

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*, *Jubbernardia* and *Isoberlinia* genera, all within the Fabaceae family, subfamily Detoroideae [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

27 climate, edaphic factors, disturbance regimes and biogeography maintain a diverse array of woodland
28 types in terms of both species composition and physiognomy [7–9].

29 The miombo ecoregion extends across the continent in a wide band that reaches north into Kenya
30 and the Democratic Republic of Congo (DRC) and south into the northeast of South Africa (Figure
31 1a). Miombo woodlands are defined both by their tree diversity and by their structure of a grassy
32 herbaceous understorey with an often sparse tree canopy. In archetypical miombo woodlands, species
33 of the genera *Brachystegia*, *Julbernardia* and *Isoberlinia* generally hold the most biomass, forming a
34 mostly open woodland canopy. Distinct from dry tropical forests, miombo woodlands generally
35 maintain a grassy understorey dominated by grass species utilizing the C₄ carbon fixation pathway
36 [10]. Miombo woodlands are heavily structured by seasonal fire and herbivory, with fire particularly
37 often preventing the creation of a closed tree canopy which would naturally occur in the absence
38 of these disturbances [11,12]. Within the miombo ecoregion, other woodland types exist, notably,
39 woodlands dominated by *Baikiaea* spp. or *Colophospermum mopane* [5].

40 Southern African woodlands are structurally complex but species poor in the tree layer compared
41 to dry tropical forests which exist at similar latitudes [13,14]. These woodlands contain many endemic
42 tree species however, and support a highly diverse woodland understorey, with an estimated 8500
43 species of vascular plants [15]. Miombo woodlands provide ecosystem service provision for an
44 estimated 150 million people [16]. Additionally miombo woodlands hold ~18-24 Pg C in woody
45 biomass and soil organic carbon, which is comparable to that held in the rainforests of the Congo basin
46 (~30 Pg C) [17]. As woodland resource extraction and conversion to agricultural land accelerates due
47 to growing human populations, the conservation of miombo woodlands as a biodiverse and unique
48 ecosystem has become a growing concern. Despite their importance however, dry tropical woodlands
49 remain understudied compared to wet forests across the globe [18].

50 Over the previous two decades, the limited ecological research in southern African woodlands has
51 been concentrated in the central and eastern parts of the miombo region, notably in southern Tanzania,
52 Mozambique, Malawi, Zimbabwe and Zambia. The southwestern extent of miombo woodlands, which
53 is found entirely within Angola has received considerably less attention [19]. Partly this is due to
54 diminished research capacity during the Angolan civil war following the country's independence,
55 which took place officially between 1975 and 2002, but with sporadic localised periods of civil unrest
56 until around 2012 [20]. While botanical surveys of woodlands in this region are more plentiful
57 [19,21], joint studies of woodland species composition and physical structure remain scarce. This is
58 despite the value of these studies in helping to estimate woodland net primary productivity, carbon
59 sequestration potential, and studies of community assembly. To properly understand spatial variation
60 in woodland species composition and physical structure across the miombo ecoregion, it is necessary
61 to fill understudied gaps. In this study we aim to address one such gap in southwest Angola, and
62 place it in context with other woodlands across the miombo ecoregion.

63 The miombo woodlands of southwest Angola are found in their most intact form in Bicuar
64 National Park and to a lesser extent in the adjacent Mupa National Park, on the Huíla plateau [22].
65 Both of these national parks have been protected to varying extents since 1938 [19]. These woodlands
66 exist in much drier conditions than other miombo woodlands, precipitation diminishes rapidly within
67 the Huíla plateau towards the Angolan coast and the Namib desert (Figure 1a). The vegetation of the
68 Huíla plateau holds many endemic species, around 83 endemic Fabaceae species [23] and the most
69 endemic plant species of any part of Angola [24]. Linder [25] and Droissart *et al.* [26] both identify the
70 western portion of the Huíla plateau as a centre of tropical African endemism.

71 Much of the historic miombo woodland area in southwest Angola surrounding the Bicuar and
72 Mupa National Parks has been deforested in recent years, with a clear increase in deforestation activity
73 since the end of the civil war owing to an increase in rural population and agricultural activity [19,27].
74 The western extent of miombo woodlands found within Bicuar National Park plateau are therefore of
75 great importance for conservation as a refuge for wildlife and endemic plant species [19].

76 It is important to focus not only on the biodiversity of undisturbed woodland areas but also
77 previously disturbed land in order to properly assess the biodiversity and woodland structure of the
78 Park. Woodland disturbance through shifting cultivation practices produces novel habitats which
79 are not necessarily of lower conservation value [28,29]. Since Bicuar National Park's rejuvenation
80 following the reinforcement of park boundaries after the civil war, many areas of woodland that were
81 previously heavily grazed, farmed via shifting cultivation techniques, and used for timber extraction
82 have been allowed to re-establish and are now protected from further human resource extraction. This
83 presents a unique opportunity to compare the species composition of these disturbed areas with areas
84 of nearby woodland that have not been farmed in living memory.

