BIODIVERSITY - ECOSYSTEM FUNCTION RELATIONSHIPS IN SOUTHERN AFRICAN WOODLANDS

THE UNIVERSITY
of EDINBURGH

John L. Godlee

Thesis submitted for the degree of Doctor of Philosophy
School of GeoSciences
The University of Edinburgh
12th September 2021

Abstract

A broad corpus of previous research has sought to understand the role of biodiversity as a driver of ecosystem structure and function. Although theory suggests that increased biodiversity should increase ecosystem function by niche complementarity among co-existing species, in natural systems wide variation in the biodiversity effect exists among vegetation types and along environmental gradients. In southern African woodlands and savannas, which experience disturbance by fire and herbivory, drought and extreme temperatures, it is unclear whether positive biodiversity effects should occur. In this thesis, I explore the ecology of southern African woodlands through the lens of the biodiversity-ecosystem function relationship, to improve our understanding of the role of tree diversity as a mediator of ecosystem function, its interactions with abiotic environment, and its effect on woodland structure.

In temperate and wet tropical forests, where the majority of biodiversity-ecosystem function studies in natural woody vegetation have been conducted, the positive effect of niche complementarity hinges on the condition that conspecific competition is the limiting factor to ecosystem function. In highly disturbed and environmentally stressed systems however, this may not hold true. I conducted a regional study investigating the role of tree species diversity and structural diversity as mediators of woody biomass, using a plot network of 1235 plots spanning wide climatic and biogeographic gradients across southern Africa. Using Structural Equation Modelling, I determined that tree species diversity has a positive effect on biomass, operating mostly via its effect on structural diversity. I found that biodiversity itself increases with water availability, and that positive biodiversity effects only arise under sufficiently high stem density.

To further understand the ecological mechanisms which drive positive biodiversity-productivity relationships, I explored the effects of tree species diversity and woodland demographic structure on patterns of land-surface phenology. I combined a dense plot-based tree census dataset across multiple deciduous Zambian woodland types with remotely sensed measures of greenness, to understand drivers of variation in pre-rain green-up, growing season length and productivity. I found that pre-rain green-up occurred earlier in more diverse sites, across all woodland types, while in non-miombo woodlands, species richness also increased post-rain senescence lag and season length. I also found that large-sized trees increase the degree of both pre-rain green-up and post-rain senescence lag, across vegetation types, with an effect size similar to that of species richness.

Southern African woodlands occur as a complex mosaic of open grassy patches and closed canopy forest-like patches, driven by positive feedbacks of fire-induced tree mortality and grass growth, but the biotic mechanisms causing variation in canopy closure are unclear. I used terrestrial LiDAR at two sites, in Tanzania and Angola, to understand at fine spatial scale the effects of species composition and diversity on canopy architecture and canopy cover. Species diversity was found to allow increased spatial clumping of trees, which drove vertical canopy layer diversity and canopy height, demonstrating an indirect role of species diversity on canopy cover via stand structure. Taken together with the regional study of the biodiversity-ecosystem function relationship, these findings suggest a nuanced role of tree species diversity on ecosystem function, operating primarily via its effect on canopy structural diversity in southern African woodlands. I propose that higher diversity communities are more likely to produce forest-like closed canopy woodlands, with a higher upper limit on biomass, and are more likely to transition from savanna to closed canopy forest under conditions of atmospheric CO_2 enrichment.

Finally, in an effort to increase our understanding of the variation in diversity and structure of woodlands across southern Africa, I conducted a study of tree species biodiversity and woodland structure in Bicuar National Park, southwest Angola, with comparison to other woodlands around the miombo ecoregion. Much of the published plot data and woodland monitoring infrastructure in miombo woodlands is located in central and eastern regions of southern Africa, while woodlands in the west of the region, which occur entirely within Angola, remain poorly represented. I found that Bicuar National Park constitutes an important woodland refuge at the transition between dry miombo woodland and *Baikiaea-Baphia* woodlands. I recorded 27 tree species not recorded elsewhere in the miombo ecoregion outside the Huíla plateau. An additional study of one-off plots in areas previously disturbed by shifting cultivation, found that this disturbance increases tree species diversity, but ultimately reduces woody biomass, even after a period of regeneration, potentially representing a directional shift to a different stable vegetation type.

Together, the findings of this thesis demonstrate multiple relationships among tree biodiversity, ecosystem structure, and ecosystem function, measured primarily through woody biomass and productivity, at multiple spatial scales. I conclude that incorporation of diversity and canopy structural information into earth system models, by scaling up plot data using cutting edge remotely sensed datasets, could improve predictions of how climate change and biodiversity change will impact the functioning of different vegetation types across southern Africa, with consequences for carbon cycle modelling, conservation management, and ecosystem service provision. Finally, I suggest that biodiversity loss of large archetypal miombo tree species will have the greatest impact on a number of ecosystem functions related to carbon cycling, raising concerns over the impacts of selective logging of these species.

Lay summary

The tropical woodlands and savannas of southern Africa are complex and heterogeneous ecological systems, defined by the coexistence of grasses and trees. They vary widely in species composition, tree cover and canopy structure, from the dry Acacia savannas of South Africa, to the dense and humid miombo woodlands of southern Congo. Ecosystem functions in tropical savannas depend on a combination of factors, including rainfall, soil fertility, disturbance from seasonal grass fires, and herbivore grazing. Understanding what controls the rate of tree growth (i.e. productivity) and the total woody biomass in tropical savannas is important for predicting how these ecosystems contribute to the global carbon cycle, as productivity sets the rate at which trees take carbon from the atmosphere and store it in woody biomass. Yet, despite knowing the environmental drivers of savanna ecosystem processes, we don't have a detailed understanding of how variation in tree species composition and structure mediates the effect of environment on ecosystem function.

In other biomes, many studies have shown that as plant biodiversity increases, so does ecosystem function. These findings are supported by theory, which predicts that ecosystems with more species will be able to make more complete use of available resources, such as light, water, and space, due to differences among species in their growth strategy.

In this thesis, I explore how tree species composition and species diversity mediate the effects of environment on ecosystem functions and ecosystem properties across southern African woodlands. My aims are 1) to add depth to our understanding of savanna ecology, and 2) to extend general theory about the effects of biodiversity on ecosystem function to ecosystems which experience disturbance and resource-scarcity.

Using a large network of woodland plots, across nine countries, I investigated how tree species diversity and tree size diversity mediated the effects of various environmental drivers of woody biomass. I found that plots with more tree species also had greater variation in tree size, and that this was the main driver of increased woody biomass, by allowing more individuals to pack together in a smaller space, by reducing competition. I also found that positive effects of species diversity on biomass only occur when trees are sufficiently close together, which is in turn controlled by resource availability. I suggest that below this tree density threshold, the positive effects of biodiversity on biomass are not realised as individuals do not compete with each other to the degree that it limits their biomass.

The timing of leaf production in response to seasonal rainfall is an important driver of productivity and growth in trees. Leaves are the primary interface between the atmosphere and the plant, without them the plant cannot absorb atmospheric carbon needed for growth. I investigated the effects of tree species diversity on leaf production using a dense network of ~600 woodland plots in Zambia. I found that plots with greater species diversity had a longer growing season, and were able to produce leaves earlier in the rainy season than plots with fewer species. I also found differences in the leaf production behaviour of woodlands based on their dominant species. These findings help to understand how fine-scale variation in biodiversity and vegetation composition impact carbon cycling across the dry tropics.

I used terrestrial LiDAR (laser-scanning) to measure savanna canopy structure in fine detail, to understand how variation in tree species richness and spatial patterns of tree diversity affect canopy cover and canopy structural complexity. I found that spatial clustering of individuals increased with species richness, allowing greater canopy cover and more complete use of available light in diverse savannas. This finding suggests that more diverse savannas are more likely to transition from savanna to closed canopy forest in the future.

Finally, much of the long-term plot-based research in southern African woodlands comes from Tanzania, Mozambique, and Zambia, while woodlands in the western part of southern Africa remain understudied, and much less is known about their diversity and vegetation dynamics. I conducted a study of tree species composition and woodland structure using 15 permanent plots constructed in Bicuar National Park, southwest Angola, to highlight the divergent floristic composition and conservation value of this region. I encountered many species not recorded elsewhere in the region, and demonstrated the effects of pervasive agriculture on the diversity of these woodlands.

Together, this thesis demonstrates multiple mechanisms by which species diversity in southern African woodlands affect ecosystem function, measured as woody biomass and productivity. I highlight the wide functional variation of savanna vegetation across the region. I conclude that incorporating information on species diversity and canopy structure into carbon cycling models could improve predictions of how climate and biodiversity change will impact the functioning of different vegetation types across southern Africa. I also suggest that biodiversity loss of keystone miombo tree species will have the greatest negative effect on ecosystem function in this biome.

Author Declaration

I declare that this thesis has been composed by myself and that the work has not been submitted, either in whole or in part, for any other degree or professional qualification. Except where otherwise acknowledged, the work presented is entirely my own.

JLG

John L. Godlee
12th September 2021

Acknowledgements

Firstly I would like to thank my two main supervisors, Kyle Dexter and Casey Ryan, for guiding me through my PhD and along the road to becoming a real academic. My PhD experience has been enriched by the many opportunities they sent my way, and by the freedom I was given to pursue my own interests throughout the project. With their guidance I have learned that research is about collaboration, creativity, and exploration.

For support during fieldwork I thank Francisco Maiato Gonçalves, who looked after me during my two visits to Angola, and who made me feel at home with his family and friends. I also thank José Tchamba, Abel Cahali, Fortunato da Silva, and Henriques Jacinto for their support and friendship during our most difficult field campaign. For braving the bees, snakes, and rain, while measuring many thousands of trees in Bicuar National Park. I also thank the rangers and support staff at Bicuar National Park for guiding us and always providing delicious food at the end of the day.

For support during my fieldwork in Kilwa District, Tanzania I thank all those who helped me from Mpingo Conservation & Development Initiative in Kilwa Masoko. In particular, I extend my deepest gratitude to Paula Whyte for helping me navigate the impenetrable Tanzanian bureaucracy, and for being a friend during the long days at the Slow Leopard as I waited for permits. For help during the fieldwork itself I thank Emanuel Mlimitho for his impressive work ethic and attention to detail, and Abdala Mpotola, village chairman of Nainokwe, for his help with identifying tree species and digging us out of many situations on the road.

Thank you to the NERC Geophysical Equipment Facility for their help with the terrestrial LiDAR, and for trusting me with such a delicate and expensive piece of equipment. Thank you also to Steven Hancock who provided so much help in analysing the LiDAR data, without which I could not have attempted

such a huge task.

This PhD was funded primarily by the NERC E3 Doctoral Training Partnership. Thank you to the Davis Expedition Fund which provided funding for the Tanzania portion of the fieldwork, and to the Centenary Agroforestry 89 Fund for the Angola part of the fieldwork. Thank you to National Geographic who provided funding for the creation of the Bicuar National Park permanent plots, which will hopefully benefit many other researchers in years to come, and without which a large portion of this thesis would not have come to fruition.

Finally, thank you to Rosie for your unwavering support, for talking me through re-wiring a generator from 5000 miles away, for listening with apparent interest to many hours of chatter about LiDAR and canopy architecture, and for being my partner as we both navigate our way through our PhD programmes. During the final months of writing up you kept me healthy and positive. Now it is my turn to do the same for you.

Table of Contents

List of Figures

List of Tables

List of Code Snippets

List of Abbreviations

AGB	Above-Ground Biomass
AIC	Akaike Information Criterion
ANOVA	Analysis of Variance
BA	Basal Area
BEF	Biodiversity-Ecosystem Function
BEFR	Biodiversity-Ecosystem Function Relationship
C	Carbon
CEC	Cation Exchange Capacity
CFI	Comparative Fit Index
COVID-19	SARS-CoV-2 Coronavirus Disease
CRU TS	Climatic Research Unit Time Series
CV	Coefficient of Variation
CWD	Climatic Water Deficit
DAG	Directed Acyclic Graph
DBH	Diameter at Breast Height (1.3 m)
DOI	Digital Object Identifier
DRC	Democratic Republic of Congo
DPM	Disc Pasture Meter
DSLR	Digital Single Lens Reflex
ENL	Effective Number of Layers
ESA CCI	European Space Agency Climate Change Initiative
EVI	Enhanced Vegetation Index
FIML	Full Information Maximum Likelihood
FOS	Forest Observation System
GAM	General Additive Model
GCRF	Global Challenges Research Fund
GEDI	Global Ecosystem Dynamics Investigation

GLONASS	Global Navigation Satellite System (Russia)
GNSS	Global Navigation Satellite System (generic)
GPP	Gross Primary Productivity
GPS	Global Positioning System (United States)
HSD	Honest Significant Difference
IGBP	International Geosphere-Biosphere Programme
ILUA	Integrated Land Use Assessment
IMERG GPM	Integrated Multi-satellite Retrievals for Global Precipitation Measurement
IQR	Inter-Quartile Range
ISCED	Instituto de Ciências da Educação
ISRIC	International Soil Reference and Information Centre
JSON	JavaScript Object Notation
LAI	Leaf Area Index
LiDAR	Light Detection And Ranging
MANOVA	Multiple Analysis of Variance
MAP	Mean Annual Precipitation
MAT	Mean Annual Temperature
MODIS	Moderate Resolution Imaging Spectroradiometer
NDVI	Normalized Difference Vegetation Index
NERC	Natural Environment Research Council
NIR	Near Infra-Red
NMDS	Non-metric Multi-Dimensional Scaling
NP	National Park
PDAL	Point Data Abstraction Library
POSIX	Portable Operating System Interface
PPK	Post-Processed Kinematic
RMSEA	Root Mean Squared Error of Approximation
SASSCAL	Southern African Science Centre for Climate Change and Adaptive Land Management
SD	Standard Deviation
SECO	SECO: Resolving the current and future carbon dynamics of the dry tropics
SEM	Structural Equation Modelling

SEOSAW	A Socio-Ecological Observatory for Southern African Woodlands
TBM	Terrestrial Biosphere Model
TRMM	Tropical Rainfall Measuring Mission
TLS	Terrestrial Laser Scanning/Scanner
UV	Ultra-Violet radiation
WDPA	World Database on Protected Areas

Chapter 1

Introduction

1.1 Overview

Savanna-woodland mosaics are the dominant vegetation type in southern Africa, covering ~2.275 million km^2 (Arino et al., 2012). Currently, these ecosystems represent the largest uncertainty in models of the terrestrial carbon cycle (Ahlstrom et al., 2015), while being simultaneously identified as the fastest increasing component of the terrestrial carbon sink (Sitch et al., 2015). In the coming century, climate and land use change are likely to cause strong directional shifts in woody carbon storage and other aspects of ecosystem function in southern African woodlands (Midgley & Thuiller, 2011; Giannecchini et al., 2007; Scholze et al., 2006), which in turn could feedback to further influence both global climate and local livelihoods (Jew et al., 2016; Kalema et al., 2015). While many studies conducted outside of the dry tropics have identified biodiversity of trees as both a driver and mediator of ecosystem productivity and carbon storage (Liang et al., 2016), there is no such consensus on whether this effect exists in disturbance prone savanna-woodland mosaics (Mensah et al., 2020; Shirima et al., 2015; McNicol et al., 2018; Loiola et al., 2015). Understanding the complex relationships between biodiversity, environment, disturbance and ecosystem function in this system is therefore critical to predict ecological change, and is the central focus of this thesis.

In this thesis I address three key research questions, with the aim to improve understanding of the role of biodiversity in shaping the structure and function of southern African woodlands:

1. *Is there a detectable relationship between biodiversity and ecosystem function across southern African woodlands, and to what extent is this mediated by environment and vegetation composition?* (Chapter 3)
   While strong effects of tree species diversity on ecosystem function have been found in temperate and wet tropical ecosystems (Liang et al., 2016), empirical evidence for such effects in the dry tropics is inconclusive. In tropical savannas there may be important climatic or structural thresholds below which the importance of biotic competition is superseded by stress tolerance and the role of abiotic environment (Loiola et al., 2015; Mensah et al., 2020).

2. *What are the possible mechanisms driving observed biodiversity-ecosystem function relationships in southern African woodlands?* (Chapter 4, Chapter 5)

A broad corpus of research has found positive relationships between biodiversity and ecosystem function, with niche complementarity emerging as an important driver of this effect (Plas, 2019). However, the underlying ecological mechanisms of biodiversity effects are less well studied (Barry et al., 2019). Understanding the causes of biodiversity effects in southern African woodlands will contribute to a more general theory of the biodiversity-ecosystem function relationship.

3. *How does the tree species diversity, composition and structure of mesic savannas vary across southern Africa?* (Chapter 7)
   There is wide variability in species composition and woodland structure across southern Africa (Solbrig et al., 1996; White, 1983), but much of the work to describe woodland types has been concentrated in the central and eastern parts of the region (SEOSAW, 2020). Greater evaluation of the biogeographic variation in miombo woodlands is needed to improve predictions of ecological change across the region.

1.2 Thesis structure

This thesis is structured around four core research chapters (Chapters 3,4,5 and 7), each of which are summarised below. The core research chapters are presented in the style of stand-alone papers, as they are either published, in the process of revision, or intended for publication later. As such, there is some overlap among chapters in introductory and methodological material. In addition, I present a synthesis of the literature on southern African woodland ecology as it relates to current biodiversity-ecosystem function theory (Chapter 2), extended methods for Chapter 5 (Chapter 6), and a short chapter which provides further detail on the extended legacy of the data collected during this thesis (Chapter 8). Finally, I summarise the results arising from this thesis (Chapter 9), and discuss their implications for understanding of both the ecology of southern African woodlands and biodiversity-ecosystem function research.

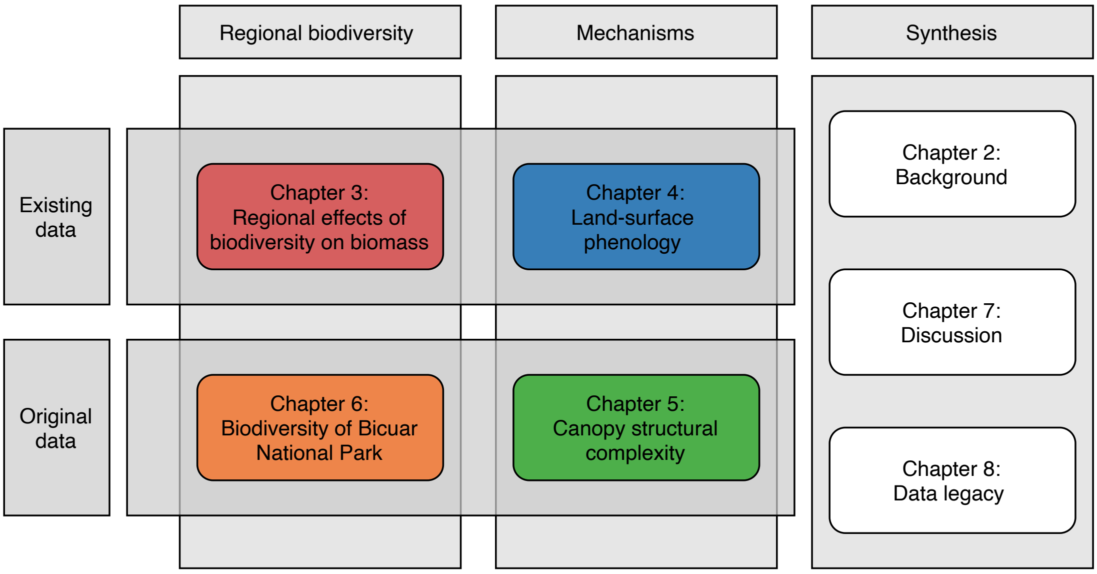


Figure 1.1: The structure of this thesis, showing the thematic focus and data usage in each chapter. Coloured boxes refer to similar colours in Figure 1.2, which shows the spatial scales of each core chapter.

1.2.1 Chapter 2: Background: The ecology, structure and function in southern African woodlands

In this chapter, I summarise the literature underpinning the thesis, focussing on two key themes: 1) biodiversity-ecosystem function theory, previous studies and latest developments, and 2) the ecology of tropical savannas, their biogeography within southern Africa, and drivers of structure and function.

1.2.2 Chapter 3: Structural diversity and tree density drives variation in the biodiversity-ecosystem function relationship of woodlands and savannas

Here, I explore whether the positive biodiversity effects on ecosystem function observed in wet tropical and temperate forested ecosystems extends to the mesic savannas of southern Africa. The biodiversity-ecosystem function relationship has been observed to various extents in many experimental and natural systems (Tilman et al., 2014; Plas, 2019), but low species richness, disturbance by fire and herbivory, and variation in climate might obscure or

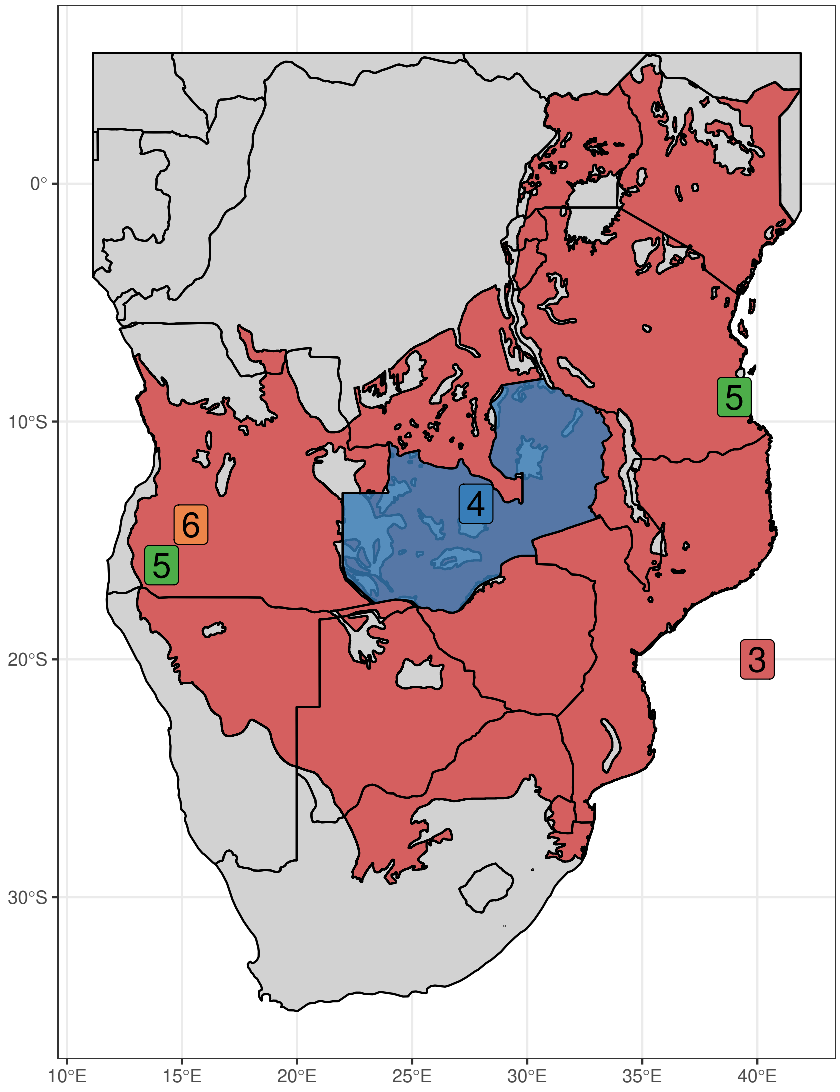


Figure 1.2: The spatial scales of the four core chapters in this thesis. Labels refer to chapter numbers. Chapter 3: The effects of biodiversity on above-ground woody biomass across southern African woodlands. The extent of southern African woodlands is defined by the SEOSAW working region, described in further detail in Figure 1.3. Chapter 4: Effects of tree diversity and composition on land-surface phenology across Zambia. Chapter 5: Biodiversity and canopy structural complexity in Bicuar National Park, Angola (west), and Mtarure Forest Reserve, Tanzania (east). Chapter 7: Woodland composition and structure in Bicuar National Park, Angola.

negate such a relationship in southern Africa. Using existing plot data from the SEOSAW database (Section 1.3.1), I test the interactive effects of: climate, resource availability, disturbance by fire, tree floristic diversity, and woodland structural diversity on woody biomass as a measure of ecosystem function.

1.2.3 Chapter 4: Diversity and vegetation type mediates land-surface phenology in Zambian deciduous woodlands

In this chapter, I test whether species composition and diversity metrics can explain some of the variation in patterns of land-surface phenology in deciduous tropical savannas not already explained by covariation with abiotic environment. The seasonal patterns of foliage growth in deciduous woodlands largely define their gross primary productivity (Penuelas et al., 2009), a key measure of ecosystem function. The pervasive pre-rain green-up observed in deciduous tropical woodlands across southern Africa (Ryan et al., 2016) has important consequences for carbon cycling and ecosystem structure (Xia et al., 2015). Climate adequately explains phenological variation across continental spatial scales, but at local scales biotic effects are hypothesised to be more important. I use plot data from the Zambian Integrated Land Use Assessment, which covers the entirety of the country, paired with remotely-sensed measures of green-ness to specifically test: 1) whether species diversity has an observable effect on pre-rain green-up of woodlands, 2) whether species diversity influences growing season length, and 3) whether models of gross primary productivity in deciduous tropical savannas would benefit from the inclusion of higher resolution species compositional data.

1.2.4 Chapter 5: Species diversity and stand structure as drivers of canopy complexity in southern African woodlands

Canopy packing and the spatial relations among tree canopies is a hypothesised vector of niche complementarity driving positive biodiversity effects on productivity in wooded ecosystems (Jucker et al., 2015; Oehri et al., 2020). Frost (1996) describes miombo woodland trees as maintaining high functional diversity, with wide variation in life-history strategies and growth forms among coexisting species. In this chapter I conduct the first assessment of tree canopy complexity using terrestrial LiDAR in southern African woodlands, to investigate: 1) the effects of neighbourhood tree species diversity on observed canopy structural complexity, 2) the role of disturbance and spatial distribution of tree stems in driving canopy complexity, and 3), the consequences of variation in tree species diversity for canopy closure and woody encroachment. In Chapter 6, I present extended methods for this chapter, covering the LiDAR data processing workflow, and explaining the behaviour of various derived canopy complexity and stand structural metrics.

1.2.5 Chapter 6: Estimation of canopy complexity with terrestrial LiDAR: extended methods

The methods used to quantify canopy complexity and stand structure in Chapter 5 comprise a mixture of existing methods adapted from published literature, and methods developed by myself. In this chapter I provide a detailed explanation of the field setup for the terrestrial LiDAR measurements, and describe the reproducible processing chain developed to extract cleaned and voxelised point clouds from the raw LiDAR data. I also provide a deeper analysis of the behaviour of the metrics used in Chapter 5 to quantify canopy complexity and stand structure, along with an explanation of how they are derived.

1.2.6 Chapter 7: Diversity and structure of an arid woodland in southwest Angola, with comparison to the wider miombo ecoregion

White (1983) classified miombo woodlands simply as “dry” or “wet”, but this ignores much of the floristic diversity to be found across the miombo eco-region. Understanding the breadth of woodland formations present across southern Africa not only provides vital information for the Dynamic Global Vegetation Models which form the foundation of models of the global carbon cycle (Conradi et al., 2020), but also raises awareness of the conservation value of this diverse phyto-geographic region (Jew et al., 2016). In this chapter, I conduct the first plot-based assessment of the species composition and woodland structure of woodlands in Bicuar National Park, Huíla Province, southwest Angola. Specifically, I investigate: 1) the floristic composition of Bicuar National Park compared to other miombo woodlands across the miombo eco-region, 2) the multiple vegetation types found within the Park, and 3) the effects of previous shifting cultivation practices on woodland structure and composition at the boundaries of the Park.

1.2.7 Chapter 8: Data legacy

An important outcome of this thesis is the data collected and the research infrastructure that has been cultivated through collaboration with colleagues based in southern Africa. In this chapter I discuss the extended value of the data collected, the steps taken to ensure the data are accessible to others, and provide some ideas for future projects that could use the data to further contribute to understanding of the carbon dynamics of southern African woodlands.

1.2.8 Chapter 9: Synthesis and conclusions

Here I discuss the key findings of the thesis. I examine: 1) tree biodiversity effects on ecosystem function as they are mediated by environment and ecological context, 2) tree canopies and physical structure of trees in southern African woodlands as both a product and driver of biodiversity, 3) the mechanisms that may drive observed biodiversity effects in tropical savannas, and 4) potential future research that will extend, clarify, and implement the findings of the thesis.

1.3 Data sources and research sites

The research presented in this thesis is drawn from three main sources:

1. Existing plot-based data
2. Publicly available geospatial data
3. Original data collected at two research sites within southern Africa

Background on the various datasets used in the thesis and how each was utilised is discussed below:

1.3.1 Existing datasets

SEOSAW

Much of the existing data analysed in this thesis, and the locations of field sites used for additional data collection, come from the SEOSAW plot network. SEOSAW - “a Socio-Ecological Observatory for Southern African Woodlands” (SEOSAW, 2020), consists of a network of woodland inventory plots across southern Africa (Figure 1.3) and a network of researchers who study the ecology of southern African woodlands. The SEOSAW plot network currently represents the largest plot network in the dry tropics. As of May 2021, it contains 9863 plots, of which 286 are permanent plots where measurement of tree productivity is possible. The plots are of varying size and shape but share a similar methodology in the way woody biomass is estimated, using allometric equations incorporating stem diameter and height measurements with species specific wood density estimates. The plot network spans wide environmental gradients (Figure 1.4) and floristic types, making it a valuable resource for studying regional variation in tree biodiversity and biomass stocks. During this PhD project I contributed to the development of the SEOSAW database, helping to formalise aspects of the data processing chain, and in developing field data collection methods, as part of SavannaChange, a project funded by the Global Challenges Research Fund (GCRF). Chapter 3 of this thesis uses a subset of 1235 plots from across the region to investigate drivers of aboveground biomass as they relate to species composition and other environmental variables.

Zambian Integrated Land Use Assessment

While The Zambian Integrated Land Use Assessment (ILUAii, Mukosha & Siampale 2009) is included in part within the SEOSAW database, this dataset deserves separate explanation. The ILUAii constitutes that largest single dataset contribution to the SEOSAW database in terms of number of plots (3886/9863) and total area covered (389/1387 ha) as of May 2021 (SEOSAW v2.12). Among other goals related to quantifying the state of natural resources in Zambia, the ILUAii aims to quantify woody biomass and vegetative composition across Zambia. In 2014 a regular grid of one-off plot surveys was conducted across the country, with very few gaps, mostly related to accessibility or lack of natural

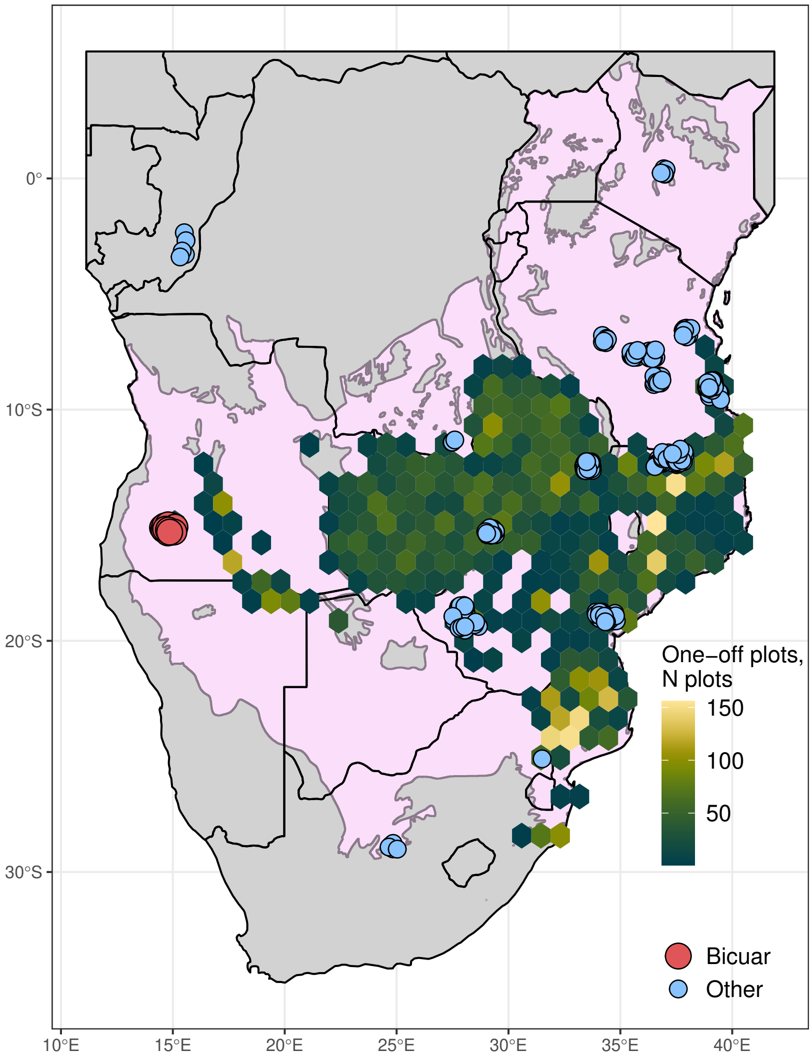


Figure 1.3: The spatial distribution of plots in the SEOSAW network. Blue circles are permanent plots, where individual stems can be matched among censuses. The new permanent plots in Bicuar National Park constructed as part of this thesis are shown as red points. The hexagonal-grid shows the density of one-off plots. The pink shading shows the working region of the SEOSAW network, defined primarily from woodland defined by White (1983) and further adapted to bound the north-eastern and southern boundaries.

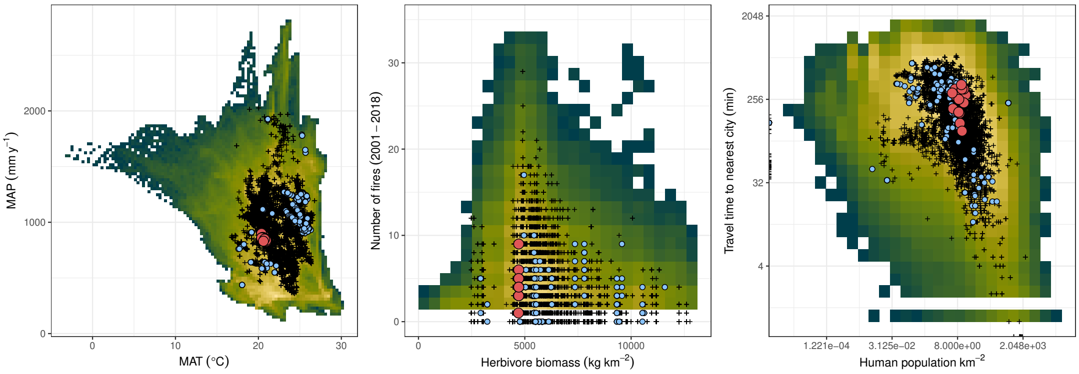


Figure 1.4: SEOSAW plots in various bivariate environmental spaces. Blue circles are permanent plots, where individual stems can be matched among censuses. The permanent plots in Bicuar National Park constructed as part of this thesis are shown as red points. Black crosses show one-off plots. The background of each plot is shaded according to the density of pixels in the SEOSAW working region, as described in Figure 1.3, from blue (low) to yellow (high). From left to right: 1) Climate space, using Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP), both extracted from the WorldClim dataset gridded at 30" (~900 m at the equator) (Fick & Hijmans, 2017). 2) 'Disturbance space', using herbivore biomass from Hempson et al. (2017) and fire frequency between 2001 and 2018 from the MODIS burned area product (MCD64A1) (Giglio et al., 2015). 3) 'Human influence space', using human population density taken from the WorldPop dataset (Linard et al., 2012), and travel time to nearest city taken from the Malaria Atlas Project (Meijer et al., 2018). Note that both axes for the human influence plot are log transformed.

vegetation. The plot survey collected data on tree species, stem diameter and metadata such as land tenure and human resource usage. Chapter 4 of this thesis uses plot data contributed to the SEOSAW database from the ILUAii to investigate the role of tree species composition and diversity in driving land surface phenology.

Climate databases: WorldClim, IMERG

I use multiple climate databases to account for variation in climate, which affects biodiversity, ecosystem function and the interaction between biodiversity and ecosystem function. WorldClim provides up to 30" (~900 m at the equator) monthly climate averages of temperature and precipitation over the period 1970-present (Fick & Hijmans, 2017). Additionally, WorldClim provides summarised data known as BioClim, with calculated variables commonly used in ecological science at an annual time-scale such as temperature seasonality and diurnal temperature range. WorldClim provides interpolated climate data utilising weather station data to produce data with known spatial uncertainty, at a higher resolution than similar products such as the CRU TS data (Harris et al., 2013). I use WorldClim throughout the thesis to characterise the climatic context of study sites, but particularly within the Structural Equation Modelling framework of Chapter 3 to understand how environmental covariates mediate biodiversity effects across the southern African subcontinent. IMERG GPM (Integrated Multi-satellitE Retrievals for Global Precipitation Measurement) provides globally available estimated precipitation daily time series (Huffman et al., 2015). IMERG has a pixel size of 0.1° (11.1 km at the equator). I use IMERG precipitation time series in Chapter 4 to quantify the extent of the pre-rain green-up phenomenon in Zambian woodlands. IMERG can be seen as the successor to the well-known TRMM (Tropical Rainfall Measuring Mission) product (Bowman et al., 2007), which no longer provides accurate measurements due to its declining altitude.

SoilGrids

ISRIC SoilGrids provides modelled estimates of the spatial distribution soil properties, globally, at 250 m resolution (Hengl et al., 2017). SoilGrids incorporates over 230,000 soil profile observations from the WoSIS database (Batjes et al., 2017), along with various environmental covariates to estimate soil properties where ground measurements are sparse. I use variables related to soil texture and soil nutrient content such as cation exchange capacity, sand content, and available organic nitrogen, to understand the effect of resource availability on the strength of biodiversity effects on woody biomass across southern African woodlands, in Chapter 3 of this thesis. While the modelled nature of the SoilGrids product relies upon interpolation of spatially sporadic ground measurements with other data such as climate and land use and carries uncertainty as a result, this trade-off also produces a consistent data product that can be used to easily compare many plots where conducting ground measurements would be prohibitively expensive.

MODIS burned area

The MODIS burned area time series product (MCD64A1) uses a combination of burn scars and active fire records to estimate instances of fire, overcoming limitations caused by cloud cover (Giglio et al., 2015). The MODIS burned area product provides estimates of burned area at a resolution of 500 m, classifying pixels as burned or unburned over a monthly time period. I used the MODIS burned area product to quantify plot level disturbance regime as mean annual fire frequency in Chapter 3 of the thesis. The majority of the plots used in analyses did not have a comprehensive fire history, thus the MODIS burned area product provided a consistent and easily interpretable alternative. There is no comparable remotely-sensed fire product available with the same spatial and temporal coverage as the MODIS burned area product.

MODIS EVI

The MODIS EVI (Enhanced Vegetation Index) time series product (MOD13Q1) provides 16 day estimates of EVI at 250 m spatial resolution (Didan, 2015). EVI uses a simple formula using the Near-InfraRed (NIR) and Red spectral bands from MODIS to estimate “green-ness”. EVI is considered an improvement over the Normalised Differential Vegetation Index (NDVI) in certain ecological contexts as it corrects for diurnal variation in atmospheric conditions and avoids saturation at higher canopy densities (Huete et al., 2002). I use EVI estimates in Chapter 4 to approximate phenological activity of trees across Zambia.

1.3.2 New datasets

Permanent plots in Bicuar National Park

With colleagues from ISCED Huíla, I set up 15 permanent 1 ha woodland survey plots in Bicuar National Park, Huíla Province, Angola (S15.1°, E14.8°). The plots were situated along a gradient of stem density. These plots aim to encompass the main woodland types found in the park, which is representative of the natural vegetation found in the larger Huíla plateau region (Huntley et al., 2019). Chapter 7 characterises the floristic and structural diversity of the permanent plots in Bicuar National Park, with respect to other plots in the wider miombo eco-region.

Forest mosaics and savanna-woodlands are the dominant vegetation type in Angola (White, 1983), and are regarded as under threat as the human population increases, particularly surrounding urban areas (Ritchie & Roser, 2018), putting pressure on woodlands to provide charcoal and timber. Weak policies in the forestry sector and inadequate government oversight has led to deforestation, particularly in the southern and eastern parts of the country, notably inside protected area boundaries (FAO, 2015; Mendelsohn, 2019). While the annual rate of deforestation in Angola was estimated at 0.2% in 2005, this has since increased following population growth and development of rural infrastructure such as roads since the end of the civil war (Röder et al., 2015), resulting in an estimated 13.7% of intact forested habitat being lost between 2000 and 2013 (Potapov et al., 2017; Hansen et al., 2013). The biota of much of Angola remains understudied (Huntley et al., 2019). While many conservation areas and national parks were created during the Portuguese colonial era, most were abandoned during the civil war period following independence (1975-2002), with some only recently coming back under active government management (Huntley et al., 2019; Ministèrio do Urbanismo e Ambiente, 2006).

Bicuar National Park constitutes the largest intact formation of miombo woodlands in the Huíla plateau. The Park has been protected to varying extents since 1938, initially as a game reserve and as a National Park from 1964. The Park was originally 790 km^2, but was reduced to ~675 km^2 in 1972 following a governmental decree to allow for the expansion of the Capelongo colonial settlement (Mendelsohn, 2019). In 2012, the Park boundaries were re-instated with a new fence and park access gates, following multiple decades of largely absent management. Around the mid-1980s the current park main station was occupied by Cuban militia. During this time many species of large herbivore became locally extinct within the Park, including the African buffalo (*Syncerus caffer*), the plains zebra (*Eqqus quagga*), and the blue wildebeest (*Connochaetes taurinus*).

Bicuar National Park lies at ~1200 m asl, sitting on wind-blown Kalahari sand deposits which extends across much of the western portion of southern Africa as far north as the Congo basin (Shaw & Goudie, 2002). The soils underlying the Park are identified as arenosols, consisting of mainly sand with some humus and clay (Jones et al., 2013; Hartemink & Huting, 2008). The Park is located at the transition between miombo woodlands found in moister conditions to the north, and *Baikiaea plurijuga* woodlands which occupy the drier region to the south. The miombo woodlands of the Park are dominated by *Brachystegia* spp. and *Julbernardia paniculata*, while the southern drier woodlands are dominated by *Baikiaea plurijuga* and *Burkea africana* (Teixeira, 1968). A distinctive catenal system occupies the north and central parts of the Park, with seasonally flooded grasslands and suffrutex shrublands at the base of the shallow valleys (locally known as “mulolas”), which drain into the Kunene river, and woodlands on the catenal ridges (locally known as “tundas”). The climate of the Park is highly seasonal, with a warm rainy season from October to April and cooler dry periods over June and July. SASSCAL provides ongoing meteorological monitoring from a weather station located near the Park centre from 2015 (Figure 1.5).

The Park currently holds many endemic plant species not found outside the Huíla plateau (Huntley et al., 2019), and is home to large herbivores such as elephants (*Loxodonta africana*), giant sable antelope (*Hippotragus niger variani*), and greater kudu (*Tragelaphus strepsiceros*), which travel between Bicuar National Park and the adjacent Mupa National Park to the south. The Park has a number of excavated watering holes to attract large herbivores for observation (Simões, 1971). Other studies indicate populations of other animal species such as the African wild dog (*Lycaon pictus*) (Beja et al., 2019; Overton et al., 2016) and a number of endemic herptiles (Baptista et al., 2019). Both Linder (2001) and Droissart et al. (2018) identify the Huíla plateau as a centre of tropical African botanical endemism, but contemporary studies characterising the exact vegetation composition of the Park are scarce. Teixeira (1968) identified six unique vegetation formations within the Park, including

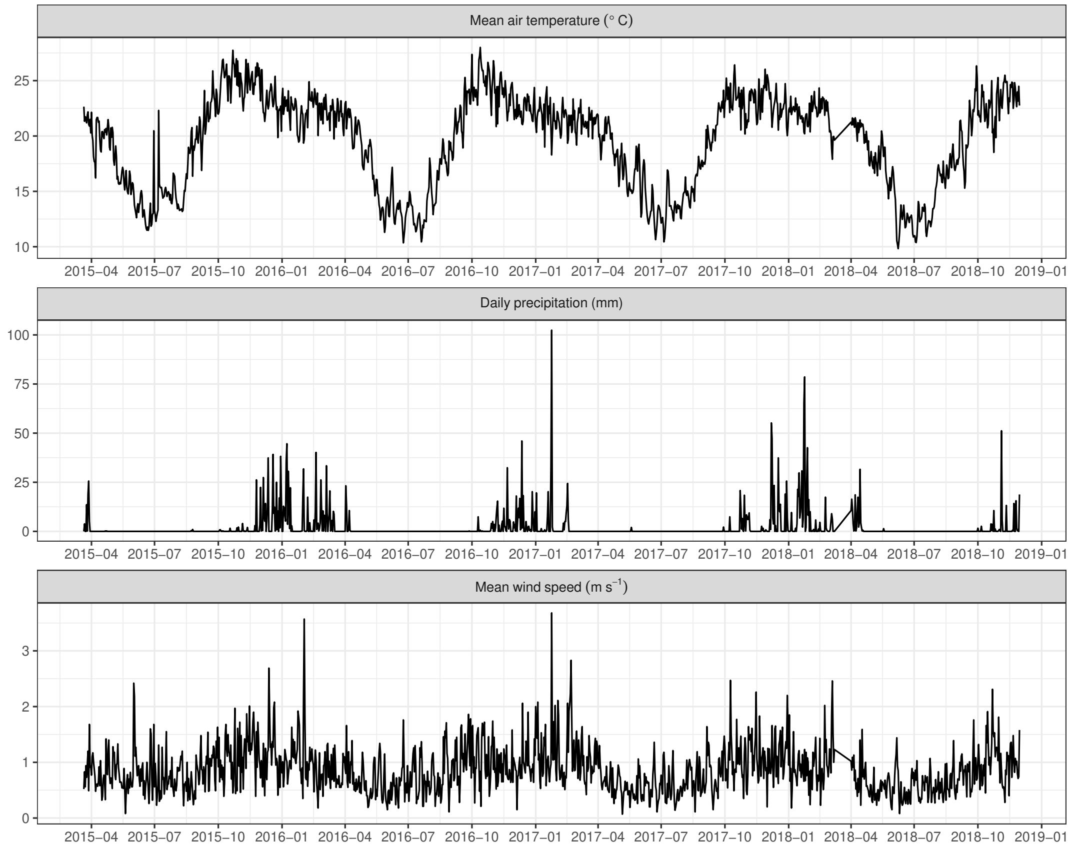
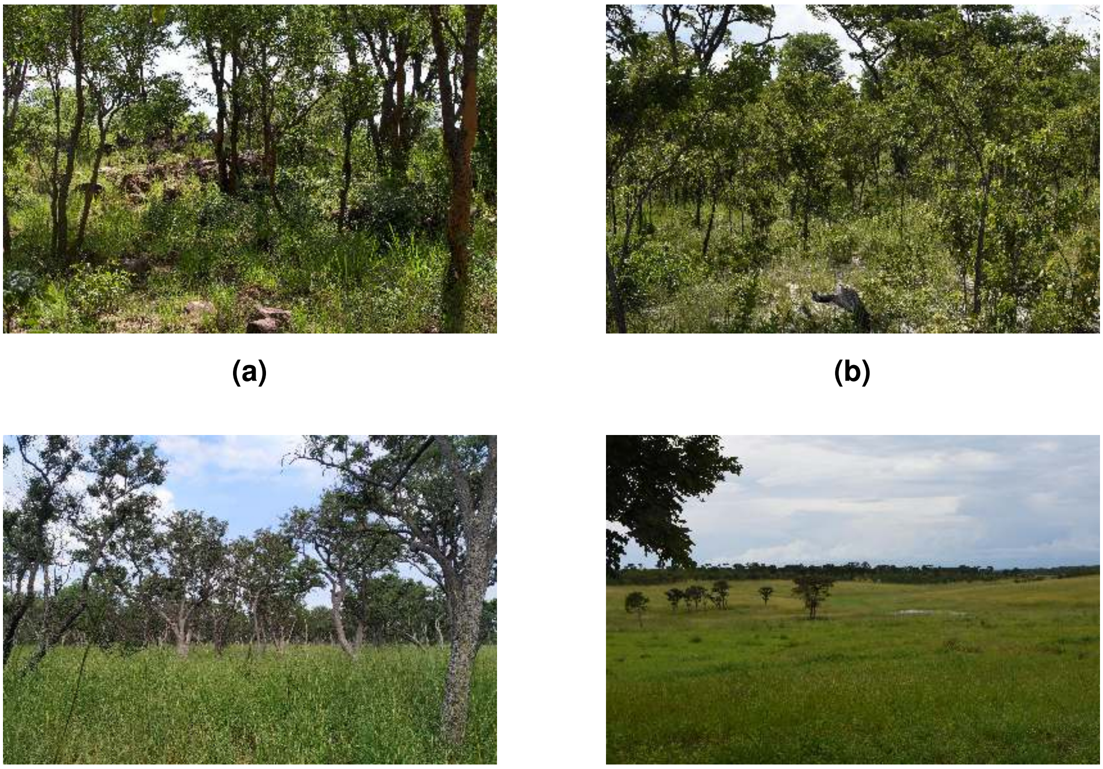


Figure 1.5: Data from the SASSCAL weather station located at the main station near the centre of Bicuar National Park. Data are daily aggregates, collected between March 2015 and June 2019.

woodlands, shrublands, and grasslands. Barbosa (1970) and Chisingui et al. (2018) both described the dominance of *Baikiaea-Baphia* woodlands particularly in the southern area of the Park. Much of the land cover around the Park has been transformed to agriculture and pasture. Of particular conservation concern is the pattern of land use change in the corridor between Bicuar National Park and Mupa National Park. Further development in this area could fragment the valuable seasonal corridor used by large mammals in the dry season to reach ephemeral water sources (Overton et al., 2016). Additionally, Catarino et al. (2020) described changing patterns of fire across protected areas in Angola, showing that Bicuar National Park is experiencing a rapid increase in fire frequency. They suggest that ingress by humans may be causing the increase in burning, with potential negative consequences for biodiversity and ecosystem integrity.

Terrestrial laser scanning

Terrestrial laser scanning (LiDAR) data was collected at two sites which span southern Africa: Bicuar National Park in southwest Angola, and Mtarure Forest Reserve in southeast Tanzania (Figure 1.2). The two sites comprise 100×100 m (1 ha) permanent plots in tropical savanna vegetation. Chapter 5 uses the terrestrial laser scanning data to investigate drivers of canopy structural complexity. Chapter 6 provides extended methods for LiDAR data processing and the derivation of canopy complexity metrics Chapter 8 discusses the future research potential of this data. Terrestrial laser scanning technology provides high-resolution point cloud data that can be analysed in innumerable ways to extend its lifespan. Traditional analogue measurements of tree canopy structure are laborious, inaccurate, imprecise and tree-centric, while LiDAR data provides valuable information on inter-tree canopy structure at sub-centimetre precision, albeit at a higher monetary cost, and requiring greater expertise (Xiao et al., 2019; Dassot et al., 2011).



(a) **(b)**

(c) **(d)**

Figure 1.6: The principal vegetation formations seen in Bicuar National Park, southwest Angola. (a) Julbernardia-Brachystegia miombo woodland, (b) Burkea-Pseudolachnostylis miombo woodland, (c) Baikiaea-Baphia woodland, and (d) open grassy wetland (“mulola”).

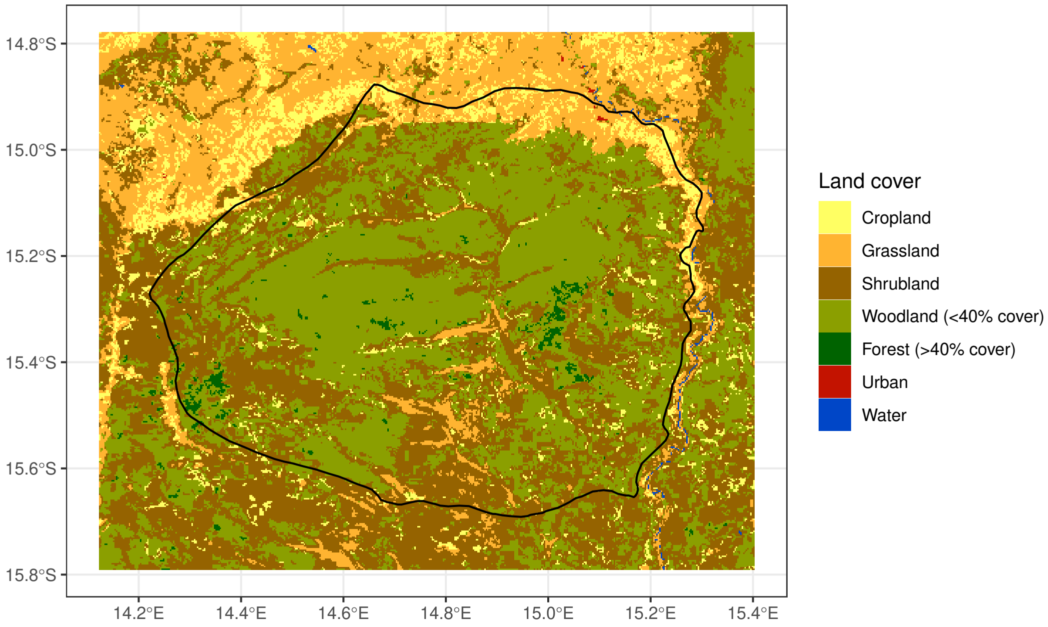


Figure 1.7: Land cover of Bicuar National Park, reclassified from the ESA CCI land cover map (v2.0.7) (ESA, 2017). This map highlights the clear deforestation north of the Park, with much land transformed to cropland and grassy pasture. The map also shows the discrepancy between the official park boundary as taken from the World Database on Protected Areas, and the park boundary fence, which is easily seen as a boundary running east-west at approximately S15.0°, E14.8°, with areas of agricultural encroachment beyond the Park boundary fence particularly to northeast of the Park, near the town of Folgares, situated along the Kunene River.

References

Ahlstrom, A., M. R. Raupach, G. Schurgers, B. Smith, A. Arneth, M. Jung, M. Reichstein, J. G. Canadell, P. Friedlingstein, A. K. Jain et al. (2015). 'The dominant role of semi-arid ecosystems in the trend and variability of the land CO2 sink'. In: *Science* 348.6237, pp. 895–899. DOI: `10.1126/science.aaa1668`.

Arino, O., J. J. Ramos Perez, V. Kalogirou, S. Bontemps, P. Defourny & E. Van Bogaert (2012). *Global Land Cover Map for 2009 (GlobCover 2009)*. PANGAEA. DOI: `10.1594/PANGAEA.787668`. (Visited on 30/05/2021).

Baptista, N. L., T. António & W. R. Branch (2019). 'The herpetofauna of Bicuar National Park and surroundings, southwestern Angola: a preliminary checklist'. In: *Amphibian and Reptile Conservation* 13.2, pp. 96–130.

Barbosa, L. A. G. (1970). *Carta Fitogeográfica de Angola*. Luanda, Angola.

Barry, K. E., L. Mommer, J. van Ruijven, C. Wirth, A. J. Wright, Y. Bai, J. Connolly, G. B. De 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`.

Batjes, N. H., E. Ribeiro, A. van Oostrum, J. Leenaars, T. Hengl & J. M. de Jesus (2017). 'WoSIS: providing standardised soil profile data for the world'. In: *Earth System Science Data* 9.1, pp. 1–14. DOI: `10.5194/essd-9-1-2017`.

Beja, P., P. V. Pinto, L. Veríssimo, E. Bersacola, E. Fabiano, J. M. Palmeirim, A. Monadjem, P. Monterroso, M. S. Scensson & P. J. Taylor (2019). 'The mammals of Angola'. In: *Biodiversity of Angola*. Ed. by B. J. Huntley, F. Lages, V. Russo & N. Ferrand. Cham, Switzerland: Springer, pp. 357–444.

Bowman, K. P., Y. Hong, E. F. Stocker & D. B. Wol (2007). 'The TRMM Multisatellite Precipitation Analysis (TMPA): Quasi-Global, Multiyear, Combined-Sensor Precipitation Estimates at Fine Scales'. In: *Journal of Hydrometeorology* 8, pp. 28–55. DOI: `10.1175/JHM560.1`.

Catarino, S., M. M. Romeiras, R. Figueira, V. Aubard, J. M. N. Silva & J. M. C. Pereira (2020). 'Spatial and Temporal Trends of Burnt Area in Angola: Implications for Natural Vegetation and Protected Area Management'. In: *Diversity* 12.8, p. 307. DOI: `10.3390/d12080307`.

Chisingui, A. V., F. M. P. Gonçalves, J. J. Tchamba, J. C. Luís, M. F. F. Rafael & J. L. M. Alexandre (2018). 'Vegetation survey of the woodlands of Huíla Province'. In: *Biodiversity and Ecology*, pp. 426–437. DOI: `10.7809/b-e.00355`.

Conradi, T., J. A. Slingsby, G. F. Midgley, H. Nottebrock, A. H. Schweiger & S. I. Higgins (2020). 'An operational definition of the biome for global change research'. In: *New Phytologist* 227.5, pp. 1294–1306. DOI: `10.1111/nph.16580`.

Dassot, M., T. Constant & M. Fournier (2011). 'The use of terrestrial LiDAR technology in forest science: application fields, benefits and challenges'. In: *Annals of Forest Science* 68.5, pp. 959–974. DOI: `10.1007/s13595-011-0102-2`.

Didan, L. (2015). *MOD13Q1 MODIS/Terra Vegetation Indices 16-Day L3 Global 250m SIN Grid V006 [Data set]*. NASA EOSDIS Land Processes DAAC. DOI: `10.5067/MODIS/MOD13Q1.006`. (Visited on 05/08/2020).

Droissart, V., G. Dauby, O. J. Hardy, V. Deblauwe, D. J. Harris, S. Janssens, B. A. Mackinder, A. Blach-Overgaard, B. Sonké, M. S. M. Sosef et al. (2018). 'Beyond trees: Biogeographical regionalization of tropical Africa'. In: *Journal of Biogeography* 45, pp. 1153–1167. DOI: `10.1111/jbi.13190`.

ESA (2017). *Land Cover CCI Product User Guide Version 2. Technical Report*. URL: `maps.elie.ucl.ac.be/CCI/viewer/download/ESACCI-LC-Ph2-PUGv2_2.0.pdf` (visited on 20/05/2021).

FAO (2015). *Southern Africa's forests and people: Investing in a sustainable future: Successes, challenges and ways forward*.

Fick, S. E. & R. J. Hijmans (2017). ‘WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas’. In: *International Journal of Climatology* 37.12, pp. 4302–4315. DOI: `10.1002/joc.5086`.

Frost, P. (1996). ‘The ecology of miombo woodlands’. In: *The miombo in transition: woodlands and welfare in Africa*. Ed. by B. M. Campbell. Bogor, Indonesia: Center for International Forestry Research, pp. 11–55.

Giannecchini, M., W. Twine & C. Vogel (2007). ‘Land-cover change and human-environment interactions in a rural cultural landscape in South Africa’. In: *The Geographical Journal* 173.1, pp. 26–42. DOI: `10.1111/j.1475-4959.2007.00227.x`.

Giglio, L., C. Justice, L. Boschetti & D. Roy (2015). *MCD64A1 MODIS/Terra+Aqua Burned Area Monthly L3 Global 500m SIN Grid V006 [Data set]*. NASA EOSDIS Land Processes DAAC. DOI: `10.5067/MODIS/MCD64A1.006`. (Visited on 20/04/2020).

Hansen, M. C., P. V. Potapov, R. Moore, M. Hancher, S. A. Turubanova, A. Tyukavina, D. Thau, S. V. Stehman, S. J. Goetz, T. R. Loveland et al. (2013). ‘High-Resolution Global Maps of 21st-Century Forest Cover Change’. In: *Science* 342.6160, pp. 850–853. DOI: `10.1126/science.1244693`.

Harris, I., P. D. Jones, T. J. Osborn & D. H. Lister (2013). ‘Updated high-resolution grids of monthly climatic observations - the CRU TS3.10 Dataset’. In: *International Journal of Climatology* 34.3, pp. 623–642. DOI: `10.1002/joc.3711`.

Hartemink, A. E. & J. Huting (2008). ‘Land Cover, Extent, and Properties of Arenosols in Southern Africa’. In: *Arid Land Research and Management* 22.2, pp. 134–147. DOI: `10.1080/15324980801957689`.

Hempson, G. P., S. Archibald & W. J. Bond (2017). ‘The consequences of replacing wildlife with livestock in Africa’. In: *Scientific Reports* 7.1. DOI: `10.1038/s41598-017-17348-4`.

Hengl, T., J. Mendes de Jesus, G. B. M. Heuvelink, M. R. Gonzalez, M. Kilibarda, A. Blagotić, W. Shangguan, M. N. Wright, X. Geng, B. Bauer-Marschallinger et al. (2017). ‘SoilGrids250m: Global gridded soil information based on machine learning’. In: *PLoS ONE* 12, pp. 1–40. DOI: `10.1371/journal.pone.0169748`.

Huete, A., K. Didan, T. Miura, E. P. Rodriguez, X. Gao & L. G. Ferreira (2002). ‘Overview of the radiometric and biophysical performance of the MODIS vegetation indices’. In: *Remote Sensing of Environment* 83.1-2, pp. 195–213. DOI: `10.1016/s0034-4257(02)00096-2`.

Huffman, G. J., E. F. Stocker, D. T. Bolvin, E. J. Nelkin & J. Tan (2015). *GPM IMERG Final Precipitation L3 1 day 0.1 degree x 0.1 degree V06 [Data set]*. Goddard Earth Sciences Data and Information Services Center (GES DISC). DOI: `10.5067/GPM/IMERGDF/DAY/06`. (Visited on 30/10/2020).

Huntley, B. J., F. Lages, V. Russo & N. Ferrand, eds. (2019). *Biodiversity of Angola: Science & conservation: A modern synthesis*. Cham, Switzerland: Springer. DOI: `10.1007/978-3-030-03083-4`.

Jew, E. K. K., A. J. . Dougill, S. M. Sallu, J. O’Connell & T. G. Benton (2016). ‘Miombo woodland under threat: Consequences for tree diversity and carbon storage’. In: *Forest Ecology and Management* 361.February, pp. 144–153. DOI: `10.1016/j.foreco.2015.11.011`.

Jones, A., H. Breuning-Madsen, M. Brossard, A. Dampha, J. Deckers, O. Dewitte, S. Hallett, R. Jones, M. Kilasara, P. Le Roux et al., eds. (2013). *Soil atlas of Africa*. Luxembourg, Luxembourg: European Commission.

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`.

Kalema, V. N., E. T. F. Witkowski, B. F. N. Erasmus & E. N. Mwavu (2015). ‘The impacts of changes in land use on woodlands in an equatorial African savanna’. In: *Land Degradation and Development* 26.7, pp. 632–641. DOI: `10.1002/ldr.2279`.

Liang, J., T. W. Crowther, N. Picard, S. Wiser, M. Zhou, G. Alberti, E.-D. Schulze, A. D. McGuire, F. Bozzato, H. Pretzsch et al. (2016). ‘Positive biodiversity-productivity relationship predominant in global forests'. In: *Science* 354.6309, aaf8957–aaf8957. DOI: `10.1126/science.aaf8957`.

Linard, C., M. Gilbert, R. W. Snow, A. M. Noor & A. J. Tatem (2012). 'Population Distribution, Settlement Patterns and Accessibility across Africa in 2010'. In: *PLoS ONE* 7.2, e31743. DOI: `10.1371/journal.pone.0031743`.

Linder, H. P. (2001). 'Plant diversity and endemism in sub-Saharan tropical Africa'. In: *Journal of Biogeography* 28, pp. 169–182. DOI: `10.1046/j.1365-2699.2001.00527.x`.

Loiola, P. P., M. Scherer-Lorenzen & M. A. Batalha (2015). 'The role of environmental filters and functional traits in predicting the root biomass and productivity in savannas and tropical seasonal forests'. In: *Forest Ecology and Management* 342, pp. 49–55. DOI: `10.1016/j.foreco.2015.01.014`.

McNicol, I. M., C. M. Ryan, K. G. Dexter, S. M. J. Ball & M. Williams (2018). 'Aboveground carbon storage and its links to stand structure, tree diversity and floristic composition in south-eastern Tanzania'. In: *Ecosystems* 21, pp. 740–754. DOI: `10.1007/s10021-017-0180-6`.

Meijer, J. R., M. A. J. Huijbregts, K. C. G. J. Schotten & A. M. Schipper (2018). 'Global patterns of current and future road infrastructure'. In: *Environmental Research Letters* 13.6, p. 064006. DOI: `10.1088/1748-9326/aabd42`.

Mendelsohn, J. M. (2019). 'Landscape changes in Angola'. In: *Biodiversity of Angola*. Ed. by B. J. Huntley, F. Lages, V. Russo & N. Ferrand. Cham, Switzerland, pp. 123–137.

Mensah, S., V. K. Salako & T. Seifert (2020). 'Structural complexity and large-sized trees explain shifting species richness and carbon relationship across vegetation types'. In: *Functional Ecology* 34.8, pp. 1731–1745. DOI: `10.1111/1365-2435.13585`.

Midgley, G. F. & W. Thuiller (2011). 'Potential responses of terrestrial biodiversity in southern Africa to anthropogenic climate change'. In: *Regional Environmental Change* 11, pp. 127–135. DOI: `10.1007/s10113-010-0191-8`.

Ministèrio do Urbanismo e Ambiente (2006). *National Biodiversity Strategy and Action Plan (2007-2012)*. Luanda, Angola.

Mukosha, J. & A. Siampale (2009). *Integrated land use assessment Zambia 2005–2008*. Lusaka, Zambia: Ministry of Tourism, Environment et al.

Oehri, J., M. Bürgin, B. Schmid & P. A. Niklaus (2020). 'Local and landscape-level diversity effects on forest functioning'. In: *PLoS ONE* 15.5, e0233104. DOI: `10.1371/journal.pone.0233104`.

Overton, J., S. Fernandes, D. Elizalde, R. Groom & P. Funston (2016). *A large mammal survey of Bicuar and Mupa National Parks, Angola. With special emphasis on the presence and status of cheetah and African wild dogs*. Luanda, Angola.

Penuelas, J., T. Rutishauser & I. Filella (2009). 'Phenology Feedbacks on Climate Change'. In: *Science* 324.5929, pp. 887–888. DOI: `10.1126/science.1173004`.

Plas, F. van der (2019). 'Biodiversity and ecosystem functioning in naturally assembled communities'. In: *Biological Reviews* 94, pp. 1220–1245. DOI: `10.1111/brv.12499`.

Potapov, P., M. C. Hansen, L. Laestadius, S. Turubanova, A. Yaroshenko, C. Thies, W. Smith, I. Zhuravleva, A. Komarova, S. Minnemeyer et al. (2017). 'The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013'. In: *Science Advances* 3.1, e1600821. DOI: `10.1126/sciadv.1600821`.

Ritchie, H. & M. Roser (2018). *Urbanization*. URL: `https://ourworldindata.org/urbanization` (visited on 15/05/2021).

Röder, A., M. Pröpper, M. Stellmes, A. Schneibel & J. Hill (2015). 'Assessing urban growth and rural land use transformations in a cross-border situation in Northern Namibia and Southern Angola'. In: *Land Use Policy* 42, pp. 340–354. DOI: `10.1016/j.landusepol.2014.08.008`.

Ryan, C. M., R. Pritchard, I. McNicol, M. Owen, J. A. Fisher & C. Lehmann (2016). 'Ecosystem services from southern African woodlands and their future under global change'. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 371.1703, p. 20150312. DOI: `10.1098/rstb.2015.0312`.

Scholze, M., W. Knorr, N. W. Arnell & I. C. Prentice (2006). ‘A climate-change risk analysis for world ecosystems’. In: *Proceedings of the National Academy of Sciences of the United States of America* 103.35, pp. 13116–13120. DOI: `10.1073/pnas.0601816103`.

SEOSAW (2020). ‘A network to understand the changing socio-ecology of the southern African woodlands (SEOSAW): Challenges, benefits, and methods’. In: *Plants, People, Planet*. DOI: `10.1002/ppp3.10168`.

Shaw, A. I. & A. S. Goudie (2002). ‘Geomorphological evidence for the extension of the mega-Kalahari into south-central Angola’. In: *South African Geographical Journal* 84.2, pp. 182–194. DOI: `10.1080/03736245.2002.9713769`.

Shirima, D. D., Ø. Totland, P. K. T. Munishi & S. R. Moe (2015). ‘Relationships between tree species richness, evenness and aboveground carbon storage in montane forests and miombo woodlands of Tanzania’. In: *Basic and Applied Ecology* 16.3, pp. 239–249. DOI: `10.1016/j.baae.2014.11.008`.

Simões, A. P. (1971). *Considerações acerca de Algumas Zonas de Protecção da Fauna, Flora e Solo de Angola*. Luanda, Angola: Instituto de Investigação Científica de Angola.

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`.

Solbrig, O. T., E. Medina & J. F. Silva (1996). *Biodiversity and Savanna Ecosystem Processes*. Berlin, Germany: Springer-Verlag.

Teixeira, J. B. (1968). *Parque Nacional do Bicuar. Carta da Vegetação (1 approximação) e Memória Descritiva*. Nova Lisboa, Angola.

Tilman, D., F. Isbell & J. M. Cowles (2014). ‘Biodiversity and ecosystem functioning’. In: *Annual Review of Ecology, Evolution, and Systematics* 45, pp. 471–493. DOI: `10.1146/annurev-ecolsys-120213-091917`.

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`.

Xia, J., S. Niu, P. Ciais, I. A. Janssens, J. Chen, C. Ammann, A. Arain, P. D. Blanken, A. Cescatti, D. Bonal et al. (2015). ‘Joint control of terrestrial gross primary productivity by plant phenology and physiology’. In: *Proceedings of the National Academy of Sciences* 112.9, pp. 2788–2793. DOI: `10.1073/pnas.1413090112`.

Xiao, J., F. Chevallier, C. Gomez, L. Guanter, J. A. Hicke, A. R. Huete, K. Ichii, W. Ni, Y. Pang, A. F. Rahman et al. (2019). ‘Remote sensing of the terrestrial carbon cycle: A review of advances over 50 years’. In: *Remote Sensing of Environment* 233, p. 111383. DOI: `10.1016/j.rse.2019.111383`.

Chapter 2

Background: The ecology, biodiversity, structure and function of southern African woodlands

2.1 Introduction

Tropical savannas are expected to experience significant shifts in vegetation structure and biodiversity in the coming century, due primarily to human induced climate change, land use change, and an increase in atmospheric carbon concentration (Ross et al., 2021; Scheiter & Higgins, 2009; Moncrieff et al., 2016). Yet, we lack a detailed understanding of how biodiversity and vegetation structure affect ecosystem function in this biome (i.e. processes controlling fluxes of energy and matter through ecosystems), how this co-varies with various environmental factors, and among distinct savanna vegetation types. A lack of clarity in the functional heterogeneity of tropical savanna vegetation has resulted in large uncertainties in models of earth system fluxes for this biome (Ahlstrom et al., 2015), and confusion over appropriate management actions (Veldman et al., 2015). This thesis examines the role of tree species diversity as a driver of ecosystem function, with a focus on woody biomass and productivity as measures of ecosystem function, in southern African savannas. Biodiversity-Ecosystem Function (BEF) theory predicts positive effects of biodiversity on ecosystem function (Tilman et al., 2014), but it is unclear whether this effect should occur in disturbance-prone and environmentally stressful ecosystems (Steudel et al., 2012; Baert et al., 2018). This chapter provides background on the ecology and biodiversity of tropical savannas and more specifically southern African savannas, then summarises current literature on BEF theory, and findings of previous studies of the biodiversity-ecosystem function relationship within southern African savannas and elsewhere, to understand in greater depth the rationale for this thesis.

2.2 The ecology of savannas

Savannas occupy ~20% of the global land surface (Scholes & Walker, 1993). They are the dominant land cover in the seasonal tropics, covering ~40% of the tropical land surface (Scholes & Archer, 1997) (Figure 2.1). While debate continues around use of the term ‘savanna’ (Lehmann et al., 2011; Ratnam et al., 2011), the generic definition used in this thesis characterises a savanna by the co-dominance of grasses and trees, with a near contiguous grass-dominated understorey, and a closed or discontinuous, but sparse, woody overstorey

(Scholes & Archer, 1997; Bond, 2008). Within this broad definition, savannas are highly heterogeneous, across local to continental scales (Bucini & Hanan, 2007), with wide variation in tree cover (Sankaran et al., 2005; Hirota et al., 2011), the structure and floristic composition of the woody overstorey (Fayolle et al., 2018; Solbrig et al., 1996), and the herbaceous understorey (Siebert & Dreber, 2019; Van Coller et al., 2018).

Historically, tropical savannas were often mis-represented as severely degraded forests (Veldman, 2016). This view has roots in the early twentieth century concept of Clementsian succession and potential vegetation (Clements, 1916; Pulsford et al., 2014), which focussed on hierarchical physiognomic vegetation classifications with closed canopy forest at the apex, rather than the horizontal floristic or functional classifications that are in greater use at present (Aleman et al., 2020). This misinterpretation of savanna vegetation dynamics was exacerbated by the vast majority of early studies of savanna ecosystems originating from regions which lacked savanna vegetation (Fairhead et al., 1996). The hangover of this outdated paradigm is still felt today, with tropical savannas receiving less conservation funding (Watson et al., 2016), experiencing the greatest rates of transformation to agriculture of any major biome (Hoekstra et al., 2004; Parr et al., 2014), and being the focus of misplaced afforestation projects (Silveira et al., 2020; Kumar et al., 2020; Laestadius et al., 2011). In recent years there has been a push to acknowledge the value of tropical savannas, both intrinsically as centres of biodiversity and endemism (Kumar et al., 2020; Pennington et al., 2018), and as providers of ecosystem services (Ryan et al., 2016). Savannas proliferated globally during the Pliocene (~3-8 Mya), as a result of climate change, C_4 grass proliferation, and an increase in the frequency and intensity of fire, with all three of these causes being inter-linked (Cerling et al., 1997; Beerling & Osborne, 2006; Osborne, 2007; Edwards & Smith, 2010). Rather than being viewed as derived landscapes that may be restored to a more forest-like environment, savannas should be considered a unique biome in their own right, with particular vegetation formations (Torello-Raventos et al., 2013), a distinct evolutionary history (Veldman et al., 2015), high species endemism (Pennington et al., 2006; Huntley, 1982), and unique responses to global environmental change (Sankaran, 2019).

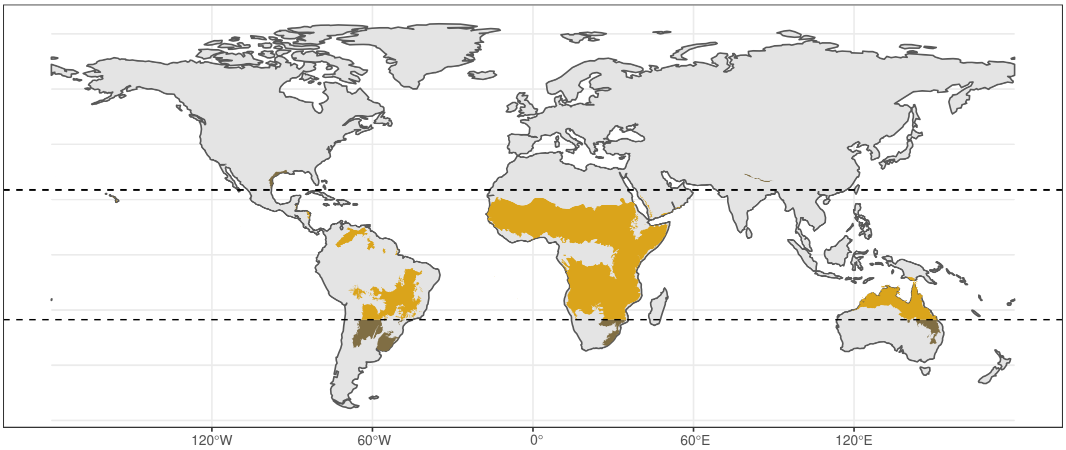


Figure 2.1: The global distribution of tropical savannas and grasslands (yellow), re-classified from the Terrestrial Ecoregions of the World (Dinerstein et al., 2017). Dashed lines mark the latitudinal extent of the tropics from N23.5° to S23.5°. Brown areas denote extra-tropical vegetation resembling tropical savannas in their floristics and structure.

2.2.1 Determinants of savanna vegetation

Savanna vegetation may occur as a result of multiple non-exclusive and interacting factors. One of the key questions in savanna ecology concerns identifying the factors driving variation in tree cover and woody biomass, and assessing their relative importance in different contexts, thus determining the global distribution of savannas (Higgins et al., 2000; Archibald et al., 2019). In this thesis I will explore the role of biodiversity and vegetation structure as mediators of tree cover and woody biomass as ecosystem functions, but first it is necessary to understand other environmental controls, before considering how they may interact with the biota to determine ecosystem function.

Controls on tree cover can be split broadly into ‘disturbance-based’ (e.g. fire, herbivory) or ‘resource-based’ (e.g. precipitation, soil fertility) (Bond, 2008; Staver & Koerner, 2015). Both resource-based and disturbance-based controls on tree cover act simultaneously to varying extents in most savannas, though it is possible to classify savannas into two broad types based on whether the dominant control on tree cover is resource limitation or disturbance, as these dominant controls drive species adaptation and thus tend to coincide with dichotomies in species composition and woodland structure (Huntley, 1982; Torello-Raventos et al., 2013).

Tropical savannas occur in areas of high rainfall seasonality (Lehmann et al., 2011). Most tropical savannas experience a prolonged dry season At the continental scale, available moisture is the most significant determinant of savanna tree cover (Sankaran et al., 2005), setting the upper boundary of tree cover by physiological limitation of tree growth. In wetter mesic savannas, competition between grasses and adult trees is low, but in arid savannas, grasses may ‘poach’ water from trees by intercepting it close to the soil surface (Scheiter & Higgins, 2007). While water availability may be the dominant resource-based determinant of savanna vegetation, edaphic properties also affect tree cover across savannas. Tropical savannas are often associated with dystrophic soils, especially in higher rainfall areas, where available nutrients are leached from the soil (February et al., 2013). Furthermore soil texture also interacts with rainfall to allow greater woody biomass and less grass biomass where the soil drains more readily (Staver et al., 2011).

While resource availability, particularly moisture sets the upper bound for tree cover, many savannas exist in areas that are climatically suitable for closed canopy forest (Sankaran et al., 2005; Lehmann et al., 2011; Staver et al., 2011; Murphy & Bowman, 2012). Even at local spatial scales, there is large heterogeneity in woody canopy cover (Dantas et al., 2016). Above ~650 mm yr^{-1}, woody cover in savannas appears to show little dependence on MAP (Sankaran et al., 2008; Sankaran et al., 2005; Good & Caylor, 2011), suggesting that other factors such as soil fertility and disturbance become more dominant above this precipitation threshold (Figure 2.2) (Staver et al., 2011).

The key premise of the “Alternative Stable States” phenomenon is that contrasting ecosystem states may occur under similar environmental conditions, due to strong stabilising positive feedbacks on vegetation structure (Staver et al., 2011). Grass is the main fuel source for fires in mesic savannas. C_4 grasses, which dominate many mesic and arid savannas, particularly in southern Africa (Still et al., 2003), are highly flammable, but require more light than C_3 grasses, meaning they are highly sensitive to variation in tree canopy cover (Charles-Dominique et al., 2018). In areas with low grass biomass, fire frequency and intensity are expected to be lower due to a lack of fuel. Simultaneously, juvenile trees are highly sensitive to fire in the grassy understorey layer due to their low stature, meaning that fire increases tree mortality, or ‘top-kill’ of these individuals which must then resprout, keeping individuals small and creating a demographic bottleneck where only a few individuals grow to adults (Bond & Midgley, 1995; Ryan et al., 2011). A positive feedback loop therefore occurs whereby disturbance by fire reduces canopy cover, allowing more frequent and intense fires, further reducing canopy cover as tree growth is suppressed. Alternatively, under reduced fire, trees can escape the ‘fire trap’ in the understorey and grow to canopy trees (Wakeling et al., 2011), which rarely burn due to adaptive traits such as insulating bark and elevated crowns, increasing canopy cover, causing competitive exclusion of grasses (Moustakas et al., 2013), which further reduces disturbance by fire (Figure 2.3).

Hirota et al. (2011), using remotely sensed measures of tree cover across tropical Africa, South America and Australia, demonstrated a distinctly bi-modal distribution of tree cover within areas of intermediate rainfall (~650-1500 mm yr^{-1}). Staver et al. (2011) showed that fire was the main source of this bimodality, and furthermore, Staver et al. (2017) showed that change in fire return interval, whether the result of management or environmental change, can result in transitions to an alternative stable state. Specifically, that longer fire return intervals result in a shift toward a more forest-like ecosystem with greater canopy closure, fewer small trees, and a greater number of large canopy trees.

Savannas in southern Africa in particular, are host to populations of large mammal herbivores (Hempson et al., 2017). Disturbance by herbivory is another key determinant of tree cover in these ecosystems. Herbivory generally has a negative effect on woody tree cover (Bond, 2008), as herbivores remove branches from adults and destroy juvenile individuals, creating a demographic bottleneck similar to that caused by fire (Bond & Keeley, 2005). Additionally, like fire, positive feedback mechanisms exist whereby many large herbivore species are discouraged from entering densely wooded patches, and instead maintain ‘grazing lawns’ in more open patches (Klop et al., 2007; Donaldson et al., 2017). The effect of herbivory on tree cover is more complex than that of fire, however. Sankaran et al. (2008) found that while certain herbivore guilds such as elephants generally decrease woody cover, foraging selectivity, combined with behavioural historic preference, led to some patches experiencing greater herbivory than others nearby. While fire is the dominant control on tree cover

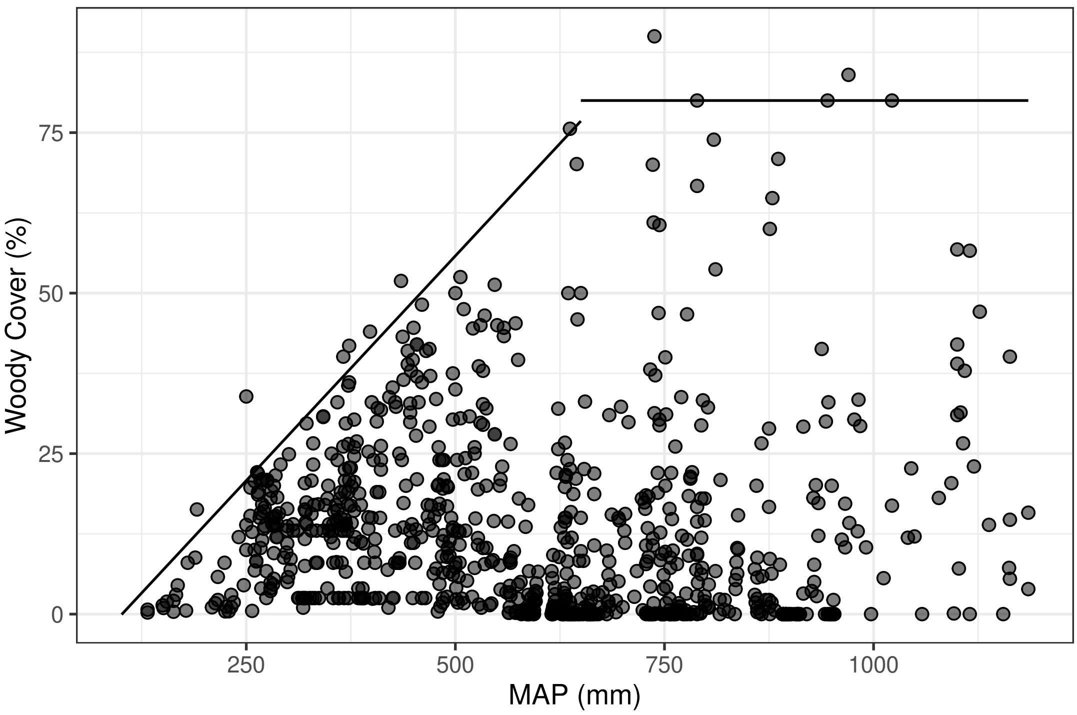


Figure 2.2: The relationship between rainfall (Mean Annual Precipitation) and proportional tree cover, across 854 savanna sites in Africa, data from Sankaran et al. (2005). The line of best fit uses a broken-stick 99th quantile piece-wise linear regression to identify the breakpoint at which rainfall no longer sets the upper limit for tree cover. Above the breakpoint (650 ± 134 mm MAP) other processes such as disturbance by fire and local edaphic limitations are thought to determine tree cover.

and biomass in wetter savannas, many drier savannas, which are unable to form a closed canopy due to underlying water limitation, experience further reduction in tree cover due to herbivory (Sankaran et al., 2008). Additionally, in drier savannas, certain grazer guilds may actually promote woody growth when grazing pressure is high, by reducing grass competition (Roques et al., 2001). Uncertainty around the complex role of herbivores in savannas is exacerbated by a dearth of consistent measurement on herbivory pressure, which hampers cross-site comparisons (Hempson et al., 2017).

The factors described above which determine savanna vegetation structure are highly interactive. Moisture availability interacts with fire disturbance, leading, seemingly paradoxically, to a situation where increased resource availability

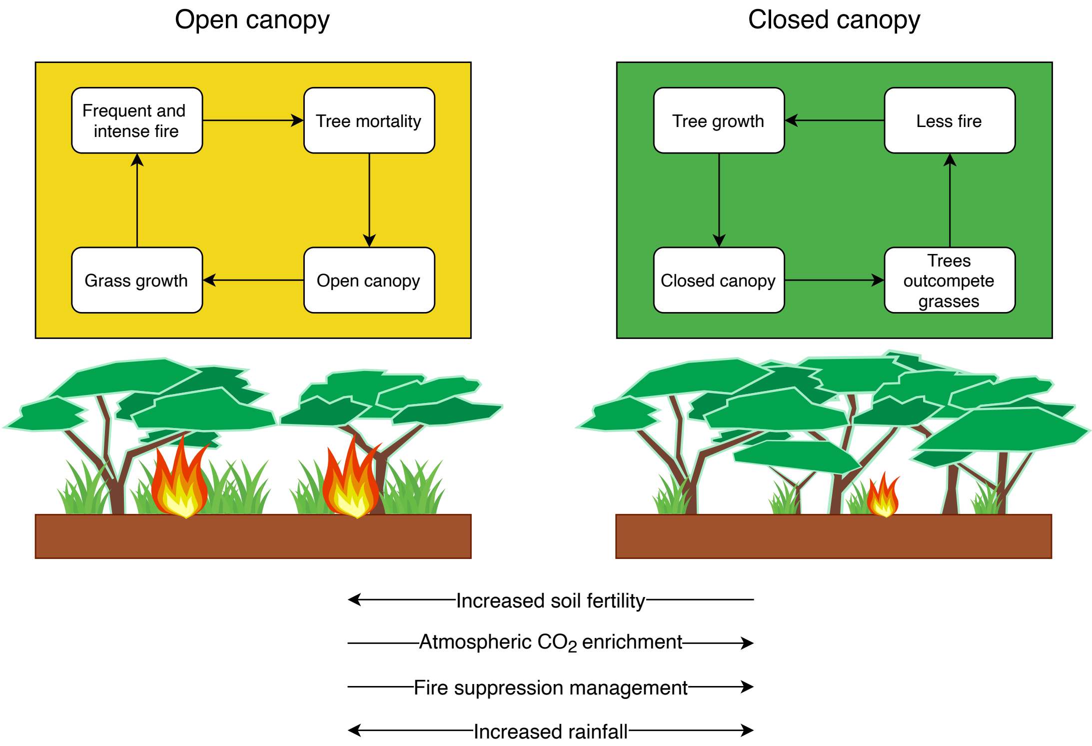


Figure 2.3: The positive feedback mechanisms which determine the alternative stable states of mesic tropical savannas. Left: increased fire increases tree mortality, which decreases canopy cover, increasing available light for grass growth, leading to more fire and a further reduction in canopy cover. Right: decreased fire decreases tree mortality, which increases canopy cover, reducing available light to the grassy understorey, causing a reduction in grass fuel load, fewer fires and a further increase in canopy cover. Bottom: stabilising feedback loops can be disrupted given a large enough perturbation, causing a switch to another stable state. Some of these perturbations have different outcomes depending on the principal limitation of woody cover. In arid savannas, increased rainfall leads to an increase in woody cover, as more water percolates to deeper tree tap roots, while in a mesic savanna where water is not limiting, increased rainfall may lead to an increase in grass growth and therefore an increase in fire, which reduces woody cover.

may lead to lower woody biomass above a given threshold resource availability, due to increased grass growth and more intense and frequent fires (Xu et al., 2015). Soil fertility also plays an interactive role with fire, increasing grass recovery rate between fires, which may lead to more frequent fires, increased tree mortality and lower woody biomass (Kellman, 1984). Interactions between environment, disturbance and tree cover, with clear thresholds of resource availability and tipping points of disturbance regime, result in a highly complex model of savanna ecosystem processes.

2.2.2 Adaptations of savanna trees

The model of ecosystem processes which determine ecosystem function in savanna ecosystems described above, the result of interactions among water availability, soil fertility, and disturbance, only becomes more complex when the biotic component and its biogeographic variation is considered. To overcome a multitude of environmental pressures, savanna trees have developed adaptations and employ various life history strategies, leading to high functional diversity within and among savanna ecosystems, despite their low tree species richness compared to tropical rainforests, for example (Solbrig et al., 1996). This functional diversity allows niche separation among species and potentially greater ecosystem function in higher diversity ecosystems, particularly by conferring greater resilience of function to environmental extremes such as drought (Díaz & Cabido, 2001). This section describes some of the key adaptations of savanna trees and their effect on ecosystem processes.

Seasonal fires are a key determinant of savanna structure in mesic savannas (>650 mm MAP) (Sankaran et al., 2005). Many savanna tree species produce thick corky bark which protects the sapwood from high temperatures during fire (Hoffmann et al., 2012; Lawes et al., 2011; Dantas & Pausas, 2013). Additionally, many savanna trees produce large below-ground root structures built to store carbohydrate, and access deep groundwater reserves, allowing individuals to re-sprout following fire (Wigley et al., 2019). There is evidence of adaptation in juveniles of some species that allows them to resprout in the same year following fire, outside the normal cycle of seasonal growth, giving them a head-start over competitors which adhere to a more rigid bud production cycle (Wiegand et al., 2006). Natural coppicing of adult savanna trees is common. If one growing tip is damaged due to fire, other stems on the same individual can continue growing, avoiding mortality. Savanna trees also sometimes have insulated buds to prevent fire reaching the sensitive growing tip (Charles-Dominique et al., 2015).

Previously, root niche separation between grasses and trees was thought to be the main method by which trees and grasses coexist in savannas (Walter, 1971). Trees were observed to have deep tap roots while grasses have a greater density of fine near-surface roots (Timberlake et al., 1993). In arid savannas, root niche separation is an important mechanism allowing tree-grass coexistence, with consequences for the timing of seasonal growth in relation to seasonal rainfall intensity. In mesic savannas however, this effect is largely absent, except under specific edaphic conditions that increase soil drainage (Case et al., 2020; Ketter & Holdo, 2018; Sankaran et al., 2004; Higgins et al., 2000). Many savanna trees in mesic savannas produce two types of roots, the first are deep tap roots which are used primarily for water uptake and for storing carbohydrates as ligno-tubers to facilitate pre-rain green-up and resprouting following fire. The second are a mesh of finer roots which occur near to the surface and compete directly with grasses. These roots are used primarily for nutrient uptake, as most savanna soils have a distinct vertical nutrient profile (Tomlinson et al., 2012; February et al., 2013). In southern Africa especially, many mesic savanna soils are denuded of phosphorus (Campbell, 1996). Thus, many dominant mesic savanna trees in the Fabaceae family, subfamily Detarioideae have mutualistic arbuscular mycorrhizal associations which improve phosphorus uptake (Gomes et al., 2021). Similarly, in drier savannas, many dominant non-Detarioideae Fabaceae species, including *Acacia* spp., *Dalbergia* spp., *Dichrostachys* spp., etc, produce root nodules to host *Rhizobia* capable of fixing atmospheric nitrogen (Hogberg, 1986).

Seasonal fire routinely removes much of the grass layer in savannas, meaning that this is an ideal time for tree seedlings to germinate, as the lack of grass fuel means another fire is unlikely for some time, and the lack of grass cover reduces competition for the growing seedling. Many tree species have adapted to having fire-activated seed dispersal (Veldman et al., 2015), with large seeds for long seed residence times, and rapid growth of newly emerged seedlings (Daibes et al., 2019), so that the seedlings can grow enough to escape the "fire-trap" before the grass fuel load has increased sufficiently to allow another fire. Wakeling et al. (2015) found that in densely grassy areas, a lack of gaps may prevent the germination of tree seeds, with long seed residence times allowing trees to take advantage of stochastic fire events that open up gaps for rooting. As an alternative to producing seed, some savanna tree species reproduce predominantly via clonal growth. Clonal suckers remain connected to the natal tree, allowing rapid growth, as they benefit from the resources of the established carbohydrate-storing root structures (Bond & Midgley, 2003).

Tropical savannas experience highly seasonal patterns of rainfall. Many savanna trees are deciduous or semi-deciduous, losing their leaves during the dry season to limit transpiration and conserve water (Dahlin et al., 2016). The phenomenon of 'pre-rain green-up' has been observed widely across tropical savanna trees (Archibald & Scholes, 2007; Borchert, 1994; Williams et al., 1997; Ryan et al., 2017), whereby trees produce foliage material in advance of the rainy season. Multiple mechanisms have been suggested to explain pre-rain green-up as an adaptive trait, such as: to optimise photosynthesis during the wet season (Archibald & Scholes, 2007), to avoid herbivory (Aide, 1988), and to maximise the length of the growing season (Scholes & Walker, 1993).

2.3 Savannas and the global carbon cycle

Tropical savannas contribute ~30% of global terrestrial Net Primary Productivity (NPP), i.e. atmospheric carbon fixed into biomass (Grace et al., 2006). Due to their large spatial extent, even a small percentage change in woody cover in savannas is expected to have large effects on the global carbon sink (Williams et al., 2005). Globally, savanna ecosystems are being degraded and lost to agricultural expansion, mining, and urban growth (Parr et al., 2014). Ross et al. (2021) predict biomass loss over most tropical savannas over the coming century, mostly due to land use change. Similarly, Aleman et al. (2016) concluded that land use change in sub-Saharan African savannas will have a greater negative effect on tree cover than changes in annual rainfall and rainfall seasonality. By 2100, the human population of sub-Saharan Africa is expected to double, increasing pressure on savanna ecosystems further (Pison, 2017). Despite this, tropical savannas are reportedly the fastest increasing component of the terrestrial carbon sink (Sitch et al., 2015), though they also represent the largest source of uncertainty in the terrestrial carbon cycle (Ahlstrom et al., 2015).

By 2050, it is expected that atmospheric CO_2 will have risen high enough that C_4 grasses no longer have a growth advantage over C_3 plants (Bond & Midgley, 2012). An increase in atmospheric CO_2 is expected to lead to faster tree growth rates, allowing saplings to more quickly escape the “fire-trap”, resulting in lower mortality, and a shift towards closed canopy forest-like landscapes. Additionally, in arid savannas, the negative effect of CO_2 enrichment on grass transpiration rates is expected to lead to less vigorous root growth and therefore more percolation of water to the deeper tree roots, increasing tree growth (Murphy & Bowman, 2012). Various studies, across the country of South Africa (Stevens et al., 2016), the neotropics (Rosan et al., 2019), and globally (Stevens et al., 2017), have reported woody encroachment of trees into previously grassland or shrubland areas, increasing carbon uptake and storage in these systems. These studies cite atmospheric CO_2 increase as the main driver of this phenomenon. Due to the complex nature of the determinants of savanna tree cover however, it is still unclear whether the positive growth effects of CO_2 enrichment will occur to the same extent in different savanna ecosystems. Most global carbon cycling models currently use broad plant functional types to describe variation in function among biomes. It is common for all mesic savannas within southern Africa to be assigned to the same plant functional type, for example (Atkin et al., 2015; Whitley et al., 2017), yet we know there are many functionally distinct vegetation types in this region (Campbell, 1996), each likely to response to concomitant changes in environmental factors in different ways.

