

Species diversity and stand structure as drivers of canopy complexity in southern African woodlands

Abstract

1 Introduction

Canopy structure describes the spatial distribution and density of canopy foliage, comprising the primary interface between trees, the atmosphere and sunlight. Canopy structural complexity, i.e. the spatial heterogeneity of foliage distribution through the canopy, has been positively linked to canopy productivity (Hardiman et al., 2011; Chen et al., 2012; Law, Cescatti, and D. D. Baldocchi, 2001; Dennis D. Baldocchi and Wilson, 2001; Morin, 2015). The characterisation of tree canopy structure in wooded ecosystems constitutes a long-standing field of research that has been fundamental to interpreting, modelling, and improving understanding of ecosystem function (Watt, 1947; Whittaker and Woodwell, 1969; Horn, 1971; Maarel, 1996). It is therefore essential to understand the drivers of variation in canopy structural complexity to improve modelling of earth-atmosphere carbon fluxes.

At continental scales, variation in canopy height and canopy cover, two coarse measures of canopy structure both of which have been shown to affect woody productivity and correlate with woody biomass (), can largely be explained by climate and edaphic data (**GEDI**). Increased resource availability allows for larger trees and greater canopy closure (). At the scale of a single tree community however, where variation in climate and soil may be negligible, variation in canopy structure is thought to be affected principally by an interacting combination of tree canopy species composition (), and disturbance history through its effect on stand physical structure (). However, empirical testing of these mechanisms thought to drive canopy structure in natural wooded ecosystems remains sparse across many biomes ().

Following established biodiversity-ecosystem function theory, the niche partitioning of canopy space, i.e. the spatial complementarity of individual tree canopies, is thought to be a key mechanism underlying positive biodiversity-productivity effects in wooded ecosystems (Pretzsch, 2014; Barry et al., 2019). Biodiversity-ecosystem function theory predicts that crown complementarity and thus canopy complexity and foliage density should increase with tree diversity in the local neighbourhood, increasing standing biomass and woody productivity, as coexisting species must occupy non-identical niche space to avoid competitive exclusion ().

As well as the species diversity of trees in a local neighbourhood, the spatial distribution and relative size of those trees, i.e. stand structure, is also expected to affect canopy structural complexity.

31 Heterogeneity in tree size, whether a result of species diversity, disturbance history or some other
32 factor, is expected to increase crown complexity and overall canopy density as individuals of differ-
33 ent sizes occupy different parts of the vertical canopy space (). Additionally, clustering of individ-
34 uals in space is expected to increase canopy structural heterogeneity across a stand, but ultimately
35 decrease total foliage density due to an increase in competitive interactions (). Clustering may oc-
36 cur as a result of disturbance history, or as a result of strong facilitation effects among individuals
37 in a hostile environment (**Ratcliffe2017**).

38 The direction of relationships between species diversity, stand structure, and canopy complex-
39 ity is unclear. While biodiversity-ecosystem function theory presents a species diversity-centric
40 view, whereby diversity affects stand structure and canopy structure, it is possible that aspects
41 of stand structure may influence observed species diversity through sampling effects. Woodlands
42 with greater stem density are likely to have greater species diversity, for example, simply because
43 there are more stems which could potentially constitute different species (). It is important there-
44 fore to account for variation in stem density within models predicting the effects of structural and
45 species diversity on canopy structure, and to design measures of structural diversity that are not
46 conflated with stem density.

47 While much work in the field of forest management has been done to test biotic drivers of tree
48 canopy structure in temperate () and boreal forests (), mostly to inform commercial forestry man-
49 agement, similar work in the tropics is comparatively scarce (). In dry tropical woodlands and sa-
50 vannas especially, tree canopy structure and its effect on ecosystem productivity has received lit-
51 tle attention, possibly due to the misplaced assumption that woody productivity in these ecosys-
52 tems does not represent a globally significant carbon flux (), or that tree canopies in these smaller
53 stature woodlands do not interact and compete for resources to the same degree as in large stature
54 forests (). In recent years however, it has been shown that dry tropical woodlands represent the
55 largest uncertainty in our estimates of the terrestrial carbon cycle (Quéré et al., 2018; Ahlstrom
56 et al., 2015). Sitch et al. (2015) demonstrated the dominant role of the dry tropics in driving vari-
57 ability in the terrestrial carbon sink, and showed that the dry tropics are the fastest increasing
58 component of the terrestrial carbon sink. Part of this uncertainty arises from our lacking a nu-
59 anced understanding of how species composition and structure affect ecosystem function in these
60 ecosystems, which conceptually underpins the Dynamic Global Vegetation Models (DGVMs) fed
61 into global carbon dynamics models. The pertinence of this knowledge gap has prompted further
62 research of the biotic drivers of variation in productivity in the dry tropics, and momentum in this
63 field of research is building, to create general theories of the ecosystem function of the dry tropics
64 ().

65 Canopy structure is multi-dimensional and has previously been explained using a plethora of sim-

ple metrics that originated in forest and community ecology (). Assessments of canopy structure in the dry tropical have most often modelled tree canopies as a series of ellipses (2D) or ellipsoids (3D) based on field measurements with measuring tapes (). Measurements of this kind are time consuming and yet are an over-simplification of canopy structure (). Alternatively, canopy cover is often measured using indirect optical methods which partition sky from canopy material, i.e. with hemispherical photography or the commonly used LAI-2000, providing a 2D representation of the canopy but lacking information on vertical canopy structure. In recent years, particularly in temperate and boreal forests, LiDAR (Light Detection And Ranging) has emerged as a suitable technology for rapidly and precisely assessing canopy structure in 3D, conserving information on 3D structure of the calibre that is required to understand it's complexities ().

