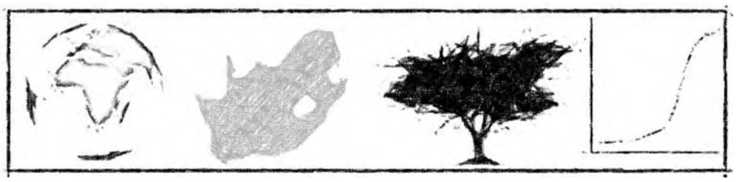
Woody plant encroachment in arid and mesic South African savanna-grasslands: same picture, different story?



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Abstract

Woody plant encroachment in South Africa's savanna-grasslands has been considered a rangeland management problem since the early 1900s. This phenomenon, which has been observed globally, is particularly important in Africa given the extent of tropical grassy biomes on the continent and their importance for rural livelihoods. In this study, local and regional scale approaches were used to investigate woody cover change in South Africa across the important savanna-grassland rainfall threshold of 650 mm mean annual precipitation (MAP). The aim was to test this threshold using remote sensing and demographic surveys in order to better understand the patterns, mechanisms and drivers of encroachment. Rates of encroachment and population demographics of *Vachelia karroo* were compared at arid and mesic savanna sites in the Eastern Cape, using time-series analysis of historical aerial photographs in conjunction with field surveys. Changes in the extent of woodland vs. grassland were then quantified at a national scale (1990–2013) by combining optical and synthetic aperture radar remote sensing data. This produced the first map of woodland-grassland shifts for South Africa and provided the basis for a spatially explicit investigation of the key drivers of change. The local studies revealed higher rates of encroachment at mesic sites than at arid sites, with a correlation between drought and rate of encroachment at the arid site. *Vachelia karroo* seedlings and stunted saplings were more prevalent at mesic sites than at arid sites and the growth form of adult trees differed significantly between sites. The national remote sensing investigation showed that woodland replaced grassland in over 5% of South Africa's savanna-grasslands between 1990 and 2014, at rates consistent with other global and regional studies. Spatially explicit models showed a pattern of incremental expansion of woodland along a 'tree front' and complex relationships between woodland increase and fire, rainfall, terrain ruggedness and temperature. Overall, the local and regional scale findings of this work highlight the importance of the savanna rainfall threshold (~650 mm MAP) and the presence / absence of fire in understanding savanna dynamics and woody cover change in the context of global drivers such as elevated atmospheric CO_2.

Table of Contents

List of figures

List of tables

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Chapter 1: General Introduction

Woody plant increase in savanna-grasslands

Woody plant encroachment in the savannas and grasslands of southern Africa has been the focus of rangeland management and ecological research since the early 1900s (Trollope, 1980; Teague & Smit, 1992; Hoffman & Ashwell, 2001; O'Connor *et al.*, 2014; Puttick *et al.*, 2014a; Russell & Ward, 2014a). The tree or shrub genera responsible vary, but prominent in the literature are indigenous Acacia species (now *Vachellia* and *Senegalia*) (Midgley & Bond, 2001; Britz & Ward, 2007; O'Connor et al., 2014). Increases in woody plant cover have been observed globally in tropical grassy biomes and have been attributed to a wide range of interacting factors (Scholes & Archer, 1997; Van Auken, 2000; Eldridge *et al.*, 2011; Parr *et al.*, 2014; Lehmann & Parr, 2016; Stevens *et al.*, 2017). These include rainfall and drought (Roques *et al.*, 2001; Fensham *et al.*, 2005), altered fire regimes (Roques *et al.*, 2001; Archibald *et al.*, 2010a), extirpation of wild browsers (O'Connor et al., 2014), changes to grazer : browser ratios (Sankaran et al., 2008; Wigley et al., 2010; Barger et al., 2011), soil nutrients and soil structure (Kraaij & Ward, 2006; Sankaran et al., 2008) and reduced fuel wood collection (Russell & Ward, 2014b). More recently, global drivers such as climate change (including temperature, rainfall and evaporation), increased atmospheric CO_2 and nitrogen deposition have been implicated in the trend of increasing woody plant cover (Bond & Midgley, 2000, 2012; Eamus & Palmer, 2007; Sankaran *et al.*, 2008; Buitenwerf *et al.*, 2012; Russell & Ward, 2014b; Devine *et al.*, 2017), with support from CO_2 enrichment experiments (Polley et al., 2003; Kgope et al., 2010) and remote sensing approaches (Donohue *et al.*, 2013; Poulter *et al.*, 2014; Hall & Scanlon, 2015).

In contrast, a number of recent papers report on decreasing woody plant cover or loss of large trees in some African protected areas – citing increased fire frequency and herbivore pressure (elephants in particular) as the drivers (Eckhardt *et al.*, 2000; Asner *et al.*, 2009; Staver *et al.*, 2011a); and in Australian savannas with drought as the key driver (Fensham *et al.*, 2009). Large-scale wood harvesting (for timber or charcoal) or land clearing (for agriculture) is also a well-documented phenomena in parts of Africa's savanna biome and complicates the interpretation of regional or continent wide trends in tree cover (Puttick *et al.*, 2011; Mitchard & Flintrop, 2013; Fisher *et al.*, 2015; Ryan *et al.*, 2016; Brandt *et al.*, 2017).

Key concepts and frameworks

Various studies of savanna determinants, function and dynamics have proposed thresholds of between the 600–1000 mm MAP as being important for classifying savannas into arid and mesic types (Higgins *et al.*, 2000; Sankaran *et al.*, 2005; Hirota *et al.*, 2011; Lehmann *et al.*, 2011; Staver *et al.*, 2011a). Archibald & Hempson (2016) describe a gradual transition from herbivore consumption to fire consumption along a rainfall-soil nutrient gradient, and show that, between 400 and 1000 mm MAP, both are capable of controlling biomass in grassy biomes in Africa (but seldom both at any specific location). At mesic sites sufficient soil moisture is present to support both woody plant establishment (i.e. seedling establishment) and high levels of grass production (which provides fuel for fires), and both fire or herbivory act to limit woody plant recruitment (i.e. release of already established plants) (O'Connor, 1995a; Higgins *et al.*, 2000; Sankaran *et al.*, 2005; O'Connor *et al.*, 2014). Above 800 mm MAP it has been shown that fire alone can play a key role as a landscape level disturbance and limit woody plant recruitment (Bond & Van Wilgen, 1996; Scholes & Archer, 1997; Bond *et al.*, 2003; Scholes, 2003; Lehmann *et al.*, 2011). At arid sites low moisture availability limits the opportunities for establishment of woody plants and limits grass production (Higgins *et al.*, 2000; Lehmann *et al.*, 2011). Recruitment at arid sites is generally limited by herbivory since fire is infrequent and / or of low intensity (due to limited fuel load production) (Higgins *et al.*, 2000; Midgley *et al.*, 2006; Lehmann *et al.*, 2011; O'Connor *et al.*, 2014). Low moisture availability at arid sites is also thought to reduce maximum potential canopy cover (Sankaran *et al.*, 2005). Some authors (e.g. Balfour & Midgley, 2008) use the term release to refer to the growth of stunted individuals in to adults, following a disruption to the disturbance regime; I follow the terminology of Higgins *et al.* (2000) and refer to both of these processes as recruitment.

Herbivory

Grazing pressure can reduce the grass layer and increase the depth to which water infiltrates after rain-fall events; potentially aiding woody plant establishment at arid sites (Teague & Smit, 1992; Kraaij & Ward, 2006). In more mesic areas sustained domestic grazing pressure can reduce the grass layer leading to lower fuel loads and hence lower fire intensity and / frequency (Trollope, 1980; Midgley *et al.*, 2006; O'Connor *et al.*, 2014); potentially enhancing the recruitment of woody saplings that are temporarily released from the "fire trap", allowing them to grow into more fire resistant adult trees (Higgins *et al.*, 2000; Balfour & Midgley, 2008; Sankaran *et al.*, 2008; O'Connor *et al.*, 2014). Browsing pressure (predominantly by domestic goats, but also by free ranging indigenous antelope) acts directly on the woody component of the vegetation, limiting growth and potentially shaping savanna structure (Teague, 1983; Hester *et al.*, 2006; Mopipi *et al.*, 2009). Even a temporary reduction in browsing pressure can release woody plants from the "browse trap" and promote woody plant recruitment (Staver & Bond, 2014).

Drought

For some arid South African savannas the successful establishment of acacia seedlings is thought to occur mostly in above-average rainfall years, as evidenced by cohorts in the demographic profile and watering experiments (O'Connor, 1995a; Kraaij & Ward, 2006). But when above average rainfall follows a drought—during which the grass layer has been reduced by sustained grazing and trampling–successful seedling establishment can lead to new cohorts of woody plants and a future increase in woody cover (Aucamp *et al.*, 1983; O'Connor & Crow, 1999; February *et al.*, 2013). Or, as O'Connor and Crow (1999, page 29) put it, "…a window of opportunity for release of the woody component because of reduced fire and competition is created".

Soils

Soil characteristics can also be important in determining the tree-grass ratios in savannas. Seasonal water logging and shallow hard B-horizons (e.g. calcrete & silcrete) can limit root growth of woody plants and favour shallow rooted grasses (Huntley & Walker, 1982; Fey, 2010). Sandy soils can allow for rapid infiltration of rainwater thus aiding the deeper rooted woody plants (by limiting competition with shallow rooted grasses) (O'Connor, 1995a; Britz & Ward, 2007). This is compounded by the generally lower nutrient status of sandy soils which result in lower grass production than more nutrient rich fine textured soils; resulting in potentially lower fuel loads and lower fire intensities (Scholes & Archer, 1997; Sankaran *et al.*, 2008; O'Connor *et al.*, 2014).

Atmospheric CO_2

Devine *et al.*(2017) reviewed the global and local drivers of woody encroachment in African savannas and argued that local effects such as fire and herbivory are unlikely to explain the observed continent-wide changes (as noted by Bond *et al.*, 2003; Bond & Midgley, 2012). The authors propose a two-system conceptual model of CO_2 driven woody encroachment in arid vs. mesic grassy biomes (Figure 1) (Devine *et al.*, 2017). In arid systems, where maximum tree cover and seedling establishment is limited by moisture availability, the increase in water use efficiency caused by CO_2 enrichment (Polley *et al.*, 2003; Eamus & Palmer, 2007; Kgope *et* *al.*, 2010) reduces this limitation and promotes woody plant establishment and contributes to woody encroachment. In mesic systems, where disturbances (i.e. fire and herbivory) typically limit woody plant growth, CO_2 enrichment allows for additional carbon allocation to roots facilitating more rapid recovery after disturbance and consequently promotes woody plant recruitment and contributes to woody encroachment (Bond & Midgley, 2000, 2012; Buitenwerf *et al.*, 2012).

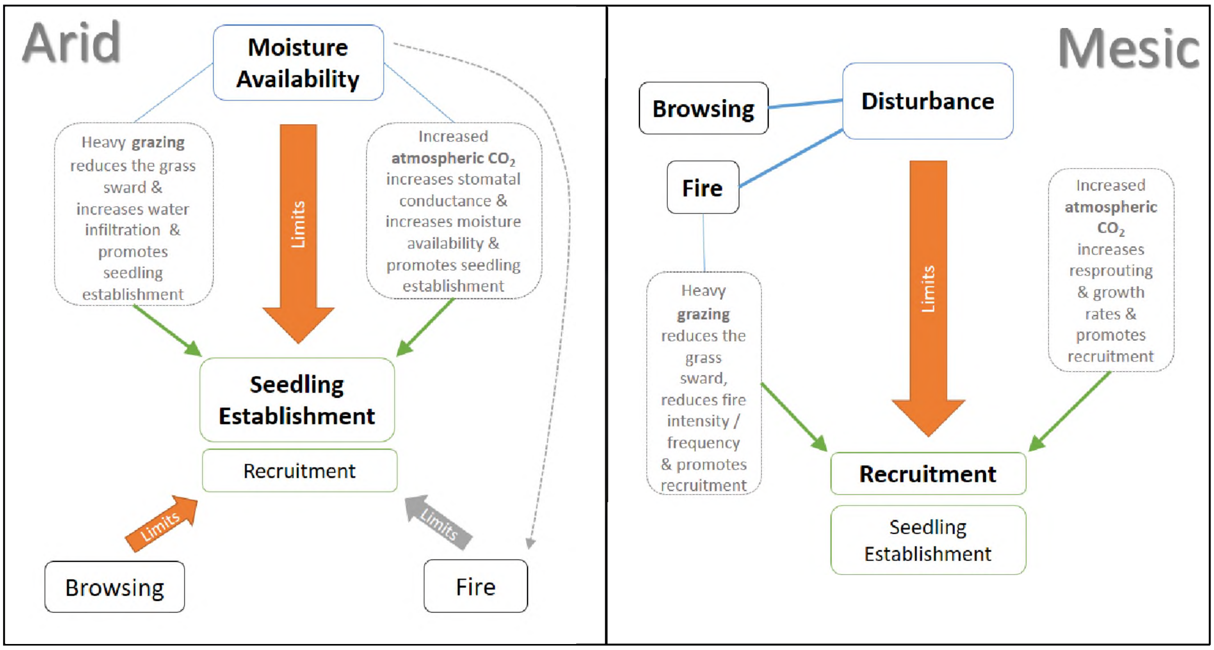

Figure 1. Conceptual diagram of the key mechanisms of woody plant encroachment in arid vs. mesic grassy biomes. At arid sites (< ~650 mm MAP) moisture availability is the key limit on woody plant seedling establishment and browsing (by large mammals) limits recruitment of seedling to adults; fire can be an important disturbance factor but is usually limited by low fuel levels and grazing can enhance seedling establishment by reducing competition from grasses. Increased atmospheric CO_2 reduces water stress and promotes seedling establishment and woody encroachment. At mesic sites (> ~650 mm MAP) fire and browsing control woody plant recruitment as seedling establishment is not limited by moisture availability. Increased atmospheric CO_2 increases root carbon stores and promotes recruitment of woody species (adapted from Higgins *et al.* (2000); Devine *et al.* (2017) & Lehmann *et al.* (2014)).