Lewis et al. (2009) suggested that although existing woodlands are thickening, this does not necessarily extend to encroachment into previously non-forested areas, due to the strong stabilising influence of fire. Similarly, Pelletier et al. (2018) concluded that while more arid savannas will likely experience woody encroachment due primarily to the effects of CO_2 enrichment on transpiration and tree-grass water relations, there is no evidence that the same will happen in non-water limited savannas such as the miombo woodlands of southern Africa. Reich et al. (2014) demonstrated that earth system models may be overly sensitive to the effects of CO_2 enrichment, and that the models suffer from a lack of mechanistic understanding of the effect of resource availability on disturbance. Körner (2017) suggested that CO_2 enrichment may serve only to increase biomass turnover through increased growth offset by fire, with 44% of all carbon emissions in savanna coming from fire (Werf et al., 2010), and 62% of fire carbon emissions coming from savanna (Werf et al., 2017), offsetting the extra carbon sequestered.

Tropical savannas remain the largest source of uncertainty in models of the terrestrial carbon cycle (Ahlstrom et al., 2015). Environmental and land use change is expected to cause drastic changes to the functioning of savanna ecosystems in the coming century (Ross et al., 2021). Clearly, there is much work needed to better understand the mechanisms which determine the role of tropical savannas in the global carbon cycle. Carbon cycling models must consider biogeographic variation, the effect of functional differences among species and vegetation types on ecosystem function, and how functional relationships may alter as a result of global change. In this thesis, I will explore the role of tree species biodiversity as a mediator of ecosystem functions related to carbon cycling, namely productivity and biomass storage. In doing so, I hope to provide a basis for incorporating information on biodiversity into carbon cycle models, to reduce their uncertainty in predicting the terrestrial carbon cycle.

2.4 Southern African woodlands

This thesis uses the mesic savannas of southern Africa as the main study location within which to explore the effects of biodiversity on ecosystem function. These savannas occur in a latitudinal band south of the Congo basin rainforest, and north of the arid savannas of the country of South Africa (Figure 2.4), covering ~2.7 million km^2 (Arino et al., 2012). Hereafter they are referred to as southern African woodlands.

Tree cover in southern African woodlands is limited through a combination of precipitation and disturbance from fire and herbivory, leading to a highly heterogeneous patchy woodland habitat across the region (Archibald et al., 2019). Fire return intervals vary at local to regional spatial scales, dependent on climate and existing vegetation which determines grass fuel load (Archibald et al., 2010). Fires in southern African woodlands rarely track up into the tree canopy, and instead burn quickly in the grass layer, causing tree mortality among juvenile trees but only occasionally in larger trees, resulting in a distinct demographic bottleneck effect that heavily influences woodland structure (Frost, 1996).

Large herbivores play an important role in determining the vegetation structure of southern African woodlands. Compared to climatically similar savannas in the neotropics or southeast Asia, large herbivores are common in southern African woodlands (Asner et al., 2009). It has been suggested that large herbivores may cause disturbance in a manner similar to fires, reducing woody biomass by increasing mortality of juvenile saplings (Bond & Keeley, 2005), though the effects of herbivory are often much more localised than fire, and the spatial distribution of herbivory cannot be predicted with the same detail (Hempson et al., 2015).

While the dominant pressure determining the coexistence of grass and trees in savannas globally is moisture availability, within southern African woodlands where rainfall is rarely a limiting factor, competition for light is more important (Vadigi & Ward, 2013). Depending on the disturbance regime, southern African woodlands occasionally form dense closed canopies, while C_4 grasses are highly sensitive to shade. Feedbacks between tree cover and grass growth determine the fire regime and lead to highly heterogeneous woodland structure.

Southern African woodlands support a growing human population, with >150 million people benefitting from ecosystem services provided (Ryan et al., 2016; Wunder et al., 2014). Vast areas of woodland in southern Africa are used for grazing cattle which requires relatively open woodland (Njana et al., 2013), while other areas are used for charcoal production, bushmeat hunting, fruit, vegetable and mushroom foraging, and timber production (Ryan et al., 2016). Wood extraction by humans is increasing in southern Africa (Hansen et al., 2013), with more than 90% of harvested wood used for energy production, mostly as charcoal in a domestic setting (May-Tobin, 2011). Other important ecosystem services provided by these woodlands to the human population include regulation of water availability throughout the dry season (Wilk et al., 2010; Hecky et al., 2003) and the provision of medicinal plants (Ryan et al., 2016; Augustino et al., 2011). Simultaneously, southern African woodlands are inhabited by a high number of charismatic endemic species (Burgess et al., 2004) and are increasingly a destination for international tourists (Vergles et al., 2015; Shackleton et al., 2007). These attributes together make southern African woodlands a hugely important natural asset, both locally and globally.

Southern African mesic savannas can be divided roughly into three main vegetation types. Miombo woodlands dominate southern Africa, and are the largest savanna vegetation type in the world by area (Ryan et al., 2011). They are dominated by species from the Fabaceae family, subfamily Detarioideae, from the genera: *Brachystegia*, *Julbernardia*, and *Isoberlinia* (Figure 2.5a). The namesake 'miombo' comes from the local name for the genus *Brachystegia* in various Bantu languages. These woodlands frequently have tall continuous but sparse tree canopies, only occasionally closing to the point of excluding grasses. They are mistakenly classified as forest by some data-driven forest cover maps (Hansen et al., 2013), but the co-dominance of grasses and trees means that they are true savannas under the definition used in this thesis. Rainfall in miombo woodlands varies between 540-1700 mm yr^{-1}, with a highly seasonal pattern of precipitation. Many miombo tree species are deciduous, losing their leaves in the dry season to conserve water and limit chances of damage by embolism (Tomlinson et al., 2013). Miombo woodlands are diverse, with >8500 vascular plant species, of which >300 are tree species, many of which are endemic to the region (Frost, 1996). Historically, miombo woodlands have been split into dry (<1000 mm y^{-1}) and wet (>1000 mm y^{-1}) (White, 1983). Although in reality the distinction between these two miombo types is clear cut, in general, dry miombo is dominated by *B. spiciformis* and *J. globiflora*, while wet miombo is dominated by *B. floribunda*, *B. longifolia*, *J. paniculata* and *I. angolensis* (Frost, 1996). While variation in water availability has dominated the classification of miombo woodlands, adaptations to edaphic conditions have recently gained traction as an alternative driver of biogeographic differences among miombo woodland types. Gomes et al. (2021) found that symbiotic arbuscular mycorrhizal associations of Detarioideae tree species coincide with phosphorus-limited landscapes, while non-Detarioideae tree species, many of which produce Rhizobia-associated root nodules, tend to be found in more nitrogen-limited landscapes.

Mopane woodlands form thin bands in the south of Zambia, Zimbabwe, central and southern Mozambique, and also across the border region of Angola and Namibia (Figure 2.4). They are characterised by the dominance of a single tree species, *Colophospermum mopane*, and generally occur in areas of lower rainfall than miombo woodlands (Figure 2.5b) (Palgrave, 2003). Reduced rainfall means that mopane soils are generally more fertile than the surrounding miombo woodlands (Makhado et al., 2014). Mopane woodlands are host to the largest diversity of large mammals in southern Africa, including populations of charismatic and highly threatened species such as the black rhinoceros (*Diceros bicornis*) and giraffe (*Giraffa camelopardalis*) (Mittermeier et al., 2003). While many mopane woodlands exists as short-stature shrubby vegetation, larger ‘cathedral mopane’ exists in some areas, forming a near closed canopy (Makhado et al., 2014).

Baikiaea woodlands occur in a belt along the Angolan-Namibian border to Zimbabwe. They are dominated by *Baikiaea plurijuga*, which grow to large trees at low densities, with a long grass and shrub understorey that burns regularly (Figure 2.5c) (Werger & Coetzee, 1978). Like *C. mopane*, *B. plurijuga* is also in the Detarioideae subfamily. Baikiaea woodlands are generally less suitable for agriculture than miombo woodlands, with sandy soil originating from windblown Kalahari sand further south, and low rainfall. Human timber extraction has removed many of the largest and oldest trees in some regions (Gambiza et al., 2005). Like mopane woodlands, Baikiaea woodlands provide habitat for large herbivores, most notably elephants (*Loxodonta africana*) (Holdo, 2007).

Although this thesis focusses primarily on the mesic Detarioideae savannas described above, other southern African savannas not dominated by Detarioideae species are also referred to throughout the thesis. Combretaceae woodlands are dominated by trees from the *Combretum* and *Terminalia* genera, both arbuscular mycorrhizal genera in the Combretaceae family (Figure 2.5d). Combretaceae woodlands are found in drier conditions than miombo woodlands, but still mainly on dystrophic soils. They differ from miombo woodlands in their woodland structure, lacking large canopy tree species (Frost, 1996). Often, Combretaceae woodland patches can be found among miombo woodland patches, in areas where drainage or intense disturbance has precluded the growth of dominant miombo species (Gonçalves et al., 2017), thus Combretaceae woodlands sometimes constitute a kind of ‘degraded’ miombo woodland. Finally, Mimosoideae woodlands occur in eutrophic areas that are drier still, often experiencing higher levels of herbivory from large mammals than other woodlands in the region. Mimosoideae genera such as *Acacia* often develop ‘cagey’ and thorny canopy architecture to protect from browsing mammals (Figure 2.5e) (Moncrieff et al., 2014). Mimosoid woodlands in southern Africa occur mainly in South Africa, Kenya and Tanzania. Unlike the other vegetation types mentioned above, tree cover in Mimosoid woodlands is generally limited by precipitation and herbivory (White, 1983).

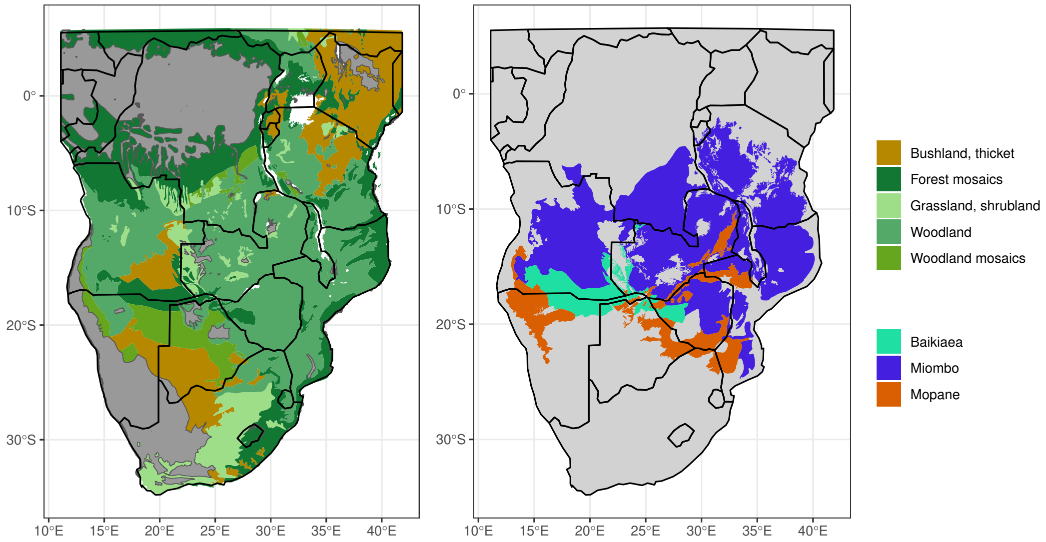
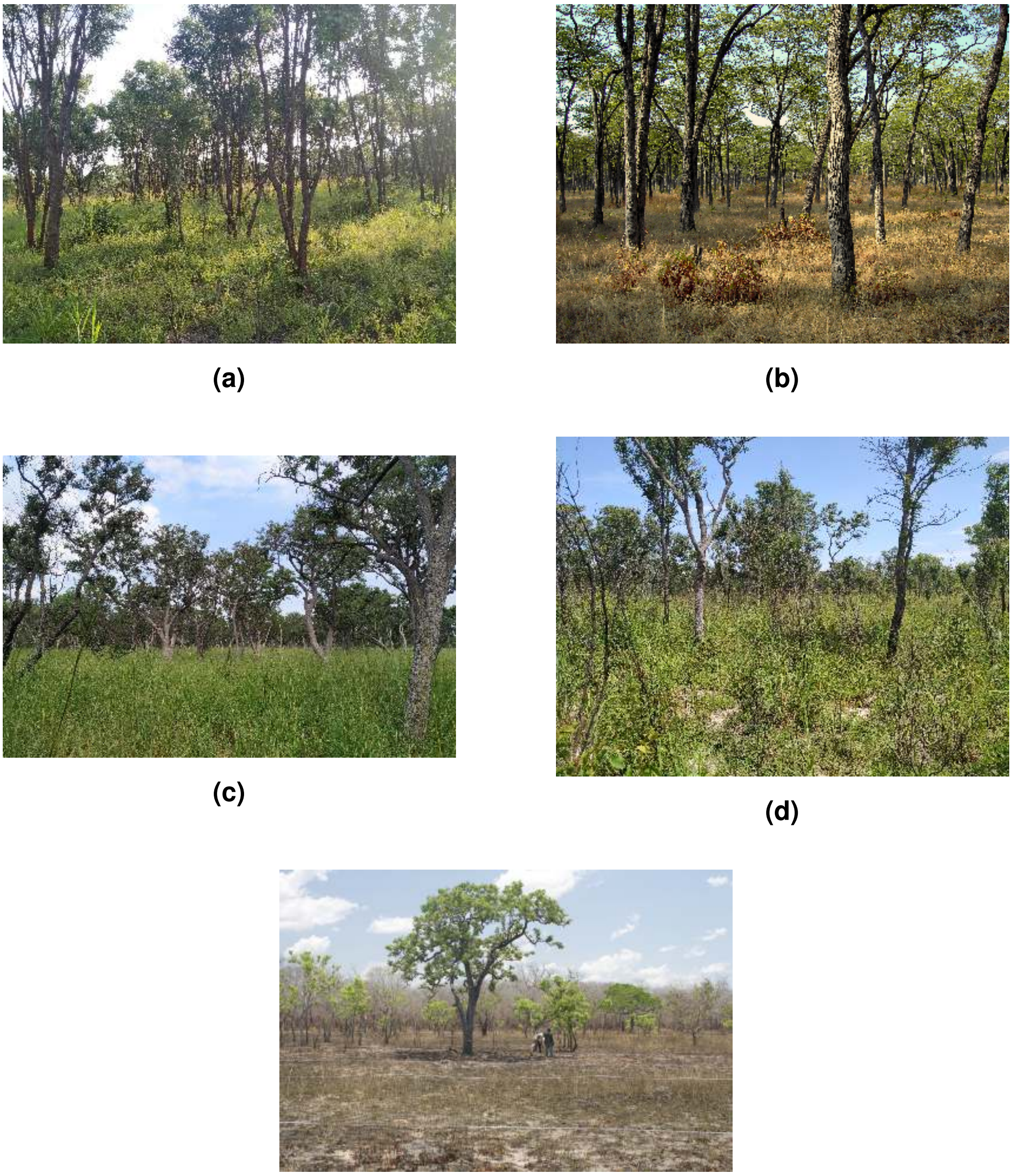


Figure 2.4: The distribution of key savanna vegetation types within southern Africa. Left: physiognomic classification adapted from White (1983). Right: floristic classification of selected savanna-woodlands adapted from Dinerstein et al. (2017), Terrestrial Ecoregions of the World.

2.5 Biodiversity and ecosystem function theory

Since the development of the concept of niches (Grinnell, 1904; MacArthur & Levins, 1967) and the coexistence of competing species (Elton, 1927), various research has touched on the potential link between species diversity, the efficiency of resource use, and therefore ecosystem function (Hairston et al., 1960; Janzen, 1970; Grime, 1973; Whittaker, 1960). In 1992, the Earth Summit in Rio de Janeiro discussed the growing concern that global patterns of biodiversity loss might negatively impact the functioning of ecosystems, and importantly damage the ecosystem services provided to humans. Later, researchers gathered in Bayreuth, Germany to discuss the role of biodiversity (B) on ecosystem function (EF), prompting the seminal work of Schulze & Mooney (1993), which formalised these initial theories. Since then, a thriving field of research has emerged which aims to assess and explain the multiple and complex relationships between biodiversity and ecosystem function (Figure 2.7), with hundreds of studies exploring biodiversity effects in both experimental and



(a)

(b)

(c)

(d)

(e)

Figure 2.5: Typical southern African woodland vegetation formations. (a) miombo woodland in Bicuar National Park, Angola, with *Julbernardia paniculata*, (b) Mopane woodland in South Luangwa National Park, Zambia, with *Colophospermum mopane* (photo: Hans Hillewaert), (c) Baikiaea woodland in Bicuar National Park, Angola, with *Baikiaea plurijuga*, (d) highly disturbed Combretaceae woodland in Bicuar National Park, Angola, and (e) Mimosoideae woodland in Kilwa District, Tanzania (photo: Casey Ryan).

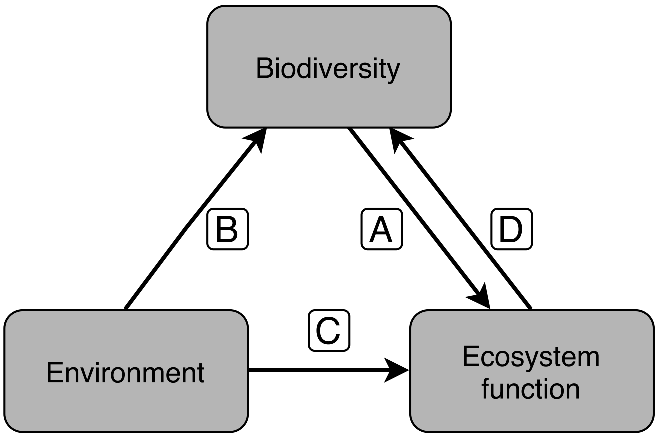


Figure 2.6: As BEF research has progressed, it has become apparent that effects of biodiversity on ecosystem function must be considered within a framework which appreciates biodiversity as both a driver of, and a response to, ecosystem function and environment. Early BEF research in experimental systems sought to isolate the effect of biodiversity on ecosystem function (A) by holding the effects of environment on ecosystem function constant (B) (e.g. Cardinale et al. 2009). More recently, studies in natural systems have incorporated the effects of environment on both biodiversity and ecosystem function (B, C), as well as the reciprocal effect of ecosystem function on biodiversity (D), in an attempt to understand the relative importance of environment and biodiversity for ecosystem function, and to account for the covariation of biodiversity with environmental factors that could otherwise lead to mistaken attribution of environmental effects to biodiversity in natural systems (e.g. Mora et al. 2014).

natural systems (Plas, 2019; Newbold et al., 2016; Tilman et al., 2014). The 1992 Earth Summit defined a paradigm shift in ecological thinking. Previously, biodiversity had mainly been considered as a *result* of environmental conditions and ecosystem function, while the research that came after redefined biodiversity as both a *driver* and result of ecosystem function (Figure 2.6).

The BEF framework and supporting empirical evidence has influenced global environmental policy by encouraging biodiversity conservation as a means of maintaining ecosystem functionality and its associated ecosystem services such as carbon storage, food provision, soil moisture retention etc. (Balvanera et al., 2014; Naeem et al., 2012). Increasingly, biodiversity conservation is encouraged as a method of indirectly maximising natural capital (perceived value of natural assets, Kareiva et al. 2011) by maximising ecosystem functionality (Scherer-Lorenzen, 2014; Cardinale et al., 2012). Many conservation policy makers and managers seek win-win conservation strategies that maximise both biodiversity and ecosystem service provision (Howe et al., 2014; Adams, 2004). Research into the role of biodiversity in maintaining ecosystem functionality has become more pertinent in the last 20 years in response to mounting evidence of startling global biodiversity losses (McRae et al., 2017; Butchart et al., 2010; Vitousek et al., 1997). There should be trepidation however, as it is still unclear whether positive biodiversity effects exist in all ecosystems (Sheil & Bongers, 2020). The vast majority of previous research has taken place in experimental settings, or in temperate and wet tropical natural systems. In tropical savannas, naive management strategies to maximise ecosystem functions that have been identified as valuable, such as carbon sequestration (Duffy et al., 2017), could lead to the decline of other ecosystem functions and services, resulting in a loss of unique savanna characteristics (Brockerhoff et al., 2017; Srivastava & Vellend, 2005).

This thesis aims to understand drivers of variation in ecosystem function across southern African woodlands through the lens of the “Biodiversity - Ecosystem Function Relationship” (BEFR). Ecosystem functions can be defined in broad terms as the rate processes which control the fluxes of energy and matter through an ecosystem (Jax, 2005). This includes basic processes of primary production such as gross primary productivity and atmospheric nitrogen fixation, but can be extended to indirect aggregate measures of function such as resilience of productivity to disturbance. Additionally, ecosystem function can be further extended to include ecosystem structural properties such as forest canopy complexity and trophic complexity, which in turn influence ecosystem processes. In this thesis, I focus on woody biomass, productivity, tree cover and associated tree canopy complexity as measures of ecosystem function, with the aim of improving understanding of the vegetation and carbon dynamics of southern African woodlands.

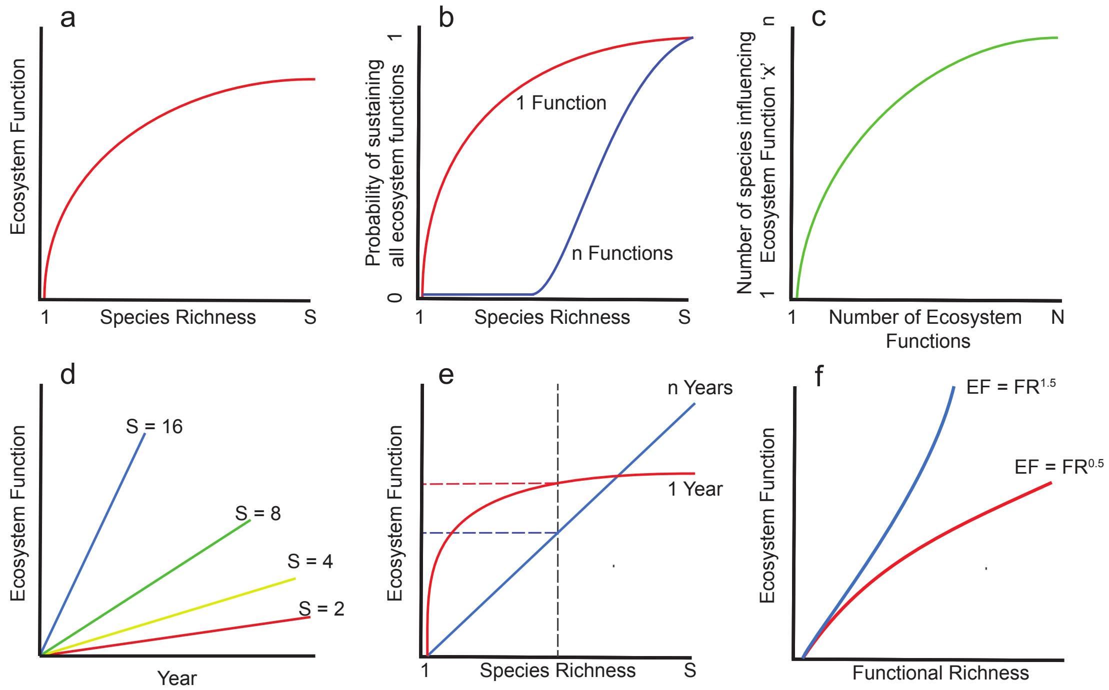


Figure 2.7: Schematic diagrams of inferences made on the Biodiversity - Ecosystem Function Relationship by previous studies. a) The classic BEF relationship found by many experiments at small spatial scales (Cardinale et al., 2009). b) As more functions are considered the proportion of functionally redundant species decreases, i.e. the curve reaches asymptote at a higher species richness (Hector & Bagchi, 2007). c) The saturating relationship of the number of ecosystem functions considered and the number of species influencing ecosystem multifunctionality (Hector & Bagchi, 2007). d) The rate of increase in ecosystem function over time increases as species richness (S) increases (Cardinale et al., 2007). e) Longer-running studies find lower functional redundancy (Reich et al., 2012). f) When functional richness is used in place of species richness, the relationship reaches asymptote at a higher richness. The relationship saturates at higher functional richness as the number of species interactions increases (Mora et al., 2014).

2.5.1 Niche complementarity, selection effects, and facilitation

There are various mechanisms underlying the observed effect of biodiversity on ecosystem function. Early experiments in artificial grasslands (Tilman & Downing, 1994) and experimental microcosms (Naeem et al., 1994), which involved introducing or removing species from random assemblages concluded that ‘selection effects’ were the strongest drivers of the BEFR. Assuming random introduction or extinction of species, it is more likely that a diverse community will contain a species which contributes to a given ecosystem function (Huston, 1997). Of course, in natural systems, species introduction and removal is rarely random and may be confounded by a species’ contribution to a given ecosystem function (Smith & Knapp, 2003). Related to selection effects, which place emphasis on the presence of species which contribute to function, Grime (1998) proposed the Mass-Ratio Hypothesis to explain biodiversity effects on ecosystem function. The Mass-Ratio Hypothesis suggests that it is not the breadth of niche space filled by a species assemblage that determines ecosystem function, but the ability of the most abundant species to optimise a given ecosystem function. Subsequent experimental studies have attempted to partition selection effects from other effects, or to remove selection effects entirely through experimental design, in an attempt to isolate other effects (Loreau, 2001).

The mechanism of niche complementarity has been the main focus of the majority of previous BEFR studies (Figure 2.8) (Wright et al., 2017). The theory of niche complementarity follows intuitively from early evolutionary theory, that coexisting species must occupy different environmental niches, in order to prevent competitive exclusion of the weaker competitor (Tobner et al., 2016; Levine & HilleRisLambers, 2009; MacArthur, 1955; MacArthur & Levins, 1967). Thus, the more species present in a given system, the more environmental niche space is filled, leading to more efficient and complete use of resources, a reduction in density dependent intra-specific competition and ‘higher’ observed values for various ecosystem functions (Isbell et al., 2013). The mechanism of niche complementarity has been corroborated by many studies, but to varying extents depending on biome, whether the study was conducted in an experimental or natural system, the duration of study, and what measures of biodiversity and ecosystem function are used (Wright et al., 2017; Cardinale et al., 2009; Cardinale et al., 2011). Niche complementarity can also mediate functionality over time, as different species are able to optimise function at different times under under varying environmental conditions; this effect is known as the biodiversity insurance hypothesis (Morin et al., 2014; Bartomeus et al., 2013; Yachi & Loreau, 1999). The insurance hypothesis also postulates that higher biodiversity at the landscape level will increase the rate at which ecosystems recover from stochastic local disturbances, by providing refugia populations in less perturbed areas (Gonzalez et al., 2009).

Facilitation effects increase the functional contribution of certain species in combination. For example, if grass species A is sensitive to high temperatures, tree species B may provide shade and thus reduce the temperature of the understorey, increasing the productivity of grass species A compared to if it was found in monoculture. Originally this specific example of facilitation was termed “nurse plant syndrome” (Padilla & Pugnaire, 2006). This effect has been studied extensively in dryland ecosystems, where adult trees act as nurse plants for juveniles below, providing shade and reducing mortality. Callaway & Walker (1997), Good et al. (2014) and Weltzin & McPherson (1999) theorised a predictable relationship between environmental stress and the nature of interactions among plants, hypothesising that facilitation effects override competitive effects in highly stressful environments. More recently, Lortie et al. (2021) conducted a meta-analysis of facilitation effects in arid shrublands, concluding that while shrubs do provide facilitative effects, the net effect of species diversity on shrub biomass turned weakly negative under high diversity, due to competitive effects. Facilitation effects remain understudied in the BEFR literature, but could be important in environmentally stressful landscapes. A history of research into partitioning niche complementarity from selection effects in biodiversity experiments has largely ignored the role of facilitation effects, presumably because they are not expected to drive large scale variation in the BEFR between systems, and because they are often context specific and it is difficult to test for their presence in natural systems (Wright et al., 2017). Wright et al. (2021) discusses how facilitation effects may have been mistakenly identified as niche complementarity as a result of the simplistic partitioning method used in previous studies.

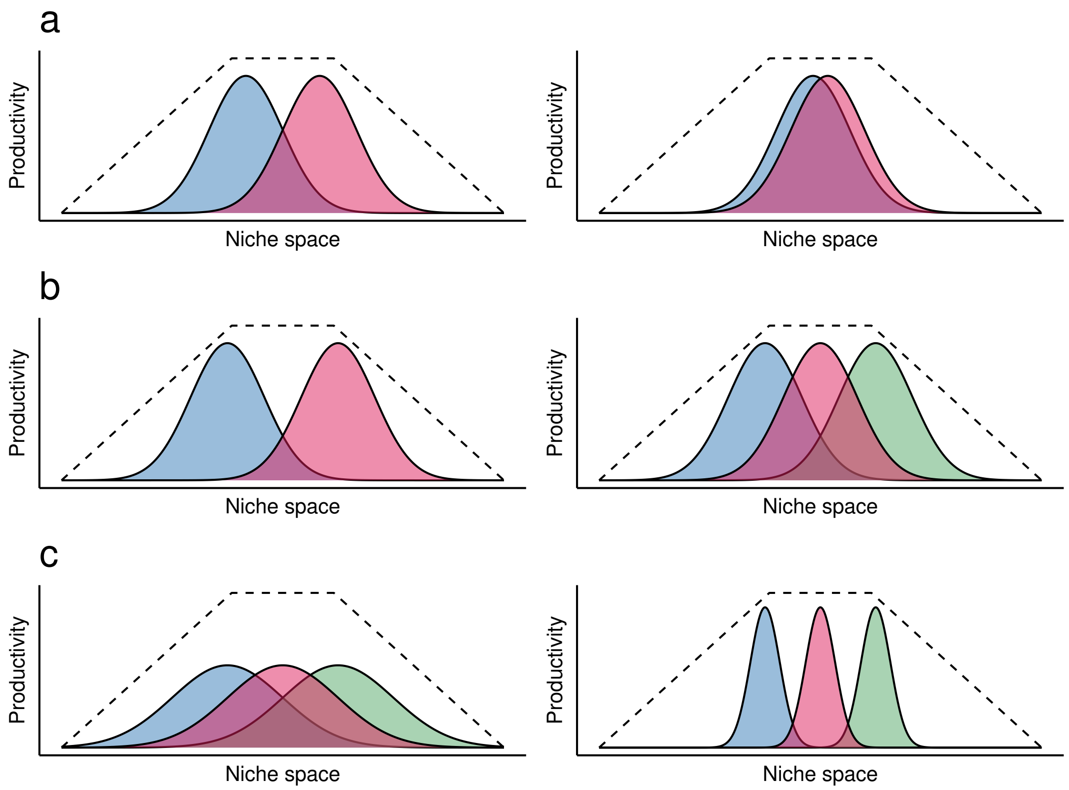


Figure 2.8: Schematic diagrams demonstrating secondary controls on the mechanism of niche complementarity. Each density plot shows species represented by their functional contribution (productivity) under different environmental conditions (niche space) within the larger environmental niche volume (dashed line). a) shows how the degree of overlap in niche space of two species affects the total utilisation of the environmental niche volume (area under all species curves). On the left, functionally distinct species utilise more of the environmental niche volume. Removal of a species in this case would greatly reduce ecosystem productivity. On the right, where functional redundancy is high, removal of a species would have negligible effects. b) shows the effect of adding a functionally distinct species to an ecosystem. c) shows the effect of niche breadth on environmental niche volume utilisation. On the left, three generalist species overlap in their functional niche. While each species has relatively incomplete utilisation of the environmental niche volume, this is offset by each species occupying a wide range of environmental niche space. If the red species was removed, there would be only a marginal reduction in ecosystem productivity. On the right, three specialist species have a narrower niche breadth but more complete environmental niche volume utilisation under ideal conditions. If a species was removed from this ecosystem, there would be a much greater reduction in ecosystem productivity.

2.5.2 Global distribution of biodiversity-ecosystem function research

Among the hundreds of published studies of the biodiversity-ecosystem function relationship (BEFR), the majority are from experimental contexts, in small grassland patches or mesocosms. The number of studies in forested ecosystems is growing, but remains restricted predominantly to temperate forests in the global north (Clarke et al., 2017). In particular, there is a paucity of BEFR research in disturbance-prone wooded ecosystems, e.g. the mesic savannas which cover ~20% of the global land surface (Scholes & Walker, 1993). Liang et al. (2016) conducted a meta-analysis of estimates of the BEFR from 777,126 forest sample plots. They found that 99.87% of these estimates followed a monotonic, positive BEFR curve, which saturated at high species richness. However, less than 600 of these plots were located in Africa, and none further south than Tanzania.

Clarke et al. (2017) reviewed four BEFR meta-analyses (Gamfeldt et al., 2015; Griffin et al., 2013; Zhang et al., 2012; Cardinale et al., 2009) and identified only two studies conducted in Africa (Foster et al., 1999; Burleigh & Yamoah, 1997), compared with 69 in Europe and 82 in North America (Figure 2.9). Both of these African studies are narrow in their scope and do not consider southern African savanna-woodland mosaics. Foster et al. (1999) studied the effect of dietary diversity on a single marine mollusc species in an experimental context. Burleigh & Yamoah (1997) is an agroforestry study primarily investigating the suitability of two Fabaceae tree species as erosion mitigators. Neither of these studies provide an understanding of the BEFR that is relevant to understanding how entire savanna ecosystems respond to changes in biodiversity. In a meta-analysis by Duffy et al. (2017), only three terrestrial field studies from southern Africa were used to compare the effects of biodiversity to those of environmental factors from a total of 167 field estimates of the BEFR. Given the unique community composition (Lehmann et al., 2011), environmental conditions (Linder, 2003) and strong role of disturbance by fire and herbivory in structuring these savannas (Staver et al., 2011), it would be simplistic to generalise the BEFR found in other systems to this region.

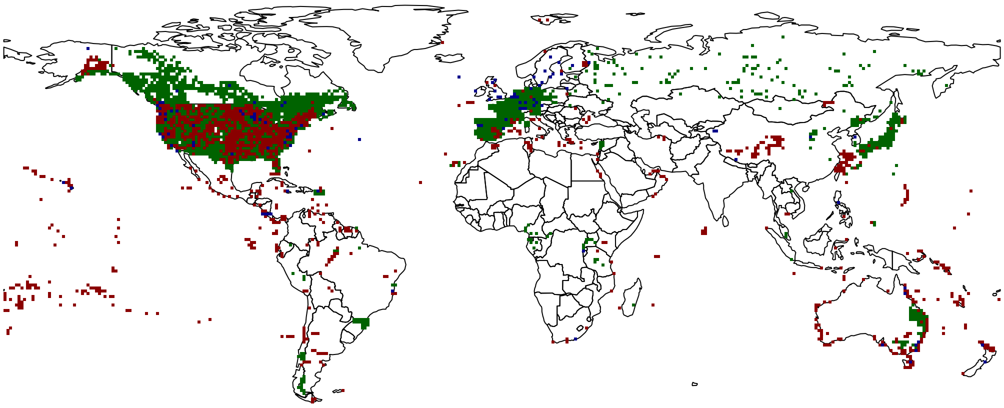


Figure 2.9: Location of studies of the biodiversity - ecosystem function relationship included in three meta-analyses of BEF research: blue Clarke et al. (2017), green Liang et al. (2016), red Duffy et al. (2017).

2.5.3 Should we expect biodiversity effects on ecosystem function in southern African woodlands?

Extensive research has linked tree biodiversity to ecosystem function in temperate and tropical forests (Liang et al., 2016), but only a small number of BEFR studies have taken place in tropical savannas, and fewer still in southern African woodlands. The effects of disturbance and water availability in particular, which serve to reduce tree cover and biomass in southern African woodlands, might weaken or even invert the positive biodiversity-ecosystem function relationship found in other biomes (Tilman et al., 2012; Tilman et al., 2014; Hooper et al., 2012).

In temperate and wet tropical closed canopy forests trees interact with each other due to their close proximity (Coomes & Allen, 2007; Purves et al., 2007). Overlapping canopies and inter-weaving root networks produce competition for light, water and nutrients among individuals. Southern African woodlands however, exist along a wide gradient of tree cover. At the extreme low end of this gradient, trees may be too far apart for canopy competition to occur, and while the root networks of savanna trees are often extensive (Belsky, 1994), root competition may also be negligible among adult trees in the most sparsely wooded ecosystems. Though Dohn et al. (2017) demonstrated strong competitive interactions at neighbourhood scales of up to 5 m for most trees in an East African savanna. Low tree densities may result from a combination of resource-based processes such as low water availability and disturbance caused by fire, herbivory, or human land use practices such as selective logging (Ryan et al., 2016). Figure 2.2 shows observed woody cover along a precipitation gradient in Africa, taken from Sankaran et al. (2005). It shows that in the majority of plots, woody cover is below the physiological maximum set by precipitation, indicating that many other factors influence woody cover other than water availability. A lack of competition would weaken the effect of tree species diversity on ecosystem function, as multiple species can often fill overlapping niches in the absence of competition. In other words, the lack of competition allows the realised niche of a species to expand to approach the volume of the fundamental niche set by physiological limitations. Niche differentiation however, would still occur, only allowing certain species to establish and optimise productivity in certain micro-habitats, suggesting at least some effect of tree diversity on ecosystem function even in the most sparsely forested ecosystems, depending on the functional overlap of the species present in the community.

While disturbance and low resource availability may reduce the strength of biodiversity effects in southern African woodlands through its effect on competition, these same environmental pressures may increase the strength of the BEFR via facilitation effects. In European forests, Ratcliffe et al. (2017) found that the strength of the effect of tree species richness on many ecosystem functions increased as water availability decreased. They suggested that facilitation effects between species became stronger than competitive effects when resource availability was low, with strong facilitation effects being more likely at high species richness. Furthermore, Baert et al. (2018) reported that environmental stress shows a humped relationship with the strength of the BEFR, with the relationship being highest at intermediate levels of stress. They suggest an interplay between niche complementarity and selection effects at low environmental stress levels, which are often accompanied by greater levels of competition due to the lack of growth limitation, and higher facilitative effects at very high levels of environmental stress. Cardinale & Palmer (2002) found that in an experimental mesocosm of caddisfly larvae, increased disturbance in the form of random individual mortality led to increased effects of species richness on productivity. They attributed this effect to a decrease in dominance of competitively superior but low productivity taxa. Fire disturbance in forests has been linked to abundance dependent mortality among smaller stems (Roques et al., 2001). A species with more small stems is more likely to experience mortality during a fire. There may therefore be a link between disturbance regime and the strength of the species richness - ecosystem function relationship in fire prone woodland ecosystems. Unlike the caddisfly larvae in Cardinale & Palmer (2002) however, tree species differ in their resilience to fire driven mortality, owing to adaptations such as corky bark (Solbrig et al., 1996). The strength of the BEFR in a given system may therefore be a product of environmental conditions, disturbance regime, and species functional composition. These factors, which remain unmeasured in many studies of the BEFR in natural systems may explain some of the variation in the observed strength of the BEFR, and may be especially important in determining the BEFR in southern African woodlands. Conducting experiments across environmental gradients will improve understanding of how biodiversity effects interact with the environment to determine ecosystem functionality (Turnbull et al., 2016; Tilman et al., 2014).

2.5.4 Structural diversity, tree cover and ecosystem function

Biodiversity in BEFR studies is most often measured as the species richness of a focal trophic level or functional group (e.g. trees). However, more complex measures of functional diversity provide better insight into the tangible mechanistic processes that underlie biodiversity effects (Finegan et al., 2015; Scherer-Lorenzen, 2014; Petchey & Gaston, 2006). Increased tree species richness appears to cause an increase in the productivity of forest stands, but is this due to a greater likelihood of including a productive species (selection effects), canopy packing complementarity, rooting depth complementarity, facilitative shading effects, or more likely a combination of all the above, with the contribution of each varying across environmental gradients? Investigating the mechanisms responsible for biodiversity effects provides better understanding of ecosystem processes in a given system, and allows for more generalisable predictions of the effects of species loss on ecosystem function (Díaz & Cabido, 2001; Petchey & Gaston, 2006).

Structural diversity, i.e. variation in tree size and physiognomy, is an important measure of functional diversity in savanna ecosystems (Ali et al., 2016;

Ali et al., 2019; Pedro et al., 2017; Lecina-Diaz et al., 2018). While most tree species are somewhat plastic in their canopy occupancy, responding to the light environment and available canopy space (Jucker et al., 2015), in disturbance prone savannas, variation in growth strategy among species as an adaptation to disturbance represents an axis of functional diversity that may partially determine niche complementarity and tree cover. Tree species in southern African woodlands exhibit wide variation in growth strategy among species (Solbrig et al., 1996). While some trees remain small, resprouting and coppicing after each fire to produce shrub-like understorey trees with large below-ground structures e.g. *Baphia massaiensis*, others grow rapidly to escape the fire zone, producing large, spreading canopies, e.g. *Julbernardia paniculata*. Similarly, tree species vary in their adaptation to environmental stress, namely water availability, by investing differentially in below-ground, above-ground woody and foliage structures, affecting their physical structure and canopy occupancy (Sankaran, 2019). Thus, variation in growth strategy and response to disturbance might also confer greater complementarity in canopy occupancy, allowing greater canopy cover, canopy density, and ultimately productivity in more diverse woodlands. Seidel et al. (2013) and Dănescu et al. (2016) both found that species richness increases tree canopy density and productivity in European temperate forests, through crown complementarity and wider niche occupancy across a range of understorey light environments. Similarly, Seidl et al. (2014) found that canopy structural complexity was related to ecosystem resilience and reduced recovery time after disturbance.

In miombo woodlands especially, where the canopy routinely closes but generally remains sparse enough to support grass growth (Frost, 1996), biodiversity driven increases in canopy complexity and the resulting reduction in understorey light availability might help to explain why some miombo woodland canopies exclude grasses more readily than others. While atmospheric CO_2 enrichment is expected to cause woody encroachment and woody thickening across southern Africa (Stevens et al., 2016), empirical studies have found unexplained variation among woodlands in the rates of encroachment and thickening (Lewis et al., 2009). Perhaps the functional diversity of tree canopy architecture could provide a mechanism for this previously unexplained variation.

2.6 Conclusions

Tropical savannas are complex, and savanna vegetation arises as a result of many interacting factors, but are understudied and represent the largest uncertainty in models of the global carbon cycle. Assumptions about the behaviour of tropical savannas cannot be based on other tropical forested ecosystems, mainly due the pervasive effect of disturbance and resource scarcity on ecosystem function. Previous studies of tropical savannas have focussed predominantly on the role of abiotic environment and disturbance as drivers of ecosystem function, with biodiversity as a passive result of these factors. This thesis aims to increase understanding of the functional effects of tree biodiversity in southern African woodlands, the world's largest savanna, through the lens of the Biodiversity-Ecosystem Function Relationship. Biodiversity - Ecosystem Function research reframes the role of biodiversity as both a driver and result of ecosystem function, and provides an intuitive prediction that biodiversity increases ecosystem function. BEF research in natural wooded ecosystems has shown that both positive and negative biodiversity effects may occur, depending on the function studied and the effect of environmental stress. It is unclear whether the biodiversity of tree species in southern African woodlands may affect ecosystem function, but there are multiple reasons why biodiversity effects might be weaker or possibly negative in this biome. Structural diversity of tree canopies however, arising as a result of differences in growth strategy among savanna tree species in response to disturbance and resource scarcity, could present an important mechanistic link between biodiversity and ecosystem function in southern African woodlands, with consequences for productivity, woody biomass, and tree cover. Ultimately this may be a key determinant of transitions between open and closed canopy stable states.

References

Adams, W. M. (2004). ‘Biodiversity Conservation and the Eradication of Poverty’. In: *Science* 306.5699, pp. 1146–1149. DOI: `10.1126/science.1097920`.

Ahlstrom, A., M. R. Raupach, G. Schurgers, B. Smith, A. Arneth, M. Jung, M. Reichstein, J. G. Canadell, P. Friedlingstein, A. K. Jain et al. (2015). ‘The dominant role of semi-arid ecosystems in the trend and variability of the land CO2 sink’. In: *Science* 348.6237, pp. 895–899. DOI: `10.1126/science.aaa1668`.

Aide, T. M. (1988). ‘Herbivory as a selective agent on the timing of leaf production in a tropical understory community’. In: *Nature* 336.6199, pp. 574–575. DOI: `10.1038/336574a0`.

Aleman, J. C., A. Fayolle, C. Favier, A. C. Staver, K. G. Dexter, C. M. Ryan, A. F. Azihou, D. Bauman, M. te Beest, E. N. Chidumayo et al. (2020). ‘Floristic evidence for alternative biome states in tropical Africa’. In: *Proceedings of the National Academy of Sciences* 117.45, pp. 28183–28190. DOI: `10.1073/pnas.2011515117`.

Aleman, J. C., O. Blarquez & C. A. Staver (2016). ‘Land-use change outweighs projected effects of changing rainfall on tree cover in sub-Saharan Africa’. In: *Global Change Biology* 22.9, pp. 3013–3025. DOI: `10.1111/gcb.13299`.

Ali, A., S. Lin, J. He, F. Kong, J. Yu & H. Jiang (2019). ‘Climate and soils determine aboveground biomass indirectly via species diversity and stand structural complexity in tropical forests’. In: *Forest Ecology and Management* 432, pp. 823–831. DOI: `10.1016/j.foreco.2018.10.024`.

Ali, A., E. Yan, H. Chen, S. X. Chang, Y. Zhao, X. Yang & M. Xu (2016). ‘Stand structural diversity rather than species diversity enhances aboveground carbon storage in secondary subtropical forests in Eastern China’. In: *Biogeosciences* 13, pp. 4627–4635. DOI: `10.5194/bg-13-4627-2016`.

Archibald, S., A. Nickless, N. Govender, R. J. Scholes & V. Lehsten (2010). ‘Climate and the inter-annual variability of fire in southern Africa: a meta-analysis using long-term field data and satellite-derived burnt area data’. In: *Global Ecology and Biogeography* 19.6, pp. 794–809. DOI: `10.1111/j.1466-8238.2010.00568.x`.

Archibald, S. & R. J. Scholes (2007). ‘Leaf green-up in a semi-arid African savanna -separating tree and grass responses to environmental cues’. In: *Journal of Vegetation Science* 18.4, pp. 583–594. DOI: `10.1111/j.1654-1103.2007.tb02572.x`.

Archibald, S., W. J. Bond, W. Hoffmann, C. Lehmann, C. Staver & N. Stevens (2019). *Distribution and Determinants of Savannas*. DOI: `10.1002/9781119081111.ch1`.

Arino, O., J. J. Ramos Perez, V. Kalogirou, S. Bontemps, P. Defourny & E. Van Bogaert (2012). *Global Land Cover Map for 2009 (GlobCover 2009)*. PANGAEA. DOI: `10.1594/PANGAEA.787668`. (Visited on 30/05/2021).

Asner, G. P., S. R. Levick, T. Kennedy-Bowdoin, D. E. Knapp, R. Emerson, J. Jacobson, M. S. Colgan & R. E. Martin (2009). ‘Large-scale impacts of herbivores on the structural diversity of African savannas’. In: *Proceedings of the National Academy of Sciences* 106.12, pp. 4947–4952. DOI: `10.1073/pnas.0810637106`.

Atkin, O. K., K. J. Bloomfield, P. B. Reich, M. G. Tjoelker, G. P. Asner, D. Bonal, G. Bönisch, M. G. Bradford, L. A. Cernusak, E. G. Cosio et al. (2015). ‘Global variability in leaf respiration in relation to climate, plant functional types and leaf traits’. In: *New Phytologist* 206.2, pp. 614–636. DOI: `10.1111/nph.13253`.

Augustino, S., J. B. Hall, F. B. S. Makonda & R. C. Ishengoma (2011). ‘Medicinal Resources of the Miombo woodlands of Urumwa, Tanzania: Plants and its uses’. In: *Journal of Medicinal Plants Research* 5.27. DOI: `10.5897/JMPR10.517`.

Baert, J. M., N. Eisenhauer, C. R. Janssen & F. D. Laender (2018). ‘Biodiversity effects on ecosystem functioning respond unimodally to environmental stress’. In: *Ecology Letters* 21.8. Ed. by J. Knops, pp. 1191–1199. DOI: `10.1111/ele.13088`.

Balvanera, P., I. Siddique, L. Dee, A. Paquette, F. Isbell, A. Gonzalez, J. Byrnes, M. I. O’Connor, B. A. Hungate & J. N. Griffin (2014). ‘Linking Biodiversity and Ecosystem Services: Current

Uncertainties and the Necessary Next Steps'. In: *BioScience* 64.1, pp. 49–57. DOI: `10.1093/biosci/bit003`.

Bartomeus, I., M. G. Park, J. Gibbs, B. N. Danforth, A. N. Lakso & R. Winfree (2013). 'Biodiversity ensures plant-pollinator phenological synchrony against climate change'. In: *Ecology Letters* 16.11, pp. 1331–1338. DOI: `10.1111/ele.12170`.

Beerling, D. J. & C. P. Osborne (2006). 'The origin of the savanna biome'. In: *Global Change Biology* 12.11, pp. 2023–2031. DOI: `10.1111/j.1365-2486.2006.01239.x`.

Belsky, A. J. (1994). 'Influences of Trees on Savanna Productivity: Tests of Shade, Nutrients, and Tree-Grass Competition'. In: *Ecology* 75.4, pp. 922–932. DOI: `10.2307/1939416`.

Bond, W. J. & J. E. Keeley (2005). 'Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems'. In: *Trends in Ecology & Evolution* 20.7, pp. 387–394. DOI: `10.1016/j.tree.2005.04.025`.

Bond, W. J. (2008). 'What Limits Trees in C_4 Grasslands and Savannas?' In: *Annual Review of Ecology, Evolution, and Systematics* 39.1, pp. 641–659. DOI: `10.1146/annurev.ecolsys.39.110707.173411`.

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`.

Bond, W. J. & J. J. Midgley (1995). 'Kill Thy Neighbour: An Individualistic Argument for the Evolution of Flammability'. In: *Oikos* 73.1, p. 79. DOI: `10.2307/3545728`.

Bond, W. J. & J. J. Midgley (2003). 'The Evolutionary Ecology of Sprouting in Woody Plants'. In: *International Journal of Plant Sciences* 164.S3, S103–S114. DOI: `10.1086/374191`.

Borchert, R. (1994). 'Soil and Stem Water Storage Determine Phenology and Distribution of Tropical Dry Forest Trees'. In: *Ecology* 75.5, pp. 1437–1449. DOI: `10.2307/1937467`.

Brockerhoff, E. G., L. Barbaro, B. Castagneyrol, D. I. Forrester, B. Gardiner, J. R. González-Olabarria, P. O. Lyver, N. Meurisse, A. Oxbrough, H. Taki et al. (2017). 'Forest biodiversity, ecosystem functioning and the provision of ecosystem services'. In: *Biodiversity and Conservation*. DOI: `10.1007/s10531-017-1453-2`.

Bucini, G. & N. P. Hanan (2007). 'A continental-scale analysis of tree cover in African savannas'. In: *Global Ecology and Biogeography* 16.5, pp. 593–605. DOI: `10.1111/j.1466-8238.2007.00325.x`.

Burgess, N., J. D'Amico Hales, E. Underwood, E. Dinerstein, D. Olson, I. Itoua, J. Schipper, T. Ricketts & K. Newman (2004). *Terrestrial Ecoregions of Africa and Madagascar: A Conservation Assessment*. Washington D. C., pp. 20–29.

Burleigh, J. R. & C. F. Yamoah (1997). 'Site factors associated with the performance of Leucaena leucocephala (Lam.) de Wit and Sesbania sesban (L.) Merill in pure and mixed stands in the northern highlands of Rwanda'. In: *Agroforestry Systems* 37.2, pp. 121–131. DOI: `10.1023/A:1005861821739`.

Butchart, S. H. M., M. Walpole, B. Collen, A. van Strien, J. P. W. Scharlemann, R. E. A. Almond, J. E. M. Baillie, B. Bomhard, C. Brown, J. Bruno et al. (2010). 'Global Biodiversity: Indicators of Recent Declines'. In: *Science* 328.5982, pp. 1164–1168. DOI: `10.1126/science.1187512`.

Callaway, R. M. & L. R. Walker (1997). 'Competition and facilitation: a synthetic approach to interactions in plant communities'. In: *Ecology* 78.7, pp. 1958–1965. DOI: `10.1890/0012-9658(1997)078[1958:cafasa]2.0.co;2`.

Campbell, B. M., ed. (1996). *The miombo in transition: Woodlands and welfare in Africa*. Bogor, Indonesia: Centre for International Forestry Research.

Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, G. M. Mace, D. Tilman, D. A. Wardle et al. (2012). 'Biodiversity loss and its impact on humanity'. In: *Nature* 489.7415, pp. 326–326. DOI: `10.1038/nature11373`.

Cardinale, B. J., K. L. Matulich, D. U. Hooper, J. E. Byrnes, E. Duffy, L. Gamfeldt, P. Balvanera, M. I. O'Connor & A. Gonzalez (2011). 'The functional role of producer diversity in ecosystems'. In: *American Journal of Botany* 98.3, pp. 572–592. DOI: `10.3732/ajb.1000364`.

Cardinale, B. J. & M. A. Palmer (2002). 'Disturbance moderates biodiversity-ecosystem function relationships: experimental evidence from caddisflies in stream mesocosms'. In: 83.7, pp. 1915–1927. DOI: `10.1890/0012-9658(2002)083[1915:dmbefr]2.0.co;2`.

Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, C. Jouseau, M. W. Cadotte, I. T. Carroll, J. J. Weis et al. (2009). 'Effects of biodiversity on the functioning of ecosystems: a summary of 164 experimental manipulations of species richness'. In: *Ecology* 90.3, pp. 854–854. DOI: `10.1890/08-1584.1`.

Cardinale, B. J., J. P. Wright, M. W. Cadotte, I. T. Carroll, A. Hector, D. S. Srivastava, M. Loreau & J. J. Weis (2007). 'Impacts of plant diversity on biomass production increase through time because of species complementarity'. In: *Proceedings of the National Academy of Sciences* 104.46, pp. 18123–8. DOI: `10.1073/pnas.0709069104`.

Case, M. F., J. B. Nippert, R. M. Holdo & A. C. Staver (2020). 'Root-niche separation between savanna trees and grasses is greater on sandier soils'. In: *Journal of Ecology* 108.6. Ed. by I. Oliveras, pp. 2298–2308. DOI: `10.1111/1365-2745.13475`.

Cerling, T. E., J. M. Harris, B. J. MacFadden, M. G. Leakey, J. Quade, V. Eisenmann & J. R. Ehleringer (1997). 'Global vegetation change through the Miocene/Pliocene boundary'. In: *Nature* 389.6647, pp. 153–158. DOI: `10.1038/38229`.

Charles-Dominique, T., H. Beckett, G. F. Midgley & W. J. Bond (2015). 'Bud protection: a key trait for species sorting in a forest/savanna mosaic'. In: *New Phytologist* 207.4, pp. 1052–1060. DOI: `10.1111/nph.13406`.

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`.

Clarke, D. A., P. H. York, M. A. Rasheed & T. D. Northfield (2017). 'Does biodiversity-ecosystem function literature neglect tropical ecosystems'. In: *Trends in Ecology & Evolution* 32.5, pp. 320–323. DOI: `10.1016/j.tree.2017.02.012`.

Clements, F. E. (1916). *Plant succession: an analysis of the development of vegetation*. Carnegie Institution of Washington, pp. 1–658.

Coomes, D. A. & R. B. Allen (2007). 'Effects of size, competition and altitude on tree growth'. In: *Journal of Ecology* 95.5, pp. 1084–1097. DOI: `10.1111/j.1365-2745.2007.01280.x`.

Dahlin, K. M., D. D. Ponte, E. Setlock & R. Nagelkirk (2016). 'Global patterns of drought deciduous phenology in semi-arid and savanna-type ecosystems'. In: *Ecography* 40.2, pp. 314–323. DOI: `10.1111/ecog.02443`.

Daibes, L. F., J. G. Pausas, N. Bonani, J. Nunes, F. A. O. Silveira & A. Fidelis (2019). 'Fire and legume germination in a tropical savanna: ecological and historical factors'. In: *Annals of Botany* 123.7, pp. 1219–1229. DOI: `10.1093/aob/mcz028`.

Dănescu, A., A. T. Albrecht & J. Bauhus (2016). 'Structural diversity promotes productivity of mixed, uneven-aged forests in southwestern Germany'. In: *Oecologia* 182.2, pp. 319–333. DOI: `10.1007/s00442-016-3623-4`.

Dantas, V. L., M. Hirota, R. S. Oliveira & J. G. Pausas (2016). 'Disturbance maintains alternative biome states'. In: *Ecology Letters* 19, pp. 12–19. DOI: `10.1111/ele.12537`.

Dantas, V. L. & J. G. Pausas (2013). 'The lanky and the corky: fire-escape strategies in savanna woody species'. In: *Journal of Ecology* 101.5. Ed. by P. Bellingham, pp. 1265–1272. DOI: `10.1111/1365-2745.12118`.

Díaz, S. & M. Cabido (2001). 'Vive la différence: plant functional diversity matters to ecosystem processes'. In: *Trends in Ecology & Evolution* 16.11, pp. 646–655. DOI: `10.1016/s0169-5347(01)02283-2`.

Dinerstein, E., D. Olson, A. Joshi, C. Vynne, N. D. Burgess, E. Wikramanayake, N. Hahn, S. Palminteri, P. Hedao, R. Noss et al. (2017). 'An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm'. In: *BioScience* 67.6, pp. 534–545. DOI: `10.1093/biosci/bix014`.

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`.

Donaldson, J. E., S. Archibald, N. Govender, D. Pollard, Z. Luhdo & C. L. Parr (2017). 'Ecological engineering through fire-herbivory feedbacks drives the formation of savanna grazing lawns'. In: *Journal of Applied Ecology* 55.1, pp. 225–235. DOI: `10.1111/1365-2664.12956`.

Duffy, J. E., C. M. Godwin & B. J. Cardinale (2017). 'Biodiversity effects in the wild are common and as strong as key drivers of productivity'. In: *Nature* 549.7671, pp. 261–264. DOI: `10.1038/nature23886`.

Edwards, E. J. & S. A. Smith (2010). 'Phylogenetic analyses reveal the shady history of C4 grasses'. In: *Proceedings of the National Academy of Sciences* 107.6, pp. 2532–2537. DOI: `10.1073/pnas.0909672107`.

Elton, C. S. (1927). *Animal ecology*. Chicago IL, USA: University of Chicago Press.

Fairhead, J., M. Leach, D. Millimouno & M. Kamano (1996). *Misreading the African landscape: society and ecology in a forest-savanna mosaic*. Cambridge, UK: Cambridge University Press.

Fayolle, A., M. D. Swaine, J. Aleman, A. F. Azihou, D. Bauman, M. te Beest, E. N. Chidumayo, J. P. G. M. Cromsigt, H. Dessard, M. Finkch et al. (2018). 'A sharp floristic discontinuity revealed by the biogeographic regionalization of African savannas'. In: *Journal of Biogeography* 46, pp. 1–12. DOI: `10.1111/jbi.13475`.

February, E. C., S. I. Higgins, W. J. Bond & L. Swemmer (2013). 'Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses'. In: *Ecology* 94.5, pp. 1155–1164. DOI: `10.1890/12-0540.1`.

Finegan, B., M. Peña-Claros, A. de Oliveira, N. Ascarrunz, M. S. Bret-Harte, G. Carreño-Rocabado, F. Casanoves, S. Díaz, P. Eguiguren Velepucha, F. Fernandez et al. (2015). 'Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses'. In: *Journal of Ecology* 103.1, pp. 191–201. DOI: `10.1111/1365-2745.12346`.

Foster, G. G., A. N. Hodgson & M. Balarin (1999). 'Effect of diet on growth rate and reproductive fitness of Turbo sarmaticus (Mollusca: Vetigastropoda: Turbinidae)'. In: *Marine Biology* 134.2, pp. 307–315. DOI: `10.1007/s002270050548`.

Frost, P. (1996). 'The ecology of miombo woodlands'. In: *The miombo in transition: woodlands and welfare in Africa*. Ed. by B. M. Campbell. Bogor, Indonesia: Center for International Forestry Research, pp. 11–55.

Gambiza, J., B. M. Campbell, S. R. Moe & P. G. H. Frost (2005). 'Fire behaviour in a semi-arid Baikiaea plurijuga savanna woodland on Kalahari sands in western Zimbabwe'. In: *South African Journal of Science* 101, pp. 239–244.

Gamfeldt, L., J. S. Lefcheck, J. E. K. Byrnes, B. J. Cardinale, J. E. Duffy & J. N. Griffin (2015). 'Marine biodiversity and ecosystem functioning: What's known and what's next?' In: *Oikos* 124.3, pp. 252–265. DOI: `10.1111/oik.01549`.

Gomes, A. L., R. Revermann, P. Meller, F. M. P. Gonçalves, M. P. M. Aidar, F. Lages & M. Finckh (2021). 'Functional traits and symbiotic associations of geoxyles and trees explain the dominance of detarioid legumes in miombo ecosystems'. In: *New Phytologist* 230.2, pp. 510–520. DOI: `10.1111/nph.17168`.

Gonçalves, F. M. P., R. Revermann, A. L. Gomes, M. P. M. Aidar, M. Finckh & N. Juergens (2017). 'Tree species diversity and composition of Miombo woodlands in South-Central Angola: A chronosequence of forest recovery after shifting cultivation'. In: *International Journal of Forestry Research* 2017, pp. 1–13. DOI: `10.1155/2017/6202093`.

Gonzalez, A., N. Mouquet & M. Loreau (2009). 'Biodiversity as spatial insurance: The effects of habitat fragmentation and dispersal on ecosystem functioning'. In: *Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective*. DOI: `10.1093/acprof:oso/9780199547951.003.0010`.

Good, M. K., P. J. Clarke, J. N. Price & N. Reid (2014). 'Seasonality and facilitation drive tree establishment in a semi-arid floodplain savanna'. In: *Oecologia* 175.1, pp. 261–271. DOI: 10.1007/s00442-014-2886-x.

Good, S. P. & K. K. Caylor (2011). 'Climatological determinants of woody cover in Africa'. In: *Proceedings of the National Academy of Sciences* 108.12, pp. 4902–4907. DOI: 10.1073/pnas.1013100108.

Grace, J., J. S. Jose, P. Meir, H. S. Miranda & R. A. Montes (2006). 'Productivity and carbon fluxes of tropical savannas'. In: *Journal of Biogeography* 33.3, pp. 387–400. DOI: 10.1111/j.1365-2699.2005.01448.x.

Griffin, J. N., J. E. K. Byrnes & B. J. Cardinale (2013). 'Effects of predator richness on prey suppression: A meta-analysis'. In: *Ecology* 94.10, pp. 2180–2187. DOI: 10.1890/13-0179.1.

Grime, J. P. (1973). 'Competitive Exclusion in Herbaceous Vegetation'. In: *Nature* 242.5396, pp. 344–347. DOI: 10.1038/242344a0.

Grime, J. P. (1998). 'Benefits of plant diversity to ecosystems: Immediate, filter and founder effects'. In: *Journal of Ecology* 86.6, pp. 902–910. DOI: 10.1046/j.1365-2745.1998.00306.x.

Grinnell, J. (1904). 'The Origin and Distribution of the Chest-Nut-Backed Chickadee'. In: *The Auk* 21.3, pp. 364–382. DOI: 10.2307/4070199.

Hairston, N. G., F. E. Smith & L. B. Slobodkin (1960). 'Community Structure, Population Control, and Competition'. In: *The American Naturalist* 94.879, pp. 421–425. DOI: 10.1086/282146.

Hansen, M. C., P. V. Potapov, R. Moore, M. Hancher, S. A. Turubanova, A. Tyukavina, D. Thau, S. V. Stehman, S. J. Goetz, T. R. Loveland et al. (2013). 'High-Resolution Global Maps of 21st-Century Forest Cover Change'. In: *Science* 342.6160, pp. 850–853. DOI: 10.1126/science.1244693.

Hecky, R. E., H. A. Bootsma & M. L. Kingdon (2003). 'Impact of Land Use on Sediment and Nutrient Yields to Lake Malawi/Nyasa (Africa)'. In: *Journal of Great Lakes Research* 29, pp. 139–158. DOI: 10.1016/s0380-1330(03)70544-9.

Hector, A. & R. Bagchi (2007). 'Biodiversity and ecosystem multifunctionality'. In: *Nature* 448.7150, pp. 188–190. DOI: 10.1038/nature05947.

Hempson, G. P., S. Archibald & W. J. Bond (2015). 'A continent-wide assessment of the form and intensity of large mammal herbivory in Africa'. In: *Science* 350.6264, pp. 1056–1061. DOI: 10.1126/science.aac7978.

Hempson, G. P., S. Archibald & W. J. Bond (2017). 'The consequences of replacing wildlife with livestock in Africa'. In: *Scientific Reports* 7.1. DOI: 10.1038/s41598-017-17348-4.

Higgins, S. I., W. J. Bond & W. S. W. Trollope (2000). 'Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna'. In: *Journal of Ecology* 88.2, pp. 213–229. DOI: 10.1046/j.1365-2745.2000.00435.x.

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.

Hoekstra, J. M., T. M. Boucher, T. H. Ricketts & C. Roberts (2004). 'Confronting a biome crisis: global disparities of habitat loss and protection'. In: *Ecology Letters* 8.1, pp. 23–29. DOI: 10.1111/j.1461-0248.2004.00686.x.

Hoffmann, W. A., E. L. Geiger, S. G. Gotsch, D. R. Rossatto, L. C. R. Silva, O. L. Lau, M. Haridasan & A. C. Franco (2012). 'Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes'. In: *Ecology Letters* 15.7, pp. 759–768. DOI: 10.1111/j.1461-0248.2012.01789.x.

Hogberg, P. (1986). 'Nitrogen-Fixation and Nutrient Relations in Savanna Woodland Trees (Tanzania)'. In: *Journal of Applied Ecology* 23.2, p. 675. DOI: 10.2307/2404045.

Holdo, R. M. (2007). 'Elephants, fire, and frost can determine community structure and composition in kalahari woodlands'. In: *Ecological Applications* 17.2, pp. 558–568. DOI: 10.1890/05-1990.

Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. K. Byrnes, B. a. Hungate, K. L. Matulich, A. Gonzalez, J. E. Duffy, L. Gamfeldt & M. I. O'Connor (2012). 'A global synthesis reveals biodiversity loss as a major driver of ecosystem change'. In: *Nature* 486.7401, pp. 105–108. DOI: `10.1038/nature11118`.

Howe, C., H. Suich, B. Vira & G. M. Mace (2014). 'Creating win-wins from trade-offs? Ecosystem services for human well-being: A meta-analysis of ecosystem service trade-offs and synergies in the real world'. In: *Global Environmental Change* 28.1, pp. 263–275. DOI: `10.1016/j.gloenvcha.2014.07.005`.

Huntley, B. J. (1982). 'Southern African savannas'. In: *Ecology of tropical savannas*. Ed. by B. J. Huntley & B. H. Walker. Berlin, Germany: Springer-Verlag, pp. 101–119. DOI: `10.1007/978-3-642-68786-0`.

Huston, M. A. (1997). 'Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity'. In: *Oecologia* 110.4, pp. 449–460. DOI: `10.1007/s004420050180`.

Isbell, F., P. B. Reich, D. Tilman, S. E. Hobbie, S. Polasky & S. Binder (2013). 'Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity'. In: *Proceedings of the National Academy of Sciences of the United States of America* 110.29, pp. 11911–6. DOI: `10.1073/pnas.1310880110`.

Janzen, D. H. (1970). 'Herbivores and the number of tree species in tropical forests'. In: *The American Naturalist* 104.940, pp. 501–528. DOI: `10.1086/282687`.

Jax, K. (2005). 'Function and "functioning" in ecology: what does it mean?' In: *Oikos* 111.3, pp. 641–648. DOI: `10.1111/j.1600-0706.2005.13851.x`.

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`.

Kareiva, P., H. Tallis, T. H. Ricketts, G. C. Daily & S. Polasky (2011). 'Natural Capital: Theory and Practice of Mapping Ecosystem Services'. In: *Progress in Physical Geography* 35.5, pp. 701–704. DOI: `10.1177/0309133311417953`.

Kellman, M. (1984). 'Synergistic Relationships Between Fire and Low Soil Fertility in Neotropical Savannas: A Hypothesis'. In: *Biotropica* 16.2, p. 158. DOI: `10.2307/2387850`.

Ketter, B. L. & R. M. Holdo (2018). 'Strong competitive effects of African savanna C4 grasses on tree seedlings do not support rooting differentiation'. In: *Journal of Tropical Ecology* 34.1, pp. 65–73. DOI: `10.1017/s0266467418000020`.

Klop, E., J. van Goethem & H. H. de Iongh (2007). 'Resource selection by grazing herbivores on post-fire regrowth in a West African woodland savanna'. In: *Wildlife Research* 34.2, pp. 77–83. DOI: `10.1071/wr06052`.

Körner, C. (2017). 'A matter of tree longevity'. In: *Science* 355.6321, pp. 130–131. DOI: `10.1126/science.aal2449`.

Kumar, D., M. Pfeiffer, C. Gaillard, L. Langan, C. Martens & S. Scheiter (2020). 'Misinterpretation of Asian savannas as degraded forest can mislead management and conservation policy under climate change'. In: *Biological Conservation* 241, p. 108293. DOI: `10.1016/j.biocon.2019.108293`.

Laestadius, L., S. Maginnis, S. Minnemeyer, P. Potapov, C. Saint-Laurent & N. Sizer (2011). 'Opportunities for forest landscape restoration'. In: *Unasylva* 62, pp. 1–238.

Lawes, M. J., H. Adie, J. Russell-Smith, B. Murphy & J. J. Midgley (2011). 'How do small savanna trees avoid stem mortality by fire? The roles of stem diameter, height and bark thickness'. In: *Ecosphere* 2.4, art42. DOI: `10.1890/es10-00204.1`.

Lecina-Diaz, J., A. Alvarez, A. Regos, P. Drapeau, A. Paquette, C. Messier & J. Retana (2018). 'The positive carbon stocks-biodiversity relationship in forests: co-occurrence and drivers across five subclimates'. In: *Ecological Applications* 28.6, pp. 1481–1493. DOI: `10.1002/eap.1749`.

Lehmann, C. E. R., S. A. Archibald, W. A. Hoffmann & W. J. Bond (2011). 'Deciphering the distribution of the savanna biome'. In: *New Phytologist* 191.1, pp. 197–209. DOI: `10.1111/j.1469-8137.2011.03689.x`.

Levine, J. M. & J. HilleRisLambers (2009). 'The importance of niches for the maintenance of species diversity'. In: *Nature* 461.7261, pp. 254–257. DOI: `10.1038/nature08251`.

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`.

Liang, J., T. W. Crowther, N. Picard, S. Wiser, M. Zhou, G. Alberti, E.-D. Schulze, A. D. McGuire, F. Bozzato, H. Pretzsch et al. (2016). 'Positive biodiversity-productivity relationship predominant in global forests'. In: *Science* 354.6309, aaf8957–aaf8957. DOI: `10.1126/science.aaf8957`.

Linder, H. P. (2003). 'The radiation of the Cape flora, southern Africa'. In: *Biological Reviews of the Cambridge Philosophical Society* 78.2003, pp. 597–638. DOI: `Doi10.1017/S1464793103006171`.

Loreau, M. (2001). 'Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges'. In: *Science* 294.5543, pp. 804–808. DOI: `10.1126/science.1064088`.

Lortie, C. J., M. Zuliani, N. Ghazian, S. Haas, J. Braun, M. Owen, F. Miguel, M. Seifan, A. Filazzola & J. Lucero (2021). 'Too much of a good thing: Shrub benefactors are less important in higher diversity arid ecosystems'. In: *Journal of Ecology* 109.5. Ed. by A. Wright, pp. 2047–2053. DOI: `10.1111/1365-2745.13596`.

MacArthur, R. (1955). 'Fluctuations of Animal Populations and a Measure of Community Stability'. In: *Ecology* 36.3, p. 533. DOI: `10.2307/1929601`.

MacArthur, R. & R. Levins (1967). 'The Limiting Similarity, Convergence, and Divergence of Coexisting Species'. In: *The American Naturalist* 101.921, pp. 377–385. DOI: `10.1086/282505`.

Makhado, R., M. Potgieter, J. Timberlake & D. Gumbo (2014). 'A review of the significance of mopane products to rural people's livelihoods in southern Africa'. In: *Transactions of the Royal Society of South Africa* 69.2, pp. 117–122. DOI: `10.1080/0035919x.2014.922512`.

May-Tobin, C. (2011). 'Wood for Fuel'. In: *The root of the problem: What's driving tropical deforestation today?* Ed. by D. Boucher, P. Elias, K. Lininger, C. May-Tobin, S. Roquemore & E. Saxon. Cambridge MA, USA: Union of Concerned Scientists, pp. 79–87.

McRae, L., S. Deinet & R. Freeman (2017). 'The Diversity-Weighted Living Planet Index: Controlling for Taxonomic Bias in a Global Biodiversity Indicator'. In: *PLoS ONE* 12.1. Ed. by H. Doi, e0169156. DOI: `10.1371/journal.pone.0169156`.

Mittermeier, R. A., C. G. Mittermeier, T. M. Brooks, J. D. Pilgrim, W. R. Konstant, G. A. B. da Fonseca & C. Kormos (2003). 'Wilderness and biodiversity conservation'. In: *Proceedings of the National Academy of Sciences* 100.18, pp. 10309–10313. DOI: `10.1073/pnas.1732458100`.

Moncrieff, G. R., C. E. R. Lehmann, J. Schnitzler, J. Gambiza, P. Hiernaux, C. M. Ryan, C. M. Shackleton, R. J. Williams & S. I. Higgins (2014). 'Contrasting architecture of key African and Australian savanna tree taxa drives intercontinental structural divergence'. In: *Global Ecology and Biogeography* 23.11, pp. 1235–1244. DOI: `10.1111/geb.12205`.

Moncrieff, G. R., S. Scheiter, L. Langan, A. Trabucco & S. I. Higgins (2016). 'The future distribution of the savannah biome: model-based and biogeographic contingency'. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 371.1703, p. 20150311. DOI: `10.1098/rstb.2015.0311`.

Mora, C., R. Danovaro & M. Loreau (2014). 'Alternative hypotheses to explain why biodiversity-ecosystem functioning relationships are concave-up in some natural ecosystems but concave-down in manipulative experiments'. In: *Scientific Reports* 4.1. DOI: `10.1038/srep05427`.

Morin, X., L. Fahse, C. de Mazancourt, M. Scherer-Lorenzen & H. Bugmann (2014). 'Temporal stability in forest productivity increases with tree diversity due to asynchrony in species dynamics'. In: *Ecology Letters* 17.12. Ed. by M. Rejmanek, pp. 1526–1535. DOI: `10.1111/ele.12357`.

Moustakas, A., W. E. Kunin, T. C. Cameron & M. Sankaran (2013). ‘Facilitation or Competition? Tree Effects on Grass Biomass across a Precipitation Gradient’. In: *PLoS ONE* 8.2. DOI: `10.1371/journal.pone.0057025`.

Murphy, B. P. & D. M. J. S. Bowman (2012). ‘What controls the distribution of tropical forest and savanna?’ In: *Ecology Letters* 15.7, pp. 748–758. DOI: `10.1111/j.1461-0248.2012.01771.x`.

Naeem, S., J. E. Duffy & E. Zavaleta (2012). ‘The functions of biological diversity in an age of extinction’. In: *Science* 336.6087, pp. 1401–1406. DOI: `10.1126/science.1215855`.

Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton & R. M. Woodfin (1994). ‘Declining biodiversity can alter the performance of ecosystems’. In: *Nature* 368, pp. 734–737. DOI: `10.1038/368734a0`.

Newbold, T., L. N. Hudson, A. P. Arnell, S. Contu, A. D. Palma, S. Ferrier, S. L. L. Hill, A. J. Hoskins, I. Lysenko, H. R. P. Phillips et al. (2016). ‘Has land use pushed terrestrial biodiversity beyond the planetary boundary?’ In: *Science* 353.6296, pp. 288–91. DOI: `10.1126/science.aaf2201`.

Njana, M. A., G. C. Kajembe & R. E. Malimbwi (2013). ‘Are miombo woodlands vital to livelihoods of rural households? Evidence from Urumwa and surrounding communities, Tabora, Tanzania’. In: *Forests Trees and Livelihoods* 22.2, pp. 124–140. DOI: `10.1080/14728028.2013.803774`.

Osborne, C. P. (2007). ‘Atmosphere, ecology and evolution: what drove the Miocene expansion of C4 grasslands?’ In: *Journal of Ecology* 96, pp. 35–45. DOI: `10.1111/j.1365-2745.2007.01323.x`.

Padilla, F. M. & F. I. Pugnaire (2006). ‘The role of nurse plants in the restoration of degraded environments’. In: *Frontiers in Ecology and the Environment* 4.4, pp. 196–202. DOI: `10.1890/1540-9295(2006)004[0196:tronpi]2.0.co;2`.

Palgrave, K. C. (2003). *Trees of southern Africa*. Cape Town, South Africa: Struik Publications.

Parr, C. L., C. E. R. Lehmann, W. J. Bond, W. A. Hoffmann & A. N. Andersen (2014). ‘Tropical grassy biomes: Misunderstood, neglected, and under threat’. In: *Trends in Ecology & Evolution* 29, pp. 205–213. DOI: `10.1016/j.tree.2014.02.004`.

Pedro, M. S., W. Rammer & R. Seidl (2017). ‘Disentangling the effects of compositional and structural diversity on forest productivity’. In: *Journal of Vegetation Science* 28, pp. 649–658. DOI: `10.1111/jvs.12505`.

Pelletier, J., A. Paquette, K. Mbindo, N. Zimba, A. Siampale, B. Chendauka, F. Siangulube & J. W. Roberts (2018). ‘Carbon sink despite large deforestation in African tropical dry forests (miombo woodlands)’. In: *Environmental Research Letters* 13, p. 094017. DOI: `10.1088/1748-9326/aadc9a`.

Pennington, R. T., C. E. R. Lehmann & L. M. Rowland (2018). ‘Tropical savannas and dry forests’. In: *Current Biology* 28.9, R541–R545. DOI: `10.1016/j.cub.2018.03.014`.

Pennington, R. T., G. P. Lewis & J. A. Ratter (2006). ‘An Overview of the Plant Diversity, Biogeography and Conservation of Neotropical Savannas and Seasonally Dry Forests’. In: *Neotropical Savannas and Seasonally Dry Forests*. Ed. by R. T. Pennington, G. P. Lewis & J. A. Ratter. Boca Raton FL, USA: CRC Press, pp. 1–30. DOI: `10.1201/9781420004496`.

Petchey, O. L. & K. J. Gaston (2006). ‘Functional diversity: back to basics and looking forward’. In: *Ecology Letters* 9.6, pp. 741–758. DOI: `10.1111/j.1461-0248.2006.00924.x`.

Pison, G. (2017). ‘The population of the world (2017)’. In: *Population and Societies* 547, pp. 1–9.

Plas, F. van der (2019). ‘Biodiversity and ecosystem functioning in naturally assembled communities’. In: *Biological Reviews* 94, pp. 1220–1245. DOI: `10.1111/brv.12499`.

Pulsford, S. A., D. B. Lindenmayer & D. A. Driscoll (2014). ‘A succession of theories: purging redundancy from disturbance theory’. In: *Biological Reviews* 91.1, pp. 148–167. DOI: `10.1111/brv.12163`.

Purves, D. W., J. W. Lichstein & S. W. Pacala (2007). ‘Crown plasticity and competition for canopy space: A new spatially implicit model parameterized for 250 North American tree species’. In: *PLoS ONE* 2.9. DOI: `10.1371/journal.pone.0000870`.

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: `10.1111/ele.12849`.

Ratnam, J., W. J. Bond, R. J. Fensham, W. A. Hoffmann, S. Archibald, C. E. R. Lehmann, M. T. Anderson, S. I. Higgins & M. Sankaran (2011). 'When is a 'forest' a savanna, and why does it matter?' In: *Global Ecology and Biogeography* 20, pp. 653–660. DOI: `10.1111/j.1466-8238.2010.00634.x`.

Reich, P. B., D. Tilman, F. Isbell, K. Mueller, S. E. Hobbie, D. F. B. Flynn & N. Eisenhauer (2012). 'Impacts of Biodiversity Loss Escalate Through Time as Redundancy Fades'. In: *Science* 336.6081, pp. 589–592. DOI: `10.1126/science.1217909`.

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`.

Roques, K. G., T. G. O'Connor & A. R. Watkinson (2001). 'Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence'. In: *Journal of Applied Ecology* 38.2, pp. 268–280. DOI: `10.1046/j.1365-2664.2001.00567.x`.

Rosan, T. M., L. E. O. C. Aragão, I. Oliveras, O. L. Phillips, Y. Malhi, E. Gloor & F. H. Wagner (2019). 'Extensive 21st-Century Woody Encroachment in South America's Savanna'. In: *Geophysical Research Letters* 46.12, pp. 6594–6603. DOI: `10.1029/2019gl082327`.

Ross, C. W., N. P. Hanan, L. Prihodko, J. Anchang, W. Ji & Q. Yu (2021). 'Woody-biomass projections and drivers of change in sub-Saharan Africa'. In: *Nature Climate Change* 11.5, pp. 449–455. DOI: `10.1038/s41558-021-01034-5`.

Ryan, C. M., M. Williams & J. Grace (2011). 'Above- and belowground carbon stocks in a miombo woodland landscape of Mozambique'. In: *Biotropica* 43.4, pp. 423–432. DOI: `10.1111/j.1744-7429.2010.00713.x`.

Ryan, C. M., M. Williams, J. Grace, E. Woollen & C. E. R. Lehmann (2017). 'Pre-rain green-up is ubiquitous across southern tropical Africa: implications for temporal niche separation and model representation'. In: *New Phytologist* 213.2, pp. 625–633. DOI: `10.1111/nph.14262`.

Ryan, C. M., R. Pritchard, I. McNicol, M. Owen, J. A. Fisher & C. Lehmann (2016). 'Ecosystem services from southern African woodlands and their future under global change'. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 371.1703, p. 20150312. DOI: `10.1098/rstb.2015.0312`.

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: `10.1038/nature04070`.

Sankaran, M. (2019). 'Droughts and the ecological future of tropical savanna vegetation'. In: *Journal of Ecology* 107.4, pp. 1531–1549. DOI: `10.1111/1365-2745.13195`.

Sankaran, M., J. Ratnam & N. Hanan (2008). 'Woody cover in African savannas: the role of resources, fire and herbivory'. In: *Global Ecology and Biogeography* 17.2, pp. 236–245. DOI: `10.1111/j.1466-8238.2007.00360.x`.

Sankaran, M., J. Ratnam & N. P. Hanan (2004). 'Tree-grass coexistence in savannas revisited - insights from an examination of assumptions and mechanisms invoked in existing models'. In: *Ecology Letters* 7.6, pp. 480–490. DOI: `10.1111/j.1461-0248.2004.00596.x`.

Scheiter, S. & S. I. Higgins (2009). 'Impacts of climate change on the vegetation of Africa: an adaptive dynamic vegetation modelling approach'. In: *Global Change Biology* 15.9, pp. 2224–2246. DOI: `10.1111/j.1365-2486.2008.01838.x`.

Scheiter, S. & S. I. Higgins (2007). 'Partitioning of Root and Shoot Competition and the Stability of Savannas'. In: *The American Naturalist* 170.4, pp. 587–601. DOI: `10.1086/521317`.

Scherer-Lorenzen, M. (2014). *The functional role of biodiversity in the context of global change*, pp. 195–238.

Scholes, R. J. & S. R. Archer (1997). 'Tree grass interactions in savannas'. In: *Annual Review of Ecology and Systematics* 28.1, pp. 517–544. DOI: `10.1146/annurev.ecolsys.28.1.517`.

Scholes, R. J. & B. H. Walker (1993). *An African savanna. Synthesis of the Nylsvley Study*. Cambridge, UK: Cambridge University Press.

Schulze, E. D. & H. A. Mooney (1993). *Biodiversity and Ecosystem Function*. Berlin, Germany: Springer Berlin Heidelberg.

Seidel, D., C. Leuschner, C. Scherber, F. Beyer, T. Wommelsdorf, M. J. Cashman & L. Fehrmann (2013). 'The relationship between tree species richness, canopy space exploration and productivity in a temperate broad-leaf mixed forest'. In: *Forest Ecology and Management* 310, pp. 366–374. DOI: `10.1016/j.foreco.2013.08.058`.

Seidl, R., W. Rammer & T. A. Spies (2014). 'Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning'. In: *Ecological Applications* 24.8, pp. 2063–2077. DOI: `10.1890/14-0255.1`.

Shackleton, C. M., S. E. Shackleton, E. Buiten & N. Bird (2007). 'The importance of dry woodlands and forests in rural livelihoods and poverty alleviation in South Africa'. In: *Forest Policy and Economics* 9.5, pp. 558–577. DOI: `10.1016/j.forpol.2006.03.004`.

Sheil, D. & F. Bongers (2020). 'Interpreting forest diversity-productivity relationships: volume values, disturbance histories and alternative inferences'. In: *Forest Ecosystems* 7.6, pp. 1–12. DOI: `10.1186/s40663-020-0215-x`.

Siebert, F. & N. Dreber (2019). 'Forb ecology research in dry African savannas: Knowledge, gaps, and future perspectives'. In: *Ecology and Evolution* 9.13, pp. 7875–7891. DOI: `10.1002/ece3.5307`.

Silveira, F. A. O., A. J. Arruda, W. Bond, G. Durigan, A. Fidelis, K. Kirkman, R. S. Oliveira, G. E. Overbeck, J. B. B. Sansevero, F. Siebert et al. (2020). 'Myth-busting tropical grassy biome restoration'. In: *Restoration Ecology* 28.5, pp. 1067–1073. DOI: `10.1111/rec.13202`.

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`.

Smith, M. D. & A. K. Knapp (2003). 'Dominant species maintain ecosystem function with non-random species loss'. In: *Ecology Letters* 6.6, pp. 509–517. DOI: `10.1046/j.1461-0248.2003.00454.x`.

Solbrig, O. T., E. Medina & J. F. Silva (1996). *Biodiversity and Savanna Ecosystem Processes*. Berlin, Germany: Springer-Verlag.

Srivastava, D. S. & M. Vellend (2005). 'Biodiversity-Ecosystem Function Research: Is It Relevant to Conservation?' In: *Annual Review of Ecology, Evolution, and Systematics* 36.1, pp. 267–294. DOI: `10.1146/annurev.ecolsys.36.102003.152636`.

Staver, A. C., S. Archibald & S. A. Levin (2011). 'The Global Extent and Determinants of Savanna and Forest as Alternative Biome States'. In: *Science* 334.6053, pp. 230–232. DOI: `10.1126/science.1210465`.

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, UK: Cambridge University Press, pp. 86–106.

Staver, A. C., J. Botha & L. Hedin (2017). 'Soils and fire jointly determine vegetation structure in an African savanna'. In: *New Phytologist* 216.4, pp. 1151–1160. DOI: `10.1111/nph.14738`.

Steudel, B., A. Hector, T. Friedl, C. Löfke, M. Lorenz, M. Wesche & M. Kessler (2012). 'Biodiversity effects on ecosystem functioning change along environmental stress gradients'. In: *Ecology Letters* 15.12. Ed. by M. Gessner, pp. 1397–1405. DOI: `10.1111/j.1461-0248.2012.01863.x`.

Stevens, N., B. F. N. Erasmus, S. Archibald & W. J. Bond (2016). 'Woody encroachment over 70 years in South African savannahs: overgrazing, global change or extinction aftershock?' In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 371.1703, p. 20150437. DOI: `10.1098/rstb.2015.0437`.

Stevens, N., C. E. R. Lehmann, B. P. Murphy & G. Durigan (2017). ‘Savanna woody encroachment is widespread across three continents’. In: *Global Change Biology* 23.1, pp. 235–244. DOI: `10.1111/gcb.13409`.

Still, C. J., J. A. Berry, G. J. Collatz & R. S. DeFries (2003). ‘Global distribution of C3 and C4 vegetation: Carbon cycle implications’. In: *Global Biogeochemical Cycles* 17.1, pp. 6–1–6–14. DOI: `10.1029/2001gb001807`.

Tilman, D. & J. A. Downing (1994). ‘Biodiversity and stability in grasslands’. In: *Nature* 367, pp. 363–365. DOI: `10.1038/367363a0`.

Tilman, D., F. Isbell & J. M. Cowles (2014). ‘Biodiversity and ecosystem functioning’. In: *Annual Review of Ecology, Evolution, and Systematics* 45, pp. 471–493. DOI: `10.1146/annurev-ecolsys-120213-091917`.

Tilman, D., P. B. Reich & F. Isbell (2012). ‘Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory’. In: *Proceedings of the National Academy of Sciences* 109.26, pp. 10394–10397. DOI: `10.1073/pnas.1208240109`.

Timberlake, J. R., G. M. Calvert, J. A. Morris & Forestry Commission (1993). *Preliminary root atlas for Zimbabwe and Zambia*. Forest Research Centre.

Tobner, C. M., A. Paquette, D. Gravel, P. B. Reich, L. J. Williams & C. Messier (2016). ‘Functional identity is the main driver of diversity effects in young tree communities’. In: *Ecology Letters* 19, pp. 638–647. DOI: `10.1111/ele.12600`.

Tomlinson, K. W., L. Poorter, F. J. Sterck, F. Borghetti, D. Ward, S. de Bie & F. van Langevelde (2013). ‘Leaf adaptations of evergreen and deciduous trees of semi-arid and humid savannas on three continents’. In: *Journal of Ecology* 101.2, pp. 430–440. DOI: `10.1111/1365-2745.12056`.

Tomlinson, K. W., F. J. Sterck, F. Bongers, D. A. da Silva, E. R. M. Barbosa, D. Ward, F. T. Bakker, M. van Kaauwen, H. H. T. Prins, S. de Bie et al. (2012). ‘Biomass partitioning and root morphology of savanna trees across a water gradient’. In: *Journal of Ecology* 100.5, pp. 1113–1121. DOI: `10.1111/j.1365-2745.2012.01975.x`.

Torello-Raventos, M., T. R. Feldpausch, E. Veenendaal, F. Schrodt, G. Saiz, T. F. Domingues, G. Djagbletey, A. Ford, J. Kemp, B. S. Marimon et al. (2013). ‘On the delineation of tropical vegetation types with an emphasis on forest/savanna transitions’. In: *Plant Ecology and Diversity* 6.1, pp. 101–137. DOI: `10.1080/17550874.2012.762812`.

Turnbull, L. A., F. Isbell, D. W. Purves, M. Loreau & A. Hector (2016). ‘Understanding the value of plant diversity for ecosystem functioning through niche theory’. In: *Proceedings of the Royal Society B: Biological Sciences* 283.1844, p. 20160536. DOI: `10.1098/rspb.2016.0536`.

Vadigi, S. & D. Ward (2013). ‘Shade, nutrients, and grass competition are important for tree sapling establishment in a humid savanna’. In: *Ecosphere* 4.11, art142. DOI: `10.1890/ES13-00239.1`.

Van Coller, H., F. Siebert, P. F. Scogings & S. Ellis (2018). ‘Herbaceous responses to herbivory, fire and rainfall variability differ between grasses and forbs’. In: *South African Journal of Botany* 119, pp. 94–103. DOI: `10.1016/j.sajb.2018.08.024`.

Veldman, J. W. (2016). ‘Clarifying the confusion: old-growth savannahs and tropical ecosystem degradation’. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 371.1703, p. 20150306. DOI: `10.1098/rstb.2015.0306`.

Veldman, J. W., E. Buisson, G. Durigan, G. W. Fernandes, S. L. Stradic, G. Mahy, D. Negreiros, G. E. Overbeck, R. G. Veldman, N. P. Zaloumis et al. (2015). ‘Toward an old-growth concept for grasslands, savannas, and woodlands’. In: *Frontiers in Ecology and the Environment* 13.3, pp. 154–162. DOI: `10.1890/140270`.

Vergles, E., H. Djoudi, R. R. Blackie, C. K. Koame & D. Gautier (2015). ‘Dry Forests, Livelihoods and Poverty Alleviation: Understanding Current Trends’. In: *International Forestry Review* 17.S2, pp. 54–69. DOI: `10.1505/146554815815834868`.

Vitousek, P. M., H. A. Mooney, J. Lubchenco & J. M. Melillo (1997). ‘Human Domination of Earth’s Ecosystems’. In: *Science* 277.5325, pp. 494–499. DOI: `10.1126/science.277.5325.494`.

Wakeling, J. L., W. J. Bond, M. Ghaui & E. C. February (2015). 'Grass competition and the savanna-grassland 'treeline': A question of root gaps?' In: *South African Journal of Botany* 101, pp. 91–97. DOI: `10.1016/j.sajb.2014.09.007`.

Wakeling, J. L., A. C. Staver & W. J. Bond (2011). 'Simply the best: The transition of savanna saplings to trees'. In: *Oikos* 120.10, pp. 1448–1451. DOI: `10.1111/j.1600-0706.2011.19957.x`.

Walter, H. (1971). *Ecology of tropical and sub-tropical vegetation*. Edinburgh, UK: Oliver and Boyd.

Watson, J. E. M., K. R. Jones, R. A. Fuller, M. D. Marco, D. B. Segan, S. H. M. Butchart, J. R. Allan, E. McDonald-Madden & O. Venter (2016). 'Persistent Disparities between Recent Rates of Habitat Conversion and Protection and Implications for Future Global Conservation Targets'. In: *Conservation Letters* 9.6, pp. 413–421. DOI: `10.1111/conl.12295`.

Weltzin, J. F. & G. R. McPherson (1999). 'Facilitation of conspecific seedling recruitment and shifts in temperate savanna ecotones'. In: *Ecological Monographs* 69.4, pp. 513–534. DOI: `10.1890/0012-9615(1999)069[0513:focsra]2.0.co;2`.

Werf, G. R. van der, J. T. Randerson, L. Giglio, G. J. Collatz, M. Mu, P. S. Kasibhatla, D. C. Morton, R. S. DeFries, Y. Jin & T. T. van Leeuwen (2010). 'Global fire emissions and the contribution of deforestation, savanna, forest, agricultural, and peat fires (1997-2009)'. In: *Atmospheric Chemistry and Physics* 10.23, pp. 11707–11735. DOI: `10.5194/acp-10-11707-2010`.

Werf, G. R. van der, J. T. Randerson, L. Giglio, T. T. van Leeuwen, Y. Chen, B. M. Rogers, M. Mu, M. J. E. van Marle, D. C. Morton, G. J. Collatz et al. (2017). 'Global fire emissions estimates during 1997-2016'. In: *Earth System Science Data* 9.2, pp. 697–720. DOI: `10.5194/essd-9-697-2017`.

Werger, M. J. A. & B. J. Coetzee (1978). 'The Sudano-Zambezian Region'. In: *Biogeography and Ecology of Southern Africa*. Springer Netherlands, pp. 301–462. DOI: `10.1007/978-94-009-9951-0_10`.

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`.

Whitley, R., J. Beringer, L. B. Hutley, G. Abramowitz, M. G. De Kauwe, B. Evans, V. Haverd, L. Li, C. Moore, Y. Ryu et al. (2017). 'Challenges and opportunities in land surface modelling of savanna ecosystems'. In: *Biogeosciences* 14.20, pp. 4711–4732. DOI: `10.5194/bg-14-4711-2017`.

Whittaker, R. H. (1960). 'Vegetation of the Siskiyou Mountains, Oregon and California'. In: *Ecological Monographs* 30.3, pp. 279–338. DOI: `10.2307/1943563`.

Wiegand, K., D. Saltz & D. Ward (2006). 'A patch-dynamics approach to savanna dynamics and woody plant encroachment - Insights from an arid savanna'. In: *Perspectives in Plant Ecology, Evolution and Systematics* 7.4, pp. 229–242. DOI: `10.1016/j.ppees.2005.10.001`.

Wigley, B. J., A. C. Staver, R. Zytkowiak, A. M. Jagodzinski & C. Wigley-Coetsee (2019). 'Root trait variation in African savannas'. In: *Plant and Soil* 441.1-2, pp. 555–565. DOI: `10.1007/s11104-019-04145-3`.

Wilk, J., L. Andersson, P. Wolski, D. Kgathi, S. Ringrose & C. Vanderpost (2010). 'Changing Flow in the Okavango Basin: Upstream Developments and Downstream Effects'. In: *Integrated Watershed Management: Perspectives and Problems*. Ed. by E. Beheim, G. S. Rajwar, M. J. Haigh & J. Krecˇek. Dordrecht, Netherlands: Springer. Chap. Changing F, pp. 99–113.