In this study we applied terrestrial LiDAR techniques to woodland-savanna mosaics at two sites in southern Africa, with the aim of increasing our understanding of how various metrics of tree canopy structural complexity are affected by tree neighbourhood diversity and stand structure. Our overarching contention is that neighbourhoods of greater tree diversity and greater structural diversity allow greater canopy complexity and foliage density, resulting in higher productivity, and ultimately a more 'forest-like' community, rather than an open canopy savanna.

2 Materials and methods

2.1 Study sites

Measurements were conducted at two sites, the first in Bicuar National Park, southwest Angola (S15.1°, E14.8°), and the second in and around Mtarure Forest Reserve, southeast Tanzania (S9.0°, E39.0°) (Figure 1). At each site, 1 ha (100x100 m) plots were sited in areas of miombo woodland vegetation, across a gradient of stem density. In Angola, 15 plots were sampled, while in Tanzania, seven were sampled following the curtailment of fieldwork due to COVID-19 travel restrictions. Fieldwork was conducted between February and April at both sites, during the peak growth period of each site in order to capture the highest foliage volume in the canopy.

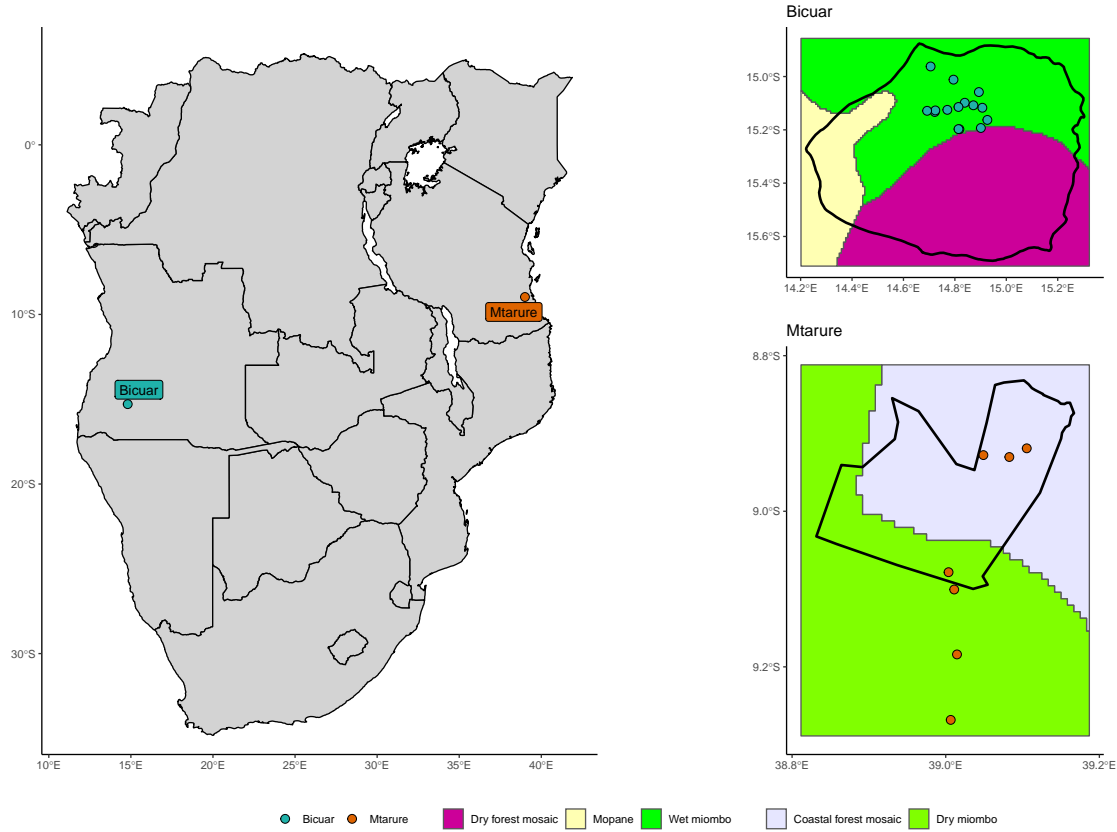


Figure 1: Location of study sites within southern Africa (left), and of 1 ha plots within each site (right). The black outlines in each site map denote the boundaries of protected areas which encompass the majority of study sites, Bicular National Park in Angola (top), and Mtarure Forest Reserve in Tanzania (bottom). The background of each site map is a re-classified version of White’s vegetation map (**White1983**). Note that all maps are on different scales.

2.2 Field measurements

Within each 1 ha plot we identified each stem >5 cm stem diameter to species, measured stem diameter (diameter at breast height - 1.3 m) and recorded stem location within the plot using tap measures. Each 1 ha plot was further subdivided into nine 10 m diameter circular subplots arranged in a regular grid, with a 15 m buffer from the plot edge and 35 m between subplots. For each subplot, we identified woody stems >5 cm diameter with canopy material inside the subplot. We measured the distance and direction from the subplot centre to each of these stems, as well as their projected crown area as an ellipse of two perpendicular crown diameter measurements.

Within each subplot, a variable number of scans were recorded using a Leica HDS6100 phase-shift Terrestrial Laser Scanner (TLS) (**Leica**). The number and position of scans within a subplot was determined by the arrangement of canopy material in the subplot. Scan positions were arranged

102 to minimise shadows within the canopy of the subplot, and to maximise canopy penetration. The
103 number of scans per subplot ranged between one and five in both sites.