South African context and terminology

The savannas and grasslands of South Africa occupy the northern and eastern portions of the country (Figure 2 & Figure 3) and are described as distinctive biomes in the vegetation map of South Africa, Swaziland and Lesotho (Rutherford *et al.*, 2006a). The majority of this region fits the general definition of the tropical grassy biome (Parr *et al.*, 2014; Lehmann & Parr, 2016) in that the grass sward is dominated by C_4 species and tree cover ranges from 0–80%. However, the grasslands of the central plateau and Drakensberg regions of South Africa are found at elevations of over 1400 m, and in some situations are dominated by C_3 grasses (Mucina *et al.*, 2006a). In addition, low temperatures and frost are thought to limit tree recruitment in some high elevation regions (Wakeling *et al.*, 2012, 2015). From a global perspective, South African savannas fall in the lower end of the rainfall envelope described for savannas (180–2500 mm MAP) (Lehmann *et al.*, 2011, 2014; Staver *et al.*, 2011a) occurring between 180–1200 mm MAP; with 50% of the extent receiving less than 500 mm MAP. I use the term savanna-grassland to refer collectively to grassy biomes in South Africa.

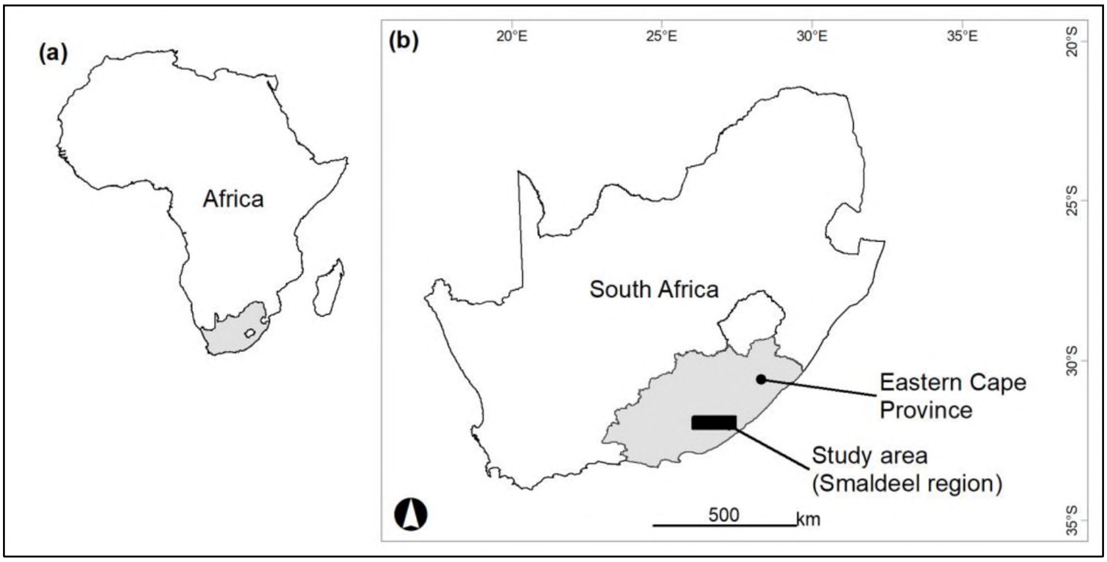

Figure 2. Location of South Africa (a), the Eastern Cape Province and the Smaldeel region in which the field surveys were conducted (b).

Encroachment

Globally, woody plant increase in grassy biomes is referred using a wide range of related terms: bush encroachment, woody thickening, shrub invasion and various combinations of these terms (reviewed by Van Auken, 2009; Eldridge *et al.*, 2011; O'Connor *et al.*, 2014). Increase in size of existing shrubs and trees and the increase in number of stems of individual plants are also considered under these broad terms (Trollope, 1980; O'Connor *et al.*, 2014). The term bush encroachment is commonly used in South Africa to refer to the increase in both shrub and tree densities in savannas, and occasionally to the invasion of grasslands by shrubs and trees (reviewed by O'Connor *et al.*, 2014). The focus is usually on native woody plant increase in these biomes; alien invasive plants are specifically excluded from consideration in most cases (but see Nackley *et al.*, 2017). In this thesis I treat the terms bush encroachment and woody plant increase as equivalent and focus primarily on the increase in woody canopy cover – that result from the establishment and recruitment to adulthood of tree species in South Africa's grassy biomes. In Chapter 4 in particular, I use the term "woodland expansion" to refer to the landscape level increase in tree canopy cover in previously open savannas and grasslands.

Previous efforts to quantify woody plant increases

Despite the attention of many rangeland scientists and ecologists, only a very small portion of the country has been sampled and a reliable estimate of bush encroachment has yet to be published for South Africa (O'Connor *et al.*, 2014). A comprehensive report on the state of land degradation in South Africa, based on extensive workshops and interviews (Hoffman & Ashwell, 2001), reported that 154 of the 367 magisterial districts of the country were affected by bush encroachment. The study was largely focussed on perceptions of degradation and did not attempt to measure the extent or rate of bush encroachment. It does, however, provide a good indication of the extent of the phenomenon nationally. An analysis of the vegetation type descriptions in the Vegetation of South Africa, Lesotho and Swaziland (Mucina & Rutherford, 2006) revealed that bush encroachment is most often noted within the Sub Escarpment Savanna, Central Bushveld and Eastern Kalahari Bushveld bioregions (Figure 3). No comparable estimates of the extent of bush encroachment within each bioregion were made, so the information cannot be used in a national estimate.

Vachelia karroo

Chapters 2 and 3 of this thesis focus on savanna-grasslands of Eastern Cape Province of South Africa (Figure 2). The tree component of savannas in Eastern Cape is dominated by *Vachelia karroo* (Hayne) Banfi & Galasso (previously *Acacia karroo*) a wide spread, woody shrub or tree in South Africa, known for its wide range of growth forms (Ross, 1971) (Figure 4). In particular, fire and herbivory are thought to drive tree growth form variation *Vachellia* species in savanna landscapes; in fire-prone environments a "pole-like" architecture is beneficial while in fire-free, herbivore dominated savannas a short, "cage-like" architecture is beneficial (Archibald & Bond, 2003; Staver *et al.*, 2012). The striking morphological differences between populations at different localities, together with the results of common garden experiments have lead numerous authors to segregate the species in various ways (reviewed by Taylor & Barker, 2012). *V. karroo* has been described as a "ring" species (Brain *et al.*, 1997), but with unusually strong differentiation between neighbouring populations (Ward, 2011). Taylor & Barker (2012), however, concluded that it is a single "panmictic entity", with no detectable genetic structuring linked to the morphological variations. The debate is sure to continue, but for the purposes of this study I follow Taylor & Barker (2012) and treat *V. karroo* as a single, though architecturally plastic, species.

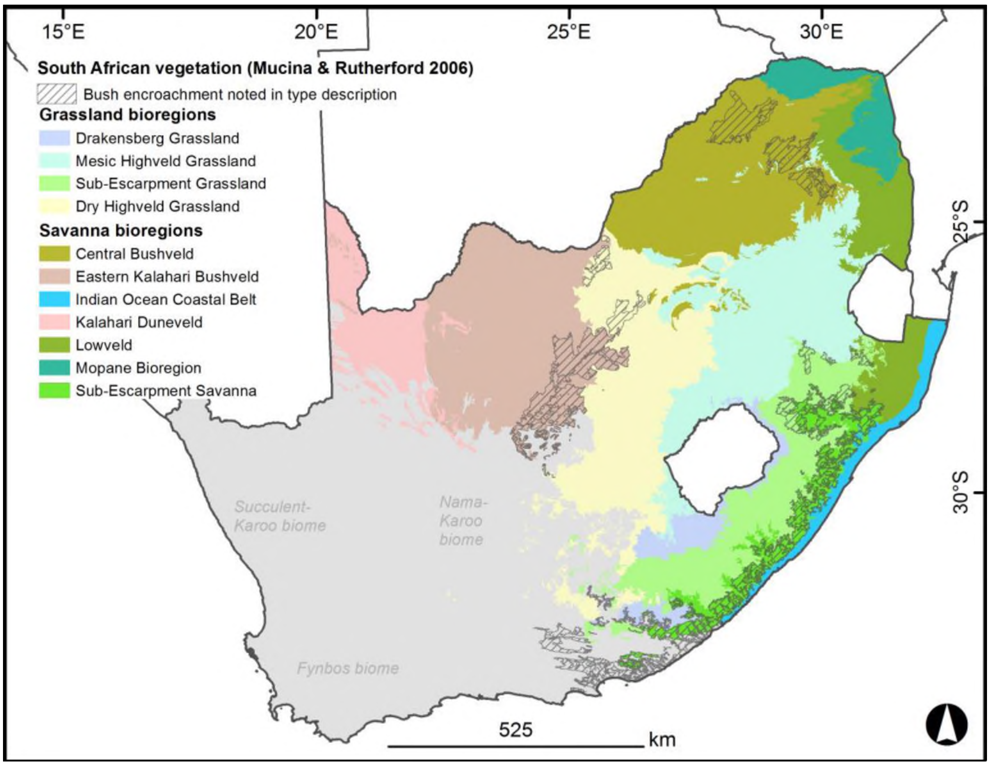

Figure 3. Map of South Africa showing the bioregions of the savanna and grassland biomes (based on Mucina & Rutherford (eds), 2006). Vegetation types with mention of bush encroachment in their descriptions are overlaid in black hatching.

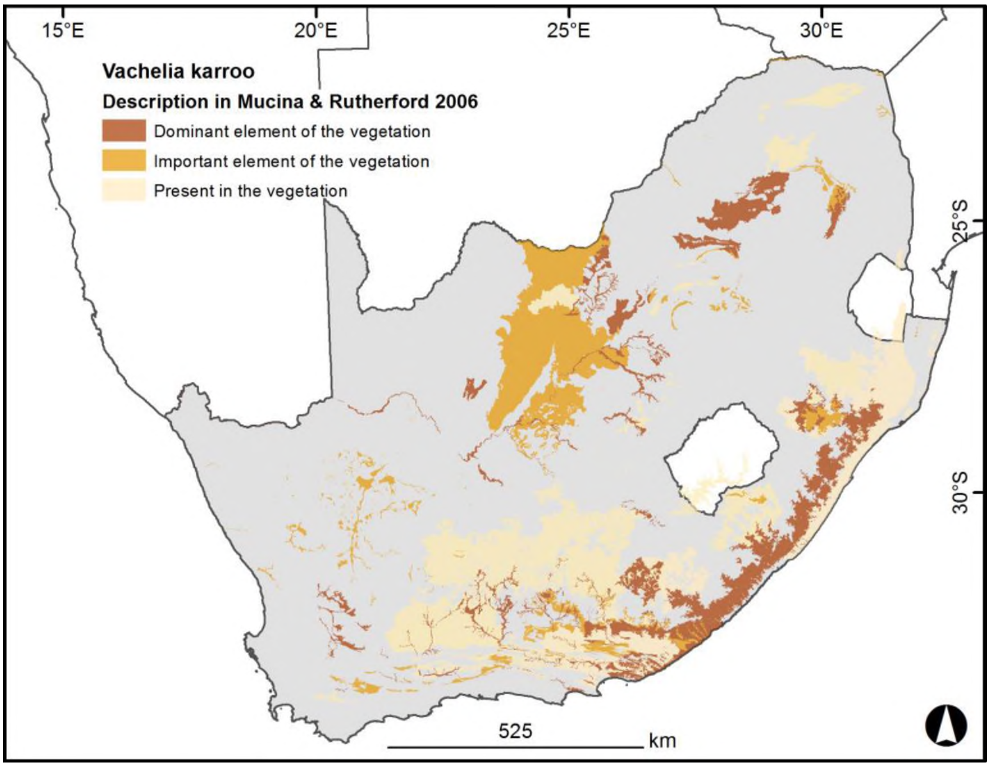

Figure 4. Distribution and abundance of *Vachelia karroo* (*Acacia karroo*) based on vegetation type descriptions in Mucina & Rutherford (2006). Mucina & Rutherford (2006) chose to follow von Breitenbach (1989) and split the species into *A. karroo* and *A. natalitia.* In this thesis and in this figure, however, *A. karroo* and *A. natalitia* are treated as conspecifics.