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

93 2. Materials and Methods

94 2.1. Study area

95 We chose three areas of miombo woodland across the miombo ecoregion to compare with those
96 in Bicuar National Park, Angola ($S15.1^{\circ}$, $E14.8^{\circ}$). The three sites were Gorongosa National Park in
97 central Mozambique ($S19.0^{\circ}$, $E34.2^{\circ}$) [30], Kilwa District in southern Tanzania ($S9.0^{\circ}$, $E39.0^{\circ}$) [31], and
98 the Mikembo Natural Reserve in Katanga, southern Democratic Republic of Congo (DRC) ($S11.5^{\circ}$,
99 $E27.7^{\circ}$) [32]. Within each of these woodland sites, multiple one hectare square plots had been installed
100 previously to monitor biodiversity and biomass dynamics. In Katanga, a larger 10 ha plot was
101 subdivided into ten 1 ha plots for this study. We used these previous censuses, collected between
102 2010 and 2019, to estimate tree biodiversity and woodland structure. Sites range in Mean Annual
103 Precipitation (MAP) from 864 mm y^{-1} in Bicuar to 1115 mm y^{-1} in Katanga. Mean Annual Temperature
104 ranges from $\sim 20.5^{\circ}\text{C}$ in Bicuar and Katanga to $\sim 25.8^{\circ}\text{C}$ in Kilwa (Figure 1b, Table 1).

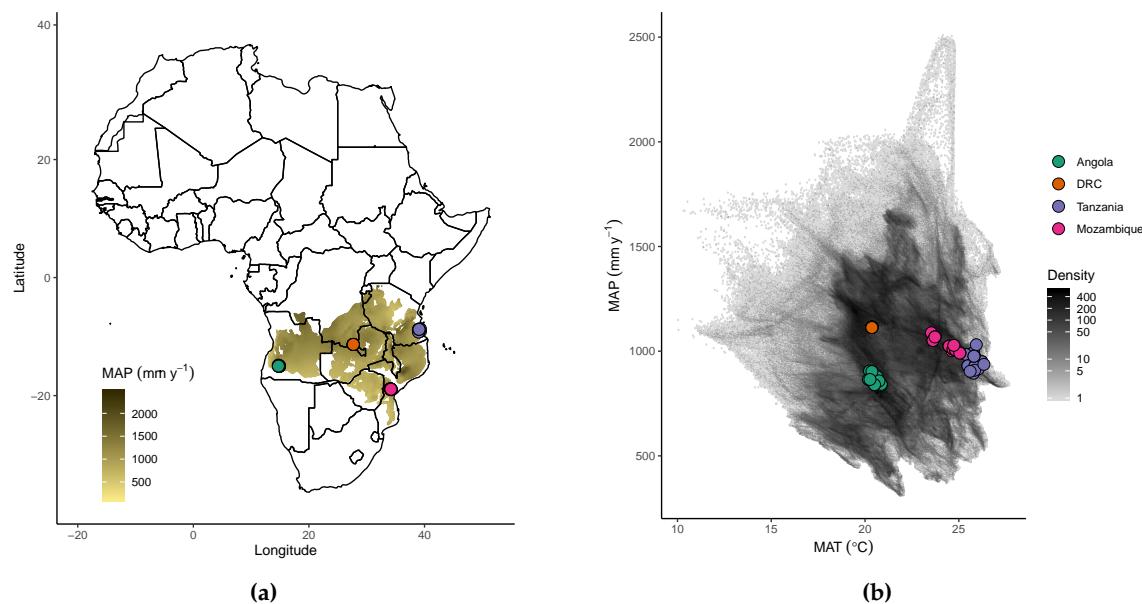


Figure 1. Locations of plots used in this study, by (a) geographic location with respect to the distribution of miombo woodland vegetation (shaded brown according to mean annual precipitation) [1], and (b) showing the plot locations compared to the climate space of the miombo ecoregion estimated using the WorldClim dataset over the Miombo woodland vegetation extent with a pixel size of 30 arc seconds (0.86 km^2 at the equator) [33]. 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

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

113 2.2. Plot data collection

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

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

121 was later checked against the African Plant Database [34]. In all sites Palgrave [35] and various other
122 texts were used as a guide for species identification in the field. Specimens that could not be identified
123 in the field, or subsequently at herbaria, were described as morphospecies. All tree species within the
124 Bicuar National Park plots were identified. Tree coppicing due to fire, herbivory, and human actions
125 is common in miombo woodlands, therefore, for trees with multiple stems, each stem ≥ 5 cm stem
126 diameter was recorded, while the parent tree was also recorded for diversity analyses described below.

127 Stem diameter was recorded at 1.3 m from the ground along the stem (diameter at breast height,
128 DBH) as per convention using a diameter tape measure [36]. Where stem abnormalities were present
129 at 1.3 m from the ground, which precluded the accurate estimation of stem diameter at 1.3 m, the
130 stem diameter was recorded at the nearest 10 cm increment above 1.3 m without significant stem
131 abnormalities [36]. To ensure consistency among stem diameter values recorded at different heights,
132 when the stem diameter was recorded at a height other than 1.3 m the stem diameter at 1.3 m was
133 estimated from the recorded stem diameter using a cubic polynomial equation which adjusts for tree
134 stem taper. This equation was calibrated on 100 stems measured at multiple heights in Niassa Province,
135 Mozambique ([Appendix A](#)). Stems below 10 cm stem diameter were not measured in the DRC plots.
136 We therefore estimated the number of 5-10 cm stems in each these plots by extrapolating a linear
137 regression of log stem abundance across the available stem diameter classes.

