

Article

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

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

John L. Godlee¹*, Francisco Maiato Gonçalves², José João Tchamba², Antonio Valter Chisingui², Jonathan Ilunga Muledi³, Mylor Ngoy Shutcha³, Casey M. Ryan¹, Thom K. Brade¹ and Kyle G. Dexter^{1,4}

¹ School of GeoSciences, University of Edinburgh, Edinburgh, United Kingdom

² Herbarium of Lubango, ISCED Huíla, Sarmento Rodrigues Str. No. 2, CP. 230, Lubango, Angola

³ Ecologie, Restauration Ecologique et Paysage, Faculté des Sciences Agronomique, Université de Lubumbashi, Route Kasapa BP 1825, Democratic Republic of Congo

⁴ Royal Botanic Garden Edinburgh, Edinburgh EH3 5LR, United Kingdom

* Correspondence: johngodlee@gmail.com

<http://>

Version March 4, 2020 submitted to Diversity

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 **south-western** 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 Detoroideae [4–6]. These genera are seldom found as dominant species outside

25 miombo woodlands, and while their contribution to the biomass of miombo woodlands is substantial,
26 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*, *Jubaeopsis* 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 south-western extent of miombo
53 woodlands, which is found entirely within Angola has received considerably less attention [19]. Partly
54 this is due to diminished research capacity during the Angolan civil war following the country's
55 independence, which took place officially between 1975 and 2002, but with sporadic localised periods
56 of civil unrest until around 2012 [20]. While botanical surveys of woodlands in this region are more
57 plentiful [19,21], joint studies of woodland species composition and physical structure remain scarce.
58 This is despite the value of these studies in helping to estimate woodland net primary productivity,
59 carbon sequestration potential, and studies of community assembly. To
60 properly understand spatial variation in woodland species composition and physical structure across
61 the miombo ecoregion, it is necessary to fill understudied gaps. In this study we aim to address
62 one such gap in southwest Angola, and place it in context with other woodlands across the miombo
63 ecoregion.

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

72 Much of the historic miombo woodland area in southwest Angola surrounding the Bicuar and
73 Mupa National Parks has been deforested in recent years, with a clear increase in deforestation activity
74 since the end of the civil war owing to an increase in rural population and agricultural activity [19,27].

75 The western extent of miombo woodlands found within Bicuar National Park plateau are therefore of
76 great importance for conservation as a refuge for wildlife and endemic plant species [19].

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 [28,29]. 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 National Park in
98 central Mozambique ($S19.0^{\circ}$, $E34.2^{\circ}$) [30], Kilwa District in southern Tanzania ($S9.0^{\circ}$, $E39.0^{\circ}$) [31], and
99 the Mikembo Natural Reserve in Katanga, southern Democratic Republic of Congo (DRC) ($S11.5^{\circ}$,
100 $E27.7^{\circ}$) [32]. 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).

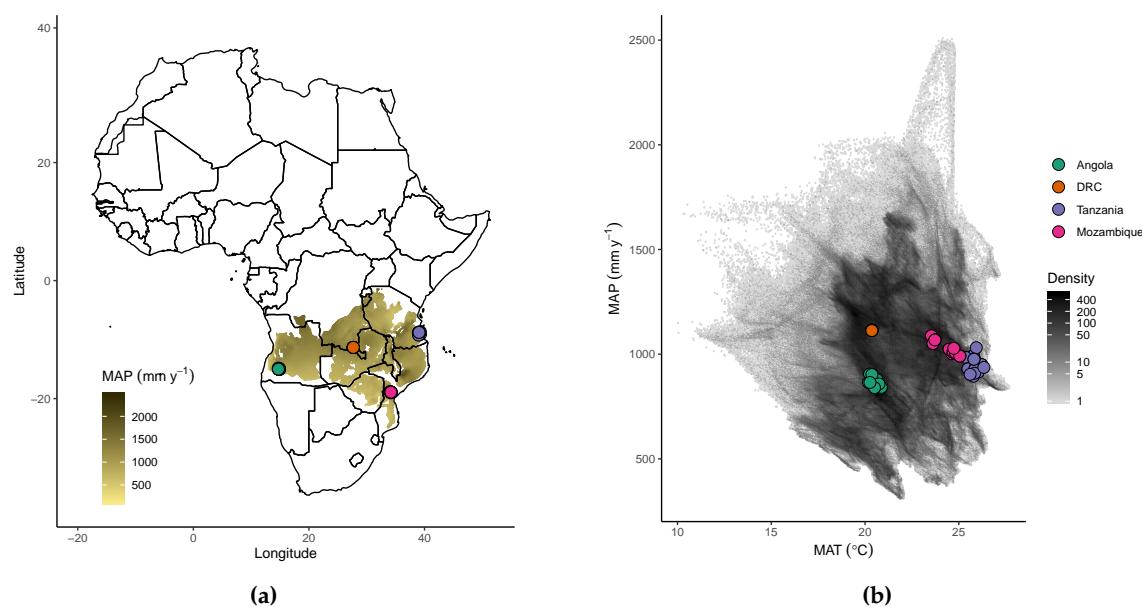


Figure 1. Locations of plots used in this study, by (a) geographic location with respect to the distribution of miombo woodland vegetation (shaded brown according to mean annual precipitation) [1], and (b) showing the plot locations compared to the climate space of the miombo ecoregion estimated using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

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 [34]. In all sites Palgrave [35] 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 [36]. 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 [36]. 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.