Potential consequences of woody plant increase

Woody plant encroachment and the expansion of woodland into grassland can have many ecological and social repercussions. It has been shown to compromise ecosystem service delivery in rangelands and directly impact on human livelihoods – largely through the impacts of canopy cover on the grass sward (O'Connor, 1995a; Hoffman & Todd, 2000; Scholes, 2003; Gillson *et al.*, 2012; Archer & Predick, 2014). From a biodiversity point of view, changes in tree-grass cover ratios have been linked to changes in bird community structure (Parmesan & Yohe, 2003; Skowno & Bond, 2003; Sirami *et al.*, 2009; Eldridge *et al.*, 2011), large mammal habitat choice (Smit & Prins, 2015) and changes in plant and invertebrate communities (Parr *et al.*, 2012). As Archer & Predick (2014) state, "Drylands prone to woody plant proliferation present a novel series of dilemmas, challenges and opportunities for mitigation".

Woody plant encroachment is generally seen as a form of ecological degradation by rangeland managers because the desired state of the ecosystem is open savanna-grassland and the perception is that poor land management practices lead to the degraded state (Van Auken, 2009; Archer & Predick, 2014; O'Connor *et al.*, 2014; Hobbs, 2016). As early as the 1980's agricultural legislation in South Africa was enacted to help address the problem of alien plant invasion and indigenous woody plant encroachment. Government resources directed at the alien plant problem were far greater than for the bush encroachment problem – which was considered to be a result of poor management practices (van Wilgen *et al.*, 2012). Despite the low level of government involvement, landowners have taken the bush encroachment problem seriously for decades, investing resources in a wide range of control methodologies (Trollope, 1980; Aucamp *et al.*, 1983; Teague & Smit, 1992; Smit, 2004; O'Connor *et al.*, 2014). Bush encroachment has recently been identified as a priority for action by the South African government, perhaps due to the multitude of scientific studies highlighting its extent, drivers and implications (O'Connor *et al.*, 2014; Nackley *et al.*, 2017). A new government programme focused on bush encroachment (Working on Land) is under development (Table 1).

South Africa is a signatory to both the United Nations Convention on Biological Diversity (CBD) and the UN Convention to Combat Desertification (CCD). The CBD has targets focussed on combatting alien invasive species (Aichi Biodiversity Target 9), while native invasions and woody plant proliferation are not specifically mentioned (Table 1). The CCD, on the other hand, has targets to combat land degradation and specifically mentions bush encroachment as a form of degradation in grassy biomes (Table 1). The IUCN have recently updated their threat schemes (for the red-listing of species and ecosystems) to include invasions by both native and alien species. Previously it was alien species alone that were considered a threat to biodiversity (Table 1).

While thicket/forest invasion of grasslands is generally classed as degradation by savanna and rangeland ecologists; in more mesic systems, where grassy biomes and forest occupy the same environmental envelop, grassy biomes are classed as degraded ecosystems in some forest landscape restoration plans (Veldman *et al.*, 2015a). Indeed, a series of recent articles address this issue and promote an "old growth" concept for grasslands, savannas and woodlands, in the hope that this will improve conservation policies and ecosystem management (Parr *et al.*, 2014; Veldman *et al.*, 2015b; Bond, 2016). Ultimately, if woody plant increase in grassy biomes is an increasingly likely consequence of elevated atmospheric CO_2, rangeland managers may need to adopt an adaptive attitude to a different (more woody) ecosystem state (Hobbs, 2016; Case & Staver, 2017).

Table 1. Recent legislative and policy developments linked to woody plant invasion

South Africa
All invasive plants (native and alien) were seen as potentially problematic and were addressed under one piece of agricultural legislation in 1983, 1985 and 2001 (CARA[1]).
Recent updates to the National Environmental Management Act, 2004 (NEMA[2]), including the invasive species regulations[3] in 2014 (which replaced part of CARA that dealt with alien species invasions) do not, however, mention native invasions or bush encroachment.
There is a new government programme within the Department of Environmental Affairs (working on land – within the NRM programme) to address bush encroachment[4]. There is no legislative basis for this under NEMA but the programme documents mention the UNCCD targets linked to reducing bush encroachment (see below).
International
The (UN) Convention on Biological Diversity (CBD) to which South Africa is a signatory has targets focussed on combatting alien invasive species (Aichi Biodiversity[5]). Native invasions are not specifically mentioned.
The (UN) Convention to Combat Desertification (CCD) to which South Africa is a signatory includes targets to combat degradation and specifically mentions bush encroachment[6] as a form of degradation in grassland and savanna eco-regions.
The IUCN have recently updated their threat schemes (for the red-listing of species and ecosystems) to include both native and alien invasive species. Previously it was alien species alone that were considered a threat to biodiversity[7].

[1] Conservation of Agricultural Resources Act (43:1983), amendment 2001
[2] National Environmental Management: Biodiversity Act (10/2004)
[3] NEMA (10/2004): Alien and Invasive Species Regulations, 2014
[4] Working on Fire (www.environment.gov.za/projectsprogrammes/wfl)
[5] Aichi Target 9
[6] UNCCD Target 14 and 15
[7] IUCN threat classification system (http://www.iucnredlist.org)

Methods and approaches

This thesis draws on a wide range of technologies and approaches; ranging from local and regional scale remote sensing of woody plant cover change over time, to in-field demographic surveys, to spatial modelling based on machine learning. The remote sensing and modelling approaches are introduced and discussed below.

Aerial photo analysis (Chapter 2)

Observations of woody plant increase based on historical and aerial photographs are some of the most accessible and striking evidence of land cover change available in South Africa and globally (O'Connor & Crow, 1999; Eckhardt *et al.*, 2000; Ansley *et al.*, 2001; Fensham *et al.*, 2002; Asner *et al.*, 2003; Bowman *et al.*, 2008; Lehmann *et al.*, 2008; Wigley *et al.*, 2010; Russell & Ward, 2014a).

The benefits of viewing change across an area of interest from a birds-eye-perspective include gaining a better understanding of the spatial patterns and trajectories of change, the ability to investigate inaccessible areas and, most importantly, allowing investigators to study regions or sites for which no historical field data exist (Howard, 1970; Morgan *et al.*, 2010). While much research is rightly focussed on making the most of the growing satellite record – which spans the last two to three decades – the aerial photograph record offers significant advantages for studies of land cover change in terms of time period covered and spatial resolution (Morgan *et al.*, 2010; Hansen & Loveland, 2012; Gómez *et al.*, 2016). Aerial photographs are usually available: a) at a high horizontal resolution (< 2 m) – thus enabling investigators to reliably estimate tree canopy cover, b) from as early as the 1940's for many regions, and c) on a 5–10 year time step – allowing for true time series analysis. The principal drawback of using historical aerial imagery is that it is time consuming to prepare for analysis and therefore poorly suited to regional and national scale studies (Morgan *et al.*, 2010). Advances in digital aerial photography and automatic geo-referencing and ortho-rectification have reduced this limitation for recent imagery (2000–present) but for historical, non-digital imagery it remains a significant challenge.

There are numerous approaches to aerial photo analysis for estimating percentage canopy cover that have been successfully applied to savanna grassland environments, including:

a) Point based estimates of canopy cover; typically, a regular or random cloud of points covering a 1–5 ha area of interest are scored for their cover type and the values are summed to estimate the % canopy cover of the study area (e.g. Fensham *et al.*, 2005), this can be applied to hard copy or digital imagery.

b) Estimates of percentage cover within a specified zone or sample area (typically a grid cell or circle with diameter between 10 and 200 m) (e.g. O'Connor & Crow, 1999), this can be applied to hard copy or digital imagery.

c) Pixel based classifications that use the difference in reflectance between tree canopies (usually dark, low reflectance values) and grass/bare ground (usually bright, high reflectance values) to assess the whole image or part thereof to automatically estimate canopy cover (e.g. Britz & Ward, 2007).

d) Object based classification in modern GIS systems that that break the image up in to areas of relative spectral homogeneity (object) and then assign a classification of canopy or grass/bare to each object (e.g. Stevens *et al.*, 2016).

Choosing the best approach depends on a number of variables including image quality and consistency across time steps (resolution and contrast required to identify the woody canopies), image geo-referencing and the extent of area of interest (Morgan *et al.*, 2010). Sites with consistent resolution images (from similar sensors) that are well matched between time steps (in terms of colour balance and spectral coverage), have high contrast between canopies and non-canopy areas and have existing geo-referencing information, are well suited to the various automated approaches which can cover large regions and are implemented in geographical information systems (Morgan *et al.*, 2010). In Chapter 2, I relied on historical aerial photographs with no geo-referencing, captured using many different cameras and processed in a variety of ways. The image sets varied between and within each time period and were better suited to a combined GIS and manual operator driven approach. Russell & Ward (2014b) provide a detailed motivation for this approach under similar circumstances.

National scale remote sensing of woodland expansion (Chapter 4)

While the horizontal resolution and depth of the time series are the strengths of using the aerial photograph approach to land cover change detection; the key drawback of the approach is the limited spatial extent (~20 to 200 km^2) that it allows (Howard, 1970; Morgan *et al.*, 2010). Satellite imagery, on the other hand, can be used to measure changes in woody cover over millions of km^2 and allows for the investigation of landscape and regional patterns, and rates of change (Franklin & Wulder, 2002; Gómez *et al.*, 2016). The trade-off for this large spatial extent is a limited (though growing) historical record of between two and four decades (for

MODIS and Landsat products respectively) and horizontal resolution of between 30 m and 500 m (for Landsat and MODIS respectively).

Multi-spectral optical data (such as Landsat) are widely used in land-cover change mapping (reviewed by Hansen & Loveland, 2012) with numerous studies aimed specifically at detecting woody plant changes (Gasparri *et al.*, 2010; Barger *et al.*, 2011; Favier *et al.*, 2012). In open savanna woodlands optical remote sensing approaches to land cover mapping tend to classify grassland and open woodlands into the same category, due primarily to the dominance in reflectance of the grass layers (Asner *et al.*, 2003; Mitchard *et al.*, 2011). This is especially true when sparse canopied trees and shrubs such as microphyllous acacias are the dominant woody species (Asner *et al.*, 2003; Turner *et al.*, 2003; Lehmann *et al.*, 2008). Synthetic aperture radar sensors measure backscatter relative to the wavelength of its active senor, the resulting data contains information on surface roughness and soil moisture (Woodhouse, 2006). L-band SAR has a wave length of 15–30 cm making it sensitive to vegetation structure, tree stems and main branches in particular. Because of this L-band SAR sensors have been successfully applied to biomass estimation studies in the savanna biome in Africa (Mitchard *et al.*, 2009, 2011; De Grandi *et al.*, 2010; Taylor *et al.*, 2011; Ryan *et al.*, 2012; Carreiras *et al.*, 2013) and several authors have noted that combining optical and SAR remote sensing products holds promise for woody cover change studies at a range of scales (Hellwich *et al.*, 2000; Hudak & Brockett, 2004; Mitchard *et al.*, 2009, 2011). In Chapter 4, I attempted this by first modifying an existing Landsat derived land cover change dataset and then combining it with L-band SAR data from the ALOS PALSAR sensor to develop a national scale map of woodland expansion.

Spatial models based on machine learning (Chapter 5)

Spatially explicit modelling approaches have the potential to combine various sources of data regarding aspects of woody plant cover change in savannas and link these aspects with external driver or covariates (Guisan & Zimmermann, 2000). Machine learning algorithms differ from statistical modelling approaches in that they learn the relationship between the response and its predictors rather than assuming an appropriate model and using the data to estimate the parameters for the model (Breiman, 2001). Boosted regression trees (BRT) are one such technique (others include random forests and neural nets) which holds the advantages of good predictive power and robustness to missing data and outliers. Importantly, non-linear relationships and interaction effects between predictors are implicitly modelled due to the hierarchical structure of decision trees (Elith *et al.*, 2008a). Thus, even though fitting multiple trees makes them more complex and less interpretable, BRT models can be summarized in ways that provide ecological insight. As a result BRT's and other machine learning approaches have recently risen to prominence in spatial ecology for examining the relationship between multiple environmental variables and species / habitat occurrence (Elith *et al.*, 2008a; Sankaran *et al.*, 2008) and are used to explore the potential drivers of woodland-grassland shifts in Chapter 5.

Summary of chapters and key questions

The overarching aims of the study were to i) describe local and regional changes in woody cover in South Africa's savanna-grasslands, using novel remote sensing and *in situ* methods (Figure 5), and then ii) to test key conceptual models of savanna canopy cover change; specifically those focused on the rainfall thresholds separating arid and mesic savannas.

