

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

John L. Godlee

4th August 2021

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 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, 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 resulting in a change 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 provides 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 those 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 the negative density dependency effect that would occur among individuals from the same species.

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 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. Thus, more diverse savannas might more effectively increase growth under elevated atmospheric CO₂ and are more likely to experience woody thickening. We also consider the functional differences among species in these communities and assess how combinations of these functional groups affect canopy structure.

2 Materials and methods

2.1 Study sites

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 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 greatest foliage volume in the canopy.

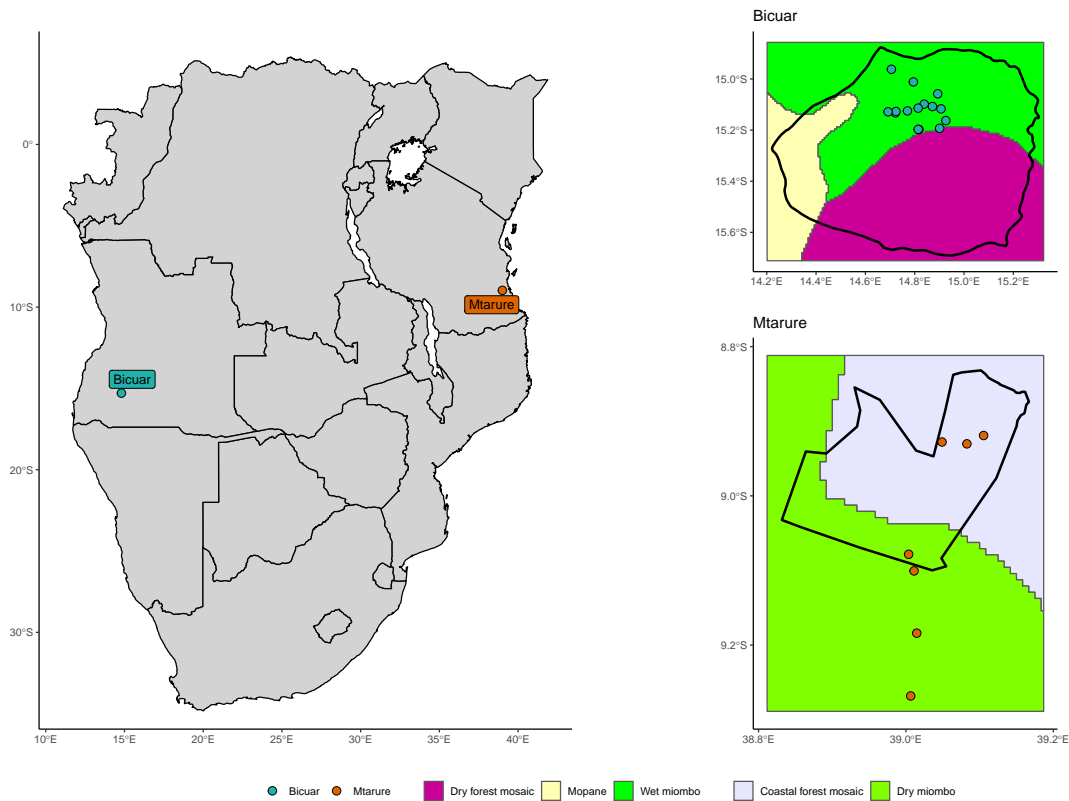


Figure 1: Location of study sites within southern Africa (left), and of 1 ha plots within each site (right). The black outlines in each site map denote the boundaries of protected areas which encompass the majority of study sites, Bicular National Park in Angola (top), and Mtarure Forest Reserve in Tanzania (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 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). 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 in 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 10 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 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 $\sim 2.9\text{e}+08$ points, $\sim 4.5\text{e}+07$ points after voxelisation, and $\sim 2.1\text{e}+07$ 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 converted to 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 0.5 m 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. The height of peak foliage density was calculated by fitting a loess model to the foliage height profile and extracting the height at which foliage density peaked.

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.

