

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

John L. Godlee

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Abstract

Atmospheric CO₂ enrichment and human-induced climate change are expected to drive woody encroachment and an increase in tree cover across African savannas, with consequences for ecosystem function, particularly related to carbon dynamics. The patch dynamics of savanna-woodland mosaics are complex however, as woody growth is mediated by seasonal fire that is itself driven by woody canopy structure. It is unclear how variation in existing tree species composition and stand structure in this ecosystem affects canopy structure, and how this might determine future vegetation dynamics. In this study, I used terrestrial LiDAR at two miombo savanna sites, in Angola and Tanzania, measuring canopy cover and canopy structure to explore relationships between tree species diversity, stand structure, and canopy structure. I found that **WHAT**

1 Introduction

Atmospheric CO₂ enrichment, coupled with climate change, is expected to drive woody encroachment, i.e. proliferation of trees in previously non-wooded areas, and woody thickening, i.e. increased growth of trees in currently wooded areas, across the savanna biome over the coming century (Criado et al., 2020; Stevens et al., 2016; Mitchard & Flintrop, 2013). As atmospheric CO₂ concentrations increase, C₃ trees are expected to gain a competitive edge over C₄ grasses due to differences in photosynthetic pathway (Buitenwerf et al., 2012), with cascading effects on canopy cover, grass growth, and therefore disturbance regime (Bond & Midgley, 2012). If realised, woody encroachment and thickening will have significant effects on the global carbon cycle, as more CO₂ is stored as woody biomass, as well as myriad other effects on ecosystem structure (Donohue et al., 2013). Indeed, tropical savannas have been identified as the fastest increasing component of the terrestrial carbon sink (Sitch et al., 2015). Previous studies however, have reported wide variation in rates of woody encroachment and thickening (Mitchard & Flintrop, 2013), particularly in disturbance-prone savannas such as miombo woodlands in southern Africa (Lewis et al., 2009), and it is unclear how the fertilisation effect of atmospheric CO₂ enrichment will interact other ecosystem properties to alter vegetation (Körner, 2017; Reich et al., 2014).

Savanna vegetation is defined by the coexistence of trees and grasses (Scholes & Archer, 1997). In the tropical mesic savannas of southern Africa, disturbance by fire and herbivory are the main limitations on tree cover, preventing the competitive exclusion of shade-sensitive C₄ grasses where climatic conditions would otherwise allow for closed canopy forest (Sankaran et al., 2005). C₄ grasses also provide the main fuel source for seasonal fires in these savannas (Frost, 1996), producing a positive feedback where an increase in tree cover reduces grass fuel load, reducing fire frequency and intensity, increasing tree cover, and so on (Staver & Koerner, 2015). As such, even small perturbations in tree cover can lead to large changes in vegetation structure if critical thresholds of tree cover are crossed (Hirota et al., 2011). Previous research has sought to identify environmental factors which affect tree cover and its responses to atmospheric CO₂ enrichment, but few have considered the functional role of the existing tree community and its effect on ecosystem processes.

Canopy structure describes the spatial distribution of tree canopy foliage (Lowman & Rinker, 2004). Canopy structural complexity, i.e. the spatial heterogeneity of foliage distribution within the canopy, has been linked to increased net ecosystem productivity (Hardiman et al., 2011; Chen et al., 2012; Law et al., 2001; Baldocchi & Wilson, 2001; Morin, 2015), increased resilience of productivity (Pretzsch, 2014), reduced understorey light penetration (Scheuermann et al., 2018; Fotis et al., 2018), and greater moderation of understorey micro-climate (Wright et al., 2017). Furthermore, in temperate and boreal forests, functional differences among coexisting tree species in their vertical and horizontal canopy occupation provide a link between species diversity, canopy structural complexity and canopy density, with canopy structure constituting a mechanism for observed positive biodiversity-ecosystem function effects in wooded ecosystems (Pretzsch, 2014; Barry et al., 2019). In tropical savannas, tree species diversity might therefore influence ecosystem-level woody thickening in response to elevated atmospheric CO₂, where diverse tree communities are less limited by competition due to niche separation, and can more effectively increase foliage density and reduce understorey light penetration, excluding grass and thus reducing disturbance.

