

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
26th July 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 separation 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.

Studies of biodiversity-ecosystem function effects typically use species diversity as their chosen biodiversity measure, but this does little to help us understand the ecological mechanisms which produce positive biodiversity effects.

To further understand these mechanisms, 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 green-ness, to understand drivers of variation in pre-rain green-up, growing season length and productivity. I found that pre-rain green-up increased with species richness 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 size 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 a spatial scale the effects of species composition and diversity on canopy architecture and canopy cover. Species diversity was found to increase with spatial clumping of trees, which drove vertical canopy layer diversity and canopy height, demonstrating an indirect role of species diversity on canopy cover via structural diversity. 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.

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 greatly improve our 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.

Lay summary

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.

John L. Godlee
26th July 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 who helped me navigate the impenetrable Tanzanian bureaucracy, and for being a friend during the long days at the Slow Leopard as I waited for things to happen. For help during the fieldwork itself I thank Emanuel Mlimitho for his impressive work ethic and attention to detail, and to 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

Abstract	iii
Lay Summary	v
Author Declaration	vii
Acknowledgements	x
Table of Contents	xiv
List of Figures	xvii
List of Tables	xx
List of Abbreviations	xxi
1 Introduction	1
1.1 Overview	1
1.2 Thesis structure	2
1.2.1 Chapter 2: Background: The ecology of structure and function in southern African woodlands	3
1.2.2 Chapter 3: A regional assessment of the biodiversity-ecosystem function relationship in southern African woodlands	5
1.2.3 Chapter 4: Tree diversity and compositional effects on land-surface phenology in deciduous Zambian woodlands	5
1.2.4 Chapter 5: Canopy structural complexity as a mechanism for biodiversity effects on productivity	6
1.2.5 Chapter 6: Bicuar National Park: a woodland refugia at the extreme western extent of the miombo eco-region	6

1.2.6	Chapter 7: Synthesis: Biodiversity and ecosystem function in southern African woodlands	7
1.2.7	Chapter 8: Data legacy	7
1.3	Data sources and research sites	7
1.3.1	Existing datasets	8
1.3.2	New datasets	12
	References	18
2	Background: The ecology, biodiversity, structure, and function of southern African woodlands	23
2.1	Introduction	23
2.2	The ecology of savannas	24
2.2.1	Determinants of savanna vegetation	25
2.2.2	Adaptations of savanna trees	27
2.2.3	The global carbon cycle and change in savannas	31
2.3	Southern African woodlands	32
2.4	Biodiversity and ecosystem function theory	35
2.4.1	Niche complementarity, selection effects, and facilitation . .	38
2.4.2	Global distribution of biodiversity-ecosystem function re- search	39
2.4.3	Should we expect biodiversity effects on ecosystem function in southern African woodlands?	41
2.4.4	Demographic structure, structural diversity and ecosystem function	45
2.5	Conclusions	46
	References	47
3	Structural diversity and tree density drives variation in the biodiversity- ecosystem function relationship of woodlands and savannas	59
3.1	Introduction	2
3.2	Materials and Methods	5
3.2.1	Study location	5
3.2.2	Data collection	6
3.2.3	Data analysis	7
3.3	Results	13
3.3.1	Structural and species diversity models	15

3.3.2	Variation among vegetation types	15
3.3.3	Moderation of Diversity-AGB relationship by stem density	16
3.3.4	Environmental covariates and tree diversity	17
3.4	Discussion	19
3.4.1	Inter-related effects of tree species and structural diversity on AGB	20
3.4.2	Organismal density and disturbance	22
3.4.3	Effects of water availability and soil fertility	23
3.4.4	Vegetation type responses	24
3.5	Conclusions	26
	References	27
3.6	Supplementary Material	34
4	Diversity mediates land-surface phenology in Zambian deciduous woodlands	43
4.1	Introduction	2
4.2	Materials and methods	4
4.2.1	Plot data	4
4.2.2	Plot data analysis	7
4.2.3	Land-surface phenology data	8
4.2.4	Statistical modelling	9
4.3	Results	11
4.4	Discussion	14
4.5	Conclusion	20
	References	21
4.6	Supplementary Material	25
5	TLS chapter	33
6	Diversity and Structure of an Arid Woodland in Southwest An- gola, with Comparison to the Wider Miombo Ecoregion	35
6.1	Introduction	2
6.2	Materials and Methods	5
6.2.1	Study area	5
6.2.2	Plot data collection	7
6.2.3	Climatic data	8

6.2.4	Data analysis	9
6.3	Results	11
6.3.1	Alpha diversity	11
6.3.2	Beta diversity	13
6.3.3	Woodland structure	15
6.3.4	Effect of disturbance via shifting cultivation on diversity within Bicuar National Park	17
6.4	Discussion	18
6.4.1	Comparison of Bicuar National Park with other woodlands across the miombo ecoregion	18
6.4.2	Delineation of woodland types within Bicuar National Park	20
6.4.3	Comparison of disturbed and undisturbed woodland plots	22
6.5	Conclusion	24
	References	25
7	Discussion	29
8	Data legacy	31
8.1	Introduction	31
8.2	Permanent plots in Bicuar National Park	31
8.2.1	Bicuar National Park as a ‘Supersite’	33
8.3	Terrestrial LiDAR	37
8.3.1	Tree taper modelling from Terrestrial LiDAR	38
8.3.2	Biomass of large trees: testing scaling theory for estimating biomass	39
8.3.3	Effects of canopy structure on understorey light environ- ment and grass biomass	45
	References	47

List of Figures

1.1	Thesis structure and data usage	3
1.2	Map of thesis study locations	4
1.3	Map of SEOSAW plot locations	9
1.4	Distribution of SEOSAW plots in environmental space	10
1.5	Bicuar National Park climate time series	14
1.6	Bicuar National Park vegetation type photographs	15
1.7	Bicuar National Park land cover	16
2.1	Map of global savanna distribution	25
2.2	Precipitation vs. tree cover in southern Africa	28
2.3	Schematic diagram of savanna positive feedback mechanisms	29
2.4	Map of savanna vegetation types in Southern Africa	35
2.5	Inferences from previous Biodiversity-Ecosystem Function Research	37
2.6	Schematic diagrams demonstrating secondary controls on niche complementarity	40
2.7	Global distribution of Biodiversity-Ecosystem Function Relationship studies	42
3.1	Plot locations used in analysis, grouped by vegetation type	10
3.2	Conceptual model path diagram	11
3.3	Correlation matrix of observed variables used in analysis	14
3.4	Path diagram for vegetation type model	16
3.5	Path coefficients for vegetation type model	17
3.6	Effect of stems density on path coefficients	18
3.7	Path diagram of full Structural Equation Model	19
3.S1	Raw histograms of observed variables	33
3.S2	Histograms of transformed observed variables	33
3.S3	Bivariate scatter plots of observed variables	40

3.S4 Path coefficients for full Structural Equation Model	41
4.1 Map of study sites in Zambia	5
4.2 Schematic diagram of plot layout within a site	6
4.3 Annotated EVI time series	10
4.4 Mean EVI GAMs per vegetation type	13
4.5 Model slope coefficients for each phenological metric	14
4.6 Marginal effects of species diversity on each phenological metric per vegetation type	15
4.7 Density distribution of phenological metrics per vegetation type .	16
4.S1 Scatter plots comparing MOD13Q1 and MODIS VIPPHEN phenological measurements	25
4.S2 Bivariate comparison of phenological metrics	26
6.1 Location of study sites within the miombo ecoregion and within climate space	6
6.2 Location of plots within Bicuar National Park	9
6.3 Alpha diversity of plots within each site	13
6.4 NMDS ordination of species composition	16
6.5 Bar plots of stem diameter abundance within each site	17
6.6 NMDS ordination of undisturbed and disturbed plots in Bicuar National Park	19
6.7 Variation in diversity and woodland structure among disturbed and undisturbed plots	20
6.8 Stem diameter class variation among disturbed and undisturbed plots	21
8.1 Concrete corner posts in Bicuar National Park	34
8.2 Spatial distribution of plots in the SEOSAW network	35
8.3 Climatic distribution of plots in the SEOSAW network	36
8.4 GEDI satellite LiDAR tracks over Bicuar National Park	37
8.5 Stem cross section cylinder interpolation to estimate stem diameter from terrestrial LiDAR	40
8.6 Scatter plot of stem diameter and biomass from GlobAllomeTree database	41
8.7 Photographs of large old trees with idiosyncratic trunk physiognomy	42
8.8 Photograph of severely fluted tree stem	43

8.9	Example tomograph visualisation and trunk cross-section photo-graph	44
8.10	Grass biomass harvesting subplot layout	47

List of Tables

3.1	Description of vegetation types	9
3.2	Model fit statistics per vegetation type	15
3.S1	Soil C correlation fit statistics	34
3.S2	Soil CEC correlation fit statistics	35
3.S3	Soil N correlation fit statistics	35
3.S4	Fire frequency correlation fit statistics	36
3.S5	MAP correlation fit statistics	36
3.S6	Precipitation seasonality correlation fit statistics	37
3.S7	Temperature stress correlation fit statistics	37
3.S8	Soil sand content correlation fit statistics	38
3.S9	Species richness correlation fit statistics	38
3.S10	Shannon equitability correlation fit statistics	38
3.S11	Tree height variation correlation fit statistics	39
3.S12	DBH variation correlation fit statistics	39
3.S13	Stem density correlation fit statistics	39
4.1	Description of vegetation types	6
4.2	Model fit statistics	14
4.S1	Model fit statistics comparing MODIS VIPPHEN and MOD13Q1 phenological metrics	26
4.S2	Cumulative EVI model selection statistics	26
4.S3	Season length model selection statistics	27
4.S4	Green-up rate model selection statistics	27
4.S5	Senescence rate model selection statistics	28
4.S6	Green-up lag model selection statistics	28
4.S7	Senescence lag model selection statistics	29
4.S8	Comparisons of species diversity interaction marginal effects using post-hoc Tukey's tests	30

4.S9 Post-hoc Tukey's pairwise comparisons among vegetation types for each phenological metric	31
6.1 Description of sites	5
6.2 Bicuar National Park species list	12
6.3 ANOVA statistics among sites	14
6.4 Pairwise Sørensen coefficient of similarity among sites	15
6.5 ANOVA statistics among disturbed and undisturbed plots in Bicuar National Park	21

List of Abbreviations

BEFR	Biodiversity-Ecosystem Function Relationship
AGB	Above-Ground Biomass
AIC	Akaike Information Criterion
C	Carbon
DBH	Diameter at Breast Height (1.3 m)
DPM	Disc Pasture Meter
TLS	Terrestrial Laser Scanning/Scanner
SEM	Structural Equation Modelling
ISCED	Instituto de Ciências da Educação
NMDS	Non-metric Multi-Dimensional Scaling
LiDAR	Light Detection And Ranging
MAP	Mean Annual Precipitation
DSLR	Digital Single Lens Reflex
ENL	Effective Number of Layers
GPS	Global Positioning System
NDVI	Normalized Difference Vegetation Index
EVI	Enhanced Vegetation Index
PPK	Post-Processed Kinematic
SASSCAL	Southern African Science Centre for Climate Change and Adaptive Land Management
WDPA	World Database on Protected Areas

Chapter 1

Introduction

1.1 Overview

Woodland-savanna mosaics are the dominant vegetation type in southern Africa, covering ~2.275 million km² (Arino et al., 2010). Currently, these ecosystems represent the largest uncertainty in models of the terrestrial carbon cycle, 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 woodland-savanna 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 our 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?

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?*

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?*

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 3-6), 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). I also summarise the results arising from this thesis (Chapter 7), and discuss their implications for our understanding of both the ecology of southern African woodlands and biodiversity-ecosystem function research. Finally, I also present a short chapter which provides further detail on the extended legacy of the data collected during this thesis (Chapter 8).

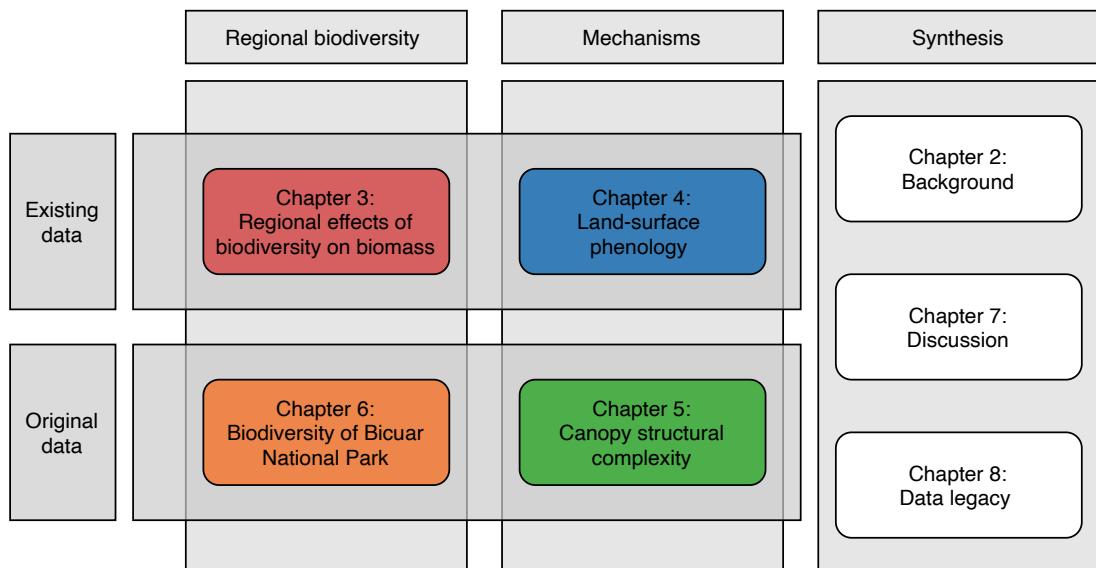


Figure 1.1: The structure of this thesis, showing the thematic focus and data usage in each chapter. Coloured boxes refer to similar colours in Figure 1.2, which shows the spatial scales of each core chapter.

1.2.1 Chapter 2: Background: The ecology of 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.

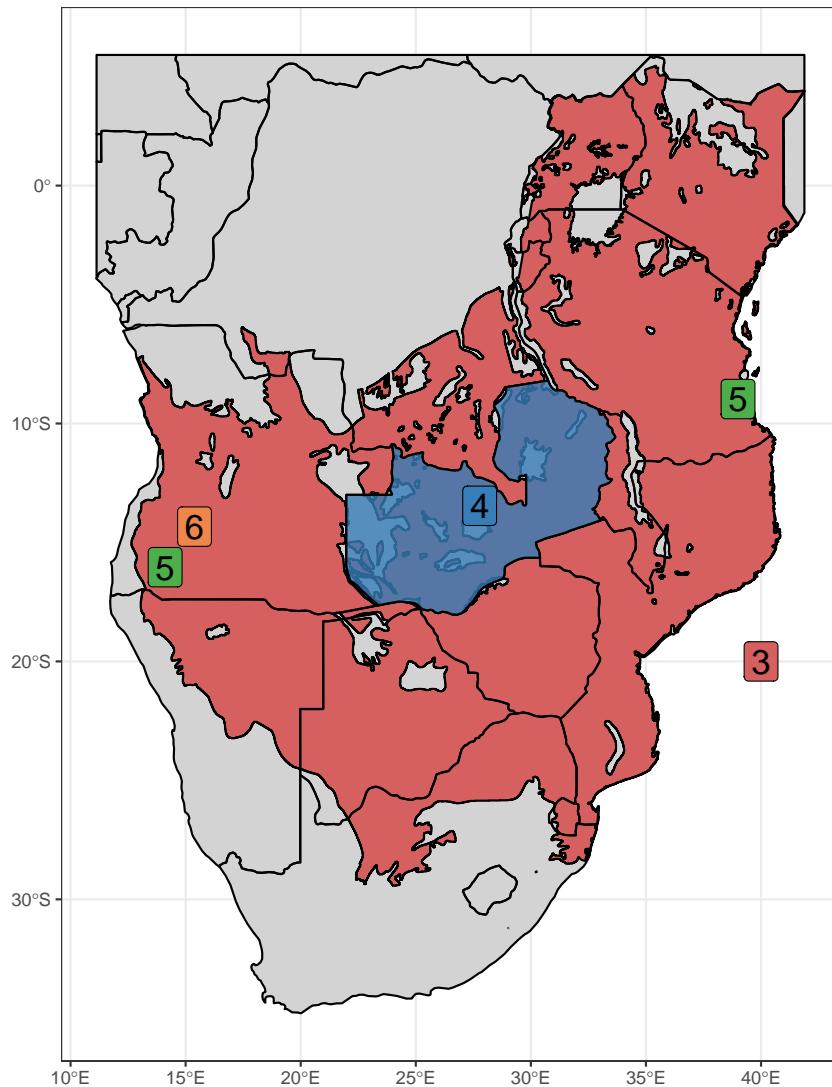


Figure 1.2: The spatial scales of the four core chapters in this thesis. Labels refer to chapter numbers: Chapter 3: The effects of biodiversity on above-ground woody biomass across southern African woodlands. The extent of southern African woodlands is defined by the SEOSAW working region, described 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 6: Woodland composition and structure in Bicuar National Park, Angola.

1.2.2 Chapter 3: A regional assessment of the biodiversity-ecosystem function relationship in southern African woodlands

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 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: Tree diversity and compositional effects on land-surface phenology in deciduous Zambian woodlands

In this chapter, I test whether species composition and diversity metrics can explain some of the remaining variation in patterns of land-surface phenology in deciduous tropical savannas. 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 used 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 affects 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: Canopy structural complexity as a mechanism for biodiversity effects on productivity

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 structure in southern African woodlands, at two sites in southern Africa, 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.

1.2.5 Chapter 6: Bicuar National Park: a woodland refugia at the extreme western extent of the miombo eco-region

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 phytogeographic 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.

1.2.6 Chapter 7: Synthesis: Biodiversity and ecosystem function in southern African woodlands

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) the potential consequences of consequences of climate and land use change on woodland ecology as it applies to biodiversity-ecosystem function theory. I conclude by outlining future research that will extend and clarify the findings of the thesis.

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 our understanding of the carbon dynamics of southern African woodlands.

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. SEO-SAW - “a Socio-Ecological Observatory for Southern African Woodlands” (SEO-SAW, 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 & Siam-pale 2009) is included in part within the SEOSAW database, this dataset deserves separate explanation. The ILUAii constitutes the 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 vegetation. The plot survey collected data on tree species, stem diameter and metadata such as

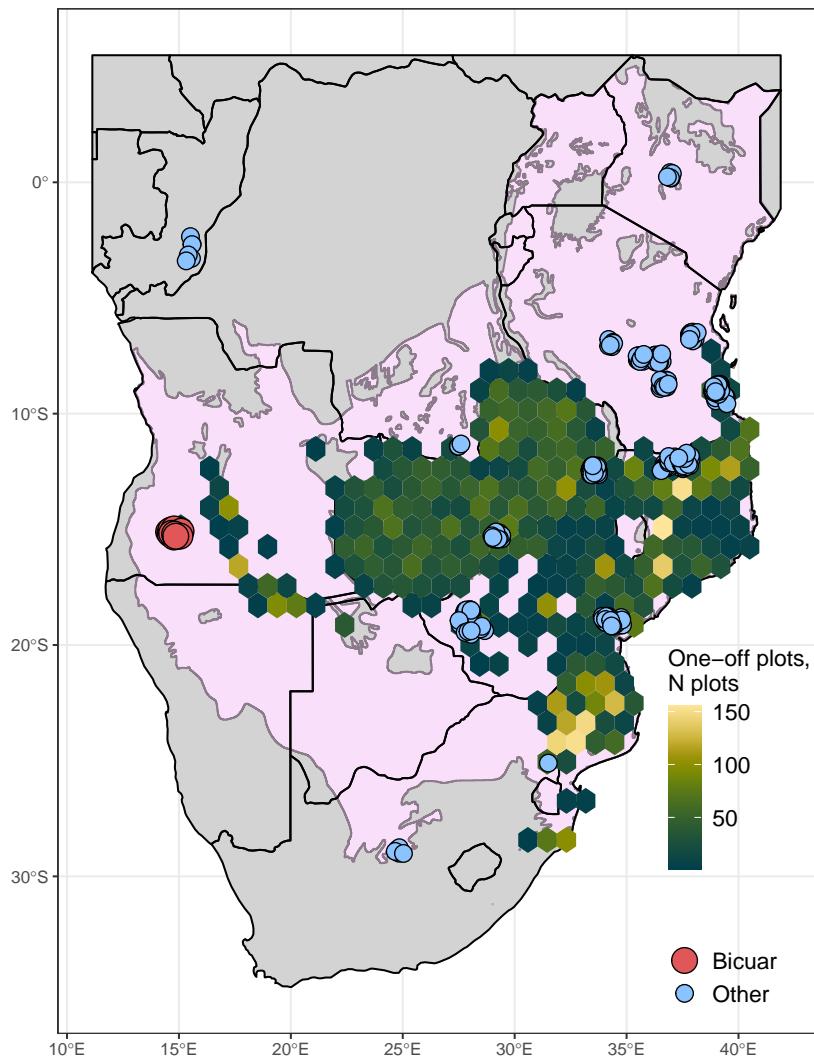


Figure 1.3: The spatial distribution of plots in the SEOSAW network. Blue circles are permanent plots, where individual stems can be matched among censuses. The new permanent plots in Bicuar National Park constructed as part of this thesis are shown as red points. The hexagonal-grid shows the density 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.

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.

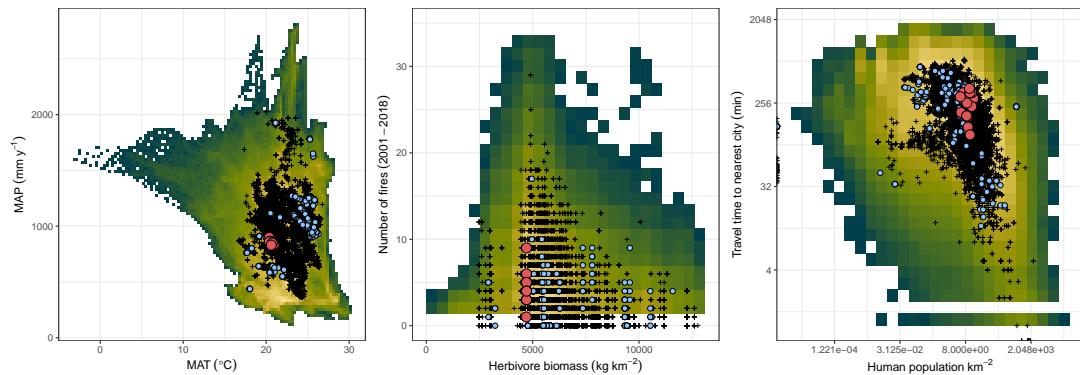


Figure 1.4: SEOSAW plots in various bivariate environmental spaces. Blue circles are permanent plots, where individual stems can be matched among censuses. The permanent plots in Bicuar National Park constructed as part of this thesis are shown as red points. Black crosses show one-off plots. The background 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" (arc seconds, ~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.

Climate databases: WorldClim, IMERG

I used 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 used 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 (Integrated Multi-satellitE Retrievals for GPM) (Huffman et al., 2015) provides globally available estimated precipitation daily time series. IMERG has a pixel size of 0.1° (11.1 km at the equator) (Huffman et al., 2015). I used 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 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 used 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) (Giglio et al., 2015) uses a combination of burn scars and active fire records to estimate instances of fire, overcoming limitations caused by cloud cover. 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. To our knowledge 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) (Didan, 2015) provides 16 day estimates of EVI at 250 m spatial resolution. 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 used 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 ($S15.1^{\circ}$, $E14.8^{\circ}$). 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 6 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; Ministério 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 km², but was reduced to ~675 km² 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

CHAPTER 1. INTRODUCTION

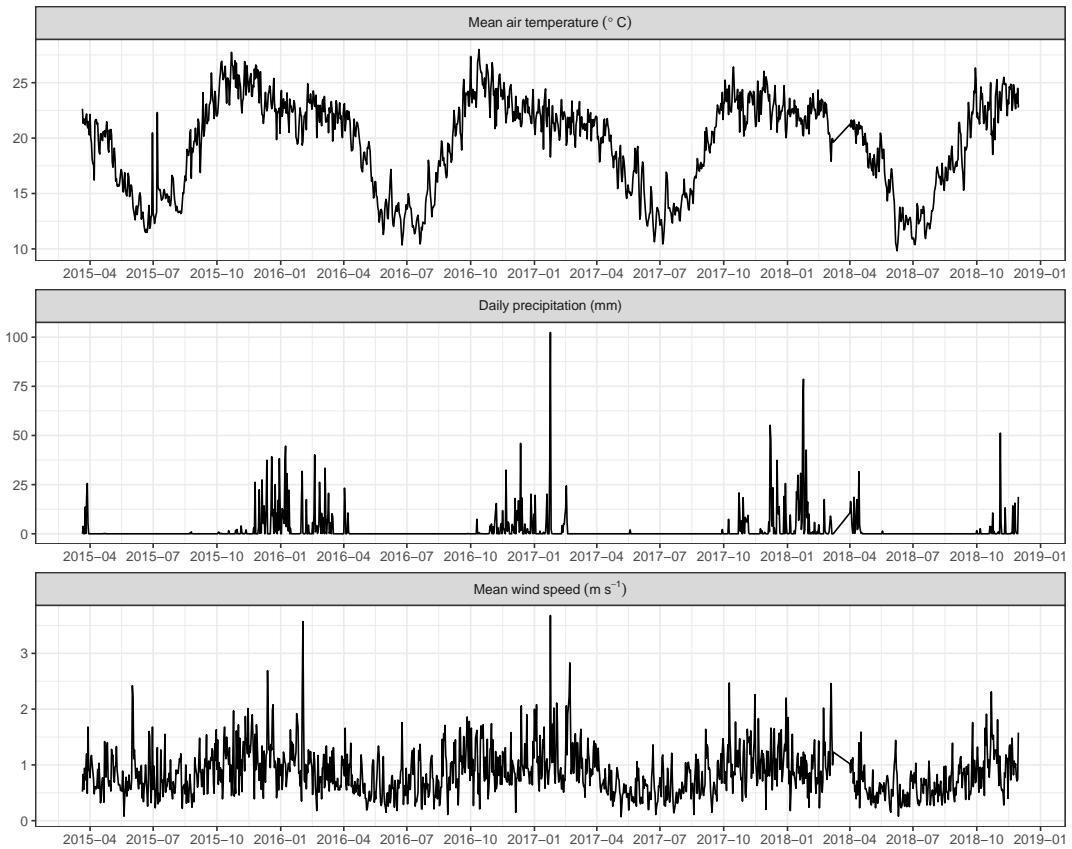


Figure 1.5: Data from the SASSCAL weather station located at the main station near the centre of Bicuar National Park. Data are daily aggregates, collected between March 2015 and June 2019.

Huila 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 Huila 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 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.

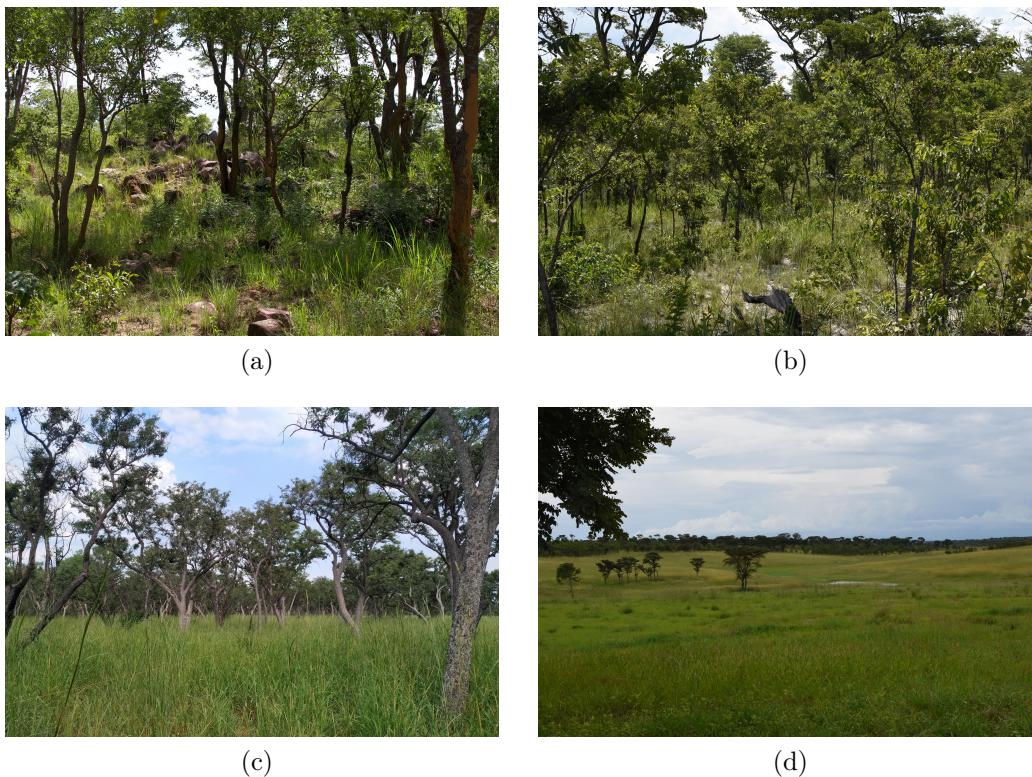


Figure 1.6: The principal vegetation formations seen in Bicuar National Park, southwest Angola. a) Julbernardia-Brachystegia miombo woodland, b) Burkea-Pseudolachnostylis miombo woodland, c) Baikiaea-Baphia woodland, and d) open grassy wetland (“mulola”).