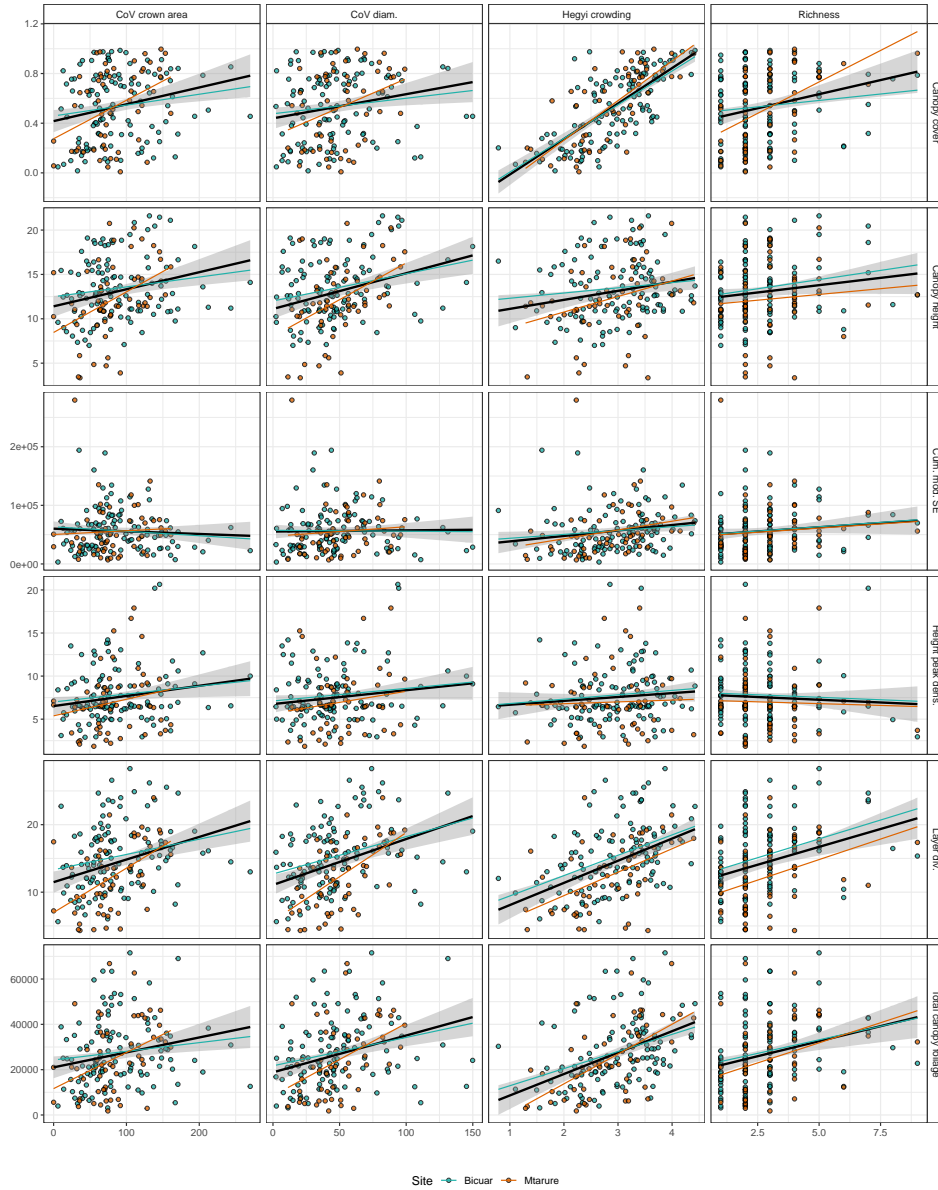


Figure 2: Bivariate relationships between subplot canopy structure metrics (y axis) and diversity/stand structure metrics (x axis). Points and linear model lines of best fit are coloured by site. The black line of best fit is a linear model including both sites. See **supp. material** for a comparison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

Bivariate plots showed that subplot species diversity, measured by species richness of the tree neighbourhood around each 10 m diameter subplot, appeared to have weak but positive effects 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**).

