

Article

Diversity and structure of an arid woodland at the western edge of the miombo ecoregion, southwest Angola

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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 conducted a plot-based study in Bicuar National Park, southwest Angola, comparing tree species composition and woodland structure with similar plots in Tanzania, Mozambique, and the Democratic Republic of Congo. We found plots in Bicuar National Park had comparatively low tree species diversity, but contained 28 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 plots in areas previously disturbed by shifting-cultivation agriculture, we found species diversity was marginally higher in disturbed plots. Our study supports that Bicuar National Park and the woodlands of the Huíla plateau should be a conservation priority, representing a unique woodland mosaic with an uncommon mixture of woodland types within a small area.

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* and *Jubbernardia* genera, both within the Fabaceae family, subfamily Detarioideae [4–6]. These genera are seldom found outside miombo woodlands, while their contribution to the biomass of miombo woodlands 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 physical woodland structure [7–9].

Southern African woodlands are structurally complex but species poor in the tree layer compared to dry tropical forests which exist at similar latitudes [10,11]. These woodlands contain many endemic

28 tree species however, and support a highly diverse woodland understorey, with an estimated 8500
29 species of vascular plants [12]. Miombo woodlands are a conservation priority, especially considering
30 their importance for ecosystem service provision for an estimated 150 million people [13]. Additionally
31 miombo woodlands hold ~18-24 Pg C in woody biomass and soil organic carbon, which is comparable
32 to that held in the rainforests of the Congo basin (~30 Pg C) [14]. Despite their importance, dry tropical
33 woodlands remain understudied compared to wet forests across the globe [15].

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

46 The miombo woodlands of southwest Angola are found in their most intact form in Bicuar
47 National Park and to a lesser extent in the adjacent Mupa National Park, on the Huíla plateau [19].
48 Both of these national parks have been protected to varying extents since 1938 [16]. These woodlands
49 exist in much drier conditions than other miombo woodlands, precipitation diminishes rapidly within
50 the Huíla plateau towards the Angolan coast and the Namib desert (Figure 1a). The vegetation of the
51 Huíla plateau holds many endemic species, around 83 endemic Fabaceae species [20] and the most
52 endemic plant species of any part of Angola [21]. Linder [22] and Droissart *et al.* [23] both identify the
53 western portion of the Huíla plateau as a centre of tropical African endemism.

54 Much of the historic miombo woodland area in southwest Angola surrounding the Bicuar and
55 Mupa National Parks has been deforested in recent years, with a clear increase in deforestation activity
56 since the end of the civil war owing to an increase in rural population and agricultural activity [16,24].
57 The western extent of miombo woodlands found within Bicuar National Park plateau are therefore of
58 great importance for conservation as a refuge for wildlife and endemic plant species [16].

59 It is important to focus not only on the biodiversity of undisturbed woodland areas but also
60 previously disturbed land in order to properly assess the biodiversity and woodland structure of the
61 Park. Woodland disturbance through shifting cultivation practices produces novel habitats which
62 are not necessarily of lower conservation value [25,26]. Since Bicuar National Park's rejuvenation
63 following the reinforcement of park boundaries after the civil war, many areas of woodland that were
64 previously heavily grazed, farmed via shifting cultivation techniques, and used for timber extraction
65 have been allowed to re-establish and are now protected from further human resource extraction. This
66 presents a unique opportunity to compare the species composition of these disturbed areas with areas
67 of nearby woodland that have not been farmed in living memory.

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

75 2. Materials and Methods

76 2.1. Study area

77 The miombo ecoregion spans 11 countries in sub-Saharan Africa, extending across the continent
78 in a wide band that reaches north into Kenya and the Democratic Republic of Congo (DRC) and south
79 into the northeast of South Africa ([Figure 1a](#)). Miombo woodlands are defined both by their tree
80 diversity and by their structure. In archetypical miombo woodlands, species of the genera *Brachystegia*
81 and *Jubbernardia* generally hold the most biomass, forming a sparse woodland canopy. Distinct from
82 dry tropical forests, miombo woodlands generally maintain a grassy understorey dominated by C4
83 grasses [27]. Miombo woodlands are heavily structured by seasonal fire and herbivory, which often
84 prevent the creation of a closed tree canopy which would naturally occur in the absence of these
85 disturbances [28,29]. Within the miombo ecoregion, other woodland types exist, notably, woodlands
86 dominated by *Baikiaea* spp. or *Colophospermum mopane* [5].

87 We chose three areas of miombo woodland across the region to compare with those in Bicuar
88 National Park, Angola ($S15.1^\circ$, $E14.8^\circ$). The three sites were Gorongosa National Park in central
89 Mozambique ($S19.0^\circ$, $E34.2^\circ$) [30], Kilwa District in southern Tanzania ($S9.0^\circ$, $E39.0^\circ$) [31], and the
90 Mikembo Natural Reserve in Katanga, southern Democratic Republic of Congo (DRC) ($S11.5^\circ$, $E27.7^\circ$)
91 [32]. Within each of these woodland sites, multiple one hectare square plots had been installed
92 previously to monitor biodiversity and biomass dynamics. We used these previous censuses, collected
93 between 2012 and 2019, to estimate tree biodiversity and woodland structure. Sites range in Mean
94 Annual Precipitation (MAP) from 864 mm y^{-1} in Bicuar to 1115 mm y^{-1} in Katanga. Mean Annual
95 Temperature ranges from $\sim 20.5^\circ\text{C}$ in Bicuar and Katanga to $\sim 25.8^\circ\text{C}$ in Kilwa ([Figure 1b](#)).