104 2.3 Data analysis

105 2.3.1 Scan processing

106 Point clouds from scans in each subplot were registered and unified using Leica Cyclone (version
107 9.1) (**Cyclone**), using five reflective targets visible to all scans. Point clouds were voxelised to
108 cubic voxel sizes of different sizes depending on the application of the data. For subplot height
109 profile estimation and gap fraction we used 5 cm³ voxels, and for whole plot canopy rugosity we
110 used 10 cm³ voxels. Voxels were classed as filled if they intersected with one or more points. Vari-
111 ation in voxel size reflects the spatial scale of each analysis, and is bounded by the beam diver-
112 gence of the scanner over longer distances (). Choosing voxels that are too small can result in
113 pock-marked representations of surfaces that are especially problematic when calculating larger
114 scale canopy structure metrics, such as canopy top roughness, while voxels that are too large can
115 result in an over-estimation of plant volume when estimating canopy foliage density at the subplot
116 scale (Seidel, Fleck, and Leuschner, 2012; Cifuentes et al., 2014). We used a noise reduction algo-
117 rithm from to discard points based on mean nearest neighbour distances. This effectively removed
118 ‘ghost points’ produced by partial interceptions and also removed many erroneous returns caused
119 by airborne dust particles, which was common at our study sites. Raw points clouds for each sub-
120 plot had a mean of $\sim 2.9 \times 10^8$ points, $\sim 4.5 \times 10^7$ points after voxelisation, and $\sim 2.1 \times 10^7$ points after
121 noise reduction.

122 Ground points were classified using the Progressive Morphological Filter (PMF) from Zhang et al.
123 (2003). Point cloud height was reclassified height based on this revised ground layer by measuring
124 the vertical distance between the nearest ground point and each point.

125 We used ray-tracing to calculate canopy cover at the subplot centre from multiple TLS scans.
126 Hemispherical images were created using the POV-ray software (). Voxels were converted to matt
127 black cubes filling the voxel volume, with a white sky box and no light source. A ‘camera’ with a
128 180° fisheye lens was placed at the subplot centre within POV-Ray, at a height of 1.8 m pointing
129 directly upwards. The images produced by POV-Ray were analysed using Hemiphot (**Steege**) to
130 estimate canopy cover as the proportion of pixels filled by canopy material.

131 We calculated a number of metrics to describe different aspects of canopy complexity within each
132 subplot in addition to canopy cover. Canopy height was measured as the 99th percentile of height
133 of canopy material within the subplot. Layer diversity was calculated using Shannon entropy on
134 foliage density of 0.5 m height bins through the tree canopy. The uniformity of foliage distribution

135 was calculated by fitting a linear model to the cumulative foliage density profile, then extracting
136 the standard error on the slope estimate of this linear model. The height of peak foliage density
137 was calculated by fitting a loess model to the foliage height profile and extracting the height at
138 which foliage density peaked.

139 At the plot level, canopy complexity was measured with six metrics. Of these, canopy top rough-
140 ness was measured as the standard deviation of canopy height across the plot, and canopy rugos-
141 ity was measured according to Hardiman et al. (2011), as the standard deviation of vertical and
142 horizontal foliage density within 0.5 m cubic bins.

143 2.4 Stand structure

144 For each subplot, we calculated an adapted version of the Hegyi index to estimate crowding, as
145 an alternative to stem density that works better to describe stand structure at small spatial scales
146 (Hegyi, 1974).

147 To estimate subplot structural diversity we calculated the coefficient of variation of stem diameter
148 as a measure of the heterogeneity of tree size in the neighbourhood, and the coefficient of variation
149 of neighbourhood crown area as a measure of the heterogeneity of tree canopy size.

150 At the plot level, we estimated the regularity of species spatial distribution using the spatial min-
151 gling index (von Gadow and Hui, 2002). We also measured the uniformity of whole plot stem dis-
152 tribution using the winkelmass, which measures the degree of clustering of stems (von Gadow and
153 Hui, 2002). Finally, we calculated plot level stem density to estimate crowding.

154 2.5 Statistical analysis

155 Linear mixed effects models tested the effects of tree species diversity and stand structural diver-
156 sity on canopy complexity. Mixed models were used to account for the highly nested sampling de-
157 sign of subplots within plots and plots within sites. Two sets of models were conducted, the first
158 at the subplot level with random effects for plot nested within site, and the second at the plot
159 level with random effects for site only. Separate models were fitted for each canopy complexity
160 metric, resulting in six models at the subplot level and five models at the plot level. We compared
161 the AIC values and Akaike weights of all models for a particular canopy complexity metric to find
162 the ‘best model’, i.e. the model which minimised variance in the fitted values, with penalties for
163 complex model structure (**Akaike**).

164 To explore variation in tree species composition among plots and sites, we conducted a Non-metric
165 Multi-dimensional Scaling (NMDS) analysis using tree species abundance in each plot. We ex-
166 cluded species with only one individual across all plots.