Williams, M., P. A. Schwarz, B. E. Law, J. Irvine & M. R. Kurpius (2005). 'An improved analysis of forest carbon dynamics using data assimilation'. In: *Global Change Biology* 11.1, pp. 89–105. DOI: `10.1111/j.1365-2486.2004.00891.x`.

Williams, R. J., B. A. Myers, W. J. Muller, G. A. Duff & D. Eamus (1997). 'Leaf phenology of woody species in a north Australian tropical savanna'. In: *Ecology* 78.8, pp. 2542–2558. DOI: `10.1890/0012-9658(1997)078[2542:lpowsi]2.0.co;2`.

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`.

Wunder, S., A. Angelsen & B. Belcher (2014). ‘Forests, Livelihoods, and Conservation: Broadening the Empirical Base’. In: *World Development* 64, S1–S11. DOI: `10.1016/j.worlddev.2014.03.007`.

Xu, X., D. Medvigy & I. Rodriguez-Iturbe (2015). ‘Relation between rainfall intensity and savanna tree abundance explained by water use strategies’. In: *Proceedings of the National Academy of Sciences* 112.42, pp. 12992–12996. DOI: `10.1073/pnas.1517382112`.

Yachi, S. & M. Loreau (1999). ‘Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis’. In: *Proceedings of the National Academy of Sciences* 96.4, pp. 1463–1468. DOI: `10.1073/pnas.96.4.1463`.

Zhang, Y., H. Y. H. Chen & P. B. Reich (2012). ‘Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis’. In: *Journal of Ecology* 100.3, pp. 742–749. DOI: `10.1111/j.1365-2745.2011.01944.x`.

Chapter 3

Structural diversity and tree density drives variation in the biodiversity-ecosystem function relationship of woodlands and savannas

The following chapter has been previously accepted as an article in *New Phytologist*:

J. L. Godlee et al. (2021). ‘Structural diversity and tree density drives variation in the biodiversity-ecosystem function relationship of woodlands and savannas’. In: *New Phytologist*. DOI: `10.1111/nph.17639`

Authors: John L. Godlee[1], Casey M. Ryan[1], David Bauman[2,3], Samuel J. Bowers[1], Joao M. B. Carreiras[4], Antonio Valter Chisingui[5], Joris P. G. M. Cromsigt[6,7,8], Dave J. Druce[9,10], Manfred Finckh[11], Francisco Maiato Gonçalves[5], Ricardo M. Holdo[12], Steve Makungwa[13], Iain M. McNicol[1], Edward T. A. Mitchard[1], Anderson Muchawona[14], Rasmus Revermann[11,15], Natasha Sofia Ribeiro[16], Abel Siampale[17], Stephen Syampungani[18], José João Tchamba[5], Hemant G. Tripathi[19], Johannes Wallenfang[11], Mariska te Beest[20,21,22], Mathew Williams[1], Kyle G. Dexter[1,23]

1. School of GeoSciences, University of Edinburgh, Edinburgh, EH9 3FF, United Kingdom
2. Environmental Change Institute, School of Geography and the Environment, University of

Oxford, Oxford, OX1 3QY, United Kingdom

3. Laboratoire d'Écologie Végétale et Biogéochimie, CP 244, Université Libre de Bruxelles, Brussels, B-1050, Belgium
4. National Centre for Earth Observation (NCEO), University of Sheffield, Hicks Building, Hounsfield Road, Sheffield, S3 7RH, United Kingdom
5. Herbarium of Lubango, ISCED Huíla, Sarmento Rodrigues Str. No. 2, CP. 230, Lubango, Angola
6. Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, SE-907 36, Sweden
7. Department of Zoology, Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth, 6031, South Africa
8. Copernicus Institute of Sustainable Development, Utrecht University, Utrecht, 3584CS, The Netherlands
9. Ecological Advice, Ezemvelo KZN Wildlife, Hluhluwe-iMfolozi Park, 3202, South Africa
10. School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, 3209, South Africa
11. Biodiversity, Evolution and Ecology of Plants, Institute of Plant Sciences and Microbiology, University of Hamburg, Ohnhorststr. 18, Hamburg, 22609, Germany
12. Odum School of Ecology, University of Georgia, 140 E. Green St., Athens, GA 30602, USA
13. Lilongwe University of Agriculture and Natural Resources (LUANAR), Lilongwe, Malawi
14. Forest Research Centre, 1 Orange Groove Highlands, Harare, Zimbabwe
15. Faculty of Natural Resources and Spatial Sciences, Namibia University of Science and Technology, Windhoek, 10005, Namibia
16. Department of Forest Engineering, Faculty of Agronomy and Forest Engineering, Universidade Eduardo Mondlane, Av. Julius Nyerere, 3453, Campus Universitario, Maputo, Mozambique
17. Ministry of Lands and Natural Resources, Cairo Road, Lusaka, Zambia
18. School of Natural Resources, Copperbelt University, Kitwe, Zambia
19. Faculty of Biological Sciences, University of Leeds, LS2 9JT, United Kingdom
20. Copernicus Institute of Sustainable Development, Utrecht University, Utrecht, 3508, The Netherlands
21. Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth, 6031, South Africa
22. South African Environmental Observation Network, Grasslands-Forests-Wetlands Node, Montrose, 3201, South Africa
23. Royal Botanic Garden Edinburgh, Edinburgh, EH3 5LR, United Kingdom

Author Contributions: JLG and KGD conceived the study. JLG conducted data analysis, data management for further versions of the SEOSAW dataset, and wrote the manuscript. CMR conceived the SEOSAW database. JLG, CMR, DB, ETAM, HGT, JMBC, KGD, MF, MW, MtB, RMH and SS contributed to manuscript revisions. JLG, AM, AS, AVC, CMR, DJD, FMG, IM, JJT, JPGMC, JW, MF, MtB, MW, NSR, RR, SJB, SM and SS contributed to experimental design, field data collection, data preparation and data management of parts of the dataset used in this study.

Abstract

Positive biodiversity-ecosystem function relationships (BEFRs) have been widely documented, but it is unclear if BEFRs should be expected in disturbance-driven systems. Disturbance may limit competition and niche differentiation, which are frequently posited to underlie BEFRs. We provide the first exploration of the relationship between tree species diversity and biomass, one measure of ecosystem function, across southern African woodlands and savannas, an ecological system rife with disturbance from fire, herbivores and humans. We used >1000 vegetation plots distributed across 10 southern African countries, and structural equation modelling, to determine the relationship between tree species diversity and aboveground woody biomass, accounting for interacting effects of resource availability, disturbance by fire, tree stem density and vegetation type. We found positive effects of tree species diversity on aboveground biomass, operating via increased structural diversity. The observed BEFR was highly dependent on organismal density, with a minimum threshold of c. 180 mature stems ha^{-1}. We found that water availability mainly affects biomass indirectly, via increasing species diversity. The study underlines the close association between tree diversity, ecosystem structure, environment and function in highly disturbed savannas and woodlands. We suggest that tree diversity is an under-appreciated determinant of wooded ecosystem structure and function.

3.1 Introduction

Understanding the relationship between biodiversity and ecosystem function has become a central endeavour in ecological science, as we seek to predict the consequences of global biodiversity change (Naeem et al., 2012). Over the past two decades, study of the Biodiversity-Ecosystem Function Relationship (BEFR) has grown from small-scale experimental studies mostly in temperate grasslands (Cardinale et al., 2009; Tilman & Downing, 1994; Tilman et al., 2014), to observational studies in natural ecosystems (Plas, 2019). While positive BEFRs which align with theory have been frequently reported, a complex picture has emerged whereby the strength and direction of the BEFR varies depending on the ecosystem studied (Liang et al., 2016), the ecosystem function(s) of interest (Hector & Bagchi, 2007), and the inclusion of environmental covariates in statistical models (Vilà et al., n.d.). The goal now should be to study the BEFR in different environmental and ecological contexts, in order to develop an ecosystem-agnostic understanding of the complex interactions between biodiversity, abiotic environment, and ecosystem function.

Ecosystem functions are defined in broad terms as rate processes and aggregate properties of ecosystems that describe the nature of biotic activity within those ecosystems (Jax, 2005). Woody productivity and biomass storage are two of the most commonly studied ecosystem functions in forests and other wooded ecosystems (e.g. savannas) (Brockerhoff et al., 2017), due to their importance in the global carbon cycle (Pan et al., 2011) and their potential leverage as a tool to mitigate the effects of anthropogenic climate change while maintaining biodiversity (Pichancourt et al., 2013). Theory predicts that biodiversity will have a positive effect on ecosystem function via three principal mechanisms: 1) niche complementarity, whereby niche partitioning and ecosystem resource use efficiency is increased in diverse communities, minimising negative density dependent effects such as conspecific competition and abundance of species-specific natural enemies (Barry et al., 2019); 2) selection effects, whereby diverse communities are more likely to include a high-yield species; and 3) facilitation effects, whereby diverse communities are more likely to contain species combinations which enhance each others' functional contribution (Wright et al., 2017).

There has been extended debate on whether positive BEFRs should be expected in all wooded ecosystems (Liang et al., 2016). In temperate and wet tropical forests, where the majority of BEFR studies in natural forest ecosystems have been conducted (Plas, 2019), the mechanism of niche complementarity, which contributes the majority of the observed biodiversity effect (Poorter et al., 2015; Sande et al., 2017; Wright et al., 2017), hinges on the condition that conspecific competition between trees is the limiting factor to ecosystem functioning, but this may not hold true in all systems.

Disturbance-driven mesic savannas and open canopy woodlands cover >20% of the global land surface (Pennington et al., 2018; Solbrig et al., 1996). They represent the dominant vegetation type in Africa, spanning >4 million km^2 (White, 1983; Ratnam et al., 2011; Ryan et al., 2016) (Figure 3.1). Taken together, the above- and below-ground carbon stored in African mesic savannas may be comparable to that found in the wet forests of the Congo basin (Houghton et al., 2009; Mayaux et al., 2008; Spawn et al., 2020). Globally, dry woodlands and savannas represent the largest, most sensitive and fastest increasing component of the terrestrial carbon sink (Ahlstrom et al., 2015). Yet their carbon dynamics remain poorly constrained (Sitch et al., 2015).

Despite their global importance, African savannas are severely under-represented in BEFR studies (Clarke et al., 2017; Liang et al., 2016). In savannas disturbance by fire (Lehmann et al., 2014) and herbivory (Sankaran et al., 2008; Levick et al., 2009) reduces woody stem density and biomass, diminishing competitive interactions between individuals, allowing competitors to co-exist where they would normally be excluded (Grime, 1979; Keddy, 1990). It is possible that a threshold woody stem density exists below which the lack of competition precludes the detection of a biodiversity effect on ecosystem function via niche differentiation. Instead, stress tolerance and the functional contribution of particular species (selection effects) may be the predominant biotic forces influencing ecosystem function in these ecosystems (Lasky et al., 2014; Tobner et al., 2016). Additionally, stressful environments appear to lessen the role of both niche complementarity and facilitation effects in driving the BEFR, by replacing competition between individuals with stress tolerance as the limiting factor on functional contribution (Ratcliffe et al., 2017; Paquette & Messier, 2010). This potential mismatch in the contribution of different mechanisms to the BEFR among resource-, disturbance-, and competition-limited ecosystems requires further investigation if we are to derive a generalisable

BEFR.

A number of studies in miombo woodlands, the dominant savanna type in southern Africa (Campbell, 1996), have found that above-ground woody carbon/biomass stocks correlate positively with tree species richness (McNicol et al., 2018; Shirima et al., 2015; Mutowo & Murwira, 2012). These studies however, lacked the spatial extent required to account for the interacting effects of variation in abiotic environment, disturbance regime, and biogeography which are expected to affect the BEFR. Studies of the BEFR often find that within a small spatial extent (<2500 km^2), biodiversity shows a strong effect on ecosystem function, but at broader extents (>100,000s km^2) biodiversity effects pale in significance compared to abiotic factors such as climate (Gonzalez et al., 2020). In West Africa, Mensah et al. (2020) found that woodlands and forests showed a positive effect of tree species richness on above-ground carbon, while sparse savannas did not, implying that tree stem density and the presence of dominant large trees may affect the strength of the observed BEFR. In the Brazilian Cerrado savanna, Loiola et al. (2015) found that disturbance by fire reduced tree productivity via its effect on functional trait values. Furthermore, Carvalho et al. (2014) found that disturbance by fire in the Brazilian Cerrado reduced soil fertility, causing an indirect effect of fire frequency on functional trait diversity via soil fertility. Other studies focussing on the herbaceous diversity in disturbance-prone grasslands in North America and Europe have shown that disturbance by fire, mowing and herbivory reduces herbaceous productivity (Grace et al., 2007), allowing weak competitors to co-exist where otherwise they would be excluded (Mason et al., 2011), thus weakening the observable BEFR. Thus, there is a case that in highly disturbed systems, a relationship between diversity and ecosystem function may not exist at all. While these studies together offer some glimpse into how the BEFR may operate in disturbance-prone systems, none provide a full and comprehensive assessment of the interacting effects of diversity, abiotic environment, disturbance and ecosystem function, particularly for wooded ecosystems. Additionally, due to differences in community assembly, evolutionary history and contemporary drivers between the neotropics and the African tropics, inferences from one continent cannot necessarily be applied to the other (Dexter et al., 2015).

In this study, we make the first known estimation of the Biodiversity-Ecosystem Function Relationship (BEFR) in disturbance-driven wooded ecosystems (savannas and woodlands), using southern Africa as our study region. We aim to understand the synergistic effects of environmental and biotic drivers of variation in the BEFR, with a view to creating a general model of the BEFR in disturbance-prone wooded ecosystems, which is currently lacking in the BEFR literature. We posit three hypotheses: (1) water availability and soil fertility will indirectly positively affect woody biomass via an increase in tree species diversity, (2) the effect of tree species diversity on woody biomass will increase with organismal density (number of stems ha^{-1}), with competitive interactions becoming more pronounced as stem proximity increases. Likewise, we expect that an increase in disturbance by fire will decrease organismal density and therefore competition, weakening the effect of tree species diversity on woody biomass. Finally, we expect that (3) tree species diversity will increase tree structural diversity due to inter-specific variation in size strategy (i.e. physiognomic diversity), providing an indirect path by which tree diversity increases woody biomass.

3.2 Materials and methods

3.2.1 Study location

The study used 1235 woodland monitoring plots from a larger pool of 5395 plots in the larger SEOSAW database (SEOSAW, 2020), located across 10 countries within southern Africa in the miombo ecoregion (Figure 3.1) (White, 1983). The study area spans the core climate space of the region, with a precipitation gradient from c. 460 mm y^{-1} in southern Mozambique and southern Zimbabwe to c. 1700 mm y^{-1} in northern Zambia, Malawi and northern Mozambique. A 2D convex hull of Mean Annual Precipitation (MAP) and Mean Annual Temperature (MAT) of the study sites covers 96.5% of the pixel-wise climate space of the miombo woodland ecoregion (White, 1983), using WorldClim estimates of Mean Annual Temperature (MAT, BIO1) and Mean Annual Precipitation (MAP, BIO12) between 1970 and 2000 with a pixel size of 30 arc seconds (926 m at equator) (Fick & Hijmans, 2017).

Plots were chosen from the SEOSAW database based on the quality and completeness of data collection, and plot configuration. Plot vegetation was identified under the broad term of ‘savanna’, which includes ‘woodland’, ‘savanna woodland', and 'tree savanna', variously defined in other areas of the scientific literature and here referred to collectively as southern African woodlands, or savannas (Ratnam et al., 2011; Hill & Hanan, 2011). Plots with evidence of farming, human resource extraction, experimental treatments such as prescribed burning or herbivore exclusion, or containing termite mounds were excluded from the initial pool. Only plots >0.1 hectares were used in analyses, as area-based biomass estimation from small plots is highly influenced by rare large trees (Stegen et al., 2011), leading to inaccurate biomass estimates. Only plots with a stem density >50 trees ha^{-1} (>10 cm stem diameter) were used, to ensure all plots represented woodland rather than 'grassy savanna', which is considered here a separate biome with very different species composition (Parr et al., 2014). 3760 plots within the SEOSAW database were arranged in clusters of four 20×50 m plots, with 20 m between plots. Plots within each spatial cluster were combined and treated as a single plot in analyses, resulting in 940 aggregate plots which were then subject to the plot filtering process described above.

3.2.2 Data collection

We considered only trees and shrubs in our calculations of Above-Ground woody Biomass (AGB), including woody species such as palms and cycads, which are functionally tree-like. Woody lianas are scarce in our study plots and were not measured. Only living stems >10 cm DBH (Diameter at Breast Height, 1.3 m) were included in analyses. Many plots in the dataset did not include data on stems <10 cm DBH. For those plots which contained stem measurements <10 cm DBH, small stems only accounted for a median of 2.1% of the plot AGB.

All stems >10 cm DBH were measured within each plot resulting in a total of 66,758 stems with measurements. A tree may be comprised of multiple stems and so tree level richness estimates, rather than stem level estimates, were used to prevent bias from species which readily coppice. For each tree, we recorded species, tree height to the top of the highest branch material, and the DBH of each stem >10 cm DBH. Height was measured through a variety of means including laser rangefinders, manual clinometers and measuring sticks. When stem DBH could not be reliably measured at 1.3 m due to trunk abnormalities, it was measured at the closest regular portion of the trunk to 1.3

m. The height of this measurement was used to estimate diameter at 1.3 m using a cubic polynomial regression to account for stem taper, with parameters estimated using a test dataset from Ryan C., (unpublished), see Godlee et al. (2020).

AGB for each plot (t ha^{-1}) was calculated as the sum of the AGB of each stem >5 cm DBH (AGB_i), divided by the plot area, using Equation 3.1 taken from Chave et al. (2014):

$$AGB_i = 0.0673 \times (\rho D^2 H)^{0.976} \times 1000 \tag{3.1}$$

where ρ is the species mean wood density (g cm^{-3}), D is the stem diameter (cm) measured or estimated at 1.3 m, and H is the tree height (m). Wood density estimates were taken from the global wood density database for each species where possible (Chave et al., 2009; Zanne et al., 2009). Wood density for species without species level estimates was estimated from the means of their respective genera. For stems where tree height was unknown, the plots' climatic parameters, estimated from plot location, were used to estimate tree height, according to Chave et al. (2014).

Climatic data were taken from the WorldClim database (Fick & Hijmans, 2017), which uses BIOCLIM to derive bioclimatic variables (Booth et al., 2014). In addition to MAT and MAP, temperature stress was calculated as the mean diurnal temperature range (BIO2) and precipitation seasonality was calculated as the mean of the coefficient of variation of monthly mean precipitation (BIO15). Soil fertility data were extracted from the ISRIC SoilGrids data product at 250 m resolution, taking the grid cell value for each plot centre (Hengl et al., 2017). We extracted Cation Exchange Capacity (CEC) (cmolc kg^{-1}), soil organic carbon stocks (kg m^{-2}) percentage soil sand content (0.05-2 mm) by weight and soil nitrogen content (g kg^{-1}). These data are a modelled product derived from various remotely sensed and directly measured data sources. The degree of fire disturbance was calculated using the MODIS monthly burned area product at 500 m resolution (MCD64A1, Giglio et al. 2015), counting the total number of times the plot pixel was classified as burning, between 2001 and 2018. We initially aimed to include disturbance by herbivory in our model, including total herbivore biomass from the Hempson et al. (2017) modelled herbivory product, but this inclusion prevented models from converging due to its collinearity with other observed variables, notably MAP and disturbance by fire.

3.2.3 Data analysis

Species diversity and structural diversity metrics

Estimated tree species richness was calculated for each plot using `ChaoRichness()` from the `iNEXT` R package (Hsieh et al., 2016). This procedure uses Hill numbers of the order $q = 0$ to extrapolate a species rarefaction curve to its predicted asymptote and uses this value as its estimated species richness value (Jost, 2006). Extrapolated species richness accounts for variation in plot size present in the dataset (0.1-10 ha) and therefore sampling effort among plots. Larger plots will tend to encompass more individuals, and therefore more species (Dengler, 2009). To measure tree species evenness, the Shannon equitability index ($E_{H'}$) was calculated as the ratio of the estimated Shannon diversity index to the natural log of estimated species richness (Smith & Wilson, 1996). Abundance evenness allows for greater niche complementarity at small scales due to potentially increased heterogeneity of functional traits. In terms of the theory of niche complementarity, both species richness and abundance evenness contribute to the positive total diversity effect on ecosystem function. Holding either species richness or abundance evenness constant while increasing the other will have the similar effect of reducing the likelihood that a neighbour is a conspecific, thus reducing the occurrence of negative density dependent competition effects and therefore increasing ecosystem function. We quantified tree structural diversity for each plot by calculating the Coefficient of Variation of DBH (DBH CV) and tree height (Height CV).

Vegetation clusters

Plots were assigned to vegetation type groups based on tree species composition. Groups were defined in a manner adapted from Fayolle et al. (2018) in an Africa-wide analysis of floristic units using plot data in savannas and woodlands with tree species diversity and relative abundance data. Group identification was conducted using unconstrained correspondence analysis, followed by hierarchical clustering based on dominant ordination axes. Plot data used in this study occurred in four compositional vegetation types. See Table 3.1 for a floristic description of each vegetation cluster, Table 3.2 for additional descriptive statistics, and Figure 3.1 for the spatial distribution of plots from each of these clusters. Cluster names were assigned post-hoc based on the dominant and indicator species in each cluster. Indicator species were identified using Dufrêne-Legendre indicator species analysis (Dufrêne & Legendre, 1997) implemented with `indval()` from the `labdsv` R package (Roberts, 2019). Dominant species also identified, as the species with the highest mean plot level proportional AGB (Above-Ground woody Biomass) within each cluster.

Table 3.1: Floristic description of vegetation types, showing the top three indicator and dominant species for each vegetation type.

Cluster	Dominant species	Indicator species
Core miombo	*Brachystegia spiciformis* *Julbernardia paniculata* *Brachystegia boehmii*	*Parinari curatellifolia* *Uapaca kirkiana* *Brachystegia spiciformis*
ex-Acacia	*Spirostachys africana* *Senegalia burkei* *Senegalia nigrescens*	*Euclea racemosa* *Vachellia nilotica* *Spirostachys africana*
Mopane	*Colophospermum mopane* *Androstachys johnsonii* *Kirkia acuminata*	*Colophospermum mopane* *Psuedolachnostylis maprouneifolia* *Lannea discolor*
Baikiaea	*Baikiaea plurijuga* *Burkea africana* *Pterocarpus angolensis*	*Burkea africana* *Baikiaea plurijuga* *Pterocarpus angolensis*

Table 3.2: Descriptive statistics for each of the vegetation type clusters to which each plot in the study was assigned. Numeric values of species richness, stems ha^{-1} and AGB represent medians and interquartile ranges (75th - 25th percentile).

Cluster	N Plots	Species Richness	Stem density (stems ha^{-1})	AGB (t ha^{-1})
Core miombo	523	20(16.9)	204(142.5)	44.2(36.11)
ex-Acacia	188	12(10.3)	181(166.5)	54.5(61.33)
Mopane	58	10(10.2)	186(125.6)	42.7(32.83)
Baikiaea	466	12(13.7)	178(129.5)	36.9(26.98)

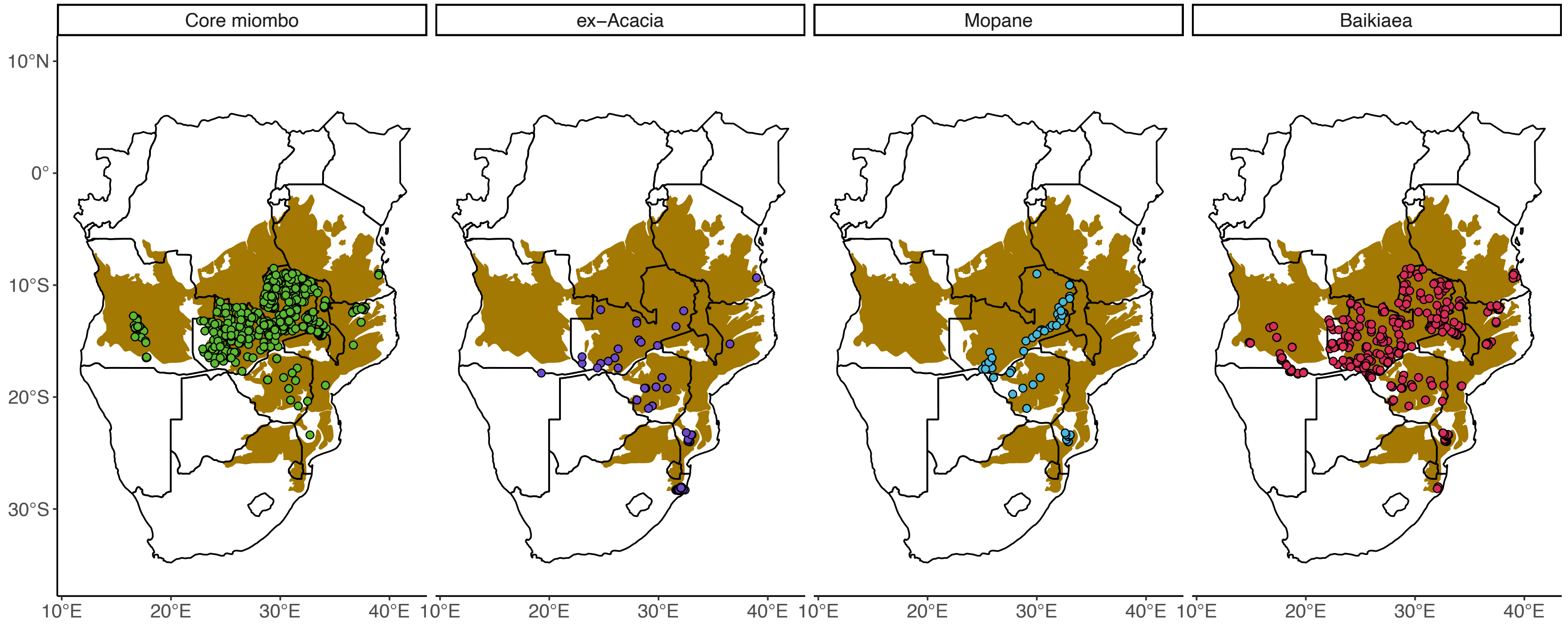


Figure 3.1: The locations of the 1235 plots used in this study, with respect to the distribution of mesic savanna vegetation according to White (1983). Each panel shows plots categorised by their vegetation type as defined by the vegetation types in Table 3.2.

Structural equation modelling

We used Structural Equation Modelling (SEM) to investigate the determinants of AGB. All SEMs were constructed and analysed in the 'lavaan' package (Rosseel, 2012) in R version 4.1.0 (R Core Team, 2020). SEM was used because of its suitability for modelling complex causal interactions in ecological systems (Lee, 2007). A key aspect consideration in our decision to use SEM is that they can explicitly model and partition variance attributed to indirect effects, which is challenging in standard multiple regressions. Using SEMs also allowed us to describe latent variables such as 'water availability', 'soil fertility', and 'disturbance' which have been suggested to act upon biodiversity and biomass/productivity in previous studies despite these factors not having directly observable measures in our dataset. SEM is also necessary to properly account for potential feedback mechanisms between aspects of environment and tree species diversity, which could otherwise increase the chances of Type I error and wrongly attribute inference due to the covariance of explanatory variables when using conventional regression analyses (Nachtigall et al., 2003).

We specified a conceptual model with factors expected to affect AGB: water availability, soil fertility, disturbance, tree species diversity, tree structural diversity and stem density (Figure 3.2).

Observed variables were transformed to achieve normality where necessary and standardised to Z-scores prior to analysis (Figure 3.S1, Figure 3.S2). Standardisation allows path regression coefficients to be easily compared between paths in the same model to assess their relative effect size, and eliminates confusion in model interpretation arising from the observed variables being on different scales (Beaujean, 2014). Standardisation also controls for variables with variation across different orders of magnitude, which could otherwise prevent adequate model estimation from the covariance matrix in 'lavaan'. To ensure that observed variables within a latent variable had consistent directions of influence, some observed variables had their sign reversed. For example, overall water availability is expected to decrease as soil sand content increases, therefore sand content was reversed for use in the water availability latent variable. Precipitation seasonality, and temperature stress were also reversed in this way to account for the direction of their effect on water availability.

The factor loading of the observed variable assumed to contribute most to each latent variable were set to one, as per convention, with other observed

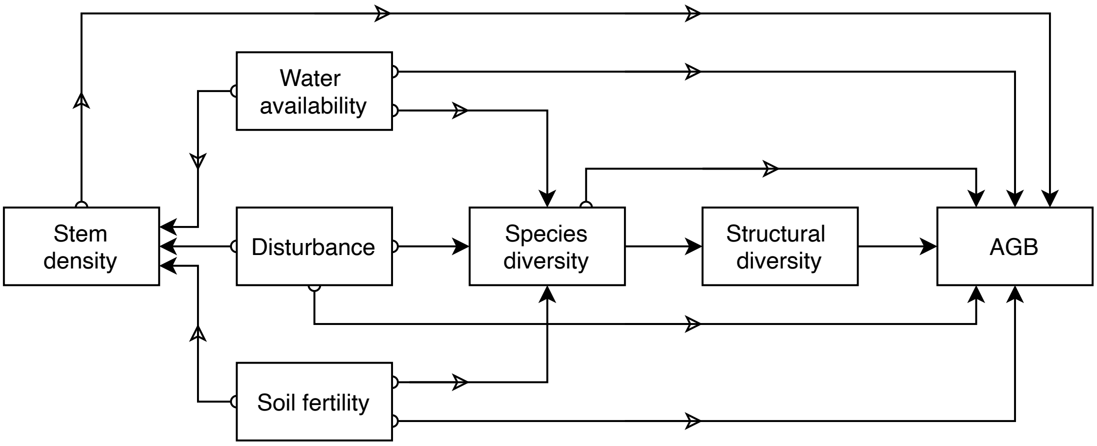


Figure 3.2: Conceptual Directed Acyclic Graph (DAG) showing the theoretical relationships between environmental factors, tree species diversity, tree structural diversity, stem density, and AGB (Above-Ground Woody Biomass). Hypothesised paths of causation are depicted as arrows from predictor to response. Open arrow heads track the direction of each arrow along its path.

variables being allowed to vary (Beaujean, 2014). We tested the robustness of our assumptions with a chi-squared test of all possible combinations of observed variable factor loadings set to one, while ensuring no factor loading were in excess of one. We found no significant difference between model specifications ($p > 0.05$). Full Information Maximum Likelihood (FIML) was used in each model to estimate the values of missing data in each latent variable (Cham et al., 2017).

First, we used a simple mediation model which excluded the environmental covariates, to assess the role of tree species diversity and tree structural diversity in determining AGB. This model allowed direct effects of species diversity, structural diversity, and stem density on AGB, and also the indirect effect of species diversity on AGB via structural diversity. To explore variation in the model among woodland vegetation types, we fit the model both at the regional scale and for each vegetation type separately. We compared unstandardised path coefficients among the models for different vegetation types to understand the effect that vegetation type has on the relationship between tree species diversity, structural diversity, stem density and AGB. Path coefficients show the effect of a given path with other paths held constant. Models were estimated using the ‘MLM’ estimator, because it is robust to multivariate non-normality (Shapiro, 1983). Model fit was evaluated using the robust Comparative Fit Index (CFI), the robust Tucker Lewis Index (TLI), the Root Mean Squared Error of Approximation (RMSEA) and the R^2 coefficient of determination for AGB. We critically assessed model fit in each case, taking into consideration the recommendations of Hu & Bentler (1999) who define threshold values of acceptability for these model fit indices: CFI >0.85, TLI >0.85, RMSEA <0.15, alongside our judgement of the model estimates.

To explore the hypothesis that biodiversity effects on ecosystem function increase in strength as stem density increases, we repeatedly sub-sampled the available plot dataset to create 50 data subsets with similar stem density. For each data subset we separately fitted a model including tree species and structural diversity latent variables to predict AGB. As we controlled for stem density via the dataset sub-sampling process, the effect of stem density on AGB was not included in the model. We examined how the unstandardised path coefficients for each path in the SEM varied according to the median stem density of the data subsets.

Second, we fitted the full model with environmental covariates, to understand the relative effects of water availability, soil fertility and disturbance on AGB, both directly and indirectly via species diversity and stem density. We compared standardised path coefficients among paths in the model to understand the relative contribution of each path to explain variance in AGB. Due to sample size issues, and because some vegetation types were narrow in their climate space, particularly in the water availability latent variable, we could not fit the model including environmental covariates separately for each vegetation type, as we encountered issues with model convergence. Preliminary models that included herbivore biomass from Hempson et al. (2017) did not converge. This is possibly due to the spatially coarse nature of the available data, or to collinearity with other variables, notably MAP and fire frequency. We therefore did not include herbivory in our final model.

3.3 Results

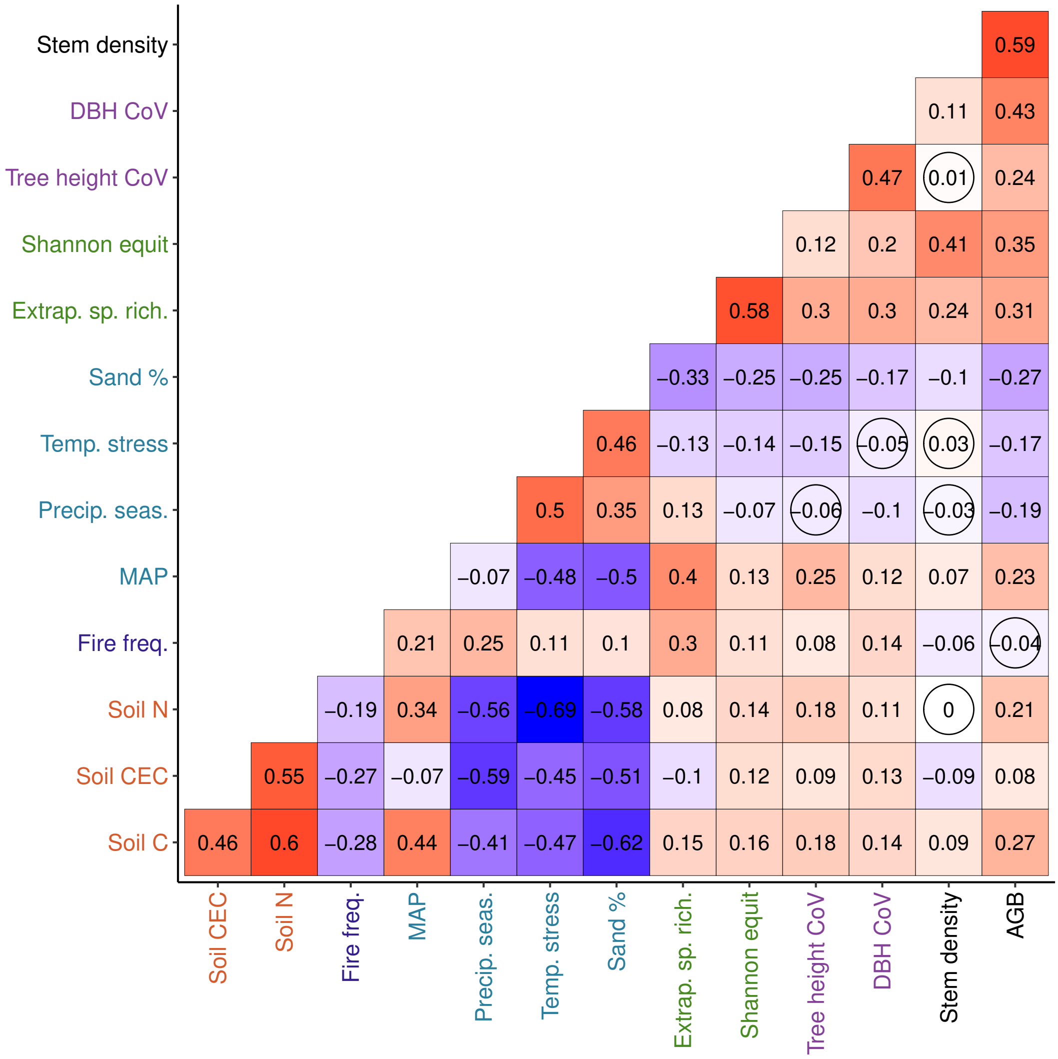
Pairwise correlations between all observed variables used in the Structural Equation Models (SEMs) showed that all tree species diversity (extrapolated tree species richness, Shannon equitability index) and structural diversity (coefficients of variation of DBH and height) variables had moderate positive correlations with AGB (Figure 3.3, Figure 3.S3). Stem density had the strongest correlation with AGB of all variables considered (r = 0.59, p <0.01). Environmental variables had weaker correlations with AGB than diversity variables, with all environmental variables having significant correlations with AGB, except fire frequency. The direction of these correlations was used as a test of our assumptions for the direction of influence of latent variables later used in the SEMs. MAP had positive correlations with all tree species diversity and structural diversity variables. Tree species diversity variables had clear positive correlations with stem density (species richness: r = 0.24, p <0.01; Shannon equitability: r = 0.58, p <0.01), but structural diversity variables showed weak correlations with stem density (DBH CV: r = 0.11, p <0.01, Height CV: r = 0.01, p = 0.86).

3.3.1 Structural and species diversity models

In the reduced SEM, which included stem density and the mediating effect of species diversity on AGB via structural diversity (Figure 3.4), species diversity showed no direct effect on AGB (β = 0.01$\pm$0.053, p=0.88), but did have an indirect positive effect via structural diversity (β = 0.18$\pm$0.039, p<0.01) (Figure 3.4). Model fit was good with high factor loading for all observed variables. All other path coefficients were significant (p <0.01) (Table 3.3). The R^2 of AGB was 0.49. The strongest direct effect on AGB was from stem density (β = 0.5$\pm$0.033, p<0.01).

3.3.2 Variation among vegetation types

When the tree species and structural diversity model (Figure 3.4) was refitted separately using data from each of the four vegetation types, we found that the effect sizes of each latent variable remained largely similar, though model fit varied. The direct effect of tree species diversity on AGB was positive and marginally significant in ex-Acacia (β = 0.16$\pm$0.121, p=0.18) but negligible in Mopane (β = 0.24$\pm$0.099, p<0.05), Baikiaea (β = 0.23$\pm$0.045, p<0.01) and Core miombo (β = 0.23$\pm$0.041, p<0.01) (Figure 3.5). Relationships among



	Soil CEC	Soil N	Fire freq.	MAP	Precip. seas.	Temp. stress	Sand %	Extrap. sp. rich.	Shannon equit	Tree height CoV	DBH CoV	Stem density	AGB
Stem density													0.59
DBH CoV												0.11	0.43
Tree height CoV											0.47	0.01	0.24
Shannon equit										0.12	0.2	0.41	0.35
Extrap. sp. rich.									0.58	0.3	0.3	0.24	0.31
Sand %								−0.33	−0.25	−0.25	−0.17	−0.1	−0.27
Temp. stress							0.46	−0.13	−0.14	−0.15	−0.05	0.03	−0.17
Precip. seas.						0.5	0.35	0.13	−0.07	−0.06	−0.1	−0.03	−0.19
MAP					−0.07	−0.48	−0.5	0.4	0.13	0.25	0.12	0.07	0.23
Fire freq.				0.21	0.25	0.11	0.1	0.3	0.11	0.08	0.14	−0.06	−0.04
Soil N			−0.19	0.34	−0.56	−0.69	−0.58	0.08	0.14	0.18	0.11	0	0.21
Soil CEC		0.55	−0.27	−0.07	−0.59	−0.45	−0.51	−0.1	0.12	0.09	0.13	−0.09	0.08
Soil C	0.46	0.6	−0.28	0.44	−0.41	−0.47	−0.62	0.15	0.16	0.18	0.14	0.09	0.27

Figure 3.3: Correlation matrix of standardised observed variables used in the SEMs (Structural Equation Models), with Pearson correlation coefficients (r) coloured according to sign (+ve red, −ve blue) and shaded by strength of correlation. Correlation coefficients marked by a circle indicate that the 95% confidence interval of r overlapped zero. Colours of variable names group them into latent variables used in the SEMs: red = soil fertility, blue = disturbance, turquoise = water availability, green = tree species diversity, purple = tree structural diversity. See Table 3.S1 for a full assessment of correlation fit statistics.

Table 3.3: Model fit statistics for Structural Equation Models investigating the effects of tree diversity and stem density on AGB (Figure 3.4). N = number of plots in cluster, χ^2 = Chi-squared fit statistic, DoF = model degrees of freedom, CFI = Comparative Fit Index, TLI = Tucker-Lewis Index, RMSEA = Root Mean Square Error of Approximation, R^2 AGB = model R^2 for AGB (Above-Ground Biomass).

Cluster	N	χ^2	DoF	CFI	TLI	RMSEA	R^2 AGB
Core miombo	523	78.67	6	0.904	0.759	0.14	0.49
ex-Acacia	188	9.57	6	0.952	0.879	0.13	0.83
Mopane	58	19.88	6	0.834	0.584	0.24	0.51
Baikiaea	466	43.87	6	0.914	0.784	0.13	0.58
All	1235	91.38	6	0.937	0.843	0.12	0.49

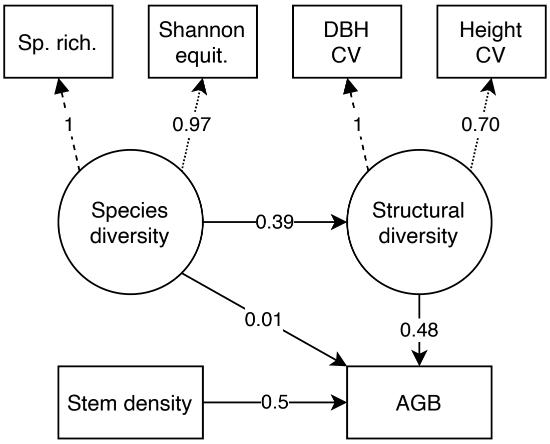


Figure 3.4: Path diagram with regression coefficients for the tree diversity SEM (Structural Equation Model), including plots from all vegetation clusters. Latent variables are shown as circles while observed variables are shown as rectangles. Standardised path coefficients are shown as solid arrows pointing from predictor to response with the effect size of the path coefficient expressed in terms of standard deviations on the latent variable response scale. The observed variables that inform the latent variables are connected by dotted arrows, and observed variables with loading set to one are connected by dashed arrows. Measurement errors of exogenous variables are omitted for clarity.

structural diversity and AGB remained generally similar, with the same sign and overlap between the 95% confidence intervals of path coefficients. The R^2 of AGB was highest in ex-Acacia shrubland (R^2 = 0.83) and lowest in Baikiaea (R^2 = 0.46). The total effect of species diversity on AGB remained strongly positive and there was a positive direct effect of species diversity on structural diversity, across all vegetation types. All models had adequate goodness-of-fit (Table 3.3), though confidence intervals around the unstandardised path coefficients were wide particularly for Mopane and ex-Acacia. χ^2 statistics were high for some vegetation types, but this appears to be highly correlated with sample size for each vegetation type (Hooper et al., 2008).

3.3.3 Moderation of diversity effect by stem density

In the sub-sampling of the plot dataset by stem density, we found an increasing positive effect of tree species diversity on AGB as stem density increased (Figure 3.6e). There appears to be a minimum stem density threshold at c. 180 stems >10 cm DBH ha^{-1} below which there appears to be a reasonably constant baseline effect of tree diversity on biomass (Figure 3.6b). The effect of structural diversity on AGB appears to remain constant with increasing stem density (Figure 3.6d). The indirect effect of tree species diversity on AGB via structural diversity increases as stem density increases (Figure 3.6c).

3.3.4 Environmental covariates and tree diversity

A model incorporating the latent variables of water availability, soil fertility and disturbance by fire showed that the total effect of tree species diversity on biomass was similar to that of water availability, soil fertility and disturbance (Figure 3.7, Figure 3.S4). The direct effects of water availability, soil fertility and disturbance on AGB were negligible (water: β = 0.1±0.13, p=0.43, soil: β = 0.1±0.155, p=0.51, disturbance: β = -0.04±0.043, p=0.32), with nearly all of their observed effects on AGB coming from the indirect paths via stem density (water: β = 0.14±0.091, p=0.12, soil: β = -0.22±0.109, p<0.05, disturbance: β = -0.12±0.03, p<0.01) and species diversity (water: β = 0.62±0.172, p<0.01, soil: β = -0.24±0.209, p=0.26, disturbance: β = 0.19±0.058, p<0.01). MAP and soil sand content had the greatest contributions to the latent variable of water

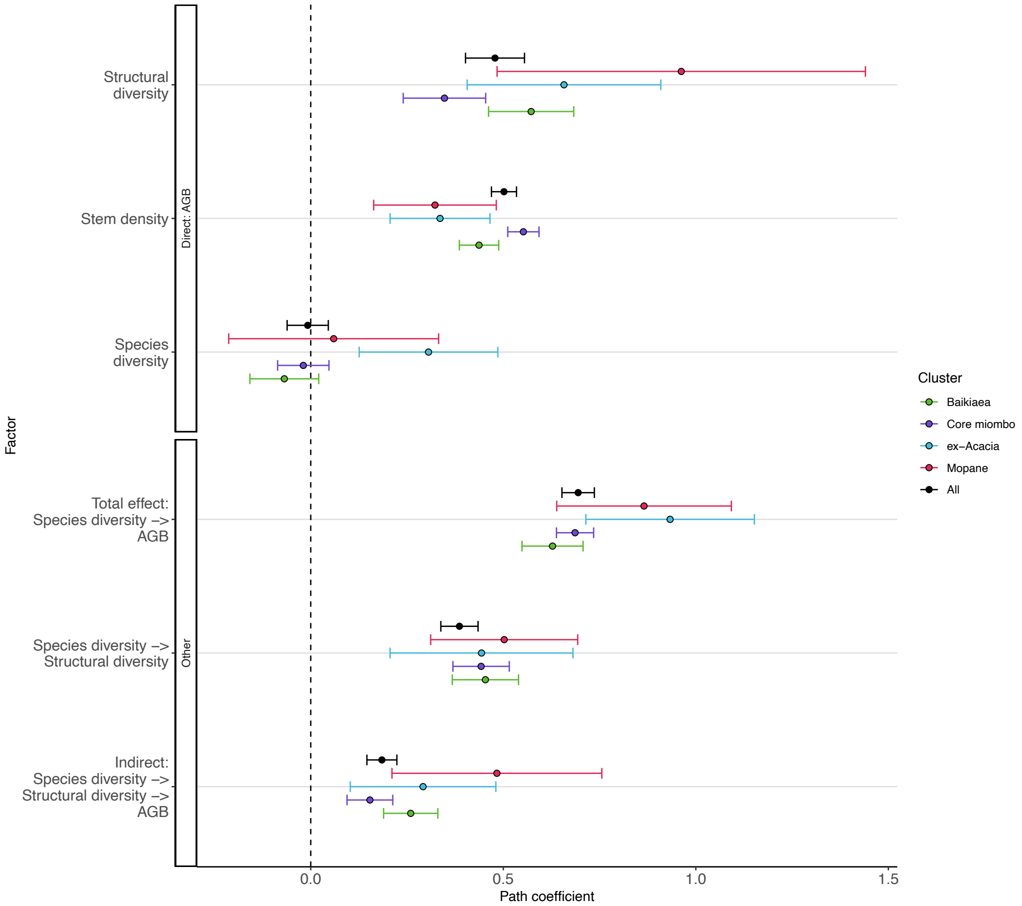


Figure 3.5: Unstandardised path coefficients for the effects of tree diversity on AGB (Above-Ground Woody Biomass), mediated by the effect of stand structural diversity. Path coefficients are ±1 standard error. Path coefficients where the interval (standard error) does not overlap zero are considered to be significant effects.

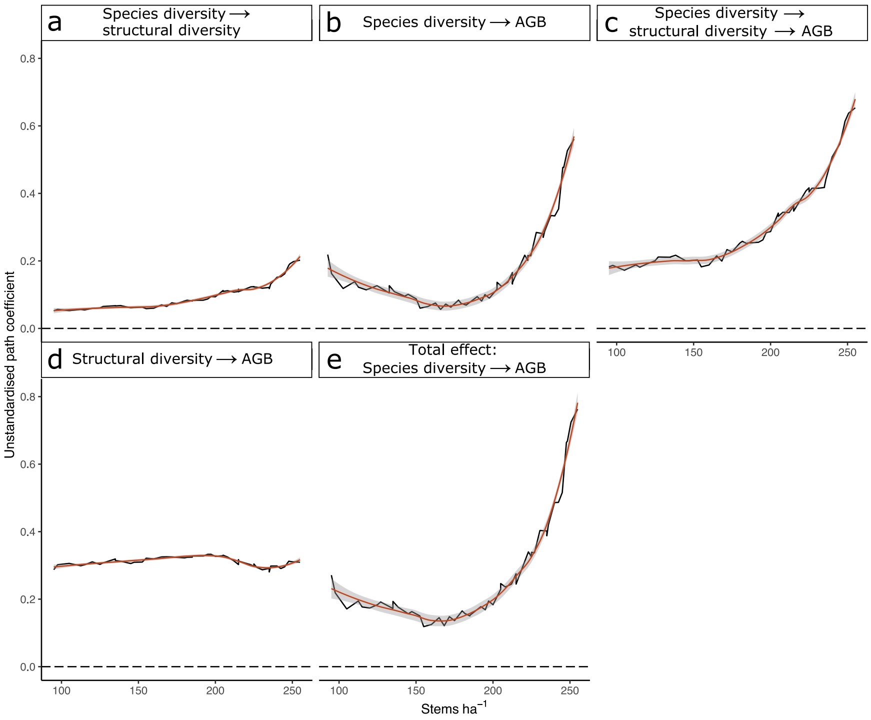


Figure 3.6: Line plots showing the variation in SEM (Structural Equation Model) path coefficients among latent variables, across datasets with different mean stem density. Smoothed lines are loess curves with ±1 standard error shaded bars. AGB = Above-Ground woody Biomass. Arrows in plot titles indicate causal paths in SEM models. Where multiple arrows are present, as in c), this indicates an indirect pathway via an intermediate variable. a) shows the direct effect of species diversity on structural diversity. b) and d) show the direct effects of species diversity and structural diversity on AGB, respectively. c) shows the indirect effect of species diversity on AGB via structural diversity. e) shows the total effect of species diversity on AGB, incorporating both the direct effect and the indirect effect via structural diversity.

availability. Model fit was acceptable: CFI = 0.925, TLI = 0.900, and RMSEA = 0.153, R^2 of AGB = 0.34.

Similar to the model that only considered tree species and structural diversity (Figure 3.4), the direct effect of species diversity on structural diversity was positive, while structural diversity itself had a positive effect on AGB, leading to a strong positive indirect effect of species diversity on AGB via structural diversity (β = 0.19±0.026, p<0.01) when environmental covariates were accounted for. Again, the direct effect of species diversity on AGB was negligible (β = -0.05±0.041, p=0.27). The total effect of species diversity on AGB was positive (β = 0.34±0.044, p<0.01). Compared to the simple model with no environmental covariates, the total explanatory power of tree species diversity and structural diversity in this model decreased, but the predictive power of the model as a whole increased.

3.4 Discussion

We assessed the importance of a) tree species diversity, b) tree structural diversity, c) resource availability, d) disturbance by fire, e) organismal density and their interactions on above-ground woody biomass (AGB) across southern African savannas and woodlands, using a network of 1235 woodland plots in conjunction with Structural Equation Modelling (SEM). We found support for a general positive relationship between tree species diversity and AGB, operating indirectly via structural diversity (H_1). Tree species diversity, structural diversity and stem density accounted for 49% of the variation in AGB across the region, while models for specific vegetation types showed even greater explanatory power in some cases (Table 3.3). Within the latent variable of tree species diversity we found similarly strong factor loading for both species richness and abundance evenness. This demonstrates that species richness and abundance evenness measure different and largely uncorrelated axes of diversity. We found that the effect of tree species diversity on AGB increased with stem density (H_2), with an apparent threshold of 180 stems >10 cm DBH ha^{-1}, below which the effect of species diversity on AGB remained at a low baseline level. The strongest direct effect on AGB was that of stem density. When the effects of water availability, soil fertility and disturbance by fire were controlled for, the total explanatory power of tree species diversity and structural diversity decreased,

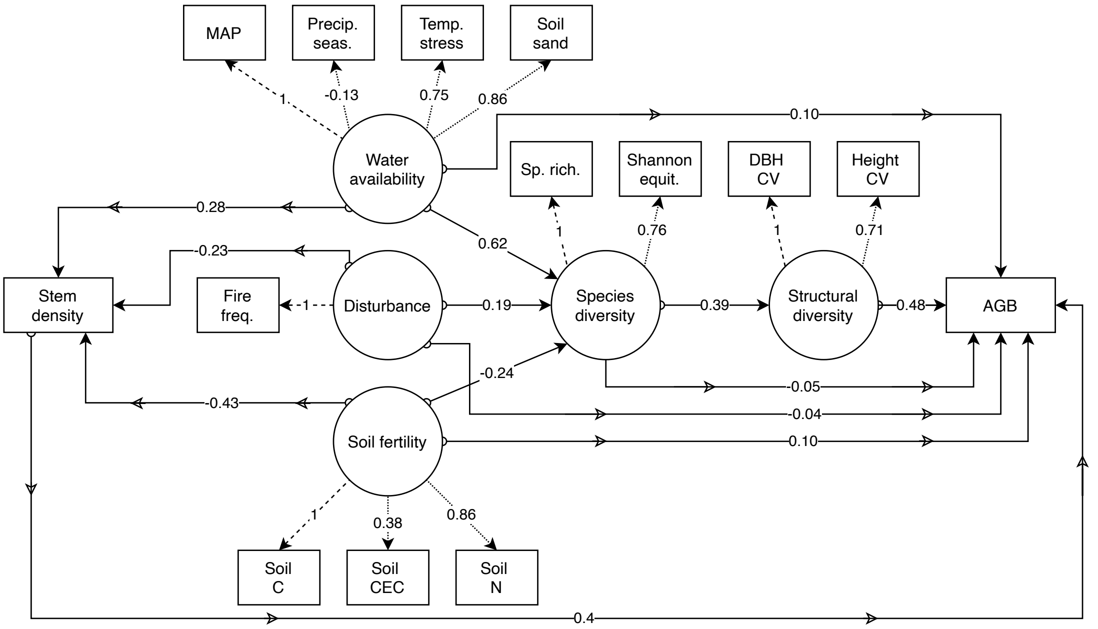


Figure 3.7: Path diagram with regression coefficients for the SEM (Structural Equation Model) incorporating environmental covariates and tree species and structural diversity across all five vegetation types. Latent variables are shown as circles while observed variables are shown as rectangles. Standardised path coefficients are shown as solid arrows pointing from predictor to response, with the effect size of the path coefficient expressed in terms of standard deviations on the latent variable response scale. Observed variables that inform the latent variables are connected by dotted arrows, observed variables with loading set to one are connected by dashed arrows. Measurement errors of exogenous variables are omitted for clarity.

but the predictive power of the model increased, suggesting that it is important to control for environmental covariates to understand the true effect of tree species diversity on AGB in regional scale assessments of the BEFR.

3.4.1 Inter-related effects of tree species and structural diversity on AGB

We found a consistent positive effect of tree species diversity on AGB. Within southern African woodlands we therefore find support for the hypothesis that higher tree species richness and evenness leads to higher above-ground woody biomass. This finding is in agreement with many other studies across different ecosystems and biomes, supporting the idea that there is a generalisable positive association between biodiversity and ecosystem function (Liang et al., 2016; Cardinale et al., 2009). Our study provides a novel dissection of the mechanisms underlying this relationship, particularly in the context of southern African woodlands, a disturbance-driven and poorly studied ecological system.

Much of the total variation in AGB was driven by variation in organismal density. It is possible that within southern African woodlands a higher species diversity allows for a higher stem density through niche separation, which reduces competition between species occupying varying niche space, leading to an increase in total AGB per unit area. The opposite causation is also plausible however, with increased stem density causing higher species richness through an increased probability of encountering new species. We attempted to correct for the correlation between species richness and stem density using extrapolated species richness, which extrapolates a rarefaction curve to its predicted asymptote, thus estimating the total landscape level species richness which is independent of plot size and stem density. We suggest therefore that an increase in tree species diversity through species richness and evenness produces an assemblage of species which can utilise more available light and moisture, resulting in greater plot level AGB. This is supported by the moderately strong indirect positive effect of tree species diversity on AGB via structural diversity, and the positive effect of water availability on AGB via stem density in the model which included environmental covariates.

We found evidence that tree species diversity led to an increase in AGB indirectly via tree structural diversity, and we therefore find support for our second hypothesis H_2. A higher tree species diversity allows for a greater structural diversity of trees, i.e. greater variation in DBH and height. This may act as a mechanism for niche complementarity, with a canopy of diversely-sized trees able to take advantage of a greater proportion of the available light. Additionally, the volume of tree above-ground structures is generally correlated with the volume of below-ground structures (Paul et al., 2019). In water and nutrient limited ecosystems especially, variation in rooting depth may constitute a second related axis of niche partitioning driving the observed positive effect of above-ground structural diversity on AGB (Kulmatiski & Beard, 2013). Although we did not measure them here, we would also expect that tree species diversity allows for a greater range of tree functional forms (Pretzsch, 2014), i.e. wider variation in canopy shape and overall growth form; broad flat crowns vs. narrow deep crowns, for example. In forests, where the tree canopy is effectively closed, as the stand matures a more diverse canopy emerges via competition and tree mortality events which open canopy gaps (Muscolo et al., 2014). Indeed, our finding that the strength of the effect of tree diversity on AGB increases with stem density supports this mechanism (Figure 3.6). At low stem densities, competition between mature trees may not occur, meaning that the niche complementarity effect provided by an increase in tree species richness may not be present, accounting for the small effect of tree species diversity on AGB below c. 180 trees ha^{-1}. In frequently disturbed woodlands such as those studied here, a woodland canopy similar to that of a forest is frequently not reached. Instead, a simple open canopy is maintained that can be made more complex and productive via an increase in species diversity.

Alternatively, due to the non-linear relationship between biomass and tree size (Bastin et al., 2018), the positive relationship between structural diversity and biomass may also be partly driven by an increased number of large sized trees in plots with higher structural diversity, with large trees contributing disproportionately to biomass. The positive effect of species diversity on AGB via structural diversity may therefore be due to selection effects, with higher diversity plots supporting larger trees due to species specific variation in functional form (Díaz et al., 2015).

3.4.2 Organismal density and disturbance

Disturbance by fire had a negative total effect on AGB, with most of this negative effect coming from the indirect pathway via stem density. This is expected as increased fire frequency is a key mechanism by which savannas maintain an open canopy, rather than shifting to a closed canopy forest (Staver et al., 2011). Previous studies have found that southern African woodlands with higher species diversity tend to experience less frequent disturbance by fire and tend to form a more closed canopy with a sparse understorey (Chidumayo, 2013; Mutowo & Murwira, 2012). In our study however, we found a positive effect of fire frequency on species diversity, perhaps suggesting that disturbance prevents domination of woodlands by a single dominant species (Chidumayo, 2013; Durigan et al., 2020; Staver et al., 2009). It is suggested that in savannas where the tree-species pool is largely adapted to fire, increased fire may actually increase tree species diversity by allowing weak competitors to co-exist.

Disturbances such as fire have the potential to reduce both species diversity and above-ground biomass in the short term, due to increased mortality (Huston, 2014). Unless this effect is accounted for, there is the potential for mistaken causality as both diversity and biomass may correlate. In our model, time since disturbance is accounted for within each plot via the stem density term. Disturbance reduces stem density of large stems (>10 cm DBH), which is expected to increase until the effects of competition preclude further increase (Johnson et al., 2012). Furthermore, our rarefied measure of species diversity accounts for variation in sampling effort and is therefore independent of stem density. Tree species richness should also increase with time since disturbance as with increased stem density the likelihood of including a new species also increases. Outside of the stem density effect, there are multiple causes for variation in tree species diversity in this study. Vegetation types and localities differ in their available species pool, for example. Variation in abiotic environmental factors will also affect species accumulation.

3.4.3 Effects of water availability and soil fertility

Water availability had a positive total effect on AGB, comparable in size to the total effect of tree species diversity on AGB, while soil fertility had a negative total effect. We expected that higher water availability and soil fertility would lead to higher AGB under the assumption that higher resource availability would allow for a greater stem density per unit area, greater productivity per unit area and additionally greater tree species diversity due to niche partitioning (Kraaij & Ward, 2006; Shirima et al., 2015). Previous studies in tropical forests have shown that water availability increases AGB both directly and indirectly via increasing tree species diversity and via increasing stand structural diversity (Ali et al., 2019a; Ali et al., 2019b; Poorter et al., 2017). In this study, we observed indirect positive effects of water availability on AGB via species diversity and a positive but only marginally significant direct effect on AGB. Compared to moist tropical forests, water availability is more of a limiting factor to tree growth in southern African woodlands, which experience frequent drought.

A negative total effect of soil fertility on AGB is in contrast to other studies in the region and general ecological theory, which predicts a positive effect of soil nutrients on biomass (Scarascia-Mugnozza et al., 2000). The negative total effect of soil fertility on AGB was driven mostly by an indirect negative effect via stem density. The direct effect on AGB however, remained positive and marginally significant, as expected. Model estimates of the effect of soil on AGB were poorly constrained compared with other latent variables. This wide standard error on the model predictions is possibly due to the coarseness and nature of the soil data we used. SoilGrids provides modelled data at 250 m resolution, while soil structure and nutrient content varies at much finer scales in southern African woodlands (Muledi et al., 2017; Bucini & Hanan, 2007). It is therefore not surprising that this model path is poorly constrained. Lehmann et al. (2014) found similarly weak and poorly constrained relationships for soil in a Structural Equation Model including precipitation, temperature, soil, and fire to predict tree basal area in southern African woodlands. Plot-specific soil data are time-consuming to collect and difficult to compare across studies when different protocols are used. Our study points to the need for further effort in this regard, which may reveal interesting findings about the complex interactions between soil, disturbance and tree diversity in southern African woodlands. Alternatively, Gourlet-Fleury et al. (2011) found that environmental filtering of fast-growing species with low wood density on resource poor soils resulted in a decoupling of the soil fertility - AGB relationship. It is possible that at regional scales, variation in species composition could offset resource availability constraints on AGB. However, unlike Gourlet-Fleury et al. (2011) disturbance by fire in our study region may further complicate this environmental filtering effect.

3.4.4 Vegetation type responses

All four vegetation types produced similar results in the simple SEM, with a positive total effect of species diversity on AGB, the majority being indirectly via structural diversity. This demonstrates the robustness of our results, showing they are generalisable across vegetation types in southern Africa. It also demonstrates that similar ecosystem processes are occurring in these vegetation types, despite variation in species composition, overall species richness and mean biomass.

Core miombo and Baikiaea woodland vegetation exhibited a small negative direct effect of tree species diversity on AGB, while the total effect, incorporating the indirect effect via structural diversity, remained positive in these vegetation types. Compared to ex-Acacia and Mopane woodlands, miombo woodlands have higher median tree species richness. Ex-Acacia and Mopane woodlands are dominated by fewer tree species, notably *Senegalia* spp. in ex-Acacia woodlands and *Colophospermum mopane* in Mopane woodlands, which can produce large canopy dominating trees in the so-called “Cathedral mopane”. We postulate that the slight negative effect of tree species richness on AGB in miombo woodlands may be due to an increase in interspecific competition through canopy crowding, but that this effect is not present in ex-Acacia and Mopane woodlands, where the top level of the woodland canopy is dominated often by a single species.

Higher functional redundancy among tree species in miombo woodlands may lead to smaller trees with lower AGB in the most diverse plots, more resembling thicket vegetation and suppressing the few species which tend to create high biomass, such as *Julbernardia* and *Brachystegia* spp.. In the species-poor Mopane and ex-Acacia woodlands however, the addition of extra species may fill a greater proportional niche space, thus increasing total AGB more.

Despite Mopane woodland having very low species diversity generally, with often monospecific stands (Timberlake et al., 2010), a positive effect of tree species diversity on AGB was observed. In previous studies across multiple biomes it has been found that the effect of adding species on ecosystem function is stronger in low diversity assemblages (Cardinale et al., 2006; Srivastava &

Vellend, 2005). This has been attributed to an increase in functional redundancy as species diversity increases. Mopane woodlands also have a negligible effect of species diversity on structural diversity. This may be due to the particular functional forms of species which co-exist with *C. mopane*, many of which are small shrub-like trees rather than large canopy trees (Timberlake et al., 2010). Larger canopy trees tend to have greater variation in physical structure (Seidel et al., 2019), which would drive an effect of species diversity on structural diversity as we observed in miombo woodlands.

Ex-Acacia woodlands showed the strongest total effect of species diversity on AGB and was the only vegetation type to show a significant positive direct effect of species diversity on AGB. Ex-Acacia woodlands also had relatively low median species richness compared to miombo, but the addition of new species appears to make a larger difference to the AGB of these plots than in Mopane woodlands. We suggest that this is due mostly to the particular identity of species found in ex-Acacia woodlands and their contribution to ecosystem functioning. Unlike Mopane woodlands, ex-Acacia woodlands contain a wider variety of species which can grow to large canopy trees, albeit at low densities, especially in transition zones with miombo woodlands. Additionally, many more species species in ex-Acacia woodlands are found in the Mimosoideae and Papilionoideae sub-families, of which most are nitrogen-fixing (Tedersoo et al., 2018). Nitrogen availability is often a limiting factor in productivity, making nitrogen-fixing species strong competitors. It is possible that in ex-Acacia dominated woodlands, the presence of a large number of nitrogen-fixing tree species reduces functional redundancy, meaning that the effect of adding species on ecosystem function saturates at a higher species richness.

3.5 Conclusion

In this study we found that even in highly disturbed southern African woodlands, there exists a generalisable positive association between tree species diversity and ecosystem function, quantified as above-ground woody biomass (AGB). Our findings contribute to our understanding of a universal biodiversity-ecosystem function relationship, one which is moderated in a predictable manner by environmental covariates and their interaction with biodiversity and ecosystem structure. We found that the multiple vegetation types which comprise southern African woodlands exhibit similarities in the relationship between species diversity and woody biomass, suggesting that similar processes operate across the region to determine ecosystem function. We advocate for explicit inclusion of environmental covariates in regional scale models of biodiversity and ecosystem function. We assert that this is necessary to develop our understanding of the biodiversity-ecosystem function relationship in real-world ecosystems, to progress from experimental mesocosms. We found that much of the effect of species diversity on biomass exists as an indirect effect by increasing the structural diversity of trees, exemplifying a key mechanism by which tree species diversity determines ecosystem function in savannas, woodlands and forests, where trees comprise a significant, canopy-forming component. The presence of a stem density threshold above which the effect of tree species diversity on AGB increases clearly implies the presence of niche complementarity effects in southern African woodlands, an aspect which has often been overlooked in previous studies despite its intuitive logic as a determinant of niche complementarity effects in wooded ecosystems. Our study shows that biodiversity change through extensive human-induced land use change in this region will have the greatest negative impact on ecosystem function in areas of high stems density, and in certain vegetation types, specifically Mopane and ex-Acacia woodlands. This raises concerns about the robustness of these ecosystems to further resource extraction and biodiversity loss. Finally, our results provide further evidence of the complex interaction of factors governing biomass and therefore carbon dynamics in disturbance-driven wooded ecosystems, which currently represent the greatest uncertainty in the global terrestrial carbon sink.

References

Ahlstrom, A., M. R. Raupach, G. Schurgers, B. Smith, A. Arneth, M. Jung, M. Reichstein, J. G. Canadell, P. Friedlingstein, A. K. Jain et al. (2015). 'The dominant role of semi-arid ecosystems in the trend and variability of the land CO2 sink'. In: *Science* 348.6237, pp. 895–899. DOI: `10.1126/science.aaa1668`.

Ali, A., S. Lin, J. He, F. Kong, J. Yu & H. Jiang (2019a). 'Big-sized trees overrule remaining trees' attributes and species richness as determinants of aboveground biomass in tropical forests'. In: *Global Change Biology* 25, pp. 2810–2824. DOI: `10.1111/gcb.14707`.

Ali, A., S. Lin, J. He, F. Kong, J. Yu & H. Jiang (2019b). 'Climate and soils determine aboveground biomass indirectly via species diversity and stand structural complexity in tropical forests'. In: *Forest Ecology and Management* 432, pp. 823–831. DOI: `10.1016/j.foreco.2018.10.024`.

Barry, K. E., L. Mommer, J. van Ruijven, C. Wirth, A. J. Wright, Y. Bai, J. Connolly, G. B. De 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`.

Bastin, J., E. Rutishauser, J. R. Kellner, S. Saatchi, R. Pélissier, B. Hérault, F. Slik, J. Bogaert, C. De Cannièire, A. R. Marshall et al. (2018). 'Pan-tropical prediction of forest structure from the largest trees'. In: *Global Ecology and Biogeography* 27.11, pp. 1366–1383. DOI: `10.1111/geb.12803`.

Beaujean, A. A. (2014). *Latent variable modeling using R*. New York NY, USA: Routledge.

Booth, T. H., H. A. Nix, J. R. Busby & M. F. Hutchinson (2014). 'BIOCLIM: the first species distribution modelling package, its early applications and relevance to most current MaxEnt studies'. In: *Diversity and Distributions* 20.1, pp. 1–9. DOI: `10.1111/ddi.12144`.

Brockerhoff, E. G., L. Barbaro, B. Castagneyrol, D. I. Forrester, B. Gardiner, J. R. González-Olabarria, P. O. Lyver, N. Meurisse, A. Oxbrough, H. Taki et al. (2017). 'Forest biodiversity, ecosystem functioning and the provision of ecosystem services'. In: *Biodiversity and Conservation*. DOI: `10.1007/s10531-017-1453-2`.

Bucini, G. & N. P. Hanan (2007). 'A continental-scale analysis of tree cover in African savannas'. In: *Global Ecology and Biogeography* 16.5, pp. 593–605. DOI: `10.1111/j.1466-8238.2007.00325.x`.

Campbell, B. M., ed. (1996). *The miombo in transition: Woodlands and welfare in Africa*. Bogor, Indonesia: Centre for International Forestry Research.

Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran & C. Jouseau (2006). 'Effects of biodiversity on the functioning of trophic groups and ecosystems'. In: *Nature* 443.7114, pp. 989–992. DOI: `10.1038/nature05202`.

Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, C. Jouseau, M. W. Cadotte, I. T. Carroll, J. J. Weis et al. (2009). 'Effects of biodiversity on the functioning of ecosystems: a summary of 164 experimental manipulations of species richness'. In: *Ecology* 90.3, pp. 854–854. DOI: `10.1890/08-1584.1`.

Carvalho, G. H., M. A. Batalha, I. A. Silva, M. V. Cianciaruso & O. L. Petchey (2014). 'Are fire, soil fertility and toxicity, water availability, plant functional diversity, and litter decomposition related in a Neotropical savanna?' In: *Oecologia* 175.3, pp. 923–935. DOI: `10.1007/s00442-014-2937-3`.

Cham, H., E. Reshetnyak, B. Rosenfeld & W. Breitbart (2017). 'Full information maximum likelihood estimation for latent variable interactions with incomplete indicators'. In: *Multivariate Behavioural Research* 52, pp. 12–30. DOI: `10.1080/00273171.2016.1245600`.

Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson & A. E. Zanne (2009). 'Towards a worldwide wood economics spectrum'. In: *Ecology Letters* 12, pp. 351–366. DOI: `10.1111/j.1461-0248.2009.01285.x`.

Chave, J., M. Réjou-Méchain, A. Búrquez, E. Chidumayo, M. S. Colgan, W. B. C. Delitti, A. Duque, T. Eid, P. M. Fearnside, R. C. Goodman et al. (2014). 'Improved allometric models to estimate the aboveground biomass of tropical trees'. In: *Global Change Biology* 20, pp. 3177–3190. DOI: `10.1111/gcb.12629`.

Chidumayo, E. N. (2013). 'Forest degradation and recovery in a miombo woodland landscape in Zambia: 22 years of observations on permanent sample plots'. In: *Forest Ecology and Management* 291, pp. 154–161. DOI: `10.1016/j.foreco.2012.11.031`.

Clarke, D. A., P. H. York, M. A. Rasheed & T. D. Northfield (2017). 'Does biodiversity-ecosystem function literature neglect tropical ecosystems'. In: *Trends in Ecology & Evolution* 32.5, pp. 320–323. DOI: `10.1016/j.tree.2017.02.012`.

Dengler, J. (2009). 'Which function describes the species-area relationship best? A review and empirical evaluation'. In: *Journal of Biogeography* 36, pp. 728–744. DOI: `10.1111/j.1365-2699.2008.02038.x`.

Dexter, K. G., B. Smart, C. Baldauf, T. R. Baker, M. P. B. Bessike Balinga, R. J. W. Brienen, S. Fauset, T. R. Feldpausch, L. Ferreira-da Silva, J. I. Muledi et al. (2015). 'Floristics and biogeography of vegetation in seasonally dry tropical regions'. In: *International Forestry Review* 17.S2, pp. 10–32. DOI: `10.1505/146554815815834859`.

Díaz, S., J. Kattge, J. H. C. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, M. Kleyer, C. Wirth, I. C. Prentice et al. (2015). 'The global spectrum of plant form and function'. In: *Nature* 529.7585, pp. 167–171. DOI: `10.1038/nature16489`.

Dufrêne, M. & P. Legendre (1997). 'Species assemblages and indicator species: The need for a flexible asymmetrical approach'. In: *Ecological Monographs* 67.3, pp. 345–366. DOI: `10.1890/0012-9615(1997)067[0345:saaist]2.0.co;2`.

Durigan, G., N. A. L. Pilon, R. C. R. Abreu, W. A. Hoffmann, M. Martins, B. F. Fiorillo, A. Z. Antunes, A. P. Carmignotto, J. B. Maravalhas, J. Vieira et al. (2020). 'No net loss of species diversity after prescribed fires in the Brazilian savanna'. In: *Frontiers in Forests and Global Change* 3. DOI: `10.3389/ffgc.2020.00013`.

Fayolle, A., M. D. Swaine, J. Aleman, A. F. Azihou, D. Bauman, M. te Beest, E. N. Chidumayo, J. P. G. M. Cromsigt, H. Dessard, M. Finkch et al. (2018). 'A sharp floristic discontinuity revealed by the biogeographic regionalization of African savannas'. In: *Journal of Biogeography* 46, pp. 1–12. DOI: `10.1111/jbi.13475`.

Fick, S. E. & R. J. Hijmans (2017). 'WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas'. In: *International Journal of Climatology* 37.12, pp. 4302–4315. DOI: `10.1002/joc.5086`.

Giglio, L., C. Justice, L. Boschetti & D. Roy (2015). *MCD64A1 MODIS/Terra+Aqua Burned Area Monthly L3 Global 500m SIN Grid V006 [Data set]*. NASA EOSDIS Land Processes DAAC. DOI: `10.5067/MODIS/MCD64A1.006`. (Visited on 20/04/2020).

Godlee, J. L., F. M. Gonçalves, J. J. Tchamba, A. V. Chisingui, J. I. Muledi, M. N. Shutcha, C. M. Ryan, T. K. Brade & K. G. Dexter (2020). 'Diversity and structure of an arid woodland in southwest Angola, with comparison to the wider miombo ecoregion'. In: *Diversity* 12, pp. 1–20. DOI: `10.3390/d12040140`.

Godlee, J. L., C. M. Ryan, D. Bauman, S. J. Bowers, J. M. B. Carreiras, A. V. Chisingui, J. P. G. M. Cromsigt, D. J. Druce, M. Finckh, F. M. Gonçalves et al. (2021). 'Structural diversity and tree density drives variation in the biodiversity-ecosystem function relationship of woodlands and savannas'. In: *New Phytologist*. DOI: `10.1111/nph.17639`.

Gonzalez, A., R. M. Germain, D. S. Srivastava, E. Filotas, L. D. Dee, D. Gravel, D. L. Thompson, F. Isbell, S. Wang, S. Kéfi et al. (2020). 'Scaling-up biodiversity-ecosystem functioning research'. In: *Ecology Letters* 23.4, pp. 757–776. DOI: `10.1111/ele.13456`.

Gourlet-Fleury, S., V. Rossi, M. Réjou-Méchain, V. Freycon, A. Fayolle, L. Saint-André, G. Cornu, J. Gérard, J. Sarrailh, J. Flores et al. (2011). 'Environmental filtering of dense-wooded species controls above-ground biomass stored in African moist forests'. In: *Journal of Ecology* 99.4, pp. 981–990. DOI: `10.1111/j.1365-2745.2011.01829.x`.

Grace, J. B., T. M. Anderson, M. D. Smith, E. Seabloom, S. J. Andelman, G. Meche, E. Weiher, L. K. Allain, H. Jutila, M. Sankaran et al. (2007). 'Does species diversity limit productivity in natural grassland communities?’ In: *Ecology Letters* 10.8, pp. 680–689. DOI: `10.1111/j.1461-0248.2007.01058.x`.

Grime, J. P. (1979). *Plant strategies and vegetation processes*. Chichester, UK: John Wiley and Sons.

Hector, A. & R. Bagchi (2007). ‘Biodiversity and ecosystem multifunctionality’. In: *Nature* 448.7150, pp. 188–190. DOI: `10.1038/nature05947`.

Hempson, G. P., S. Archibald & W. J. Bond (2017). ‘The consequences of replacing wildlife with livestock in Africa’. In: *Scientific Reports* 7.1. DOI: `10.1038/s41598-017-17348-4`.

Hengl, T., J. Mendes de Jesus, G. B. M. Heuvelink, M. R. Gonzalez, M. Kilibarda, A. Blagotić, W. Shangguan, M. N. Wright, X. Geng, B. Bauer-Marschallinger et al. (2017). ‘SoilGrids250m: Global gridded soil information based on machine learning’. In: *PLoS ONE* 12, pp. 1–40. DOI: `10.1371/journal.pone.0169748`.

Hill, M. J. & N. P. Hanan, eds. (2011). *Ecosystem function in savannas*. Boca Raton FL, USA: CRC Press. DOI: `10.1201/b10275`.

Hooper, D., J. Coughlan & M. R. Mullen (2008). ‘Structural equation modelling: Guidelines for determining model fit’. In: *Electronic Journal of Business Research Methods* 6, pp. 53–60.

Houghton, R. A., F. Hall & S. J. Goetz (2009). ‘Importance of biomass in the global carbon cycle’. In: *Journal of Geophysical Research* 114, pp. 1–13. DOI: `10.1029/2009JG000935`.

Hsieh, T. C., K. H. Ma & A. Chao (2016). ‘iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers)’. In: *Methods in Ecology and Evolution* 7, pp. 1451–1456. DOI: `10.1111/2041-210X.12613`.

Hu, L. & P. M. Bentler (1999). ‘Cutoff criteria for fit indexes in covariance structure analysis: Conventional criteria versus new alternatives’. In: *Structural Equation Modeling: A Multidisciplinary Journal* 6, pp. 1–55. DOI: `10.1080/10705519909540118`.

Huston, M. A. (2014). ‘Disturbance, productivity, and species diversity: Empiricism vs. logic in ecological theory’. In: *Ecology* 95.9, pp. 2382–2396. DOI: `10.1890/13-1397.1`.

Jax, K. (2005). ‘Function and “functioning” in ecology: what does it mean?’ In: *Oikos* 111.3, pp. 641–648. DOI: `10.1111/j.1600-0706.2005.13851.x`.

Johnson, D. J., W. T. Beaulieu, J. D. Bever & K. Clay (2012). ‘Conspecific Negative Density Dependence and Forest Diversity’. In: *Science* 336.6083, pp. 904–907. DOI: `10.1126/science.1220269`.

Jost, L. (2006). ‘Entropy and diversity’. In: *Oikos* 113.2, pp. 363–375. DOI: `10.1111/j.2006.0030-1299.14714.x`.

Keddy, P. A. (1990). ‘Competitive hierarchies and centrifugal organization in plant communities’. In: *Perspectives on plant competition*. Ed. by J. B. Grace & D. Tilman. San Diego CA, USA: Academic Press, pp. 266–287.

Kraaij, T. & D. Ward (2006). ‘Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa’. In: *Plant Ecology* 186, pp. 235–246. DOI: `10.1007/s11258-006-9125-4`.

Kulmatiski, A. & K. H. Beard (2013). ‘Root niche partitioning among grasses, saplings, and trees measured using a tracer technique’. In: *Oecologia* 171.1, pp. 25–37. DOI: `10.1007/s00442-012-2390-0`.

Lasky, J. R., M. Uriarte, V. K. Boukili, D. L. Erickson, W. J. Kress & R. L. Chazdon (2014). ‘The relationship between tree biodiversity and biomass dynamic changes with tropical forest succession’. In: *Ecology Letters* 17, pp. 1158–1167. DOI: `10.1111/ele.12322`.

Lee, S. Y. (2007). *Structural Equation Modeling: A Bayesian Approach*. New York, USA: Wiley.

Lehmann, C. E. R., T. M. Anderson, M. Sankaran, S. I. Higgins, S. Archibald, W. A. Hoffmann, N. P. Hanan, R. J. Williams, F. R. J., J. Felfili et al. (2014). ‘Savanna vegetation-fire-climate relationships differ among continents’. In: *Science* 343, pp. 548–552. DOI: `10.1126/science.1247355`.

Levick, S. R., G. P. Asner, T. Kennedy-Bowdoin & D. E. Knapp (2009). ‘The relative influence of fire and herbivory on savanna three-dimensional vegetation structure’. In: *Biological Conservation* 142, pp. 1693–1700. DOI: `10.1016/j.biocon.2009.03.004`.

Liang, J., T. W. Crowther, N. Picard, S. Wiser, M. Zhou, G. Alberti, E.-D. Schulze, A. D. McGuire, F. Bozzato, H. Pretzsch et al. (2016). 'Positive biodiversity-productivity relationship predominant in global forests'. In: *Science* 354.6309, aaf8957–aaf8957. DOI: `10.1126/science.aaf8957`.

Loiola, P. P., M. Scherer-Lorenzen & M. A. Batalha (2015). 'The role of environmental filters and functional traits in predicting the root biomass and productivity in savannas and tropical seasonal forests'. In: *Forest Ecology and Management* 342, pp. 49–55. DOI: `10.1016/j.foreco.2015.01.014`.

Mason, N. W. H., F. de Bello, J. Doležal & J. Lepš (2011). 'Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities'. In: *Journal of Ecology* 99.3, pp. 788–796. DOI: `10.1111/j.1365-2745.2011.01801.x`.

Mayaux, P., H. Eva, A. Brink, F. Achard & A. Belward (2008). 'Remote sensing of land-cover and land-use dynamics'. In: *Earth Observation of Global Change: The Role of Satellite Remote Sensing in Monitoring the Global Environment*. Berlin, Germany: Springer-Verlag, pp. 85–108. DOI: `10.1007/978-1-4020-6358-9_5`.

McNicol, I. M., C. M. Ryan, K. G. Dexter, S. M. J. Ball & M. Williams (2018). 'Aboveground carbon storage and its links to stand structure, tree diversity and floristic composition in south-eastern Tanzania'. In: *Ecosystems* 21, pp. 740–754. DOI: `10.1007/s10021-017-0180-6`.

Mensah, S., V. K. Salako & T. Seifert (2020). 'Structural complexity and large-sized trees explain shifting species richness and carbon relationship across vegetation types'. In: *Functional Ecology* 34.8, pp. 1731–1745. DOI: `10.1111/1365-2435.13585`.

Muledi, J. I., D. Bauman, T. Drouet, J. Vleminckx, A. Jacobs, J. Lejoly, P. Meerts & M. N. Shutcha (2017). 'Fine-scale habitats influence tree species assemblage in a miombo forest'. In: *Journal of Plant Ecology* 10, pp. 958–969. DOI: `10.1093/jpe/rtw104`.

Muscolo, A., S. Bagnato, M. Sidari & R. Mercurio (2014). 'A review of the roles of forest canopy gaps'. In: *Journal of Forestry Research* 25, pp. 725–736. DOI: `10.1007/s11676-014-0521-7`.

Mutowo, G. & A. Murwira (2012). 'Relationship between remotely sensed variables and tree species diversity in savanna woodlands of Southern Africa'. In: *International Journal of Remote Sensing* 33, pp. 6378–6402. DOI: `10.1080/01431161.2012.687472`.

Nachtigall, C., U. Kroehne, F. Funke & R. Steyer (2003). '(Why) should we use SEM? Pros and cons of Structural Equation Modeling'. In: *Methods of Psychological Research* 8, pp. 1–22.

Naeem, S., J. E. Duffy & E. Zavaleta (2012). 'The functions of biological diversity in an age of extinction'. In: *Science* 336.6087, pp. 1401–1406. DOI: `10.1126/science.1215855`.

Pan, Y., R. A. Birdsey, J. Fang, R. Houghton, P. E. Kauppi, W. A. Kurz, O. L. Phillips, A. Shvidenko, S. L. Lewis, J. G. Canadell et al. (2011). 'A large and persistent carbon sink in the world's forests'. In: *Science* 333.6045, pp. 988–993. DOI: `10.1126/science.1201609`.

Paquette, A. & C. Messier (2010). 'The effect of biodiversity on tree productivity: from temperate to boreal forests'. In: *Global Ecology and Biogeography* 20.1, pp. 170–180. DOI: `10.1111/j.1466-8238.2010.00592.x`.

Parr, C. L., C. E. R. Lehmann, W. J. Bond, W. A. Hoffmann & A. N. Andersen (2014). 'Tropical grassy biomes: Misunderstood, neglected, and under threat'. In: *Trends in Ecology & Evolution* 29, pp. 205–213. DOI: `10.1016/j.tree.2014.02.004`.

Paul, K. I., J. Larmour, S. A., A. Zerihun, P. Ritson, S. H. Roxburgh, S. Sochacki, T. Lewis, C. V. M. Barton, J. R. England et al. (2019). 'Testing the generality of below-ground biomass allometry across plant functional types'. In: *Forest Ecology and Management* 432, pp. 102–114. DOI: `10.1016/j.foreco.2018.08.043`.

Pennington, R. T., C. E. R. Lehmann & L. M. Rowland (2018). 'Tropical savannas and dry forests'. In: *Current Biology* 28.9, R541–R545. DOI: `10.1016/j.cub.2018.03.014`.

Pichancourt, J., J. Firn, I. Chadès & T. G. Martin (2013). 'Growing biodiverse carbon-rich forests'. In: *Global Change Biology* 20.2, pp. 382–393. DOI: `10.1111/gcb.12345`.

Plas, F. van der (2019). ‘Biodiversity and ecosystem functioning in naturally assembled communities’. In: *Biological Reviews* 94, pp. 1220–1245. DOI: `10.1111/brv.12499`.

Poorter, L., M. T. van der Sande, E. J. M. M. Arets, N. Ascarrunz, B. J. Enquist, B. Finegan, J. C. Licona, M. Martínez-Ramos, L. Mazzei, J. A. Meave et al. (2017). ‘Biodiversity and climate determine the functioning of neotropical forests’. In: *Global Ecology and Biogeography* 26, pp. 1423–1434. DOI: `10.1111/geb.12668`.

Poorter, L., M. T. van der Sande, J. Thompson, E. J. M. M. Arets, A. Alarcòn, J. àlvarez-Sànchez, N. Ascarrunz, P. Balvanera, G. Barajas-Guzmàn, A. Boit et al. (2015). ‘Diversity enhances carbon storage in tropical forests’. In: *Global Ecology and Biogeography* 24, pp. 1314–1328. DOI: `10.1111/geb.12364`.

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: `10.1016/j.foreco.2014.04.027`.

R Core Team (2020). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. Vienna, Austria. URL: `https://www.R-project.org/`.

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: `10.1111/ele.12849`.

Ratnam, J., W. J. Bond, R. J. Fensham, W. A. Hoffmann, S. Archibald, C. E. R. Lehmann, M. T. Anderson, S. I. Higgins & M. Sankaran (2011). ‘When is a ‘forest’ a savanna, and why does it matter?’ In: *Global Ecology and Biogeography* 20, pp. 653–660. DOI: `10.1111/j.1466-8238.2010.00634.x`.

Roberts, D. W. (2019). *labdsv: Ordination and Multivariate Analysis for Ecology*. R package version 2.0-1. URL: `https://CRAN.R-project.org/package=labdsv`.

Rosseel, Y. (2012). ‘lavaan: An R Package for Structural Equation Modeling’. In: *Journal of Statistical Software* 48.2. DOI: `10.18637/jss.v048.i02`. URL: `http://www.jstatsoft.org/v48/i02/`.

Ryan, C. M., R. Pritchard, I. McNicol, M. Owen, J. A. Fisher & C. Lehmann (2016). ‘Ecosystem services from southern African woodlands and their future under global change’. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 371.1703, p. 20150312. DOI: `10.1098/rstb.2015.0312`.

Sande, M. T. van der, L. Poorter, L. Kooistra, P. Balvanera, K. Thonicke, J. Thompson, E. J. M. M. Arets, N. G. Alaniz, L. Jones, F. Mora et al. (2017). ‘Biodiversity in species, traits, and structure determines carbon stocks and uptake in tropical forests’. In: *Biotropica* 49, pp. 593–603. DOI: `10.1111/btp.12453`.

Sankaran, M., J. Ratnam & N. Hanan (2008). ‘Woody cover in African savannas: the role of resources, fire and herbivory’. In: *Global Ecology and Biogeography* 17.2, pp. 236–245. DOI: `10.1111/j.1466-8238.2007.00360.x`.

Scarascia-Mugnozza, G., G. A. Bauer, H. Persson, G. Matteucci & A. Masci (2000). ‘Tree biomass, growth and nutrient pools’. In: *Ecological Studies*. Springer Berlin Heidelberg, pp. 49–62. DOI: `10.1007/978-3-642-57219-7_3`.

Seidel, D., M. Ehbrecht, Y. Dorji, J. Jambay, C. Ammer & P. Annighöfer (2019). ‘Identifying architectural characteristics that determine tree structural complexity’. In: *Trees* 33, pp. 911–919. DOI: `10.1007/s00468-019-01827-4`.

SEOSAW (2020). ‘A network to understand the changing socio-ecology of the southern African woodlands (SEOSAW): Challenges, benefits, and methods’. In: *Plants, People, Planet*. DOI: `10.1002/ppp3.10168`.

Shapiro, A. (1983). ‘Asymptotic distribution theory in the analysis of covariance structures (A unified approach)’. In: *South African Statistical Journal* 17, pp. 33–81.

Shirima, D. D., M. Pfeifer, P. J. Platts, Ø. Totland & S. R. Moe (2015). ‘Interactions between canopy structure and herbaceous biomass along environmental gradients in moist forest and dry miombo woodland of Tanzania'. In: *PLoS ONE* 10, pp. 1–15. DOI: `10.1371/journal.pone.0142784`.

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`.

Smith, B. & J. B. Wilson (1996). 'A consumer's guide to evenness indices'. In: *Oikos* 76, pp. 70–82. DOI: `10.2307/3545749`.

Solbrig, O. T., E. Medina & J. F. Silva (1996). *Biodiversity and Savanna Ecosystem Processes*. Berlin, Germany: Springer-Verlag.

Spawn, S. A., C. C. Sullivan, T. J. Lark & H. K. Gibbs (2020). 'Harmonized global maps of above and belowground biomass carbon density in the year 2010'. In: *Scientific Data* 7.1. DOI: `10.1038/s41597-020-0444-4`.

Srivastava, D. S. & D. S. Vellend (2005). 'Biodiversity-ecosystem function research: Is it relevant to conservation?' In: *Annual Review of Ecology, Evolution, and Systematics* 36.1, pp. 267–294. DOI: `10.1146/annurev.ecolsys.36.102003.152636`.

Staver, A. C., S. Archibald & S. A. Levin (2011). 'The Global Extent and Determinants of Savanna and Forest as Alternative Biome States'. In: *Science* 334.6053, pp. 230–232. DOI: `10.1126/science.1210465`.

Staver, A. C., W. J. Bond, W. D. Stock, S. J. van Rensburg & M. S. Waldram (2009). 'Browsing and fire interact to suppress tree density in an African savanna'. In: *Ecological Applications* 19, pp. 1909–1919. DOI: `10.1890/08-1907.1`.

Stegen, J. C., N. G. Swenson, B. J. Enquist, E. P. White, O. L. Phillips, P. M. Jørgensen, M. D. Weiser, A. M. Mendoza & P. N. Vargas (2011). 'Variation in above-ground forest biomass across broad climatic gradients'. In: *Global Ecology and Biogeography* 20, pp. 744–754. DOI: `10.1111/j.1466-8238.2010.00645.x`.

Tedersoo, L., L. Laanisto, S. Rahimlou, A. Toussaint, T. Hallikma & M. Pärtel (2018). 'Global database of plants with root-symbiotic nitrogen fixation: NodDB'. In: *Journal of Vegetation Science* 29.3, pp. 560–568. DOI: `10.1111/jvs.12627`.

Tilman, D. & J. A. Downing (1994). 'Biodiversity and stability in grasslands'. In: *Nature* 367, pp. 363–365. DOI: `10.1038/367363a0`.

Tilman, D., F. Isbell & J. M. Cowles (2014). 'Biodiversity and ecosystem functioning'. In: *Annual Review of Ecology, Evolution, and Systematics* 45, pp. 471–493. DOI: `10.1146/annurev-ecolsys-120213-091917`.

Timberlake, J., E. Chidumayo & L. Sawadogo (2010). 'Distribution and characteristics of African dry forests and woodlands'. In: *The Dry Forests and Woodlands of Africa: Managing for Products and Services*. London, UK: EarthScan, pp. 11–42.

Tobner, C. M., A. Paquette, D. Gravel, P. B. Reich, L. J. Williams & C. Messier (2016). 'Functional identity is the main driver of diversity effects in young tree communities'. In: *Ecology Letters* 19, pp. 638–647. DOI: `10.1111/ele.12600`.

Vilà, M., P. Inchausti, J. Vayreda, O. Barrantes, C. Gracia, J. J. Ibáñez & T. Mata (n.d.). 'Confounding Factors in the Observational Productivity-Diversity Relationship in Forests'. In: *Forest Diversity and Function*. Springer-Verlag, pp. 65–86. DOI: `10.1007/3-540-26599-6_4`.

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`.

Zanne, A. E., G. Lopez-Gonzalez, D. A. Coomes, J. Ilic, S. Jansen, S. L. Lewis, R. B. Miller, N. G. Swenson, M. C. Wiemann & J. Chave (2009). *Global wood density database*. http://hdl.handle.net/10255/dryad.235. Dryad.

3.6 Supplementary material

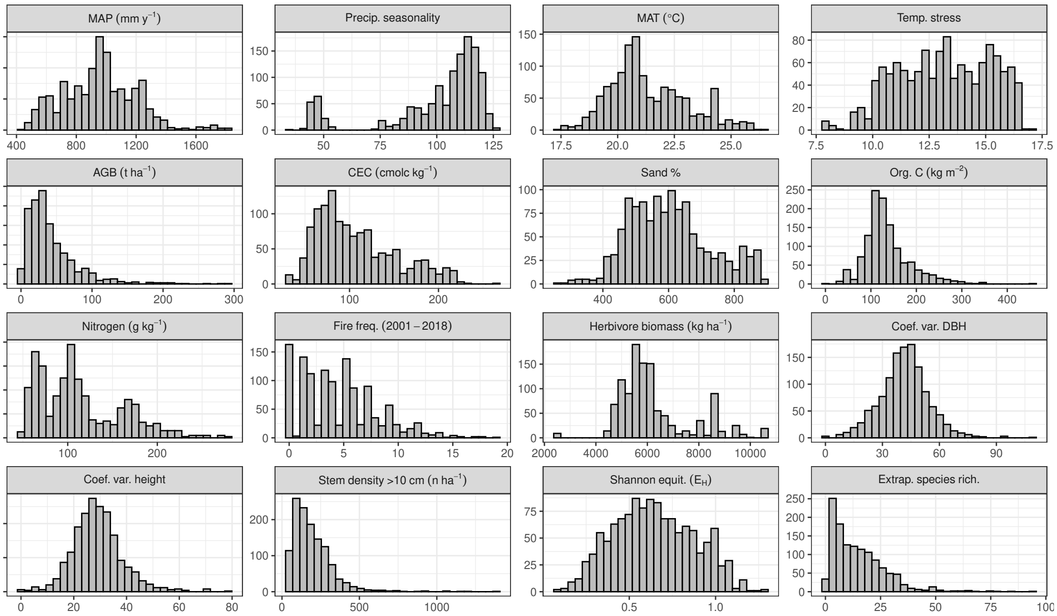


Figure 3.S1: Histograms of raw untransformed observed variables used in final analyses.