As well as the species diversity of trees in a local neighbourhood, the spatial distribution and relative size of trees, i.e. stand structure, is also expected to affect canopy structural complexity (Stark et al., 2015). Heterogeneity in tree size, whether a result of species diversity, disturbance history or some other factor, is expected to increase canopy complexity and canopy density as individuals of different sizes occupy different parts of the vertical canopy space (Panzou et al., 2020), and may differ in light requirements (Charles-Dominique et al., 2018). Additionally, clustering of individuals in space is expected to increase canopy structural heterogeneity across the wider savanna landscape, but ultimately decrease total foliage density due to an increase in competitive interactions (Dohn et al., 2017). Clustering may occur as a result of disturbance history, or as a result of strong facilitation effects among individuals in stressful environments (Ratcliffe et al., 2017). More diverse communities may allow more dense clustering, as differences in canopy occupancy among species can reduce competition, meaning that diversity may reduce the negative effect of disturbance on tree cover ().

Canopy structure is multi-dimensional and has previously been explained using a plethora of simple metrics that originated in forest and community ecology (Kershaw et al., 2017). Assessments of canopy structure have most often modelled tree canopies as a series of ellipses (2D), ellipsoids or cones (3D) based on field measurements with measuring tapes (Jucker et al., 2015). 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 (Jonckheere et al., 2004). 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 its complexities (Muir et al., 2018; Calters et al., 2020).

In this study I 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 relate to tree neighbourhood diversity and stand structure. I aim to develop our understanding of how biotic ecosystem properties in savannas might mediate responses to atmospheric CO₂ enrichment and climate change. I hypothesise that neighbourhoods with greater tree diversity and greater structural diversity allow greater canopy complexity, and foliage density. Thus, more diverse savannas might more effectively increase growth under elevated atmospheric CO₂ and are more likely to experience woody thickening through their greater occupation of environmental niche space. I also consider the functional differences among tree species in these communities and assess how combinations of these functional groups affect

canopy structure and understorey light environment.

2 Materials and methods

2.1 Study sites

Field measurements were conducted at two sites, the first in Bicular 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 located in areas of savanna-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 greatest foliage volume in the canopy.