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

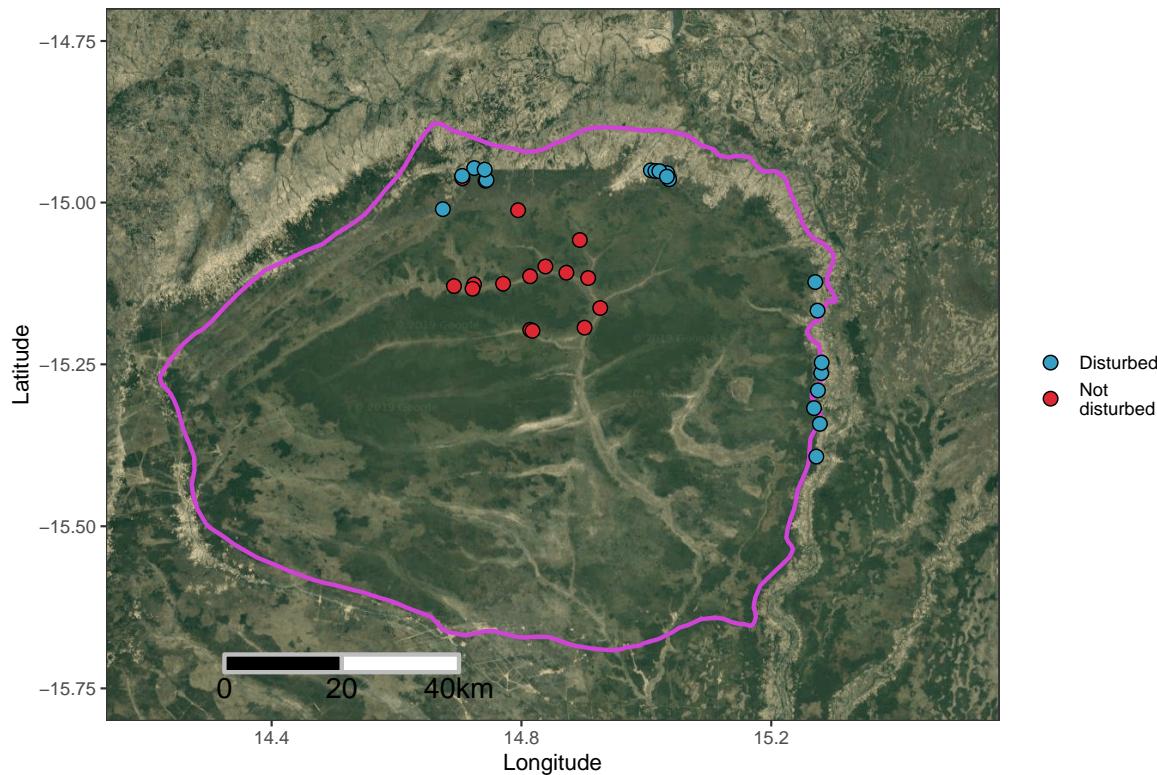


Figure 2. Location of plots in Bicuar National Park, southwest Angola. The Park boundary is shown as a pink outline, according to UNEP-WCMC and IUCN [37]. One hectare undisturbed plots are shown as red points, while disturbed 20x50 m (0.1 hectare) plots are shown as blue points. The map background is a true colour composite satellite image generated using the Google Maps Static Maps API in the `ggmap` R package [38].

147 2.3. Climatic data

148 The WorldClim dataset [33] was used to gather data on plot-level climatic conditions. We
 149 estimated Mean Annual Precipitation (MAP) as the mean of total annual precipitation values between
 150 1970 and 2000, and Mean Annual Temperature (MAT) as the mean of mean annual temperatures
 151 between 1970 and 2000. The seasonality of temperature (MAT SD) was calculated as the standard
 152 deviation of monthly temperature per year, respectively. We estimated Climatic Water Deficit (CWD)
 153 for each plot according to [39], as the sum of the difference between monthly rainfall and monthly
 154 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.

156 2.4. Data analysis

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

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

158 Where d_i is the estimated stem diameter of stem i at 1.3 m having accounted for tree taper. We
 159 then calculated the total basal area of each plot as the sum of each stem's basal area. For the DRC plots
 160 which lacked 5–10 cm stems, we estimated basal area in this stem diameter class from our extrapolation
 161 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 [40]. We calculated the pairwise beta diversity among sites using the Sørensen coefficient (S_S) [41]. 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 ($E_{H'}$) [42] 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 [43]. 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 [44].