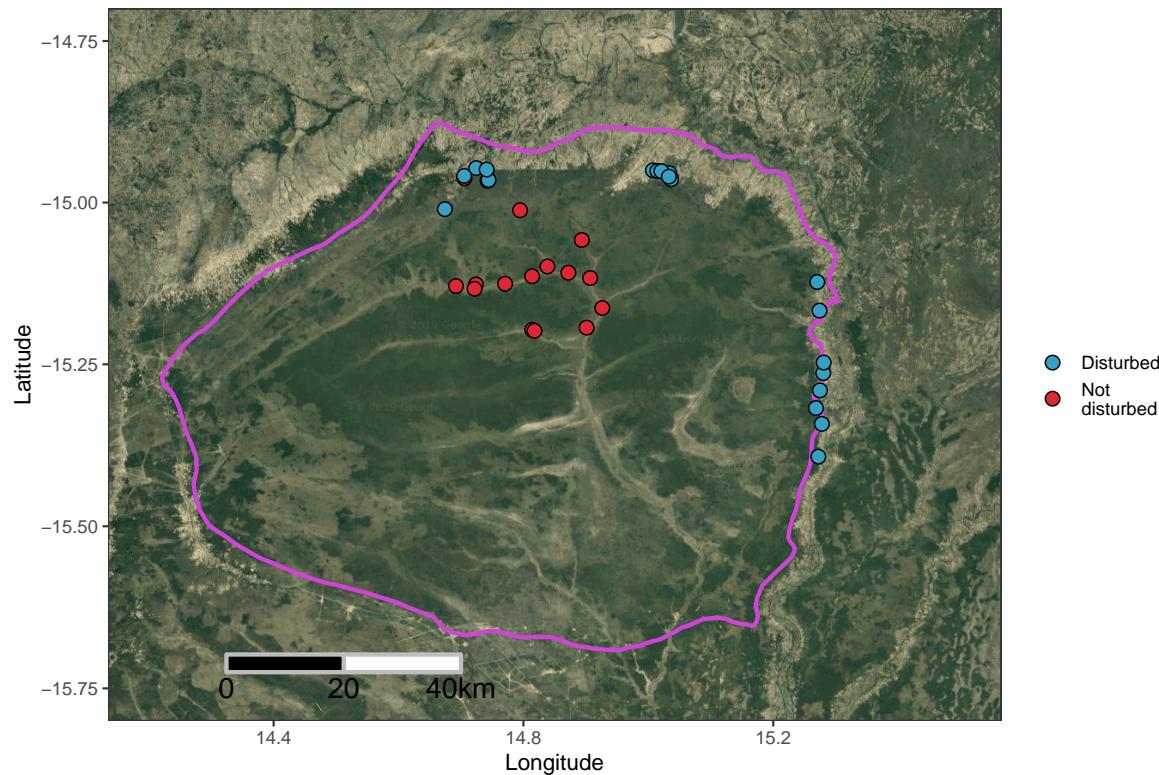


Figure 2. Location of plots in Bicuar National Park, southwest Angola. The Park boundary is shown as a pink outline, according to UNEP-WCMC and IUCN [37]. One hectare undisturbed plots are shown as red points, while disturbed 20x50 m (0.1 hectare) plots are shown as blue points. The map background is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

148 2.3. Climatic data

149 The WorldClim dataset [33] 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 [39], 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.
 156

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 [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	<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)

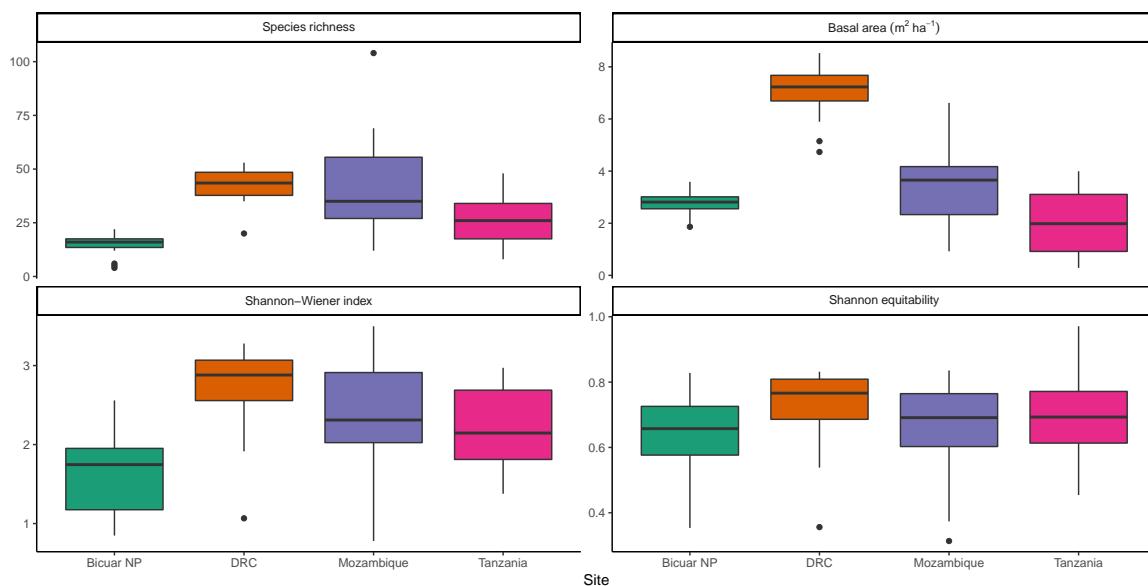


Figure 3. Variation of alpha diversity estimates and basal area among sites. Boxes bound the 1st and 3rd quartiles, with the median within the box. Whiskers represent 1.5 times the interquartile range plus or minus the 1st and 3rd quartiles, respectively. Values found beyond the whiskers are shown individually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

204 3.2. Beta diversity

205 The NMDS of plot species composition among one hectare plots was run with four dimensions.
 206 The stress value was 0.10. Plot diversity in Bicuar National Park formed three distinct groups within
 207 axes 1 and 2 of the NMDS ordination. Bicuar plots 9, 13, and 15 were characterised by high abundances
 208 of *Baikiaea plurijuga*, *Baphia massaiensis* and *Croton gratissimus*, according to species scores from the
 209 NMDS. Bicuar plots 4, 11, and 12 were characterised by *Brachystegia tamarindoides*, and *Ochna pulchra*.
 210 The third group consisting of the remaining seven plots surprisingly had a species composition most
 211 similar to that of plots in the DRC group according to the NMDS, sharing the core miombo species
 212 of *Julbernardia paniculata* and *Pterocarpus angolensis*. This group of plots in Bicuar National Park was
 213 further characterised by the abundance of *Pterocarpus lucens*, *Strychnos pungens* and *Bridelia mollis*
 214 however, which were not present in the DRC plots. All environmental factors fitted to the NMDS
 215 ordination correlated significantly with the grouping of plots (Figure 4a). MAT explained the most
 216 variation in plot position on the first two NMDS axes ($R^2 = 0.75$, $p < 0.01$), followed by CWD ($R^2 =$
 217 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
 218 MAP explained much of the difference among plots in Bicuar National Park versus those in Tanzania
 219 and Mozambique. Axes 3 and 4 showed a greater degree of overlap in species composition among
 220 plot groups, with plots from Bicuar National Park similar to a select few plots in both Tanzania and
 221 Mozambique (Figure 4b). Axis 3 distinguished plots in Bicuar NP from those in DRC, while plots
 222 from all geographic area overlapped in their distribution across Axis 4. Axes 3 and 4 largely reflected
 223 distribution patterns of less abundant species and not the dominant species in the vegetation.