In Chapter 2, I used aerial photograph time-series data to investigate woody canopy cover changes in relation to rainfall and drought at a mesic and an arid site – spanning the conceptual rainfall threshold described in Figure 1. The sites were well matched in terms of species composition, soils, topography and herbivore management; allowing for a comparison of patterns and rates of encroachment at a mesic and an arid site. Given the moisture-limited seedling-establishment concept presented in Figure 1; do the arid sites show the expected link between rainfall / drought and woody encroachment rates, and is this link absent at mesic sites which are not moisture limited?

Demonstrating mechanisms for differential encroachment in arid versus mesic savannas is crucial. In Chapter 3, I used a demographic approach, based on field transect data, to test the proposed mechanisms of woody plant encroachment at the same Eastern Cape sites as in Chapter 2. The transect data focussed on growth form and size class distributions of the dominant encroaching woody species (*V. karroo*). Do arid sites (which are establishment limited) (Figure 1) have a relatively even demographic profile, and do mesic sites (which are recruitment limited) have a demographic profile that is skewed toward small and or stunted individuals; and do the two sites differ in term of V. karroo architecture?

Chapter 4 describes the development of South Africa's first national scale, remotely sensed map of grassland-woodland shifts (in the period 1990–2013). The study focused on estimating the extent and pattern of woodland increase and decrease over the whole savanna – grassland biome, allowing me to explore the changes in relation to bioregion, rainfall and land tenure, in a spatially explicit manner.

In Chapter 5, I used the map produced in Chapter 4 to construct the national-scale models of woodland increase and woodland decrease for South Africa. I used a machine-learning approach (BRT) to investigate a suite of 11 potential environmental correlates of woodland-grassland change, with the aim of better understanding the patterns and the key drivers of woodland increase and decrease.

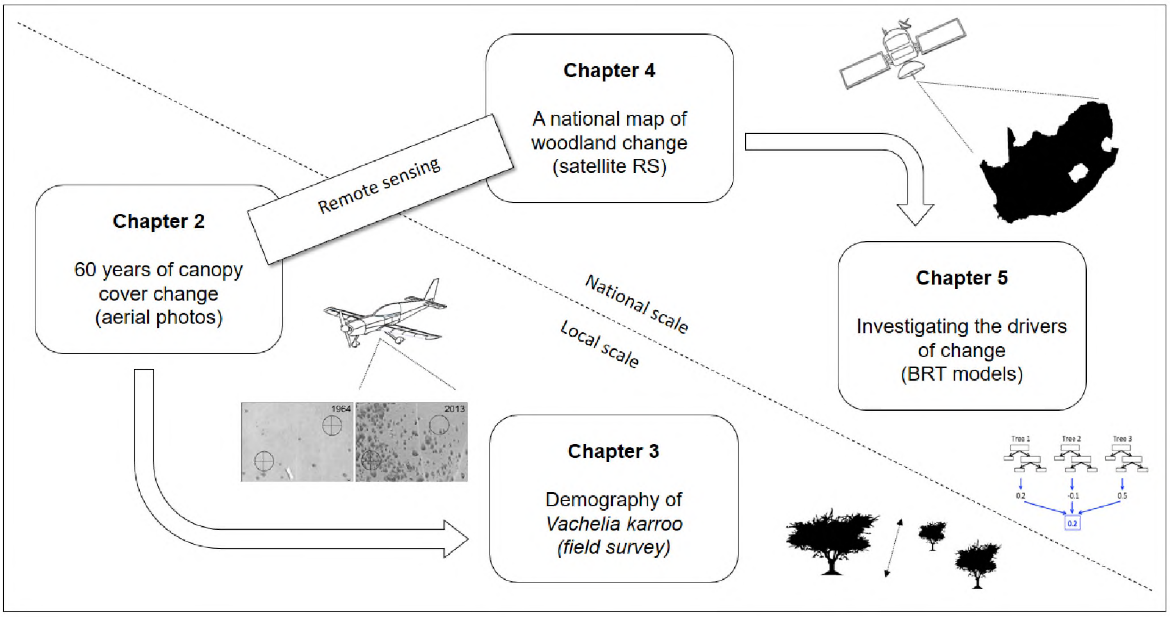

Figure 5. Diagram of thesis structure showing the links between the chapters and range of approaches.

Chapter 2: Six decades of woody canopy cover change across a savanna rainfall gradient in the Eastern Cape, South Africa

Abstract

Aerial photograph time series data were used to compare the long term changes in woody canopy cover at an arid site (468 mm mean annual precipitation (MAP)) and a mesic site (762 mm MAP); within a single *Vachelia karroo* dominated savanna type in the Eastern Cape Province of South Africa. Woody canopy cover change was estimated for each site and compared with rainfall and drought records. I ask the following questions: are arid and mesic sites different in terms of woody canopy cover change direction and magnitude and are the rates of change in woody canopy cover linked to rainfall and fire? Overall, woody canopy cover doubled (from 13 to 26%) at the arid site (1949 –2013) and almost quadrupled (from 7 to 27%) at the mesic site (1953–2013). The mean rate of woody canopy cover change at the arid site was 0.2% y^{-1}, with a maximum 0.49% y^{-1} in the period 2005–2013. At the mesic site the mean was 0.34% y^{-1}, with a maximum of 1.13% y^{-1} between 1992 and 2005. The rates of encroachment observed in this study are well aligned with both regional and continental observations. Woody canopy cover increased in two pulses at the arid site (1967–1985 & 1996–2013) and in a single strong pulse (1992–2005) at the mesic site. At the arid site the rate of woody cover increase was positively correlated with the standardised precipitation index (SPI), derived from long term median rainfall. The regression analysis failed to align drought and rainfall with observed woody cover increase at mesic sites, which are not usually water limited. The finding that woody canopy cover increased dramatically at both sites from the 1960s onwards is well aligned with observations by numerous other investigators from sites across the savanna biome globally. Additional explanations for this relatively recent phenomenon range from release from high levels of herbivory – by (now extirpated) mega-herbivores in the late 19th century and by livestock whose numbers peaked in the middle of the 20th century – to facilitation by increasing atmospheric CO_2 levels over the last century.

Introduction

The interplay between rainfall and disturbance in the structure, function and dynamics of savanna-grasslands was introduced in Chapter 1. Woody plant encroachment is thought to be limited by woody plant recruitment at mesic sites, with fire and / or herbivory playing key disturbance / consumer roles (Higgins *et al.*, 2000; Sankaran *et al.*, 2008; O'Connor *et al.*, 2014; Archibald & Hempson, 2016; Devine *et al.*, 2017). At arid sites encroachment is thought to be limited by woody plant establishment (linked to low moisture availability) and recruitment (linked to herbivory) (Higgins *et al.*, 2000; Sankaran *et al.*, 2008; O'Connor *et al.*, 2014; Archibald & Hempson, 2016; Devine *et al.*, 2017) (Figure 1). Increased grazing pressure can also indirectly promote woody plant establishment and recruitment by reducing fuel loads for fires and / or increasing water infiltration depth (Trollope, 1980; Teague & Smit, 1992; Kraaij & Ward, 2006; Midgley *et al.*, 2006); while reduced browsing pressure can directly promote woody plant recruitment (Staver & Bond, 2014). At arid sites woody plant establishment is most often successful during above average rainfall years (O'Connor, 1995a; Kraaij & Ward, 2006), especially when preceded by a drought (Aucamp *et al.*, 1983; O'Connor & Crow, 1999; February *et al.*, 2013) (Figure 1).

The rate and trajectory of land cover change remains a key research question in South Africa, especially in the savanna and grasslands biomes which cover over 65% of the country and are considered sensitive to both local and global drivers of change. This study continues the tradition of aerial photograph based woody canopy cover mapping, by comparing an arid and a mesic savanna site from the Eastern Cape using all the available time points between 1940 and 2013. To minimize the impact of the complex interactions discussed above the arid and mesic sites chosen for this study are 120 km apart and are situated at the same altitude, on similar soils and topography and share very similar plant species composition and dominance. They differ significantly in terms of long term mean annual precipitation; at 468 mm the arid site falls well within the range of arid savannas (Sankaran *et al.*, 2005, 2008; Higgins *et al.*, 2010; Staver *et al.*, 2011a, 2011b; Lehmann *et al.*, 2014) and at 762 mm the mesic site falls above the threshold for mesic savanna according to some authors (~650 mm MAP) (Sankaran *et al.*, 2008; Staver *et al.*, 2011a; Lehmann *et al.*, 2014) and just below the threshold according to others (~1000 mm) (Higgins *et al.*, 2010). The region has a mix of commercial freehold land tenure and traditional communal tenure, which result in clear land use management differences. Numerous studies have focussed on these differences and how they relate to woody plant encroachment. (Puttick *et al.*, 2011, 2014a, 2014b; Buitenwerf *et al.*, 2012). The overall message from these studies is that woody plants have increased under both tenure systems. In this study both sites fall in the commercial freehold tenure system. The study region is therefore well suited to a comparison of canopy cover change in arid vs. mesic savannas. The trade-off, however, is that the narrow biogeographic setting limits the generality of the analysis.

Aims and key questions

I ask the following questions aimed at testing a key element of the conceptual model presented in the introductory chapter (Figure 1); do the arid sites show the expected links between rainfall / drought and woody encroachment rates (i.e woody plant establishment is promoted by higher than average moisture availability), and is this link absent at mesic sites which are not moisture limited? I use three key metrics of change in the study; overall direction of change at a site (i.e. from low canopy cover to high canopy cover or *visa versa*); magnitude of change (i.e. the percentage point difference in canopy cover between start and end of time period) and the rate of change for each time period.

- Are arid and mesic sites different in terms of the overall direction (e.g. grassy to woody) and magnitude (e.g. 10% cover to 35% cover) of woody canopy cover change?
- Are the arid and mesic sites different in terms of the proportion of plots showing woody canopy cover increase, decrease and stability?
- Is the rate of woody canopy cover change at each site linked to rainfall patterns and fire frequency at a decadal scale?
- How do these results compare to previous research, locally, regionally and globally?

Methods

Study site

The study area is an east-west orientated band of savanna complex habitats in the Eastern Cape Province of South Africa; stretching from the town of Bedford in the west to the village of Kei Road in the east, a region known locally as the "Smaldeel" (Figure 6a,b,c). The dominant vegetation types in the region are Bedford Dry Grassland and the floristically similar Bhisho Thornveld, with Eastern Cape Escarpment Thicket in deep valley and escarpment situations (Hoare *et al.*, 2006; Mucina *et al.*, 2006a; Rutherford *et al.*, 2006b) (Figure 6d). *Vachelia* *karroo (*formerly *Acacia karroo*) is the dominant tree in the study area and only in the thicket patches and riverine forest are other tree species present in significant numbers. The grass sward generally increases in density from west to east (along the rainfall gradient) and dominant species, which vary from site to site according to grazing history, include *Themeda triandra, Eragrostis obtusa, Panicum maximum, Digitaria eriantha, Sporobolus fimbratus.* The underlying geology of the region is sandstone and shale of the Ecca and Beaufort series and the topography is mostly rounded hills with moderately steep valleys. The resulting soil forms are mostly Glenrosa and Mispah, with high silt and fine sand content (Fey, 2010).

Two field study sites, representative of the bioregion in terms of topography, management and history, were identified within the study area. Importantly the owners of the sites were prepared to offer full access to investigators over a number of years, an increasingly difficult situation in South Africa. Haddon Farm (the arid site) lies in the arid western portion of the Smaldeel – with MAP of 468 mm (Schulze *et al.*, 2008); and Killaloe Farm (the mesic site) lies in the relatively mesic eastern portion of the Smaldeel – with MAP of 762 mm (Schulze *et al.*, 2008) (Figure 6c). The land use history of the sites is relatively well known and consists of mixed cattle, goat and sheep ranching, with limited interventions in terms of bush clearing. Fire is used as a management tool in the eastern site (Killaloe) but not in the arid western site (Haddon) due to low fuel accumulation rates.

Historical aerial photograph analysis

Preparation of historical imagery

Flight plans of historical and recent aerial photography missions were used to identify a set of 100 images captured at the two sites between 1949 and 2013. These images were ordered from the National Department of Land Reform and Rural Development, Chief Directorate: National Geo-Spatial Information (CD:NGI). For images captured pre 1998 the original panchromatic photo negatives were scanned by CD:NGI at 1200 dpi and provided in TIF format with no geo-referencing information. Imagery captured post 1998 were supplied in geo-referenced and ortho-rectified TIF format. The unique aerial photo job number, scale of the imagery and date of capture is listed in Table 2.