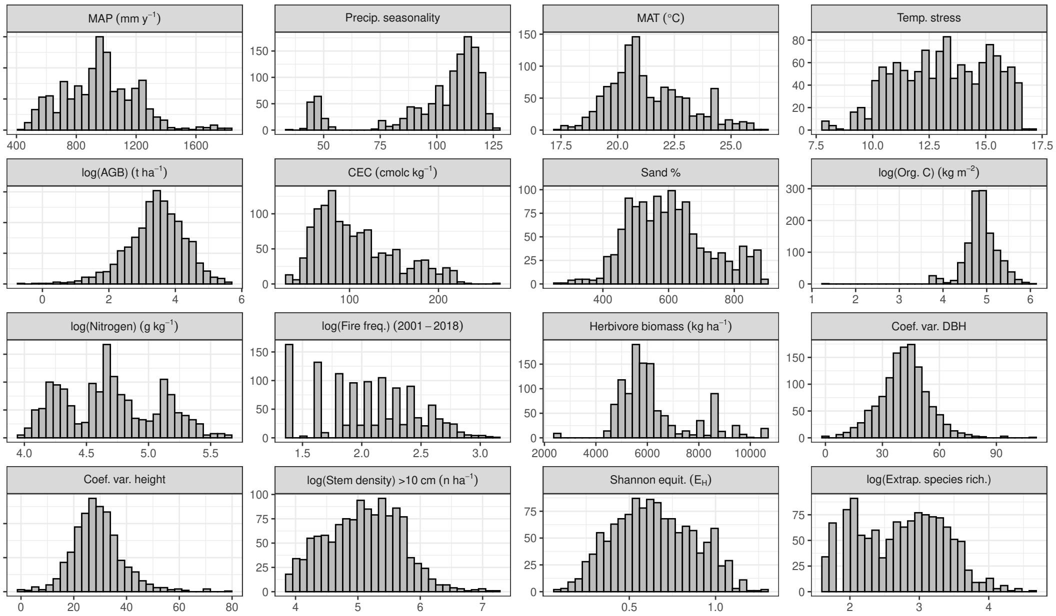


Figure 3.S2: Histograms of observed variables transformed to achieve a normal frequency distribution.

Table 3.S1: Correlation fit statistics among observed variables used in path analysis. Showing the Pearson correlation coefficient (*r*), correlation confidence interval upper and lower bounds, number of plots used in the correlation (n), and the p-value of the correlation (Prob.).

X	Y	*r*	Lower	Upper	N	Prob.
Soil CEC	Soil C	0.26	0.21	0.31	1239	<0.01
Soil N	Soil C	0.85	0.82	0.87	644	<0.01
Fire freq.	Soil C	–0.07	–0.13	–0.01	1239	<0.05
MAP	Soil C	0.51	0.46	0.55	1239	<0.01
Precip. seas.	Soil C	–0.56	–0.60	–0.52	1239	<0.01
Temp. stress	Soil C	–0.63	–0.67	–0.60	1239	<0.01
Sand %	Soil C	–0.57	–0.61	–0.54	1239	<0.01
Species rich.	Soil C	0.25	0.20	0.30	1239	<0.01
Shannon equit.	Soil C	0.23	0.18	0.28	1239	<0.01
Height CV	Soil C	0.23	0.17	0.29	981	<0.01
DBH CV	Soil C	0.16	0.11	0.22	1237	<0.01
Stem density	Soil C	0.07	0.02	0.13	1239	<0.05
AGB	Soil C	0.26	0.21	0.32	1239	<0.01
Soil N	Soil CEC	0.44	0.37	0.50	644	<0.01
Fire freq.	Soil CEC	–0.47	–0.51	–0.43	1239	<0.01
MAP	Soil CEC	–0.28	–0.33	–0.22	1239	<0.01
Precip. seas.	Soil CEC	–0.71	–0.73	–0.68	1239	<0.01
Temp. stress	Soil CEC	–0.25	–0.30	–0.20	1239	<0.01
Sand %	Soil CEC	–0.21	–0.27	–0.16	1239	<0.01
Species rich.	Soil CEC	–0.38	–0.43	–0.33	1239	<0.01
Shannon equit.	Soil CEC	–0.09	–0.15	–0.04	1239	<0.01
Height CV	Soil CEC	–0.11	–0.17	–0.05	981	<0.01
DBH CV	Soil CEC	–0.01	–0.07	0.04	1237	0.62
Stem density	Soil CEC	–0.02	–0.08	0.03	1239	0.43
AGB	Soil CEC	–0.04	–0.09	0.02	1239	0.17
Fire freq.	Soil N	–0.25	–0.32	–0.18	644	<0.01
MAP	Soil N	0.37	0.30	0.44	644	<0.01
Precip. seas.	Soil N	–0.76	–0.79	–0.73	644	<0.01

Continued overleaf

X	Y	*r*	Lower	Upper	N	Prob.
Temp. stress	Soil N	–0.80	–0.82	–0.77	644	<0.01
Sand %	Soil N	–0.66	–0.70	–0.61	644	<0.01
Species rich.	Soil N	0.44	0.38	0.50	644	<0.01
Shannon equit.	Soil N	0.35	0.28	0.42	644	<0.01
Height CV	Soil N	0.27	0.18	0.36	386	<0.01
DBH CV	Soil N	0.26	0.18	0.33	642	<0.01
Stem density	Soil N	–0.03	–0.11	0.05	644	0.47
AGB	Soil N	0.31	0.24	0.38	644	<0.01
MAP	Fire freq.	0.37	0.32	0.42	1239	<0.01
Precip. seas.	Fire freq.	0.36	0.31	0.41	1239	<0.01
Temp. stress	Fire freq.	0.21	0.16	0.26	1239	<0.01
Sand %	Fire freq.	0.06	0.00	0.11	1239	<0.05
Species rich.	Fire freq.	0.38	0.34	0.43	1239	<0.01
Shannon equit.	Fire freq.	0.12	0.07	0.18	1239	<0.01
Height CV	Fire freq.	0.15	0.09	0.22	981	<0.01
DBH CV	Fire freq.	0.12	0.07	0.18	1237	<0.01
Stem density	Fire freq.	–0.02	–0.07	0.04	1239	0.52
AGB	Fire freq.	0.03	–0.03	0.08	1239	0.33
Precip. seas.	MAP	–0.07	–0.12	–0.01	1239	<0.05
Temp. stress	MAP	–0.49	–0.53	–0.44	1239	<0.01
Sand %	MAP	–0.33	–0.38	–0.28	1239	<0.01
Species rich.	MAP	0.41	0.36	0.45	1239	<0.01
Shannon equit.	MAP	0.15	0.10	0.20	1239	<0.01
Height CV	MAP	0.25	0.19	0.30	981	<0.01
DBH CV	MAP	0.11	0.06	0.17	1237	<0.01
Stem density	MAP	0.02	–0.03	0.08	1239	0.47
AGB	MAP	0.24	0.18	0.29	1239	<0.01
Temp. stress	Precip. seas.	0.50	0.45	0.54	1239	<0.01
Sand %	Precip. seas.	0.31	0.26	0.36	1239	<0.01
Species rich.	Precip. seas.	0.12	0.07	0.18	1239	<0.01
Shannon equit.	Precip. seas.	–0.07	–0.12	–0.01	1239	<0.05
Height CV	Precip. seas.	–0.05	–0.11	0.01	981	0.11
DBH CV	Precip. seas.	–0.10	–0.15	–0.04	1237	<0.01

Continued overleaf

X	Y	*r*	Lower	Upper	N	Prob.
Stem density	Precip. seas.	–0.04	–0.10	0.01	1239	0.12
AGB	Precip. seas.	–0.18	–0.23	–0.13	1239	<0.01
Sand %	Temp. stress	0.30	0.25	0.35	1239	<0.01
Species rich.	Temp. stress	–0.13	–0.18	–0.07	1239	<0.01
Shannon equit.	Temp. stress	–0.13	–0.18	–0.07	1239	<0.01
Height CV	Temp. stress	–0.14	–0.20	–0.08	981	<0.01
DBH CV	Temp. stress	–0.04	–0.10	0.01	1237	0.12
Stem density	Temp. stress	0.03	–0.02	0.09	1239	0.27
AGB	Temp. stress	–0.17	–0.22	–0.11	1239	<0.01
Species rich.	Sand %	–0.27	–0.32	–0.22	1239	<0.01
Shannon equit.	Sand %	–0.21	–0.26	–0.16	1239	<0.01
Height CV	Sand %	–0.24	–0.30	–0.18	981	<0.01
DBH CV	Sand %	–0.16	–0.21	–0.10	1237	<0.01
Stem density	Sand %	–0.14	–0.19	–0.08	1239	<0.01
AGB	Sand %	–0.22	–0.27	–0.16	1239	<0.01
Shannon equit.	Species rich.	0.60	0.56	0.63	1249	<0.01
Height CV	Species rich.	0.31	0.25	0.36	981	<0.01
DBH CV	Species rich.	0.32	0.26	0.36	1247	<0.01
Stem density	Species rich.	0.23	0.17	0.28	1249	<0.01
AGB	Species rich.	0.33	0.28	0.38	1249	<0.01
Height CV	Shannon equit.	0.14	0.07	0.20	981	<0.01
DBH CV	Shannon equit.	0.23	0.17	0.28	1247	<0.01
Stem density	Shannon equit.	0.41	0.36	0.45	1249	<0.01
AGB	Shannon equit.	0.38	0.33	0.42	1249	<0.01
DBH CV	Height CV	0.49	0.44	0.54	981	<0.01
Stem density	Height CV	0.00	–0.06	0.06	981	0.95
AGB	Height CV	0.24	0.18	0.30	981	<0.01
Stem density	DBH CV	0.11	0.05	0.16	1247	<0.01
AGB	DBH CV	0.44	0.40	0.49	1247	<0.01
AGB	Stem density	0.57	0.53	0.61	1249	<0.01

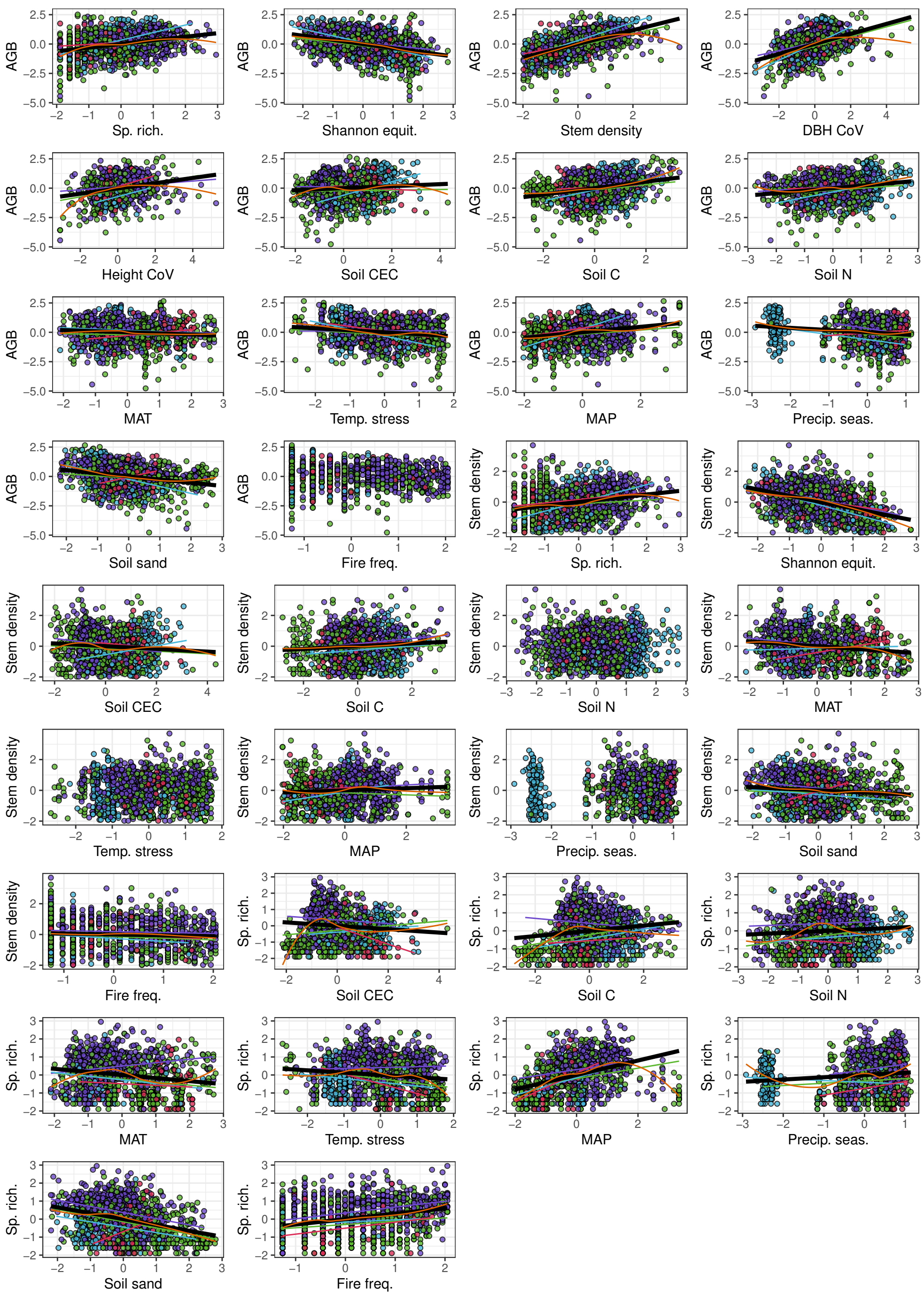


Figure 3.S3: Bivariate scatter plots for each variable used in the SEMs (Structural Equation Models), based on hypothesised causality. Points are coloured by vegetation type: green = Baikiaea, purple = Core miombo, blue = ex-Acacia, red = Mopane. The black line combines all vegetation types in a single linear regression, while loess trend lines are fitted for each vegetation type, separately. An orange loess trend line is fitted for all the data. All data is standardised to a mean of zero and a standard deviation of one. Variables are transformed where it was appropriate for analysis.

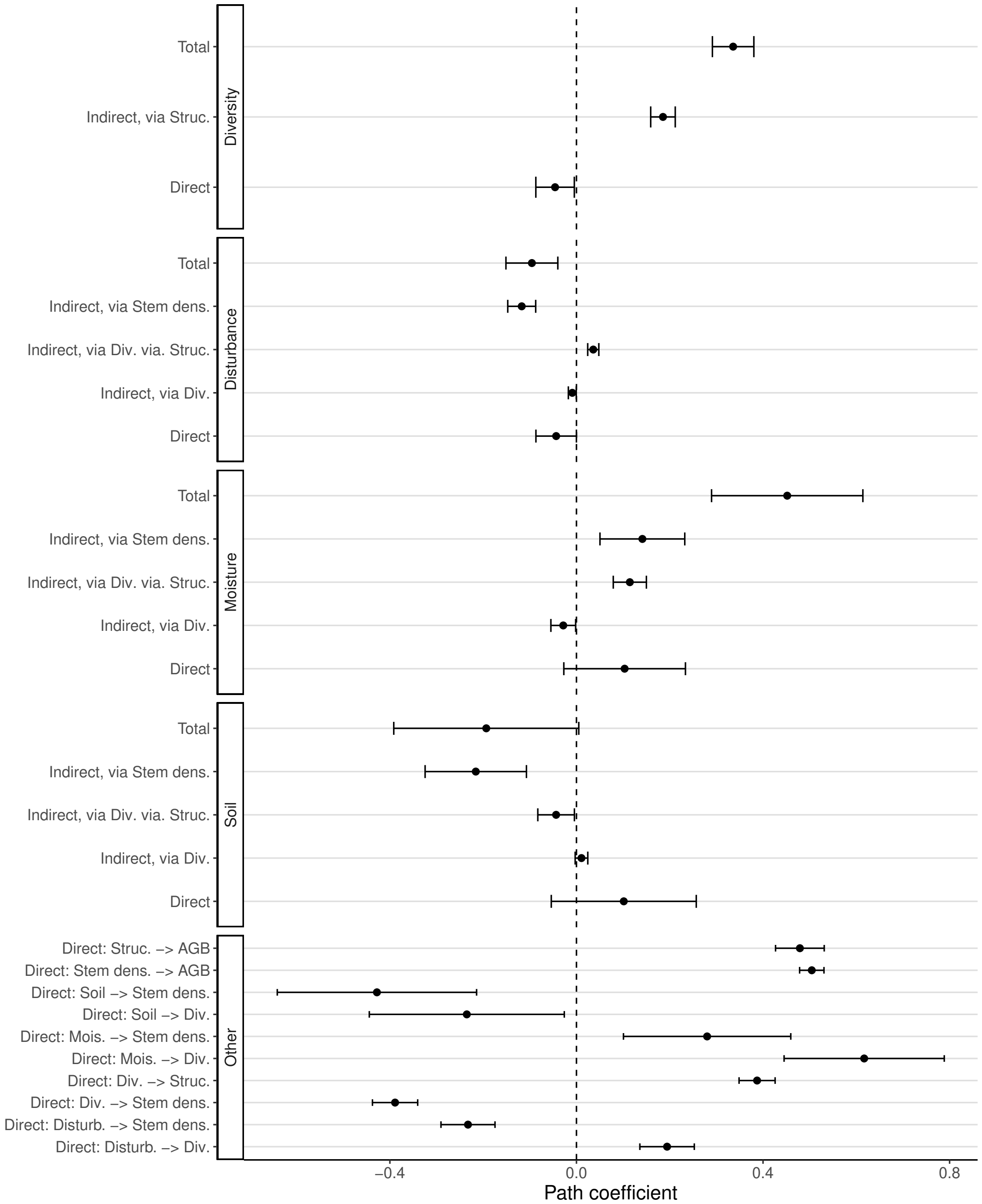


Figure 3.S4: Unstandardised path coefficients for the full model including tree species diversity, environmental covariates and stem density. Path coefficients are ±1 standard error. Path coefficients where the interval (standard error) does not overlap zero are considered to be significant effects.

Chapter 4

Diversity and vegetation type mediates land-surface phenology in Zambian deciduous woodlands

The following chapter has been prepared for submission to *Biotropica*.

Authors: John L. Godlee[1], Casey M. Ryan[1], Abel Siampale[2], Kyle G. Dexter[1,3]

1. School of GeoSciences, University of Edinburgh, Edinburgh, EH9 3FF, United Kingdom
2. Ministry of Lands and Natural Resources, Cairo Road, Lusaka, Zambia
3. Royal Botanic Garden Edinburgh, Edinburgh, EH3 5LR, United Kingdom

Author Contributions: JLG conceived the study, conducted the analysis, and wrote the first draft of the manuscript. AS coordinated plot data collection in Zambia, and initial data management. All authors contributed to manuscript revisions.

Abstract

Land-surface phenology is a key determinant of ecosystem function across the dry tropics, and measures of land-surface phenology are routinely included in earth system models to constrain estimates of productivity. Future variation in phenology can be predicted to some extent from climatic variables, but our understanding of how ecosystem structure and composition mediates variation in phenology is lacking, commonly limited to coarse plant functional types. We combined a dense plot network of 617 sites across deciduous Zambian woodlands with remotely sensed land-surface phenology metrics to investigate the role of tree species diversity, composition, and tree size on phenological patterns, including the phenomenon of pre-rain green-up. We found that tree species diversity caused earlier pre-rain green-up across all studied vegetation types, and caused longer total growing season length in drier woodlands. We found variation among miombo and non-miombo vegetation types in their phenological patterns and biotic drivers of phenology, with Combretaceae-dominated woodlands exhibiting a positive effect of evenness on season length, while miombo woodlands exhibited a negative effect. Finally, we found that while species richness had positive effects on phenological metrics, species evenness had negative effects, suggesting that land-surface phenology is driven by a few dominant canopy-forming tree species in dry tropical woodlands. The study clarifies the role of biotic diversity as a determinant of ecosystem function, and offers new insights into the factors which determine land-surface phenology across the dry tropics, which could improve the accuracy of earth system models of the carbon cycle.

4.1 Introduction

The seasonal timing and duration of foliage production (land-surface phenology) is a key mediator of land-atmosphere exchanges. Foliage forms the primary interface between plants, the atmosphere and sunlight (Gu et al., 2003; Penuelas et al., 2009), and land-surface phenology plays an important role in regulating global carbon, water and nitrogen cycles (Richardson et al., 2013). Carbon-cycling models routinely incorporate land-surface phenological processes, most commonly through remotely-sensed data products (e.g. Bloom et al. 2016), but our understanding of the ecological mechanisms which determine these phenological processes remains under-developed (Whitley et al., 2017). This limits our ability to predict how land-surface phenology will respond to climate and biodiversity change, and how these responses will vary among species and vegetation types (Xia et al., 2015).

At regional scales, land-surface phenology can be predicted using only climatic factors, namely precipitation, diurnal temperature, and light environment (Adole et al., 2018b), but significant local variation exists within biomes in the timing of leaf production which cannot be attributed solely to abiotic environment (Stöckli et al., 2011). It has been repeatedly suggested that the diversity, composition, and demographic structure of plant species plays a role in determining how ecosystems respond to abiotic cues that may drive phenology (Adole et al., 2018a; Jeganathan et al., 2014; Fuller, 1999), owing to differences in life history strategy among species and demographic groups, but current implementation of biotic variation in earth system models is often limited to coarse plant functional types, which are unable to represent the wide variation in phenological patterns observed at local scales (Scheiter et al., 2013; Pavlick et al., 2013).

Across the dry tropics, seasonal oscillations in water availability produce strong cycles of foliage production (Chidumayo, 2001; Dahlin et al., 2016), with knock-on effects for ecosystem function. The phenomenon of pre-rain green-up seen in some tree species within the dry tropics serves as a striking example of adaptation to seasonal variation in water availability (Ryan et al., 2017). Conservative species, i.e. slower growing, with robust leaves and denser wood, may initiate leaf production (green-up) before the wet season has commenced. More acquisitive species and juveniles however, tend to green-up during the wet season creating a dense leaf-flush during the mid-season peak of growth and dropping their leaves earlier as the wet season ends (Lasky et al., 2016). Both strategies have associated costs and benefits which allow coexistence of species exhibiting a range of phenological syndromes along this spectrum. While conservative species gain a competitive advantage from having fully emerged leaves when the wet season starts, they must also invest heavily in deep root architecture to access dry season groundwater reserves in order to produce foliage during the dry season. Similarly, while acquisitive species minimise the risk of hydraulic failure and mortality by only producing leaves when conditions are amenable, they forfeit growing season length. It has been suggested that variation in phenological strategy among tree species is one mechanism by which increased species diversity increases resilience to drought and maximises productivity in water-limited woodland ecosystems (Stan & Sanchez-Azofeifa, 2019; Morellato et al., 2016). By providing functional redundancy within the ecosystem, leaf production can be maintained under a wider range of conditions, therefore maximising long-term productivity.

In addition to determining productivity, variation in leaf phenology also affects broader ecosystem function. Woodlands with a longer tree growth period support a greater diversity and abundance of wildlife, particularly birds, but also browsing mammals and invertebrates (Cole et al., 2015; Araujo et al., 2017; Morellato et al., 2016; Ogutu et al., 2013). As climate change increases the frequency and severity of drought in water-limited woodlands, it is feared that this will result in severe negative consequences for biodiversity (Bale et al., 2002). The periods of green-up and senescence which bookend the growing season are key times for invertebrate reproduction (Prather et al., 2012) and herbivore browsing activity (Velasque & Del-Claro, 2016; Morellato et al., 2016). Pre-rain green-up provides a valuable source of moisture and nutrients before the wet season, and can moderate the understorey microclimate, increasing humidity, reducing UV exposure, moderating diurnal oscillations in temperature, and reducing ecophysiological stress which otherwise can lead to mortality during the dry season. Additionally, a slower rate of green-up caused by tree species greening at different times, i.e. reduced synchronicity, provides an extended period of bud-burst, maintaining the important food source of nutrient rich young leaves for longer. Thus, understanding the determinants of seasonal patterns of tree leaf production in dry deciduous woodlands can provide valuable information on spatial variation in their vulnerability to climate change, and help to model the contribution of these woodlands to earth system fluxes under climate change.

In this study we investigated how tree species diversity, composition, and demographic structure influence three key measurable aspects of the tree phenological cycle of dry tropical woodlands: (1) the lag time between green-up/senescence and the start/end of the wet season, (2) the rates of greening and senescence at the start and end of the seasonal growth phase, and (3) the overall length of the growing period. We hypothesise that: (H_1) sites with greater species diversity will exhibit a longer growing season and greater cumulative green-ness over the course of the growing season, due to a higher diversity of phenological strategies, including timing of foliage production. Additionally, we hypothesise that: (H_2) in sites with greater species diversity the start of the growing season will occur earlier with respect to the onset of rain due to an increased likelihood of containing a species which can green-up early, and that (H_3) due to variation among species in phenological strategy and minimum water requirement, sites with greater tree species diversity will exhibit slower rates of greening and senescence as different species green-up and senesce at different times. We further hypothesise that: (H_4) irrespective of species diversity, variation in tree species composition and vegetation type will cause variation in the phenological metrics outlined above. Finally, we hypothesise that: (H_5) sites with larger trees will exhibit earlier pre-rain green-up and later senescence, under the assumption that large trees can better access resilient deep groundwater reserves outside of the wet season.

4.2 Materials and methods

4.2.1 Plot data

We used data on tree species diversity and composition across 617 sites from the Zambian Integrated Land Use Assessment Phase II (ILUA-II), conducted in 2014 (Mukosha & Siampale, 2009; Pelletier et al., 2018). Each site consisted of four 20×50 m (0.1 ha) plots positioned in a square around a central point, with a distance of 500 m between each plot (Figure 4.2). The original census contained 993 sites, which was filtered in order to define study bounds and to ensure data quality. Only sites with $\geq$50 stems ha^{-1} $\geq$10 cm DBH (Diameter at Breast Height) were included in the analysis, to ensure all sites represented woodlands rather than ‘grassy savanna’, which is considered a separate biome with different species composition and ecosystem processes governing phenology (Parr et al., 2014). Sites dominated by non-native tree species ($\geq$50% of individuals), e.g. *Pinus* spp. and *Eucalyptus* spp. were excluded, as these species may exhibit atypical patterns of foliage production (Broadhead et al., 2003). Of the 56634 trees recorded, 90.3% were identified to species, 1.9% were identified to genus only, 0.1% were identified to family only, and 7.7% could not be identified at all. There were no significant correlations between the number of trees identified per site and any of the phenological metrics, diversity or structural variables used in analyses.

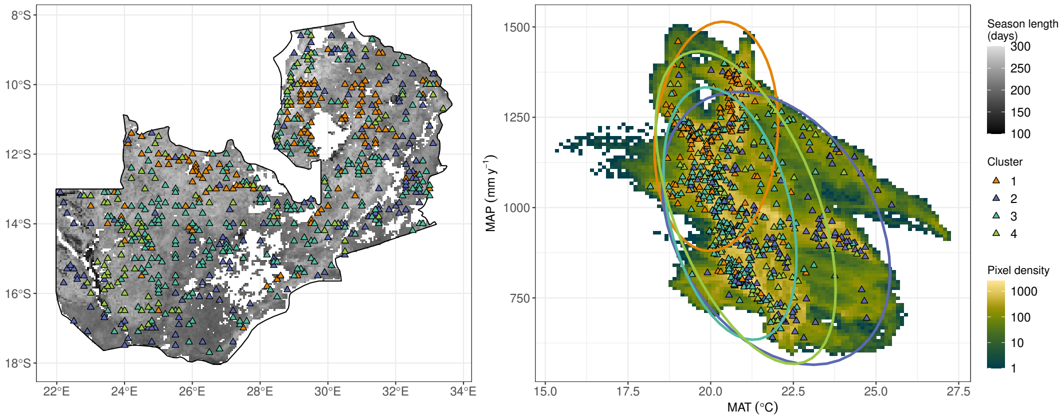


Figure 4.1: Distribution of study sites, within Zambia (left), and in climate space (right). Sites are shown as triangles, each consisting of four plots, coloured according to vegetation type cluster. Zambia is shaded according to growing season length, estimated by the MODIS VIPPHEN-EVI2 product, at 0.05° spatial resolution (Didan & Barreto, 2016). The growing season length layer is masked by the MODIS MCD12Q1 land cover map from 2015 (Friedl & Sulla-Menashe, 2019), using the International Geosphere-Biosphere Programme (IGBP) classification to remove all pixels occurring in wetlands, croplands, water bodies, and urban areas. Climate space is represented by Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP), extracted from the WorldClim dataset at 30 arc second resolution, between 1970 and 2000 (Fick & Hijmans, 2017). The shaded area in the right panel shows the climate space of Zambia, showing the density of pixels for given values of MAT and MAP. The ellipses in the right panel show the 95% confidence interval for the climate space of each site.

Table 4.1: Climatic information and Dufrêne-Legendre indicator species analysis for the vegetation type clusters identified using the Ward algorithm, based on basal area weighted species abundances. The three species per cluster with the highest indicator values are shown along with other key statistics for each cluster. MAP (Mean Annual Precipitation) and dT (Diurnal temperature range) are reported as the mean and 1 standard deviation in parentheses. Species richness is reported as the median and the interquartile range in parentheses.

Cluster	N sites	Richness	MAP	Diurnal dT	Species	Indicator value
1	134	17(7)	1176(156)	13(1.5)	*Brachystegia longifolia*	0.397
					Uapaca kirkiana	0.390
					Marquesia macroura	0.285
2	144	14(5)	955(173)	14(1.6)	*Combretum molle*	0.258
					Lannea discolor	0.228
					Combretum zeyheri	0.214
3	243	17(6)	977(158)	14(1.5)	*Julbernardia paniculata*	0.559
					Brachystegia boehmii	0.540
					Pseudolachnostylis maprouneifolia	0.226
4	96	14(6)	1012(186)	14(1.7)	*Brachystegia spiciformis*	0.582
					Cryptosepalum exfoliatum	0.285
					Guibourtia coleosperma	0.281

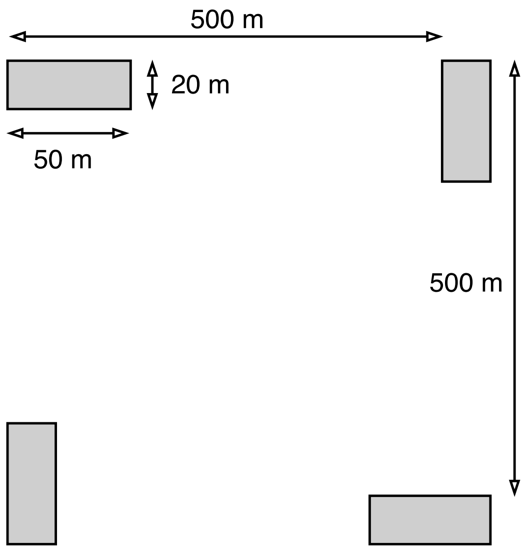


Figure 4.2: Schematic diagram of plot layout within a site. Each 20×50 m (0.1 ha) plot is shaded grey. Note that the plot dimensions are not to scale.

Within each plot, the species of all trees with at least one stem ≥10 cm DBH were recorded. Plot data were aggregated to the site level for analyses to avoid pseudo-replication, and to link with the more spatially coarse phenology data. Tree species composition varied little among the four plots within a site, and were treated as representative of the woodland in the local area. Using the Bray-Curtis dissimilarity index on species basal area data (Faith et al., 1987), we calculated that the mean pairwise compositional distance between plots within a site was lower than the mean compositional distance across all pairs of plots in 92% of cases.

4.2.2 Plot data analysis

To classify variation in tree species composition we used agglomerative hierarchical clustering on species basal area data (Kreft & Jetz, 2010; Fayolle et al., 2014). To guard against sensitivity to rare individuals, which can preclude meaningful cluster delineation across such a large species compositional range, we excluded species with less than five records. We used Ward's algorithm to define clusters (Murtagh & Legendre, 2014), based on the Bray-Curtis distance between pairs of sites. We determined the optimal number of clusters by maximising the mean silhouette width among clusters (Rousseeuw, 1987).

Vegetation type clusters were used later as interaction terms in linear models. We described the vegetation types represented by each of the clusters using a Dufrêne-Legendre indicator species analysis (Dufrêne & Legendre, 1997). Four vegetation type clusters were identified during hierarchical clustering. The silhouette value of the clustering algorithm reached 0.59.

To describe the species diversity of each site, we calculated the Shannon-Wiener index (H') from species basal area rather than individual abundance, as a measure of species diversity effectively weighted by a species' contribution to canopy occupancy and thus by contribution to the phenological signal. H' was transformed to the first order numbers-equivalent (${}^1D$) of H', calculated as $e^{H'}$ (Jost, 2007). We use ${}^1D$ as the primary measure of species diversity in our statistical models, and is subsequently referred to as species diversity. Additionally, we calculated a separate measure of abundance evenness, using the Shannon Equitability index ($E_{H'}$) (Smith & Wilson, 1996). $E_{H'}$ was calculated as the ratio of basal area Shannon-Wiener diversity index to the natural log of total basal area per site. To describe average tree size, we calculated the quadratic mean of stem diameters per site (Curtis & Marshall, 2000). The quadratic mean gives more weight to large trees and is thus more appropriate for our use, where we are interested in the contribution of large trees to land-surface phenology.

4.2.3 Land-surface phenology data

To quantify phenology at each site, we used the MODIS MOD13Q1 satellite data product at 250 m resolution (Didan, 2015). The MOD13Q1 product provides an Enhanced Vegetation Index (EVI) time series at 16 day intervals. EVI is widely used as a measure of vegetation growth and the cumulative sum of EVI is well-correlated with Gross Primary Productivity (GPP), thus providing a measure of land-surface phenology that is relevant to carbon cycling (Sjöström et al., 2011). We used all scenes from January 2010 to December 2020 with less than 20% cloud cover covering the study area. All sites were determined to have a single annual growing season according to the MODIS VIPPHEN product (Didan & Barreto, 2016), which assigns pixels (0.05°, 5.55 km at equator) up to three growing seasons per year. We stacked yearly data between 2010 and 2020 and fit a General Additive Model (GAM) to produce an average EVI curve

(Figure 4.3). We estimated the start and end of the growing season using first derivatives of the GAM. The start of the growing season was identified as the first day where the model slope exceeds half of the maximum positive model slope for a continuous period of 20 or more days, using only backwards looking data, following White et al. (2009). Similarly, we defined the end of the growing season as the final day of the latest 20 day period where the GAM slope meets or exceeds half of the maximum negative slope. We estimated the length of the growing season as the number of days between the start and end of the growing season. We calculated cumulative EVI as the area under the EVI curve during the growing season, and is reported in the results divided by 1e+05, to put it on a similar scale to other variables. We estimated the green-up rate as the slope of a linear model across EVI values between the start of the growing season and the point at which the slope reduces below half of the maximum positive slope. Similarly the senescence rate was estimated as the slope of a linear model between the latest point where the slope of decrease fell below half of the maximum negative slope and the end of the growing season. We validated our calculations of cumulative EVI, mean annual EVI, growing season length, season start date, season end date, green-up rate and senescence rate with calculations made by the MODIS VIPPHEN product with linear models comparing the two datasets across our study sites (Figure 4.S1, Table 4.S1). We chose not to use the MODIS VIPPHEN product directly due to its more coarse spatial resolution (0.05°, 5.55 km at equator).

Precipitation data were gathered using the "GPM IMERG Final Precipitation L3 1 day V06" dataset, which has a pixel size of 0.1°(11.1 km at the equator) (Huffman et al., 2015), between 2010 and 2020. Daily total precipitation was separated into three periods: precipitation during the growing season (wet season precipitation), precipitation in the 90 day period before the onset of the growing season (pre-green-up precipitation), and precipitation in 90 day period before the onset of senescence at the end of the growing season (pre-senescence precipitation). Wet season limits were defined as for the EVI data, using the first derivative of a GAM to create a curve for each site using stacked yearly precipitation data, from which we estimated the half-maximum positive and negative slope to identify where the GAM model exceeded these slope thresholds for a consistent period of 20 days or more. Mean diurnal temperature range (Diurnal dT) was calculated as the mean of monthly temperature range from the WorldClim database, using the BioClim variables, with a pixel size of 30 arc seconds (926 m at the equator) (Fick & Hijmans, 2017), averaged across all years of available data (1970-2000).

We calculated the lag between the onset of the growing season and the onset of the wet season as the difference between these two dates. We performed a similar calculation to estimate the lag between the end of the growing season and the end of the wet season. These two metrics are referred to as “green-up lag” and “senescence lag” hereafter. To aid interpretation, we reversed the sign of the green-up lag measurements, so that larger values indicate earlier pre-rain green-up.

4.2.4 Statistical modelling

We used multivariate linear models to assess the role of tree species diversity and woodland structure on each phenological metric. We defined a maximal model structure including the explanatory variables of species diversity, evenness, and tree size alongside climatic variables shown by previous studies to strongly influence land-surface phenology. We included interaction terms of species diversity, species evenness, and tree size with vegetation type. The maximal model was compared to models with different subsets of explanatory variables, using the model log likelihood, AIC (Akaike Information Criteria), and adjusted R^2 values for each model, to determine which combination of explanatory variables and their interactions with vegetation type best explained each phenological metric. Where two similar models were within 2 AIC points of each other, the model with fewer terms was chosen as the best model, to maximise model parsimony. Explanatory variables in each model were transformed to achieve normality where necessary and standardised to Z-scores prior to modelling to allow comparison of slope coefficients within a given model.

We used the `ggeffects` package to estimate the marginal means of the effects of species diversity, species evenness, and tree size on each phenological metric among vegetation types, where those terms appeared in the best model identified during model selection (Lüdecke, 2018). Estimating marginal means entails generating model predictions across values of a focal variable, while holding non-focal variables constant at their reference value.

To describe variation in land-surface phenology within and among vegetation

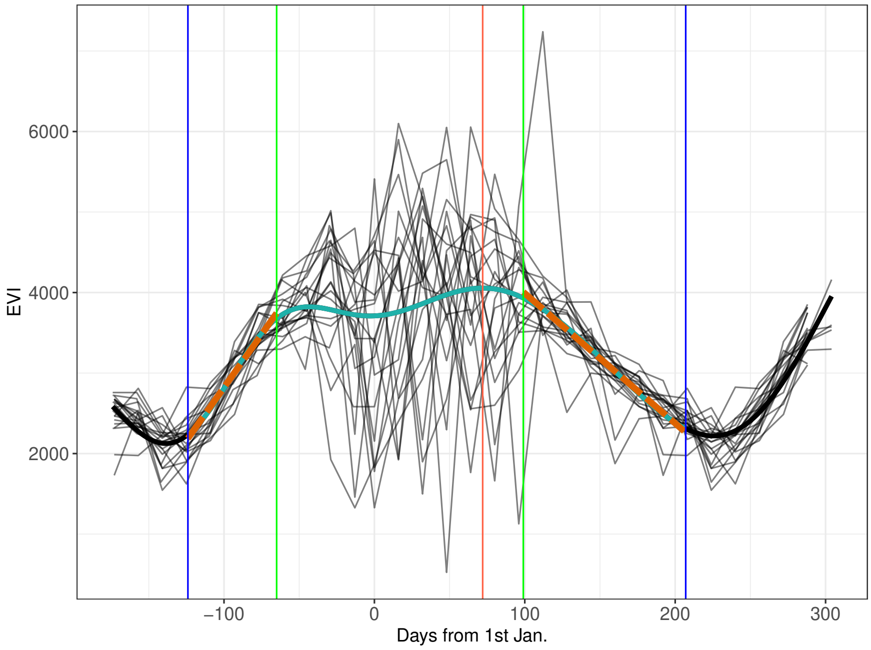


Figure 4.3: Example EVI time series, demonstrating the metrics derived from it. Thin black lines show the raw EVI time series, with one line for each annual growing season. The thick cyan line shows the GAM fit. The blue vertical lines show the minima which bound the growing season. The green vertical lines show the end of the green-up period and start of the senescence period, respectively. The red vertical line shows the maximum EVI value reached within the growing season. The shaded cyan area of the GAM fit shows the growing season, as defined by the first derivative of the GAM curve. The two orange dashed lines are linear regressions predicting the green-up rate and senescence rate at the start and end of the growing season, respectively. Note that while the raw EVI time series fluctuate greatly around the middle of the growing season, mostly due to cloud cover, the GAM fit effectively smooths this variation to estimate the average EVI over the 10 years of data.

clusters we conducted a simple MANOVA using the phenological metrics as response variables, followed by post-hoc Tukey's tests between each pairwise combination of vegetation clusters per phenological metric, to test whether vegetation clusters differed significantly in their land-surface phenology. We also visually compared the mean EVI GAM fits for each cluster within the growing season. All statistical analyses were conducted in R version 4.1.0 (R Core Team, 2020).

4.3 Results

Our models effectively predicted cumulative EVI, season length, green-up lag, and green-up rate, while senescence lag and senescence rate were poorly constrained even in the best fitting models. Nevertheless, all models were of better quality than a naive model including only mean annual precipitation and mean annual diurnal temperature range (Table 4.2). Model selection showed that both tree species diversity and evenness were significant predictors of cumulative EVI, growing season length, and green-up lag, while senescence lag, senescence rate, and green-up rate were better explained by climate only (Figure 4.5). Despite the 'best' model for senescence lag including diversity as an explanatory variable, the slope of this effect was negligible, with a wide standard error, and the model itself only explained 11%.

As expected (H_1), species diversity and wet season precipitation both had positive significant effects on cumulative EVI and growing season length. In contrast, abundance evenness, the other aspect of tree species diversity in our models, had a significant negative effect on these three phenological metrics (Figure 4.5). Similarly, species diversity increased green-up lag, i.e. the length of the period between green-up and wet season onset, while evenness caused a decrease in green-up lag (H_2). The positive effect of diversity was comparable to the effects of pre-green-up precipitation and diurnal temperature range, which also increased green-up lag. The best model predicting green-up lag explained 32% of the variance in this phenological metric.

Larger average tree size, measured by the quadratic mean of stem DBH per site, was only included and significant in the best model for senescence lag, where it caused earlier senescence with respect to the end of the wet season (H_5). None of the other phenological metrics were significantly affected by average tree size. As mentioned previously however, senescence lag was poorly constrained in our models, with the best model explaining only 11% of the variance in senescence lag.

The four vegetation type clusters exhibited some spatial and climatic stratification (Figure 4.1). Cluster 1 was largely absent from the southwest of the country, occurring predominantly in higher rainfall regions to the north. Cluster 4 dominated the southwest of the country (Table 4.1). Cluster 2, consists of small stature Zambesian Combretaceae woodlands, as described by Dinerstein et al. (2017) and Chidumayo (2001), and is not dominated by the same archetypal Detarioideae canopy tree species as miombo woodland. It is possible that these woodlands represent highly disturbed miombo woodlands where large trees may have been removed by humans or by fire induced mortality. Cluster 2 occurs over a wide climatic range, and contains some of the warmest sites in the dataset. Clusters 1, 3 and 4 represent varieties of miombo woodland, dominated by *Brachystegia* spp. and *Julbernardia* spp., with different secondary species. Cluster 1, occurring in predominantly in the north, represents wet miombo, as defined by White (1983), while Cluster 3 represents the corresponding dry miombo. Cluster 4, possibly represents the eastern extent of the biogeographically distinct Angolan miombo woodlands, with the notable abundance of *Guibourtia coleosperma* and *Cryptosepalum exfoliatum* (Huntley & Matos, 1994). Median species richness and the range of species richness values per site is similar across all vegetation clusters (Table 4.1).

The slope of the relationship between species diversity and phenological metrics varied among vegetation types (H_4) (Figure 4.6). According to post-hoc Tukey's tests on marginal effects (Table 4.S2), Cluster 2 differed from all other clusters in the effect of species diversity on cumulative EVI, growing season length, and pre-rain green-up lag. Clusters 1 and 4 appear to show no positive effect of diversity on cumulative EVI and Cluster 4 also showed a negative effect of diversity on season length. The effect of diversity and evenness on green-up lag were consistent among all vegetation types. Cluster 2 appears to show a divergent positive effect of evenness on cumulative EVI compared to the other clusters.

Clusters, 1, 3 and 4 were largely similar in their density distribution of the six phenological metrics, while Cluster 2 had more plots with lower cumulative EVI and a shorter growing season (Figure 4.7). A MANOVA including all

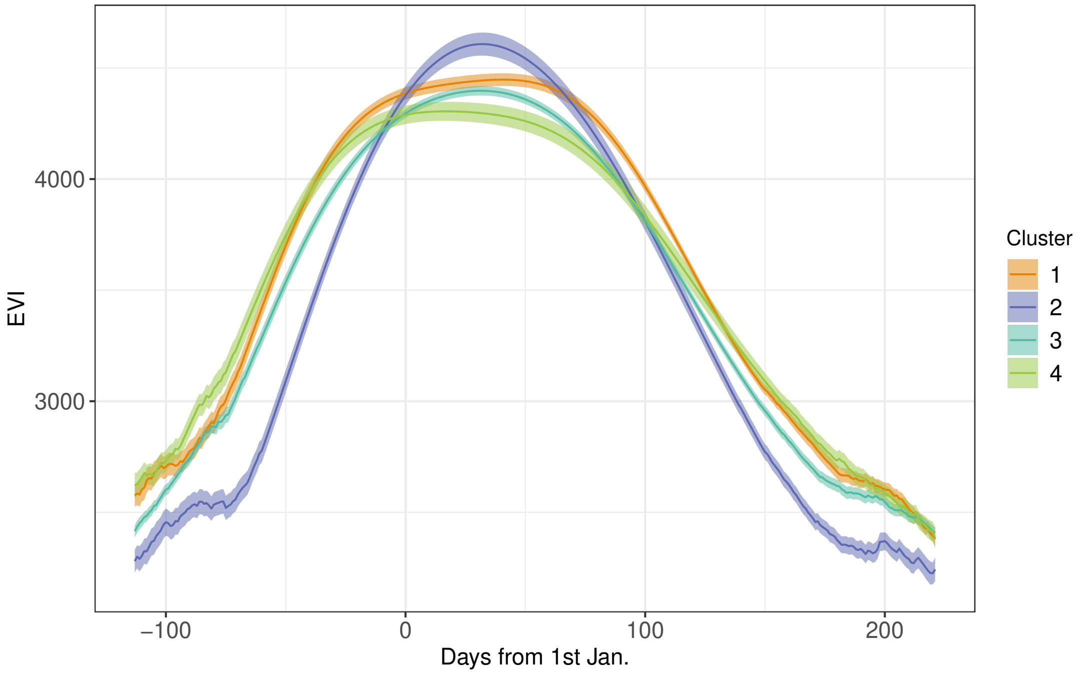


Figure 4.4: Mean GAMs of EVI over the growing season for each vegetation type cluster. Shaded ribbons are 95% confidence intervals.

phenological metrics showed a significant difference among vegetation clusters (F(3,613)=14.06, p<0.01). Post-hoc Tukey's tests showed significant differences between Cluster 2 and the other three clusters for all phenological metrics (Table 4.S3). Cluster 2 had a significantly shorter growing season than the other clusters, caused by both later green-up and earlier senescence. Cluster 2 also had a higher maximum EVI than the other clusters (Figure 4.4). The vast majority of plots, regardless of vegetation type, exhibited some degree of pre-rain green-up, and all plots exhibited some degree of senescence lag (Figure 4.7).

4.4 Discussion

In this study we have demonstrated clear and measurable effects of tree species diversity, evenness, and composition on various aspects of land-surface phenology in Zambian deciduous savannas, independent of the effects of climatic variation. We showed that tree species diversity led to an increase in cumulative EVI and growing season length in certain vegetation types. Additionally, species

Table 4.2: Model fit statistics for the best model describing each phenological metric.

Response	δAIC	R^2_{adj}	δlogLik
Cumulative EVI	74.8	0.34	–52.38
Season length	75.3	0.20	–52.63
Green-up rate	48.2	0.21	–39.09
Senescence rate	83.2	0.15	–56.59
Green-up lag	100.3	0.33	–65.15
Senescence lag	21.3	0.11	–25.64

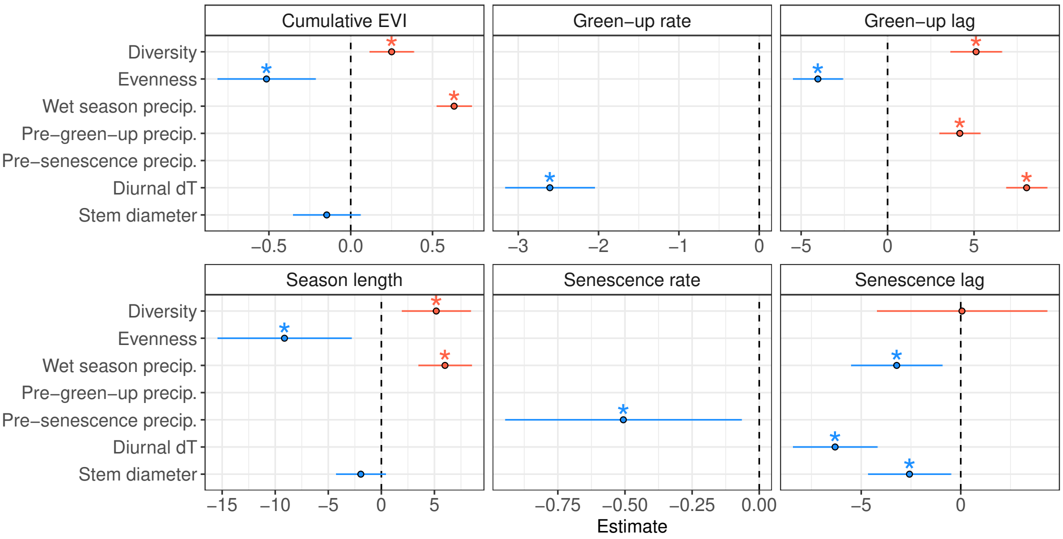


Figure 4.5: Standardised slope coefficients for each best model of a phenological metric. Slope estimates are ±1 standard error. Slope estimates where the interval does not overlap zero are considered to be significant effects and are marked by asterisks.

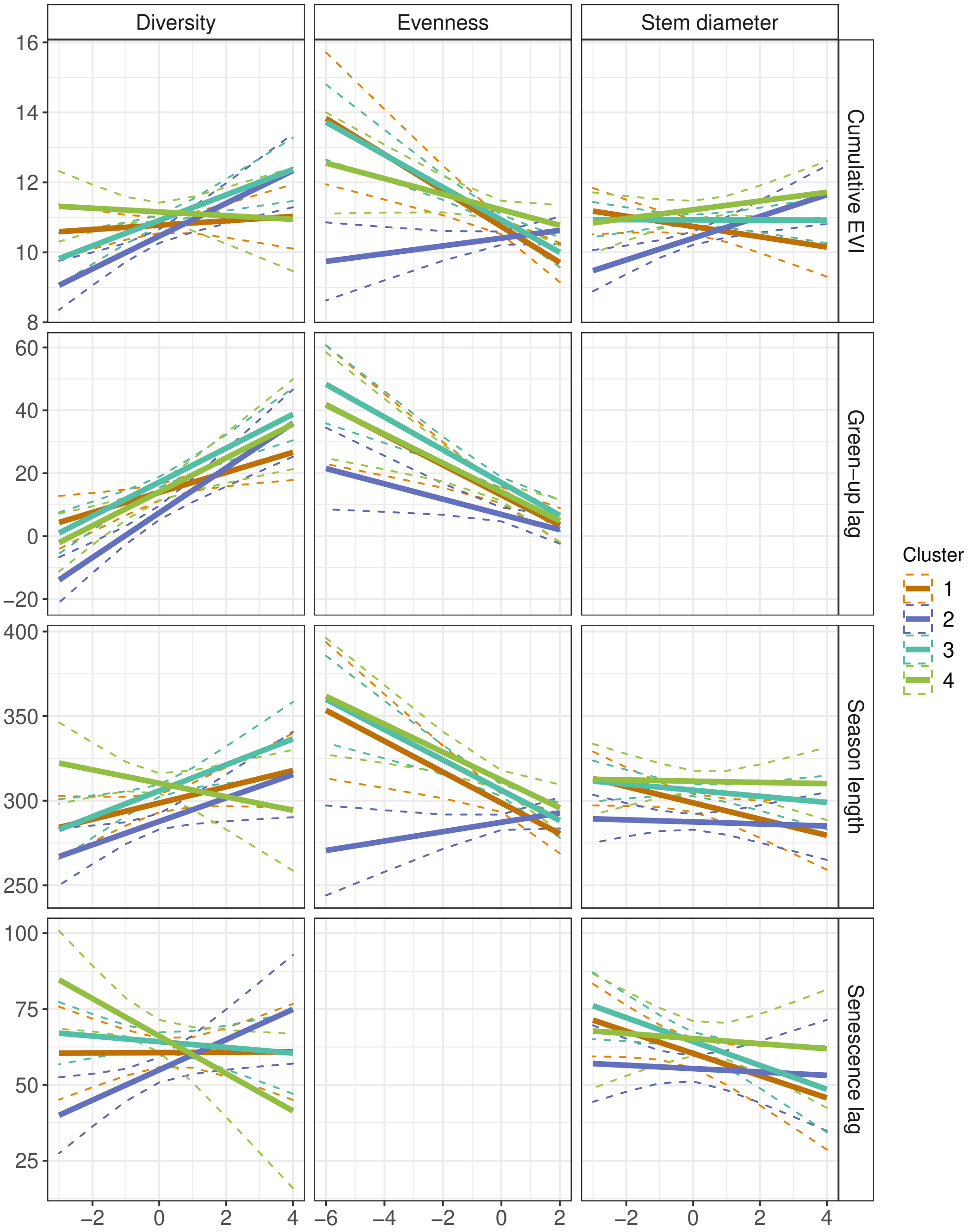


Figure 4.6: Marginal effects of tree species diversity, evenness, and tree size on each of the phenological metrics, using the maximal mixed effects model, for each vegetation cluster. Dotted lines represent 95% confidence intervals.

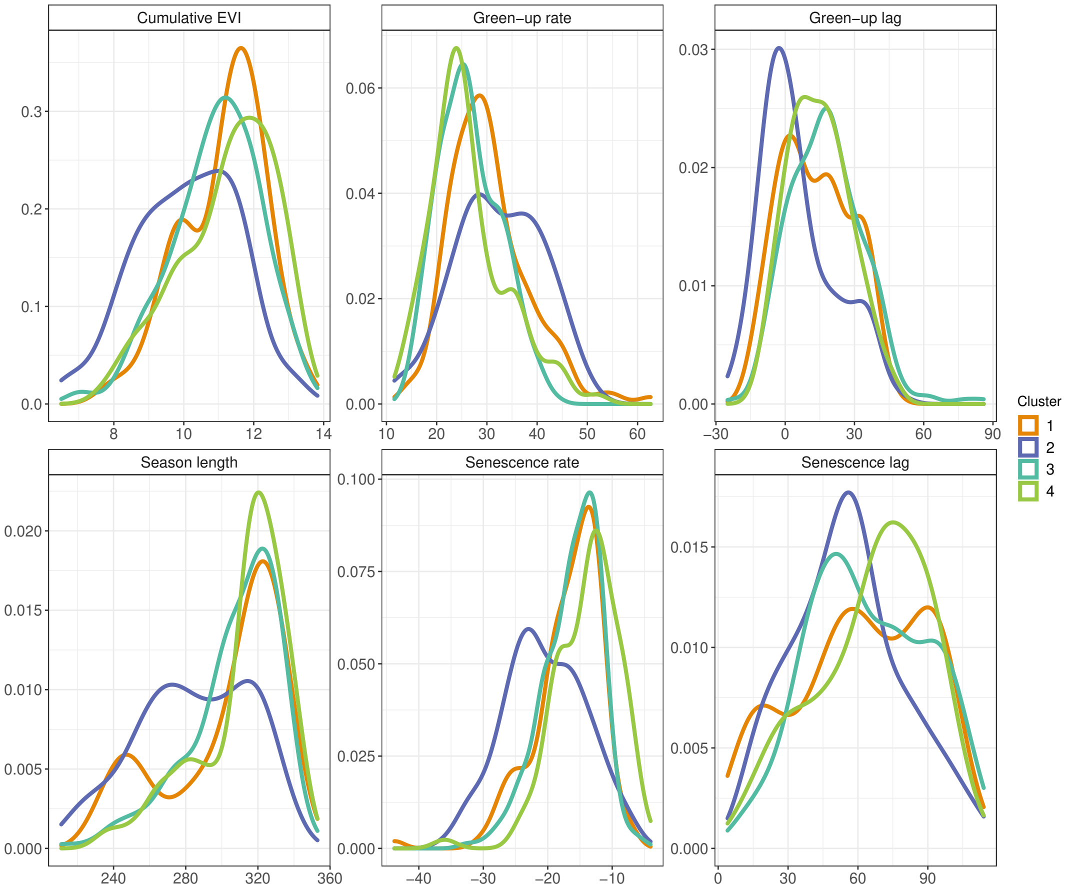


Figure 4.7: Density distribution of the six phenological metrics used in the study, grouped by vegetation cluster.

diversity caused the onset of greening to occur earlier with respect to the start of the wet season, in all vegetation types. Our study lends support for a positive biodiversity-ecosystem function relationship in deciduous savannas, operating through its influence on land-surface phenology, with a longer growing season and greater cumulative EVI suggesting greater primary productivity in species rich woodlands. Additionally, our finding that species diversity causes earlier pre-rain green-up suggests that diverse woodlands are more resilient to varying precipitation patterns, by producing foliage in advance of seasonal rainfall. This provides early forage for herbivores (Morellato et al., 2016), and provides facilitative effects such as cover and hydraulic lift which benefit understorey plants (Domec et al., 2010; Yu & D'Odorico, 2015). Our results highlight the role of tree species diversity as a driver of key ecosystem processes, which affect ecosystem structure, the wildlife provisioning role, and gross primary productivity.

Our finding that species diversity strongly affects patterns of land-surface phenology in deciduous Zambian woodlands provides earth surface system modellers with a means to better understand how future changes in species diversity and composition will affect land-surface phenology and therefore the carbon cycle. Incorporating predictions of biotic change into carbon cycling models has been limited (Ahlstrom et al., 2015; Bodegom et al., 2011), owing to large uncertainties in the effects of diversity on Gross Primary Productivity (GPP). Our study provides a link by demonstrating a strong positive relationship between species diversity and cumulative EVI, which itself correlates with GPP (Sjöström et al., 2011).

While species diversity is a common measure of biodiversity, abundance evenness constitutes a second key related axis (Wilsey et al., 2005; Hillebrand et al., 2008; Jost, 2010). In this study, we found contrasting effects of diversity and evenness on cumulative EVI, growing season length and green-up lag. Evenness caused a decrease in these phenological metrics in miombo woodland vegetation, contrary to our hypothesis. It is possible that the negative effect of abundance evenness occurred because an increase in evenness is associated with a reduction in the dominance of a few large canopy-forming tree species (e.g. *Brachystegia* spp. and *Julbernardia paniculata*). Large canopy tree species have access to groundwater for a longer part of the year, due to their deep root systems and conservative growth patterns, allowing them to green-up in advance of seasonal rains and remain resilient to mid-season fluctuations in water availability (Zhou et al., 2020). Indeed, our study found that plots with larger trees tend to senesce later with respect to the end of the wet season. We found that while the three miombo vegetation types showed a negative effect of evenness on cumulative EVI and season length, Cluster 2, which was not dominated by miombo canopy tree species, showed a positive effect of evenness on these phenological metrics.

The effect of species diversity on cumulative EVI and growing season length was driven largely by the response of vegetation Clusters 2 and 3. Cluster 2 consisted of shorter stature non-miombo vegetation. Clusters 1, and 4, which consisted of miombo vegetation, exhibited negligible species diversity effects on these two phenological metrics. However, Cluster 3, the remaining miombo vegetation type also showed a positive effect of evenness on cumulative EVI. Cluster 3 had lower annual precipitation than the other two miombo clusters, with a precipitation regime closer to that of Cluster 2, representing the dry miombo vegetation type identified by White (1983). In high precipitation miombo vegetation, it appears that the dominant archetypal miombo tree species can grow to large canopy forming trees, and that these individuals determine cumulative EVI as a result. Meanwhile, in the drier woodlands represented by Clusters 2 and 3, a genuine species diversity effect driven by niche complementarity exists. We suggest that in these drier woodlands, higher species diversity provides ecosystem level resilience to drought by increasing the breadth of water use strategies.

Patterns of senescence were poorly predicted by species diversity and evenness in our models. Cho et al. (2017) found that tree cover, measured by MODIS LAI data, had a significant negative effect on senescence rates in savannas in South Africa, which have similar climatic conditions to the sites in our study. In most savannas, including sparse savannas, while the onset of the growing season is often driven by tree photosynthetic activity, which may precede the onset of precipitation, the end of the growing season is conversely driven by the understorey grass layer, which itself can be dependent on tree cover (Cho et al., 2017; Guan et al., 2014). Grass activity is more reactive to short-term changes in soil moisture than tree activity, and may oscillate within the senescence period (Archibald & Scholes, 2007). This may explain the lack of a strong precipitation signal for senescence lag and senescence rate in our models. Our finding that sites with larger trees may prolong the growing season beyond the end of the rainy season corroborates these earlier studies. As average tree stem size increases, tree cover is also likely to increase (Panzou et al., 2020), reducing the relative contribution of the understorey grass layer to land-surface phenology and producing a more consistent decline in EVI during the senescence period.

Other studies both globally and within southern African savannas have largely ignored patterns of senescence, instead focussing patterns of green-up (Gallinat et al., 2015). Most commonly, these studies simply correlate the decline of rainfall with senescence (Guan et al., 2014), but our best model suggests that diurnal temperature range is a stronger determinant of the end of the growing season than precipitation. Diurnal temperature range effectively measures mean daily temperature variability. We suggest that diurnal temperature fluctuations, particularly minimum night time temperatures, may provide cues for senescence toward the end of the wet season. In temperate ecosystems which experience autumn senescence, lower night time temperatures have been shown to increase the rate of senescence (Michelson et al., 2017; Gárate-Escamilla et al., 2020), thus leaves remain green for longer when the diurnal temperature range is smaller. Similarly, our models showed that larger diurnal temperature range caused earlier pre-rain green-up, and possibly acts as a cue to initiate the growing season as well.

Alternatively, Zani et al. (2020) suggests that in resource limited environments, senescence times may largely be set by the preceding photosynthetic activity and sink-limitations on growth. For example, limited nutrient supply may prohibit photosynthesis late in the season if the preceding photosynthetic activity has depleted that supply. Reich et al. (1992) suggested that there are many direct constraints on leaf life-span such as drought and herbivory, especially in the dry tropics, which would lead to timing of senescence being set largely by the time of bud-burst. Our study corroborates this theory, showing that precipitation across the entire wet season was a better predictor of senescence lag than pre-senescence precipitation, while pre-senescence precipitation does cause variation in the rate of senescence. However, we did not find a strong correlation between green-up lag and senescence lag (Figure 4.S2).

While leaf senescence may not be as important for the survival of browsing herbivores as the green-up period, the timing of senescence with respect to temperature and precipitation has important consequences for the savanna understorey microclimate. The longer leaf material remains in the canopy after the end of the wet season, the greater the microclimatic buffer for herbaceous understorey plants and animals, which require water and protection from high levels of insolation and dry air which can prevail rapidly after the end of the wet season (Guan et al., 2014). Our study merely demonstrates that more work needs to be done to properly characterise the drivers of senescence in this biome, which were poorly constrained in our models.

Our coverage of very short growing season lengths in Zambia was restricted, with a notable absence of available plot data in the northeast of the country around E30.5°, S11.5°, and E23.0°, S15.0°. These regions are largely seasonally water-logged floodplain and swampland (White, 1983; Dinerstein et al., 2017), and were likely excluded by the ILUA-II assessment for this reason. This also explains their divergent phenological patterns as observed in the MODIS EVI data (Figure 4.1). The plot data does however, provide representative coverage of growing season lengths in wooded ecosystems. While our study focusses on woodlands, the phenological behaviour of these other vegetation types should also be considered in future studies, as these may be even more sensitive to changes in climate (Dean et al., 2018) and under greater land-use change pressures (Langan et al., 2018).

It is important to note that the remotely sensed EVI data used here do not only measure trees, they represent the landscape as a single unit. Nevertheless, seasonal patterns of tree leaf phenology in southern African deciduous woodlands, particularly the pre-rain green-up phenomenon, is driven almost exclusively by trees, while grass phenology tends to follow patterns of precipitation more closely (Whitecross et al., 2017; Archibald & Scholes, 2007; Higgins et al., 2011). Grasses make a significant contribution to savanna gross primary productivity (Lloyd et al., 2008), and it was therefore in our interests to include their response in our analysis as we seek to demonstrate how tree species diversity can affect cycles of carbon exchange. Additionally, the micro-climatic effects of tree leaf canopy coverage and hydraulic lift through tree deep root systems will benefit the productivity of grasses as well as understorey tree individuals.

4.5 Conclusion

Here we explored how tree species diversity, composition and woodland structure influence land surface phenology across Zambia. We showed that species diversity clearly causes earlier pre-rain green-up, across all vegetation types studied here. The length of the growing season, and ultimately woodland productivity as measured by cumulative EVI, appeared to increase with species diversity in drier woodlands only, while wetter miombo woodlands were dominated by a few canopy-forming archetypal miombo Detarioideae species regardless of species diversity. Interestingly, species evenness had a consistently negative effect on green-up lag, suggesting that pre-rain green-up is driven by canopy-forming Detarioideae species when they are dominant. Finally, we have demonstrated variation in phenological patterns among vegetation types within Zambia that are commonly not distinguished in earth system models. Our results have a range of consequences for earth system modellers as well as conservation managers working in Zambia and across the dry tropics, and lend further support to an already well established corpus of study demonstrating the positive effect of species diversity on ecosystem function.

References

Adole, T., J. Dash & P. M. Atkinson (2018a). ‘Characterising the land surface phenology of Africa using 500 m MODIS EVI’. In: *Applied Geography* 90, pp. 187–199. DOI: `10.1016/j.apgeog.2017.12.006`.

Adole, T., J. Dash & P. M. Atkinson (2018b). ‘Large-scale prerain vegetation green-up across Africa’. In: *Global Change Biology* 24.9, pp. 4054–4068. DOI: `10.1111/gcb.14310`.

Ahlstrom, A., M. R. Raupach, G. Schurgers, B. Smith, A. Arneth, M. Jung, M. Reichstein, J. G. Canadell, P. Friedlingstein, A. K. Jain et al. (2015). ‘The dominant role of semi-arid ecosystems in the trend and variability of the land CO2 sink’. In: *Science* 348.6237, pp. 895–899. DOI: `10.1126/science.aaa1668`.

Araujo, H. F. P. de, A. H. Vieira-Filho, M. R. V. Barbosa, J. A. F. Diniz-Filho & J. M. C. da Silva (2017). ‘Passerine phenology in the largest tropical dry forest of South America: Effects of climate and resource availability’. In: *Emu - Austral Ornithology* 117.1, pp. 78–91. DOI: `10.1080/01584197.2016.1265430`.

Archibald, S. & R. J. Scholes (2007). ‘Leaf green-up in a semi-arid African savanna -separating tree and grass responses to environmental cues’. In: *Journal of Vegetation Science* 18.4, pp. 583–594. DOI: `10.1111/j.1654-1103.2007.tb02572.x`.

Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, J. Farrar et al. (2002). ‘Herbivory in global climate change research: direct effects of rising temperature on insect herbivores’. In: *Global Change Biology* 8.1, pp. 1–16. DOI: `10.1046/j.1365-2486.2002.00451.x`.

Bloom, A. A., J. Exbrayat, I. R. van der Velde, L. Feng & M. Williams (2016). ‘The decadal state of the terrestrial carbon cycle: Global retrievals of terrestrial carbon allocation, pools, and residence times’. In: *Proceedings of the National Academy of Sciences* 113.5, pp. 1285–1290. DOI: `10.1073/pnas.1515160113`.

Bodegom, P. M. V., J. C. Douma, J. P. M. Witte, J. C. Ordoñez, R. P. Bartholomeus & R. Aerts (2011). ‘Going beyond limitations of plant functional types when predicting global ecosystem-atmosphere fluxes: exploring the merits of traits-based approaches’. In: *Global Ecology and Biogeography* 21.6, pp. 625–636. DOI: `10.1111/j.1466-8238.2011.00717.x`.

Broadhead, J. S., C. K. Ong & C. R. Black (2003). ‘Tree phenology and water availability in semi-arid agroforestry systems’. In: *Forest Ecology and Management* 180.1-3, pp. 61–73. DOI: `10.1016/s0378-1127(02)00602-3`.

Chidumayo, E. N. (2001). ‘Climate and phenology of savanna vegetation in southern Africa’. In: *Journal of Vegetation Science* 12.3, p. 347. DOI: `10.2307/3236848`.

Cho, M. A., A. Ramoelo & L. Dziba (2017). ‘Response of land surface phenology to variation in tree cover during green-up and senescence periods in the semi-arid savanna of southern Africa’. In: *Remote Sensing* 9.7, p. 689. DOI: `10.3390/rs9070689`.

Cole, E. F., P. R. Long, P. Zelazowski, M. Szulkin & B. C. Sheldon (2015). ‘Predicting bird phenology from space: Satellite-derived vegetation green-up signal uncovers spatial variation in phenological synchrony between birds and their environment’. In: *Ecology and Evolution* 5.21, pp. 5057–5074. DOI: `10.1002/ece3.1745`.

Curtis, R. O. & D. D. Marshall (2000). ‘Why Quadratic Mean Diameter?’ In: *Western Journal of Applied Forestry* 15.3, pp. 137–139. DOI: `10.1093/wjaf/15.3.137`.

Dahlin, K. M., D. D. Ponte, E. Setlock & R. Nagelkirk (2016). ‘Global patterns of drought deciduous phenology in semi-arid and savanna-type ecosystems’. In: *Ecography* 40.2, pp. 314–323. DOI: `10.1111/ecog.02443`.

Dean, J. F., J. J. Middelburg, T. Röckmann, R. Aerts, L. G. Blauw, M. Egger, M. S. M. Jetten, A. E. E. de Jong, O. H. Meisel, O. Rasigraf et al. (2018). ‘Methane Feedbacks to the Global Climate System in a Warmer World’. In: *Reviews of Geophysics* 56.1, pp. 207–250. DOI: `10.1002/2017rg000559`.

Didan, L. (2015). *MOD13Q1 MODIS/Terra Vegetation Indices 16-Day L3 Global 250m SIN Grid V006 [Data set]*. NASA EOSDIS Land Processes DAAC. DOI: `10.5067/MODIS/MOD13Q1.006`. (Visited on 05/08/2020).

Didan, L. & A. Barreto (2016). *NASA MEaSUREs Vegetation Index and Phenology (VIP) Phenology EVI2 Yearly Global 0.05Deg CMG [Data set]*. NASA EOSDIS Land Processes DAAC. DOI: `10.5067/MEaSUREs/VIP/VIPPHEN_EVI2.004`. (Visited on 05/08/2020).

Dinerstein, E., D. Olson, A. Joshi, C. Vynne, N. D. Burgess, E. Wikramanayake, N. Hahn, S. Palminteri, P. Hedao, R. Noss et al. (2017). 'An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm'. In: *BioScience* 67.6, pp. 534–545. DOI: `10.1093/biosci/bix014`.

Domec, J.-C., J. S. King, A. Noormets, E. Treasure, M. J. Gavazzi, G. Sun & S. G. McNulty (2010). 'Hydraulic redistribution of soil water by roots affects whole-stand evapotranspiration and net ecosystem carbon exchange'. In: *New Phytologist* 187.1, pp. 171–183. DOI: `10.1111/j.1469-8137.2010.03245.x`.

Dufrêne, M. & P. Legendre (1997). 'Species assemblages and indicator species: The need for a flexible asymmetrical approach'. In: *Ecological Monographs* 67.3, pp. 345–366. DOI: `10.1890/0012-9615(1997)067[0345:saaist]2.0.co;2`.

Faith, D. P., P. R. Minchin & L. Belbin (1987). 'Compositional dissimilarity as a robust measure of ecological distance'. In: *Vegetatio* 69.1-3, pp. 57–68. DOI: `10.1007/bf00038687`.

Fayolle, A., M. D. Swaine, J. Bastin, N. Bourland, J. A. Comiskey, G. Dauby, J. Doucet, J. Gillet, S. Gourlet-Fleury, O. J. Hardy et al. (2014). 'Patterns of tree species composition across tropical African forests'. In: *Journal of Biogeography* 41.12, pp. 2320–2331. DOI: `10.1111/jbi.12382`.

Fick, S. E. & R. J. Hijmans (2017). 'WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas'. In: *International Journal of Climatology* 37.12, pp. 4302–4315. DOI: `10.1002/joc.5086`.

Friedl, M. & D. Sulla-Menashe (2019). *MCD12Q1 MODIS/Terra+Aqua Land Cover Type Yearly L3 Global 500m SIN Grid V006 [Data set]*. NASA EOSDIS Land Processes DAAC. DOI: `10.5067/MODIS/MCD12Q1.006`. (Visited on 23/07/2021).

Fuller, D. O. (1999). 'Canopy phenology of some mopane and miombo woodlands in eastern Zambia'. In: *Global Ecology and Biogeography* 8.3-4, pp. 199–209. DOI: `10.1046/j.1365-2699.1999.00130.x`.

Gallinat, A. S., R. B. Primack & D. L. Wagner (2015). 'Autumn, the neglected season in climate change research'. In: *Trends in Ecology & Evolution* 30.3, pp. 169–176. DOI: `10.1016/j.tree.2015.01.004`.

Gárate-Escamilla, H., C. C. Brelsford, A. Hampe, T. M. Robson & M. B. Garzón (2020). 'Greater capacity to exploit warming temperatures in northern populations of European beech is partly driven by delayed leaf senescence'. In: *Agricultural and Forest Meteorology* 284, p. 107908. DOI: `10.1016/j.agrformet.2020.107908`.

Gu, L., W. M. Post, D. Baldocchi, T. A. Black, S. B. Verma, T. Vesala & S. C. Wofsy (2003). 'Phenology of vegetation photosynthesis'. In: *Phenology: An Integrative Environmental Science*, pp. 467–485. DOI: `10.1007/978-94-007-0632-3_29`.

Guan, K., E. F. Wood, D. Medvigy, J. Kimball, M. Pan, K. K. Caylor, J. Sheffield, C. Xu & M. O. Jones (2014). 'Terrestrial hydrological controls on land surface phenology of African savannas and woodlands'. In: *Journal of Geophysical Research: Biogeosciences* 119.8, pp. 1652–1669. DOI: `10.1002/2013jg002572`.

Higgins, S. I., M. D. Delgado-Cartay, E. C. February & H. J. Combrink (2011). 'Is there a temporal niche separation in the leaf phenology of savanna trees and grasses?' In: *Journal of Biogeography* 38.11, pp. 2165–2175. DOI: `10.1111/j.1365-2699.2011.02549.x`.

Hillebrand, H., D. M. Bennett & M. W. Cadotte (2008). 'Consequences of dominance: A review of evenness effects on local and regional ecosystem processes'. In: *Ecology* 89.6, pp. 1510–1520. DOI: `10.1890/07-1053.1`.

Huffman, G. J., E. F. Stocker, D. T. Bolvin, E. J. Nelkin & J. Tan (2015). *GPM IMERG Final Precipitation L3 1 day 0.1 degree x 0.1 degree V06 [Data set]*. Goddard Earth Sciences Data and Information Services Center (GES DISC). DOI: `10.5067/GPM/IMERGDF/DAY/06`. (Visited on 30/10/2020).

Huntley, B. J. & E. M. Matos (1994). 'Botanical diversity and its conservation in Angola'. In: *Botanical Diversity in Southern Africa*. Ed. by B. J. Huntley. Pretoria, South Africa: National Botanical Institute, pp. 53–74.

Jeganathan, C., J. Dash & P. M. Atkinson (2014). 'Remotely sensed trends in the phenology of northern high latitude terrestrial vegetation, controlling for land cover change and vegetation type'. In: *Remote Sensing of Environment* 143, pp. 154–170. DOI: `10.1016/j.rse.2013.11.020`.

Jost, L. (2007). 'Partitioning diversity into independent alpha and beta components'. In: *Ecology* 88.10, pp. 2427–2439. DOI: `10.1890/06-1736.1`.

Jost, L. (2010). 'The relation between evenness and diversity'. In: *Diversity* 2.2, pp. 207–232. DOI: `10.3390/d2020207`.

Kreft, H. & W. Jetz (2010). 'A framework for delineating biogeographical regions based on species distributions'. In: *Journal of Biogeography* 37.11, pp. 2029–2053. DOI: `10.1111/j.1365-2699.2010.02375.x`.

Langan, C., J. Farmer, M. Rivington & J. U. Smith (2018). 'Tropical wetland ecosystem service assessments in East Africa: A review of approaches and challenges'. In: *Environmental Modelling & Software* 102, pp. 260–273. DOI: `10.1016/j.envsoft.2018.01.022`.

Lasky, J. R., M. Uriarte & R. Muscarella (2016). 'Synchrony, compensatory dynamics, and the functional trait basis of phenological diversity in a tropical dry forest tree community: effects of rainfall seasonality'. In: *Environmental Research Letters* 11, p. 115003. DOI: `10.1088/1748-9326/11/11/115003`.

Lloyd, J., M. I. Bird, L. Vellen, A. C. Miranda, E. M. Veenendaal, G. Djagbletey, H. S. Miranda, G. Cook & G. D. Farquhar (2008). 'Contributions of woody and herbaceous vegetation to tropical savanna ecosystem productivity: a quasi-global estimate'. In: *Tree Physiology* 28.3, pp. 451–468. DOI: `10.1093/treephys/28.3.451`.

Lüdecke, D. (2018). 'ggeffects: Tidy data frames of marginal effects from regression models'. In: *Journal of Open Source Software* 3.26, p. 772. DOI: `10.21105/joss.00772`.

Michelson, I. H., P. K. Ingvarsson, K. M. Robinson, E. Edlund, M. E. Eriksson, O. Nilsson & S. Jansson (2017). 'Autumn senescence in aspen is not triggered by day length'. In: *Physiologia Plantarum* 162.1, pp. 123–134. DOI: `10.1111/ppl.12593`.

Morellato, L. P. C., B. Alberton, S. T. Alvarado, B. Borges, E. Buisson, M. G. G. Camargo, L. F. Cancian, D. W. Carstensen, D. F. E. Escobar, P. T. P. Leite et al. (2016). 'Linking plant phenology to conservation biology'. In: *Biological Conservation* 195, pp. 60–72. DOI: `10.1016/j.biocon.2015.12.033`.

Mukosha, J. & A. Siampale (2009). *Integrated land use assessment Zambia 2005–2008*. Lusaka, Zambia: Ministry of Tourism, Environment et al.

Murtagh, F. & P. Legendre (2014). 'Ward's hierarchical agglomerative clustering method: Which algorithms implement Ward's criterion?' In: *Journal of Classification* 31.3, pp. 274–295. DOI: `10.1007/s00357-014-9161-z`.

Ogutu, J. O., H. Piepho & H. T. Dublin (2013). 'Responses of phenology, synchrony and fecundity of breeding by African ungulates to interannual variation in rainfall'. In: *Wildlife Research* 40.8, p. 698. DOI: `10.1071/wr13117`.

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`.

Parr, C. L., C. E. R. Lehmann, W. J. Bond, W. A. Hoffmann & A. N. Andersen (2014). 'Tropical grassy biomes: Misunderstood, neglected, and under threat'. In: *Trends in Ecology & Evolution* 29, pp. 205–213. DOI: `10.1016/j.tree.2014.02.004`.

Pavlick, R., D. T. Drewry, K. Bohn, B. Reu & A. Kleidon (2013). ‘The Jena Diversity-Dynamic Global Vegetation Model (JeDi-DGVM): A diverse approach to representing terrestrial biogeography and biogeochemistry based on plant functional trade-offs’. In: *Biogeosciences* 10.6, pp. 4137–4177. DOI: `10.5194/bg-10-4137-2013`.

Pelletier, J., A. Paquette, K. Mbindo, N. Zimba, A. Siampale, B. Chendauka, F. Siangulube & J. W. Roberts (2018). ‘Carbon sink despite large deforestation in African tropical dry forests (miombo woodlands)’. In: *Environmental Research Letters* 13, p. 094017. DOI: `10.1088/1748-9326/aadc9a`.

Penuelas, J., T. Rutishauser & I. Filella (2009). ‘Phenology Feedbacks on Climate Change’. In: *Science* 324.5929, pp. 887–888. DOI: `10.1126/science.1173004`.

Prather, C. M., S. L. Pelini, A. Laws, E. Rivest, M. Woltz, C. P. Bloch, I. Del Toro, C. Ho, J. Kominoski, T. A. S. Newbold et al. (2012). ‘Invertebrates, ecosystem services and climate change’. In: *Biological Reviews* 88.2, pp. 327–348. DOI: `10.1111/brv.12002`.

R Core Team (2020). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. Vienna, Austria. URL: `https://www.R-project.org/`.

Reich, P. B., M. B. Walters & D. S. Ellsworth (1992). ‘Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems’. In: *Ecological Monographs* 62.3, pp. 365–392. DOI: `10.2307/2937116`.

Richardson, A. D., T. F. Keenan, M. Migliavacca, Y. Ryu, O. Sonnentag & M. Toomey (2013). ‘Climate change, phenology, and phenological control of vegetation feedbacks to the climate system’. In: *Agricultural and Forest Meteorology* 169, pp. 156–173. DOI: `10.1016/j.agrformet.2012.09.012`.

Rousseeuw, P. J. (1987). ‘Silhouettes: A graphical aid to the interpretation and validation of cluster analysis’. In: *Journal of Computational and Applied Mathematics* 20, pp. 53–65. DOI: `10.1016/0377-0427(87)90125-7`.

Ryan, C. M., M. Williams, J. Grace, E. Woollen & C. E. R. Lehmann (2017). ‘Pre-rain green-up is ubiquitous across southern tropical Africa: implications for temporal niche separation and model representation’. In: *New Phytologist* 213.2, pp. 625–633. DOI: `10.1111/nph.14262`.

Scheiter, S., L. Langan & S. I. Higgins (2013). ‘Next-generation dynamic global vegetation models: Learning from community ecology’. In: *New Phytologist* 198.3, pp. 957–969. DOI: `10.1111/nph.12210`.

Sjöström, M., J. Ardö, A. Arneth, N. Boulain, B. Cappelaere, L. Eklundh, A. de Grandcourt, W. L. Kutsch, L. Merbold & Y. Nouvellon (2011). ‘Exploring the potential of MODIS EVI for modeling gross primary production across African ecosystems’. In: *Remote Sensing of Environment* 115.4, pp. 1081–1089. DOI: `10.1016/j.rse.2010.12.013`.

Smith, B. & J. B. Wilson (1996). ‘A consumer’s guide to evenness indices’. In: *Oikos* 76, pp. 70–82. DOI: `10.2307/3545749`.

Stan, K. & A. Sanchez-Azofeifa (2019). ‘Tropical dry forest diversity, climatic response, and resilience in a changing climate’. In: *Forests* 10.5, p. 443. DOI: `10.3390/f10050443`.

Stöckli, R., T. Rutishauser, I. Baker, M. A. Liniger & A. S. Denning (2011). ‘A global reanalysis of vegetation phenology’. In: *Journal of Geophysical Research* 116.G3. DOI: `10.1029/2010jg001545`.

Velasque, M. & K. Del-Claro (2016). ‘Host plant phenology may determine the abundance of an ecosystem engineering herbivore in a tropical savanna’. In: *Ecological Entomology* 41.4, pp. 421–430. DOI: `10.1111/een.12317`.

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`.

White, M. A., K. M. de Beurs, K. Didan, D. W. Inouye, A. D. Richardson, O. P. Jensen, J. O’Keefe, G. Zhang, R. R. Nemani, W. J. D. Van Leeuwen et al. (2009). ‘Intercomparison, interpretation, and assessment of spring phenology in North America estimated from remote sensing for 1982-2006’. In: *Global Change Biology* 15.10, pp. 2335–2359. DOI: `10.1111/j.1365-2486.2009.01910.x`.

Whitecross, M. A., E. T. F. Witkowski & S. Archibald (2017). ‘Savanna tree-grass interactions: A phenological investigation of green-up in relation to water availability over three seasons’. In: *South African Journal of Botany* 108, pp. 29–40. DOI: `10.1016/j.sajb.2016.09.003`.

Whitley, R., J. Beringer, L. B. Hutley, G. Abramowitz, M. G. De Kauwe, B. Evans, V. Haverd, L. Li, C. Moore, Y. Ryu et al. (2017). ‘Challenges and opportunities in land surface modelling of savanna ecosystems’. In: *Biogeosciences* 14.20, pp. 4711–4732. DOI: `10.5194/bg-14-4711-2017`.

Wilsey, B. J., D. R. Chalcraft, C. M. Bowles & M. R. Willig (2005). ‘Relationships among indices suggest that richness is an incomplete surrogate for grassland biodiversity’. In: *Ecology* 86.5, pp. 1178–1184. DOI: `10.1890/04-0394`.

Xia, J., S. Niu, P. Ciais, I. A. Janssens, J. Chen, C. Ammann, A. Arain, P. D. Blanken, A. Cescatti, D. Bonal et al. (2015). ‘Joint control of terrestrial gross primary productivity by plant phenology and physiology’. In: *Proceedings of the National Academy of Sciences* 112.9, pp. 2788–2793. DOI: `10.1073/pnas.1413090112`.

Yu, K. & P. D’Odorico (2015). ‘Hydraulic lift as a determinant of tree-grass coexistence on savannas’. In: *New Phytologist* 207.4, pp. 1038–1051. DOI: `10.1111/nph.13431`.

Zani, D., T. W. Crowther, L. Mo, S. S. Renner & C. M. Zohner (2020). ‘Increased growing-season productivity drives earlier autumn leaf senescence in temperate trees’. In: *Science* 370.6520, pp. 1066–1071. DOI: `10.1126/science.abd8911`.

Zhou, Y., B. J. Wigley, M. F. Case, C. Coetsee & A. C. Staver (2020). ‘Rooting depth as a key woody functional trait in savannas’. In: *New Phytologist* 227.5, pp. 1350–1361. DOI: `10.1111/nph.16613`.

4.6 Supplementary material

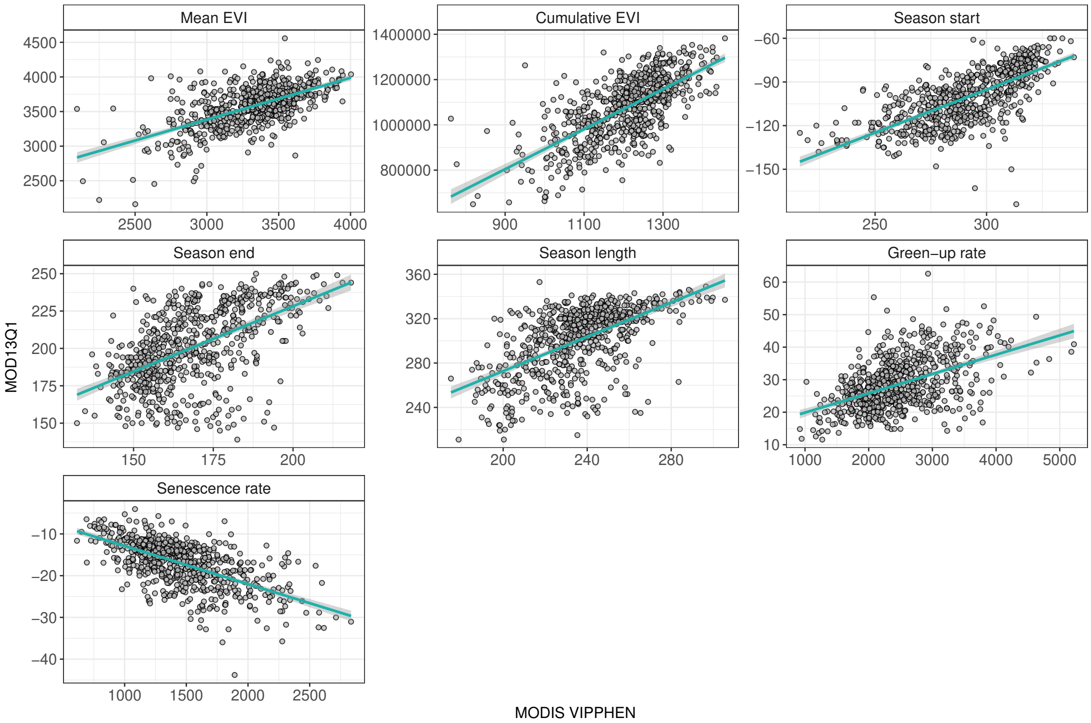


Figure 4.S1: Scatter plots showing a comparison of phenological metrics from the MODIS VIPPHEN product (Didan & Barreto, 2016) and those extracted from the MOD13Q1 data (Didan, 2015), for each of the sites in our study. The cyan line shows a linear model of the data, with a 95% confidence interval.

Table 4.S1: Model fit statistics for comparison of MODIS VIPPHEN and MOD13Q1 products across each of our study sites.

Response	DoF	F	R^2	Prob.
Mean EVI	672	387.0	0.37	<0.05
Cumulative EVI	672	592.6	0.47	<0.05
Season start	672	660.3	0.50	<0.05
Season end	672	285.0	0.30	<0.05
Season length	672	325.0	0.33	<0.05
Green-up rate	672	217.2	0.24	<0.05
Senescence rate	672	412.3	0.38	<0.05

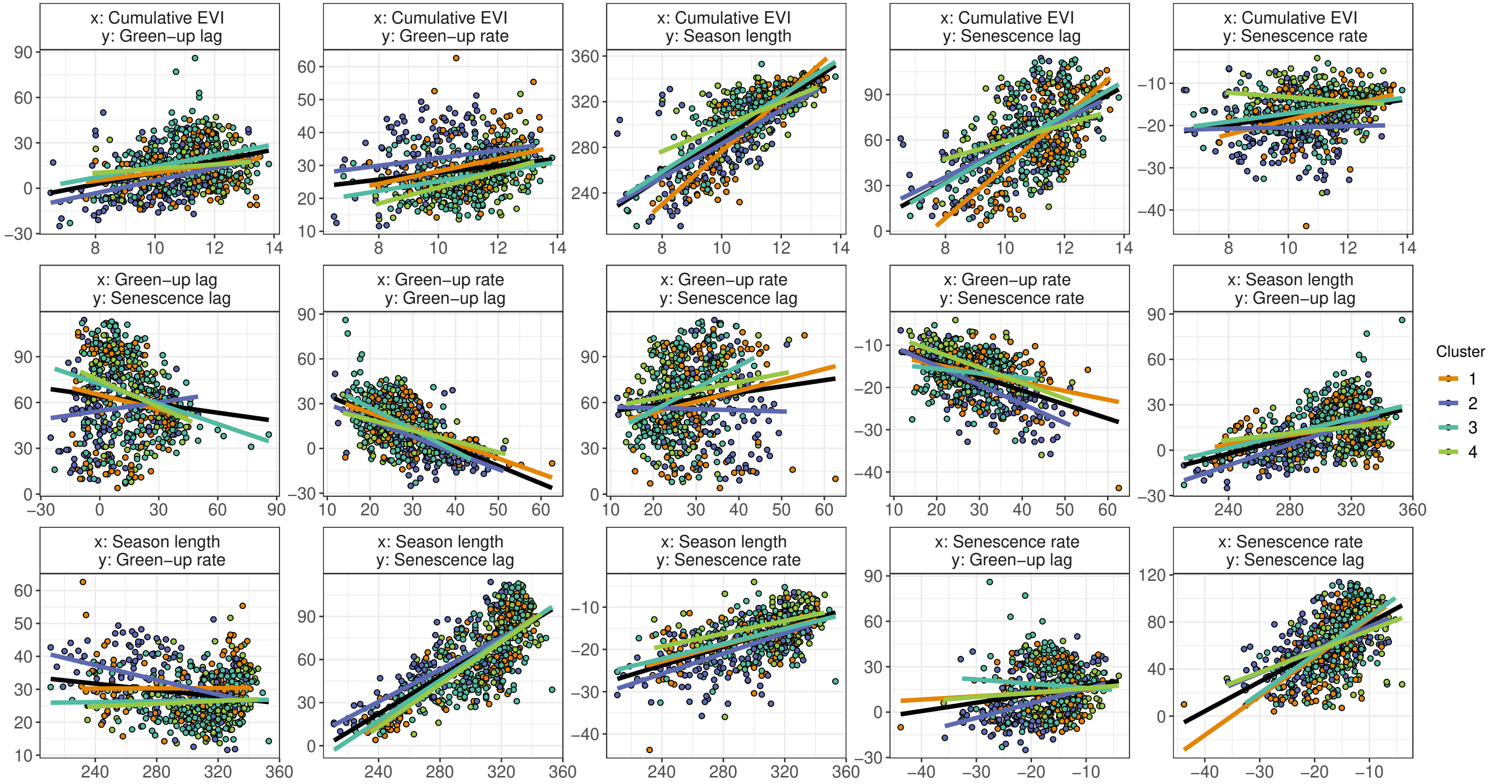


Figure 4.S2: Scatter plots showing pairwise comparisons of the six phenological metrics used in this study, extracted from the MODIS MOD13Q1 product (Didan, 2015). Points represent study sites and are coloured by vegetation cluster. Linear regression line of best fit for all sites is shown as a black line, while linear regressions are shown for each vegetation cluster as coloured lines.

Table 4.S2: Comparisons of species diversity interaction marginal effects using post-hoc Tukey's tests.

Response	Clusters	Estimate	SE	DoF	T ratio	Prob.
Cumulative EVI	1-2	0.3	0.16	600	1.99	0.19
	1-3	–0.1	0.14	600	–0.97	0.77
	1-4	–0.4	0.18	600	–2.14	0.14
	2-3	–0.4	0.12	600	–3.62	<0.01
	2-4	–0.7	0.17	600	–4.11	<0.01
	3-4	–0.2	0.15	600	–1.57	0.40
Season length	1-2	10.8	3.76	603	2.89	<0.05
	1-3	–7.3	3.39	603	–2.14	0.14
	1-4	–11.7	4.06	603	–2.88	<0.05
	2-3	–18.1	2.98	603	–6.07	<0.01
	2-4	–22.5	3.90	603	–5.78	<0.01
	3-4	–4.4	3.54	603	–1.24	0.60
Green-up lag	1-2	6.5	1.70	606	3.80	<0.01
	1-3	–3.3	1.57	606	–2.08	0.16
	1-4	–0.2	1.94	606	–0.10	1.00
	2-3	–9.7	1.44	606	–6.75	<0.01
	2-4	–6.7	1.84	606	–3.62	<0.01
	3-4	3.1	1.69	606	1.83	0.26
Senescence lag	1-2	5.7	3.29	606	1.73	0.31
	1-3	–3.6	2.94	606	–1.22	0.61
	1-4	–5.5	3.64	606	–1.50	0.44
	2-3	–9.3	2.61	606	–3.56	<0.01
	2-4	–11.2	3.48	606	–3.21	<0.01
	3-4	–1.9	3.14	606	–0.60	0.93

Table 4.S3: Post-hoc Tukey's pairwise comparisons among vegetation types for each phenological metric.

Response	Clusters	Mean diff.	Interval	Prob.
Cumulative EVI	2-1	−0.74	−1.04 – −0.45	<0.01
	3-1	−0.14	−0.40 – 0.13	0.55
	4-1	0.09	−0.24 – 0.42	0.89
	3-2	0.61	0.35 – 0.87	<0.01
	4-2	0.84	0.51 – 1.16	<0.01
	4-3	0.23	−0.07 – 0.53	0.19
Season length	2-1	−0.58	−0.88 – −0.29	<0.01
	3-1	0.16	−0.10 – 0.43	0.37
	4-1	0.31	−0.01 – 0.64	0.07
	3-2	0.75	0.49 – 1.01	<0.01
	4-2	0.9	0.58 – 1.22	<0.01
	4-3	0.15	−0.15 – 0.44	0.56
Green-up rate	2-1	0.26	−0.03 – 0.55	0.11
	3-1	−0.48	−0.74 – −0.22	<0.01
	4-1	−0.51	−0.84 – −0.19	<0.01
	3-2	−0.74	−1.00 – −0.48	<0.01
	4-2	−0.77	−1.1 – −0.45	<0.01
	4-3	−0.03	−0.33 – 0.26	0.99
Senescence rate	2-1	−0.65	−0.94 – −0.37	<0.01
	3-1	0.09	−0.16 – 0.35	0.79
	4-1	0.52	0.20 – 0.84	<0.01
	3-2	0.75	0.49 – 1.00	<0.01
	4-2	1.17	0.86 – 1.49	<0.01
	4-3	0.43	0.14 – 0.71	<0.01
Green-up lag	2-1	−0.49	−0.79 – −0.2	<0.01
	3-1	0.28	0.01 – 0.54	<0.05
	4-1	0.08	−0.25 – 0.41	0.91
	3-2	0.77	0.51 – 1.03	<0.01
	4-2	0.58	0.25 – 0.90	<0.01
	4-3	−0.19	−0.49 – 0.10	0.34
Senescence lag	2-1	−0.19	−0.50 – 0.12	0.38
	3-1	0.15	−0.12 – 0.43	0.47
	4-1	0.22	−0.12 – 0.56	0.36
	3-2	0.34	0.08 – 0.61	<0.01
	4-2	0.41	0.07 – 0.74	<0.05
	4-3	0.06	−0.25 – 0.37	0.95

Table 4.S4: Cumulative EVI model selection candidate models, with fit statistics. The overall best model is marked by bold text, according to AIC and model parsimony.