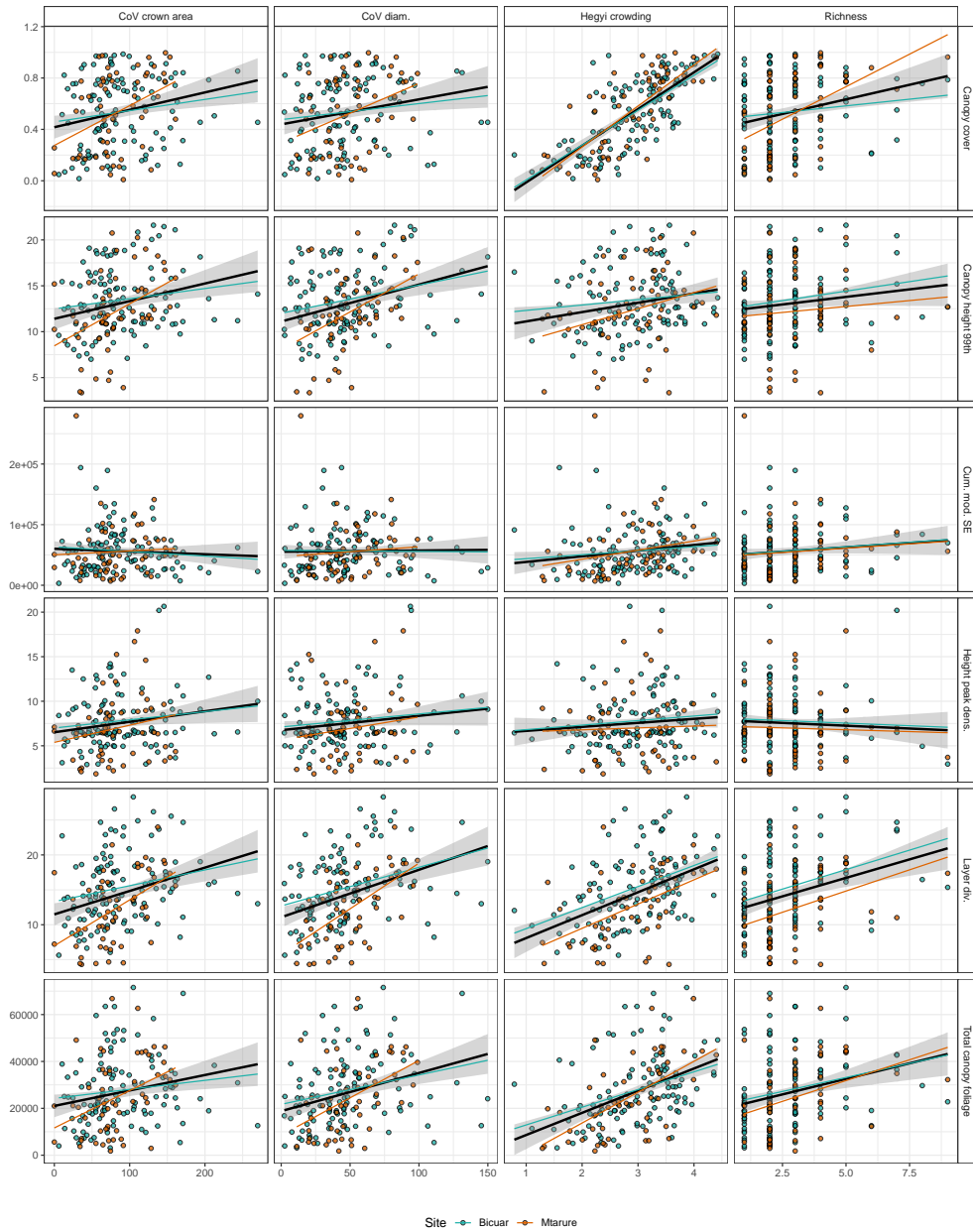
168 **3.1 Vertical canopy complexity**

Figure 2: Bivariate relationships between subplot canopy structure metrics (y axis) and diversity/stand structure metrics (x axis). Points and linear model lines of best fit are coloured by site. The black line of best fit is a linear model including both sites. See **supp. material** for a comparison of linear model fits by site.

169 Bivariate plots showed that subplot species diversity, measured by species richness of the tree
 170 neighbourhood around each 10 m diameter subplot, appeared to have weak but positive effects
 171 on canopy layer diversity and total canopy cover (Figure 2). The Hegyi crowding index and both

stand structural diversity metrics had strong positive effects on canopy complexity, for all metrics except for uniformity of foliage distribution and height of peak foliage density. The two sites in our study had similar bivariate relationships, with interaction effects of site in the bivariate linear models being non-significant in all cases (supp. material).

Linear mixed effects models showed that species richness of the subplot neighbourhood had variable effects across different measures of canopy structure, but the effect sizes were not significant (slope standard errors not overlapping zero) for any model (Figure 3). One exception is the negative effect of richness on canopy height in Mtarure only. As in the bivariate plots, the Hegyi crowding index had strong positive effects on three of six canopy complexity metrics. Heterogeneity of stem diameter had a positive effect on layer diversity and total foliage density, and a marginally significant positive effect on canopy height. Variation in crown area was only seen to have significant effects in Bicular plots, where it correlated with a decrease in vertical uniformity of foliage distribution, and total canopy foliage density.

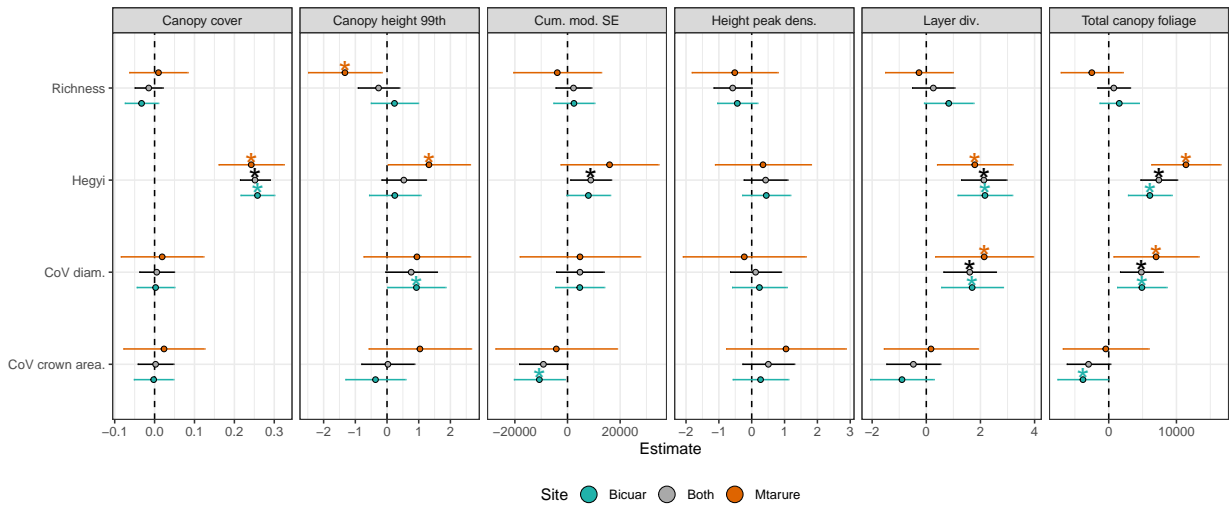


Figure 3: Standardized fixed effect slopes for each model of a canopy structure metric. Slope estimates are ± 1 standard error. Slope estimates where the interval (standard error) does not overlap zero are considered to be significant effects. Points are coloured according to site.

