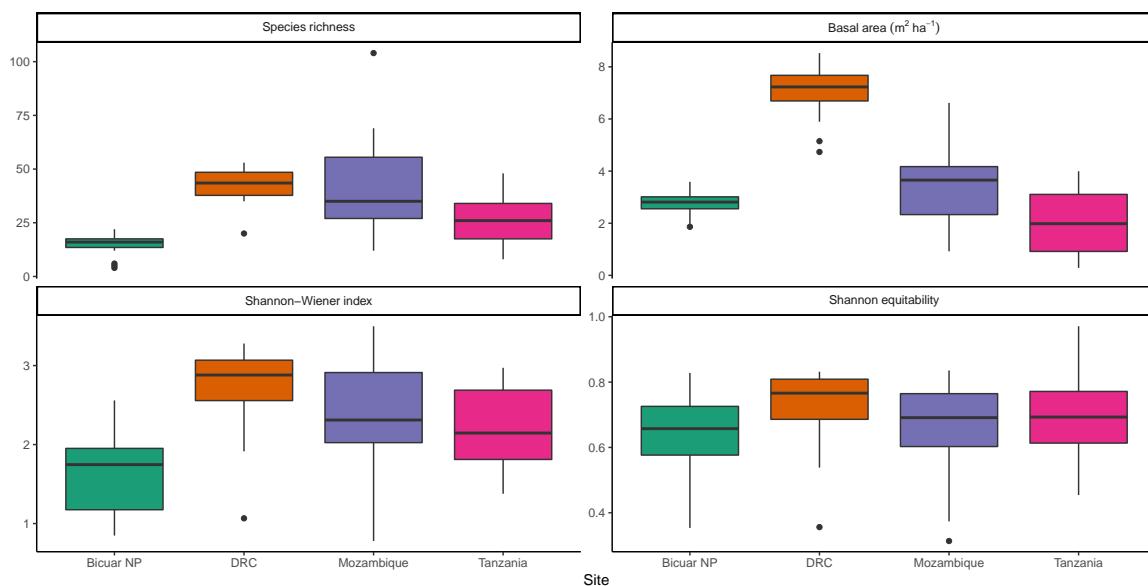


Figure 3. Variation of alpha diversity estimates and basal area among sites. Boxes bound the 1st and 3rd quartiles, with the median within the box. Whiskers represent 1.5 times the interquartile range plus or minus the 1st and 3rd quartiles, respectively. Values found beyond the whiskers are shown individually as points.

204 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 within axes 1 and 2 of the NMDS ordination. Bicuar plots 9, 13, and 15 were characterised by high abundances of *Baikiaea plurijuga*, *Baphia massaiensis* and *Croton gratissimus*, according to species scores from the NMDS. Bicuar plots 4, 11, and 12 were characterised by *Brachystegia tamarindoides*, and *Ochna pulchra*. The third group consisting of the remaining seven plots surprisingly had a species composition most similar to that of plots in the DRC group according to the NMDS, sharing the core miombo species of *Julbernardia paniculata* and *Pterocarpus angolensis*. This group of plots in Bicuar National Park was further characterised by the abundance of *Pterocarpus lucens*, *Strychnos pungens* and *Bridelia mollis* however, which were not present in the DRC plots. All environmental factors fitted to the NMDS ordination correlated significantly with the grouping of plots (Figure 4a). MAT explained the most variation in plot position on the first two NMDS axes ($R^2 = 0.75$, $p < 0.01$), followed by CWD ($R^2 = 0.54$, $p < 0.01$), the seasonality of MAT ($R^2 = 0.46$, $p < 0.01$) and MAP ($R^2 = 0.4$, $p < 0.01$). Variation in MAP explained much of the difference among plots in Bicuar National Park versus those in Tanzania and Mozambique. Axes 3 and 4 showed a greater degree of overlap in species composition among plot groups, with plots from Bicuar National Park similar to a select few plots in both Tanzania and Mozambique (Figure 4b). Axis 3 distinguished plots in Bicuar NP from those in DRC, while plots from all geographic area overlapped in their distribution across Axis 4. Axes 3 and 4 largely reflected distribution patterns of less abundant species and not the dominant species in the vegetation.