Rank	Precip.	Stem diam.	Diurnal dT	Richness	Evenness	DoF	logLik	AIC	W_i
1	**✓**	**✓+**	**✓**	**✓+**	**✓+**	**19**	**-932**	**1903**	**0.380**
2	✓	✓+		✓+	✓+	18	-933	1903	0.366
3	✓	✓+	✓	✓	✓+	16	-937	1906	0.065
4	✓	✓+		✓	✓+	15	-938	1907	0.048
5	✓	✓	✓	✓+	✓+	16	-938	1907	0.040
6	✓	✓		✓+	✓+	15	-939	1908	0.027
7	✓			✓+	✓+	14	-940	1908	0.022
8	✓		✓	✓+	✓+	15	-939	1909	0.018
9	✓	✓	✓	✓	✓+	13	-942	1910	0.008
10	✓	✓+		✓+	✓	15	-941	1911	0.005

Table 4.S5: Season length model selection candidate models, with fit statistics. The overall best model is marked by bold text, according to AIC and model parsimony.

Rank	Precip.	Stem diam.	Diurnal dT	Richness	Evenness	DoF	logLik	AIC	W_i
1	✓	✓	✓	✓+	✓+	16	-2898	5829	0.198
2	**✓**	**✓**	**✓**	**✓**	**✓+**	**13**	**-2901**	**5829**	**0.187**
3	✓	✓		✓+	✓+	15	-2900	5830	0.106
4	✓	✓		✓	✓+	12	-2903	5830	0.097
5	✓			✓+	✓+	14	-2901	5830	0.077
6	✓		✓	✓+	✓+	15	-2900	5831	0.074
7	✓			✓	✓+	11	-2904	5831	0.068
8	✓		✓	✓	✓+	12	-2903	5831	0.064
9	✓	✓+	✓	✓+	✓+	19	-2897	5832	0.036
10	✓	✓+	✓	✓	✓+	16	-2900	5832	0.034

Table 4.S6: Green-up rate model selection candidate models, with fit statistics. The overall best model is marked by bold text, according to AIC and model parsimony.

Rank	Precip.	Stem diam.	Diurnal dT	Richness	Evenness	DoF	logLik	AIC	W_i
1			**✓**			**6**	**-2071**	**4154**	**0.165**
2		✓+	✓			10	-2068	4156	0.074
3		✓	✓			7	-2071	4156	0.074
4			✓	✓		7	-2071	4156	0.072
5			✓		✓	7	-2071	4156	0.068
6	✓		✓			7	-2071	4156	0.067
7	✓	✓+	✓			11	-2068	4157	0.038
8		✓+	✓	✓		11	-2068	4157	0.036
9		✓	✓	✓		8	-2071	4157	0.033
10		✓	✓		✓	8	-2071	4157	0.033

Table 4.S7: Senescence rate model selection candidate models, with fit statistics. The overall best model is marked by bold text, according to AIC and model parsimony.

Rank	Precip.	Stem diam.	Diurnal dT	Richness	Evenness	DoF	logLik	AIC	W_i
1	✓		✓			7	-1884	3783	0.079
2	**✓**					**6**	**-1886**	**3783**	**0.059**
3	✓		✓	✓	✓	9	-1883	3784	0.055
4			✓			6	-1886	3784	0.048
5	✓	✓	✓			8	-1884	3784	0.045
6	✓	✓	✓	✓	✓	10	-1882	3784	0.044
7	✓		✓	✓		8	-1884	3784	0.039
8	✓		✓		✓	8	-1884	3784	0.037
9	✓			✓	✓	8	-1884	3785	0.034
10	✓				✓	7	-1885	3785	0.030

Table 4.S8: Green-up lag model selection candidate models, with fit statistics. The overall best model is marked by bold text, according to AIC and model parsimony.

Rank	Precip.	Stem diam.	Diurnal dT	Richness	Evenness	DoF	logLik	AIC	W_i
1	**✓**		**✓**	**✓**	**✓**	**9**	**-2464**	**4946**	**0.203**
2	✓		✓	✓+	✓	12	-2461	4946	0.190
3	✓	✓	✓	✓+	✓	13	-2460	4947	0.119
4	✓	✓	✓	✓	✓	10	-2463	4947	0.118
5	✓		✓	✓+	✓+	15	-2458	4947	0.109
6	✓		✓	✓	✓+	12	-2461	4947	0.105
7	✓	✓	✓	✓	✓+	13	-2461	4948	0.061
8	✓	✓	✓	✓+	✓+	16	-2458	4948	0.059
9	✓	✓+	✓	✓	✓	13	-2462	4951	0.015
10	✓	✓+	✓	✓+	✓	16	-2460	4952	0.009

Table 4.S9: Senescence lag model selection candidate models, with fit statistics. The overall best model is marked by bold text, according to AIC and model parsimony.

Rank	Precip.	Stem diam.	Diurnal dT	Richness	Evenness	DoF	logLik	AIC	W_i
2	**✓**	**✓**	**✓**	**✓+**		**12**	**-2840**	**5704**	**0.149**
3	✓	✓	✓	✓+	✓	13	-2839	5704	0.143
4	✓	✓+	✓	✓+	✓+	19	-2833	5704	0.119
5	✓	✓	✓		✓+	12	-2841	5705	0.061
6	✓	✓	✓	✓	✓+	13	-2840	5706	0.058
7	✓	✓	✓			8	-2845	5706	0.038
8	✓	✓+	✓	✓	✓+	16	-2837	5707	0.029
9	✓	✓+	✓	✓+	✓	16	-2838	5707	0.026
10	✓	✓+	✓		✓+	15	-2839	5707	0.025

Chapter 5

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

The following chapter has been prepared for submission to *Journal of Ecology*. Extended methods are presented in Chapter 6.

Authors: John L. Godlee[1], Francisco Maiato Gonçalves[2], José João Tchamba[2], Antonio Valter Chisingui[2], Casey M. Ryan[1], Kyle G. Dexter[1,3]

1. School of GeoSciences, University of Edinburgh, Edinburgh, EH9 3FF, United Kingdom
2. Herbarium of Lubango, ISCED Huíla, Sarmento Rodrigues Str. No. 2, CP. 230, Lubango, Angola
3. Royal Botanic Garden Edinburgh, Edinburgh, EH3 5LR, United Kingdom

Author Contributions: JLG conceived the study, conducted the analysis, and wrote the first draft of the manuscript. FMG, JJT, and AVC assisted with data collection in Angola. CMR was responsible for plot data in Tanzania. KGD and CMR contributed to manuscript editing.

Abstract

Atmospheric CO_2 enrichment and human-induced climate change are expected to drive woody encroachment and increased tree growth rates across African savannas, with consequences for ecosystem function, particularly related to carbon dynamics. The vegetation dynamics of savanna-woodland mosaics are complex however, as woody growth is mediated by seasonal fire that is itself driven by properties of the woody overstorey. It is unclear how variation in tree species composition and stand structure in this ecosystem affects woody canopy complexity, and how this might determine future vegetation dynamics. Here, I conducted a study of canopy structure in southern African savannas using terrestrial LiDAR, at sites in Bicuar National Park, Angola and Mtarure Forest Reserve, Tanzania, to explore relationships between tree species diversity, species composition, the spatial distribution of trees, variation in tree size and canopy complexity. Species diversity was found to have consistent weak positive effects on plot scale canopy complexity metrics related to canopy density, but a negative effect on metrics related to the spatial heterogeneity of canopy material distribution. Species diversity was associated with an increase in canopy height, canopy closure, and within-canopy structural complexity, together suggesting that diverse canopies may promote woody encroachment and exhibit higher upper limits on biomass. Stochasticity in neighbourhood scale stand structure partially weakened species diversity effects at small spatial scales. Finally, while tree species diversity did affect tree size variation, tree size variation itself did not influence canopy complexity. As species diversity also influenced canopy foliage volume, this suggests a partial decoupling of tree stem size and canopy foliage volume, highlighting species-specific differences in crown shape that are independent from tree size.

5.1 Introduction

Atmospheric CO_2 enrichment, coupled with climate change and changing disturbance regimes, is expected to drive woody encroachment, i.e. the proliferation of trees into previously non-wooded areas, along with increased stem density and growth of trees in currently wooded areas, here termed woody densification, across the savanna biome over the coming century (Mitchard & Flintrop, 2013; Criado et al., 2020; Stevens et al., 2017). As atmospheric CO_2 concentrations increase, C_3 trees are expected to gain a competitive edge over C_4 grasses due to differences in photosynthetic pathway and carbon use efficiency (Buitenwerf et al., 2012), allowing trees to increase their productivity. This is expected to have cascading effects on canopy cover, grass growth, and disturbance regime (Bond & Midgley, 2012). If realised, woody encroachment and woody densification will have significant effects on the global carbon cycle, as more CO_2 is stored in 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 densification (Mitchard & Flintrop, 2013), particularly in disturbance-prone savannas such as miombo woodlands in southern Africa (Axelsson & Hanan, 2018), and it is unclear how the fertilisation effect of atmospheric CO_2 enrichment interacts with other ecosystem properties and processes to alter vegetation structure (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 C_4 grasses where climatic conditions would otherwise allow for closed canopy forest (Sankaran et al., 2005). C_4 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 CO_2 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 and density 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 (Gough et al., 2019; 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; Sercu et al., 2017; Fotis et al., 2018), and greater moderation of understorey micro-climate (Wright et al., 2017). 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 complexity constituting a mechanism for positive biodiversity-ecosystem function effects observed 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 CO_2, where competition effects in diverse tree communities are reduced due to niche separation, and can more effectively increase foliage density and reduce understorey light penetration (Sercu et al., 2017), excluding grass and thus reducing both the likelihood and intensity of disturbance.

As well as the species diversity of trees, the spatial distribution and relative size of tree stems, i.e. stand structure, is also expected to affect canopy structural complexity (Stark et al., 2015). Heterogeneity in stem 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 at local spatial scales (Schertzer et al., 2015; Groen, 2007), facilitation effects among individuals in stressful environments (Ratcliffe et al., 2017), due to other limitations on dispersion arising from growth strategy (Silva & Batalha, 2011), or from environmental heterogeneity (Getzin et al., 2008). More diverse communities may allow greater stem density and greater foliage density within clusters, as differences in canopy occupancy among species reduce negative effects competition among individuals on growth (Gough et al., 2019), and reduce the number of natural enemies, which causes negative density dependence in low diversity wooded ecosystems (Janzen, 1970).

Functional differences among floristic types of savanna may also drive variation in canopy complexity, irrespective of species diversity. Some savanna trees form denser canopies than others, as a result of variation in leaf size and branch architecture (Charles-Dominique et al., 2018). Previous studies have compared the branch architecture of ex-Acacia (e.g. *Senegalia* and *Vachellia* spp.) and miombo (e.g. *Julbernardia*, *Brachystegia*, and *Isoberlinia*) archetypal tree species. While ex-Acacia species tend to inhabit drier, heavily grazed areas, miombo species tend to inhabit dystrophic wetter areas structured heavily by fire (Ribeiro et al., 2020). These studies have shown that ex-Acacia species develop sparser canopies, cagey branch architecture, and wider spreading crowns, while dominant Fabaceae species from the miombo develop thicker, taller canopies, and can grow to larger sizes (Mugasha et al., 2013; Archibald & Bond, 2003; Privette et al., 2004). Similarly, dominant miombo Fabaceae species from the Detarioideae subfamily have been shown to develop wider crowns and grow taller than coexisting miombo species from the Combretaceae family. Shenkin et al. (2020) showed that Fabaceae tree species from tropical forests develop wider and more voluminous tree crowns than other common families of tropical trees. Under identical stem densities, miombo woodland species may therefore exclude grass more effectively than ex-Acacia or Combretaceae species given these differences in growth form.

Canopy complexity 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 complexity 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 remain an over-simplification of canopy structure. Alternatively, canopy closure 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 it's complexities (Muir et al., 2018; Calders et al., 2020). In tropical savannas, very few studies have used terrestrial LiDAR for vegetation analyses, and in southern Africa all existing studies have been located at the Skukuza Flux Tower in Kruger National Park, South Africa (Muumbe et al., 2021). Pioneering work describing the ecology of southern African savannas placed large emphasis on canopy structural diversity as a mediator of ecosystem function (Solbrig et al., 1996), but much of that understanding of savanna vegetation structure was derived from traditional mensuration methods. Using terrestrial LiDAR to measure canopy complexity in southern African savannas therefore offers a unique chance to validate accepted theory and to describe differences in canopy structure among savanna vegetation types in finer detail than previously possible.

In this study I applied terrestrial LiDAR techniques to savanna-woodland mosaics at two sites in southern Africa, with the aim of increasing understanding of how various measures of tree canopy complexity relate to tree diversity and stand structure. I hypothesise that tree neighbourhoods with greater tree species diversity, greater heterogeneity in stem size, and greater spatial variation in stem density, allow greater canopy complexity and foliage density. Thus, more diverse savannas might exhibit a higher potential woody biomass, greater productivity, and more effectively increase their growth under elevated atmospheric CO_2, promoting woody thickening. I also consider the functional differences in canopy architecture among tree communities and how this affects canopy closure and total canopy occupancy.

5.2 Materials and methods

5.2.1 Study sites

Field measurements were conducted at two sites, Bicuar National Park, in southwest Angola (S15.1°, E14.8°), and Mtarure Forest Reserve, in southeast

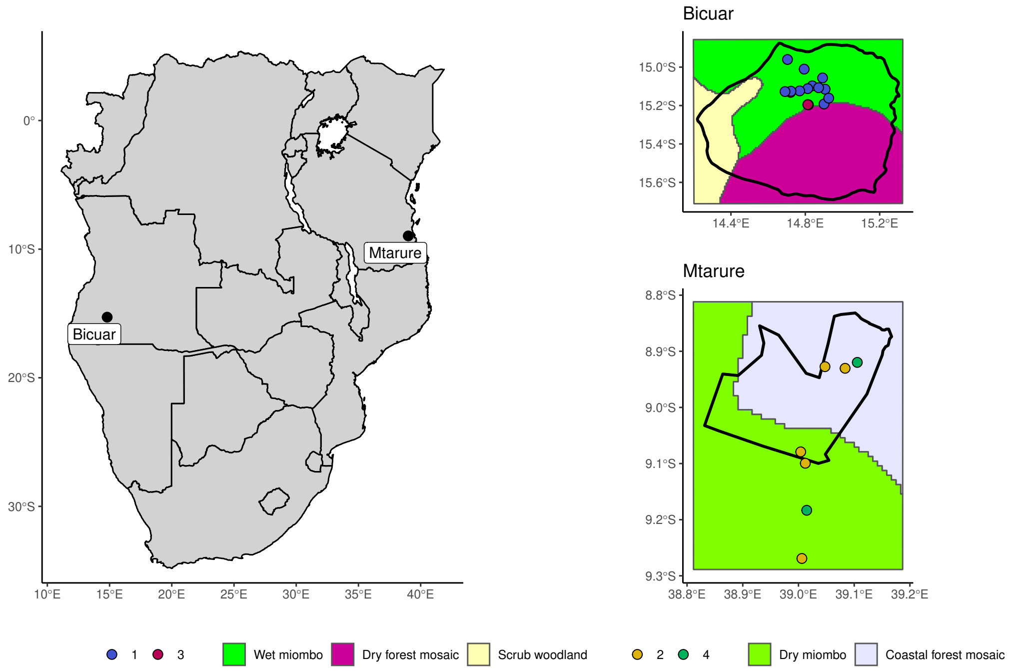


Figure 5.1: Location of study sites within southern Africa (left), and of 1 ha plots within each site (right). The black outlines in each site map denote the boundaries of protected areas which encompass the majority of study sites, Bicuar National Park in Angola (top), and Mtarure Forest Reserve in Tanzania (bottom). The background of each site map is a re-classified version of White's vegetation map (White, 1983). Points in site maps are shaded according to vegetation type identified by hierarchical clustering of tree genera abundances. Note that all maps are on different scales.

Tanzania (S9.0°, E39.0°) (Figure 5.1). At each site, 1 ha (100×100 m) plots were located in areas of savanna-woodland vegetation, across a gradient of stem density and covering a range of savanna floristic archetypes. In Angola, 15 plots were sampled, while in Tanzania only 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 maximum foliage volume in the canopy.

5.2.2 Field measurements

Within each 1 ha plot, each woody stem $\geq$5 cm stem diameter was identified to species, the stem Diameter at Breast Height (DBH) was measured at 1.3 m above the ground, and the stem location within the plot was recorded using tape measures. Each 1 ha plot was sampled by 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, the distance and direction from the subplot centre of each stem >5 cm diameter with canopy material inside the subplot was recorded. 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, to minimise shadows within the canopy of the subplot, and to maximise canopy penetration (Béland & Kobayashi, 2021). The number of scans per subplot ranged between one and five across both sites. Extended field methods and data analysis methods are described in Chapter 6.

5.2.3 Data analysis

TLS processing

Point clouds from scans in each subplot were registered and unified using Leica Cyclone (version 9.1), with five reflective cross targets visible to all scans used as anchor points. Point clouds were voxelised to cubic voxels of different sizes depending on the application of the data. Subplot height profiles and canopy closure estimates were calculated using 5 cm^3 voxels, while whole plot canopy rugosity and canopy surface roughness were calculated using 50 cm^3 voxels. Voxels were classified as ‘filled’ if they intersected 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 (Cifuentes et al., 2014). Choosing voxels that are too small can result in pock-marked representations of surfaces that are especially problematic when calculating larger scale canopy complexity 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).

The noise reduction algorithm from Rusu et al. (2008) was used to discard points based on mean nearest neighbour distances, with a number of neighbours of eight, and a standard deviation threshold of 1.96. 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 these study sites. Raw points clouds for each subplot had a mean of ~2.9e+08 points, ~4.5e+07 points after voxelisation to 5 cm^3, 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 based on this revised ground layer by measuring the vertical distance between the nearest ground point and each point. Points below 1.3 m height above ground were discarded for calculations of foliage density, canopy cover, and canopy complexity, as points below this threshold were often occupied by long grass.

Canopy complexity metrics

Ray-tracing was used to estimate canopy closure in each subplot, i.e. the proportion of the sky hemisphere occluded by plant material at the subplot centre from multiple TLS scans. Hemispherical images were created using the POV-Ray ray-tracing software (Persistence of Vision Pty. Ltd., 2004). Filled voxels were represented as 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 1.3 m pointing directly upwards. The images produced by POV-Ray were analysed using Hemiphot to estimate canopy closure (ter Steege, 2018). Canopy closure estimates from the TLS were validated with hemispherical photographs taken at the same location and processed using the same method in Hemiphot, and compared using Pearson’s correlation ($r(195)=0.87$, $p<0.001$). A plot level estimate of canopy closure was calculated as the mean of subplot canopy closure measurements. See Chapter 6 for expanded methods and explanation of the behaviour of the different canopy complexity metrics.

Effective Number of Layers (ENL) was calculated according to Ehbrecht et al. (2016) to measure vertical variation in subplot foliage density. ENL is calculated as the exponential Shannon index (i.e. the Hill number of order $q = 1$) of foliage density among 50 cm vertical layers within each subplot:

$$\text{ENL} = \exp\Big(-\sum_{i=1}^{N} p_i \times \ln p_i \Big) \tag{5.1}$$

Where p_i is the proportion of filled voxels in the 50 cm layer i, and N is the total number of layers. ENL increases with canopy height and thus with number of layers, and also with variation in foliage density among those layers, but not with increased total foliage density.

Total foliage density was calculated within each subplot as the area under the curve of the foliage height profile. Total foliage density was also calculated at the plot level as the sum of filled 50 cm^3 voxels across the plot. Vertical variation in subplot foliage density was calculated by fitting a linear model to the cumulative foliage density profile, then calculating the sum of squared residuals of that model. If foliage was distributed evenly throughout the vertical canopy profile, the residuals from the linear model would be zero, while clumping of foliage would cause departures from a linear cumulative foliage density profile.

Plot level canopy surface models were extracted using the 99th percentile of canopy height in 10 cm^2 columns. A pit-filling algorithm provided by Khosravipour et al. (2014) was applied at 50 cm^2 resolution to reduce the effects of incomplete canopy penetration in dense canopies. Whole plot canopy complexity was measured by three metrics. Canopy top roughness was measured as the coefficient of variation (CV) of canopy surface height across the plot. Canopy rugosity was measured according to Hardiman et al. (2011), as the CV of vertical and horizontal foliage density within 50 cm^3 cubic bins. Finally, canopy height was calculated as the mean of the canopy surface model across the plot.

Stand structure and diversity

An adapted version of the iterative Hegyi index was used to estimate crowding at the subplot scale. The iterative Hegyi index was used as an alternative to stem density, which does not adequately capture crowding at small spatial scales when only a small number of trees are included in the sample (Hegyi, 1974). The CV of stem basal area was calculated as a measure of the heterogeneity of tree size in the subplot neighbourhood. The iterative Hegyi index positively scales with stem diameter, number of stems, and the proximity of stems to the sample point (Chapter 6).

At the plot level, the regularity of species spatial distribution was estimated using the spatial mingling index (von Gadow & Hui, 2002), which scores each tree based on whether it shares species identity with its nearest neighbours. The spatial regularity of tree location was estimated using the uniform angle index (winkelmass) (von Gadow & Hui, 2002), which scores each tree based on the angles between nearest neighbours. Additionally, the degree of spatial clustering of trees was measured using Voronoi tessellation of tree locations, as the CV of Voronoi cell areas (Ong et al., 2012). Voronoi cell area CV increases as the spatial clustering of trees increases (Chapter 6). Finally, plot level tree density was calculated to estimate crowding at the plot scale. See Chapter 6 for more information on the behaviour of the spatial mingling index, uniform angle index, and Voronoi cell area CV.

Species diversity at both the subplot and plot level was measured using the exponential Shannon index (i.e. the Hill number of order $q = 1$), calculated using tree species abundances (Hill, 1973; Jost, 2006). At the subplot level trees were included if they had canopy material inside the 10 m diameter subplot, while at the plot level trees were included if the base of the largest stem was inside the plot boundaries.

Statistical analysis

Non-metric Multi-dimensional Scaling (NMDS) was used to describe variation in species composition among plots, using genus-level basal area weighted abundance in each plot. Trees that could not be identified to genus were excluded from this analysis, which accounted for 0.2% of the total basal area recorded. Four distinct vegetation types, two from each site (Table 5.1), were identified using hierarchical clustering of the four dominant NMDS ordination axes using Ward's algorithm. Clusters were further described using Dufrêne-Legendre indicator species analysis and by ranking tree species according to abundance across all plots within each cluster.

Linear mixed effects models tested the effects of tree species diversity and stand structural diversity on subplot canopy complexity metrics. Mixed models used a nested random intercept structure to account for the sampling design of subplots within plots and plots within vegetation types. Separate

Table 5.1: Description of vegetation type clusters. AGB = Above-Ground woody Biomass. Species richness, stem density and AGB are reported as the median among plots, with the interquartile range in parentheses.

Site	Cluster	N plots	Richness	Stem density (stems ha^{-1})	AGB (t ha^{-1})
Bicuar	1	12	17(2)	642(194)	41(8.4)
Mtarure	2	5	23(4)	411(137)	72(11.9)
Bicuar	3	3	6(1)	196(55)	77(7.3)
Mtarure	4	2	12(2)	288(73)	9(0.2)

models were fitted for each canopy complexity metric. Effect sizes among fixed effects in maximal models were compared for each canopy complexity metric, significance of fixed effects was determined by whether the 95% confidence interval overlapped zero (Nakagawa & Cuthill, 2007). AIC values and Akaike weights of models with different combinations of fixed effects were compared to determine which combination of diversity and structural metrics best explained variation in each canopy complexity metric.

Statistical analyses of the determinants of plot level canopy complexity metrics were conducted using linear models. The ex-Acacia vegetation type was represented by only two plots and could not be included in this model due to lack of replication. As with the subplot linear mixed models, effect sizes were used to assess predictor variable significance, and comparison of candidate models using AIC, Akaike weights, and model R^2 values was used to determine which combination of predictors best explained each canopy complexity metric.

Path analysis was used to test whether tree species diversity influences canopy complexity indirectly through its effect on stand structure, using the `piecewiseSEM` R package (Lefcheck, 2016). Two path analyses were conducted, one at the plot level and one at the subplot level. Subplot path analysis investigated the direct effect of species diversity on canopy closure, as well as the indirect effect of diversity on canopy closure via the CV of basal area, with random intercept terms for each vegetation type. Plot level path analysis investigated the direct effects of species diversity and spatial mingling of species on mean canopy height, as well as the indirect effects of these metrics on canopy height via tree density and basal area CV. Again, these models excluded the ex-Acacia vegetation type due to lack of replication.

Table 5.2: Floristic description of the vegetation type clusters. Dominant species are the most abundant individuals across all plots within each cluster. Indicator species are the three species with the highest indicator values, from Dufrêne-Legendre indicator species analysis.

Cluster	Dominant species	Indicator species	Indicator value
1	Julbernardia paniculata	Strychnos spinosa	0.83
	Burkea africana	Combretum collinum	0.74
	Combretum collinum	Julbernardia paniculata	0.70
2	Diplorhynchus condylocarpon	Pteleopsis myrtifolia	1.00
	Pseudolachnostylis maprouneifolia	Diplorhynchus condylocarpon	0.89
	Gymnosporia senegalensis	Pseudolachnostylis maprouneifolia	0.81
3	Baikiaea plurijuga	Baikiaea plurijuga	0.94
	Baphia massaiensis	Baphia massaiensis	0.83
	Philenoptera nelsii	Philenoptera nelsii	0.45
4	Combretum apiculatum	Vachellia nilotica	0.99
	Burkea africana	Combretum apiculatum	0.70
	Bauhinia petersiana	Senegalia polyacantha	0.62

5.3 Results

5.3.1 Description of vegetation types

Indicator species analysis shows that the four vegetation types identified by hierarchical clustering constitute common southern African savanna floristic archetypes (Table 5.2). Cluster 1, found in Bicuar National Park contains typical miombo species from the Detarioideae subfamily, such as *Julbernardia paniculata*. Cluster 1 is the most frequent vegetation type in this study, with 12 plots. Cluster 1 has the highest stem density, but lower Above-Ground woody Biomass (AGB) than Clusters 2 or 3, which contain larger individuals with disproportionately higher biomass. Cluster 2, found in Mtarure Forest Reserve, is dominated by *Pteleopsis myrtifolia*, a common miombo species from the Combretaceae family. Indeed, Cluster 2 also contained other common miombo species shared with plots in Cluster 1, such as *Julbernardia globiflora* and *Pseudolachnostylis maprouneifolia*, but these clusters remain distinct due to biogeographic variation in endemic genera at the longitudinal extremes of the miombo ecoregion represented by the two sites in this study. Cluster 3 represents *Baikiaea* woodland, found on Kalahari sands in southern Angola. It is species poor and dominated by *Baikiaea plurijuga* which forms large spreading canopy trees with high AGB. Other shrubby species that coppice readily in response to disturbance by fire such as *Baphia massaiensis* are also common. Cluster 4, found in Mtarure is a type of ex-Acacia woodland, dominated by *Vachellia* and *Senegalia* spp. This vegetation type was not well represented in the study, with only two plots, precluding its use in some multi-level statistical analyses at the plot level due to lack of replication. Cluster 4 had far lower AGB than the other clusters (Table 5.1).

Differences in canopy structure among the four vegetation types are evident through observation of canopy surface models for typical plots within each vegetation type (Figure 5.5), and by comparing canopy complexity metrics (Figure 5.6). Cluster 1 shows many overlapping crowns forming a nearly contiguous canopy surface, and the highest plot foliage density of all clusters. Though the tallest trees in Cluster 1 have smaller crowns than those in Cluster 2, which also forms a nearly contiguous canopy. The largest trees in Cluster 2 grow taller and have a wider spreading canopy than those in other vegetation types. Cluster 3 shows two distinct size classes of tree, the large *Baikiaea* *plurijuga* forming clear isolated canopies, and much smaller scattered shrubby individuals in the understorey. Cluster 4 shows many small shrubby individuals with irregular canopy shapes, but a greater total crown area coverage than Cluster 3.

5.3.2 Bivariate relationships

Bivariate plots and linear models show that subplot species diversity, measured as the true-numbers equivalent of the Shannon diversity index of the tree neighbourhood around each 10 m diameter subplot, appears to have weak positive effects on subplot canopy layer diversity, canopy closure and foliage density (Figure 5.3, Table 5.3). The Hegyi crowding index had strong positive effects on canopy closure and layer diversity, as expected. The effect of Hegyi crowding on subplot canopy complexity metrics was similar across all vegetation types (Table 5.S1). Structural diversity, measured as the CV of subplot stem basal area had significant weak positive effects on total canopy foliage, layer diversity, and canopy closure.

At the plot level, effects of species diversity and stand structure on canopy complexity were similarly weak, but not strictly significant except for the effect on canopy height, which explained more variance in canopy height than tree density (Table 5.3, Figure 5.4). The effect of spatial regularity of trees on canopy closure, measured by uniform angle index, was clearly negative, while the effect of spatial clustering of stems, measured by Voronoi cell area CV, was negligible. Additionally, there was a non-significant negative effect of basal area CV on whole canopy rugosity. As expected, tree density had strong positive and significant effects on foliage density and canopy closure, but negative effects on canopy roughness and canopy rugosity. Cluster 4 represented an outlier in plot level bivariate relationships, with low canopy closure, low canopy height, low species diversity, and low variation in stem size.

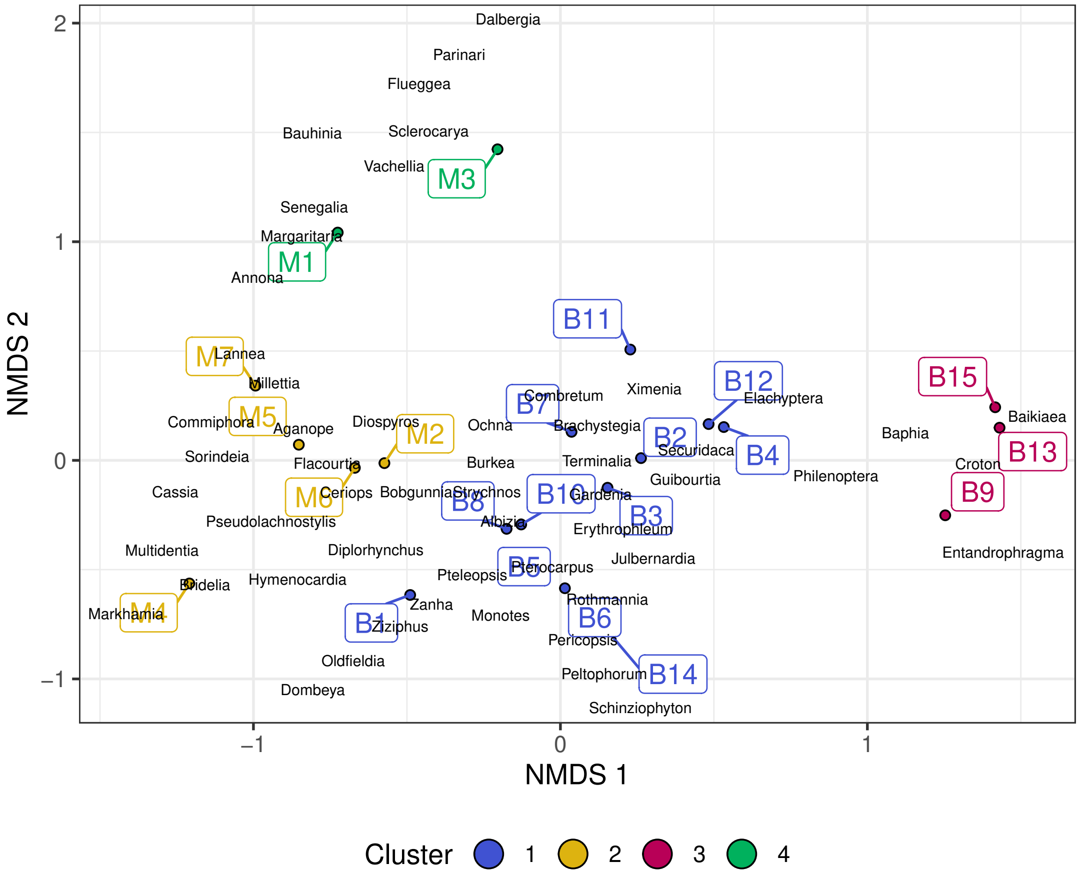


Figure 5.2: The first two axes of a Non-metric Multi-Dimensional Scaling (NMDS) analysis of tree genus diversity in each plot. Genus scores are labelled as black text, while plot scores are labelled as coloured points. Plots are shaded by vegetation type, identified by hierarchical clustering: 1) B1-B8, B10-B12, B14, dominated by core miombo species such as *Julbernardia* spp., *Brachystegia* spp.; 2) M2, M5, M6, and M7, also dominated by core miombo genera with some genera not found in Bicuar National Park such as *Commiphora* and *Sorindeia*; 3) B9, B13 and B15, dominated by *Baikiaea plurijuga*; and 4) M1, M3, and M4, dominated by *Senegalia* spp., *Vachellia* spp., and *Combretum* spp.

Table 5.3: Summary statistics of bivariate linear models comparing canopy complexity metrics with diversity and stand structural metrics across all vegetation types. Slope refers to the slope of the predictor term in the model, ±1 standard error. T is the t-value of the slope of the predictor term in the model, Asterisks indicate the p-value of these terms (***<0.001, **<0.01, *<0.05).

Response	Predictor	Slope	F	R^2	T
Foliage density	Basal area CV	8.7e+01±3.0e+01	8.6(167)	0.05	2.93**
	Hegyi	7.8e+03±1.6e+03	25.5(184)	0.12	5.05***
	Shannon	3.2e+03±1.1e+03	8.9(180)	0.05	2.98**
Canopy closure	Basal area CV	1.2e-03±4.8e-04	6.3(168)	0.04	2.52*
	Hegyi	2.4e-01±2.1e-02	132.8(185)	0.42	11.52***
	Shannon	4.7e-02±1.7e-02	7.3(181)	0.04	2.70**
Foliage uniformity	Basal area CV	4.1e+00±3.0e+00	1.9(167)	0.01	1.37
	Hegyi	4.0e+02±1.6e+02	6.2(184)	0.03	2.49*
	Shannon	2.2e+02±1.1e+02	4.1(180)	0.02	2.04*
Layer diversity	Basal area CV	3.2e-02±7.6e-03	17.6(167)	0.10	4.20***
	Hegyi	2.7e+00±3.9e-01	46.8(184)	0.20	6.84***
	Shannon	1.1e+00±2.7e-01	16.8(180)	0.09	4.10***
Canopy roughness	Basal area CV	3.0e-02±5.0e-02	0.4(16)	0.02	0.60
	Voronoi CV	7.5e-01±5.9e-01	1.6(16)	0.09	1.26
	Mingling	-2.8e+01±3.3e+01	0.7(16)	0.04	–0.86
	Tree density	-2.6e-02±1.7e-02	2.3(16)	0.12	–1.51
	Shannon	-1.9e+00±9.5e-01	4.0(16)	0.20	–2.01
	Uniform angle index	1.6e+02±1.6e+02	1.0(16)	0.06	0.98
Canopy height	Basal area CV	7.1e-03±7.3e-03	0.9(16)	0.06	0.97
	Voronoi CV	-4.7e-02±9.1e-02	0.3(16)	0.02	–0.52
	Mingling	3.8e+00±4.8e+00	0.6(16)	0.04	0.79
	Tree density	4.3e-03±2.5e-03	3.1(16)	0.16	1.76
	Shannon	3.3e-01±1.3e-01	6.0(16)	0.27	2.45*
	Uniform angle index	-2.2e+01±2.4e+01	0.8(16)	0.05	–0.90

Continued overleaf

Response	Predictor	Slope	F	R^2	T
Canopy closure	Basal area CV	8.5e-04±5.7e-04	2.2(20)	0.10	1.50
	Voronoi CV	2.4e-03±5.8e-03	0.2(20)	0.01	0.41
	Mingling	7.2e-03±3.7e-01	0.0(20)	0.00	0.02
	Tree density	4.7e-04±1.9e-04	6.3(20)	0.24	2.50*
	Shannon	1.0e-02±1.2e-02	0.7(20)	0.04	0.86
	Uniform angle index	-3.4e+00±1.7e+00	3.9(20)	0.16	–1.98
Foliage density	Basal area CV	5.8e+01±3.2e+01	3.3(16)	0.17	1.80
	Voronoi CV	5.8e+02±4.1e+02	2.1(16)	0.11	1.43
	Mingling	6.6e+03±2.3e+04	0.1(16)	0.01	0.29
	Tree density	3.0e+01±1.0e+01	8.6(16)	0.35	2.93**
	Shannon	1.1e+03±6.9e+02	2.5(16)	0.13	1.57
	Uniform angle index	-2.1e+04±1.1e+05	0.0(16)	0.00	–0.18
Canopy rugosity	Basal area CV	-1.0e+00±5.3e-01	3.7(16)	0.19	–1.92
	Voronoi CV	-6.0e+00±7.0e+00	0.7(16)	0.04	–0.86
	Mingling	1.3e+02±3.8e+02	0.1(16)	0.01	0.33
	Tree density	-5.2e-01±1.7e-01	10.0(16)	0.38	–3.16**
	Shannon	-1.3e+01±1.2e+01	1.2(16)	0.07	–1.11
	Uniform angle index	-1.8e+03±1.9e+03	0.9(16)	0.06	–0.97

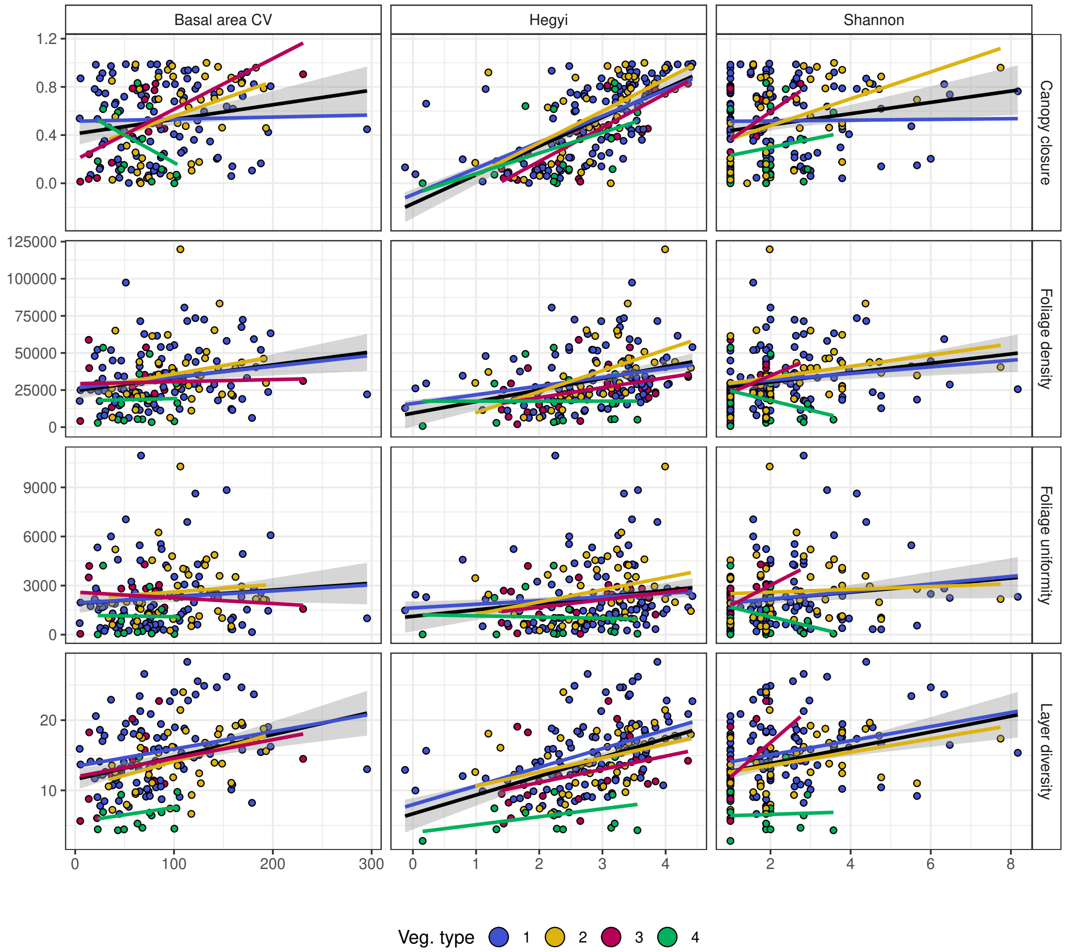


Figure 5.3: Subplot level bivariate relationships between diversity/stand structure metrics (x axis) and canopy complexity metrics (y axis). Points and linear model lines of best fit are coloured by vegetation type. Black lines of best fit are linear models including all plots, with a 95% confidence interval. See Table 5.S1 for a comparison of linear model fits by vegetation type.

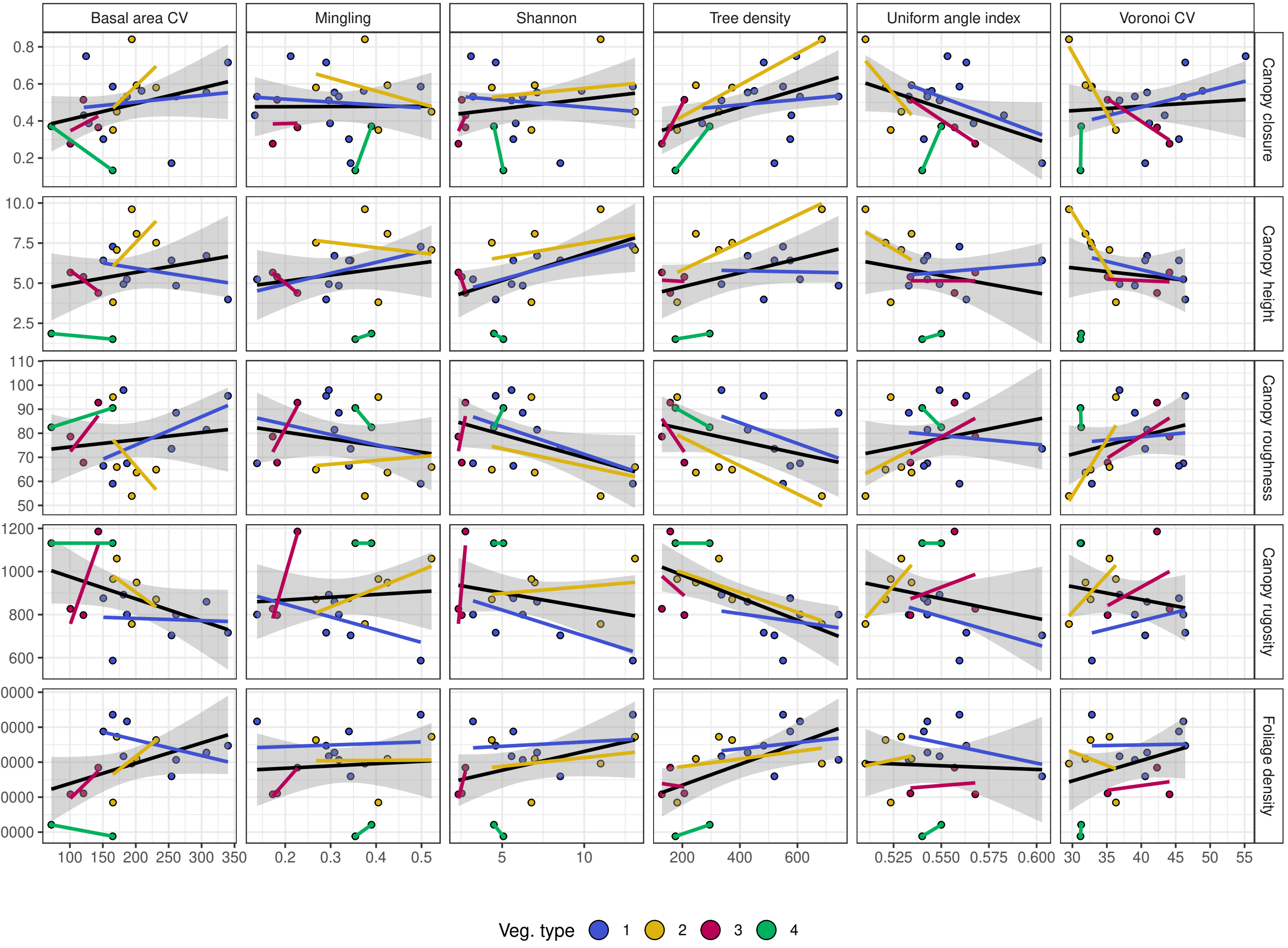


Figure 5.4: Plot level bivariate relationships between diversity/stand structure metrics (x axis) and canopy complexity metrics (y axis). Points and linear model lines of best fit are coloured by vegetation type. Black lines of best fit are linear models including all plots, with a 95% confidence interval. See Table 5.S1 for a comparison of linear model fits by vegetation type.

Table 5.4: Explanatory variables included in the best model for each subplot canopy complexity variable. ΔAIC shows the difference in model AIC value compared to a null model which included only the random effects of vegetation type and plot. ΔAIC values >2 indicate that the model is of better quality than the null model. 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.

Response	Hegyi	Shannon	Basal area CV	ΔAIC	R^2_c	R^2_m
Layer diversity	✓	✓	✓	37.0	0.50	0.17
Foliage density	✓		✓	47.6	0.27	0.09
Foliage uniformity	✓			13.1	0.28	0.02
Canopy closure	✓	✓		101.9	0.60	0.46

5.3.3 Subplot mixed models

Linear mixed effects models showed that species diversity of the subplot neighbourhood contributed to both layer diversity and canopy closure (Table 5.4), despite their low R^2 in bivariate linear models (Table 5.3), and low effect sizes in maximal linear mixed models (Figure 5.7). As also seen in the subplot bivariate relationships (Figure 5.3), the Hegyi crowding index had strong positive effects on canopy closure and layer diversity, though these effects were non-significant for vegetation Clusters 3 and 4. Stem basal area CV had a significant positive effect on layer diversity and foliage density, but there was wide variation in vegetation type marginal effects for Clusters 3 and 4, due to low levels of replication. Cluster 3 had strong positive effects of species diversity on foliage uniformity and layer diversity. The random effects of vegetation type and plot identity described most of the variation in layer diversity and foliage density. Foliage uniformity was poorly explained by all combinations of fixed effects, with the best model only explaining 29%. All models were better than random effects only models according to AIC values (Table 5.4).

5.3.4 Plot level linear models

While species diversity had varying effects on different plot level canopy complexity metrics, the confidence intervals on these effect sizes were wide (Figure 5.8).

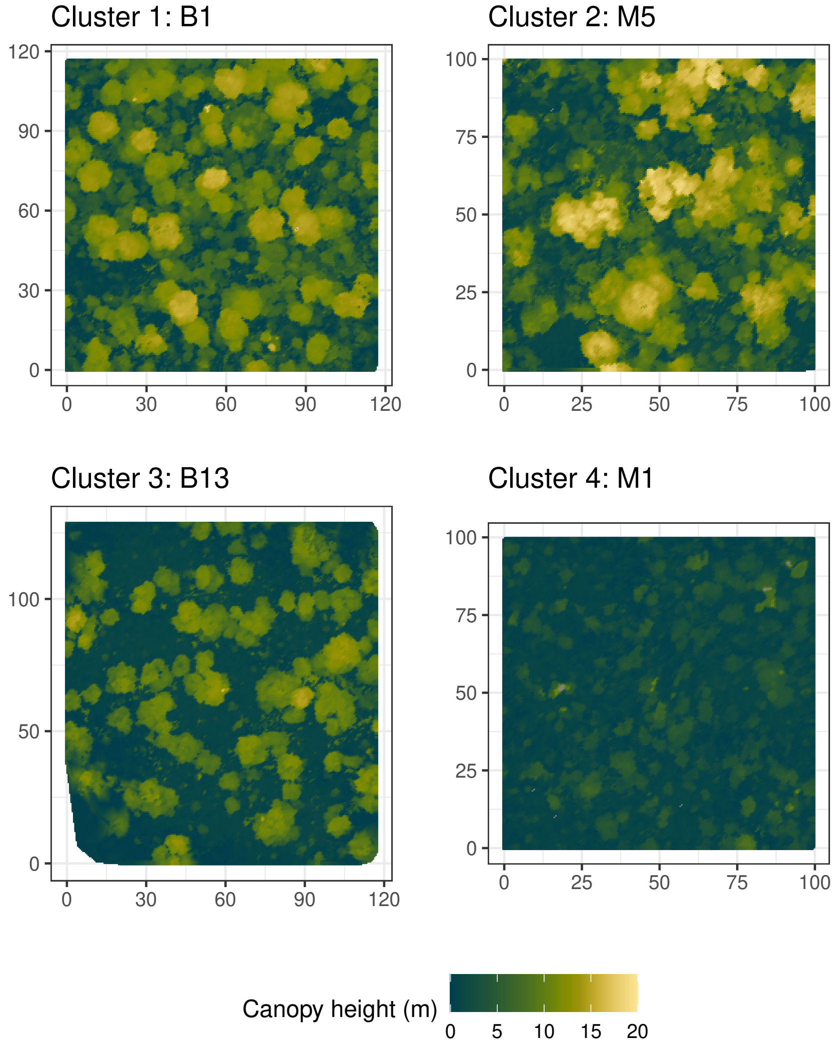


Figure 5.5: Representative canopy surface models for each vegetation type identified in the hierarchical clustering analysis. Panel titles show the plot name and the vegetation type cluster.

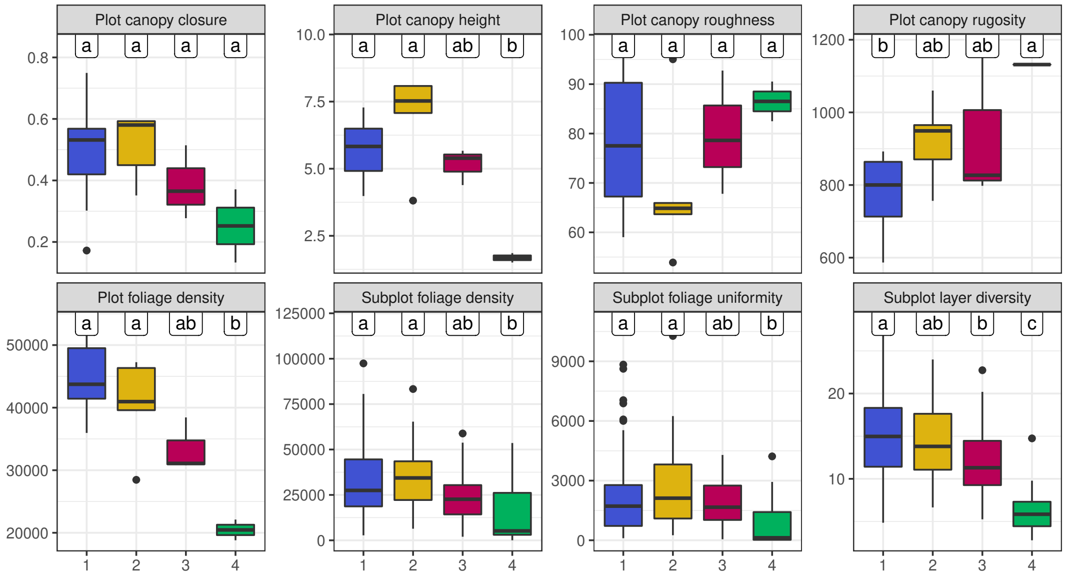


Figure 5.6: Box plots showing variation in canopy complexity metrics among the four vegetation types identified in the hierarchical clustering analysis. Thick lines show the median, boxes show the interquartile range (IQR), whiskers show 1.5×IQR, and points show outliers beyond these limits. Labels above each box plot group vegetation types according to significant differences in pairwise Tukey's tests; vegetation types sharing a letter are not significantly different.

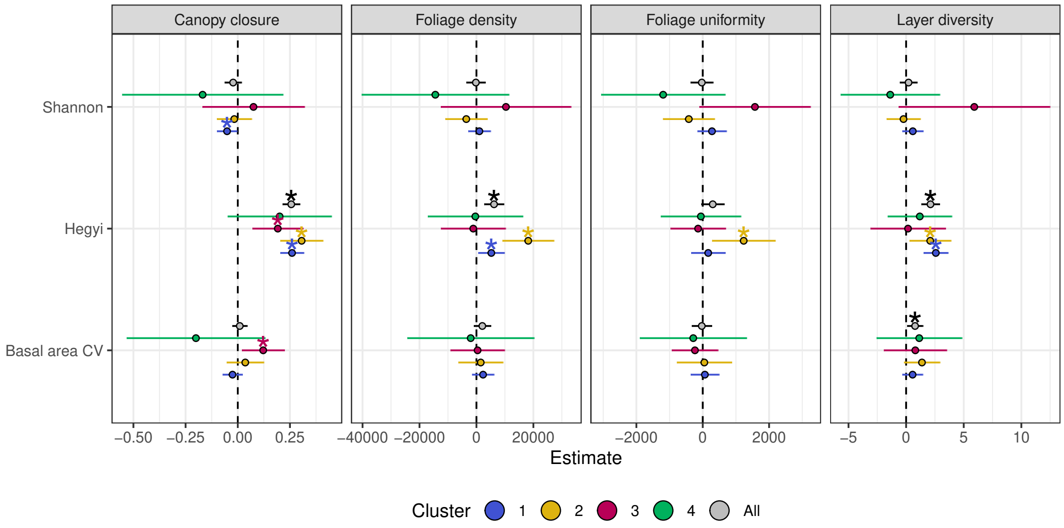


Figure 5.7: Standardised fixed effect slopes for each subplot canopy complexity metric model metric. Slope estimates where the interval (±1 standard error) does not overlap zero are considered to be significant effects, marked with asterisks. Points are coloured according to vegetation type.

Species diversity had a significant positive effect on canopy height (β=3±0.96, p<0.05), a non-significant positive effect on canopy closure (β=0.07±0.085, p=0.41), but a negative effect on canopy surface roughness (β=-13±6.8, p=0.09) and whole canopy rugosity (β=-111±71, p=0.15). Spatial mingling of tree species had a positive effect on canopy surface roughness and canopy rugosity, but a negative effect on canopy height. Plot tree density had negligible effects on canopy complexity, except for canopy rugosity (β=-61±42, p=0.17), in contrast to the effect of Hegyi crowding on subplot canopy complexity. Measures of structural diversity, measured by the uniform angle index, Voronoi cell area CV, and basal area CV, had smaller effects on canopy complexity than species diversity, and were generally insignificant. One exception was the effect of uniform angle index, i.e. the spatial clustering of stems, on canopy closure, which was clearly negative, though still insignificant (β=-0.08±0.043, p=0.1), the effect of Voronoi cell area CV on foliage density, which was positive (β=6199±3312, p=0.09), and the effect of basal area CV on canopy closure, which was positive (β=0.06±0.042, p=0.19).

Despite the weak effect sizes of species diversity on canopy complexity at the plot level, model selection showed that foliage density, canopy height and

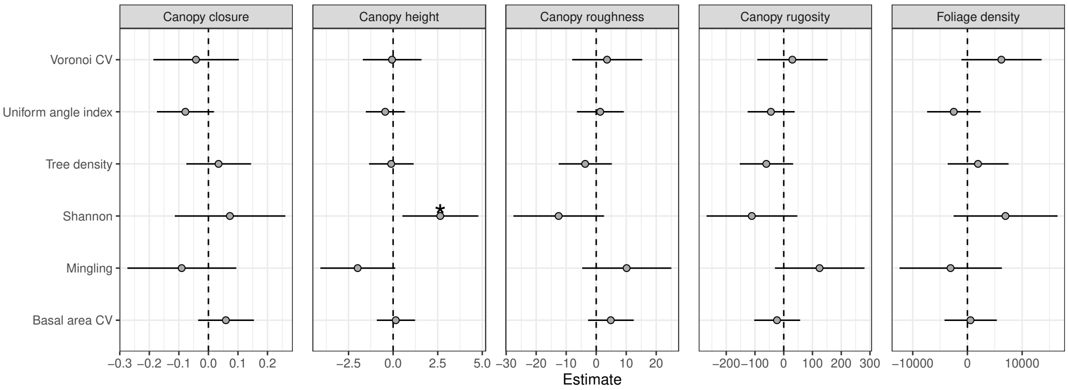


Figure 5.8: Standardised effect sizes for whole-plot canopy rugosity. Slope estimates where the interval (±1 standard error) does not overlap zero are considered to be significant effects, marked with asterisks.

canopy roughness were better explained by models which included species diversity (Table 5.5). Additionally, the best models for canopy height and canopy roughness also included spatial mingling of tree species. The model for canopy roughness was only marginally better than a null model and the model did not have a significant p-value.

Table 5.5: Explanatory variables included in the best linear model for each plot-level canopy complexity metric. ΔAIC shows the difference in model AIC value compared to a null model. ΔAIC values >2 indicate that the model is of better quality than the null model.

Response	Shannon	Tree density	Basal area CV	Mingling	Uniform angle index	Voronoi CV	ΔAIC	R^2	Prob.
Foliage density	✓					✓	5.8	0.42	<0.05
Canopy closure			✓		✓		5.8	0.42	<0.05
Canopy height	✓			✓			8.2	0.49	<0.01
Canopy roughness	✓			✓			2.5	0.30	0.07
Canopy rugosity		✓			✓		6.9	0.45	<0.05

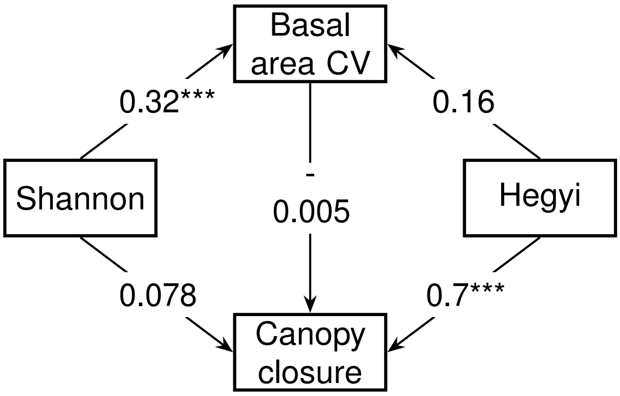


Figure 5.9: Directed Acyclic Graph showing standardised path coefficients of paths in the path analysis of the indirect effect of subplot species diversity (Shannon diversity index) on canopy closure via basal area CV. Asterisks define p-value thresholds: *<0.05, **<0.01, ***<0.001.

5.3.5 Path analysis

The subplot level path analysis investigating the indirect effect of subplot species diversity on canopy closure via the basal area CV showed that while species diversity had a strong positive significant effect on basal area variation, the effect of basal area variation on canopy closure remained negligible (Figure 5.9). The indirect effect of species diversity on canopy closure via basal area CV was -0.0016, while the direct effect was 0.078. The R^2 of this model was 0.47. As in the bivariate relationships and plot level linear models, species diversity had a weak positive significant effect on canopy closure, while the major driver of canopy closure was the Hegyi crowding index.

The plot level path analysis, which tested the effects of species diversity and species mingling on canopy height, showed that the main effect of species diversity on canopy height was direct (1.3*), while the indirect effects via basal area CV (0.0210), and tree density (-0.0294), remained small and insignificant. Shannon diversity had a strong positive effect on tree density. Species mingling had a moderately strong negative but insignificant direct effect on canopy height, as in the linear mixed models and bivariate relationships.

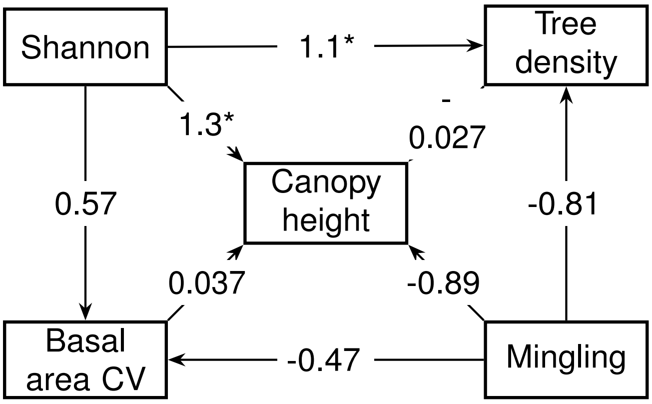


Figure 5.10: Directed Acyclic Graph showing standardised path coefficients of paths in the path analysis of the indirect effect of plot species diversity (Shannon diversity index) and species mingling on mean canopy height via stand structural metrics of basal area CV and tree density. Asterisks define p-value thresholds: *<0.05, **<0.01, ***<0.001.

5.3.6 Covariance of subplot and plot measures of canopy complexity

Plot and subplot canopy complexity metrics were highly correlated in many cases, with similar relationships among vegetation types (Figure 5.8, Figure 5.S1, Figure 5.S2). Most subplot and plot level canopy metrics covaried in a predictable manner. For example, increased canopy height led to an increase in canopy closure. Plot canopy height especially, tended to be strongly positively correlated with subplot canopy complexity metrics. Additionally, as canopy rugosity increased, many subplot canopy complexity and density metrics decreased. Subplot metrics varied greatly within plots, producing large uncertainty in plot level estimates of these metrics. All subplot level canopy complexity metrics positive correlated with each other (Figure 5.S2). Plot level canopy complexity also generally correlated (Figure 5.S1). Plot level measures of spatial heterogeneity in canopy structure, i.e. canopy surface roughness and canopy rugosity, were negatively correlated with measures of canopy density, i.e. foliage density, canopy closure, and canopy height. Measures of canopy spatial heterogeneity positively correlated with each other, as did measures of canopy density.

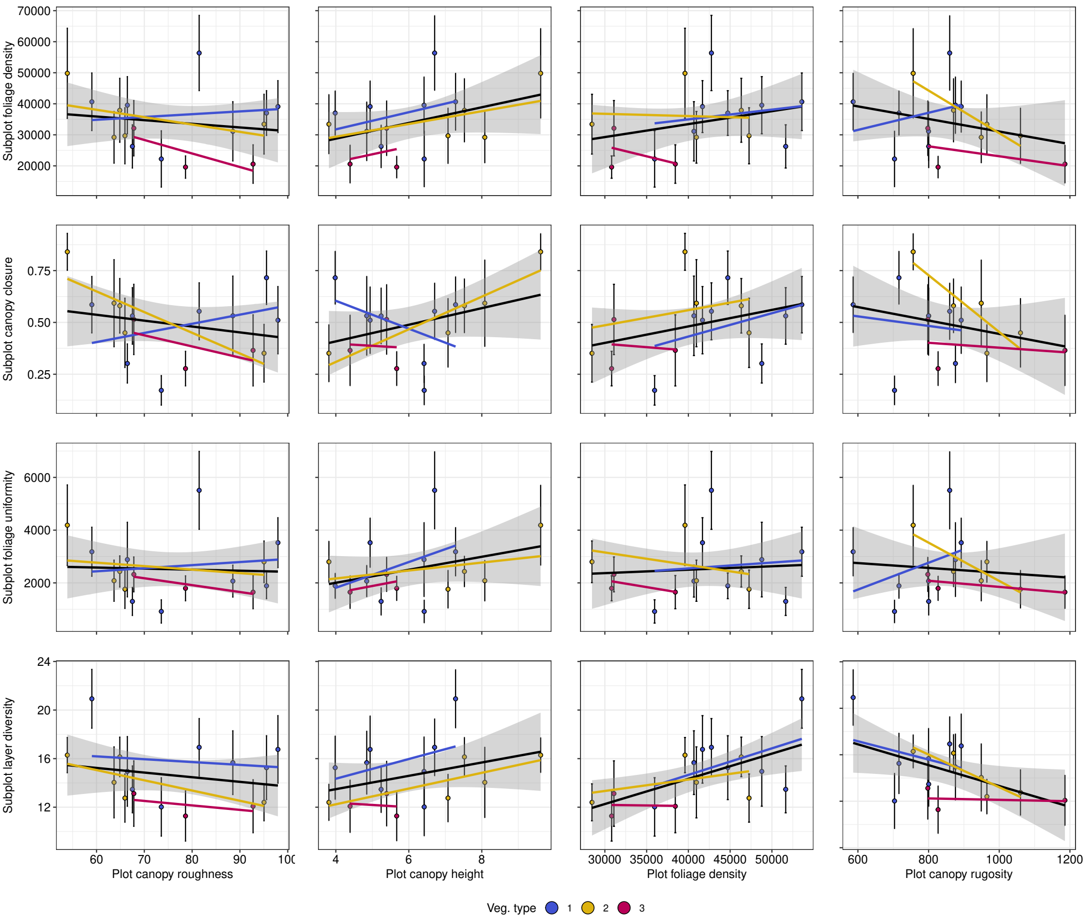


Figure 5.11: Bivariate plots comparing canopy structural metrics at the plot (x axis) and subplot scale (y axis). Each point represents the mean values of a single plot. Points and linear model fits are coloured according to vegetation type. The black linear model combines all vegetation types. Error bars on points are the standard deviation of mean subplot metrics across the plot. Note that because plot level canopy closure is calculated as the mean of subplot canopy closure, a comparison of subplot and plot canopy closure is not made in this figure.

5.4 Discussion

This study investigated relationships between tree species diversity, stand structure, and several metrics of tree canopy complexity using terrestrial LiDAR in southern African savannas, with a view to improving understanding of the biotic drivers of variation in canopy complexity and vegetation dynamics. Species diversity appeared to generally have weak positive effects on canopy complexity metrics related to canopy density at both the subplot and plot scales. While biodiversity effects were weak this is not unexpected, as environmental heterogeneity and landscape history lead to a great deal of stochasticity in canopy structure at small spatial scales, which could obscure biodiversity effects. Plots with greater species diversity produced taller tree canopies, with greater canopy closure and foliage density. Species diversity had negative effects on canopy surface roughness and canopy rugosity, canopy complexity metrics both related to the spatial heterogeneity of foliage distribution. The study did not however, find support for the hypothesis that increased heterogeneity in tree stem size is related to an increase in canopy complexity, and only partial support for the hypothesis that greater spatial clustering of stems is associated with increased canopy complexity. This study supports previous studies in forests which found a positive association between tree species diversity and canopy space-filling (Seidel et al., 2013; Shirima et al., 2015).

5.4.1 Ecological consequences of a species diversity effect on canopy complexity

The result that species diversity increases metrics of canopy density suggests that diverse stands can more effectively close the tree canopy under a given set of environmental conditions. Of course, environmental conditions remain the largest determinant of canopy cover and were not incorporated here. There are climate thresholds which may prevent canopy closure even in diverse savannas (Devine et al., 2017). Increased canopy closure reduces light penetration to the ground (Pilon et al., 2020), reducing grass fuel load, and so could promote woody densification in diverse stands under atmospheric CO_2 enrichment. Similarly, the finding that species diversity is associated with an increase in foliage density and canopy height suggests that more diverse stands could more effectively upregulate productivity in response to atmospheric CO_2 fertilisation, and can maintain stands with greater woody biomass. Taller trees hold disproportionately higher biomass than shorter trees (King, 1990). In mesic savannas that are prone to disturbance by fire, increased growth rate and canopy height could increase the likelihood of trees escaping the “fire trap”, and facilitate their growth to larger canopy trees (Wakeling et al., 2011). This finding concurs with many previous studies, which have found that species diversity leads to greater woody productivity in both forests and savannas (Plas, 2019; Liang et al., 2016). This study adds further information on the mechanisms underlying the species diversity effect on ecosystem function in savannas, that niche complementarity among species promotes greater canopy occupancy.

5.4.2 Species diversity and variation in tree size

Path analysis showed that indirect effects of species diversity on canopy complexity via tree stem size (basal area CV) were negligible, due to the lack of an effect of tree stem size on canopy complexity at both the subplot and plot scale. This finding suggests that the effects of species diversity on canopy complexity are not simply due to covariation with heterogeneity of tree stem size, which could also arise due to demographic effects, rather they are due to differences among species in their canopy dimensions and growth strategy. This strengthens support for the hypothesis that species diversity genuinely increases canopy complexity and canopy density, and is not merely an artefactual relationship. Previous studies in temperate and boreal forests have suggested that increasing tree stem size diversity through active management and thinning can offset productivity losses caused by reduced species diversity (Levick et al., 2009), but this study suggests that in southern African savannas at least, this is not the case.

The lack of a strong effect of tree size variation on canopy complexity suggests a partial decoupling of tree size and foliage volume. This finding highlights that there are likely species-specific differences in growth strategy which influence crown shape, and physiological limits on crown architecture that lead to species diversity effects on canopy packing that are separate from those driven by tree size (Panzou et al., 2020). Thus, structural diversity in crown architecture appears to be a key mechanism by which species diversity affects ecosystem function in these savannas. Seminal work in southern African woodlands described the wide variety of tree functional forms in southern African woodlands (Solbrig et al., 1996), with highly adaptive growth strategies to escape the “fire-trap” (Dantas & Pausas, 2013). Recently this earlier work has been validated using terrestrial LiDAR on individual trees, demonstrating wide variation in crown structure among species (Luck et al., 2020).

Shannon diversity did have strong positive effects on tree stem size variation and tree density. This can be interpreted as a niche complementarity effect, where diverse savannas are able to support a greater density of trees by reducing the effects of intraspecific competition and promoting canopy occupation in different vertical layers by trees of different sizes. Although basal area CV was included in best models for subplot layer diversity and foliage density, subplot level path analysis suggests that covariance between basal area CV and species diversity, and the effect of species diversity on canopy complexity, means that any observed effect of basal area CV on subplot canopy complexity is actually due to species diversity rather than covarying with basal area CV.

Despite tree density having strong positive observed effects on canopy density, and negative effects on canopy heterogeneity metrics in bivariate relationships, tree density only appeared in the best quality plot level mixed model for canopy rugosity. Additionally, the effect sizes for tree density in maximal mixed models were small. At the subplot level however, the Hegyi crowding index, which can be seen as analogous to tree density at neighbourhood scales, was a strong determinant of canopy complexity. Tree density was shown to covary with basal area CV and Voronoi cell area CV at the plot scale, which described variation in tree size and degree of spatial clustering, respectively. This covariance may have led to the effect dropping out in the best models at the plot scale, while at the subplot scale there were no measures of spatial clustering included. Hegyi crowding and tree density are expected to positively correlate with resource availability, and negatively correlate with disturbance which causes tree mortality and reduces tree growth. The study sites sampled here did cover a gradient of tree density, but variation in tree density within vegetation types was small. As vegetation type was included as a random effect in mixed models, this may have led to tree density not having a larger effect size in the models.

Variation in tree size was related to positive canopy complexity effects for within-canopy structural metrics such as layer diversity and canopy surface roughness, but had negligible effects on canopy density. This is in line with other studies in forest ecosystems, which report that variation in tree size increases total canopy volume occupancy by increasing the number of canopy layers, but does not necessarily result in a concomitant increase in canopy closure, as the resulting canopies are often more sparse, due to increased competition for light (Béland & Baldocchi, 2021). Both path analyses also support this conclusion, where species diversity was found to cause an increase in stand structural diversity, but this did not extend to an increase in canopy closure.

5.4.3 Spatial clustering effects

Spatial regularity of stems, measured using the uniform angle index, was associated with a clear decrease in canopy closure, with similar behaviour across vegetation types. Uniform angle index was also included in the best multivariate model predicting canopy closure. Concurrently, spatial clustering of stems, measured by Voronoi cell area CV was included in the best model for foliage density but had a positive effect on this canopy complexity metric. This finding is expected, as spatial clustering results in reduced canopy cover in areas outside clusters, and a non-compensatory increase in canopy closure within clusters, due to competition among individuals (Martens et al., 2000). In contrast, changes in spatial regularity of trees do not imply changes in the distance of stems, only their relative angular positions, though this does generally correlate with spatial clustering (von Gadow & Hui, 2002).

Spatial mingling of species at the plot level had a moderately strong negative effect on canopy height. Mingling also had a negative effect on tree density and on tree size variation, and a positive effect on canopy surface roughness. These results are in line with initial expectations that conspecific clustering reduces canopy complexity and thus foliage volume, by increasing competition among nearby conspecific individuals. Spatial mingling was lowest in the *Baikiaea* woodlands in Cluster 3, which also are expected to experience the most frequent and intense disturbance by fire of the vegetation types studied here, as a result of their sparse canopy and prolific grass growth on sandy well-drained soils (Figure 1.6c, Figure 5.5). Together, these findings suggest that conspecific clustering is increased in the most disturbed plots, where clustering is promoted by a positive feedback where clustered individuals create protection from fire by reducing grass growth and forming thickets (Charles-Dominique et al., 2018). Additionally, fire-adapted species frequently reproduce by suckering (Hoffmann, 1998), creating a positive density dependence effect whereby neighbouring trees are more likely to be of the same species. Spatial mingling is therefore probably a result of fire disturbance, which in turn correlates with other canopy complexity and structural metrics also affected by disturbance.

5.4.4 Plot vs. subplot scale results

The standardised effect sizes of species diversity on canopy complexity metrics were generally greater at the plot level than at the subplot level. While positive and significant relationships between species diversity and subplot canopy complexity metrics were observed in the subplot bivariate models, subplot linear mixed effects models did not show strong species diversity effects, and models were instead dominated by the effect of crowding. This finding suggests a large degree of stochastic variability in canopy complexity within plots, that can mask species effects at smaller spatial scales. The prevalence of disturbance events such as fire and damage by elephants in southern African woodlands (Bond, 2008), as well as tree-fall, small-scale variability in edaphic factors, and stochastic tree mortality all contribute to heterogeneity in canopy complexity (Shirima et al., 2015). While disturbances are controlled to some extent by stand structure and composition, due to the stochastic nature of disturbance events, a snapshot study such as this cannot capture the average disturbance regime and there is therefore a great deal of noise in models predicting canopy complexity from species diversity. The contrast in strength of species diversity effects at the subplot and plot level demonstrates the importance of large sample units, a high degree of spatial replication, and ideally a longer time scale when measuring canopy complexity, especially in disturbed systems, to effectively account for inherent heterogeneity in the system. Even with the one hectare plots used in this study, these plots may still be too small to fully capture larger scale patch dynamics arising from disturbance feedbacks and edaphic heterogeneity.

5.4.5 Variation among vegetation types

Bivariate relationships showed that some of the observed species diversity effect on canopy closure and foliage density may be driven by vegetation type, and the variation in species diversity among vegetation types. The linear mixed model framework however, which accounted for differences among vegetation types, still shows weak species diversity effects even after vegetation type is controlled for, strengthening the validity of the result. Canopy complexity metrics also differed among vegetation types, but significant differences among vegetation types only occurred in a few cases, mostly between miombo and non-miombo vegetation clusters. Canopy density and total foliage volume was lowest in ex-Acacia plots, as expected, while the highest canopy density occurred in miombo plots in Clusters 1 and 2. Miombo woodlands frequently have contiguous canopies with overlapping individual tree canopies (Solbrig et al., 1996), while ex-Acacia savannas show greater negative density dependence of individuals, forming patchy canopies with simpler vertical profiles (Pillay & Ward, 2012). From this result it is suggested that under identical disturbance and climatic regimes, ex-Acacia savannas may not be as effective at closing their canopy to exclude grasses. Particularly, the lower maximum tree height of trees in the ex-Acacia plots may preclude these savannas from forming a multi-layer canopy that may be necessary to allow increased biomass.

While vegetation types differed in mean values for stand structural and species diversity metrics, variation in these metrics produced results of similar direction and magnitude among vegetation types in most cases where strong effects were observed, suggesting that ecosystem processes driving canopy complexity are similar, even across these varied savanna types. Small sample sizes for *Baikiaea* and ex-Acacia vegetation however, led to wide errors on most relationships, especially at the plot level, such that it is impossible to draw deep conclusions about the behaviour of these vegetation types. Variation in mean values of canopy complexity metrics among vegetation types is likely driven by species identity and variation in physiological limits on tree physiognomy (Seidel et al., 2013; Sercu et al., 2017), though species composition itself is driven by environmental factors and disturbance regime (Ribeiro et al., 2020).

5.5 Conclusion

Here I explored how tree species diversity and stand structure influence canopy complexity in southern African savannas, using terrestrial LiDAR methods. I determined that species diversity was related an increase in canopy metrics related to foliage density, and was independently related to variation in tree size and tree density. Together these results suggest that diverse savannas may be able to upregulate their productivity and more effectively exclude grasses under atmospheric CO_2 enrichment conditions. Miombo woodlands exhibited stronger diversity effects than ex-Acacia or *Baikiaea* woodlands, but replication in these other woodland types prevents deeper conclusions on this matter. The findings presented here have a range of consequences for savanna land managers that wish to predict future vegetation dynamics, particularly related to woody encroachment. This study also highlights and compares a number of novel and easy to calculate metrics for estimating different aspects of canopy complexity using terrestrial LiDAR, and sets a precedent as one of the few initial studies using terrestrial LiDAR in mesic savanna landscapes worldwide.

References

Archibald, S. & W. J. Bond (2003). 'Growing tall vs growing wide: tree architecture and allometry of Acacia karroo in forest, savanna, and arid environments'. In: *Oikos* 102.1, pp. 3–14. DOI: `10.1034/j.1600-0706.2003.12181.x`.

Axelsson, C. R. & N. P. Hanan (2018). 'Rates of woody encroachment in African savannas reflect water constraints and fire disturbance'. In: *Journal of Biogeography* 45.6, pp. 1209–1218. DOI: `10.1111/jbi.13221`.

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. De 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`.

Béland, M. & D. D. Baldocchi (2021). 'Vertical structure heterogeneity in broadleaf forests: Effects on light interception and canopy photosynthesis'. In: *Agricultural and Forest Meteorology* 307, p. 108525. DOI: `10.1016/j.agrformet.2021.108525`.

Béland, M. & H. Kobayashi (2021). 'Mapping forest leaf area density from multiview terrestrial lidar'. In: *Methods in Ecology and Evolution* 12.4, pp. 619–633. DOI: `10.1111/2041-210x.13550`.

Bond, W. J. (2008). 'What Limits Trees in C_4 Grasslands and Savannas?' In: *Annual Review of Ecology, Evolution, and Systematics* 39.1, pp. 641–659. DOI: `10.1146/annurev.ecolsys.39.110707.173411`.

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 CO_2 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, GB1019. 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`.

Dantas, V. L. & J. G. Pausas (2013). 'The lanky and the corky: fire-escape strategies in savanna woody species'. In: *Journal of Ecology* 101.5. Ed. by P. Bellingham, pp. 1265–1272. DOI: `10.1111/1365-2745.12118`.

Devine, A. P., R. A. McDonald, T. Quaife & I. M. D. Maclean (2017). 'Determinants of woody encroachment and cover in African savannas'. In: *Oecologia* 183.4, pp. 939–951. DOI: `10.1007/s00442-017-3807-6`.

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 CO_2 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`.

Ehbrecht, M., P. Schall, J. Juchheim, C. Ammer & D. Seidel (2016). 'Effective number of layers: A new measure for quantifying three-dimensional stand structure based on sampling with terrestrial LiDAR'. In: *Forest Ecology and Management* 380, pp. 212–223. DOI: `10.1016/j.foreco.2016.09.003`.

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. M. Campbell. Bogor, Indonesia: Center for International Forestry Research, pp. 11–55.

Getzin, S., T. Wiegand, K. Wiegand & F. He (2008). 'Heterogeneity influences spatial patterns and demographics in forest stands'. In: *Journal of Ecology* 96.4, pp. 807–820. DOI: `10.1111/j.1365-2745.2008.01377.x`.

Gough, C. M., J. W. Atkins, R. T. Fahey & B. S. Hardiman (2019). 'High rates of primary production in structurally complex forests'. In: *Ecology* 100.10. DOI: `10.1002/ecy.2864`.

Groen, T. A. (2007). 'Spatial matters: how spatial processes and patterns affect savanna dynamics'. PhD thesis. Netherlands.

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`.

Hegyi, 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.

Hill, M. O. (1973). 'Diversity and Evenness: A Unifying Notation and Its Consequences'. In: *Ecology* 54.2, pp. 427–432. DOI: `10.2307/1934352`.

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`.

Hoffmann, W. A. (1998). 'Post-burn reproduction of woody plants in a neotropical savanna: the relative importance of sexual and vegetative reproduction'. In: *Journal of Applied Ecology* 35.3, pp. 422–433. DOI: `10.1046/j.1365-2664.1998.00321.x`.

Janzen, D. H. (1970). 'Herbivores and the number of tree species in tropical forests'. In: *The American Naturalist* 104.940, pp. 501–528. DOI: `10.1086/282687`.

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`.

Jost, L. (2006). 'Entropy and diversity'. In: *Oikos* 113.2, pp. 363–375. DOI: `10.1111/j.2006.0030-1299.14714.x`.

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.

Khosravipour, A., A. K. Skidmore, M. Isenburg, T. Wang & Y. A. Hussin (2014). 'Generating Pit-free Canopy Height Models from Airborne LiDAR'. In: *Photogrammetric Engineering & Remote Sensing* 80.9, pp. 863–872. DOI: `10.14358/pers.80.9.863`.

King, D. A. (1990). 'The Adaptive Significance of Tree Height'. In: *The American Naturalist* 135.6, pp. 809–828. DOI: `10.1086/285075`.

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`.

Lefcheck, J. S. (2016). 'piecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics'. In: *Methods in Ecology and Evolution* 7.5, pp. 573–579. DOI: `10.1111/2041-210X.12512`.

Levick, S. R., G. P. Asner, T. Kennedy-Bowdoin & D. E. Knapp (2009). 'The relative influence of fire and herbivory on savanna three-dimensional vegetation structure'. In: *Biological Conservation* 142, pp. 1693–1700. DOI: `10.1016/j.biocon.2009.03.004`.

Liang, J., T. W. Crowther, N. Picard, S. Wiser, M. Zhou, G. Alberti, E.-D. Schulze, A. D. McGuire, F. Bozzato, H. Pretzsch et al. (2016). 'Positive biodiversity-productivity relationship predominant in global forests'. In: *Science* 354.6309, aaf8957–aaf8957. DOI: `10.1126/science.aaf8957`.

Lowman, M. D. & H. B. Rinker (2004). *Forest Canopies*. Physiological Ecology. Burlington MA, USA: Elsevier Science. ISBN: 9780080491349.

Luck, L., L. B. Hutley, K. Calders & S. R. Levick (2020). 'Exploring the Variability of Tropical Savanna Tree Structural Allometry with Terrestrial Laser Scanning'. In: *Remote Sensing* 12.23, p. 3893. DOI: `10.3390/rs12233893`.

Martens, S. N., D. D. Breshears & C. W. Meyer (2000). 'Spatial distributions of understory light along the grassland/forest continuum: effects of cover, height, and spatial pattern of tree canopies'. In: *Ecological Modelling* 126.1, pp. 79–93. DOI: `10.1016/s0304-3800(99)00188-x`.

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`.

Mugasha, W. A., O. M. Bollandsås & T. Eid (2013). 'Relationships between diameter and height of trees in natural tropical forest in Tanzania'. In: *Southern Forests: a Journal of Forest Science* 75.4, pp. 221–237. DOI: `10.2989/20702620.2013.824672`.

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`.

Muumbe, T. P., J. Baade, J. Singh, C. Schmullius & C. Thau (2021). 'Terrestrial Laser Scanning for Vegetation Analyses with a Special Focus on Savannas'. In: *Remote Sensing* 13.3, p. 507. DOI: `10.3390/rs13030507`.

Nakagawa, S. & I. C. Cuthill (2007). 'Effect size, confidence interval and statistical significance: a practical guide for biologists'. In: *Biological Reviews* 82.4, pp. 591–605. DOI: `10.1111/j.1469-185x.2007.00027.x`.

Ong, M. S., Y. C. Kuang & M. P.-L. Ooi (2012). 'Statistical measures of two dimensional point set uniformity'. In: *Computational Statistics & Data Analysis* 56.6, pp. 2159–2181. DOI: `10.1016/j.csda.2011.12.005`.

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`.

Persistence of Vision Pty. Ltd. (2004). *Persistence of Vision Raytracer (Version 3.7)*. [Computer software].

Pillay, T. & D. Ward (2012). 'Spatial pattern analysis and competition between Acacia karroo trees in humid savannas'. In: *Plant Ecology* 213.10, pp. 1609–1619. DOI: `10.1007/s11258-012-0115-4`.

Pilon, N. A. L., G. Durigan, J. Rickenback, R. T. Pennington, K. G. Dexter, W. A. Hoffmann, R. C. R. Abreu & C. E. R. Lehmann (2020). 'Shade alters savanna grass layer structure and function along a gradient of canopy cover'. In: *Journal of Vegetation Science* 32.1. DOI: `10.1111/jvs.12959`.

Plas, F. van der (2019). 'Biodiversity and ecosystem functioning in naturally assembled communities'. In: *Biological Reviews* 94, pp. 1220–1245. DOI: `10.1111/brv.12499`.

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: `10.1016/j.foreco.2014.04.027`.

Privette, J. L., Y. Tian, G. Roberts, R. J. Scholes, Y. Wang, K. K. Caylor, P. Frost & M. Mukelabai (2004). 'Vegetation structure characteristics and relationships of Kalahari woodlands and savannas'. In: *Global Change Biology* 10, pp. 281–291. DOI: `10.1111/j.1529-8817.2003.00740.x`.

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: `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`.

Ribeiro, N. S., P. L. Silva de Miranda & J. Timberlake (2020). 'Biogeography and Ecology of Miombo Woodlands'. In: *Miombo Woodlands in a Changing Environment: Securing the Resilience and Sustainability of People and Woodlands*. Ed. by N. S. Ribeiro, Y. Katerere, P. W. Chirwa & I. M. Grundy. Cham, Switzerland: Springer International Publishing, pp. 9–53. DOI: `10.1007/978-3-030-50104-4_2`.

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: `10.1038/nature04070`.

Schertzer, E., A. C. Staver & S. A. Levin (2015). 'Implications of the spatial dynamics of fire spread for the bistability of savanna and forest'. In: *Journal of Mathematical Biology* 70.1-2, pp. 329–341. DOI: `10.1007/s00285-014-0757-z`.

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* 28.1, pp. 517–544. DOI: `10.1146/annurev.ecolsys.28.1.517`.

Seidel, D., C. Leuschner, C. Scherber, F. Beyer, T. Wommelsdorf, M. J. Cashman & L. Fehrmann (2013). 'The relationship between tree species richness, canopy space exploration and productivity in a temperate broad-leaf mixed forest'. In: *Forest Ecology and Management* 310, pp. 366–374. DOI: `10.1016/j.foreco.2013.08.058`.

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`.

Sercu, B. K., L. Baeten, F. van Coillie, A. Martel, L. Lens, K. Verheyen & D. Bonte (2017). 'How tree species identity and diversity affect light transmittance to the understory in mature temperate forests'. In: *Ecology and Evolution* 7.24, pp. 10861–10870. DOI: `10.1002/ece3.3528`.

Shenkin, A., L. P. Bentley, I. Oliveras, N. Salinas, S. Adu-Bredu, B. H. Marimon-Junior, B. S. Marimon, T. Peprah, E. L. Choque, L. T. Rodriguez et al. (2020). 'The Influence of Ecosystem and Phylogeny on Tropical Tree Crown Size and Shape'. In: *Frontiers in Forests and Global Change* 3. DOI: `10.3389/ffgc.2020.501757`.

Shirima, D. D., M. Pfeifer, P. J. Platts, Ø. Totland & S. R. Moe (2015). 'Interactions between canopy structure and herbaceous biomass along environmental gradients in moist forest and dry miombo woodland of Tanzania'. In: *PLoS ONE* 10, pp. 1–15. DOI: `10.1371/journal.pone.0142784`.

Silva, I. A. & M. A. Batalha (2011). 'Plant functional types in Brazilian savannas: The niche partitioning between herbaceous and woody species'. In: *Perspectives in Plant Ecology, Evolution and Systematics* 13.3, pp. 201–206. DOI: `10.1016/j.ppees.2011.05.006`.

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`.

Solbrig, O. T., E. Medina & J. F. Silva (1996). *Biodiversity and Savanna Ecosystem Processes*. Berlin, Germany: Springer-Verlag.

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, UK: Cambridge University Press, pp. 86–106.

Stevens, N., C. E. R. Lehmann, B. P. Murphy & G. Durigan (2017). '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'. In: *Proceedings of the IUFRO International workshop 'Sustainable forestry in temperate regions'*. Ed. by L. Bjoerk. Lund, Sweden, pp. 20–30.

Wakeling, J. L., A. C. Staver & W. J. Bond (2011). 'Simply the best: The transition of savanna saplings to trees'. In: *Oikos* 120.10, pp. 1448–1451. DOI: `10.1111/j.1600-0706.2011.19957.x`.

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`.

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`.

5.6 Supplementary material

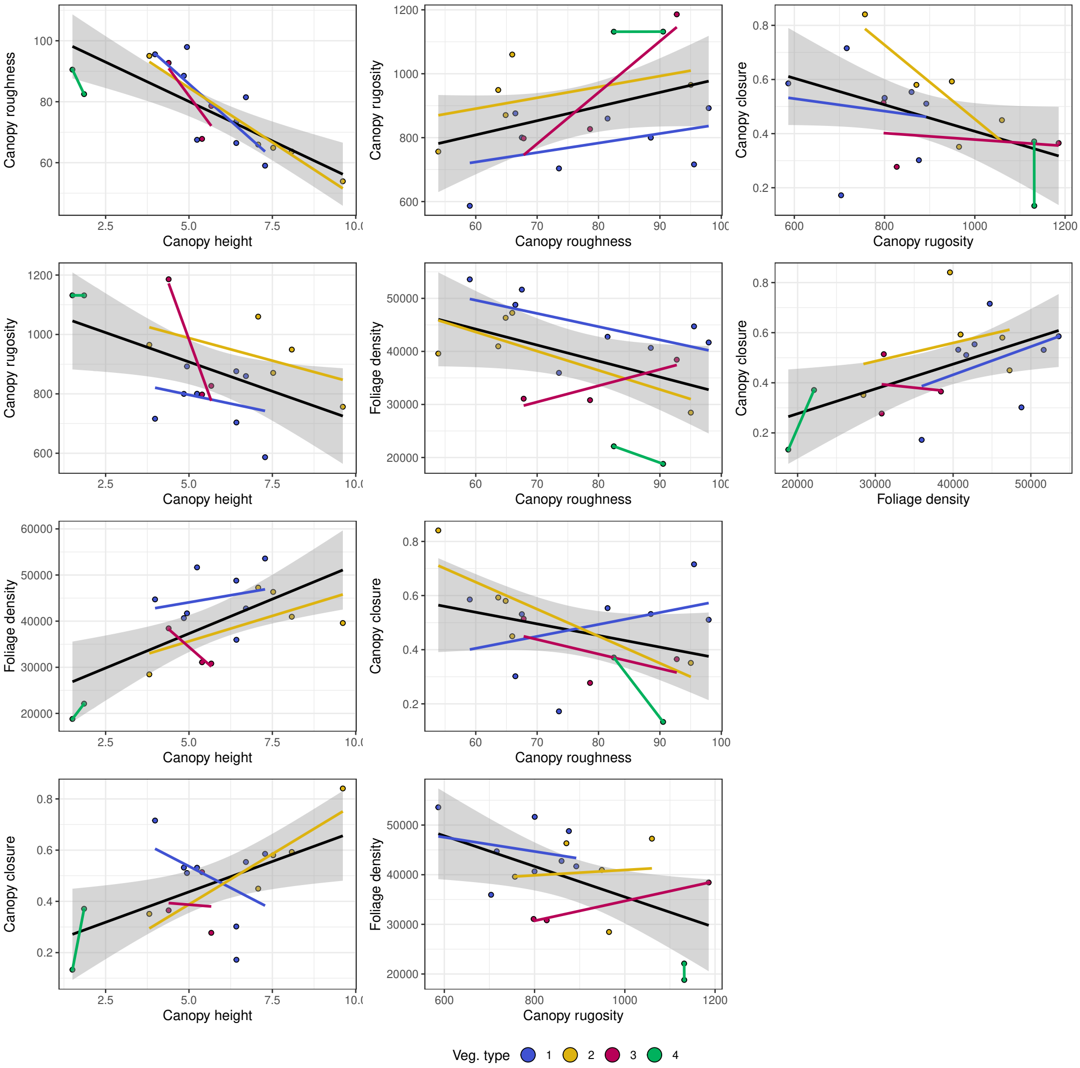


Figure 5.S1: Bivariate scatter plots of plot level canopy complexity metrics.

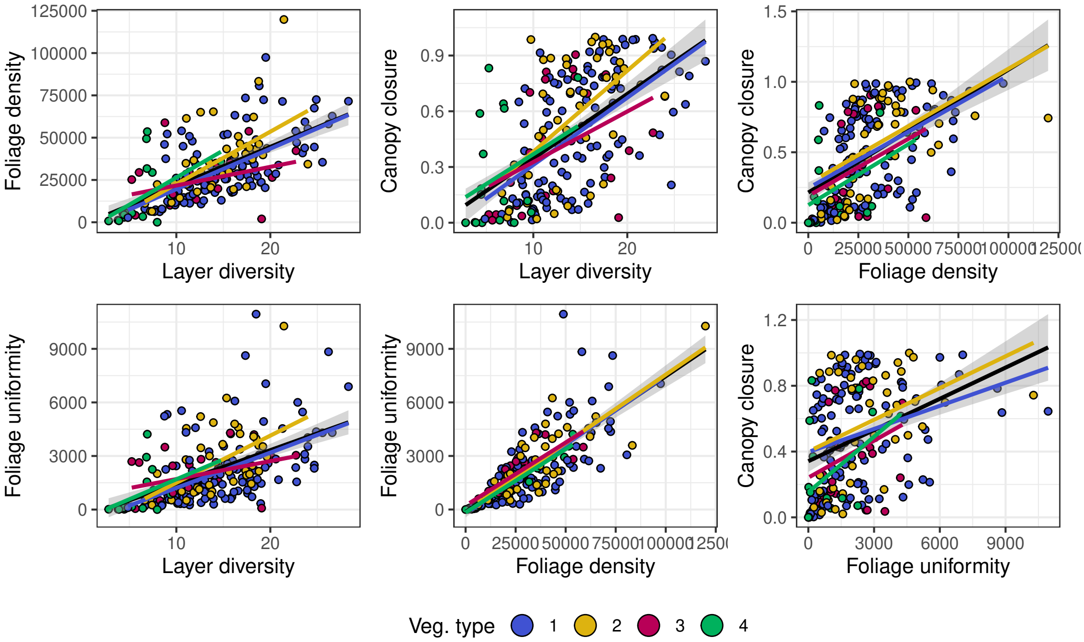


Figure 5.S2: Bivariate scatter plots of subplot level canopy complexity metrics.

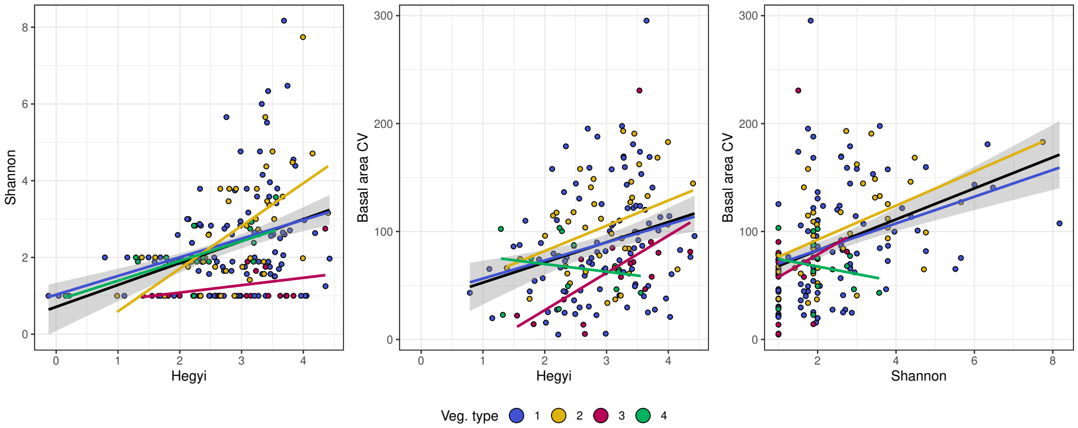


Figure 5.S3: Bivariate scatter plots of subplot level diversity and stand structural metrics.