The model selection process showed that the best model for layer diversity included species richness. Stand structural diversity metrics were included in the best models for all canopy complexity metrics except for canopy cover, which was predicted solely by the Hegyi crowding index. Models of layer diversity, total foliage density, and canopy cover were predicted well by a combination of crowding and stand structural diversity. Models of height of peak foliage density, canopy height, and uniformity of foliage distribution were poorly constrained by the fixed effects, with R^2_m of $\sim 5\%$. The majority of the total model effect on canopy height came from the random effects of site and plot identity.

Response	Richness	Hegyi crowding	CoV diameter	CoV crown area	ΔAIC	R^2_c	R^2_m
Layer div.		✓	✓		10.1	0.44	0.24
Total canopy foliage		✓	✓	✓	52.1	0.30	0.24
Height peak dens.	✓			✓	-0.3	0.09	0.05
Canopy height 99th			✓		1.2	0.29	0.06
Cum. mod. SE		✓		✓	53.1	0.10	0.05
Canopy cover		✓			-23.7	0.64	0.52

Table 1: Explanatory variables included in the best model for each canopy structure variable.

ΔAIC shows the difference in model AIC value compared to a null model which included only the hegyl crowding index and the random effects of site and plot. R^2_c is the R^2 of the best model, while R^2_m is the R^2 of the model fixed effects only.

3.2 Canopy rugosity

Similar to the subplot analyses, at the whole-plot scale tree species diversity, measured here by the Shannon index, tended to have weak positive effects on canopy complexity metrics, while stand structural diversity metrics had stronger positive effects (Figure 4). Strong positive relationships of basal area on canopy complexity are driven mostly by two plots with particularly low basal area in Mtarure, M3 and M4. These plots are sparse thorny savanna, dominated by *Senegalia* spp. (Figure 6). Indeed, linear models using only plots in bicuar show divergent relationships. These two plots also have particularly low canopy cover, canopy height, and canopy top roughness, despite having similar tree species diversity and spatial distribution of trees (winkelmass) as other plots.