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

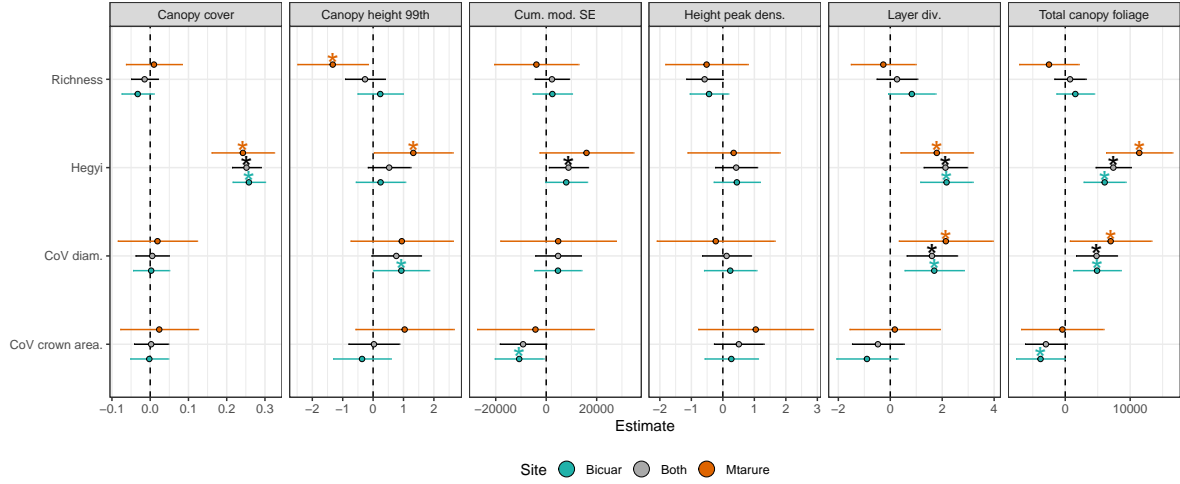


Figure 3: Standardized fixed effect slopes for each model of a canopy structure metric. Slope estimates are ± 1 standard error. Slope estimates where the interval (standard error) does not overlap zero are considered to be significant effects. Points are coloured according to site.

194 The model selection process showed that the best model for layer diversity included species
 195 richness. Stand structural diversity metrics were included in the best models for all canopy
 196 complexity metrics except for canopy cover, which was predicted solely by the Hegyi crowding
 197 index. Models of layer diversity, total foliage density, and canopy cover were predicted well by a
 198 combination of crowding and stand structural diversity. Models of height of peak foliage density,
 199 canopy height, and uniformity of foliage distribution were poorly constrained by the available
 200 fixed effects, with R^2_m of $\sim 5\%$. The majority of the total model effect on canopy height came
 201 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			✓		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.