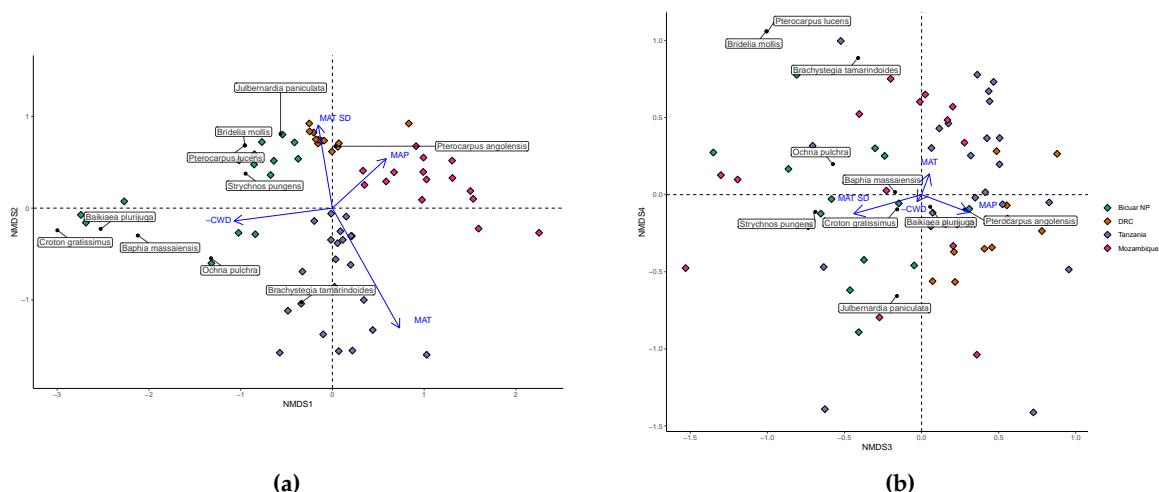


Figure 4. Environmental factors fitted to axes 1 and 2 (a), 3 and 4 (b) of the NMDS ordination of species composition of one hectare plots, showing the variation in plot species composition within and among sites. Diamonds are plot scores coloured by site. The lengths of arrows indicating environmental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

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

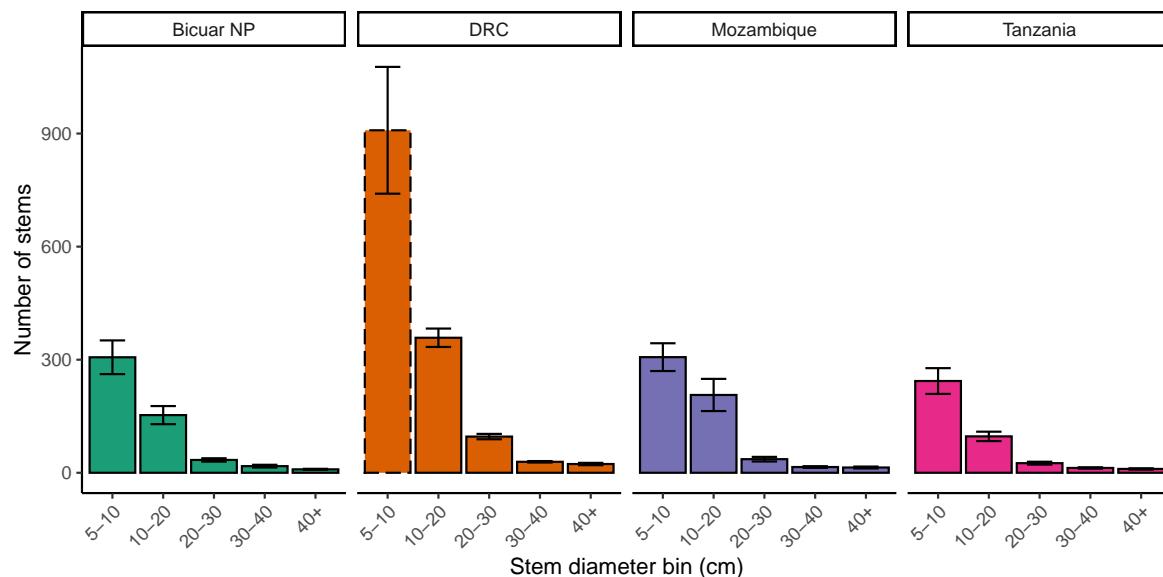


Figure 5. Ranked variation between plots in stem number within each site, with bars according to stem diameter class. Error bars are the mean ± 1 standard error. The dashed bar for the DRC 5-10 cm stem diameter class indicates that these measurements were estimated from the average proportion of 5-10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

241 3.4. Effect of disturbance via shifting cultivation on diversity within Bicuar National Park

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

262 Mean stem density was higher in disturbed plots ($900 \pm 338.36 \text{ stems ha}^{-1}$) than undisturbed plots
 263 ($520.3 \pm 220.22 \text{ stems ha}^{-1}$). The stem diameter abundance distribution in disturbed plots showed
 264 that many more stems were from the 5-10 cm diameter class in disturbed plots, while the disturbed
 265 plots had fewer stems in the 10-20 cm size class. Both disturbed and undisturbed plots had a similar
 266 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).

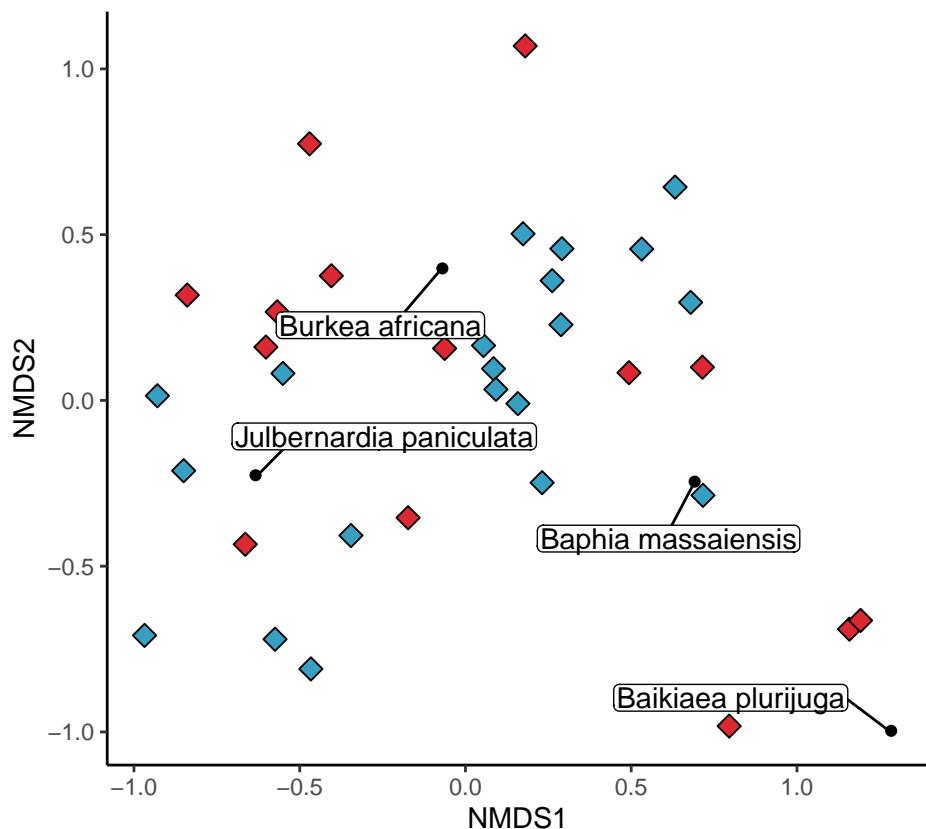


Figure 6. NMDS ordination of species composition of 20x50 m (0.1 ha) plots showing plot scores as coloured diamonds located in disturbed (blue) and undisturbed (red) areas of woodland in Bicuar National Park.