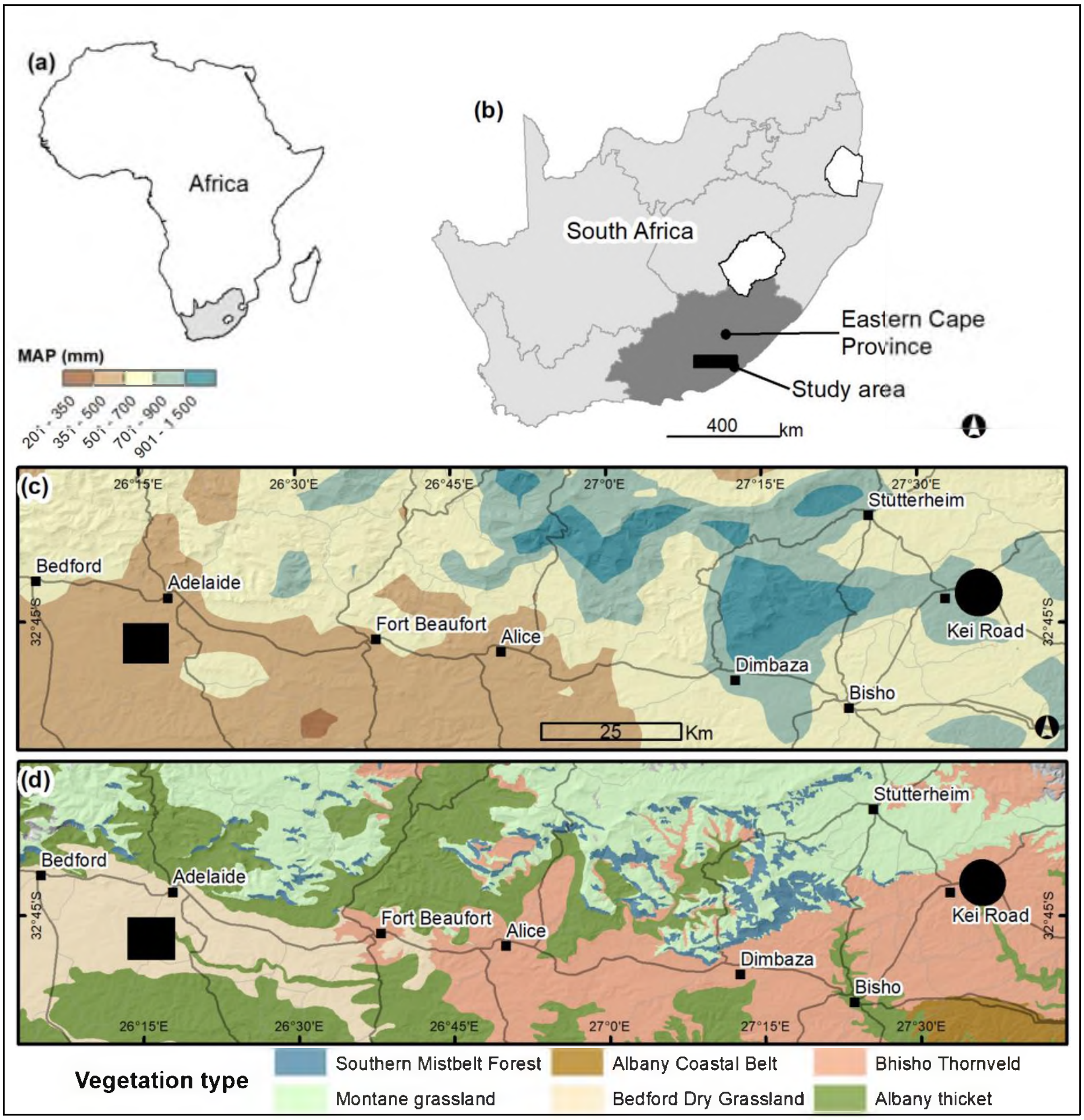

Figure 6. Location of the study sites in South Africa (a) and the Eastern Cape Province (b). Study area in the Samldeel region with mean annual precipitation (MAP) from Schulze *et al.* (2008) (c) and vegetation units (Mucina and Rutherford 2006) (d). The arid site (Haddon farm) is shown with a black square and the mesic site (Kilalloe farm) is shown with a black circle.

Due to costs of scanning and the time consuming process of geo-referencing historical imagery, the historical aerial photo analysis was limited to the selected farms and their immediate neighbours; an area of approximately 1000 ha per site.

The historical images were geo-referenced and mosaicked in ARCGIS 10.3 using a minimum of 10 tie-points per image and second order polynomial transformation with root mean square error of less than 6.5 m; the 2013 digital ortho-rectified imagery provided by CD:NGI was used as the basis for the geo-referencing of the historical images. Geo-referencing progressively older images in series allowed for the identification of sufficient tie-points between the imagery dates. The spatial reference system used was the transverse Mercator projection (central meridian = 27°, reference latitude = 0°, datum = WGS84).

Table 2. Aerial photographs used in the study

Date	Job & Scale	Site	Format
1949	234 (1:30 000)	Haddon (arid)	Scanned negative (Tiff)
1953	332 (1:36 000)	Killaloe (mesic)	Scanned negative (Tiff)
1964	494 (1:30 000)	Killaloe (mesic)	Scanned negative (Tiff)
1967	544 (1:40 000)	Haddon (arid)	Scanned negative (Tiff)
1975	732 (1:50 000)	Haddon (arid) & Killaloe (mesic)	Scanned negative (Tiff)
1985	884 (1:30 000)	Haddon (arid)	Scanned negative (Tiff)
1992	970 (1:30 000)	Killaloe (mesic)	Scanned negative (Tiff)
1996	981 (1:50 000)	Haddon (arid)	Scanned negative (Tiff)
2005	1:30 000	Haddon (arid) & Killaloe (mesic)	Digital (GeoTiff)
2013	1:30 000	Haddon (arid) & Killaloe (mesic)	Digital (GeoTiff)

Estimating woody canopy cover change

Using ARCGIS 10.3, a network of 111 circular plots was generated for each study site in order to quantify changes in canopy cover. Each plot was 1000 m^2 (diameter = 35.68 m) and was arranged on a regular point grid of 400 m x 400 m, resulting in circular plots 364 m apart. Plots without natural vegetation cover were excluded (e.g. cultivated lands, homesteads, dams and roads). Previously cultivated lands (i.e. prior to the study) with secondary vegetation cover (usually identified by presence of linear plough lines or terraces) were also excluded from the time series analysis.

The shapefile of the 1000 m^2 plots was over-lain on the historical aerial photograph mosaics in ARCGIS 10.3. The percentage canopy cover of each plot, at each time interval, was estimated visually on-screen (23 inch Dell Monitor) at a scale of 1:1000, using 5% canopy cover bins. The plots were divided into quarters by an additional overlay to aid in estimation of canopy cover. This method is a combination of contrasting techniques developed in similar studies of savanna change (O'Connor & Crow, 1999; Fensham *et al.*, 2002; Russell & Ward, 2014b). The techniques were combined to accommodate the spatial scale of this study and the natural heterogeneity in canopy cover in this particular savanna complex (Figure 7 & Figure 8).

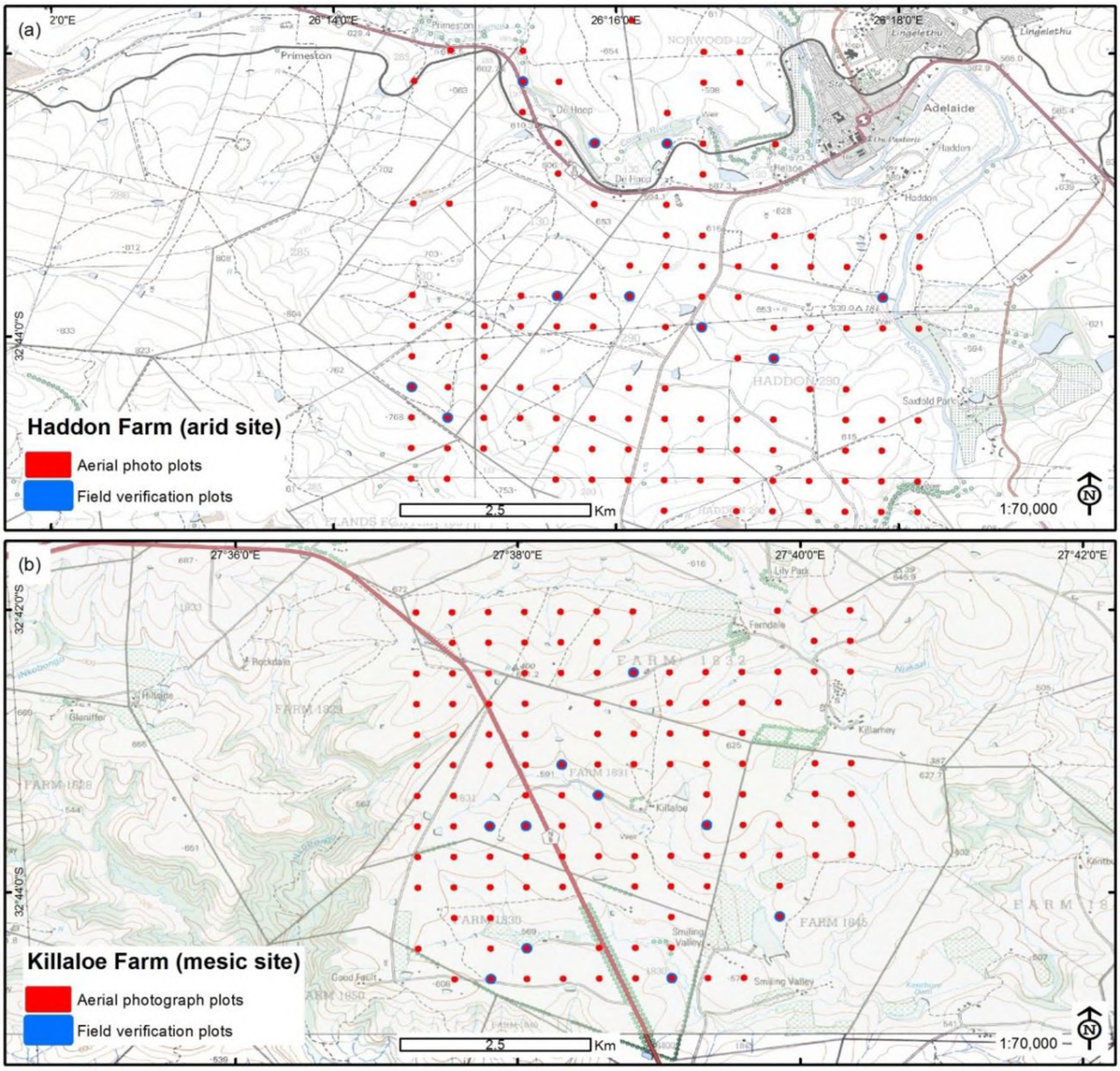

Figure 7. Layout of aerial photograph plots and field verification transects at (a) arid site (Haddon Farm) and (b) mesic site (Killaloe Farm). Each plot is a circular area of 1000 m^2.

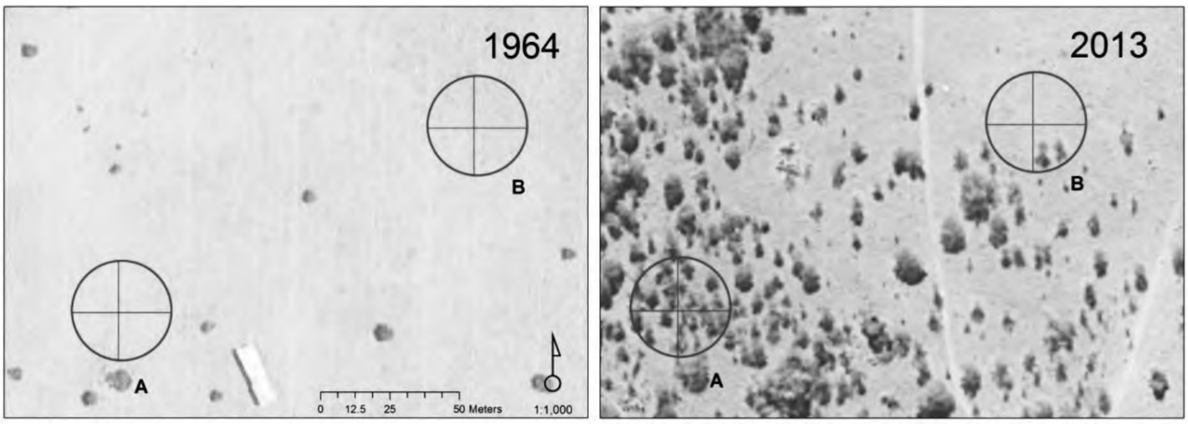

Figure 8. Illustration of the aerial photo based woody canopy cover estimation process and layout of the field verification transects. The 1964 image is shown on the left (a) and the 2013 image is shown on the right (b).

Verification of the GIS based canopy cover estimates for 2013 was made by field observations at 10 randomly selected plots at each site. The centre point of each of the selected plots was located using a hand held GPS. From the centre point a short transect of 18 m was set up in each cardinal direction using a measured section of rope. The tree canopy cover was estimated at 0.5 m intervals along each transect (point-intercept method) and the mean was calculated for each plot (trees were defined as *V. karroo* plants > 2 m in height). These field estimates of canopy cover were compared to the desktop aerial photograph estimates using a paired t-test.