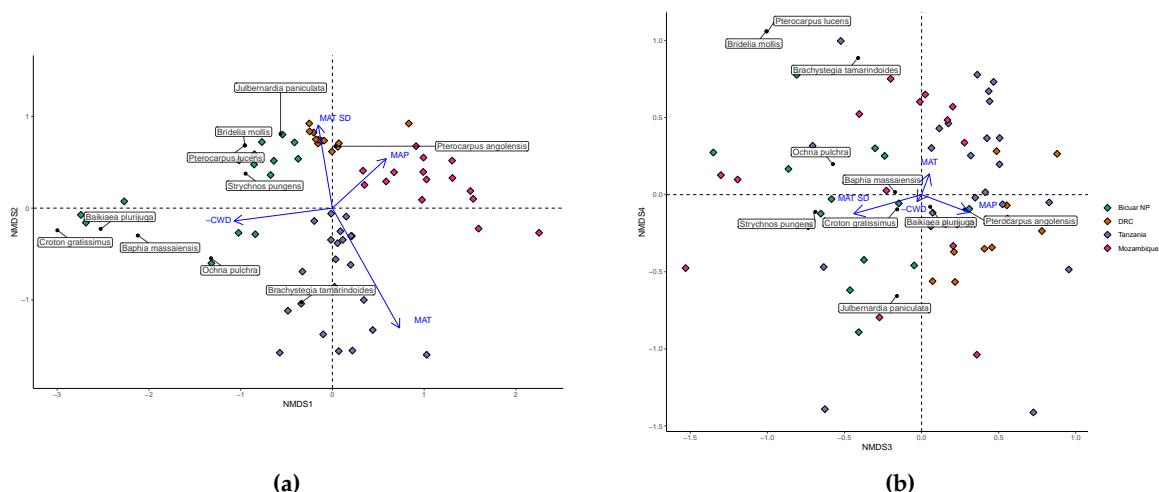


Figure 4. Environmental factors fitted to axes 1 and 2 (a), 3 and 4 (b) of the NMDS ordination of species composition of one hectare plots, showing the variation in plot species composition within and among sites. Diamonds are plot scores coloured by site. The lengths of arrows indicating environmental factor fits to the first two ordination axes are scaled by R^2 . Arrows point in the direction of increasing values of that environmental factor. Note that Climatic Water Deficit (CWD) is expressed in more intuitively as the negative inverse of CWD, thus larger values indicate higher levels of CWD.

The pairwise Sørensen coefficient of percentage similarity (S_S) showed that the species composition of plots in Bicuar National Park had low similarity with other sites in the study, sharing few species with other sites (Table 3). Similar to the NMDS, these results show that plots in Bicuar National Park are most similar to those found in DRC.

Table 3. Pairwise beta diversity comparison of plot groups measured by the Sørensen coefficient (S_S) of percentage similarity of aggregated plot level data from each of the four sites. Values in parentheses are the number of species unique to each site in each comparison.

Site 1	Site 2	S_S	Shared species
Bicuar NP(34)	DRC(74)	20.6	14
Bicuar NP(34)	Tanzania(147)	13.4	14
Bicuar NP(37)	Mozambique(236)	7.5	11
DRC(64)	Tanzania(137)	19.3	24
DRC(69)	Mozambique(228)	11.3	19
Tanzania(139)	Mozambique(225)	10.8	22

3.3. Woodland structure

Mean basal area of plots in Bicuar National Park was $2.78 \pm 0.122 \text{ m}^2 \text{ ha}^{-1}$, ranging from 1.86 to $8.53 \text{ m}^2 \text{ ha}^{-1}$ (Figure 3). An ANOVA showed a significant difference in basal area among sites ($F(3,60) = 48.04$, $p < 0.01$), and a post-hoc Tukey's test showed that basal area in Bicuar National Park was significantly lower than plots in DRC ($\text{BA} = 6.95 \pm 0.327 \text{ m}^2 \text{ ha}^{-1}$, $p < 0.01$), but there were no significant differences between Bicuar and Mozambique ($\text{BA} = 3.43 \pm 0.409 \text{ m}^2 \text{ ha}^{-1}$, $p = 0.43$) or Tanzania ($\text{BA} = 2.06 \pm 0.253 \text{ m}^2 \text{ ha}^{-1}$, $p = 0.26$) (Figure 3). Additionally, Bicuar plots had less variation in basal area among plots than other sites. Plots in Bicuar with the highest basal area were dominated by *Baikaea plurijuga* and *Baphia massaiensis* (Plots 9, 13, and 15).