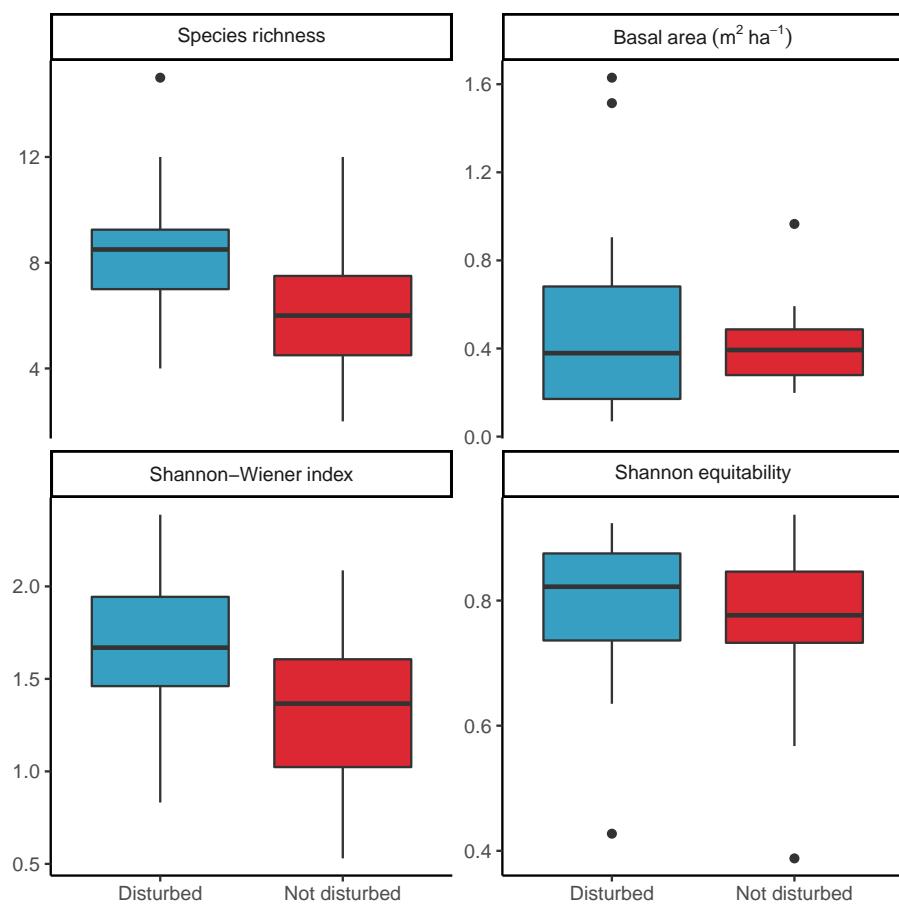


Figure 7. The variation in diversity and woodland structure between disturbed and undisturbed 20x50 m (0.1 ha) plots in Bicuar National Park. Boxes bound the 1st and 3rd quartiles, with the median within the box. Whiskers represent 1.5 times the interquartile range plus or minus the 1st and 3rd quartiles,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

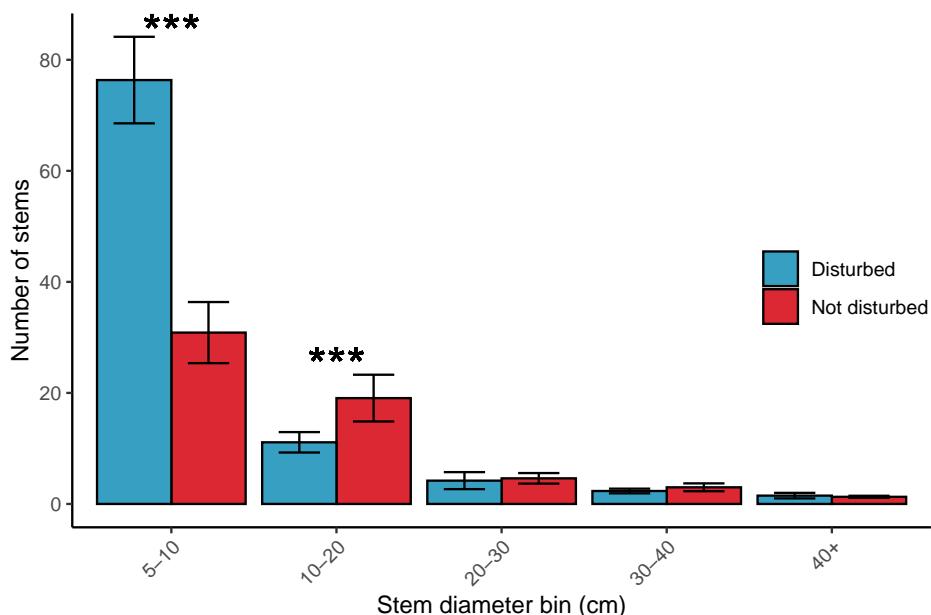


Figure 8. Ranked variation between disturbed and undisturbed plots in stem number, with bars according to stem diameter class. Error bars are the mean \pm 1 standard error. Asterisks above pairs of bars refer to the p-values of Poisson general linear models which tested whether disturbed and undisturbed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

269 4. Discussion

270

271 4.1. Comparison of Bicuar National Park with other woodlands across the miombo ecoregion

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

285

286 4.2. Delineation of woodland types within Bicuar National Park

287 Within Bicuar National Park, three distinct woodland types were identified. The first, dominated
 288 by *Baikiaea plurijuga* and *Baphia massaiensis* represents the Baikiaea woodland type commonly found to
 289 the south of the miombo ecoregion [47]. This is supported by Chisingui *et al.* [22] who also found
 290 Baikiaea woodlands as a distinct woodland type in the Park. *B. plurijuga* has been identified as an
 291 important species for conservation, being attractive for selective logging due to its large stature [48,49].
 292 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 Huila 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 in 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 Huila 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 the 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 [19], 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.

309

310 4.3. Comparison of disturbed and undisturbed woodland plots

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

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

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

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

359 **Funding:** Final data preparation across all sites was funded by SEOSAW (a Socio-Ecological Observatory for the
360 Southern African Woodlands), a NERC-funded project (Grant No. NE/P008755/1). The installation of woodland
361 plots in Bicuar National Park and their data collection was funded by the National Geographic Society (Grant No.
362 EC-51464R-18) to FMG, AVC, KGD and JLG. JLG was supported by a NERC E3 Doctoral Training Programme
363 PhD studentship (Grant No. NE/L002558/1). The APC was funded by the University of Edinburgh.

364 **Acknowledgments:** The rangers at Bicuar National Park are gratefully acknowledged for their help in installing
365 the woodland survey plots and for their help with numerous other incidental challenges during fieldwork.
366 Domingos Fortunato P. Félix da Silva, Abel C. E. Cahali, Felisberto Gomes Armando, José Camôngua Luís, Manuel
367 Jundo Cachissapa and Henrique Jacinto are acknowledged for their help in conducting plot measurements in
368 Bicuar National Park.