96 Bicuar National Park covers an area of $\sim 7900\text{ km}^2$, established as a hunting reserve in 1938,
97 and later as a national park in 1964 ([Figure 2](#)). While fauna populations in the Park were severely
98 damaged by the Angolan civil war, the interior of the Park remains as a largely intact mosaic of miombo
99 woodland, Baikiaea-Burkea woodland, shrub/thicket vegetation and seasonally flooded grassland.
100 Encroachment of agriculture and grazing, particularly along the northwest and western boundaries of
101 the Park, has led to a fragmented park boundary with patches of diminished thicket and woodland in
102 areas of previously farmed land that have been protected since park boundaries were re-established
103 following the end of the civil war.

104 2.2. Plot data collection

105 We sampled 15 one hectare plots in Bicuar National Park and a total of 64 plots across the miombo
106 ecoregion across four sites. [Figure 1a](#) and [Table 1](#) show the locations and general description of each
107 site, respectively. Plots in Bicuar were situated at least 500 m from the edge of a woodland patch to
108 prevent edge effects which may have altered tree species composition.

109 Within each plot, every tree stem $\geq 5\text{ cm}$ stem diameter was recorded. For each tree stem the
110 species and stem diameter were recorded. Tree species were identified using local botanists at each site
111 and taxonomy was later checked against the African Plant Database [33]. In all sites Palgrave [34] and
112 various other texts were used as a guide for species identification in the field. Specimens that could not
113 be identified in the field, or subsequently at herbaria, were described as morphospecies. All species
114 in Bicuar National Park were identified. Tree coppicing due to fire, herbivory, and human actions
115 is common in miombo woodlands, therefore, for trees with multiple stems, each stem $\geq 5\text{ cm}$ stem
116 diameter was recorded, while the parent tree was also recorded for diversity analyses described below.

117 Stem diameter was recorded at 1.3 m from the ground along the stem as per convention using
118 a diameter tape measure. Where stem abnormalities were present at 1.3 m from the ground, which
119 precluded the accurate estimation of stem diameter at 1.3 m, the stem diameter was recorded at the
120 nearest 10 cm increment above 1.3 m without significant stem abnormalities [35]. To ensure consistency
121 among stem diameter values recorded at different heights, when the stem diameter was recorded at a

height other than 1.3 m the stem diameter at 1.3 m was estimated from the recorded stem diameter using a cubic polynomial equation which adjusts for tree stem taper. This equation was calibrated on 100 stems measured at multiple heights in Niassa Province, Mozambique (Appendix A). Stems below 10 cm stem diameter were not measured in the DRC plots. We therefore estimated the number of 5-10 cm stems from the average proportion of 5-10 cm stems in all other plots. We first assured that there was not a significant difference among the three other sites in the proportion of total stems in the 5-10 cm size class, using an ANOVA ($F(2,49) = 1.93, p = 0.16$).

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

2.3. Climatic data

The WorldClim dataset [36] was used to gather data on plot-level climatic conditions. We estimated Mean Annual Precipitation (MAP) as the mean of total annual precipitation values between 1970 and 2000, and Mean Annual Temperature (MAT) as the mean of mean annual temperatures between 1970 and 2000. The seasonality of temperature was calculated as the standard deviation of monthly temperature per year, respectively. We estimated Climatic Water Deficit (CWD) for each plot according to [37], as the sum of the difference between monthly rainfall and monthly evapotranspiration when the difference is negative, using the dataset available at http://ups-tlse.fr/pantropical_allometry.htm, which uses data from the WorldClim dataset 1970-2000.

2.4. Data analysis

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

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

Where D is the estimated stem diameter at 1.3 m having accounted for tree taper. We then calculated the total basal area of each plot as the sum of each stem's basal area. For the DRC plots which lacked 5-10 cm stems, we estimated basal area in this stem diameter class from the mean proportional basal area of 5-10 cm stems in all other plots. Similar to our estimation of stem DBH in the DRC plots, we first assured that there was not a significant difference among the other three sites in the proportion of total basal area in the 5-10 cm class using an ANOVA ($F(2,49) = 1.45, p = 0.24$).

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 [38]. We calculated the pairwise beta diversity among sites using the Sørensen coefficient (S_S) [39]. 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 ($E_{H'}$) [40] 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 [41]. We fit plot-level estimates of MAP, MAT, the seasonality of MAT and CWD to the first two axes of the resulting ordination to investigate how these environmental factors influenced the grouping of species composition among plots. All analyses were conducted in R version 3.6.1 [42].

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. 27 tree species were found in Bicuar National Park which were not found in the other miombo woodland plots (Table 3). The most common of these unique species were *Brachystegia 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 1.62 ± 0.135 . 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 ($H' = 2.67 \pm 0.186$, $p < 0.01$), Mozambique ($H' = 2.41 \pm 0.197$, $p < 0.01$) and Tanzania ($H' = 2.22 \pm 0.112$, $p < 0.05$). 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.