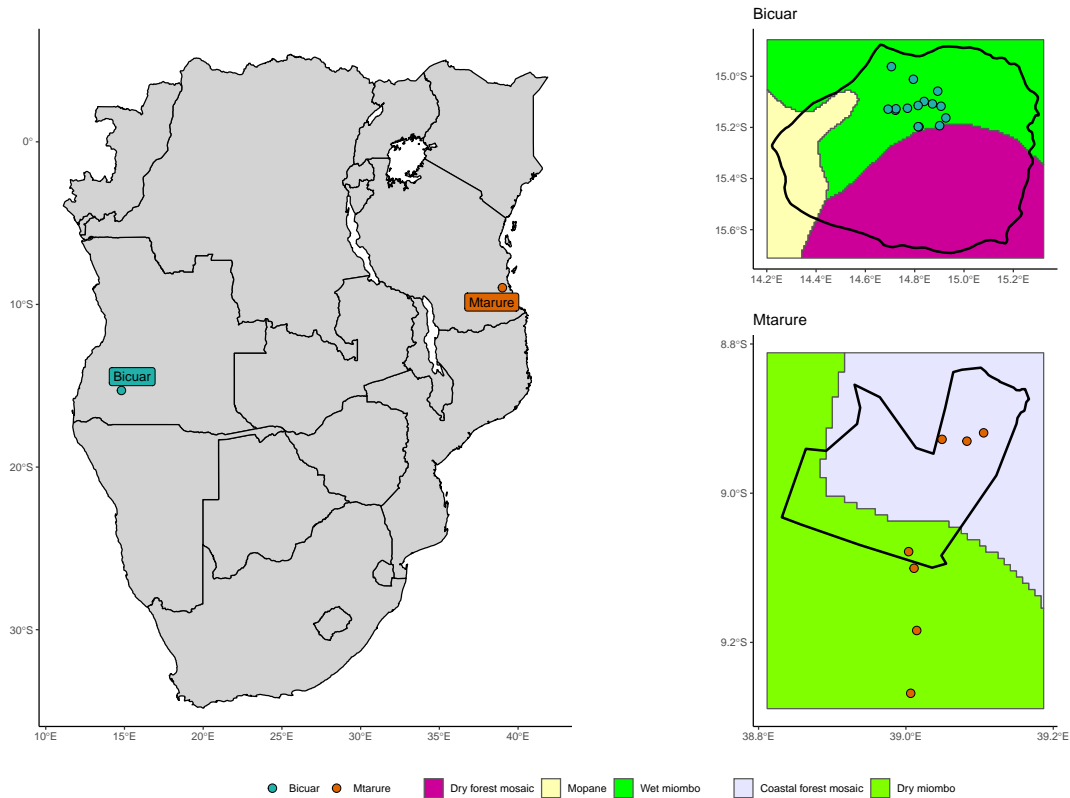


Figure 1: Location of study sites within southern Africa (left), and of 1 ha plots within each site (right). The black outlines in each site map denote the boundaries of protected areas which encompass the majority of study sites, Bicular National Park in Angola (top), and Mtarure Forest Reserve in Tanzania (bottom). The background of each site map is a re-classified version of White’s vegetation map (White, 1983). 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 tape 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 recorded the distance and direction from the subplot centre of each woody stem >5 cm diameter with canopy material inside the subplot. Within each subplot, a variable number of scans were recorded using a Leica HDS6100 phase-shift Terrestrial Laser Scanner (TLS). The number and position of scans within a subplot was determined by the arrangement of canopy material in the subplot. Scan positions were arranged to minimise shadows within the canopy of the subplot, and to maximise canopy penetration. The number of scans per subplot ranged between one and five across both sites.

2.3 Data analysis

2.3.1 Scan processing

Point clouds from scans in each subplot were registered and unified using Leica Cyclone (version 9.1), using five reflective cross targets visible to all scans. Point clouds were voxelised to cubic voxel sizes of different sizes depending on the application of the data. For subplot height profile estimation and gap fraction we used 5 cm³ voxels, and for whole plot canopy rugosity we used 50 cm³ voxels. Voxels were classified as filled if they intersected with one or more points. Variation in voxel size reflects the spatial scale of each analysis, and is bounded by the beam divergence of the scanner over longer distances (). Choosing voxels that are too small can result in pock-marked representations of surfaces that are especially problematic when calculating larger scale canopy structure metrics, such as canopy top roughness, while voxels that are too large can result in an over-estimation of plant volume when estimating canopy foliage density at the subplot scale (Seidel et al., 2012; Cifuentes et al., 2014). We used the noise reduction algorithm from Rusu et al. (2008) to discard points based on mean nearest neighbour distances. This effectively removed ‘ghost points’ produced by partial beam interceptions and also removed many erroneous returns caused by airborne dust particles, which was common at our study sites. Raw points clouds for each subplot had a mean of ~2.9e+08 points, ~4.5e+07 points after voxelisation, and ~2.1e+07 points after noise reduction.

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

We used ray-tracing to calculate canopy cover at the subplot centre from multiple TLS scans. Hemispherical images were created using the POV-ray software (). Voxels were represented as matt black cubes filling the voxel volume, with a white sky box and no light source. A ‘camera’ with a 180° fisheye lens was placed at the subplot centre within POV-Ray, at a height of 1.8 m pointing directly upwards. The images produced by POV-Ray were analysed using Hemiphot (ter Steege, 2018) to estimate canopy cover as the proportion of pixels filled by canopy material.

We calculated a number of metrics to describe different aspects of canopy complexity within each subplot in addition to canopy cover. Canopy height was measured as the 99th percentile of height of canopy material within the subplot. Layer diversity was calculated using Shannon entropy on foliage density of 50 cm height bins through the tree canopy. The uniformity of foliage distribution was calculated by fitting a linear model to the cumulative foliage density profile, then extracting the standard error on the slope estimate of this linear model.

At the plot level, canopy complexity was measured with six metrics. Of these, canopy top roughness was measured as the standard deviation of canopy height across the plot, and canopy rugosity was measured according to Hardiman et al. (2011), as the standard deviation of vertical and horizontal foliage density within 0.5 m cubic bins.

2.4 Stand structure

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

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

At the plot level, we estimated the regularity of species spatial distribution using the spatial mingling index (von Gadow & Hui, 2002). We also measured the uniformity of whole plot stem distribution using the winkelmass, which measures the degree of clustering of stems (von Gadow & Hui, 2002). Finally, we calculated plot level stem density to estimate crowding.

2.5 Statistical analysis

Linear mixed effects models tested the effects of tree species diversity and stand structural diversity on canopy complexity. Mixed models were used to account for the highly nested sampling design of subplots within plots and plots within sites. Two sets of models were conducted, the first at the subplot level with random effects for plot nested within site, and the second at the plot level with random effects for site only. Separate models were fitted for each canopy complexity metric, resulting in six models at the subplot level and five models at the plot level. We compared the AIC values and Akaike weights of all models for a particular canopy complexity metric to find the ‘best model’, i.e. the model which minimised variance in the fitted values, with penalties for complex model structure (Akaike, 1992).

