



**SPATIO-TEMPORAL ANALYSIS OF WOODY VEGETATION DATA AT VARIOUS
HEIGHT CLASSES WITHIN A SEMI-ARID SAVANNA: INSIGHTS ON
ENVIRONMENTAL DRIVERS, DISTRIBUTIONS AND DYNAMICS**


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**Submitted in fulfilment of the academic requirements for the degree of Doctor of Philosophy in
the School of Life Sciences, University of KwaZulu-Natal, Durban**

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ABSTRACT

Savanna vegetation is regulated by bottom-up (e.g. soil and rainfall) and top-down (e.g. fire and herbivory) factors. Little is known about how these factors influence biodiversity at regional scales, particularly spatial patterns of woody plant cover, species richness, distribution and composition at various height classes. Vegetation studies are often restricted to hillslope or catchment-level scales due to time and/or logistical constraints, however there is a need to understand patterns of vegetation dynamics at regional scales as well. The main aim of this thesis was to better understand the factors (bottom-up and top-down) that influence vegetation structural dynamics in terms of species richness, distribution, composition and woody cover at regional scales.

Using a rapid data collecting technique within $n > 1800$ field sites across the entire Kruger National Park, South Africa, woody species were identified and categorized into one of three height classes; shrub (0.75m – 2.5m), brush (2.5m-5.5m) and tree (>5.5 m). From this, several vegetation attributes were collated; such as species composition, richness and woody cover at each height class. A range of covariates related to disturbance (i.e. fire frequency and elephant density), landscape (e.g. aspect, altitude) and climate (temperature, rainfall) were used to identify which covariates were significantly associated with each attribute of interest.

A primary finding of this research highlights the importance of bottom-up factors, such as geology and rainfall, for woody vegetation spatial distribution at regional scales. However, depending on the response variable (e.g. species richness, woody cover, species distribution), the various height classes were not influenced equally by each specific environmental factor. Overall, both climatic and non-climatic factors were highly associated with species distribution and richness, but top-down factors such as fire and herbivory were significantly associated with maintaining plant structural variation. This influenced species community composition but not species richness at each height class. Similarities in composition were related to degree of disturbance rather than the disturbance alone at specific height classes. Therefore, while species distribution and woody cover were spatially regulated by specific climatic and non-climatic factors, top-down disturbances were essential in preserving structural heterogeneity. Future vegetation monitoring campaigns in disturbance-driven systems should be cognizant of the importance of vegetation structure.

PREFACE

The experimental work described in this dissertation “Spatio-temporal analysis of woody vegetation at various height classes with a semi-arid savanna” insights on environmental drivers, distributions and dynamics” was carried out in the School of Life Sciences, University of KwaZulu-Natal, Durban, from May 2013 to March 2015, under the supervision of A/Prof Gregory A. Kiker, Dr. U. Scharler, Prof. Henry G. Mwambi and Dr. I.P.J. Smit.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

DECLARATION 1 - PLAGIARISM

I, RHEINHARDT SCHOLTZ declare that;

1. The research reported in this thesis, except where otherwise indicated, and is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
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DECLARATION 2 - PUBLICATIONS

PUBLICATION 1

Kiker, G. A., Scholtz, R., Smit, I. P. J. & Venter, F. J., 2014, 'Exploring an extensive dataset to establish woody vegetation cover and composition in Kruger National Park for the late 1980s', *Koedoe-African Protected Area Conservation and Science* 56 (1).

Author Contributions:

G.A.K. was the project leader and provided the first-level database preparation and analysis. R.S. performed all spatial statistical analysis and developed all continuous map estimates. I.P.J.S. provided both conceptual and detailed analysis methodologies in addition to guiding data interpretation. F.J.V. recorded all field data and provided conceptual and detailed contributions to the analysis.

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Author Contributions:

R.S. was the project leader and developed the original study idea and conducted all data analyses. G.A.K. provided prepared database for conducting species distribution models. I.P.J.S. provided conceptual insights to data and results interpretation. F.J.V. recorded all field data and provided detailed contributions to the results.

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Author Contributions:

R.S. was the project leader, developed the original study and conducted all data analyses. I.P.J.S. provided insight into methodological approaches on data analyses and insights into the results. C.C-W provided both conceptual sight to the manuscript and additional ideas for data analysis. G.A.K. provided prepared database for analyses and conceptual insight on results. F.J.V. recorded all field data and provided detailed contributions to the results.

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R.S. was the project leader, developed the original study and conducted all data analyses. G.A.K. provided prepared database for analyses and provided conceptual insight on results. U.M.S. provided conceptual insight on the study. H.G.M and G.D. provided advice and input on data analyses

employed. F.J.V. recorded all field data and provided detailed contributions to the significance of the study.

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CHAPTER 1: INTRODUCTION

1.1 Savannas as dynamic ecosystems

Savannas are characterized by a unique co-existence of two major plant life forms; grass and a discontinuous tree layer (Skarpe 1992; Scholes & Archer 1997; Bond 2008). Their co-existence has intrigued researchers for many years, in particular, variation in woody cover, distribution and communities (Sankaran et al. 2005; Levick & Rogers 2011; Stevens et al. 2013). For this reason, woody vegetation dynamics has received a substantial amount of global attention in recent years (e.g. Scholes & Archer 1997; Scholes, Bond & Eckhardt 2003; Sankaran, Ratnam & Hanan 2004; Sankaran, Ratnam & Hanan 2008; Accatino et al. 2010), yet the processes and patterns that give rise to woody vegetation persistence are only marginally understood (Smit et al. 2010; Vanak et al. 2012). These processes, including stochastic events (e.g. disturbances such as fire and herbivory and their interaction) occur at various scales and at irregular intervals (Levin 1992; Bucini & Hanan 2007), indicative of a non-linear complex system. There have been many attempts to explain the interactions between ecological processes and patterns that give rise to savanna vegetation (Lehmann et al. 2014). However, the lack of predictability of how factors such as a changing climate, soil, fire and herbivory affects woody vegetation has led to many open-ended theories, except perhaps for the evidence of a rainfall gradient setting the upper asymptote for woody cover in African savannas and variation below this threshold by disturbances (Sankaran et al. 2005).

A large body of research on woody vegetation dynamics has provided essential information for researchers and managers of protected areas within savannas (e.g. Peel, McNamara & Jacobs 1993; Enslin et al. 2000; Scholes, Bond & Eckhardt 2003; Govender, Trollope & Van Wilgen 2006; Bucini & Hanan 2007; Smith et al. 2013), but a unified view of the drivers influencing woody vegetation in savanna systems has been slow to emerge (Midgley, Lawes & Chammille-Jammes 2010). This is partly due to top-down disturbances such as fire and herbivory that impact vegetation at various scales and at irregular intervals having major influences on the spatial distribution of woody vegetation (van Langevelde et al. 2003). The magnitude of the interactive effect between fire and herbivory are often non-linear, making it difficult to predict and patterns are generally not held across the numerous scales in savannas ecosystems (e.g. scale can range from an organisms home range to catenal sequences related to soil or a river catchment (Du Toit, Biggs & Rogers 2003)).

Landscape heterogeneity is a crucial determinant of species diversity and richness and is a term widely used throughout the ecological literature (Allouche et al. 2012). It is defined by Li and Reynolds (1995) as “the complexity and/or variability of a system property in space and/or time”. Quantifying heterogeneity poses many challenges, particularly with regard to spatial scale (Levin 1992) and temporal changes such as during periods of drought (Viljoen 1995; Porensky et al. 2013). Habitat heterogeneity can be created by various sources; for example, variation in woody vegetation

structure and the spatial arrangement of termite mounds (Erpenbach, Wittig & Hahn 2014). Managing biodiversity in a heterogeneous system is challenging, therefore management adaptation is essential in dynamic systems (Biggs & Rogers 2003; Gardner & Engelhardt 2008; Biggs et al. 2011). Since dynamic savanna systems are constantly influenced by disturbances such as fire and herbivory, the intermediate disturbance hypothesis (IDH) proposes that the highest diversity would be found in areas of intermediate disturbance (Connell 1978). This theory has received a substantial amount of attention in many ecosystems since its inception (e.g. Jeltsch et al. 1998; Roxburgh, Shea & Wilson 2004; Bongers et al. 2009) and well-studied, disturbance-driven systems such as savannas provide an opportunity to test the IDH.

1.2 Drivers of dynamic savanna systems

Of the many drivers, ecological processes and stochastic disturbances that influence savanna ecosystems (e.g. predation, migration, droughts, floods (see Sinclair et al. 2007 for a summary)), most research on vegetation dynamics appears to agree that rainfall and soil (known as “bottom-up” drivers) and fire and herbivory (known as “top-down” drivers) influence African savanna vegetation dynamics substantially, while the relative effects of these predictors vary according to scale (Scholes, Bond & Eckhardt 2003; Venter, Scholes & Eckhardt 2003; Ekblom & Gillson 2010; Levick & Rogers 2011). Bottom-up drivers interact substantially to promote persistence of savanna vegetation in both the herbaceous and woody vegetation layers (Knoop & Walker 1985; Sankaran et al. 2005; Treydte et al. 2008; Accatino et al. 2010). This in turn influences top-down drivers such as fire intensity and frequency by influencing biomass (fuel load) fluctuations (Sankaran, Ratnam & Hanan 2008; Smit et al. 2010; Smit et al. 2013b; Smith et al. 2013) and reduces vegetation biomass. All of these processes in turn have cascading effects on ecosystem function and processes such as nutrient cycling (Anderson et al. 2007; Sinclair et al. 2007; Holdo, Holt & Fryxell 2009).

Within Kruger National Park, South Africa (KNP), a semi-arid savanna; two long-term experiments provided valuable information regarding the importance of bottom up process influencing vegetation dynamics. February et al. (2013) showed that increasing rainfall will increase the competitive pressure exerted by grasses on trees to the extent that trees will only recruit into the adult stage during drought years. However, Kulmatiski and Beard (2013) showed that if total rainfall stays constant, but the rainfall intensity is increased, it will favor woody species over herbaceous species. Both of these experiments were conducted within herbivore exclosures and therefore ignore the interactive effect of herbivory on plant persistence. Nevertheless, these examples demonstrate the complexities that give rise to the heterogeneous landscapes seen within the KNP savanna system and highlight the importance of understanding the mechanisms through which rainfall influences vegetation dynamics.

Fire frequency and intensity, which are closely related to rainfall, are important in maintaining a mixture of trees and grass in savanna systems worldwide (Scholes & Archer 1997; Archibald et al. 2005; Govender, Trollope & Van Wilgen 2006; Sankaran, Ratnam & Hanan 2008; Smit et al. 2010; Diouf et al. 2012; Staver & Levin 2012). The importance of fire in many African savanna systems (e.g. Sinclair et al. 2007; Holdo, Holt & Fryxell 2009), and worldwide in maintaining savanna and forest boundaries has been well documented (Staver, Archibald & Levin 2011). Fire is also crucial in shaping savanna vegetation structure (Govender, Trollope & Van Wilgen 2006; Smit et al. 2010).

Fire manipulation experiments in African savannas are well documented since the 1940s (van Wilgen et al. 2000) and many fire-related projects are still ongoing in southern African protected areas (SANParks Research Report 2013). In KNP, the Experimental Burn Plots (EBPs) were established in 1954 in four rainfall regions of the park and remain one of the longest running fire manipulation experiments in Africa. These plots were established to better understand the effects of fire frequency and season on the parks flora and fauna (Biggs et al. 2003). Several other versions of these plots exist in KNP, such as the Nkhuhlu, Letaba and Makohlolo exclosures (Figure 1.1); some like the Nkhuhlu exclosures maintain fire manipulation experiments as well as restricting access to certain herbivores based on body size (Siebert & Eckhardt 2008; Siebert, Eckhardt & Siebert 2010).

One of the most important outcomes of fire research in savanna ecosystems is that woody vegetation is structurally responsive but compositionally resilient to fire, and that these effects are tightly related to season and rainfall (Govender, Trollope & Van Wilgen 2006; Smit et al. 2010). This has led to the idea that savanna tree demography is regulated by a fire-trap, a zone that is generally 3m above ground level in which growing trees are killed by fire (Bond & Van Wilgen 1996; Hoffmann et al. 2009). It is also known that complete mortality by fire is highly unlikely since flames are seldom carried in to the canopy of larger trees. More recently, it has been postulated that the long term effects of fire regimes (van Wilgen et al. 2014) may have restricted recruitment of certain keystone species, and potential compositional changes may only emerge over longer time periods (Helm & Witkowski 2013) or in extreme events (Andersen, Woinarski & Parr 2012). Nevertheless, vegetation structure has been shown to influence plant and animal biodiversity (Karr & Roth 1971; Fuhlendorf & Smeins 1997; Fuhlendorf et al. 2006; Hovick et al. 2014), therefore, maintaining vegetation structural heterogeneity should promote higher biodiversity.



Plate 1.1 Fire breaks around the Makohlolo enclosure in Lower Sabie, Kruger National Park. Photo Source: R Scholtz

The other major top-down driver affecting savannas is herbivore impact, in particular by the African elephant (*Loxodonta africana*). Elephant impact exists in various forms, of which some may lead to tree mortality (e.g. toppling trees as seen in Figure 1.2) (Whyte et al. 1999; Owen-Smith et al. 2006; Hayward & Zawadzka 2010; Midgley, Lawes & Chammille-Jammes 2010; Shannon et al. 2011; Vanak et al. 2012; Sankaran, Augustine & Ratnam 2013). Here the impact is perceived to be an overall reduction of biodiversity and ecosystem functioning (Kalwij et al. 2010), including cascading effects on other herbivores (Fritz et al. 2002; Kohi et al. 2011; Hilbers et al. 2015). Elephants have been shown to utilize woody vegetation more during the dry season (Stokke & Toit 2000) which potentially influences the spatial distribution of other herbivores (Hilbers et al. 2015).

Studies by Asner and Levick (2012) and Levick and Asner (2012) showed that elephant impact was most prominent on trees found within the 5m- 9m height class and these studies agree with similar research in the same study area (Shannon et al. 2008; Shannon et al. 2011). In the Chobe National Park, Botswana, a similar result was found where a growing elephant population resulted in a decrease in tall trees (Kalwij et al. 2010). The density of elephants during that study was estimated at approximately 3.34 individuals/km² from aerial census data compared to approximately 0.7

individuals/km² in 2007 for KNP studies (Smit & Ferreira 2010). These elephant population densities exceed the proposed “threshold” of 0.5 individuals/km² as suggested by Cumming et al. (1997) who postulated that savanna woodlands would be converted to shrub-lands or grasslands if elephant population density exceeded 0.5 individuals/km².

Even though research has shown that elephant population densities can exceed these threshold amounts (Scheiter & Higgins 2012), it is important to acknowledge that the distribution of elephants and their associated impacts are largely influenced by their space use, the distribution of water in the area (Smit, Grant & Whyte 2007; Smit & Ferreira 2010) and rainfall (Birkett et al. 2012) over the landscape. Importantly, the elephant population in Chobe National Park is unfenced compared to one in KNP, and are therefore open to historical migration patterns across the landscape (Skarpe & Ringrose 2014). Ultimately, understanding how elephants use space will improve understanding on how they impact the landscape. However, this is a great challenge for researchers and managers alike as historical practices (e.g. culling) can have long-term influences on elephant behavior.



Plate 1.2 An example of elephant damage to woody trees in KNP. This is an *Acacia nigrescens*, a preferred forage species. Photo Source: R Scholtz

The interaction of fire and herbivory and the associated effects on vegetation is both fascinating and complex. For example, Sankaran et al. (2005; 2008) highlighted the importance of mean annual precipitation in regulating woody cover across African savannas and acknowledged fire as the second most important factor in determining plant woody cover. Higgins et al. (2007) found that the density of woody individuals was in fact unresponsive to fire treatments in the EBPs (a combination of season and fire frequency over a rainfall gradient). However, the relative dominance of small trees was highly responsive to fire, suggesting that fire indeed has a major effect on vegetation structure (Govender, Trollope & Van Wilgen 2006). These treatments are not isolated from herbivory, and perhaps this might have led Sankaran et al. (2008) to suggest that fire may be more important than herbivory in predicting woody cover in savannas.

Although the effects of fire on trees is less clear where herbivores are present (Staver et al. 2009; Staver & Bond 2014), the effects of herbivores, in particular elephants, have only been quantified at small scales (Asner & Levick 2012; Levick & Asner 2013). Recently, Wigley et al. (2014) showed that woody species communities are indeed affected by browsers, in terms of species distribution, density and population structure by actively browsing for selected, preferred species with particular traits making them more desirable. These traits were, but perhaps not limited to, high leaf nitrogen, low total phenolic content and low acid detergent lignin, all of which are directly related to soil and geology type. Similarly, Staver et al. (2009) showed how the effect of fire and herbivory suppress tree density in maturing saplings. In addition, they showed that the interactive effect of fire and browsing had a much greater effect on tree density, and therefore has a strong influence on the co-existence of trees and grasses in savannas (Scholes & Archer 1997). More recently, Staver and Bond (2014) alluded to a “browse-trap” highlighting that a reduction in browsing pressure on trees has a profound effect on tree establishment events. While grazers reduced grass biomass in a short time after reintroduction, tree release from browsing persisted regardless of tree size. This highlights the need to evaluate the global extent of herbivore effects in savannas (Staver & Bond 2014), particularly the pressure exerted on seedlings by top-down disturbances, while acknowledging that seedling recruitment could be resource limited as well (Holdo, Anderson & Morrison 2014).

It is clear that there are various drivers that interact and influence savanna vegetation dynamics depending on their height class, and a central theme throughout this thesis is to understand the importance of woody vegetation structure in relation to species distribution, composition and woody cover in semi-arid savannas.

1.3 Current concerns relating to vegetation change in African savannas

Managing an area within African savannas can be confounded by various factors relating to additional socio-ecological aspects of conservation. Not only are animals conserved in these areas, humans also rely on savannas for various ecosystem services such as grazing fields for cattle and fuel

wood for cooking purposes (Kalema et al. 2014). Managing and monitoring the use of these resources has become increasingly important over recent years (Twine 2005; Wessels et al. 2011) since savannas contain a large and rapidly growing proportion of the world's human population (Scholes & Archer 1997). A critical evaluation of human-disturbance interactions, particularly in light of climate change and its associated affects such as woody encroachment (Buitenwerf et al. 2012) and land degradation (Scholes 2009; Kalema et al. 2014) is therefore needed.

Understanding vegetation change (compositionally and structurally) and the factors responsible for these changes will enable sustainable resource use in savanna systems. Although this thesis is not aimed at highlighting how vegetation change may influence communal land users, the consequences of vegetation change will indeed be experienced by communal land users who rely on their environment for their daily livelihoods, as is the case in most parts of Africa. In this light, two current concerns surrounding woody vegetation dynamics in savannas are highlighted in this thesis; (i) woody encroachment (or bush thickening) (Roques, O'Connor & Watkinson 2001) and (ii) tall tree loss (Trollope et al. 1998; Shannon et al. 2008; Shannon et al. 2011). These structural changes in the woody vegetation layer are associated with an overall loss in biodiversity and ecosystem function (Noss 1990), although tall tree loss may be a concern specific to KNP in recent years (SANParks Research Report 2013).

The relative effect that top-down disturbances, in particular herbivory, has had on savanna vegetation remains largely unknown (Staver et al. 2009; Staver & Bond 2014). Attempts to monitor changes in the structural heterogeneity of the woody vegetation layer in KNP were established in 1996 with the implementation of the woody veld condition assessments (wVCAs), with four successful surveys completed to date in 1996, 2002, 2005 and 2008. Although data from the wVCA surveys has received minimal attention over recent years, it may provide the first evidence of woody vegetation structural changes. While the causes of woody encroachment are not fully understood (Ward 2005), actions to mitigate or control woody encroachment are currently being tested (Govender 2014).

The loss of tall trees has become a big concern in KNP over the past few decades (Trollope et al. 1998; Smit, Grant & Whyte 2007; Smit & Ferreira 2010; De Knegt et al. 2011) and creating baseline information on woody tall tree dynamics from the late 1980s will provide a much needed baseline for future research considering the political changes that took place in the 1990s in South Africa and KNP (e.g. moratorium on elephant culling (Whyte et al. 1999; Biggs & Rogers 2003)). Monitoring tall trees loss without a combination of fieldwork and technological advancements such as Light Detection and Ranging (LiDAR) will be challenging and perhaps inefficient (Asner & Levick 2012; Baldeck et al. 2014). Yet acknowledging the high costs involved with LiDAR, it may not be a management option for protected areas in most savannas of the world in the foreseeable future.

Substantial information exists regarding the rates of tall tree loss using repeat field-based surveys (Shannon et al. 2008; Shannon et al. 2011; Asner & Levick 2012) although these studies were conducted at small scales, they provide convincing evidence for the observed structural changes in savannas. These studies highlight rates of tall tree loss are constantly linked to an increasing elephant population in KNP. The latest census in KNP that took place in 2013 suggests an increase in the elephant population from the 2007 reported value (0.7 individuals/km²) to approximately 0.83 individuals/km² (Ferreira et al. 2013). However, the scales at which the effects of elephants are observed have often been restricted to small, less than park-wide scales. Therefore, whether the influence of an increasing elephant population on woody vegetation is restricted to small scales; remains to be seen.

The rationale of this thesis lies within the need to understand vegetation dynamics at regional scales. Currently, the vast body of research on savanna vegetation dynamics has largely been restricted to small, fine scaled studies due to logistical constraints associated with working in savanna systems as well as the scaling properties of the system. This highlights the importance of scale in savanna systems and that certain patterns and processes are more prominent at particular scales than others. With this in mind, vegetation height/structure adds to landscape heterogeneity, and understanding how vegetation in specific height classes responds to the various bottom-up and top-down drivers is largely unknown at regional scales. This knowledge gap will be specifically addressed in this thesis, as management of protected areas often occur on regional scales. Therefore, the main objective of this thesis is to identify the factors that influence the spatial distribution of species composition, species richness and woody cover at three height classes in a semi-arid savanna with one main question:

Are the drivers of savanna woody plants the same across all height classes?

This will be unpacked by answering the following sub-questions:

- a) Are the drivers of species distribution and composition similar across height classes?
- b) Are woody plant communities shaped by top-down disturbances? How does this relate to specific height classes?
- c) Do drivers of woody cover differ according to height class?

The culmination of this thesis aims to highlight the importance of vegetation structure that creates heterogeneous landscapes in savanna systems. Some repetition may occur throughout the thesis as each data chapter has been written up in the form of a scientific publication some of which are already published.

1.4 Structure of thesis

Part 1 of this thesis includes this introductory chapter along with introducing the woody vegetation dataset that will be used throughout the thesis (Chapter 2, which has been published in *Koedoe - African Protected Area Conservation and Science*).

Part 2 of this thesis teases some of the most important vegetation attributes attained from Chapter 2. In Chapter 3 (which has been published in *Ecosphere*) I aim to highlight the importance of vegetation height in species distributions by identifying drivers of some commonly occurring species at various height classes. This also serves as one of the first studies to document drivers of species distribution per height class within a semi-arid savanna. Chapter 4 (submitted for publication to *Diversity and Distributions*) aims to assess spatial patterns of species richness and identify if species composition at various height classes clusters in relation to geology and disturbance. Using the results obtained from Chapter 4, Chapter 5 (in final preparation for publication to *Landscape Ecology*) ignores species composition and aims to assess drivers of woody cover at various height classes at regional scales.

In part 3, Chapter 6 synthesizes the findings of this thesis and answers the questions set forward in this introductory chapter.

CHAPTER 2: EXPLORING AN EXTENSIVE DATASET TO ESTABLISH WOODY VEGETATION COVER AND COMPOSITION IN KRUGER NATIONAL PARK FOR THE LATE 1980s¹

2.1 Abstract

Woody plant cover and species composition play an important role in defining the type and function of savanna ecosystems. Approximately two thousand sites in the Kruger National Park (KNP) were surveyed by F.J Venter over a period from 1985 to 1989, recording vegetation, soil and topological characteristics. At each of these sites (approximately 20mx20m each), woody vegetation cover and species were recorded using a rapid, Braun-Blanquet classification for three height classes; Shrub (0.75m-2.5m), Brush (2.5m-5.5m) and Tree (>5.5m). The objective of this study is to re-analyze the vegetation component of the field data, with a specific focus to provide a spatially-explicit, height-differentiated, benchmark dataset in terms of species occurrence, species richness and structural canopy cover. Overall, 145 different woody species were recorded in the dataset out of the 458 species documented to occur in the park. The dataset describes a woody layer dominated by a relatively small number of widely occurring species, as 24 of the most common woody species accounted for all woody species found on over 80% of all sites. The less-common woody species (101) were each recorded on 20 sites or less. Species richness varied from 12 to 1 species per site. Structural canopy cover averaged 9.34%, 8.16% and 2.89% for shrub, brush and tree cover, respectively. The dataset provides a useful benchmark for woody species distribution in KNP and can be used to explore woody species and height class distributions as well as comparison with more recent or future woody vegetation surveys. The results provide evidence that large-scale, woody vegetation surveys conducted along roads provide useful ecosystem level information. However, such an approach fails to pick up less common species. The data presented here provide a useful snapshot of KNP woody vegetation structure and composition and provide excellent opportunities for spatio-temporal comparisons.

2.2 Introduction

Woody plant cover and species composition play an important role in defining the type and function of savanna ecosystems (Sankaran et al. 2005; Bucini & Hanan 2007; Wagenseil & Samimi 2007; Sankaran, Ratnam & Hanan 2008). When assessing the vulnerability or resilience of savannas to environmental or anthropomorphic drivers, changes in woody composition and density are often cited as evidence (Vanak et al. 2012). Analysis of woody plant height and locality data can have useful application to current issues in the Kruger National Park, South Africa (KNP). For example, monitoring of the various thresholds of potential concern (TPCs) as outlined by Biggs and Rogers (2003) aid KNP managers to monitor and assess biodiversity levels (Grant, Peel & Bezuidenhout

¹ Kiker, G. A., Scholtz, R., Smit, I. P. J. & Venter, F. J., 2014, 'Exploring an extensive dataset to establish woody vegetation cover and composition in Kruger National Park for the late 1980s', *Koedoe-African Protected Area Conservation and Science* 56 (1).

2011) and provide benchmark analysis for assessing when specific management interventions are needed (Scholes & Kruger 2011).

Within the KNP, considerable scientific and management effort has been invested into monitoring and studying woody vegetation dynamics, yet large-scale detailed vegetation cover and species data is often limited making it hard to generalize results (Sankaran, Ratnam & Hanan 2008). While more recent studies employing advanced remote sensing technology have provided useful information about the woody plant layer (Bucini et al. 2010; Asner & Levick 2012; Levick, Asner & Smit 2012; Smit & Asner 2012), one essential gap in these analyses of woody cover change is a comprehensive, KNP-wide, historical dataset for comparison.

Earlier studies of the KNP woody vegetation layer have been focused mostly on taxonomical descriptions with ecological groupings created to broadly define landscape-scale management areas (Coetzee & Nel 1978; Coetzee 1983; Gertenbach 1983). In more recent years, a variety of methods have been used to estimate percent woody cover or changes in woody cover for different KNP areas. These studies fall into two broad categories; detailed field-based surveys in limited, but representative areas and remote sensing-based studies over larger scales. Using a combination of aerial and fixed point photographs ranging from 1940 to 1998 along with field sampling, Eckhardt et al. (2001) reported woody cover increases of 12% on granite substrates (inclusive of trees and shrubs) and decreases of 64% on basalt substrates. Within the long-term fire exclusion plots (Experimental Burn Plots or EBPs), several studies have explored the role of fire and herbivory in various rainfall regimes within the park (van Wilgen et al. 2000). Using remote sensing techniques such as airborne LiDAR (Light Detection and Ranging), canopy cover, vegetation height cover and canopy structure was accurately estimated over thousands of hectares at a 0.5m-1m horizontal resolution (Asner, Levick & Smit 2011; Wessels et al. 2011). With the advances in satellite remote sensing technology, Bucini et al. (2010) used a combination of optical and radar imagery to estimate percent woody cover over the entire KNP. In addition to producing a percent woody cover map for KNP at a horizontal resolution of 90m, it was accompanied by a standard deviation map (at the 1km grid scale) which can be used as a metric for woody cover heterogeneity. Bucini et al. (2010) suggests that percent woody cover ranges between 0% to approximately 65% across the KNP landscape. To date, this is the most widely “accepted” percent woody cover map for KNP and extensively used in current research projects (e.g. De Knegt et al. 2011; Smit et al. 2013b). However, this map does not differentiate between vertical structure and as such includes all woody cover, irrespective of height class. This lack of vertical information in the Bucini et al. (2010) woody cover map is a critical gap, especially considering the management concern around the diminishing populations of tall (>5m) trees over recent years, as well as the concern with bush encroachment in certain areas of the park (Buitenwerf et al. 2012). This highlights the need for both current and historical data for detecting trends in woody vegetation structure and composition.

Between the descriptive studies of the 1970s and 1980s and the more recent remote sensing studies is the large and comprehensive field effort of Venter (Venter 1990). In the middle to late 1980s, Venter (1990) conducted a study in the KNP in which he used a rapid Braun-Blanquet (BB) survey method (Coetzee & Nel 1978) to describe vegetation at 1985 observation sites (Figure 2.1). Each selected site was visually examined over a 20m x 20m quadrat to determine the species present and the estimated canopy cover for three height classes (shrub 0.75-2.5m; Brush 2.5-5.5m and Tree > 5.5m). The assessment relied on ordinal scales rather than specific measurements to describe woody cover in each height class. For each species identified at a site, three BB codes were recorded for each height class using the number of canopy diameters separating occurrences of that species (Supplementary Material, Table S2.1). To allow multiple sites to be efficiently assessed, sites were selected systematically approximately every 2.5 km along tourist and management roads over the entire KNP (Figure 2.1). The results of soil, vegetation and topological features present at sites were used along with stereoscopic aerial photography to create functional land type maps for management and to estimate the percent areas of various land type and terrain unit areas (Venter 1990).

Venter (1990) and Venter et al. (2003) provided a critical analysis of landscape-level functionality in soils, topology and ecozones. However, we argue that further value can be gained by additional analysis of the original dataset. Significant management changes and climatic conditions occurred in the 1990s, including management changes for elephant population (Whyte et al. 1999; Shannon et al. 2008), fire management (van Wilgen et al. 2000), artificial water provision (Smit, Grant & Devereux 2007), herbaceous layer monitoring (Zambatis 2005) and the largest drought recorded (Viljoen 1995; Zambatis & Biggs 1995). A methodical re-analysis of the Venter (1990) dataset would therefore provide a valuable benchmark for comparison with later datasets to explore the ecosystem response to such large-scale ecosystem and management alterations. This dataset provides a unique opportunity to assess park-wide, field based data on woody species richness, occurrence and canopy cover at various height classes.

The objective of this study is to provide a comprehensive overview of the Venter (1990) dataset, followed by a re-analysis of the vegetation component of the field data in order to address the following key questions:

- *How is woody vegetation spatially distributed in the KNP landscape?*
- *Do the size classes (shrub, brush or tree) of a particular species have a different spatial distribution across the landscape?*
- *How many species were reported using a spatially diverse yet rapid, field monitoring campaign?*

- *Does woody species richness vary widely throughout the KNP? Does woody species richness vary with size classes?*
- *What was the structural distribution of KNP woody cover in terms of shrub (0.75m to 2.5m), brush (2.5m to 5.5m) and tall trees (greater than 5.5m) in the late 1980s?*

Over and above the ecological significance of our results, we believe that the lessons learned from our reanalysis will provide critical information to inform and guide future woody vegetation monitoring programmes.