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. 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 significantly influenced the grouping of plots (Figure 4). 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 drove much of the difference between plots in Bicuar National Park versus those in Tanzania and Mozambique.

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 2). Similar to the NMDS, these results show that plots in Bicuar National Park are most similar to those found in DRC.

211 3.3. Woodland structure

212 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
213 $8.53 \text{ m}^2 \text{ ha}^{-1}$ ([Figure 3](#)). An ANOVA showed a significant difference in basal area among sites ($F(3,60)$
214 = 48.04, $p < 0.01$), and a post-hoc Tukey's test showed that basal area in Bicuar National Park was
215 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
216 differences between Bicuar and Mozambique ($\text{BA} = 3.43 \pm 0.409 \text{ m}^2 \text{ ha}^{-1}$, $p = 0.43$) or Tanzania (BA
217 = $2.06 \pm 0.253 \text{ m}^2 \text{ ha}^{-1}$, $p = 0.26$) ([Figure 3](#)). Additionally, Bicuar plots had less variation in basal area
218 among plots than other sites. Plots in Bicuar with the highest basal area were dominated by *Baikiaea*
219 *plurijuga* and *Baphia massaiensis* (Plots 9, 13, and 15).

220 The stem diameter abundance distribution in Bicuar National Park was comparable with other
221 sites ([Figure 5](#)), albeit with fewer stems in each class. The slope of log mean stem size distribution
222 among diameter bins was -0.92 ± 0.067 in Bicuar National Park, -1.07 ± 0.044 in DRC, -0.89 ± 0.065 in
223 Tanzania, and -0.87 ± 0.075 in Mozambique.

224 3.4. Effect of disturbance via shifting cultivation on diversity within Bicuar National Park

225 There was a clear difference in the species composition of previously farmed disturbed woodland
226 plots and undisturbed woodland plots, but with some overlap ([Figure 7](#)). Notably, Plots 4 and 7 in
227 putatively undisturbed woodland have a species composition more resembling the disturbed plots.
228 These two plots were dominated by *Brachystegia tamarindoides* and *Burkea africana*, with *B. africana* being
229 a species which occurred frequently as a pioneer in the disturbed plots. The undisturbed plots 15, 13,
230 and 9 represent distinct outliers in the NMDS. These three plots were dominated by *Baikiaea plurijuga*
231 which was not encountered in the disturbed plots. The most common species in the disturbed plots
232 was *Baphia massaiensis* ($n = 158$), with a mean stem diameter of $6.1 \pm 1.87 \text{ cm}$, while in the undisturbed
233 plots the most common species was *Julbernardia paniculata* ($n = 182$), with a mean stem diameter of
234 $11.8 \pm 7.24 \text{ cm}$. Mean alpha diversity was marginally higher in disturbed plots ($H' = 1.68 \pm 0.082$) than
235 in undisturbed plots ($H' = 1.31 \pm 0.119$) and an ANOVA showed that there was a significant difference
236 in H' between the two plot types ($F(1,33) = 7.04$, $p < 0.05$). Mean plot species richness was also lower
237 in undisturbed plots (6.2 ± 0.691) than disturbed plots (8.65 ± 0.534). Mean $E_{H'}$ was 0.79 ± 0.027 in
238 disturbed plots and 0.76 ± 0.037 undisturbed plots but there was no significant difference between
239 disturbed and undisturbed plots according to an ANOVA ($F(1,33) = 0.62$, $p = 0.44$). 13 species were
240 found only in the disturbed plots and not in the undisturbed plots. The most common of these were
241 *Combretum celastroides* ($n = 30$), *Acacia reficiens* ($n = 14$), and *Gardenia ternifolia* ($n = 11$). 8 were found
242 only in undisturbed plots, the most common being *Brachystegia spiciformis* ($n = 53$), *Baikiaea plurijuga* (n
243 = 18) and *Combretum apiculatum* ($n = 13$). Mean basal area was higher in undisturbed plots (0.42 ± 0.051
244 $\text{m}^2 \text{ ha}^{-1}$) than disturbed plots ($0.51 \pm 0.098 \text{ m}^2 \text{ ha}^{-1}$).

245 3.5. Figures and Tables

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
Angola	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