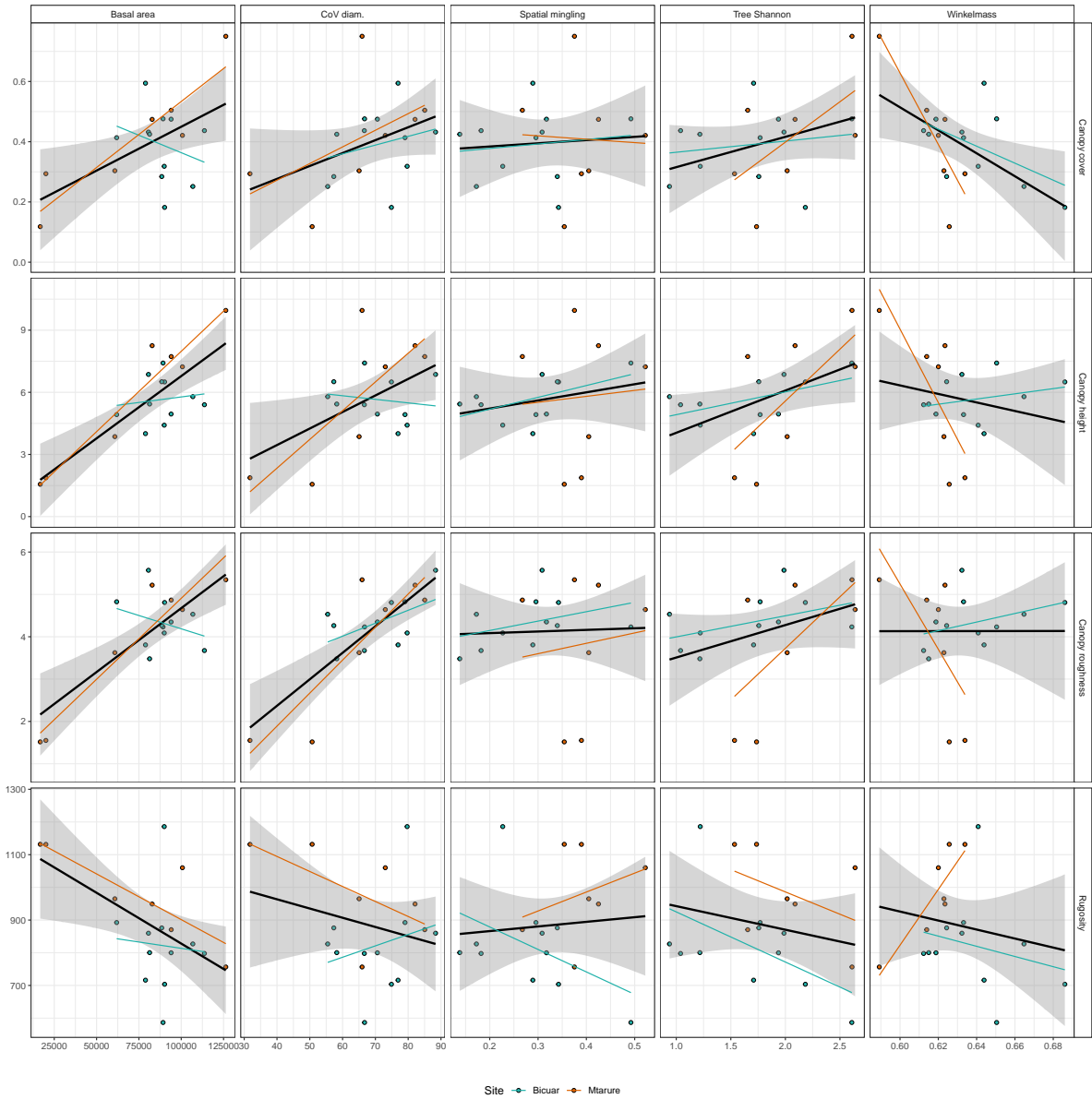


Figure 4: Bivariate relationships between diversity and stand structure metrics (x axis) and whole-plot canopy structure metrics (y axis). Points and linear model lines of best fit are coloured by site. The thick black line of best fit is a linear model including both sites.

Linear mixed effects models show that increased spatial clustering of trees causes a decrease in

213 canopy cover. Increased spatial mingling of tree species causes an increase in canopy rugosity,
 214 while in contrast an increase in overall tree species diversity appears to cause a decrease in
 215 canopy rugosity. An increase in the heterogeneity of stem diameter causes an increase in canopy
 216 top roughness.

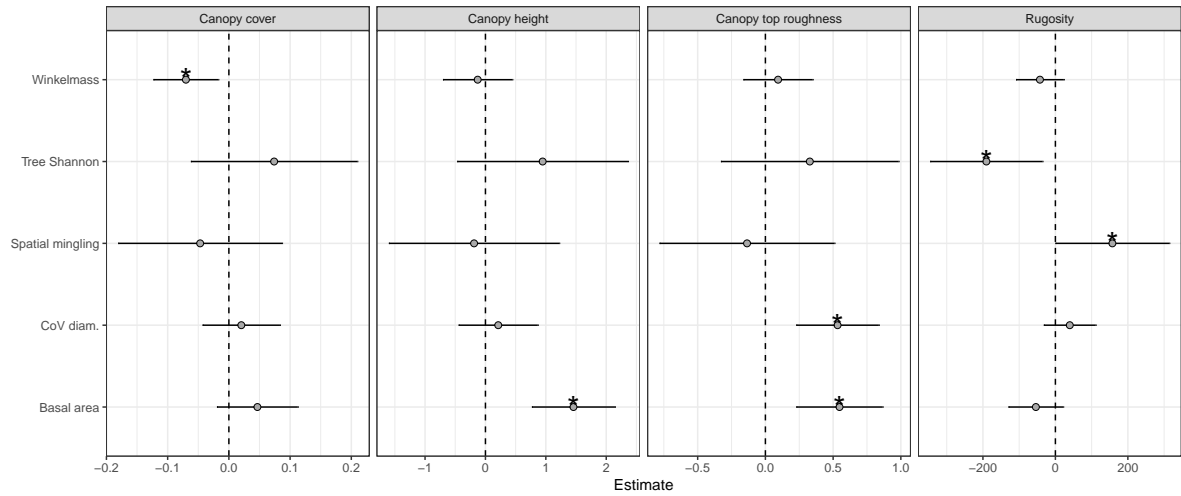


Figure 5: Standardized fixed effect slopes for whole-plot canopy rugosity. Slope estimates are ± 1 standard error. Slope estimates where the interval (standard error) does not overlap zero are considered to be significant effects.