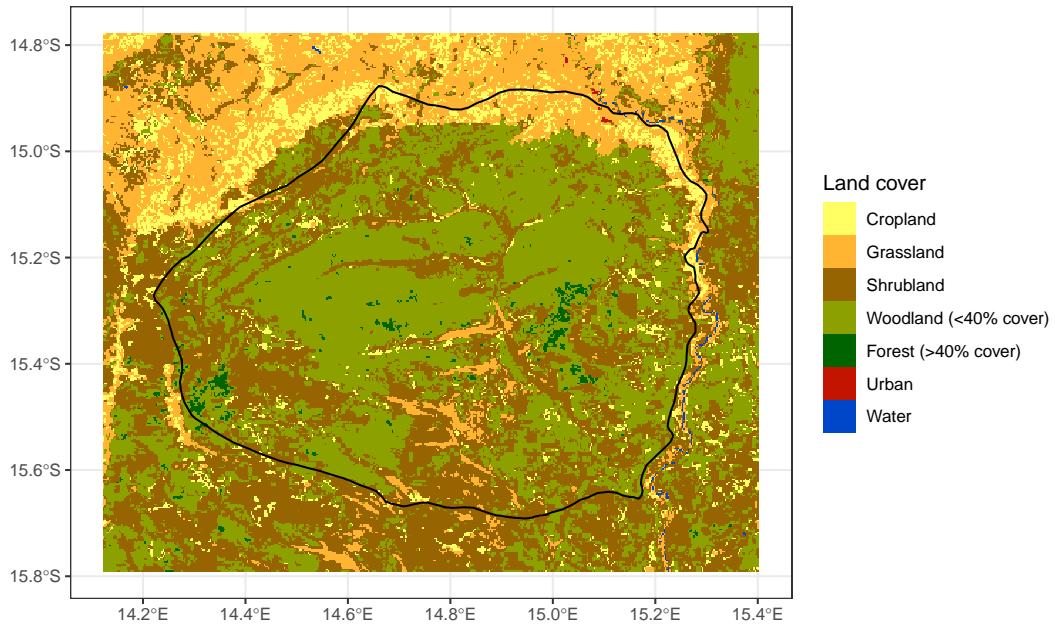


Figure 1.7: Land cover of Bicuar National Park, reclassified from the ESA CCI land cover map (v2.0.7) (ESA, 2017). This map highlights the clear deforestation north of the Park, with much land transformed to cropland and grassy pasture. The map also shows the discrepancy between the official park boundary 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.

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 both comprise 100x100 m (1 ha) permanent plots in tropical savanna vegetation of varying species composition and stem density. Chapter 5 uses the terrestrial laser scanning data to investigate drivers of canopy structural complexity. 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 post-hoc 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).

References

- Arino, O., J. R. Perez, V. Kalogirou, P. Defourny & F. Achard (2010). ‘GlobCover 2009’. In: *ESA Living Planet Symposium*, pp. 1–3.
- Baptista, N. L., T. António & W. R. Branch (2019). ‘The herpetofauna of Bicuar National Park and surroundings, southwestern Angola: a preliminary checklist’. In: *Amhidian 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, Niels H., Eloi Ribeiro, Ad van Oostrum, Johan Leenaars, Tom Hengl & Jorge Mendes 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). ‘TRMM multi-satellite precipitation analysis: Quasi-global, multi-year, combined-sensor precipitation estimates at finescale’. In: *Journal of Hydrometeorology* 8, pp. 28–55.
- Catarino, Silvia, Maria Manuel Romeiras, Rui Figueira, Valentine Aubard, João M. N. Silva & José 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, António Valter, Francisco M. P. Gonçalves, José João Tchamba, José Camóngua Luís, Marina Filomena F. Rafael & José L. M. Alexandre (2018). ‘Vegetation survey of the woodlands of Huíla Province’. In: *Biodiversity & Ecology* 6, 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, Mathieu, Thiéry Constant & Meriem Fournier (2011). ‘The use of terrestrial LiDAR technology in forest science: application fields, benefits and challenges’. In: 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. Tech. Rep.* 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: 34.3, pp. 623–642. DOI: 10.1002/joc.3711.
- Hartemink, Alfred E. & Jan 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, Gareth P., Sally Archibald & William 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 & Jackson 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, Catherine, Marius Gilbert, Robert W. Snow, Abdisalan M. Noor & Andrew 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.

CHAPTER 1. INTRODUCTION

- 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, Priscilla P., Michael Scherer-Lorenzen & Marco Antônio 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, Johan R, Mark A J Huijbregts, Kees C G J Schotten & Aafke 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, Sylvanus, Valère K. Salako & Thomas 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.
- Ministério 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, Jacqueline, Marvin Bürgin, Bernhard Schmid & Pascal 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, Peter, Matthew C. Hansen, Lars Laestadius, Svetlana Turubanova, Alexey Yaroshenko, Christoph Thies, Wynet Smith, Ilona Zhuravleva, Anna Komarova, Susan 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, Hannah & Max Roser (2018). *Urbanization*. URL: <https://ourworldindata.org/urbanization> (visited on 15/05/2021).
- Röder, Achim, Michael Pröpper, Marion Stellmes, Anne Schneibel & Joachim 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, Casey M., Rose Pritchard, Iain McNicol, Matthew Owen, Janet A Fisher & Caroline 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, Marko, Wolfgang Knorr, Nigel W Arnell & I Colin 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, Deo D., Ørjan Totland, Pantaleo K.T. Munishi & Stein 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, Jingfeng, Frederic Chevalier, Cecile Gomez, Luis Guanter, Jeffrey A. Hicke, Alfredo R. Huete, Kazuhito Ichii, Wenjian Ni, Yong Pang, Abdullah 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 and land use change (Ross et al., 2021; Scheiter & Higgins, 2009; Moncrieff et al., 2016). Yet we lack a detailed understanding of how biodiversity and vegetation structure vary and affect ecosystem function (i.e. processes controlling fluxes of energy and matter through ecosystem across this highly heterogeneous biome, resulting in large uncertainty in earth system flux estimates across this biome (Ahlstrom 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 productivity (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 woodlands, then summarises current literature on biodiversity-ecosystem function theory, 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 predominantly found in the seasonal tropics (Scholes & Archer, 1997), and to a lesser extent in temperate regions (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 grass and trees, with a near contiguous grass-dominated understorey, and a closed or open 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 canopy cover (Sankaran et al., 2005; Hirota et al., 2011), the functional and floristic composition of the woody overstorey (Fayolle et al., 2018; Solbrig et al., 1996), and the composition of 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 nineteenth century idea of Clementsian succession and potential vegetation (Pulsford et al., 2014), which focussed on hierarchical physiognomic vegetation classifications with closed canopy forest at the top, rather than floristic or functional classifications that are in greater use today (Aleman et al., 2020). The misinterpretation was exacerbated by the vast majority of early studies of savanna ecosystems originating from regions which lacked savanna vegetation. 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 reforestation 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, C4 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; 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), and unique responses to global environmental change ()).

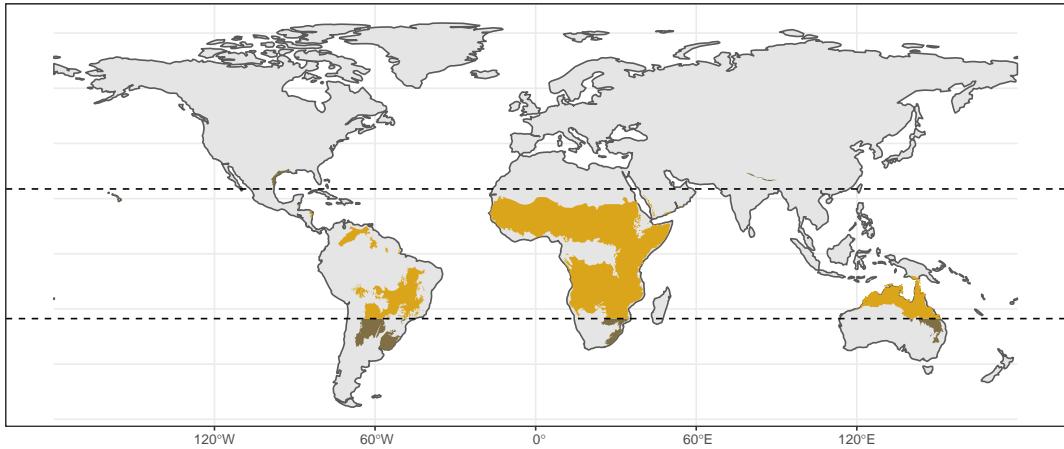


Figure 2.1: The global distribution of tropical (yellow) and extra-tropical (pale brown) savanna ecosystems, re-classified from the Terrestrial Ecoregions of the World (Dinerstein et al., 2017). Dashed lines mark the latitudinal extent of the tropics from N23.5° to S23.5°.

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 assessing their relative importance in different contexts, thus determining the global distribution of savannas (Higgins et al., 2000; Archibald et al., 2019). Controls on tree cover can be split broadly into ‘disturbance-based’ or ‘resource-based’ (Bond, 2008; Staver & Körner, 2015). For example, a lack of available moisture may limit tree growth to form an arid savanna (resource-based), while disturbance by fire or herbivory may cause tree mortality in a mesic savanna (disturbance-based). It is possible to classify savannas based on whether tree cover is primarily resource limited, or disturbance limited, and these two major types of savanna are expected to respond differently to future environmental change (Torello-Raventos et al., 2013).

Tropical savannas occur in areas of high rainfall seasonality (Lehmann et al., 2011). At the continental scale, available moisture is the most significant deter-

inant 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 trees is low, but in arid savannas, grasses may ‘poach’ water from trees by intercepting it closer 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 nutrient-poor 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 grassy biomass where there is greater drainage (Staver et al., 2011).

While resource availability, particularly moisture sets the upper bounds 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). Above $\sim 650 \text{ mm yr}^{-1}$, woody cover in savannas appears to show no dependence on MAP (Figure 2.2) (Sankaran et al., 2008; Sankaran et al., 2005; Good & Caylor, 2011). In mesic savannas, where climatic conditions are suitable for closed canopy forest, there exists large heterogeneity in woody canopy cover at local spatial scales (Dantas et al., 2015). Mesic savannas often form a complex mosaic of open grassy patches and closed canopy forest-like patches, with their distribution dependent on local edaphic conditions and historical disturbance patterns (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. C₄ grasses, which dominate many mesic savannas, particularly in southern Africa (Still et al., 2003), are particularly flammable, but require more light than C₃ grasses, meaning they are highly sensitive to variation in tree canopy cover (Charles-Dominique et al., 2018). In areas with low grassy 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 (Ryan et al., 2011), keeping individuals small and creating a demographic bottleneck where only a few individuals grow to adults. 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 (\sim 650-1500 mm yr $^{-1}$). Staver et al. (2011) further showed that fire is the main source of this bi-modality. Furthermore, Staver et al. (2017) showed that change in fire return interval, whether the result of management or environmental change, can result in changes in ecosystem structure. 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.

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 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 nutrient availability 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

Savanna trees are subject to a multitude of environmental pressures. To overcome these, savanna trees have a number of adaptations and employ various life history strategies, leading to a high functional diversity within tropical savanna trees (Solbrig et al., 1996), despite their low species diversity compared to tropical rainforests (Solbrig et al., 1996), for example.

Seasonal fires are a key determinant of savanna structure in mesic savannas

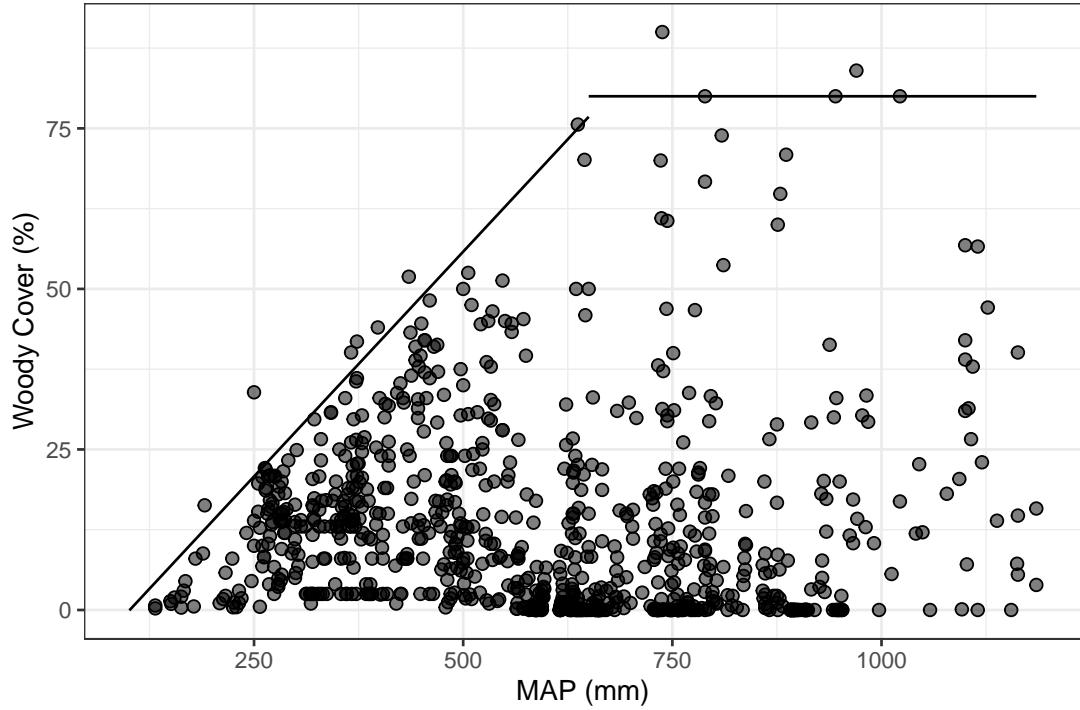


Figure 2.2: The relationship between rainfall (Mean Annual Precipitation) and proportional tree cover, across 854 savanna sites in Africa, adapted from Sankaran et al. (2005). The line of best fit uses a broken-stick 99th quantile piece-wise linear regression to identify the breakpoint at which rainfall 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.

(>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 that are able to store carbohydrate, 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, 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

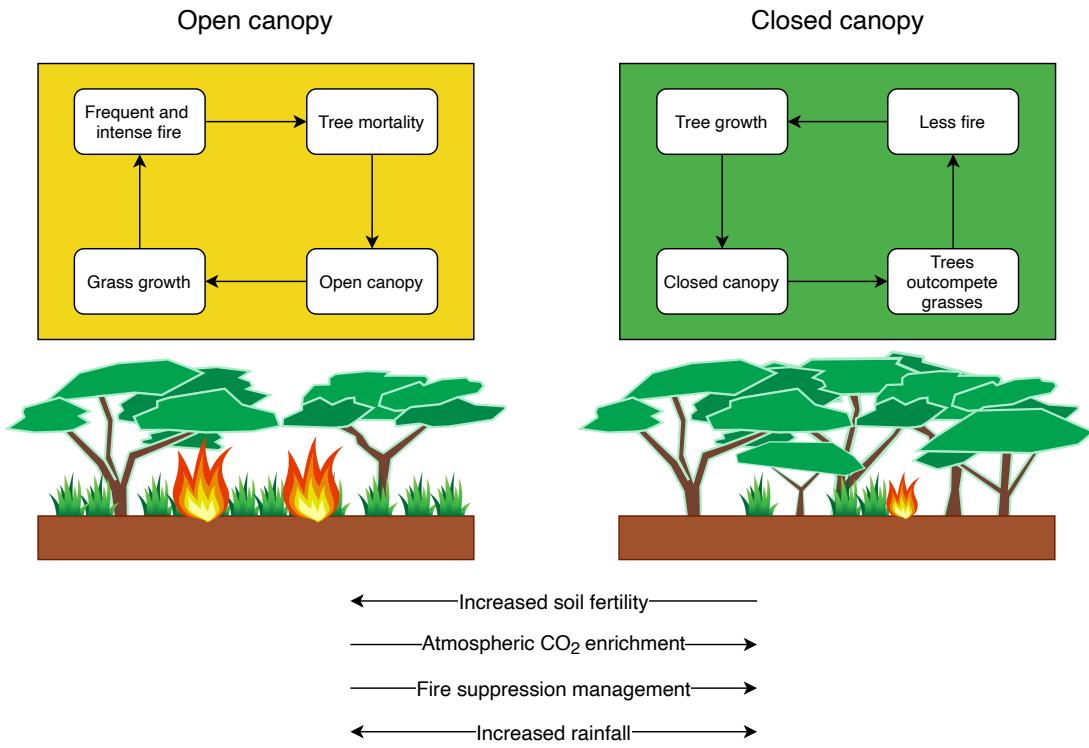


Figure 2.3: The positive feedback mechanisms which determine the alternative stable states of mesic tropical savannas. Left: increased fire increases tree mortality, which decreases canopy cover, increasing available light for grass growth, leading to more fire and a further reduction in canopy cover. 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.

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 (Case et al., 2020; Ketter & Holdo, 2018; Sankaran et

CHAPTER 2. BACKGROUND

al., 2004; Higgins et al., 2000). Recent work has shown that 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). As an additional adaptation to overcome nutrient poor soils, many savanna trees readily produce root nodules with mutualistic *Rhizobia* bacteria capable of fixing atmospheric nitrogen. The dominant canopy forming mesic savanna trees are dominated by species from the Fabaceae family which produce root nodules (Hogberg, 1986).

Fire removes much of the grass layer in a savanna, 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 means less 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, many savanna trees 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, 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), 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 avoid competition for light and water (Ryan et al., 2017), to avoid herbivory (Aide, 1988),

and to maximise the length of the growing season (Scholes & Walker, 1993).

The many adaptations of savanna trees to disturbance and resource availability represent axes of functional variation which could lead to a greater contribution to ecosystem function under higher biodiversity. Specifically, greater resilience to disturbances and higher productivity maintained under seasonal variation in climate (Díaz & Cabido, 2001; Mori et al., 2012).

2.2.3 The global carbon cycle and change in savannas

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, tree planting, 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 rainfall. By 2100, the human population of sub-Saharan Africa is expected to double, increasing pressure on savanna ecosystems (Pison, 2017). Despite this, tropical savannas are reportedly the fastest increasing component of the terrestrial carbon sink (Sitch et al., 2015).

By 2050, it is expected that atmospheric CO₂ will have risen high enough that C₄ grasses no longer have a growth advantage over C₃ plants (Bond & Midgley, 2012). An increase in atmospheric CO₂ 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 a closed canopy forest-like environment. Additionally, in arid savannas, the negative effect of CO₂ enrichment on grass transpiration rates (Murphy & Bowman, 2012) is expected to lead to less vigorous root growth and therefore more percolation of water to the deeper tree roots, increasing tree growth.

Various studies, across the country of South Africa (Stevens et al., 2016b), the neotropics (Rosan et al., 2019), and globally (Stevens et al., 2016a), have reported woody encroachment of trees into previously grassland or shrubland areas. However, due to the complex interactive nature of the determinants of savanna carbon cycling, it is still unclear whether these predicted effects of at-

mospheric CO₂ enrichment will materialise. Lewis et al. (2009) suggested that although existing woodlands are thickening, this does not necessarily extend to encroachment into previously unforested areas, due to the strong stabilising influence of fire. Pelletier et al. (2018) concluded that while more arid savannas will likely experience woody encroachment due primarily to the effects of CO₂ 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. Similarly, (Reich et al., 2014) demonstrated that earth system models may be overly sensitive to the effects of CO₂ enrichment, and that the models suffer from a lack of mechanistic understanding of the effect of resource availability on disturbance. Körner (2017) suggested that CO₂ 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. Clearly, there is much work needed to better understand the interactive mechanisms which determine the role of tropical savannas in the global carbon cycle, and how these relations vary across environmental and biogeographic gradients. The wide functional diversity of savanna trees means that ecosystem level responses to global change will be complex, as adaptive traits determine varied individual responses, resulting likely in shifts in carbon storage and turnover of species in response to changes in rainfall, temperature, fire regime, and atmospheric carbon.

2.3 Southern African woodlands

This thesis focusses specifically on the mesic savannas of southern African woodlands, the savanna formations occurring in a latitudinal band south of Congo basin rainforest, and north of the more temperate savannas of the country of South Africa (Figure 2.4). These savannas cover approximately 2.7 million km² (Arino et al., 2010). Hereafter they are referred to as southern African woodlands.

The structure of southern African woodlands is driven primarily by disturb-

ance from fire and herbivory, leading to a highly heterogeneous patchy woodland habitat (Archibald et al., 2019). Fire return interval varies locally, dependent on climate and existing vegetation which determines grass fuel load (Archibald et al., 2010). 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 savannas throughout southern Africa (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 closed canopies, while C₄ 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). Deforestation 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.

CHAPTER 2. BACKGROUND

Southern African mesic savannas can be divided roughly into three dominant vegetation types. Miombo woodlands dominate southern Africa, and are the largest savanna vegetation type in the world (Ryan et al., 2011). They are dominated by species from the Fabaceae family, subfamily Detarioideae, from the genera: *Brachystegia*, *Julbernardia*, and *Isoberlinia*, with the namesake ‘miombo’ coming from the local name for the genus *Brachystegia* in various Bantu languages. These woodlands frequently have tall tree canopies that occasionally close, and are therefore frequently classified as forest by some forest cover maps (Hansen et al., 2013). Rainfall in miombo woodlands varies between 540-1700 mm yr⁻¹, with a highly seasonal pattern of precipitation. Miombo woodlands are highly diverse, with >8500 vascular plant species, of which >300 are tree species, many of which are endemic to the region (Frost, 1996).

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 (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 hippopotamus (*Hippopotamus amphibius*) (Mittermeier et al., 2003). While much of the 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 on sandy soils, in a wide belt along the Angolan-Namibian border to Zimbabwe. They are dominated by *Baikiaea plurijuga*, which grow to large trees at low densities, with a grass and shrub understorey that burns regularly (Werger & Coetzee, 1978). Baikiaea woodlands are generally less suitable for agriculture than miombo woodlands, with highly sandy soil and low rainfall, though logging pressures have removed many of the largest and oldest trees in some regions (). Like mopane woodlands, Baikiaea woodlands provide habitat for many large herbivores ()�.

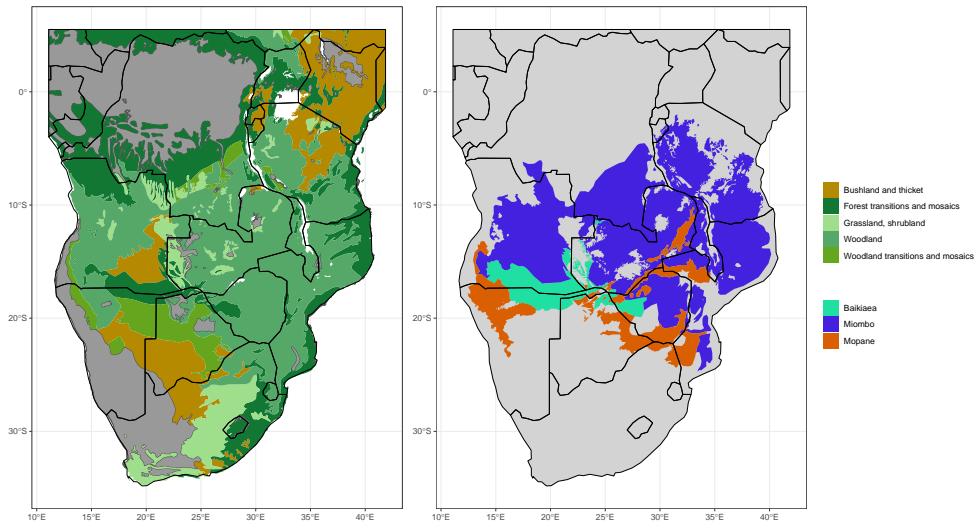


Figure 2.4: The distribution of key savanna vegetation types within southern Africa. Left: physiognomic classification adapted from White (1983). Right: floristic classification of selected savanna-woodlands adapted from Dinerstein et al. (2017), Terrestrial Ecoregions of the World.

2.4 Biodiversity and ecosystem function theory

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) (Schulze & Mooney, 1993). 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 2.5), with hundreds of studies exploring biodiversity effects in both experimental and 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 a passive result of environmental conditions and ecosystem function, while the research that came after redefined biodiversity as both a driver and result of ecosystem function. BEF theory provides intuitive reasoning as to why increased biodiversity should lead to increased ecosystem function.

BEF theory and supporting empirical evidence has informed global environmental policy by encouraging biodiversity conservation as a means of maintaining

CHAPTER 2. BACKGROUND

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 being encouraged as a method of maximising natural capital (perceived value of natural assets, Kareiva et al. 2011) indirectly by maximising ecosystem functionality (Scherer-Lorenzen, 2014; Cardinale et al., 2012). Many conservation policy makers are seeking win-win conservation strategies which will 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 is trepidation however, that as ecosystems are transformed as a result of conservation meant to maximise ecosystem function, or rather a subset of ecosystem functions that are easily measured and have been identified as valuable, such as carbon sequestration (Duffy et al., 2017), other ecosystem functions and services may suffer and the ecosystem may lose unique characteristics (Brockhoff et al., 2017; Srivastava & Vellend, 2005).

This thesis aims to understand variation in ecosystem function and community structure in 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 ecosystem properties such as forest canopy complexity and trophic complexity, which in turn influence ecosystem processes. In this thesis, I focus only on biomass and productivity of trees as measures of ecosystem function, with the aim of improving our understanding of the carbon dynamics of southern African woodlands.

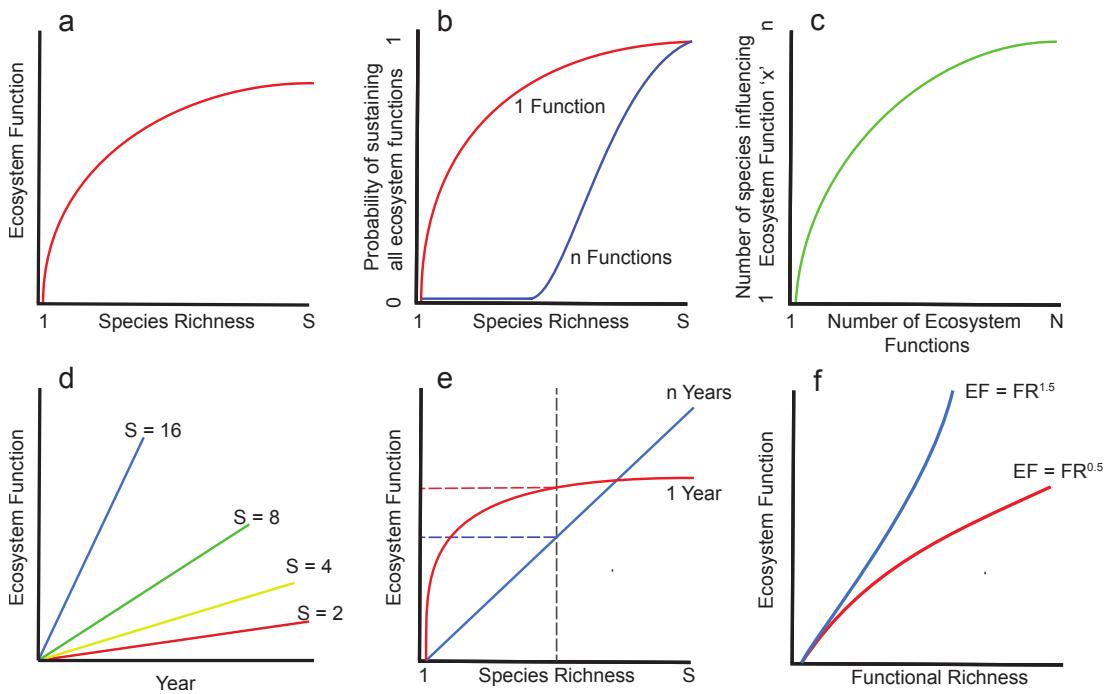


Figure 2.5: Schematic diagrams illustrating various inferences made on the Biodiversity - Ecosystem Function Relationship by previous studies. a) The classic BEF relationship found by many small scale experiments (Cardinale et al., 2009). b) As more functions are considered simultaneously the minimum species richness needed to maintain overall ecosystem functionality increases, also showing how the proportion of functionally redundant species increases as less functions are considered (i.e. the curve reaches asymptote at a lower 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) As studies progress through time the strength of the BEF relationship increases, the rate of increase in ecosystem function increases as species richness (S) grows (Cardinale et al., 2007). e) As studies progress through time the shape of the relationship becomes more linear, saturating at progressively higher species richnesses. Studies averaged over longer periods exhibit a greater loss in ecosystem function in response to an equivalent species richness reduction (Reich et al., 2012). f) When functional richness is used in place of species richness, the relationship reaches asymptote at a higher richness. Additionally the relationship becomes more concave as a power coefficient representing the strength and number of species interactions increases. $FR^{>1}$ (interspecific competition $>$ intraspecific competition (unstable)) results in a convex relationship, while $FR^{<1}$ results in a concave relationship (Mora et al., 2014).

2.4.1 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 ecosystem functionality (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 functionality, but the ability of the most abundant species to optimise a chosen 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 (Wright et al., 2017) (Figure 2.6). 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). 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, 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 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 increasing species diversity turned weakly negative under high diversity, due to competitive effects. Facilitation effects remain understudied in BEFR literature. 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 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.