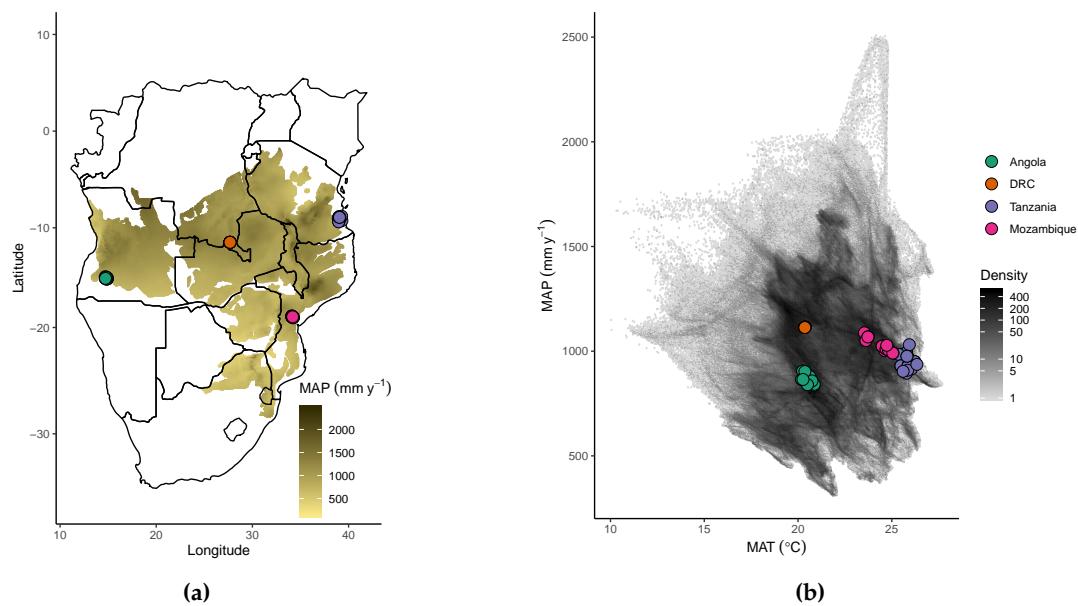


Figure 1. Locations of plots used in this study, by (a) geographic location with respect to the distribution of miombo woodland vegetation (shaded brown according to mean annual precipitation) [1], and (b) showing the plot locations compared to the climate space of the miombo ecoregion estimated using the WorldClim dataset over the Miombo woodland vegetation extent with a pixel size of 30 arc seconds (0.86 km² at the equator) [36]. Note that the density colour scale is log-transformed for visual clarity.

Table 2. 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 brackets are the number of species unique to each site in each comparison.

Site 1	Site 2	S_S	Shared species
Angola(34)	DRC(74)	20.6	14
Angola(34)	Tanzania(147)	13.4	14
Angola(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

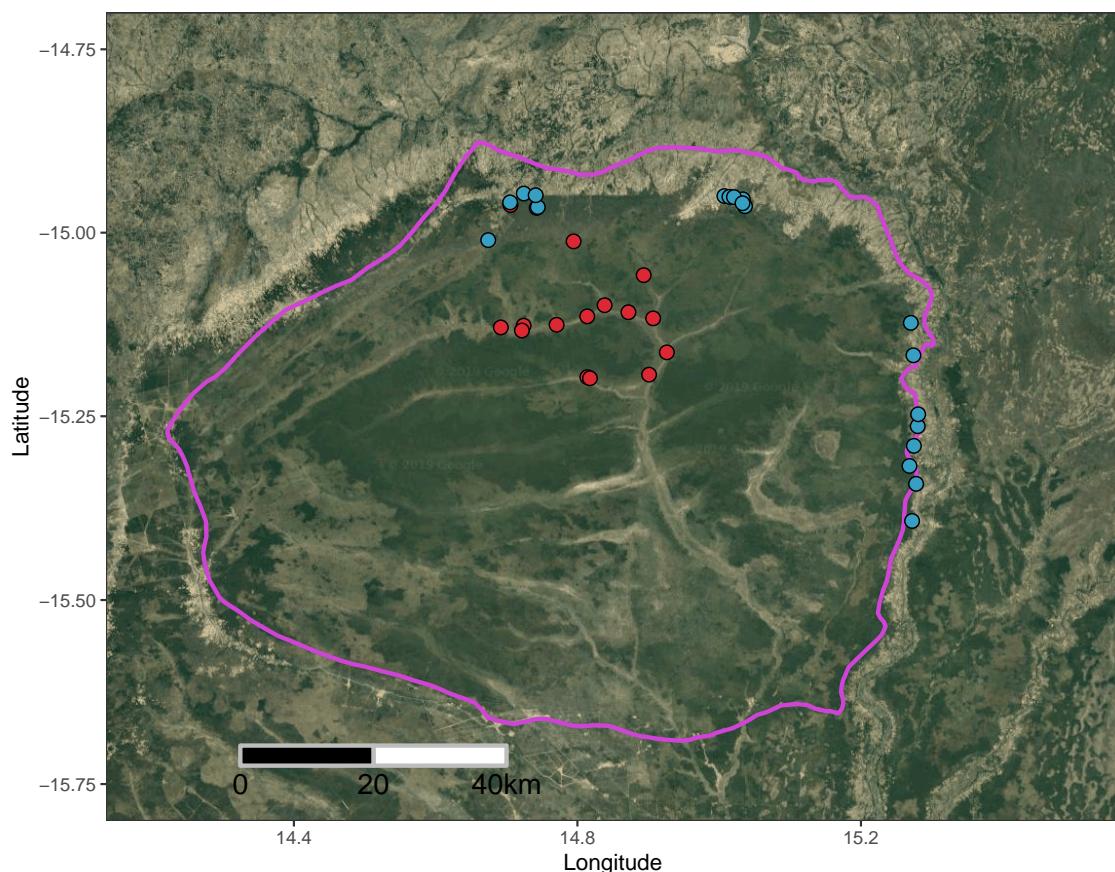


Figure 2. Location of plots in Bicuar National Park, southwest Angola. The Park boundary is shown as a pink outline, according to UNEP-WCMC and IUCN [43]. One hectare undisturbed plots are shown as red points, while disturbed 20x50 m (0.1 hectare) plots are shown as blue points. The map background is a true colour composite satellite image generated using the Google Maps Static Maps API in the `ggmap` R package [44].