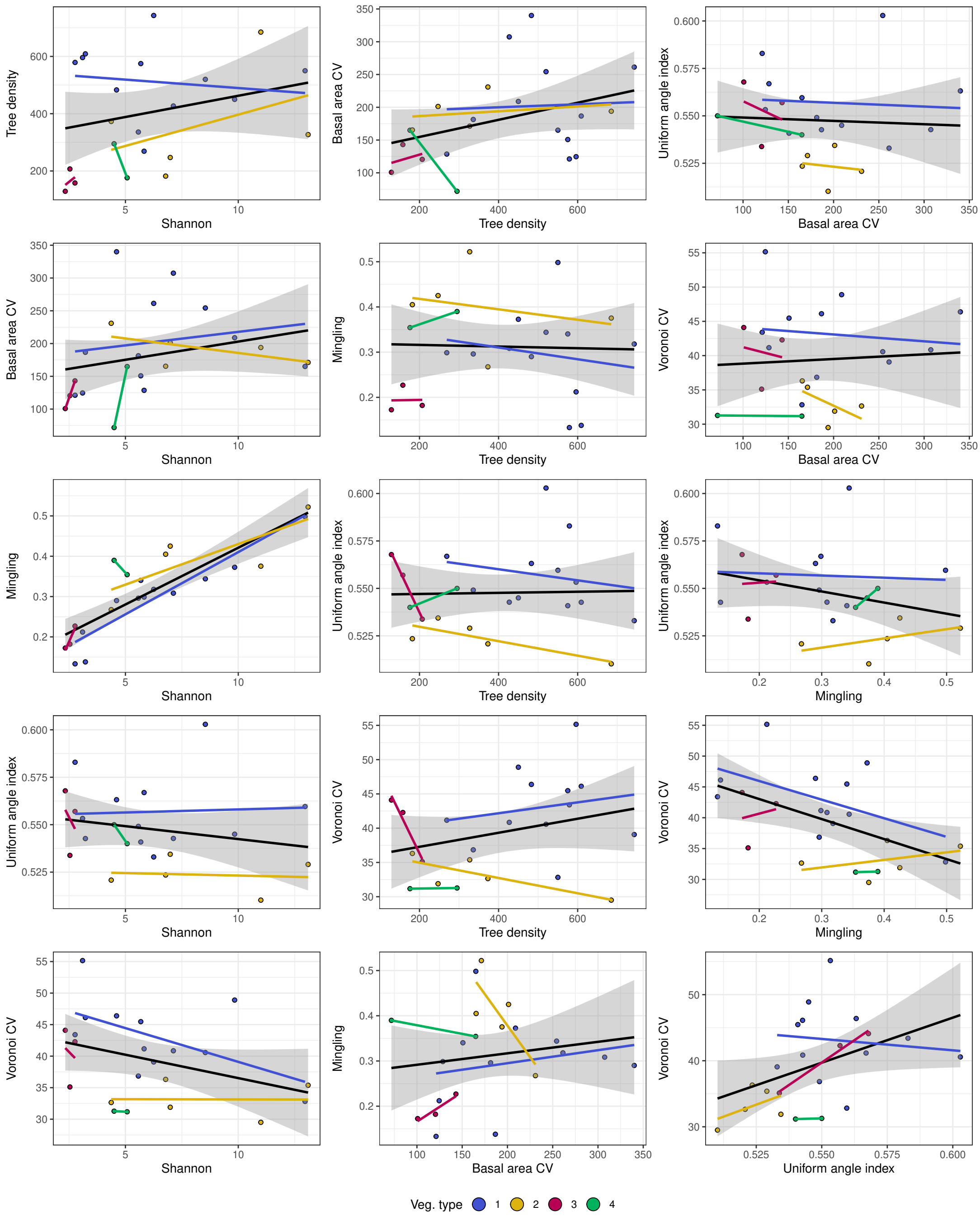


Figure 5.S4: Bivariate scatter plots of plot level diversity and stand structural metrics.

Table 5.S1: Summary statistics of bivariate linear models comparing canopy complexity metrics with diversity and stand structural metrics, grouped by vegetation type. Note that models plot level canopy complexity metrics could not be fitted for Cluster 4, as this cluster only contained two plots. Slope refers to the slope of the predictor term in the model, ±1 standard error. T is the t-value of the slope of the predictor term in the model, Asterisks indicate the p-value of these terms (***<0.001, **<0.01, *<0.05).

Response	Predictor	Cluster	Slope	F	R^2	T
Foliage density	Basal area CV	1	7.3e+01±3.7e+01	4.0(2,97)	0.04	1.99*
		2	1.1e+02±7.9e+01	2.1(2,38)	0.05	1.44
		3	1.4e+01±7.2e+01	0.0(2,14)	0.00	0.20
		4	1.6e+01±2.0e+02	0.0(2,12)	0.00	0.08
Foliage density	Hegyi	1	5.9e+03±2.1e+03	8.2(2,102)	0.07	2.86**
		2	1.4e+04±3.6e+03	15.2(2,40)	0.28	3.90***
		3	6.6e+03±3.0e+03	4.8(2,23)	0.17	2.18*
		4	1.5e+01±5.5e+03	0.0(2,13)	0.00	0.00
Foliage density	Shannon	1	2.2e+03±1.3e+03	2.8(2,102)	0.03	1.67
		2	3.8e+03±2.4e+03	2.6(2,39)	0.06	1.61
		3	1.1e+04±6.5e+03	3.1(2,20)	0.13	1.77
		4	-6.5e+03±6.5e+03	1.0(2,13)	0.07	–1.01

Continued overleaf

Response	Predictor	Cluster	Slope	F	R^2	T
Canopy closure	Basal area CV	1	1.7e-04±6.0e-04	0.1(2,97)	0.00	0.28
		2	2.9e-03±1.1e-03	6.9(2,39)	0.15	2.62*
		3	4.2e-03±1.1e-03	15.1(2,14)	0.52	3.89**
		4	-4.6e-03±3.0e-03	2.2(2,12)	0.16	–1.50
Canopy closure	Hegyi	1	2.2e-01±2.8e-02	62.3(2,102)	0.38	7.89***
		2	2.6e-01±5.1e-02	27.0(2,41)	0.40	5.19***
		3	2.8e-01±4.0e-02	50.7(2,23)	0.69	7.12***
		4	1.7e-01±8.0e-02	4.5(2,13)	0.26	2.12
Canopy closure	Shannon	1	3.1e-03±2.2e-02	0.0(2,102)	0.00	0.14
		2	1.1e-01±3.2e-02	12.1(2,40)	0.23	3.48**
		3	2.3e-01±1.4e-01	2.9(2,20)	0.13	1.69
		4	6.7e-02±1.1e-01	0.4(2,13)	0.03	0.60
Foliage uniformity	Basal area CV	1	3.7e+00±4.0e+00	0.9(2,97)	0.01	0.92
		2	4.5e+00±7.4e+00	0.4(2,38)	0.01	0.61
		3	-3.5e+00±5.9e+00	0.4(2,14)	0.02	–0.59
		4	-9.3e-01±1.5e+01	0.0(2,12)	0.00	–0.06

Continued overleaf

Response	Predictor	Cluster	Slope	F	R^2	T
Foliage uniformity	Hegyi	1	2.2e+02±2.3e+02	1.0(2,102)	0.01	0.98
		2	7.5e+02±3.7e+02	4.0(2,40)	0.09	2.00
		3	4.5e+02±2.6e+02	2.9(2,23)	0.11	1.72
		4	-7.5e+01±4.0e+02	0.0(2,13)	0.00	–0.19
Foliage uniformity	Shannon	1	2.3e+02±1.4e+02	2.6(2,102)	0.02	1.61
		2	8.6e+01±2.2e+02	0.1(2,39)	0.00	0.38
		3	1.3e+03±5.1e+02	6.1(2,20)	0.23	2.48*
		4	-5.9e+02±4.7e+02	1.6(2,13)	0.11	–1.27
Layer diversity	Basal area CV	1	2.5e-02±9.3e-03	7.1(2,97)	0.07	2.66**
		2	3.9e-02±1.4e-02	8.0(2,38)	0.17	2.83**
		3	2.7e-02±2.3e-02	1.3(2,14)	0.09	1.15
		4	2.1e-02±3.1e-02	0.5(2,12)	0.04	0.67
Layer diversity	Hegyi	1	2.7e+00±4.9e-01	29.1(2,102)	0.22	5.39***
		2	2.0e+00±7.5e-01	7.1(2,40)	0.15	2.66*
		3	1.9e+00±1.0e+00	3.6(2,23)	0.13	1.89
		4	1.1e+00±8.5e-01	1.8(2,13)	0.12	1.33

Continued overleaf

Response	Predictor	Cluster	Slope	F	R^2	T
Layer diversity	Shannon	1	1.0e+00±3.4e-01	8.7(2,102)	0.08	2.95**
		2	9.5e-01±4.3e-01	4.8(2,39)	0.11	2.18*
		3	4.9e+00±1.8e+00	7.2(2,20)	0.26	2.68*
		4	1.8e-01±1.1e+00	0.0(2,13)	0.00	0.16
Canopy roughness	Basal area CV	1	1.2e-01±6.9e-02	2.9(2,6)	0.33	1.72
		2	-3.2e-01±2.9e-01	1.2(2,3)	0.29	−1.10
		3	3.5e-01±4.7e-01	0.6(2,1)	0.36	0.74
		4				
Canopy roughness	Voronoi CV	1	2.6e-01±1.2e+00	0.0(2,6)	0.01	0.22
		2	4.6e+00±1.9e+00	6.1(2,3)	0.67	2.48
		3	1.8e+00±1.9e+00	1.0(2,1)	0.49	0.99
		4				
Canopy roughness	Mingling	1	-4.2e+01±5.7e+01	0.5(2,6)	0.08	−0.74
		2	1.6e+01±9.7e+01	0.0(2,3)	0.01	0.17
		3	3.5e+02±2.5e+02	2.0(2,1)	0.67	1.42
		4				

Continued overleaf

Response	Predictor	Cluster	Slope	F	R^2	T
Canopy roughness	Tree density	1	-4.3e-02±4.5e-02	0.9(2,6)	0.13	–0.96
		2	-5.9e-02±3.1e-02	3.6(2,3)	0.54	–1.89
		3	-1.8e-01±2.6e-01	0.5(2,1)	0.31	–0.68
		4				
Canopy roughness	Shannon	1	-2.3e+00±1.7e+00	1.7(2,6)	0.22	–1.32
		2	-1.4e+00±2.4e+00	0.4(2,3)	0.11	–0.60
		3	3.4e+01±4.7e+01	0.5(2,1)	0.34	0.72
		4				
Canopy roughness	Uniform angle index	1	-7.4e+01±2.6e+02	0.1(2,6)	0.01	–0.28
		2	4.1e+02±9.5e+02	0.2(2,3)	0.06	0.43
		3	4.4e+02±5.7e+02	0.6(2,1)	0.37	0.76
		4				
Canopy height	Basal area CV	1	-6.5e-03±6.1e-03	1.1(2,6)	0.16	–1.07
		2	4.3e-02±4.0e-02	1.2(2,3)	0.28	1.08
		3	-3.1e-02±8.7e-03	12.3(2,1)	0.92	–3.51
		4				

Continued overleaf

Response	Predictor	Cluster	Slope	F	R^2	T
Canopy height	Voronoi CV	1	-1.0e-01±8.6e-02	1.5(2,6)	0.20	–1.21
		2	-7.0e-01±2.0e-01	12.7(2,3)	0.81	–3.57*
		3	-1.8e-02±1.4e-01	0.0(2,1)	0.02	–0.13
		4				
Canopy height	Mingling	1	6.8e+00±3.8e+00	3.2(2,6)	0.34	1.78
		2	-3.3e+00±1.3e+01	0.1(2,3)	0.02	–0.25
		3	-2.3e+01±9.3e-01	619.2(2,1)	1.00	–24.88*
		4				
Canopy height	Tree density	1	-3.5e-04±3.8e-03	0.0(2,6)	0.00	–0.09
		2	8.6e-03±4.0e-03	4.7(2,3)	0.61	2.16
		3	-1.0e-03±1.7e-02	0.0(2,1)	0.00	–0.06
		4				
Canopy height	Shannon	1	2.8e-01±1.1e-01	7.1(2,6)	0.54	2.66*
		2	1.7e-01±3.3e-01	0.3(2,3)	0.08	0.52
		3	-3.0e+00±9.0e-01	11.1(2,1)	0.92	–3.32
		4				

Continued overleaf

Response	Predictor	Cluster	Slope	F	R^2	T
Canopy height	Uniform angle index	1	1.0e+01±2.1e+01	0.2(2,6)	0.04	0.49
		2	-7.2e+01±1.3e+02	0.3(2,3)	0.09	–0.56
		3	6.0e-02±3.9e+01	0.0(2,1)	0.00	0.00
		4				
Canopy closure	Basal area CV	1	3.6e-04±6.9e-04	0.3(2,10)	0.03	0.53
		2	3.5e-03±3.5e-03	1.0(2,3)	0.24	0.98
		3	1.9e-03±5.3e-03	0.1(2,1)	0.11	0.35
		4				
Canopy closure	Voronoi CV	1	9.3e-03±8.2e-03	1.3(2,10)	0.11	1.13
		2	-6.6e-02±7.9e-03	69.7(2,3)	0.96	–8.35**
		3	-2.5e-02±4.6e-03	29.0(2,1)	0.97	–5.39
		4				
Canopy closure	Mingling	1	-1.6e-01±5.1e-01	0.1(2,10)	0.01	–0.31
		2	-6.9e-01±1.1e+00	0.4(2,3)	0.12	–0.63
		3	7.6e-02±4.1e+00	0.0(2,1)	0.00	0.02
		4				

Continued overleaf

Response	Predictor	Cluster	Slope	F	R^2	T
Canopy closure	Tree density	1	1.4e-04±4.0e-04	0.1(2,10)	0.01	0.36
		2	8.5e-04±2.4e-04	12.2(2,3)	0.80	3.50*
		3	3.0e-03±4.3e-06	499683.9(2,1)	1.00	706.88***
		4				
Canopy closure	Shannon	1	-7.6e-03±1.7e-02	0.2(2,10)	0.02	–0.45
		2	8.5e-03±3.0e-02	0.1(2,3)	0.03	0.28
		3	1.9e-01±5.2e-01	0.1(2,1)	0.12	0.37
		4				
Canopy closure	Uniform angle index	1	-3.9e+00±2.3e+00	2.9(2,10)	0.23	–1.71
		2	-1.2e+01±9.3e+00	1.7(2,3)	0.36	–1.30
		3	-6.9e+00±3.9e-01	306.2(2,1)	1.00	–17.50*
		4				
Foliage density	Basal area CV	1	-4.5e+01±2.9e+01	2.3(2,6)	0.28	–1.52
		2	1.5e+02±1.4e+02	1.1(2,3)	0.27	1.05
		3	1.8e+02±8.9e+01	4.2(2,1)	0.81	2.06
		4				

Continued overleaf

Response	Predictor	Cluster	Slope	F	R^2	T
Foliage density	Voronoi CV	1	3.5e+01±5.0e+02	0.0(2,6)	0.00	0.07
		2	-7.7e+02±1.5e+03	0.3(2,3)	0.08	–0.51
		3	2.7e+02±8.7e+02	0.1(2,1)	0.09	0.31
		4				
Foliage density	Mingling	1	4.5e+03±2.5e+04	0.0(2,6)	0.01	0.18
		2	8.0e+02±4.7e+04	0.0(2,3)	0.00	0.02
		3	1.5e+05±2.0e+04	54.1(2,1)	0.98	7.35
		4				
Foliage density	Tree density	1	8.8e+00±2.0e+01	0.2(2,6)	0.03	0.45
		2	1.1e+01±2.1e+01	0.3(2,3)	0.08	0.51
		3	-1.3e+01±1.1e+02	0.0(2,1)	0.01	–0.12
		4				
Foliage density	Shannon	1	2.5e+02±8.1e+02	0.1(2,6)	0.02	0.31
		2	5.0e+02±1.2e+03	0.2(2,3)	0.05	0.42
		3	1.8e+04±9.1e+03	3.9(2,1)	0.80	1.98
		4				

Continued overleaf

Response	Predictor	Cluster	Slope	F	R^2	T
Foliage density	Uniform angle index	1	-1.1e+05±1.0e+05	1.3(2,6)	0.18	–1.15
		2	1.2e+05±4.7e+05	0.1(2,3)	0.02	0.25
		3	4.3e+04±2.5e+05	0.0(2,1)	0.03	0.18
		4				
Canopy rugosity	Basal area CV	1	-1.0e-01±6.1e-01	0.0(2,6)	0.00	–0.17
		2	-2.2e+00±2.2e+00	1.1(2,3)	0.26	–1.03
		3	8.7e+00±5.4e+00	2.6(2,1)	0.73	1.62
		4				
Canopy rugosity	Voronoi CV	1	7.9e+00±8.2e+00	0.9(2,6)	0.13	0.96
		2	3.5e+01±1.3e+01	6.8(2,3)	0.69	2.61
		3	1.8e+01±4.2e+01	0.2(2,1)	0.15	0.42
		4				
Canopy rugosity	Mingling	1	-5.9e+02±3.6e+02	2.7(2,6)	0.31	–1.63
		2	8.5e+02±5.2e+02	2.7(2,3)	0.47	1.63
		3	7.2e+03±1.7e+03	17.6(2,1)	0.95	4.19
		4				

Continued overleaf

Response	Predictor	Cluster	Slope	F	R^2	T
Canopy rugosity	Tree density	1	-1.9e-01±3.4e-01	0.3(2,6)	0.05	–0.56
		2	-4.6e-01±2.1e-01	4.9(2,3)	0.62	–2.22
		3	-1.2e+00±5.4e+00	0.0(2,1)	0.05	–0.22
		4				
Canopy rugosity	Shannon	1	-2.4e+01±1.0e+01	5.3(2,6)	0.47	–2.31
		2	6.4e+00±1.8e+01	0.1(2,3)	0.04	0.35
		3	8.5e+02±5.4e+02	2.5(2,1)	0.71	1.57
		4				
Canopy rugosity	Uniform angle index	1	-2.6e+03±1.6e+03	2.5(2,6)	0.30	–1.58
		2	1.0e+04±4.1e+03	6.1(2,3)	0.67	2.47
		3	3.4e+03±1.2e+04	0.1(2,1)	0.07	0.28
		4				

Chapter 6

Estimation of canopy complexity with terrestrial LiDAR: extended methods

6.1 Introduction

This chapter provides expanded field and analytical methods for the study of tree canopy structure in southern African woodlands, presented in brief in Chapter 5. The study aimed to understand the effects of tree species diversity and stand structure on tree canopy structural complexity, using terrestrial LiDAR. Firstly, I provide technical details on the field setup for the terrestrial LiDAR and the hemispherical photography used to validate terrestrial LiDAR canopy closure estimates. Secondly, I describe the processing chain used to extract canopy complexity metrics from the terrestrial LiDAR point clouds. Thirdly, I describe in further detail the behaviour and suitability of the different canopy complexity and stand structural metrics used in the study.

6.2 Terrestrial LiDAR field setup

Within each 1 ha (100×100 m) square plot, nine 10 m diameter circular subplots were laid out in a grid, with 35 m between subplot centre points (Figure 6.1). These subplots constitute the basic sampling unit of the study. Within each subplot, a Leica HDS6100 phase-shift Terrestrial Laser Scanner (TLS) was

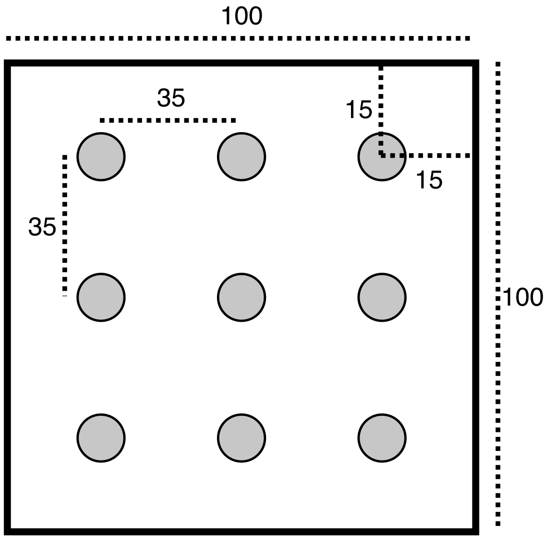
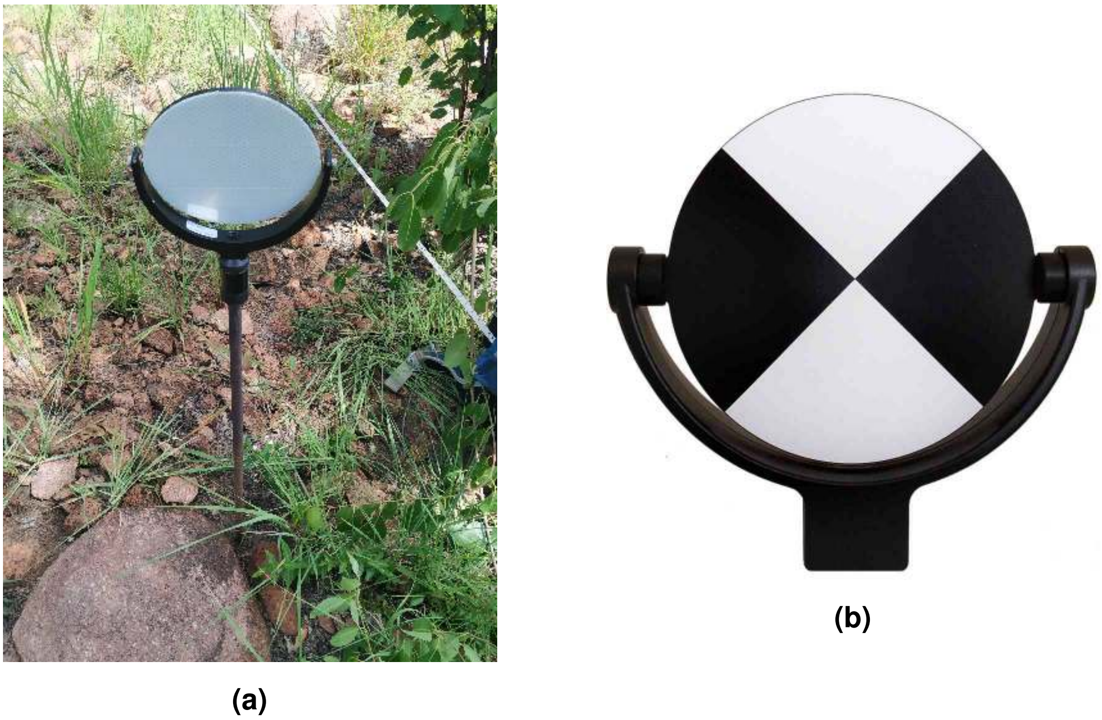


Figure 6.1: The layout of 10 m diameter subplots within each 1 ha plot. Each subplot is situated inside a 15 m buffer from the plot edge, with 35 m between subplot centres. Subplots are arranged in a 3×3 grid. All distances are in metres.

used to capture woodland canopy structure. The number and position of scan locations within a subplot was determined by the arrangement and density of canopy material in the subplot, with the aim to minimise shadows within the canopy, and to maximise canopy penetration (Béland & Kobayashi, 2021). Between one and five scans were recorded per subplot, across all plots. Further information on the field setup of the TLS is presented in Table 6.1.

Five Leica 6" (15.24 cm) diameter planar tilt-and-turn cross-pattern reflective targets were located in each subplot to facilitate alignment of scans (Figure 6.2). The five targets were located roughly in a quincunx pattern, with one target at the subplot centre and the remaining four targets arranged in a cross pattern around the edges of the subplot, ensuring that all scans could see all five targets. To facilitate alignment of scans among subplots, the location of each target in real space was recorded using a Leica VIVA GS10 GNSS (Global Navigation Satellite Systems) unit (Figure 6.3). The GNSS was set up in a Post-Processing Kinematic (PPK) configuration with a base-station located ~100 m from the edge of each 1 ha plot with an unobstructed view of the sky hemisphere where possible. The location of each target was measured for at least four minutes to minimise measurement error (Figure 6.4).



(a)

(b)

Figure 6.2: Example of a Leica 6" diameter reflective target, (a) in situ mounted on a length of threaded bar, and (b) showing the cross pattern face of the target.

Figure 6.3: A Leica VIVA GS10 GNSS unit in the field, showing the antenna atop an aluminium pole, attached to the base station on the ground, and the rover terminal in the hand of a research assistant.

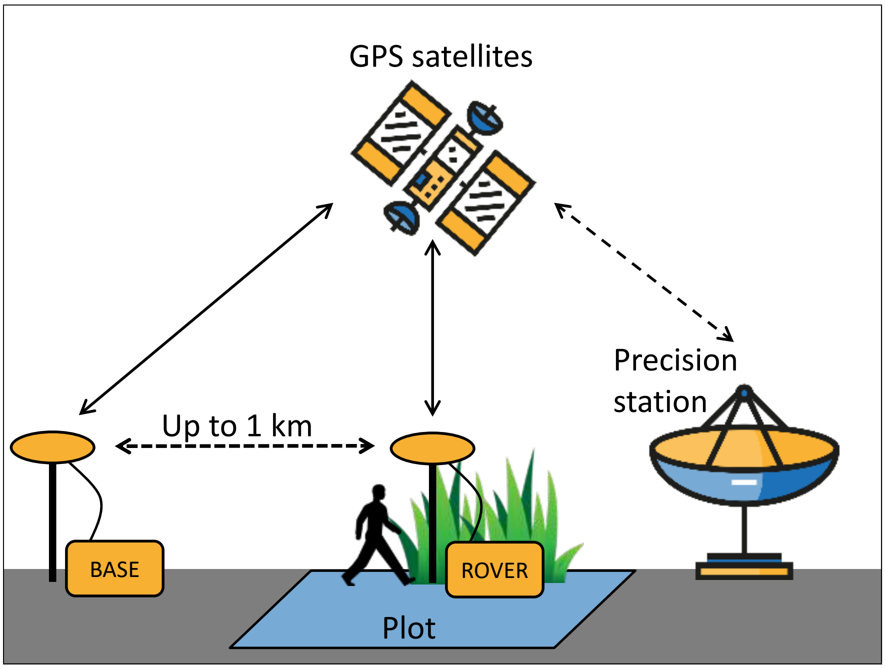


Figure 6.4: Schematic diagram of the GNSS PPK configuration used to precisely locate targets in real space. The base station is located in an area with a full unobstructed view of the sky hemisphere, up to ~1 km from the plot, and is left in the same location for the duration of the data collection, recording its location once per second. The rover is moved around inside the plot to record the location of each target, for >4 minutes at each target. The rover and the base station both utilise GPS and GLONASS satellites to record their position. After data collection, a two stage validation technique is used to improve the precision of the recorded positions, firstly using the base station, and secondly using the TrimbleRTX service which utilises highly precise distributed regional stations.

Table 6.1: Description of scan settings used for each scan.

Setting	Value
TLS model	Leica HDS6100
Wavelength	650-690 nm
Spot size at exit	3 mm
Beam divergence	0.22 mrad
Range	79 m @90%; 50 m @18% albedo
Azimuth range	0-360°
Zenith range	0-155°
Increment	0.018°
Point spacing over 25 m	7.9 mm
Pixels per line	20 000
Lines	10 000
Compressed file size	~800 MB
Duration of scan	6 minutes 44 seconds

6.3 Hemispherical photography field setup

To validate TLS canopy closure estimates, at the centre of each subplot a single photograph was taken with a full-frame DSLR camera, equipped with a circular fisheye lens. Further information on the hemispherical photography setup is presented in Table 6.2.

The fisheye lens had an equisolid (equal area) projection, with a projection function given by:

$$R = 2f \sin\left(\frac{\theta}{2}\right) \tag{6.1}$$

Where R is the radial position of a point on the image, f is the focal length of the lens, and θ is the angle in radians of incident light on the lens. Equisolid lenses are preferred for hemispherical photography because they maintain an equal area for each pixel, i.e. a pixel projected through the lens has the same solid angle irrespective of the incident light angle, meaning that canopy closure estimations are not biased towards any part of the sky hemisphere (Herbert, 1987).

Photographs were taken facing directly to zenith using a camera-mounted spirit level, with the top of the camera body facing magnetic north, at a height of 1.3 m or above understorey vegetation, whichever was higher. Photographs

Table 6.2: Description of camera settings used for hemispherical photographs. Note that shutter speed and ISO are deliberately variable within sensible thresholds to allow adjustments for ambient light conditions.

Setting	Value
Camera model	Nikon D750
Lens model	Sigma 8 mm f/3.5 EX DG Circular Fisheye
Pixel pitch	5.95 µm
Sensor resolution	24.3 MP
Shutter speed	>1/60s
Aperture	5-7
ISO	100-200
Exposure compensation	-0.7 (Brusa & Bunker, 2014)
Focus	∞ (Hu & Zhu, 2009; Frazer et al., 2001)
Image size	Large Fine JPEG - circular image 4016×4016 px
Orientation	Landscape

were captured under uniform light conditions as much as possible, either under overcast skies or early in the day before direct sunlight could be seen on the photograph, to minimise lens flare, which can preclude accurate differentiation of plant material and sky, and to minimise 'blooming', a phenomenon where light 'bleeds' into dark areas of the image in highly contrasting light conditions (Frazer et al., 2001).

ImageJ (Fiji version 2.1.0/1.53c) was used to binarise hemispherical photographs, to separate plant material from sky (Schneider et al., 2012). Images were binarised using the Huang algorithm (Huang & Wang, 1995) using only the blue channel of the image, under the assumption that plant material reflects little blue light, while the sky reflects much more (Brusa & Bunker, 2014). Images were saved as PNG files at the original pixel resolution, with a circular image of 4016×4016 pixels.

6.4 Terrestrial LiDAR processing

6.4.1 Scan alignment and registration

Point clouds within a subplot were aligned using the reflective targets as anchor points. Point cloud alignment was conducted in Leica Cyclone (version 9.1)

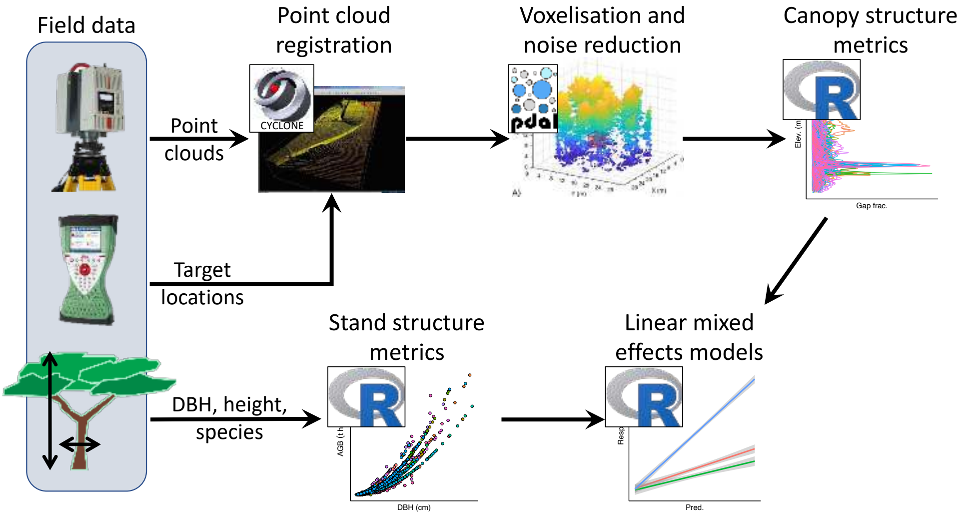


Figure 6.5: Schematic diagram summarising the data processing and analysis workflow for the TLS data. Processing steps are labelled according to the principal software used during that step.

(Leica Camera AG, 2009). Reflective targets were manually located within each point cloud, then the precise centre of each target was identified automatically by Cyclone. Anchor points were discarded if they had a location uncertainty of >3 cm. After alignment, subplot point clouds were exported from Cyclone as PTX files for further processing.

GNSS measurements of target locations were used to register point clouds in real space. The TrimbleRTX GNSS post-processing service was used to improve the precision of target locations recorded with GNSS, using distributed regional stations to validate the rover and base station GNSS measurements (Table 6.3) (Chen et al., 2011). Following point cloud registration, subplot point clouds were combined to a plot level point cloud.

PTX files were converted to compressed LAZ files using PDAL (PDAL Contributors, 2018), to reduce file size and speed up further processing. Code 6.1 contains the code used to transform PTX to LAZ.

```
# Get file name without extension
noext=${1%.ptx}

# Find the PTX scan array dimension header material
lines=$(grep -E -n '^.{1,10}$' $1 |
  cut -f1 -d: |
  awk 'NR%2!=0' |
  tr '\n' ' ' |
  sed 's/^[0-9]\s//g')

# Split PTX file into individual scans
csplit -f "$noext" -b "_%d.ptx" $1 $lines

$ Find split files
ptxsplit=$(find . -type f -regex ".*/${noext}_[0-9].ptx")

# For each file:
for j in ${ptxsplit} ; do
  jnoext="${j%.ptx}"
  matrix=$(head -n 10 $j | tail -4 | sed -r 's/0\s+?$/0.0/g' | dos2unix)
  pdal pipeline ptx_laz.json --readers.text.filename=$j \
    --filters.transformation.matrix="${matrix}" \
    --writers.las.filename=${jnoext}.laz
done

# List LAZ files
lazsplit=$(find . -type f -regex ".*/${noext}_[0-9].laz")

# Merge LAZ files
pdal merge ${lazsplit} ${noext}.laz
```

Code 6.1: The processing chain used to convert Leica Cyclone PTX files to LAZ files, using PDAL, POSIX-compliant shell scripting, and common UNIX utilities. The `ptx_laz.json` JSON pipeline is shown in Code 6.2.

Table 6.3: The five closest regional base stations to each site, used by TrimbleRTX to refine GNSS measurements

Site	Receiver	Distance (km)
Bicuar	JAVAD TRE 3	863
	JAVAD TRE 3 DELTA	1448
	TRIMBLE NETRS	1630
	TRIMBLE NETRS	1648
	JAVAD TRE G3TH DELTA	1796
Mtarure	SEPT POLARX5	686
	TRIMBLE ALLOY	795
	LEICA GRX1200GGPRO	903
	JAVAD TRE 3 DELTA	1119
	JAVAD TRE 3 DELTA	1315

```json
[
  {
    "type" : "readers.text",
    "filename" : "input.txt",
        "header" : "X Y Z I",
        "skip" : 10
  },
   {
        "type" : "filters.transformation",
        "matrix" : "0 -1  0  1  1  0  0  2  0  0  1  3  0  0  0  1"
    },
    {
        "type" : "writers.las",
        "compression" : "true",
        "minor_version" : "2",
        "dataformat_id" : "0",
        "forward" : "all",
        "filename" : "output.laz"
    }
]
```

Code 6.2: The JSON pipeline used in Code 6.1 to convert PTX files to LAZ files, and applying a rotation matrix.

6.4.2 Voxelisation

Point clouds were voxelised to different voxel sizes depending on the application of the data. 5 cm^3 cubic voxels were used for subplot height profile estimation, while 50 cm^3 voxels were used for whole plot canopy rugosity. Variation in voxel size reflects the spatial scale of each analysis, and is bounded by the beam divergence of the TLS over longer distances (Grau et al., 2017). 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, especially when foliage is clumped (Seidel et al., 2012; Cifuentes et al., 2014). Voxels were classified as ‘filled’ if they intersected one or more points.

6.4.3 Noise reduction

Outlier detection and noise reduction of point clouds was conducted in PDAL, using the “statistical method” of `filters.outlier` (Rusu et al., 2008), with $k = 8$ (mean number of neighbours), and $m = 1.96$ (outlier distance threshold multiplier, here approximating a 95% confidence interval):

$$\begin{aligned}
\overline{\mu} &= \frac{1}{N}\sum_{i=1}^{N}\mu_i \\
\sigma &= \sqrt{\frac{1}{N-1}\sum_{i=1}^{N}(\mu_i - \overline{\mu})^2} \\
t &= \mu + m\sigma \\
\text{with } outlier_i &= \begin{cases} \text{true}, & \text{if } \mu_i >= t \\ \text{false}, & \text{otherwise} \end{cases}
\end{aligned} \tag{6.2}$$

Where μ_i is the mean distance from point i to all k nearest neighbour points, N is the number of points in the scene, $\overline{\mu}$ is the mean distance to nearest neighbour points, σ is the standard deviation of these mean distances, t is the threshold distance used to define an outlier and $outlier_i$ is the condition of a

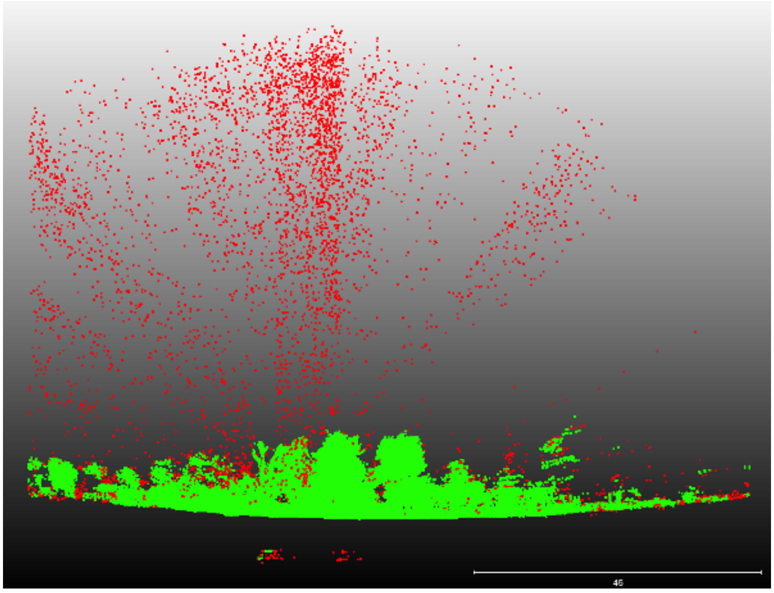


Figure 6.6: A 2 m deep cross section of a subplot point cloud showing the efficacy of the noise reduction and voxelisation process. Red points are excluded by the process, while green points are preserved for further analysis.

point in the scene being identified as an outlier.

6.4.4 Foliage density profiles

To calculate subplot foliage density profiles, the 5 cm^3 voxelised point cloud was first cropped to a 10 m diameter cylinder of infinite height. Ground points were identified using `filters.pmf` (Progressive Morphological Filter - PMF) in PDAL (Zhang et al., 2003), and the height above ground of all points was calculated using `filters.hag_nn` (Nearest Neighbour) in PDAL. Points below ground level and above the 99th percentile of height were excluded from further analyses. Height profile points were exported to XYZ coordinates then imported into R for further processing.

In R, foliage density was calculated in 5 cm layers as the proportion of filled 5 cm^3 voxels. A loess model with a span of 0.1 was fitted to the foliage density values in each layer to estimate the foliage density profile (Figure 6.7). The foliage density profile was further filtered to only tree canopy material, by discarding all points below 1.3 m.

6.5 Subplot canopy complexity metrics

6.5.1 Effective Number of Layers

The Effective Number of Layers (ENL) in the foliage density profile was used to estimate canopy structural complexity, using the true-numbers equivalent Shannon entropy of foliage density among 50 cm vertical layers (Ehbrecht et al., 2016):

$$\mathrm{ENL} = \exp\left(-\sum_{i=1}^{N} p_i \times \ln p_i \right) \tag{6.3}$$

Where N is the number of 50 cm bins in the height profile, and p_i is the proportion of filled voxels in layer i (foliage density). While Ehbrecht et al. (2016) used 1 m layers, their study was conducted in temperate deciduous forest where the maximum height of the sampled forest stands was 40 m, whereas the maximum canopy height in this study was only 22 m. Both Ehbrecht et al. (2016) and Montes et al. (2004) assert that the choice of layer thickness is largely arbitrary, but should be determined with respect to the variability within the canopy, thus in the sparse and highly variable savanna tree canopies measured in this study, narrower layers were chosen. As with the conventional Shannon-Wiener diversity index, ENL increases with number of layers and so increases with canopy height, and also increases with increasing variation in the proportion of filled voxels per layer (Jost, 2006), but not with increasing total foliage density.

6.5.2 Foliage density profiles and foliage uniformity

Subplot canopy foliage density was calculated as the area under the curve of the canopy foliage density profile, using trapezoid estimation. Foliage density correlates with Gross Primary Productivity (GPP), as a greater foliage surface area allows more complete usage of the available light in the canopy (Kotchenova et al., 2004). To describe the uniformity of the foliage density distribution through the canopy, a linear model of cumulative foliage volume vs. height was fitted (Figure 6.7). Under a completely even distribution of foliage material through the canopy, the residuals of the linear model tend to zero, while clumping causes deviations from this uniform distribution and increases the sum of squared residuals. Vertical distribution of foliage is a key measure of canopy complexity. Increased foliage clumping has been linked to increased biodiversity within the canopy (Ishii et al., 2004), deeper light penetration in the canopy (Béland & Baldocchi, 2021), and overall greater canopy photosynthesis (Baldocchi & Hutchison, 1986; Béland & Baldocchi, 2021).

Maximum canopy height has been used in other studies to describe canopy structural complexity (Scheuermann et al., 2018). At the small spatial scale of the subplots used in this study however, there proved to be too much stochastic variation in canopy height among subplots due to the distribution of individual trees to make this statistic informative as a measure of canopy complexity. Canopy height was instead calculated later at the plot level.

6.5.3 Canopy closure

Subplot canopy closure, i.e. the proportion of the sky hemisphere occluded by plant material, a.k.a. gap fraction or site factor (Jennings, 1999), was measured by simulating a hemispherical image at the centre of the subplot using the point cloud data from all scans per subplot. The point cloud was first cropped to a 20 m diameter cylinder around the subplot centre using PDAL. Points below 1.3 m and within a 50 cm sphere around the subplot centre at 1.3 m height were discarded, to prevent the simulated hemispherical image being occluded by understorey vegetation. POV-Ray was used to simulate the hemispherical image using ray-tracing (Persistence of Vision Pty. Ltd., 2004). Filled voxels were represented in POV-Ray as non-reflective black cubes filling the 5 cm^3 voxel volume, with a white uniform sky box and no light source. POV-Ray produced an image with identical qualities to that of the real hemispherical photograph, using a fisheye lens with an equisolid projection and a view angle of 180°, located at the subplot centre at 1.3 m above the ground, with the top of the camera facing magnetic north and the camera facing directly to zenith, producing a circular image of 4016×4016 pixels.

Hemiphot was used to estimate closure from both the hemispherical photographs and the TLS POV-Ray simulation (ter Steege, 2018). Images were cropped to a circle of 60° zenith angle. It can be supposed that below 60°, under most woodland canopies, variation in tree canopy density does little to

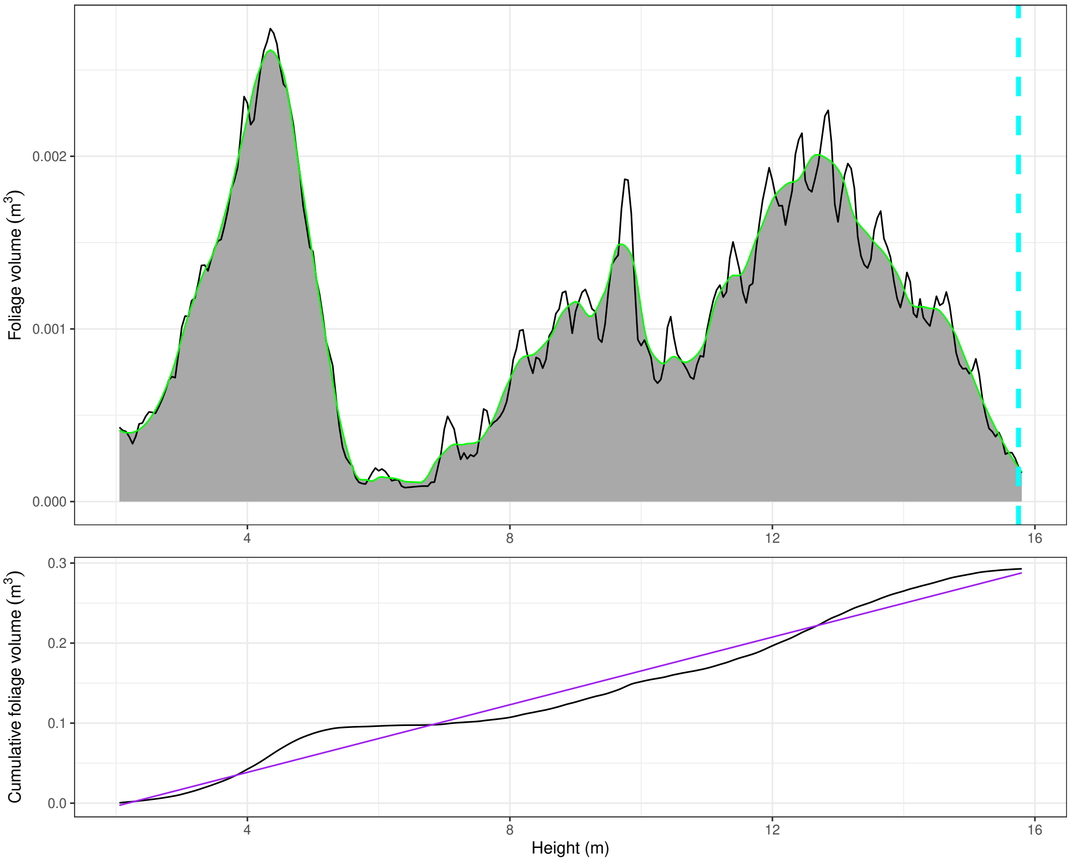


Figure 6.7: Subplot foliage volume height profile (top) and cumulative foliage volume profile (bottom) for a subplot in Bicuar National Park, Angola, to illustrate some of the canopy structure metrics extracted from each height profile. In the top panel: the dashed cyan line shows the 99th percentile of canopy height, used here as a measure of canopy top height in plot level canopy surface modelling. The black trace shows the foliage density height profile, and the green trace shows the loess model fitted to the data, with the area under the canopy shaded grey. The bottom panel: the black trace shows the cumulative foliage volume through the canopy, taken from the loess fit in the top panel. The purple line shows the line of best fit of a linear model through this data. Not illustrated is the Effective Number of Layers (ENL) metric.

affect sunlight penetration, due to the greater depth of canopy at these angles (Jupp et al., 2008). To obtain the total closure (C_α) of a circular image:

$$C_\alpha = 1 - G_{\text{tot}} = \sum_{\alpha=0.5}^{\alpha=60.0} (G_\alpha A_\alpha / A_{\text{tot}}) \tag{6.4}$$

Where G_α is the fraction of unfilled pixels in ring α, A_α is the sky area of the ring segment, and A_{tot} is the total sky area of the hemisphere.

Canopy closure estimates from the TLS were validated using estimates from hemispherical photography. A Pearson's correlation analysis showed that both methods were highly correlated (r(195)=0.87, p<0.001). TLS estimates of closure were almost exclusively higher than hemispherical photography estimates, except in a few subplots with particularly low canopy closure. At higher canopy closure the over-estimation of canopy closure by TLS was larger (Figure 6.8). This finding is in agreement with previous studies which have found that that the magnitude of TLS canopy closure over-estimation depends on gap size distribution, where a site with greater canopy cover and a gap fraction dominated by small within crown gaps will have a larger over-estimate than a more open site with a gap fraction dominated by large between crown gaps (Seidel et al., 2012). A linear mixed model which included nested random intercept effects for subplots within plots was used to identify if sites differed significantly in their relationship between hemispherical photography and TLS estimates of canopy closure. There was no significant difference in model fixed effect slope between plots in Bicuar National Park, Angola, and those in Mtarure, Tanzania (β(173)=0.13±0.011, p=0.21).

Measurements of canopy closure are expected to positively correlate with foliage density, as increased foliage density will reduce the number and size of canopy gaps. However, canopy closure and foliage density do access subtly different aspects of canopy complexity. Clumping of foliage affects the relationship between canopy closure and foliage density. As clumping increases, all else being equal the value of foliage density will remain constant, while the value of canopy closure may decrease as between canopy gaps increase in size (Béland & Baldocchi, 2021). Foliage density is more often related to productivity as it is a more direct measure of leaf area (Seidel et al., 2013), while canopy closure is more often related to understorey processes and light penetration, as it is only a 2D measurement of canopy structure.

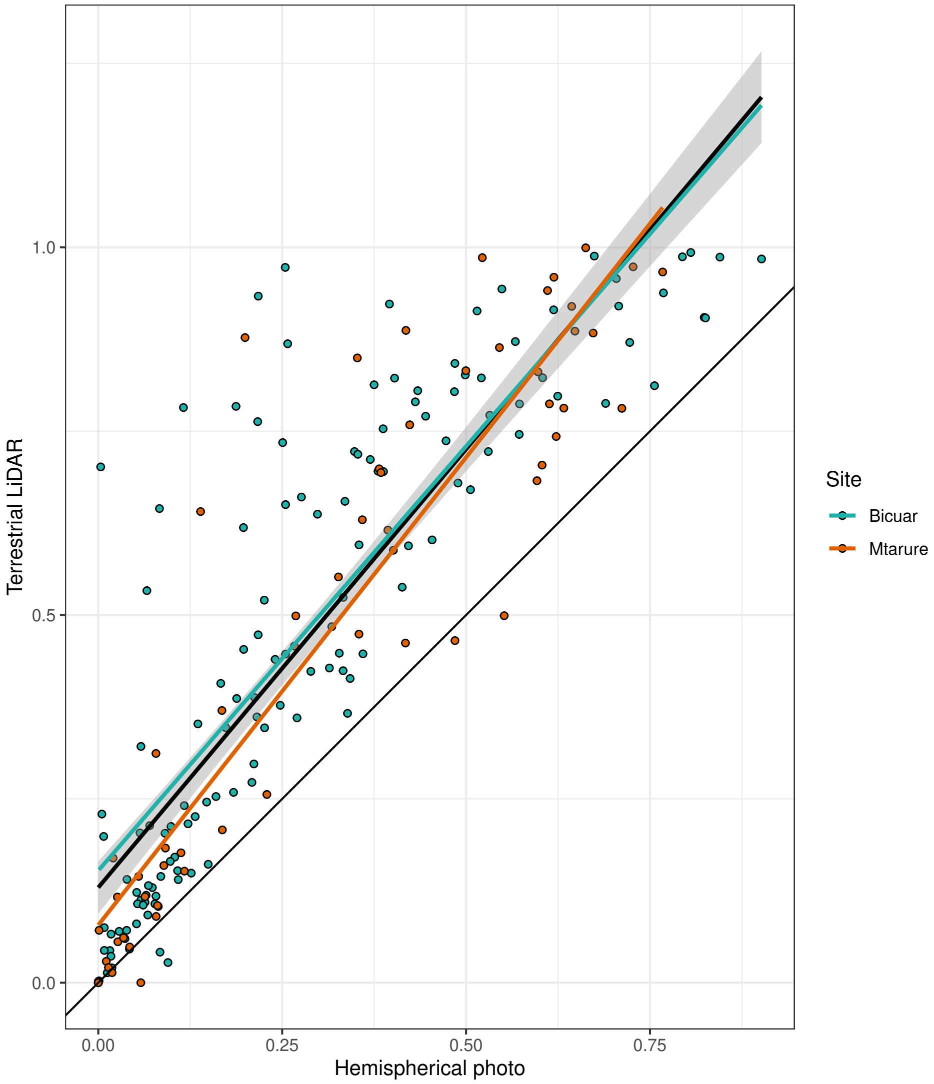
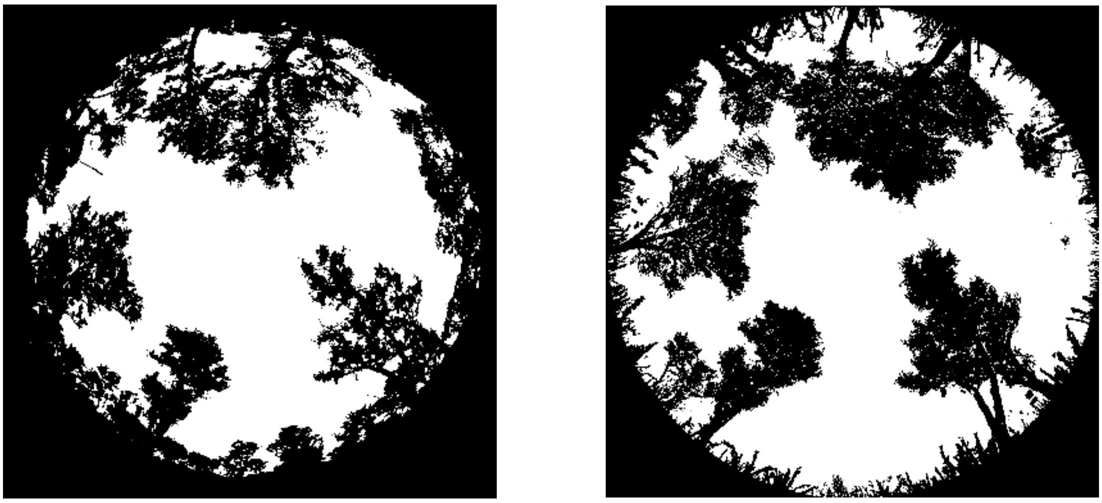
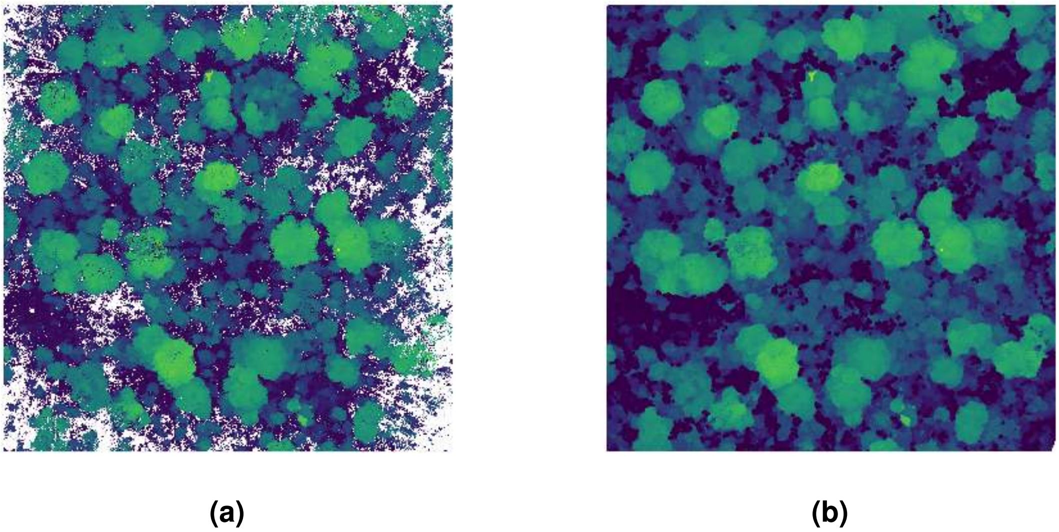


Figure 6.8: Comparison of canopy closure estimation from TLS and hemispherical photography. The thick black line of best fit is a linear model of all points ±1 standard error, while the coloured lines are site specific linear models. The thin black line shows the 1:1 fit.



(a) **(b)**

Figure 6.9: Comparison of hemispherical images for a subplot in Bicuar National Park, Angola. (a) A hemispherical photograph, and (b) a multi-scan point cloud modelled as cubic voxels with POV-Ray. The hemispherical photograph (left) shows some blooming, especially in the tree on the bottom right of the image, where light is seen ‘bleeding’ through the darker canopy material, causing an under-estimation in canopy closure. Note also that while there are minor variations in image height between TLS and hemispherical photos, this does not affect canopy closure estimates, as images were first cropped to a 60° angle of view.



(a) (b)

Figure 6.10: Top-down view of a 1 ha plot in Bicuar National Park. (a) The point cloud after voxelisation, noise reduction, and taking the 99th percentile of tree height in each 5 cm vertical bin. (b) The same point cloud after pit filling to generate a smooth canopy height profile. Points are coloured according to point height from the ground.

6.6 Whole plot canopy complexity metrics

6.6.1 Canopy height

The canopy height of each 1 ha plot was estimated using unified point clouds from all subplots. The unified point cloud was voxelised to 10 cm^3, and the 99th percentile of height was recorded as the canopy height of each 10 cm^2 column. Maximum height was not used as this occasionally constituted a severe outlier which skewed further canopy surface model smoothing. The point cloud was then cropped to the plot boundaries, located using PPK GNSS similar to the TLS targets. A pit-filling algorithm described in Khosravipour et al. (2014) was used to smooth the canopy surface model, at a resolution of 50 cm, removing gaps within trees caused by incomplete penetration of the LiDAR beam (Figure 6.10).

Mean canopy height across the plot and the coefficient of variation (CV) of canopy height were extracted from the canopy surface model for use in statistical analyses. Canopy height CV describes canopy structural diversity measured by the heterogeneity of the canopy surface (Parker & Russ, 2004). Other studies in closed canopy temperate and boreal forests have used metrics similar to the Topographic Roughness Index to measure canopy surface heterogeneity, by comparing canopy height to that of neighbouring pixels in the canopy height model (Weligepolage et al., 2012; Herrero-Huerta et al., 2020). In this study however, the sparse nature of the tree canopies meant that these metrics were overly influenced by canopy density and the edges of individual tree canopies.

6.6.2 Canopy rugosity and foliage density

Canopy rugosity (R_c) was calculated to describe structural complexity across the entire canopy profile of each plot, rather than just the canopy surface (Hardiman et al., 2011). R_c first calculates the standard deviation of foliage density in 50 cm^2 columns across the plot (σG_z), then calculates the standard deviation of those standard deviations:

$$R_c = \sigma(\sigma G_z)_x \tag{6.5}$$

Where G_z is the vertical height axis z, x is the horizontal axis, and σ is the standard deviation. Additionally, foliage density was calculated at the plot level as the sum of filled 50 cm^3 voxels across the plot, and plot canopy closure was calculated as the mean of all subplot canopy closure estimates.

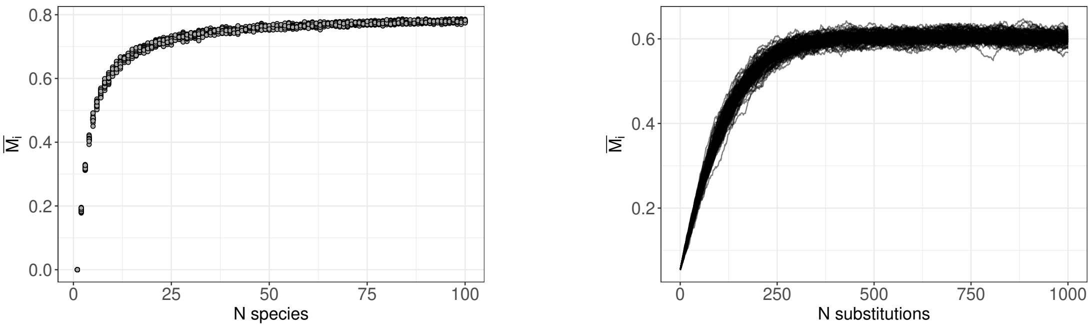
6.7 Stand structure metrics

6.7.1 Spatial mingling of species

The spatial mingling index (M_i) is a spatially explicit estimate of the degree to which species are spatially mixed within a plot. Here, M was calculated at the plot level as the mean of M_i (von Gadow & Hui, 2002), with the adjustment for potential neighbourhood species pool suggested by Hui et al. (2011):

$$
\begin{aligned}
M &= \overline{M_i} \\
M_i &= \frac{S_i}{n_{\max}} \frac{1}{k} \sum_{j=1}^{k} v_j \\
\text{with } v_j &= \begin{cases} 0, & \text{neighbour } j \text{ same species as reference } i \\ 1, & \text{otherwise} \end{cases}
\end{aligned}
\tag{6.6}
$$

Where k is the number of nearest neighbours considered for each reference tree, S_i is the number of species found among the k nearest neighbours of tree i, $n_{\max}$ is the potential number of species in the neighbourhood, i.e. $k+1$, and N is the total number of trees in the plot. The conventional value of $k = 4$ was used here (von Gadow & Hui, 2002; Hui et al., 2007). The value of M_i increases with greater mixing of species, and all else being equal will increase with number of species within the plot (Figure 6.11).



(a) **(b)**

Figure 6.11: The behaviour of the spatial mingling index (M_i) with increasing number of species (a), and increasing spatial mixing of species (b). The left panel was generated by randomly assigning different numbers of species, in equal proportions, to an evenly spaced grid of individuals. 20 replicates were conducted for each number of species. The right panel was generated by randomly swapping pairs of individuals in a plot with 9 species arranged in mono-specific square blocks in an evenly spaced grid. Each line shows a single replicate, where individuals were swapped in an additive fashion, with 100 total.

6.7.2 Uniform angle index

The uniform angle index (winkelmass, W) was calculated to estimate the degree of spatial regularity in tree spatial distribution. Here, W was calculated at the plot level as the mean of W_i (von Gadow & Hui, 2002):

$$\begin{aligned} W &= \overline{W_i} \\ W_i &= \frac{1}{k}\sum_{j=1}^{k} v_j \\ \text{with } v_j &= \begin{cases} 0, & \alpha_j \leq \alpha_0 \\ 1, & \text{otherwise} \end{cases} \end{aligned} \tag{6.7}$$

Where k is the number of neighbours considered, α_j is the angle between consecutive neighbours and α_0 is the critical angle, where $\alpha_0 = 72°$ (Hui & Gadow, 2002). Figure 6.12 demonstrates how the value of W_i varies according to spatial distribution of neighbours. The value of the uniform angle index increases with increasing spatial clumping (decreasing spatial regularity) of individuals (Figure 6.13), and in a plot with random tree distribution will increase as more neighbours are considered (Figure 6.14).

6.7.3 Voronoi tessellation

In addition to spatial regularity, the spatial uniformity of trees is another important aspect of tree spatial distribution. While the uniform angle index effectively measures similarity to a grid-like distribution of individuals, it does not account for variation in the relative distance of trees from their neighbours over the plot area. Spatial uniformity is defined here by two criteria: equality of spacing among individuals within the plot, and even coverage of individuals across the plot (Ong et al., 2012). Departures from spatial uniformity indicate clustering of individuals. Voronoi tessellation is a method of partitioning an n-dimensional space into regions according to the closest individual (Figure 6.15). Voronoi tessellation was conducted using tree location within each plot. The CV of the area of Voronoi cells was then used as a measure of spatial clustering which is sensitive to both the criteria defining spatial uniformity, and is independent of

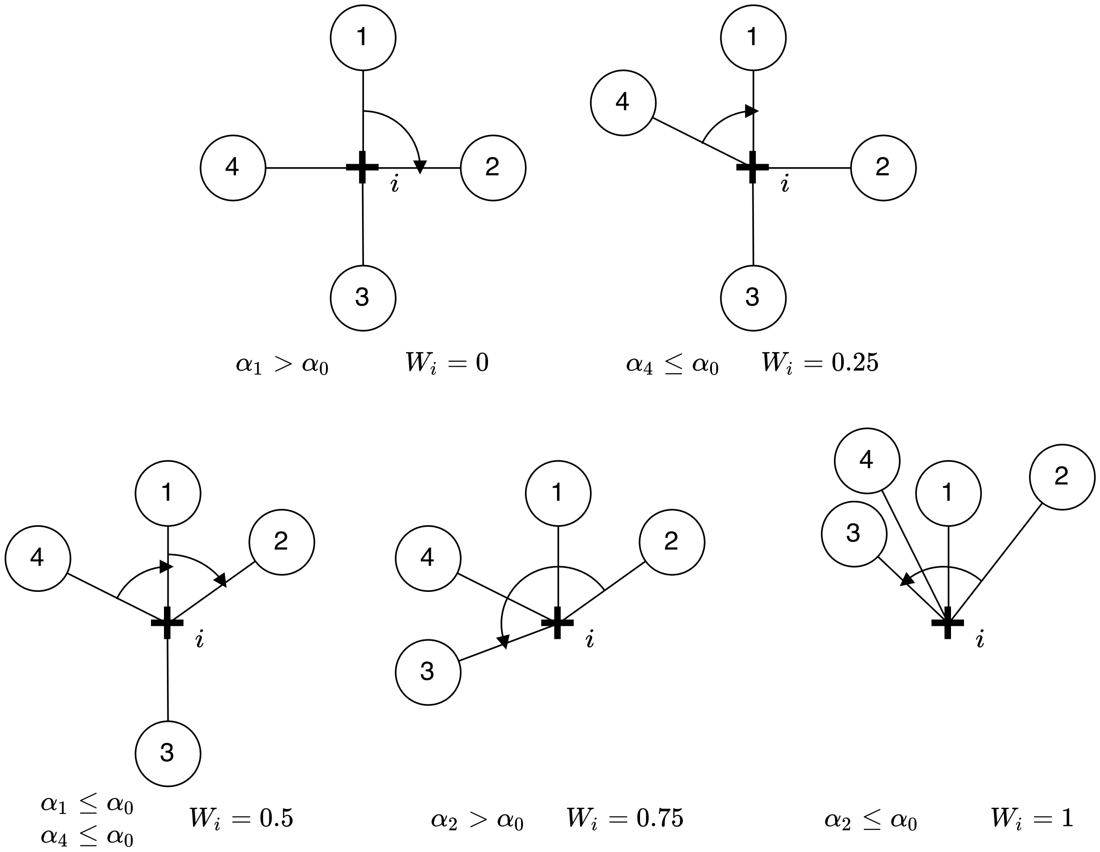


Figure 6.12: Possible values of W_i at a sample point i, denoted by a cross. Neighbours are represented as circles numbered sequentially from 1 to 4, where k = 4. The angles of arrows in each example are given below, along with the uniform angle index for that example.

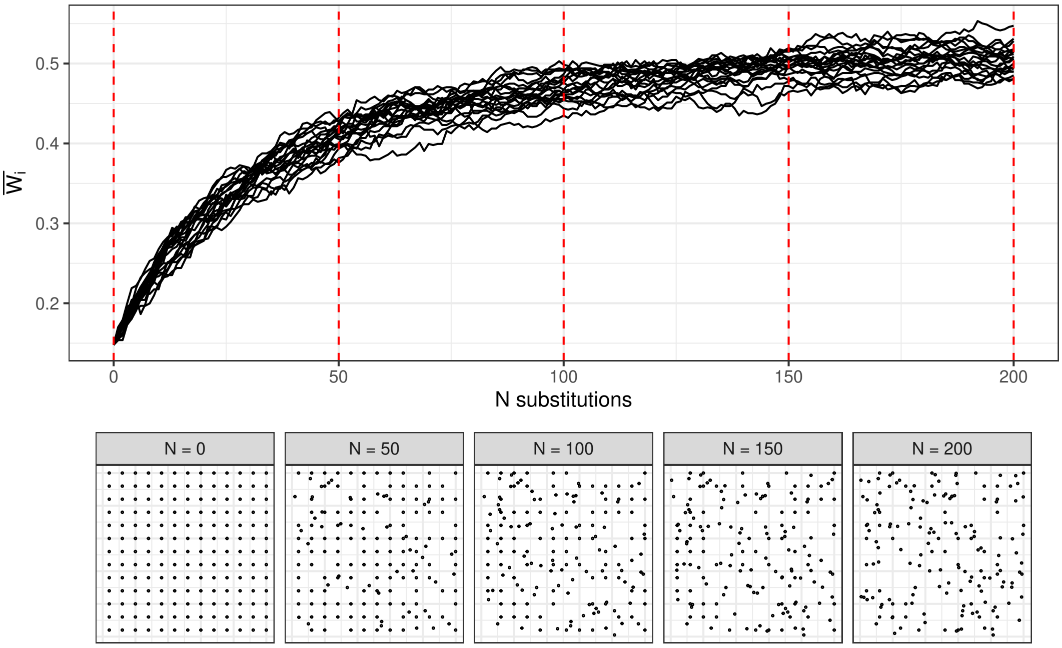


Figure 6.13: Variation in uniform angle index with increasing spatial irregularity of individuals. The top panel shows variation of uniform angle index in 20 plots as individuals are sequentially moved to a random location within the plot. Red dotted lines correspond to the panels below which show the spatial distribution of individuals after a given number of random individual movements.

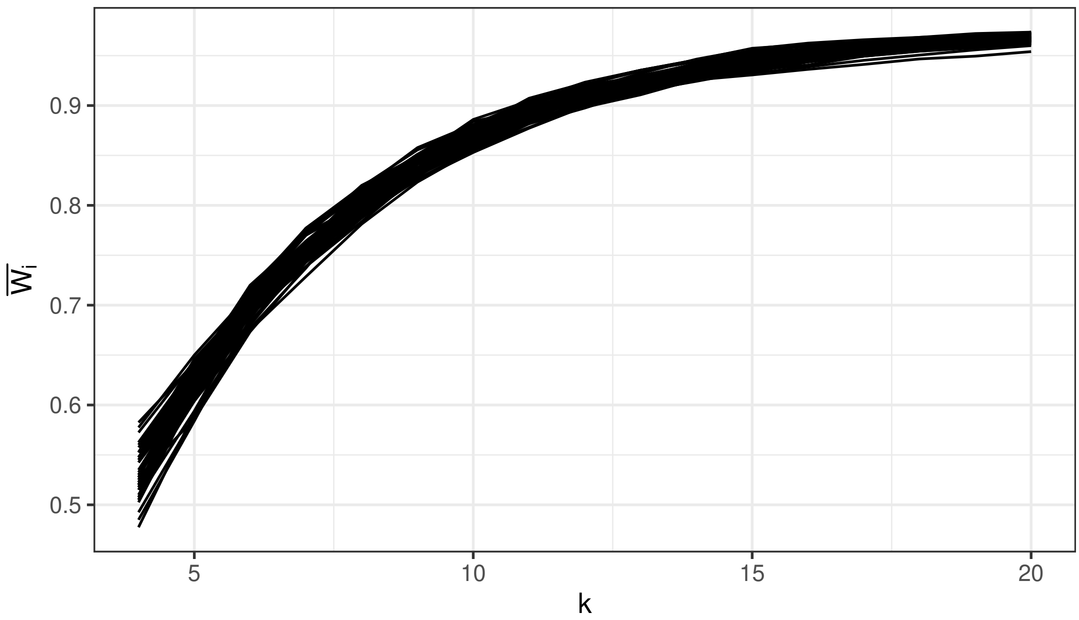


Figure 6.14: Variation in uniform angle index with increasing number of neighbours *k* considered in the calculation. 50 replicate plots were used, each with 100 individuals randomly distributed in space.

tree density (Figure 6.16). As clustering increases, individuals within clusters will exhibit progressively smaller Voronoi cells, while individuals at the edges of clusters will exhibit progressively larger Voronoi cells, thus increasing the cell area CV.

6.7.4 Subplot canopy crowding

An adapted version of the iterative Hegyi index (H_i) was used to estimate tree spatial structure in subplots (Hegyi, 1974). The adapted formula used here allows the index to be based on a point rather than a focal tree, transforming it from a tree-centric competition index to a point-centric crowding index:

$$H_i = log \sum_{j=1}^{n} (\frac{1}{L_{ij}} D_j) \tag{6.8}$$

Where n is the number of trees with canopy material within the subplot, D_j is the diameter of stem j and L_{ij} is the distance of stem j from the subplot centre i. H_i uses an iterative method for choosing active canopy occupants at the

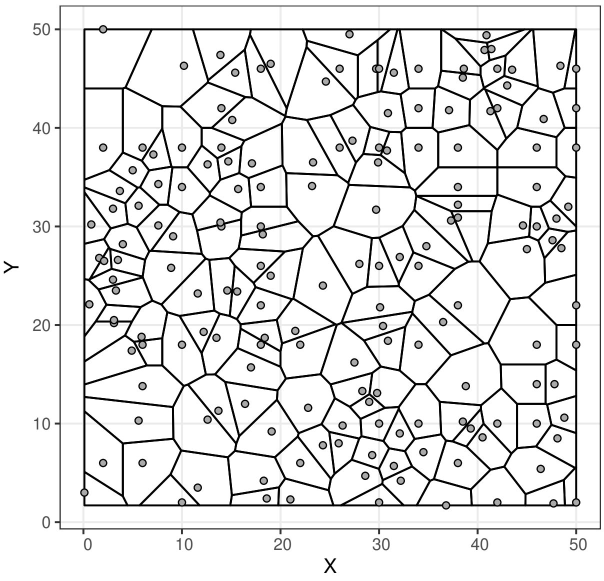


Figure 6.15: An example of a square plot with 100 randomly located individuals, with polygons constructed by Voronoi tessellation.

subplot centre, where the nearest individual to the subplot centre from each of 12 equally sized sectors is classified as the active stem (Figure 6.17). H_i was preferred over stem density to describe stem crowding in subplots because it is sensitive to how close a stem is to the subplot centre, which will affect canopy closure even if the number of stems in the subplot remains the same. H_i increases with stem diameter and number of stems, and decreases with the distance of those stems from the sample points (Figure 6.18).

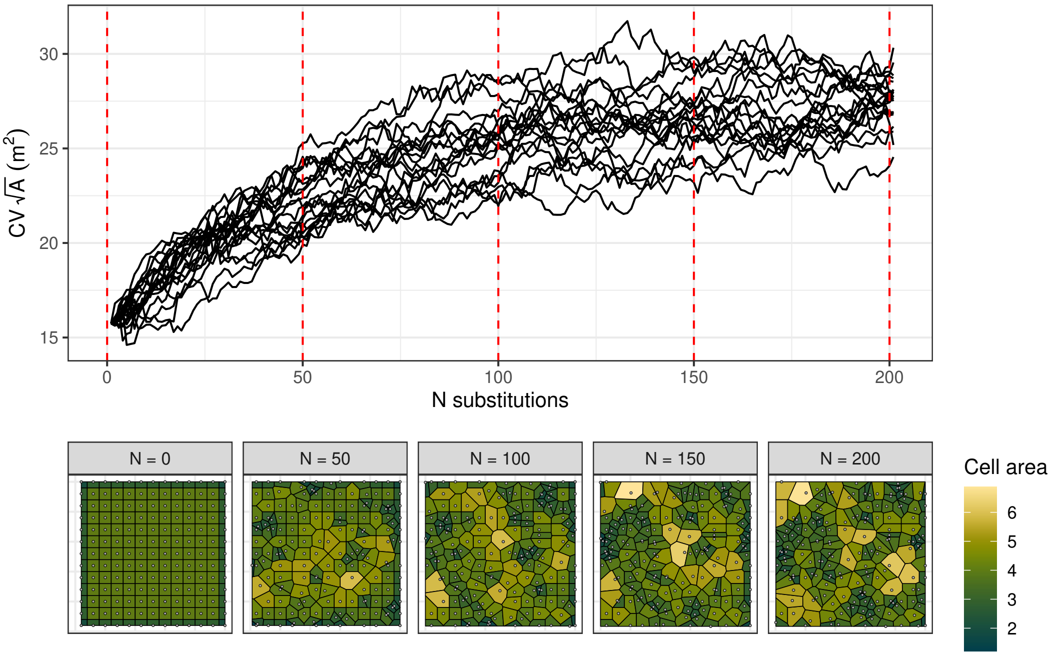


Figure 6.16: Voronoi cell area CV with increasing spatial irregularity of individuals. The top panel shows variation in Voronoi cell area CV in 20 plots as individuals are sequentially moved to a random location within the plot. Red dotted lines correspond to the panels below which show the spatial distribution of individuals after a given number of random individual movements. Voronoi cells in the bottom panels are shaded according to their area.

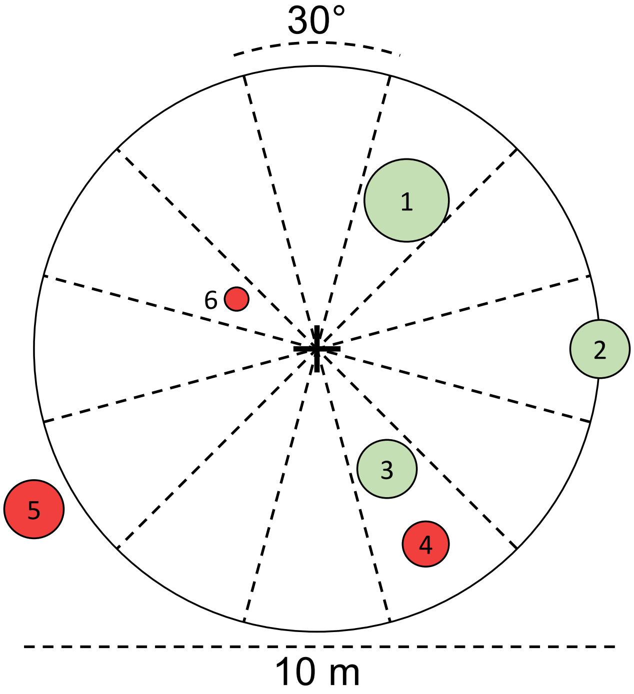
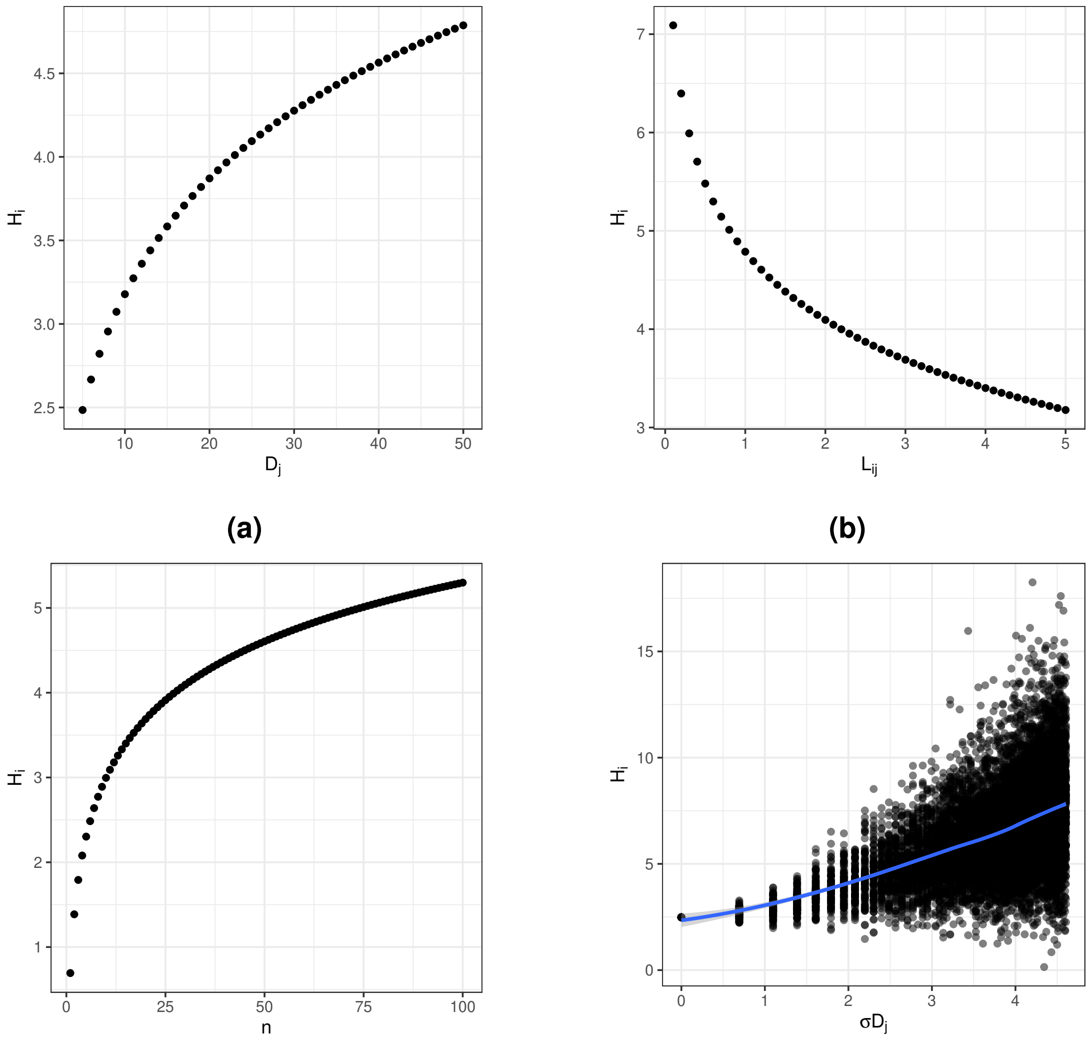


Figure 6.17: Schematic diagram demonstrating use of the iterative Hegyi index to assess crowding within each subplot. The 10 metre diameter subplot is divided into 12 equally sized sectors. Within each sector, the nearest stem of sufficient size (>5 cm diameter) to the subplot centre is recorded (e.g. 1). All stems with any canopy material inside the subplot are valid (e.g. 2). Stem 4 is not valid as it is behind stem 3. Stem 5 is invalid as all its canopy is outside the subplot. Stem 6 is too small to be recorded.



(a) **(b)**

(c) **(d)**

Figure 6.18: Variation in the iterative Hegyi index with: (a) increasing diameter (D_j) of 12 equally distant stems, (b) increasing distance (L_{ij}) of 12 stems of equal stem diameter, (c) increasing number (n) of equally distant stems with equal diameter, (d) and increasing variance in stem diameter (σD_j), measured by drawing 12 random samples from a log normal distribution with increasing standard deviation, and a mean of 5, repeated 100 times. The blue line shows a loess fit.

References

Baldocchi, D. D. & B. A. Hutchison (1986). 'On estimating canopy photosynthesis and stomatal conductance in a deciduous forest with clumped foliage'. In: *Tree Physiology* 2.1-2-3, pp. 155–168. DOI: `10.1093/treephys/2.1-2-3.155`.

Béland, M. & D. D. Baldocchi (2021). 'Vertical structure heterogeneity in broadleaf forests: Effects on light interception and canopy photosynthesis'. In: *Agricultural and Forest Meteorology* 307, p. 108525. DOI: `10.1016/j.agrformet.2021.108525`.

Béland, M. & H. Kobayashi (2021). 'Mapping forest leaf area density from multiview terrestrial lidar'. In: *Methods in Ecology and Evolution* 12.4, pp. 619–633. DOI: `10.1111/2041-210x.13550`.

Brusa, A. & D. E. Bunker (2014). 'Increasing the precision of canopy closure estimates from hemispherical photography: Blue channel analysis and under-exposure'. In: *Agricultural and Forest Meteorology* 195-196, pp. 102–107. DOI: `10.1016/j.agrformet.2014.05.001`.

Chen, X., T. Allison, W. Cao, K. Ferguson, S. Grünig, V. Gomez, A. Kipka, J. Köhler, H. Landau, R. Leandro et al. (2011). *Trimble RTX, an innovative new approach for network RTK*. Tech. rep. Portland OR, USA: International Technical Meeting of the Satellite Division of the Institute of Navigation, ION GNSS, pp. 2214–2219.

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`.

Ehbrecht, M., P. Schall, J. Juchheim, C. Ammer & D. Seidel (2016). 'Effective number of layers: A new measure for quantifying three-dimensional stand structure based on sampling with terrestrial LiDAR'. In: *Forest Ecology and Management* 380, pp. 212–223. DOI: `10.1016/j.foreco.2016.09.003`.

Frazer, G. W., R. A. Fournier, J. A. Trofymow & R. J. Hall (2001). 'A comparison of digital and film fisheye photography for analysis of forest canopy structure and gap light transmission'. In: *Agricultural and Forest Meteorology* 109.4, pp. 249–263. DOI: `10.1016/s0168-1923(01)00274-x`.

Grau, E., S. Durrieu, R. Fournier, J.-P. Gastellu-Etchegorry & T. Yin (2017). 'Estimation of 3D vegetation density with Terrestrial Laser Scanning data using voxels. A sensitivity analysis of influencing parameters'. In: *Remote Sensing of Environment* 191, pp. 373–388. DOI: `10.1016/j.rse.2017.01.032`.

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`.

Hegyi, 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.

Herbert, T. J. (1987). 'Area projections of fisheye photographic lenses'. In: *Agricultural and Forest Meteorology* 39.2-3, pp. 215–223. DOI: `10.1016/0168-1923(87)90039-6`.

Herrero-Huerta, M., A. Bucksch, E. Puttonen & K. M. Rainey (2020). 'Canopy Roughness: A New Phenotypic Trait to Estimate Aboveground Biomass from Unmanned Aerial System'. In: *Plant Phenomics* 2020, pp. 1–10. DOI: `10.34133/2020/6735967`.

Hu, L. & J. Zhu (2009). 'Determination of the tridimensional shape of canopy gaps using two hemispherical photographs'. In: *Agricultural and Forest Meteorology* 149.5, pp. 862–872. DOI: `10.1016/j.agrformet.2008.11.008`.

Huang, L. & M. J. Wang (1995). 'Image thresholding by minimizing the measures of fuzziness'. In: *Pattern Recognition* 28.1, pp. 41–51. DOI: `0031-3203/95`.

Hui, G., K. von Gadow, Y. Hu & H. Xu (2007). *Structure-based forest management*. Beijing, China: China Forestry Publishing House.

Hui, G., X. Zhao, Z. Zhao & K. von Gadow (2011). 'Evaluating tree species spatial diversity based on neighbourhood relationships'. In: *Forest Science* 57.4, pp. 292–300. DOI: `10.1093/forestscience/57.4.292`.

Hui, G. & K. Gadow (2002). 'Das Winkelmass-Theoretische überlegungen zum optimalen Standardwinkel'. In: *Allgemeine Forst und Jagdzeitung* 173 (9), pp. 173–177.

Ishii, H. T., S.-i. Tanabe & T. Hiura (2004). 'Exploring the relationships among canopy structure, stand productivity, and biodiversity of temperate forest ecosystems'. In: *Forest Science* 50.3, pp. 342–355. DOI: `10.1093/forestscience/50.3.342`.

Jennings, S. (1999). 'Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures'. In: *Forestry* 72.1, pp. 59–74. DOI: `10.1093/forestry/72.1.59`.

Jost, L. (2006). 'Entropy and diversity'. In: *Oikos* 113.2, pp. 363–375. DOI: `10.1111/j.2006.0030-1299.14714.x`.

Jupp, D. L. B., D. S. Culvenor, J. L. Lovell, G. J. Newnham, A. H. Strahler & C. E. Woodcock (2008). 'Estimating forest LAI profiles and structural parameters using a ground-based laser called 'Echidna''. In: *Tree Physiology* 29, pp. 171–181. DOI: `10.1093/treephys/tpn022`.

Khosravipour, A., A. K. Skidmore, M. Isenburg, T. Wang & Y. A. Hussin (2014). 'Generating Pit-free Canopy Height Models from Airborne LiDAR'. In: *Photogrammetric Engineering & Remote Sensing* 80.9, pp. 863–872. DOI: `10.14358/pers.80.9.863`.

Kotchenova, S. Y., X. Song, N. V. Shabanov, C. S. Potter, Y. Knyazikhin & R. B. Myneni (2004). 'Lidar remote sensing for modeling gross primary production of deciduous forests'. In: *Remote Sensing of Environment* 92.2, pp. 158–172. DOI: `10.1016/j.rse.2004.05.010`.

Leica Camera AG (2009). *Leica Cyclone*. Version 9.1.

Montes, F., I. Cañellas, M. del Río, R. Calama & G. Montero (2004). 'The effects of thinning on the structural diversity of coppice forests'. In: *Annals of Forest Science* 61.8, pp. 771–779. DOI: `10.1051/forest:2004074`.

Ong, M. S., Y. C. Kuang & M. P.-L. Ooi (2012). 'Statistical measures of two dimensional point set uniformity'. In: *Computational Statistics & Data Analysis* 56.6, pp. 2159–2181. DOI: `10.1016/j.csda.2011.12.005`.

Parker, G. G. & M. E. Russ (2004). 'The canopy surface and stand development: assessing forest canopy structure and complexity with near-surface altimetry'. In: *Forest Ecology and Management* 189.1-3, pp. 307–315. DOI: `10.1016/j.foreco.2003.09.001`.

PDAL Contributors (2018). *PDAL Point Data Abstraction Library*. DOI: `10.5281/zenodo.2556738`.

Persistence of Vision Pty. Ltd. (2004). *Persistence of Vision Raytracer (Version 3.7)*. [Computer software].

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`.

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`.

Schneider, C. A., W. S. Rasband & K. W. Eliceiri (2012). 'NIH Image to ImageJ: 25 years of image analysis'. In: *Nature Methods* 9.7, pp. 671–675. DOI: `10.1038/nmeth.2089`.

Seidel, D., C. Leuschner, C. Scherber, F. Beyer, T. Wommelsdorf, M. J. Cashman & L. Fehrmann (2013). 'The relationship between tree species richness, canopy space exploration and productivity in a temperate broad-leaf mixed forest'. In: *Forest Ecology and Management* 310, pp. 366–374. DOI: `10.1016/j.foreco.2013.08.058`.

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`.

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’. In: *Proceedings of the IUFRO International workshop ‘Sustainable forestry in temperate regions’*. Ed. by L. Bjoerk. Lund, Sweden, pp. 20–30.

Weligepolage, K., A. S. M. Gieske & Z. Su (2012). ‘Surface roughness analysis of a conifer forest canopy with airborne and terrestrial laser scanning techniques’. In: *International Journal of Applied Earth Observation and Geoinformation* 14.1, pp. 192–203. DOI: `10.1016/j.jag.2011.08.014`.

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`.

Chapter 7

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

The following chapter has been previously accepted as an article in *Diversity*:

J. L. Godlee et al. (2020). 'Diversity and structure of an arid woodland in southwest Angola, with comparison to the wider miombo ecoregion'. In: *Diversity* 12, pp. 1–20. DOI: `10.3390/d12040140`

Authors: John L. Godlee[1], Francisco Maiato Gonçalves[2], José João Tchamba[2], Antonio Valter Chisingui[2], Jonathan Ilunga Muledi[3], Mylor Ngoy Shutcha[3], Casey M. Ryan[1], Thom K. Brade[1], Kyle G. Dexter[1,4]

1. School of GeoSciences, University of Edinburgh, Edinburgh, EH9 3FF, United Kingdom
2. Herbarium of Lubango, ISCED Huíla, Sarmento Rodrigues Str. No. 2, CP. 230, Lubango, Angola
3. Restauration Ecologique et Paysage, Faculté des Sciences Agronomique, Université de Lubumbashi, Route Kasapa BP 1825, Congo
4. Royal Botanic Garden Edinburgh, Edinburgh, EH3 5LR, United Kingdom

Author Contributions: Data collection was conducted by JLG, FMG, JJT, AVC (Bicuar National Park), CMR, TKB (Tanzania, Mozambique), JIM, and MNS (Democratic Republic of Congo). The study was conceived by JLG and KGD. Methodology, analysis and writing was conducted by JLG.

Abstract

Seasonally dry woodlands are the dominant land cover across southern Africa. They are biodiverse, structurally complex, and important for ecosystem service provision. Species composition and structure vary across the region, producing a diverse array of woodland types. The woodlands of the Huíla plateau in southwest Angola represent the extreme southwestern extent of the miombo ecoregion and are markedly drier than other woodlands within this ecoregion. They remain understudied however, compared to woodlands further east in the miombo ecoregion. We aimed to elucidate further the tree diversity found within southwestern Angolan woodlands by conducting a plot-based study in Bicuar National Park, comparing tree species composition and woodland structure with similar plots in Tanzania, Mozambique, and the Democratic Republic of Congo. We found that Bicuar had comparatively low tree species diversity, but contained 27 tree species not found in other plots. Plots in Bicuar had low basal area, excepting plots dominated by *Baikiaea plurijuga*. In a comparison of plots in intact vegetation with areas previously disturbed by shifting-cultivation agriculture, we found species diversity was marginally higher in previously farmed plots. Bicuar remains an important woodland refuge in Angola, with an uncommon mosaic of woodland types within a small area. While we highlight wide variation in species composition and woodland structure across the miombo ecoregion, plot-based studies with wider sampling across the ecoregion are clearly needed to understand regional variation in vegetation diversity, composition and structure in greater detail.

7.1 Introduction

Tropical woodlands extend over 12 countries in central and southern Africa, with an estimated area of ~3.7 million km^2 (White, 1983; Mayaux et al., 2004; Arino et al., 2012). Within this, miombo woodlands are the dominant vegetation type, characterised by trees of the *Brachystegia*, *Julbernardia* and *Isoberlinia* genera, all within the Fabaceae family, subfamily Detarioideae (Chidumayo, 1997; Campbell et al., 2002; LPWG et al., 2017). These genera are seldom found as dominant species outside miombo woodlands, and while their contribution to the biomass of miombo woodlands is substantial, it varies throughout the region (Campbell et al., 2002). Across the range of southern African woodlands, variation in climate, edaphic factors, disturbance regimes and biogeography maintain a diverse array of woodland types in terms of both species composition and physiognomy (Privette et al., 2004; Caylor et al., 2004; Chidumayo, 2002). Many of these woodlands have a flammable grassy understorey and thus are also considered as a form of savanna (Ratnam et al., 2011).

The miombo ecoregion extends across the continent in a wide band that reaches north into Kenya and the Democratic Republic of Congo (DRC) and south into the northeast of South Africa (Figure 7.1). Miombo woodlands are defined both by their tree diversity and by their structure, consisting of a grassy herbaceous understorey with an often sparse tree canopy. In archetypal miombo woodlands, species of the genera *Brachystegia*, *Julbernardia* and *Isoberlinia* generally hold the most biomass, forming a sparse but frequently contiguous woodland canopy. Distinct from dry tropical forests, miombo woodlands generally maintain a grassy understorey dominated by grass species utilising the C_4 carbon fixation pathway (Dexter et al., 2015). Miombo woodlands are heavily structured by seasonal fire and herbivory, with fire particularly often preventing the creation of a dense closed tree canopy which would naturally occur in the absence of these disturbances (Oliveras & Malhi, 2016; Dantas et al., 2016). Within the miombo ecoregion, other woodland types exist, notably, woodlands dominated by *Baikiaea plurijuga* or *Colophospermum mopane* (Campbell et al., 2002).

Southern African woodlands are structurally complex but species poor in the tree layer compared to dry tropical forests which exist at similar latitudes (DRYFLOR et al., 2016; Torello-Raventos et al., 2013). These woodlands contain many endemic tree species however, and support a highly diverse woodland understorey, with an estimated 8500 species of vascular plants (Frost, 1996). Miombo woodlands provide ecosystem services for an estimated 150 million people (Ryan et al., 2016). Additionally miombo woodlands hold ~18-24 Pg C in woody biomass and soil organic carbon, which is comparable to that held in the rainforests of the Congo basin (~30 Pg C) (Mayaux et al., 2008). As woodland resource extraction and conversion to agricultural land accelerates due to growing human populations, the conservation of miombo woodlands as a biodiverse and unique ecosystem has become a growing concern. Despite their importance however, dry tropical woodlands remain understudied compared to wet forests across the globe (Clarke et al., 2017).

Over the previous two decades, the limited ecological research in southern African woodlands has been concentrated in the central and eastern parts of the miombo region, notably in southern Tanzania, Mozambique, Malawi, Zimbabwe and Zambia. The southwestern extent of miombo woodlands, which is found entirely within Angola has received considerably less attention (Huntley et al., 2019). Partly this is due to diminished research capacity during the Angolan civil war following the country's independence, which took place officially between 1975 and 2002, but with sporadic localised periods of civil unrest until around 2012 (Soares de Oliveira, 2015). While botanical surveys of woodlands in this region are more plentiful (Huntley et al., 2019; Figueiredo et al., 2009), joint studies of woodland species composition and physical structure remain scarce. This is despite the value of these studies in helping to estimate woodland net primary productivity, carbon sequestration potential, and community assembly. To properly understand spatial variation in woodland species composition and physical structure across the miombo ecoregion, it is necessary to fill understudied gaps. In this study we aim to address one such gap in southwest Angola, and place it in context with other woodlands across the miombo ecoregion.