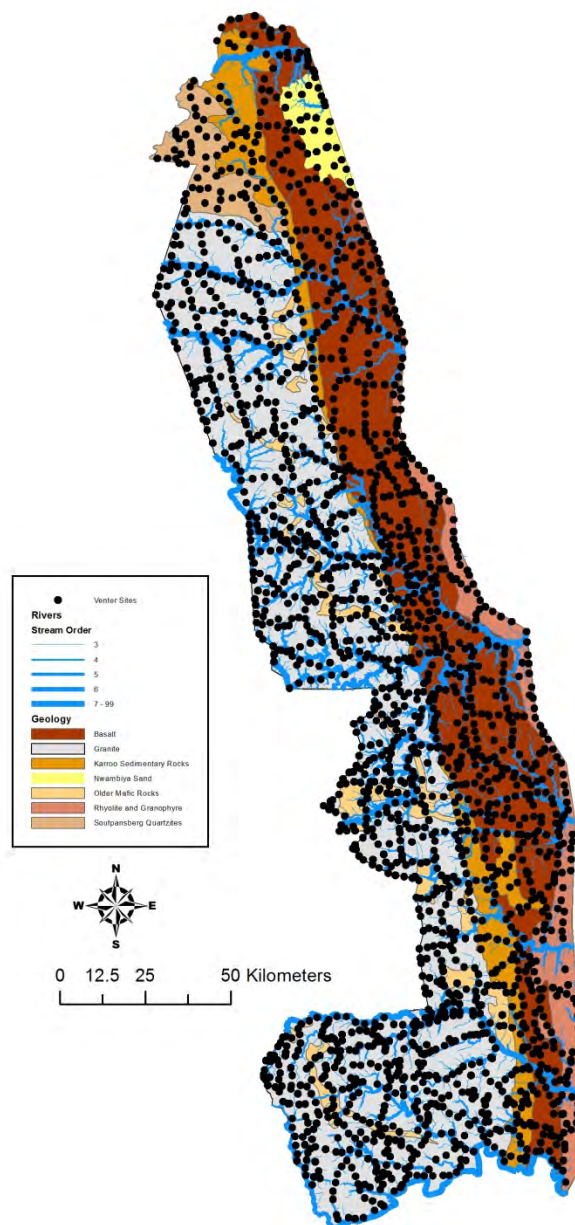


Figure 2.1 Venter (1990) field sites (n=1985) displayed as points with rivers and base geology.

2.3 Materials and methods

Originally, Venter (1990) utilized the SAS statistical package (SAS Institute Inc. 1988) for analysis of constituent soil, grass and tree species within land type and terrain unit classifications from the 1985 sites. These same field data files were translated into database and spreadsheet formats and were joined with site points digitalized from 1:50000 scale maps using ArcGIS (ESRI 2011) to create point-based maps of structural woody cover, species counts and species occurrence. From the original 1985 woody presence sites, 1820 sites were totaled and linked with the digitized sampling locations (the reduction in sites is due to missing location data for 165 sites).

The assessment sites were sorted to include only woody plant classifications and the BB data was used to calculate cover estimations for each of three height classes (Shrub: 0.75m-2.5m; Brush 2.5 - 5.5m; Tree >5.5m). As the BB categories vary within a pre-set percent estimate (Supplementary Material, Table S2.1), BB cover codes were assigned to low, average and high category values to explore potential variations in cover estimations. Thus, a BB record of “2a” denoted a range of 5% to 12% crown cover with 2-3 canopy diameters separating canopies. The subsequent woody cover calculations would assume 5% cover as a minimum estimate, 8.5% as a mean estimate and 12% as a maximum estimate. For each assessment site, all the recorded species were summed within their respective height classes to estimate a minimum, mean and maximum canopy cover (assuming no canopy overlap within a height class). In addition, the number of non-zero species recorded at each site and within each height class was summed to estimate a woody plant species richness value. Table 2.1 provides an example of woody data recorded for a typical site (#382) and the results of calculations for woody canopy cover and species richness. In addition, the five woody species recorded at the site (*Combretum zeyheri*, *Terminalia sericea*, *Acacia exuvialis*, *Combretum apiculatum* and *Combretum collinum*) were included as presence points in their respective height classes and their canopy covers were used in subsequent canopy cover estimates.

Table 2.1 Example of Venter (1990) field data and subsequent cover and species richness estimations for site number 382. The recorded Braun-Blanquet (BB) codes are used to create three canopy cover (%) estimates for each height class of each species. The Cover Total row sums all canopy cover estimates within a height class. Interspecies overlap within a height class is assumed to be negligible. The species richness row records the number of different species listed with non-zero occurrence for all height classes and within each height class.

| Site No. | SPECIES CODE | Field Data (BB code) | | 0.75m-2.5m (Shrub) | | | 2.5m - 5.5m (Brush) | | | >5.5m (Tree) | | | |
|-------------------------|--------------|----------------------|-------|--------------------|------------|------------|---------------------|--------------|------------|--------------|----------|----------|----------|
| | | Shrub | Brush | Tree | Mean | Min | Max | Mean | Min | Max | Mean | Min | Max |
| 382 | COMZEY | 1 | - | - | 3 | 1 | 5 | 0 | 0 | 0 | 0 | 0 | 0 |
| 382 | TERCER | + | 2A | - | 0.55 | 0.1 | 1 | 8.5 | 5 | 12 | 0 | 0 | 0 |
| 382 | ACAEXU | + | - | - | 0.55 | 0.1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 382 | COMAPI | - | 1 | 1 | 0 | 0 | 0 | 3 | 1 | 5 | 3 | 1 | 5 |
| 382 | COMCOL | - | + | - | 0 | 0 | 0 | 0.55 | 0.1 | 1 | 0 | 0 | 0 |
| Cover Total | | | | | 4.1 | 1.2 | 7 | 12.05 | 6.1 | 18 | 3 | 1 | 5 |
| Species Richness | | | | | 5 | 3 | | 3 | | | 1 | | |

Species occurrence data were sorted and ranked for each site to assess the most and least commonly recorded species with their respective number of sites. Two methods were used to interpolate the point data into continuous grids. For species-based maps, an estimation of probability of occurrence was calculated by the Indicator Kriging (IK) method (Lloyd & Atkinson 2001). IK is a non-parametric method of interpolation that was chosen since all species were recorded at each site, thus providing true absence/presence data. To develop continuous spatial maps for selected woody species, presence/absence data were compiled from the occurrence data and used to interpolate the binary data into a continuous map that indicates relative probability of occurrence (Auerbach & Shmida 1987). The semi-variogram was estimated using a maximum of 5 and a minimum of 2 neighboring data points. Data at unknown locations are estimated using the binary input values of known locations and the semi-variogram (Isaaks & Srivastava 1989).

For height-based, structural cover and woody species richness maps, continuous maps were obtained through Empirical Bayesian Kriging (EBK) (Pilz & Spoeck 2008). EBK was chosen to create interpolated maps as it accounts for user error in estimating the underlying semi-variogram through repeated simulations which is not done by ordinary Kriging methods. One hundred simulations were run to estimate the semi-variogram with a search neighborhood maximum of 15 and a minimum of 10 neighboring data points (Delfiner 2009).

Validation of the interpolation techniques was done by using the Root Mean Square Error (RMSE) which estimates the prediction error. The RMSE ranges from 0 to ∞ , where values of 0 indicate a perfect fit (Ritter & Munoz-Carpena 2013). Predicted values were extracted at the same point locations where field data was collected to compare observed vs predicted values. Prediction errors can be found in the Supplementary Material (Table S2.2).

All interpolation analyses were conducted using ArcMap 10.1 (ESRI 2011). RMSE values were calculated using the hydroGOF (Zambrano-Bigiarini 2013) package in R v.3.0.2 (R Development Core Team 2013).

2.4 Results

The following sections provide summary information for woody species frequency, selected species maps, species richness and structural cover. While each following section provides a brief summary with example tables and maps, more comprehensive field data files and meta-data will be made available through the SANParks Data Management system (<http://dataknp.sanparks.org>).

Woody Species Frequency and Occurrence

In viewing the diversity and abundance of individual woody tree species recorded by the Venter (1990) survey on 1985 woody presence sites, 145 different species were recorded from a possible total of 458 species known to occur in the park (Coetzee 1983; van Wyk 1984). Of these 145 species recorded, 24 species account for over 80 percent of all occurrences recorded (Table 2.2). Seventy percent of all woody species recorded were found on 20 sites or less. Just under half of the recorded species (65 of 145) occurred in 5 or less sites. These results show that even with a significant level of spatially diverse field sites ($n = 1985$ locations), locating and monitoring less common woody species remains a significant challenge.

Table 2.2 Ranked list of the 24 most frequently recorded tree species and the percentage of total sites that recorded their presence (n=1985 sites with woody vegetation recorded).

| Species Code | Species | # of sites recorded | Rank | Percent of Sites | Percent of all sightings | Cumulative Sightings |
|--------------|----------------------------------|---------------------|------|------------------|--------------------------|----------------------|
| COLMOP | <i>Colophospermum mopane</i> | 790 | 1 | 39.80 | 10.1 | 10.1 |
| COMAPI | <i>Combretum apiculatum</i> | 708 | 2 | 35.67 | 9.0 | 19.1 |
| ACANIG | <i>Acacia nigrescens</i> | 497 | 3 | 25.04 | 6.3 | 25.5 |
| DICAFR | <i>Dichrostachys cinnerea</i> | 455 | 4 | 22.92 | 5.8 | 31.3 |
| GREBIC | <i>Grewia bicolor</i> | 371 | 5 | 18.69 | 4.7 | 36.0 |
| TERCER | <i>Terminalia sericea</i> | 357 | 6 | 17.98 | 4.6 | 40.6 |
| EUCDIV | <i>Euclea divinorum</i> | 317 | 7 | 15.97 | 4.0 | 44.6 |
| COMHER | <i>Combretum hereroense</i> | 306 | 8 | 15.42 | 3.9 | 48.5 |
| SCLBIR | <i>Sclerocarya birrea</i> | 300 | 9 | 15.11 | 3.8 | 52.3 |
| LONCAP | <i>Lonchocarpus capassa</i> | 241 | 10 | 12.14 | 3.1 | 55.4 |
| COMIMB | <i>Combretum imberbe</i> | 202 | 11 | 10.18 | 2.6 | 58.0 |
| ALBHAR | <i>Albizia harveyi</i> | 191 | 12 | 9.62 | 2.4 | 60.4 |
| COMZEY | <i>Combretum zeyheri</i> | 190 | 13 | 9.57 | 2.4 | 62.9 |
| ACATOR | <i>Acacia tortilis</i> | 168 | 14 | 8.46 | 2.1 | 65.0 |
| PTEROT | <i>Pterocarpus rotundifolius</i> | 147 | 15 | 7.41 | 1.9 | 66.9 |
| ACAGER | <i>Acacia gerrardii</i> | 138 | 16 | 6.95 | 1.8 | 68.6 |
| COMCOL | <i>Combretum collinum</i> | 138 | 17 | 6.95 | 1.8 | 70.4 |
| PELAFR | <i>Peltophorum africanum</i> | 128 | 18 | 6.45 | 1.6 | 72.0 |
| CISCON | <i>Cissus cornifolia</i> | 127 | 19 | 6.35 | 1.6 | 73.7 |
| ACEEXU | <i>Acacia exuvialis</i> | 126 | 20 | 6.30 | 1.6 | 75.2 |
| TERPRU | <i>Terminalia prunioides</i> | 125 | 21 | 5.49 | 1.4 | 76.6 |
| MAYSEN | <i>Maytenus senegalensis</i> | 109 | 22 | 5.19 | 1.3 | 78.0 |
| SECVIR | <i>Securinea virosa</i> | 103 | 23 | 4.94 | 1.3 | 79.2 |
| SPIAFR | <i>Spirostachys africana</i> | 91 | 24 | 4.58 | 1.2 | 80.4 |

From the original 1985 woody presence sites, 1820 sites were totaled and linked with the digitized location sampling points to create species occurrence and richness maps. For all interpolated maps, the output grid resolution size was 1.7km, which is the minimum distance between points for each grid to contain at least one sample point.

Species occurrence maps for four of the six most common woody species were created for each of the three height classes to show the utility of the Venter (1990) data to estimate the probability of presence/absence. Figures 2.2a-d show interpolated maps created from IK using presence/absence data for *Terminalia sericea* (Silver Cluster Leaf) at each height class and for all height classes combined. The figures show similar presence maps for each height class in the southwest KNP (Pretoriuskop) region with some wider distribution of shrub and brush heights in the northern KNP.

Figures 2.3a-d show the interpolated maps for *Colophospermum mopane* (Mopane) showing quite similar probability distributions for all height classes along with the expected distribution northwards from the Olifants River. The presence uniformity amongst the Tree, Brush and Shrub height classes is not observed for *Acacia nigrescens* (Knob Thorn) (Figures 2.4a-d) nor for *Combretum apiculatum* (Red Bush Willow) (Figures 2.5a-d). The interpolated *Acacia nigrescens* maps show similar probabilities for shrub and brush heights with tall trees distributed more widely in riverine areas and the extreme southern KNP.

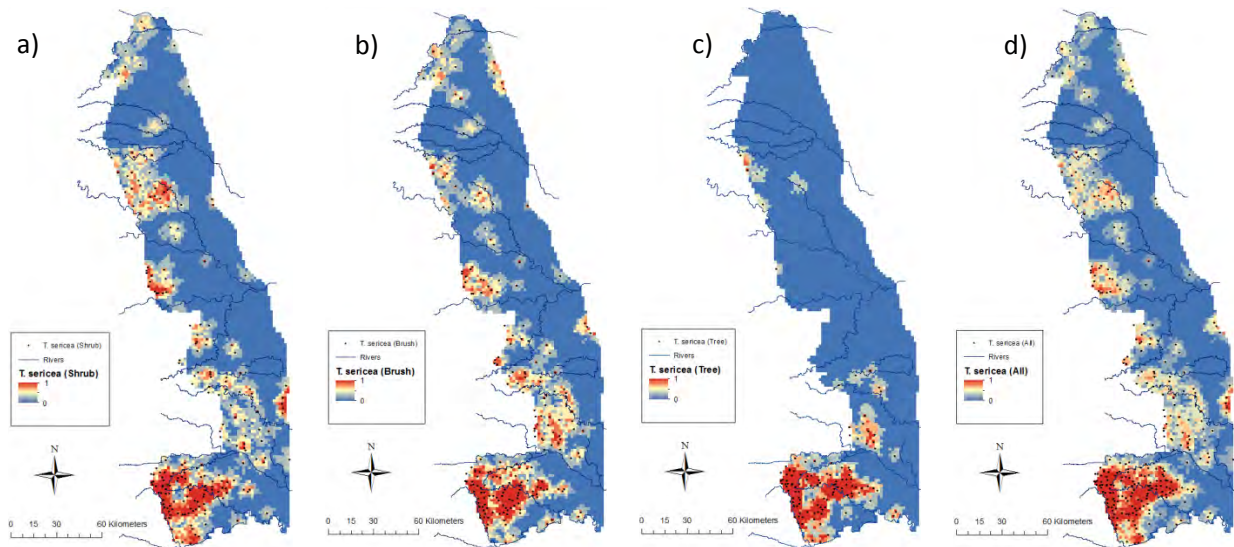


Figure 2.2a-d. Interpolated map from Indicator Kriging showing potential probability of *Terminalia sericea* based on presence/absence data at each structural height class; a) shrub (0.75m-2.5m) b) brush (2.5m-5.5m) c) tree (>5.5m) and d) all sizes combined.

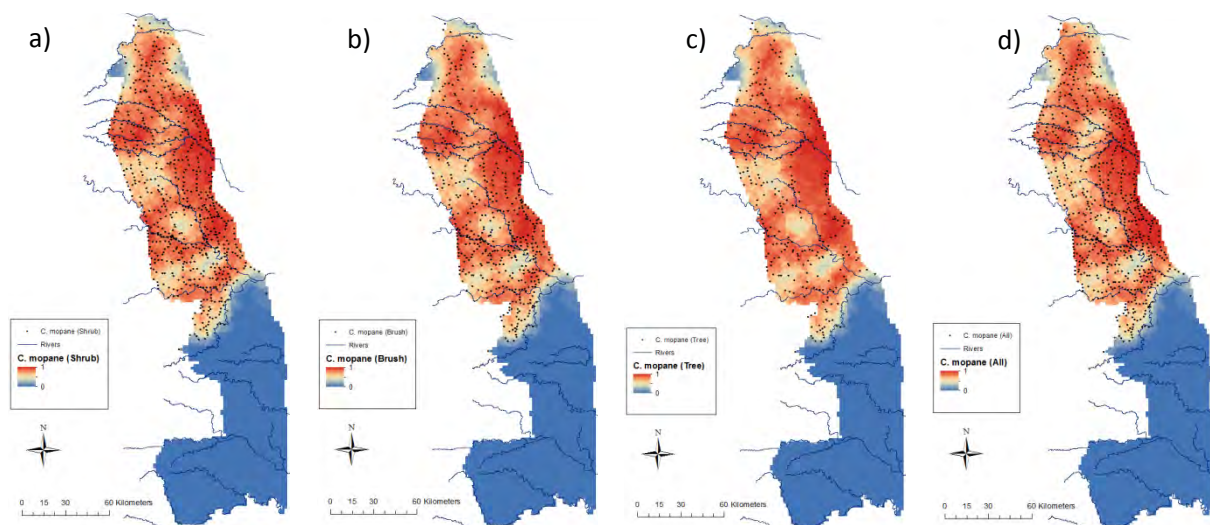


Figure 2.3a-d. Interpolated map from Indicator Kriging showing potential probability of *Colophospermum*

mopane based on presence/absence data at each structural height class; a) shrub (0.75m-2.5m) b) brush (2.5m-5.5m) c) tree (>5.5m) and d) all sizes combined.

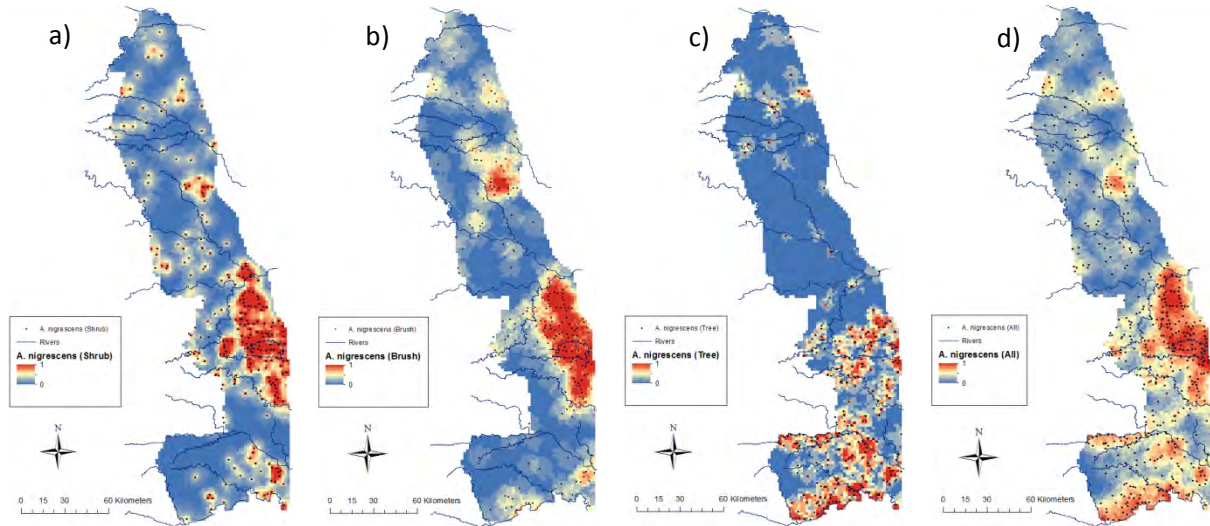


Figure 2.4a-d. Interpolated map from Indicator Kriging showing potential probability of *Acacia nigrescens* at each structural height class; a) shrub (0.75m-2.5m) b) brush (2.5m-5.5m), c) tree (>5.5m), and d) all sizes combined.

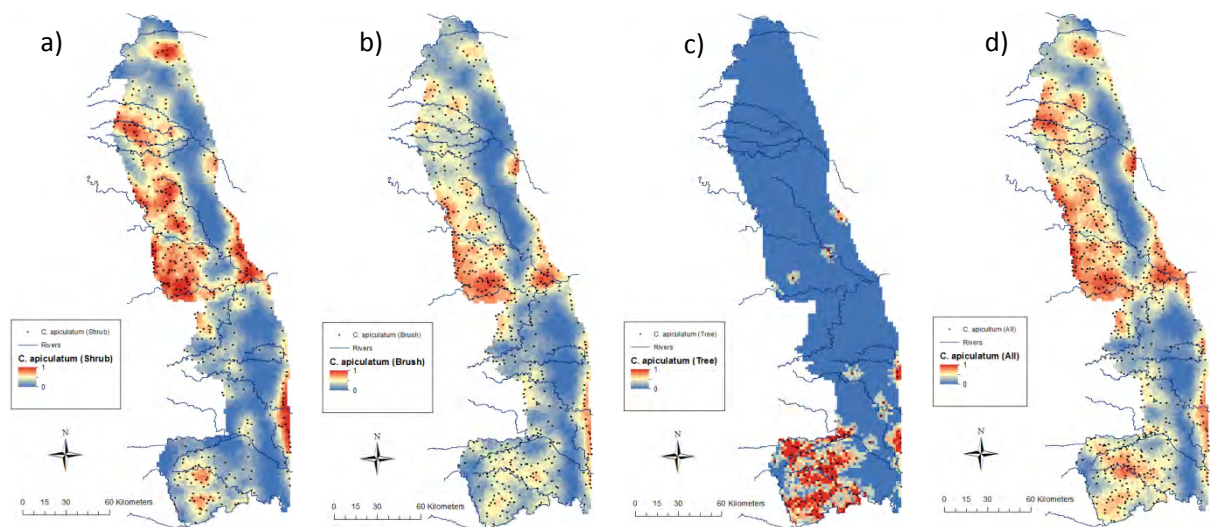


Figure 2.5a-d. Interpolated map from Indicator Kriging showing potential probability of *Combretum apiculatum* based on presence/absence data at each structural height class; a) shrub (0.75m-2.5m) b) brush (2.5m-5.5m) c) tree (>5.5m) and d) all sizes combined.

Woody Species Richness

Overall woody species richness for all heights varied from 12 to 1 species recorded per site with a mean of 3.95 species and a standard deviation of 1.8 (Table 2.3). Over 90 percent of sites had 6 or less recorded species with 3 and 4 species as the most commonly encountered. Within the height differentiated classes, the shrub layer had the highest species richness (Mean=2.76, SD=1.43) with declining levels for brush (Mean=1.82, SD=1.16) and tree (Mean=0.93, SD=1.00) height classes. Figures 2.6 a-d shows the total woody species richness along with the interpolated species richness for each height class. The highest species richness for the shrub layer is found in the southeast region dominated by basalt areas whereas brush and tree species richness (Figures 2.6b and 2.6c) are higher in the south-southwest granite/ecca shales regions.

Table 2.3 Number of woody species recorded at each field site compared with the percentage of all woody presence sites (n=1985) for all height classes and for species numbers found only in shrub, brush and tree categories.

| Number of Woody Species Recorded at a Site | Percentage of Sites with Woody Presence (n=1985) | | | |
|---|--|---------------------------------------|----------------------|-----------------|
| | All Classes | Height Shrub Layer (0.75m-2.5m) | Brush (2.5m-5.5m) | Tree (>5.5m) |
| 0 | 0.0 | 2.5 | 11.0 | 41.9 |
| 1 | 6.1 | 16.1 | 31.2 | 33.3 |
| 2 | 16.1 | 27.1 | 32.6 | 15.9 |
| 3 | 22.8 | 29.1 | 18.0 | 7.8 |
| 4 | 20.6 | 14.0 | 5.1 | 0.9 |
| 5 | 14.7 | 7.1 | 1.1 | 0.2 |
| 6 | 10.6 | 2.8 | 0.7 | 0.1 |
| 7 | 5.6 | 0.9 | 0.2 | 0.0 |
| 8 | 2.4 | 0.4 | 0.0 | 0.0 |
| 9 | 0.8 | 0.1 | 0.0 | 0.0 |
| 10 | 0.2 | 0.1 | 0.0 | 0.0 |
| 11 | 0.0 | 0.0 | 0.0 | 0.0 |
| 12 | 0.2 | 0.0 | 0.0 | 0.0 |

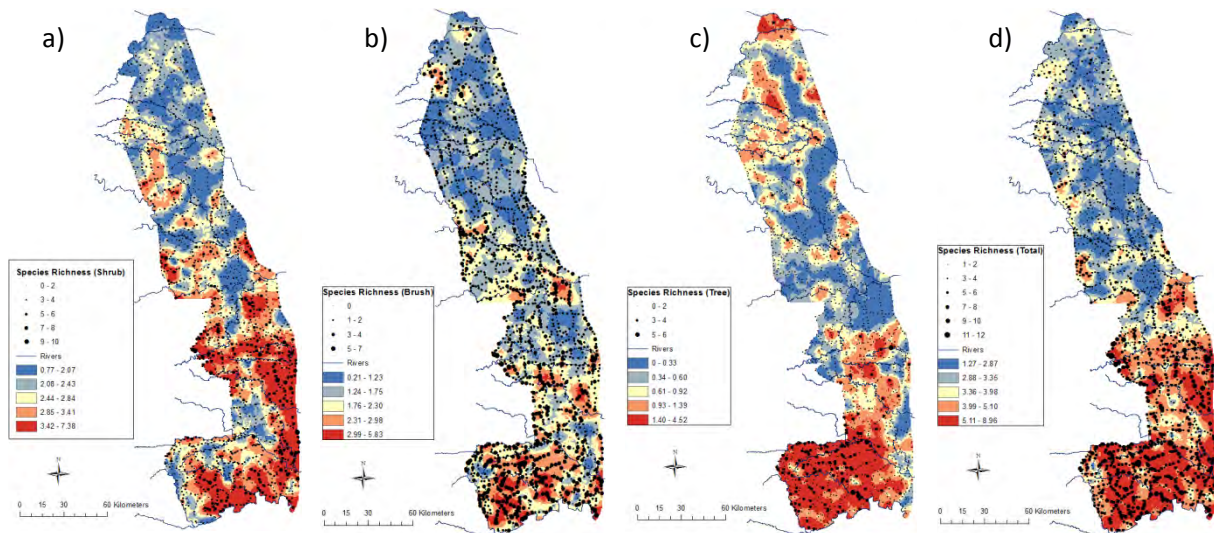


Figure 6a-d. Interpolated maps from Empirical Bayesian Kriging showing woody species richness for structural height class; a) shrub (0.75m-2.5m) (Mean=2.76, SD=1.43) b) brush (2.5m-5.5m) (Mean=1.82, SD=1.16) c) tree (>5.5m) (Mean=0.93, SD=1.00) and d) all sizes combined (Mean=4.01, SD=1.81).

Structural Cover for Shrub, Brush and Tree Height Classes

The majority of the Shrub layer (54.5%) is distributed within the 5-10% cover range with significant patches in the higher cover range. The Brush layer has a similar distribution to the Shrub layer, with 47.9% of cover totals in the 5-10% cover range. Tall trees are more skewed towards lower cover totals with 41.9% and 45.3% of all sites in the 0-5% and 5-10% cover ranges, respectively (Table 2.4). For each woody monitoring site, as shown in Table 2.1, the various species covers within a height class were totaled using the mean, minimum and maximum cover category values. Assuming no overlap amongst height classes, three estimates were created for each site and binned according to total cover, as shown in Table 2.4. Using the different BB cover category valuations, most KNP sites fall under the 35% total cover. Table 2.4 shows the maximum estimation with a longer tailed distribution of total cover so that about 87% of all sites fall below 60% total cover. Figures 2.7 show interpolated percent cover maps for the three height classes (Figure 2.7a-c) and a total canopy cover created from the mean BB category value and assuming no overlap between height layers (Figure 2.7d). The most prevalent cover amounts, especially in the central and southern KNP are contributed from the Brush (2.5m to 5.5m) class (Figure 2.7b). Given that no data concerning the overlap of woody canopy were recorded among height classes, one singular estimate of total woody cover using the dataset is not supportable without further analysis and comparison with additional datasets such as Bucini et al. (2010) and Asner et al. (2011).

Table 2.4 Structural Cover for each height class as a percentage of woody presence sites (n=1985).

| Percent Cover | Percentage of Sites (n=1985) | | | Total Structural Canopy Cover (Percentage of Sites) | | | | | |
|---------------|------------------------------|----------------------|-----------------|---|----------------|---------------------|----------------|---------------------|----|
| | Shrub Layer (0.75m-2.5m) | Brush (2.5m-5.5m) | Tree (>5.5m) | Mean Estimate | BB Estimate | Minimum Estimate | BB Estimate | Maximum Estimate | BB |
| 0-5 | 2.5 | 11.0 | 41.9 | 0.0 | | 0.0 | | 0.0 | |
| 5-10 | 54.5 | 47.9 | 45.3 | 13.8 | | 33.9 | | 7.1 | |
| 10-15 | 19.7 | 18.5 | 6.6 | 17.9 | | 28.5 | | 10.6 | |
| 15-20 | 6.3 | 6.9 | 1.7 | 19.9 | | 16.2 | | 14.5 | |
| 20-25 | 6.6 | 6.8 | 2.2 | 12.3 | | 4.5 | | 12.6 | |
| 25-30 | 2.6 | 2.1 | 0.1 | 11.2 | | 1.2 | | 10.3 | |
| 30-35 | 0.8 | 0.3 | 0.1 | 5.4 | | 7.3 | | 11.5 | |
| 35-40 | 0.0 | 0.0 | 0.0 | 2.2 | | 2.1 | | 6.9 | |
| 40-45 | 3.2 | 4.0 | 1.2 | 3.9 | | 0.6 | | 4.6 | |
| 45-50 | 0.6 | 0.7 | 0.1 | 3.9 | | 0.1 | | 3.5 | |
| 50-55 | 0.2 | 0.1 | 0.0 | 1.8 | | 0.4 | | 1.2 | |
| 55-60 | 0.1 | 0.0 | 0.1 | 1.3 | | 2.9 | | 4.1 | |
| 60-65 | 0.0 | 0.0 | 0.0 | 0.4 | | 0.9 | | 2.6 | |
| 65-70 | 1.6 | 1.5 | 0.7 | 1.9 | | 0.4 | | 1.8 | |
| 70-75 | 0.3 | 0.2 | 0.1 | 1.1 | | 0.1 | | 1.6 | |
| 75-80 | 0.2 | 0.0 | 0.0 | 0.8 | | 0.3 | | 1.1 | |
| 80-85 | 0.1 | 0.0 | 0.0 | 0.5 | | 0.7 | | 1.9 | |
| 85-90 | 0.0 | 0.0 | 0.0 | 0.4 | | 0.1 | | 0.8 | |
| 90-95 | 0.6 | 0.2 | 0.3 | 0.6 | | 0.1 | | 0.7 | |
| 95-100 | 0.1 | 0.0 | 0.0 | 0.3 | | 0.0 | | 0.5 | |
| 100 | 0.1 | 0.0 | 0.0 | 0.5 | | 0.1 | | 2.2 | |

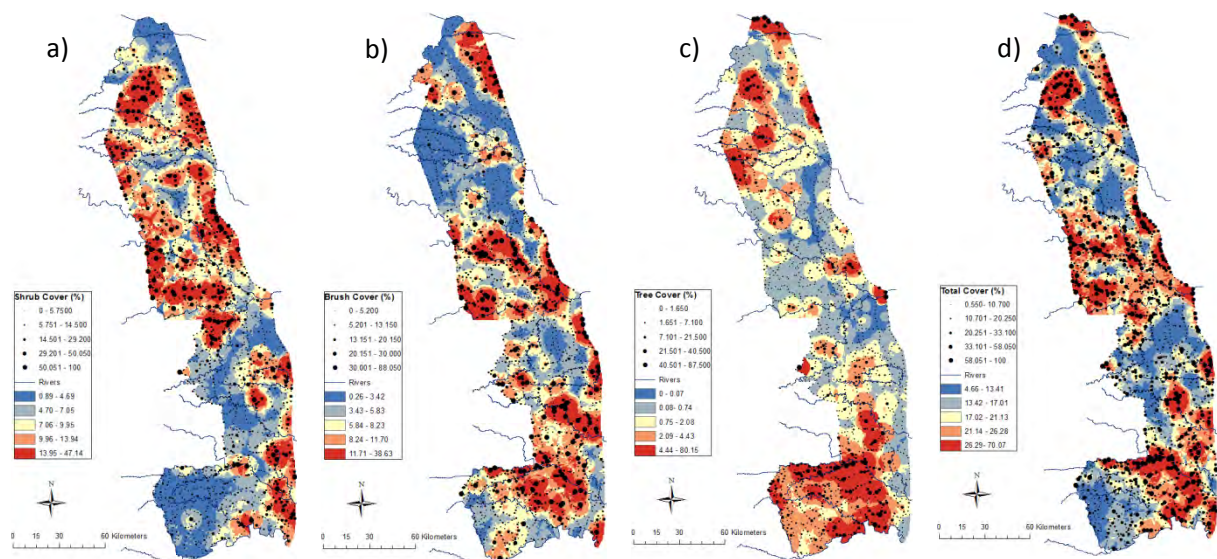


Figure 2.7a-d. Structural maps of the total woody cover estimates for each height class; a) shrub (0.75m-2.5m) b) brush (2.5m-5.5m), c) tree (>5.5m) and d) total cover, over the entire KNP area.