The stem diameter abundance distribution in Bicuar National Park was comparable with other sites (Figure 5), albeit with fewer stems in each class. The slope of log mean stem size distribution

among diameter bins was -0.92 ± 0.067 in Bicuar National Park, -0.99 ± 0.067 in DRC, -0.89 ± 0.065 in Tanzania, and -0.87 ± 0.075 in Mozambique.

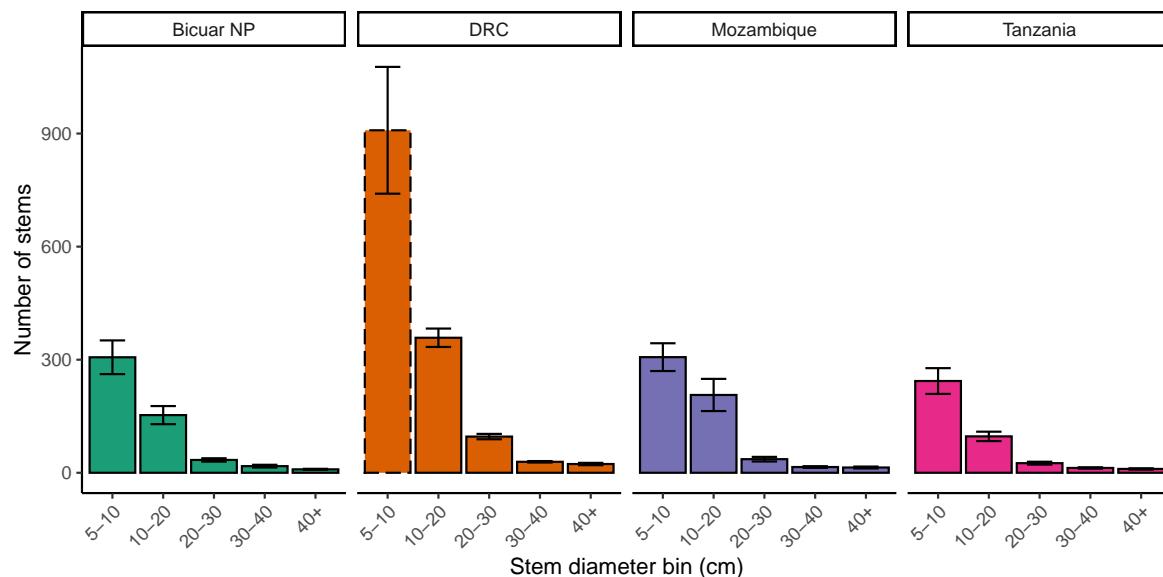


Figure 5. Ranked variation between plots in stem number within each site, with bars according to stem diameter class. Error bars are the mean ± 1 standard error. The dashed bar for the DRC 5-10 cm stem diameter class indicates that these measurements were estimated by extrapolating a linear regression of log stem abundance across the available stem diameter classes for DRC.