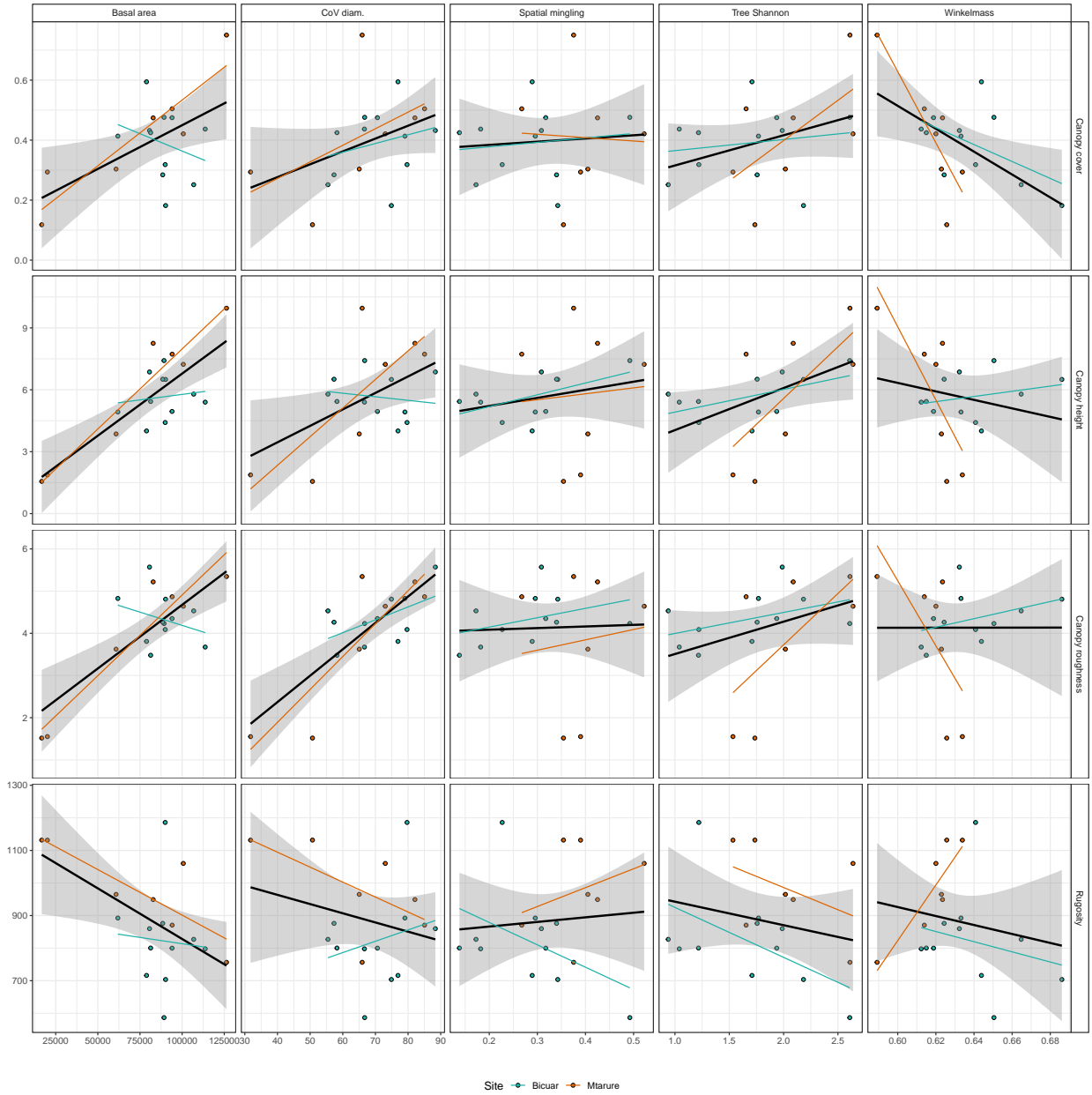


Figure 4: Bivariate relationships between diversity and stand structure metrics (x axis) and whole-plot canopy structure metrics (y axis). Points and linear model lines of best fit are coloured by site. The thick black line of best fit is a linear model including both sites.

203 Linear mixed effects models show that increased spatial clustering of trees causes a decrease in
 204 canopy cover. Increased spatial mingling of tree species causes an increase in canopy rugosity,
 205 while in contrast an increase in overall tree species diversity appears to cause a decrease in canopy
 206 rugosity. An increase in the heterogeneity of stem diameter causes an increase in canopy top rough-
 207 ness.

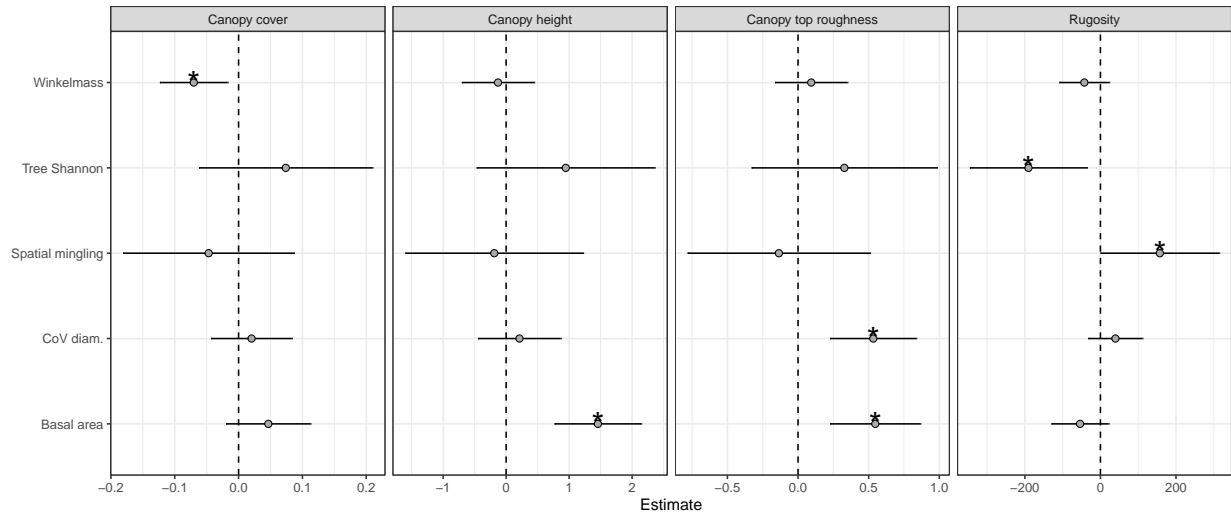


Figure 5: Standardized fixed effect slopes for whole-plot canopy rugosity. Slope estimates are ± 1 standard error. Slope estimates where the interval (standard error) does not overlap zero are considered to be significant effects.

208 Model selection showed that all plot canopy complexity metrics except canopy rugosity were best
 209 modelled by a combination of basal area and either species diversity or structural diversity.

Response	Shannon	Basal area	CoV diameter	Mingling	Winkelmass	ΔAIC	R^2_c	R^2_m
Canopy cover		✓			✓	3.4	0.64	0.64
Canopy height	✓	✓				2.8	0.81	0.81
Canopy roughness		✓	✓			10.0	0.85	0.85
Rugosity		✓				0.9	0.58	0.58

Table 2: Explanatory variables included in the best model for each plot-level canopy complexity metric. ΔAIC shows the difference in model AIC value compared to a null model which included only the hegyi crowding index and the random effects of site and plot. R^2_c is the R^2 of the best model, while R^2_m is the R^2 of the model fixed effects only.