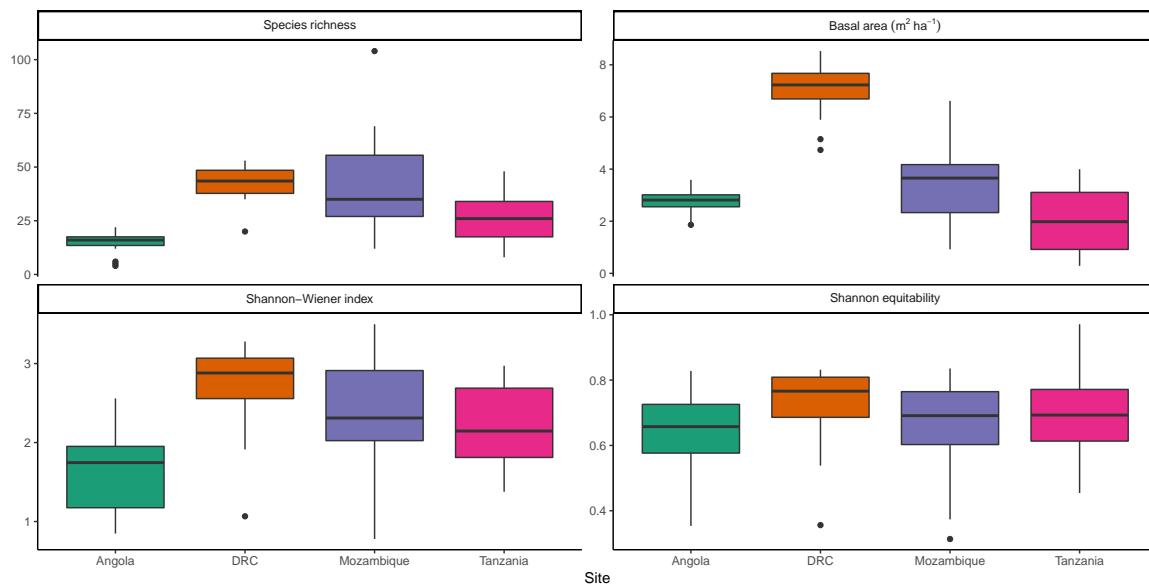


Figure 3. Variation of alpha diversity estimates and basal area among sites. Boxes bound the 1st and 3rd quartiles, with the median within the box. Whiskers represent 1.5 times the interquartile range plus or minus the 1st and 3rd quartiles, respectively. Values found beyond the whiskers are shown individually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

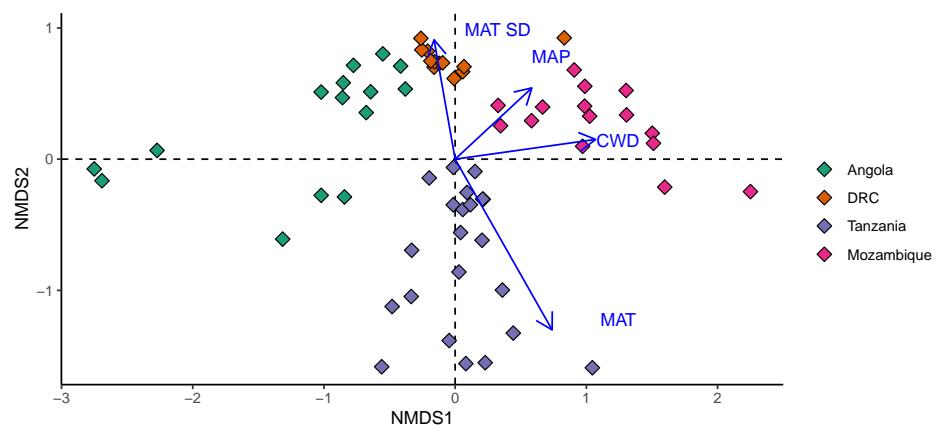


Figure 4. Environmental factors fitted to the first two axes of the NMDS ordination of species composition of one hectare plots, showing the variation in plot species composition within and among sites. Diamonds are plot scores coloured by site. The lengths of arrows indicating environmental factor fits are scaled by R^2 . Arrows point in the direction of increasing values of that environmental factor.