2.4.2 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

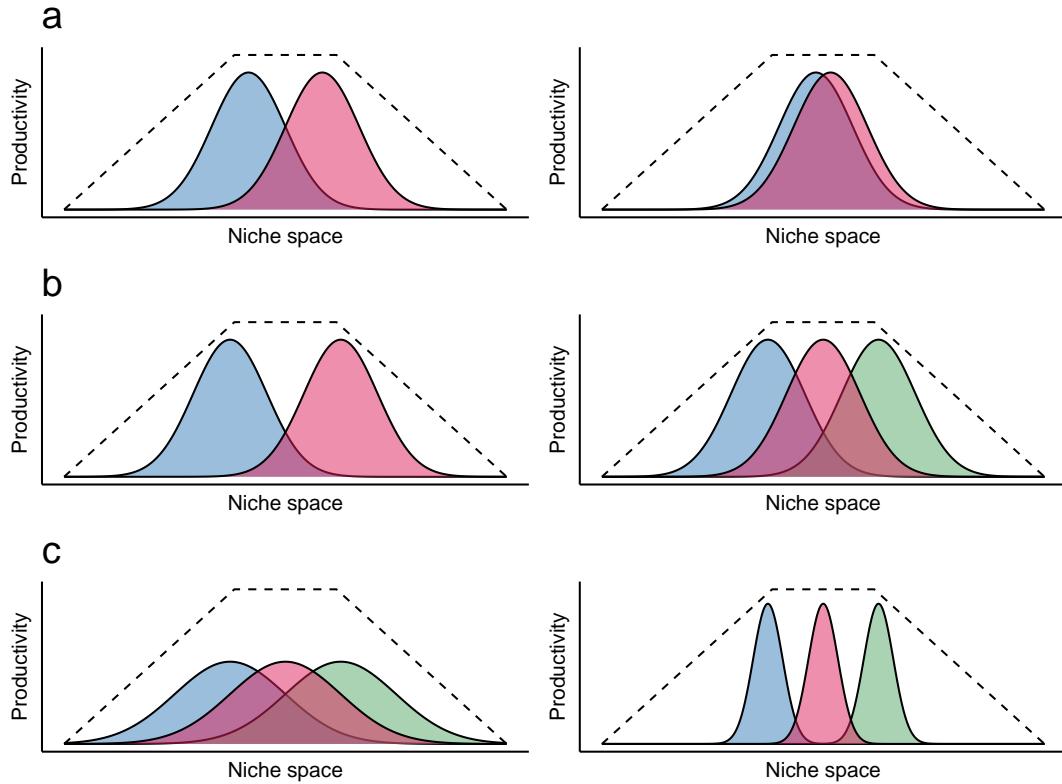


Figure 2.6: Schematic diagrams demonstrating niche occupation and secondary controls on the mechanism of niche complementarity. Each density plot shows a number of species, each represented by the species functional contribution (productivity) under different environmental conditions (niche space) within the larger environmental niche volume (dashed line). a) shows how the degree of overlap in functional niche of two species affects the total utilisation of the environmental niche volume (area under all species curves). When species are functionally distinct (left), more of the environmental niche volume is utilised. Removal of a species in this case would result in a large reduction in ecosystem productivity, while on the right, where functional redundancy is high, removal of a single 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 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 as each species may occupy a wide range of environmental conditions. 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 a more complete utilisation of the environmental niche under ideal conditions. If a species was removed from this ecosystem, there would be a much greater reduction in ecosystem productivity.

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, 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 2.7). Both of these African studies are narrow in their scope and do not consider southern African woodland-savanna 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 Duffy et al.'s (2017) meta-analysis, 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, it would be unfeasible to generalise the BEFR found in other systems to this region.

2.4.3 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 tropical savannas differ in the environmental pressures they experience, and in the mechanisms which determine ecosystem structure. Conclusions drawn from BEFR research conducted in forests cannot necessarily be directly applied to disturbance driven and resource

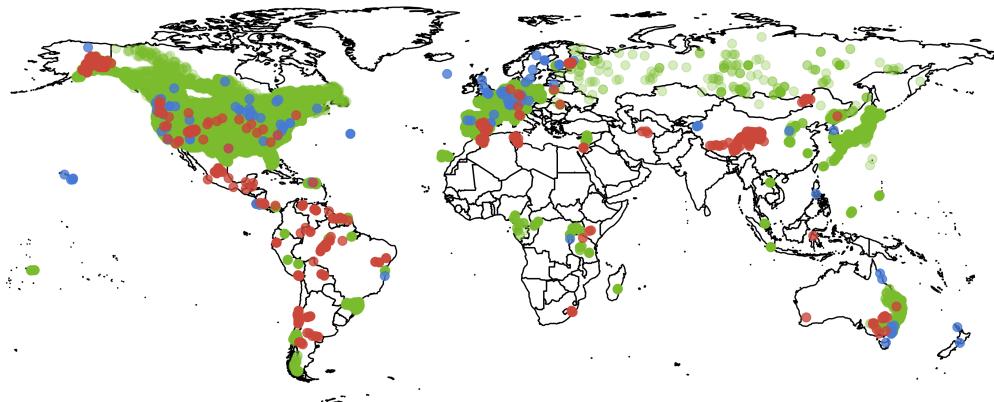


Figure 2.7: Location of studies of the biodiversity - ecosystem function relationship included in three meta-analyses of BEF research: blue Clarke et al. (2017), green Liang et al. (2016), red Duffy et al. (2017) - 67 field studies.

limited systems.

Despite the current trend in conservation strategy to maximise biodiversity under the assumption that it will ensure ecosystem functionality, it remains unclear how important the BEFR is in determining ecosystem functionality compared to environmental factors (Tilman et al., 2014). It is also unclear to what extent the BEFR itself varies over environmental and biogeographical gradients (Scherer-Lorenzen, 2014). Many observed biodiversity effects could potentially be better explained by variation in unmeasured environmental variables, with which biodiversity merely correlates. Plant biodiversity has been shown to increase in areas with climatic conditions conducive to growth (Fischer et al., 2014; Bunker et al., 2005), and it is clear that temperature and precipitation also have a direct role in determining ecosystem functions such as net primary productivity and woody biomass (Urban et al., 2017; Michaletz et al., 2014).

A strong positive BEFR may not exist in all landscapes, with previous experimental and field studies producing many contrasting results. Duffy et al. (2017) conducted a meta-analysis of 133 estimates of the BEFR from 67 studies, suggesting comparable effects of biodiversity and climate or nutrient availability, but this generalisation remains largely speculative, especially for regions with a paucity of data, such as southern Africa (Figure 2.7). Resource availability

and disturbance frequency/intensity have been identified as two environmental factors that modulate the effect that biodiversity has on ecosystem functionality (Tilman et al., 2012; Tilman et al., 2014; Hooper et al., 2012). 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. These environmental 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. 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). 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.

Biodiversity is often crudely measured as local species richness of a focal trophic level or functional group (e.g. trees). However, more complex measures such as functional richness provide better insight into the tangible organ-

ism level processes, which drive apparent species richness effects (Finegan et al., 2015; Scherer-Lorenzen, 2014; Petchey & Gaston, 2006). For example, increased tree species richness appears to cause an increase in the productivity of forest stands, but is this due to there being a higher likelihood of having a productive species (selection effects), canopy packing complementarity, root depth complementarity, facilitative shading effects, or more likely a combination of all the above? It is likely that species richness is merely correlated with many other aspects of biodiversity which actually affect ecosystem function (Mlambo, 2014; Scherer-Lorenzen, 2014). Ultimately, there is no biological reason why two species should exhibit niche complementarity according to differences in species name. Of course, this is not to discount the role of phylogenetic and taxonomic separation as a proxy for degree of potential niche differentiation among species (Flynn et al., 2011; Petchey & Gaston, 2002). Additionally, the distribution of relative contributions to a given function among species within an ecosystem is likely to affect the provision of that ecosystem function, through selection effects and the mass ratio hypothesis (Chisholm et al., 2013). *i.e.* a species with a high photosynthetic capacity will contribute little to overall ecosystem level productivity if it is found at very low abundances, but see Viole et al. (2017) and Soliveres et al. (2016), which suggest that rare species often exhibit the least redundant traits and are therefore as functionally important common species. Functional diversity should ideally be used to more directly quantify the functional contribution of species and individuals within an ecosystem, to understand better the mechanisms that drive biodiversity effects.

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 between individuals. Southern African woodlands however, exist along a wide gradient of tree cover. At the extreme low end of this gradient, trees are often 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 approach zero between adult trees in the most sparsely wooded ecosystems. Low tree densities may result from a combination of “resource-based” processes such as low water availability and “disturbance-based” processes of disturbance caused by fire, herbivory, or human land use practices such as selective logging or tree felling for beehive harvesting (Ryan et al., 2016). Fig-

ure 2.2 shows percentage woody cover along a precipitation gradient in Africa from Sankaran et al. (2005). It shows that the majority of plots have a woody cover below the physiological maximum set by precipitation, indicating that many other factors influence woody cover other than water availability. A lack of competition would certainly weaken any effect of tree species diversity on ecosystem productivity, as multiple species can often fill overlapping niches in the absence of competition. Niche differentiation however, would still serve to only allow 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. 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. Additionally, many savanna tree species do not grow well under shade (Belsky, 1994), unlike those in forests. Adult savanna trees will therefore compete with seedlings and saplings from their own species and from other species. Differences in competitive interactions amongst trees across tree cover gradients are likely to have an impact on the strength of the BEFR.

2.4.4 Demographic structure, structural diversity and ecosystem function

Disturbance by fire and herbivory, as well as drought and extreme temperature, create a bottleneck in the demographic structure of savannas, with high mortality of juveniles. The extent of this demographic bottleneck effect causes variation in tree canopy structure in different savannas. In the same way that co-existing tree species are expected to occupy different niche space to produce the positive niche complementarity effect on ecosystem function, it can be assumed that individuals occupying different demographic stages and with different canopy occupancy also occupy different niche space. Thus, demographic and physical structure may represent a form of structural diversity that also influences ecosystem function.

In wet tropical forests () and temperate forests (Dănescu et al., 2016), canopy layer diversity has been shown to increase productivity. Presumably an increase in canopy layer diversity

2.5 Conclusions

Savannas are complex, and savanna vegetation arises as a result of many interacting factors. Despite their complexity tropical savannas are understudied and represent the largest uncertainty in models of the global carbon cycle. Assumptions about the behaviour of tropical savannas cannot be made based on other tropical forested ecosystems, mainly due the pervasive role of disturbance and resource scarcity as drivers of ecosystem functioning. 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. 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. However, BEF research in natural forested ecosystems has shown that both positive and negative biodiversity effects may occur, depending on the function studied and the intensity of environmental stress. It is unclear how biodiversity of tree species in southern African woodlands may affect productivity, but there are multiple reasons why biodiversity effects might be weaker or possibly negative in this biome. This thesis aims to increase our understanding of tree biodiversity in southern African woodlands, the world's largest savanna, through the lens of the Biodiversity-Ecosystem Function Relationship.

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. Mitchell (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, Julie C., Olivier Blarquez & Carla 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.
- 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, Sally, William J. Bond, William Hoffmann, Caroline Lehmann, Carla Staver & Nicola Stevens (2019). *Distribution and Determinants of Savannas*. DOI: 10.1002/9781119081111.ch1.
- Arino, O., J. R. Perez, V. Kalogirou, P. Defourny & F. Achard (2010). ‘GlobCover 2009’. In: *ESA Living Planet Symposium*, pp. 1–3.
- 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.
- 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, Jan M., Nico Eisenhauer, Colin R. Janssen & Frederik De Laender (2018). ‘Biodiversity effects on ecosystem functioning respond unimodally to environmental stress’. In: *Ecology Letters* 21.8. Ed. by Johannes Knops, pp. 1191–1199. DOI: 10.1111/ele.13088.
- Balvanera, Patricia, Ilyas Siddique, Laura Dee, Alain Paquette, Forest Isbell, Andrew Gonzalez, Jarrett Byrnes, Mary I. O’Connor, Bruce A. Hungate & John 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, Ignasi, Mia G. Park, Jason Gibbs, Bryan N. Danforth, Alan N Lakso & Rachael 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. Joy (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 and Evolution* 20.7, pp. 387–394. DOI: 10.1016/j.tree.2005.04.025.

CHAPTER 2. BACKGROUND

- Bond, William J. (2008). ‘What Limits Trees in C4 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, William J. & Guy 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, William J. & Jeremy 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.
- Brokerhoff, Eckehard G., Luc Barbaro, Bastien Castagnéyrol, David I. Forrester, Barry Gardiner, José Ramón González-Olabarria, Phil O’B. Lyver, Nicolas Meurisse, Anne Oxbrough, Hisatomo 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, Gabriela & Niall 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.
- Bunker, D, F DeClerck, J Bradford & R Colwell (2005). ‘Species loss and aboveground carbon storage in a tropical forest’. In: *Science* 310.November, pp. 1029–1031. DOI: 10.1126/science.1117682.
- Burgess, Neil, Jennifer D’Amico Hales, Emma Underwood, Eric Dinerstein, David Olson, Illana Itoua, Jan Schipper, Taylor Ricketts & Kate 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, Ragan M. & Lawrence 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.
- Cardinale, Bradley J, Justin P Wright, Marc W Cadotte, Ian T Carroll, Andy Hector, Diane S Srivastava, Michel Loreau & Jerome 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 of the United States of America* 104.46, pp. 18123–8. DOI: 10.1073/pnas.0709069104.
- Cardinale, Bradley J., J. Emmett Duffy, Andrew Gonzalez, David U. Hooper, Charles Perrings, Patrick Venail, Anita Narwani, Georgina M. Mace, David Tilman, David A. Wardle et al. (2012). ‘Biodiversity loss and its impact on humanity’. In: *Nature* 489.7415, pp. 326–326. DOI: 10.1038/nature11373.
- Cardinale, Bradley J., Kristin L. Matulich, David U. Hooper, Jarrett E. Byrnes, Emmett Duffy, Lars Gamfeldt, Patricia Balvanera, Mary I. O’Connor & Andrew 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, Bradley J. & Margaret A. Palmer (2002). ‘Disturbance Moderates biodiversity-ecosystem function relationships- experimental evidence from caddisflies in stram mesocosms’. In: *Ecology*, 83 (7)-1915-1927 83.7, pp. 1915–1927. DOI: 10.1890/0012-9658(2002)083[1915:DMBEFR]2.0.CO;2.

- Cardinale, Bradley J., Diane S. Srivastava, J. Emmett Duffy, Justin P. Wright, Amy L. Downing, Mahesh Sankaran, Claire Jouseau, Marc W Cadotte, Ian T. Carroll, Jerome 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.
- Case, Madelon F., Jesse B. Nippert, Ricardo M. Holdo & A. Carla Staver (2020). ‘Root-niche separation between savanna trees and grasses is greater on sandier soils’. In: *Journal of Ecology* 108.6. Ed. by Imma Oliveras, pp. 2298–2308. DOI: 10.1111/1365-2745.13475.
- Cerling, Thure E., John M. Harris, Bruce J. MacFadden, Meave G. Leakey, Jay Quade, Vera Eisenmann & James R. Ehleringer (1997). ‘Global vegetation change through the Miocene/Pliocene boundary’. In: *Nature* 389.6647, pp. 153–158. DOI: 10.1038/38229.
- Charles-Dominique, Tristan, Heath Beckett, Guy F. Midgley & William 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, Tristan, Guy F. Midgley, Kyle W. Tomlinson & William 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.
- Chisholm, Ryan A., Helene C. Muller-Landau, Kassim Abdul Rahman, Daniel P. Bebber, Yue Bin, Stephanie A Bohlman, Norman A Bourg, Joshua Brinks, Sarayudh Bunyavejchewin, Nathalie Butt et al. (2013). ‘Scale-dependent relationships between tree species richness and ecosystem function in forests’. In: *Journal of Ecology* 101.5. Ed. by David Coomes, pp. 1214–1224. DOI: 10.1111/1365-2745.12132.
- 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.
- Coomes, David A. & Robert 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, Kyla M., Dominick Del Ponte, Emily Setlock & Ryan 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 Felipe, Juli G Pausas, Nathalia Bonani, Jessika Nunes, Fernando A O Silveira & Alessandra 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, Adrian, Axel T. Albrecht & Jürgen Bauhus (2016). ‘Structural diversity promotes productivity of mixed, uneven-aged forests in southwestern Germany’. In: 182.2, pp. 319–333. DOI: 10.1007/s00442-016-3623-4.
- Dantas, V. L., M. Hirota, R. S. Oliveira & J. G. Pausas (2015). ‘Disturbance maintains alternative biome states’. In: *Ecology Letters* 19.1, 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 Peter Bellingham, pp. 1265–1272. DOI: 10.1111/1365-2745.12118.
- Díaz, Sandra & Marcelo 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, Eric, David Olson, Anup Joshi, Carly Vynne, Neil D. Burgess, Eric Wikramanayake, Nathan Hahn, Suzanne Palminteri, Prashant Hedao, Reed 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, Justin, David J. Augustine, Niall P. Hanan, Jayashree Ratnam & Mahesh 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.

CHAPTER 2. BACKGROUND

- Duffy, J. Emmett, Casey M. Godwin & Bradley 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.
- Fayolle, A., M. D. Swaine, J. Aleman, A. F. Azihou, D. Bauman, M. te Beest, E. N. Chidumayo, J. P. G. M. Cronsigt, 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, Edmund C., Steven I. Higgins, William J. Bond & Louise 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, Bryan, Marielos Peña-Claros, Alexandre de Oliveira, Nataly Ascarrunz, M. Syndonia Bret-Harte, Geovana Carreño-Rocabado, Fernando Casanoves, Sandra Díaz, Paul Eguiguren Velepucha, Fernando 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.
- Fischer, Rico, Amanda Armstrong, Herman H. Shugart & Andreas Huth (2014). ‘Simulating the impacts of reduced rainfall on carbon stocks and net ecosystem exchange in a tropical forest’. In: *Environmental Modelling and Software* 52, pp. 200–206. DOI: 10.1016/j.envsoft.2013.10.026.
- Flynn, Dan F. B., Nicholas Mirochnick, Meha Jain, Matthew I. Palmer & Shahid Naeem (2011). ‘Functional and phylogenetic diversity as predictors of biodiversity ecosystem-function relationships’. In: *Ecology* 92.8, pp. 1573–1581. DOI: 10.1890/10-1245.1.
- 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.
- Gamfeldt, Lars, Jonathan S. Lefcheck, Jarrett E. K. Byrnes, Bradley J. Cardinale, J. Emmett Duffy & John 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.
- Gonzalez, Andrew, Nicolas Mouquet & Michel 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, Megan K., Peter J. Clarke, Jodi N. Price & Nick 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, John, Jose San Jose, Patrick Meir, Heloisa S. Miranda & Ruben 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, John N., Jarrett E K Byrnes & Bradley 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. (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.

- 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, Robert E., Harvey A. Bootsma & Murray 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, Andy & Robert 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.
- Higgins, Steven I., William J. Bond & Winston 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, Jonathan M., Timothy M. Boucher, Taylor H. Ricketts & Carter 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, William A., Erika L. Geiger, Sybil G. Gotsch, Davi R. Rossatto, Lucas C. R. Silva, On Lee Lau, M. Haridasan & Augusto 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. Ed. by Francisco Lloret, 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: *The Journal of Applied Ecology* 23.2, p. 675. DOI: 10.2307/2404045.
- Hooper, David U., E. Carol Adair, Bradley J. Cardinale, Jarrett E. K. Byrnes, Bruce a. Hungate, Kristin L. Matulich, Andrew Gonzalez, J. Emmett Duffy, Lars Gamfeldt & Mary 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, Caroline, Helen Suich, Bhaskar Vira & Georgina 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.
- 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, Forest, Peter B Reich, David Tilman, Sarah E Hobbie, Stephen Polasky & Seth 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.
- Jax, Kurt (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.
- 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, Martin (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, Benjamin L. & Ricardo 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.

CHAPTER 2. BACKGROUND

- Körner, Christian (2017). ‘A matter of tree longevity’. In: *Science* 355.6321, pp. 130–131. DOI: 10.1126/science.aal2449.
- Kumar, Dushyant, Mirjam Pfeiffer, Camille Gaillard, Liam Langan, Carola Martens & Simon 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, Michael J., Hylton Adie, Jeremy Russell-Smith, Brett Murphy & Jeremy 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.
- 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, Jonathan M. & Janneke HilleRisLambers (2009). ‘The importance of niches for the maintenance of species diversity’. In: *Nature* 461.7261, pp. 254–257. DOI: 10.1038/nature08251.
- Lewis, Simon L., Gabriela Lopez-Gonzalez, Bonaventure Sonké, Kofi Affum-Baffoe, Timothy R. Baker, Lucas O. Ojo, Oliver L. Phillips, Jan M. Reitsma, Lee White, James 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. Peter (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, Christopher J., Mario Zuliani, Nargol Ghazian, Stephanie Haas, Jenna Braun, Malory Owen, Florencia Miguel, Merav Seifan, Alessandro Filazzola & Jacob 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 Alexandra Wright, pp. 2047–2053. DOI: 10.1111/1365-2745.13596.
- MacArthur, Robert (1955). ‘Fluctuations of Animal Populations and a Measure of Community Stability’. In: *Ecology* 36.3, p. 533. DOI: 10.2307/1929601.
- Makhado, Rudzani, Martin Potgieter, Jonathan Timberlake & Davison 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, Louise, Stefanie Deinet & Robin Freeman (2017). ‘The Diversity-Weighted Living Planet Index: Controlling for Taxonomic Bias in a Global Biodiversity Indicator’. In: *PLOS ONE* 12.1. Ed. by Hideyuki Doi, e0169156. DOI: 10.1371/journal.pone.0169156.
- Michaletz, Sean T., Dongliang Cheng, Andrew J. Kerkhoff & Brian J. Enquist (2014). ‘Convergence of terrestrial plant production across global climate gradients’. In: *Nature* 512.1, pp. 39–43. DOI: 10.1038/nature13470.
- 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.

- Mlambo, Musa C. (2014). ‘Not all traits are ‘functional’: Insights from taxonomy and biodiversity-ecosystem functioning research’. In: *Biodiversity and Conservation* 23.3, pp. 781–790. DOI: 10.1007/s10531-014-0618-5.
- Moncrieff, Glenn R., Simon Scheiter, Liam Langan, Antonio Trabucco & Steven 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, Camilo, Roberto Danovaro & Michel 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.
- Mori, Akira S., Takuwa Furukawa & Takehiro 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.
- Morin, Xavier, Lorenz Fahse, Claire de Mazancourt, Michael Scherer-Lorenzen & Harald Buggmann (2014). ‘Temporal stability in forest productivity increases with tree diversity due to asynchrony in species dynamics’. In: *Ecology Letters* 17.12. Ed. by Marcel Rejmanek, pp. 1526–1535. DOI: 10.1111/ele.12357.
- Moustakas, Aristides, William E. Kunin, Tom C. Cameron & Mahesh 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, Brett P. & David 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, Shahid, 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.
- Newbold, Tim, Lawrence N Hudson, Andrew P Arnell, Sara Contu, Adriana De Palma, Simon Ferrier, Samantha L L Hill, Andrew J Hoskins, Igor Lysenko, Helen R P Phillips et al. (2016). ‘Has land use pushed terrestrial biodiversity beyond the planetary boundary?’ In: *Science* 353.6296, pp. 288–91.
- Njana, Marco Andrew, George Chamungwana Kajembe & Rogers Ernest 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.
- Padilla, Francisco M. & Francisco 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 and Evolution* 29, pp. 205–213. DOI: 10.1016/j.tree.2014.02.004.
- 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.
- Petchey, Owen L. & Kevin J. Gaston (2002). ‘Functional diversity (FD), species richness and community composition’. In: *Ecology Letters* 5.3, pp. 402–411. DOI: 10.1046/j.1461-0248.2002.00339.x.

CHAPTER 2. BACKGROUND

- Petchey, Owen L. & Kevin 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, Stephanie A., David B. Lindenmayer & Don 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, Drew W., Jeremy W. Lichstein & Stephen 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, Peter B., Sarah E. Hobbie & Tali 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, Thais M., Luiz E. O. C. Aragão, Imma Oliveras, Oliver L. Phillips, Yadvinder Malhi, Emanuel Gloor & Fabien 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. Wade, Niall P. Hanan, Lara Prihodko, Julius Anchang, Wenjie Ji & Qiuyan 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, Casey M., Rose Pritchard, Iain McNicol, Matthew Owen, Janet A Fisher & Caroline 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, Mahesh, Jayashree Ratnam & Niall 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, Mahesh, Jayashree Ratnam & Niall 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, Simon & Steven 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 - Scholes and Archer - 1997’. In: *Annual Review of Ecology and Systematics*.
- Scholes, R. J. & B. H. Walker (1993). *An African savanna. Synthesis of the Nylsvley Study*. Cambridge, United Kingdom: Cambridge University Press.
- Schulze, E. D. & H. A. Mooney (1993). *Biodiversity and Ecosystem Function*. Berlin, Germany: Springer Berlin Heidelberg.
- Shackleton, Charlie M., Sheona E. Shackleton, Erik Buitenhuis & Neil 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.forepol.2006.03.004.
- Siebert, Frances & Niels 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, Fernando A. O., André J. Arruda, William Bond, Giselda Durigan, Alessandra Fidelis, Kevin Kirkman, Rafael S. Oliveira, Gerhard E. Overbeck, Jerônimo B. B Sansevero, Frances 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, Melinda D. & Alan 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.
- Soliveres, Santiago, Peter Manning, Daniel Prati, Martin M. Gossner, Fabian Alt, Hartmut Arndt, Vanessa Baumgartner, Julia Binkenstein, Klaus Birkhofer, Stefan 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.
- Srivastava, Diane S. & Mark 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, United Kingdom: Cambridge University Press, pp. 86–106.

CHAPTER 2. BACKGROUND

- Staver, A. Carla, Judith Botha & Lars 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, Bastian, Andy Hector, Thomas Friedl, Christian Löfke, Maike Lorenz, Moritz Wesche & Michael Kessler (2012). ‘Biodiversity effects on ecosystem functioning change along environmental stress gradients’. In: *Ecology Letters* 15.12. Ed. by Mark Gessner, pp. 1397–1405. DOI: 10.1111/j.1461-0248.2012.01863.x.
- Stevens, N., C. E. R. Lehmann, B. P. Murphy & G. Durigan (2016a). ‘Savanna woody encroachment is widespread across three continents’. In: *Global Change Biology* 23.1, pp. 235–244. DOI: 10.1111/gcb.13409.
- Stevens, Nicola, B. F. N. Erasmus, S. Archibald & W. J. Bond (2016b). ‘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.
- Still, Christopher J., Joseph A. Berry, G. James Collatz & Ruth 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, Kyle W., Frank J. Sterck, Frans Bongers, Dulce A. da Silva, Eduardo R. M. Barbosa, David Ward, Freek T. Bakker, Martijn van Kaauwen, Herbert H. T. Prins, Steven 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, Mireia, Ted R. Feldpausch, Elmar Veenendaal, Franziska Schrödt, Gustavo Saiz, Tomas F. Domingues, Gloria Djagbletey, Andrew Ford, Jeanette Kemp, Beatriz 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.
- Turnbull, Lindsay A., Forest Isbell, Drew W. Purves, Michel Loreau & Andy 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.
- Urban, Josef, Miles Ingwers, Mary Anne McGuire & Robert O. Teskey (2017). ‘Stomatal conductance increases with rising temperature’. In: *Plant Signaling and Behavior* 12.8, pp. 1–4. DOI: 10.1080/15592324.2017.1356534.
- Vadigi, Snehalatha & David 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, Joseph W, Elise Buisson, Giselda Durigan, G Wilson Fernandes, Soizig Le Stradic, Gregory Mahy, Daniel Negreiros, Gerhard E Overbeck, Robin G Veldman, Nicholas 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.
- Veldman, Joseph 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.
- Vergles, E., H. Djoudi, R R Blackie, C Koffi 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.
- Violle, Cyrille, Wilfried Thuiller, Nicolas Mouquet, François Munoz, Nathan J. B. Kraft, Marc W. Cadotte, Stuart W. Livingstone & David Mouillot (2017). ‘Functional Rarity: The Ecology of Outliers’. In: *Trends in Ecology and Evolution* 32.5, pp. 356–367. DOI: 10.1016/j.tree.2017.02.002.
- Vitousek, Peter M, Harold a Mooney, Jane Lubchenco & Jerry 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, Julia L., A. Carla Staver & William 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, United Kingdom: Oliver and Boyd.
- Watson, James E. M., Kendall R. Jones, Richard A. Fuller, Moreno Di Marco, Daniel B. Segan, Stuart H. M. Butchart, James R. Allan, Eve McDonald-Madden & Oscar 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, Jake F. & Guy 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:focrsa]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, Guido R. van der, James T. Randerson, Louis Giglio, Thijs T. van Leeuwen, Yang Chen, Brendan M. Rogers, Mingquan Mu, Margreet J. E. van Marle, Douglas C. Morton, G. James 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.
- 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.

CHAPTER 2. BACKGROUND

- Wigley, Benjamin J., A. Carla Staver, Roma Zytkowiak, Andrzej M. Jagodzinski & Corli 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. Kreček. Dordrecht, Netherlands: Springer. Chap. Changing F, pp. 99–113.
- Williams, Mathew, Paul A. Schwarz, Beverly E. Law, James Irvine & Meredith 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 and Evolution* 32, pp. 383–390. DOI: 10.1016/j.tree.2017.02.011.
- Wright, Alexandra J., Kathryn E. Barry, Christopher J. Lortie & Ragan 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 Mark Rees, pp. 1962–1968. DOI: 10.1111/1365-2745.13665.
- Wunder, Sven, Arild Angelsen & Brian 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, Xiangtao, David Medvigy & Ignacio 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, Yu, Han Y. H. Chen & Peter 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**

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., 2005). 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) (Brokerhoff 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 km² (Hopkins & White, 1987; 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 car-

bon/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 ($<2500 \text{ km}^2$), biodiversity shows a strong effect on ecosystem function, but at broader extents ($>100,000 \text{ km}^2$) 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. Relatedly, 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, Hopkins & White, 1987). 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 (Hopkins & White, 1987), 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 20x50 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):

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

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, using the BioClim variables (Fick & Hijmans, 2017). 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 gridded soil information 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’ package in R (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 ($E_{H'}$) (Smith & Wilson, 1996) was calculated as the ratio of the estimated Shannon diversity index to the natural log of estimated species richness. 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 CoV) and tree height (Height CoV).

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 description of each vegetation cluster 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.

Table 3.1: Description of the biogeographical clusters to which each plot in the study was assigned. Indicator species were generated using Dufrene-Legendre indicator species analysis (Dufrêne & Legendre, 1997) implemented with `indval()` from the `labdsv` R package (Roberts, 2019) and represent species which define the given cluster. Dominant species were identified by choosing the species with the largest mean plot level proportional AGB (Above-Ground woody Biomass) within each cluster. N = number of plots in cluster. Numeric values of species richness, stems ha^{-1} and AGB represent medians and interquartile ranges (75th percentile - 25th percentile).