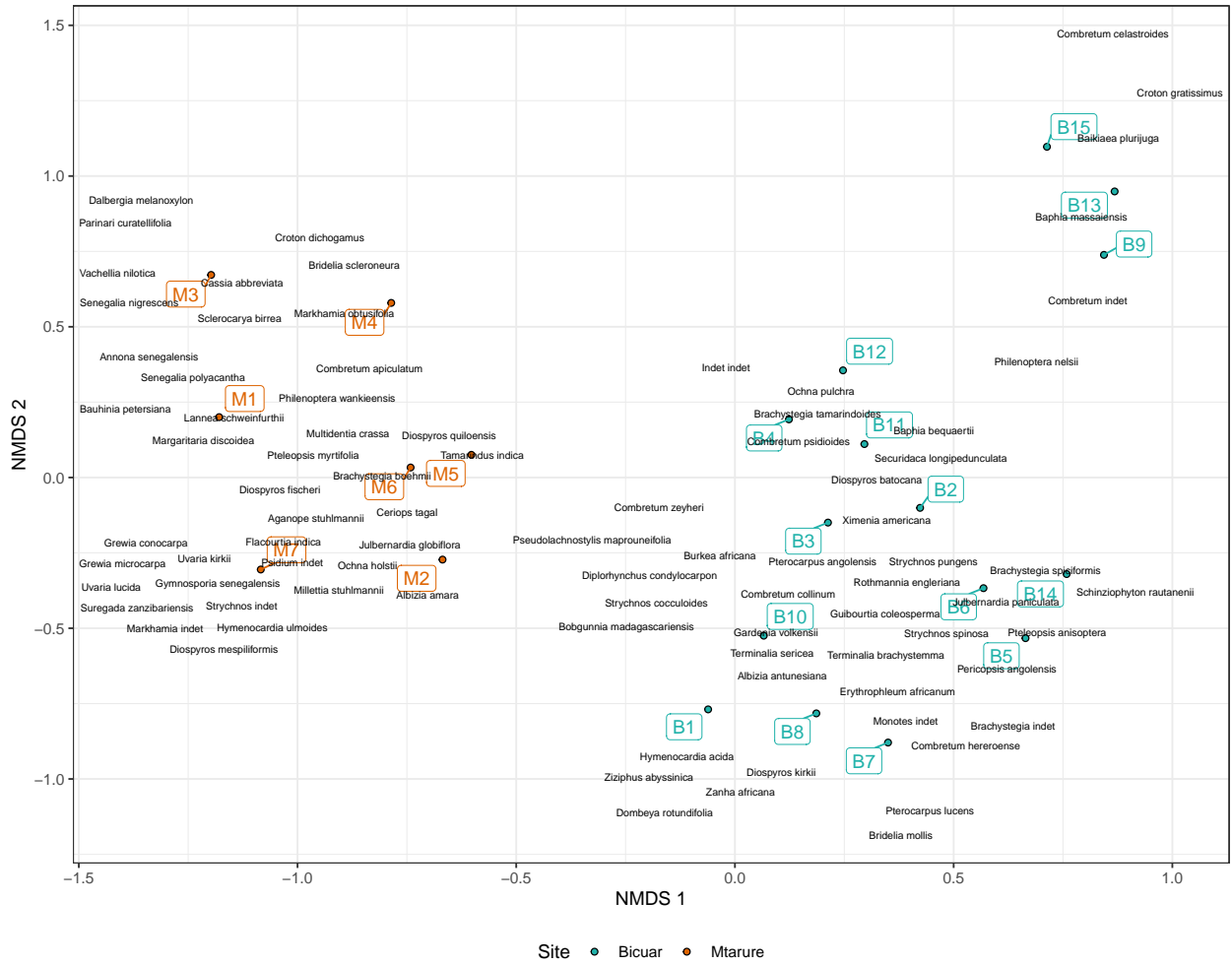


Figure 6: The first two axes of a Non-metric Multi-Dimensional Scaling (NMDS) analysis of tree species diversity in each plot. Species scores are labelled as black text, while plot scores are labelled as coloured points. Plots can be split into four principal groups: 1) B9, B13 and B15, dominated by *Baikiaea plurijuga*; 2) the other Bicular plots; 3) M2, M5, M6, and M7, dominated by *Julbernardia* spp., *Brachystegia* spp. and *Ochna* spp.; 4) M1, M3, and M4, dominated by *Senegalia* spp. and *Vachellia* spp..

3.3 Comparing subplot and plot measures of canopy structure

Plot-level and subplot-level canopy structure metrics were highly correlated in many cases (Figure 5). Plot canopy height especially, tended to be strongly positively correlated with subplot canopy complexity. Additionally, as canopy top roughness increases, many subplot canopy complexity and density metrics increase. In the majority of cases, both sites had similar correlations of subplot and plot measures of canopy structure, with notable exceptions for plot roughness vs. layer diversity, plot roughness vs. canopy cover, and plot canopy height vs. canopy cover.

Variance of plot canopy height and plot roughness was larger in Mtarure than Bicular. The in-

crease in variance was caused by two particularly sparse thorny savanna plots in Mtarure, M3 and M4, which had very low canopy height and roughness.

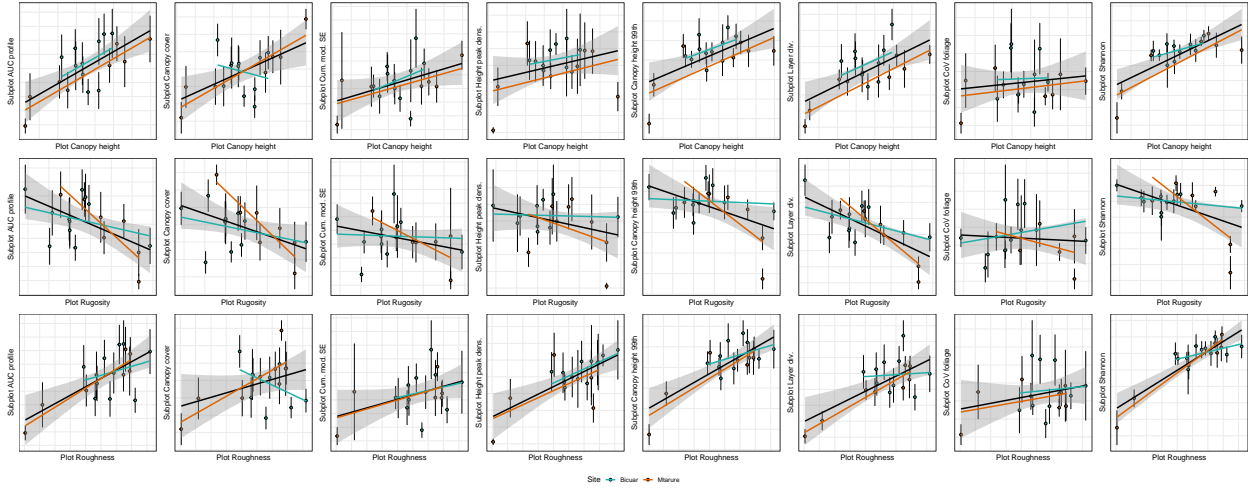


Figure 7: Bivariate plots of canopy structural metrics at the subplot (y axis) and plot level (x axis). Each point represents the mean values of a single plot. Points and linear model fits are coloured according to site. The black linear model combines both sites. Error bars on points are the standard deviation of mean subplot metrics across the plot.