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

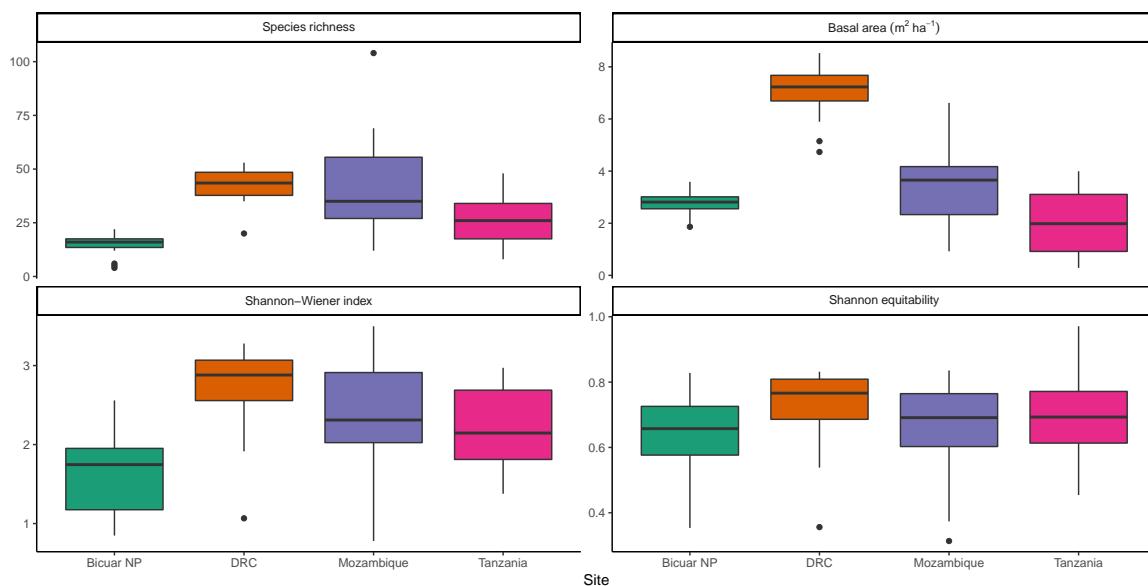


Figure 3. Variation of alpha diversity estimates and basal area among sites. Boxes bound the 1st and 3rd quartiles, with the median within the box. Whiskers represent 1.5 times the interquartile range plus or minus the 1st and 3rd quartiles, respectively. Values found beyond the whiskers are shown individually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

203 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.

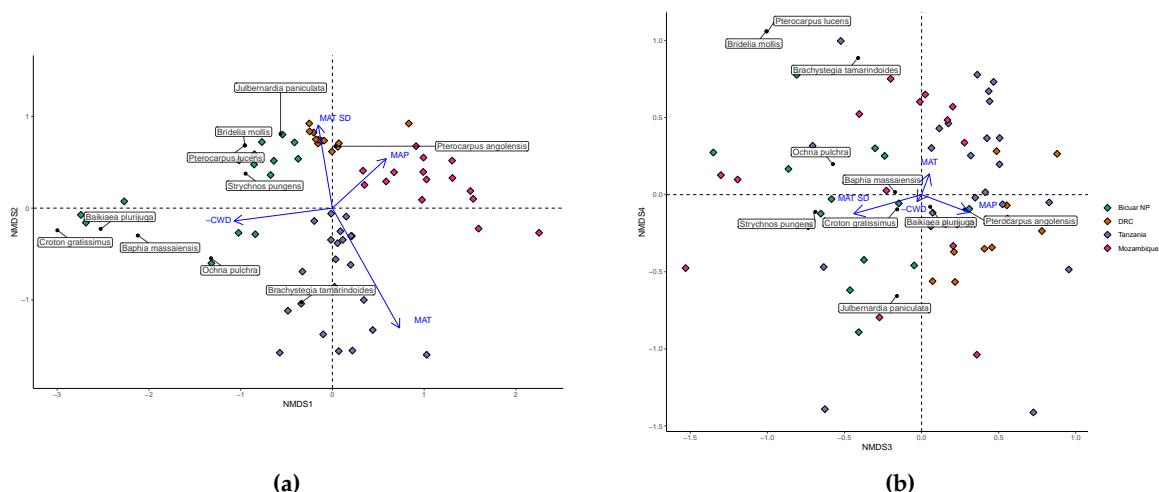


Figure 4. Environmental factors fitted to axes 1 and 2 (a), 3 and 4 (b) of the NMDS ordination of species composition of one hectare plots, showing the variation in plot species composition within and among sites. Diamonds are plot scores coloured by site. The lengths of arrows indicating environmental 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

²³⁸ among diameter bins was -0.92 ± 0.067 in Bicuar National Park, -0.99 ± 0.067 in DRC, -0.89 ± 0.065 in
²³⁹ Tanzania, and -0.87 ± 0.075 in Mozambique.

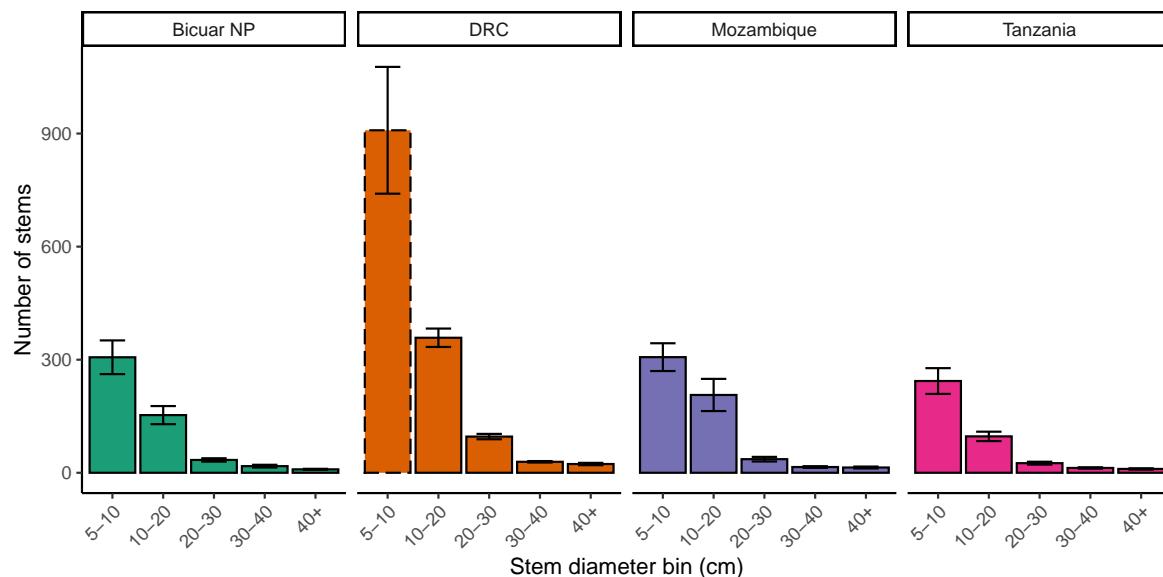


Figure 5. Ranked variation between plots in stem number within each site, with bars according to stem diameter class. Error bars are the mean ± 1 standard error. The dashed bar for the DRC 5-10 cm stem diameter class indicates that these measurements were estimated from the average proportion of 5-10 cm stems in all other plots.