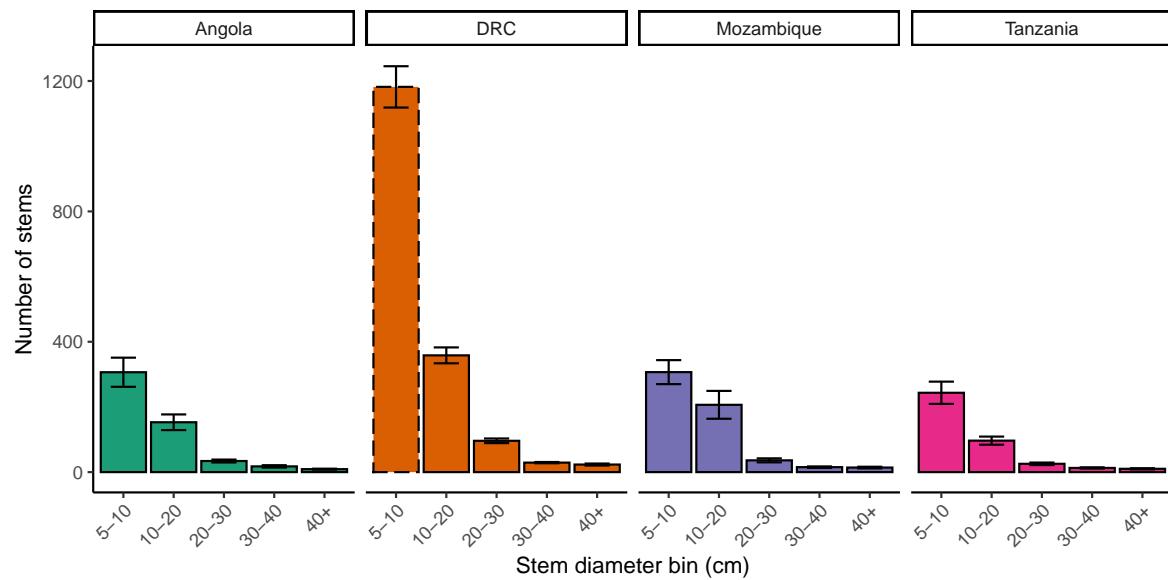


Figure 5. Ranked variation between plots in stem number within each site, with bars stacked according to stem diameter class. Error bars are the mean \pm 1 standard error. The dashed bar for the DRC 5-10 cm stem diameter class indicates that these measurements were estimated from the average proportion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

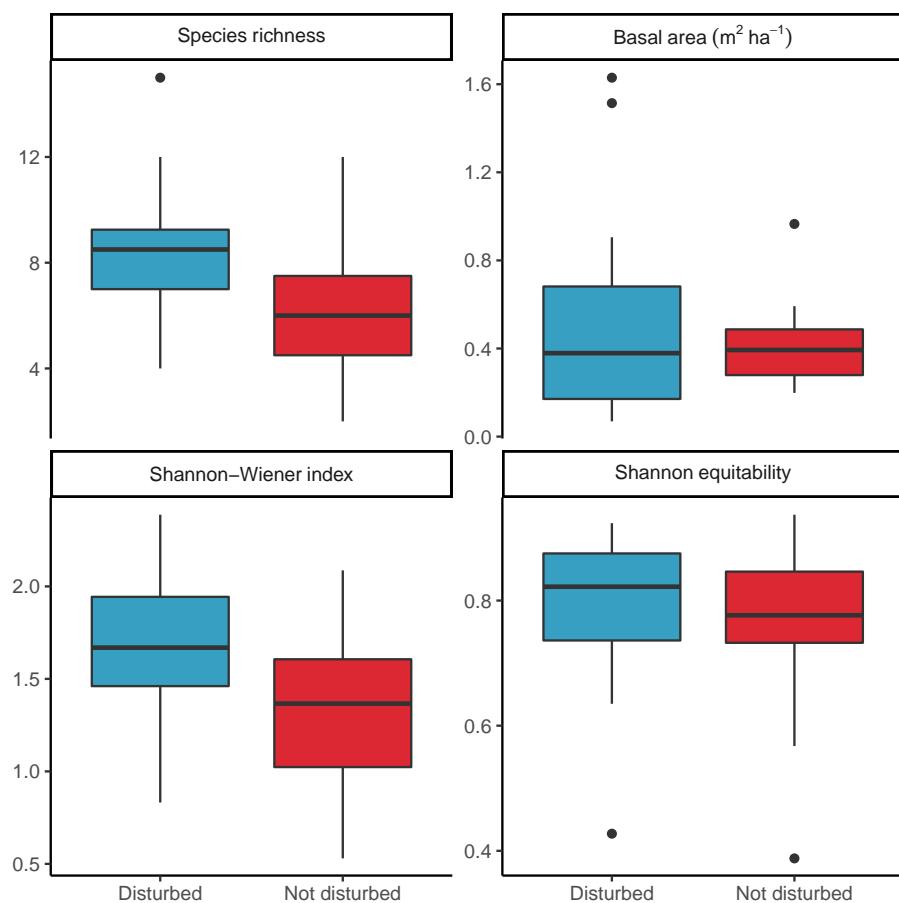


Figure 6. The variation in diversity and woodland structure between disturbed and undisturbed 20x50 m (0.1 ha) plots in Bicuar National Park. Boxes bound the 1st and 3rd quartiles, with the median within the box. Whiskers represent 1.5 times the interquartile range plus or minus the 1st and 3rd quartiles, respectively. Values found beyond the whiskers are shown individually as points.