217 Model selection showed that all plot canopy complexity metrics except canopy rugosity were
 218 best 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.

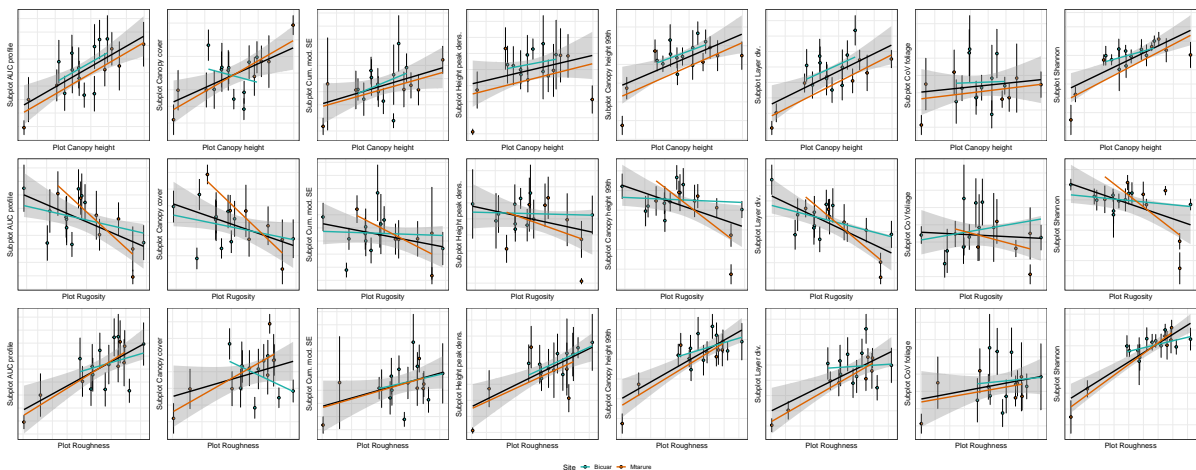


Figure 7: Bivariate plots of canopy structural metrics at the subplot (y axis) and plot level (x axis). Each point represents the mean values of a single plot. Points and linear model fits are coloured according to site. The black linear model combines both sites. Error bars on points are the standard 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. Jucker et al. (2015) 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 of stand and canopy structure ().

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

Facilitation might be more important in these woodlands than in temperate woodlands. Large canopy trees may cause micro-climate amelioration for understorey saplings, protecting them from drying conditions caused by the sun and wind. Facilitation has been under-played in BEFR research (Wright et al., 2021).

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	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	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	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	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).