Rainfall trends

To compare woody cover change and rainfall trends I obtained daily precipitation records for the town of Adelaide (3 km from the arid site at Haddon Farm) and Kei Road (7 km from the mesic site at Killaloe Farm) from the South African Weather Services (SAWS). Additional global data on rainfall was obtained from Global Precipitation Climatology Centre (GPCC) data portal (www.esrl.noaa.gov). The global 0.5° gridded monthly rainfall data 1901–2015 (precip.mon.total.v7.nc ; downloaded June 2016) (Schneider *et al.*, 2013) was converted to monthly rainfall grids (in TIF format) of 0.5° resolution using ARCGIS 10.3 – Multidimension toolbox. The daily rainfall data was summarised into monthly and annual precipitation totals for all available dates starting in 1950. Missing data for 1964, 1992 and 2003 at Kei Road and 1992, 1996 and 2002 at Adelaide were supplemented with GPCC raster data.

To approximate drought conditions on an annual basis I used the standardised precipitation index (SPI) (World Meteorological Organization, 2012), using a three month period. This results in an annual SPI value that is sensitive to changes in median rainfall on a seasonal basis without a long lag period (World Meteorological Organization, 2012). I used the package “precintcon” (Povoa & Nery, 2016) for R v3.02 (R Core Team, 2014) to calculate SPI using the function [spi.per.year].

Fire records

Long term fire records for the sites were not available from the land owners so I used Google Earth Engine (Google Earth Engine Team, 2015) and the US Geological Survey’s Landsat viewing portal (https://landsatlook.usgs.gov/viewer.html) to develop maps of monthly burnt area at the study sites for all available image dates for all Landsat missions (Landsat 5,7 & 8) (1990–2013) (Figure 9). Images from earlier Landsat missions (1–4) were not regularly captured over the sites and only two cloud free images were collected in the dry season (fire season) between 1972 and 1990. The Landsat 5, 7 and 8 record from 1990 to 2013 is more comprehensive, but significant gaps remain (2008, 2009 and 2012). Unfortunately, combination of cloud cover and sensor issues (the major scan line error in 2003 in Landsat 7 that affected all subsequent images) prevented the collection of a full burnt area time series, making comparison between periods impossible (Table 3). No burnt areas were detected at the arid site between 1990 and 2013), confirming that fire is not a significant landscape level process at MAP ~460 mm.

Table 3. Landsat derived fire history for the mesic site 1990–2013; c = cloud obscured view, y = no burnt area observed, Fire = burnt area observed and mapped. Blanks indicate that no imagery was available for that date. The number of data gaps after 2005 made it impossible to compare the 1992–2005 period with the 2005–2013 period.

Year	May	Jun	Jul	Aug	Sep	Oct	Year	May	Jun	Jul	Aug	Sep	Oct
1990	y	y	y	c	y	y	2002	y	y	y	Fire	y	y
1991	y	y	y	c	c	x	2003	y	y	c	y	y	y
1992	x	y	y	x	x	y	2004	y	y	y	y	c	c
1993	y	y	c	y	y	y	2005	y	y	y	c	c	y
1994	y	y	y	y	y	y	2006	c	y	y	y	Fire	c
1995	y	y	y	y	Fire	y	2007	c	y	y	y	y	y
1996	c	y	y	c	Fire	c	2008	-	-	-	-	-	-
1997	y	y	c	c	y	c	2009	y	-	c	c	c	y
1998	c	y	y	Fire	c	x	2010	-	-	-	-	-	-
1999	y	y	c	y	y	y	2011	y	-	-	-	-	-
2000	y	y	y	y	y	Fire	2012	-	-	-	-	-	-
2001	Fire	y	y	y	Fire	y	2013	-	-	y	y	y	y

Analyses

Woody canopy cover change, estimated within each of the 111 plots at each site, was analysed in three ways:

1) General trends

Overall changes in canopy cover were evaluated by calculating the mean and maximum woody canopy cover at each time point at each site and by calculating the mean and maximum rate of change between the time points.

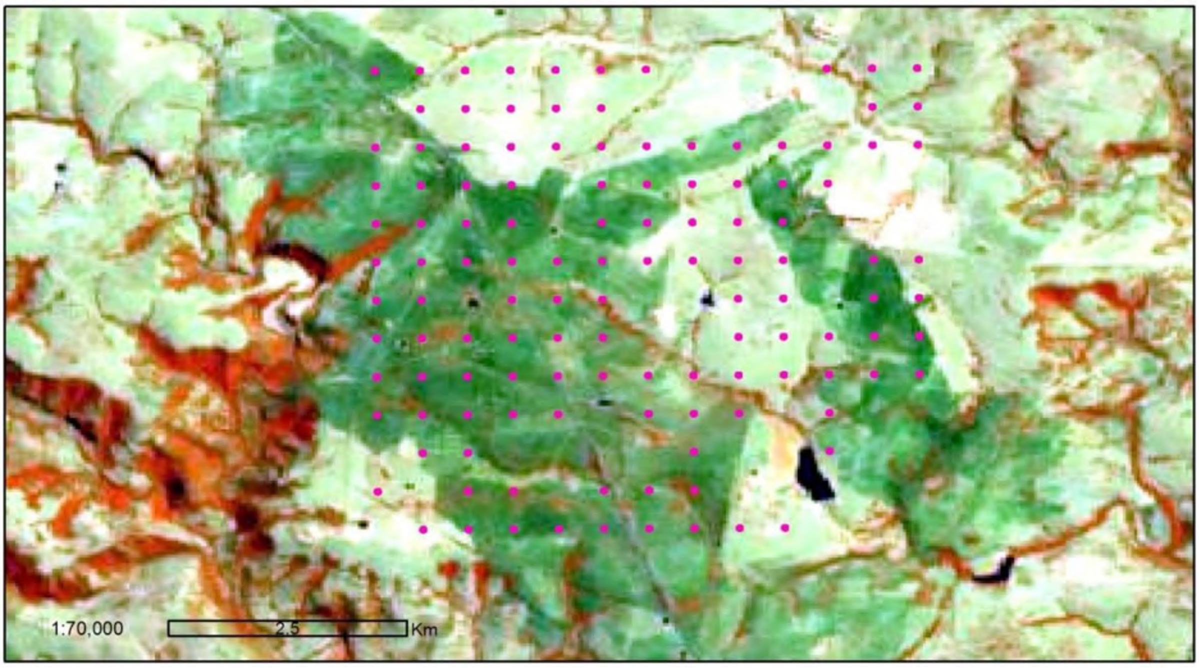

Figure 9. Example of burnt area visible (dark green) in Landsat 5 image (false colour with 4:5:3 band combination in R:G:B) at the mesic site, circa September 1996 – exported from Google Earth Engine.

2) Type analysis

For this analysis plots were categorised according to level of woody cover and to change in woody cover. Stable plots were defined as those that showed between 0 and 10% woody canopy cover change. Low woody cover sites were defined as those with less than 20% woody canopy cover and high woody cover sites those with greater than 20% cover. This classification system results in a small number of "stable" plots with very low levels of increase or decrease in woody canopy cover. Variation in woody canopy cover change between plots was evaluated by counting the number of plots at each site that showed woody cover increase of more than 10% (grassland to woodland ("GW")), decrease of more than 10% (woodland to grassland ("WG")), stable low woody cover (grassland to grassland ("GG")) and stable high woody cover (woodland to woodland ("WW")).

3) Rate analysis

Rate and timing of change in woody canopy cover for each site was evaluated by calculating the absolute rate of woody canopy cover change between each aerial photo time point (i.e. change in canopy cover percentage points per year)

$\frac{CC_{t2} - CC_{t1}}{t_2 - t_1}$, where CC = canopy cover percentage, t_1 = start year and t_2 = end year.

I tested the relationship between the rate of woody canopy cover change for the aerial photo period and both MAP and SPI. Given the length of time required for savanna tree species to establish and or grow into adults it is possible that the observed canopy cover changes for a specific period are correlated with rainfall and drought conditions for the previous period. To address this I summarised MAP and SPI for the aerial photo period (e.g. MAP for period 1949 to 1967) and for a 10 year period, ending five years prior to the end of the aerial photo period (e.g. MAP for 1953 to 1962).

Semi-partial correlation analyses were used to test the relationship between absolute rate of woody cover change and SPI and MAP, while controlling for initial canopy cover. Differences in the absolute rate of canopy cover change between the aerial photo periods were tested using Kruskal-Wallis rank sum tests. The statistical programme R v3.02 (R Core Team, 2014) was used for all statistics and graphs were produced using the R package "ggplot2" (Wickham, 2009) and "ppcor" (Seongho, 2015).

Results

Validation of method

A paired t-test based on 20 random samples (10 from arid site and 10 from the mesic site) showed that the in-field canopy cover estimates (transect based) vs. desk-top (aerial photograph based) estimates of canopy cover were not significantly different ($t = 1.0717$, $df = 19$, p-value $= 0.2973$).

General trends at each site

The woody canopy cover change between each time point for all the aerial photo plots is shown in Figure 10. A wide range of trajectories and magnitudes of canopy cover change are evident. Overall, woody canopy cover increased at both the arid and mesic sites over the approximately 60 year study period. The average woody canopy cover doubled at the arid site (from 13% to 26% between 1949 and 2013; 0.2% per annum) and almost quadrupled at the mesic site (from 7% to 27% between 1953 and 2013; 0.34% per annum) (Figure 12, Figure 13 & Table 4). Woody canopy cover increased relatively consistently at the arid site, with the highest rate of increase between 1990 and 2013. The mesic site, on the other hand, showed a relatively rapid and recent increase in the woody canopy cover between 1992 and 2005 years.

Table 4. Overall changes in canopy cover from start to the end of the study period.

Trend in canopy cover	Arid site			Mesic site		
	mean	sd	n	mean	sd	n
Starting (%) woody canopy cover 1949/53	12.7	10.2	111	7.2	12.0	111
Ending (%) woody canopy cover 2013	25.7	19.5	111	27.3	22.0	111
Percentage point change	13			20		
Percentage change	102			281		
Study period (years)	64			60		
Rate of woody canopy cover change (%change/y)*	0.203	0.32	111	0.336	0.32	111

**This figure assumes a linear increase in canopy cover and is included to aid in comparisons with existing studies of woody canopy cover change.*

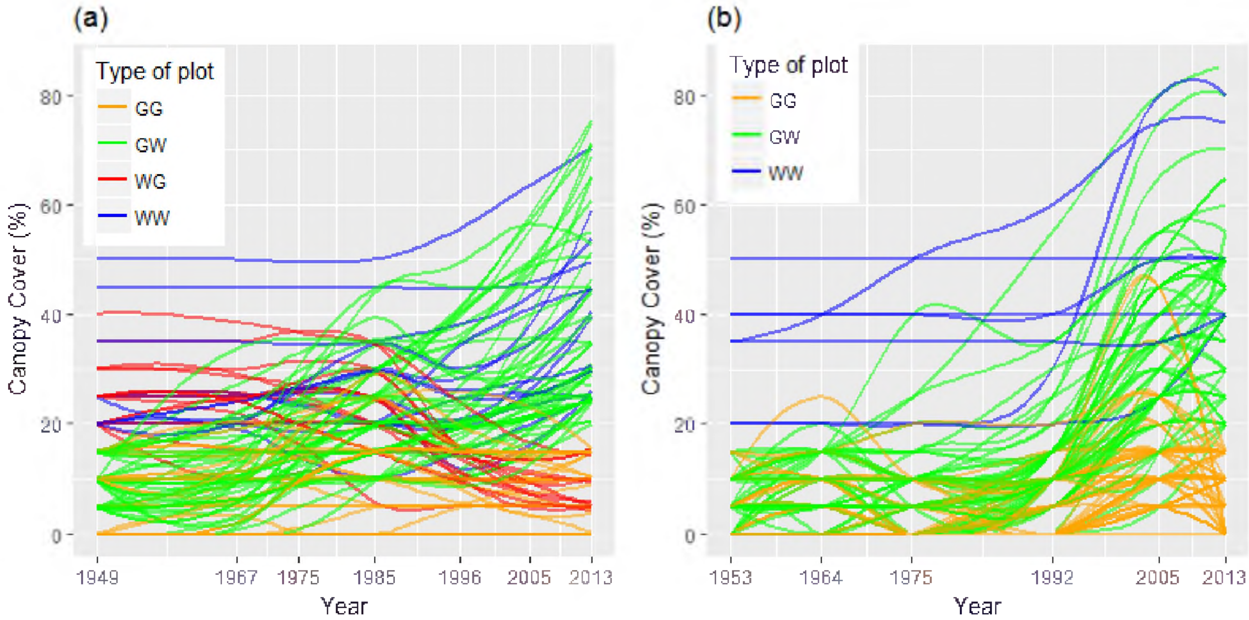

Figure 10. Woody canopy cover change over time for the arid (a) and mesic (b) site. All 111 aerial photograph plots for each site are shown. To aid in interpreting the figure colours representing the main trajectories of change have been added: GG = grassland to grassland (i.e. stable), GW = grassland to woodland (i.e. increase in woody canopy cover), WG = woodland to grassland (i.e. decrease in woody canopy cover) and WW = woodland to woodland (i.e. stable).