2.5 Discussion

Given the significant resource constraints and technical challenges in monitoring woody vegetation, efforts to analyze historical data can be useful and efficient for addressing current research and management concerns and for providing historical context. The Venter (1990) dataset provides a useful and critical benchmark for analyzing woody presence/absence and canopy cover for subsequent ecosystem management changes implemented since the 1990s. In reflecting on the initial research questions in this paper, the following answers can be offered.

Spatial distribution of woody vegetation across the KNP

The Venter (1990) dataset describes a woody layer dominated by a small number of commonly occurring species (24) that are found in a large number of sites (>80%) with a concomitant large number (121) of different species occurring in the remaining 20% of sites. In addition, higher species numbers are found within the smaller height classes with diminishing diversity found in the taller height classes. This is not surprising as many woody species do not grow into the taller height classes. In addition, the Venter (1990) dataset has utility in providing spatially-explicit presence/absence data to characterize both species occurrence and structure maps.

Species size class distribution across the KNP

One interesting feature worth further exploration is the different spatial distributions of the various height classes of the same species. Certain species (*Terminalia sericea* and *Colophospermum mopane*) show similar presence patterns regardless of height classes while other species (*Acacia nigrescens* and *Combretum apiculatum*) show a break in presence distributions for tall Tree classes. The database shows promise in identifying which species and structural classes of specific species may be more sensitive to additional ecosystem drivers (Currie 1991).

Woody species diversity across the KNP

In terms of monitoring species occurrence, analysis of this database shows that even with a large sampling regime (n=1985), more than two thirds of woody species known to occur in the park were not ever recorded during the extensive sampling campaign, and that 73% of recorded species are found in less than 1.5% of the sites (i.e. 30 sites or less). This may prove problematic for designing random monitoring schemes to track less common species. Our results suggest that a sampling design like the one employed here will be more effective in detecting dominance changes for the common species. However, targeted monitoring at preselected, non-random sites may be needed to monitor the less common species occurring in the tail of the species dominance curve. These rare species may respond to system changes before the more dominant species and directed monitoring effort may be needed.

Is woody species richness uniform throughout the KNP?

Species richness varies significantly both horizontally and vertically. The southern KNP has higher woody species richness with differing levels depending on area and height class. These differences can be explored further with respect to environmental drivers such as fire (frequency and intensity), browsing (including elephant effects) and rainfall.

Structural distribution of woody cover across the KNP

The Venter (1990) dataset describes a mostly shrub and brush dominated KNP landscape with small percent cover contributions from tall trees. Visual assessment of the interpolated maps shows that tree locations are often near river courses and are mostly found in the higher rainfall regions in the southern KNP. In all height classes, woody cover was greatest nearest to perennial rivers in accordance with Smit et al. (2013). Depending on which BB cover estimate is used for each height class and which overlap assumption is used, woody cover estimates for each height class can be calculated and then combined to form an estimate of total woody cover. In this paper, no attempt was made to compare the woody cover estimates with other woody cover totals such as Bucini et al. (2010) or Asner et al. (2011) as these studies have used quite different technical means and spatial scales to estimate woody cover. Still, a comparison of estimations may be helpful to determine methods for future monitoring programs and their connection to developing remote sensing technologies.

There are advantages and drawbacks to the method used here for estimating woody cover. Advantages include that the Venter (1990) dataset provides a somewhat quantitative snapshot into the late 1980s with on-site measurements for approximately 2000 locations recording both species presences and their general height distributions. Venter (1990) sampling locations are distributed mainly along roads for efficient access and cover a wide range of land types and terrain units. BB cover surveys are rapid site estimates. In this case, all estimates were by one individual with significant expertise. In addition, cover estimations for height classes include direct observations of land type/terrain unit features for additional comparison with other research and monitoring efforts.

Potential drawbacks include the concept that the total summed cover within a size class is not simply the sum of the recorded species covers as no information concerning overlap or within site distribution was recorded. While a large number of sampling points exist, they are not continuous like remotely sensed datasets (Bucini et al. 2010). Matching different sampling techniques employed over different scales makes it challenging to compare and to establish how woody cover is fluctuating over a heterogeneous landscape. When estimating the canopy separation between occurrences of a particular species, canopy interactions or overlaps with other species may be missed. In reducing the

set into more localized analysis for specific land types or terrain units, sampling bias along roads may be evident.

The dataset presented in this paper provides a useful benchmark for woody species distribution in KNP in middle to late 1980s. The data can be used to explore woody species and height class distributions spatially explicitly as well as the creation of functional groups of species for comparisons with later SANParks woody Vegetation Composition Assessment (wVCA) datasets compiled in 1996, 2002, 2005 and 2008 (Zambatis 2005). The results have particular value as they represent the woody layer in the light of management practices during that time before significant changes in terms of fire management, elephant population control and artificial water point provision. Thus, the dataset can be used as a historical point in time to compare with subsequent field and remote sensing derived woody datasets. Since there is an apparent concern over the loss of tall trees and a densification in the lower height classes, woody vegetation monitoring is of vital importance for KNP to maintain structural heterogeneity. The ability to generate canopy cover maps and probability occurrence maps at the species level and height class provides a detailed account and benchmark of species demographic profiles throughout the park. While this study presented the database and its initial creation and analysis, significant opportunities lie ahead in its use in more detailed analysis and scientific applications.

CHAPTER 3: IDENTIFYING DRIVERS THAT INFLUENCE THE SPATIAL DISTRIBUTION OF WOODY VEGETATION IN KRUGER NATIONAL PARK, SOUTH AFRICA ²

In Chapter two I introduced the dataset that forms the basis of this thesis. Chapter three aims to tease apart drivers relating to species distribution at various height classes.

3.1 Abstract

Understanding the dynamics of woody tree species distribution in savanna systems remains a challenge despite considerable attention the topic has received in recent years. Disturbances such as fire and elephant effects on woody vegetation are well documented, yet the influence of these factors on emerging landscape-scale patterns such as height and species distributions continue to be poorly understood. The aim of this study was to identify how a suite of environmental variables (rainfall, temperature, aspect, slope, geology, fire frequency and elephant density) and their relative contributions, may affect woody species distribution in relation to structural height classes. Using the Maximum Entropy model for three structural height classes of the fifteen most frequently occurring woody species in the Kruger National Park (South Africa), the environmental variables best explaining each species distribution were identified. The three structural classes were defined to capture canopy height categories of specific management interest, namely Shrub (0.75-2.5m), Brush (2.5m-5.5m) and Tree (over 5.5m). The weighted contributions of environmental variables for each species and its associated size class were further analyzed for similarities using a resemblance matrix based on the Bray-Curtis similarity index coupled with a hierarchical clustering test. Our main findings suggest that the patterns and processes driving woody composition and structure are largely decoupled and that the distribution of different structural classes of a particular species may not be driven by the same environmental variables. Future studies should take cognizance of this as ignoring one or the other may lead to confounding results.

3.2 Introduction

The dynamics of woody vegetation within savannas around the world are poorly understood (Lehmann et al. 2008). This is especially true in Africa, yet understanding plant dynamics is essential for effective management of these ecosystems (Sankaran et al. 2005; Higgins et al. 2007; Ekblom & Gillson 2010; Smit et al. 2010; Vanak et al. 2012). Four main drivers or factors have been reported to influence vegetation in savannas; these are rainfall, soil, fire and herbivory (Scholes, Bond & Eckhardt 2003; Venter, Scholes & Eckhardt 2003). Abiotic drivers such as rainfall, soil and nutrients (known as bottom-up drivers) have been shown to substantially influence woody and herbaceous vegetation in savannas (Scholes, Bond & Eckhardt 2003; Sankaran et al. 2005; Sankaran, Ratnam & Hanan 2008; Treydte et al. 2008; Accatino et al. 2010). Competition between trees and grasses in

² Scholtz, R., Kiker, G. A., Smit, I. P. J. & Venter, F. J., 2014, 'Identifying drivers that influence the spatial distribution of woody vegetation in Kruger National Park, South Africa', *Ecosphere* 5 (6).

savannas is a complex topic. Rainfall and nutrient manipulation studies are becoming more common to increase understanding of tree-grass co-existence (e.g. Skarpe 1991; Jeltsch et al. 1998; February et al. 2013). Recently, February et al. (2013) showed that additional rainfall tends to increase the competitive pressure exerted by grasses on trees to the extent that trees will only recruit into the adult stage during drought years. However, Kulmatiski and Beard (2013) have shown that if total rainfall remains constant, while the rainfall intensity is increased, woody species are favored over herbaceous species. The significance of these seemingly conflicting results highlights the importance of understanding the underlying mechanisms through which rainfall may possibly influence woody vegetation composition and structure in savannas.

The same challenge is evident when assessing fire as a driver in savanna systems. Fire is a top-down driver of vegetation (Scholes, Bond & Eckhardt 2003) that influences the global distribution of savanna ecosystems (Staver, Archibald & Levin 2011). Fire can act as a generalist herbivore (Bond & Keeley 2005) or as a facilitator of woody cover change within the ecosystem (Sankaran, Ratnam & Hanan 2004). Fire intensity and frequency are largely controlled by the available herbaceous biomass, and this is often a positive relationship (van Wilgen et al. 2000; Bond & Keeley 2005; van Wilgen, Govender & Biggs 2007; Ekblom & Gillson 2010; Kulmatiski & Beard 2013; Smith et al. 2013). Smit et al. (2010) showed that long-term exposure to fire reduces woody vegetation in the Kruger National Park (KNP) South Africa. They showed that average fire intensity was positively correlated with the magnitude of changes in woody vegetation structure with more frequent fires and late dry season fires reducing woody vegetation cover the most. However, the interactions among seasonality, intensity and frequency remain poorly understood (Govender, Trollope & Van Wilgen 2006).

Similarly, herbivory (also a top-down driver), particularly by mega-herbivores such as African elephants (*Loxidonta africana*) and their associated space use dynamics, also have a major influence on vegetation structure (Asner & Levick 2012). Large trees play an important role within the ecosystem by providing habitat and shade to several species and food for many browsers (Shannon et al. 2008), as well as increasing the nutritional status of the herbaceous layer for grazers (Treydte et al. 2008). Trollope et al. (1998) showed that the interaction of elephant impact and fire can have a profound effect on woody vegetation structure and composition, and suggested that an increase in elephant density (>0.36 individuals/km²) could lead to structural changes across the KNP landscape. According to Asner and Levick (2012), who used repeat Light Detection and Ranging (LiDAR) over a two year period, trees were toppled at rates 6 times higher in areas accessible to elephants compared to “back-ground” rates of treefall in an adjacent area where elephants were excluded.

Not only are woody vegetation structure dynamics influenced through a multitude of interacting drivers as explained above, but woody vegetation community assemblages are also controlled and influenced through a host of processes occurring at various spatiotemporal scales (e.g. competitive

exclusion, herbivory, stochastic disturbance and seed dispersal strategies, etc.) (Gaston 2003). Earlier research on woody vegetation species distributions and community assembly in the KNP has been restricted to field assessments and descriptive analysis (e.g. Gertenbach 1983; Venter & Gertenbach 1986; Venter 1990; Venter, Scholes & Eckhardt 2003). Venter et al. (2003) provided an in-depth description of the soil types and their associated vegetation, from the broadest (landscape scale) to the finest scale (catenal sequences). Baldeck et al. (2014) recently conducted a study in the KNP that showed, using airborne species mapping, that species composition found within catenal sequences varied substantially, highlighting the heterogeneous landscapes found within KNP. Species distribution studies are seldom conducted at the landscape scale in the KNP due to the time and financial constraints associated with field data collection. Stevens et al. (2013) conducted research on the potential limits to the range expansion of mopane (*Colophospermum mopane*) in South Africa. They found that both non-climatic (dry season day length) and climatic (minimum temperature) environmental variables at the national scale appear to be the limiting factors that restrict mopane to the warmer parts of the country. Similarly, Kiker et al. (2014, Chapter 2 of this thesis) re-analyzed the woody vegetation component of the Venter (1990) dataset and presented insights to the possibilities of expanding species distribution modeling within the KNP.

Understanding the drivers of the spatial distribution of woody vegetation composition and structure are important for managers, especially the top-down drivers which can be influenced by management policies. For example, in KNP both the fire policy (van Wilgen et al. 2014) and the water provision policies (Smit 2013) are cognizant of the possible impact that management fires and artificial water provision may have on vegetation composition and structure. Varying distance to permanent water sources (i.e. creating a herbivory gradient) and a range of fire frequencies/intensities create a gradient of disturbance regimes, which is presumed to be beneficial for biodiversity.

Recently, species distribution models have become popular in landscape ecology allowing empirical data to be used to predict the probability of presence under selected abiotic and biotic conditions. Here we employ a multivariate analysis approach that involves analyzing the patterns of the Maximum Entropy (MaxEnt) model (Phillips & Dudik 2008). Our main objectives were the following: (1) to identify environmental variables that best predict woody species distribution and their structural classes in the KNP, and (2) to determine whether the suite of environmental variables best predicting woody species distribution is similar among species and structural classes. I expect species to group together compositionally rather than structurally in relation to the drivers of species distribution.

3.3 Materials and Methods

Study Area

Kruger National Park (KNP) in South Africa covers almost 2 000 000ha within the low lying savannas of north eastern South Africa (Figure 3.1). The vegetation in KNP is dominated by several woody species including: mopane (*Colophospermum mopane*), red-bush willow (*Combretum apiculatum*), knobthorn (*Acacia nigrescens*), umbrella thorn (*Acacia tortilis*), silver cluster leaf (*Terminalia sericea*) and marula (*Sclerocarya birrea*) (Gertenbach 1983). There is a marked increase in mean annual precipitation from the north to the south of the park ranging from about 440mm.y⁻¹ in the north to about 740mm.y⁻¹ in the south (Venter & Gertenbach 1986). The park is geologically divided into two main parts; granites and their erosion products to the west and basalts and their erosion products to the east (Venter, Scholes & Eckhardt 2003).

Data Selection

Fifteen woody species that are considered dominant throughout the KNP (Kiker et al. 2014, Chapter 2 of this thesis) were chosen from data collected between 1986 and 1990 by Venter (1990). Data were collected in 20m x 20m plots selected along major roads throughout the park. Every 2.5 km all woody species were identified and percent cover was estimated using a rapid Braun-Blanquet sampling method (Appendix, Table S3.1). Edaphic and catenal features of the plot were estimated as well (see Chapter 2 for a description of the sampling technique). Recorded woody tree species were subdivided into three height classes; Shrub <2.5m, Brush 2.5-5.5m and Tree >5.5m. Each site may contain more than one species and height class of any particular species. A total of 1985 sites were recorded throughout the park (Figure 3.1) between the years 1986-1989 (Venter, 1990), of which 1820 sites were matched to geo-referenced locations (Kiker et al. 2014, Chapter 2 of this thesis). The list of the most common species (included in this study) can be found in Table 3.1 and a more comprehensive list can be found in Chapter 2 of this thesis.

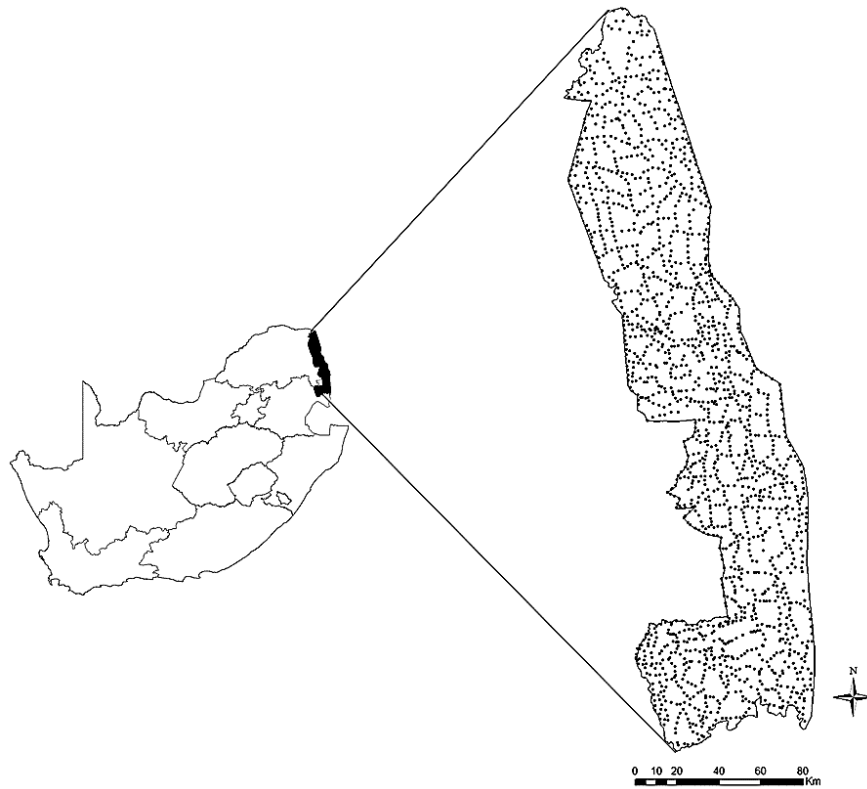


Figure 3.1 Location of the sample sites within Kruger National Park, South Africa

Table 3.1 List of species used in the analysis and the percentage of total sites (n = 1985)

| Species | # of sites recorded | Percent of All Sites |
|----------------------------------|---------------------|----------------------|
| <i>Colophospermum mopane</i> | 790 | 39.80 |
| <i>Combretum apiculatum</i> | 708 | 35.67 |
| <i>Acacia nigrescens</i> | 497 | 25.04 |
| <i>Dichrostachys cinerea</i> | 455 | 22.92 |
| <i>Grewia bicolor</i> | 371 | 18.69 |
| <i>Terminalia sericea</i> | 355 | 17.88 |
| <i>Euclea divinorum</i> | 317 | 15.97 |
| <i>Combretum hereroense</i> | 306 | 15.42 |
| <i>Sclerocarya birrea</i> | 300 | 15.11 |
| <i>Lonchocarpus capassa</i> | 241 | 12.14 |
| <i>Combretum imberbe</i> | 202 | 10.18 |
| <i>Albizia harveyi</i> | 191 | 9.62 |
| <i>Combretum zeyheri</i> | 190 | 9.57 |
| <i>Acacia tortilis</i> | 168 | 8.46 |
| <i>Pterocarpus rotundifolius</i> | 147 | 7.41 |

Seven predictor variables that are believed to influence woody tree species distribution were chosen. These were geology (<http://dataknpsanparks.org> 2012), long-term fire frequency (Smit et al. 2013b), long-term elephant density (Smit & Ferreira 2010), average and minimum seasonal temperature, aspect, slope, and seasonal rainfall obtained from Schulze et al. (2008). Minimum temperature was included in the analysis as the region experiences relatively low temperatures during the dry season and potentially has an influence on woody vegetation dynamics (Auerbach & Shmida 1987). Geology was treated as a categorical variable, while the rest of the predictor variables were treated as continuous variables. Geology referred mainly to the soil type derived from the underlying parent rock material. Average elephant densities based on dry-season aerial surveys conducted between 1985-2007 were adapted from Smit and Ferreira (2010) and fire frequency was calculated from fire scar maps from 1941 – 1990 as described in Smit et al. (2013b).

The layers of aspect, slope, elephant density and fire frequency grids were created using ESRI Arc Map™ V.10 (ESRI 2011). For rainfall and temperature, data from the WorldClim database (Hijmans et al. 2005) as well as the South African Atlas of Climatology and Agrohydrology (SA Atlas) (Schulze et al. 2008) were tested and compared. As no major discrepancies were identified between the two modeled climatic datasets, the SA Atlas data were used in analysis to align with methods previously used for species distribution modeling in KNP (Smith et al. 2012). Monthly rainfall and temperature datasets were combined into seasons; (1) “early wet season” is the sum of October, November and December, (2) “late wet season” is the sum of January, February and March, (3) “early dry season” is the sum of April, May and June and (4) “late dry season” is the sum of July, August and September. This was done to capture vegetation responses linked to seasonal climatic conditions, such as growing seasons (October to March) and dry seasons (April to September) (see Figure 3 in Smit et al. (2013a) for the phenological cycle of KNP).

Data Analysis

The analyses consisted of two stages; (1) application of the MaxEnt species niche modeling software to identify the environmental variables that best explained the observed distribution and (2) application of a cluster analysis using the weighted percentage contribution of all environmental variables identified by MaxEnt to assess similarities of the relative contributions of all environmental predictor variables among species and heights.

The Maximum Entropy Model. The software program MaxEnt V3.3.3k (Phillips & Dudik 2008) was used to estimate the potential distribution of each of the fifteen species/height class combinations using the environmental covariates as predictor variables. Only samples that had $n \geq 50$ presences were used in the model. This meant that where a species had $n \geq 50$ in one structural height class and not in

any other structural height class, only the structural height class where $n \geq 50$ was used for the analysis. Even though Hernandez et al. (2006) showed that MaxEnt performs reasonably well with low sample sizes ($n=5, 10$ or 25), the authors showed that samples of 50 produced the best results for MaxEnt. Using presence-only data, the geographic true distribution of a species was represented as a probability distribution y over the set X of sites in the study area. Y assigns a proportional probability value to every site X and all values of y at all sites sum to one. The model output is a product of y , a probability distribution that was regulated by a set of constraints derived from the presence data. The constraints were expressed in terms of simple functions of the environmental covariates (see Phillips & Dudik 2008 for a full description). Following a similar methodology to Smith et al. (2012), the model was executed for 50 iterations per species/height class combination along with a cross-validation to test model accuracy with standard default settings and auto features (Phillips & Dudik 2008). These settings are listed in the supplemental information. The program produces a species probability distribution map and the associated environmental covariate contributions based on the average of the iterations. These contributions are given as a percentage based on the weight that each variable has on the distribution of the species modeled. While species probability distribution maps are a useful MaxEnt model output (see Figure 3.2 for examples), these products were not the primary focus of this study. Given the large combination of species and height class combinations, the primary MaxEnt output of interest was the model accuracy and the contribution of each environmental covariate that drives species distribution.

Model fit and evaluation for MaxEnt. The Area Under the Curve (AUC) was used as a measure of model fit for MaxEnt. The AUC is a common method in machine learning for determining fit of the model by calculating the area under the receiver operating curve (ROC) (Manel, Williams & Ormerod 2001). Model accuracy was defined as the percentage of correctly classified cases predicted by the model. AUC ranges from 0 to 1; values that are close to 0.5 indicate a fit no better than that expected by random, while a value of 1 indicates a perfect fit and are highly unlikely in ecological models. AUC values of >0.9 were considered very good, 0.7-0.9 were considered good and <0.7 were considered uninformative (Phillips & Dudik 2008; Baldwin 2009). In addition to the AUC, MaxEnt also ranks (from highest to lowest percentage contribution) each predictor variable according to the degree to which each variable influences the total distribution. This is called the heuristic approach to model importance and is influenced by the increase in gain in the model provided by each variable (Baldwin 2009).

Cluster analysis. Each of the 50 iterations produced by MaxEnt contains results from the single run as well as an average of the 50 iterations. For each species and its respective height class, (which will be referred to as samples), results from the average run were used to perform a hierarchical cluster analysis (Maechler et al. 2013). All covariate contributions (from rainfall, fire, elephants, etc.) were weighted by their respective AUC values to standardize each variable contribution. A

resemblance matrix was constructed using the weighted contributions based on the Bray-Curtis similarity index without any data transformation. The hierarchical cluster analysis was performed to combine similar suites of covariates for each sample into clusters, which are displayed in a tree-like dendrogram (Quinn & Keough 2002; Maechler et al. 2013). Using the resemblance matrix, a cluster dendrogram was generated (grouping by average) using the similarity indices. Because the Bray-Curtis similarity measure incorporated the contribution of each variable, the average dissimilarity between variables of groups is expressed in terms of the average contribution from each variable.

Unlike previous vegetation analyses in the KNP that were mainly descriptive (e.g. Gertenbach 1983; Venter & Gertenbach 1986; Venter 1990; Venter, Scholes & Eckhardt 2003) the cluster analysis was used to statistically identify similarities between drivers of woody vegetation throughout the KNP. MaxEnt was used to identify and rank drivers that are most important to a species/height class distribution. The cluster analysis was used to identify whether drivers would be similar across differing species or height classes. The cluster analysis was performed in R v3.0.2 (R Development Core Team 2013) using the *vegan* (Oksanen et al. 2013) and *cluster* (Maechler et al. 2013) packages.

3.4 Results

The AUC values varied among samples with an average $AUC \pm SD$ equal to 0.75 ± 0.14 . About eighty percent (25 of 31) of the calculated AUC values indicated that the model was a good fit to the data ($AUC > 0.7-0.9$). Rainfall and geology were the explanatory variables that contributed the most to the model fit (Table 3.2). Table 3.2 shows the summary results from the MaxEnt model, as well as the most important variable and an example of the weighted contribution per species per height class.