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

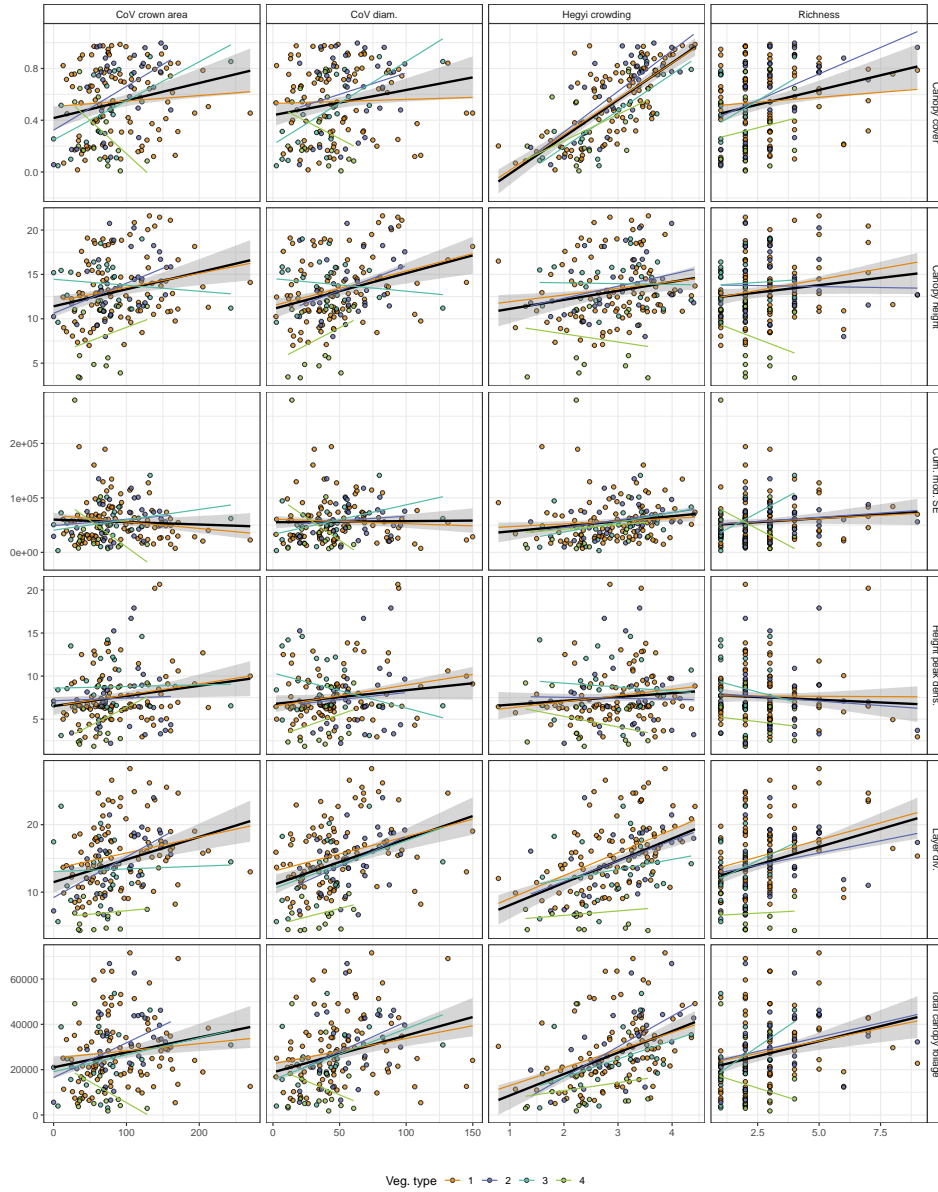
175 **3.1 Vertical canopy complexity**

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.

176 Bivariate plots showed that subplot species diversity, measured by species richness of the tree
 177 neighbourhood around each 10 m diameter subplot, appeared to have weak but positive effects
 178 on canopy layer diversity and total canopy cover (Figure 2). The Hegyi crowding index and
 179 both stand structural diversity metrics had strong positive effects on canopy complexity, for
 180 all metrics except for uniformity of foliage distribution and height of peak foliage density. The
 181 two sites in our study had similar bivariate relationships, with interaction effects of site in the
 182 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 being 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.