References

- Akaike, H. (1992). ‘Information theory and an extension of the maximum likelihood principle’. In: *Breakthroughs in Statistics*, pp. 610–624. DOI: http://dx.doi.org/10.1007/978-1-4612-0919-5_38.
- Baldocchi, D. D. & K. B. Wilson (2001). ‘Modeling CO₂ and water vapor exchange of a temperate broadleaved forest across hourly to decadal time scales’. In: *Ecological Modelling* 142.1-2, pp. 155–184. DOI: 10.1016/S0304-3800(01)00287-3.
- Barry, K. E., L. Mommer, J. van Ruijven, C. Wirth, A. J. Wright, Y. Bai, J. Connolly, G. B. D. Deyn, H. de Kroon, F. Isbell et al. (2019). ‘The Future of Complementarity: Disentangling Causes from Consequences’. In: *Trends in Ecology & Evolution* 34.2, pp. 167–180. DOI: 10.1016/j.tree.2018.10.013.
- Bond, W. J. & G. F. Midgley (2012). ‘Carbon dioxide and the uneasy interactions of trees and savannah grasses’. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 367.1588, pp. 601–612. DOI: 10.1098/rstb.2011.0182.
- Buitenwerf, R., W. J. Bond, N. Stevens & W. S. W. Trollope (2012). ‘Increased tree densities in South African savannas: >50 years of data suggests CO₂ as a driver’. In: *Global Change Biology* 18.2, pp. 675–684. DOI: 10.1111/j.1365-2486.2011.02561.x.
- Calders, K., J. Adams, J. Armston, H. Bartholomeus, S. Bauwens, L. P. Bentley, J. Chave, F. M. Danson, M. Demol, M. Disney et al. (2020). ‘Terrestrial laser scanning in forest ecology: Expanding the horizon’. In: *Remote Sensing of Environment* 251, p. 112102. DOI: 10.1016/j.rse.2020.112102.
- Charles-Dominique, T., G. F. Midgley, K. W. Tomlinson & W. J. Bond (2018). ‘Steal the light: shade vs fire adapted vegetation in forest-savanna mosaics’. In: *New Phytologist* 218.4, pp. 1419–1429. DOI: 10.1111/nph.15117.
- Chen, J. M., G. Mo, J. Pisek, J. Liu, F. Deng, M. Ishizawa & D. Chan (2012). ‘Effects of foliage clumping on the estimation of global terrestrial gross primary productivity’. In: *Global Biogeochemical Cycles* 26.1, n/a–n/a. DOI: 10.1029/2010gb003996.
- Cifuentes, R., D. V. der Zande, J. Farifteh, C. Salas & P. Coppin (2014). ‘Effects of voxel size and sampling setup on the estimation of forest canopy gap fraction from terrestrial laser scanning data’. In: *Agricultural and Forest Meteorology* 194, pp. 230–240. DOI: 10.1016/j.agrformet.2014.04.013.
- Criado, M. G., I. H. Myers-Smith, A. D. Bjorkman, C. E. R. Lehmann & N. Stevens (2020). ‘Woody plant encroachment intensifies under climate change across tundra and savanna biomes’. In: *Global Ecology and Biogeography* 29.5, pp. 925–943. DOI: 10.1111/geb.13072.
- Dohn, J., D. J. Augustine, N. P. Hanan, J. Ratnam & M. Sankaran (2017). ‘Spatial vegetation patterns and neighborhood competition among woody plants in an East African savanna’. In: *Ecology* 98.2, pp. 478–488. DOI: 10.1002/ecy.1659.
- Donohue, R. J., M. L. Roderick, T. R. McVicar & G. D. Farquhar (2013). ‘Impact of CO₂ fertilization on maximum foliage cover across the globe’s warm, arid environments’. In: *Geophysical Research Letters* 40.12, pp. 3031–3035. DOI: 10.1002/grl.50563.
- Fotis, A. T., T. H. Morin, R. T. Fahey, B. S. Hardiman, G. Bohrer & P. S. Curtis (2018). ‘Forest structure in space and time: Biotic and abiotic determinants of canopy complexity and their effects on net primary productivity’. In: *Agricultural and Forest Meteorology* 250-251, pp. 181–191. DOI: 10.1016/j.agrformet.2017.12.251.
- Frost, P. (1996). ‘The ecology of miombo woodlands’. In: *The miombo in transition: woodlands and welfare in Africa*. Ed. by B. Campbell. Bogor, Indonesia: Center for International Forestry Research, pp. 11–55.
- Hardiman, B. S., G. Bohrer, C. M. Gough, C. S. Vogel & P. S. Curtis (2011). ‘The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest’. In: *Ecology* 92.9, pp. 1818–1827. DOI: 10.1890/10-2192.1.