Cluster	Dominant species	Indicator species	N	Species Richness	Stem density (stems ha^{-1})	AGB (t ha^{-1})
Core miombo	<i>Brachystegia spiciformis</i>	<i>Parinari curatellifolia</i>	523	20(16.9)	204(142.5)	44.2(36.11)
	<i>Julbernardia paniculata</i>	<i>Uapaca kirkiana</i>				
	<i>Brachystegia boehmii</i>	<i>Brachystegia spiciformis</i>				
ex-Acacia	<i>Spirostachys africana</i>	<i>Euclea racemosa</i>	188	12(10.3)	181(166.5)	44.5(61.33)
	<i>Senegalia burkei</i>	<i>Vachellia nilotica</i>				
	<i>Senegalia nigrescens</i>	<i>Spirostachys africana</i>				
Mopane	<i>Colophospermum mopane</i>	<i>Colophospermum mopane</i>	58	10(10.2)	186(125.6)	22.7(32.83)
	<i>Androstachys johnsonii</i>	<i>Psuedolachnostylis maprouneifolia</i>				
	<i>Kirkia acuminata</i>	<i>Lannea discolor</i>				
Sparse miombo / Baikiaeae	<i>Baikiaea plurijuga</i>	<i>Burkea africana</i>	466	12(13.7)	178(129.5)	26.9(26.98)
	<i>Burkea africana</i>	<i>Baikiaea plurijuga</i>				
	<i>Pterocarpus angolensis</i>	<i>Pterocarpus angolensis</i>				

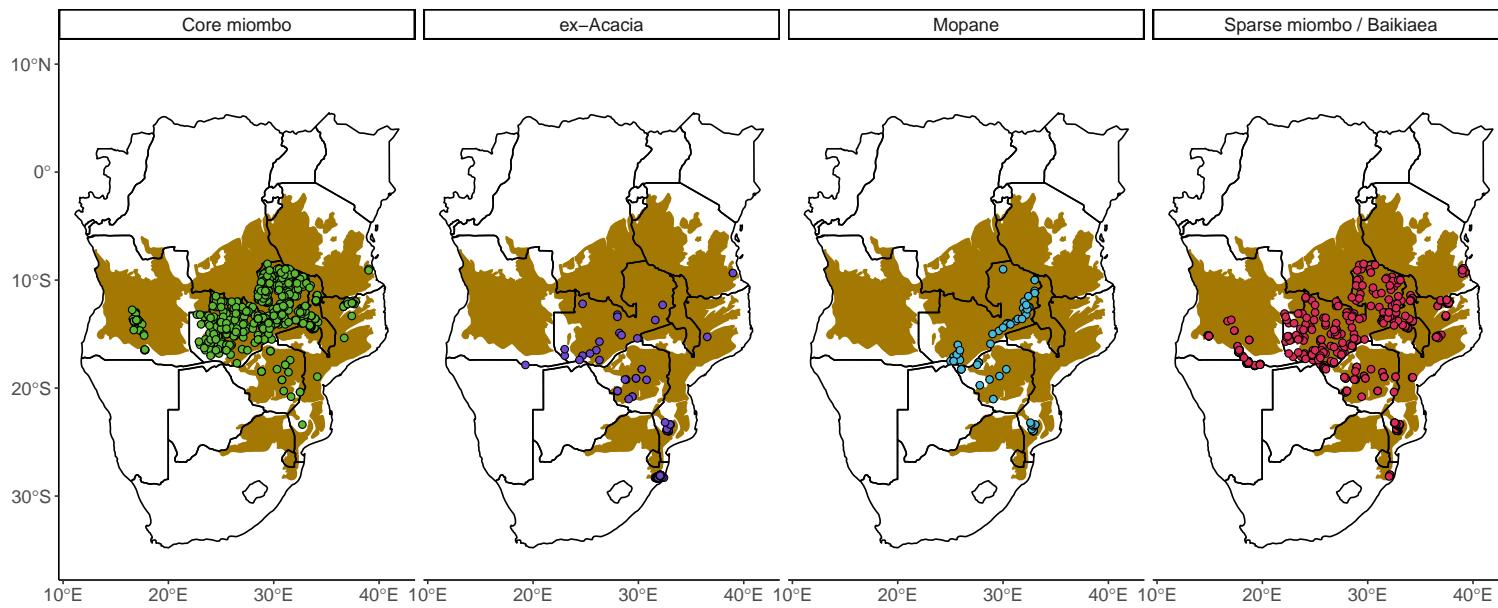


Figure 3.1: The locations of the 1235 plots used in this study, with respect to the distribution of mesic savanna vegetation according to Hopkins & White (1987). Each panel shows plots categorized by their vegetation type as defined by the vegetation types in Table 3.1.

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 3.6.0 (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).

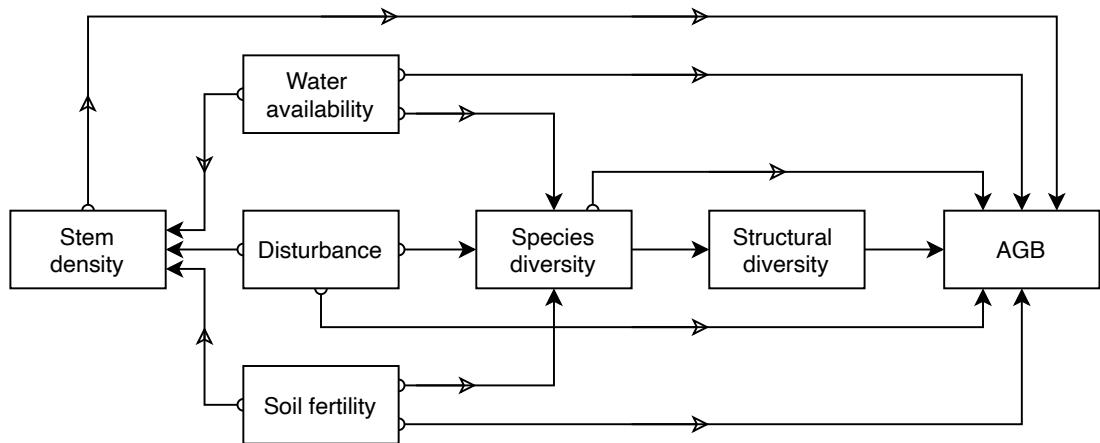


Figure 3.2: Conceptual Directed Acyclic Graph (DAG) showing the theoretical relationships between environmental factors, tree species diversity, tree structural diversity, stem density, and AGB (Above-Ground Woody Biomass). Hypothesised paths of causation are depicted as arrows from predictor to response.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

Observed variables were transformed to achieve normality where necessary

and standardised to Z-scores prior to analysis (Figure S1, Figure 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 loadings of the observed variable assumed to contribute most to each latent variable were set to one, as per convention, with other observed 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 loadings 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 (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 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 CoV: $r = 0.11$, $p < 0.01$, Height CoV: $r = 0.01$, $p = 0.86$).

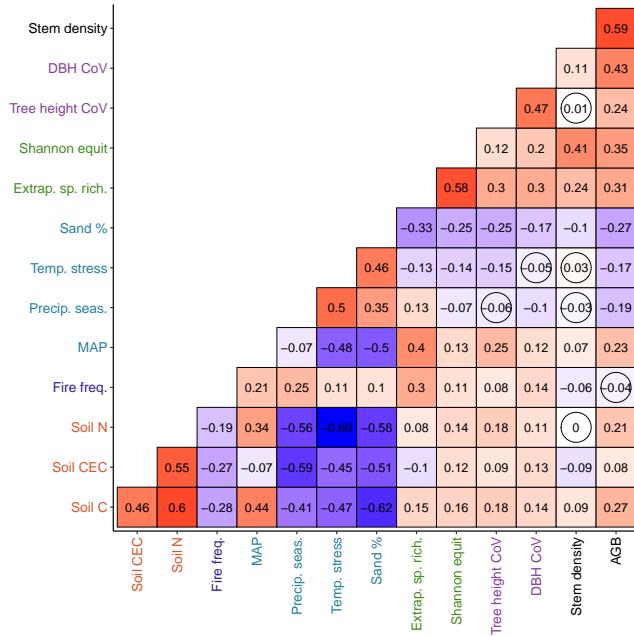


Figure 3.3: Correlation matrix of standardised observed variables used in the SEMs (Structural Equation Models), with Pearson correlation coefficients (r) coloured according to sign (+ve red, -ve blue) and shaded by strength of correlation. Correlation coefficients marked by a circle indicate that the 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 S1 for a full assessment of correlation fit statistics.

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 ($\beta = 0.01 \pm 0.053$, $p = 0.88$), but did have an indirect positive effect via structural diversity ($\beta = 0.18 \pm 0.039$, $p < 0.01$) (Figure 3.4). Model fit was good with high factor loadings for all observed variables. All other path coefficients were significant ($p < 0.01$) (Table 3.2). The R^2 of AGB was 0.49. The strongest direct effect on AGB was from stem density ($\beta = 0.5 \pm 0.033$, $p < 0.01$).

Table 3.2: 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 = R-squared of AGB (Above-Ground Biomass).

Cluster	N	χ^2	DoF	CFI	TLI	RMSEA	R^2 AGB
Core miombo	523	78.670	6	0.904	0.759	0.140	0.490
ex-Acacia	188	9.570	6	0.952	0.879	0.130	0.830
Mopane	58	19.880	6	0.834	0.584	0.240	0.510
Sparse miombo / Baikiaea	466	43.870	6	0.914	0.784	0.130	0.580
All	1235	91.380	6	0.937	0.843	0.120	0.490

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 ($\beta = 0.16 \pm 0.121$, $p = 0.18$) but negligible in Mopane ($\beta = 0.24 \pm 0.099$, $p < 0.05$), sparse miombo / *Baikiaea* ($\beta = 0.23 \pm 0.045$, $p < 0.01$) and Core miombo ($\beta = 0.23 \pm 0.041$, $p < 0.01$) (Figure 3.5). Relationships among 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 sparse miombo / *Baikiaea* ($R^2 = 0.46$). The total effect of species diversity on

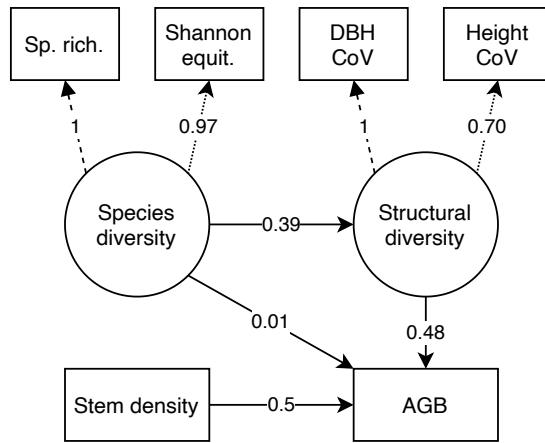


Figure 3.4: Path diagram with regression coefficients for the tree diversity SEM (Structural Equation Model), including plots from all vegetation clusters. Latent variables are shown as circles while observed variables are shown as rectangles. Standardised path coefficients are shown as solid arrows 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 loadings set to one are connected by dashed arrows. Measurement errors of exogenous variables are omitted for clarity.

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 3.2), 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-AGB relationship 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

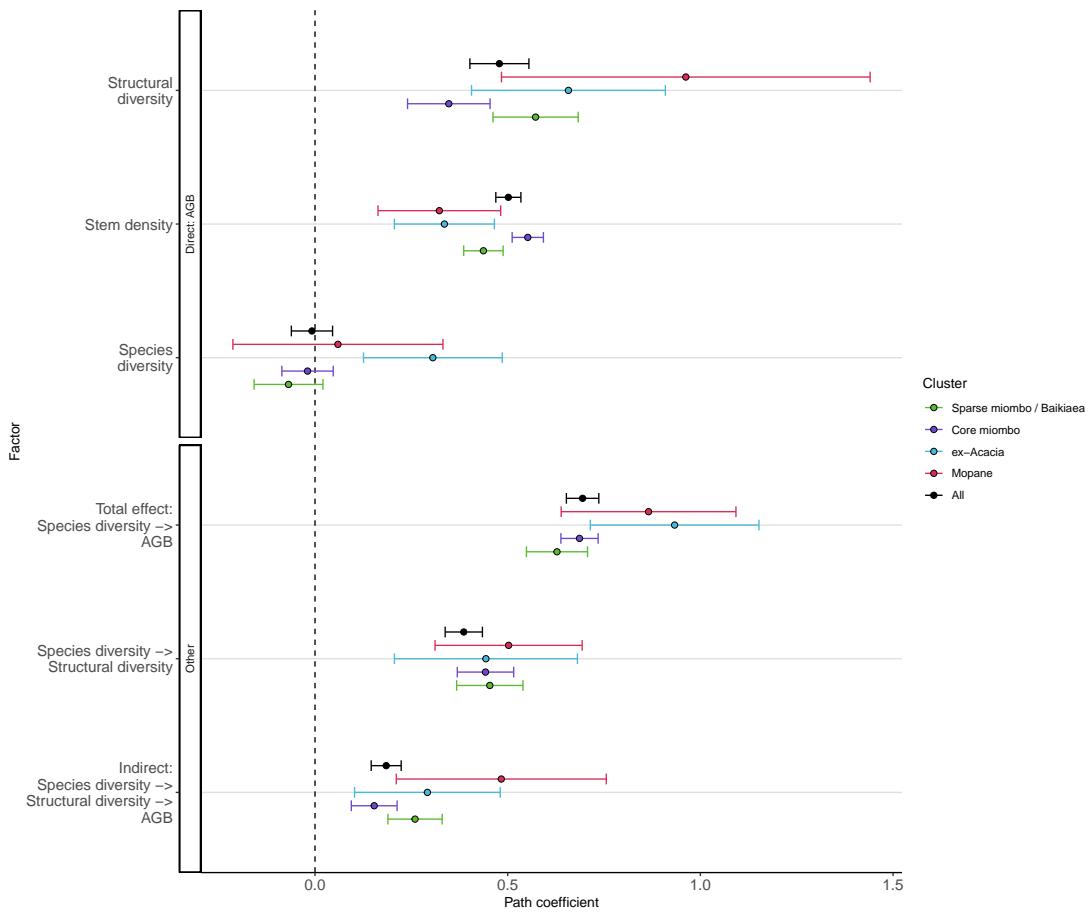


Figure 3.5: Unstandardised path coefficients for the effects of tree diversity on AGB (Above-Ground Woody Biomass), mediated by the effect of stand structural diversity. Path coefficients are ± 1 standard error. Path coefficients where the interval (standard error) does not overlap zero are considered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

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 S4). The direct effects of water availability, soil fertility and disturbance on AGB were negligible (water: $\beta = 0.1 \pm 0.13$, $p = 0.43$, soil: $\beta = 0.1 \pm 0.155$, $p = 0.51$, disturbance: $\beta = -0.04 \pm 0.043$, $p = 0.32$), with nearly all of their observed effects on AGB coming from the indirect paths via stem density (water:

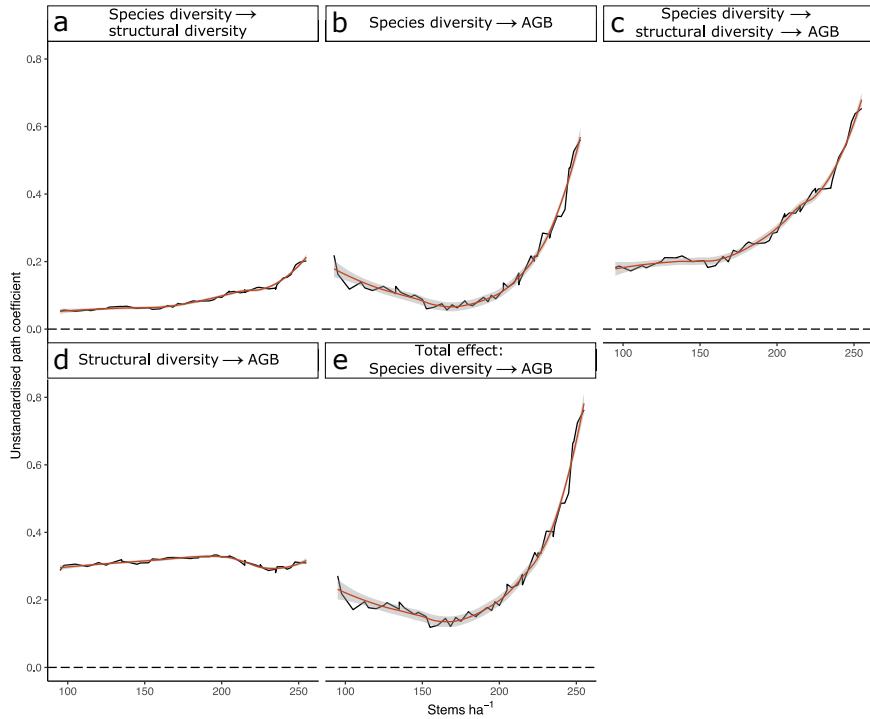


Figure 3.6: Line plots showing the variation in SEM (Structural Equation Model) path coefficients among latent variables, across datasets with different mean stem density. Smoothed lines are loess curves with ± 1 standard error shaded bars. AGB = Above-Ground woody Biomass. Arrows in plot titles indicate 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.

$\beta = 0.14 \pm 0.091$, $p = 0.12$, soil: $\beta = -0.22 \pm 0.109$, $p < 0.05$, disturbance: $\beta = -0.12 \pm 0.03$, $p < 0.01$) and species diversity (water: $\beta = 0.62 \pm 0.172$, $p < 0.01$, soil: $\beta = -0.24 \pm 0.209$, $p = 0.26$, disturbance: $\beta = 0.19 \pm 0.058$, $p < 0.01$). MAP and soil sand content had the greatest contributions to the latent variable of water availability. Model fit was acceptable: CFI = 0.925, TLI = 0.900, and RMSEA = 0.153, R² 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 di-

versity ($\beta = 0.19 \pm 0.026$, $p < 0.01$) when environmental covariates were accounted for. Again, the direct effect of species diversity on AGB was negligible ($\beta = -0.05 \pm 0.041$, $p = 0.27$). The total effect of species diversity on AGB was positive ($\beta = 0.34 \pm 0.044$, $p < 0.01$). 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.

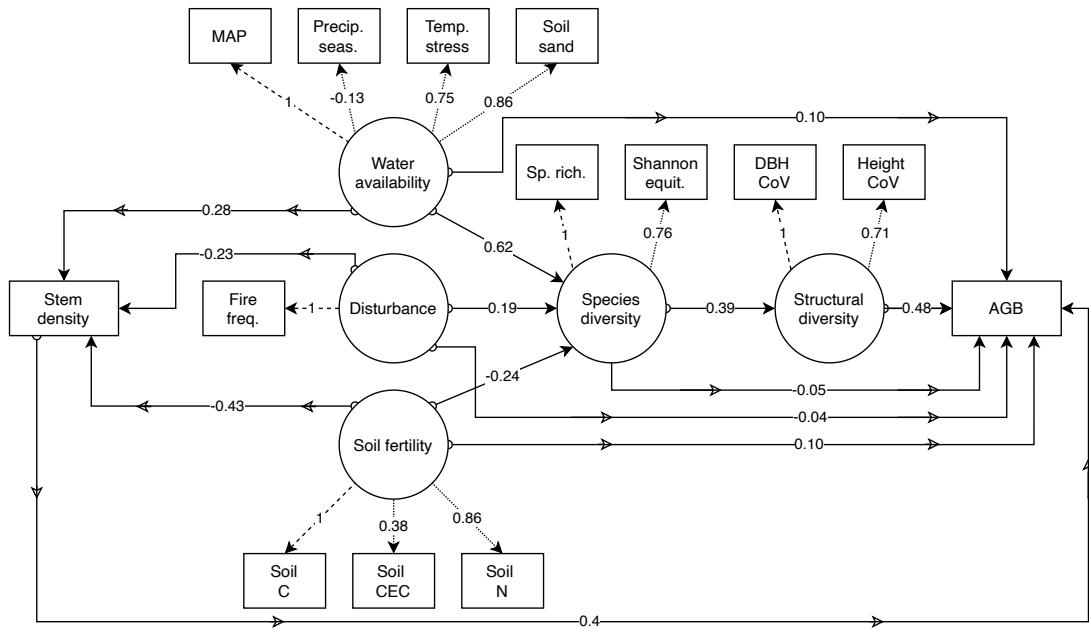


Figure 3.7: Path diagram with regression coefficients for the SEM (Structural Equation Model) incorporating environmental covariates and tree species and structural diversity across all five vegetation types. Latent variables are shown as circles while observed variables are shown as rectangles. Standardised 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.

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 3.2). Within the latent variable of tree species diversity we found similarly strong factor loadings 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, 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 H₂. 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 sparse miombo / 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 Conclusions

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.
- (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 Cannière, 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.
- Brockhoff, Eckehard G., Luc Barbaro, Bastien Castagnéyrol, David I. Forrester, Barry Gardiner, José Ramón González-Olabarria, Phil O'B. Lyver, Nicolas Meurisse, Anne Oxbrough, Hisatomo 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, Gabriela & Niall 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, Bradley J., Diane S. Srivastava, J. Emmett Duffy, Justin P. Wright, Amy L. Downing, Mahesh Sankaran, Claire Jouseau, Marc W Cadotte, Ian T. Carroll, Jerome 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. Bürquez, 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. [Accessed 2020-04-20].
- 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.
- 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. Sarraih, 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, Andy & Robert Bagchi (2007). ‘Biodiversity and ecosystem multifunctionality’. In: *Nature* 448.7150, pp. 188–190. DOI: 10.1038/nature05947.

- Hempson, Gareth P., Sally Archibald & William 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.
- Hopkins, B. & F. White (1987). ‘Vegetation Map of Africa. The vegetation of Africa: A descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa’. In: *The Journal of Ecology* 75. DOI: 10.2307/2260340.
- 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* 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, Kurt (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, Fensham 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 relation-

- ship predominant in global forests'. In: *Science* 354.6309, aaf8957–aaf8957. DOI: 10.1126/science.aaf8957.
- Loiola, Priscilla P., Michael Scherer-Lorenzen & Marco Antônio 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, Sylvanus, Valère K. Salako & Thomas 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 and Evolution* 29, pp. 205–213. DOI: 10.1016/j.tree.2014.02.004.
- Paul, K. I., J. Larmour, Spechtm 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. Alarcón, J. Álvarez-Sánchez, N. Ascarrunz, P. Balvanera, G. Barajas-Guzmán, 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, pp. 1–36. URL: <http://www.jstatsoft.org/v48/i02/>.
- Ryan, Casey M., Rose Pritchard, Iain McNicol, Matthew Owen, Janet A Fisher & Caroline 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, Mahesh, Jayashree Ratnam & Niall 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, United Kingdom: 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 (2005). 'Confounding factors in the observational productivity-diversity relationship in forests'. In: *Ecological Studies* 176, pp. 65–86.
- 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 and 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.2> Dryad.

CHAPTER 3. REGIONAL BIODIVERSITY-BIOMASS RELATIONSHIP

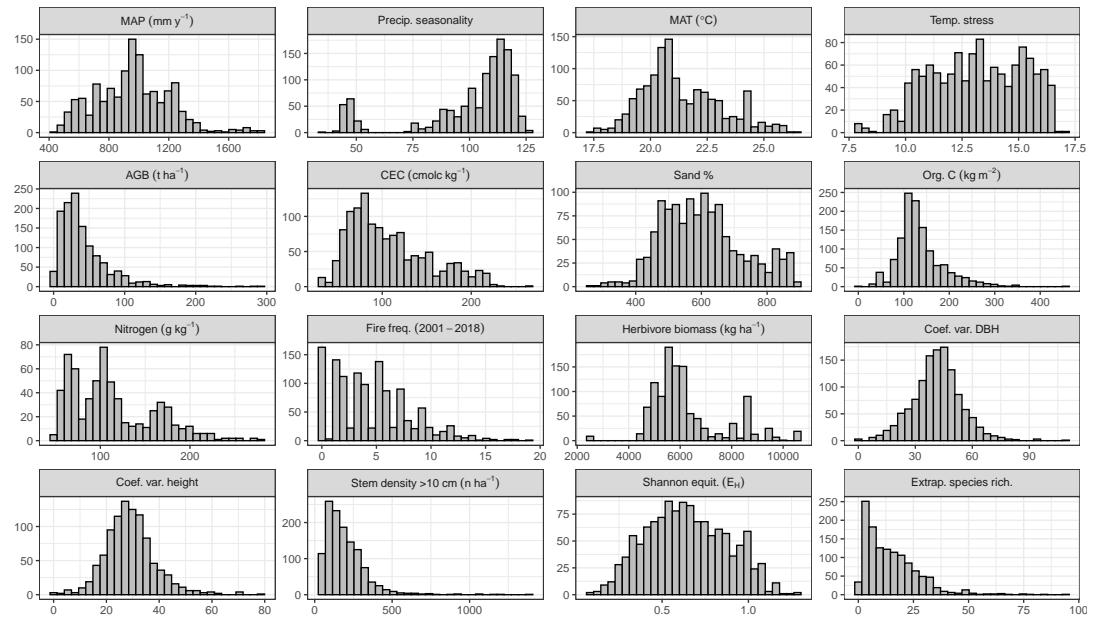


Figure 3.S1: Histograms of raw untransformed observed variables used in final analyses.

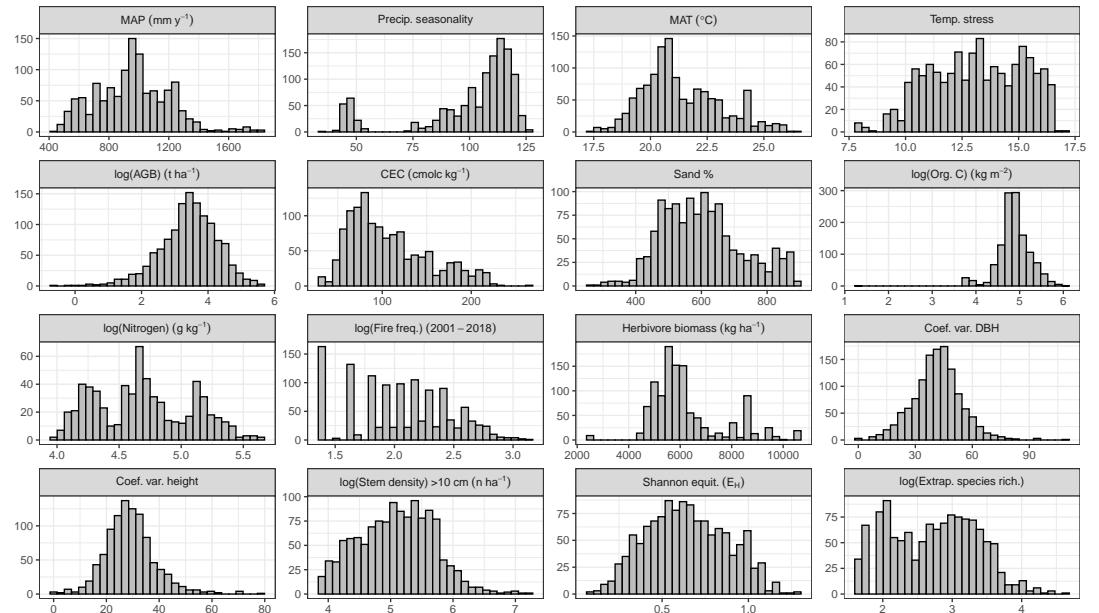


Figure 3.S2: Histograms of observed variables transformed to achieve a normal frequency distribution.