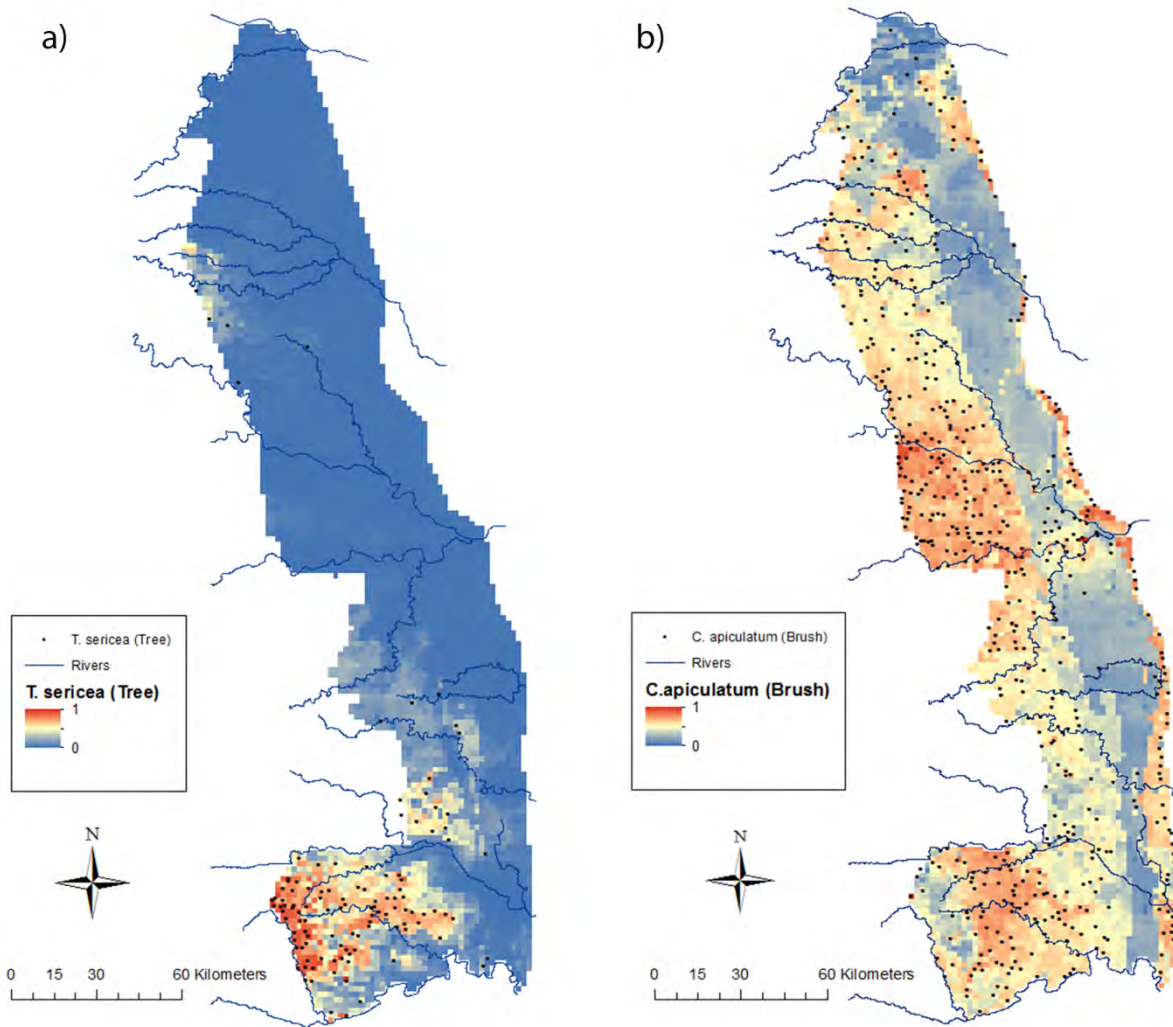


Figure 3.2 a) *T. sericea* (Tree) probability map ($AUC \pm SD = 0.90 \pm 0.08$), b) *C. apiculatum* (Brush) probability map ($AUC \pm SD = 0.63 \pm 0.09$). Black dots indicate species presence. All maps are at a 1.7km grid resolution

Table 3.2 Summary results from MaxEnt model showing model fit and the variable that contributed the most to the model

| Sample | n | Mean AUC±SD | Most Important Variable | Weighted contribution of most important variable (%) | |
|-------------------------|-----------------|----------------|-------------------------|---|-------|
| Species | Height Class | | | | |
| <i>A. nigrescens</i> | Brush | 230 | 0.71±0.16 | Geology | 27.20 |
| | Shrub | 244 | 0.72±0.13 | Geology | 19.71 |
| | Tree | 239 | 0.75±0.09 | Late Dry Season Rainfall | 49.44 |
| <i>A. tortilis</i> | Brush | 90 | 0.81±0.15 | Geology | 20.04 |
| | Shrub | 107 | 0.83±0.13 | Geology | 25.67 |
| <i>C. apiculatum</i> | Brush | 560 | 0.63±0.09 | Geology | 34.22 |
| | Shrub | 442 | 0.65±0.08 | Geology | 25.37 |
| | Tree | 117 | 0.87±0.09 | Early Dry Season Rainfall | 27.80 |
| <i>C. mopane</i> | Brush | 567 | 0.75±0.06 | Late Dry Season Rainfall | 46.09 |
| | Shrub | 706 | 0.72±0.05 | Late Dry Season Rainfall | 52.88 |
| | Tree | 334 | 0.74±0.07 | Late Dry Season Rainfall | 38.34 |
| <i>D. cinerea</i> | Brush | 148 | 0.86±0.08 | Late Dry Season Rainfall | 47.77 |
| | Shrub | 422 | 0.73±0.06 | Late Dry Season Rainfall | 44.61 |
| <i>S. birrea</i> | Tree | 267 | 0.79±0.07 | Late Dry Season Rainfall | 44.26 |
| | | 217 | 0.78±0.10 | Late Wet Season Average | 28.59 |
| <i>T. sericea</i> | Brush | | | Temperature | |
| | Shrub | 210 | 0.77±0.11 | Geology | 24.93 |
| | Tree | 116 | 0.90±0.08 | Early Wet Season Average | 26.84 |
| | Shrub | 151 | 0.75±0.13 | Late Dry Season Average | 12.65 |
| <i>A. harveyi</i> | | | | Temperature | |
| <i>C. hereroense</i> | Brush | 175 | 0.59±0.15 | Elephant Density/km ² | 13.28 |
| | Shrub | 78 | 0.70±0.25 | Late Dry Season Rainfall | 19.97 |
| <i>C. imherbe</i> | Brush | 87 | 0.78±0.20 | Geology | 45.12 |
| | Shrub | 81 | 0.76±0.23 | Geology | 54.21 |
| | Tree | 63 | 0.64±0.28 | Geology | 33.25 |
| <i>C. zeyheri</i> | Brush | 85 | 0.82±0.20 | Geology | 44.97 |
| | Shrub | 56 | 0.83±0.17 | Geology | 32.19 |
| <i>E. divinorum</i> | Shrub | 81 | 0.82±0.12 | Late Dry Season Rainfall | 57.64 |
| <i>G. bicolor</i> | Shrub | 257 | 0.73±0.11 | Geology | 25.41 |
| <i>L. capassa</i> | Brush | 52 | 0.59±0.30 | Geology | 35.50 |
| | Shrub | 139 | 0.76±0.14 | Geology | 36.10 |
| | Tree | 55 | 0.61±0.29 | Elephant Density/km ² | 22.57 |
| <i>P. rotundifolius</i> | Shrub | 95 | 0.85±0.15 | Geology | 27.98 |

Two main groups emerged from the dendrogram denoted by the vertical dotted line (Figure 3.3). The groups were roughly 35% similar given the suite of drivers per sample. These two groups mainly related to abiotic properties that drive species distribution. Group 1 had nine samples, all of which had rainfall as the most important variable. Initial analyses showed that mean annual rainfall had surprisingly low explanatory power for species distribution, thus it was suggested that seasonal rainfall and seasonal temperature, would improve these results. It is therefore not only the total annual rainfall, but possibly the timing of rainfall that may be of importance. For example, rainfall events occurring at the end or beginning of a growing or dry season might have a disproportionate effect on species community structure throughout the landscape.

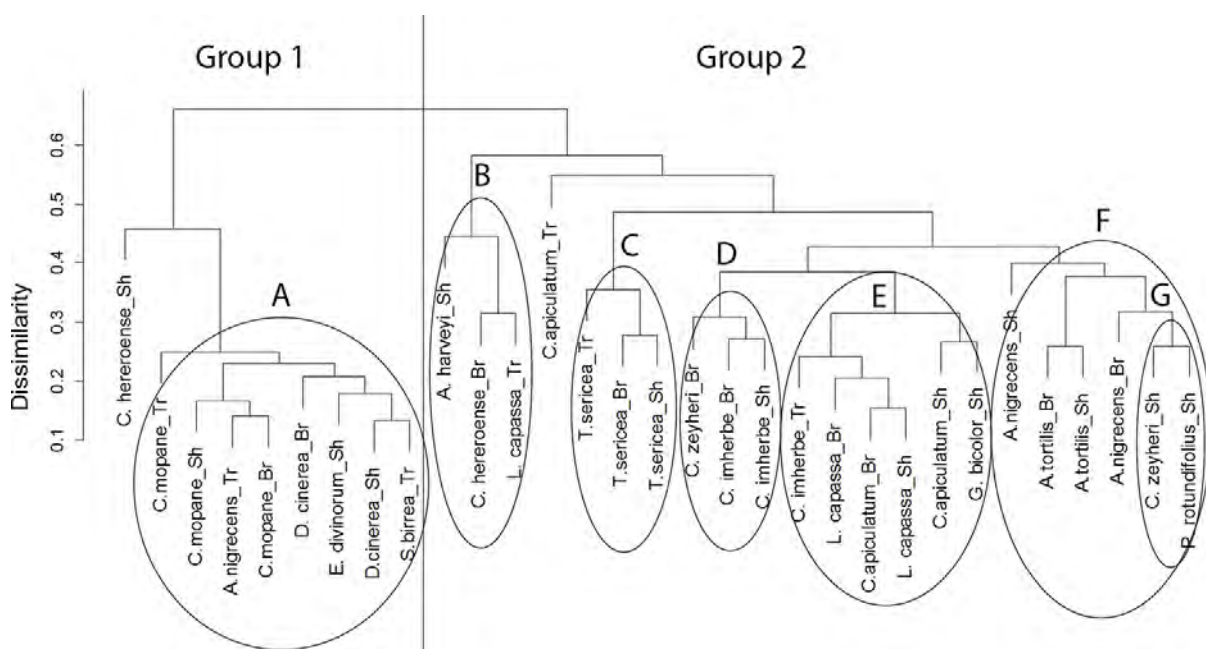


Figure 3.3. Dendrogram depicting dissimilarities (by fraction) and groups between species and structure. Letters A through G refers to ecological groupings (see main text for details).

Group 2 had 22 samples, of which the majority (15) had geology as the most important variable driving the distribution. This group contained *T. sericea* species of all height classes and a few species such as *C. apiculatum* that are known to prefer granitic, sandy soils along catenal sequences. All structural forms of a specific species did not group together, except for *T. sericea*, suggesting that environmental variables driving woody vegetation composition and structure were different.

Of the 24 samples in the brush and shrub class, 15 had geology as the most important driver for their distribution, six rainfall, two temperature and one driven by elephant density. Of the seven samples in the tree class, four had rainfall as their most important driver for their distribution, one

geology, one temperature and one elephant density (Table 3.2). Besides a few samples, it is clear that the two groups formed were driven largely by bottom-up drivers; rainfall and geology (soil type).

The letters A-G indicate the main ecological similarities. “A” represented species commonly found in high (e.g. *S. birrea* and *A. nigrescens*) and low (e.g. *C. mopane*) rainfall regions. Contrary to what was found on a much larger scale by Stevens et al. (2013), our study suggested that rainfall rather than minimum temperature was a major contributor to the probability distribution of *C. mopane* in KNP. “B” represented species commonly found in valley bottom regions of catenal sequences predominantly on granites (Venter, Scholes & Eckhardt 2003). “C” represented the grouping together of *T. sericea* at all structural classes, where these species are preferentially found on granite-based soils. “D” represented species commonly found in the valley bottom and foot slopes of catenal sequences. “E” showed a combination of species commonly found in the mid- and foot slopes of catenal sequences. “F” showed the grouping of both *Acacia tortilis* and *Acacia nigrescens* in the brush and shrub forms, both forms are commonly found in areas of higher rainfall. Group “G” were two species commonly found on the crests and midslopes of catenal sequences. Certain groups were leaf phenotypically specific; circles B, C, D, E and G are all broad leaved species while circle F is the only fine leaved group, and A contained a mixture of fine and broad leaved species. These groups of ecological relevance agree with qualitative observations from Gertenbach (1983), Venter (1990) and Venter et al. (2003). The results presented here show a clear indication that drivers of woody species vegetation differ depending on structural class.

3.5 Discussion

Understanding vegetation community assemblages in disturbance-driven ecosystems such as savannas are challenging. The aim of this research was to increase our current knowledge of the environmental variables that drive species distribution and community assemblages in KNP. Our results showed that species and their associated height classes did not always group together as expected, suggesting that the processes driving composition and structure are decoupled. Environmental factors responsible for woody vegetation structure are distinct from those influencing woody species distribution. Thus, drivers of woody vegetation community structure appear to be more similar across height classes of different species than among height classes of the same species.

Our finding that the two main drivers of species structural distribution were geology and rainfall is in agreement with previous studies. Using aerial remote sensing mapping techniques, Baldeck et al. (2014) illustrated that patterns in community structure were strongly linked to catenal positions, alluding to the importance of geomorphology and the associated soil types in shaping savanna vegetation communities. Furthermore Sankaran et al. (2005) highlighted the importance of rainfall in maintaining woody cover in savannas, particularly how future changes in precipitation may

influence global savanna distribution and dynamics (complimented by recent work done by February et al (2013) and Kulmatiski and Beard (2013)).

On a global scale, the techniques presented here may provide useful insight for other savannas, such as mesic savannas, where fire is the main driver of savanna persistence (Staver, Archibald & Levin 2011). Given the results found for the KNP ecosystem, it is possible that in mesic savannas, the influence of fire may be more pronounced as Higgins et al. (2007) and Smit et al. (2010) showed that the effects of fire are greater within wetter landscapes.

In this paper, we presented a novel technique using the output results of the MaxEnt model and cluster analysis to show the relationship between the environmental drivers of woody vegetation in relation to structural classes. Our results suggest that the environmental variables (such as rainfall and geology) are more important drivers of woody structure and composition in the KNP than disturbance factors such as fire and herbivory (mainly by elephants), at the scales considered here. In a subsequent manuscript, semi-variance was assessed using additional response variables (e.g. % woody canopy cover, woody species richness) and found that nearby sites were very different to one another (R. Scholtz. *unpublished data*). This small-scale heterogeneity within the KNP landscape provides a possible reason for fire frequency seeming to have a minor effect on species distribution in this study. There may be a mismatch between the larger scale of fire mapping compared to the fine-scale observations recorded in a 20m x 20m plot. Nevertheless, similar to what was found in our study, Govender et al. (2006) have shown that fire (season and intensity) influences woody vegetation structure but not woody vegetation composition and community assembly.

Overall results showed that grouping among structural classes was more common than among similar species, which was unexpected. These results suggest that environmental drivers influence structure more than species across the KNP landscape. The study provides a useful base for subsequent research to disentangle environmental variables that influence structural patterns from variables that drive species composition.

CHAPTER 4: DOES LONG-TERM DISTURBANCE INFLUENCE PATTERNS OF WOODY PLANT SPECIES COMPOSITION IN A SEMI-ARID SAVANNA? ³

In Chapter three, I assessed species distributions at various height classes of some of the most commonly occurring species in KNP. Here, I will assess community assemblages at various height classes in response to top-down disturbance.

4.1 Abstract

Savanna vegetation is controlled by bottom-up (e.g. soil and rainfall) and top-down (e.g. fire and herbivory) factors, all of which have an effect on biodiversity. Little is known about the relative contribution of these factors to biodiversity, particularly the long term effects of top-down disturbance on patterns of woody plant composition. The aim of this study was to identify if there were distinct woody species community assemblages under various degrees of disturbance regimes. Using a rapid data collecting technique within 1820 field plots of 20m x 20m across the entire Kruger National Park, South Africa, woody species were identified and categorized into one of three height classes; shrub (0.75m – 2.5m), brush (2.5m-5.5m) and tree (>5.5m). Species richness and composition were calculated for each site and height class. A combination of long-term fire frequency and elephant density data were used to delineate areas with varying degrees of top-down disturbance (i.e. low, medium and high). Using these degrees of disturbance, species composition was identified and community assemblages constructed according to disturbance regime. Our results suggest that areas with similar disturbance histories have more similar species composition to each other than to areas with different disturbance regimes. Shrub community composition were mainly responsive to fire and tree composition to elephant disturbance. A few dominant species were found under all degrees of disturbance at all height classes, while others were only found under specific disturbance regimes at particular height classes. This study highlights that while species richness does not appear to be influenced by long-term top-down disturbance regimes, species community composition may be responsive to these disturbances. While most species and structural classes persisted across all disturbance regimes, the long-term effects of top-down disturbances can have effects on compositional and structural biodiversity. Managers of protected areas can use this information to provide context for policies related to management of artificial water provision, elephants and fire.

³ Scholtz, R., Smit, I. P. J., Coetsee-Wigley C, Kiker, G. A., & Venter, F. J., 2014, 'Does long-term disturbance influence patterns of woody plant species composition in a semi-arid savanna?', Submitted to *Diversity and Distributions*. March 2015

4.2 Introduction

Plant diversity is important in natural systems for several reasons. Plant functional diversity leads to higher plant productivity and ecosystem processes (Tilman *et al.*, 1997). A review of biodiversity and productivity across 11 studies (and >7000 measurements) found that increases in grassland diversity caused dramatic increases in biomass and productivity (Tilman *et al.*, 2012). Costanza *et al.* (2007) further showed that at various locations around the globe in areas of high temperatures (with an average of 13°C) that contained long term ecological research (LTER) stations acquiring data on vascular plant diversity and net primary plant productivity (NPP), NPP was positively correlated with biodiversity (e.g. Africa and South America). Higher diversity has not only been linked with higher primary productivity, and has important consequences for fauna. For instance, higher plant diversity has been found to stabilize invertebrate communities across trophic levels in Oak savanna (Haddad *et al.*, 2011). Greater spatial heterogeneity in vegetation created by patchy burning and grazing provides greater diversity (Fuhlendorf *et al.*, 2006) and stability (Hovick *et al.*, 2014) in grassland bird communities in North American prairies. Simplification of ecosystems will have escalating effects on ecosystem functioning over time as redundancy disappears (Reich *et al.*, 2012).

Plant communities in savanna ecosystems are affected by a range of factors which can be characterized into two broad categories; bottom-up drivers such as rainfall and nutrients, and top-down drivers (e.g. disturbances) such as fire and herbivory (Scholes & Archer, 1997; Pickett *et al.*, 2003; Scholes *et al.*, 2003; Venter *et al.*, 2003). Studies covering numerous spatial and temporal scales have investigated how these factors affect savanna processes (or function) and productivity (van Langevelde *et al.*, 2003; Sankaran *et al.*, 2005; Smit *et al.*, 2010; Staver *et al.*, 2011; Lehmann *et al.*, 2014). However, the relative importance of different drivers on plant species composition and richness across large scales has received less attention and remains obscure (Gotelli *et al.*, 2009).

Herbivory, in particular elephant impact, can alter woody vegetation structure (Shannon *et al.*, 2008; Shannon *et al.*, 2011; Asner & Levick, 2012; Vanak *et al.*, 2012). Elephant impact can lead to a reduction in woody vegetation structure and changes in species composition since elephants preferentially target palatable woody species such as marula (*Sclerocarya birrea*) and knobthorn (*Acacia nigrescens*) (Shannon *et al.*, 2008; Shannon *et al.*, 2011). Both these studies showed that marula and knobthorn species in height classes >5m were removed at higher rates than they were replaced. The cascading effects of this process has led to increases in density of less preferred species such as tamboti (*Spirostachys africana*) and silver-cluster leaf (*Terminalia sericea*). Recent evidence using repeat LiDAR (Light Detection and Ranging) technology has also shown that elephant impact on woody vegetation structure are more evident when trees are 5-9m in height (Asner & Levick, 2012). Similarly, other studies have shown that browsers other than elephants may have a substantial

influence on species richness and composition (Levick & Rogers, 2008; Belay *et al.*, 2013; Wigley *et al.*, 2014) by decreasing seedling establishment and sapling recruitment (O'Kane *et al.*, 2012; Holdo *et al.*, 2014). Additionally other studies have shown that browsers directly impact plant species distribution, densities and population structures by actively selecting palatable species (Levick & Rogers, 2008; Wigley *et al.*, 2014).

Over the past ten million years, adaptations of savanna vegetation to fire have been credited for plant species diversification and resultant richness in tropical cerrado savanna (Simon *et al.*, 2009). Rainfall interacts with fire in maintaining savanna where forest has the potential to establish (Staver *et al.*, 2011). Evidence from savanna systems show that woody vegetation responds structurally rather than compositionally to fire with a strong effect of season on fire frequency and intensity (Govender *et al.*, 2006; Higgins *et al.*, 2007). Anderson *et al.* (2012) found that savanna biota in general is very resilient to frequent fire, and only riparian vegetation decrease with frequent fire in northern Australia. In contrast, unburned oak savanna has the highest woody diversity, but understory (and total) plant richness is highest at intermediate fire frequencies (Peterson & Reich, 2008).

Vegetation structural diversity is one of the characteristics that have been shown to promote animal biodiversity (Karr & Roth, 1971; Erdelen, 1984; Tews *et al.*, 2004) and as such may provide a useful indicator for inventorying, monitoring and assessing terrestrial biodiversity (Noss, 1990). However, woody thickening, also known as bush encroachment, may lead to reduced structural diversity, as one or a few 'woody encroaching' species, usually multi-stemmed woody shrubs, may dominate and lead to an overall reduction in diversity (Roques *et al.*, 2001). Changes in woody biomass can also influence biogeochemical processes such as nutrient cycling and fire regime (van Langevelde *et al.*, 2003; Pellegrini *et al.*, 2014) as well as invertebrate species diversity and composition (Parr *et al.*, 2012). The lack of tall trees in the landscape also influences savanna function as they provide shade, forage and refuge (Jeltsch *et al.*, 1998; Trollope *et al.*, 1998). Tews *et al.* (2004) proposed that large trees are vital keystone structures in savannas that enhance animal diversity by their presence.

Fire and herbivory are natural ecosystem processes essential in maintaining savanna systems (van Langevelde *et al.*, 2003; Vanak *et al.*, 2012), and all plant stages are exposed to the effects of these top down disturbances from seedling establishment (Bond & Van Wilgen, 1996; Hoffmann *et al.*, 2009) to tall, mature trees (Asner & Levick, 2012). The aim of this study was to identify whether disparate fire and elephant disturbance regimes gave rise to distinct woody species communities. The following questions will be addressed for three different structural classes of woody vegetation (shrubs; brush and trees); (i) does species richness differ between areas with different disturbance histories? (ii) Does community composition differ between areas with different disturbance histories?

Patterns in community assemblages as influenced by disturbance regimes, which can in some cases be manipulated by managers, will assist managers and policy makers alike.

4.3 Materials and methods

Study area

Kruger National Park is situated in the northeast corner of South Africa, and covers about 20 000km² within the low-lying savannas of South Africa (Figure 4.1). The vegetation in KNP is characterized by several woody species including marula (*Sclerocarya birrea*), mopane (*Colophospermum mopane*), red-bush willow (*Combretum apiculatum*), knobthorn (*Acacia nigrescens*), umbrella thorn (*Acacia tortilis*) and silver cluster leaf (*Terminalia sericea*) (Gertenbach 1983). There is a marked increase in mean annual rainfall from the north to the south of the park ranging from about 440mm.y⁻¹ in the north to about 740mm.y⁻¹ in the south (Venter and Gertenbach 1986). In general, the park is divided geologically into two main parts, granites and their erosion products to the west and basalts and their erosion products to the east (Venter et al. 2003).

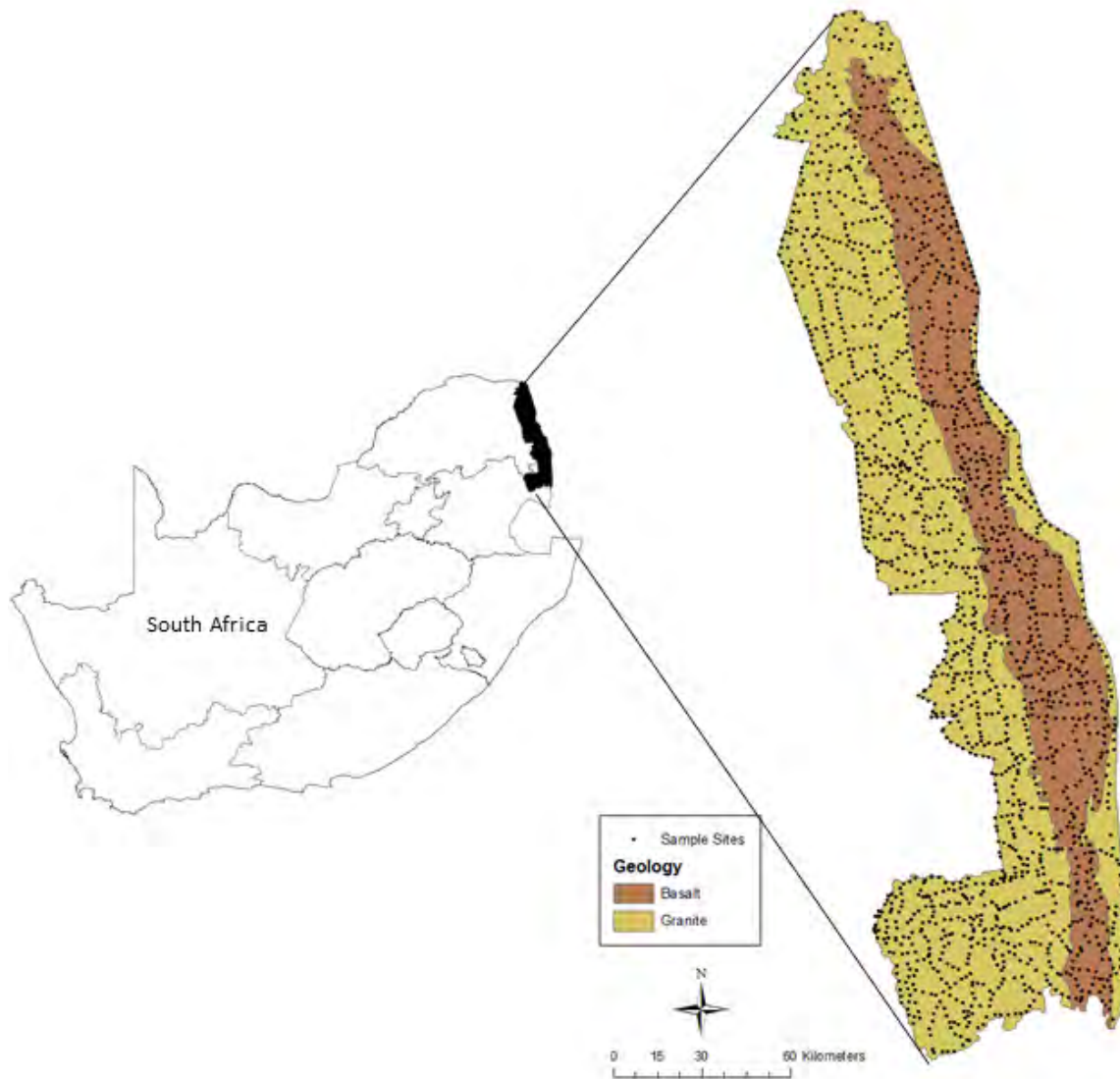


Figure 4.1. Sampling sites within Kruger National Park with underlying geology; granite and basalt.

Data selection

Using a Braun-Blanquet rapid sampling technique, woody species were identified within 20m x 20m plots (spaced about 2.5km apart along roads), and categorized into height classes (Shrub >0.75m-2.5m, Brush 2.5m – 5.5m and Tree >5.5m). Subsequently woody plant species richness was calculated and composition identified for each plot (separately for each of the three height classes). A total of n=1985 sites were sampled between 1986 and 1989, of which n=1820 were linked with digitized sampling points and will subsequently be used in our analysis (Kiker *et al.*, 2014).

Environmental covariates

Spatially explicit average elephant densities based on dry-season aerial surveys conducted between the years 1985-2007 were adapted from Smit & Ferreira (2010). Elephant censuses takes

place yearly (in most cases) in KNP and we calculated the average density over a 22 year period to create a habitat suitability index (per $\sim 1\text{km}^2$) showing areas of high utilization versus areas with low utilization over the landscape. Based on these long-term average locational densities of elephants, we delineated areas of low (0-33rd percentile), medium (33rd percentile – 66th percentile) and high (66th percentile – maximum) elephant utilization. This translated into low elephant density which ranged from 0 - 0.26 individuals per km^2 , medium elephant density which ranged from 0.26 - 0.48 individuals per km^2 and high elephant density which ranged from 0.48 - 3.23 individuals per km^2 . The number of fires (fire frequency) was calculated from fire scar maps from 1941 – 1990 as described in Smit *et al.* (2013), and similar to the elephant densities, using the 33rd and 66th percentiles, the park was delineated into areas that burn at low, medium and high frequency. This translated into low fire frequency which ranged from 0 - 9 years, medium fire frequency which ranged from 9 – 12 years and high fire frequency which ranged from 12 - 22 years. Using a combination of the three fire frequency and elephant density classes described above, each sample location was assigned to one of nine possible disturbance regimes (i.e. based on the different combinations of the three fire and three elephant disturbance classes). Abbreviations used in the Results section stemming from the combinations of fire and elephant were constructed according to the disturbance regime. For example, areas that were within High Fire Frequency (12-22 years) zone were labelled “HighFire” and High Elephant density (0.48-3.23 indiv. km^2) were labelled “HighEle”, and together they create the group labelled “HighFire - HighEle”. Therefore, samples within the groups were labelled according to the degree of disturbance and type accordingly.

Data Analyses

Species richness at all height classes was plotted against the disturbance regime combinations to identify whether there were trends in species richness associated with the varying degrees of disturbance. In addition, areas of extreme disturbance (upper and lower 5% elephant density and fire frequency areas, see Appendix) were also plotted to test whether these regions influenced species richness over the study area within a geological context.

In order to examine community assemblages under varying degrees of disturbance, a cluster analyses with all species identified for each site and height class was conducted. All data analyses were performed in R v. 3.1.2 (R Development Core Team, 2013) using base and vegan (Oksanen *et al.*, 2013) packages. Each site was assigned to one of the nine fire*elephant disturbance regimes, as described in Table 1. Species presence data was calculated per regime which was used to construct dendograms over the disturbance regimes (n=9) (separately for each height class). From these dendograms, communities were identified under specific disturbance conditions. Communities occurring under similar disturbance regimes (high, medium, low or combinations thereof) will be grouped and deconstructed into species lists. Using these identified groups from the dendograms, a

similarity percentages (SIMPER) test with 100 permutations was conducted to identify the species most contributing to group resemblance as well as group uniqueness. Thereafter an analysis of similarities (ANOSIM) test was performed to identify significant differences in species composition between groups identified in the dendrogram. ANOSIM computes R values where values close to 1 indicate high separation between groups and values close or equal to 0 indicate no or low separation between groups. As a rule of thumb, R values <0.25 is interpreted as barely separable groups, R values between 0.5 and 0.75 as overlapping, but separate to certain extent, and R values >0.75 as well separated. The species composition information was used to identify species responsible for group dissimilarity at each height class. The total number of sites that contained a particular species was weighted by the number of sites per group identified in the dendrogram at each height class.

4.4 Results

Species richness was not influenced by disturbance (see Figure 4.2). This result was consistent across all height classes (see Appendix). Furthermore, areas of extreme disturbance (using 5th and 95th percentiles instead of 33rd and 66th percentiles for low, medium and high fire frequency and elephant density) also showed no signs of disturbance influencing species richness within each height class (detailed results provided in Appendix; Figure 4.1 and 4.2).

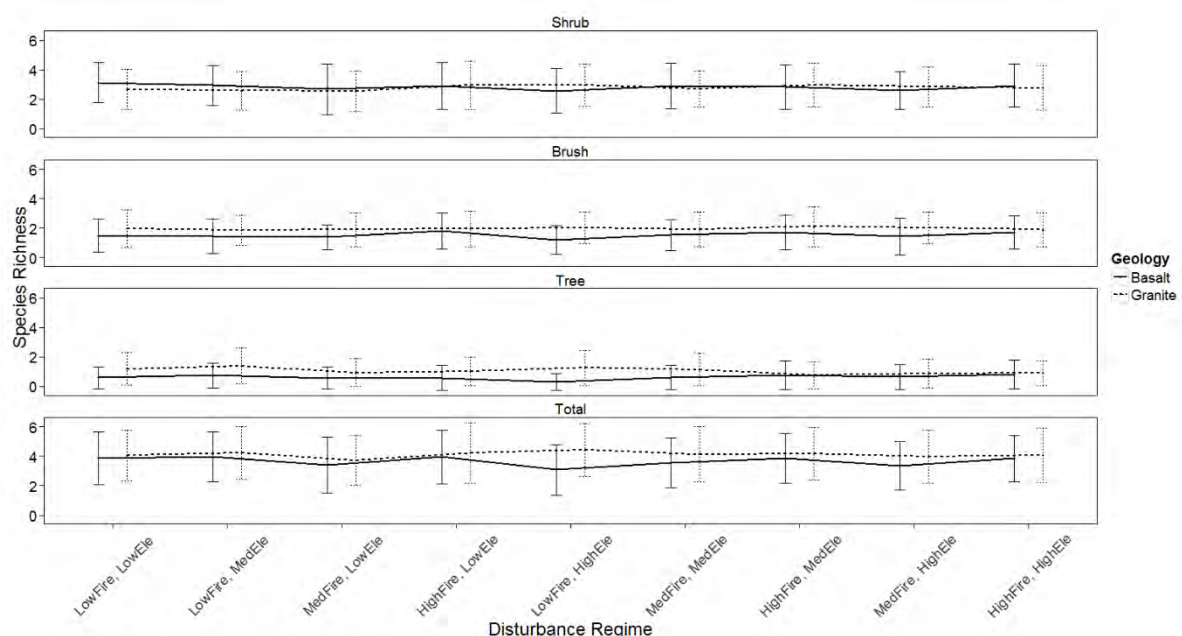


Figure 4.2. Species richness over varying degrees of disturbance.

Except for the outlier community grouping resulting under the “HighFire-MedEle” regime, the shrub community composition clustered predominantly in response to fire frequency (Figure 2). Two

main groups formed; the first contained communities within low fire areas with varying degrees of elephant density (Group 1 – low fire disturbance), and the second within medium and high fire areas with varying degrees of elephant density (Group 2 – medium - high fire and elephant disturbance). Even though these two distinct groups formed, group species composition between the groups was similar (Global R = 0.26).