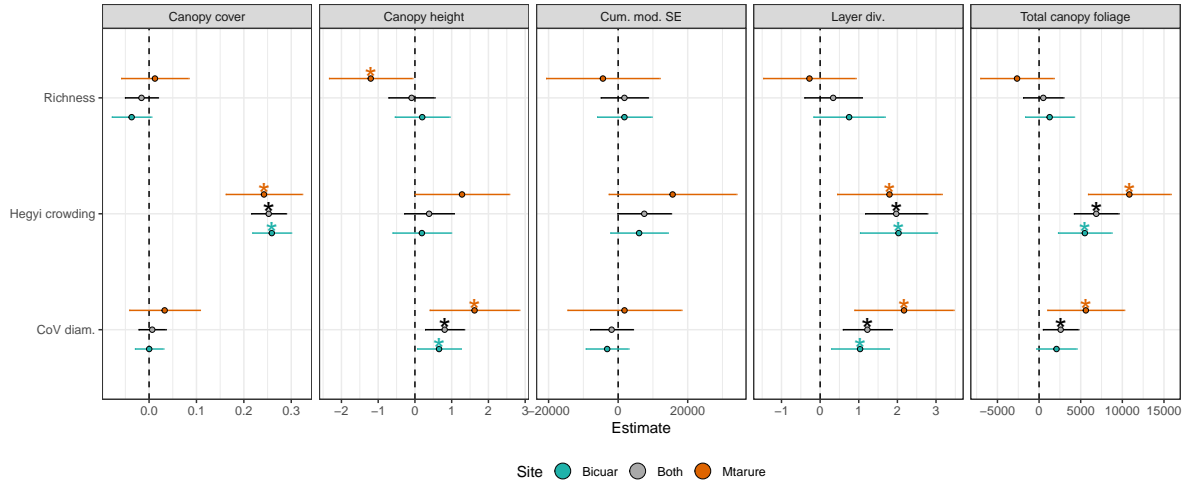


Figure 3: Standardized fixed effect slopes for each model of a canopy structure metric. Slope estimates are ± 1 standard error. Slope estimates where the interval (standard error) does not overlap zero are considered to be significant effects. Points are coloured according to site.

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 available 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.