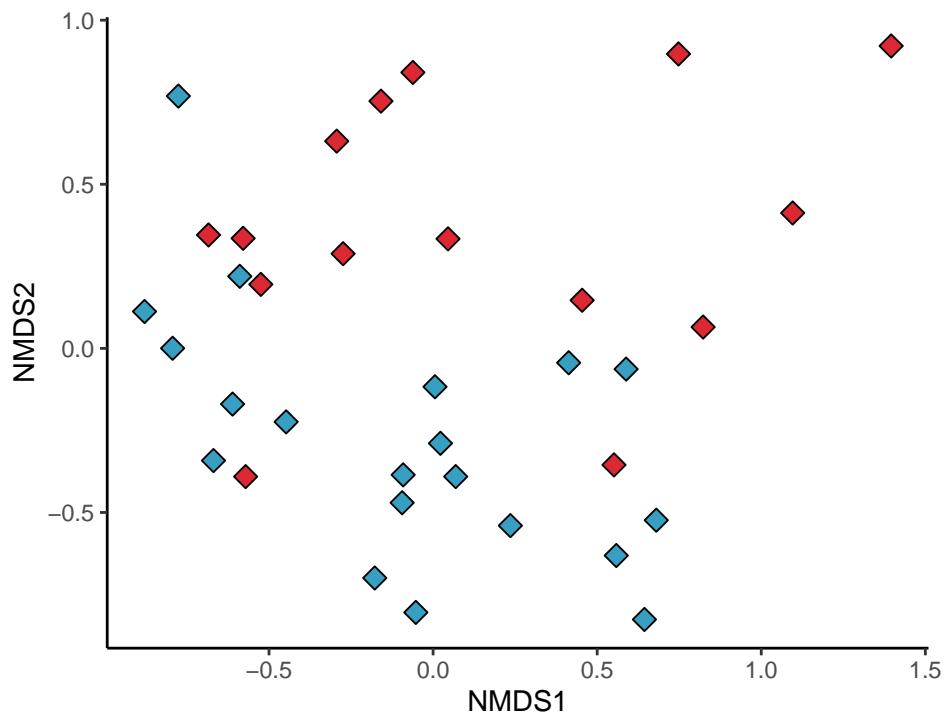


Figure 7. NMDS ordination of species composition of 20x50 m (0.1 ha) plots showing plot scores as coloured diamonds located in disturbed (blue) and undisturbed (red) areas of woodland in Bicuar National Park.

246 4. Discussion

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

260 Within Bicuar National Park, three distinct woodland types were identified. The first, dominated
 261 by *Baikiaea plurijuga* and *Baphia massaiensis* represents the Baikiaea woodland type commonly found to
 262 the south of the miombo ecoregion [47]. This is supported by Chisingui *et al.* [19] which also found
 263 Baikiaea woodlands as a distinct woodland type in the Park. *B. plurijuga* has been identified as an
 264 important species for conservation, being attractive for selective logging due to its large stature [48,49].

Table 3. Species found in one hectare plots in Bicuar National Park. Stem diameter and basal area are the mean of all stems with the standard error of the mean in brackets. Number of stems per hectare is mean of the number of stems in all one hectare plots where stems of that species are present with the standard error of the mean in brackets. 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)

The woodlands created by *B. plurijuga* are also an important habitat for elephants (*Loxodonta africana*) [50,51], with Bicuar National Park and Mupa National Park being key refugia for this animal in the Huíla plateau region. The second woodland type, dominated by *Brachystegia tamarindoides* and *Ochna pulchra* represents a form of small stature woodland with a shrubby understorey and sparse canopy trees, which commonly occurs as a result of repeated disturbance by fire, or poor soil structure [52]. The remaining plots resemble the more archetypical miombo woodland with *Julbernardia paniculata*, though with a number of species not seen in plots further to the east of the miombo ecoregion such as *Strychnos pungens*. This mosaic of woodland types makes Bicuar National Park a valuable reservoir of diversity and strengthens the case for the Park being a key conservation asset within the Huíla plateau and the larger southern African region. While there are regional boundaries between Baikiaeae and miombo woodlands [1], within Bicuar National Park it is likely that mosaic of woodland types has been created by a combination of soil water capacity and disturbance history. Bicuar has a distinct landscape of wide shallow grassy valleys surrounded by woodland on higher ground (Figure 2). On some of these high points the soil is particularly sandy, resembling the Kalahari sand soils found further east and south [16], and these areas coincide with the presence of Baikiaeae woodlands [5]. High levels of disturbance by fire in these Baikiaeae patches may additionally prevent a transition to an alternative woodland type via the control of sapling growth.

Previously disturbed woodlands around the edge of Bicuar National Park were found to share many species with undisturbed plots in the Park, but with some additional species which did not occur in the undisturbed plots. They also lacked notable archetypical miombo species which tend to form larger canopy trees such as *Brachystegia spiciformis* and contained very few *Julbernardia paniculata*, leading to a distinct woodland composition. The species diversity of these disturbed patches was higher than was found in the undisturbed plots, a result which has been corroborated by other studies in miombo woodlands [53–55]. Other studies have shown a peak in species richness during woodland regrowth as pioneer species take advantage of a low competition environment, while some later stage woodland species remain from before the original disturbance [26,56]. This suggests that reclamation of previously farmed and abandoned land for landscape conservation in this ecological context is a valuable management strategy.