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

²⁴¹ There was a clear difference in the species composition of previously farmed disturbed woodland
²⁴² plots and undisturbed woodland plots, but with some overlap ([Figure 6](#)). Notably, Plots 4 and 7 in
²⁴³ putatively undisturbed woodland have a species composition more resembling the disturbed plots.
²⁴⁴ These two plots were dominated by *Brachystegia tamarindoides* and *Burkea africana*, with *B. africana* being
²⁴⁵ a species which occurred frequently as a pioneer in the disturbed plots. The undisturbed plots 15, 13,
²⁴⁶ and 9 represent distinct outliers in the NMDS. These three plots were dominated by *Baikiaea plurijuga*
²⁴⁷ which was not encountered in the disturbed plots. The most common species in the disturbed plots
²⁴⁸ was *Baphia massaiensis* ($n = 158$), with a mean stem diameter of 6.1 ± 1.87 cm, while in the undisturbed
²⁴⁹ plots the most common species was *Julbernardia paniculata* ($n = 125$), with a mean stem diameter of
²⁵⁰ 11.8 ± 7.24 cm. Mean alpha diversity was marginally higher in disturbed plots ($H' = 1.7 \pm 0.08$) than
²⁵¹ in undisturbed plots ($H' = 1.3 \pm 0.14$) and an ANOVA showed that there was a significant difference
²⁵² in H' between the two plot types ($F(1,33) = 5.91$, $p < 0.05$) ([Figure 7](#)). Mean plot species richness was
²⁵³ also lower in undisturbed plots (6.4 ± 0.86) than disturbed plots (8.7 ± 0.53). Mean $E_{H'}$ was 0.8 ± 0 in
²⁵⁴ disturbed plots and 0.7 ± 0.04 in undisturbed plots but there was no significant difference between
²⁵⁵ disturbed and undisturbed plots according to an ANOVA ($F(1,33) = 1.54$, $p = 0.22$). 11 species were
²⁵⁶ found only in the disturbed plots and not in the undisturbed plots. The most common of these were
²⁵⁷ *Combretum celastroides* ($n = 30$), *Acacia reficiens* ($n = 14$), and *Gardenia ternifolia* ($n = 11$). 7 were found
²⁵⁸ only in undisturbed plots, the most common being *Brachystegia spiciformis* ($n = 61$), *Baikiaea plurijuga* (n
²⁵⁹ = 43) and *Combretum apiculatum* ($n = 9$). Mean basal area was higher in undisturbed plots ($0.5 \pm 0.07 \text{ m}^2 \text{ ha}^{-1}$)
²⁶⁰ than disturbed plots ($0.5 \pm 0.1 \text{ m}^2 \text{ ha}^{-1}$).

²⁶¹ Mean stem density was higher in disturbed plots ($900 \pm 338.36 \text{ stems ha}^{-1}$) than undisturbed plots
²⁶² ($520.3 \pm 220.22 \text{ stems ha}^{-1}$). The stem diameter abundance distribution in disturbed plots showed
²⁶³ that many more stems were from the 5-10 cm diameter class in disturbed plots, while the disturbed
²⁶⁴ plots had fewer stems in the 10-20 cm size class. Both disturbed and undisturbed plots had a similar
²⁶⁵ abundance of stems in larger stem diameter classes ([Figure 8](#)). Multi-stemmed trees in disturbed plots

²⁶⁶ tended to have a greater number of stems per tree (3.4 ± 2.35) than multi-stemmed trees in undisturbed
²⁶⁷ plots (2.4 ± 0.8).