369 **Conflicts of Interest:** The authors declare no conflict of interest. The funders had no role in the design of the
370 study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to
371 publish the results.

372 Abbreviations

373 The following abbreviations are used in this manuscript:

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

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

```

377
378 1 ##' @author Casey M. Ryan
379 2 ##' @return d130, the estimated diameter at a POM of 1.3 m (in cm).
380 3 ##' @param d_in the diameter measured at the POM (in cm)
381 4 ##' @param POM the height of the POM (in m)
382 5 ##' @details The adjustment based on tree taper model developed as part of
383 6 ##' the ACES project (Abrupt Changes in Ecosystem Services
384 7 ##' https://miomboaces.wordpress.com/), using data from the miombo of Niassa.
385 8 ##' The model is a cubic polynomial, with three equations for different sized stems.
386 9 ##' @section Warning: POMs >1.7 m are not adjusted.
387 10 POMadj <- function(d_in, POM) {
388 11   stopifnot(is.numeric(d_in),
389 12     is.numeric(POM),
390 13     POM >= 0,
391 14     sum(is.na(POM))==0,
392 15     length(POM) == length(d_in))
393 16   if (any(POM > 1.7))
394 17     warning("POMs >1.7 m are outside the calibration data, no correction applied")
395 18   NAS <- is.na(d_in)
396 19   d_in_clean <- d_in[!NAS]
397 20   POM_clean <- POM[!NAS]
398 21   # define the size class edges:
399 22   edges <- c(5.0, 15.8, 26.6, 37.4)
400 23   sm <- d_in_clean < edges[2]
401 24   med <- d_in_clean >= edges[2] & d_in_clean < edges[3]
402 25   lg <- d_in_clean >= edges[3]
403 26
404 27   # compute predictions for delta_d, for all size classes
405 28   delta_d <- data.frame(
406 29     # if small:
407 30     small = 3.4678+-5.2428 *
408 31     POM_clean + 2.9401 *
409 32     POM_clean^2+-0.7141 *
410 33     POM_clean^3,
411 34     # if med
412 35     med = 4.918+-8.819 *
413 36     POM_clean + 6.367 *
414 37     POM_clean^2+-1.871 *
415 38     POM_clean^3,
416 39     # if large
417 40     large = 9.474+-18.257 *
418 41     POM_clean + 12.873 *
419 42     POM_clean^2+-3.325 *
420 43     POM_clean^3
421 44   )
422 45   # index into the right size class
423 46   dd <- NA_real_
424 47   dd[sm] <- delta_d$small[sm]
425 48   dd[med] <- delta_d$med[med]
426 49   dd[lg] <- delta_d$large[lg]
427 50   dd[POM_clean > 1.7] <- 0 # to avoid extrapolation mess
428 51
429 52   # add NAs back in
430 53   d130 <- NA
431 54   d130[NAS] <- NA
432 55   d130[!NAS] <- d_in_clean - dd
433 56
434 57   if (any(d130[!NAS] < 0))
435 58     warning("Negative d130 estimated, replaced with NA")
436 59   d130[d130 <= 0 & !is.na(d130)] <- NA
437 60   return(d130)
438 61 }
```

440 References

- 441 1. White, F. *The Vegetation of Africa: A descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation*
442 *map of Africa.*; UNESCO: Paris, France, 1983. doi:<http://dx.doi.org/10.2307/2260340>.
- 443 2. Mayaux, P.; Bartholomé, E.; Fritz, S.; Belward, A. A new land-cover map of Africa for the year 2000. *Journal*
444 *of Biogeography* **2004**, *31*, 861–877. doi:<http://dx.doi.org/10.1111/j.1365-2699.2004.01073.x>.
- 445 3. Arino, O.; Perez, J.R.; Kalogirou, V.; Defourny, P.; Achard, F. Globcover 2009. *ESA Living Planet Symposium*
446 **2010**, pp. 1–3.
- 447 4. Chidumayo, E. *Miombo ecology and management: An introduction*; Intermediate Technology Publications:
448 London, UK, 1997.
- 449 5. Campbell, B.M.; Jeffrey, S.; Kozanayi, W.; Luckert, M.; Mutamba, M. *Household Livelihoods in Semi-Arid*
450 *Regions: Options and constraints*; Center for International Forestry Research: Bogor, Indonesia, 2002; p. 153.
- 451 6. LPWG, Azani, N.; Babineau, M.; Bailey, C.D.; Banks, H.; Barbosa, A.R.; Pinto, R.B.; Boatwright, J.S.; Borges,
452 L.M.; Brown, G.K.; Bruneau, A.; Candido, E.; Cardoso, D.; Chung, K.; Clark, R.P.; Conceição, A.d.S.; Crisp,
453 M.; Cubas, P.; Delgado-Salinas, A.; Dexter, K.G.; Doyle, J.J.; Dumiljil, J.; Egan, A.N.; de la Estrella, M.;
454 Falcão, M.J.; Filatov, D.A.; Fortuna-Perez, A.P.; Fortunato, R.H.; Gagnon, E.; Gasson, P.; Rando, J.G.; de
455 Azevedo Tozzi, A.M.G.; Gunn, B.; Harris, D.; Haston, E.; Hawkins, J.A.; Herendeen, P.S.; Hughes, C.E.;
456 Iganci, J.R.; Javadi, F.; Kanu, S.A.; Kazempour-Osaloo, S.; Kite, G.C.; Klitgaard, B.B.; Kochanovski, F.J.;
457 Koenen, E.J.; Kovar, L.; Lavin, M.; le Roux, M.; Lewis, G.P.; de Lima, H.C.; López-Roberts, M.C.; Mackinder,
458 B.; Maia, V.H.; Malécot, V.; Mansano, V.; Marazzi, B.; Mattapha, S.; Miller, J.T.; Mitsuyuki, C.; Moura,
459 T.; Murphy, D.J.; Nageswara-Rao, M.; Nevado, B.; Neves, D.; Ojeda, D.I.; Pennington, R.T.; Prado, D.E.;
460 Prenner, G.; de Queiroz, L.P.; Ramos, G.; Filardi, F.L.R.; Ribeiro, P.G.; de Lourdes Rico-Arce, M.; Sanderson,
461 M.J.; Santos-Silva, J.; São-Mateus, W.M.; Silva, M.J.; Simon, M.F.; Sinou, C.; Snak, C.; de Souza, É.R.; Sprent,
462 J.; Steele, K.P.; Steier, J.E.; Steeves, R.; Stirton, C.H.; Tagane, S.; Torke, B.M.; Toyama, H.; da Cruz, D.T.;
463 Vatanparast, M.; Wieringa, J.J.; Wink, M.; Wojciechowski, M.; Yahara, T.; Yi, T.; Zimmerman, E. A new
464 subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny: The
465 Legume Phylogeny Working Group (LPWG). *Taxon* **2017**, *66*, 44–77. doi:<http://dx.doi.org/10.12705/661.3>.
- 466 7. Privette, J.L.; Tian, Y.; Roberts, G.; Scholes, R.J.; Wang, Y.; Taylor, K.K.; Frost, P.; Mukelabai, M. Vegetation
467 structure characteristics and relationships of Kalahari woodlands and savannas. *Global Change Biology*
468 **2004**, *10*, 281–291. doi:<http://dx.doi.org/10.1111/j.1529-8817.2003.00740.x>.
- 469 8. Taylor, K.K.; Dowty, P.R.; Shugart, H.H.; Ringrose, S. Relationship between small-scale structural variability
470 and simulated vegetation productivity across a regional moisture gradient in southern Africa. *Global*
471 *Change Biology* **2004**, *10*, 374–382. doi:<http://dx.doi.org/10.1046/j.1529-8817.2003.00704.x>.
- 472 9. Chidumayo, E.N. Changes in miombo woodland structure under different land tenure
473 and use systems in central Zambia. *Journal of Biogeography* **2002**, *29*, 1619–1626.
474 doi:<http://dx.doi.org/10.1046/j.1365-2699.2002.00794.x>.
- 475 10. Dexter, K.G.; Smart, B.; Baldauf, C.; Baker, T.R.; Bessike Balinga, M.P.B.; Brienen, R.J.W.; Fauset, S.;
476 Feldpausch, T.R.; Ferreira-da Silva, L.; Muledi, J.I.; Lewis, S.L.; Lopez-Gonzalez, G.; Marimon-Junior,
477 B.H.; Marimon, B.S.; Meerts, P.; Page, B.; Parthasarathy, N.; Phillips, O.L.; Sunderland, T.C.H.; Theilade,
478 I.; Weinritt, J.; Affum-Baffoe, K.; Araujo, A.; Arroyo, L.; Begne, S.K.; Carvalho-das Neves, E.; Collins, M.;
479 Cuni-Sánchez, A.; Djuiukouo, M.N.K.; Elias, F.; Foli, E.G.; Jeffery, K.J.; Killeen, T.J.; Malhi, Y.; Maracahipes,
480 L.; Mendoza, C.; Monteagudo-Mendoza, A.; Morandi, P.; Oliveira-dos Santos, C.; Parada, A.G.; Pardo,
481 G.; Peh, K.S.H.; Salomão, R.P.; Silveira, M.; Sinatura-Miranda, H.; Slik, J.W.F.; Sonke, B.; Taedoumg,
482 H.E.; Toledo, M.; Umetsu, R.K.; Villaroel, R.G.; Vos, V.A.; White, L.J.T.; Pennington, R.T. Floristics and
483 biogeography of vegetation in seasonally dry tropical regions. *International Forestry Review* **2015**, *17*, 10–32.
484 doi:<http://dx.doi.org/10.1505/146554815815834859>.
- 485 11. Oliveras, I.; Malhi, Y. Many shades of green: The dynamic tropical forest-savannah transition
486 zones. *Philosophical Transactions of the Royal Society B: Biological Sciences* **2016**, *371*, 1–15.
487 doi:<http://dx.doi.org/10.1098/rstb.2015.0308>.
- 488 12. Dantas, V.L.; Hirota, M.; Oliveira, R.S.; Pausas, J.G. Disturbance maintains alternative biome states. *Ecology*
489 *Letters* **2016**, *19*, 12–19. doi:<http://dx.doi.org/10.1111/ele.12537>.
- 490 13. DRYFLOR, Banda-R, K.; Delgado-Salinas, A.; Dexter, K.G.; Linares-Palomino, R.; Oliveira-Filho, A.;
491 Prado, D.; Pullan, M.; Quintana, C.; Riina, R.; Rodríguez, G.M.; Weinritt, J.; Acevedo-Rodríguez, P.;