The miombo woodlands of southwest Angola are found in their most intact form in Bicuar National Park and to a lesser extent in the adjacent Mupa National Park, on the Huíla plateau (Chisingui et al., 2018). Both of these national parks have been protected to varying extents since 1938 (Huntley et al., 2019). These woodlands exist in much drier conditions than other miombo woodlands; precipitation diminishes rapidly within the Huíla plateau towards the Angolan coast and the Namib desert (Figure 7.1). The vegetation of the

Huíla plateau holds many endemic species, around 83 endemic Fabaceae species (Soares et al., 2007) and the most endemic plant species of any part of Angola (Figueiredo et al., 2009). Linder (2001) and Droissart et al. (2018) both identify the western portion of the Huíla plateau as a centre of tropical African endemism.

Much of the historic miombo woodland area in southwest Angola surrounding the Bicuar and Mupa National Parks has been deforested in recent years, with a clear increase in deforestation activity since the end of the civil war owing to an increase in rural population and agricultural activity (Schneibel et al., 2013; Huntley et al., 2019). The western extent of miombo woodlands found within Bicuar National Park are therefore of great importance for conservation as a refuge for wildlife and endemic plant species (Huntley et al., 2019; Silva et al., 2020).

It is important to focus not only on the biodiversity of 'pristine' (i.e. not utilised by humans) woodland areas but also land that has been previously utilised by humans, in order to properly assess the biodiversity and woodland structure of the Park. Woodland disturbance through shifting cultivation practices produces novel habitats which are not necessarily of lower conservation value (McNicol et al., 2015; Gonçalves et al., 2017). Since Bicuar National Park's rejuvenation following the reinforcement of park boundaries after the civil war, many areas of woodland that were previously heavily grazed, farmed via shifting cultivation techniques, and used for timber extraction have been allowed to re-establish and are now protected from further human resource extraction. This presents a unique opportunity to compare the species composition of these previously farmed areas with areas of nearby 'pristine' woodland that have not been farmed in living memory.

In this study we present results of the tree diversity and woodland structure of miombo woodlands found at the far western extent of miombo woodlands in Bicuar National Park, Huíla province, Angola. Our study utilised recently installed biodiversity monitoring plots set up within the Park in 2018 and 2019. We compare the tree diversity and woodland structure of Bicuar National Park with biodiversity monitoring plots previously established in other areas of miombo woodland across the miombo ecoregion which use a common plot biodiversity census methodology. In addition, we take advantage of a unique opportunity to compare the tree species composition of areas of abandoned and now protected farmland that have begun to re-establish as woodland. Specifically, this study aims to:

1. Describe the tree species diversity and structure of woodlands in Bicuar National Park, and compare this composition with other woodlands across the miombo eco-region.
2. Explore the role of environmental factors in driving changes in tree species composition across the miombo ecoregion.
3. Describe variation in tree species composition and woodland structure between ‘pristine’ woodland patches and those previously utilised by humans within Bicuar National Park.

7.2 Materials and methods

7.2.1 Study area

We chose three areas of miombo woodland across the miombo ecoregion to compare with those in Bicuar National Park, Angola (S15.1°, E14.8°). The three sites were Gorongosa District in central Mozambique (S19.0°, E34.2°) (Ryan et al., 2011), Kilwa District in southern Tanzania (S9.0°, E39.0°) (McNicol et al., 2018a), and the Mikembo Natural Reserve in Katanga, southern Democratic Republic of Congo (DRC) (S11.5°, E27.7°) (Muledi et al., 2017). Within each of these woodland sites, multiple one hectare square plots had been installed previously to monitor biodiversity and biomass dynamics. In Katanga, a larger 10 ha plot was subdivided into ten 1 ha plots for this study. We used these previous censuses, collected between 2010 and 2019, to estimate tree biodiversity and woodland structure. Sites range in Mean Annual Precipitation (MAP) from 864 mm y^{-1} in Bicuar to 1115 mm y^{-1} in Katanga. Mean Annual Temperature ranges from ~20.5 ℃ in Bicuar and Katanga to ~25.8 ℃ in Kilwa (Figure 7.1, Figure 7.2, Table 7.1).

Bicuar National Park covers an area of ~7900 km^2, established as a hunting reserve in 1938, and later as a national park in 1964 (Figure 7.3). While fauna populations in the Park were severely damaged by the Angolan civil war, the interior of the Park remains as a largely intact mosaic of miombo woodland,

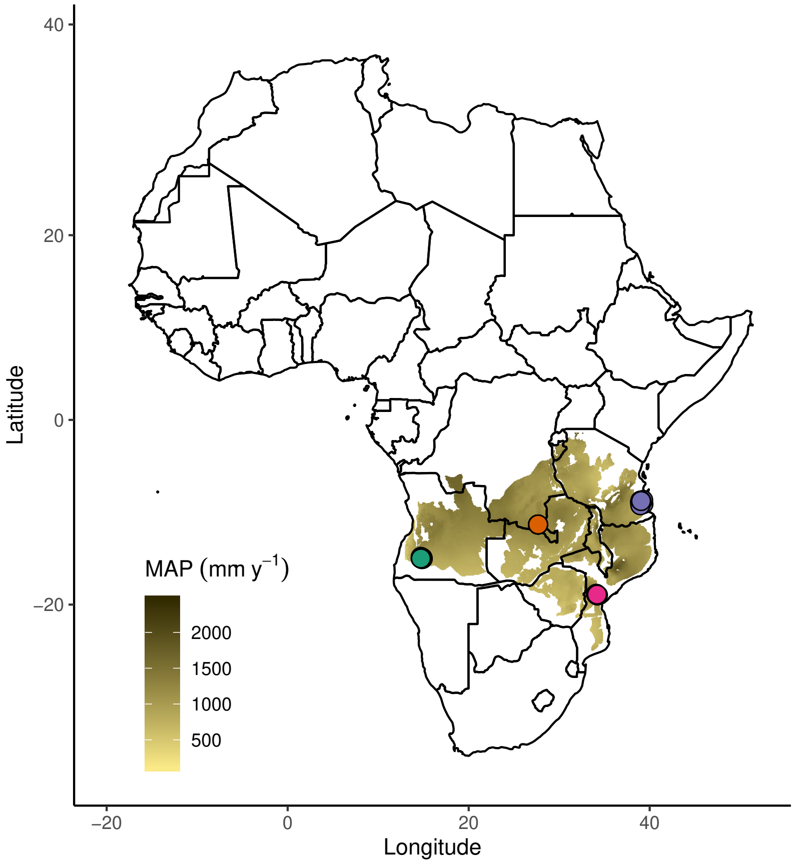


Figure 7.1: Locations of plots used in this study, with respect to the distribution of miombo woodland vegetation (White, 1983), shaded according to Mean Annual Precipitation (MAP) (Fick & Hijmans, 2017).

Table 7.1: Description of each group of plots used in the analysis. MAT = Mean Annual Temperature, MAP = Mean Annual Precipitation, CWD = Climatic Water Deficit, DD = Decimal Degrees.

Plot group	MAT (℃)	MAP (mm y^{-1})	CWD (mm y^{-1})	Latitude (DD)	Longitude (DD)	N plots	N species
Bicuar NP	20.5	864	−815	−15.12	14.81	15	49
DRC	20.4	1115	−762	−11.49	27.67	12	89
Mozambique	24.4	1029	−662	−18.95	34.16	15	162
Tanzania	25.8	956	−754	−9.05	39.05	22	248

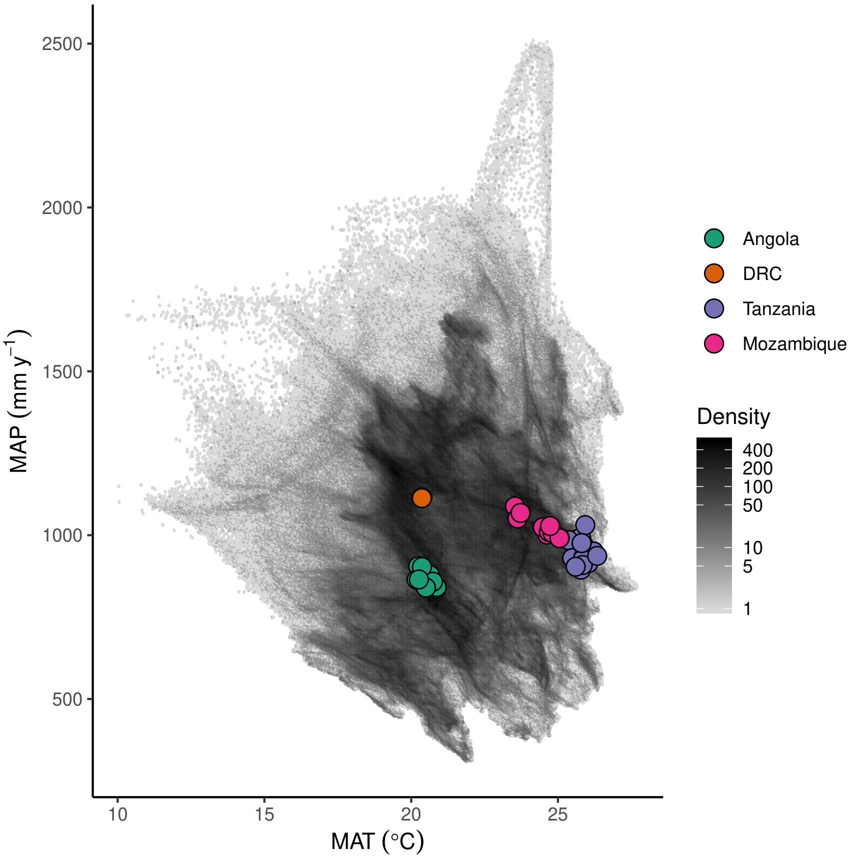


Figure 7.2: The plots used in this study within the climate space of the miombo ecoregion, estimated using the WorldClim dataset over the miombo ecoregion extent with a pixel size of 30 arc seconds (0.86 km^2 at the equator) (Fick & Hijmans, 2017). Note that the density colour scale is log-transformed for visual clarity.

Baikiaea-Burkea woodland, shrub/thicket vegetation and seasonally flooded grassland. Encroachment of agriculture and grazing, particularly along the northwest and western boundaries of the Park, has led to a fragmented park boundary with patches of diminished thicket and woodland in areas of previously farmed land that have been protected since park boundaries were re-established following the end of the civil war.

Plots in Tanzania were located predominantly within or near the Mtarure Forest Reserve, administrated by the Tanzania Forest Service and protected from human incursion since their installation. Plots were established between 2010 and 2011 in grassy savanna/woodland areas, with plots located along the road network with a 1 km buffer from the road. Plots in Mozambique were established in 2004, in areas of miombo woodland, some of which had been previously used for agriculture but since left fallow, with all plots >250 m from the road. Plots in DRC were established in 2009 and located within a larger 800 ha miombo woodland reserve. All plots were located quasi-randomly, with consideration to accessibility for future woodland censuses.

7.2.2 Plot data collection

We sampled 15 one hectare plots in Bicuar National Park and collated data from a total of 64 one hectare plots across the miombo ecoregion within the four sites. Figure 7.1 and Table 7.1 show the locations and provide a general description of each site, respectively. Plots in Bicuar were situated at least 500 m from the edge of a woodland patch to prevent edge effects which may have altered tree species composition.

Within each plot, every tree stem $\geq$5 cm stem diameter was recorded, except in the DRC plots, where only stems $\geq$10 cm stem diameter were recorded. For each tree stem the species and stem diameter were recorded. Tree species were identified using local botanists at each site and taxonomy was later checked against the *African Plant Database (version 3.4.0)* (2020). At all sites, Palgrave (2003) was used, along with other texts, to identify tree species. Specimens that could not be identified in the field, or subsequently at herbaria, were described as morphospecies. All tree species within the Bicuar National Park plots were identified. Tree coppicing due to fire, herbivory, and human actions is common in miombo woodlands, therefore, for trees with multiple stems, each stem $\geq$5 cm stem diameter was recorded, while the parent tree was also recorded for diversity analyses described below.

Stem diameter was recorded at 1.3 m from the ground along the stem (diameter at breast height, DBH) as per convention using a diameter tape measure (Kershaw et al., 2017). Where stem abnormalities were present at 1.3 m from the ground, which precluded the accurate estimation of stem diameter at 1.3 m, the stem diameter was recorded at the nearest 10 cm increment above 1.3 m without significant stem abnormalities (Kershaw et al., 2017). To ensure consistency among stem diameter values recorded at different heights, when the stem diameter was recorded at a height other than 1.3 m the stem diameter at 1.3 m was estimated from the recorded stem diameter using a cubic polynomial equation which adjusts for tree stem taper. This equation was calibrated on 100 stems measured at multiple heights in Niassa Province, Mozambique (Code 7.S1). Stems below 10 cm stem diameter were not measured in the DRC plots. We therefore estimated the number of 5-10 cm stems in each these plots by extrapolating a linear regression of log stem abundance across the available stem diameter classes.

In addition to the one hectare plots across the miombo ecoregion, we compared the tree biodiversity of ‘pristine’ areas of miombo woodland in Bicuar National Park with areas of woodland around the edge of the Park that had been previously farmed via shifting cultivation methods, and had since been abandoned and reclaimed within the Park boundaries (Figure 7.3). We identified areas previously farmed with the help of park rangers and local residents who identified these areas from memory. We conducted 20 plot surveys of woodland diversity and structure in these areas with 20×50 m (0.1 ha) plots, and compared their diversity and structure with 20×50 m subsamples of the 15 one hectare plots within the Park interior. Like the one hectare plots, within these smaller 20×50 m plots we recorded the species and stem diameter of every tree stem $\geq$5 cm stem diameter.

7.2.3 Climatic data

The WorldClim dataset (Fick & Hijmans, 2017) was used to gather data on plot level climatic conditions. We estimated Mean Annual Precipitation (MAP) as the mean of total annual precipitation values between 1970 and 2000, and Mean

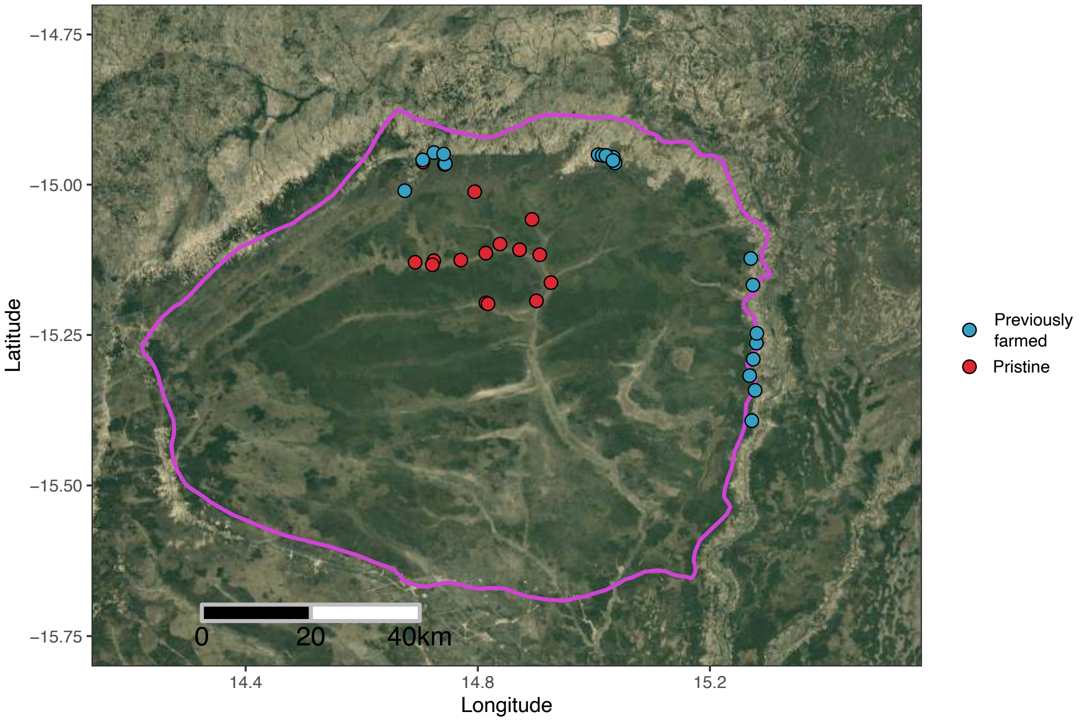


Figure 7.3: Location of plots in Bicuar National Park, southwest Angola. The Park boundary is shown as a pink outline, according to UNEP-WCMC and IUCN (2019). One hectare ‘pristine’ plots are shown as red points, while previously farmed 20×50 m (0.1 hectare) plots are shown as blue points. The map background is a true colour composite satellite image generated using Google Maps Static Maps.

Annual Temperature (MAT) as the mean of mean annual temperatures between 1970 and 2000. The seasonality of temperature (MAT SD) was calculated as the standard deviation of monthly temperature per year, respectively. We estimated Climatic Water Deficit (CWD) for each plot according to Chave et al. (2014), as the sum of the difference between monthly rainfall and monthly evapotranspiration when the difference is negative, using data from WorldClim.

7.2.4 Data analysis

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

$$g_i = \pi \times (d_i/2)^2 \tag{7.1}$$

Where d_i is the estimated stem diameter of stem i at 1.3 m having accounted for tree taper. We then calculated the total basal area of each plot as the sum of each stem's basal area. For the DRC plots which lacked 5-10 cm stems, we estimated basal area in this stem diameter class from our extrapolation of stem abundance in the 5-10 cm diameter class, assuming a mean stem diameter of 7.5 cm.

All diversity measures were calculated on individual tree level data, rather than stem level data, to avoid artificial inflation of abundance for those species which readily coppice. We calculated the alpha diversity of each plot using both the tree species richness of trees with stems $\geq$5 cm diameter, and the Shannon-Wiener index (H') (Equation 7.2), using the `vegan` package in R (Oksanen et al., 2019):

$$H' = -\sum_{i=1}^{S} p_i \ln p_i \tag{7.2}$$

Where S is the total number of species in the plot, p_i is the proportional abundance of the ith species and ln is the natural logarithm.

We calculated the pairwise beta diversity among sites using the Sørensen coefficient (S_S) (Equation 7.3) (Koleff et al., 2003):

$$S_S = \frac{2a}{2a + b + c} \tag{7.3}$$

Where a is the number of species shared between two sites, b is the number of species unique to site 1 and c is the number of species unique to site 2. We calculated S_S for each pairwise combination of sites using aggregated species composition data from all plots in each site. The value of S_S, which ranges between zero and one, was multiplied by 100 to give a "percentage similarity" between communities in species composition.

We estimated abundance evenness for each plot using the Shannon equitability index ($E_{H'}$) (Smith & Wilson, 1996) which is the ratio of H' to the log transformed species richness.

We analysed the difference in alpha diversity measures and woodland structural variables among groups of plots using Analysis of Variance (ANOVA) statistical models, with a null hypothesis that there was no difference among the mean values of groups of plots. Post-hoc Tukey's HSD tests were used to investigate the degree to which pairwise combinations of plot groups differed in each case.

We used Non-metric Multidimensional Scaling (NMDS) to assess the variation in species composition among one hectare plots, and also between previously farmed and 'pristine' 20×50 m plots within Bicuar National Park, using the `vegan` R package. The number of dimensions for NMDS was minimised while ensuring the stress value of the NMDS fit was $\leq$0.1. NMDS analyses were run with 500 random restarts to ensure a global solution was reached. We used Bray-Curtis dissimilarity as the optimal measure of ecological distance (Legendre & De Cáceres, 2013). We fit plot level estimates of MAP, MAT, the seasonality of MAT and CWD to the first two axes of the resulting ordination using the `envfit` function in the `vegan` R package to investigate how these environmental factors influenced the grouping of species composition among plots. All analyses were conducted in R version 4.1.0 (R Core Team, 2020).

7.3 Results

7.3.1 Alpha diversity

In Bicuar National Park we measured a total of 6565 trees within the one hectare plots, and across the four sites, a total of 25525 trees were sampled. Trees in Bicuar National Park belonged to 48 species within 18 families. Across all four sites we recorded 468 species from 43 families. The most diverse family within each site and among all plots was Fabaceae with 61 species. We encountered 27 tree species in Bicuar National Park which were not found in the other miombo woodland plots (Table 7.2). The most common of these unique species were *Brachystegia tamarindoides* (n = 576), *Baikiaea plurijuga* (n = 331) and *Baphia massaiensis* (n = 303). Four species unique to Bicuar National Park within this dataset only had one individual recorded: *Elachyptera parvifolia*, *Entandrophragma spicatum*, *Oldfieldia dactylophylla*, *Peltophorum africanum*.

Table 7.2: Species found in one hectare plots in Bicuar National Park. Stem diameter and basal area are the mean of all stems with the standard error of the mean in parentheses. Number of stems per hectare is the mean of the number of stems in all one hectare plots where stems of that species are present with the standard error of the mean in parentheses. Species found only in Bicuar National Park are marked in bold text with an asterisk.

Family	Species	Stem diam. (cm)	Basal area (m^2 ha^{-1})	N stems	N stems ha^{-1}
Fabaceae	Albizia antunesiana	9.1(2.03)	0.07(0.040)	40	8(4.81)
Fabaceae	**⋆Baikiaea plurijuga**	28.9(0.75)	1.72(0.570)	331	55.2(17.83)
Fabaceae	**⋆Baphia bequaertii**	7.4(0.36)	0.08(0.050)	127	31.8(18.14)
Fabaceae	**⋆Baphia massaiensis**	6.6(0.17)	0.05(0.020)	303	30.3(11.20)
Fabaceae	Bobgunnia madagascariensis	7.8(0.91)	0.04(0.020)	32	10.7(9.67)
Fabaceae	**⋆Brachystegia longifolia**	12.9(0.48)	1.14(0.430)	576	115.2(72.67)
Fabaceae	Brachystegia spiciformis	11.4(0.52)	0.74(0.430)	326	81.5(46.56)
Phyllanthaceae	**⋆Bridelia mollis**	5.7(0.31)	0.02(NA)	23	23(NA)
Fabaceae	Burkea africana	8.5(0.33)	0.39(0.120)	863	71.9(19.11)
Combretaceae	Combretum apiculatum	7.6(0.45)	0.06(0.040)	60	30(15.00)
Combretaceae	Combretum celastroides	5.6(0.34)	<0.01(0.000)	7	3.5(2.50)
Combretaceae	Combretum collinum	6.3(0.09)	0.07(0.020)	609	50.8(20.48)
Combretaceae	**⋆Combretum hereroense**	6.7(0.26)	0.02(0.010)	73	12.2(5.69)
Combretaceae	**⋆Combretum psidioides**	7.4(0.43)	0.01(0.010)	33	6.6(4.17)

Continued overleaf

Family	Species	Stem diam. (cm)	Basal area (m^2 ha^{-1})	N stems	N stems ha^{-1}
Combretaceae	Combretum zeyheri	6.3(0.35)	0.01(0.000)	61	10.2(3.03)
Euphorbiaceae	⋆**Croton gratissimus**	6.1(1.55)	<0.01(NA)	4	4(NA)
Ebenaceae	⋆**Diospyros batocana**	8.4(2.14)	<0.01(0.000)	2	1(0.00)
Ebenaceae	⋆**Diospyros kirkii**	9.3(1.64)	0.03(NA)	11	11(NA)
Apocynaceae	Diplorhynchus condylocarpon	8.2(0.52)	0.08(0.060)	174	19.3(7.57)
Malvaceae	⋆**Dombeya rotundifolia**	5.5(0.19)	<0.01(NA)	2	2(NA)
Celastraceae	⋆**Elachyptera parvifolia**	7.3(NA)	<0.01(NA)	1	1(NA)
Meliaceae	⋆**Entandrophragma spicatum**	14.6(NA)	<0.01(NA)	1	1(NA)
Fabaceae	Erythrophleum africanum	9.0(0.84)	0.10(0.040)	128	18.3(6.82)
Rubiaceae	⋆**Gardenia volkensii**	5.6(1.15)	<0.01(0.000)	5	2.5(1.50)
Fabaceae	⋆**Guibourtia coleosperma**	7.2(1.00)	0.02(0.010)	31	6.2(3.54)
Phyllanthaceae	Hymenocardia acida	5.9(1.25)	<0.01(NA)	6	6(NA)
Fabaceae	Julbernardia paniculata	10.1(0.21)	0.92(0.200)	1624	162.4(50.60)
Fabaceae	⋆**Lonchocarpus nelsii**	13.4(0.88)	0.15(0.030)	165	15(2.77)
Dipterocarpaceae	⋆**Monotes angolensis**	7.4(0.83)	<0.01(0.000)	2	1(0.00)
Ochnaceae	⋆**Ochna pulchra**	6.5(0.80)	0.01(0.000)	26	8.7(3.76)
Picrodendraceae	⋆**Oldfieldia dactylophylla**	8.5(NA)	<0.01(NA)	1	1(NA)
Fabaceae	⋆**Peltophorum africanum**	11.5(NA)	<0.01(NA)	1	1(NA)
Fabaceae	Pericopsis angolensis	8.4(0.61)	0.06(0.020)	97	12.1(5.08)

Continued overleaf

Family	Species	Stem diam. (cm)	Basal area (m^2 ha^{-1})	N stems	N stems ha^{-1}
Phyllanthaceae	Pseudolachnostylis maprouneifolia	6.7(0.45)	0.03(0.010)	84	9.3(3.00)
Combretaceae	⋆**Pteleopsis anisoptera**	6.8(0.46)	0.07(0.020)	81	20.2(15.11)
Fabaceae	Pterocarpus angolensis	13.0(0.61)	0.15(0.100)	102	17(8.65)
Fabaceae	⋆**Pterocarpus lucens**	6.9(0.94)	<0.01(NA)	4	4(NA)
Rubiaceae	⋆**Rothmannia engleriana**	6.8(0.66)	<0.01(0.000)	5	1.7(0.67)
Euphorbiaceae	⋆**Schinziophyton rautanenii**	8.0(2.82)	<0.01(NA)	3	3(NA)
Polygalaceae	Securidaca longepedunculata	7.3(1.12)	<0.01(0.010)	4	2(1.00)
Loganiaceae	Strychnos cocculoides	10.4(1.17)	0.03(0.020)	19	6.3(3.53)
Loganiaceae	⋆**Strychnos pungens**	6.1(0.48)	<0.01(0.000)	18	3.6(0.93)
Loganiaceae	Strychnos spinosa	6.8(0.36)	0.02(0.010)	97	9.7(4.07)
Combretaceae	⋆**Terminalia brachystemma**	6.5(0.21)	0.04(0.020)	174	29(12.04)
Combretaceae	Terminalia sericea	7.1(0.28)	0.06(0.030)	214	23.8(12.18)
Ximeniaceae	Ximenia americana	6.1(0.53)	<0.01(0.000)	7	1.8(0.25)
Sapindaceae	Zanha africana	9.4(1.12)	0.01(NA)	6	6(NA)
Rhamnaceae	⋆**Ziziphus abyssinica**	5.9(1.13)	<0.01(NA)	2	2(NA)

Alpha diversity in Bicuar National Park was low compared to other sites (Figure 7.4). Mean H' across plots in Bicuar National Park was 1.6±0.13. An ANOVA showed a significant difference in H' among sites (F(3,60) = 7.54, p<0.01, Table 7.3), and a post-hoc Tukey's test showed that H' in plots in Bicuar National Park was significantly different from those in DRC (H' = 2.7±0.19, p<0.01), Mozambique (H' = 2.4±0.2, p<0.01) and Tanzania (H' = 2.2±0.11, p<0.05). Variation in H' is large within Bicuar National Park, with H' ranging from 0.85 to 2.56, but this was a similar range to other sites. In contrast, the range of species richness within Bicuar National Park was much lower than other sites, suggesting that the wide range in H' was caused by variation in abundance evenness.

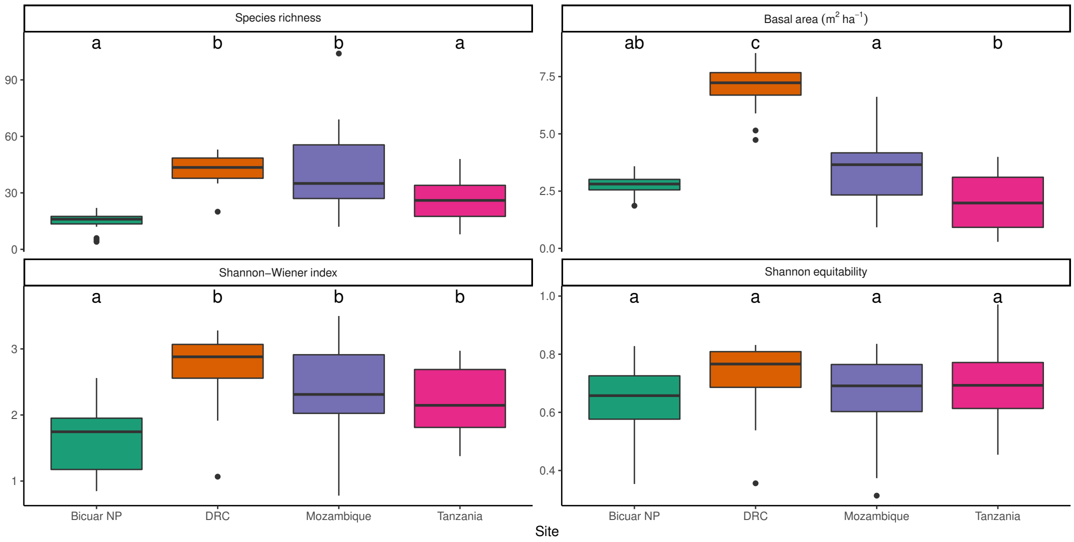


Figure 7.4: Variation of alpha diversity estimates and basal area among sites. Boxes bound the 1st and 3rd quartiles, with the median within the box. Whiskers represent 1.5 times the interquartile range plus or minus the 1st and 3rd quartiles, respectively. Values found beyond the whiskers are shown individually as points. Letter labels above each box refer to groupings from post-hoc Tukey's tests on the ANOVA of each diversity/structure variable. Sites sharing a letter do not differ significantly (p<0.05)

.

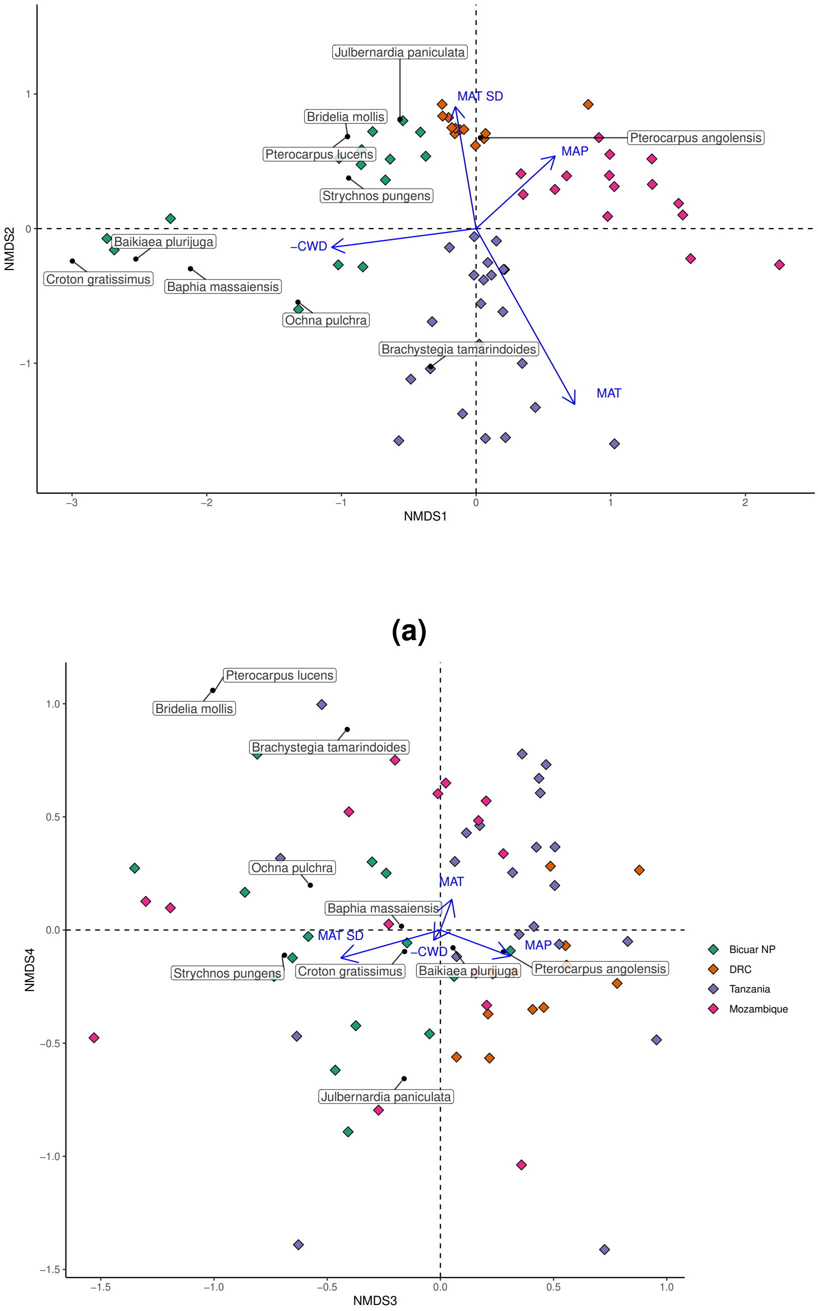
Table 7.3: Results of ANOVA tests for alpha diversity metrics and plot basal area, among the four sites. Mean values for each site with standard errors in parentheses are shown. Asterisks indicate the p-value of individual sites in each ANOVA (***<0.001, **<0.01, *<0.05, .<0.1).

	Dependent variable			
	Species richness	Basal area	Shannon (H')	Shannon equit. (E_H)
DRC	27.920*** (5.538)	4.175*** (0.452)	1.055*** (0.236)	0.080 (0.053)
Tanzania	12.440** (4.788)	–0.721* (0.391)	0.605*** (0.204)	0.064 (0.046)
Mozambique	27.930*** (5.221)	0.653 (0.427)	0.792*** (0.223)	0.028 (0.050)
Constant	14.330*** (3.692)	2.778*** (0.302)	1.617*** (0.158)	0.631*** (0.035)
Observations	64	64	64	64
Adjusted R^2	0.363	0.691	0.237	0.003
Residual Std. Error (df = 60)	14.300	1.168	0.611	0.137
F Statistic (df = 3; 60)	12.980***	48.040***	7.537***	1.000

7.3.2 Beta diversity

The NMDS of plot species composition among one hectare plots was run with four dimensions. The stress value was 0.10. Plot diversity in Bicuar National Park formed three distinct groups within axes 1 and 2 of the NMDS ordination. Bicuar plots 9, 13, and 15 were characterised by high abundances of *Baikiaea plurijuga*, *Baphia massaiensis* and *Croton gratissimus*, according to species scores from the NMDS. Bicuar plots 4, 11, and 12 were characterised by *Brachystegia tamarindoides*, and *Ochna pulchra*. The third group consisting of the remaining seven plots surprisingly had a species composition most similar to that of plots in the DRC group according to the NMDS, sharing the core miombo species of *Julbernardia paniculata* and *Pterocarpus angolensis*. This group of plots in Bicuar National Park was further characterised by the abundance of *Pterocarpus lucens*, *Strychnos pungens* and *Bridelia mollis* however, which were not present in the DRC plots. All environmental factors fitted to the NMDS ordination correlated significantly with the grouping of plots (Figure 7.5a). MAT explained the most variation in plot position on the first two NMDS axes (R^2 = 0.75, $p<0.01$), followed by CWD (R^2 = 0.54, $p<0.01$), the seasonality of MAT (R^2 = 0.46, $p<0.01$) and MAP (R^2 = 0.4, $p<0.01$). Variation in MAP explained much of the difference among plots in Bicuar National Park versus those in Tanzania and Mozambique. Axes 3 and 4 showed a greater degree of overlap in species composition among plot groups, with plots from Bicuar National Park similar to a select few plots in both Tanzania and Mozambique (Figure 7.5b). Axis 3 distinguished plots in Bicuar NP from those in DRC, while plots from all geographic area overlapped in their distribution across Axis 4. Axes 3 and 4 largely reflected distribution patterns of less abundant species and not the dominant species in the vegetation.

The pairwise Sørensen coefficient of percentage similarity (S_S) showed that the species composition of plots in Bicuar National Park had low similarity with other sites in the study, sharing few species with other sites (Table 7.4). Similar to the NMDS, these results show that plots in Bicuar National Park are most similar to those found in DRC.



(a)

(b)

Figure 7.5: Environmental factors fitted to (a) axes 1 and 2, and (b) axes 3 and 4 of the NMDS ordination of plot species composition. Diamonds are plot scores coloured by site. Arrows indicate environmental fits, scaled by R^2. Climatic Water Deficit (CWD) is expressed more intuitively as the inverse of CWD, thus larger values indicate higher CWD.

Table 7.4: Pairwise beta diversity comparison of plot groups measured by the Sørensen coefficient (S_s) of percentage similarity of aggregated plot level data from each of the four sites. Values in parentheses are the number of species unique to each site in each comparison.

Site 1	Site 2	S_s	Shared species
Bicuar NP(34)	DRC(74)	20.6	14
Bicuar NP(34)	Tanzania(147)	13.4	14
Bicuar NP(37)	Mozambique(236)	7.5	11
DRC(64)	Tanzania(137)	19.3	24
DRC(69)	Mozambique(228)	11.3	19
Tanzania(139)	Mozambique(225)	10.8	22

7.3.3 Woodland structure

Mean basal area of plots in Bicuar National Park was 2.78±0.122 m^2 ha^{-1}, ranging from 1.86 to 8.53 m^2 ha^{-1} (Figure 7.4). An ANOVA showed a significant difference in basal area among sites (F(3,60) = 48.04, $p<0.01$), and a post-hoc Tukey's test showed that basal area in Bicuar National Park was significantly lower than plots in DRC (BA = 6.95±0.327 m^2 ha^{-1}, $p<0.01$), but there were no significant differences between Bicuar and Mozambique (BA = 3.43±0.409 m^2 ha^{-1}, $p = 0.43$) or Tanzania (BA = 2.06±0.253 m^2 ha^{-1}, $p = 0.26$) (Figure 7.4). Additionally, Bicuar plots had less variation in basal area among plots than other sites. Plots in Bicuar with the highest basal area were dominated by *Baikiaea plurijuga* and *Baphia massaiensis* (Plots 9, 13, and 15).

The stem diameter abundance distribution in Bicuar National Park was comparable with other sites (Figure 7.6), albeit with fewer stems in each class. The slope of log mean stem size distribution among diameter bins was -0.92±0.067 in Bicuar National Park, -0.99±0.067 in DRC, -0.89±0.065 in Tanzania, and -0.87±0.075 in Mozambique.

7.3.4 Effect of shifting cultivation on diversity within Bicuar National Park

There was a clear difference in the species composition of previously farmed plots and 'pristine' woodland plots, but with some overlap (Figure 7.7). Notably,

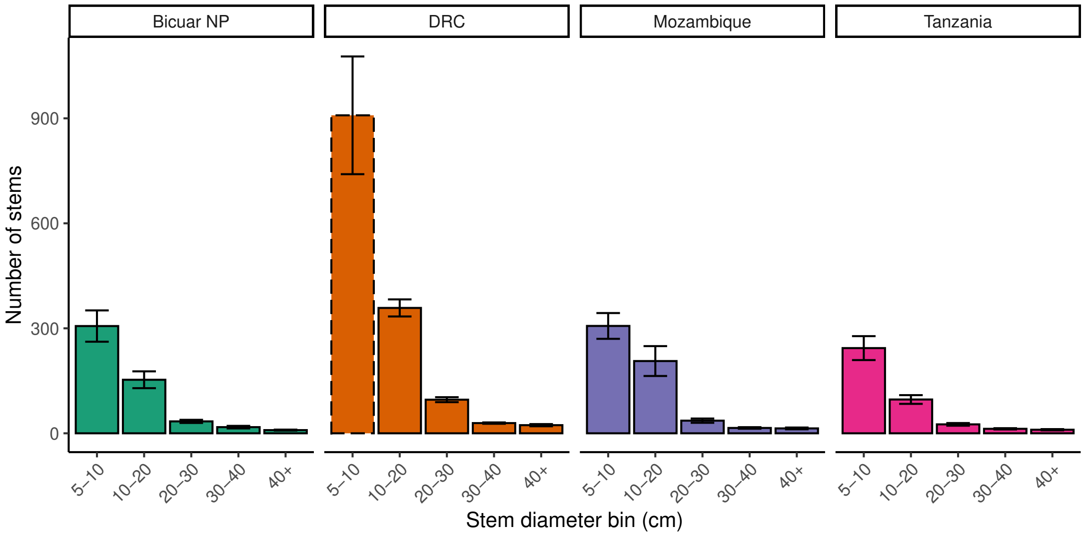


Figure 7.6: Ranked variation between plots in stem number within each site, with bars according to stem diameter class. Error bars are the mean ±1 standard error. The dashed bar for the DRC 5-10 cm stem diameter class indicates that these measurements were estimated by extrapolating a linear regression of log stem abundance across the available stem diameter classes for DRC.

Plots 4 and 7 in have a species composition more resembling the previously farmed plots. These two plots were dominated by *Brachystegia tamarindoides* and *Burkea africana*, with *B. africana* being a species which occurred frequently as a pioneer in the previously farmed plots. The 'pristine' plots 15, 13, and 9 represent distinct outliers in the NMDS. These three plots were dominated by *Baikiaea plurijuga* which was not encountered in the previously farmed plots. The most common species in the previously farmed plots was *Baphia massaiensis* (n = 158), with a mean stem diameter of 6.1±1.87 cm, while in the 'pristine' plots the most common species was *Julbernardia paniculata* (n = 125), with a mean stem diameter of 11.8±7.24 cm. Mean alpha diversity was marginally higher in previously farmed plots (H' = 1.7±0.08) than in non-farmed plots (H' = 1.3±0.14) and an ANOVA showed that there was a significant difference in H' between the two plot types (F(1,33) = 5.91, $p<0.05$) (Figure 7.8, Table 7.5). Mean plot species richness was also lower in 'pristine' plots (6.4±0.86) than previously farmed plots (8.7±0.53). Mean $E_{H'}$ was 0.8±0 in previously farmed plots and 0.7±0.04 in 'pristine' plots but there was no significant difference between groups according to an ANOVA (F(1,33) = 1.54, p = 0.22). 11 species were found only in the previously farmed plots. The most common of these were *Combretum celastroides* (n = 30), *Acacia reficiens* (n = 14), and *Gardenia ternifolia* (n = 11). 7 were found only in the 'pristine' plots, the most common being *Brachystegia spiciformis* (n = 61), *Baikiaea plurijuga* (n = 43) and *Combretum apiculatum* (n = 9). Mean basal area was higher in the 'pristine' plots (0.5±0.07 m^2 ha^{-1}) than previously farmed plots (0.5±0.1 m^2 ha^{-1}).

Mean stem density was higher in previously farmed plots (900±338.36 stems ha^{-1}) than 'pristine' plots (520.3±220.22 stems ha^{-1}). The stem diameter abundance distribution in previously farmed plots showed that many more stems were from the 5-10 cm diameter class in these plots, while the previously farmed plots had fewer stems in the 10-20 cm size class. Both groups of plots had a similar abundance of stems in larger stem diameter classes (Figure 7.9). Multi-stemmed trees in previously farmed plots tended to have a greater number of stems per tree (3.4±2.35) than multi-stemmed trees in 'pristine' plots (2.4±0.8).

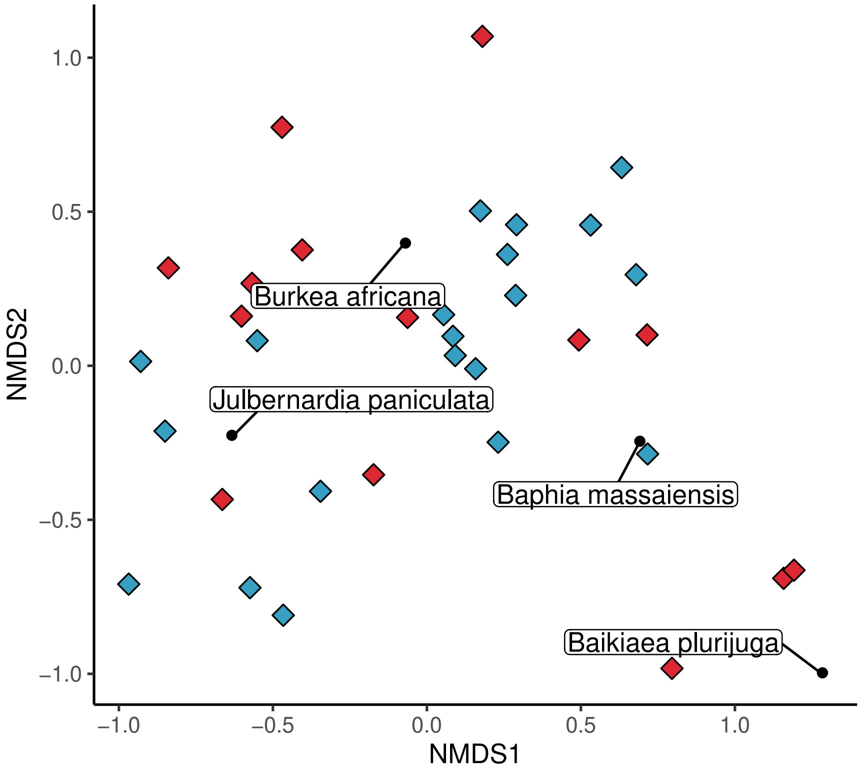


Figure 7.7: NMDS ordination of species composition of 20×50 m (0.1 ha) plots showing plot scores as coloured diamonds located in previously farmed (blue) and ‘pristine’ (red) areas of woodland in Bicuar National Park.

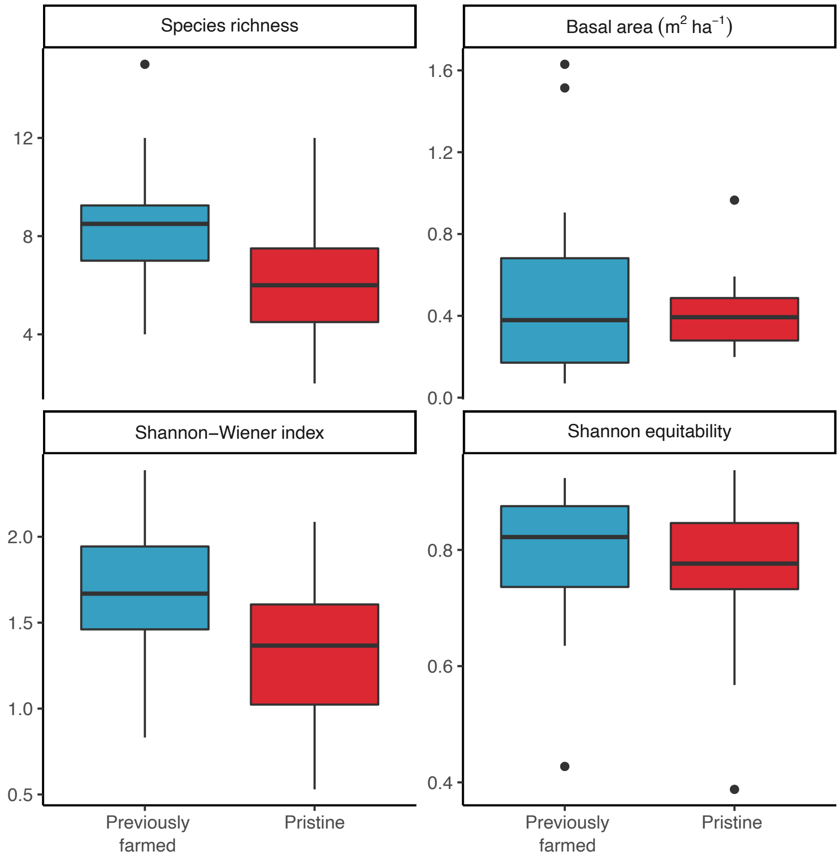


Figure 7.8: The variation in diversity and woodland structure between previously farmed and non-farmed 20×50 m (0.1 ha) plots in Bicuar National Park. Boxes bound the 1st and 3rd quartiles, with the median within the box. Whiskers represent 1.5 times the interquartile range plus or minus the 1st and 3rd quartiles, respectively. Values found beyond the whiskers are shown individually as points.

Table 7.5: Results of ANOVA tests for alpha diversity metrics and plot basal area, between previously farmed and ‘pristine’ plots in Bicuar National Park. Mean values for each group of plots with standard errors in parentheses are shown. Asterisks indicate the p-value of individual sites in each ANOVA (***<0.001, **<0.01, *<0.05, .<0.1).

	Dependent variable:			
	Species richness	Basal area	Shannon (H')	Shannon equit. (E_H)
Previously farmed	2.450***	0.098	0.372**	0.035
	(0.859)	(0.122)	(0.140)	(0.045)
Constant	6.200***	0.416***	1.311***	0.756***
	(0.650)	(0.092)	(0.106)	(0.034)
Obs.	35	35	35	35
R^2	0.198	0.019	0.176	0.018
Res. Std. Err. (df = 33)	2.516	0.357	0.410	0.131
F (df = 1; 33)	8.126***	0.639	7.040**	0.617

7.4 Discussion

7.4.1 Comparison of Bicuar National Park with other woodlands across the miombo ecoregion

We compared the tree species diversity and woodland structure of arid woodlands in Bicuar National Park in southwest Angola with three other woodland sites across the miombo ecoregion. Our results show that Bicuar National Park is distinct in both woodland structure and species composition from these other woodlands. Notably, plots in Bicuar National Park contained 27 tree species which did not occur at other sites. This lends support for the Huíla Plateau as an important area for conservation of southern African woodland landscapes. The woodlands in Bicuar National Park were of low tree basal area, with few large trees except in plots dominated by *Baikiaea plurijuga*. Many other studies have drawn a relationship between water availability and basal area (Terra et al., 2018; Strickland et al., 2016), and our study supports this, with Bicuar National Park being the most arid of the four sites considered in our study. The NMDS of species composition also suggests that plots in Bicuar National Park are influenced by aridity. While there are more arid woodlands within southern Africa, with Mopane woodlands for example often being particularly dry, these plots in Bicuar National park represent particularly dry miombo woodlands.

7.4.2 Delineation of woodland types within Bicuar National Park

Within Bicuar National Park, three distinct woodland types were identified. The first, dominated by *Baikiaea plurijuga* and *Baphia massaiensis* represents the Baikiaea woodland type commonly found to the south of the miombo ecoregion (Timberlake et al., 2010). This is supported by Chisingui et al. (2018) who also found Baikiaea woodlands as a distinct woodland type in the Park. *B. plurijuga* has been identified as an important species for conservation efforts, being attractive for selective logging due to its large stature (Ng'andwe et al., 2017; Wallenfang et al., 2015). The woodlands created by *B. plurijuga* are also an important habitat for elephants (*Loxodonta africana*) (Sianga & Fynn, 2017; Mukwashi et al., 2012), with Bicuar National Park and Mupa National Park being

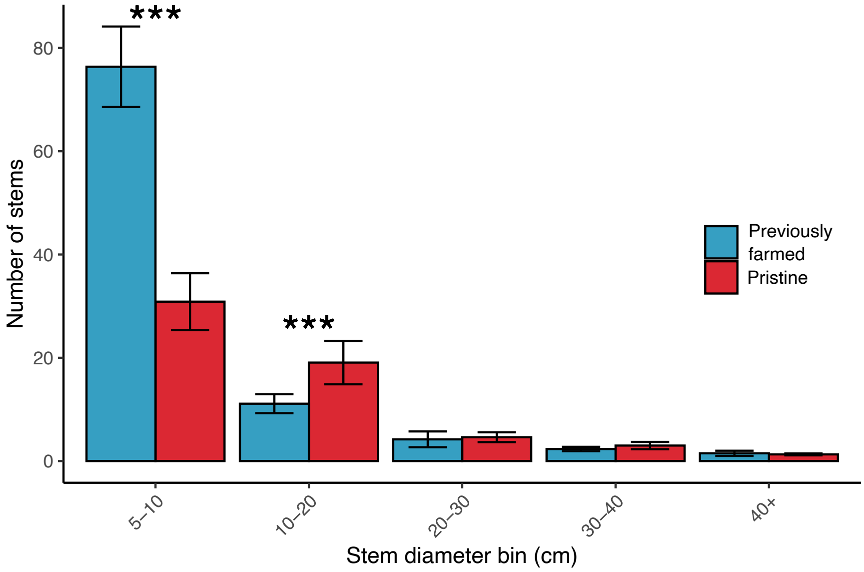


Figure 7.9: Ranked variation between previously farmed and 'pristine' plots in stem number, with bars according to stem diameter class. Error bars are the mean ±1 standard error. Asterisks above pairs of bars refer to the p-values of Poisson general linear models which tested whether previously farmed and 'pristine' plots differ in the number of stems for different stem diameter classes (***<0.001, **<0.01, *<0.05, .<0.1).

key refugia for this animal in the Huíla plateau region. The second woodland type, dominated by *Brachystegia tamarindoides* and *Ochna pulchra* represents a form of small stature woodland with a shrubby understorey and sparse canopy trees, which commonly occurs as a result of repeated disturbance by fire, or poor soil structure (Smith & Allen, 2004). The remaining plots resemble the more archetypal miombo woodland with *Julbernardia paniculata*, though with a number of species not seen in plots further to the east in the miombo ecoregion such as *Strychnos pungens*. This mosaic of woodland types makes Bicuar National Park a valuable reservoir of diversity and strengthens the case for the Park being a key conservation asset within the Huíla plateau and the larger southern African region. While there are biogeographic boundaries between Baikiaea and miombo woodlands (White, 1983), within Bicuar National Park it is likely that the mosaic of woodland types has been created by a combination of soil water capacity and disturbance history. Bicuar has a distinct landscape of wide shallow grassy valleys surrounded by woodland on higher ground (Figure 7.3). On some of these high points the soil is particularly sandy, resembling the Kalahari sand soils found further east and south (Huntley et al., 2019), and these areas coincide with the presence of Baikiaea woodlands (Campbell et al., 2002). High levels of disturbance by fire in these Baikiaea patches may additionally prevent a transition to an alternative woodland type via the control of sapling growth.

7.4.3 Comparison of previously farmed and ‘pristine’ woodland plots

Previously farmed woodlands around the edge of Bicuar National Park were found to share many species with the ‘pristine’ plots in the Park, but with some additional species which did not occur in the ‘pristine’ plots. They also lacked notable archetypal miombo species which tend to form larger canopy trees such as *Brachystegia spiciformis* and contained very few *Julbernardia paniculata*, leading to a distinct woodland composition. The species diversity of these disturbed patches was higher on average than was found in the ‘pristine’ plots, a result which has been corroborated by other studies in miombo woodlands (Caro, 2001; McNicol et al., 2018b; Shackleton, 2000). Other studies have shown a peak in species richness during woodland regrowth as pioneer species take advantage of a low competition environment, while some later stage woodland species remain as residuals that survived the original disturbance (Gonçalves et al., 2017; Kalaba et al., 2013). Gonçalves et al. (2017), notes the dominance of *Pericopsis angolensis* and *Combretum* spp. as light-demanding pioneer species, which were found to be abundant in the previously farmed plots here. This suggests that reclamation of previously farmed and abandoned land for landscape conservation in this ecological context is a valuable management strategy.

In previously farmed plots near the edge of the Park, there was a lack of species which tend to grow to large canopy trees, possibly due to them being repeatedly felled for timber prior to reclamation by the Park, or due to them being unable to recruit into a more open, shrubby woodland. Despite this lack of canopy forming tree species, some previously farmed plots had a greater basal area than ‘pristine’ plots, possibly due to high levels of coppicing in these plots or a divergent fire history. Indeed, mean stem density was higher in ‘pristine’ plots. This can lead to species that would otherwise remain small producing a much larger basal area as they grow multiple stems under intense disturbance conditions (Luoga et al., 2004). The most common species in the previously farmed plots were *Combretum psidioides*, *Combretum collinum* and *Terminalia sericea*, members of the Combretaceae family, all of which more commonly remain as smaller multi-stemmed trees in disturbed woodlands, rather than growing to larger canopy trees (van Wyk & van Wyk, 2014). This result could be considered at odds with other studies which report lower woody biomass in plots that have experienced harvesting (e.g. Muvengwi et al. 2020). It is important to consider however that our study took place in plots that were measured after farming had been abandoned for at least seven years, with time for regeneration to occur. It is possible that over time tree basal area will decrease as coppiced shrubby trees are replaced by core miombo species in the transition back to miombo woodland (Gonçalves et al., 2017). Indeed, other studies in miombo woodlands across the ecoregion have reported substantial recovery within seven years, with high levels of biomass accumulation in previously farmed plots (Chidumayo, 2013; Gonçalves et al., 2017). Bicuar National Park offers a valuable case study to track woodland regeneration in real-time over the next decade in these previously farmed and now protected woodland plots, which could improve our understanding of this potential post-disturbance peak in basal area.

7.5 Conclusion

The woodlands of Bicuar National Park represent an important woodland refuge at the far western extent of the miombo ecoregion. These woodlands, both those disturbed by previous farming activity and those which remain ‘pristine’, possess a number of species not found commonly in other miombo woodland plots around the region. They may also maintain important genetic variation for widespread species, representing populations adapted to more arid conditions. Our study highlights the variation in species composition across the miombo ecoregion and underlines the need for studies which incorporate plot data from multiple locations to reach generalisable conclusions about the region as a whole. Additionally, the installation of 15 one hectare woodland monitoring plots and a further twenty 20×50 m plots in previously farmed and now protected land offer a valuable natural laboratory to further explore the dynamics of dry miombo woodlands of the Huíla plateau. Bicuar National Park should be considered a key conservation asset within the Huíla plateau and within the miombo ecoregion as a whole, as a successfully protected example of an arid woodland mosaic.

References

African Plant Database (version 3.4.0) (2020). Accessed: 2019-11-05. Conservatoire et Jardin botaniques de la Ville de Genève and South African National Biodiversity Institute.

Arino, O., J. J. Ramos Perez, V. Kalogirou, S. Bontemps, P. Defourny & E. Van Bogaert (2012). *Global Land Cover Map for 2009 (GlobCover 2009)*. PANGAEA. DOI: `10.1594/PANGAEA.787668`. (Visited on 30/05/2021).

Campbell, B. M., S. Jeffrey, W. Kozanayi, M. Luckert & M. Mutamba (2002). *Household Livelihoods in Semi-Arid Regions: Options and constraints*. Bogor, Indonesia: Center for International Forestry Research, p. 153.

Caro, T. M. (2001). 'Species richness and abundance of small mammals inside and outside and African national park'. In: *Biological Conservation* 98, pp. 251–257. DOI: `10.1016/S0006-3207(00)00105-1`.

Caylor, K. K., P. R. Dowty, H. H. Shugart & S. Ringrose (2004). 'Relationship between small-scale structural variability and simulated vegetation productivity across a regional moisture gradient in southern Africa'. In: *Global Change Biology* 10, pp. 374–382. DOI: `10.1046/j.1529-8817.2003.00704.x`.

Chave, J., M. Réjou-Méchain, A. Búrquez, E. Chidumayo, M. S. Colgan, W. B. C. Delitti, A. Duque, T. Eid, P. M. Fearnside, R. C. Goodman et al. (2014). 'Improved allometric models to estimate the aboveground biomass of tropical trees'. In: *Global Change Biology* 20, pp. 3177–3190. DOI: `10.1111/gcb.12629`.

Chidumayo, E. (1997). *Miombo ecology and management: An introduction*. London, UK: Intermediate Technology Publications.

Chidumayo, E. N. (2002). 'Changes in miombo woodland structure under different land tenure and use systems in central Zambia'. In: *Journal of Biogeography* 29, pp. 1619–1626. DOI: `10.1046/j.1365-2699.2002.00794.x`.

Chidumayo, E. N. (2013). 'Forest degradation and recovery in a miombo woodland landscape in Zambia: 22 years of observations on permanent sample plots'. In: *Forest Ecology and Management* 291, pp. 154–161. DOI: `10.1016/j.foreco.2012.11.031`.

Chisingui, A. V., F. M. P. Gonçalves, J. J. Tchamba, J. C. Luís, M. F. F. Rafael & J. L. M. Alexandre (2018). 'Vegetation survey of the woodlands of Huíla Province'. In: *Biodiversity and Ecology*, pp. 426–437. DOI: `10.7809/b-e.00355`.

Clarke, D. A., P. H. York, M. A. Rasheed & T. D. Northfield (2017). 'Does biodiversity-ecosystem function literature neglect tropical ecosystems'. In: *Trends in Ecology & Evolution* 32.5, pp. 320–323. DOI: `10.1016/j.tree.2017.02.012`.

Dantas, V. L., M. Hirota, R. S. Oliveira & J. G. Pausas (2016). 'Disturbance maintains alternative biome states'. In: *Ecology Letters* 19, pp. 12–19. DOI: `10.1111/ele.12537`.

Dexter, K. G., B. Smart, C. Baldauf, T. R. Baker, M. P. B. Bessike Balinga, R. J. W. Brienen, S. Fauset, T. R. Feldpausch, L. Ferreira-da Silva, J. I. Muledi et al. (2015). 'Floristics and biogeography of vegetation in seasonally dry tropical regions'. In: *International Forestry Review* 17.S2, pp. 10–32. DOI: `10.1505/146554815815834859`.

Droissart, V., G. Dauby, O. J. Hardy, V. Deblauwe, D. J. Harris, S. Janssens, B. A. Mackinder, A. Blach-Overgaard, B. Sonké, M. S. M. Sosef et al. (2018). 'Beyond trees: Biogeographical regionalization of tropical Africa'. In: *Journal of Biogeography* 45, pp. 1153–1167. DOI: `10.1111/jbi.13190`.

DRYFLOR Banda-R, K., A. Delgado-Salinas, K. G. Dexter, R. Linares-Palomino, A. Oliveira-Filho, D. Prado, M. Pullan, C. Quintana, R. Riina, G. M. Rodríguez et al. (2016). 'Plant diversity patterns in neotropical dry forests and their conservation implications'. In: *Science* 353.6306, pp. 1383–1387. DOI: `10.1126/science.aaf5080`.

Fick, S. E. & R. J. Hijmans (2017). 'WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas'. In: *International Journal of Climatology* 37.12, pp. 4302–4315. DOI: `10.1002/joc.5086`.

Figueiredo, E., G. F. Smith & J. César (2009). 'The flora of Angola: First record of diversity and endemism'. In: *Taxon* 58.1, pp. 233–236. DOI: `10.1002/tax.581022`.

Frost, P. (1996). 'The ecology of miombo woodlands'. In: *The miombo in transition: woodlands and welfare in Africa*. Ed. by B. M. Campbell. Bogor, Indonesia: Center for International Forestry Research, pp. 11–55.

Godlee, J. L., F. M. Gonçalves, J. J. Tchamba, A. V. Chisingui, J. I. Muledi, M. N. Shutcha, C. M. Ryan, T. K. Brade & K. G. Dexter (2020). 'Diversity and structure of an arid woodland in southwest Angola, with comparison to the wider miombo ecoregion'. In: *Diversity* 12, pp. 1–20. DOI: `10.3390/d12040140`.

Gonçalves, F. M. P., R. Revermann, A. L. Gomes, M. P. M. Aidar, M. Finckh & N. Juergens (2017). 'Tree species diversity and composition of Miombo woodlands in South-Central Angola: A chronosequence of forest recovery after shifting cultivation'. In: *International Journal of Forestry Research* 2017, pp. 1–13. DOI: `10.1155/2017/6202093`.

Huntley, B. J., F. Lages, V. Russo & N. Ferrand, eds. (2019). *Biodiversity of Angola: Science & conservation: A modern synthesis*. Cham, Switzerland: Springer. DOI: `10.1007/978-3-030-03083-4`.

Kalaba, F. K., C. H. Quinn, A. J. Dougill & R. Vinya (2013). 'Floristic composition, species diversity and carbon storage in charcoal and agriculture fallows and management implications in Miombo woodlands of Zambia'. In: *Forest Ecology and Management* 304, pp. 99–109. DOI: `10.1016/j.foreco.2013.04.024`.

Kershaw, J. A., M. J. Ducey, T. W. Beers & B. Husch (2017). *Forest Mensuration*. Chichester, UK: John Wiley & Sons.

Koleff, P., K. J. Gaston & J. J. Lennon (2003). 'Measuring beta diversity for presence-absence data'. In: *Journal of Animal Ecology* 72, pp. 367–382. DOI: `10.1046/j.1365-2656.2003.00710.x`.

Legendre, P. & M. De Cáceres (2013). 'Beta diversity as the variance of community data: dissimilarity coefficients and partitioning'. In: *Ecology Letters* 16.8, pp. 951–963. DOI: `10.1111/ele.12141`.

Linder, H. P. (2001). 'Plant diversity and endemism in sub-Saharan tropical Africa'. In: *Journal of Biogeography* 28, pp. 169–182. DOI: `10.1046/j.1365-2699.2001.00527.x`.

LPWG Azani, N., M. Babineau, C. D. Bailey, H. Banks, A. R. Barbosa, R. B. Pinto, J. S. Boatwright, L. M. Borges, G. K. Brown, A. Bruneau et al. (2017). 'A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny: The Legume Phylogeny Working Group (LPWG)'. In: *Taxon* 66, pp. 44–77. DOI: `10.12705/661.3`.

Luoga, E. J., E. T. F. Witkowski & K. Balkwill (2004). 'Regeneration by coppicing (resprouting) of miombo (African savanna) trees in relation to land use'. In: *Forest Ecology and Management* 189, pp. 23–25. DOI: `10.1016/j.foreco.2003.02.001`.

Mayaux, P., E. Bartholomé, S. Fritz & A. Belward (2004). 'A new land-cover map of Africa for the year 2000'. In: *Journal of Biogeography* 31, pp. 861–877. DOI: `10.1111/j.1365-2699.2004.01073.x`.

Mayaux, P., H. Eva, A. Brink, F. Achard & A. Belward (2008). 'Remote sensing of land-cover and land-use dynamics'. In: *Earth Observation of Global Change: The Role of Satellite Remote Sensing in Monitoring the Global Environment*. Berlin, Germany: Springer-Verlag, pp. 85–108. DOI: `10.1007/978-1-4020-6358-9_5`.

McNicol, I. M., C. M. Ryan, K. G. Dexter, S. M. J. Ball & M. Williams (2018a). 'Aboveground carbon storage and its links to stand structure, tree diversity and floristic composition in south-eastern Tanzania'. In: *Ecosystems* 21, pp. 740–754. DOI: `10.1007/s10021-017-0180-6`.

McNicol, I. M., C. M. Ryan & E. T. A. Mitchard (2018b). 'Carbon losses from deforestation and widespread degradation offset by extensive growth in African woodlands'. In: *Nature Communications* 9, pp. 1–11. DOI: `10.1038/s41467-018-05386-z`.

McNicol, I. M., C. M. Ryan & M. Williams (2015). 'How resilient are African woodlands to disturbance from shifting cultivation?' In: *Ecological Applications* 25.8, pp. 2320–2336. DOI: `10.1890/14-2165.1`.

Mukwashi, K., E. Gandiwa & S. Kativu (2012). 'Impact of African elephants on *Baikiaea plurijuga* woodland around natural and artificial watering points in northern Hwange National Park, Zimbabwe'. In: *International Journal of Environmental Sciences* 2.3, pp. 1355–1368. DOI: `10.6088/ijes.002020300022`.

Muledi, J. I., D. Bauman, T. Drouet, J. Vleminckx, A. Jacobs, J. Lejoly, P. Meerts & M. N. Shutcha (2017). 'Fine-scale habitats influence tree species assemblage in a miombo forest'. In: *Journal of Plant Ecology* 10, pp. 958–969. DOI: `10.1093/jpe/rtw104`.

Muvengwi, J., T. Chisango, K. Mpakairi, M. Mbiba & E. T. F. Witkowski (2020). 'Structure, composition and regeneration of miombo woodlands within harvested and unharvested areas'. In: *Forest Ecology and Management* 458, pp. 1–10. DOI: `10.1016/j.foreco.2019.117792`.

Ng'andwe, P., D. Chungu, O. Shakacite & L. Vesa (2017). 'Abundance and distribution of top five most valuable hardwood timber species in Zambia and their implications on sustainable supply'. In: *6th International Conference on Hardwood Processing*. Ed. by V. Möttönen & E. Heinonen. Natural Resources Institute Finland, Helsinki: Natural Resources Institute Finland, pp. 18–27.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos et al. (2019). *vegan: Community Ecology Package*. R package version 2.5-5. URL: `https://CRAN.R-project.org/package=vegan`.

Oliveras, I. & Y. Malhi (2016). 'Many shades of green: The dynamic tropical forest-savannah transition zones'. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 371.20150308, pp. 1–15. DOI: `10.1098/rstb.2015.0308`.

Palgrave, K. C. (2003). *Trees of southern Africa*. Cape Town, South Africa: Struik Publications.

Privette, J. L., Y. Tian, G. Roberts, R. J. Scholes, Y. Wang, K. K. Caylor, P. Frost & M. Mukelabai (2004). 'Vegetation structure characteristics and relationships of Kalahari woodlands and savannas'. In: *Global Change Biology* 10, pp. 281–291. DOI: `10.1111/j.1529-8817.2003.00740.x`.

R Core Team (2020). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. Vienna, Austria. URL: `https://www.R-project.org/`.

Ratnam, J., W. J. Bond, R. J. Fensham, W. A. Hoffmann, S. Archibald, C. E. R. Lehmann, M. T. Anderson, S. I. Higgins & M. Sankaran (2011). 'When is a 'forest' a savanna, and why does it matter?' In: *Global Ecology and Biogeography* 20, pp. 653–660. DOI: `10.1111/j.1466-8238.2010.00634.x`.

Ryan, C. M., M. Williams & J. Grace (2011). 'Above- and belowground carbon stocks in a miombo woodland landscape of Mozambique'. In: *Biotropica* 43.4, pp. 423–432. DOI: `10.1111/j.1744-7429.2010.00713.x`.

Ryan, C. M., R. Pritchard, I. McNicol, M. Owen, J. A. Fisher & C. Lehmann (2016). 'Ecosystem services from southern African woodlands and their future under global change'. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 371.1703, p. 20150312. DOI: `10.1098/rstb.2015.0312`.

Schneibel, A., M. Stellmes, R. Revermann, M. Finckh, A. Röder & J. Hill (2013). 'Agricultural expansion during the post-civil war period in southern Angola based on bi-temporal Landsat data'. In: *Biodiversity and Ecology* 5, pp. 311–319. DOI: `10.7809/b-e.00285`.

Shackleton, C. M. (2000). 'Comparison of plant diversity in protected and communal lands in the Bushbuckridge lowveld savanna, South Africa'. In: *Biological Conservation* 94, pp. 273–285. DOI: `10.1016/S0006-3207(00)00001-X`.

Sianga, K. & R. Fynn (2017). 'The vegetation and wildlife habitats of the Savuti-Mababe-Linyati ecosystem, northern Botswana'. In: *KOEDOE* 59.2, pp. 1–16. DOI: `10.4102/koedoe.v59i2.1406`.

Silva, D. F. D., A. E. Cahali, F. A. Gomes, J. J. Tchamba & F. M. Gonçalves (2020). 'Caracterização da diversidade de espécies do Parque Nacional do Bicuar e implicações para a gestão e conservação da biodiversidade'. In: *Revista Internacional de Educação Saúde e Ambiente* 3.1, pp. 46–58. DOI: `10.37334/riesa.v3i1.33`.

Smith, B. & J. B. Wilson (1996). 'A consumer's guide to evenness indices'. In: *Oikos* 76, pp. 70–82. DOI: `10.2307/3545749`.

Smith, P. & Q. Allen (2004). *Field guide to the trees and shrubs of the miombo woodlands*. London, UK: Royal Botanic Gardens, Kew.

Soares, M., J. Abreu, H. Nunes, P. Silveira, B. Schrire & E. Figueiredo (2007). 'The leguminosae of Angola: Diversity and endemism'. In: *Systematics and Geography of Plants* 77.2, pp. 141–212. DOI: `10.2307/20649738`.

Soares de Oliveira, R. (2015). *Magnificent and Beggar Land: Angola since the civil war*. London, UK: Hurst Publishers.

Strickland, C., A. C. Liedloff, G. D. Cook, G. Dangelmayr & P. D. Shipman (2016). 'The role of water and fire in driving tree dynamics in Australian savannas'. In: *Journal of Ecology* 104, pp. 828–840. DOI: `10.1111/1365-2745.12550`.

Terra, M. C. N. S., d. R. M., J. A. Prado Júnior, J. M. de Mello, J. R. S. Scolforo, M. A. L. Fontes & H. ter Steege (2018). 'Water availability drives gradients of tree diversity, structure and functional traits in the Atlantic-Cerrado-Caatinga transition, Brazil'. In: *Journal of Plant Ecology* 11.6, pp. 803–814. DOI: `10.1093/jpe/rty017`.

Timberlake, J., E. Chidumayo & L. Sawadogo (2010). 'Distribution and characteristics of African dry forests and woodlands'. In: *The Dry Forests and Woodlands of Africa: Managing for Products and Services*. London, UK: EarthScan, pp. 11–42.

Torello-Raventos, M., T. R. Feldpausch, E. Veenendaal, F. Schrodt, G. Saiz, T. F. Domingues, G. Djagbletey, A. Ford, J. Kemp, B. S. Marimon et al. (2013). 'On the delineation of tropical vegetation types with an emphasis on forest/savanna transitions'. In: *Plant Ecology and Diversity* 6.1, pp. 101–137. DOI: `10.1080/17550874.2012.762812`.

UNEP-WCMC and IUCN (2019). *Protected Planet: the world database on protected areas (WDPA)*. [Online; 15-January-2019]. URL: `https://www.protectedplanet.net`.

van Wyk, B. & P. van Wyk (2014). *Field guide to trees of southern Africa*. Cape Town, South Africa: Struik Nature.

Wallenfang, J., M. Finckh, J. Oldeland & R. Revermann (2015). 'Impact of shifting cultivation on dense tropical woodlands in southeast Angola'. In: *Tropical Conservation Science* 8.4, pp. 863–892. DOI: `10.1177/194008291500800402`.

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`.

7.6 Supplementary material

```
##’ @author Casey M. Ryan
##’ @param d_in diameter measured at the POM (in cm)
##’ @param POM height of the POM (in m)
##’ @return d130, estimated diameter at a POM of 1.3 m (in cm).
POMadj <- function(d_in, POM) {
  d_in_clean <- d_in[!is.na(d_in)]
  POM_clean <- POM[!is.na(d_in)]
  edges <- c(5.0, 15.8, 26.6, 37.4)
  sm <- d_in_clean < edges[2]
  med <- d_in_clean >= edges[2] & d_in_clean < edges[3]
  lg <- d_in_clean >= edges[3]
  delta_d <- data.frame(
    small = 3.4678-5.2428 * POM_clean+2.9401 *
      POM_clean^2-0.7141 * POM_clean^3,
    med = 4.918-8.819 * POM_clean+6.367 *
      POM_clean^2-1.871 * POM_clean^3,
    large = 9.474+-18.257 * POM_clean + 12.873 *
      POM_clean^2+-3.325 * POM_clean^3)
  dd <- NA_real_
  dd[sm] <- delta_d$small[sm]
  dd[med] <- delta_d$med[med]
  dd[lg] <- delta_d$large[lg]
  dd[POM_clean > 1.7] <- 0
  d130 <- NA
  d130[is.na(d_in)] <- NA
  d130[!is.na(d_in)] <- d_in_clean - dd
  if (any(d130[!is.na(d_in)] < 0)) {
    warning("Negative d130, replaced with NA")
  }
  d130[d130 <= 0 & !is.na(d130)] <- NA
  return(d130)
}
```

Code 7.S1: R function to estimate stem diameter at 1.3 m from a model of tree taper

Chapter 8

Data legacy

8.1 Introduction

In the spirit of expanding the definition of academic success (Goring et al., 2014) and fostering open collegiate science (Hampton et al., 2015), this chapter discusses the products of this PhD project outwith the immediate results-based thesis chapters. It is my hope that the data and research infrastructure generated during this PhD will have a legacy beyond the uses I have found for it thus far, providing value to myself as I progress through my academic career, and to other researchers. Specifically, this chapter discusses the extended value of the data collected during the PhD, the steps taken to ensure that data are visible to and usable by other researchers, existing research outputs by colleagues utilising the data, and a non-exhaustive list of future projects which could use the data in novel and impactful ways.

There are two principal non-chapter outputs of this PhD project. Firstly the network of permanent plots and accompanying census data in Bicuar National Park, southwest Angola, and secondly the terrestrial LiDAR data collected in 22 1 ha plots, including all 15 in Bicuar National Park and a further seven in Kilwa District, southern Tanzania.

8.2 Permanent plots in Bicuar National Park

The 15 1 ha permanent plots in Bicuar National Park were set up in collaboration with Dr. Francisco Maiato Gonçalves from the Herbarium of Lubango, Huíla province, Angola, with the help of a National Geographic Society grant (Grant No. EC-51464R-18). These plots provide not only a valuable dataset of woody stem measurements but also an infrastructure for further ecological research and an opportunity for continued scientific collaboration between the University of Edinburgh and the Herbarium of Lubango.

The Herbarium of Lubango is located ~300 km from Bicuar National Park. During their installation and in the year after, the plots were used by the Instituto de Ciências da Educação Huíla (ISCED), which is partnered with the Herbarium of Lubango, to teach Ecology Masters students about woody biomass estimation techniques and plant taxonomy. As teaching resources at public institutions in Angola can be scarce, this partnership with ISCED provides a clear capacity building benefit that will hopefully strengthen academic interest in woodland monitoring programmes at the institution.

A number of voucher specimens from tagged trees in the plots are held in the Herbarium of Lubango, with duplicates of most currently held in the Royal Botanic Gardens at Kew, London, UK. We hope to conduct more botanical collections during future censuses to update the checklist of plant species found in Bicuar National Park, with the hope of raising the profile of this valuable woodland refuge at the far western extent of the miombo ecoregion, and of improving its protection and development as a natural resource by the Angolan government. To this end, in 2019, in addition to setting up the 1 ha permanent plots, we conducted 20 one-off 20×50 m samples of previously abandoned agricultural land at the edge of the park boundaries, to improve coverage of different land-use types in the Park and to better understand the biodiversity recovery of regenerating agricultural landscapes.

Steps have been taken to ensure the longevity of the permanent plots. The value of a plot focussed monitoring programme generally increases over time as more data is accrued and temporal trends can be identified, so efforts must be made to ensure that regular censuses and maintenance are conducted. In 2020 all plot corners were marked permanently with concrete posts (Figure 8.1), and have been located with highly accurate differential-GNSS, to an accuracy of $\leq$3 cm. Knowing the plot boundaries to a high degree of accuracy will increase their value as plots to be matched with highly precise satellite data products that are currently emerging (Exbrayat et al., 2019; George-Chacon et al., 2019; Wagner et al., 2018).

Data from the first census of the plots are held in the SEOSAW database (SEOSAW, 2020). The SEOSAW database holds standardised woody stem measurements from plots spanning southern Africa. The data in SEOSAW are available to all researchers following agreement by the data holder and all other SEOSAW members. The permanent plots in Bicuar are the most westerly permanent plots in the SEOSAW plot network (Figure 8.2), occupying a climate space within the region not currently served by other permanent plots (Figure 8.3), and representing a unique floristic assemblage not seen elsewhere in the network (Chapter 7). Holding the plot data from Bicuar in SEOSAW also acts as a permanent data backup repository, extending the lifespan of the data.

A second woody stem biomass survey is planned for all plots in 2022/2023, with the aim of improving the quality of data collected and assessing mortality

Figure 8.1: An example of the concrete posts installed to a depth of 1 m at the plot corners of all 1 ha plots in Bicuar National Park, to ensure that plot boundaries are not lost and do not drift over repeated censuses.

and productivity over time. This re-census will likely happen as part of either the SEOSAW or SECO projects, both operating out of the University of Edinburgh. Data from the second census will be provided to SEOSAW and eventually uploaded along with the first census to ForestPlots.net (Lopez-Gonzalez et al., 2011), increasing visibility of the data further.

Data from these plots have already been utilised in four peer-reviewed articles led by colleagues:

- G. J. L. Panzou et al. (2020). ‘Pantropical variability in tree crown allometry’. In: *Global Ecology and Biogeography* 30.2, pp. 459–475. DOI: `10.1111/geb.13231`

- SEOSAW (2020). ‘A network to understand the changing socio-ecology of the southern African woodlands (SEOSAW): Challenges, benefits, and methods'. In: *Plants, People, Planet*. DOI: `10.1002/ppp3.10168`

- D. F. D. Silva et al. (2020). 'Caracterização da diversidade de espécies do Parque Nacional do Bicuar e implicações para a gestão e conservação da biodiversidade'. In: *Revista Internacional de Educação Saúde e Ambiente* 3.1, pp. 46–58. DOI: `10.37334/riesa.v3i1.33`
- Esquivel-Muelbert, A. ... (in prep. Nature Communications 2021). Bridging scales in monitoring tree mortality globally.

8.2.1 Bicuar National Park as a 'supersite'

There has been a recent push to establish certain long-term ecological monitoring sites as 'supersites'. A supersite is defined here as a "highly-instrumented research site where all ecosystem compartments and fluxes are covered" (Mikkelsen et al., 2013). Establishment of supersites has been identified as a goal by a number of international projects which seek to improve global land-atmosphere modelling and monitoring of the effects of climate change on ecosystem structure and function. Notable organisations include the Forest Observation System (FOS, Chave et al. 2019), and the upcoming SECO project at the University of Edinburgh (NERC Large Grant NE/T01279X/1). The impetus behind the supersite model is that it is more cost-effective to prioritise a small number of sites that are representative of a given landscape's ecology as locations for concentrating multiple expensive measurements, such as LiDAR and atmospheric flux towers. These highly-instrumented sites then form the apex of a hierarchy of sites within the landscape most of which only have limited monitoring measurements. Measurements from the supersites can then be used to 'scale up' to the landscape scale with the help of the less-provisioned sites and remotely-sensed data (Anderson, 2018). Concentrating multiple measurements within a few sites allows more ready comparison of these measurements, which when scattered among nearby sites can severely decrease their predictive power due to individual site conditions (Mikkelsen et al., 2013).

Some of the common requirements for supersites outlined by various projects have already been fulfilled for the plots in Bicuar National Park. Since 2015, SASSCAL (Southern African Science Service Centre for Climate Change

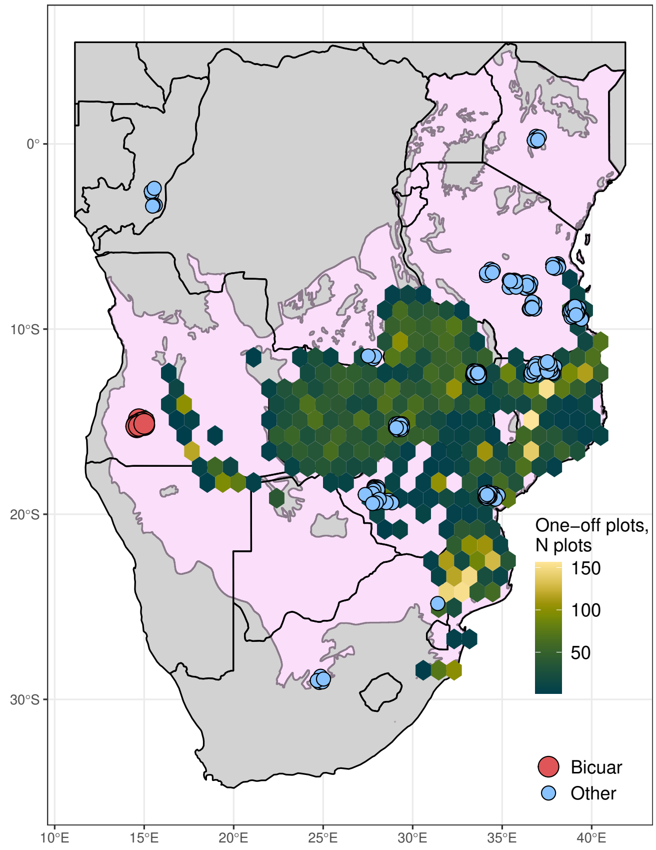


Figure 8.2: The spatial distribution of plots in the SEOSAW network. Blue circles are permanent plots, where individual stems are tagged and can be matched among censuses. The permanent plots in Bicuar National Park are shown as red points. The hexagon grid shows the density of one-off plots. The pink shading shows the working region of the SEOSAW network, defined primarily from woodland defined by White (1983) and further adapted to bound the north-eastern and southern boundaries.

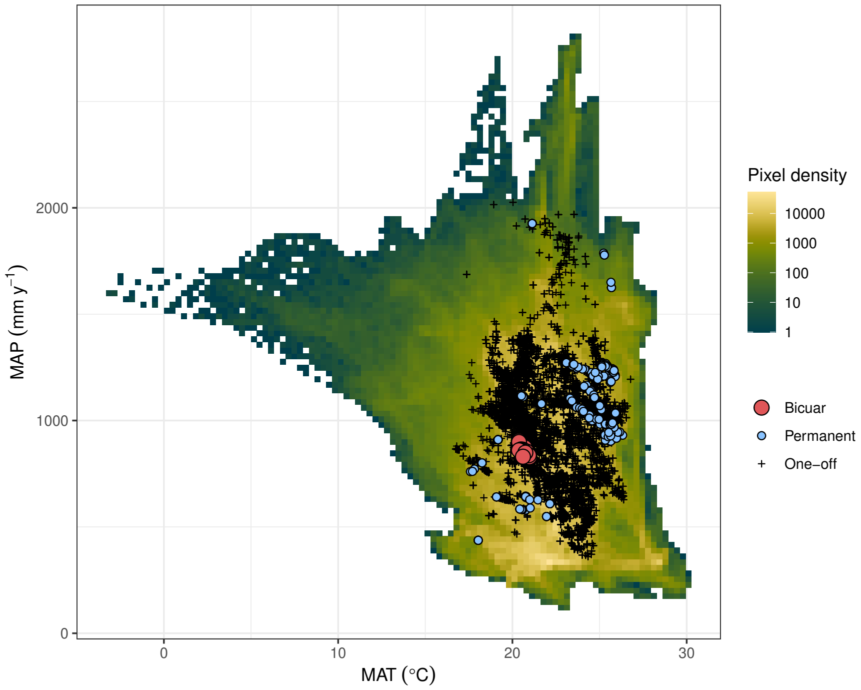


Figure 8.3: The distribution of SEOSAW plots in climate space, using Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP) from the WorldClim database (Fick & Hijmans, 2017). Blue circles are permanent plots, where individual stems can be matched among censuses. The permanent plots in Bicuar National Park are shown as red points. Black crosses show one-off plots. The background is shaded according to the density of pixels in the SEOSAW working region, described in Figure 8.2.

and Adaptive Land Management) has maintained a weather station at Bicuar National Park, providing freely available hourly data on air temperature, solar irradiance, wind speed and direction, soil moisture, precipitation and air pressure (SASSCAL, 2020). The weather station is located within 20 km of all the permanent plots. A critical requirement for a supersite in many projects is that it has a combination of either terrestrial and/or airborne LiDAR measurements. LiDAR provides invaluable information on forest structure that is precisely georeferenced, helping to bridge the scale gap between ground measurements and satellite measurements. The 15 plots in Bicuar National Park already have a comprehensive terrestrial LiDAR dataset, with precise geo-referencing, collected in 2019. The possibility of repeat LiDAR measurements in combination with an airborne LiDAR campaign would make Bicuar National Park an extremely valuable resource. Additionally, the GEDI L2B satellite LiDAR product has good coverage over Bicuar National Park, with the potential to compare these measurements with the terrestrial LiDAR in the plots (Figure 8.4). To our knowledge there are no other plot-based terrestrial LiDAR datasets of miombo woodlands in southern Africa. Our hope is that Bicuar National Park can be registered as a supersite with one or more research organisations and become a destination for researchers, strengthening the representation of Angolan science, and advertising Bicuar National Park and the Herbarium of Lubango as a destination for researchers, building capacity, research potential and conservation awareness in the region.

8.3 Terrestrial LiDAR

In addition to the value of terrestrial LiDAR data to qualify as a supersite, as described above, the terrestrial LiDAR data collected as part of this thesis has other uses and values. The LiDAR data has been archived on the University of Edinburgh DataShare, with a permanent DOI (10.7488/ds/3114), along with details of the largely free and open source reproducible workflow for processing the data, which is also seen in Chapter 6 of this thesis. When Chapter 5 is eventually published as a peer-reviewed article, the data repository will be advertised in the article. It is my hope that other researchers will use the data for their own research, extending its lifespan to that which befits the effort expended to collect it. An alternative method to increase visibility of the dataset

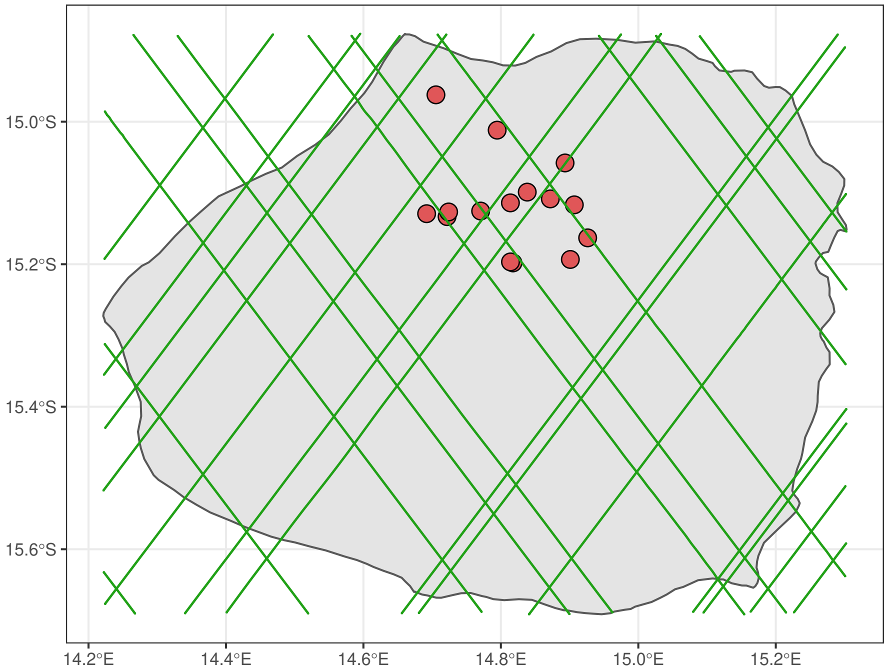


Figure 8.4: 50 m wide flight-paths of the GEDI L2B satellite LiDAR product (red lines), with the extent of Bicuar National Park (grey polygon), and the locations of the 15 1 ha permanent plots (blue points). Note that in reality each 25 m track consists of a series of 25 m radius circles which contain LiDAR data.

and encourage its use by others could be to publish an article in a journal like "*Data in Brief*", which specialises in short reports on open-access datasets.

The LiDAR data was collected in a way to maximise its potential future uses. The sampling density is sufficient to reliably estimate the canopy height profile of an entire plot, to segment individual trees from the point cloud and to distinguish internal tree canopy architecture. A key application of terrestrial LiDAR is in linking to air- and space-borne LiDAR, and other remotely sensed data products to bridge the scale gap between plot and landscape studies (Xiao et al., 2019). Recent studies have used a combination of terrestrial LiDAR and other remotely-sensed data products to scale up models of functional traits from individual leaves to landscapes (Martínez et al., 2016), calibrate landscape models of biomass distribution (Réjou-Méchain et al., 2019), and infer 3D forest structure with satellite data products (Fischer et al., 2020). My hope is that the LiDAR data may be used by other researchers to answer questions pertinent to the functioning of southern African woodlands. Currently, very few studies using terrestrial LiDAR have been conducted in savannas (Muumbe et al., 2021). In southern African, to my knowledge, all existing studies have been located at Skukuza Flux Tower, Kruger National Park (Singh et al., 2018). Yet, terrestrial LiDAR could provide a useful tool to measure the biomass and physiognomy of shrubs and idiosyncratic trees that comprise a large part of the biomass in these disturbed ecosystems (Muir et al., 2018). The data collected during this thesis therefore make an important contribution to the field of savanna ecology, and by making the data available to other researchers I hope to raise the profile of TLS as a tool for savanna ecology. The following sections contain justifications for future studies I wish to undertake personally using the data collected during this project.

8.3.1 Tree taper modelling from terrestrial LiDAR

The most common way of assessing aboveground woody biomass of trees is through allometric models which estimate biomass from a combination of stem diameter, tree height and wood density (Chave et al., 2014). These allometric models often assume that stem diameter is measured at a height of 1.3 m, a convention that is widely followed across forestry and ecology (Brokaw & Thompson, 2000). Peculiarities in stem shape occasionally require the measurement of stem diameter at a different height however, to avoid abnormalities such as burls, fluting, or branch nodes that would otherwise provide an unrepresentative estimate of stem diameter if measured at the conventional height (Kershaw et al., 2017). On average, stem diameter tapers towards the top of a tree (Kozak et al., 1969), meaning that without proper correction, biomass estimates generated from these diameter measurements at unconventional heights will over- or under-estimate biomass.

Many models of stem taper have been developed, being used by foresters for over a century to estimate harvestable timber volumes, and are still the subject of active development (MacFarlane & Weiskittel, 2016; Luoma et al., 2019). As well as estimating harvestable volume, stem taper models can be used to correct for variation in stem diameter measurement height, to ensure consistent estimates of woody biomass or harvestable volume. Previously these models have been parametrised through multiple measures of stem diameter at different heights with a tape measure, but this is time-consuming and suffers from the same imprecision and human error as any other diameter tape measurement (Saarinen et al., 2019).

Plot-based estimation of woody biomass across the globe currently relies on measuring stem diameter (SEOSAW, 2020; Chave et al., 2005; Schepaschenko et al., 2019). Being able to accurately reconcile stem diameters measured at different heights is therefore paramount to improving our models of above-ground woody biomass.

Rapid progress has been made in methods to model woody stem diameter from terrestrial LiDAR point clouds (Bogdanovich et al., 2021; Hopkinson et al., 2004; Srinivasan et al., 2015; Ravaglia et al., 2019; Wang et al., 2016). These methods estimate a cylinder of the stem from a slice of points, with recent advancements allowing interpolation of the cylinder even when the coverage of laser returns on the stem surface is incomplete. Others have extended the method to generate estimates of stem taper (Henning & Radtke, 2006; Thies et al., 2004), but to our knowledge this has not been done for any tree species growing the dry tropics. The terrestrial LiDAR data collected in Angola and Tanzania provide the opportunity to conduct this first study of stem taper from LiDAR measurements in the dry tropics. The species, locations, and stem diameters of all stems >5 cm diameter is known within these plots, meaning that these data can be matched with stems observable in the LiDAR point

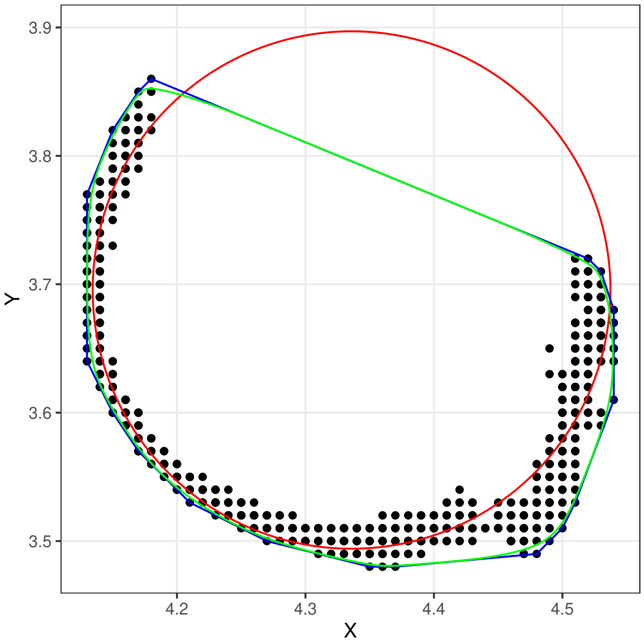


Figure 8.5: Example output of the prototype stem cylinder interpolation method used to estimate stem diameter from an incomplete point cloud. Voxelised points at 2 cm^3 are shown as black points. Interpolation methods are shown as coloured polygons. The interpolated stem cylinder method based on Umbach & Jones (2003) is shown in red. A convex hull of all points is shown in blue. A kernel smoothing method using Gaussian kernel regression is shown in green.

cloud. As a proof of concept, I have developed a prototype stem segmentation using `treeseg` (Burt et al., 2018), and a cylinder interpolation method based on Umbach & Jones (2003), which estimates stem diameter at multiple heights along the tree stem (Figure 8.5).