3.4. Effect of disturbance via shifting cultivation on diversity within Bicuar National Park

There was a clear difference in the species composition of previously farmed disturbed woodland plots and undisturbed woodland plots, but with some overlap (Figure 6). Notably, Plots 4 and 7 in putatively undisturbed woodland have a species composition more resembling the disturbed plots. These two plots were dominated by *Brachystegia tamarindoides* and *Burkea africana*, with *B. africana* being a species which occurred frequently as a pioneer in the disturbed plots. The undisturbed plots 15, 13, and 9 represent distinct outliers in the NMDS. These three plots were dominated by *Baikiaea plurijuga* which was not encountered in the disturbed plots. The most common species in the disturbed plots was *Baphia massaiensis* ($n = 158$), with a mean stem diameter of 6.1 ± 1.87 cm, while in the undisturbed plots the most common species was *Julbernardia paniculata* ($n = 125$), with a mean stem diameter of 11.8 ± 7.24 cm. Mean alpha diversity was marginally higher in disturbed plots ($H' = 1.7 \pm 0.08$) than in undisturbed plots ($H' = 1.3 \pm 0.14$) and an ANOVA showed that there was a significant difference in H' between the two plot types ($F(1,33) = 5.91$, $p < 0.05$) (Figure 7). Mean plot species richness was also lower in undisturbed plots (6.4 ± 0.86) than disturbed plots (8.7 ± 0.53). Mean $E_{H'}$ was 0.8 ± 0 in disturbed plots and 0.7 ± 0.04 in undisturbed plots but there was no significant difference between disturbed and undisturbed plots according to an ANOVA ($F(1,33) = 1.54$, $p = 0.22$). 11 species were found only in the disturbed plots and not in the undisturbed plots. The most common of these were *Combretum celastroides* ($n = 30$), *Acacia reficiens* ($n = 14$), and *Gardenia ternifolia* ($n = 11$). 7 were found only in undisturbed plots, the most common being *Brachystegia spiciformis* ($n = 61$), *Baikiaea plurijuga* ($n = 43$) and *Combretum apiculatum* ($n = 9$). Mean basal area was higher in undisturbed plots ($0.5 \pm 0.07 \text{ m}^2 \text{ ha}^{-1}$) than disturbed plots ($0.5 \pm 0.1 \text{ m}^2 \text{ ha}^{-1}$).

Mean stem density was higher in disturbed plots ($900 \pm 338.36 \text{ stems ha}^{-1}$) than undisturbed plots ($520.3 \pm 220.22 \text{ stems ha}^{-1}$). The stem diameter abundance distribution in disturbed plots showed that many more stems were from the 5-10 cm diameter class in disturbed plots, while the disturbed plots had fewer stems in the 10-20 cm size class. Both disturbed and undisturbed plots had a similar abundance of stems in larger stem diameter classes (Figure 8). Multi-stemmed trees in disturbed plots

²⁶⁷ tended to have a greater number of stems per tree (3.4 ± 2.35) than multi-stemmed trees in undisturbed
²⁶⁸ plots (2.4 ± 0.8).

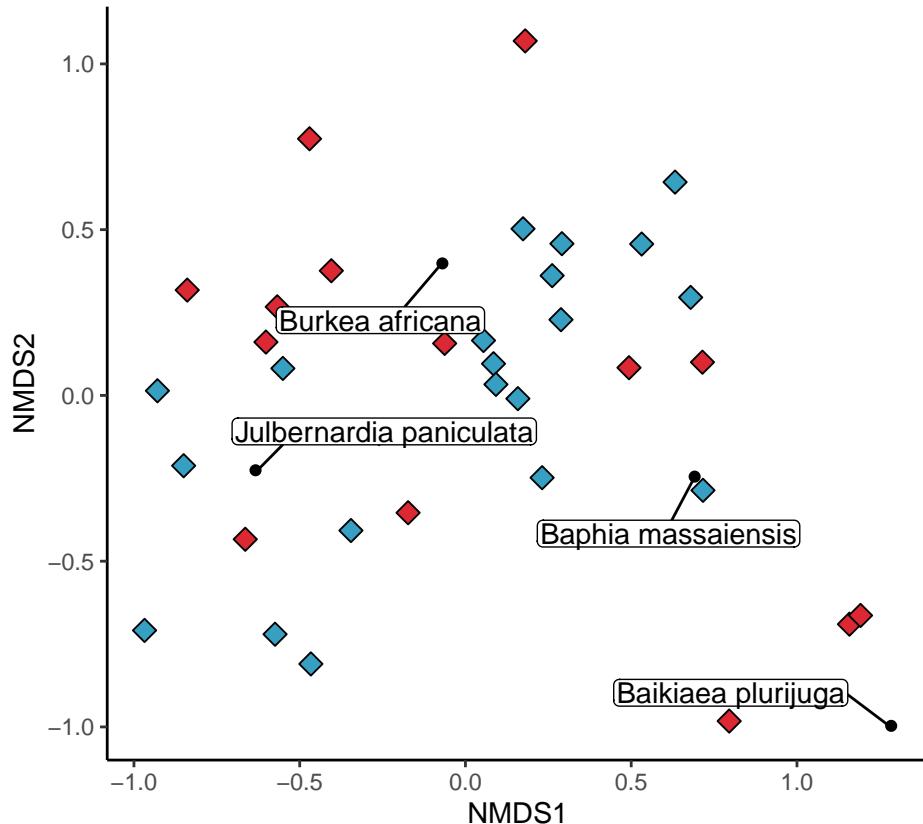


Figure 6. NMDS ordination of species composition of 20x50 m (0.1 ha) plots showing plot scores as coloured diamonds located in disturbed (blue) and undisturbed (red) areas of woodland in Bicuar National Park.