- 492 Adarve, J.; Álvarez, E.; Aranguren, A.; Arteaga, J.C.; Aymard, G.; Castaño, A.; Ceballos-Mago, N.; Cogollo,
493 A.; Cuadros, H.; Delgado, F.; Devia, A.W.; Dueñas, H.; Fajardo, L.; Fernández, A.; Fernández, M.A.;
494 Franklin, J.; Freid, E.H.; Galetti, L.A.; Gonto, R.; González-M., A.; Graveson, R.; Helmer, E.H.; Idárraga,
495 A.; López, R.; Marcano-Vega, H.; Martínez, O.G.; Maturo, H.M.; McDonald, M.; McLaren, K.; Melo,
496 O.; Mijares, F.; Mogni, V.; Molina, D.; Moreno, N.P.; Nassar, J.M.; Neves, D.M.; Oakley, L.J.; Oatham,
497 M.; Olvera-Luna, A.R.; Pezzini, F.F.; Dominguez, O.J.R.; Ríos, M.E.; Rivera, O.; Rodríguez, N.; Rojas,
498 A.; Sarkinen, T.; Sánchez, R.; Smith, M.; Vargas, C.; Villanueva, B.; Pennington, R.T. Plant diversity
499 patterns in neotropical dry forests and their conservation implications. *Science* **2016**, *353*, 1383–1387.
500 doi:<http://dx.doi.org/10.1126/science.aaf5080>.
- 501 14. Torello-Raventos, M.; Feldpausch, T.R.; Veenendaal, E.; Schrodt, F.; Saiz, G.; Domingues, T.F.; Djagbletey,
502 G.; Ford, A.; Kemp, J.; Marimon, B.S.; Marimon Jr, B.H.; Lenza, E.; Ratter, J.A.; Maracahipes, L.; Sasaki, D.;
503 Sonké, B.; Zapfack, L.; Taedoumg, H.; Villarroel, D.; Schwarz, M.; Quesada, C.A.; Ishida, F.Y.; Nardoto, G.B.;
504 Affum-Baffoe, K.; Arroyo, L.; Bowman, D.M.J.S.; Compaore, H.; Davies, K.; Diallo, A.; Fyllas, N.M.; Gilpin,
505 M.; Hien, F.; Johnson, M.; Killeen, T.J.; Metcalfe, D.; Miranda, H.S.; Steininger, M.; Thomson, J.; Sykora, K.;
506 Mougin, E.; Hiernaux, P.; Bird, M.I.; Grace, J.; Lewis, S.L.; Phillips, O.L.; Lloyd, J. On the delineation of
507 tropical vegetation types with an emphasis on forest/savanna transitions. *Plant Ecology & Diversity* **2013**,
508 *6*, 101–137. doi:<http://dx.doi.org/10.1080/17550874.2012.762812>.
- 509 15. Frost, P. The ecology of miombo woodlands. In *The miombo in transition: woodlands and welfare in Africa*;
510 Campbell, B., Ed.; Center for International Forestry Research: Bogor, Indonesia, 1996; pp. 11–55.
- 511 16. Ryan, C.M.; Pritchard, R.; McNicol, I.; Owen, M.; Fisher, J.A.; Lehmann, C. Ecosystem services from
512 southern African woodlands and their future under global change. *Philosophical Transactions of the Royal
513 Society B: Biological Sciences* **2016**, *371*, 1–16. doi:<http://dx.doi.org/10.1098/rstb.2015.0312>.
- 514 17. Mayaux, P.; Eva, H.; Brink, A.; Achard, F.; Belward, A. Remote sensing of land-cover and land-use dynamics.
515 In *Earth Observation of Global Change: The Role of Satellite Remote Sensing in Monitoring the Global Environment*;
516 Springer-Verlag: Berlin, Germany, 2008; pp. 85–108. doi:http://dx.doi.org/10.1007/978-1-4020-6358-9_5.
- 517 18. Clarke, D.A.; York, P.H.; Rasheed, M.A.; Northfield, T.D. Does biodiversity-ecosystem function
518 literature neglect tropical ecosystems. *Trends in Ecology & Evolution* **2017**, *32*, 320–323.
519 doi:<http://dx.doi.org/10.1016/j.tree.2017.02.012>.
- 520 19. Huntley, B.J.; Lages, F.; Russo, V.; Ferrand, N., Eds. *Biodiversity of Angola: Science & conservation: A modern
521 synthesis*; Springer: Cham, Switzerland, 2019. doi:<http://dx.doi.org/10.1007/978-3-030-03083-4>.
- 522 20. Soares de Oliveira, R. *Magnificent and Beggar Land: Angola since the civil war*; Hurst Publishers: London, UK,
523 2015.
- 524 21. Figueiredo, E.; Smith, G.F.; César, J. The flora of Angola: First record of diversity and endemism. *Taxon*
525 **2009**, *58*, 233–236. doi:<http://dx.doi.org/10.1002/tax.581022>.
- 526 22. Chisingui, A.V.; Gonçalves, F.M.P.; Tchamba, J.J.; Camôngua, L.J.; Rafael, M.F.F.; Alexandre, J.L.M.
527 *Vegetation survey of the woodlands of Huíla Province*. Göttingen, Germany & Windhoek, Namibia, 2018.
528 doi:<http://dx.doi.org/10.7809/b-e.00355>.
- 529 23. Soares, M.; Abreu, J.; Nunes, H.; Silveira, P.; Schrire, B.; Figueiredo, E. The leguminosae
530 of Angola: Diversity and endemism. *Systematics and Geography of Plants* **2007**, *77*, 141–212.
531 doi:<http://dx.doi.org/10.2307/20649738>.
- 532 24. Figueiredo, E.; Smith, G.F. Plants of Angola/Plantas de Angola. *Strelitzia* **2008**, *22*, 1–279.
- 533 25. Linder, H.P. Plant diversity and endemism in sub-Saharan tropical Africa. *Journal of Biogeography* **2001**,
534 *28*, 169–182. doi:<http://dx.doi.org/10.1046/j.1365-2699.2001.00527.x>.
- 535 26. Droissart, V.; Dauby, G.; Hardy, O.J.; Deblauwe, V.; Harris, D.J.; Janssens, S.; Mackinder, B.A.;
536 Blach-Overgaard, A.; Sonké, B.; Sosef, M.S.M.; Stévert, T.; Svenning, J.; Wieringa, J.J.; Couvreur, T.L.P.
537 Beyond trees: Biogeographical regionalization of tropical Africa. *Journal of Biogeography* **2018**, *45*, 1153–1167.
538 doi:<http://dx.doi.org/10.1111/jbi.13190>.
- 539 27. Schneibel, A.; Stellmes, M.; Revermann, R.; Finckh, M.; Roder, A.; Hill, J. Agricultural expansion during
540 the post-civil war period in southern Angola based on bi-temporal Landsat data. *Biodiversity and Ecology*
541 **2013**, *5*, 311–319. doi:<http://dx.doi.org/10.7809/b-e.00285>.
- 542 28. McNicol, I.M.; Ryan, C.M.; Williams, M. How resilient are African woodlands to disturbance from shifting
543 cultivation? *Ecological Applications* **2015**, *25*, 2320–2336. doi:<http://dx.doi.org/10.1890/14-2165.1>.