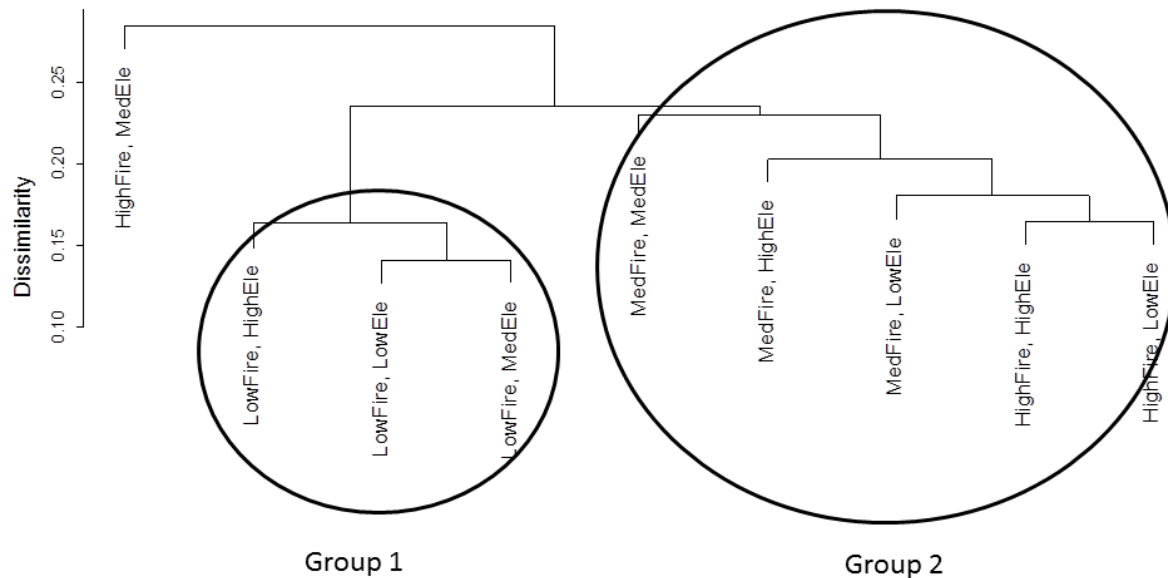


Figure 4.2. Shrub communities showing low fire assemblages (Group 1) and med-high (fire and elephant) disturbance assemblages (Group 2)

Similarly, brush communities were also 75% similar in composition and clustered into two groups (Figure 4.3); one which was mostly in high fire areas with varying degrees of elephant density (Group 3 - med-high fire and elephant disturbance), and the other in the medium and low fire areas with varying degrees of elephant density (Group 4 - med-low fire and elephant disturbance). Further inspection of the species that make up group composition suggest that the groups identified have high composition similarity (Global R = 0.17) but this was not significant ($p > 0.05$).

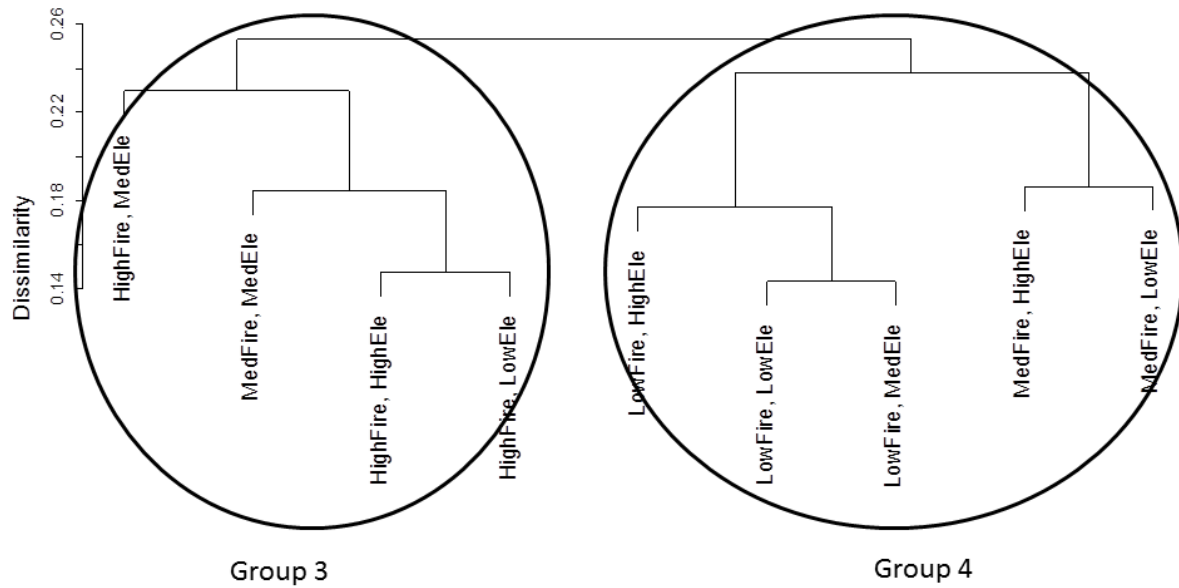


Figure 4.3 Brush communities showing med- high disturbance assemblages (Group 3) and med-low disturbance assemblages (Group 4)

Tree communities were almost 70% compositionally similar. These also clustered into two main groups (Figure 4.4). However, elephant density was the main driver of community structure. The first group comprised of the communities in highest elephant density within both high and low fire areas (Group 5 – high elephant and low fire disturbance) while the second group comprised of medium and low elephant density with medium and high fires areas (Group 6 – med-low elephant and med-high fire disturbance). While acknowledging that three disturbance regimes did fall within a group at 75% similarity, they were nonetheless highly different (Global $R = 0.63$) even though not significant ($p > 0.05$). In general, results suggest that the shrub community responds to the number of fires in an area more so than elephant density, while the tree community responds to long-term elephant density more so than the number of fires.

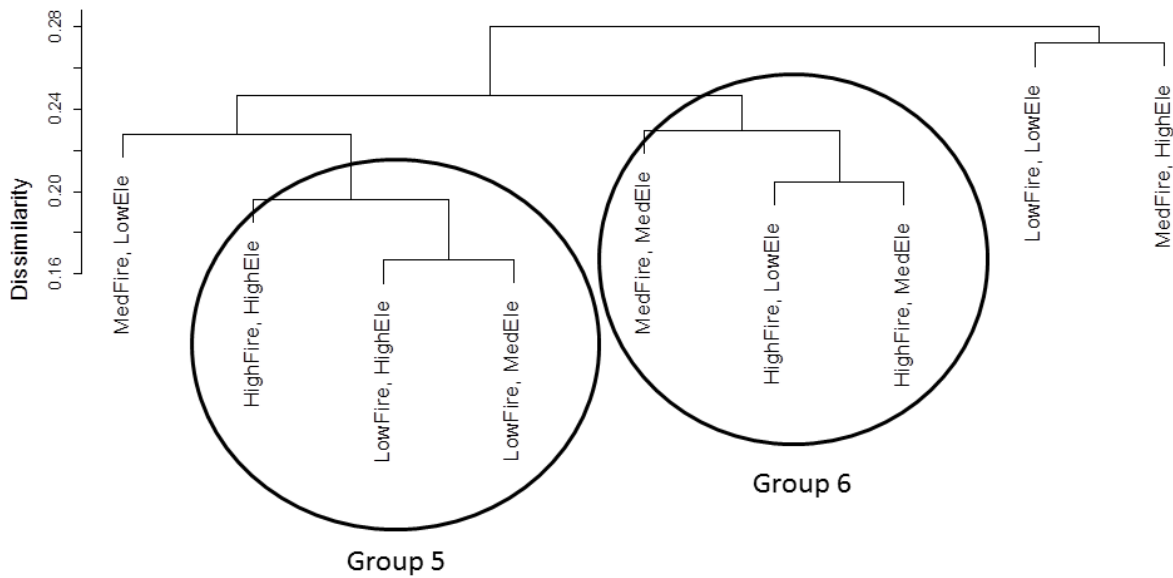


Figure 4.4. Tree communities showing high disturbance assemblages (Group 5) and med-high disturbance assemblages (Group 6)

Using the groups that were defined, the results from the group community analysis showed that most common shrub species responsible for group dissimilarity were higher represented in areas with lower number of fires (Figure 4.5). There were a few species in the shrub class such as *C. hereroense*, *A. harveyi* and *E. divinorum* that were relatively equally represented in both groups (ratio ~ 1).

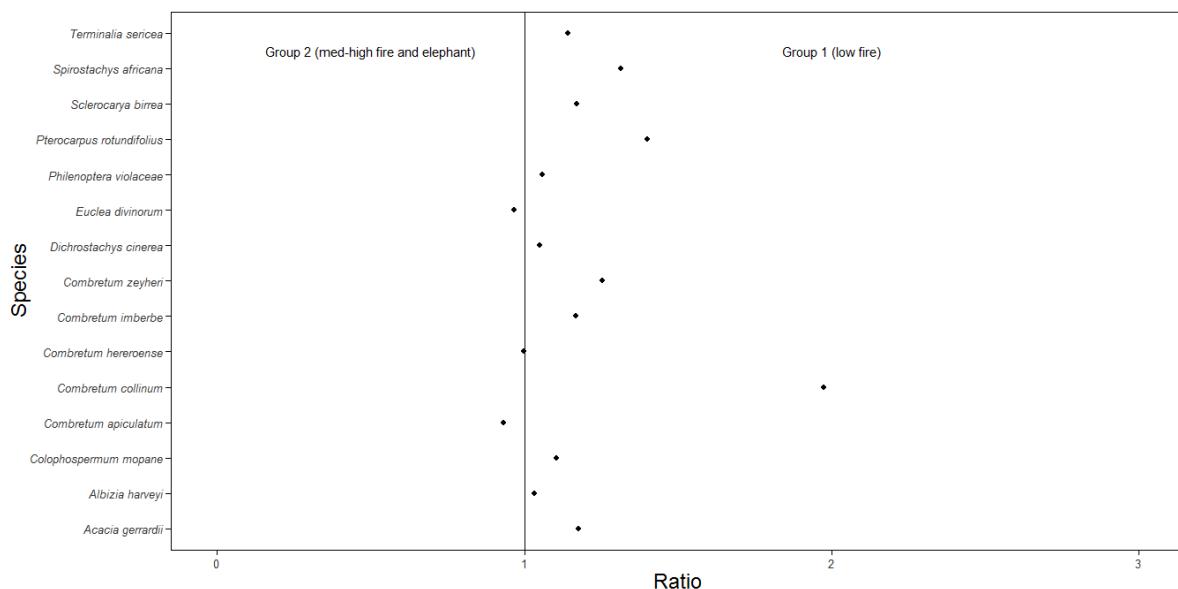


Figure 4.5. Ratio of the common species in the shrub communities between Group 1 and 2. The vertical line is where species are equally represented in both groups. Points on either side of line denote species that were more common in that particular group. This description is consistent for

Figures 4.6 and 4.7.

Most of the common brush species were higher represented in areas of low to medium fire frequency and elephant density (Figure 4.6), however there were a number of species that occurred in similar proportions across the two groups (e.g. *Philenoptera violaceae*, *C. apiculatum*, *A. nigrescens* and *A. exuvialis*). Additionally, species such as *D. cinerea* was present in higher proportions in areas of medium to high fire frequency and elephant density (Figure 4.6). Full species lists used in group comparisons at each height class can be found in the Appendix (Table S4.1).

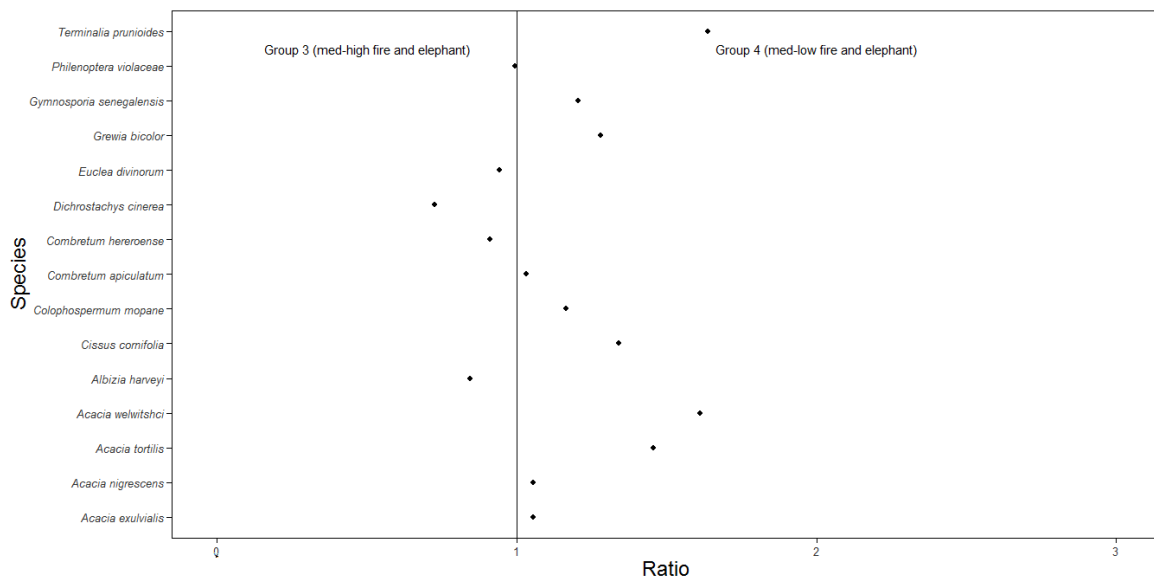


Figure 4.6. Ratio of the common species in the brush communities between Groups 3 and 4.

Several species were found in all height classes under varying disturbances, attributed to their widespread distribution and their ability to persist in disturbance-driven environments (e.g. *C. mopane*, *C. apiculatum* and *C. hereroense*). Certain trees were more responsive to specific disturbances (e.g. *A. grandicornuta*, *P. rotundifolius* and *S. birrea* trees in relation to elephant density) while others were more evenly spread across identified groups (e.g. *E. divinorum*, *C. hereroense*, *C. mopane*, and *A. nigrescens* in the tree class with a ratio ~ 1) (Figure 4.7). Species such as *A. welwitshci* was proportionately higher in areas of medium to high elephant density and low fire.

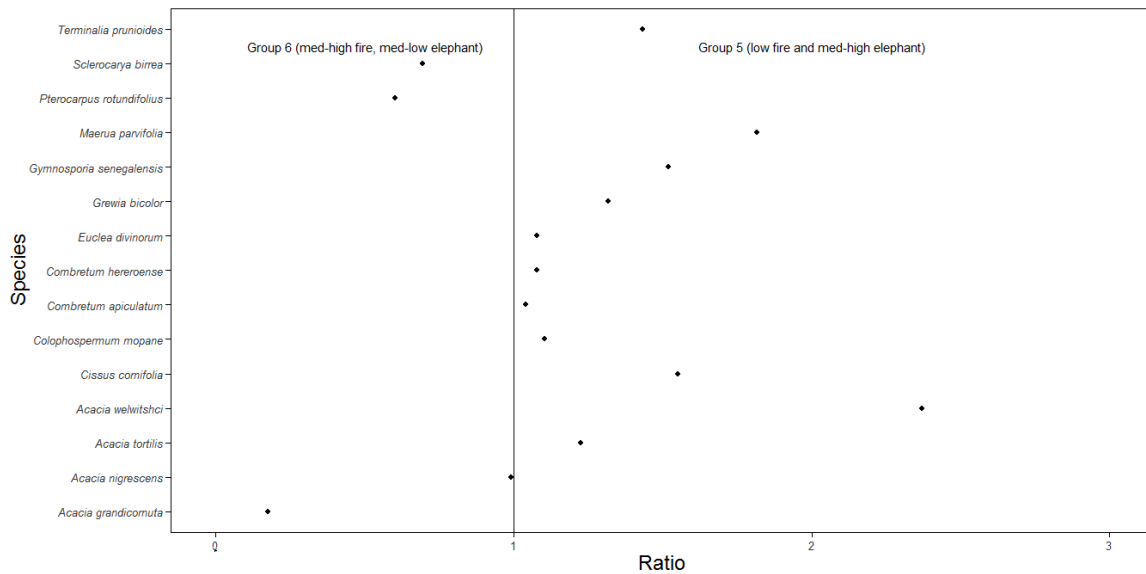


Figure 4.7. Ratio of the common species in the tree community between Groups 5 and 6.

In general, our results suggest that the tree communities may respond the strongest to disturbance by elephants if we assume elephant density as a proxy for elephant impact. The shrub community responds to the number of fires more so than to elephant density with some indication of different species assemblages with low vs. high fire frequencies. The brush layer appears very resilient to disturbance. Overall, our results suggest that areas with similar disturbance histories have more similar species composition to each other than to areas with different disturbance regimes, albeit not significantly so when considering the Global R. However, since woody plant species richness within the region is low (Kiker *et al.*, 2014), species responsible for group dissimilarity were almost identical at all height classes.

4.5 Discussion

Does top-down disturbance influence plant community composition and species richness?

The main aim of this study was to investigate whether varying degrees of long-term fire and elephant densities are associated with patterns of species community assemblages. Species community assemblages are often used to identify whether disturbances are associated with change in the ecosystem (Legendre & Gauthier, 2014). First, we investigated whether elephant density and fire frequency had a noticeable effect on species composition. Our results show that disturbance as indicated by elephant density and fire frequency, had a negligible effect on species richness. Previous work on the topic has delivered variable results; some work suggest that elephants do not affect species richness (Penzhorn et al. , Stuart-Hill) while species richness was found to decrease with time exposed to elephants in Addo National Park, South Africa (Lombard et al. 2001). Regardless of whether net species richness changed, many species report a decline in specific species with high elephant densities. For instance, very low numbers of baobab trees are present in Tsavo East and South Luangwa parks (Leuthold 1996) and *A. xanthophloea* in Amboseli Park in Kenya (Western & Maitumo 2004) as a result of elephant impact.

While no evidence of disturbance influencing species richness at various height classes was found in the current study, areas with similar long-term disturbance histories have more similar species composition than to areas with different long-term disturbance histories. This findings is in line with previous work that has shown that elephants (Leuthold, 1996; Augustine & McNaughton, 1998; Johnson *et al.*, 1999; Skarpe *et al.*, 2004; Western & Maitumo, 2004) and other browsers (Levick & Rogers, 2008; Staver & Bond, 2014; Wigley *et al.*, 2014) as well as fire (e.g. Andersen et al 2012) affect species composition (often only in extreme cases).

Further investigation showed that some species responded to specific disturbances related to height class. Species such as *P. violacaea*, *Euclea natalensis*, *D. cinerea* and *C. hereroense* were not affected by fire frequency. This is not surprising as these species are well adapted to disturbance by fire; for instance, *D. cinerea* can establish from seed as well as expand rapidly by root suckering, even when exposed to annual burning (Wakeling and Bond 2007). In the brush class this patterns were similarly unclear, however, species such as *D. cinerea*, which is a commonly occurring bush thickening species within the study area, was proportionately higher in areas of medium to high fire frequency and elephant density. *D. cinerea* appears to be stimulated by disturbance and occurs in higher numbers outside of herbivore exclosures (Wigley et al. 2015). Some of the dominant species occurred more frequently in the low fire group, for example *Combretum collinum*. Although this species may be widespread in savanna that burns frequently, the seeds are not very resistant to fire and frequent fire leads to low seedbanks (Gashaw & Michelsen 2002).

Certain species in the tree class associated to the degree of disturbance (e.g. *S. birrea* and *P. rotundifolius* and *A. grandicornuta*) and were proportionately higher in areas of lower elephant density. This supports previous small scale studies (Shannon *et al.*, 2008; Helm *et al.*, 2011; Shannon *et al.*, 2011; Vanak *et al.*, 2012) that highlighted the potential influence of elephants on the demography of highly palatable species such as *S. birrea*. Elephant-related disturbance on woody plant species distribution and persistence is dependent on a range of factors relating to the plant's ability to cope with disturbance. For instance, O'Connor *et al.*, (2007) suggested that trees such as *S. birrea* and *Pterocarpus* spp. are particularly sensitive to elephant utilization because the adults experience high levels of pollarding, uprooting and ring-barking, and mortality is not compensated by regeneration and recruitment. Factors such as artificial water provision influences elephant distribution and movement (Smit *et al.*, 2007; Smit & Ferreira, 2010) which can cause local extirpation of certain favored species as the probability of encounter with elephant increases (O'Connor *et al.*, 2007).

Testament to their widespread distribution, species such as *C. mopane*, *A. nigrescens* and *C. apiculatum* were commonly seen over various degrees of disturbances at all height classes (Kiker *et al.*, 2014) suggesting these species have an ability to cope with a range of top-down disturbances (both fire and herbivory). These resilient species occur across most major geologies as well (granite and basalt), however structural distribution of these common species depend on a range of factors (both top-down and bottom-up) that vary according to height class over the landscape (Chapter 3, Scholtz *et al.*, 2014). Wigley *et al.* (2015) suggested that species that were not responsive to high levels of browsing have three main mechanisms to deal with this disturbance; species are either well adapted to browsing (e.g., *D. cinerea*), well defended (e.g., *Gymnosporia senegalensis* has high levels of secondary compounds) or both (e.g., *Acacia nigrescens* has both tolerance traits such as fast growth rates and resistance traits such as close thorn spacing).

Does similar disturbances influence plant composition and richness at various height classes?

The study has shown that the effect of disturbance on plant communities and structure is largely decoupled. Shrub species were most responsive to the fire frequency, however, this pattern was less clear in the brush class, while tree species composition was most responsive to elephant density. There are a few common species that escape the effects of both fire and herbivory at smaller size classes and enter into the taller size classes, as many species have the ability to coppice or resprout (Luoga *et al.*, 2004; O'Connor *et al.*, 2007). Most semi-arid savannas are dominated by a few common species (Kiker *et al.*, 2014) and fires have evolved along with savanna vegetation over millions of years (Simon *et al.*, 2009). Therefore, while the effect of fire on vegetation structure is well documented, the long-term effect of fire on plant communities has received minimal attention.

Consequently, species within these areas of disturbance may become adapted to their conditions over the long-term (Bond *et al.*, 2005).

In summary, areas with different disturbance histories do not differ in species richness, yet areas with similar long-term disturbance histories have more similar species assemblages to each other than to areas with different long-term disturbance histories. This suggests that disturbance histories may have some influence on community assemblage. However, having stated that, the assemblages between the different disturbance regimes overlapped significantly and we noticed that most species persisted under all disturbance regimes. This implies that species are resilient to persist under various disturbance regimes (or lack of disturbance) (at least at the disturbance intensities available in this study). This has possible implications for management of protected areas, as natural tools (such as fire) for combating bush thickening needs careful consideration. Since decision-makers can influence these top down disturbances to some degree (e.g., fire frequency and elephant density), our results have important implications for future policies related to artificial water provision, elephants and fire.

CHAPTER 5: DRIVERS OF WOODY PLANT STRUCTURAL HETEROGENEITY IN A SEMI-ARID AFRICAN SAVANNA ⁴

Chapters three and four highlighted the importance of geology and disturbance in regulating spatial distribution of species and community assemblages. In this chapter, I ignored species composition, and focused on drivers of woody cover at specific height classes.

5.1 Abstract

Woody cover in savannas is essential for maintaining natural processes and ecosystem function. Important drivers of total woody cover in African savannas are rainfall, soil and nutrients, fire and herbivory, however, very little is known about drivers of woody cover at various height classes. The main aim of this study was to identify which of these drivers are the best predictors of woody cover at three height classes; shrub (0.75m – 2.5m), brush (2.5m – 5.5m) and tree (>5.5m). Data on percent woody cover at the three structural height classes were collected using Braun-Blanquet rapid monitoring technique over 1700 sites in Kruger National Park, South Africa. Geology (basalt and granite), mean annual rainfall, fire frequency and elephant density were analysed in this study as potential drivers of woody cover. Woody cover estimates obtained from the Braun-Blanquet rapid technique shows little variation between the two major geologies compared to previous studies of woody cover in KNP. Nevertheless, patterns associated with woody cover at specific height classes showed that the significant drivers were mean annual rainfall which is negatively associated with shrub cover, fire frequency which is negatively associated with brush cover and elephant density which is negatively associated with tree cover. While geology influences the spatial distribution of horizontal woody cover, variation in vertical vegetation structure is created and maintained by top-down disturbances such as fire and herbivory.

5.2 Introduction

Woody cover in African savannas is an essential attribute influencing many natural processes such as rates of transpiration, nutrient cycling and hydrology that give rise to savanna form and function (Sankaran, Ratnam & Hanan 2008). Savanna function is consistently under pressure considering the potential impacts of climate change such as woody encroachment (Buitenwerf et al. 2012) which will influence woody biomass and related natural processes such as fires. Studies on the drivers of woody cover on large spatial scales highlight the importance of a few major factors; top-down factors such as fire, herbivory, and bottom-up factors such as soil and rainfall (Sankaran et al. 2005; Bucini & Hanan 2007; Sankaran, Ratnam & Hanan 2008; Staver, Archibald & Levin 2011). Yet at smaller scales such as river catchments or areas with similar underlying geology, information on drivers of woody cover at specific height classes is only marginally understood.

⁴ R Scholtz, G.A. Kiker, U. M. Scharler, H.G. Mwambi, G. D. Duckworth, F.J. Venter. 2015. 'Drivers of woody plant structural heterogeneity in a semi-arid African savanna', In final preparation for submission to *Landscape Ecology*.

At continental scales, rainfall, soil and nutrients have been shown on numerous occasions to be the best predictor variables for woody cover (Sankaran et al. 2005; Bucini & Hanan 2007; Sankaran, Ratnam & Hanan 2008), particularly with respect to coexistence with grasses (February et al. 2013; Kulmatiski & Beard 2013). Rainfall dictates the upper potential of woody cover in African savannas, which increase linearly for mean annual precipitation (MAP) <650mm, after which it reaches the upper asymptote and the variation under this upper asymptote is due to top-down disturbances (Sankaran et al. 2005). Studies that have highlighted the influence of top-down disturbance factors such as fire and herbivory, particularly elephant impact on woody vegetation, have shown how these disturbances lead to a reduction in woody cover, yet these factors are essential in maintaining heterogeneity (Sankaran, Ratnam & Hanan 2008; Staver, Archibald & Levin 2011; Asner & Levick 2012; Levick, Baldeck & Asner 2015). Due to logistical challenges, studies showing a reduction of woody cover, particularly by elephant impact, have been conducted mainly at small scales (Shannon et al. 2008; Vanak et al. 2012; Shannon et al. 2013) and here we explore whether these patterns are evident at regional or landscape scales.

Other drivers of total woody cover such as rainfall and fire are evident at continental and global scales (Sankaran et al. 2005; Staver, Archibald & Levin 2011), however, less is known about how these drivers influence cover at various height classes. As such, most larger-scale studies explore drivers of horizontal cover without distinguishing how the drivers of cover may differ for woody vegetation in different height classes (i.e. vertical structure). More importantly, it is unclear how woody cover fluctuates in areas of varying degrees of long-term top-down disturbance over rainfall and geological gradients. This is a knowledge gap for decision makers of protected areas, particularly in light of biodiversity monitoring and maintaining structural heterogeneity (Noss 1990). Therefore, the main aim of this study is to identify which known drivers of woody cover (rainfall, soil, fire and herbivory) are affecting woody cover at three structural height classes in a semi-arid savanna at regional scales.

5.3 Materials and methods

Study Area

Kruger National Park covers about 2 000 000ha within the low lying savannas of northeastern South Africa (Figure 5.1). The vegetation is characterized by savannas with common species such as mopane (*Colophospermum mopane*), red-bush willow (*Combretum apiculatum*), knobthorn (*Acacia nigrescens*), marula (*Sclerocarya birrea*) and silver cluster leaf (*Terminalia sericea*) (Kiker et al. 2014, Chapter 2 of this thesis). Rainfall increases from 350mm.y⁻¹ in the north to about 750mm.y⁻¹ in the south. In general, the park is divided geologically into two main parts, granites and their erosion products to the west and basalts and their erosion products to the east. Previous studies have shown

that woody cover in KNP varies between 0 and 65% (Bucini et al. 2010) with the lowest areas of cover experienced in the basalts (Venter et al. 2003).

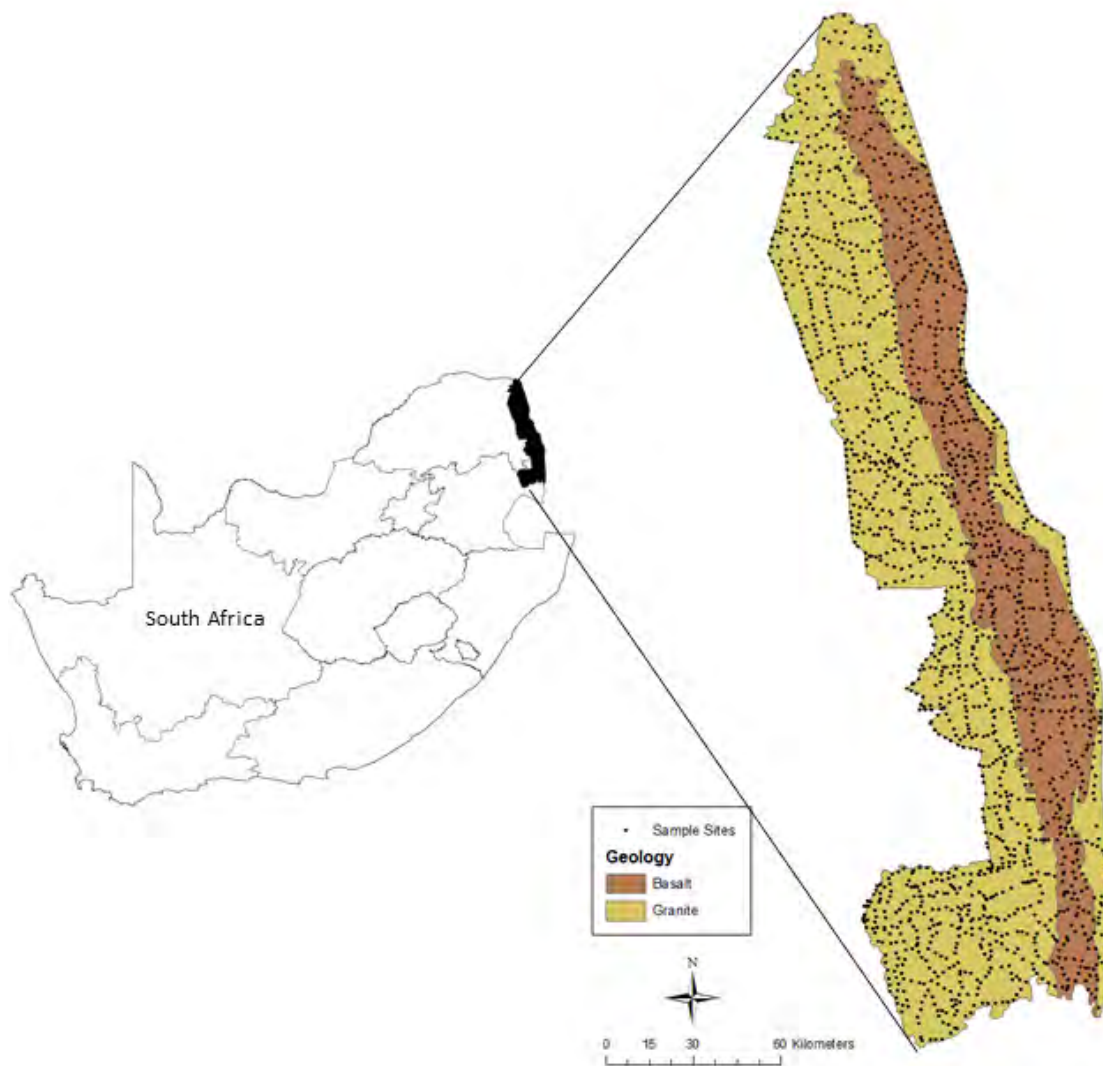


Figure. 5.1 Field sites within Kruger National Park, South Africa with underlying major geology types

Data selection

Between the years 1986 - 1990, Venter (1990) collected various field data and developed a new “land system” (consisting of 11 land systems) and a “land type” system (consisting of 56 land types) for KNP, based on geology type, soils and vegetation (Venter, Scholes & Eckhardt 2003). Information on the woody tree layer collected at 1803 unique field sites can be found in Kiker et al. (2014, Chapter 2 of this thesis). Sites were selected every 2.5km along major roads in the park. Using the Braun-Blanquet (BB) method, woody plants were classified into one of three height classes (Shrub 0.75m-2.5m; Brush 2.5 - 5.5m; Tree >5.5m) after identification at each site. BB categories varied within a preset percent estimate and these were assigned to minimum, mean, and maximum values per height

class (Kiker et al. 2014, Chapter 2 of this thesis). For example, a BB record of “2a” denoted a range of 5% to 12% crown cover with 2-3 canopy diameters separating canopies. Thus, cover calculations would assume 5% cover as the minimum estimate, 8.5% as the mean estimate and 12% as the maximum estimate (see Appendix Table 2.1, for the full list of canopy overlap assumptions). At each site n , each species per height class was identified and placed in a BB category (see Kiker et al. 2014, Chapter 2 for species lists). The mean per cent cover x was extracted (as shown above) per species and used to calculate per cent cover at each site by summation across all species ($\sum_{i=1}^n x_i$) per height class. This estimate per site within each height class (shrub, brush and tree) was used to calculate the mean per cent cover for each height class per site.