In disturbed plots near the edge of the Park, there was a lack of species which tend to grow to large canopy trees, possibly due to them being repeatedly felled for timber prior to reclamation by the Park, or due to them being unable to recruit into a more open, shrubby woodland. Despite this lack of canopy forming tree species, some disturbed plots had a greater basal area than undisturbed plots, possibly due to high levels of coppicing in these plots. Indeed, stem density was higher in undisturbed plots. This can lead to species that would otherwise remain small producing a much larger basal area as they grow multiple stems under high disturbance conditions [57]. The most common species in the disturbed plots were *Combretum psidoides*, *Combretum collinum* and *Terminalia sericea*, members of the Combretaceae family all of which more commonly remain as smaller multi-stemmed trees in disturbed woodlands, rather than growing to larger canopy trees [58]. This result could be considered at odds with other studies which report lower woody biomass in plots that have experienced harvesting (e.g. Muvengwi *et al.* 59). It is important to consider however that our study took place in plots that were measured after farming had been abandoned for at least 7 years, with time for regeneration to occur. It is possible that over time tree basal area will decrease as coppiced shrubby trees are replaced by core miombo species in the transition back to miombo woodland [26]. Bicuar National Park offers a valuable case study to track woodland regeneration in real-time over the next decade in these previously farmed and now protected woodland plots, which could improve our understanding of this potential post-disturbance peak in basal area.

In conclusion, the woodlands of Bicuar National Park represent an important woodland refugia at the far western extent of the miombo ecoregion. These woodlands, both those disturbed by previous farming activity and those which remain undisturbed, possess a number of species not found commonly in other miombo woodland plots around the region. They may also house important genetic

315 variation for widespread species, representing populations adapted to more arid conditions. Our study
316 highlights the variation in species composition across the miombo ecoregion and underlines the need
317 for studies which incorporate plot data from multiple locations to reach generalisable conclusions
318 about the region as a whole. Additionally, the installation of 15 one hectare woodland monitoring
319 plots and a further twenty 20x50 m plots in previously farmed and now protected land offer a valuable
320 natural laboratory to further explore the dynamics of dry miombo woodlands of the Huíla plateau.
321 Bicuar National Park should be considered a key conservation asset within the Huíla plateau and
322 within the miombo ecoregion, as a whole as a successfully protected example of an arid woodland
323 mosaic.

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341 Abbreviations

342 The following abbreviations are used in this manuscript:

343 MAP	Mean Annual Precipitation
MAT	Mean Annual Temperature
344 NMDS	Non-metric Multidimensional Scaling
DD	Decimal Degrees
ANOVA	Analysis of Variance

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

```

346
347 1 ##' @author Casey M. Ryan
348 2 ##' @return d130, the estimated diameter at a POM of 1.3 m (in cm).
349 3 ##' @param d_in the diameter measured at the POM (in cm)
350 4 ##' @param POM the height of the POM (in m)
351 5 ##' @details The adjustment based on tree taper model developed as part of
352 6 ##' the ACES project (Abrupt Changes in Ecosystem Services
353 7 ##' https://miomboaces.wordpress.com/), using data from the miombo of Niassa.
354 8 ##' The model is a cubic polynomial, with three equations for different sized stems.
355 9 ##' @section Warning: POMs >1.7 m are not adjusted.
356 10 POMadj <- function(d_in, POM) {
357 11   stopifnot(is.numeric(d_in),
358 12     is.numeric(POM),
359 13     POM >= 0,
360 14     sum(is.na(POM))==0,
361 15     length(POM) == length(d_in))
362 16   if (any(POM > 1.7))
363 17     warning("POMs >1.7 m are outside the calibration data, no correction applied")
364 18   NAS <- is.na(d_in)
365 19   d_in_clean <- d_in[!NAS]
366 20   POM_clean <- POM[!NAS]
367 21   # define the size class edges:
368 22   edges <- c(5.0, 15.8, 26.6, 37.4)
369 23   sm <- d_in_clean < edges[2]
370 24   med <- d_in_clean >= edges[2] & d_in_clean < edges[3]
371 25   lg <- d_in_clean >= edges[3]
372 26
373 27   # compute predictions for delta_d, for all size classes
374 28   delta_d <- data.frame(
375 29     # if small:
376 30     small = 3.4678+-5.2428 *
377 31     POM_clean + 2.9401 *
378 32     POM_clean^2+-0.7141 *
379 33     POM_clean^3,
380 34     # if med
381 35     med = 4.918+-8.819 *
382 36     POM_clean + 6.367 *
383 37     POM_clean^2+-1.871 *
384 38     POM_clean^3,
385 39     # if large
386 40     large = 9.474+-18.257 *
387 41     POM_clean + 12.873 *
388 42     POM_clean^2+-3.325 *
389 43     POM_clean^3
390 44   )
391 45   # index into the right size class
392 46   dd <- NA_real_
393 47   dd[sm] <- delta_d$small[sm]
394 48   dd[med] <- delta_d$med[med]
395 49   dd[lg] <- delta_d$large[lg]
396 50   dd[POM_clean > 1.7] <- 0 # to avoid extrapolation mess
397 51
398 52   # add NAs back in
399 53   d130 <- NA
400 54   d130[NAS] <- NA
401 55   d130[!NAS] <- d_in_clean - dd
402 56
403 57   if (any(d130[!NAS] < 0))
404 58     warning("Negative d130 estimated, replaced with NA")
405 59   d130[d130 <= 0 & !is.na(d130)] <- NA
406 60   return(d130)
407 61 }

```

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