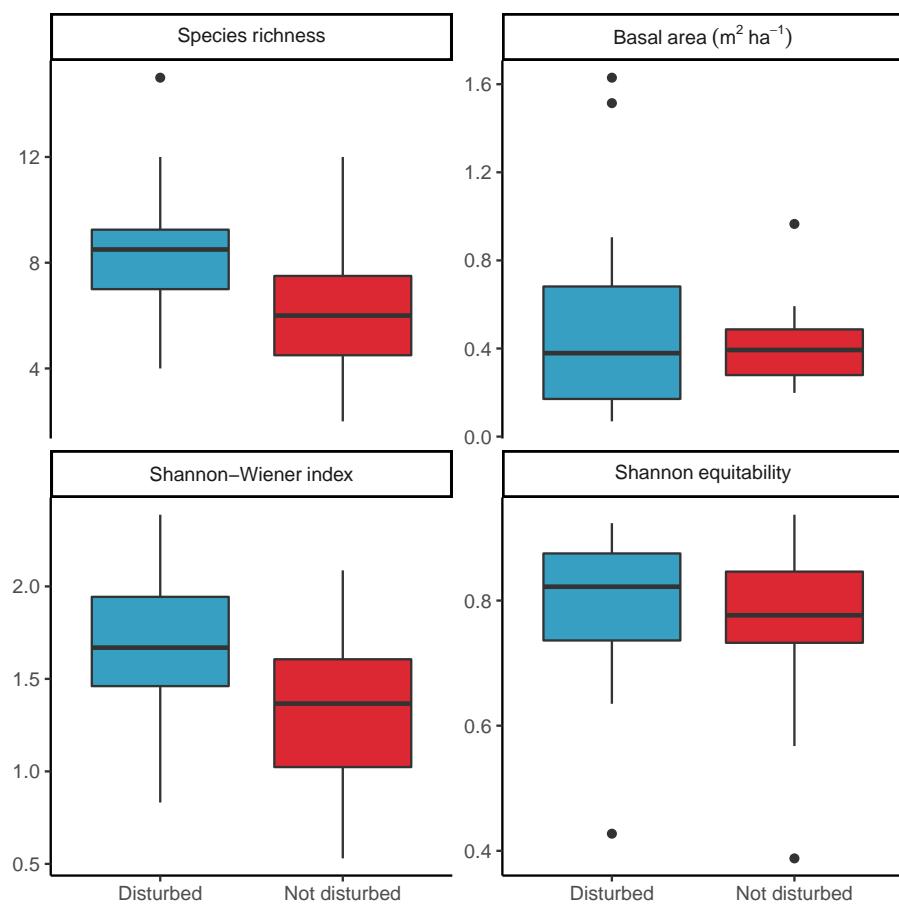


Figure 7. The variation in diversity and woodland structure between disturbed and undisturbed 20x50 m (0.1 ha) plots in Bicuar National Park. Boxes bound the 1st and 3rd quartiles, with the median within the box. Whiskers represent 1.5 times the interquartile range plus or minus the 1st and 3rd quartiles, respectively. Values found beyond the whiskers are shown individually as points.