8.3.2 Biomass of large trees: testing scaling theory for estimating biomass

Large diameter trees hold a disproportionately large amount of woody biomass in most wooded ecosystems (Bastin et al., 2015; Lutz et al., 2018). To accurately describe the woody biomass stocks of a particular system, more effort should therefore be allocated to accurately estimating the biomass of the largest trees. Woody biomass is most commonly estimated through allometric equations which rely on measures of stem diameter, tree height and woody density. At the root of these allometric equations are a limited number of destructive biomass harvests, which define the relationship between tree physiognomic measurements and the biomass of the harvested tree (Chave et al., 2005). Biomass harvesting is time consuming, expensive, and understandably not a popular activity among ecologists due to its destructive nature (Roxburgh et al., 2015). Furthermore, allometric equations are often least well defined for the largest trees, as large trees are scarcer than small trees (Lutz et al., 2018; Lindenmayer et al., 2012), and even less likely to be cut down during destructive harvests due to the cultural and aesthetic value they hold as living organisms (Blicharska & Mikusiński, 2014). Specifically the parametrisation of the exponent term of traditional diameter-biomass allometry power-models is often poor for large trees, and there is a heteroscedastic relationship between diameter and biomass at higher stem diameters (Figure 8.6) (Chave et al., 2004; Chave et al., 2014). Recently, the suitability of power-models for diameter-biomass allometries has even been drawn into question, though an alternative that works globally has not yet been found (Picard et al., 2015). Weighting procedures so that large rare trees with higher intrinsic variability in biomass do not overly influence model coefficients have been used successfully previously (Chave et al., 2014; McNicol et al., 2015), but this does not solve the root problem that the biomass of newly encountered large trees will likely be poorly estimated.

As the age of a tree increases, it generates an idiosyncratic physiognomy due to the amassed disturbances and variations in environment it has encountered (Lindenmayer & Laurance, 2016). Large trees often have hollow trunks (fluting) or areas of punky wood (Chambers et al., 2001; Ruxton, 2014), which may lead to a large over-estimation of biomass if not accounted for (Figure 8.8). The correlation between main stem diameter and the woody biomass held in other tree components such upper canopy branches tends to become weaker in larger trees, meaning that simple stem diameter measurements cannot accurately represent whole tree biomass (Goodman et al., 2014; Saglam et al., 2020). In disturbance-prone tropical savannas, it may be expected that the issue of idiosyncratic physiognomy is even greater, as trees repeatedly re-grow following seasonal fire and damage by large herbivores, further reducing the accuracy of biomass estimations (Figure 8.7). Luck et al. (2020) raised concern that traditional stem diameter allometries were particularly unreliable in disturbance-

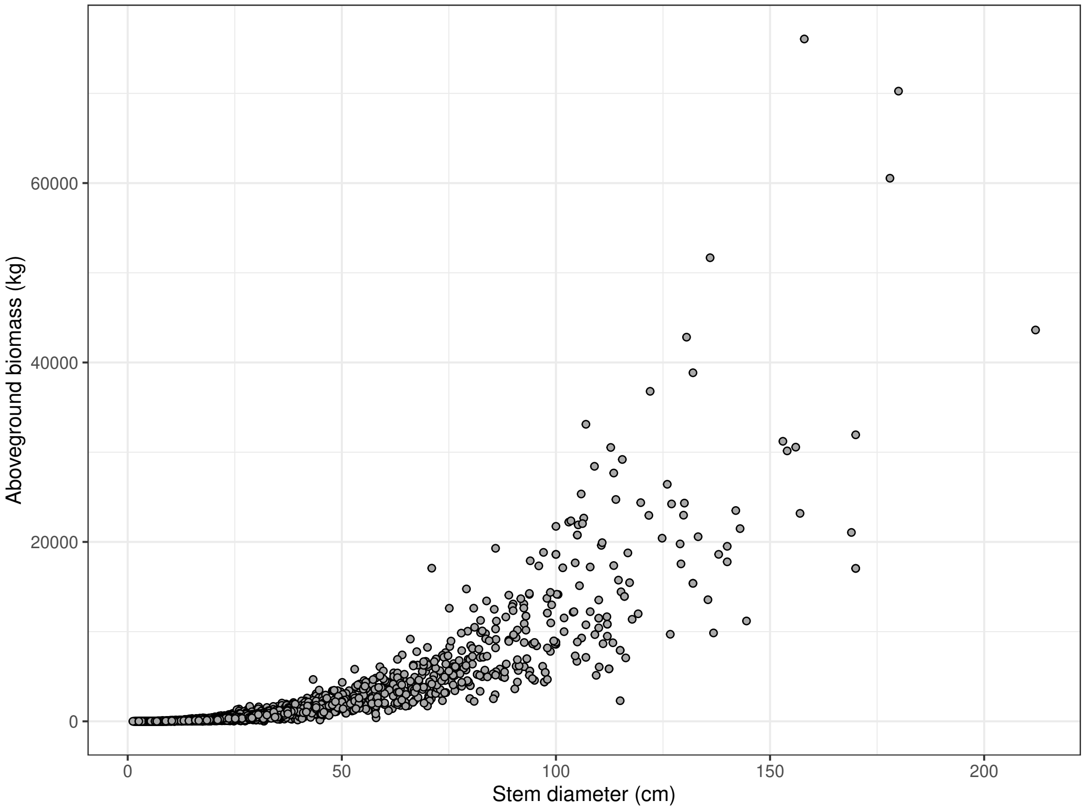


Figure 8.6: The relationship between tree stem diameter and aboveground biomass calculated from destructive harvest from all 872 records held in the GlobAllomeTree database (Henry et al., 2013) and all 4004 records reported in Chave et al. (2014). The heteroscedasticity of the relationship between stem diameter and aboveground biomass can be seen, with increased variance in biomass at higher stem diameters.

Figure 8.7: Two large old trees in Kilwa District, southeast Tanzania, with particularly idiosyncratic trunks. Using conventional stem diameter allometries will likely produce an inaccurate estimate of above-ground biomass. Photos by Ellie Wood.

prone savannas, in a study which compared terrestrial LiDAR biomass estimates with traditional allometries. For the reasons outlined above, it is therefore of great importance to develop an optimal method for estimating biomass of the largest trees. But how do we reconcile the disproportionate contribution of large trees to plot-based estimates of biomass with the scarcity of destructive large tree measurements?

Terrestrial LiDAR provides an opportunity to accurately estimate the woody volume of very large trees. Recent advances have provided a number of methods for segmenting individual trees from a point cloud (Burt et al., 2018; Koma et al., 2018), and for generating 3D surface models from point clouds (Calders et al., 2014; Malhi et al., 2018) to build voluminous models of individual trees. The plots covered by the terrestrial LiDAR dataset collected during this thesis contain 86 trees >50 cm stem diameter with 360° point cloud coverage, providing decent replication if each tree is successfully segmented.

Figure 8.8: A severely fluted *Brachystegia tamarindoides* stem found in Bicuar National Park, Angola. Due to the decomposition of wood in the stem interior, simple stem diameter based biomass allometries will over-estimate the biomass of this stem.

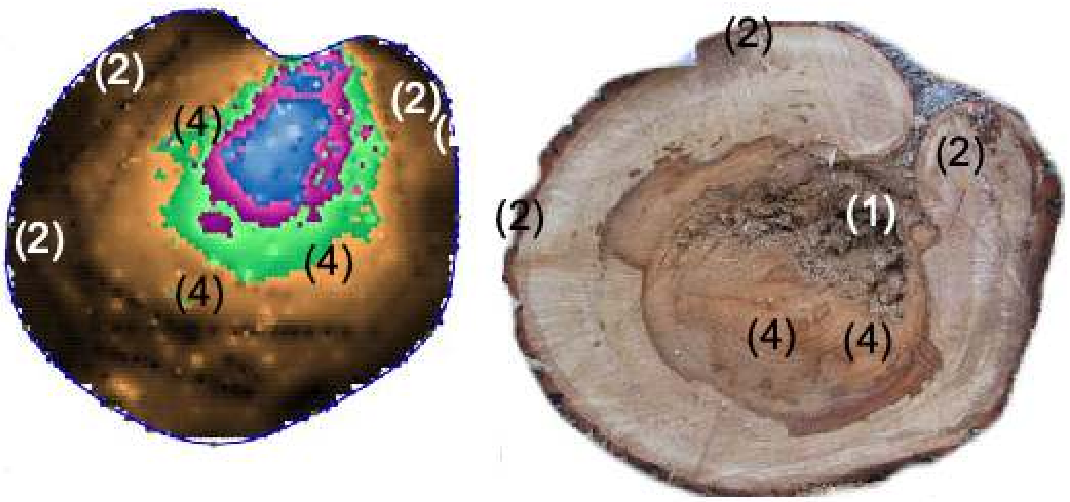


Figure 8.9: An example of a sonic tomograph image (left) and across section of the same tree (right), annotated to show internal features of the stem: (1) cavity or dead dry wood, (2) sound wood, (4) active decay with dense wood. Taken from Argus Electronic GmbH (2016).

While terrestrial LiDAR may address inaccurate biomass estimates caused by idiosyncratic physiognomy present on the exterior surface of large trees, and has been used successfully for this purpose in other studies (Takoudjou et al., 2017), it cannot address the internal variation caused by fluting and hollowing that is pervasive in large trees. It is also affected by the thick bark present in many fire-adapted savanna trees, which can lead to an over-estimation of woody biomass (Kozak & Smith, 1993; Hoffmann et al., 2012; Solbrig et al., 1996). Sonic tomography has been developed as a method to measure the decay of wood within tree trunks (Gilbert et al., 2016), and is currently used routinely to detect structural weaknesses in large trees in urban and parkland areas (Karlinasari et al., 2018). The PiCUS sonic tomograph (Argus Electronics GmbH, Rostock, Germany) is suitable for detecting internal abnormalities in large woody stems, and has been used previously to estimate biomass in forest trees (Marra et al., 2018).

I aim to test a novel method for estimating the biomass of the largest trees in the 22 plots already covered by the terrestrial LiDAR dataset, using a combination of terrestrial LiDAR and sonic tomography, to map the exterior and interior of the tree, respectively. LiDAR and tomography measurements will be combined with conventional measurements of tree stem diameter, tree height, and wood density, to build a multi-input allometric model of large trees with the hope of further reducing the large uncertainty in the woody biomass stocks of southern African woodlands. Additionally, the new biomass estimations will be compared to biomass estimates generated from existing allometric equations for dry tropical trees, e.g. Chave et al. (2014) and Ryan et al. (2011), to assess whether these allometries produce an over- or under-estimation of biomass. Specifically, I propose to use the PiCUS 3 sonic tomograph with the protocol outlined in Gilbert et al. (2016) to measure internal structure, and the pipe-fitting algorithm from Calders et al. (2014) to create 3D branch models of exterior structure. Ideally the fieldwork for this project could be carried out alongside a repeat census of the permanent plots, which in Bicuar National Park will happen in either 2022 or 2023, taking advantage of the existing plot monitoring infrastructure and existing LiDAR data.

8.3.3 Effects of canopy structure on understorey light environment and grass biomass

The competitive balance between grass and trees defines mesic savanna ecosystems (Frost, 1996). Where rainfall does not preclude a closed tree canopy (Sankaran et al., 2005), disturbance by fire can prevent canopy closure via a positive feedback loop whereby an open canopy allows grass growth, providing fuel for more frequent and intense fires, causing tree mortality, particularly among juveniles, preventing canopy closure, and so on (Staver et al., 2011). This positive feedback drives the phenomenon of 'alternative stable states', where nearby and environmentally similar patches can maintain different vegetation based on previous disturbance history. This commonly produces a mosaic of open savanna patches and closed canopy forest-like patches.

Much previous research has tried to identify the factors which determine the spatial patterning of closed and open canopy patches in mesic savannas, and particularly the factors determining the resilience of patches to state transitions (Devine et al., 2017; Case & Staver, 2016; Hirota et al., 2011). Of particular interest has been the transition from open savanna to a closed canopy forest-like state, as evidence suggests that atmospheric carbon fertilisation may be driving woody encroachment and woody thickening across mesic savannas

(Stevens et al., 2017). Most previous work has focussed on climatic (Case et al., 2020), edaphic (Colgan et al., 2012) and disturbance factors (Case & Staver, 2016), and how these interact with tree and grass growth to determine their competitive balance, but few have considered biotic factors such as tree demographic structure, canopy architecture and tree species composition (but see Pilon et al. 2020), which may also influence grass growth (Jennings, 1999). The LiDAR data collected during this PhD provides a unique opportunity to investigate the relationship between canopy tree attributes and grass biomass, to draw conclusions about the tree canopy conditions which provide resilience in open and closed canopy states.

Although the data was not included in the thesis due to lack of time for analysis, the terrestrial LiDAR dataset collected in Bicuar National Park was paired with systematic grass biomass harvest samples and grass sward height measurements using a Disc Pasture Meter (DPM), across all 15 plots (Figure 8.10). Cooper et al. (2017) provides a method for estimating grass volume from terrestrial LiDAR, which could be extended in this study to estimate grass biomass through an allometric equation linking grass volume to sward height and biomass harvests. The sample locations of the grass measurements are precisely known from differential-GPS and can therefore be matched precisely with the LiDAR measurements, providing data on canopy structure at the fine spatial scale relevant to grass growth.

Using simple linear mixed effects models to explore the relative importance of different tree canopy architectural and structural properties, these data could be used to improve our understanding the drivers of woody encroachment and alternative stable states, which could be applied to earth system models at regional spatial scales to predict how resilient different vegetation types are to environmental change, with consequences for biomass and carbon cycling predictions.

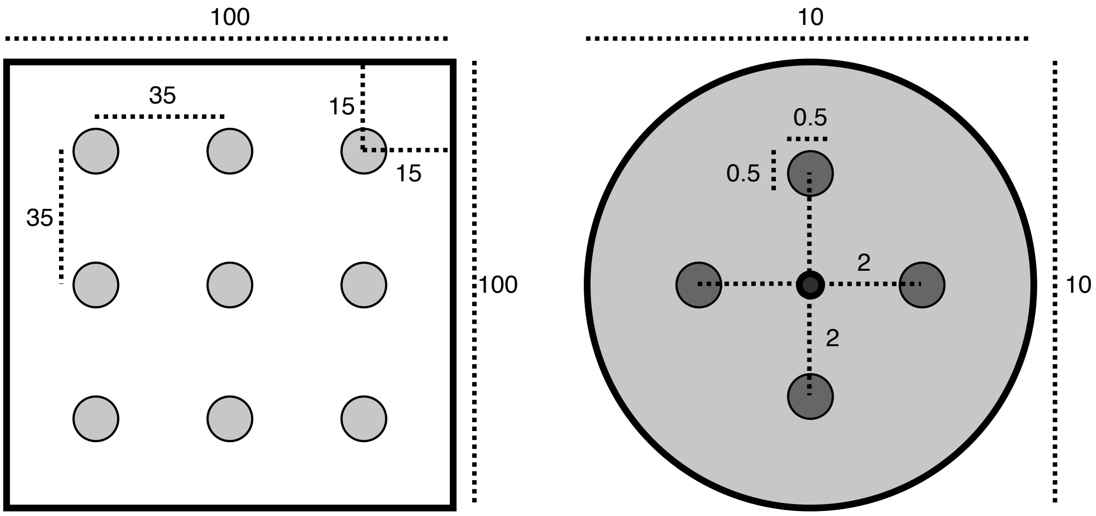


Figure 8.10: The layout of 10 m diameter subplots within each 1 ha square plot. Distances are marked by dotted lines, in metres. Each subplot is situated inside a 15 m buffer from the plot edge, with 35 m between subplot centres. Subplots are arranged in a 3×3 grid. Disc Pasture Measurements (DPM) and biomass samples are located in cardinal directions 2 m from the centre of the subplot. All distances are in metres. Biomass harvests were conducted at one randomly selected DPM sample point per subplot, resulting in nine biomass harvests and 36 DPM samples per 1 ha plot.

References

Anderson, C. B. (2018). ‘Biodiversity monitoring, earth observations and the ecology of scale’. In: *Ecology Letters* 21.10, pp. 1572–1585. DOI: `10.1111/ele.13106`.

Argus Electronic GmbH (2016). *PiCUS tree tomography methods at a glance*. Rostock, Germany: Argus Electronic GmbH.

Bastin, J.-F., N. Barbier, M. Réjou-Méchain, A. Fayolle, S. Gourlet-Fleury, D. Maniatis, T. de Haulleville, F. Baya, H. Beeckman, D. Beina et al. (2015). ‘Seeing Central African forests through their largest trees’. In: *Scientific Reports* 5.1. DOI: `10.1038/srep13156`.

Blicharska, M. & G. Mikusiński (2014). ‘Incorporating Social and Cultural Significance of Large Old Trees in Conservation Policy’. In: *Conservation Biology* 28.6, pp. 1558–1567. DOI: `10.1111/cobi.12341`.

Bogdanovich, E., O. Perez-Priego, T. S. El-Madany, M. Guderle, J. Pacheco-Labrador, S. R. Levick, G. Moreno, A. Carrara, M. P. Martín & M. Migliavacca (2021). ‘Using terrestrial laser scanning for characterizing tree structural parameters and their changes under different management in a Mediterranean open woodland’. In: *Forest Ecology and Management* 486, p. 118945. DOI: `10.1016/j.foreco.2021.118945`.

Brokaw, N. & J. Thompson (2000). ‘The H for DBH’. In: *Forest Ecology and Management* 129.1-3, pp. 89–91. DOI: `10.1016/s0378-1127(99)00141-3`.

Burt, A., M. Disney & K. Calders (2018). ‘Extracting individual trees from lidar point clouds using treeseg’. In: *Methods in Ecology and Evolution* 10 (3), pp. 438–445. DOI: `10.1111/2041-210x.13121`.

Calders, K., G. Newnham, A. Burt, S. Murphy, P. Raumonen, M. Herold, D. Culvenor, V. Avitabile, M. Disney, J. Armston et al. (2014). ‘Nondestructive estimates of above-ground biomass using terrestrial laser scanning’. In: *Methods in Ecology and Evolution* 6.2, pp. 198–208. DOI: `10.1111/2041-210x.12301`.

Case, M. F., J. B. Nippert, R. M. Holdo & A. C. Staver (2020). ‘Root-niche separation between savanna trees and grasses is greater on sandier soils’. In: *Journal of Ecology* 108.6. Ed. by I. Oliveras, pp. 2298–2308. DOI: `10.1111/1365-2745.13475`.

Case, M. F. & A. C. Staver (2016). ‘Fire prevents woody encroachment only at higher-than-historical frequencies in a South African savanna’. In: *Journal of Applied Ecology* 54.3, pp. 955–962. DOI: `10.1111/1365-2664.12805`.

Chambers, J. Q., J. dos Santos, R. J. Ribeiro & N. Higuchi (2001). ‘Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest’. In: *Forest Ecology and Management* 152.1-3, pp. 73–84. DOI: `10.1016/s0378-1127(00)00591-0`.

Chave, J., C. Andalo, S. Brown, M. A. Cairns, J. Q. Chambers, D. Eamus, H. Fölster, F. Fromard, N. Higuchi, T. Kira et al. (2005). ‘Tree allometry and improved estimation of carbon stocks and balance in tropical forests’. In: *Oecologia* 145.1, pp. 87–99. DOI: `10.1007/s00442-005-0100-x`.

Chave, J., M. Réjou-Méchain, A. Búrquez, E. Chidumayo, M. S. Colgan, W. B. C. Delitti, A. Duque, T. Eid, P. M. Fearnside, R. C. Goodman et al. (2014). ‘Improved allometric models to estimate the aboveground biomass of tropical trees’. In: *Global Change Biology* 20, pp. 3177–3190. DOI: `10.1111/gcb.12629`.

Chave, J., R. Condit, S. Aguilar, A. Hernandez, S. Lao & R. Perez (2004). ‘Error propagation and scaling for tropical forest biomass estimates’. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 359.1443, pp. 409–420. DOI: `10.1098/rstb.2003.1425`.

Chave, J., S. J. Davies, O. L. Phillips, S. L. Lewis, P. Sist, D. Schepaschenko, J. Armston, T. R. Baker, D. Coomes, M. Disney et al. (2019). ‘Ground Data are Essential for Biomass Remote Sensing Missions’. In: *Surveys in Geophysics* 40.4, pp. 863–880. DOI: `10.1007/s10712-019-09528-w`.

Colgan, M. S., G. P. Asner, S. R. Levick, R. E. Martin & O. A. Chadwick (2012). 'Topo-edaphic controls over woody plant biomass in South African savannas'. In: *Biogeosciences* 9.5, pp. 1809–1821. DOI: `10.5194/bg-9-1809-2012`.

Cooper, S., D. Roy, C. Schaaf & I. Paynter (2017). 'Examination of the Potential of Terrestrial Laser Scanning and Structure-from-Motion Photogrammetry for Rapid Nondestructive Field Measurement of Grass Biomass'. In: *Remote Sensing* 9.6, p. 531. DOI: `10.3390/rs9060531`.

Devine, A. P., R. A. McDonald, T. Quaife & I. M. D. Maclean (2017). 'Determinants of woody encroachment and cover in African savannas'. In: *Oecologia* 183.4, pp. 939–951. DOI: `10.1007/s00442-017-3807-6`.

Exbrayat, J.-F., A. A. Bloom, N. Carvalhais, R. Fischer, A. Huth, N. MacBean & M. Williams (2019). 'Understanding the Land Carbon Cycle with Space Data: Current Status and Prospects'. In: *Surveys in Geophysics* 40.4, pp. 735–755. DOI: `10.1007/s10712-019-09506-2`.

Fick, S. E. & R. J. Hijmans (2017). 'WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas'. In: *International Journal of Climatology* 37.12, pp. 4302–4315. DOI: `10.1002/joc.5086`.

Fischer, F. J., N. Labrière, G. Vincent, B. Hérault, A. Alonso, H. Memiaghe, P. Bissiengou, D. Kenfack, S. Saatchi & J. Chave (2020). 'A simulation method to infer tree allometry and forest structure from airborne laser scanning and forest inventories'. In: *Remote Sensing of Environment* 251, p. 112056. DOI: `10.1016/j.rse.2020.112056`.

Frost, P. (1996). 'The ecology of miombo woodlands'. In: *The miombo in transition: woodlands and welfare in Africa*. Ed. by B. M. Campbell. Bogor, Indonesia: Center for International Forestry Research, pp. 11–55.

George-Chacon, S. P., J. M. Dupuy, A. Peduzzi & J. L. Hernandez-Stefanoni (2019). 'Combining high resolution satellite imagery and lidar data to model woody species diversity of tropical dry forests'. In: *Ecological Indicators* 101, pp. 975–984. DOI: `10.1016/j.ecolind.2019.02.015`.

Gilbert, G. S., J. O. Ballesteros, C. A. Barrios-Rodriguez, E. F. Bonadies, M. L. Cedeño-Sánchez, N. J. Fossatti-Caballero, M. M. Trejos-Rodríguez, J. M. Pérez-Suñiga, K. S. Holub-Young, L. A. W. Henn et al. (2016). 'Use of Sonic Tomography to Detect and Quantify Wood Decay in Living Trees'. In: *Applications in Plant Sciences* 4.12, p. 1600060. DOI: `10.3732/apps.1600060`.

Goodman, R. C., O. L. Phillips & T. R. Baker (2014). 'The importance of crown dimensions to improve tropical tree biomass estimates'. In: *Ecological Applications* 24.4, pp. 680–698. DOI: `10.1890/13-0070.1`.

Goring, S. J., K. C. Weathers, W. K. Dodds, P. A. Soranno, L. C. Sweet, K. S. Cheruvelil, J. S. Kominoski, J. Rüegg, A. M. Thorn & R. M. Utz (2014). 'Improving the culture of interdisciplinary collaboration in ecology by expanding measures of success'. In: *Frontiers in Ecology and the Environment* 12.1, pp. 39–47. DOI: `10.1890/120370`.

Hampton, S. E., S. S. Anderson, S. C. Bagby, C. Gries, X. Han, E. M. Hart, M. B. Jones, W. C. Lenhardt, A. MacDonald, W. K. Michener et al. (2015). 'The Tao of open science for ecology'. In: *Ecosphere* 6.7, art120. DOI: `10.1890/es14-00402.1`.

Henning, J. G. & P. J. Radtke (2006). 'Detailed stem measurements of standing trees from ground-based scanning LiDAR'. In: *Forest Science* 52.1, pp. 67–80. DOI: `10.1093/forestscience/52.1.67`.

Henry, M., A. Bombelli, C. Trotta, A. Alessandrini, L. Birigazzi, G. Sola, G. Vieilledent, P. Santenoise, F. Longuetaud, R. Valentini et al. (2013). 'GlobAllomeTree: international platform for tree allometric equations to support volume, biomass and carbon assessment'. In: *iForest - Biogeosciences and Forestry* 6.6, pp. 326–330. DOI: `10.3832/ifor0901-006`.

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`.

Hoffmann, W. A., E. L. Geiger, S. G. Gotsch, D. R. Rossatto, L. C. R. Silva, O. L. Lau, M. Haridasan & A. C. Franco (2012). 'Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes'. In: *Ecology Letters* 15.7, pp. 759–768. DOI: `10.1111/j.1461-0248.2012.01789.x`.

Hopkinson, C., L. Chasmer, C. Young-Pow & P. Treitz (2004). 'Assessing forest metrics with a ground-based scanning lidar'. In: *Canadian Journal of Forest Research* 34.3, pp. 573–583. DOI: `10.1139/x03-225`.

Jennings, S. (1999). 'Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures'. In: *Forestry* 72.1, pp. 59–74. DOI: `10.1093/forestry/72.1.59`.

Karlinasari, L., A. T. Lestari, M. Y. S. Nababan, I. Z. Siregar & D. Nandika (2018). 'Assessment of urban tree condition using sonic tomography technology'. In: *IOP Conference Series: Earth and Environmental Science* 203, p. 012030. DOI: `10.1088/1755-1315/203/1/012030`.

Kershaw, J. A., M. J. Ducey, T. W. Beers & B. Husch (2017). *Forest Mensuration*. Chichester, UK: John Wiley & Sons.

Koma, Z., M. Rutzinger & M. Bremer (2018). 'Automated Segmentation of Leaves From Deciduous Trees in Terrestrial Laser Scanning Point Clouds'. In: *IEEE Geoscience and Remote Sensing Letters* 15.9, pp. 1456–1460. DOI: `10.1109/lgrs.2018.2841429`.

Kozak, A., D. D. Munro & J. H. G. Smith (1969). 'Taper Functions and their Application in Forest Inventory'. In: *The Forestry Chronicle* 45.4, pp. 278–283. DOI: `10.5558/tfc45278-4`.

Kozak, A. & J. H. G. Smith (1993). 'Standards for evaluating taper estimating systems'. In: *The Forestry Chronicle* 69.4, pp. 438–444. DOI: `10.5558/tfc69438-4`.

Lindenmayer, D. B., W. F. Laurance & J. F. Franklin (2012). 'Global Decline in Large Old Trees'. In: *Science* 338.6112, pp. 1305–1306. DOI: `10.1126/science.1231070`.

Lindenmayer, D. B. & W. F. Laurance (2016). 'The ecology, distribution, conservation and management of large old trees'. In: *Biological Reviews* 92.3, pp. 1434–1458. DOI: `10.1111/brv.12290`.

Lopez-Gonzalez, G., S. L. Lewis, M. Burkitt & O. L. Phillips (2011). 'ForestPlots.net: a web application and research tool to manage and analyse tropical forest plot data'. In: *Journal of Vegetation Science* 22.4, pp. 610–613. DOI: `10.1111/j.1654-1103.2011.01312.x`.

Luck, L., L. B. Hutley, K. Calders & S. R. Levick (2020). 'Exploring the Variability of Tropical Savanna Tree Structural Allometry with Terrestrial Laser Scanning'. In: *Remote Sensing* 12.23, p. 3893. DOI: `10.3390/rs12233893`.

Luoma, V., N. Saarinen, V. Kankare, T. Tanhuanpää, H. Kaartinen, A. Kukko, M. Holopainen, J. Hyyppä & M. Vastaranta (2019). 'Examining Changes in Stem Taper and Volume Growth with Two-Date 3D Point Clouds'. In: *Forests* 10.5, p. 382. DOI: `10.3390/f10050382`.

Lutz, J. A., T. J. Furniss, D. J. Johnson, S. J. Davies, D. Allen, A. Alonso, K. J. Anderson-Teixeira, A. Andrade, J. Baltzer, K. M. L. Becker et al. (2018). 'Global importance of large-diameter trees'. In: *Global Ecology and Biogeography* 27.7, pp. 849–864. DOI: `10.1111/geb.12747`.

MacFarlane, D. W. & A. R. Weiskittel (2016). 'A new method for capturing stem taper variation for trees of diverse morphological types'. In: *Canadian Journal of Forest Research* 46.6, pp. 804–815. DOI: `10.1139/cjfr-2016-0018`.

Malhi, Y., T. Jackson, L. P. Bentley, A. Lau, A. Shenkin, M. Herold, K. Calders, H. Bartholomeus & M. I. Disney (2018). 'New perspectives on the ecology of tree structure and tree communities through terrestrial laser scanning'. In: *Interface Focus* 8.2, p. 20170052. DOI: `10.1098/rsfs.2017.0052`.

Marra, R. E., N. J. Brazee & S. Fraver (2018). 'Estimating carbon loss due to internal decay in living trees using tomography: implications for forest carbon budgets'. In: *Environmental Research Letters* 13.10, p. 105004. DOI: `10.1088/1748-9326/aae2bf`.

Martínez, O. J. A., A. K. Fremier, S. Günter, Z. R. Bendaña, L. Vierling, S. M. Galbraith, N. A. Bosque-Pérez & J. C. Ordoñez (2016). 'Scaling up functional traits for ecosystem services with remote sensing: concepts and methods'. In: *Ecology and Evolution* 6.13, pp. 4359–4371. DOI: `10.1002/ece3.2201`.

McNicol, I. M., N. J. Berry, T. B. Bruun, K. Hergoualc'h, O. Mertz, A. de Neergaard & C. M. Ryan (2015). 'Development of allometric models for above and belowground biomass in swidden cultivation fallows of Northern Laos'. In: *Forest Ecology and Management* 357, pp. 104–116. DOI: `10.1016/j.foreco.2015.07.029`.

Mikkelsen, T. N., N. Clarke, A. Danielewska & R. Fischer (2013). 'Towards Supersites in Forest Ecosystem Monitoring and Research'. In: *Developments in Environmental Science* 13, pp. 475–496. DOI: `10.1016/b978-0-08-098349-3.00022-0`.

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`.

Muumbe, T. P., J. Baade, J. Singh, C. Schmullius & C. Thau (2021). 'Terrestrial Laser Scanning for Vegetation Analyses with a Special Focus on Savannas'. In: *Remote Sensing* 13.3, p. 507. DOI: `10.3390/rs13030507`.

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`.

Picard, N., E. Rutishauser, P. Ploton, A. Ngomanda & M. Henry (2015). 'Should tree biomass allometry be restricted to power models?' In: *Forest Ecology and Management* 353, pp. 156–163. DOI: `10.1016/j.foreco.2015.05.035`.

Pilon, N. A. L., G. Durigan, J. Rickenback, R. T. Pennington, K. G. Dexter, W. A. Hoffmann, R. C. R. Abreu & C. E. R. Lehmann (2020). 'Shade alters savanna grass layer structure and function along a gradient of canopy cover'. In: *Journal of Vegetation Science* 32.1. DOI: `10.1111/jvs.12959`.

Ravaglia, Fournier, Bac, Véga, Côté, Piboule & Rémillard (2019). 'Comparison of Three Algorithms to Estimate Tree Stem Diameter from Terrestrial Laser Scanner Data'. In: *Forests* 10.7, p. 599. DOI: `10.3390/f10070599`.

Réjou-Méchain, M., N. Barbier, P. Couteron, P. Ploton, G. Vincent, M. Herold, S. Mermoz, S. Saatchi, J. Chave, F. de Boissieu et al. (2019). 'Upscaling Forest Biomass from Field to Satellite Measurements: Sources of Errors and Ways to Reduce Them'. In: *Surveys in Geophysics* 40.4, pp. 881–911. DOI: `10.1007/s10712-019-09532-0`.

Roxburgh, S. H., K. I. Paul, D. Clifford, J. R. England & R. J. Raison (2015). 'Guidelines for constructing allometric models for the prediction of woody biomass: How many individuals to harvest?' In: *Ecosphere* 6.3, art38. DOI: `10.1890/es14-00251.1`.

Ruxton, G. D. (2014). 'Why are so many trees hollow?' In: *Biology Letters* 10.11, p. 20140555. DOI: `10.1098/rsbl.2014.0555`.

Ryan, C. M., M. Williams & J. Grace (2011). 'Above- and belowground carbon stocks in a miombo woodland landscape of Mozambique'. In: *Biotropica* 43.4, pp. 423–432. DOI: `10.1111/j.1744-7429.2010.00713.x`.

Saarinen, N., V. Kankare, J. Pyörälä, T. Yrttimaa, X. Liang, M. A. Wulder, M. Holopainen, J. Hyyppä & M. Vastaranta (2019). 'Assessing the Effects of Sample Size on Parameterizing a Taper Curve Equation and the Resultant Stem-Volume Estimates'. In: *Forests* 10.10, p. 848. DOI: `10.3390/f10100848`.

Saglam, S., E. Ozdemir, U. Y. Ozkan, T. Demirel & E. Makineci (2020). 'Biomass estimation of aboveground tree components for Turkey oak (Quercus cerris L.) in south-eastern Turkey'. In: *Environmental Monitoring and Assessment* 192.7. DOI: `10.1007/s10661-020-08386-z`.

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: `10.1038/nature04070`.

SASSCAL (2020). *SASSCAL WeatherNet*. URL: `www.sasscalweathernet.org` (visited on 26/04/2021).

Schepaschenko, D., J. Chave, O. L. Phillips, S. L. Lewis, S. J. Davies, M. Réjou-Méchain, P. Sist, K. Scipal, C. Perger, B. Herault et al. (2019). 'The Forest Observation System, building a global reference dataset for remote sensing of forest biomass'. In: *Scientific Data* 6.1. DOI: `10.1038/s41597-019-0196-1`.

SEOSAW (2020). 'A network to understand the changing socio-ecology of the southern African woodlands (SEOSAW): Challenges, benefits, and methods'. In: *Plants, People, Planet.* DOI: `10.1002/ppp3.10168`.

Silva, D. F. D., A. E. Cahali, F. A. Gomes, J. J. Tchamba & F. M. Gonçalves (2020). 'Caracterização da diversidade de espécies do Parque Nacional do Bicuar e implicações para a gestão e conservação da biodiversidade'. In: *Revista Internacional de Educação Saúde e Ambiente* 3.1, pp. 46–58. DOI: `10.37334/riesa.v3i1.33`.

Singh, J., S. R. Levick, M. Guderle, C. Schmullius & S. E. Trumbore (2018). 'Variability in fire-induced change to vegetation physiognomy and biomass in semi-arid savanna'. In: *Ecosphere* 9.12, e02514. DOI: `10.1002/ecs2.2514`.

Solbrig, O. T., E. Medina & J. F. Silva (1996). *Biodiversity and Savanna Ecosystem Processes*. Berlin, Germany: Springer-Verlag.

Srinivasan, S., S. Popescu, M. Eriksson, R. Sheridan & N.-W. Ku (2015). 'Terrestrial Laser Scanning as an Effective Tool to Retrieve Tree Level Height, Crown Width, and Stem Diameter'. In: *Remote Sensing* 7.2, pp. 1877–1896. DOI: `10.3390/rs70201877`.

Staver, A. C., S. Archibald & S. A. Levin (2011). 'The Global Extent and Determinants of Savanna and Forest as Alternative Biome States'. In: *Science* 334.6053, pp. 230–232. DOI: `10.1126/science.1210465`.

Stevens, N., C. E. R. Lehmann, B. P. Murphy & G. Durigan (2017). 'Savanna woody encroachment is widespread across three continents'. In: *Global Change Biology* 23.1, pp. 235–244. DOI: `10.1111/gcb.13409`.

Takoudjou, S. M., P. Ploton, B. Sonké, J. Hackenberg, S. Griffon, F. Coligny, N. G. Kamdem, M. Libalah, G. I. Mofack, G. L. Moguédec et al. (2017). 'Using terrestrial laser scanning data to estimate large tropical trees biomass and calibrate allometric models: A comparison with traditional destructive approach'. In: *Methods in Ecology and Evolution* 9.4, pp. 905–916. DOI: `10.1111/2041-210x.12933`.

Thies, M., N. Pfeifer, D. Winterhalder & B. G. H. Gorte (2004). 'Three-dimensional reconstruction of stems for assessment of taper, sweep and lean based on laser scanning of standing trees'. In: *Scandinavian Journal of Forest Research* 19.6, pp. 571–581. DOI: `10.1080/02827580410019562`.

Umbach, D. & K. N. Jones (2003). 'A few methods for fitting circles to data'. In: *IEEE Transactions on Instrumentation and Measurement* 52.6, pp. 1881–1885. DOI: `10.1109/tim.2003.820472`.

Wagner, F. H., M. P. Ferreira, A. Sanchez, M. C. M. Hirye, M. Zortea, E. Gloor, O. L. Phillips, C. R. de Souza Filho, Y. E. Shimabukuro & L. E. O. C. Aragão (2018). 'Individual tree crown delineation in a highly diverse tropical forest using very high resolution satellite images'. In: *ISPRS Journal of Photogrammetry and Remote Sensing* 145, pp. 362–377. DOI: `10.1016/j.isprsjprs.2018.09.013`.

Wang, D., M. Hollaus, E. Puttonen & N. Pfeifer (2016). 'Fast and robust stem reconstruction in complex environments using terrestrial laser scanning'. In: *The International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences*, pp. 411–417. DOI: `10.5194/isprsarchives-xli-b3-411-2016`.

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`.

Xiao, J., F. Chevallier, C. Gomez, L. Guanter, J. A. Hicke, A. R. Huete, K. Ichii, W. Ni, Y. Pang, A. F. Rahman et al. (2019). 'Remote sensing of the terrestrial carbon cycle: A review of advances over 50 years'. In: *Remote Sensing of Environment* 233, p. 111383. DOI: `10.1016/j.rse.2019.111383`.

Chapter 9

Synthesis and conclusions

This thesis aimed to improve understanding of the role of tree biodiversity in shaping the structure and of southern African woodlands. Dry tropical savanna-woodland mosaics form the dominant vegetation type in southern Africa (Arino et al., 2012). Their vegetation dynamics are complex (Scholes & Archer, 1997), their ecology is understudied compared to other dominant tropical vegetation formations (Hill & Hanan, 2011), and they represent the largest uncertainty in models of the terrestrial carbon cycle (Sitch et al., 2015; Williams et al., 2007).

I framed the studies conducted in this thesis in relation to the "Biodiversity-Ecosystem Function Relationship" (BEFR), which predicts positive effects of biodiversity on ecosystem function, and is supported by hundreds of previous studies in other biomes (Tilman et al., 2014; Plas, 2019). BEFR theory predicts positive biodiversity effects mainly via the mechanism of niche complementarity (Cardinale et al., 2009), but it was unclear whether positive biodiversity effects would be observable in highly disturbed and resource-limited savanna-woodland ecosystems (Tilman et al., 2014).

This thesis tests theory formulated in temperate and wet tropical ecosystems, in a highly disturbed and resource-limited system, southern African woodlands. The findings of this thesis contribute both to understanding the determinants of ecosystem function in southern African woodlands, and to BEFR theory more generally. To recap, the investigative chapters of this thesis explored:

1. The effect of tree species diversity on above-ground woody biomass across southern African mesic savannas, and mediation of this effect by environment and vegetation composition (Chapter 3).

2. Land-surface phenology as a mechanism by which tree species diversity might increase gross primary productivity (Chapter 4).
3. The role of tree species diversity and composition in driving canopy complexity (Chapter 5).
4. Regional variation in species composition and woodland structure in miombo woodlands across southern Africa, with particular reference to the understudied Huíla plateau, Angola (Chapter 7).

These chapters aimed to advance understanding of three broader research questions:

1. Is there a detectable relationship between biodiversity and ecosystem function across southern African woodlands, and to what extent is this mediated by environment and vegetation composition?
2. What are the possible mechanisms driving observed biodiversity-ecosystem function relationships in southern African woodlands?
3. How does the tree species diversity, composition and structure of mesic savannas vary across southern Africa?

Here, I synthesise the key findings of the thesis, set them in the context of the principal research questions, and discuss the implications of this thesis for understanding savanna ecology and biodiversity-ecosystem function theory. Furthermore, I provide a perspective for future research based on the results of this thesis.

9.1 Summary of findings

9.1.1 Evidence and implications of positive biodiversity effects in southern African woodlands

In Chapter 3, I conducted a regional study of the effects of tree species diversity, abiotic environment, and disturbance on above-ground woody biomass (AGB) and stand structure, using a network of plots distributed across southern Africa.

I found that diverse plots generally held greater AGB, supporting the results of hundreds of previous studies of the biodiversity-ecosystem function relationship conducted in other natural ecosystems across the world (Plas, 2019), and of previous experimental studies (Tilman et al., 2014). This study however, joins only a handful of studies conducted in drylands and savannas (Maestre et al., 2012; Grace et al., 2016; Plas, 2019; Clarke et al., 2017).

As well as the regional study presented in Chapter 3, I conducted two more studies which demonstrated the influence of tree biodiversity on ecosystem function in southern African woodlands. In Chapter 4, I found that species diversity correlated with increased growing season length and earlier pre-rain green-up. In Chapter 5 I found some evidence for a positive species diversity effect on woodland canopy complexity at hectare spatial scales. These studies are more mechanistic in nature, and contribute to understanding the functional contribution of different species and individuals in a way that broad studies such as that conducted in Chapter 3 cannot.

In southern Africa, the human population is rapidly increasing and urbanising (United Nations, 2018), placing greater strain on natural resources in the region to provide ecosystem services, particularly provisioning services for timber, charcoal and fuel wood (Wessels et al., 2013; Ryan et al., 2016). Selective timber extraction in the region often targets large archetypal miombo species for their high quality timber (Sitoe et al., 2010). These species are predominantly from the Detarioideae subfamily, within the Fabaceae family. The results in this thesis suggest that removal of these individuals will have disproportionate negative effects on ecosystem function, functional resilience, and therefore on ecosystem service provision.

The mutually supporting findings from Chapter 3, Chapter 4, and Chapter 5 suggest that biodiversity loss, particularly of large archetypal miombo tree species, negatively impacts ecosystem functions related to biomass and productivity, and the resilience of those functions. Southern African woodlands are a globally important carbon sink (Grace et al., 2006; Pelletier et al., 2018), and even small changes to the biomass or productivity could have global consequences (Williams et al., 2005). These findings highlight the potential for biodiversity loss to negatively impact the carbon sequestration potential of southern African woodlands, by reducing both productivity and potential woody biomass. Over the coming century, biodiversity ‘intactness’ in southern Africa is expected to decrease by around 40% (Biggs et al., 2008).

Previously, the influence of BEFR research on land management and policy has been limited (Manning et al., 2019). This thesis did not focus on strategies for management of natural resources, but a few tentative suggestions for management practices can be made. Variation in tree size was found to be a key vector for positive biodiversity effects, therefore appropriate management actions at small spatial scales should prioritise maintaining viable populations of species which differ in their growth strategy and average physiognomy. Furthermore, due to the dominant role of Detarioideae species on ecosystem functions related to productivity and biomass in miombo woodlands, I suggest that maintenance of these large canopy forming individuals should be prioritised.

Terrestrial Biosphere Models (TBMs) routinely use plant functional types (PFTs) to model spatial variation in biosphere function as it relates to carbon cycling (Fisher et al., 2014). PFTs represent broad groupings of species which co-exist to produce vegetation with unifying characteristics (Bonan et al., 2002). The studies conducted in this thesis also used vegetation type classifications to account for biogeographic variation in species composition that affects ecosystem function irrespective of species diversity. In these studies, it was consistently found that there was large variation in ecosystem function both within and among vegetation types. The vegetation types identified during the studies in this thesis were of greater specificity than the PFTs typically employed in TBMs (Ustin & Gamon, 2010; Krinner et al., 2005), which raises the question of whether existing PFTs are detailed enough resolution to capture variation in ecosystem function and structural properties driven by biogeography and biodiversity (Osborne et al., 2018; Torello-Raventos et al., 2013). As remote-sensing technology and its applications continue to develop rapidly, this thesis prompts discussion that variation in ecosystem properties detected via remote-sensing could be used to infer biodiversity and to refine maps of PFTs based on their functional signature. For example, in Chapter 4, it was found that woodlands dominated by Combretaceae species have a greater peak in mid-rainy season productivity, but a shorter overall growing season than adjacent miombo woodlands. PFTs used in other studies however, routinely combine these woodlands into a single “Deciduous woodlands” PFT (Krinner et al., 2005). Variation in functional signature could be used to refine PFTs in a data-driven fashion, or potentially replace PFTs with continuous variation in traits and functional signature (Peaucelle et al., 2019). Of course, incorporating greater detail on vegetation type into TBMs would necessitate greater computing power and could result in greater uncertainty in model predictions if the information on vegetation types is incomplete or carries its own uncertainty. I suggest that earth system models up to regional spatial scales could look to incorporate these new developments which are supported by this thesis, but global models would have little to gain until higher resolution data are available that can surpass climatic correlates.

Most studies of biodiversity effects use biodiversity measures related to the number of species (Tilman et al., 2014). In this thesis, it was recognised that abundance evenness is another important facet of biodiversity that can provide further understanding of the mechanisms driving observed biodiversity effects (Chalcraft et al., 2004). In Chapter 3, I found that species richness and abundance evenness had similarly strong factor loadings on the latent variable of species diversity, implying similar contributions to overall biodiversity effects. In Chapter 4, I found that in miombo woodlands, while species richness caused an increase in cumulative EVI, longer season length, and earlier pre-rain green-up, abundance evenness caused a decrease in these metrics. This contrasting result suggests that selection effects may be driving much of the diversity effect in these woodlands, as an increase in evenness is necessarily associated with a decrease in the dominance of large canopy forming tree species which drive the phenological signal. Thus, while an increase in the number of species increases the likelihood of including these dominant species within the plot, an increase in evenness is associated with a reduction in their dominance. The dominant Detarioideae miombo species, grow to large canopy forming trees, with roots that can access deep groundwater reserves outside of the rainy season. Indeed, in the only non-miombo vegetation cluster encountered in data collection for Chapter 4, abundance evenness did cause an increase in cumulative EVI and season length.

Alternatively, this result may say more about the effects of disturbance and succession on ecosystem function than they do about biodiversity effects *per se*. As succession continues following a large disturbance, i.e. an intense fire, evenness (measured in Chapter 4 by basal area contribution) is expected to decrease, potentially approaching something similar to a Fisher's alpha species abundance curve, with a long tail of rare species (Morozov & Li, 2008; Sheil, 2001). Greater abundance evenness isn't necessarily the 'natural' or desirable state in wooded ecosystems. Thus, high abundance evenness is also possibly associated with tree size and other attributes related to succession following disturbance (Holdo, 2006), explaining the negative correlation of evenness with green-up lag, and cumulative EVI, as more mature woodland communities are expected to optimise productivity and resilience (Hector & Bagchi, 2007).

The analytical approach taken in Chapter 3 reflects the inter-connected nature of biodiversity, ecosystem function, and external factors such as disturbance and resource availability. Structural Equation Modelling (SEM) provides the means to effectively account for the simultaneous effect of environment on both species diversity and ecosystem function (Figure 2.6). Previous experimental studies have largely ignored the moderating effects of environment, and this has hampered efforts to scale up predictions of biodiversity effects to entire regions (Thompson et al., 2021). While other studies have used a similar analytical framework (Poorter et al., 2015; Poorter et al., 2017), none have implemented it in disturbed mesic savannas, nor have they included the effects of disturbance or the mechanistic connection between species diversity and structural diversity in statistical models. The powerful analytical framework, coupled with the broad regional scale dataset, raises various points about the limitations and moderating factors of biodiversity effects in this biome.

9.1.2 Thresholds on biodiversity effects

In the introduction and background to the thesis, I suggested that there may be key climatic and structural thresholds below which biodiversity effects driven by competition do not occur in dry tropical woodlands. This hypothesis is drawn from fundamental biodiversity-ecosystem function theory, which suggests that niche complementarity effects are predicated on inter-specific competition (Isbell et al., 2013). In dry tropical woodlands however, resource limitation, environmental stress, and disturbance may limit the role of competition, as abundance is kept below carrying capacity (Sankaran et al., 2005). In Chapter 3, I found that biodiversity effects became stronger with increasing organismal density, i.e. tree stem density. Tree stem density was in turn driven by water availability and reduced by fire frequency. This finding suggests that there are indeed environmental factors which either limit or mask the role of biodiversity in driving ecosystem function in stressful conditions. The majority of previous biodiversity-ecosystem function relationship studies do not incorporate the effects of environment, and instead focus on a given location where environmental conditions are assumed to vary little across the study site (Cardinale et al., 2009; Plas, 2019). The threshold effects identified in Chapter 3 could explain the varying strength and sign of the observed BEFR in other studies (Liang et al., 2016).

A number of studies in southern African woodlands have investigated ecological thresholds that determine the transition from open savanna to a closed canopy forest-like condition (Staver et al., 2011; Hirota et al., 2011; Staver et al., 2017). These studies have identified disturbance thresholds that maintain "alternative stable states" under similar climatic conditions. The findings in Chapter 3 and Chapter 5, suggest that tree species biodiversity itself could moderate these threshold conditions, by allowing greater biomass, greater diversity in tree physiognomy, greater canopy closure, and taller canopies, in more diverse woodlands. This variation in canopy structure with diversity is expected to further moderate disturbance through its effect on understorey grass fuel load.

In Chapter 4, it was found that in Zambian woodlands, a positive evenness effect was observed on cumulative EVI and growing season length in vegetation where there was more moisture limitation, while in more mesic miombo woodlands the effect of evenness remained negative. In higher precipitation woodlands, it appears that the dominant archetypal miombo tree species can grow to large canopy forming trees, and these individuals define cumulative EVI as a result. Meanwhile, in drier woodlands, a genuine niche complementarity effect occurs. In these drier woodlands, higher species diversity provides ecosystem level resilience to drought by increasing the breadth of water use strategies. This aligns with Ratcliffe et al. (2017), who conducted a study in dry Mediterranean woodlands, finding that facilitation and niche complementarity effects increased under greater seasonal drought stress.

9.1.3 Mechanisms for positive biodiversity effects in mesic savannas

A multitude of previous studies have found that biodiversity positively correlates with productivity, AGB (Liang et al., 2016), and the resilience of these ecosystem functions to environmental perturbations (Mori et al., 2012), but fewer have investigated the ecological mechanisms by which biodiversity affects ecosystem function (Barry et al., 2019). Identifying these pathways of effect not only improves understanding of the ecological processes underlying these observed effects, but also builds a more nuanced understanding of how ecosystem structure and function may change as a result of climate change or changes to disturbance regime (Huston, 2014).

Land-surface phenology

In Chapter 4, I found that species diversity led to increased growing season length, and earlier pre-rain green-up. Land-surface phenology plays an important regulating role in the global carbon, water, and nitrogen cycles (Richardson et al., 2013), and is frequently incorporated into Terrestrial Biosphere Models (TBMs), as a proxy for gross primary productivity (Bloom et al., 2016). In southern African woodlands particularly, a large body of scholarship has grown to investigate the pre-rain green-up phenomenon (Ryan et al., 2017; Adole et al., 2018). My findings suggest that variation in phenological strategy among tree species is one mechanism by which species diversity increases resilience to drought and maximises productivity in water-limited ecosystems (Stan & Sanchez-Azofeifa, 2019; Morellato et al., 2016). In southern African woodlands especially, where woody growth is highly seasonal and ecosystem structure is determined by disturbance, controls on land-surface phenology constitute a key ecosystem function. Patterns of growth determine which individuals are able to escape the “fire-trap” (Dantas & Pausas, 2013), with feedbacks between fire and woody growth determining whether a patch remains as open grassy savanna or woodland (Staver et al., 2011).

While pre-rain green-up has been explained by a multitude of climatic and now biodiversity variables, controls on senescence have not received as much attention (Gallinat et al., 2015). Previous studies have suggested that senescence is largely driven by date of green-up, suggesting that resource limitation limits the length of the growing season (Zani et al., 2020), while others have suggested the end of season signal is dominated by grasses which more closely follow rainfall patterns. In Chapter 4, I found that the proportion of larger trees in plots also caused delayed senescence, extending the growing season and ultimately increasing productivity. This is a novel result which demonstrates the effect of large trees and older woodland patches in providing a buffer to environmental factors, i.e. the decline of water availability towards the end of the growing season. This result is in contrast to previous studies in forests, which found that larger trees are at greater risk from drought due to an increased risk of embolism (Bennett et al., 2015). I suggest that in drought-adapted savannas with a distinct seasonal rainfall pattern, larger trees can access deep groundwater reserves, making them more resilient to oscillations in rainfall. In deciduous water-limited savannas, large trees could also provide resilience to longer-term drought, which is expected to become more prevalent as human-induced climate change progresses (Kusangaya et al., 2014).

The incorporation of biodiversity and biotic change into carbon cycle modelling has been limited (Ahlstrom et al., 2015; Bodegom et al., 2011). Large uncertainties in the effects of diversity on Gross Primary Productivity, and difficulties in measuring diversity over regional spatial scales has hampered attempts to include this data in large spatial scale models. The results presented in Chapter 4 provide a link by demonstrating a strong positive relationship between species diversity and cumulative EVI, which itself correlates with gross primary productivity (GPP) (Sjöström et al., 2011).

Canopy complexity

Previous work has linked canopy complexity to various ecosystem functions, such as increased productivity (Gough et al., 2019; Hardiman et al., 2011), increased resilience of productivity (Pretzsch, 2014), and recently a mechanistic link has been found between canopy complexity and solar-induced chlorophyll fluorescence triggered by photosynthesis (Regaieg et al., 2021). At local spatial scales, canopy complexity is highly variable, with much variation not accounted for in existing studies (Guan et al., 2014). In Chapter 5, I hypothesised that species diversity might explain some of this local scale variation. I found that tree species diversity in miombo woodlands correlated with increased canopy closure, taller canopies, and increased foliage density. Species diversity effects were weak, though this was not unexpected, as stochasticity in canopy structure caused by small spatial scale environmental heterogeneity, and landscape history, could have obscured biodiversity effects at this spatial scale. Indeed, at whole plot scales, biodiversity effects were stronger.

Unlike in Chapter 3, where tree size diversity was identified as a mechanism by which species diversity caused increases in woody biomass, in Chapter 5 tree size variation had negligible effects. Tree size variation only affected subplot canopy layer diversity. However, species diversity did still influence both tree size variation and canopy complexity separately. This suggests the presence of species-specific differences in the plasticity and physiological limits of crown shape that are independent of tree size. It also points to a genuine species diversity effect acting through structural diversity in these woodlands.

Species diversity was found to increase canopy complexity metrics related to foliage volume, i.e. canopy closure and foliage density, but decreased metrics related to spatial heterogeneity of foliage, i.e. canopy surface roughness and whole-canopy rugosity. I suggest that in the sparser canopies encountered in the sampled woodlands, variation in spatial heterogeneity was driven by empty space within the canopy, i.e 'between-canopy gaps', whereas in forests spatial heterogeneity is related more to 'within-canopy gaps' and overall foliage density. Therefore, as species diversity increased in savanna-woodlands, canopy density also increased, reducing the proportion of empty space in the canopy, thus reducing these measures of heterogeneity. This finding therefore prompts discussion of the suitability of these metrics for estimating canopy complexity in savannas, and their ecological significance. Hardiman et al. (2011) assert that canopy rugosity, i.e. whole canopy heterogeneity in foliage density, drives Net Primary Productivity (NPP) by increasing light transmission through the canopy profile, and this is supported by earlier conceptual work (Horn, 1971). However, this previous work was conducted in forests, with a denser and more closed canopy. In savannas, where light penetration is less of a limiting factor to tree growth (Frost, 1996), foliage heterogeneity may not exert such an effect on productivity.

Structural diversity

Large trees drive land-surface phenology (Chapter 4), and hold disproportionate biomass (Chapter 7). Large sized trees are frequently identified in other studies as contributing disproportionately to ecosystem function, and resilience of function (Ali & Wang, 2021). In Chapter 3, I found that structural diversity, i.e. variance in stem diameter and tree height, led to greater AGB, and provided an indirect pathway for the effect of species diversity on AGB (Ali et al., 2016; Pedro et al., 2017). In Chapter 5, I found no evidence that structural diversity influenced canopy complexity. I did however, find that species diversity influenced both tree size diversity and canopy complexity separately, suggesting that foliage volume is partially independent of tree size. This result highlights variation among species in their average physiognomy that is independent of their size, and reinforces the conclusion that structural diversity is a key mechanism in southern African woodlands by which species diversity drives ecosystem function. This result supports seminal work describing southern African woodlands which described them as harbouring great variety of tree functional forms with low functional redundancy, despite their low species diversity compared to other wooded ecosystems (Solbrig et al., 1996). Taken further, this finding could imply that biodiversity loss in these woodlands could have greater negative effects on ecosystem function than in more diverse ecosystems, due to their low functional redundancy.

In Chapter 5, I considered not only the diversity of species, but also their spatial arrangement within the plot. It was hypothesised that greater spatial mingling of species would lead to greater canopy closure, under the assumption that a diversity of functional forms in the local neighbourhood would reduce competition and increase foliage density. In practice however, the opposite was found, where increased spatial mingling was associated with lower canopy closure and shorter canopy height. I interpreted that this result occurred due to the covariation of both canopy closure and spatial mingling with disturbance. Disturbance by fire is expected to promote conspecific spatial clustering, and simultaneously reduce canopy closure (Martens et al., 2000). This result highlights the complexity of savanna ecosystem processes compared to forests in temperate and wet tropical regions, and the inter-dependence of diversity, environment, and disturbance, with feedback effects which can lead to non-intuitive outcomes in vegetation dynamics. Theory developed in competition dominated wooded ecosystems cannot be naively applied to savannas without considering the role of disturbance.

9.1.4 Regional variation in woodland structure and tree diversity across the miombo ecoregion

Biodiversity is defined most frequently in studies of the biodiversity-ecosystem function relationship in terms of the variety of organisms which co-inhabit a given ecosystem, i.e. alpha diversity. Variation in species composition over space, i.e. beta diversity, constitutes another perspective on biodiversity that was investigated in this thesis. All four investigative chapters presented in this thesis included a 'vegetation type' element in their statistical analyses in order to describe variation in ecosystem function among plots that was not due to variation in the diversity of organisms found within plots, but due to the particular identity of the species combinations found therein (Grime, 1998). Distinct vegetation formations are easily distinguishable in southern African woodlands, with visible differences in structure and function driven by functional differences between their dominant tree species (Solbrig et al., 1996). Distinct vegetation types arise as a result of climatic variation, disturbance history, and biogeography (Fayolle et al., 2018). I found that southern African woodland vegetation types differed in their aboveground biomass (Chapter 3), growing season phenological patterns (Chapter 4), and markedly in their canopy structure (Chapter 5). They also differed in the strength of observed biodiversity effects.

In general, miombo woodlands tended to have stronger biodiversity effects than mopane, ex-Acacia and *Baikiaea* woodland types. Miombo woodlands were found to contain more tree species than other vegetation types, and generally existed in less environmentally stressful areas. Mensah et al. (2020) found that woodlands and forests in West Africa had positive tree species richness effects, while in sparse savannas richness effects were negligible. Miombo woodlands are frequently misclassified as forest by vegetation maps and remote-sensing studies, as they often possess a contiguous but sparse canopy (Solbrig et al., 1996). Possibly the tree communities in the miombo woodlands encountered in this thesis are structured more similar to forests than to arid savannas with a non-contiguous canopy. While resource limitation does appear to strongly moderate biodiversity effects, disturbance by fire, which is common across miombo woodlands and other savanna types in southern Africa (Saito et al., 2014), does not appear to have the same weakening effects on the biodiversity-ecosystem function relationship. Possibly this is because miombo tree species are highly adapted to deal with fire (Dantas & Pausas, 2013).

The plots used in the thesis include the major savanna-woodland vegetation types in southern Africa (White, 1983), notably multiple forms of miombo, *Baikiaea* woodlands, mopane woodlands, and ex-Acacia woodlands. Arid savannas, which are found at the southern and north-eastern limits of the miombo ecoregion, were not considered in the thesis. In Chapter 3 it was demonstrated that water availability remained a key driving force behind the detection of biodiversity effects. Similarly in Chapter 5 the drier ex-Acacia savannas did not show positive biodiversity effects on canopy complexity. I suggest that in severely water-limited savannas, biodiversity effects driven by niche complementarity may be negligible. However, facilitation effects may be more important in these systems than could be detected in this thesis. Ratcliffe et al. (2017), working in dry Mediterranean forests, found that the strength of the effect of tree species richness on many ecosystem functions increased as water availability decreased.

In Chapter 5, I discussed how ex-Acacia species develop sparser canopies, with shorter stature and wider crowns. This condition reduces canopy complexity and prevents the formation of a vertically stratified complex canopy. This means that acacia savannas may be less likely to close their canopy than miombo woodlands, for instance. This could be conflated with environment however, as Acacia savannas occur most often in water-limited and heavily grazed habitats, where complex canopies are less likely to form anyway (Archibald & Bond, 2003).

In Chapter 7, I found that woodlands at the western edge of the miombo are floristically distinct from those in the east. Core ‘miombo’ species are generally shared by sites across the region, while the floristic variation arises mainly from smaller understorey species that inhabit disturbed areas. In Chapter 5 and Chapter 7, I showed how even with similar species composition, woodland structure differs among miombo woodlands in different parts of the miombo ecoregion. Woodlands in Tanzania had taller canopies and wider spreading crowns than those in Angola. These differences are likely due to climate.

Woodlands encountered in Tanzania were warmer and wetter than those in southwest Angola. Miombo woodlands studied in southwest Angola are possibly closer to the edge of their bioclimatic envelope, explaining the shorter and less full canopies (Scholes et al., 2002). These woodlands may therefore be at greater risk from the effects of climate change, which is predicted to cause reductions in precipitation across southern Africa over the coming century (Kusangaya et al., 2014).

9.2 Limitations and directions for future research

While hundreds of experimental studies of the biodiversity-ecosystem function relationship have been conducted, most of these have used mesocosms or grass patches as the unit of study. Few have experimentally manipulated the diversity of organisms as large as trees (Huang et al., 2018; Ewers et al., 2011), and none have done this in dry tropical woodlands or savannas. The current trend is to conduct BEFR studies in real-world ecosystems, in order to test theory established in experimental settings (Plas, 2019). One key limitation of these real-world studies, and of the studies conducted in this thesis, is that they are ultimately correlative. While variation in environment, species composition, and disturbance were accounted for in statistical analyses, there is still the potential for third variable effects and even reverse causation, where ecosystem function may actually influence biodiversity (Eisenhauer et al., 2016). With the proliferation of plot-based studies in southern African woodlands (SEOSAW, 2020), a valuable exercise would be scaling up previous experiments to whole woodland plots, and manipulating their species diversity over the course of multiple growing seasons to track changes in ecosystem functions related to ecosystem productivity, canopy complexity, and phenology. Such an experimental study would add further clarification and potentially support the findings of this thesis.

This thesis focussed on the biodiversity of trees, and on ecosystem functions related to trees. Southern African woodlands however, are characterised by the coexistence of trees and herbaceous understorey vegetation, notably C_4 grasses. Grasses in savannas have been estimated to account for between 40% (Whitley et al., 2011) and 59% (Lloyd et al., 2008) of total GPP, and provide other ecosystem functions not performed by other functional groups (Soliveres et al., 2016). While positive biodiversity effects were observed for ecosystem functions related to tree cover, productivity, and woody biomass, other important ecosystem functions not related to trees were ignored, such as grass biomass, soil nutrient retention, and wildlife fodder provision. In Chapter 5, I concluded that in miombo woodlands, greater tree species diversity could accelerate woody thickening and potentially woody encroachment, which would increase values of various ecosystem functions related to tree growth. The vast majority of studies of the biodiversity-ecosystem function relationship in wooded ecosystems focus on ecosystem functions related to primary productivity, biomass, and carbon fixation, presumably because these are interpreted as globally important (Grace, 2004), but possibly also because they are straightforward to quantify. Previous studies have suggested that when multiple functions are considered, that the positive effect of biodiversity increases (Hector & Bagchi, 2007), but few studies have considered combinations of ecosystem functions generated by different functional groups of species, i.e. trees and grasses (Hooper et al., 2005). While tree species diversity appears to promote ecosystem functions related to tree cover and woody biomass in southern African woodlands, it could decrease ecosystem functions dominated by the non-tree portion of the biota, such as soil water retention and soil carbon retention (Oliveira et al., 2005).

As well as altering ecosystem function, by reducing grass growth and understorey plant production, greater woody biomass and tree cover could reduce overall biodiversity by excluding herbaceous species and the many animal species that rely upon them (Ratajczak et al., 2012; Grellier et al., 2013). It is a frequent adage among savanna scientists that the majority of biodiversity in savannas lies in the herbaceous layer (Veldman et al., 2015). If the goal is to maintain and improve biodiversity in savannas, irrespective of functional group or trophic level, perhaps tree cover should be kept at an intermediate level to prevent exclusion of herbaceous species. If the goal is to sequester carbon however, perhaps tree biodiversity should be a greater concern.

Now that a broad corpus of literature exists which demonstrates positive biodiversity effects in a variety of ecological contexts, I suggest that future studies work to more fully understand the functional contribution of different species, and optimal combinations of species which maximise multiple facets of ecosystem function. Chapter 5 of this thesis was particularly enlightening as I was able to investigate the effects of specific species combinations on canopy complexity. I concluded that species from the Detarioideae subfamily, i.e. the dominant miombo canopy tree species, had a greater effect on canopy complexity than other species. Similarly, in Chapter 4, I found that Detarioideae miombo species dominated the phenological signal, particularly during the green-up and senescence phases. Variation in growth strategy and trait values among species affects their contribution to ecosystem function, aligning somewhat with Grime's Mass Ratio Hypothesis (Grime, 1998), which suggests that it is not the breadth of filled niche space that determines ecosystem function, but the ability of the most abundant species to optimise ecosystem function. Indeed, there is no logical reason why the species should contribute equally to a given ecosystem function, and it is sensible to predict that species maximise different ecosystem functions, depending on their life history strategy (Bengtsson, 1998). This is not to diminish the role of species richness in driving ecosystem function, as niche complementarity may still operate under this framework.

Even with the 1 ha plot size used in Chapter 5, there was still a great deal of stochasticity in canopy complexity and stand structure among plots, which made it difficult to unequivocally attribute diversity effects to canopy complexity metrics. In Chapter 7, similarly there was a lot of stochastic variation in stem density within plots, which led to wide variation in reported AGB. Spatial clustering of trees and the self-reinforcing effects of disturbance by fire and herbivory in mesic savannas produces a patchwork mosaic of open grassy patches and woodland patches (Staver et al., 2011; Schertzer et al., 2015). Plot-based studies can fail to capture this spatial variation in ecosystem structure and result in biased estimates of landscape-scale ecosystem properties such as AGB. I suggest that future studies in the region move towards fewer, larger plots with a concentration of measurement types in one area, rather than many smaller and less provisioned plots (Kreyling et al., 2018). Indeed, this approach is already being pioneered by the ForestGEO project, which includes some 50 ha plots (Davies et al., 2021). The emergence of supersites in other regions of the world shows that this method of data collection is becoming more popular (Schepaschenko et al., 2019), but as yet there are no sites in the miombo ecoregion which would qualify for supersite status by the major supersite networks. In Chapter 8 I proposed that the plots set up as part of this thesis would be suitable candidates for supersite status, and I hope that in the coming years the profile of this understudied region of southern Africa is elevated to match that of the longer-running plot sites in Mozambique (Ryan et al., 2011) and Tanzania (McNicol et al., 2018).

9.3 Concluding remarks

In this thesis I demonstrated the role of tree species diversity as a determinant of ecosystem structure and function in southern African woodlands. This thesis has provided nuance on the vegetation dynamics of this understudied biome. It has also contributed valuable case studies to the already broad corpus of biodiversity-ecosystem function research, testing theory developed in temperate and wet tropical systems in a highly disturbed and resource-limited system. In doing so, I have demonstrated the limits of biodiversity effects, and raised questions about the generality of the frequently reported biodiversity-ecosystem function relationship. I suggest that future work continues to focus on ecological mechanisms driving observed biodiversity effects, and broadens the scope of studies to include multiple functional groups of organisms along with environmental effects, to account for their inter-connected nature. I hope that future studies can leverage the current explosion in plot-based ecological monitoring data and novel data collection techniques employing state of the art technology to delve deeper into this pertinent field of study, which sits at the heart of community ecology, conservation, and earth system modelling.

References

Adole, T., J. Dash & P. M. Atkinson (2018). 'Large-scale prerain vegetation green-up across Africa'. In: *Global Change Biology* 24.9, pp. 4054–4068. DOI: `10.1111/gcb.14310`.

Ahlstrom, A., M. R. Raupach, G. Schurgers, B. Smith, A. Arneth, M. Jung, M. Reichstein, J. G. Canadell, P. Friedlingstein, A. K. Jain et al. (2015). 'The dominant role of semi-arid ecosystems in the trend and variability of the land CO2 sink'. In: *Science* 348.6237, pp. 895–899. DOI: `10.1126/science.aaa1668`.

Ali, A., E. Yan, H. Chen, S. X. Chang, Y. Zhao, X. Yang & M. Xu (2016). 'Stand structural diversity rather than species diversity enhances aboveground carbon storage in secondary subtropical forests in Eastern China'. In: *Biogeosciences* 13, pp. 4627–4635. DOI: `10.5194/bg-13-4627-2016`.

Ali, A. & L.-Q. Wang (2021). 'Big-sized trees and forest functioning: Current knowledge and future perspectives'. In: *Ecological Indicators* 127, p. 107760. DOI: `10.1016/j.ecolind.2021.107760`.

Archibald, S. & W. J. Bond (2003). 'Growing tall vs growing wide: tree architecture and allometry of Acacia karroo in forest, savanna, and arid environments'. In: *Oikos* 102.1, pp. 3–14. DOI: `10.1034/j.1600-0706.2003.12181.x`.

Arino, O., J. J. Ramos Perez, V. Kalogirou, S. Bontemps, P. Defourny & E. Van Bogaert (2012). *Global Land Cover Map for 2009 (GlobCover 2009)*. PANGAEA. DOI: `10.1594/PANGAEA.787668`. (Visited on 30/05/2021).

Barry, K. E., L. Mommer, J. van Ruijven, C. Wirth, A. J. Wright, Y. Bai, J. Connolly, G. B. De 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`.

Bengtsson, J. (1998). 'Which species? What kind of diversity? Which ecosystem function? Some problems in studies of relations between biodiversity and ecosystem function'. In: *Applied Soil Ecology* 10.3, pp. 191–199. DOI: `10.1016/s0929-1393(98)00120-6`.

Bennett, A. C., N. G. McDowell, C. D. Allen & K. J. Anderson-Teixeira (2015). 'Larger trees suffer most during drought in forests worldwide'. In: *Nature Plants* 1.10. DOI: `10.1038/nplants.2015.139`.

Biggs, R., H. Simons, M. Bakkenes, R. J. Scholes, B. Eickhout, D. van Vuuren & R. Alkemade (2008). 'Scenarios of biodiversity loss in southern Africa in the 21st century'. In: *Global Environmental Change* 18.2, pp. 296–309. DOI: `10.1016/j.gloenvcha.2008.02.001`.

Bloom, A. A., J. Exbrayat, I. R. van der Velde, L. Feng & M. Williams (2016). 'The decadal state of the terrestrial carbon cycle: Global retrievals of terrestrial carbon allocation, pools, and residence times'. In: *Proceedings of the National Academy of Sciences* 113.5, pp. 1285–1290. DOI: `10.1073/pnas.1515160113`.

Bodegom, P. M. V., J. C. Douma, J. P. M. Witte, J. C. Ordoñez, R. P. Bartholomeus & R. Aerts (2011). 'Going beyond limitations of plant functional types when predicting global ecosystem-atmosphere fluxes: exploring the merits of traits-based approaches'. In: *Global Ecology and Biogeography* 21.6, pp. 625–636. DOI: `10.1111/j.1466-8238.2011.00717.x`.

Bonan, G. B., S. Levis, L. Kergoat & K. W. Oleson (2002). 'Landscapes as patches of plant functional types: An integrating concept for climate and ecosystem models'. In: *Global Biogeochemical Cycles* 16.2, pp. 5–1–5–23. DOI: `10.1029/2000gb001360`.

Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, C. Jouseau, M. W. Cadotte, I. T. Carroll, J. J. Weis et al. (2009). 'Effects of biodiversity on the functioning of ecosystems: a summary of 164 experimental manipulations of species richness'. In: *Ecology* 90.3, pp. 854–854. DOI: `10.1890/08-1584.1`.

Chalcraft, D. R., J. W. Williams, M. D. Smith & M. R. Willig (2004). 'Scale dependence in the species-richness-productivity relationship: the role of species turnover'. In: *Ecology* 85.10, pp. 2701–2708. DOI: `10.1890/03-0561`.

Clarke, D. A., P. H. York, M. A. Rasheed & T. D. Northfield (2017). ‘Does biodiversity-ecosystem function literature neglect tropical ecosystems’. In: *Trends in Ecology & Evolution* 32.5, pp. 320–323. DOI: `10.1016/j.tree.2017.02.012`.

Dantas, V. L. & J. G. Pausas (2013). ‘The lanky and the corky: fire-escape strategies in savanna woody species’. In: *Journal of Ecology* 101.5. Ed. by P. Bellingham, pp. 1265–1272. DOI: `10.1111/1365-2745.12118`.

Davies, S. J., I. Abiem, K. A. Salim, S. Aguilar, D. Allen, A. Alonso, K. Anderson-Teixeira, A. Andrade, G. Arellano, P. S. Ashton et al. (2021). ‘ForestGEO: Understanding forest diversity and dynamics through a global observatory network’. In: *Biological Conservation* 253, p. 108907. DOI: `10.1016/j.biocon.2020.108907`.

Eisenhauer, N., A. D. Barnes, S. Cesarz, D. Craven, O. Ferlian, F. Gottschall, J. Hines, A. Sendek, J. Siebert, M. P. Thakur et al. (2016). ‘Biodiversity-ecosystem function experiments reveal the mechanisms underlying the consequences of biodiversity change in real world ecosystems’. In: *Journal of Vegetation Science* 27.5. Ed. by M. Palmer, pp. 1061–1070. DOI: `10.1111/jvs.12435`.

Ewers, R. M., R. K. Didham, L. Fahrig, G. Ferraz, A. Hector, R. D. Holt, V. Kapos, G. Reynolds, W. Sinun, J. L. Snaddon et al. (2011). ‘A large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems Project’. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 366.1582, pp. 3292–3302. DOI: `10.1098/rstb.2011.0049`.

Fayolle, A., M. D. Swaine, J. Aleman, A. F. Azihou, D. Bauman, M. te Beest, E. N. Chidumayo, J. P. G. M. Cromsigt, H. Dessard, M. Finkch et al. (2018). ‘A sharp floristic discontinuity revealed by the biogeographic regionalization of African savannas’. In: *Journal of Biogeography* 46, pp. 1–12. DOI: `10.1111/jbi.13475`.

Fisher, J. B., D. N. Huntzinger, C. R. Schwalm & S. Sitch (2014). ‘Modeling the Terrestrial Biosphere’. In: *Annual Review of Environment and Resources* 39.1, pp. 91–123. DOI: `10.1146/annurev-environ-012913-093456`.

Frost, P. (1996). ‘The ecology of miombo woodlands’. In: *The miombo in transition: woodlands and welfare in Africa*. Ed. by B. M. Campbell. Bogor, Indonesia: Center for International Forestry Research, pp. 11–55.

Gallinat, A. S., R. B. Primack & D. L. Wagner (2015). ‘Autumn, the neglected season in climate change research’. In: *Trends in Ecology & Evolution* 30.3, pp. 169–176. DOI: `10.1016/j.tree.2015.01.004`.

Gough, C. M., J. W. Atkins, R. T. Fahey & B. S. Hardiman (2019). ‘High rates of primary production in structurally complex forests’. In: *Ecology* 100.10. DOI: `10.1002/ecy.2864`.

Grace, J. B., T. M. Anderson, E. W. Seabloom, E. T. Borer, P. B. Adler, W. S. Harpole, Y. Hautier, H. Hillebrand, E. M. Lind, M. Pärtel et al. (2016). ‘Integrative modelling reveals mechanisms linking productivity and plant species richness’. In: *Nature* 529.7586, pp. 390–393. DOI: `10.1038/nature16524`.

Grace, J. (2004). ‘Understanding and managing the global carbon cycle’. In: *Journal of Ecology* 92.2, pp. 189–202. DOI: `10.1111/j.0022-0477.2004.00874.x`.

Grace, J., J. S. Jose, P. Meir, H. S. Miranda & R. A. Montes (2006). ‘Productivity and carbon fluxes of tropical savannas’. In: *Journal of Biogeography* 33.3, pp. 387–400. DOI: `10.1111/j.1365-2699.2005.01448.x`.

Grellier, S., D. Ward, J.-L. Janeau, P. Podwojewski, S. Lorentz, L. Abbadie, C. Valentin & S. Barot (2013). ‘Positive versus negative environmental impacts of tree encroachment in South Africa’. In: *Acta Oecologica* 53, pp. 1–10. DOI: `10.1016/j.actao.2013.08.002`.

Grime, J. P. (1998). ‘Benefits of plant diversity to ecosystems: Immediate, filter and founder effects’. In: *Journal of Ecology* 86.6, pp. 902–910. DOI: `10.1046/j.1365-2745.1998.00306.x`.

Guan, K., E. F. Wood, D. Medvigy, J. Kimball, M. Pan, K. K. Caylor, J. Sheffield, C. Xu & M. O. Jones (2014). ‘Terrestrial hydrological controls on land surface phenology of African savannas and woodlands’. In: *Journal of Geophysical Research: Biogeosciences* 119.8, pp. 1652–1669. DOI: `10.1002/2013jg002572`.

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`.

Hector, A. & R. Bagchi (2007). 'Biodiversity and ecosystem multifunctionality'. In: *Nature* 448.7150, pp. 188–190. DOI: `10.1038/nature05947`.

Hill, M. J. & N. P. Hanan, eds. (2011). *Ecosystem function in savannas*. Boca Raton FL, USA: CRC Press. DOI: `10.1201/b10275`.

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`.

Holdo, R. M. (2006). 'Tree growth in an African woodland savanna affected by disturbance'. In: *Journal of Vegetation Science* 17.3, pp. 369–378. DOI: `10.1111/j.1654-1103.2006.tb02457.x`.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem et al. (2005). 'Effects of biodiversity on ecosystem functioning: a consensus of current knowledge'. In: *Ecological Monographs* 75.1, pp. 3–35. DOI: `10.1890/04-0922`.

Horn, H. S. (1971). *The adaptive geometry of trees*. Princeton NJ, USA: Princeton University Press. ISBN: 0691080895.

Huang, Y., Y. Chen, N. Castro-Izaguirre, M. Baruffol, M. Brezzi, A. Lang, Y. Li, W. Härdtle, G. von Oheimb, X. Yang et al. (2018). 'Impacts of species richness on productivity in a large-scale subtropical forest experiment'. In: *Science* 362.6410, pp. 80–83. DOI: `10.1126/science.aat6405`.

Huston, M. A. (2014). 'Disturbance, productivity, and species diversity: Empiricism vs. logic in ecological theory'. In: *Ecology* 95.9, pp. 2382–2396. DOI: `10.1890/13-1397.1`.

Isbell, F., P. B. Reich, D. Tilman, S. E. Hobbie, S. Polasky & S. Binder (2013). 'Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity'. In: *Proceedings of the National Academy of Sciences of the United States of America* 110.29, pp. 11911–6. DOI: `10.1073/pnas.1310880110`.

Kreyling, J., A. H. Schweiger, M. Bahn, P. Ineson, M. Migliavacca, T. Morel-Journel, J. R. Christiansen, N. Schtickzelle & K. S. Larsen (2018). 'To replicate, or not to replicate - that is the question: how to tackle nonlinear responses in ecological experiments'. In: *Ecology Letters* 21.11. Ed. by J. Chase, pp. 1629–1638. DOI: `10.1111/ele.13134`.

Krinner, G., N. Viovy, N. de Noblet-Ducoudré, J. Ogée, J. Polcher, P. Friedlingstein, P. Ciais, S. Sitch & I. C. Prentice (2005). 'A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system'. In: *Global Biogeochemical Cycles* 19.1. DOI: `10.1029/2003gb002199`.

Kusangaya, S., M. L. Warburton, E. A. van Garderen & G. P. W. Jewitt (2014). 'Impacts of climate change on water resources in southern Africa: A review'. In: *Physics and Chemistry of the Earth, Parts A/B/C* 67-69, pp. 47–54. DOI: `10.1016/j.pce.2013.09.014`.

Liang, J., T. W. Crowther, N. Picard, S. Wiser, M. Zhou, G. Alberti, E.-D. Schulze, A. D. McGuire, F. Bozzato, H. Pretzsch et al. (2016). 'Positive biodiversity-productivity relationship predominant in global forests'. In: *Science* 354.6309, aaf8957–aaf8957. DOI: `10.1126/science.aaf8957`.

Lloyd, J., M. I. Bird, L. Vellen, A. C. Miranda, E. M. Veenendaal, G. Djagbletey, H. S. Miranda, G. Cook & G. D. Farquhar (2008). 'Contributions of woody and herbaceous vegetation to tropical savanna ecosystem productivity: a quasi-global estimate'. In: *Tree Physiology* 28.3, pp. 451–468. DOI: `10.1093/treephys/28.3.451`.

Maestre, F. T., J. L. Quero, N. J. Gotelli, A. Escudero, V. Ochoa, M. Delgado-Baquerizo, M. Garcia-Gomez, M. A. Bowker, S. Soliveres, C. Escolar et al. (2012). 'Plant Species Richness and Ecosystem Multifunctionality in Global Drylands'. In: *Science* 335.6065, pp. 214–218. DOI: `10.1126/science.1215442`.

Manning, P., J. Loos, A. D. Barnes, P. Batáry, F. J. J. A. Bianchi, N. Buchmann, G. B. D. Deyn, A. Ebeling, N. Eisenhauer, M. Fischer et al. (2019). ‘Transferring biodiversity-ecosystem function research to the management of ‘real-world’ ecosystems’. In: *Advances in Ecological Research*, pp. 323–356. DOI: `10.1016/bs.aecr.2019.06.009`.

Martens, S. N., D. D. Breshears & C. W. Meyer (2000). ‘Spatial distributions of understory light along the grassland/forest continuum: effects of cover, height, and spatial pattern of tree canopies’. In: *Ecological Modelling* 126.1, pp. 79–93. DOI: `10.1016/s0304-3800(99)00188-x`.

McNicol, I. M., C. M. Ryan, K. G. Dexter, S. M. J. Ball & M. Williams (2018). ‘Aboveground carbon storage and its links to stand structure, tree diversity and floristic composition in south-eastern Tanzania’. In: *Ecosystems* 21, pp. 740–754. DOI: `10.1007/s10021-017-0180-6`.

Mensah, S., V. K. Salako & T. Seifert (2020). ‘Structural complexity and large-sized trees explain shifting species richness and carbon relationship across vegetation types’. In: *Functional Ecology* 34.8, pp. 1731–1745. DOI: `10.1111/1365-2435.13585`.

Morellato, L. P. C., B. Alberton, S. T. Alvarado, B. Borges, E. Buisson, M. G. G. Camargo, L. F. Cancian, D. W. Carstensen, D. F. E. Escobar, P. T. P. Leite et al. (2016). ‘Linking plant phenology to conservation biology’. In: *Biological Conservation* 195, pp. 60–72. DOI: `10.1016/j.biocon.2015.12.033`.

Mori, A. S., T. Furukawa & T. Sasaki (2012). ‘Response diversity determines the resilience of ecosystems to environmental change’. In: *Biological Reviews* 88.2, pp. 349–364. DOI: `10.1111/brv.12004`.

Morozov, A. & B.-L. Li (2008). ‘Abundance patterns in multi-species communities exposed to habitat destruction’. In: *Journal of Theoretical Biology* 251.4, pp. 593–605. DOI: `10.1016/j.jtbi.2008.01.011`.

Oliveira, R. S., L. Bezerra, E. A. Davidson, F. Pinto, C. A. Klink, D. C. Nepstad & A. Moreira (2005). ‘Deep root function in soil water dynamics in cerrado savannas of central Brazil’. In: *Functional Ecology* 19.4, pp. 574–581. DOI: `10.1111/j.1365-2435.2005.01003.x`.

Osborne, C. P., T. Charles-Dominique, N. Stevens, W. J. Bond, G. Midgley & C. E. R. Lehmann (2018). ‘Human impacts in African savannas are mediated by plant functional traits’. In: *New Phytologist* 220.1, pp. 10–24. DOI: `10.1111/nph.15236`.

Peaucelle, M., C. Bacour, P. Ciais, N. Vuichard, S. Kuppel, J. Peñuelas, L. B. Marchesini, P. D. Blanken, N. Buchmann, J. Chen et al. (2019). ‘Covariations between plant functional traits emerge from constraining parameterization of a terrestrial biosphere model’. In: *Global Ecology and Biogeography* 28.9. Ed. by J. Lenoir, pp. 1351–1365. DOI: `10.1111/geb.12937`.

Pedro, M. S., W. Rammer & R. Seidl (2017). ‘Disentangling the effects of compositional and structural diversity on forest productivity’. In: *Journal of Vegetation Science* 28, pp. 649–658. DOI: `10.1111/jvs.12505`.

Pelletier, J., A. Paquette, K. Mbindo, N. Zimba, A. Siampale, B. Chendauka, F. Siangulube & J. W. Roberts (2018). ‘Carbon sink despite large deforestation in African tropical dry forests (miombo woodlands)’. In: *Environmental Research Letters* 13, p. 094017. DOI: `10.1088/1748-9326/aadc9a`.

Plas, F. van der (2019). ‘Biodiversity and ecosystem functioning in naturally assembled communities’. In: *Biological Reviews* 94, pp. 1220–1245. DOI: `10.1111/brv.12499`.

Poorter, L., M. T. van der Sande, E. J. M. M. Arets, N. Ascarrunz, B. J. Enquist, B. Finegan, J. C. Licona, M. Martínez-Ramos, L. Mazzei, J. A. Meave et al. (2017). ‘Biodiversity and climate determine the functioning of neotropical forests’. In: *Global Ecology and Biogeography* 26, pp. 1423–1434. DOI: `10.1111/geb.12668`.

Poorter, L., M. T. van der Sande, J. Thompson, E. J. M. M. Arets, A. Alarcòn, J. àlvarez-Sànchez, N. Ascarrunz, P. Balvanera, G. Barajas-Guzmàn, A. Boit et al. (2015). ‘Diversity enhances carbon storage in tropical forests’. In: *Global Ecology and Biogeography* 24, pp. 1314–1328. DOI: `10.1111/geb.12364`.

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: `10.1016/j.foreco.2014.04.027`.

Ratajczak, Z., J. B. Nippert & S. L. Collins (2012). ‘Woody encroachment decreases diversity across North American grasslands and savannas’. In: *Ecology* 93.4, pp. 697–703. DOI: `10.1890/11-1199.1`.

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: `10.1111/ele.12849`.

Regaieg, O., T. Yin, Z. Malenovský, B. D. Cook, D. C. Morton & J.-P. Gastellu-Etchegorry (2021). ‘Assessing impacts of canopy 3D structure on chlorophyll fluorescence radiance and radiative budget of deciduous forest stands using DART’. In: *Remote Sensing of Environment* 265, p. 112673. DOI: `10.1016/j.rse.2021.112673`.

Richardson, A. D., T. F. Keenan, M. Migliavacca, Y. Ryu, O. Sonnentag & M. Toomey (2013). ‘Climate change, phenology, and phenological control of vegetation feedbacks to the climate system’. In: *Agricultural and Forest Meteorology* 169, pp. 156–173. DOI: `10.1016/j.agrformet.2012.09.012`.

Ryan, C. M., M. Williams & J. Grace (2011). ‘Above- and belowground carbon stocks in a miombo woodland landscape of Mozambique’. In: *Biotropica* 43.4, pp. 423–432. DOI: `10.1111/j.1744-7429.2010.00713.x`.

Ryan, C. M., M. Williams, J. Grace, E. Woollen & C. E. R. Lehmann (2017). ‘Pre-rain green-up is ubiquitous across southern tropical Africa: implications for temporal niche separation and model representation’. In: *New Phytologist* 213.2, pp. 625–633. DOI: `10.1111/nph.14262`.

Ryan, C. M., R. Pritchard, I. McNicol, M. Owen, J. A. Fisher & C. Lehmann (2016). ‘Ecosystem services from southern African woodlands and their future under global change’. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 371.1703, p. 20150312. DOI: `10.1098/rstb.2015.0312`.

Saito, M., S. Luyssaert, B. Poulter, M. Williams, P. Ciais, V. Bellassen, C. M. Ryan, C. Yue, P. Cadule & P. Peylin (2014). ‘Fire regimes and variability in aboveground woody biomass in miombo woodland’. In: *Journal of Geophysical Research: Biogeosciences* 119.5, pp. 1014–1029. DOI: `10.1002/2013jg002505`.

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: `10.1038/nature04070`.

Schepaschenko, D., J. Chave, O. L. Phillips, S. L. Lewis, S. J. Davies, M. Réjou-Méchain, P. Sist, K. Scipal, C. Perger, B. Herault et al. (2019). ‘The Forest Observation System, building a global reference dataset for remote sensing of forest biomass’. In: *Scientific Data* 6.1. DOI: `10.1038/s41597-019-0196-1`.

Schertzer, E., A. C. Staver & S. A. Levin (2015). ‘Implications of the spatial dynamics of fire spread for the bistability of savanna and forest’. In: *Journal of Mathematical Biology* 70.1-2, pp. 329–341. DOI: `10.1007/s00285-014-0757-z`.

Scholes, R. J. & S. R. Archer (1997). ‘Tree grass interactions in savannas’. In: *Annual Review of Ecology and Systematics* 28.1, pp. 517–544. DOI: `10.1146/annurev.ecolsys.28.1.517`.

Scholes, R. J., P. R. Dowty, K. Caylor, D. A. B. Parsons, P. G. H. Frost & H. H. Shugart (2002). ‘Trends in savanna structure and composition along an aridity gradient in the Kalahari’. In: *Journal of Vegetation Science* 13.3, pp. 419–428. DOI: `10.1111/j.1654-1103.2002.tb02066.x`.

SEOSAW (2020). ‘A network to understand the changing socio-ecology of the southern African woodlands (SEOSAW): Challenges, benefits, and methods’. In: *Plants, People, Planet*. DOI: `10.1002/ppp3.10168`.

Sheil, D. (2001). ‘Long-term observations of rain forest succession, tree diversity and responses to disturbance’. In: *Plant Ecology* 155.2, pp. 183–199. DOI: `10.1023/a:1013243411819`.

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`.

Sitoe, A., E. Chidumayo & M. Alberto (2010). 'Timber and wood products'. In: *The dry forests and woodlands of Africa: Managing for products and services*. Ed. by E. N. Chidumayo & D. J. Gumbo. London, UK: Earthscan, pp. 131–154.

Sjöström, M., J. Ardö, A. Arneth, N. Boulain, B. Cappelaere, L. Eklundh, A. de Grandcourt, W. L. Kutsch, L. Merbold & Y. Nouvellon (2011). 'Exploring the potential of MODIS EVI for modeling gross primary production across African ecosystems'. In: *Remote Sensing of Environment* 115.4, pp. 1081–1089. DOI: `10.1016/j.rse.2010.12.013`.

Solbrig, O. T., E. Medina & J. F. Silva (1996). *Biodiversity and Savanna Ecosystem Processes*. Berlin, Germany: Springer-Verlag.

Soliveres, S., P. Manning, D. Prati, M. M. Gossner, F. Alt, H. Arndt, V. Baumgartner, J. Binkenstein, K. Birkhofer, S. Blaser et al. (2016). 'Locally rare species influence grassland ecosystem multifunctionality'. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 371.1694, p. 20150269. DOI: `10.1098/rstb.2015.0269`.

Stan, K. & A. Sanchez-Azofeifa (2019). 'Tropical dry forest diversity, climatic response, and resilience in a changing climate'. In: *Forests* 10.5, p. 443. DOI: `10.3390/f10050443`.

Staver, A. C., S. Archibald & S. A. Levin (2011). 'The Global Extent and Determinants of Savanna and Forest as Alternative Biome States'. In: *Science* 334.6053, pp. 230–232. DOI: `10.1126/science.1210465`.

Staver, A. C., J. Botha & L. Hedin (2017). 'Soils and fire jointly determine vegetation structure in an African savanna'. In: *New Phytologist* 216.4, pp. 1151–1160. DOI: `10.1111/nph.14738`.

Thompson, P. L., S. Kéfi, Y. R. Zelnik, L. E. Dee, S. Wang, C. de Mazancourt, M. Loreau & A. Gonzalez (2021). 'Scaling up biodiversity-ecosystem functioning relationships: the role of environmental heterogeneity in space and time'. In: *Proceedings of the Royal Society B: Biological Sciences* 288.1946, p. 20202779. DOI: `10.1098/rspb.2020.2779`.

Tilman, D., F. Isbell & J. M. Cowles (2014). 'Biodiversity and ecosystem functioning'. In: *Annual Review of Ecology, Evolution, and Systematics* 45, pp. 471–493. DOI: `10.1146/annurev-ecolsys-120213-091917`.

Torello-Raventos, M., T. R. Feldpausch, E. Veenendaal, F. Schrodt, G. Saiz, T. F. Domingues, G. Djagbletey, A. Ford, J. Kemp, B. S. Marimon et al. (2013). 'On the delineation of tropical vegetation types with an emphasis on forest/savanna transitions'. In: *Plant Ecology and Diversity* 6.1, pp. 101–137. DOI: `10.1080/17550874.2012.762812`.

World Urbanization Prospects: The 2018 Revision (2018). New York NY, USA.

Ustin, S. L. & J. A. Gamon (2010). 'Remote sensing of plant functional types'. In: *New Phytologist* 186.4, pp. 795–816. DOI: `10.1111/j.1469-8137.2010.03284.x`.

Veldman, J. W., E. Buisson, G. Durigan, G. W. Fernandes, S. L. Stradic, G. Mahy, D. Negreiros, G. E. Overbeck, R. G. Veldman, N. P. Zaloumis et al. (2015). 'Toward an old-growth concept for grasslands, savannas, and woodlands'. In: *Frontiers in Ecology and the Environment* 13.3, pp. 154–162. DOI: `10.1890/140270`.

Wessels, K. J., M. S. Colgan, B. F. N. Erasmus, G. P. Asner, W. C. Twine, R. Mathieu, J. A. N. van Aardt, J. T. Fisher & I. P. J. Smit (2013). 'Unsustainable fuelwood extraction from South African savannas'. In: *Environmental Research Letters* 8.1, p. 014007. DOI: `10.1088/1748-9326/8/1/014007`.

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`.

Whitley, R. J., C. M. O. Macinnis-ng, L. B. Hutley, J. Beringer, M. Zeppel, M. Williams, D. Taylor & D. Eamus (2011). 'Is productivity of mesic savannas light limited or water limited? Results of a simulation study'. In: *Global Change Biology* 17.10, pp. 3130–3149. DOI: `10.1111/j.1365-2486.2011.02425.x`.

Williams, C. A., N. P. Hanan, J. C. Neff, R. J. Scholes, J. A. Berry, A. S. Denning & D. F. Baker (2007). 'Africa and the global carbon cycle'. In: *Carbon Balance and Management* 2.1. DOI: `10.1186/1750-0680-2-3`.

Williams, M., P. A. Schwarz, B. E. Law, J. Irvine & M. R. Kurpius (2005). 'An improved analysis of forest carbon dynamics using data assimilation'. In: *Global Change Biology* 11.1, pp. 89–105. DOI: `10.1111/j.1365-2486.2004.00891.x`.

Zani, D., T. W. Crowther, L. Mo, S. S. Renner & C. M. Zohner (2020). 'Increased growing-season productivity drives earlier autumn leaf senescence in temperate trees'. In: *Science* 370.6520, pp. 1066–1071. DOI: `10.1126/science.abd8911`.