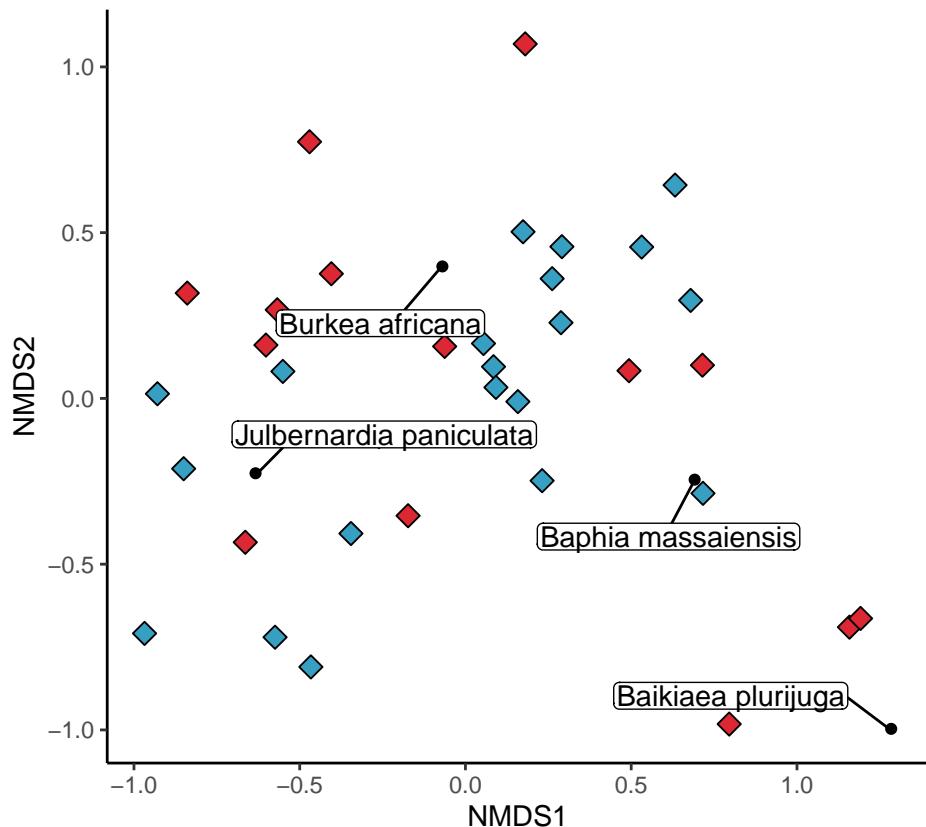


Figure 6. NMDS ordination of species composition of 20x50 m (0.1 ha) plots showing plot scores as coloured diamonds located in disturbed (blue) and undisturbed (red) areas of woodland in Bicuar National Park.

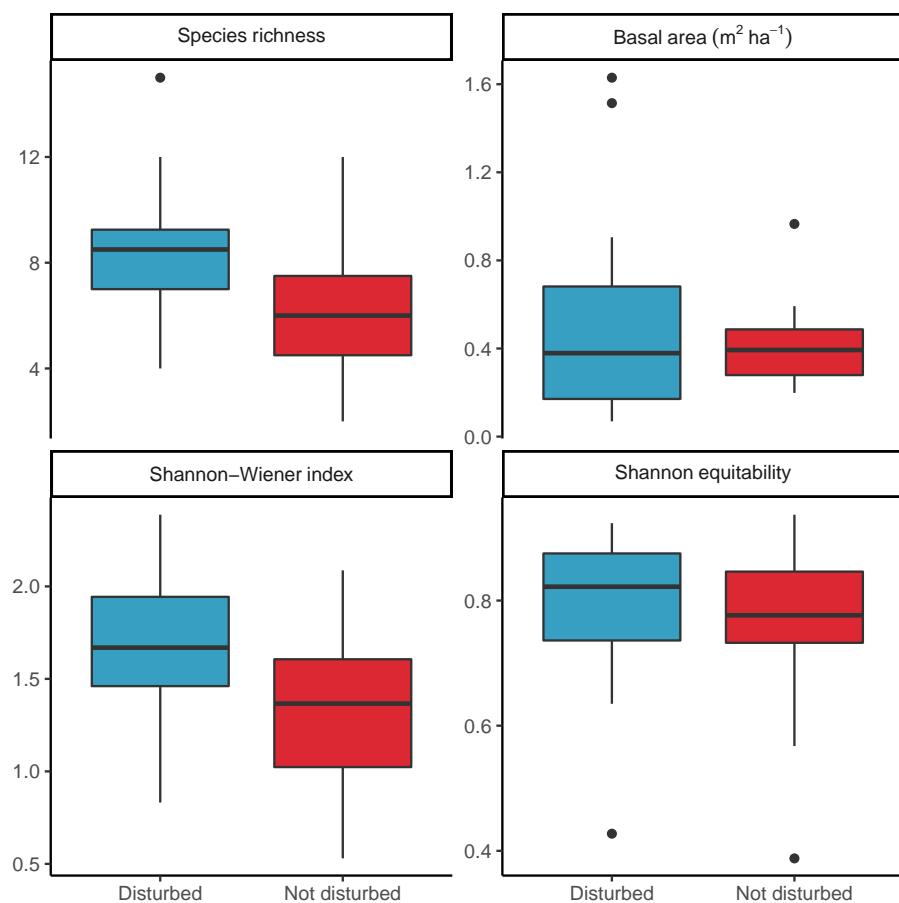


Figure 7. The variation in diversity and woodland structure between disturbed and undisturbed 20x50 m (0.1 ha) plots in Bicuar National Park. Boxes bound the 1st and 3rd quartiles, with the median within the box. Whiskers represent 1.5 times the interquartile range plus or minus the 1st and 3rd quartiles,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