- 544 29. Gonçalves, F.M.P.; Revermann, R.; Gomes, A.L.; Aidar, M.P.M.; Finckh, M.; Juergens, N. Tree species
545 diversity and composition of Miombo woodlands in South-Central Angola: A chronosequence of
546 forest recovery after shifting cultivation. *International Journal of Forestry Research* **2017**, *2017*, 1–13.
547 doi:<http://dx.doi.org/10.1155/2017/6202093>.
- 548 30. Ryan, C.M.; Williams, M.; Grace, J. Above- and belowground carbon stocks in
549 a miombo woodland landscape of Mozambique. *Biotropica* **2011**, *43*, 423–432.
550 doi:<http://dx.doi.org/10.1111/j.1744-7429.2010.00713.x>.
- 551 31. McNicol, I.M.; Ryan, C.M.; Dexter, K.G.; Ball, S.M.J.; Williams, M. Aboveground carbon storage and its
552 links to stand structure, tree diversity and floristic composition in south-eastern Tanzania. *Ecosystems* **2018**,
553 *21*, 740–754. doi:<http://dx.doi.org/10.1007/s10021-017-0180-6>.
- 554 32. Muledi, J.I.; Bauman, D.; Drouet, T.; Vleminckx, J.; Jacobs, A.; Lejoly, J.; Meerts, P.; Shutcha, M.N. Fine-scale
555 habitats influence tree species assemblage in a miombo forest. *Journal of Plant Ecology* **2017**, *10*, 958–969.
556 doi:<http://dx.doi.org/10.1093/jpe/rtw104>.
- 557 33. Fick, S.E.; Hijmans, R.J. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas.
558 *International Journal of Climatology* **2017**, *37*, 4302–4315. doi:<http://dx.doi.org/10.1002/joc.5086>.
- 559 34. Conservatoire et Jardin botaniques de la Ville de Genève and South African National Biodiversity Institute.
560 *African Plant Database (version 3.4.0)*, 2020. Accessed: 2019-11-05.
- 561 35. Palgrave, K.C. *Trees of southern Africa*; Struik Publications: Cape Town, South Africa, 2003.
- 562 36. Kershaw, J.A.; Ducey, M.J.; Beers, T.W.; Husch, B. *Forest Mensuration*; John Wiley & Sons: Chichester, UK,
563 2017.
- 564 37. UNEP-WCMC and IUCN. *Protected Planet: the world database on protected areas (WDPA)*, 2019. [Online;
565 15-January-2019].
- 566 38. Kahle, D.; Wickham, H. ggmap: Spatial visualization with ggplot2. *The R Journal* **2013**, *5*, 144–161.
- 567 39. Chave, J.; Réjou-Méchain, M.; Búrquez, A.; Chidumayo, E.; Colgan, M.S.; Delitti, W.B.C.; Duque,
568 A.; Eid, T.; Fearnside, P.M.; Goodman, R.C.; Henry, M.; Martínez-Yrízar, A.; Mugasha, W.A.;
569 Muller-Landau, H.C.; Mencuccini, M.; Nelson, B.W.; Ngomanda, A.; Nogueira, E.M.; Ortiz-Malavassi,
570 E.; Pélassier, R.; Ploton, P.; Ryan, C.M.; Saldaña, J.G.; Vieilledent, G. Improved allometric models
571 to estimate the aboveground biomass of tropical trees. *Global Change Biology* **2014**, *20*, 3177–3190.
572 doi:<http://dx.doi.org/10.1111/gcb.12629>.
- 573 40. Oksanen, J.; Blanchet, F.G.; Friendly, M.; Kindt, R.; Legendre, P.; McGlinn, D.; Minchin, P.R.; O'Hara, R.B.;
574 Simpson, G.L.; Solymos, P.; Stevens, M.H.H.; Szoecs, E.; Wagner, H. *vegan: Community Ecology Package*,
575 2019. R package version 2.5-5.
- 576 41. Koleff, P.; Gaston, K.J.; Lennon, J.J. Measuring beta diversity for presence-absence data. *Journal of Animal
577 Ecology* **2003**, *72*, 367–382. doi:<http://dx.doi.org/10.1046/j.1365-2656.2003.00710.x>.
- 578 42. Smith, B.; Wilson, J.B. A consumer's guide to evenness indices. *Oikos* **1996**, *76*, 70–82.
579 doi:<http://dx.doi.org/10.2307/3545749>.
- 580 43. Legendre, P.; De Cáceres, M. Beta diversity as the variance of community data: dissimilarity coefficients
581 and partitioning. *Ecology Letters* **2013**, *16*, 951–963. doi:<http://dx.doi.org/10.1111/ele.12141>.
- 582 44. R Core Team. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical
583 Computing, Vienna, Austria, 2019.
- 584 45. Terra, M.C.N.S.; M., d.R.; Prado Júnior, J.A.; de Mello, J.M.; Scolforo, J.R.S.; Fontes, M.A.L.; ter
585 Steege, H. Water availability drives gradients of tree diversity, structure and functional traits
586 in the Atlantic-Cerrado-Caatinga transition, Brazil. *Journal of Plant Ecology* **2018**, *11*, 803–814.
587 doi:<http://dx.doi.org/10.1093/jpe/rtv017>.
- 588 46. Strickland, C.; Liedloff, A.C.; Cook, G.D.; Dangelmayr, G.; Shipman, P.D. The role of water
589 and fire in driving tree dynamics in Australian savannas. *Journal of Ecology* **2016**, *104*, 828–840.
590 doi:<http://dx.doi.org/10.1111/1365-2745.12550>.
- 591 47. Timberlake, J.; Chidumayo, E.; Sawadogo, L. Distribution and characteristics of African dry forests and
592 woodlands. In *The Dry Forests and Woodlands of Africa: Managing for Products and Services*; EarthScan:
593 London, United Kingdom, 2010; pp. 11–42. doi:<http://dx.doi.org/>.
- 594 48. Ng'andwe, P.; Chungu, D.; Shakacite, O.; Vesa, L. Abundance and distribution of top five most valuable
595 hardwood timber species in Zambia and their implications on sustainable supply. 6th International