Maximum woody canopy cover increased from 55% to 80% at the arid site and from 90% to 100% at the mesic site start and end of the study (Figure 10). Both sites were dominated by low canopy cover plots at the start of the study period (1949 and 1953); after six decades (2013) a wider range of canopy cover values are evident. While the overall trend was increasing woody canopy cover at both sites (Figure 12, Figure 13), there were plots at both sites that remained unchanged (as predominantly grassy or woody) and plots that showed decreasing woody canopy cover at the arid site (Figure 10). This heterogeneity is addressed in the “type” and “rate” analyses below.

<u>Type analysis</u>

At both the arid and mesic site (111 plots at each sites) the majority of the plots show an increase in woody canopy cover (45 arid plots and 51 mesic plots) and a large proportion of plots are stable grassland with low woody canopy cover (30 arid plots and 43 mesic plots)(Figure 11). The sites differ in two key ways. Firstly, while 12 arid plots showed a decrease in woody canopy cover, no mesic plots display this trend. Secondly, 17 arid plots were either stable woodlands or woodlands that showed an increase in woody canopy cover while only eight mesic plots displayed this trend of woodland thickening or stability (Figure 11).

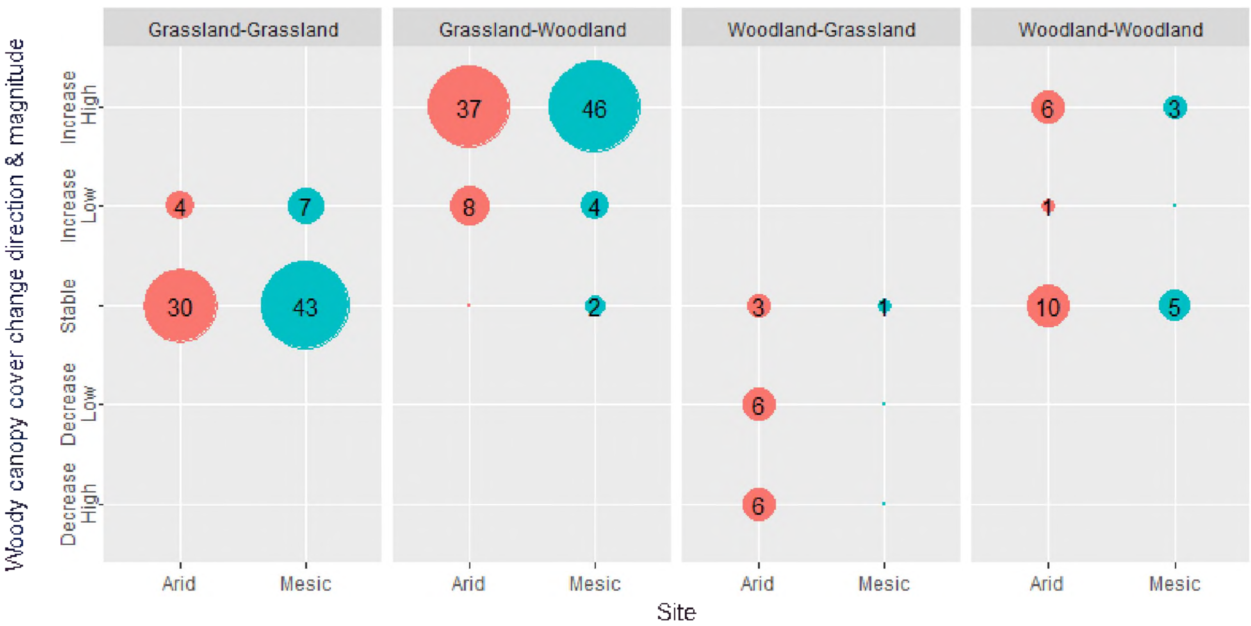

Figure 11. Number of plots in each woody canopy cover type – defined by the state at start and end of the period (grassland vs. woodland) and the direction and magnitude of change (increase high and increase low, stable, decrease low and decrease high). Each site had 111 plots and the circles are scaled according to number of plots in each class. **Plots showing less than 10% change are classed as "stable" – as a result a small number of "stable" sites switch between grassland and woodland due to a 5% change in canopy cover and are placed in the GW or WG bin*.

Rate analysis

The woody canopy cover (%) and the absolute rate of woody canopy cover change (% y^{-1}) estimated from the aerial photograph time series data, were plotted with the mean annual precipitation data and the standardised precipitation index data for the same time (Figure 12 & Figure 13). For the arid site the absolute rate of woody canopy cover change is highest in the most recent time period (2005–2013) (0.49% y^{-1}) and lowest between 1985 and 1996 (-0.04% y^{-1}) (Table 5, Figure 12). Two separate pulses of woody canopy cover increase are evident (1967–1985 and 1996–2013). A Kruskal-Wallis rank sum test showed that absolute rate of change varied significantly between the aerial photo periods (chi = 46, p-value < 0.001). In the period between 1949 and 1967, there was substantially less variation in the rate of woody canopy cover change between plots than in recent years. Since 1967, the rate of woody canopy cover change varied widely between plots – illustrated by the standard deviation bars. The two pulses of woody canopy cover increase at the arid site align with periods of high MAP and SPI and are preceded by short periods of abnormally low rainfall and SPI (1966–1968 and 1997–1999) (Figure 12). For the mesic site a single strong pulse of woody canopy cover increase is evident (1992–2005) (1.125% y^{-1}). The lowest rate of woody canopy cover change is between 1964 and 1975 (-0.04% y^{-1}) (Table 6).

A Kruskal-Wallis rank sum test showed that rate of woody canopy cover change varied significantly between the aerial photo periods (chi = 155, $P < 0.001$). Like the arid site, the rate of woody canopy cover change is far more variable in recent years (since 1964). At the mesic site rainfall and the number of drought months were relatively consistent across all time periods (Table 6). The rainfall / drought record does not link in any obvious way with the strong woody cover increase observed between 1992 and 2005.

The analysis of burnt areas in the available Landsat record revealed that seven of the eight separate fire events observed occurred in the aerial photo period 1992–2005. However, Table 3 shows that very few useful images were captured in the fire season for the period 2008–2013, so comparisons between aerial photo periods are of limited value.

The rainfall at the arid and mesic sites tracked each other closely from 1950 to 1977 and again from 1996 to 2013, but fell out of sync during the period between 1978 and 1995; when the mesic site received above average rainfall and the arid site received below average rainfall, this despite the sites being only 120 km apart (Figure 12 & Figure 13).

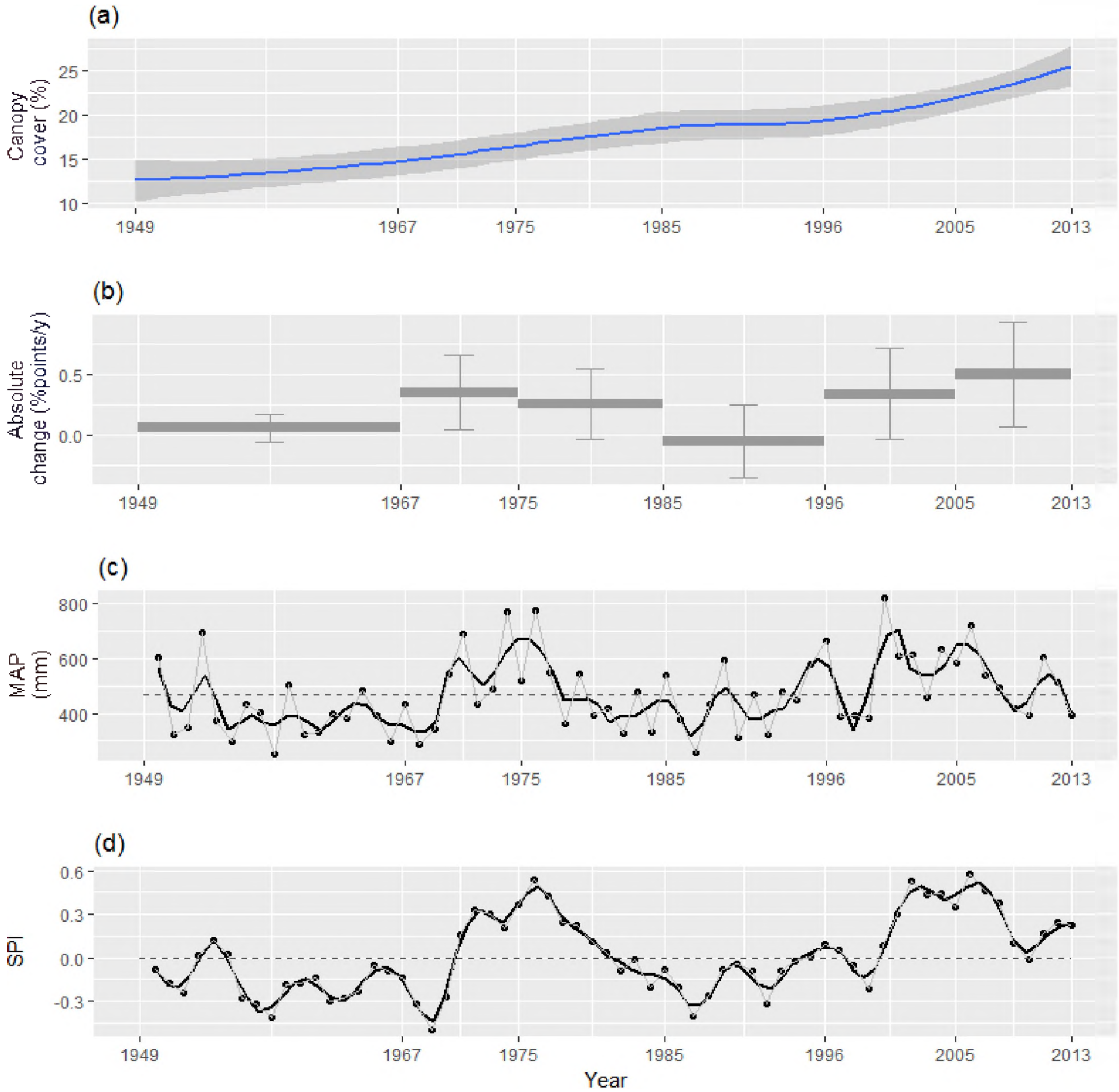

Figure 12. Arid site (Haddon farm, near Adelaide, EC). (a) canopy cover (%), (b) rate of woody canopy cover change between aerial photo time points, (c) mean annual precipitation (mm per year) and (d) standardised precipitation index.

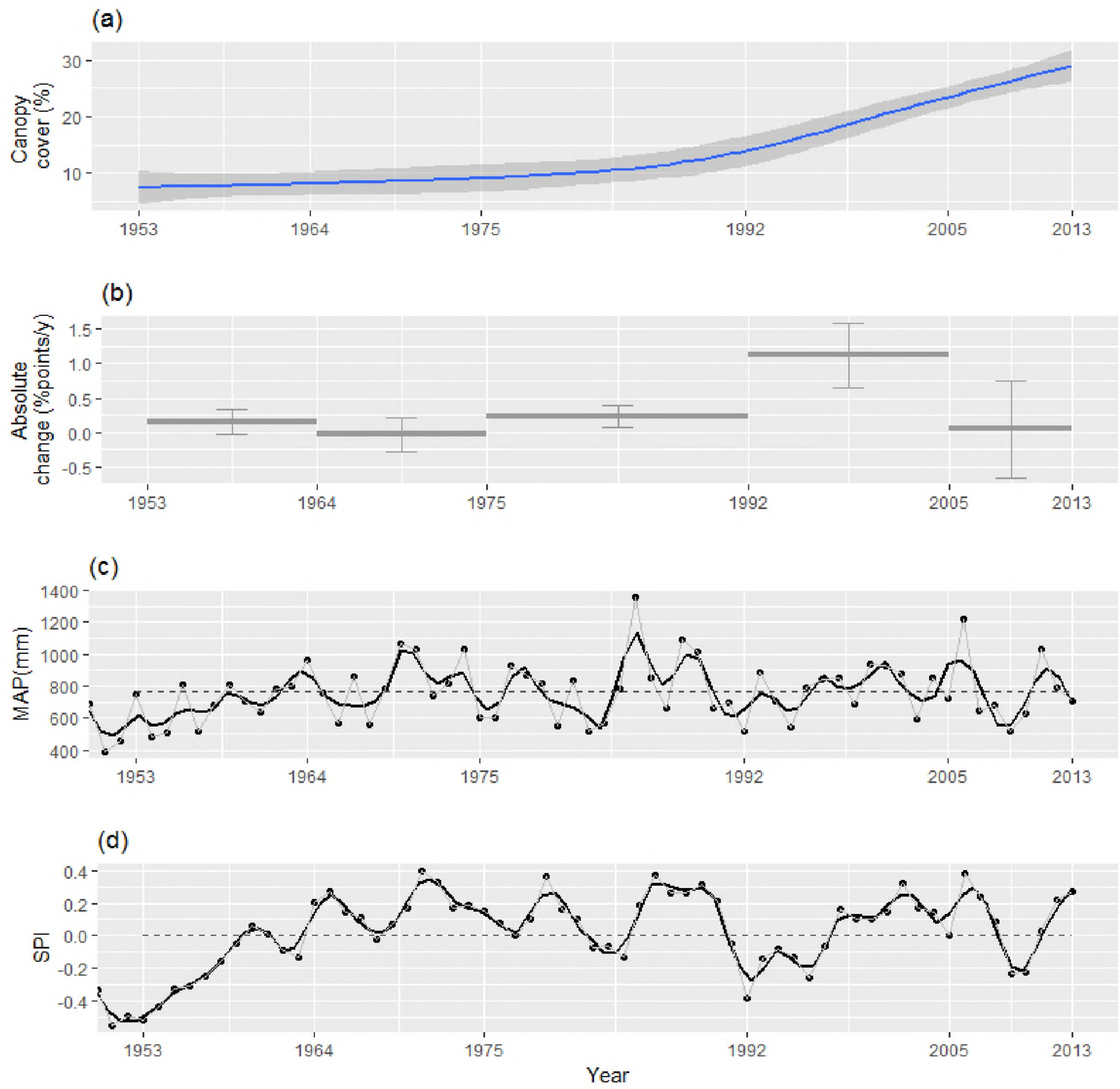

Figure 13. Mesic site (Killaloe farm, near Kei Road, EC): (a) canopy cover (%), (b) rate of woody canopy cover change between aerial photo time points, (c) mean annual precipitation (mm per year) and (d) standardised precipitation index.