- Hegy, F. (1974). 'A simulation model for managing jack-pine stands'. In: *Royal College of Forestry*, editor. Stockholm, Sweden: Royal College of Forestry, pp. 74–90.
- Hirota, M., M. Holmgren, E. H. Van Nes & M. Scheffer (2011). 'Global resilience of tropical forest and savanna to critical transitions'. In: *Science* 334, pp. 232–235. DOI: 10.1126/science.1210657.
- Jonckheere, I., S. Fleck, K. Nackaerts, B. Muys, P. Coppin, M. Weiss & F. Baret (2004). 'Review of methods for in situ leaf area index determination'. In: *Agricultural and Forest Meteorology* 121.1-2, pp. 19–35. DOI: 10.1016/j.agrformet.2003.08.027.
- Jucker, T., O. Bouriaud & D. A. Coomes (2015). 'Crown plasticity enables trees to optimize canopy packing in mixed-species forests'. In: *Functional Ecology* 29.8, pp. 1078–1086. DOI: 10.1111/1365-2435.12428.
- Kershaw, J. A., M. J. Ducey, T. W. Beers & B. Husch (2017). *Forest Mensuration*. Chichester, UK: John Wiley & Sons. ISBN: 9781118902035.
- Körner, C. (2017). 'A matter of tree longevity'. In: *Science* 355.6321, pp. 130–131. DOI: 10.1126/science.aal2449.
- Law, B. E., A. Cescatti & D. D. Baldocchi (2001). 'Leaf area distribution and radiative transfer in open-canopy forests: implications for mass and energy exchange'. In: *Tree Physiology* 21.12-13, pp. 777–787. DOI: 10.1093/treephys/21.12-13.777.
- Lewis, S. L., G. Lopez-Gonzalez, B. Sonké, K. Affum-Baffoe, T. R. Baker, L. O. Ojo, O. L. Phillips, J. M. Reitsma, L. White, J. A. Comiskey et al. (2009). 'Increasing carbon storage in intact African tropical forests'. In: *Nature* 457.7232, pp. 1003–1006. DOI: 10.1038/nature07771.
- Lowman, M. D. & H. B. Rinker (2004). *Forest Canopies*. Physiological Ecology. Burlington MA, USA: Elsevier Science. ISBN: 9780080491349.
- Mitchard, E. T. A. & C. M. Flintrop (2013). 'Woody encroachment and forest degradation in sub-Saharan Africa's woodlands and savannas 1982-2006'. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 368.1625, p. 20120406. DOI: 10.1098/rstb.2012.0406.
- Morin, X. (2015). 'Species richness promotes canopy packing: a promising step towards a better understanding of the mechanisms driving the diversity effects on forest functioning'. In: *Functional Ecology* 29.8, pp. 993–994. DOI: 10.1111/1365-2435.12473.
- Muir, J., S. Phinn, T. Eyre & P. Scarth (2018). 'Measuring plot scale woodland structure using terrestrial laser scanning'. In: *Remote Sensing in Ecology and Conservation* 4.4, pp. 320–338. DOI: 10.1002/rse2.82.
- Panzou, G. J. L., A. Fayolle, T. Jucker, O. L. Phillips, S. Bohlman, L. F. Banin, S. L. Lewis, K. Affum-Baffoe, L. F. Alves, C. Antin et al. (2020). 'Pantropical variability in tree crown allometry'. In: *Global Ecology and Biogeography* 30.2, pp. 459–475. DOI: 10.1111/geb.13231.
- Pretzsch, H. (2014). 'Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures'. In: *Forest Ecology and Management* 327, pp. 251–264. DOI: <http://dx.doi.org/10.1016/j.foreco.2014.04.027>.
- Ratcliffe, S., C. Wirth, T. Jucker, F. van der Plas, M. Scherer-Lorenzen, K. Verheyen, E. Allan, R. Benavides, H. Bruelheide, B. Ohse et al. (2017). 'Biodiversity and ecosystem functioning relations in European forests depend on environmental context'. In: *Ecology Letters* 20, pp. 1414–1426. DOI: <http://dx.doi.org/10.1111/ele.12849>.
- Reich, P. B., S. E. Hobbie & T. D. Lee (2014). 'Plant growth enhancement by elevated CO₂ eliminated by joint water and nitrogen limitation'. In: *Nature Geoscience* 7.12, pp. 920–924. DOI: 10.1038/ngeo2284.
- Rusu, R. B., Z. C. Marton, N. Blodow, M. Dolha & M. Beetz (2008). 'Towards 3D Point cloud based object maps for household environments'. In: *Robotics and Autonomous Systems* 56.11, pp. 927–941. DOI: 10.1016/j.robot.2008.08.005.
- Sankaran, M., N. P. Hanan, R. J. Scholes, J. Ratnam, D. J. Augustine, B. S. Cade, J. Gignoux, S. I. Higgins, X. Le Roux, F. Ludwig et al. (2005). 'Determinants of woody cover in African savannas'. In: *Nature* 438.8, pp. 846–849. DOI: <http://dx.doi.org/10.1038/nature04070>.