3.6 Supplementary Material

X	Y	r	Lower bound	Upper bound	n	Prob.
Soil CEC	Soil C	0.260	0.210	0.310	1239	p <0.01
Soil N	Soil C	0.850	0.820	0.870	644	p <0.01
Fire freq.	Soil C	-0.070	-0.130	-0.010	1239	p <0.05
MAP	Soil C	0.510	0.460	0.550	1239	p <0.01
Precip. seas.	Soil C	-0.560	-0.600	-0.520	1239	p <0.01
Temp. stress	Soil C	-0.630	-0.670	-0.600	1239	p <0.01
Sand %	Soil C	-0.570	-0.610	-0.540	1239	p <0.01
Extrap. sp. rich.	Soil C	0.250	0.200	0.300	1239	p <0.01
Shannon equit	Soil C	0.230	0.180	0.280	1239	p <0.01
Tree height CoV	Soil C	0.230	0.170	0.290	981	p <0.01
DBH CoV	Soil C	0.160	0.110	0.220	1237	p <0.01
Stem density	Soil C	0.070	0.020	0.130	1239	p <0.05
AGB	Soil C	0.260	0.210	0.320	1239	p <0.01

Table 3.S1: Correlation fit statistics for soil C and other variables identified in path analysis. Showing the Pearson correlation coefficient (r), the 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 bound	Upper bound	n	Prob.
Soil N	Soil CEC	0.440	0.370	0.500	644	p <0.01
Fire freq.	Soil CEC	-0.470	-0.510	-0.430	1239	p <0.01
MAP	Soil CEC	-0.280	-0.330	-0.220	1239	p <0.01
Precip. seas.	Soil CEC	-0.710	-0.730	-0.680	1239	p <0.01
Temp. stress	Soil CEC	-0.250	-0.300	-0.200	1239	p <0.01
Sand %	Soil CEC	-0.210	-0.270	-0.160	1239	p <0.01
Extrap. sp. rich.	Soil CEC	-0.380	-0.430	-0.330	1239	p <0.01
Shannon equit	Soil CEC	-0.090	-0.150	-0.040	1239	p <0.01
Tree height CoV	Soil CEC	-0.110	-0.170	-0.050	981	p <0.01
DBH CoV	Soil CEC	-0.010	-0.070	0.040	1237	p = 0.62
Stem density	Soil CEC	-0.020	-0.080	0.030	1239	p = 0.43
AGB	Soil CEC	-0.040	-0.090	0.020	1239	p = 0.17

Table 3.S2: Correlation fit statistics for soil CEC and other variables identified in path analysis. Showing the Pearson correlation coefficient (r), the 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 bound	Upper bound	n	Prob.
Fire freq.	Soil N	-0.250	-0.320	-0.180	644	p <0.01
MAP	Soil N	0.370	0.300	0.440	644	p <0.01
Precip. seas.	Soil N	-0.760	-0.790	-0.730	644	p <0.01
Temp. stress	Soil N	-0.800	-0.820	-0.770	644	p <0.01
Sand %	Soil N	-0.660	-0.700	-0.610	644	p <0.01
Extrap. sp. rich.	Soil N	0.440	0.380	0.500	644	p <0.01
Shannon equit	Soil N	0.350	0.280	0.420	644	p <0.01
Tree height CoV	Soil N	0.270	0.180	0.360	386	p <0.01
DBH CoV	Soil N	0.260	0.180	0.330	642	p <0.01
Stem density	Soil N	-0.030	-0.110	0.050	644	p = 0.47
AGB	Soil N	0.310	0.240	0.380	644	p <0.01

Table 3.S3: Correlation fit statistics for soil N and other variables identified in path analysis. Showing the Pearson correlation coefficient (r), the 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 bound	Upper bound	n	Prob.
MAP	Fire freq.	0.370	0.320	0.420	1239	p <0.01
Precip. seas.	Fire freq.	0.360	0.310	0.410	1239	p <0.01
Temp. stress	Fire freq.	0.210	0.160	0.260	1239	p <0.01
Sand %	Fire freq.	0.060	0	0.110	1239	p <0.05
Extrap. sp. rich.	Fire freq.	0.380	0.340	0.430	1239	p <0.01
Shannon equit	Fire freq.	0.120	0.070	0.180	1239	p <0.01
Tree height CoV	Fire freq.	0.150	0.090	0.220	981	p <0.01
DBH CoV	Fire freq.	0.120	0.070	0.180	1237	p <0.01
Stem density	Fire freq.	-0.020	-0.070	0.040	1239	p = 0.52
AGB	Fire freq.	0.030	-0.030	0.080	1239	p = 0.33

Table 3.S4: Correlation fit statistics for fire frequency and other variables identified in path analysis. Showing the Pearson correlation coefficient (r), the 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 bound	Upper bound	n	Prob.
Precip. seas.	MAP	-0.070	-0.120	-0.010	1239	p <0.05
Temp. stress	MAP	-0.490	-0.530	-0.440	1239	p <0.01
Sand %	MAP	-0.330	-0.380	-0.280	1239	p <0.01
Extrap. sp. rich.	MAP	0.410	0.360	0.450	1239	p <0.01
Shannon equit	MAP	0.150	0.100	0.200	1239	p <0.01
Tree height CoV	MAP	0.250	0.190	0.300	981	p <0.01
DBH CoV	MAP	0.110	0.060	0.170	1237	p <0.01
Stem density	MAP	0.020	-0.030	0.080	1239	p = 0.47
AGB	MAP	0.240	0.180	0.290	1239	p <0.01

Table 3.S5: Correlation fit statistics for MAP and other variables identified in path analysis. Showing the Pearson correlation coefficient (r), the 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 bound	Upper bound	n	Prob.
Temp. stress	Precip. seas.	0.500	0.450	0.540	1239	p <0.01
Sand %	Precip. seas.	0.310	0.260	0.360	1239	p <0.01
Extrap. sp. rich.	Precip. seas.	0.120	0.070	0.180	1239	p <0.01
Shannon equit	Precip. seas.	-0.070	-0.120	-0.010	1239	p <0.05
Tree height CoV	Precip. seas.	-0.050	-0.110	0.010	981	p = 0.11
DBH CoV	Precip. seas.	-0.100	-0.150	-0.040	1237	p <0.01
Stem density	Precip. seas.	-0.040	-0.100	0.010	1239	p = 0.12
AGB	Precip. seas.	-0.180	-0.230	-0.130	1239	p <0.01

Table 3.S6: Correlation fit statistics for precipitation seasonality and other variables identified in path analysis. Showing the Pearson correlation coefficient (r), the 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 bound	Upper bound	n	Prob.
Sand %	Temp. stress	0.300	0.250	0.350	1239	p <0.01
Extrap. sp. rich.	Temp. stress	-0.130	-0.180	-0.070	1239	p <0.01
Shannon equit	Temp. stress	-0.130	-0.180	-0.070	1239	p <0.01
Tree height CoV	Temp. stress	-0.140	-0.200	-0.080	981	p <0.01
DBH CoV	Temp. stress	-0.040	-0.100	0.010	1237	p = 0.12
Stem density	Temp. stress	0.030	-0.020	0.090	1239	p = 0.27
AGB	Temp. stress	-0.170	-0.220	-0.110	1239	p <0.01

Table 3.S7: Correlation fit statistics for temperature stress and other variables identified in path analysis. Showing the Pearson correlation coefficient (r), the 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 bound	Upper bound	n	Prob.
Extrap. sp. rich.	Sand %	-0.270	-0.320	-0.220	1239	p <0.01
Shannon equit	Sand %	-0.210	-0.260	-0.160	1239	p <0.01
Tree height CoV	Sand %	-0.240	-0.300	-0.180	981	p <0.01
DBH CoV	Sand %	-0.160	-0.210	-0.100	1237	p <0.01
Stem density	Sand %	-0.140	-0.190	-0.080	1239	p <0.01
AGB	Sand %	-0.220	-0.270	-0.160	1239	p <0.01

Table 3.S8: Correlation fit statistics for soil sand content and other variables identified in path analysis. Showing the Pearson correlation coefficient (r), the 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 bound	Upper bound	n	Prob.
Shannon equit	Extrap. sp. rich.	0.600	0.560	0.630	1249	p <0.01
Tree height CoV	Extrap. sp. rich.	0.310	0.250	0.360	981	p <0.01
DBH CoV	Extrap. sp. rich.	0.320	0.260	0.360	1247	p <0.01
Stem density	Extrap. sp. rich.	0.230	0.170	0.280	1249	p <0.01
AGB	Extrap. sp. rich.	0.330	0.280	0.380	1249	p <0.01

Table 3.S9: Correlation fit statistics for species richness and other variables identified in path analysis. Showing the Pearson correlation coefficient (r), the 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 bound	Upper bound	n	Prob.
Tree height CoV	Shannon equit	0.140	0.070	0.200	981	p <0.01
DBH CoV	Shannon equit	0.230	0.170	0.280	1247	p <0.01
Stem density	Shannon equit	0.410	0.360	0.450	1249	p <0.01
AGB	Shannon equit	0.380	0.330	0.420	1249	p <0.01

Table 3.S10: Correlation fit statistics for shannon equitability and other variables identified in path analysis. Showing the Pearson correlation coefficient (r), the 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 bound	Upper bound	n	Prob.
DBH CoV	Tree height CoV	0.490	0.440	0.540	981	p <0.01
Stem density	Tree height CoV	0	-0.060	0.060	981	p = 0.95
AGB	Tree height CoV	0.240	0.180	0.300	981	p <0.01

Table 3.S11: Correlation fit statistics for tree height variation and other variables identified in path analysis. Showing the Pearson correlation coefficient (r), the 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 bound	Upper bound	n	Prob.
Stem density	DBH CoV	0.110	0.050	0.160	1247	p <0.01
AGB	DBH CoV	0.440	0.400	0.490	1247	p <0.01

Table 3.S12: Correlation fit statistics for DBH variation and other variables identified in path analysis. Showing the Pearson correlation coefficient (r), the 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 bound	Upper bound	n	Prob.
AGB	Stem density	0.570	0.530	0.610	1249	p <0.01

Table 3.S13: Correlation fit statistics for stem density and other variables identified in path analysis. Showing the Pearson correlation coefficient (r), the correlation confidence interval upper and lower bounds, number of plots used in the correlation (n), and the p-value of the correlation (Prob.).

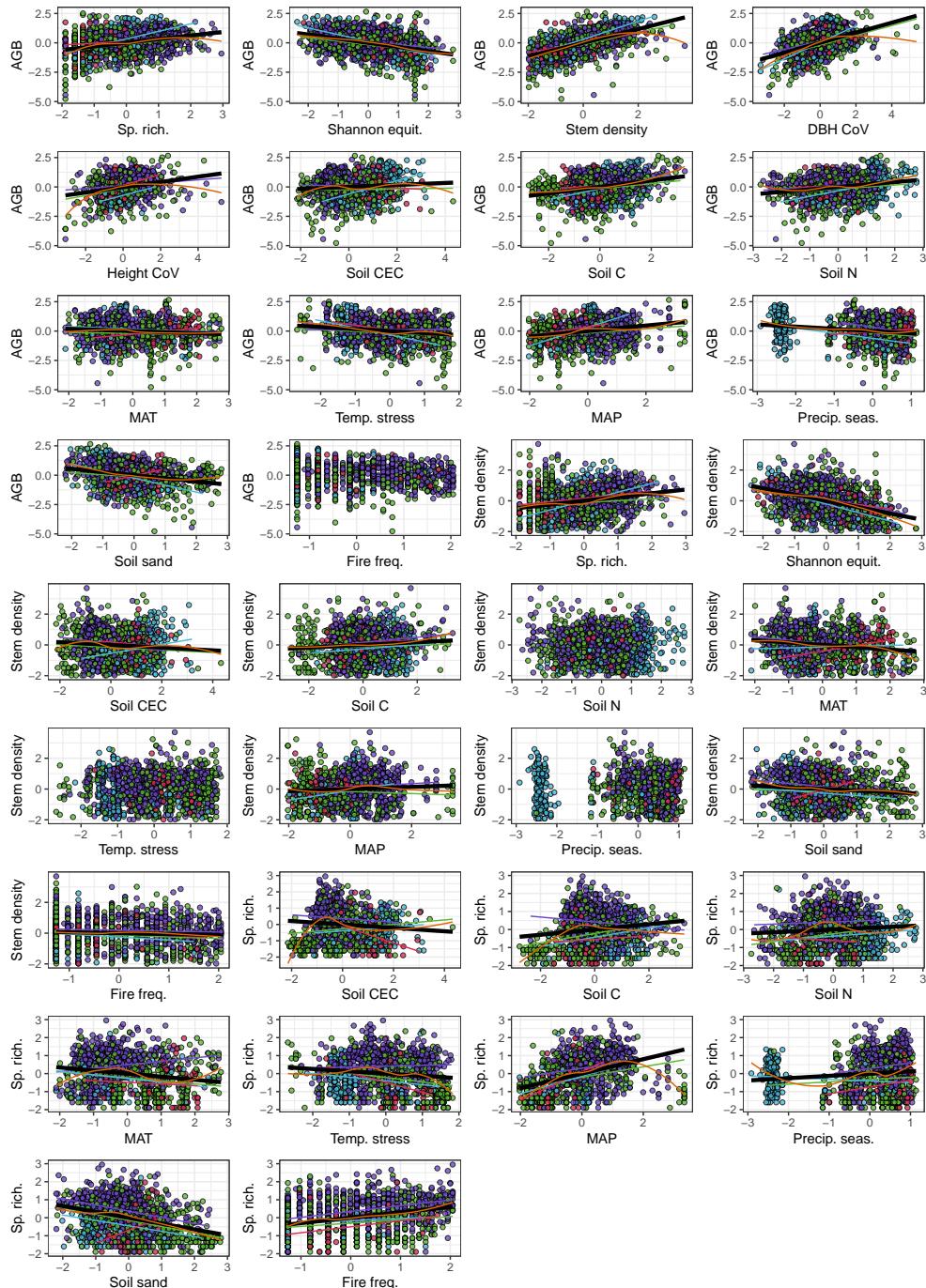


Figure 3.S3: Bivariate scatter plots for each observed variable used in the SEMs (Structural Equation Models), based on hypothesised paths of causality. Points are coloured according to vegetation type: green = Sparse miombo/Baikiaea, purple = Core miombo, blue = ex-Acacia, red = Mopane. The black line 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.

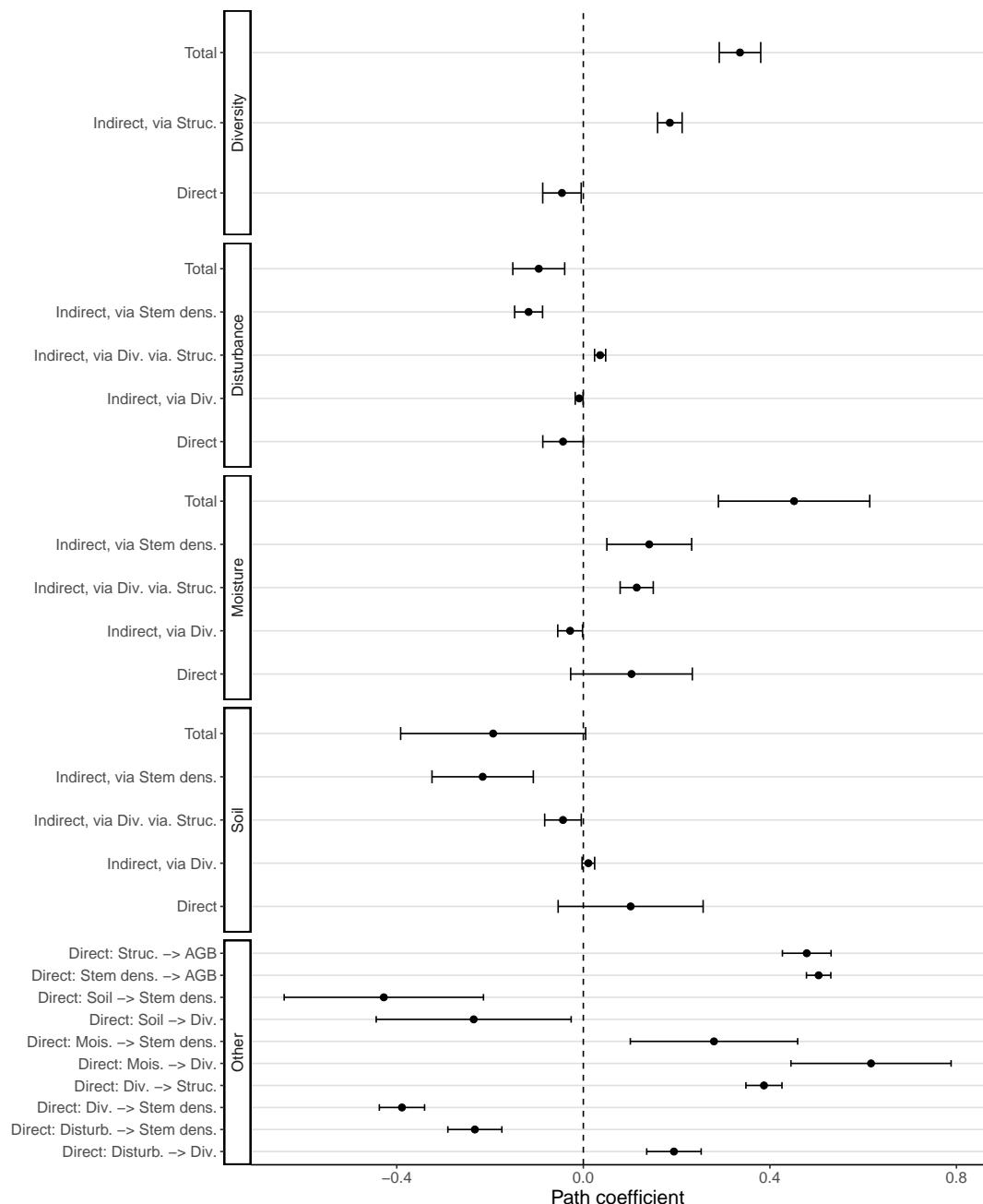


Figure 3.S4: Unstandardised path coefficients for the full model including tree species diversity, environmental covariates and stem density. Path coefficients are ± 1 standard error. Path coefficients where the interval (standard error) does not overlap zero are considered to be significant effects.

Chapter 4

Diversity mediates land-surface phenology in Zambian deciduous woodlands

This chapter was made by me, and some other people, and has been prepared for submission to dsfv davdfv.

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 season length in drier woodlands. We found variation among miombo and non-miombo vegetation types in their phenological patterns and biotic drivers of phenology. Finally, we found that species evenness had contrasting effects on phenology to species diversity, 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 are essential for earth system modelling approaches.

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. 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 20x50 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 ≥ 50 stems ha^{-1} ≥ 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.

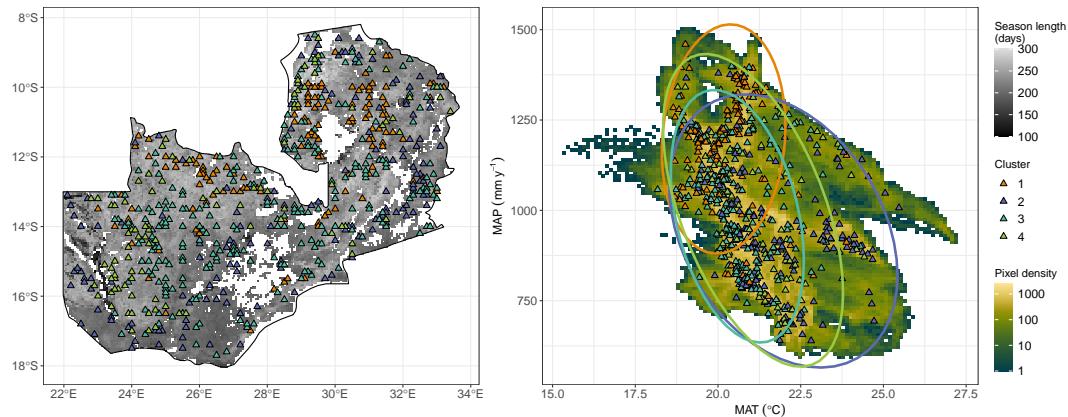


Figure 4.1: Distribution of study sites, within Zambia (left), and in climate space (right). Sites are shown as triangles, each consisting of four plots, coloured according to vegetation type cluster. Zambia is shaded according to growing season length, estimated by the MODIS VIPPHEN-EVI2 product, at 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.

Cluster	N sites	Richness	MAP	δT	Species	Indicator va
1	134	17(7)	1176(156.1)	13(1.5)	<i>Brachystegia longifolia</i>	0.397
					<i>Uapaca kirkiana</i>	0.390
					<i>Marquesia macroura</i>	0.285
2	144	14(5)	955(172.8)	14(1.6)	<i>Combretum molle</i>	0.258
					<i>Lannea discolor</i>	0.228
					<i>Combretum zeyheri</i>	0.214
3	243	17(6)	997(157.8)	14(1.5)	<i>Julbernardia paniculata</i>	0.559
					<i>Brachystegia boehmii</i>	0.540
					<i>Pseudolachnostylis maprouneifolia</i>	0.226
4	96	14(6)	1012(185.5)	14(1.7)	<i>Brachystegia spiciformis</i>	0.582
					<i>Cryptosepalum exfoliatum</i>	0.285
					<i>Guibourtia coleosperma</i>	0.281

Table 4.1: Climatic information and Dufrene-Legendre indicator species analysis for the vegetation type clusters identified by the PAM 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 δT (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.

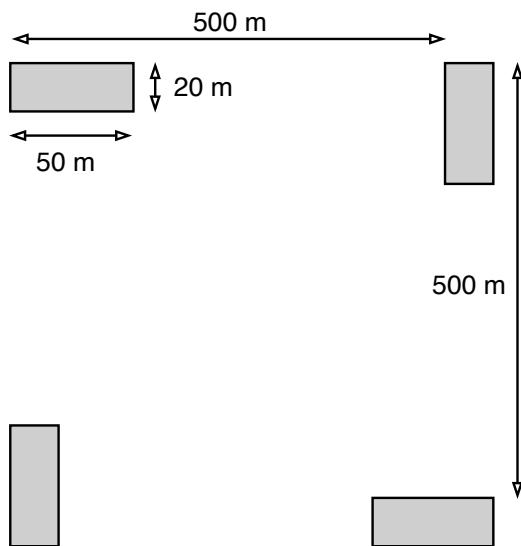


Figure 4.2: Schematic diagram of plot layout within a site. Each 20x50 m (0.1 ha) plot is shaded grey. Note that the plot dimensions are not to scale.

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 δT) 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

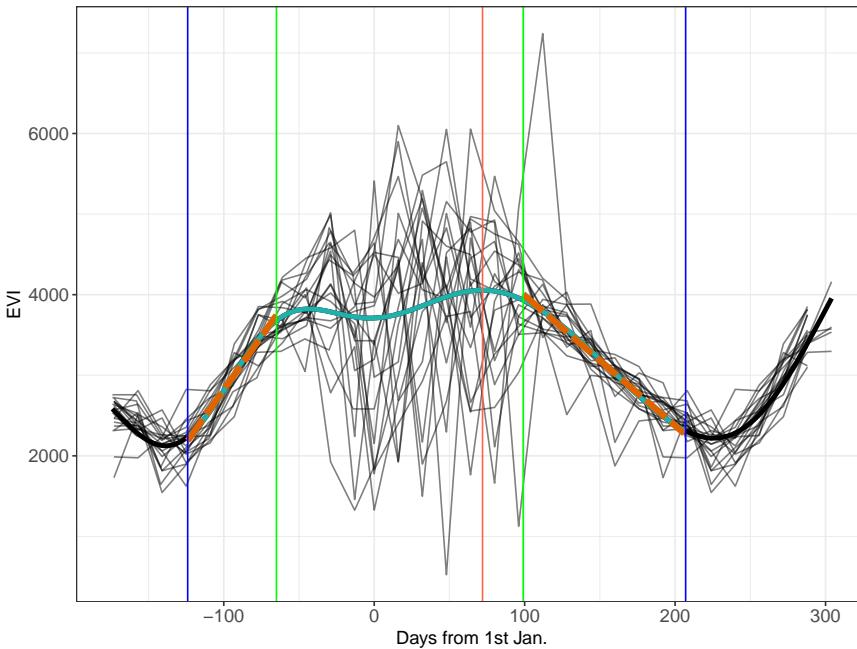


Figure 4.3: Example EVI time series, demonstrating the metrics derived from it. Thin black lines show the raw EVI time series, with one line for each annual growing season. The thick cyan line shows the GAM fit. The blue vertical lines show the minima which bound the growing season. The green vertical 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.

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 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 4.0.2 (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.

Vegetation type clusters exhibited some spatial and climatic stratification (Figure 4.1). The key emergent trends were that Cluster 1 was largely absent from the southwest of the country, occurring predominantly in higher rainfall regions. Cluster 4 dominated the southwest of the country, possibly representing drier Angolan miombo woodland (Table 4.1). Of the four vegetation clusters identified, Cluster 2, consists of small stature Zambesian 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. Median species richness and the range of species richness values per site is similar across 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.S8), 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 cumu-

lative EVI and a shorter growing season (Figure 4.7). A MANOVA including all 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.S9). 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).

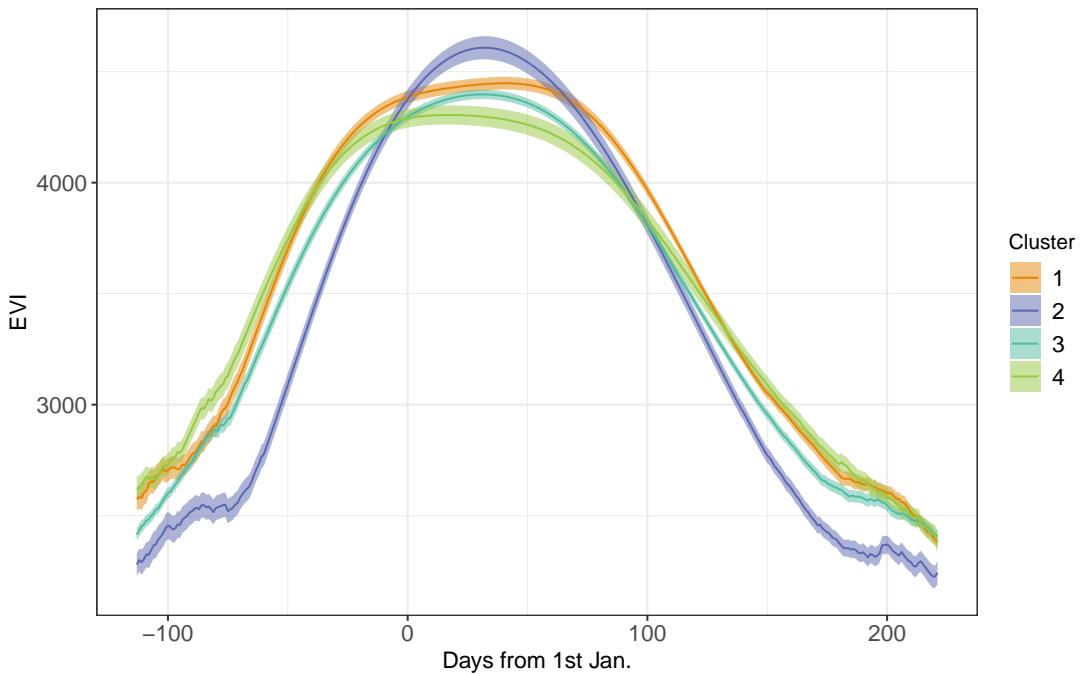


Figure 4.4: Mean GAMs of EVI over the growing season for each vegetation type cluster. Shaded ribbons are 95% confidence intervals.

	Response	δAIC	R^2_{adj}	$\delta \log Lik$
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	

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

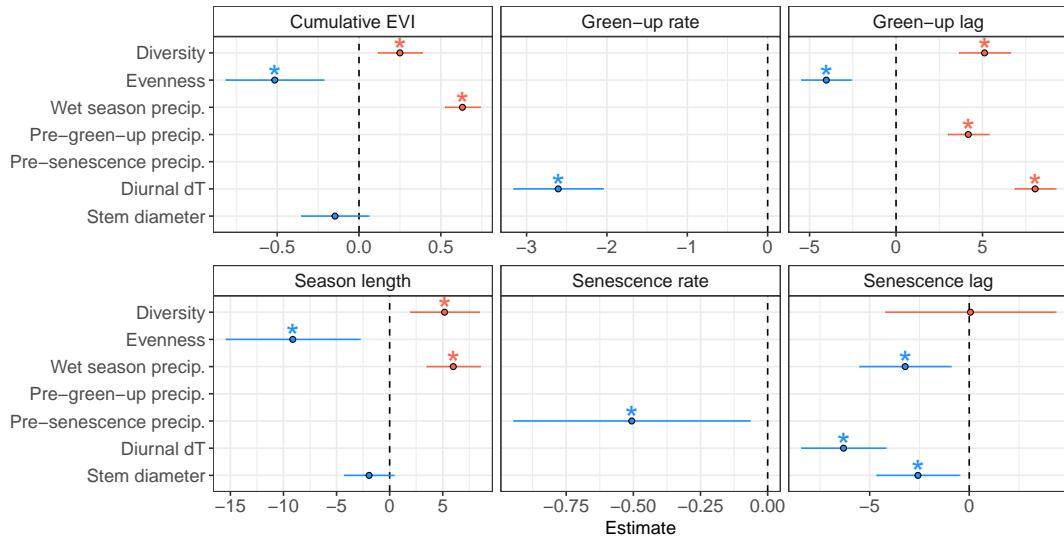


Figure 4.5: Standardized slope coefficients for each best model of a phenological metric. Slope estimates are ± 1 standard error. Slope estimates where the interval does not overlap zero are considered to be significant effects and are marked by asterisks.

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

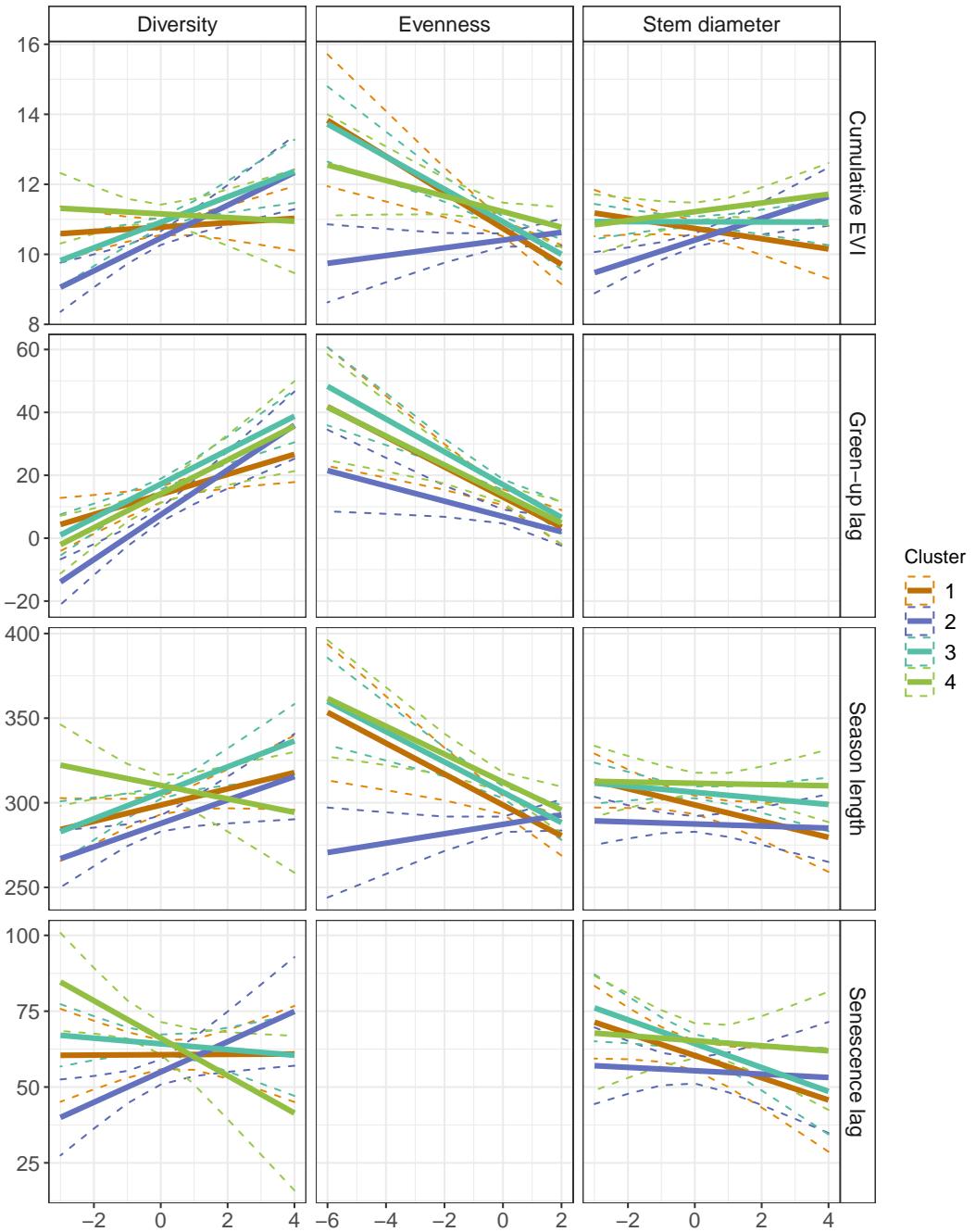


Figure 4.6: Marginal effects of tree species diversity, evenness, and tree size on each of the phenological metrics, using the maximal mixed effects model, for each vegetation cluster. Dotted lines represent 95% confidence intervals.