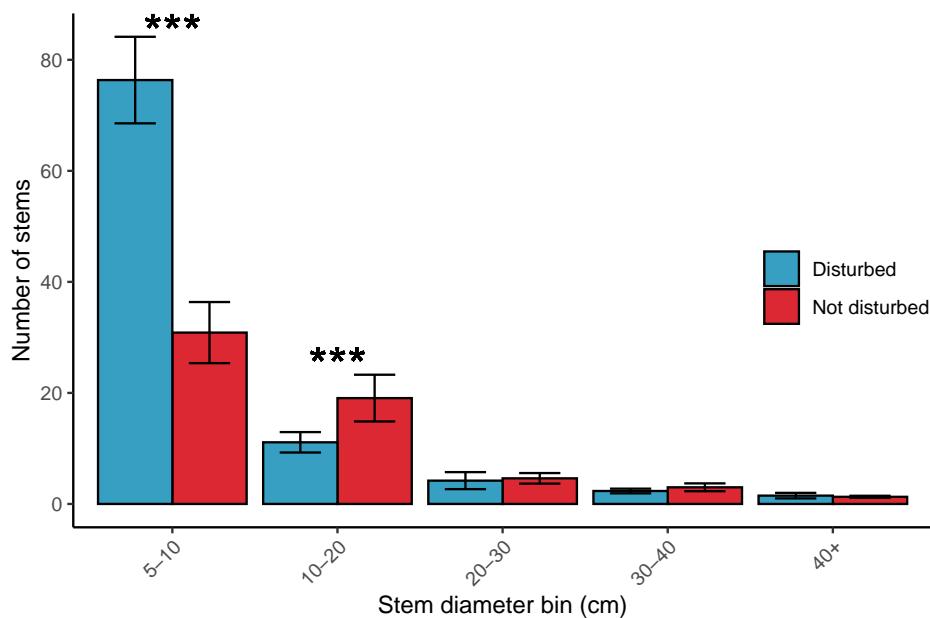


Figure 8. Ranked variation between disturbed and undisturbed plots in stem number, with bars according to stem diameter class. Error bars are the mean \pm 1 standard error. Asterisks above pairs of bars refer to the p-values of Poisson general linear models which tested whether disturbed and undisturbed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

268 4. Discussion

269 4.1. Comparison of Bicuar National Park with other woodlands across the miombo ecoregion

270 We compared the tree species diversity and woodland structure of arid woodlands in Bicuar
 271 National Park in southwest Angola with three other woodland sites across the miombo ecoregion. Our
 272 results show that Bicuar National Park is distinct in both woodland structure and species composition
 273 from these other woodlands. Notably, plots in Bicuar National Park contained 27 tree species which did
 274 not occur at other sites. This lends support for the Huíla Plateau as an important area for conservation
 275 of southern African woodland landscapes. The woodlands in Bicuar National Park were of low tree
 276 basal area, with few large trees except in plots dominated by *Baikiaea plurijuga*. Many other studies
 277 have drawn a relationship between water availability and basal area [45,46], and our study supports
 278 this, with Bicuar National Park being the most arid of the four sites considered in our study. The
 279 NMDS of species composition also suggests that plots in Bicuar National Park are influenced by aridity.
 280 While there are more arid woodlands within southern Africa, with Mopane woodlands for example
 281 often being particularly dry, these plots in Bicuar National park represent particularly dry miombo
 282 woodlands.

283 4.2. Delineation of woodland types within Bicuar National Park

284 Within Bicuar National Park, three distinct woodland types were identified. The first, dominated
 285 by *Baikiaea plurijuga* and *Baphia massaiensis* represents the Baikiaea woodland type commonly found
 286 to the south of the miombo ecoregion [47]. This is supported by Chisingui *et al.* [22] who also found
 287 Baikiaea woodlands as a distinct woodland type in the Park. *B. plurijuga* has been identified as an
 288 important species for conservation, being attractive for selective logging due to its large stature [48,49].
 289 The woodlands created by *B. plurijuga* are also an important habitat for elephants (*Loxodonta africana*)
 290 [50,51], with Bicuar National Park and Mupa National Park being key refugia for this animal in the
 291 Huíla plateau region. The second woodland type, dominated by *Brachystegia tamarindoides* and *Ochna*

292 *pulchra* represents a form of small stature woodland with a shrubby understorey and sparse canopy
293 trees, which commonly occurs as a result of repeated disturbance by fire, or poor soil structure [52].
294 The remaining plots resemble the more archetypical miombo woodland with *Jubbernardia paniculata*,
295 though with a number of species not seen in plots further to the east in the miombo ecoregion such as
296 *Strychnos pungens*. This mosaic of woodland types makes Bicuar National Park a valuable reservoir of
297 diversity and strengthens the case for the Park being a key conservation asset within the Huíla plateau
298 and the larger southern African region. While there are regional boundaries between Baikiaeae and
299 miombo woodlands [1], within Bicuar National Park it is likely that the mosaic of woodland types has
300 been created by a combination of soil water capacity and disturbance history. Bicuar has a distinct
301 landscape of wide shallow grassy valleys surrounded by woodland on higher ground (Figure 2). On
302 some of these high points the soil is particularly sandy, resembling the Kalahari sand soils found
303 further east and south [19], and these areas coincide with the presence of Baikiaeae woodlands [5].
304 High levels of disturbance by fire in these Baikiaeae patches may additionally prevent a transition to an
305 alternative woodland type via the control of sapling growth.

306 4.3. Comparison of disturbed and undisturbed woodland plots

307 Previously disturbed woodlands around the edge of Bicuar National Park were found to share
308 many species with undisturbed plots in the Park, but with some additional species which did not
309 occur in the undisturbed plots. They also lacked notable archetypical miombo species which tend to
310 form larger canopy trees such as *Brachystegia spiciformis* and contained very few *Jubbernardia paniculata*,
311 leading to a distinct woodland composition. The species diversity of these disturbed patches was
312 higher on average than was found in the undisturbed plots, a result which has been corroborated by
313 other studies in miombo woodlands [53–55]. Other studies have shown a peak in species richness
314 during woodland regrowth as pioneer species take advantage of a low competition environment, while
315 some later stage woodland species remain as residuals that survived the original disturbance [29,56].
316 Gonçalves *et al.* [29] particularly, notes the dominance of *Pericopsis angolensis* and *Combretum* spp. as
317 light-demanding pioneer species, which were found to be abundant in the disturbed plots here. This
318 suggests that reclamation of previously farmed and abandoned land for landscape conservation in this
319 ecological context is a valuable management strategy.