4 Discussion

We investigated the effects of tree species diversity and structural diversity on several metrics of canopy complexity that were hypothesised to affect plot productivity. Species diversity appeared to generally have weak positive effects on canopy complexity at both the subplot and plot scales, while stand structural diversity had much stronger effects. The strongest determinant of canopy complexity was stem crowding, as measured by basal area and the Hegyi crowding index.

The positive relationships between species richness and subplot canopy complexity metrics observed in the subplot bivariate models were not seen in the linear mixed effects models. This is likely because the observed species richness effect was itself driven by stand structure. The Hegyi crowding index increases with stem density, i.e. decreased distance of individuals from the subplot centre. Species richness also increases with stem density, as a greater number of individuals is more likely to hold more species simply through sampling effects. **Jucker2015** however, did find that increased species diversity led to greater canopy packing in European forests, with trees in mixed forests having generally larger crowns. Our result that species diversity did not have consistent effects on canopy complexity may be specific to the vegetation type studied here. Southern African open woodlands are much more heavily affected by disturbance from fire and herbivory than temperate forests, meaning the effects of inter-specific competition are weakened as a driver

237 of stand and canopy structure ().

238 Canopy structure at the plot level was less well predicted by stand structure and species diversity
239 than subplot level canopy structure. Results at the plot level suggest that woodland vegetation
240 type and basal area has the greatest effect on canopy complexity. The two thorny savanna plots
241 in Mtarure produced strong positive effects of basal area and diameter variation on canopy cover,
242 canopy height, and canopy roughness, but when these plots are removed the remaining points do
243 not produce strong relationships.

244 5 Conclusion

Response	Predictor	Slope	F	R ²	Pred. T	Int. T
Total canopy foliage	CoV crown area	38.3±27.80	4.1(4,163)	0.07	0.17 -	2.03 *
Canopy cover	CoV crown area	0.0±0.00	4.3(4,163)	0.07	0.09 -	2.01 *
Cum. mod. SE	CoV crown area	-76.1±72.69	0.4(4,163)	0.01	0.30 -	0.89 -
Height peak dens.	CoV crown area	0.0±0.01	2.4(4,163)	0.04	0.14 -	0.77 -
Canopy height 99th	CoV crown area	0.0±0.01	6.6(4,163)	0.11	0.10 -	2.41 *
Layer div.	CoV crown area	0.0±0.01	12.0(4,163)	0.18	0.01 *	2.27 *
Total canopy foliage	CoV diam.	125.4±45.35	7.4(4,163)	0.12	0.01 **	1.96 -
Canopy cover	CoV diam.	0.0±0.00	3.2(4,163)	0.06	0.15 -	1.78 -
Cum. mod. SE	CoV diam.	-15.9±122.19	0.2(4,163)	0.00	0.90 -	0.67 -
Height peak dens.	CoV diam.	0.0±0.01	2.0(4,163)	0.04	0.16 -	0.49 -
Canopy height 99th	CoV diam.	0.0±0.01	9.1(4,163)	0.14	0.01 **	2.16 *
Layer div.	CoV diam.	0.1±0.01	17.6(4,163)	0.24	0.00 ***	2.43 *
Total canopy foliage	Hegyi crowding	7555.9±1784.72	15.2(4,163)	0.22	0.00 ***	1.78 -
Canopy cover	Hegyi crowding	0.3±0.03	62.1(4,163)	0.53	0.00 ***	1.06 -
Cum. mod. SE	Hegyi crowding	6586.3±5018.81	2.0(4,163)	0.04	0.19 -	0.95 -
Height peak dens.	Hegyi crowding	0.5±0.43	1.3(4,163)	0.02	0.24 -	-0.39 -
Canopy height 99th	Hegyi crowding	0.6±0.48	4.0(4,163)	0.07	0.22 -	1.38 -
Layer div.	Hegyi crowding	3.0±0.58	19.7(4,163)	0.27	0.00 ***	0.45 -
Total canopy foliage	Richness	2393.9±874.72	5.4(4,163)	0.09	0.01 **	0.73 -
Canopy cover	Richness	0.0±0.02	6.5(4,163)	0.11	0.20 -	2.79 **
Cum. mod. SE	Richness	2968.3±2306.08	0.8(4,163)	0.01	0.20 -	-0.03 -
Height peak dens.	Richness	-0.1±0.20	0.9(4,163)	0.02	0.56 -	0.09 -
Canopy height 99th	Richness	0.4±0.22	2.7(4,163)	0.05	0.06 -	-0.39 -
Layer div.	Richness	1.1±0.28	13.0(4,163)	0.19	0.00 ***	0.20 -

Table 3: Summary statistics of bivariate linear models for subplot canopy complexity metrics. Slope refers to the slope of the predictor term in the model, ± 1 standard error. R² refers to the whole model. Pred. T refers to the t-value of the slope of the predictor term in the model, while Int. T refers to the t-value of the interaction of the predictor and the effect of site. Asterisks indicate the p-value of these terms (***<0.001, **<0.01, *<0.05, .<0.1).

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