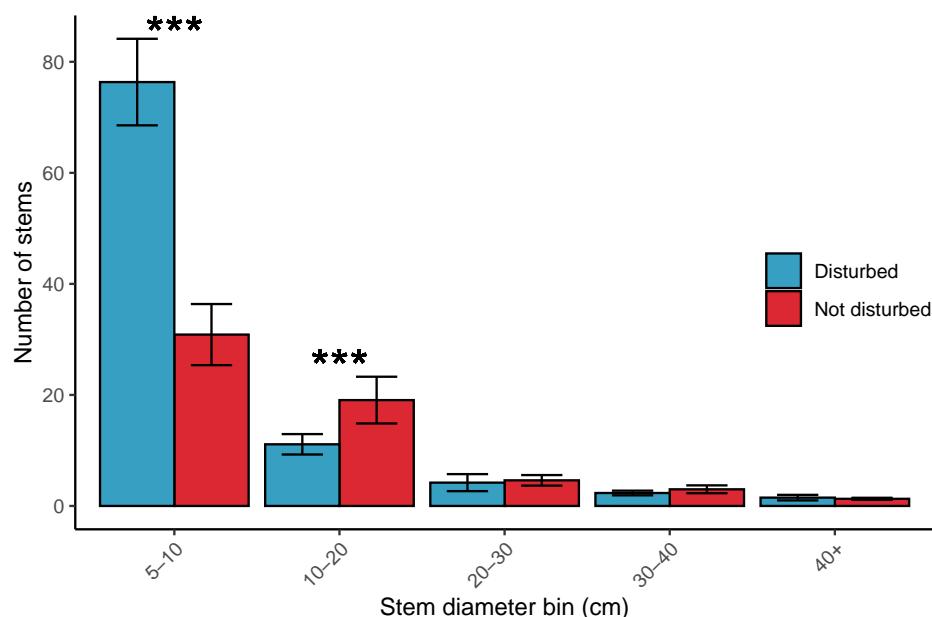


Figure 8. Ranked variation between disturbed and undisturbed plots in stem number, with bars according to stem diameter class. Error bars are the mean \pm 1 standard error. Asterisks above pairs of bars refer to the p-values of Poisson general linear models which tested whether disturbed and undisturbed plots differ in the number of stems for different stem diameter classes ('***' < 0.001, '**' < 0.01, '*' < 0.05, '.' < 0.1).

269 4. Discussion

270 4.1. Comparison of Bicuar National Park with other woodlands across the miombo ecoregion

271 We compared the tree species diversity and woodland structure of arid woodlands in Bicuar
 272 National Park in southwest Angola with three other woodland sites across the miombo ecoregion. Our
 273 results show that Bicuar National Park is distinct in both woodland structure and species composition
 274 from these other woodlands. Notably, plots in Bicuar National Park contained 27 tree species which did
 275 not occur at other sites. This lends support for the Huíla Plateau as an important area for conservation
 276 of southern African woodland landscapes. The woodlands in Bicuar National Park were of low tree
 277 basal area, with few large trees except in plots dominated by *Baikiaea plurijuga*. Many other studies
 278 have drawn a relationship between water availability and basal area [46,47], and our study supports
 279 this, with Bicuar National Park being the most arid of the four sites considered in our study. The
 280 NMDS of species composition also suggests that plots in Bicuar National Park are influenced by aridity.
 281 While there are more arid woodlands within southern Africa, with Mopane woodlands for example
 282 often being particularly dry, these plots in Bicuar National park represent particularly dry miombo
 283 woodlands.

284 4.2. Delineation of woodland types within Bicuar National Park

285 Within Bicuar National Park, three distinct woodland types were identified. The first, dominated
 286 by *Baikiaea plurijuga* and *Baphia massaiensis* represents the Baikiaea woodland type commonly found
 287 to the south of the miombo ecoregion [48]. This is supported by Chisingui *et al.* [23] who also found
 288 Baikiaea woodlands as a distinct woodland type in the Park. *B. plurijuga* has been identified as an
 289 important species for conservation, being attractive for selective logging due to its large stature [49,50].
 290 The woodlands created by *B. plurijuga* are also an important habitat for elephants (*Loxodonta africana*)
 291 [51,52], with Bicuar National Park and Mupa National Park being key refugia for this animal in the
 292 Huíla plateau region. The second woodland type, dominated by *Brachystegia tamarindoides* and *Ochna*