320 In disturbed plots near the edge of the Park, there was a lack of species which tend to grow to large
321 canopy trees, possibly due to them being repeatedly felled for timber prior to reclamation by the Park,
322 or due to them being unable to recruit into a more open, shrubby woodland. Despite this lack of canopy
323 forming tree species, some disturbed plots had a greater basal area than undisturbed plots, possibly
324 due to high levels of coppicing in these plots. Indeed, mean stem density was higher in undisturbed
325 plots. This can lead to species that would otherwise remain small producing a much larger basal area
326 as they grow multiple stems under high disturbance conditions [57]. The most common species in the
327 disturbed plots were *Combretum psidioides*, *Combretum collinum* and *Terminalia sericea*, members of the
328 Combretaceae family, all of which more commonly remain as smaller multi-stemmed trees in disturbed
329 woodlands, rather than growing to larger canopy trees [58]. This result could be considered at odds
330 with other studies which report lower woody biomass in plots that have experienced harvesting (e.g.
331 Muvengwi *et al.* [59]). It is important to consider however that our study took place in plots that were
332 measured after farming had been abandoned for at least 7 years, with time for regeneration to occur.
333 It is possible that over time tree basal area will decrease as coppiced shrubby trees are replaced by
334 core miombo species in the transition back to miombo woodland [29]. Bicuar National Park offers
335 a valuable case study to track woodland regeneration in real-time over the next decade in these
336 previously farmed and now protected woodland plots, which could improve our understanding of
337 this potential post-disturbance peak in basal area.

338 In conclusion, the woodlands of Bicuar National Park represent an important woodland refuge
339 at the far western extent of the miombo ecoregion. These woodlands, both those disturbed by
340 previous farming activity and those which remain undisturbed, possess a number of species not found

341 commonly in other miombo woodland plots around the region. They may also house important genetic
342 variation for widespread species, representing populations adapted to more arid conditions. Our study
343 highlights the variation in species composition across the miombo ecoregion and underlines the need
344 for studies which incorporate plot data from multiple locations to reach generalisable conclusions
345 about the region as a whole. Additionally, the installation of 15 one hectare woodland monitoring
346 plots and a further twenty 20x50 m plots in previously farmed and now protected land offer a valuable
347 natural laboratory to further explore the dynamics of dry miombo woodlands of the Huíla plateau.
348 Bicuar National Park should be considered a key conservation asset within the Huíla plateau and
349 within the miombo ecoregion as a whole, as a successfully protected example of an arid woodland
350 mosaic.

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

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367 publish the results.

368 Abbreviations

369 The following abbreviations are used in this manuscript:

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

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

```

373
374 1 ##' @author Casey M. Ryan
375 2 ##' @return d130, the estimated diameter at a POM of 1.3 m (in cm).
376 3 ##' @param d_in the diameter measured at the POM (in cm)
377 4 ##' @param POM the height of the POM (in m)
378 5 ##' @details The adjustment based on tree taper model developed as part of
379 6 ##' the ACES project (Abrupt Changes in Ecosystem Services
380 7 ##' https://miomboaces.wordpress.com/), using data from the miombo of Niassa.
381 8 ##' The model is a cubic polynomial, with three equations for different sized stems.
382 9 ##' @section Warning: POMs >1.7 m are not adjusted.
383 10 POMadj <- function(d_in, POM) {
384 11   stopifnot(is.numeric(d_in),
385 12     is.numeric(POM),
386 13     POM >= 0,
387 14     sum(is.na(POM))==0,
388 15     length(POM) == length(d_in))
389 16   if (any(POM > 1.7))
390 17     warning("POMs >1.7 m are outside the calibration data, no correction applied")
391 18   NAS <- is.na(d_in)
392 19   d_in_clean <- d_in[!NAS]
393 20   POM_clean <- POM[!NAS]
394 21   # define the size class edges:
395 22   edges <- c(5.0, 15.8, 26.6, 37.4)
396 23   sm <- d_in_clean < edges[2]
397 24   med <- d_in_clean >= edges[2] & d_in_clean < edges[3]
398 25   lg <- d_in_clean >= edges[3]
399 26
400 27   # compute predictions for delta_d, for all size classes
401 28   delta_d <- data.frame(
402 29     # if small:
403 30     small = 3.4678+-5.2428 *
404 31     POM_clean + 2.9401 *
405 32     POM_clean^2+-0.7141 *
406 33     POM_clean^3,
407 34     # if med
408 35     med = 4.918+-8.819 *
409 36     POM_clean + 6.367 *
410 37     POM_clean^2+-1.871 *
411 38     POM_clean^3,
412 39     # if large
413 40     large = 9.474+-18.257 *
414 41     POM_clean + 12.873 *
415 42     POM_clean^2+-3.325 *
416 43     POM_clean^3
417 44   )
418 45   # index into the right size class
419 46   dd <- NA_real_
420 47   dd[sm] <- delta_d$small[sm]
421 48   dd[med] <- delta_d$med[med]
422 49   dd[lg] <- delta_d$large[lg]
423 50   dd[POM_clean > 1.7] <- 0 # to avoid extrapolation mess
424 51
425 52   # add NAs back in
426 53   d130 <- NA
427 54   d130[NAS] <- NA
428 55   d130[!NAS] <- d_in_clean - dd
429 56
430 57   if (any(d130[!NAS] < 0))
431 58     warning("Negative d130 estimated, replaced with NA")
432 59   d130[d130 <= 0 & !is.na(d130)] <- NA
433 60   return(d130)
434 61 }

```

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