- 596 Conference on Hardwood Processing; Mottonen, V.; Heinonen, E., Eds.; Natural Resources Institute
597 Finland: Natural Resources Institute Finland, Helsinki, 2017; pp. 18–27.
- 598 49. Wallenfang, J.; Finckh, M.; Oldeland, J.; Revermann, R. Impact of shifting cultivation on
599 dense tropical woodlands in southeast Angola. *Tropical Conservation Science* **2015**, *8*, 863–892.
600 doi:<http://dx.doi.org/10.1177/194008291500800402>.
- 601 50. Sianga, K.; Flynn, R. The vegetation and wildlife habitats of the Savuti-Mababe-Linyati ecosystem, northern
602 Botswana. *KOEDOE* **2017**, *59*, 1–16. doi:<http://dx.doi.org/10.4102/koedoe.v59i2.1406>.
- 603 51. Mukwashi, K.; Gandiwa, E.; Kativu, S. Impact of African elephants on *Baikiaea plurijuga* woodland around
604 natural and artificial watering points in northern Hwange National Park, Zimbabwe. *International Journal*
605 *of Environmental Sciences* **2012**, *2*, 1355–1368. doi:<http://dx.doi.org/10.6088/ijes.002020300022>.
- 606 52. Smith, P.; Allen, Q. *Field guide to the trees and shrubs of the miombo woodlands*; Royal Botanic Gardens, Kew:
607 London, UK, 2004.
- 608 53. Caro, T.M. Species richness and abundance of small mammals inside and outside African national
609 park. *Biological Conservation* **2001**, *98*, 251–257. doi:[http://dx.doi.org/10.1016/S0006-3207\(00\)00105-1](http://dx.doi.org/10.1016/S0006-3207(00)00105-1).
- 610 54. McNicol, I.M.; Ryan, C.M.; Mitchard, E.T.A. Carbon losses from deforestation and widespread
611 degradation offset by extensive growth in African woodlands. *Nature Communications* **2018**, *9*, 1–11.
612 doi:<http://dx.doi.org/10.1038/s41467-018-05386-z>.
- 613 55. Shackleton, C.M. Comparison of plant diversity in protected and communal lands in the
614 Bushbuckridge lowveld savanna, South Africa. *Biological Conservation* **2000**, *94*, 273–285.
615 doi:[http://dx.doi.org/10.1016/S0006-3207\(00\)00001-X](http://dx.doi.org/10.1016/S0006-3207(00)00001-X).
- 616 56. Kalaba, F.K.; Quinn, C.H.; Dougill, A.J.; Vinya, R. Floristic composition, species diversity and carbon
617 storage in charcoal and agriculture fallows and management implications in Miombo woodlands of Zambia.
618 *Forest Ecology and Management* **2013**, *304*, 99–109. doi:<http://dx.doi.org/10.1016/j.foreco.2013.04.024>.
- 619 57. Luoga, E.J.; Witkowski, E.T.F.; Balkwill, K. Regeneration by coppicing (resprouting) of miombo
620 (African savanna) trees in relation to land use. *Forest Ecology and Management* **2004**, *189*, 23–25.
621 doi:<http://dx.doi.org/10.1016/j.foreco.2003.02.001>.
- 622 58. van Wyk, B.; van Wyk, P. *Field guide to trees of southern Africa*; Struik Nature: Cape Town, South Africa,
623 2014.
- 624 59. Muvengwi, J.; Chisango, T.; Mpakairi, K.; Mbiba, M.; Witkowski, E.T.F. Structure, composition and
625 regeneration of miombo woodlands within harvested and unharvested areas. *Forest Ecology and*
626 *Management* **2020**, *458*, 1–10. doi:<http://dx.doi.org/10.1016/j.foreco.2019.117792>.

627 © 2020 by the authors. Submitted to *Diversity* for possible open access publication under the terms and conditions
628 of the Creative Commons Attribution (CC BY) license (<http://creativecommons.org/licenses/by/4.0/>).