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

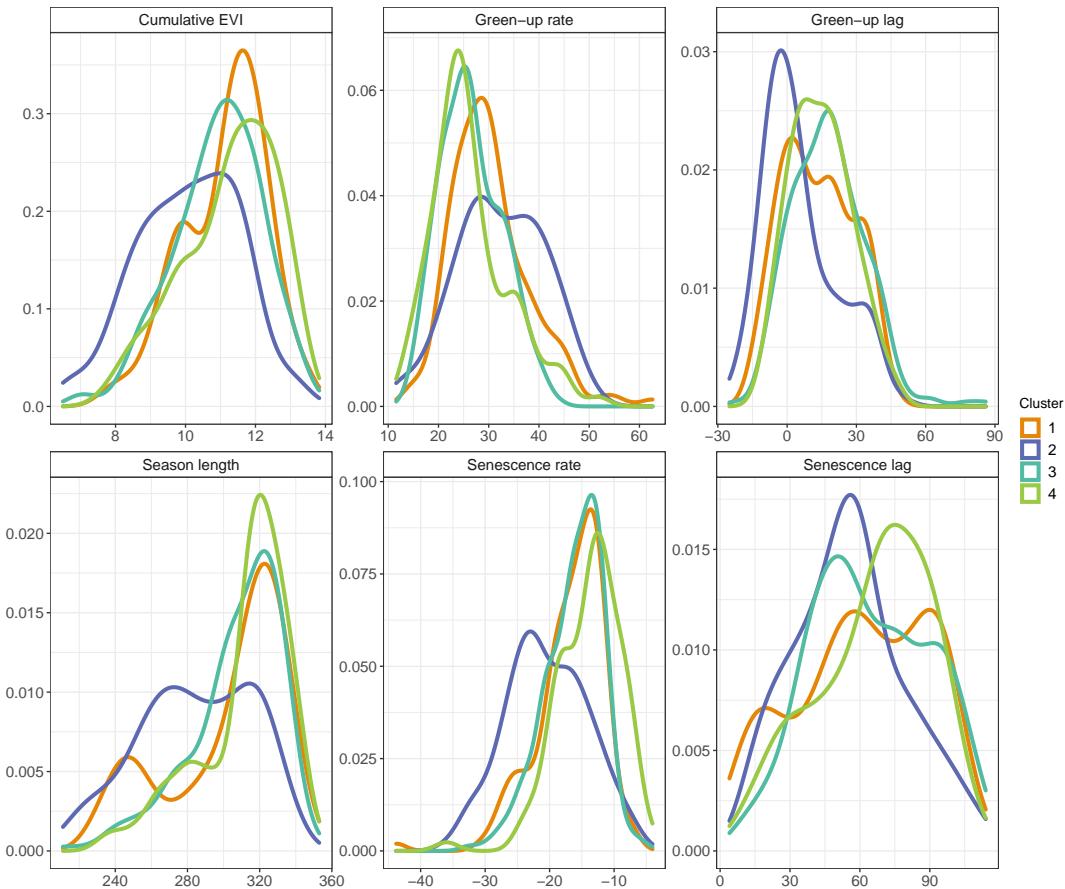


Figure 4.7: Density distribution of the six phenological metrics used in the study, grouped by vegetation cluster.

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, 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 also 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 Cluster 2, which 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. 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 (Stevens et al., 2016; 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 30.5°E, 11.5°S, and 23.0°E, 15.0°S. These regions are largely seasonally water-logged floodplain and swampland, 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 measurements used here aren't specific only to trees, they represent the landscape as a single unit. Nev-

ertheless, 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 contribute to gross primary productivity, 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 the role of tree species diversity, composition and woodland structure on 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 dominant species. 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 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.
- (2018b). ‘Large-scale prairie 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. Hodgkinson, 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. Van, 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: 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, Robert O. & David D. Marshall (2000). ‘Technical Note: Why Quadratic Mean Diameter?’ In: 15.3, pp. 137–139. DOI: 10.1093/wjaf/15.3.137.
- Dahlin, Kyla M., Dominick Del Ponte, Emily Setlock & Ryan 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, Joshua F., Jack J. Middelburg, Thomas Röckmann, Rien Aerts, Luke G. Blauw, Matthias Egger, Mike S. M. Jetten, Anniek E. E. de Jong, Ove H. Meisel, Olivia 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.

CHAPTER 4. DIVERSITY AND PHENOLOGY IN ZAMBIA

- 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, Eric, David Olson, Anup Joshi, Carly Vynne, Neil D. Burgess, Eric Wikramanayake, Nathan Hahn, Suzanne Palminteri, Prashant Hedao, Reed 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, Jean-Christophe, John S. King, Asko Noormets, Emrys Treasure, Michael J. Gavazzi, Ge Sun & Steven G. McNulty (2010). ‘Hydraulic redistribution of soil water by roots affects whole-stand evapotranspiration and net ecosystem carbon exchange’. In: 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, Daniel P., Peter R. Minchin & Lee 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: 30.3, pp. 169–176. DOI: 10.1016/j.tree.2015.01.004.
- Gárate-Escamilla, Homero, Craig C. Brelsford, Arndt Hampe, T. Matthew Robson & Marta Benito Garzón (2020). ‘Greater capacity to exploit warming temperatures in northern populations of European beech is partly driven by delayed leaf senescence’. In: 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*. Springer Netherlands, 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 & Jackson 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).
- 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.
- (2010). ‘The relation between evenness and diversity’. In: *Diversity* 2.2, pp. 207–232. doi: 10.3390/d2020207.
- Kreft, Holger & Walter 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, Charlie, Jenny Farmer, Mike Rivington & Jo U. Smith (2018). ‘Tropical wetland ecosystem service assessments in East Africa: A review of approaches and challenges’. In: 102, pp. 260–273. doi: 10.1016/j.envsoft.2018.01.022.
- Lasky, Jesse R., María Uriarte & Robert 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: 11.11, p. 115003. doi: 10.1088/1748-9326/11/11/115003.
- 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, Ingrid H., Pär K. Ingvarsson, Kathryn M. Robinson, Erik Edlund, Maria E Eriksson, Ove Nilsson & Stefan Jansson (2017). ‘Autumn senescence in aspen is not triggered by day length’. In: 162.1, pp. 123–134. doi: 10.1111/ppb.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, Grace Jopaul Loubota, Adeline Fayolle, Tommaso Jucker, Oliver L. Phillips, Stephanie Bohlman, Lindsay F. Banin, Simon L. Lewis, Kofi Affum-Baffoe, Luciana F. Alves, Cécile Antin et al. (2020). ‘Pantropical variability in tree crown allometry’. In: 30.2. Ed. by Andrew Kerkhoff, 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 and 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. Mbendo, 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: 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.
- Stevens, N., C. E. R. Lehmann, B. P. Murphy & G. Durigan (2016). ‘Savanna woody encroachment is widespread across three continents’. In: *Global Change Biology* 23.1, pp. 235–244. DOI: 10.1111/gcb.13409.
- 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, 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, Kailiang & Paolo D’Odorico (2015). ‘Hydraulic lift as a determinant of tree–grass coexistence on savannas’. In: 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: 370.6520, pp. 1066–1071. DOI: 10.1126/science.abd8911.
- Zhou, Yong, Benjamin J. Wigley, Madelon F. Case, Corli Coetsee & Ann Carla Staver (2020). ‘Rooting depth as a key woody functional trait in savannas’. In: 227.5, pp. 1350–1361. DOI: 10.1111/nph.16613.

4.6 Supplementary Material

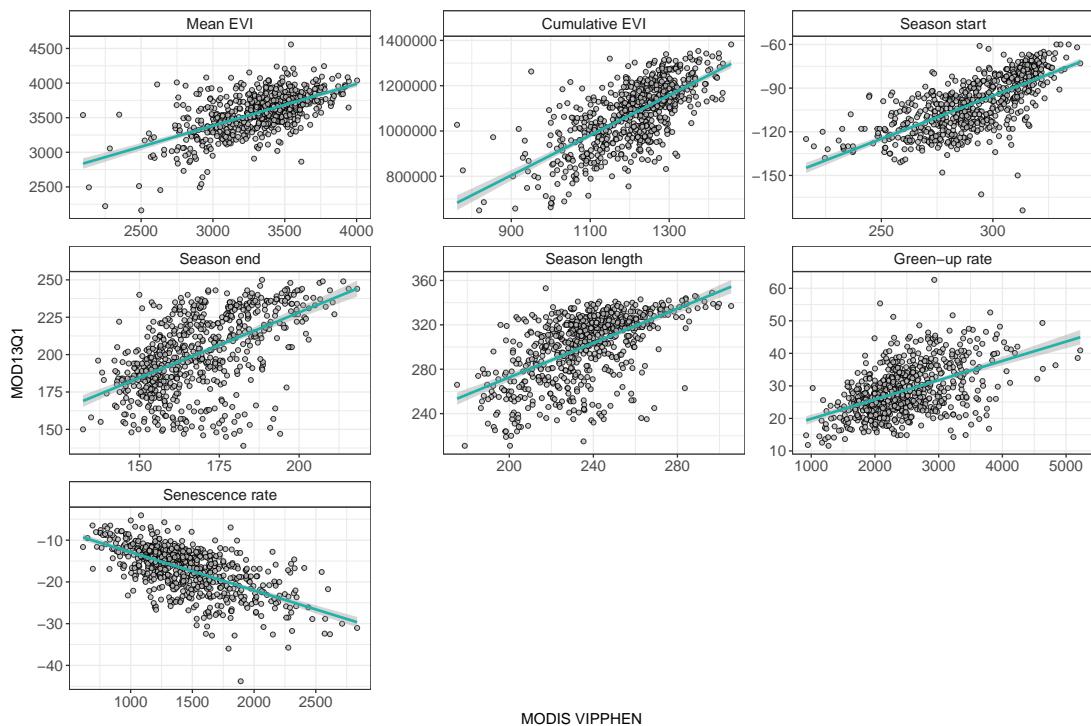


Figure 4.S1: Scatter plots showing a comparison of phenological metrics from the MODIS VIPPHEN product (Didan & Barreto, 2016) and those extracted from the MOD13Q1 data (Didan, 2015), for each of the sites in our study. The cyan line shows a linear model of the data, with a 95% confidence interval.

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

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

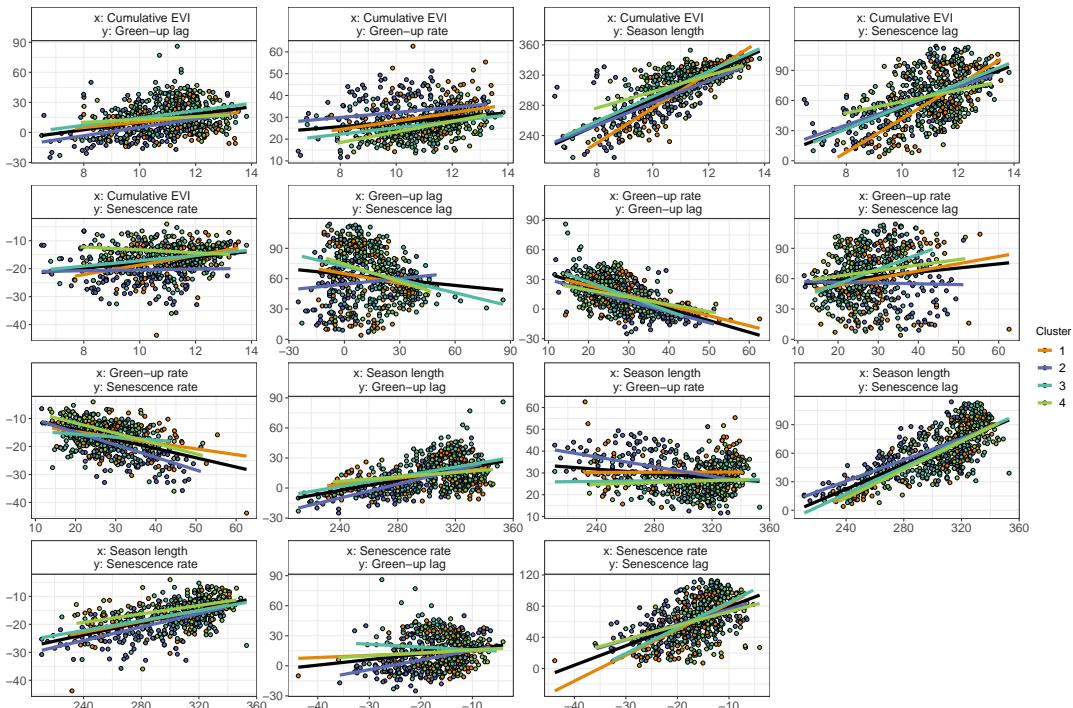


Figure 4.S2: Scatter plots showing pairwise comparisons of the six phenological metrics used in this study, extracted from the MODIS MOD13Q1 product (Didan, 2015). Points represent study sites and are coloured by vegetation cluster. Linear regression line of best fit for all sites is shown as a black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

Rank	Precipitation	Stem diameter	Diurnal	dT	Richness	Evenness	DoF	logLik	AIC	Δ	W _i
1	✓	✓+	✓+	✓	✓+	✓+	19	-932	1903	0	0.380
2	✓	✓+			✓+	✓+	18	-933	1903	0	0.366
3	✓	✓+		✓	✓	✓+	16	-937	1906	4	0.065
4	✓	✓+			✓	✓+	15	-938	1907	4	0.048
5	✓	✓	✓	✓	✓+	✓+	16	-938	1907	5	0.040
6	✓	✓	✓	26	✓+	✓+	15	-939	1908	5	0.027
7	✓				✓+	✓+	14	-940	1908	6	0.022
8	✓			✓	✓+	✓+	15	-939	1909	6	0.018
9	✓	✓	✓	✓	✓	✓+	13	-942	1910	8	0.008
10	✓	✓+	✓+		✓+	✓	15	-941	1911	9	0.005

Rank	Precipitation	Stem diameter	Diurnal	dT	Richness	Evenness	DoF	logLik	AIC	Δ	W_i
1	✓	✓	✓	✓	✓+	✓+	16	-2898	5829	0	0.198
2	<u>✓</u>	<u>✓</u>	<u>✓</u>	<u>✓</u>	<u>✓</u>	<u>✓</u>	13	-2901	5829	0	0.187
3	✓	✓	✓		✓+	✓+	15	-2900	5830	1	0.106
4	✓	✓	✓		✓	✓+	12	-2903	5830	1	0.097
5	✓				✓+	✓+	14	-2901	5830	2	0.077
6	✓			✓	✓+	✓+	15	-2900	5831	2	0.074
7	✓				✓	✓+	11	-2904	5831	2	0.068
8	✓			✓	✓	✓+	12	-2903	5831	2	0.064
9	✓		✓+	✓	✓+	✓+	19	-2897	5832	3	0.036
10	✓	✓+	✓+	✓	✓	✓+	16	-2900	5832	3	0.034

Table 4.S3: 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	Precipitation	Stem diameter	Diurnal	dT	Richness	Evenness	DoF	logLik	AIC	Δ	W_i
1					<u>✓</u>				6	-2071	4154
2		✓+		✓			10	-2068	4156	2	0.074
3		✓		✓			7	-2071	4156	2	0.074
4			✓	✓			7	-2071	4156	2	0.072
5			✓			✓	7	-2071	4156	2	0.068
6	✓			✓			7	-2071	4156	2	0.067
7	✓	✓+		✓			11	-2068	4157	3	0.038
8		✓+		✓		✓	11	-2068	4157	3	0.036
9		✓		✓		✓	8	-2071	4157	3	0.033
10		✓		✓		✓	8	-2071	4157	3	0.033

Table 4.S4: 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	Precipitation	Stem diameter	Diurnal	dT	Richness	Evenness	DoF	logLik	AIC	Δ	W_i
1	✓			✓			7	-1884	3783	0	0.079
2	<u>✓</u>						6	-1886	3783	1	0.059
3	✓			✓	✓	✓	9	-1883	3784	1	0.055
4				✓			6	-1886	3784	1	0.048
5	✓		✓	✓			8	-1884	3784	1	0.045
6	✓		✓	✓	✓	✓	10	-1882	3784	1	0.044
7	✓			✓	✓		8	-1884	3784	1	0.039
8	✓			✓		✓	8	-1884	3784	2	0.037
9	✓				✓	✓	8	-1884	3785	2	0.034
10	✓					✓	7	-1885	3785	2	0.030

Table 4.S5: 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	Precipitation	Stem diameter	Diurnal	dT	Richness	Evenness	DoF	logLik	AIC	Δ	W_i
1	<u>✓</u>			✓	✓	✓	9	-2464	4946	0	0.203
2	✓			✓	✓+	✓	12	-2461	4946	0	0.190
3	✓		✓	✓	✓+	✓	13	-2460	4947	1	0.119
4	✓		✓	✓	✓	✓	10	-2463	4947	1	0.118
5	✓			✓	✓+	✓+	15	-2458	4947	1	0.109
6	✓			✓	✓	✓+	12	-2461	4947	1	0.105
7	✓		✓	✓	✓	✓+	13	-2461	4948	2	0.061
8	✓		✓	✓	✓+	✓+	16	-2458	4948	2	0.059
9	✓		✓+	✓	✓	✓	13	-2462	4951	5	0.015
10	✓		✓+	✓	✓+	✓	16	-2460	4952	6	0.009

Table 4.S6: 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	Precipitation	Stem diameter	Diurnal	dT	Richness	Evenness	DoF	logLik	AIC	Δ	W_i
1	✓	✓	✓	✓	✓+	✓+	16	-2836	5703	0	0.185
2	<u>✓</u>	<u>✓</u>	<u>✓</u>	<u>✓</u>	<u>✓+</u>				12	-2840	5704
3	✓	✓	✓	✓	✓+	✓	13	-2839	5704	1	0.143
4	✓	✓+	✓	✓	✓+	✓+	19	-2833	5704	1	0.119
5	✓	✓	✓	✓		✓+	12	-2841	5705	2	0.061
6	✓	✓	✓	✓	✓	✓+	13	-2840	5706	2	0.058
7	✓	✓	✓	✓					8	-2845	5706
8	✓	✓+	✓	✓	✓	✓+	16	-2837	5707	4	0.029
9	✓	✓+	✓	✓	✓+	✓	16	-2838	5707	4	0.026
10	✓	✓+	✓			✓+	15	-2839	5707	4	0.025

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

Response	Clusters	Estimate	SE	DoF	T ratio	Prob.
Cumulative EVI	1-2	3.1E-01	1.57E-01	600	1.99	p = 0.19
	1-3	-1.4E-01	1.41E-01	600	-0.97	p = 0.77
	1-4	-3.8E-01	1.77E-01	600	-2.14	p = 0.14
	2-3	-4.5E-01	1.24E-01	600	-3.62	p<0.01
	2-4	-6.9E-01	1.68E-01	600	-4.11	p<0.01
	3-4	-2.4E-01	1.54E-01	600	-1.57	p = 0.40
Season length	1-2	1.1E+01	3.76E+00	603	2.89	p<0.05
	1-3	-7.3E+00	3.39E+00	603	-2.14	p = 0.14
	1-4	-1.2E+01	4.06E+00	603	-2.88	p<0.05
	2-3	-1.8E+01	2.98E+00	603	-6.07	p<0.01
	2-4	-2.3E+01	3.90E+00	603	-5.78	p<0.01
	3-4	-4.4E+00	3.54E+00	603	-1.24	p = 0.60
Green-up lag	1-2	6.5E+00	1.70E+00	606	3.80	p<0.01
	1-3	-3.3E+00	1.57E+00	606	-2.08	p = 0.16
	1-4	-1.9E-01	1.94E+00	606	-0.10	p = 1.00
	2-3	-9.7E+00	1.44E+00	606	-6.75	p<0.01
	2-4	-6.7E+00	1.84E+00	606	-3.62	p<0.01
	3-4	3.1E+00	1.69E+00	606	1.83	p = 0.26
Senescence lag	1-2	5.7E+00	3.29E+00	606	1.73	p = 0.31
	1-3	-3.6E+00	2.94E+00	606	-1.22	p = 0.61
	1-4	-5.5E+00	3.64E+00	606	-1.50	p = 0.44
	2-3	-9.3E+00	2.61E+00	606	-3.56	p<0.01
	2-4	-1.1E+01	3.48E+00	606	-3.21	p<0.01
	3-4	-1.9E+00	3.14E+00	606	-0.60	p = 0.93

Table 4.S8: Comparisons of species diversity interaction marginal effects using post-hoc Tukey's tests.

Response	Clusters	Mean diff.	Interval	Prob.
Cumulative EVI	2-1	-0.74	-1.04 - -0.45	p<0.01
	3-1	-0.14	-0.4 - 0.13	p = 0.55
	4-1	0.09	-0.24 - 0.42	p = 0.89
	3-2	0.61	0.35 - 0.87	p<0.01
	4-2	0.84	0.51 - 1.16	p<0.01
	4-3	0.23	-0.07 - 0.53	p = 0.19
Season length	2-1	-0.58	-0.88 - -0.29	p<0.01
	3-1	0.16	-0.1 - 0.43	p = 0.37
	4-1	0.31	-0.01 - 0.64	p = 0.07
	3-2	0.75	0.49 - 1.01	p<0.01
	4-2	0.9	0.58 - 1.22	p<0.01
	4-3	0.15	-0.15 - 0.44	p = 0.56
Green-up rate	2-1	0.26	-0.03 - 0.55	p = 0.11
	3-1	-0.48	-0.74 - -0.22	p<0.01
	4-1	-0.51	-0.84 - -0.19	p<0.01
	3-2	-0.74	-1 - -0.48	p<0.01
	4-2	-0.77	-1.1 - -0.45	p<0.01
	4-3	-0.03	-0.33 - 0.26	p = 0.99
Senescence rate	2-1	-0.65	-0.94 - -0.37	p<0.01
	3-1	0.09	-0.16 - 0.35	p = 0.79
	4-1	0.52	0.2 - 0.84	p<0.01
	3-2	0.75	0.49 - 1	p<0.01
	4-2	1.17	0.86 - 1.49	p<0.01
	4-3	0.43	0.14 - 0.71	p<0.01
Green-up lag	2-1	-0.49	-0.79 - -0.2	p<0.01
	3-1	0.28	0.01 - 0.54	p<0.05
	4-1	0.08	-0.25 - 0.41	p = 0.91
	3-2	0.77	0.51 - 1.03	p<0.01
	4-2	0.58	0.25 - 0.9	p<0.01
	4-3	-0.19	-0.49 - 0.1	p = 0.34
Senescence lag	2-1	-0.19	-0.5 - 0.12	p = 0.38
	3-1	0.15	-0.12 - 0.43	p = 0.47
	4-1	0.22	-0.12 - 0.56	p = 0.36
	3-2	0.34	0.08 - 0.61	p<0.01
	4-2	0.41	0.07 - 0.74	p<0.05
	4-3	0.06	-0.25 - 0.37	p = 0.95

Table 4.S9: Post-hoc Tukey's pairwise comparisons among vegetation types for each phenological metric.

Chapter 5

TLS chapter

TLS chapter

Chapter 6

Diversity and Structure of an Arid Woodland in Southwest Angola, with Comparison to the Wider Miombo Ecoregion

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 Bicuar National Park had comparatively low tree species diversity, but contained 27 tree species not found in other plots. Plots in Bicuar had low basal area, excepting plots dominated by *Baikiaea plurijuga*. In a comparison of plots in intact vegetation with areas previously disturbed by shifting-cultivation agriculture, we found species diversity was marginally higher in disturbed plots. Bicuar National Park remains an important woodland refuge in Angola, with an uncommon mosaic of woodland types within a small area. While we highlight wide variation in species composition and woodland structure across the miombo ecoregion, plot-based studies with more dense sampling across the ecoregion are clearly needed to more broadly understand regional variation in vegetation diversity, composition and structure.

6.1 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., 2010). 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 Detaroideae (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 understory 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 1a). Miombo woodlands are defined both by their tree diversity and by their structure of a grassy herbaceous understory with an often sparse tree canopy. In archetypical miombo woodlands, species of the genera *Brachystegia*, *Julbernardia* and *Isoberlinia* generally hold the most biomass, forming a mostly open woodland canopy. Distinct from dry tropical forests, miombo woodlands generally maintain a grassy understory dominated by grass species utilizing the C₄ 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 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 (DRY-FLOR et al., 2016; Torello-Raventos et al., 2013). These woodlands contain many endemic tree species however, and support a highly diverse woodland understory, with an estimated 8500 species of vascular plants (Frost, 1996). Miombo wood-

lands provide ecosystem service provision for an estimated 150 million people (Ryan et al., 2016). Additionally miombo woodlands hold \sim 18-24 Pg C in woody biomass and soil organic carbon, which is comparable to that held in the rainforests of the Congo basin (\sim 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 studies of 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 1a). 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 &

Smith, 2008). 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 plateau are therefore of great importance for conservation as a refuge for wildlife and endemic plant species (Huntley et al., 2019).

It is important to focus not only on the biodiversity of undisturbed woodland areas but also previously disturbed land 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 disturbed areas with areas of nearby 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 disturbed and undisturbed woodland patches within Bicuar National Park

6.2 Materials and Methods

6.2.1 Study area

We chose three areas of miombo woodland across the miombo ecoregion to compare with those in Bicuar National Park, Angola ($S15.1^{\circ}$, $E14.8^{\circ}$). The three sites were Gorongosa District in central Mozambique ($S19.0^{\circ}$, $E34.2^{\circ}$) (Ryan et al., 2011), Kilwa District in southern Tanzania ($S9.0^{\circ}$, $E39.0^{\circ}$) (McNicol et al., 2018a), and the Mikembo Natural Reserve in Katanga, southern Democratic Republic of Congo (DRC) ($S11.5^{\circ}$, $E27.7^{\circ}$) (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 $\sim 20.5^{\circ}\text{C}$ in Bicuar and Katanga to $\sim 25.8^{\circ}\text{C}$ in Kilwa (Figure 1b, Table 6.1).

Table 6.1: 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 ($^{\circ}\text{C}$)	MAP (mm y^{-1})	CWD (mm y^{-1})	Latitude (DD)	Longitude (DD)	N plots	N species
Bicuar NP	20.5	864	-815	-15.12	14.81	15	49
DRC	20.4	1115	-762	-11.49	27.67	12	89
Mozambique	24.4	1029	-662	-18.95	34.16	15	162
Tanzania	25.8	956	-754	-9.05	39.05	22	248

Bicuar National Park covers an area of $\sim 7900 \text{ km}^2$, established as a hunting reserve in 1938, and later as a national park in 1964 (Figure 6.2). While fauna populations in the Park were severely damaged by the Angolan civil war,

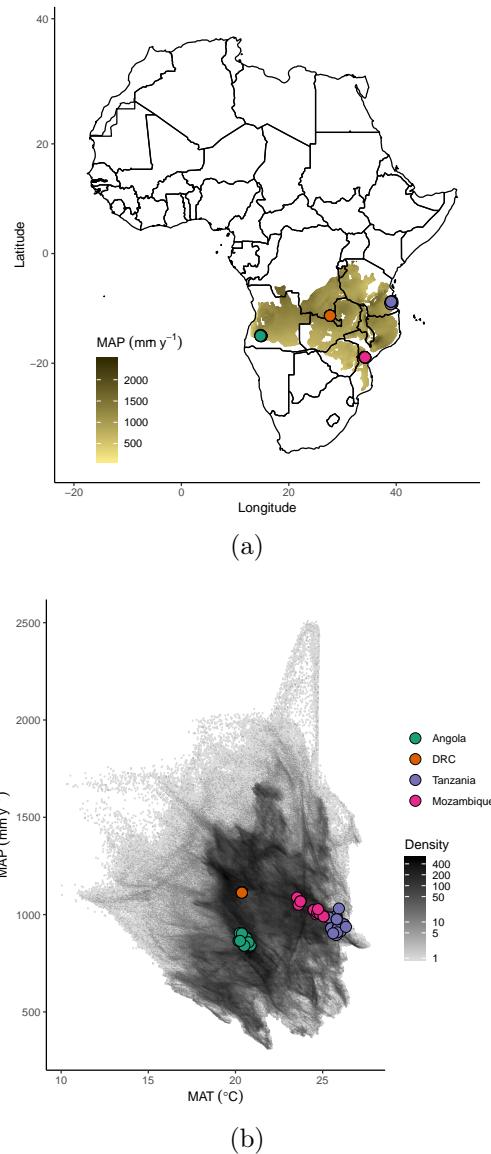


Figure 6.1: Locations of plots used in this study, by (a) geographic location with respect to the distribution of miombo woodland vegetation (shaded brown according to mean annual precipitation) (White, 1983), and (b) showing the plot locations compared to the climate space of the miombo ecoregion estimated using the WorldClim dataset over the Miombo woodland vegetation extent with a pixel size of 30 arc seconds (0.86 km^2 at the equator) (Fick & Hijmans, 2017). Note that the density colour scale is log-transformed for visual clarity.

the interior of the Park remains as a largely intact mosaic of miombo woodland, Baikiaea-Burkea woodland, shrub/thicket vegetation and seasonally flooded grassland. Encroachment of agriculture and grazing, particularly along the north-west 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 that had been previously used for agriculture but since left fallow, and areas of undisturbed miombo woodland, located along the road network, 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, which consists of undisturbed miombo woodlands. All plots were located quasi-randomly, with consideration to accessibility for future woodland censuses.

6.2.2 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 four sites. Figure 1a and Table 6.1 show the locations and 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 ≥ 5 cm stem diameter was recorded, except in the DRC plots, where only stems ≥ 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 (*African Plant Database (version 3.4.0)* 2020). At all sites, we used Palgrave (2003), 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 ≥ 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 (dia-

meter 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 (Appendix A). 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 undisturbed areas of miombo woodland in Bicuar National Park with areas of disturbed 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 6.2. 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 20x50 m (0.1 ha) plots, and compared their diversity and structure with 20x50 m subsamples of the 15 one hectare plots within the Park interior. Like the one hectare plots, within these smaller 20x50 m plots we recorded the species and stem diameter of every tree stem ≥ 5 cm stem diameter.