200 3.2 Canopy rugosity

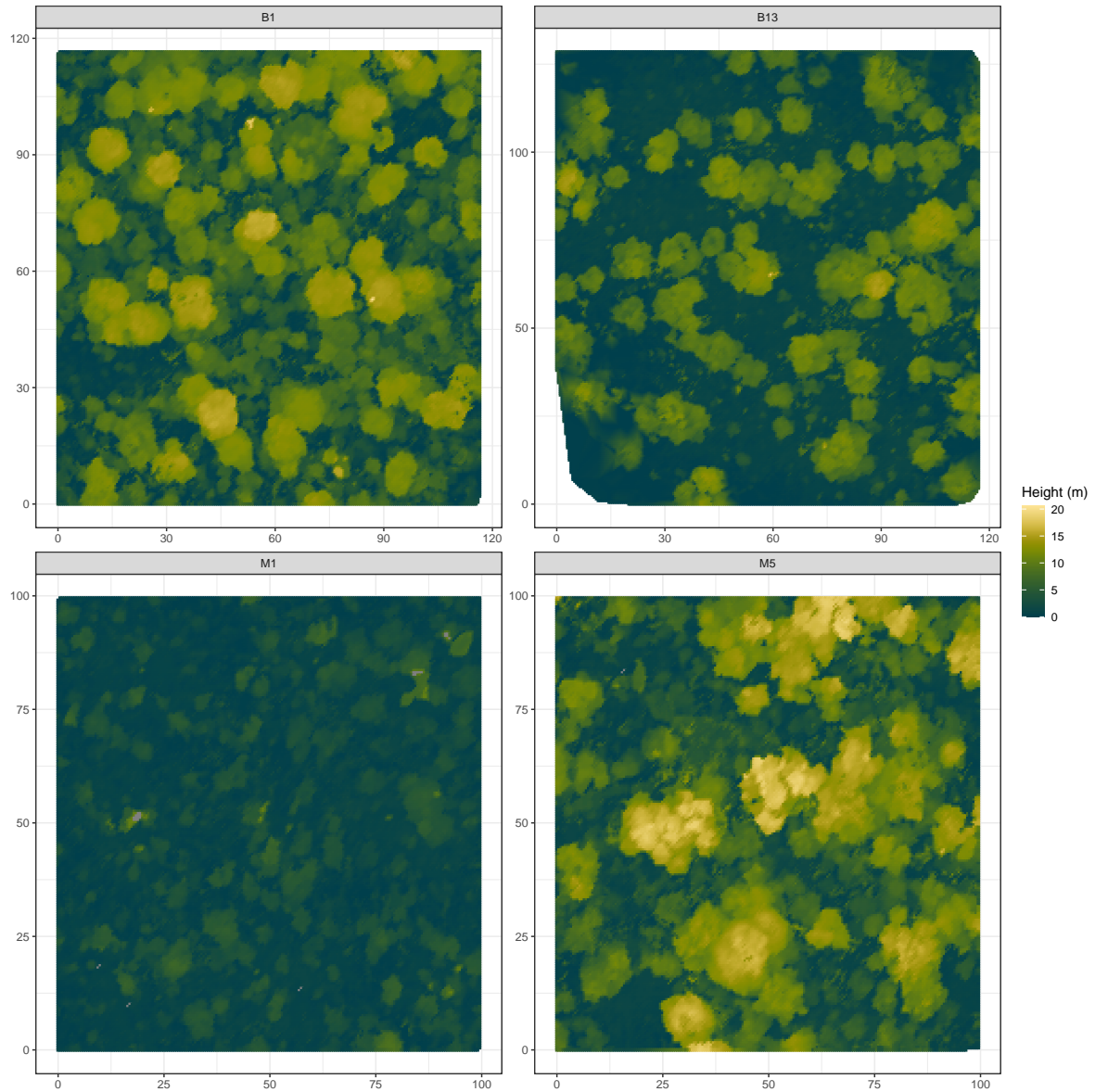


Figure 4: Representative canopy surface models for each vegetation type identified in the Non-metric Multi-dimensional Scaling (NMDS) analysis. Plot titles show the plot name and the vegetation type.

201 Similar to the subplot analyses, at the whole-plot scale tree species diversity, measured here
 202 by the Shannon index, tended to have weak positive effects on canopy complexity metrics,
 203 while stand structural diversity metrics had stronger positive effects (Figure 5). Strong positive
 204 relationships of basal area on canopy complexity are driven mostly by two plots with particularly
 205 low basal area in Mtarure, M3 and M4. These plots are sparse thorny savanna, dominated
 206 by *Senegalia* spp. (Figure 7). Indeed, linear models using only plots in bicuar show divergent
 207 relationships. These two plots also have particularly low canopy cover, canopy height, and
 208 canopy top roughness, despite having similar tree species diversity and spatial distribution of
 209 trees (winkelmass) as other plots.