- Scheuermann, C. M., L. E. Nave, R. T. Fahey, K. J. Nadelhoffer & C. M. Gough (2018). ‘Effects of canopy structure and species diversity on primary production in upper Great Lakes forests’. In: *Oecologia* 188.2, pp. 405–415. DOI: 10.1007/s00442-018-4236-x.
- Scholes, R. J. & S. R. Archer (1997). ‘Tree grass interactions in savannas’. In: *Annual Review of Ecology and Systematics*.
- Seidel, D., S. Fleck & C. Leuschner (2012). ‘Analyzing forest canopies with ground-based laser scanning: A comparison with hemispherical photography’. In: *Agricultural and Forest Meteorology* 154-155, pp. 1–8. DOI: 10.1016/j.agrformet.2011.10.006.
- Sitch, S., P. Friedlingstein, N. Gruber, S. D. Jones, G. Murray-Tortarolo, A. Ahlström, S. C. Doney, H. Graven, C. Heinze, C. Huntingford et al. (2015). ‘Recent trends and drivers of regional sources and sinks of carbon dioxide’. In: *Biogeosciences* 12.3, pp. 653–679. DOI: 10.5194/bg-12-653-2015.
- Stark, S. C., B. J. Enquist, S. R. Saleska, V. Leitold, J. Schietti, M. Longo, L. F. Alves, P. B. Camargo & R. C. Oliveira (2015). ‘Linking canopy leaf area and light environments with tree size distributions to explain Amazon forest demography’. In: *Ecology Letters* 18.7, pp. 636–645. DOI: 10.1111/ele.12440.
- Staver, A. C. & S. E. Koerner (2015). ‘Top-down and bottom-up interactions determine tree and herbaceous layer dynamics in savanna grasslands’. In: *Trophic Ecology: Bottom-up and Top-Down Interactions Across Aquatic and Terrestrial Systems*. Ed. by K. J. La Pierre & T. C. Hanley. Cambridge, United Kingdom: Cambridge University Press, pp. 86–106.
- Stevens, N., C. E. R. Lehmann, B. P. Murphy & G. Durigan (2016). ‘Savanna woody encroachment is widespread across three continents’. In: *Global Change Biology* 23.1, pp. 235–244. DOI: 10.1111/gcb.13409.
- ter Steege, H. (2018). *Hemiphot.R: Free R scripts to analyse hemispherical photographs for canopy openness, leaf area index and photosynthetic active radiation under forest canopies*. Unpublished report. Leiden, The Netherlands: Naturalis Biodiversity Center. URL: <https://github.com/Naturalis/Hemiphot>.
- von Gadow, K. & G. Hui (2002). *Characterising forest spatial structure and diversity*. Ed. by L. Bjoerk. Lund, Sweden, pp. 20–30.
- White, F. (1983). *The Vegetation of Africa: A descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa*. Paris, France: UNESCO. DOI: 10.2307/2260340.
- Wright, A. J., W. D. A. Wardle, W. R. Callaway & A. Gaxiola (2017). ‘The overlooked role of facilitation in biodiversity experiments’. In: *Trends in Ecology & Evolution* 32, pp. 383–390. DOI: 10.1016/j.tree.2017.02.011.
- Wright, A. J., K. E. Barry, C. J. Lortie & R. M. Callaway (2021). ‘Biodiversity and ecosystem functioning: Have our experiments and indices been underestimating the role of facilitation?’ In: *Journal of Ecology* 109.5. Ed. by M. Rees, pp. 1962–1968. DOI: 10.1111/1365-2745.13665.
- Zhang, K., S.-C. Chen, D. Whitman, M.-L. Shyu, J. Yan & C. Zhang (2003). ‘A progressive morphological filter for removing nonground measurements from airborne LIDAR data’. In: *IEEE Transactions on Geoscience and Remote Sensing* 41.4, pp. 872–882. DOI: 10.1109/tgrs.2003.810682.