6.2.3 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 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

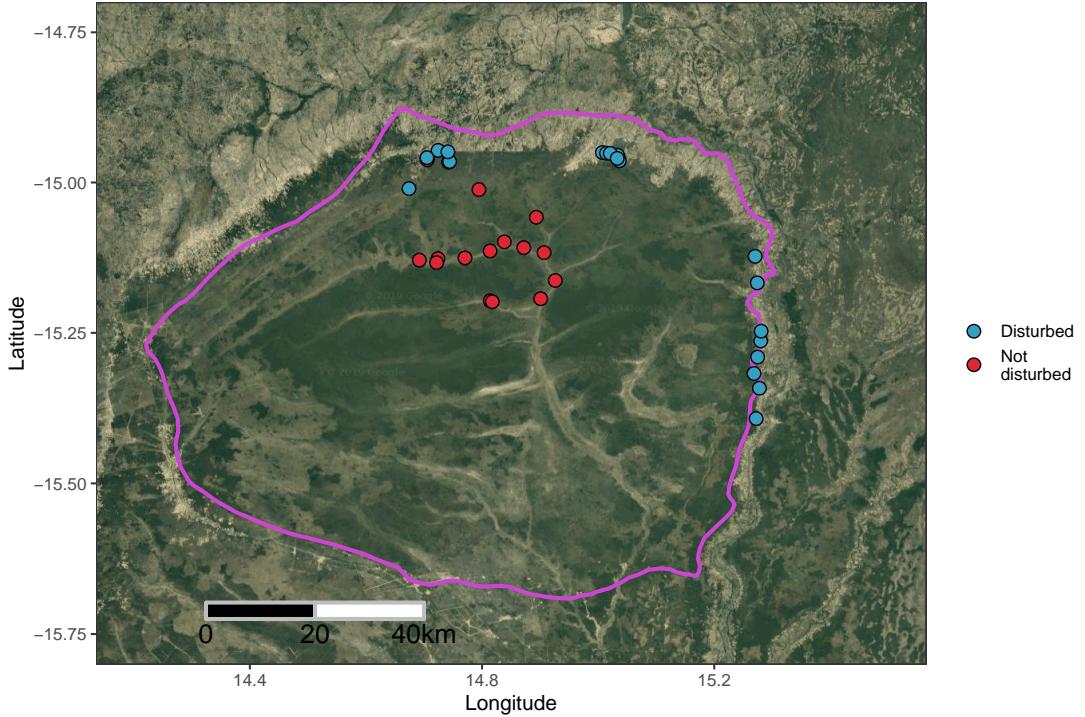


Figure 6.2: Location of plots in Bicuar National Park, southwest Angola. The Park boundary is shown as a pink outline, according to UNEP-WCMC and IUCN (2019). One hectare undisturbed plots are shown as red points, while disturbed 20x50 m (0.1 hectare) plots are shown as blue points. The map background is a true colour composite satellite image generated using the Google Maps Static Maps API in the `ggmap` R package (Kahle & Wickham, 2013).

al., 2014), as the sum of the difference between monthly rainfall and monthly evapotranspiration when the difference is negative, using the dataset available at http://ups-tlse.fr/panropical_allometry.htm, which uses data from the WorldClim dataset 1970-2000.

6.2.4 Data analysis

We calculated the basal area of each stem (g_i) using:

$$g_i = \pi \times (d_i/2)^2 \quad (6.1)$$

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 ≥ 5 cm diameter, and the Shannon-Wiener index (H') (Equation 6.2), using the `vegan` package in R (Oksanen et al., 2019):

$$H' = - \sum_{i=1}^S p_i \ln p_i \quad (6.2)$$

Where S is the total number of species in the plot, p_i is the proportional abundance of the i th species and \ln is the natural logarithm.

We calculated the pairwise beta diversity among sites using the Sørensen coefficient (S_S) (Equation 6.3) (Koleff et al., 2003):

$$S_S = \frac{2a}{2a + b + c} \quad (6.3)$$

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 vari-

ation in species composition among one hectare plots, and also between disturbed and undisturbed 20x50 m plots within Bicuar National Park, using the `vegan` R package. The number of dimensions for NMDS was minimised while ensuring the stress value of the NMDS fit was ≤ 0.1 . NMDS analyses were run with 500 random restarts to ensure a global solution was reached. We used Bray-Curtis dissimilarity as the optimal measure of ecological distance (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 3.6.1 (R Core Team, 2020).

6.3 Results

6.3.1 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 6.2). The most common of these unique species were *Brachystegia tamarindoides* ($n = 576$), *Baikiaea plurijuga* ($n = 331$) and *Baphia massaiensis* ($n = 303$). Four species unique to Bicuar National Park within this dataset only had one individual recorded: *Elachyptera parvifolia*, *Entandrophragma spicatum*, *Oldfieldia dactylophylla*, *Peltophorum africanum*.

Alpha diversity in Bicuar National Park was low compared to other sites (Figure 6.3). Mean H' across plots in Bicuar National Park was 1.6 ± 0.13 . An ANOVA showed a significant difference in H' among sites ($F(3,60) = 7.54$, $p < 0.01$, Table 6.3), and a post-hoc Tukey's test showed that H' in plots in Bicuar National Park was significantly different from those in DRC ($H' = 2.7 \pm 0.19$, $p < 0.01$), Mozambique ($H' = 2.4 \pm 0.2$, $p < 0.01$) and Tanzania ($H' = 2.2 \pm 0.11$, $p < 0.05$). Variation in H' is large within Bicuar National Park, with H' ranging from 0.85 to 2.56, but this was a similar range to other sites. In contrast, the range of species

CHAPTER 6. BICUAR NATIONAL PARK

Table 6.2: 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
Fabaceae	<i>Albizia antunesiana</i>	9.1(2.03)	0.07(0.040)	40	8(4)
Fabaceae	*Baikiae plurijuga	28.9(0.75)	1.72(0.570)	331	55.2(
Fabaceae	*Baphia bequaertii	7.4(0.36)	0.08(0.050)	127	31.8(
Fabaceae	*Baphia massaiensis	6.6(0.17)	0.05(0.020)	303	30.3(
Fabaceae	<i>Bobgunnia madagascariensis</i>	7.8(0.91)	0.04(0.020)	32	10.7(
Fabaceae	*Brachystegia longifolia	12.9(0.48)	1.14(0.430)	576	115.2(
Fabaceae	<i>Brachystegia spiciformis</i>	11.4(0.52)	0.74(0.430)	326	81.5(
Phyllanthaceae	*Bridelia mollis	5.7(0.31)	0.02(NA)	23	23(
Fabaceae	<i>Burkea africana</i>	8.5(0.33)	0.39(0.120)	863	71.9(
Combretaceae	<i>Combretum apiculatum</i>	7.6(0.45)	0.06(0.040)	60	30(1
Combretaceae	<i>Combretum celastroides</i>	5.6(0.34)	<0.01(0.000)	7	3.5(1
Combretaceae	<i>Combretum collinum</i>	6.3(0.09)	0.07(0.020)	609	50.8(1
Combretaceae	*Combretum hereroense	6.7(0.26)	0.02(0.010)	73	12.2(
Combretaceae	*Combretum psidiooides	7.4(0.43)	0.01(0.010)	33	6.6(4
Combretaceae	<i>Combretum zeyheri</i>	6.3(0.35)	0.01(0.000)	61	10.2(
Euphorbiaceae	*Croton gratissimum	6.1(1.55)	<0.01(NA)	4	4(N
Ebenaceae	*Diospyros batocana	8.4(2.14)	<0.01(0.000)	2	1(0
Ebenaceae	*Diospyros kirkii	9.3(1.64)	0.03(NA)	11	11(1
Apocynaceae	<i>Diplorhynchus condylocarpon</i>	8.2(0.52)	0.08(0.060)	174	19.3(
Malvaceae	*Dombeya rotundifolia	5.5(0.19)	<0.01(NA)	2	2(N
Celastraceae	*Elachyptera parvifolia	7.3(NA)	<0.01(NA)	1	1(N
Meliaceae	*Entandrophragma spicatum	14.6(NA)	<0.01(NA)	1	1(N
Fabaceae	<i>Erythrophleum africanum</i>	9.0(0.84)	0.10(0.040)	128	18.3(
Rubiaceae	*Gardenia volkensii	5.6(1.15)	<0.01(0.000)	5	2.5(
Fabaceae	*Guibourtia coleosperma	7.2(1.00)	0.02(0.010)	31	6.2(3
Phyllanthaceae	<i>Hymenocardia acida</i>	5.9(1.25)	<0.01(NA)	6	6(N
Fabaceae	<i>Julbernardia paniculata</i>	10.1(0.21)	0.92(0.200)	1624	162.4(
Fabaceae	*Lonchocarpus nelsii	13.4(0.88)	0.15(0.030)	165	15(2
Dipterocarpaceae	*Monotes angolensis	7.4(0.83)	<0.01(0.000)	2	1(0
Ochnaceae	*Ochna pulchra	6.5(0.80)	0.01(0.000)	26	8.7(3
Picridendraceae	*Oldfieldia dactylophylla	8.5(NA)	<0.01(NA)	1	1(N
Fabaceae	*Peltophorum africanum	11.5(NA)	<0.01(NA)	1	1(N
Fabaceae	<i>Pericopsis angolensis</i>	8.4(0.61)	0.06(0.020)	97	12.1(
Phyllanthaceae	<i>Pseudolachnostylis maprouneifolia</i>	6.7(0.45)	0.03(0.010)	84	9.3(3
Combretaceae	*Pteleopsis anisoptera	6.8(0.46)	0.07(0.020)	81	20.2(
Fabaceae	<i>Pterocarpus angolensis</i>	13.0(0.61)	0.15(0.100)	102	17(8
Fabaceae	*Pterocarpus lucens	6.9(0.94)	<0.01(NA)	4	4(N
Rubiaceae	*Rothmannia engleriana	6.8(0.66)	<0.01(0.000)	5	1.7(0
Euphorbiaceae	*Schinziophyton rautanenii	8.0(2.82)	<0.01(NA)	3	3(N
Polygalaceae	<i>Securidaca longepedunculata</i>	7.3(1.12)	<0.01(0.010)	4	2(1
Loganiaceae	<i>Strychnos cocculoides</i>	10.4(1.17)	0.03(0.020)	19	6.3(3
Loganiaceae	*Strychnos pungens	6.1(0.48)	<0.01(0.000)	18	3.6(0

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.

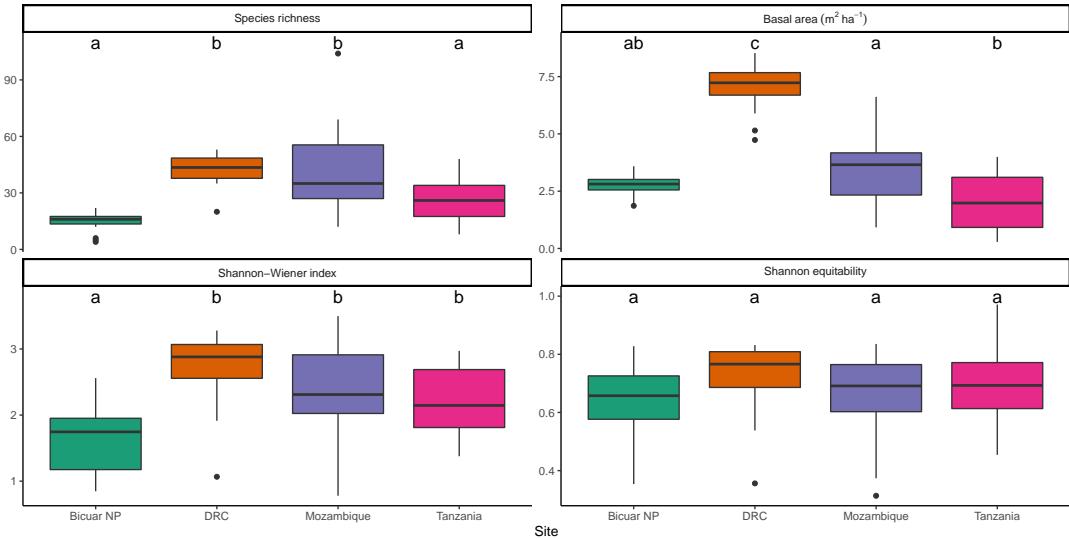


Figure 6.3: Variation of alpha diversity estimates and basal area among sites. Boxes bound the 1st and 3rd quartiles, with the median within the box. Whiskers represent 1.5 times the interquartile range plus or minus the 1st and 3rd quartiles, respectively. Values found beyond the whiskers are shown individually as points. 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 ($p < 0.05$)

6.3.2 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 *Jubaea paniculata* and *Pterocarpus angolensis*. This group of plots in Bicuar National Park was further characterised by the abundance of *Pterocarpus lucens*,

Table 6.3: 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).

	<i>Dependent variable:</i>			
	Species richness	Basal area	Shannon (H')	Shannon equit. (E_H)
	(1)	(2)	(3)	(4)
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

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 4a). 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 4b). 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 6.4). Similar to the NMDS, these results show that plots in Bicuar National Park are most similar to those found in DRC.

Table 6.4: 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

6.3.3 Woodland structure

Mean basal area of plots in Bicuar National Park was $2.78 \pm 0.122 \text{ m}^2 \text{ ha}^{-1}$, ranging from 1.86 to $8.53 \text{ m}^2 \text{ ha}^{-1}$ (Figure 6.3). An ANOVA showed a significant difference in basal area among sites ($F(3,60) = 48.04$, $p < 0.01$), and a post-hoc Tukey's test showed that basal area in Bicuar National Park was significantly lower than

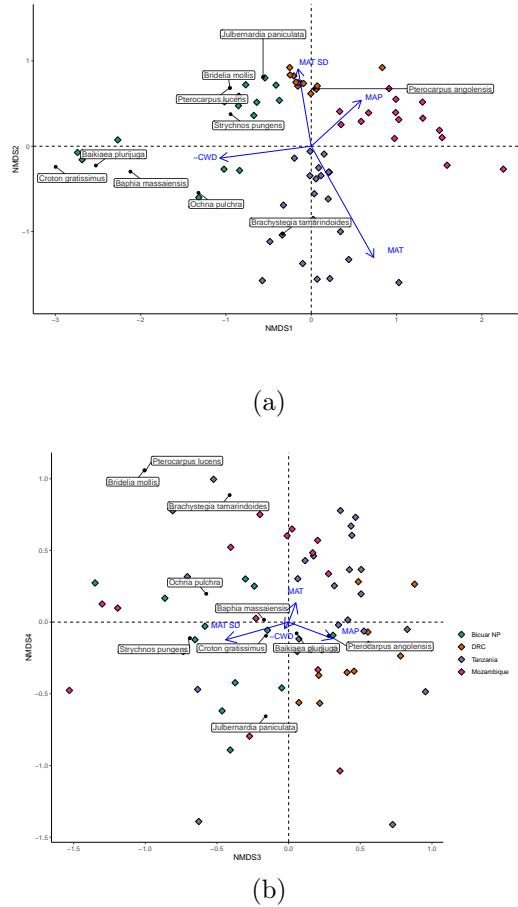


Figure 6.4: Environmental factors fitted to axes 1 and 2 (a), 3 and 4 (b) of the NMDS ordination of species composition of one hectare plots, showing the variation in plot species composition within and among sites. Diamonds are plot scores coloured by site. The lengths of arrows indicating environmental factor fits to the first two ordination axes are scaled by R^2 . Arrows point in the direction of increasing values of that environmental factor. Note that Climatic Water Deficit (CWD) is expressed in more intuitively as the negative inverse of CWD, thus larger values indicate higher levels of CWD.

plots in DRC ($BA = 6.95 \pm 0.327 \text{ m}^2 \text{ ha}^{-1}$, $p < 0.01$), but there were no significant differences between Bicuar and Mozambique ($BA = 3.43 \pm 0.409 \text{ m}^2 \text{ ha}^{-1}$, $p = 0.43$) or Tanzania ($BA = 2.06 \pm 0.253 \text{ m}^2 \text{ ha}^{-1}$, $p = 0.26$) (Figure 6.3). Additionally, Bicuar plots had less variation in basal area among plots than other sites. Plots in Bicuar with the highest basal area were dominated by *Baikiaea plurijuga* and *Baphia massaiensis* (Plots 9, 13, and 15).

The stem diameter abundance distribution in Bicuar National Park was com-

parable with other sites (Figure 6.5), 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.

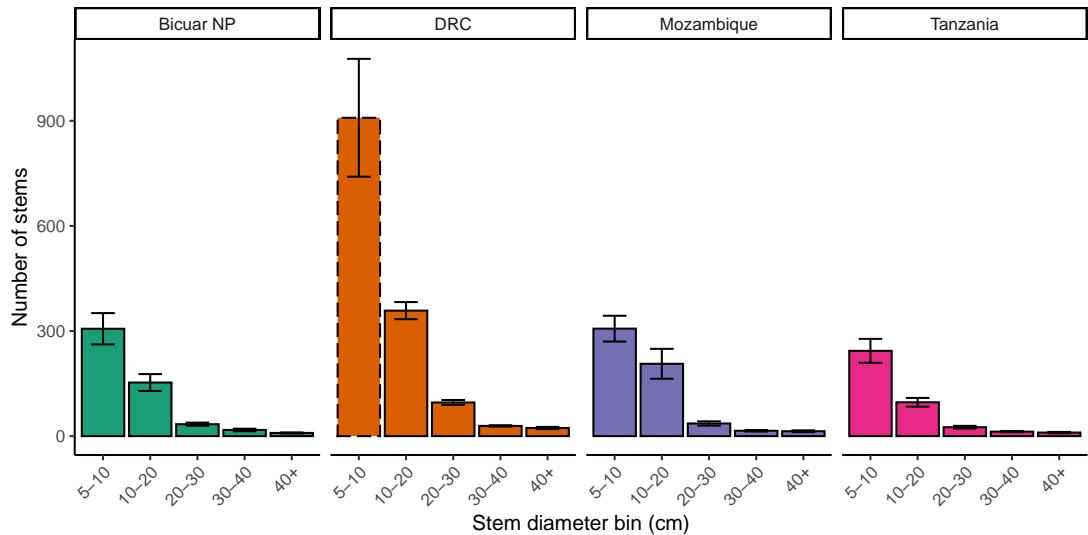


Figure 6.5: Ranked variation between plots in stem number within each site, with bars according to stem diameter class. Error bars are the mean ± 1 standard error. The dashed bar for the DRC 5-10 cm stem diameter class indicates that these measurements were estimated by extrapolating a linear regression of log stem abundance across the available stem diameter classes for DRC.

6.3.4 Effect of disturbance via shifting cultivation on diversity within Bicuar National Park

There was a clear difference in the species composition of previously farmed disturbed woodland plots and undisturbed woodland plots, but with some overlap (Figure 6.6). Notably, Plots 4 and 7 in putatively undisturbed woodland have a species composition more resembling the disturbed 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 disturbed plots. The undisturbed 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 disturbed plots. The most common species in the disturbed plots was *Baphia massaiensis* ($n = 158$), with a mean stem diameter of 6.1 ± 1.87 cm, while in the

undisturbed 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 disturbed plots ($H' = 1.7 \pm 0.08$) than in undisturbed plots ($H' = 1.3 \pm 0.14$) 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 6.7, Table 6.5). Mean plot species richness was also lower in undisturbed plots (6.4 ± 0.86) than disturbed plots (8.7 ± 0.53). Mean $E_{H'}$ was 0.8 ± 0 in disturbed plots and 0.7 ± 0.04 in undisturbed plots but there was no significant difference between disturbed and undisturbed plots according to an ANOVA ($F(1,33) = 1.54$, $p = 0.22$). 11 species were found only in the disturbed plots and not in the undisturbed 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 undisturbed plots, the most common being *Brachystegia spiciformis* ($n = 61$), *Baikiaea plurijuga* ($n = 43$) and *Combretum apiculatum* ($n = 9$). Mean basal area was higher in undisturbed plots ($0.5 \pm 0.07 \text{ m}^2 \text{ ha}^{-1}$) than disturbed plots ($0.5 \pm 0.1 \text{ m}^2 \text{ ha}^{-1}$).

Mean stem density was higher in disturbed plots ($900 \pm 338.36 \text{ stems ha}^{-1}$) than undisturbed plots ($520.3 \pm 220.22 \text{ stems ha}^{-1}$). The stem diameter abundance distribution in disturbed plots showed that many more stems were from the 5-10 cm diameter class in disturbed plots, while the disturbed plots had fewer stems in the 10-20 cm size class. Both disturbed and undisturbed plots had a similar abundance of stems in larger stem diameter classes (Figure 6.8). Multi-stemmed trees in disturbed plots tended to have a greater number of stems per tree (3.4 ± 2.35) than multi-stemmed trees in undisturbed plots (2.4 ± 0.8).

6.4 Discussion

6.4.1 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

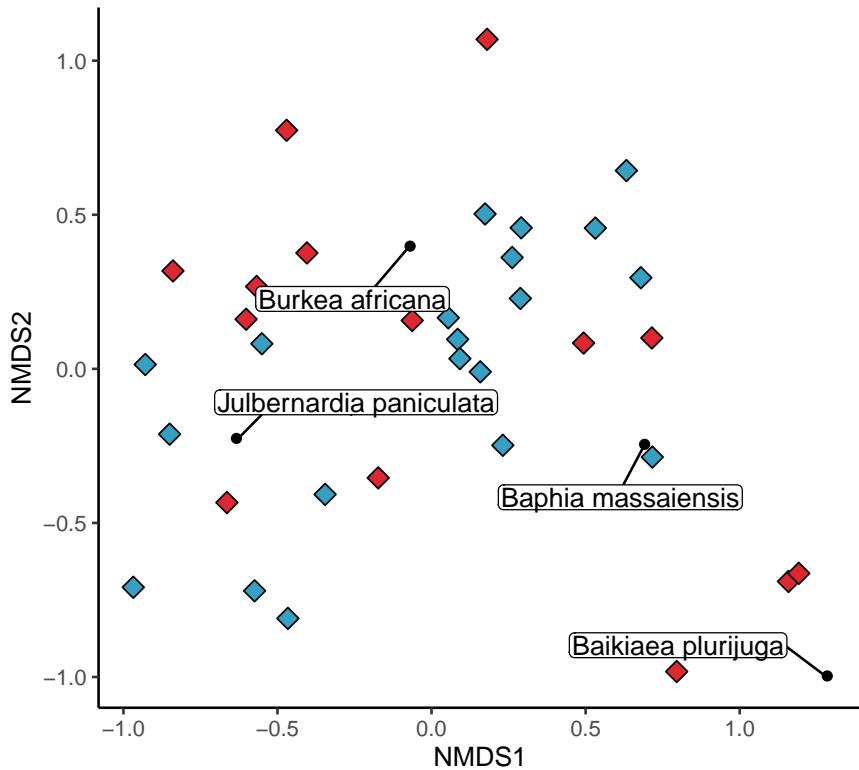


Figure 6.6: NMDS ordination of species composition of 20x50 m (0.1 ha) plots showing plot scores as coloured diamonds located in disturbed (blue) and undisturbed (red) areas of woodland in Bicuar National Park.

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.

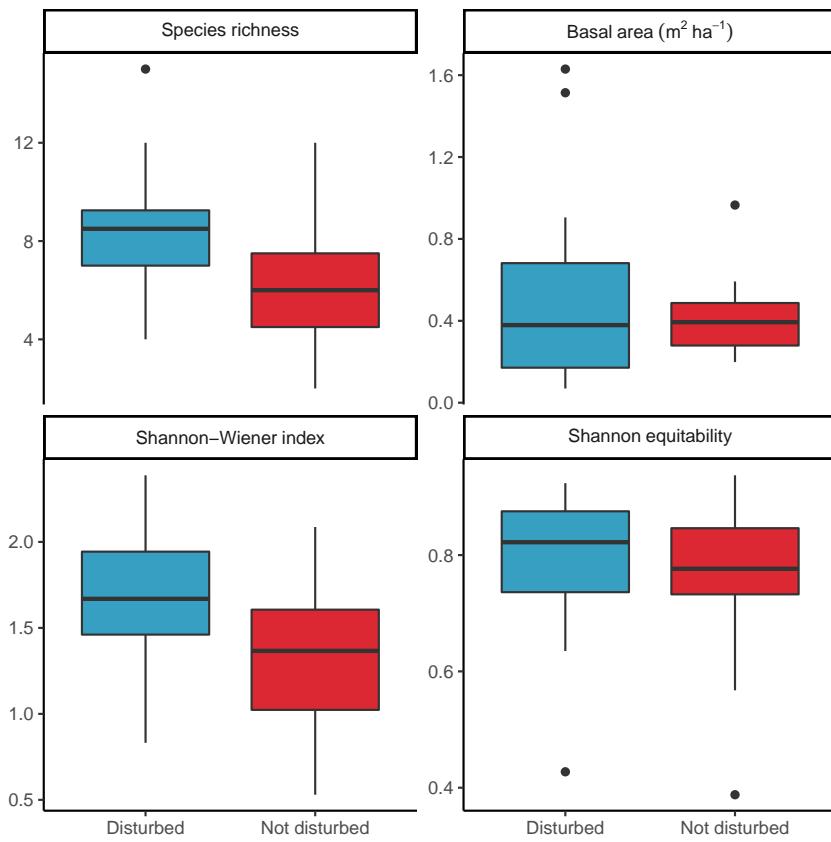


Figure 6.7: The variation in diversity and woodland structure between disturbed and undisturbed 20x50 m (0.1 ha) plots in Bicuar National Park. Boxes bound the 1st and 3rd quartiles, with the median within the box. Whiskers represent 1.5 times the interquartile range plus or minus the 1st and 3rd quartiles, respectively. Values found beyond the whiskers are shown individually as points.

6.4.2 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, 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),

Table 6.5: Results of ANOVA tests for alpha diversity metrics and plot basal area, between disturbed and undisturbed 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')
Disturbed	2.450*** (0.859)	0.098 (0.122)	0.372** (0.140)	0.035 (0.045)
Constant	6.200*** (0.650)	0.416*** (0.092)	1.311*** (0.106)	0.756*** (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

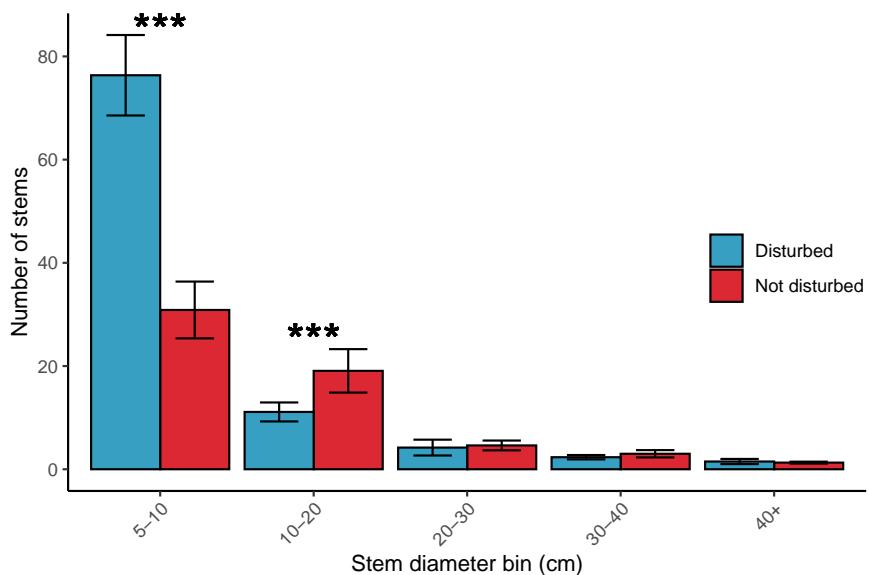


Figure 6.8: Ranked variation between disturbed and undisturbed plots in stem number, with bars according to stem diameter class. Error bars are the mean \pm 1 standard error. Asterisks above pairs of bars refer to the p-values of Poisson general linear models which tested whether disturbed and undisturbed plots differ in the number of stems for different stem diameter classes ($^{***}<0.001$, $^{**}<0.01$, $^{*}<0.05$, $.<0.1$).

with Bicuar National Park and Mupa National Park being key refugia for this animal in the Huila plateau region. The second woodland type, dominated by *Brachystegia tamarindoides* and *Ochna pulchra* represents a form of small stature woodland with a shrubby understorey and sparse canopy trees, which commonly occurs as a result of repeated disturbance by fire, or poor soil structure (Smith & Allen, 2004). The remaining plots resemble the more archetypical miombo woodland with *Julbernardia paniculata*, though with a number of species not seen in plots further to the east in the miombo ecoregion such as *Strychnos pungens*. This mosaic of woodland types makes Bicuar National Park a valuable reservoir of diversity and strengthens the case for the Park being a key conservation asset within the Huila plateau and the larger southern African region. While there are regional boundaries between Baikiaeae and miombo woodlands (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 6.2). 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 Baikiaeae woodlands (Campbell et al., 2002). High levels of disturbance by fire in these Baikiaeae patches may additionally prevent a transition to an alternative woodland type via the control of sapling growth.

6.4.3 Comparison of disturbed and undisturbed woodland plots

Previously disturbed woodlands around the edge of Bicuar National Park were found to share many species with undisturbed plots in the Park, but with some additional species which did not occur in the undisturbed plots. They also lacked notable archetypical 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 undisturbed 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) particularly, notes the dominance of *Pericopsis angolensis* and *Combretum* spp. as light-demanding pioneer species, which were found to be abundant in the disturbed 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 disturbed 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 disturbed plots had a greater basal area than undisturbed plots, possibly due to high levels of coppicing in these plots or a divergent fire history. Indeed, mean stem density was higher in undisturbed plots. This can lead to species that would otherwise remain small producing a much larger basal area as they grow multiple stems under high disturbance conditions (Luoga et al., 2004). The most common species in the disturbed 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 7 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 disturbed 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.