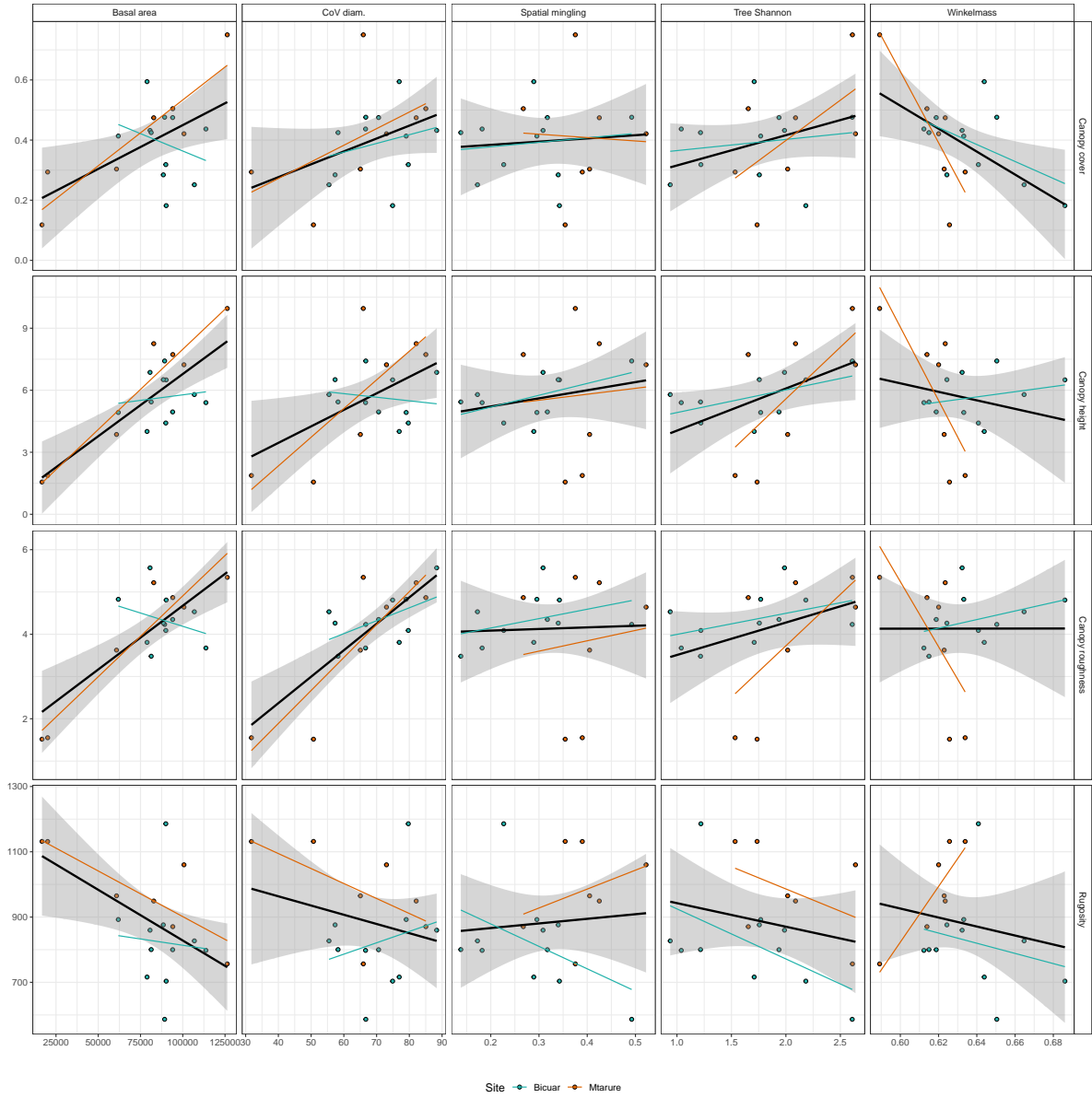


Figure 5: Bivariate relationships between diversity and stand structure metrics (x axis) and whole-plot canopy structure metrics (y axis). Points and linear model lines of best fit are coloured by site. The thick black line of best fit is a linear model including both sites.

210 Linear mixed effects models show that increased spatial clustering of trees causes a decrease in
 211 canopy cover. Increased spatial mingling of tree species causes an increase in canopy rugosity,
 212 while in contrast an increase in overall tree species diversity appears to cause a decrease in
 213 canopy rugosity. An increase in the heterogeneity of stem diameter causes an increase in canopy
 214 top roughness.

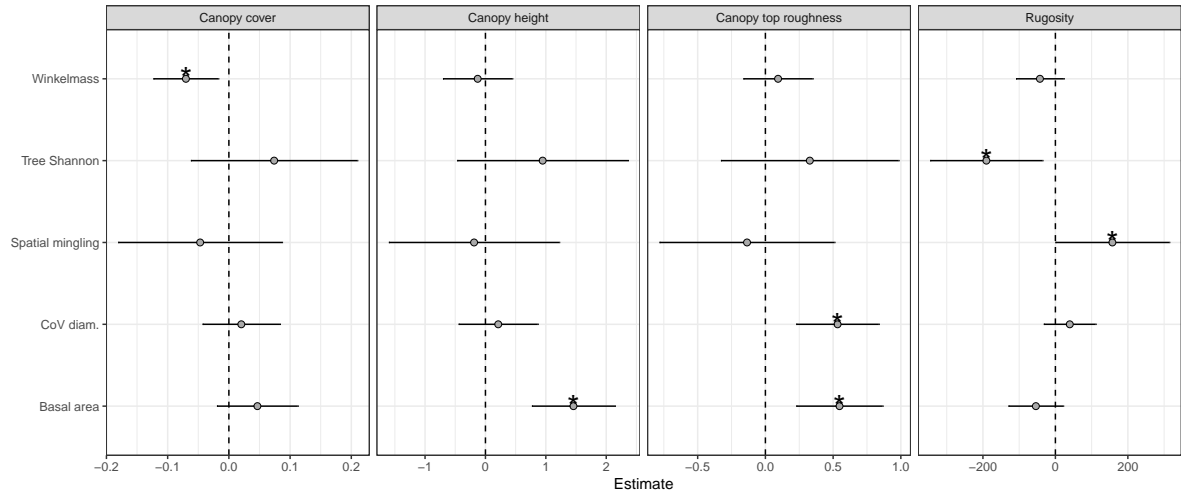


Figure 6: Standardized fixed effect slopes for whole-plot canopy rugosity. Slope estimates are ± 1 standard error. Slope estimates where the interval (standard error) does not overlap zero are considered to be significant effects.