293 *pulchra* represents a form of small stature woodland with a shrubby understorey and sparse canopy
294 trees, which commonly occurs as a result of repeated disturbance by fire, or poor soil structure [53].
295 The remaining plots resemble the more archetypical miombo woodland with *Julbernardia paniculata*,
296 though with a number of species not seen in plots further to the east in the miombo ecoregion such as
297 *Strychnos pungens*. This mosaic of woodland types makes Bicuar National Park a valuable reservoir of
298 diversity and strengthens the case for the Park being a key conservation asset within the Huíla plateau
299 and the larger southern African region. While there are regional boundaries between Baikiaeae and
300 miombo woodlands [1], within Bicuar National Park it is likely that the mosaic of woodland types has
301 been created by a combination of soil water capacity and disturbance history. Bicuar has a distinct
302 landscape of wide shallow grassy valleys surrounded by woodland on higher ground (Figure 2). On
303 some of these high points the soil is particularly sandy, resembling the Kalahari sand soils found
304 further east and south [20], and these areas coincide with the presence of Baikiaeae woodlands [5].
305 High levels of disturbance by fire in these Baikiaeae patches may additionally prevent a transition to an
306 alternative woodland type via the control of sapling growth.

307 *4.3. Comparison of disturbed and undisturbed woodland plots*

308 Previously disturbed woodlands around the edge of Bicuar National Park were found to share
309 many species with undisturbed plots in the Park, but with some additional species which did not
310 occur in the undisturbed plots. They also lacked notable archetypical miombo species which tend to
311 form larger canopy trees such as *Brachystegia spiciformis* and contained very few *Julbernardia paniculata*,
312 leading to a distinct woodland composition. The species diversity of these disturbed patches was
313 higher on average than was found in the undisturbed plots, a result which has been corroborated by
314 other studies in miombo woodlands [54–56]. Other studies have shown a peak in species richness
315 during woodland regrowth as pioneer species take advantage of a low competition environment, while
316 some later stage woodland species remain as residuals that survived the original disturbance [30,57].
317 Gonçalves *et al.* [30] particularly, notes the dominance of *Pericopsis angolensis* and *Combretum* spp. as
318 light-demanding pioneer species, which were found to be abundant in the disturbed plots here. This
319 suggests that reclamation of previously farmed and abandoned land for landscape conservation in this
320 ecological context is a valuable management strategy.

321 In disturbed plots near the edge of the Park, there was a lack of species which tend to grow to
322 large canopy trees, possibly due to them being repeatedly felled for timber prior to reclamation by the
323 Park, or due to them being unable to recruit into a more open, shrubby woodland. Despite this lack of
324 canopy forming tree species, some disturbed plots had a greater basal area than undisturbed plots,
325 possibly due to high levels of coppicing in these plots or a divergent fire history. Indeed, mean stem
326 density was higher in undisturbed plots. This can lead to species that would otherwise remain small
327 producing a much larger basal area as they grow multiple stems under high disturbance conditions
328 [58]. The most common species in the disturbed plots were *Combretum psidoides*, *Combretum collinum*
329 and *Terminalia sericea*, members of the Combretaceae family, all of which more commonly remain as
330 smaller multi-stemmed trees in disturbed woodlands, rather than growing to larger canopy trees [59].
331 This result could be considered at odds with other studies which report lower woody biomass in plots
332 that have experienced harvesting (e.g. Muvengwi *et al.* 60). It is important to consider however that
333 our study took place in plots that were measured after farming had been abandoned for at least 7 years,
334 with time for regeneration to occur. It is possible that over time tree basal area will decrease as coppiced
335 shrubby trees are replaced by core miombo species in the transition back to miombo woodland [30].
336 Indeed, other studies in miombo woodlands across the ecoregion have reported substantial recovery
337 within seven years, with high levels of biomass accumulation in previously disturbed plots [30,61].
338 Bicuar National Park offers a valuable case study to track woodland regeneration in real-time over the
339 next decade in these previously farmed and now protected woodland plots, which could improve our
340 understanding of this potential post-disturbance peak in basal area.