Data analyses

Descriptive analysis

Kiker et al. (2014, Chapter 2 of this thesis) provided baseline information at the park-wide scale on variation of woody cover at all height classes. In this study, using fire frequency and elephant density (i.e. factors that are partially managed), sampling sites were divided into three equally distributed spatial regions (33rd and 66th, 100th percentiles). This provided an overall distribution of low, medium and high disturbance areas in terms of fire frequency and elephant density. Using this scale of disturbance intensity, the distribution of woody cover at all height classes across the two major geologies were assessed.

Inferential analyses

Percent woody cover is frequently collected during vegetation surveys and data are bounded between 0 and 1 (or 0% and 100% in the case of woody cover). This type of data does not conform to the assumptions of standard statistical procedures (Eskelson et al. 2011). Typically, when a proportional response is analysed using traditional linear models (with normal/Gaussian distribution) there is major heteroscedasticity observed in the residuals. This violates linear model assumptions such as unbounded response variables, and renders model results biased or inaccurate. Alternative methods for dealing with percent or proportion data include binomial generalized linear model (glm) (Venables & Ripley 2002). Here, the bounded response must be given weights based on number of successes within a number of trials (successes and trials). Since our field data were collected once at each site (i.e. number of trials = 1), we cannot assume that this proportion data is appropriate for the binomial distribution. Another approach is using beta regression (an extension of glms), and is relatively common when the response is bounded between 0 and 1 (Crawley 2012) or is a proportion. However, this method cannot process observations that are equal to 0 or 1. To overcome this, popular smooth transformations such as the arcsine transformation (Smithson & Verkuilen 2006; Crawley 2012), probit (Finney 1947) and Box-Cox (Sakia 1992) have been shown to be useful transformations

for bounded response variables. However, these popular smooth transformations do not always provide a solution (Warton & Hui 2010), in particular, if the dataset is severely skewed towards 0 or 1 (Ospina & Ferrari 2012a). However, one solution that has shown promise when dealing with zero-inflated bounded data is zero-one inflated beta regression (ZOIB) (Wieczorek & Hawala 2011; Ospina & Ferrari 2012b; Liu & Kong 2014). In addition and of high importance, it accounts for excess observations at zero and one and has been shown to produce robust results in other studies on percent vegetation cover (Nishii & Tanaka 2013). In our dataset, data transformations (arc-sine, probit, Box-Cox) were explored for standard statistical approaches as well as running the ZOIB model in a Bayesian framework via Markov Chain Monte Carlo (MCMC) random walk approach.

Bayesian Model settings

The number of iterations per chain in the MCMC sampling was 25 000 with a thinning period of 5, and a burn-in of 5000, over 3 chains. Model priors used at each height class was $\beta_i \sim N(0, C)$, where C is set to 10^{-3} , while acknowledging the benefits of a large sample size as available in this dataset (priors generally will not influence the posterior distribution with large sample sizes). An expanded description of this technique as well as model convergence histograms and traceplot samples can be found in Appendix S5.2. Model fit was assessed using a combination of plotting tools and MCMC convergence diagnostics. The diagnostic test, Gelman and Rubin (Cowles & Carlin 1996) as well as trace and density plots were used to assess model convergence and mixing, by visual inspection (Appendix S5.2). The Gelman and Rubin test calculates within-chain and between-chain variance. This is called the potential scale reduction factor. Generally, a mean R-hat value equal or below 1.1 suggests model convergence. Diagnostic testing provided evidence to suggest the model parameters (i.e. number of iterations) are sufficient to draw inferences from the posterior distribution. Beta coefficients with their 95% credible interval (C.I.) (Bayesian analogue for confidence interval) for each predictor variable can be assessed by looking at their mean value in relation to zero where credible interval overlapping zero suggests little influence.

Model procedure

The primary interest of this study was to assess how percent woody cover is affected by predictor variables at each of the three structural height classes (shrub, brush, and tree). The predictors used have in previous research been shown to affect total woody cover on the African continent as well as on global scales (Sankaran, Ratnam & Hanan 2008; Holdo, Holt & Fryxell 2009; Staver, Archibald & Levin 2011). These were geology (soil type) with two levels; granites and basalts, fire frequency (years), elephant density (individuals.km⁻²), average annual rainfall (mm.yr⁻¹) (Table 5.1) and land system was used as an experimental unit in the model (Venter, Scholes & Eckhardt 2003). A single full model (i.e. including all predictors) for each height class was run, therefore, ending up with three models.

Table 5.1. Covariates used in each model, predicting the structural height classes shrub, brush or tree in KNP in three separate models

| Covariate | Type | Levels/Range | Source |
|----------------------|-------------|--|---|
| Geology | Categorical | Basalt and Granite | (http://dataknp.sanparks.org 2012) |
| Fire frequency | Continuous | 0 – 22 years | (Smit et al. 2013b) |
| Elephant density | Continuous | 0 – 3.23 individuals per km ² | (adapted from Smit & Ferreira 2010) |
| Mean annual rainfall | Continuous | 217mm - 762mm | (Schulze et al. 2008) |

Plots were created using *ggplot2* (Wickham 2009) and analyses conducted using the *zoib* (Liu & Kong 2014) and *zibHelpers* (Gandrud 2014) packages with MCMC convergence diagnostics assessed using package *coda* (Plummer et al. 2012) in R (R Development Core Team 2013).

5.4 Results

Descriptive results

Percent woody cover estimates per land system (Venter et al. 2003) can be found in Table 5.2. These estimates were surprising, showing very little difference between woody cover over granite and basalt soils contradicting several studies on per cent woody cover in KNP (Eckhardt, Wilgen & Biggs 2001; Bucini et al. 2010; Wessels et al. 2011). Nevertheless, the basalts indeed contained more sites with 0% cover at all height classes (Appendix Figure S5.1). Over the three degrees of disturbance (low, medium and high), there were no noticeable differences in the spread of woody cover between geologies at all height classes (Figure 5.2). Although mean estimates of cover were low, shrub cover in the basalts was higher over both disturbance agents and higher in areas of low fire frequency (Figure 5.2). While there were no clear patterns between brush cover over both disturbances, there were differences in medium fire disturbance and high elephant disturbance between geologies. Tree cover was the lowest cover (see Figure 2.7c in Chapter 2 and Appendix Figure S5.1) and no clear trends associated with disturbances (Figure 5.2).

Table 5.2 % woody cover (mean \pm s.e.) estimates over 11 land systems (# sites) in Kruger National Park, South Africa (see Appendix Figure S5.2 for map)

| Landsystem | Height Class | | | |
|------------------|-----------------|------------------|------------------|-----------------|
| | Main Geology | Shrub | Brush | Tree |
| Bulweni (31) | Basalt | 27.07 \pm 5.71 | 8.33 \pm 2.76 | 7.18 \pm 2.4 |
| Letaba (307) | Basalt | 12.51 \pm 0.87 | 5.79 \pm 0.64 | 0.62 \pm 0.11 |
| Vutome (62) | Basalt | 9.32 \pm 1.61 | 14.65 \pm 2.22 | 5.47 \pm 1.36 |
| Satara (266) | Basalt | 8.16 \pm 0.74 | 5.81 \pm 0.53 | 1.84 \pm 0.4 |
| Pafuri (52) | Granite | 5.5 \pm 0.97 | 6.45 \pm 1.72 | 8.78 \pm 2.74 |
| Nwambiya (48) | Granite | 8.02 \pm 1.75 | 14.17 \pm 2.83 | 5.03 \pm 1.71 |
| Malelane (37) | Granite | 4.52 \pm 1.1 | 7.02 \pm 1.3 | 2.85 \pm 0.66 |
| Klipkoppies (58) | Granite | 14.25 \pm 2.57 | 12.53 \pm 1.95 | 4.52 \pm 1.77 |
| Phalaborwa (453) | Granite | 11.09 \pm 0.76 | 7.78 \pm 0.52 | 1.83 \pm 0.24 |
| Sabiepoort (77) | Granite | 12.46 \pm 1.75 | 11.53 \pm 1.7 | 0.48 \pm 0.09 |
| Skukuza (412) | Granite | 5.61 \pm 0.38 | 9.37 \pm 0.56 | 4.78 \pm 0.47 |

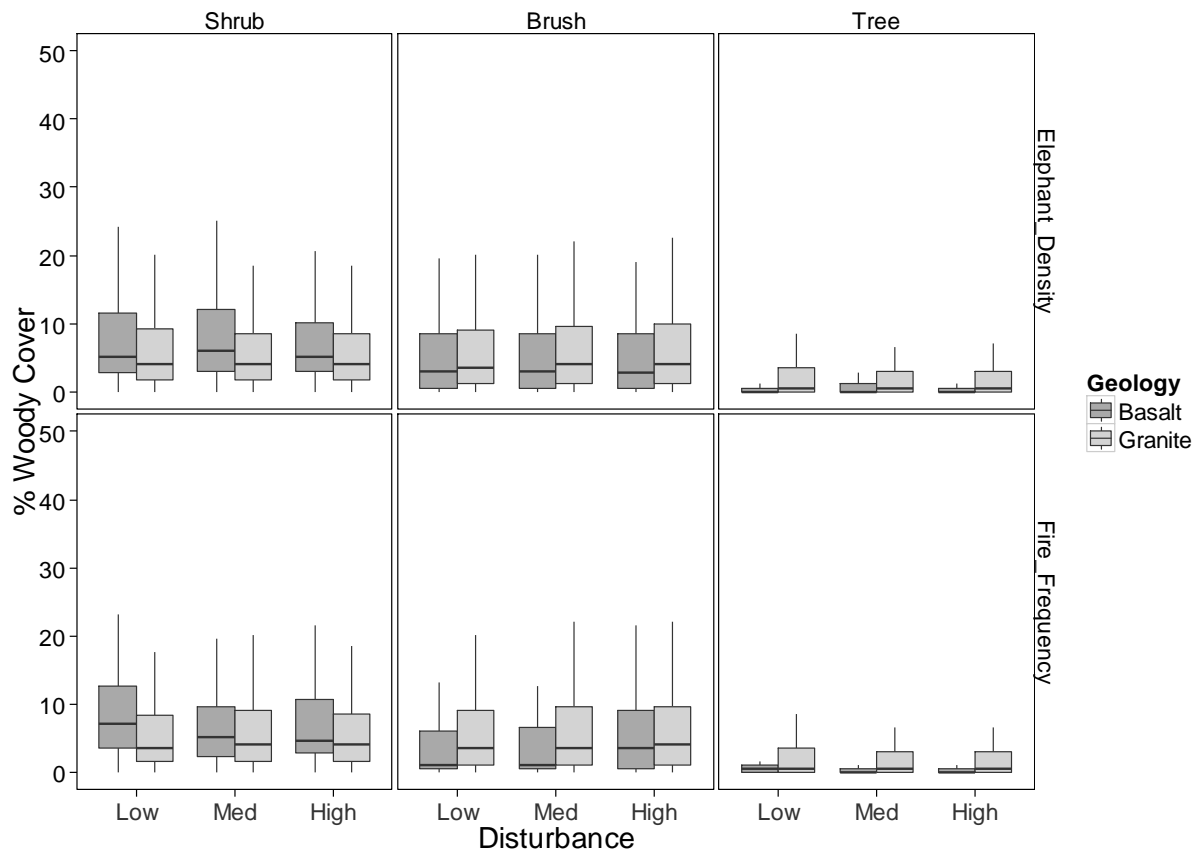


Figure. 5.2 The spread of woody cover at various height classes across three degrees of top-down disturbance. The spread of the data signifies the extremes (maximum and minimum), the interquartile range (within the box) as well as the median (indicated by the horizontal line within the box).

Bayesian model results

Smooth transformations did not assist standard statistical approaches, and therefore the zero-one inflated beta regression approach was used. Convergence results from the Gelman-Rubin diagnostic test ($R\hat{=} = 1$, upper C.I. <1.1 , Appendix Table S5.1.) suggest that our models have converged. Using Table 5.3 to identify significant drivers in the model requires that 95% of the posterior distribution not overlap zero. Geology was a significant factor at all height classes. Fire frequency was significantly negatively associated with brush cover suggesting that areas with the lowest fire frequency had the highest brush cover. Here, basalt soils had a negative association with brush cover, while granite soils had a positive association. Elephant density was significantly associated with tree cover implying that areas with low elephant density have the highest tree cover.

Rainfall was negatively associated with shrub cover implying that areas of less rainfall are associated with higher shrub cover. This finding is partially supported by Stevens et al. (2015) who

showed an increase in woody cover in drier savannas over South Africa in the last 70 years. Both the findings of this study and that of Stevens et al. (2015) contrast with the woody cover predictions of Sankaran et al. (2005). The rainfall gradient of KNP lies between 400mm and 750mm, the park lies within the zone between the two linear estimates reported by Sankaran et al. (2005). Additionally, sites obtained from KNP and subsequently used by Sankaran et al. (2005, Supplemental data), were restricted to $n=109$ sites with % woody cover equal to 14.02 ± 1.17 (mean \pm s.e.), which is somewhat low when compared to other estimates and less representative than previous studies (Eckhardt, Wilgen & Biggs 2001; Bucini et al. 2010; Wessels et al. 2011). For example, woody cover estimates of Bucini et al. (2010) taken at the geographic coordinates reported by Sankaran et al. (2005, Supplemental data) data points was $29.33\% \pm 1.13$ (mean \pm s.e.), which is about double the estimate used in the Sankaran et al. (2005) model for KNP. Given this high variation of woody cover estimates within the rainfall gradient of KNP, it is suspected that rainfall is one of many influences (including the disturbances previously mentioned) on woody cover in this region. This relationship of woody cover, within specific height classes is even more complicated in this transition zone.

Table 5.3. Results from posterior distribution of model parameters for each model run (for each height class) * Denotes a significant predictor at the 5% significance level.

| Height Class | Variable | Mean | sd | 2.5% | Median | 97.5% |
|--------------|-------------------|--------|-------|--------|--------|--------|
| Shrub | geoBasalt* | -1.225 | 0.194 | -1.553 | -1.232 | -0.882 |
| | geoGranite* | -0.136 | 0.048 | -0.212 | -0.129 | -0.056 |
| | Rainfall* | -0.002 | 0.004 | -0.002 | -0.002 | -0.001 |
| | Elephant density | -0.017 | 0.067 | -0.119 | -0.016 | 0.072 |
| | FireFreq | 0.002 | 0.005 | -0.004 | 0.003 | 0.013 |
| Brush | geoBasalt* | -2.109 | 0.205 | -2.489 | -2.125 | -1.508 |
| | geoGranite* | 0.168 | 0.050 | 0.067 | 0.173 | 0.281 |
| | Rainfall | 0 | 0 | -0.001 | 0 | 0.001 |
| | Elephant density | -0.034 | 0.071 | -0.191 | -0.043 | 0.078 |
| | FireFreq* | -0.011 | 0.006 | -0.023 | -0.011 | -0.001 |
| Tree | geoBasalt* | -3.071 | 0.261 | -3.487 | -3.016 | -1.367 |
| | geoGranite* | 0.161 | 0.069 | 0.167 | 0.156 | 0.301 |
| | Rainfall | 0 | 0 | -0.001 | 0.001 | 0.001 |
| | Elephant* density | -0.174 | 0.089 | -0.383 | -0.163 | -0.004 |
| | FireFreq | -0.007 | 0.009 | -0.019 | -0.006 | 0.004 |

Overall, our results show woody cover responds to varying degrees of disturbances across geologies. Specific factors at different height levels were significant in predicting woody cover; in general, shrub cover is most responsive to rainfall, brush cover is mainly responsive to fire frequency and less responsive to both rainfall and elephants, and tree cover strongly associated with elephant density and not influenced by rainfall or fire.

5.5 Discussion

This study aimed to identify the drivers of woody cover at three structural height classes in a semi-arid savanna, and the response of woody cover in areas of high, medium and low top-down disturbance. The main findings of this study suggest that except for geology type, factors influencing woody cover at various height classes were not the same across all height classes. Previous research at similar scales also identified geology type as a significant predictor of woody species distribution at various height classes (Scholtz et al. 2014, Chapter 3 of this thesis). Here, I show that irrespective of species composition, different drivers are significantly associated with woody cover according to height classes. The significance of these results highlights the importance of understanding vegetation dynamics not only compositionally, but also structurally. Previous studies assessing factors that influence woody cover (e.g. Sankaran et al. 2008) have not explored these relationships at various height classes. Since woody vegetation is constantly exposed to top-down disturbances, understanding which factors influence woody cover at various height classes further increases our understanding of savanna vegetation dynamics.

Results obtained for the percent cover estimates over the geological template were different to what was found in other studies predicting woody cover. For example, Eckhardt et al. (2001) found that total woody cover increased from 19.7% to 22.1% on the granites, and 11.9% to 4.3% on the basalts using aerial photographs from 1940, 1974 and 1998. Similarly, Wessels et al. (2011) measured 27.9% total woody cover over the granites and 6.3% total woody cover on the basalts (gabbro soils) in KNP using LiDAR imagery. While our estimate for granitic soils was similar to Eckhardt, Wilgen & Biggs (2001), the estimate over the basalt areas was above average with a lack of discrepancy between woody cover over both geologies. Other studies on total woody cover in the entire KNP also points out a dramatic decrease in woody cover in the basaltic areas of KNP (Bucini et al. 2010) compared to granitic areas using a combination of field measurements and remotely sensed imagery. Bucini et al. (2010) measurements at Venter (1990) data points show 38.17% woody cover on the granites and 25.81% woody cover on the basalts also alluding to large differences in woody cover between granites and basalts. There is however large differences in woody cover estimates between land systems (Table 5.2) which takes geology into account at a finer scale than the base geology types (granite and basalt). While information on fire intensity was not available for this study, it is possible that the observed negative relationship with fire on the basalt soils at all height classes could be due to higher fire intensity on the basalt soils.

Obtaining field woody cover estimates over large spatial scales using rapid techniques indeed enables greater spatial coverage (Kiker et al. 2014, Chapter 2 of this thesis). However, employing a rapid technique poses many challenges and shortcomings when collecting data on percent woody

cover from ordinal scales. Some of these shortcomings are highlighted in Kiker et al. (2014, Chapter 2 of this thesis) and one aspect requires further attention; estimating average per cent cover per site. In Chapter 2, I presented the method employed to obtain mean estimates of woody cover at each height class (Chapter 2, Table 2.1). The exact cover estimates of this dataset may not be a true representation of the KNP landscape, particularly compared to fine scaled remote sensing products (e.g. Bucini et al 2010). However, the distribution over the landscape is relatively accurate; areas of known higher cover are indeed higher, and similarly for the areas of lower cover (Figures 2.7 a-d in Chapter 2). Therefore, while our woody cover estimates are carefully considered along with canopy overlap assumptions, the difference between woody cover over both geologies do not agree previous studies' estimates. Nevertheless, no method of data collection is flawless, even technological advancements such as LiDAR has limitations when estimating percent woody cover. Wessels et al. (2011) showed that LiDAR underestimated plants below ~2m (see Figure 2 in Wessels et al. (2011)), an aspect that may be measured with higher accuracy by field measurements. While rapid techniques aid greater spatial coverage, field collections are often restricted to plots with "manageable" dimensions (e.g. 20m x 20m). In heterogeneous landscapes such as KNP, small plots can be very misleading or under-representative of the landscape in terms of descriptive statistics on per cent woody cover as shown in this Chapter. Therefore, while the absolute values of woody cover may be underestimated, the patterns associated with woody cover at specific height classes are still valuable for comparison.

There are only a few studies highlighting the drivers of total woody cover on continental and global scales (Sankaran et al. 2005; Bucini & Hanan 2007), and this is the first attempt to describe drivers of woody cover at various structural height classes in semi-arid savannas. Since our study considers woody cover at specific height classes, the underlying mechanisms that influence woody cover within a specific height class may be different than when combined to create an estimate of total woody cover. According to Sankaran et al. (2005), woody cover in areas below 650mm is limited by rainfall. This study shows that shrub cover (<2.5m) proliferates in areas of lower rainfall in a semi-arid savanna. While this finding does not dispute that of Sankaran et al. (2005) assessing total cover, it highlights the complexities when understanding the drivers of woody cover at specific height classes. To this extent, previously conducted studies on percent woody cover of KNP did not reach the upper potential as predicted by Sankaran et al. (2005) suggesting that factors other than rainfall are more important in maintaining woody cover fluctuation over the landscape. Nevertheless, in support for evidence presented by Bucini and Hanan (2007), it is suspected that due to climate variability and disturbance events, woody cover is well below the mean climate potential woody cover and therefore rainfall alone is not the limiting factor for proliferation of shrub cover. Furthermore, this is supported by our results where rainfall in fact had a minor influence (approximates zero in Table 5.3) on woody cover at all height classes. Perhaps this has something to do with the scale at which data were

collected, thereby not capturing the entire spectrum of the KNP rainfall gradient. Nevertheless, future studies on percent woody cover should not ignore structurally differentiated cover estimates.

In conclusion, the analyses presented in this paper highlight the usefulness of Bayesian approaches, particularly for zero-inflated data in savanna ecology. Since woody cover in semi-arid savannas is generally low (Bucini et al. 2010; Kiker et al. 2014, Chapter 2 of this thesis), dealing with zero-inflated, bounded response variables should receive special analytical attention for proper inference. Here I provide an additional method to analyse percent woody cover in savannas. The ecological patterns obtained for woody cover at the tree class agrees with previous studies showing that an increasing elephant population can have negative effects on woody cover. This links to the conclusions presented in Scholtz et al. (2014, Chapter 3 of this thesis). Future studies on woody cover in semi-arid savanna should be cognizant of vertical woody vegetation structure as woody plants are constantly exposed to top-down disturbances in savannas.

CHAPTER 6: SYNTHESIS AND CONCLUSION

The central theme of this thesis highlights the importance of vegetation structure in understanding woody vegetation dynamics in savanna systems. This original work presents new ideas in assessing vegetation structural dynamics in woody cover, species richness and composition as well as distribution at different height classes which to date has received minimal attention.

Some of the most detailed woody vegetation datasets available for one of South Africa's largest and oldest protected areas, Kruger National Park, South Africa (KNP) were used to demonstrate the importance of vegetation structure in savanna systems. Key findings include documenting localities of 145 species in KNP with which species probability distribution maps can be produced (Chapter 2 and 3). I also produced the first continuous maps of species richness and % woody cover at various height classes for KNP. The % cover maps at the smaller height classes (shrub and brush) are supplementary to pioneering work done by Bucini et al. (2010) and Mathieu et al. (2013) that created products of total woody cover. These products form the basis of many studies and management decisions relating to woody cover in KNP.

a) Are the drivers of species distribution and composition similar across height classes?

Following the basic work presented in Chapter 2, coupled with a novel technique using similarity indices of the findings from a presence-only species distribution model, I showed that drivers of woody vegetation composition and structure are largely decoupled (Chapter 3). That is, drivers of woody species may not be the same across the height classes. This complements earlier work done highlighting the importance of the geological template for species distributions (Gertenbach 1983; Venter & Gertenbach 1986) in spite of top-down disturbances. This also sets the framework for subsequent chapters as this result permeates throughout this thesis, irrespective of response variable.

b) Are woody plant communities shaped by top-down disturbances? How does this relate to specific height classes?

The results from Chapter 3 present an interesting question since the importance of the bottom-up drivers such as geology have been highlighted as a major influence for species distribution. That is; do long-term, top-down disturbance influence vegetation communities? I found that species richness did not fluctuate over varying degrees of long-term disturbance. This was not surprising considering that semi-arid savannas are generally dominated by a few common woody plant species (Wigley et al. 2014, Chapter 2). Van Coller et al. (2013) and Smith et al. (2013) found the highest number of herbaceous species in areas of highest disturbance. Nevertheless, when considering woody plant species composition in these areas under varying degrees of disturbance, I found that communities in

the high disturbance areas were either fire tolerant (e.g. shrub class) or elephant-impact adapted (e.g. tree class). This result tends to contradict other small scale studies for example on the Experimental Burn Plots (EBPs) in KNP (Govender, Trollope & Van Wilgen 2006; Higgins et al. 2007; Smit et al. 2010). It is most likely because the EBPs are found mainly on the crests over major geologies. However, KNP vegetation is dominated by a few species (Chapter 2) and therefore rare species may not be found on the EBP sites.

Since KNP has a long history of fire (Trollope 1993; van Wilgen et al. 2000) and elephant (Whyte et al. 1999; Whyte, Van Aarde & Pimm 2003) policy changes, I postulate that the species found in areas of long-term disturbance adapt to their conditions. It is also most likely that species community shifts may only manifest when exposed to prolonged periods of disturbance. These communities are mainly dominated by a few common driver-adapted species. However the differences in the number of sites that contained these common species within a particular disturbance regime lead to the specific community matrix within these areas. This provides pivotal information as management of these disturbances will have consequences over the long term. Similarly the effect of not managing for these disturbances will influence species composition as well while acknowledging the disturbances such as fire (frequency and intensity) are largely climate-dependent (Archibald et al. 2009). Therefore, understanding these effects assists the decision-making process as predictive models can inform decision makers of the potential changes in community composition.

c) Do drivers of woody cover differ according to height class?

In Chapter 4, I concluded that species composition may change over long term exposure to top-down disturbances. Understanding the cascading effects of vegetation change on biodiversity remains a challenge. Therefore, ignoring species composition, I looked at predictors of woody cover at various height classes in Chapter 5. Many successful studies have highlighted empirical relationships between a few of the most important drivers of woody cover such as rainfall, soil, fire and herbivory at both continental and regional scales (Sankaran et al. 2005; Bucini & Hanan 2007; Sankaran, Ratnam & Hanan 2008; Bucini et al. 2010; Staver, Archibald & Levin 2011; Lehmann et al. 2014). Within a Bayesian hierarchical framework, I highlighted the importance of each of these drivers in relation to specific height classes. Drivers of woody cover differ according to height class. The main findings suggest that mean annual rainfall is negatively associated with shrub cover; fire frequency is negatively associated with brush cover and elephant density is negatively associated with tree cover. Previous studies on % woody cover have employed various statistical techniques such as nonlinear quantile regression methods (Sankaran et al. 2005), multiple linear regression (Bucini et al. 2010) as well as boosted regression trees (Sankaran, Ratnam & Hanan 2008). With taking a Bayesian approach, especially when data are zero-inflated as is the case for woody cover within semi-arid savannas; I present an additional method that can model bounded response variables appropriately.

Understanding the predictors of woody cover at specific height classes provides important insight in light of woody encroachment and potential woody vegetation structure homogeneity, which can have cascading (negative) effects on biodiversity (Fuhlendorf et al. 2006; Hovick et al. 2014). In support of my previous chapters, geology type influences the horizontal distribution of woody cover at all height classes while top-down disturbances are essential in maintaining heterogeneous vertical structure. In light of the shortcomings mentioned in Chapter 6 on the woody cover estimates from ordinal data, I acknowledge that the absolute values may not be representative or in accordance with previous studies of woody cover in KNP (Eckhardt, Wilgen & Biggs 2001; Bucini et al. 2010; Wessels et al. 2011). Nevertheless, the observed trends are plausible, particularly in the tree class where tree cover is lower in areas of high elephant density which is substantiated by Bayesian model results. The link between Chapters 4 and 5 has major implications for current and future management decisions regarding the fire policy and artificial waterhole distribution which can influence herbivore distribution (Smit, Grant & Devereux 2007) and subsequently influence species composition. Understanding and implementing these policies are part of a learning process; however these disturbances can have cascading effects on compositional and structural biodiversity and therefore requires adequate information to make informed decisions.

It is important to acknowledge that woody vegetation at specific height classes is a snapshot of the landscape during collection time. Data in the brush class depends on successful recruitment and escape from the shrub class, and similarly for the tree class with respect to the brush height class. Since there is no temporal component to this dataset, it is difficult to infer on long-term vegetation dynamics. Therefore, while the topic of demographic bottlenecks is not a central theme to this thesis, the importance thereof in disturbance driven systems has to be acknowledged. For example, in areas of frequent fires, many shrubs will not escape the effects of fire. For example, Figure 2.4 a) and b) shows the distribution of shrub and brush *A. nigrescens* respectively. Here, these individuals are found in areas that burn on average every 2-3 years (van Wilgen et al. 2014) and are potentially caught within the so called “fire trap”. This information is pivotal to managers that can potentially manipulate fires in protected areas.

To answer my overall thesis question: Are the drivers of savanna woody plants the same across all height classes?

Drivers of species distribution, structure and composition are not the same across height classes. Drivers of woody cover are also different according to height class, something which has not received attention despite the numerous studies on drivers of total woody cover in savannas. Additionally, I have shown the influence of top-down disturbances (such as fire and elephant impact) on woody vegetation cover, composition and distribution can be detected at regional scales. These findings agree with small, fine-scaled studies highlighting patterns of decreasing woody cover in areas

highly utilized by elephants. More so, these patterns can be detected at regional scales as well. Overall, the results obtained from this thesis highlight several key aspects of structural dynamics of woody vegetation in savanna systems. Bottom-up factors such as geology and rainfall are influential in predicting species structural distribution and composition, richness and woody cover at various height classes at regional scales. However, since factors that influence woody vegetation dynamics differ according to height class in disturbance-driven environments, disturbances are essential in maintaining structural heterogeneity. This provides pertinent information for future studies and management indicators in disturbance-driven savannas.