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

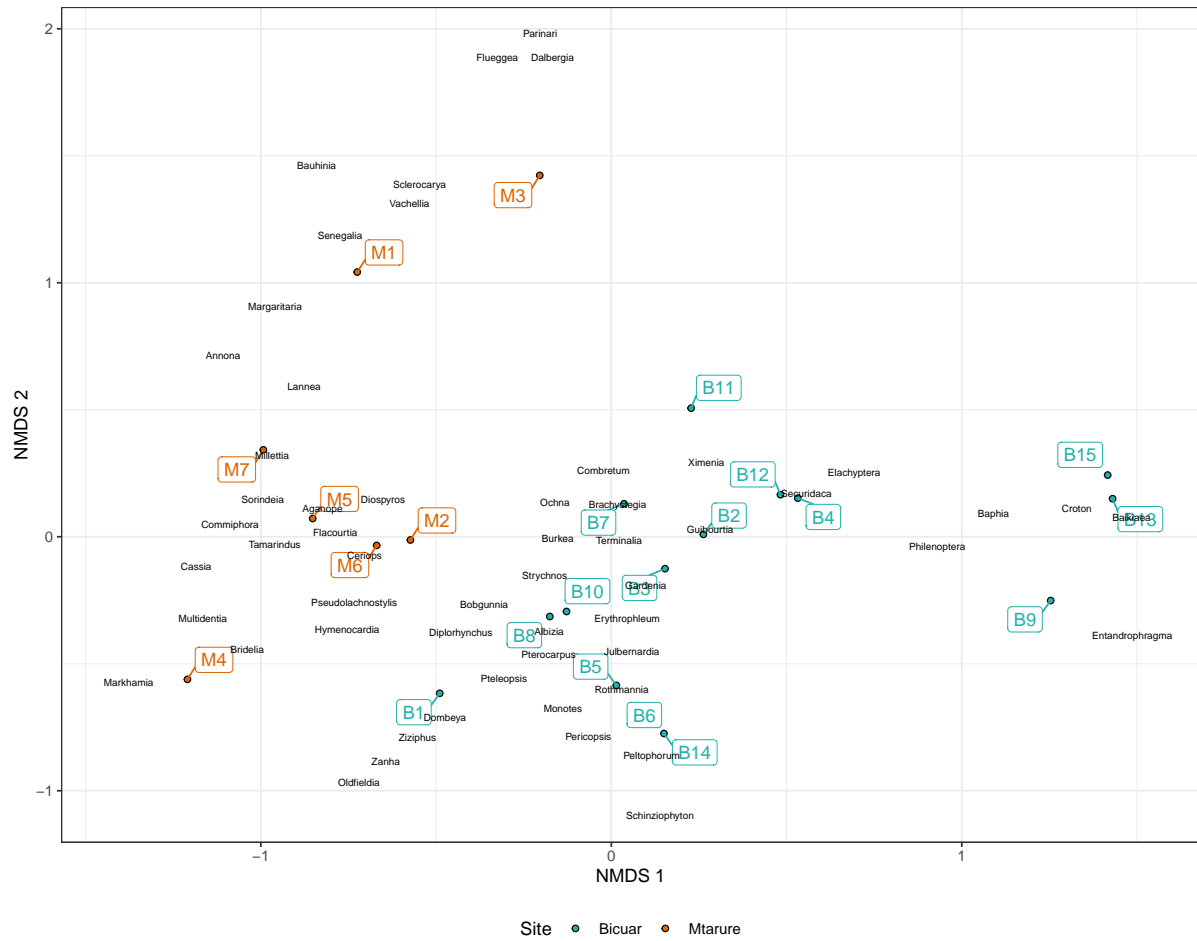


Figure 7: The first two axes of a Non-metric Multi-Dimensional Scaling (NMDS) analysis of tree species diversity in each plot. Species scores are labelled as black text, while plot scores are labelled as coloured points. Plots can be split into four principal groups: 1) B9, B13 and B15, dominated by *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 6). 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 increase in variance was caused by two particularly sparse thorny savanna plots in Mtarure, M3 and M4, which had very low canopy height and roughness.

5 Conclusion

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