341 In conclusion, the woodlands of Bicuar National Park represent an important woodland refuge
342 at the far western extent of the miombo ecoregion. These woodlands, both those disturbed by
343 previous farming activity and those which remain undisturbed, possess a number of species not found
344 commonly in other miombo woodland plots around the region. They may also house important genetic
345 variation for widespread species, representing populations adapted to more arid conditions. Our study
346 highlights the variation in species composition across the miombo ecoregion and underlines the need
347 for studies which incorporate plot data from multiple locations to reach generalisable conclusions
348 about the region as a whole. Additionally, the installation of 15 one hectare woodland monitoring
349 plots and a further twenty 20x50 m plots in previously farmed and now protected land offer a valuable
350 natural laboratory to further explore the dynamics of dry miombo woodlands of the Huíla plateau.
351 Bicuar National Park should be considered a key conservation asset within the Huíla plateau and
352 within the miombo ecoregion as a whole, as a successfully protected example of an arid woodland
353 mosaic.

354 **Author Contributions:** Investigation and project administration was conducted by J.L.G., F.M.G., J.J.T. and A.V.T.
355 (Bicuar National Park), C.M.R. (Tanzania, Mozambique), J.I.M. and M.N.S. (DRC). The study was conceived
356 by J.L.G. and K.G.D.. Data curation, methodology, formal analysis and writing—original draft preparation was
357 conducted by J.L.G.. All authors contributed to writing—review and editing.

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370 publish the results.

371 Abbreviations

372 The following abbreviations are used in this manuscript:

373	ANOVA	Analysis of Variance
	DD	Decimal Degrees
	MAP	Mean Annual Precipitation
374	MAT	Mean Annual Temperature
	MAT SD	Standard Deviation of Mean Annual Temperature (Seasonality)
	NMDS	Non-metric Multidimensional Scaling
	NP	National Park

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

```

376
377 1 ##' @author Casey M. Ryan
378 2 ##' @return d130, the estimated diameter at a POM of 1.3 m (in cm).
379 3 ##' @param d_in the diameter measured at the POM (in cm)
380 4 ##' @param POM the height of the POM (in m)
381 5 ##' @details The adjustment based on tree taper model developed as part of
382 6 ##' the ACES project (Abrupt Changes in Ecosystem Services
383 7 ##' https://miomboaces.wordpress.com/), using data from the miombo of Niassa.
384 8 ##' The model is a cubic polynomial, with three equations for different sized stems.
385 9 ##' @section Warning: POMs >1.7 m are not adjusted.
38610 POMadj <- function(d_in, POM) {
38711   stopifnot(is.numeric(d_in),
38812             is.numeric(POM),
38913             POM >= 0,
39014             sum(is.na(POM))==0,
39115             length(POM) == length(d_in))
39216   if (any(POM > 1.7))
39317     warning("POMs >1.7 m are outside the calibration data, no correction applied")
39418   NAS <- is.na(d_in)
39519   d_in_clean <- d_in[!NAS]
39620   POM_clean <- POM[!NAS]
39721   # define the size class edges:
39822   edges <- c(5.0, 15.8, 26.6, 37.4)
39923   sm <- d_in_clean < edges[2]
40024   med <- d_in_clean >= edges[2] & d_in_clean < edges[3]
40125   lg <- d_in_clean >= edges[3]
40226
40327   # compute predictions for delta_d, for all size classes
40428   delta_d <- data.frame(
40529     # if small:
40630     small = 3.4678+-5.2428 *
40731       POM_clean + 2.9401 *
40832       POM_clean^2+-0.7141 *
40933       POM_clean^3,
41034     # if med
41135     med = 4.918+-8.819 *
41236       POM_clean + 6.367 *
41337       POM_clean^2+-1.871 *
41438       POM_clean^3,
41539     # if large
41640     large = 9.474+-18.257 *
41741       POM_clean + 12.873 *
41842       POM_clean^2+-3.325 *
41943       POM_clean^3
42044   )
42145   # index into the right size class
42246   dd <- NA_real_
42347   dd[sm] <- delta_d$small[sm]
42448   dd[med] <- delta_d$med[med]
42549   dd[lg] <- delta_d$large[lg]
42650   dd[POM_clean > 1.7] <- 0 # to avoid extrapolation mess
42751
42852   # add NAs back in
42953   d130 <- NA
43054   d130[NAS] <- NA
43155   d130[!NAS] <- d_in_clean - dd
43256
43357   if (any(d130[!NAS] < 0))
43458     warning("Negative d130 estimated, replaced with NA")
43559   d130[d130 <= 0 & !is.na(d130)] <- NA
43660   return(d130)
43761 }
```

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