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APPENDICES

Chapter 2:

Table S2.1 Woody vegetation canopy cover classes field data for site-based calculations (after Venter, 1990) along with the percent cover estimates used in subsequent calculations.

| Braun- Blanquet Symbol | Crown Cover (%) | Number of Diameters Separating Canopies | Mean % Cover | Minimum % Cover | Maximum % Cover |
|------------------------------|-----------------------|---|-----------------|--------------------|--------------------|
| R | - | > 30 | 0.0 | 0.0 | 0.0 |
| + | 0.1 – 1 | 8 – 30 | 0.55 | 0.1 | 1.0 |
| 1 | 1 – 5 | 3 – 8 | 3.0 | 1.0 | 5.0 |
| 2a | 5 - 12 | 2 - 3 | 8.5 | 5.0 | 12.0 |
| 2b | 12 – 25 | 1 – 2 | 18.5 | 12.0 | 25.0 |
| 3 | 25 - 50 | Touching | 37.5 | 25.0 | 50.0 |
| 4 | 50 – 75 | Touching | 62.5 | 50.0 | 75.0 |
| 5 | 75 - 100 | Overlapping | 87.5 | 75.0 | 100.0 |

Table S2.2 RMSE values of observed vs predicted for all interpolation methods

| Indicator Kriging | Shrub | Brush | Tree | Total |
|----------------------------|-------|-------|------|-------|
| <i>T. sericea</i> | 0.29 | 0.30 | 0.20 | 0.33 |
| <i>C. mopane</i> | 0.29 | 0.29 | 0.29 | 0.29 |
| <i>A. nigrescens</i> | 0.30 | 0.29 | 0.31 | 0.40 |
| <i>C. apiculatum</i> | 0.39 | 0.42 | 0.22 | 0.44 |
| Empirical Bayesian Kriging | | | | |
| Species richness | 1.31 | 1.18 | 0.86 | 1.55 |
| % Cover | 13.95 | 11.43 | 7.4 | 17.6 |

Chapter 3:

MaxEnt software

MaxEnt was based on machine learning response that is developed for predicting the distribution of species using niche modeling techniques from incomplete data (Phillips & Dudik 2008; Baldwin 2009). The software uses raster based approach in which occurrence and environmental conditions are recorded in cells of defined size. The relative likelihood of finding a species in each cell is calculated and plotted as a distribution probability map ranging from zero to one with increasing likelihood (Phillips & Dudik 2008; Smith et al. 2012). MaxEnt uses two methods to

describe variable importance which is mentioned in the manuscript, the heuristic approach and the jackknife approach, and the strength of each prediction is measured through the receiver operating characteristic (ROC) plots. The heuristic approach to model importance is influenced by the increase in gain in the model provided by each variable; this method of variable selection was used for the subsequent cluster analysis. ROC plots are constructed by assigning a certain percentage of the data for training data, and the other portion for test data. The significance of this curve is quantified by the AUC which ranges from zero to one. Higher AUC values correspond to better species prediction than those with lower AUC values. The version of MaxEnt used was 3.3.3k (<http://www.cs.princeton.edu/~schapire/maxent/>). The following options were chosen for each model run; Linear features, Quadratic features, Product features, Threshold features, Hinge features. These together create the Auto features option. The output format chosen was Logistic, and file type was ASC. These options are default and are known to yield robust results (Phillips & Dudik 2008).

Outputs

MaxEnt produces a range of visual outputs such as prediction maps, table of variable importance, ROC plots, AUC plots, response curves for each variable and jackknife graphs depending on the user selection before the model is run. None of these outputs were used in this manuscript, except the table of variable importance for the cluster analysis.

Cluster Analysis

From the model outputs, once each sample was weighted by its respective AUC, each sample contained a value corresponding to each predictor variable that was used in the model, arranged in a matrix. Using a combination of the packages *vegan* and *cluster* in R, a distance matrix (pairwise dissimilarities) was calculated between samples using Euclidean distance. A hierarchical cluster was thereafter constructed by average grouping based on the distance matrix.

Chapter 4:

Section 1

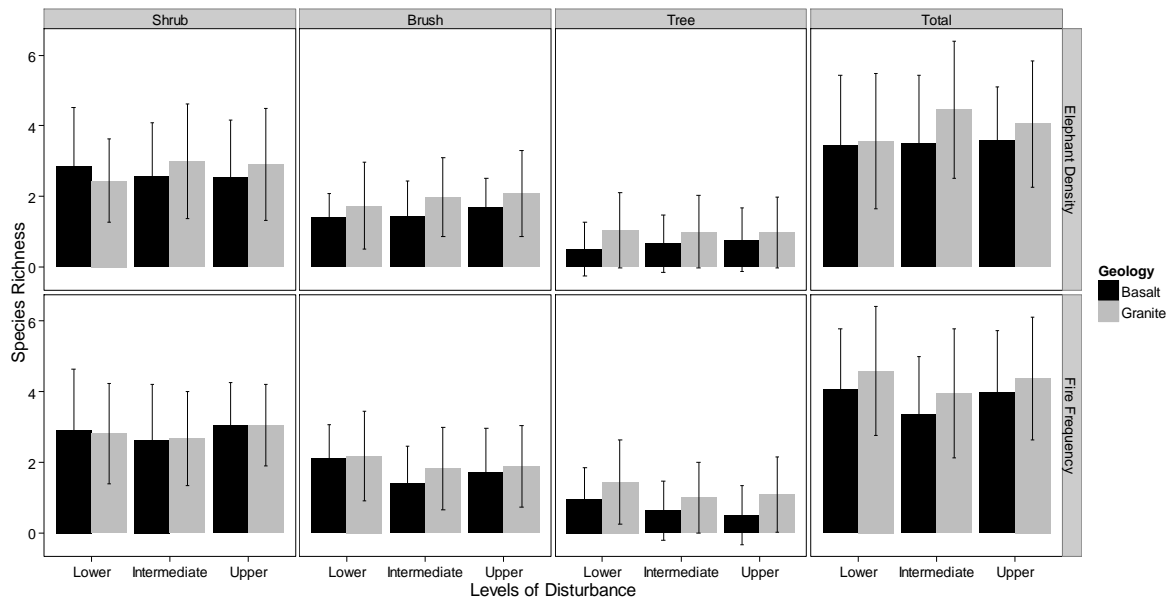


Figure S4.1 Species richness at lower, intermediate and upper 5% percentiles of top-down disturbances.

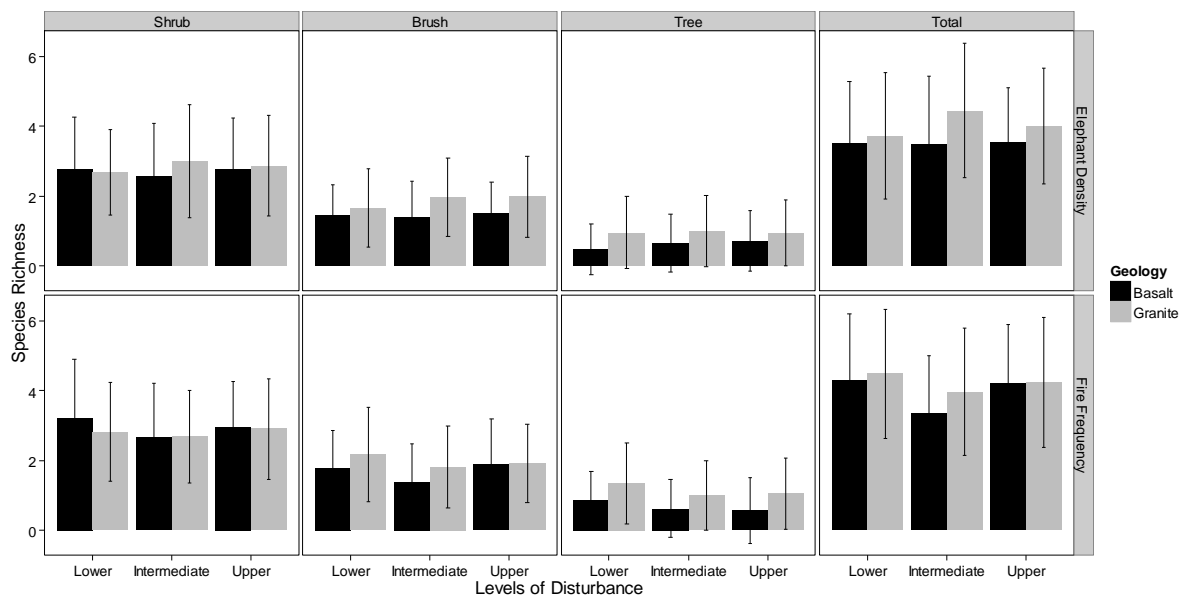


Figure S4.2 Species richness at lower, intermediate and upper 10% percentiles of top-down disturbances.

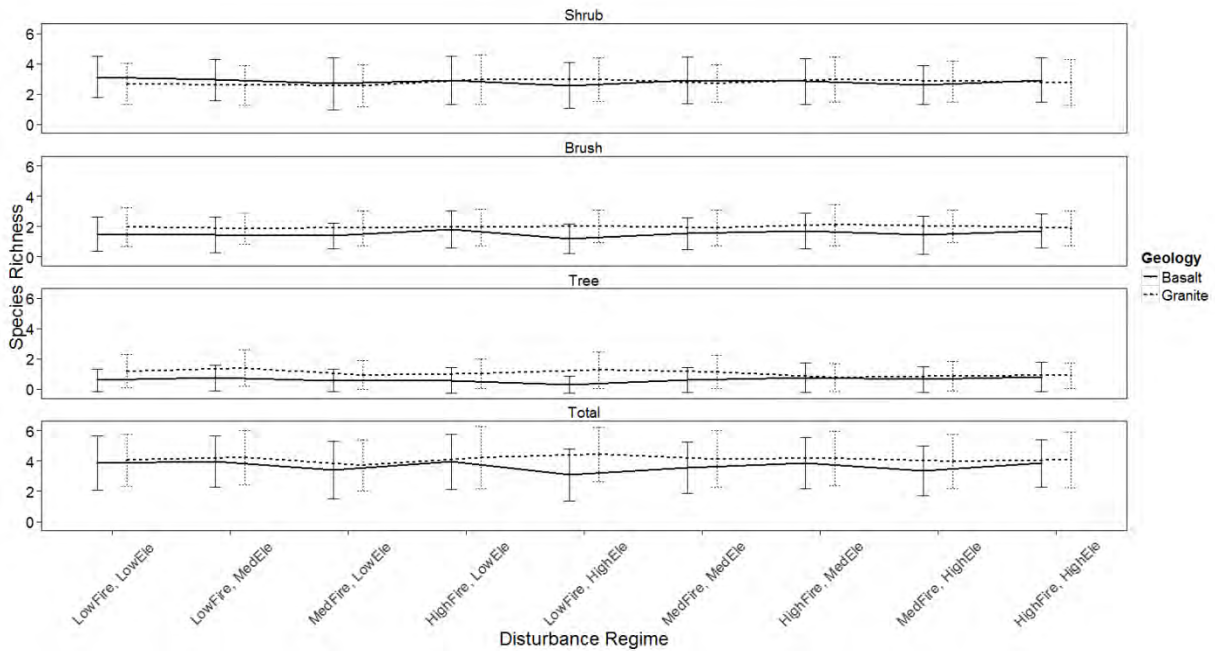


Figure S4.3. Species richness at all height classes over varying degrees of top-down disturbance and geology type.

There appears to be a substantial amount of variability within species richness across all height classes over the landscape. Initial work with species richness explored geostatistical techniques at the regional scale. Here, I tried to improve on the species richness maps at each height class as presented in Chapter 2 of this thesis using standardized approaches. However, this proved challenging as spatial autocorrelation was not as high as I suspected. This was the case for % woody cover (Figure S4.4). I suspect this may be the cause of the variation of species richness. In the Figure S4.4 below, using semi-variance as a unit of spatial variability (the distance between sites) suggests that as semi-variance increases, the similarity in brush cover decreases, however, even the closest sites were not particularly similar as seen by the large “nugget effect” in Figure 4.4. The same pattern was identified for shrub and tree (both species richness and % cover).

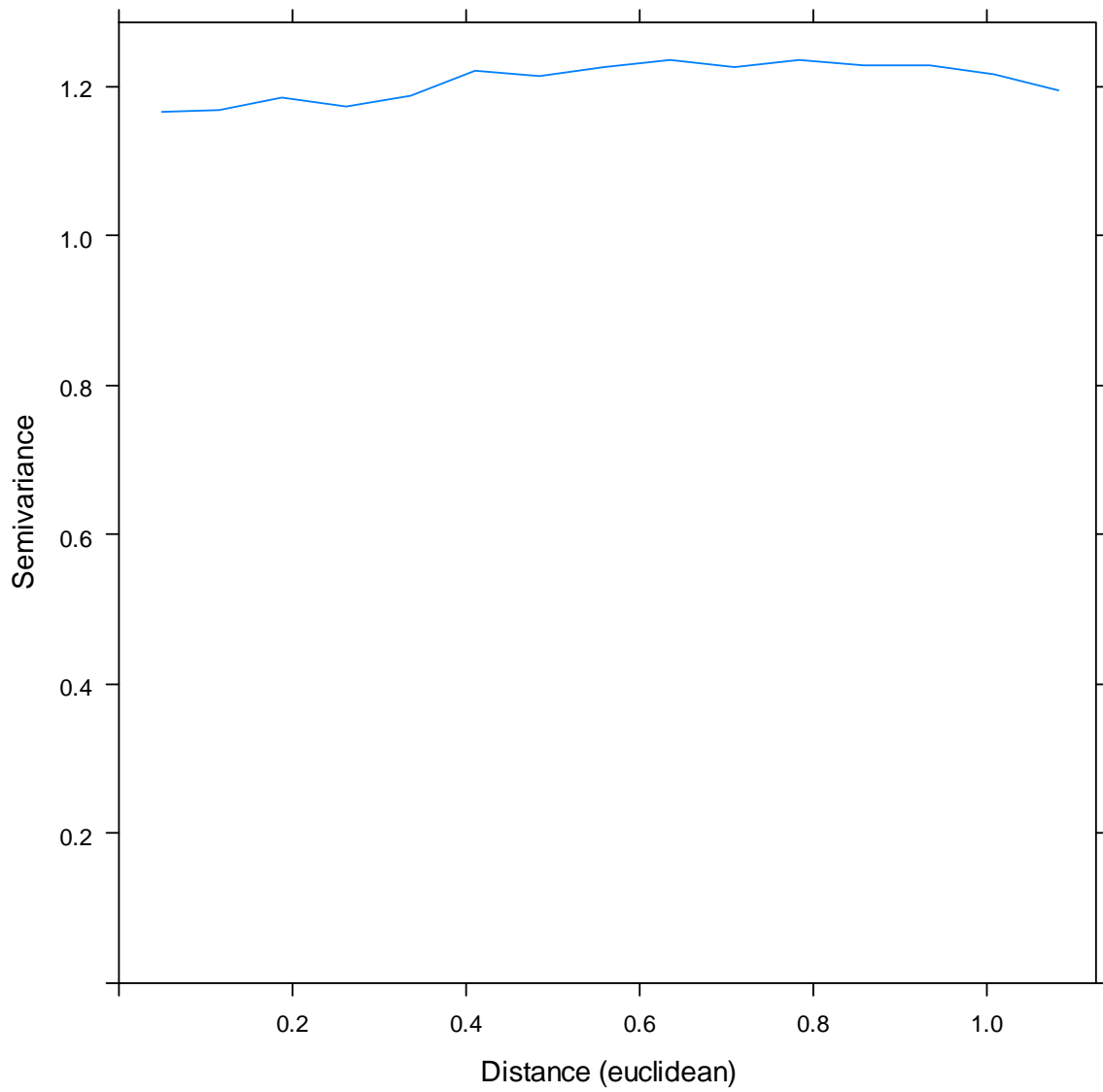


Figure S4.4. An example of the semi-variogram for brush species richness. Distance is Euclidean. Semi-variance values closer to 0 indicates site similarity.

Table. S4.1 Species lists as used in group comparison

| Shrub | Brush | Tree |
|-----------------------------------|----------------------------------|----------------------------------|
| <i>Colophospermum mopane</i> | <i>Colophospermum mopane</i> | <i>Colophospermum mopane</i> |
| <i>Combretum apiculatum</i> | <i>Combretum apiculatum</i> | <i>Combretum apiculatum</i> |
| <i>Dichrostachys cinerea</i> | <i>Grewia bicolor</i> | <i>Grewia bicolor</i> |
| <i>Terminalia sericea</i> | <i>Acacia nigrescens</i> | <i>Acacia nigrescens</i> |
| <i>Sclerocarya birrea</i> | <i>Acacia tortilis</i> | <i>Euclea divinorum</i> |
| <i>Combretum collinum</i> | <i>Euclea divinorum</i> | <i>Combretum hereroense</i> |
| <i>Combretum imberbe</i> | <i>Terminalia prunioides</i> | <i>Cissus cornifolia</i> |
| <i>Pterocarpus rotundifolius</i> | <i>Combretum hereroense</i> | <i>Gymnosporia senegalensis</i> |
| <i>Combretum hereroense</i> | <i>Philenoptera violaceae</i> | <i>Terminalia prunioides</i> |
| <i>Combretum zeyheri</i> | <i>Acacia exulvialis</i> | <i>Acacia tortilis</i> |
| <i>Euclea divinorum</i> | <i>Cissus cornifolia</i> | <i>Acacia welwitschii</i> |
| <i>Philenoptera violaceae</i> | <i>Gymnosporia senegalensis</i> | <i>Pterocarpus rotundifolius</i> |
| <i>Albizia harveyi</i> | <i>Dichrostachys cinerea</i> | <i>Acacia grandicornuta</i> |
| <i>Acacia gerrardii</i> | <i>Albizia harveyi</i> | <i>Sclerocarya birrea</i> |
| <i>Spirostachys africana</i> | <i>Acacia welwitschii</i> | <i>Maerua parvifolia</i> |
| <i>Strychnos madagascariensis</i> | <i>Spirostachys africana</i> | <i>Combretum collinum</i> |
| <i>Acacia borleae</i> | <i>Maerua parvifolia</i> | <i>Grewia hexamita</i> |
| <i>Peltophorum africanum</i> | <i>Combretum imberbe</i> | <i>Dichrostachys nyasa</i> |
| <i>Acacia grandicornuta</i> | <i>Securinega virosa</i> | <i>Albizia harveyi</i> |
| <i>Dalbergia melanoxylon</i> | <i>Combretum collinum</i> | <i>Combretum zeyheri</i> |
| <i>Securinega virosa</i> | <i>Grewia hexamita</i> | <i>Acacia exulvialis</i> |
| <i>Mundulea sericea</i> | <i>Dalbergia melanoxylon</i> | <i>Securinega virosa</i> |
| <i>Acacia exulvialis</i> | <i>Capassa tomentosa</i> | <i>Dichrostachys cinnerea</i> |
| <i>Maerua parvifolia</i> | <i>Pterocarpus rotundifolius</i> | <i>Combretum imberbe</i> |
| <i>Ormocarpum trichocarpum</i> | <i>Acacia gerrardii</i> | <i>Philenoptera violaceae</i> |
| <i>Dombeya rotundifolia</i> | <i>Ziziphus mucronata</i> | <i>Grewia flava</i> |
| <i>Ozoroa engleri</i> | <i>Dichrostachys nyasa</i> | <i>Ziziphus mucronata</i> |
| <i>Acacia nilotica</i> | <i>Mundulea sericea</i> | <i>Acacia gerrardii</i> |
| <i>Grewia flava</i> | <i>Terminalia sericea</i> | <i>Terminalia sericea</i> |

| | | |
|---------------------------------|-----------------------------------|-----------------------------------|
| <i>Pterocarpus angolensis</i> | <i>Ozoroa engleri</i> | <i>Maytenus heterophylla</i> |
| <i>Grewia bicolor</i> | <i>Sclerocarya birrea</i> | <i>Dombeya rotundifolia</i> |
| <i>Dichrostachys nyasa</i> | <i>Pterocarpus angolensis</i> | <i>Acacia robusta</i> |
| <i>Combretum mossambicense</i> | <i>Strychnos madagascariensis</i> | <i>Strychnos madagascariensis</i> |
| <i>Terminalia prunioides</i> | <i>Acacia robusta</i> | <i>Ficus sycomorus</i> |
| <i>Cassia petersiana</i> | <i>Ficus sycomorus</i> | <i>Lannea stuhlmannii</i> |
| <i>Ficus sycomorus</i> | <i>Grewia monticola</i> | <i>Ozoroa engleri</i> |
| <i>Boscia albitrunca</i> | <i>Combretum mossambicense</i> | <i>Acacia borleae</i> |
| <i>Pappea capensis</i> | <i>Grewia villosa</i> | <i>Dalbergia melanoxylon</i> |
| <i>Acacia tortilis</i> | <i>Dombeya rotundifolia</i> | <i>Albizia petersiana</i> |
| <i>Grewia monticola</i> | <i>Boscia albitrunca</i> | <i>Capassa tomentosa</i> |
| <i>Ximenia caffra</i> | <i>Euclea undulata</i> | <i>Xanthocercis zambesiaca</i> |
| <i>Acacia erubescens</i> | <i>Hyphaene natalensis</i> | <i>Acacia albida</i> |
| <i>Tephrosia cerisea</i> | <i>Ximenia caffra</i> | <i>Acacia schweinfurthii</i> |
| <i>Acacia daviesii</i> | <i>Acacia xanthophloea</i> | <i>Euphorbia ingens</i> |
| <i>Rhus guenzii</i> | <i>Ximenia americana</i> | <i>Combretum mossambicense</i> |
| <i>Hyphaene natalensis</i> | <i>Boscia foetida</i> | <i>Balanites maughamii</i> |
| <i>Ximenia americana</i> | <i>Kirkia acuminata</i> | <i>Kigelia africana</i> |
| <i>Diospyros mespiliformis</i> | <i>Ormocarpum trichocarpum</i> | <i>Croton megalobotrys</i> |
| <i>Acacia robusta</i> | <i>Acacia erubescens</i> | <i>Pterocarpus angolensis</i> |
| <i>Xanthocercis zambesiaca</i> | <i>Cassia petersiana</i> | <i>Acacia senegal</i> |
| <i>Acacia albida</i> | <i>Pappea capensis</i> | <i>Piliostigma thonningii</i> |
| <i>Schotia brachypetala</i> | <i>Xanthocercis zambesiaca</i> | <i>Bolusanthus speciosus</i> |
| <i>Commiphora africana</i> | <i>Acacia schweinfurthii</i> | <i>Pappea capensis</i> |
| <i>Euclea schimperi</i> | <i>Euphorbia ingens</i> | <i>Albizia versicolor</i> |
| <i>Piliostigma thonningii</i> | <i>Acacia albida</i> | <i>Combretum molle</i> |
| <i>Acacia schweinfurthii</i> | <i>Carissa bispinosa</i> | <i>Kirkia acuminata</i> |
| <i>Euphorbia ingens</i> | <i>Bauhinia galpinii</i> | <i>Adansonia digitata</i> |
| <i>Gymnosporia senegalensis</i> | <i>Cassia abbreviata</i> | <i>Ximenia caffra</i> |
| <i>Ziziphus mucronata</i> | <i>Combretum zeyheri</i> | <i>Boscia foetida</i> |
| <i>Capassa tomentosa</i> | <i>Acacia nilotica</i> | <i>Acacia nilotica</i> |

| | | |
|--|--------------------------------|--|
| <i>Croton megalobotrys</i> | <i>Grewia flava</i> | <i>Hyphaene natalensis</i> |
| <i>Acacia sengal</i> | <i>Diospyros mespiliformis</i> | <i>Grewia monticola</i> |
| <i>Pseudolachnostylis maprouneifolia</i> | <i>Acacia sengal</i> | <i>Acacia xanthophloea</i> |
| <i>Phoenix reclinata</i> | <i>Tephrosia cerisea</i> | <i>Spirostachys africana</i> |
| <i>Bolusanthus speciosus</i> | <i>Salvadora angustifolia</i> | <i>Carissa bispinosa</i> |
| <i>Acacia schweinfurthii</i> | <i>Euclea schimperi</i> | <i>Cassine aethiopica</i> |
| <i>Combretum molle</i> | <i>Cordea ovalis</i> | <i>Schotia brachypetala</i> |
| <i>Carissa bispinosa</i> | <i>Albizia versicolor</i> | <i>Acacia schweinfurthii</i> |
| <i>Olea africana</i> | <i>Combretum molle</i> | <i>Afzelia quanzensis</i> |
| <i>Albizia versicolor</i> | <i>Maytenus heterophylla</i> | <i>Euclea undulata</i> |
| <i>Acacia nigrescens</i> | <i>Acacia borleae</i> | <i>Garcinia transvaalensis</i> |
| <i>Cissus cornifolia</i> | <i>Croton megalobotrys</i> | <i>Ozoroa insignis</i> |
| <i>Salvadora angustifolia</i> | <i>Piliostigma thonningii</i> | <i>Ximenia americana</i> |
| <i>Balanites maughamii</i> | <i>Lannea stuhlmannii</i> | <i>Olea africana</i> |
| <i>Cordia gharaf</i> | <i>Maytenus tennispina</i> | <i>Bauhinia galpinii</i> |
| <i>Maytenus tennispina</i> | <i>Cordia gharaf</i> | <i>Gardenia volkensii</i> |
| <i>Croton pseudopulchellus</i> | <i>Androstachys johnsonii</i> | <i>Scotia capitata</i> |
| <i>Kigelia africana</i> | <i>Rhus guenzii</i> | <i>Panier curatellifolia</i> |
| <i>Acacia burkei</i> | <i>Phoenix reclinata</i> | <i>Strychnos spinosa</i> |
| <i>Cassia abbreviata</i> | <i>Cordia sinensis</i> | <i>Ormocarpum trichocarpum</i> |
| <i>Ximenia americana</i> | <i>Kigelia africana</i> | <i>Mundulea sericea</i> |
| <i>Euphorbia confinalis</i> | <i>Acacia swazica</i> | <i>Cassia petersiana</i> |
| <i>Grewia hexamita</i> | <i>Zanthoxylum capense</i> | <i>Tephrosia cerisea</i> |
| <i>Acacia welwitschii</i> | <i>Garcinia transvaalensis</i> | <i>Salvadora angustifolia</i> |
| <i>Acacia xanthophloea</i> | <i>Ozoroa insignis</i> | <i>Acacia burkei</i> |
| <i>Boscia foetida</i> | <i>Ximenia americana</i> | <i>Commiphora africana</i> |
| <i>Cordea ovalis</i> | <i>Acacia luederitzii</i> | <i>Pseudolachnostylis maprouneifolia</i> |
| <i>Lannea stuhlmannii</i> | <i>Antidesma venosum</i> | <i>Cassia abbreviata</i> |
| <i>Kirkia acuminata</i> | <i>Peltophorum africanum</i> | <i>Cordia sinensis</i> |
| <i>Androstachys johnsonii</i> | <i>Acacia grandicornuta</i> | <i>Acacia swazica</i> |
| <i>Guibourtia conjugata</i> | <i>Albizia petersiana</i> | <i>Acacia daviesii</i> |

| | | |
|--|---|---|
| <i>Commiphora gracilifrons</i> | <i>Balanites maughamii</i> | <i>Croton pseudopulchellus</i> |
| <i>Panier curatellifolia</i> | <i>Commiphora africana</i> | <i>Guibourtia conjugata</i> |
| <i>Ochoa natalensis</i> | <i>Bolusanthus speciosus</i> | <i>Neuracanthus africanus var africanus</i> |
| <i>Ficus capitata</i> | <i>Acacia burkei</i> | <i>Phoenix reclinata</i> |
| <i>Lippia javanica</i> | <i>Cassine aethiopica</i> | <i>Rhus pyroides</i> |
| <i>xeromphis obovata</i> | <i>Acacia daviesii</i> | <i>Ficus capitata</i> |
| <i>Zanthoxylum huile</i> | <i>Guibourtia conjugata</i> | <i>Lippia javanica</i> |
| <i>Rhus leptodictya</i> | <i>Acacia schweinfurthii</i> | <i>Xeromphis obovata</i> |
| <i>Rhus rehmanniana</i> | <i>Olea africana</i> | <i>Zanthoxylum huile</i> |
| <i>Acacia mellifera</i> | <i>Baphia massaiensis</i> | <i>Boscia albitrunca</i> |
| <i>Faurea saligna</i> | <i>Commiphora gracilifrons</i> | <i>Euphorbia confinalis</i> |
| <i>Gyrocarpus americanus</i> | <i>Panier curatellifolia</i> | <i>Rhus leptodictya</i> |
| <i>Croton gratissimus</i> | <i>Gardenia volkensii</i> | <i>Rhus rehmanniana</i> |
| <i>Combretum microphyllum</i> | <i>Acacia mellifera</i> | <i>Acacia mellifera</i> |
| <i>Pavetta catophylla</i> | <i>Faurea saligna</i> | <i>Faurea saligna</i> |
| <i>Salvadora persica</i> | <i>Gyrocarpus americanus</i> | <i>Gyrocarpus americanus</i> |
| <i>Trichilia emetica</i> | <i>Combretum microphyllum</i> | <i>Maytenus tennispina</i> |
| <i>Combretum collinum subsp. gazense</i> | <i>Pavetta catophylla</i> | <i>Antidesma venosum</i> |
| <i>Thilachium africanum</i> | <i>Salvadora persica</i> | <i>combretum collinum subsp. gazense</i> |
| <i>Maytenus heterophylla</i> | <i>Trichilia emetica</i> | <i>Thilachium africanum</i> |
| <i>Albizia petersiana</i> | <i>Combretum collinum subsp. gazense</i> | <i>Peltophorum africanum</i> |
| <i>Grewia villosa</i> | <i>Thilachium africanum</i> | <i>Diospyros mespiliformis</i> |
| <i>Adansonia digitata</i> | <i>Neuracanthus africanus var africanus</i> | <i>Grewia villosa</i> |
| <i>Afzelia quanzensis</i> | <i>Rhus pyroides</i> | <i>Euclea schimperii</i> |
| <i>Bauhinia galpinii</i> | <i>Rhus leptodictya</i> | <i>Rhus guenzii</i> |
| <i>Euclea undulata</i> | <i>Rhus rehmanniana</i> | <i>Cordia gharaf</i> |
| <i>Cordia sinensis</i> | <i>Ochoa natalensis</i> | <i>Acacia erubescens</i> |
| <i>Acacia swazica</i> | <i>Ficus capitata</i> | <i>Androstachys johnsonii</i> |
| <i>Cassia abbreviata</i> | <i>Lippia javanica</i> | <i>Croton gratissimus</i> |
| <i>Scotia capitata</i> | <i>xeromphis obovata</i> | <i>Ximenia americana</i> |
| <i>Zanthoxylum capense</i> | <i>Zanthoxylum huile</i> | <i>Baphia massaiensis</i> |

| | | |
|---------------------------|--|-----------------------------------|
| <i>Baphia massaiensis</i> | <i>Pseudolachnostylis maprouneifolia</i> | <i>Commiphora gracilifrondosa</i> |
| <i>Strychnos spinosa</i> | <i>Schotia brachypetala</i> | |
| <i>Acacia luederitzii</i> | <i>Croton pseudopulchellus</i> | |
| <i>Antidesma venosum</i> | <i>Cassia abbreviata</i> | |
| <i>Cassine aethiopica</i> | <i>Afzelia quanzensis</i> | |
| <i>Gardenia volkensii</i> | <i>Adansonia digitata</i> | |

Section 2

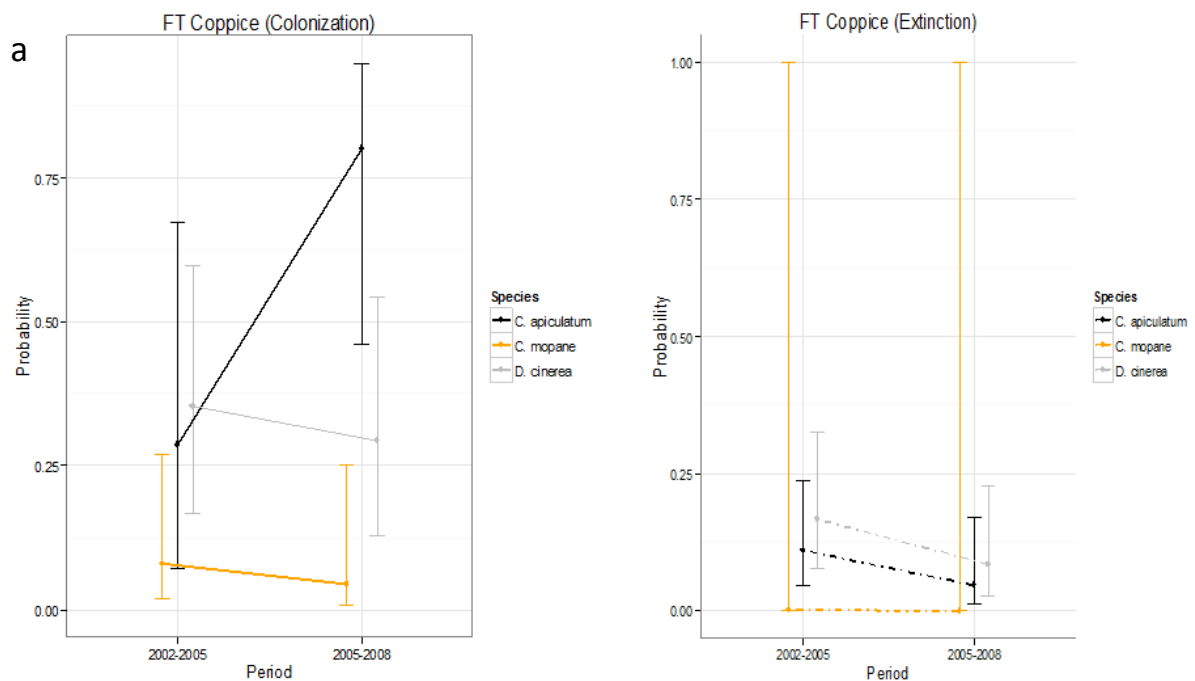
The work presented here is based on “Scholtz, R., Duckworth, G. D., Kiker, G. A. & Smit, I. P. J., 2014, 'On the use and applications of large scale survey data over long periods: A case from a well-managed protected area in a semi-arid savanna', *Unpublished manuscript*”.