6.5 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 undisturbed, possess a number of species not found commonly in other miombo woodland plots around the region. They may also house 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 20x50 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. R. Perez, V. Kalogirou, P. Defourny & F. Achard (2010). ‘GlobCover 2009’. In: *ESA Living Planet Symposium*, pp. 1–3.
- 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 an 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. Bürquez, 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.
- (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, António Valter, Francisco M. P. Gonçalves, José João Tchamba, José Camóngua Luís, Marina Filomena F. Rafael & José L. M. Alexandre (2018). ‘Vegetation survey of the woodlands of Huíla Province’. In: *Biodiversity & Ecology* 6, 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. Baldau, 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.

CHAPTER 6. BICUAR NATIONAL PARK

- Figueiredo, E. & G. F. Smith (2008). ‘Plants of Angola/Plantas de Angola’. In: *Strelitzia* 22, pp. 1–279.
- 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.
- 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.
- Kahle, D. & H. Wickham (2013). ‘ggmap: Spatial visualization with ggplot2’. In: *The R Journal* 5.1, pp. 144–161. URL: <https://journal.r-project.org/archive/2013-1/kahle-wickham.pdf>.
- 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 Azami, 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. Mottonen & 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. Taylor, 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, Casey M., Rose Pritchard, Iain McNicol, Matthew Owen, Janet A Fisher & Caroline 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. Roder & 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.

CHAPTER 6. BICUAR NATIONAL PARK

- 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., dos Santos 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, United Kingdom: 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 & 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.

Chapter 7

Discussion

The discussion

CHAPTER 7. DISCUSSION

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 Huila (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, our 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 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 20x50 m samples of previously abandoned agricultural land at the edge of the park boundaries, to improve our coverage of 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-GPS, to an accuracy of ≤ 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). 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 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 three peer-reviewed articles led by colleagues:

- Grace Jopaul Loubota Panzou et al. (2020). ‘Pantropical variability in tree crown allometry’. In: 30.2. Ed. by Andrew Kerkhoff, pp. 459–475. DOI: [10.1111/geb.13231](https://doi.org/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](https://doi.org/10.1002/ppp3.10168)
- 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



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.

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

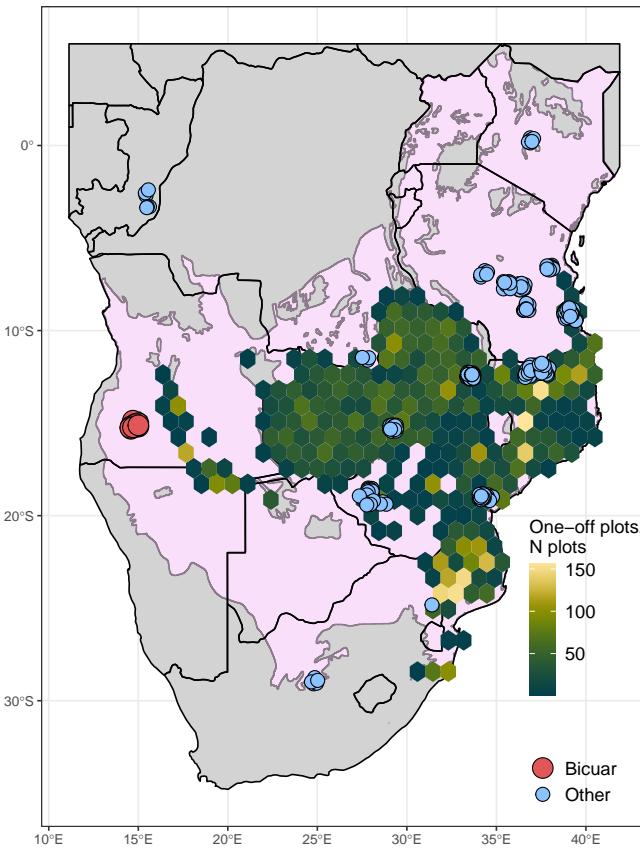


Figure 8.2: The spatial distribution of plots in the SEOSAW network. Blue circles are permanent plots, where individual stems are tagged and can be matched among censuses. The permanent plots in Bicuar National Park are shown as red points. The hexagon grid shows the density of one-off plots. The pink 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.

(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 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.

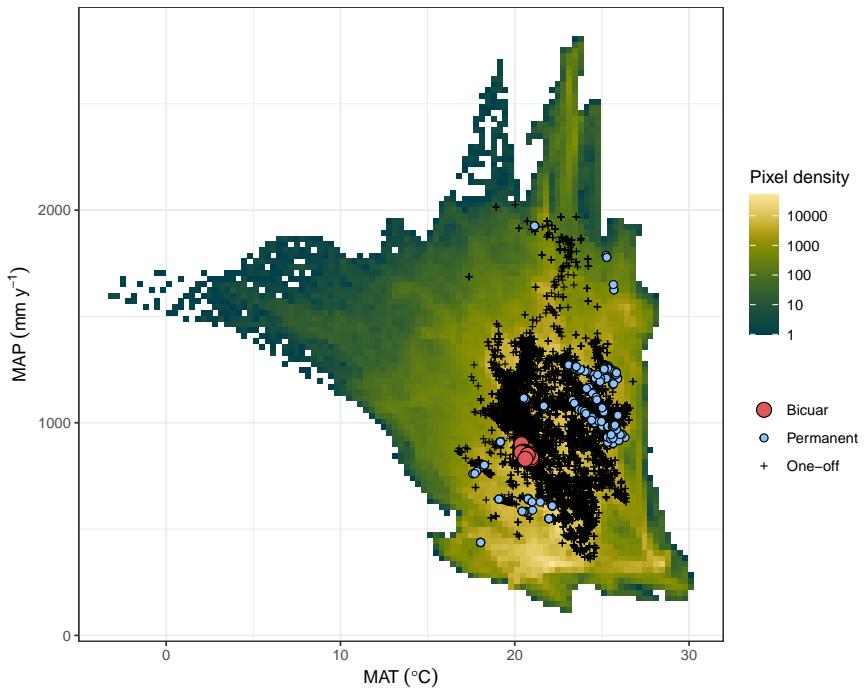


Figure 8.3: The distribution of SEOSAW plots in climate space, using Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP) from the WorldClim database (Fick & Hijmans, 2017). Blue circles are permanent plots, where individual stems can be matched among censuses. The permanent plots in Bicuar 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.

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 dry tropical woodlands in southern Africa. Our hope is that Bicuar National Park can be registered as a supersite with one or more research organisation and become a destination for researchers, strengthening the representation of Angolan science, and advert-

ising Bicuar National Park and the Herbarium of Lubango as a destination for researchers, building capacity, research potential and conservation awareness in the region.

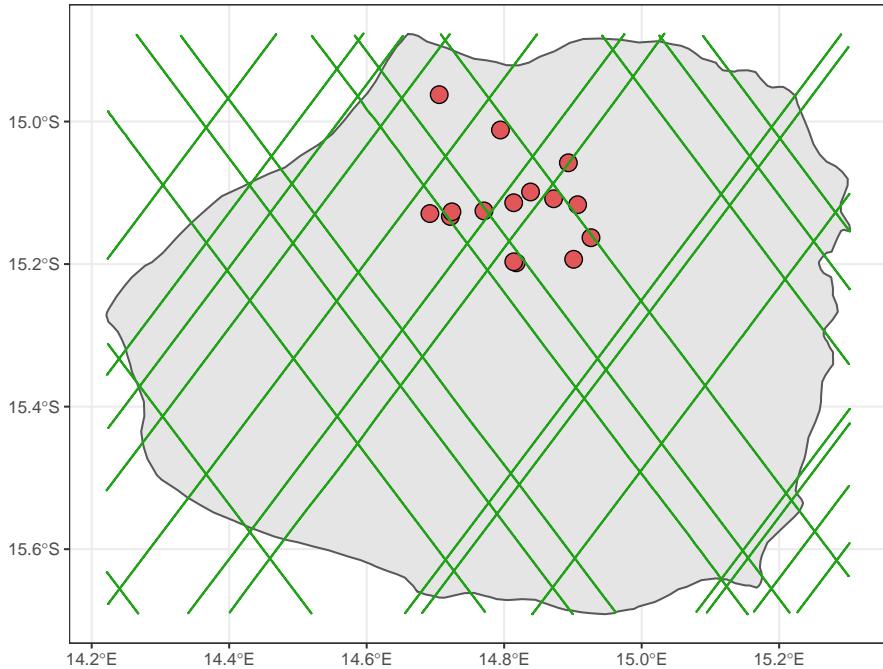


Figure 8.4: 50 m wide flight-paths of the GEDI L2B satellite LiDAR product (red lines), with the extent of Bicuar National Park (grey polygon), and the locations of the 15 1 ha permanent plots (blue points). Note that in reality each 25 m track consists of a series of 25 m radius circles which contain LiDAR data.

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 ([DOI ID](#)), along with details of the largely free and open source reproducible workflow for processing the data, which is also seen in Chapter 5 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 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 with multiple uses in mind. 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). Our hope is that the LiDAR data may be used by other researchers in a similar manner to answer questions pertinent to southern African woodlands. 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 parameterised 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). 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 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.

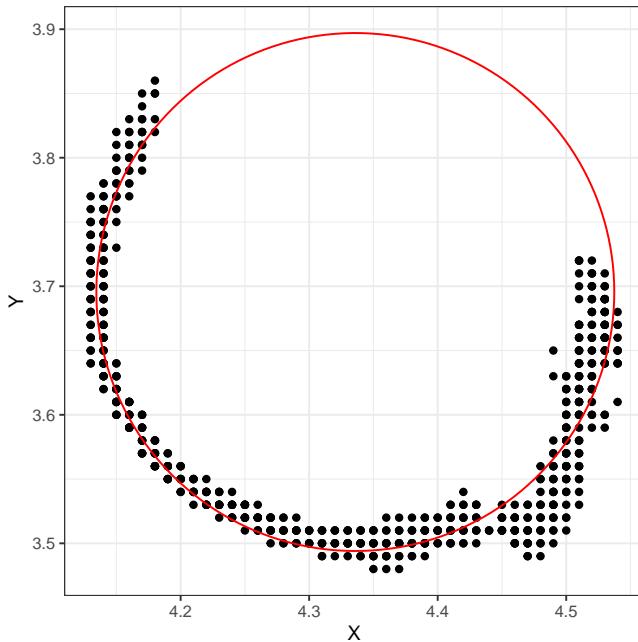


Figure 8.5: Example output of the prototype stem cylinder interpolation method used to estimate stem diameter from an incomplete point cloud. Voxelised points at 2 cm^3 are shown as black points, while the interpolated stem cylinder is shown as a red circle.

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 parameterisation 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.

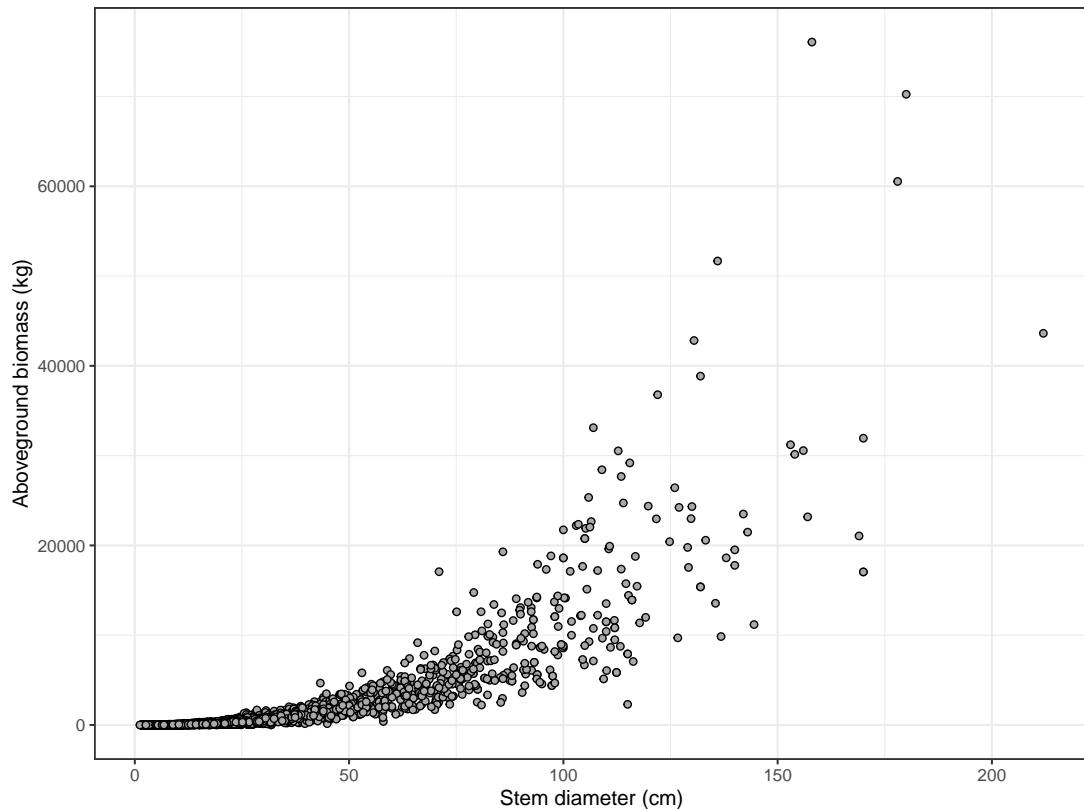


Figure 8.6: The relationship between tree stem diameter and aboveground biomass calculated from destructive harvest from all 872 records held in the GlobAllomeTree database (Henry et al., 2013) and all 4004 records reported in Chave et al. (2014). The heteroscedasticity of the relationship between stem diameter and aboveground biomass can be seen, with increased variance in biomass at higher stem diameters.

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 lar-

ger 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). 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?

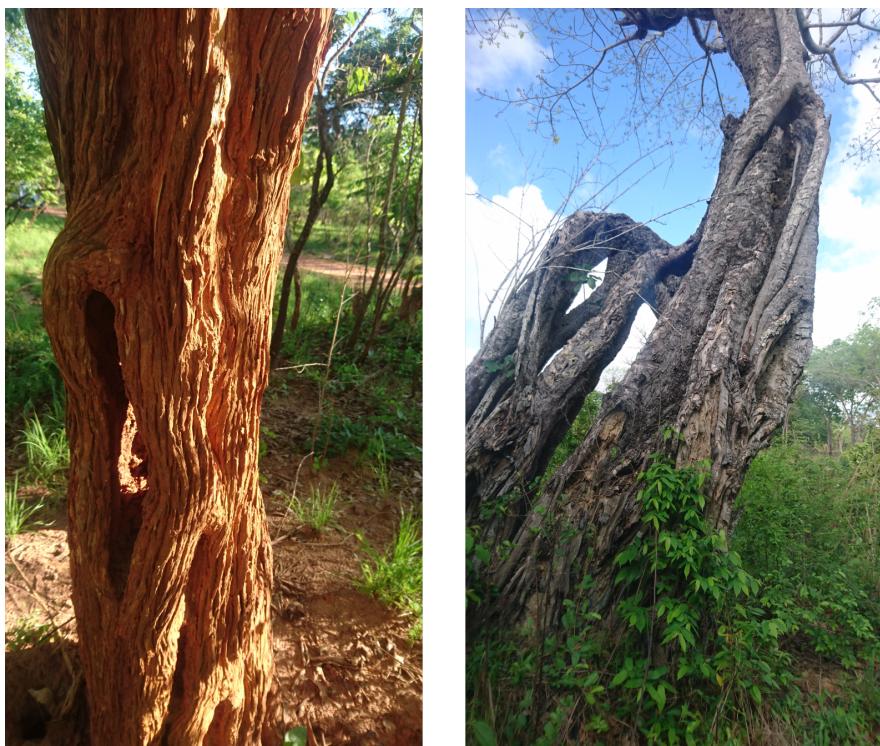


Figure 8.7: Two large old trees in Kilwa District, southeast Tanzania, with particularly idiosyncratic trunks. Using conventional stem diameter allometries will likely produce an inaccurate estimate of above-ground biomass. Photos by Ellie Wood.

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



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.

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.

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).

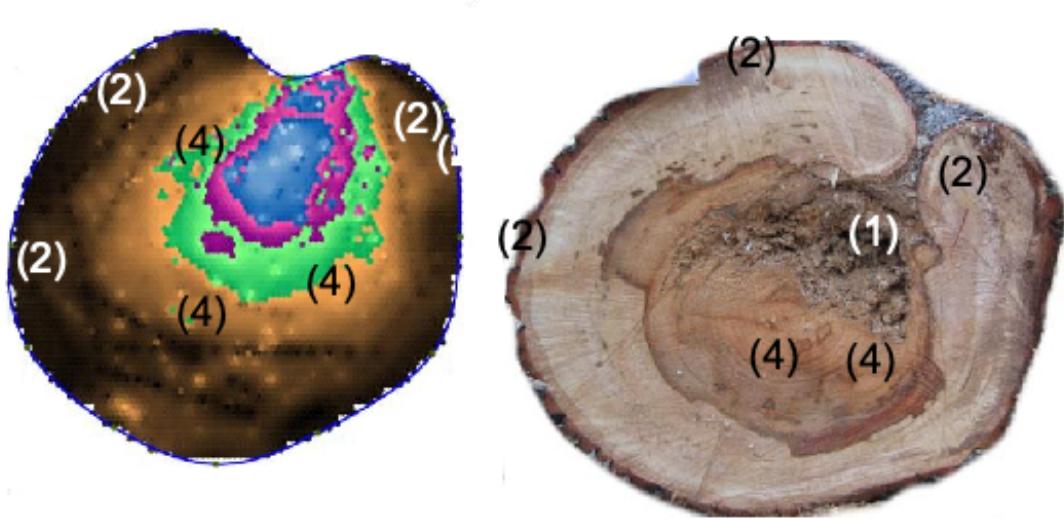


Figure 8.9: An example of a sonic tomograph image (left) and across section of the same tree (right), annotated to show internal features of the stem: (1) cavity or dead dry wood, (2) sound wood, (4) active decay with dense wood. Taken from Argus Electronic GmbH (2016).

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.

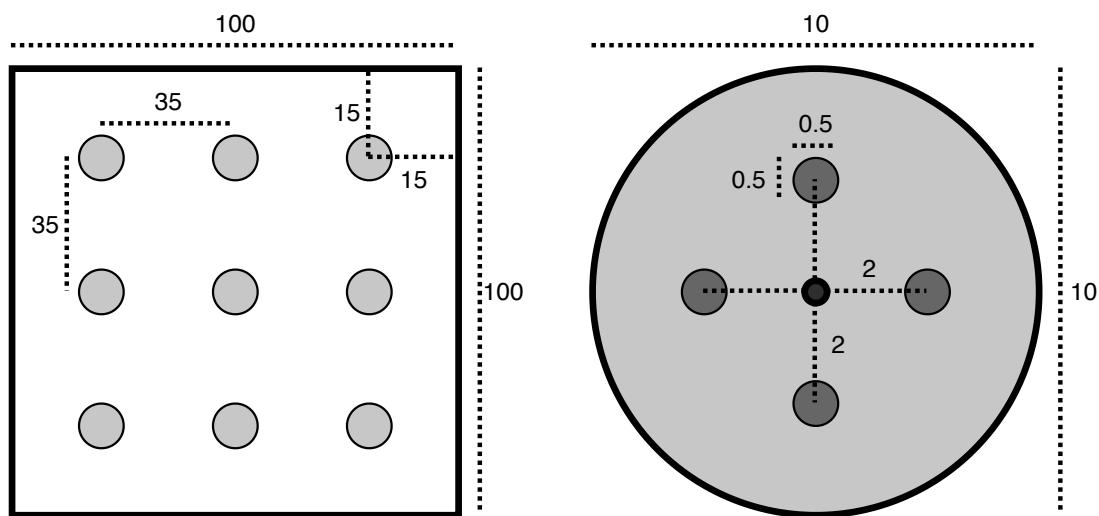


Figure 8.10: The layout of 10 m diameter subplots within each 1 ha square plot. Distances are marked by dotted lines, in metres. Each subplot is situated inside a 15 m buffer from the plot edge, with 35 m between subplot centres. Subplots are arranged in a 3x3 grid. Disc Pasture Measurements (DPM) and 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, Christopher B. (2018). ‘Biodiversity monitoring, earth observations and the ecology of scale’. In: *Ecology Letters* 21.10. Ed. by Nick Haddad, pp. 1572–1585. DOI: [10.1111/ele.13106](https://doi.org/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](https://doi.org/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](https://doi.org/10.1111/cobi.12341).
- Bogdanovich, Ekaterina, Oscar Perez-Priego, Tarek S. El-Madany, Marcus Guderle, Javier Pacheco-Labrador, Shaun R. Levick, Gerardo Moreno, Arnaud Carrara, M. Pilar Martín & Mirco 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](https://doi.org/10.1016/j.foreco.2021.118945).
- Brokaw, Nicholas & Jill 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](https://doi.org/10.1016/s0378-1127(99)00141-3).
- Burt, Andrew, Mathias Disney & Kim Calders (2018). ‘Extracting individual trees from lidar point clouds using treeseg’. In: *Methods in Ecology and Evolution*. Ed. by Sarah Goslee. DOI: [10.1111/2041-210x.13121](https://doi.org/10.1111/2041-210x.13121).

- Calders, Kim, Glenn Newnham, Andrew Burt, Simon Murphy, Pasi Raumonen, Martin Herold, Darius Culvenor, Valerio Avitabile, Mathias Disney, John Armston et al. (2014). ‘Nondestructive estimates of above-ground biomass using terrestrial laser scanning’. In: *Methods in Ecology and Evolution* 6.2. Ed. by Sean McMahon, pp. 198–208. DOI: 10.1111/2041-210x.12301.
- Case, Madelon F., Jesse B. Nippert, Ricardo M. Holdo & A. Carla Staver (2020). ‘Root-niche separation between savanna trees and grasses is greater on sandier soils’. In: *Journal of Ecology* 108.6. Ed. by Imma Oliveras, pp. 2298–2308. DOI: 10.1111/1365-2745.13475.
- Case, Madelon F. & A. Carla Staver (2016). ‘Fire prevents woody encroachment only at higher-than-historical frequencies in a South African savanna’. In: 54.3. Ed. by Jeremy James, pp. 955–962. DOI: 10.1111/1365-2664.12805.
- Chambers, Jeffrey Q., Joaquim dos Santos, Ralrh J Ribeiro & Niro 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. Bürquez, 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, Jerome, Richard Condit, Salomon Aguilar, Andres Hernandez, Suzanne Lao & Rolando Perez (2004). ‘Error propagation and scaling for tropical forest biomass estimates’. In: *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 359.1443. Ed. by Y. Malhi & O. L. Phillips, pp. 409–420. DOI: 10.1098/rstb.2003.1425.
- Chave, Jérôme, Stuart J. Davies, Oliver L. Phillips, Simon L. Lewis, Plinio Sist, Dmitry Schepaschenko, John Armston, Tim R. Baker, David Coomes, Mathias 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: 9.5, pp. 1809–1821. DOI: 10.5194/bg-9-1809-2012.
- Cooper, Sam, David Roy, Crystal Schaaf & Ian Paynter (2017). ‘Examination of the Potential of Terrestrial Laser Scanning and Structure-from-Motion Photogrammetry for Rapid Nondestructive Field Measurement of Grass Biomass’. In: 9.6, p. 531. DOI: 10.3390/rs9060531.
- Devine, Aisling P., Robbie A. McDonald, Tristan Quaife & Ilya M. D. Maclean (2017). ‘Determinants of woody encroachment and cover in African savannas’. In: 183.4, pp. 939–951. DOI: 10.1007/s00442-017-3807-6.
- Exbrayat, Jean-François, A. Anthony Bloom, Nuno Carvalhais, Rico Fischer, Andreas Huth, Natasha MacBean & Mathew 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. Héault, A. Alonso, H Memiaghe, P. Bissengou, 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, Stephanie P., Juan Manuel Dupuy, Alicia Peduzzi & J. Luis 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, Gregory S., Javier O. Ballesteros, Cesar A. Barrios-Rodriguez, Ernesto F. Bonadies, Marjorie L. Cedeño-Sánchez, Nohely J. Fossatti-Caballero, Mariam M. Trejos-Rodríguez, José Moises Pérez-Suñiga, Katharine S. Holub-Young, Laura 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, Rosa C., Oliver L. Phillips & Timothy 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, Simon J., Kathleen C Weathers, Walter K Dodds, Patricia A Soranno, Lynn C Sweet, Kendra S Cheruvellil, John S Kominoski, Janine Rüegg, Alexandra M Thorn & Ryan 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, Stephanie E., Sean S. Anderson, Sarah C. Bagby, Corinna Gries, Xueying Han, Edmund M. Hart, Matthew B. Jones, W. Christopher Lenhardt, Andrew MacDonald, William 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, William A., Erika L. Geiger, Sybil G. Gotsch, Davi R. Rossatto, Lucas C. R. Silva, On Lee Lau, M. Haridasan & Augusto 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. Ed. by Francisco Lloret, pp. 759–768. DOI: 10.1111/j.1461-0248.2012.01789.x.
- Hopkinson, Chris, Laura Chasmer, Colin Young-Pow & Paul 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: 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, Zs., 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, David B. & William 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, Gabriela, Simon L. Lewis, Mark Burkitt & Oliver L. Phillips (2011). ‘Forest-Plots.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.
- Luoma, Ville, Ninni Saarinen, Ville Kankare, Topi Tanhuanpää, Harri Kaartinen, Antero Kukko, Markus Holopainen, Juha Hyppä & Mikko 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, James A., Tucker J. Furniss, Daniel J. Johnson, Stuart J. Davies, David Allen, Alfonso Alonso, Kristina J. Anderson-Teixeira, Ana Andrade, Jennifer Baltzer, Kendall 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, David W. & Aaron 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, Yadavinder, Tobias Jackson, Lisa Patrick Bentley, Alvaro Lau, Alexander Shenkin, Martin Herold, Kim Calders, Harm Bartholomeus & Mathias 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, Robert E, Nicholas J Brazee & Shawn 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, Oscar J. Abelleira, Alexander K. Fremier, Sven Günter, Zayra Ramos Bendaña, Lee Vierling, Sara M. Galbraith, Nilsa A. Bosque-Pérez & Jenny 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, Iain M., Nicholas J. Berry, Thilde Bech Bruun, Kristell Hergoualc'h, Ole Mertz, Andreas de Neergaard & Casey 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, Teis Nørgaard, Nicholas Clarke, Alina Danielewska & Richard Fischer (2013). ‘Towards Supersites in Forest Ecosystem Monitoring and Research’. In: *Developments in Environmental Science*. Elsevier, pp. 475–496. DOI: 10.1016/b978-0-08-098349-3.00022-0.
- Panzou, Grace Jopaul Loubota, Adeline Fayolle, Tommaso Jucker, Oliver L. Phillips, Stephanie Bohlman, Lindsay F. Banin, Simon L. Lewis, Kofi Affum-Baffoe, Luciana F. Alves, Cécile Antin et al. (2020). ‘Pantropical variability in tree crown allometry’. In: 30.2. Ed. by Andrew Kerkhoff, pp. 459–475. DOI: 10.1111/geb.13231.
- Picard, Nicolas, Ervan Rutishauser, Pierre Ploton, Alfred Ngomanda & Matieu 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, Natasha A. L., Giselda Durigan, Jess Rickenback, R. Toby Pennington, Kyle G. Dexter, William A. Hoffmann, Rodolfo C. R. Abreu & Caroline E. R. Lehmann (2020). ‘Shade alters savanna grass layer structure and function along a gradient of canopy cover’. In: 32.1. Ed. by Francisco Pugnaire. 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, Maxime, Nicolas Barbier, Pierre Couteron, Pierre Ploton, Grégoire Vincent, Martin Herold, Stéphane Mermoz, Sassan Saatchi, Jérôme Chave, Florian 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, Graeme 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, Ninni, Ville Kankare, Jiri Pyörälä, Tuomas Yrttimaa, Xinlian Liang, Michael A. Wulder, Markus Holopainen, Juha Hyypää & Mikko Vastaranta (2019). ‘Assessing the Effects of Sample Size on Parametrizing a Taper Curve Equation and the Resultant Stem-Volume Estimates’. In: *Forests* 10.10, p. 848. DOI: 10.3390/f10100848.
- Saglam, Serhun, Emrah Ozdemir, Ulas Yunus Ozkan, Tufan Demirel & Ender 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, Dmitry, Jérôme Chave, Oliver L. Phillips, Simon L. Lewis, Stuart J. Davies, Maxime Réjou-Méchain, Plinio Sist, Klaus Scipal, Christoph Perger, Bruno 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.
- Solbrig, O. T., E. Medina & J. F. Silva (1996). *Biodiversity and Savanna Ecosystem Processes*. Berlin, Germany: Springer-Verlag.
- Srinivasan, Shruthi, Sorin Popescu, Marian Eriksson, Ryan Sheridan & Nian-Wei 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, Nicola, Caroline E. R. Lehmann, Brett P. Murphy & Giselda Durigan (2017). ‘Savanna woody encroachment is widespread across three continents’. In: 23.1, pp. 235–244. DOI: 10.1111/gcb.13409.
- Takoudjou, Stéphane Momo, Pierre Ploton, Bonaventure Sonké, Jan Hackenberg, Sébastien Griffon, Francois Coligny, Narcisse Guy Kamdem, Moses Libalah, Gislain II Mofack, Gilles Le 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. Ed. by Sean McMahon, pp. 905–916. DOI: [10.1111/2041-210x.12933](https://doi.org/10.1111/2041-210x.12933).
- Thies, Michael, Norbert Pfeifer, Daniel Winterhalder & Ben 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](https://doi.org/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](https://doi.org/10.1109/tim.2003.820472).
- Wagner, Fabien Hubert, Matheus Pinheiro Ferreira, Alber Sanchez, Mayumi C.M. Hirye, Maciel Zortea, Emanuel Gloor, Oliver L. Phillips, Carlos Roberto de Souza Filho, Yosio Edemir Shimabukuro & Luiz 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](https://doi.org/10.1016/j.isprsjprs.2018.09.013).
- 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](https://doi.org/10.2307/2260340).
- Xiao, Jingfeng, Frederic Chevallier, Cecile Gomez, Luis Guanter, Jeffrey A. Hicke, Alfredo R. Huete, Kazuhito Ichii, Wenjian Ni, Yong Pang, Abdullah 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](https://doi.org/10.1016/j.rse.2019.111383).