This manuscript attempts to identify change in woody species distribution over a 6 year period within the KNP landscape using repeat surveys. Six commonly occurring species were chosen based on their broad distributions (Kiker et al. 2014, Chapter 2 of this thesis) and for the following reasons; two species are known to be highly utilized by elephants; marula (*Sclerocarya birrea*), knobthorn (*Acacia nigrescens*) (Viljoen 1995; Shannon et al. 2008), two potential bush-encroaching species; sicklebush (*Dichrostachys cinera*), red bush willow (*Combretum apiculatum*) (Govender 2014) and two species of interest; mopane (*Colophospermum mopane*) due to its dominance in northern KNP and some concern that climate change may drive its distribution southwards, and silver clusterleaf (*Terminalia sericea*) due to concerns of increase in abundance of this relatively unpalatable species (Shannon et al. 2011). These species were placed into two groups for the study; multi-stemmed species (mopane, red bush willow and sicklebush) (or “coppice” group) and single-stemmed species (marula, knobthorn and silver cluster leaf (or “iconic” group).

Data were extracted from the wVCA assessments for the years 2002, 2005 and 2008 (Zambatis 2005). The survey year 1996 was excluded as the number of sites was too low (n=103) compared to the other survey years (n=442, 462 and 445 in 2002, 2005 and 2008 respectively). All identified individuals were categorized into one of three height class categories; Fire-trap (FT) <4m in height (adapted from Wessels et al. 2011), Elephant-trap (ET) $\geq 4\text{m} \leq 8\text{m}$ (Asner and Levick 2012) and Escaped (ES; >8m) (Asner and Levick 2012). The fire trap can be loosely defined as vegetation that is caught within the flame zone. Vegetation within the “elephant-trap”, as the name suggests, is vegetation of a specific height that is often targeted by elephants for browse. And “escaped” class loosely translates to vegetation that has a higher probability of escaping the synergistic effects of fire and elephants. Presence/absence matrices were developed for each species and group per height class combination throughout 53 landtypes within the study area. Assessing vegetation change was

conducted in an occupancy framework (Mackenzie et al. 2003) with particular interest in the dynamic components (colonization and extinction).

Unfortunately, sites were not sampled each survey year within the wVCA dataset, which meant that an analysis of each site through each time period could not be conducted. Therefore, all wVCA sites were aggregated up to the landtype level which became the primary “site” in terms of the analyses. However, the scale at which the analyses was conducted resulted in many probability predictions of both dynamic components (colonization and extinction) equal to 0 or 1, which was accompanied by confidence intervals between 0 and 1 (Figures S4.4-S4.6). In summary, these estimates proved uninformative in predicting change in the dynamic components over time and are most likely attributed to sparse data as suggested by Welsh, Lindenmayer & Donnelly (2013).



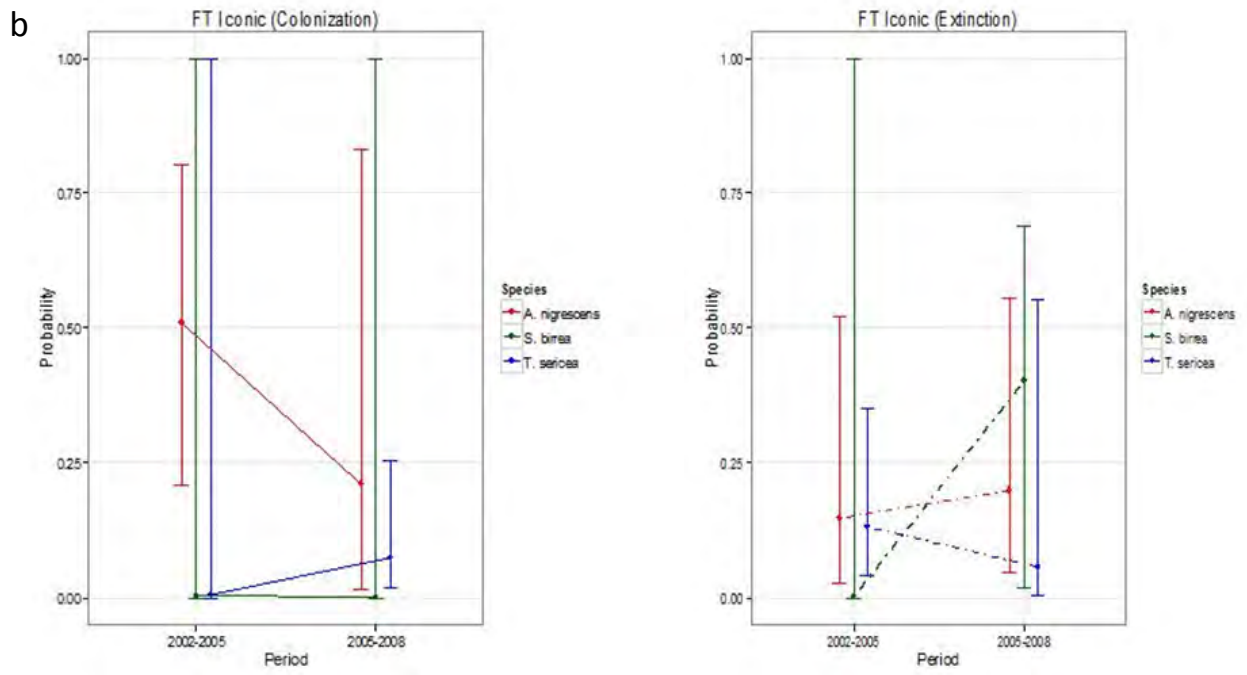
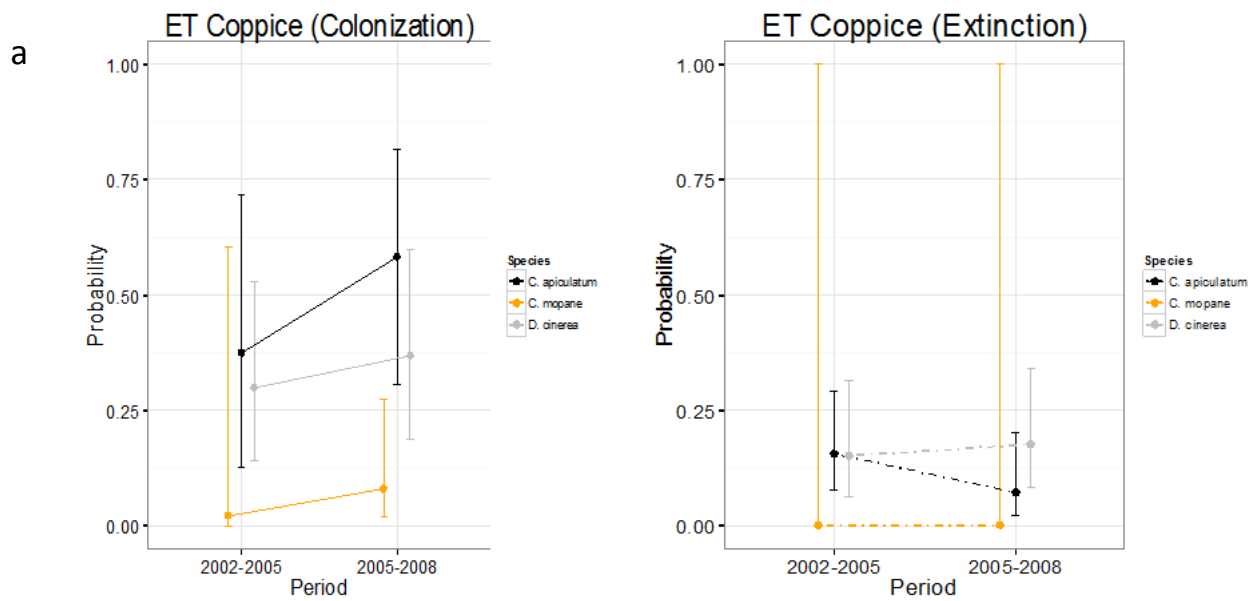


Figure S4.4. a) coppice group FT col-ext rates and b) iconic group FT col-ext rates



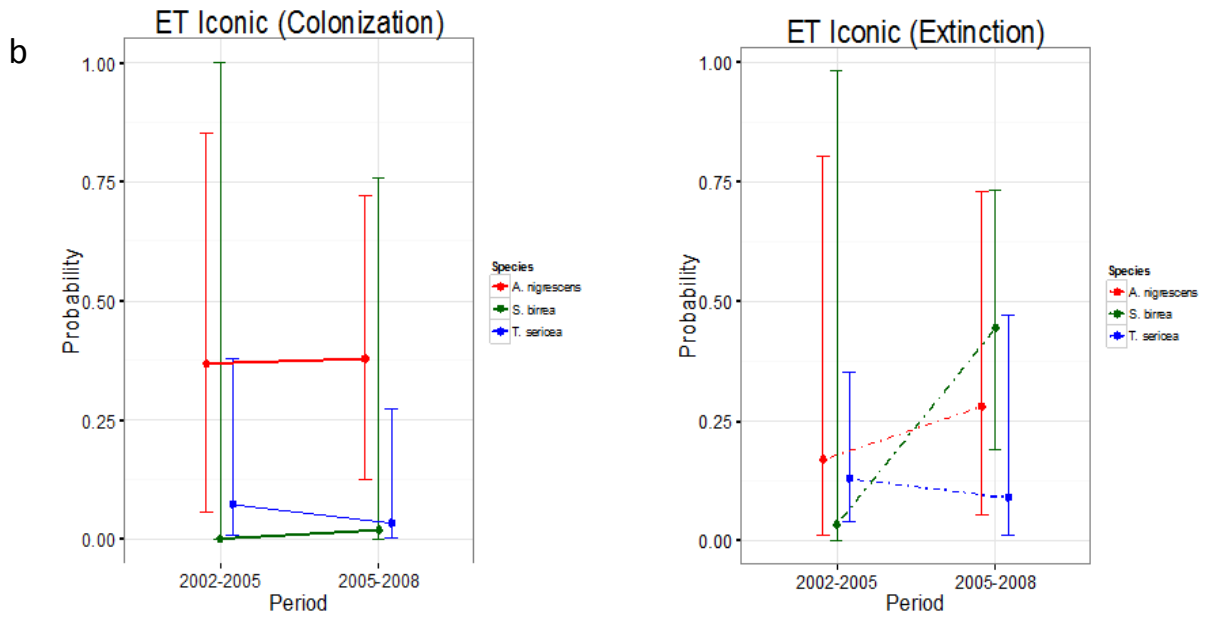
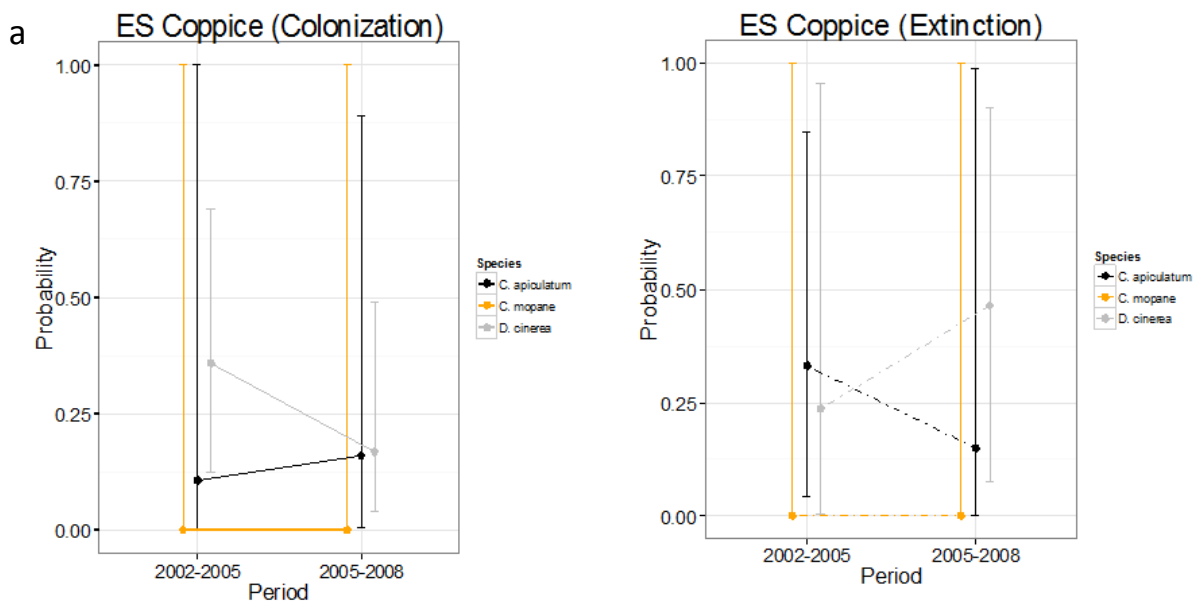


Figure S4.5 a) coppice group ET colext rates and b) iconic group ET colext rates



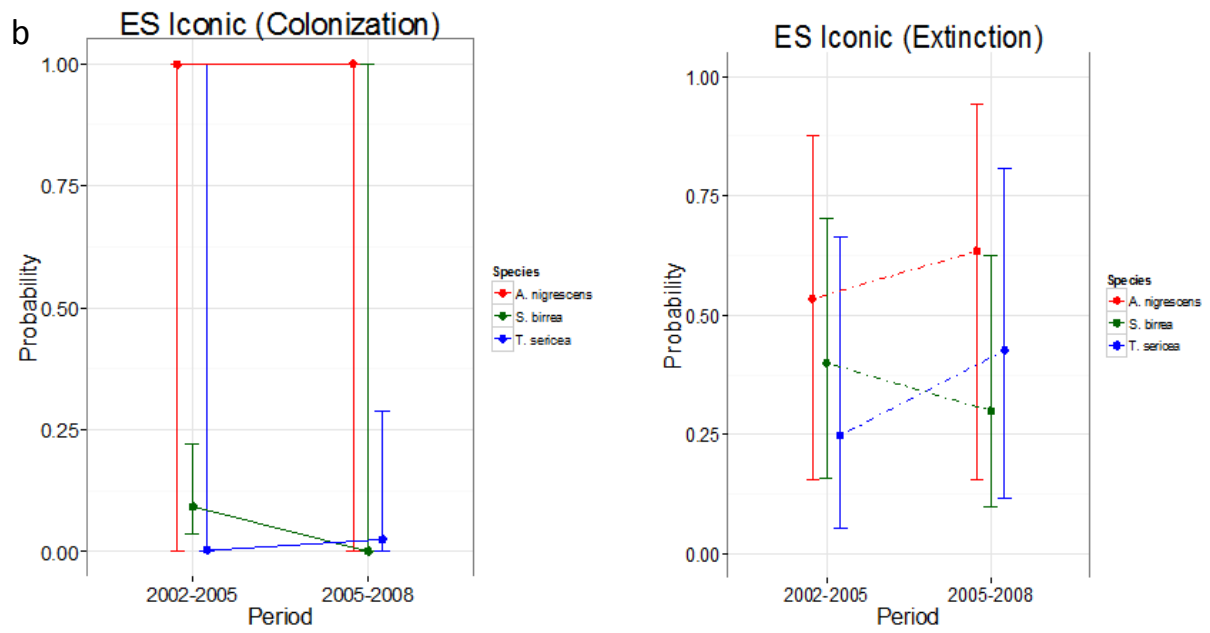


Figure S4.6 a) coppice group ES colext rates and b) iconic group ES colext rates

Chapter 5:

Appendix 5.1

Table S5.1. Diagnostic Results from Gelman-Rubin test.

| R-hat (upper C.I.) | Height class | | |
|--------------------|--------------|-------------|-------------|
| | Shrub | Brush | Tree |
| Predictor | | | |
| geoBasalt | 1 (1) | 0.99 (0.99) | 1 (1.005) |
| geoGranite | 0.99 (0.99) | 1 (1) | 1 (1.005) |
| Rainfall | 1 (1) | 0.99 (1) | 1 (1.005) |
| Elephant density | 1 (1) | 1 (1) | 0.99 (0.99) |
| FireFreq | 0.99 (1) | 1 (1) | 0.99 (1) |

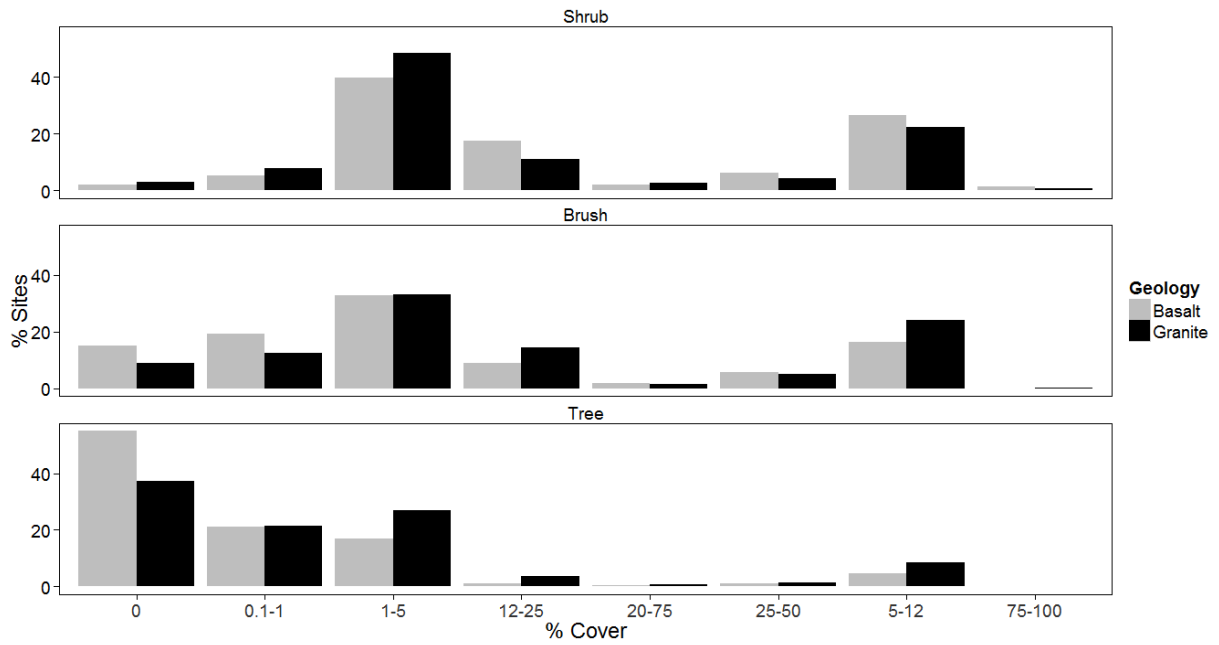


Figure S5.1. Percentage sites with estimated specific woody cover per height class

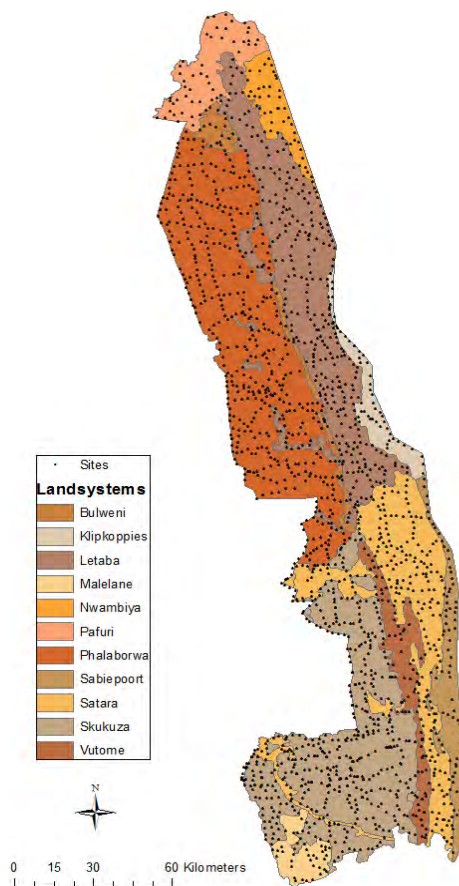


Figure S5.2. Kruger National Park, South Africa showing land systems (Venter et al. 2003) and sampling sites

Appendix 5.2

The most critical parts when using the zero-one beta regression for this chapter are the following:

Uninformative priors are distributed in the following manner: $\beta_0 \sim N(0, 10^{-3})$ at all height classes, within the following simplified equation taken from Lui and Kong (2014).

$$f(x) = \begin{cases} p & \text{if } y = 0 \\ (1-p)q & \text{if } y = 1 \\ (1-p)(1-q)\text{Beta}(\alpha_1, \alpha_2) & \text{if } y = \varepsilon(0,1) \end{cases}$$

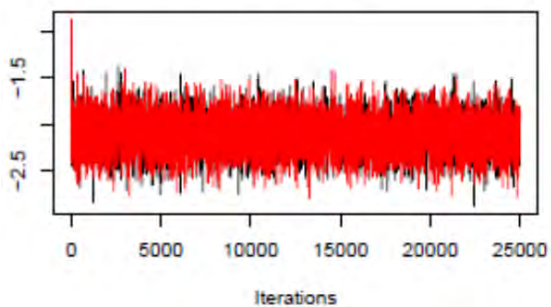
P is the probability of $y = 0$ and q is the conditional probability $\Pr(y = 1|y \neq 0)$. α are shape parameters of which the default was used.

Initial parameters did not require adjustment as model convergence was achieved under the model parameters as described in the methods section in Chapter 5. These were; the number of iterations per chain in the MCMC sampling was 25 000 with a thinning period of 5, and a burn-in of 5000, over 3 chains (i.e. 3 sets of initial conditions). Model fit was assessed using a combination of plotting tools and MCMC convergence diagnostics. The diagnostic test, Gelman and Rubin (Cowles & Carlin, 1996) as well as trace and density plots were used to assess model convergence and mixing, by visual inspection. The Gelman and Rubin test calculates within-chain and between-chain variance. This is called the potential scale reduction factor. Generally, a mean R-hat value equal or below 1.1 suggests model convergence. Diagnostic testing provided evidence to suggest the model parameters (i.e. number of iterations) are sufficient to draw inferences from the posterior distribution. Beta coefficients with their 95% credible interval (C.I.) (Bayesian analogue for confidence interval) for each predictor variable can be assessed by looking at their mean value in relation to zero where credible interval overlapping zero suggests little influence. DIC (Deviance Information Criterion), the Bayesian analogue for AIC, was not used to assess model fit, as model selection was not done in this exercise.

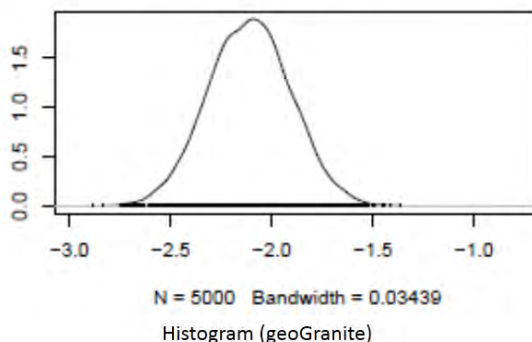
Model Convergence

An example of the traceplots and histograms for brush cover.

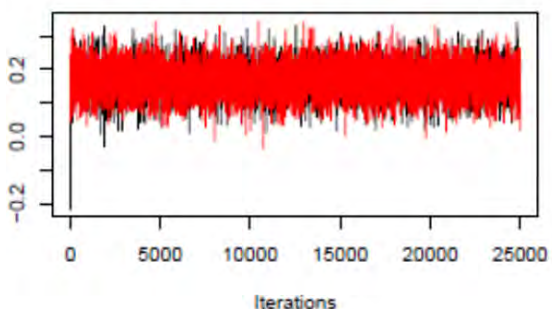
Traceplot (geoBasalt)



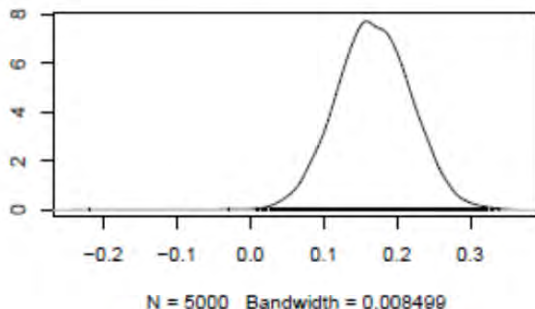
Histogram (geoBasalt)



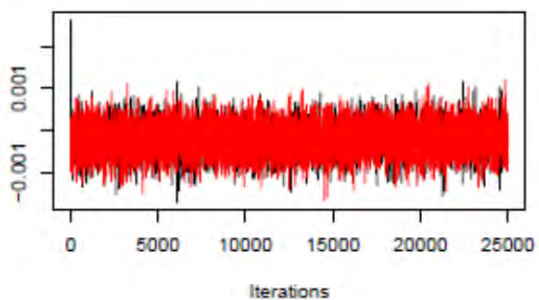
Traceplot (geoGranite)



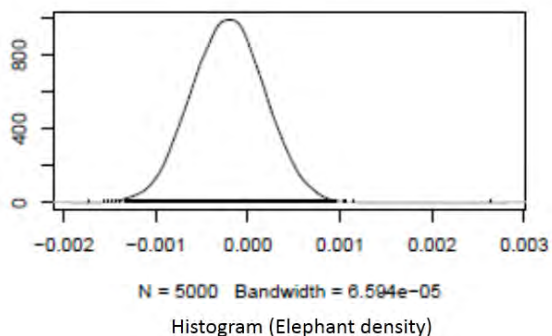
Histogram (geoGranite)



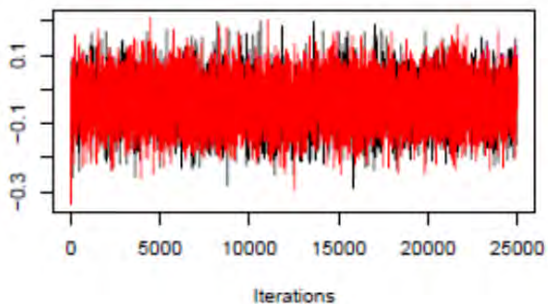
Traceplot (Rainfall)



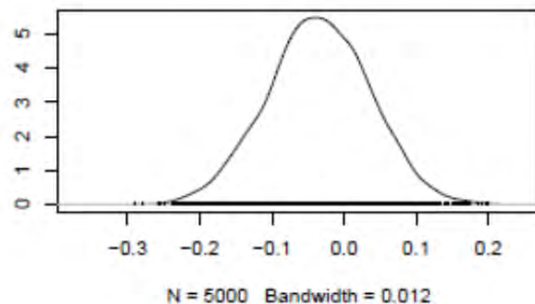
Histogram (Rainfall)



Traceplot (Elephant density)



Histogram (Elephant density)



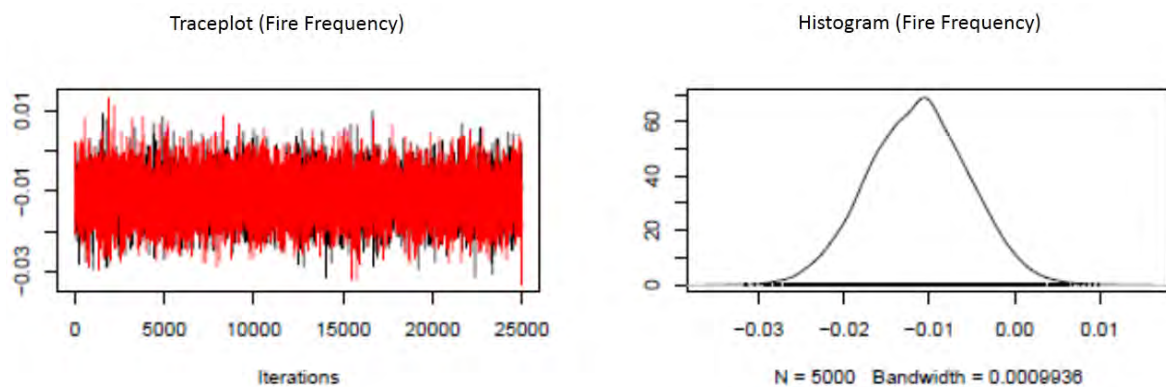


Figure S5.3. Traceplots and histograms showing model convergence for brush cover

References

- Cowles, M.K. & Carlin, B.P. (1996) Markov chain Monte Carlo convergence diagnostics: a comparative review. *Journal of the American Statistical Association*, 91, 883-904.
- Liu, F. & Kong, Y. (2014) zoib: an R package for Bayesian Inference for Zero/One Inflated Beta Regression Model.