Table 5. Arid Site. Rate of woody canopy cover change, rainfall and SPI for the aerial photo period and for a ten year period ending five years prior to the end of the aerial photo period. The long term MAP is 468 mm (1950–2013).

Period	Rate of woody canopy cover change	Mean rainfall for period (mm)	Mean rainfall for prior 10 years (mm)	Mean SPI for period	Mean SPI for prior 10 years
1949 to 1967	0.058	397	401	-0.166	-0.164
1967 to 1975	0.358	508	389	0.016	-0.232
1975 to 1985	0.259	471	551	0.143	0.291
1985 to 1996	-0.041	448	411	-0.124	-0.147
1996 to 2005	0.338	542	494	0.202	-0.055
2005 to 2013	0.492	509	585	0.277	0.334

Table 6. Mesic site. Rate of woody canopy cover change, rainfall and SPI for the aerial photo period and for a ten year period ending five years prior to the end of the aerial photo period. The long term MAP is 762 mm (1950–2013).

Period	Rate of woody canopy cover change	Mean rainfall for period (mm)	Mean rainfall for prior 10 years (mm)	Mean SPI for period	Mean SPI for prior 10 years
1953 to 1964	0.169	705	611	-0.165	-0.342
1964 to 1975	-0.036	801	777	0.182	0.075
1975 to 1992	0.225	785	783	0.105	0.13
1992 to 2005	1.125	803	747	0.007	-0.073
2005 to 2013	0.005	772	780	0.085	0.092

Controlling for initial canopy cover in rate analysis

The relationship between the rate of woody canopy cover change and each rainfall variable was tested using semi-partial correlation analysis in order to control for the effect of canopy cover at the start of each period. The only significant correlation was found at the arid site, where the rate of woody canopy cover change and the standardised precipitation index for the period had a positive relationship ($R^2 = 0.924$, p-value = 0.025) (Figure 14 & Table 5). No significant relationship between rate of woody cover change and any rainfall metric was found at the mesic site, not a surprising finding when one considers the consistency of rainfall across all the time periods. One noteworthy trend was the exceptionally dry period that preceded the first time point at the mesic site (1948–1952) (Table 6), but did not seem to influence woody canopy cover change in the period between 1953 and 1964.

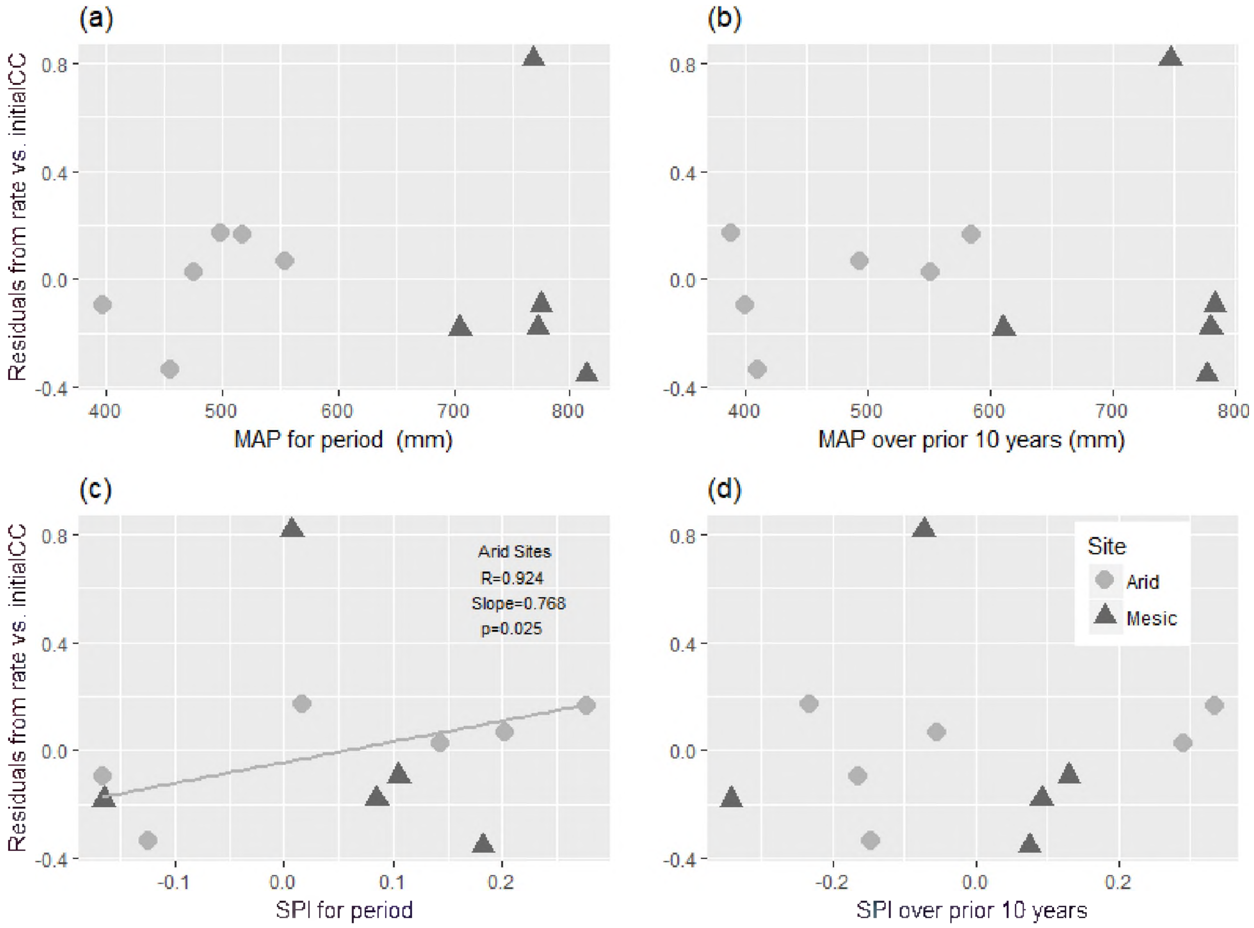

Figure 14. Scatter plot graphs showing the semi-partial correlation between the rate of woody cover change during each aerial photo period and four metrics related to rainfall, while controlling for initial canopy cover. The residuals of a regression between rate and initial canopy cover are plotted against (a) mean annual precipitation (MAP) for each aerial photo time period, (b) MAP for the ten year period ending five years prior to the end of the aerial photo period, (c) standardised precipitation index (SPI) during the period (c) and SPI for the ten year period ending five years prior to the end of the aerial photo period (d).

Discussion

Overall trends

While woody canopy cover increased at both the arid and the mesic site over the six decade study period, the rate of change for the mesic site was almost double that for the arid site. Maximum canopy cover was higher at the mesic site than at the arid site; a result consistent with contemporary models of arid grassy biomes which suggest that moisture availability is a key determinant of the maximum canopy cover that can be attained (Sankaran *et al.*, 2005; Hirota *et al.*, 2011; Lehmann *et al.*, 2011; O'Connor *et al.*, 2014).

At both sites the majority of plots either remained stable in a grass dominated state or shifted from a grassy to a woody state. The difference was that some of the arid plots showed decreased woody canopy cover, a trend that was not observed at the mesic site and that would have contributed to the lower overall rate of woody canopy cover increase at the arid site. The decreases in woody cover at the arid site are assumed to be driven by natural tree mortality during drought as management records from the sites show no active tree / shrub clearing efforts at the plot locations. Drought related mortality has been implicated in decreases in savanna canopy cover (Skarpe, 1991; Fensham *et al.*, 2009; Archer *et al.*, 2012). The results also highlight the fact that within a particular site there can be many different trajectories of change, and that obtaining a reliable estimate of overall change requires a significant sampling effort.

Rates of encroachment and rainfall/drought

Apart from the higher overall and maximum rate of increase at the mesic site, the sites differ in terms of the timing of woody canopy cover increase. The arid site shows two pulses of woody canopy cover increase (1967–1985 and 1996–2013) that are significantly correlated with periods of high moisture availability (i.e. high MAP and SPI). Although no correlation was found between rate and SPI in the prior 10 year period at the arid site, Figure 12 shows that immediately prior to each pulse of encroachment there were two or three dry years (1968–1969 and 1997–1999).

The observations of change at the arid site provide some support for previously published suggestions that periods of drought followed by periods of high rainfall may promote woody plant establishment and recruitment in arid savannas where fire is infrequent or absent (Teague, 1983; O'Connor & Crow, 1999; Kraaij & Ward, 2006). This explanation is a fusion of the demographic bottle neck and tree-grass competition models of woody encroachment (see reviews by Sankaran *et al.*, 2005; O'Connor *et al.*, 2014). In drought years grass production is reduced (potentially exacerbated by grazing pressure) which makes space for the establishment and recruitment of woody plants in the ensuing wet periods. Since the system is assumed to be water limited a high rainfall period is required to facilitate tree seedling establishment and subsequent recruitment to adult trees. The mesic site showed a single, dramatic pulse of increase in woody canopy cover between 1992 and 2005 that was not correlated with rainfall or drought and rainfall was more consistent at the mesic site than the arid site. The proposed model for mesic savannas is that drought years cause a reduction in grass production (potentially exacerbated by grazing pressure) reducing the fuel available for fire, thus promoting woody plant escape from the fire trap (Higgins *et al.*, 2000). The results suggest that the rate of encroachment at the mesic site is not related to rainfall and that without detailed fire records for the six decade time period it is impossible to evaluate the potential interaction between rainfall, grass production and fire frequency / intensity.

Alignment with previous studies

The range in rates of change reported in this study (Table 5 & Table 6) (-0.04% y^{-1} to 1.13% y^{-1}) are similar to those reported for southern Africa by O'Connor *et al.* (2014) (-0.13% y^{-1} to 1.3% y^{-1}) – where the majority of authors employ similar aerial photo based methodology. The mean rates of woody canopy cover increase observed in this study (0.34% y^{-1} for mesic sites and 0.2% y^{-1} for arid sites) bracket the mean rate of change described for African savannas (0.25% y^{-1}) (O'Connor *et al.*, 2014; Stevens *et al.*, 2017). In comparison, these rates are consistently lower than those reported for South American savannas (0.49% y^{-1}) and higher than those reported for Australian savannas (0.1% y^{-1}). The reviews undertaken by O'Connor *et al.* (2014) and Stevens *et al.* (2017) showed that the rates of change were higher in mesic than in arid sites. The reviews differ in that Stevens *et al.* (2017) ascribe accelerating rates of change to CO_2 as central, overarching driver of woody plant increase; while O'Connor *et al.* (2014) highlight the extensive changes to local herbivory and fire regimes since the mind 1900s. Bond & Midgley (2012) argue that in mesic savannas CO_2 enrichment is a more compelling driver of woody encroachment than local effects, while in arid savannas the local effects may be dominant. CO_2 enrichment allows for additional carbon allocation to the roots of encroaching woody plants, potentially accelerating woody plant growth and facilitating more rapid recovery after disturbance, leading to increasing woody plant cover (Hoffmann *et al.*, 2000; Kgope *et al.*, 2010; Bond & Midgley, 2012). Devine *et al.* (2017) take this argument further and propose that in both arid and mesic savannas CO_2 enrichment is the dominant driver of woody encroachment. In arid systems increased plant water use efficiency, caused by CO_2 enrichment (Polley, 1997), increases soil water availability and reduces the inherent limitation on maximum woody cover, resulting in increased woody plant recruitment and growth (Devine *et al.*, 2017).

In this study area *Vachelia karroo* is the dominant encroaching species and experimental evidence suggests that it has limited seedling survival below 500 mm of MAP (O'Connor, 1995b). At the arid site long term MAP is 468 mm and only wet years tend to surpass 500 mm, providing additional landscape level support for the idea that encroachment may be driven by enhanced seedling survival during abnormally wet periods (O'Connor, 1995a, 1995b). The relationships between drought / rainfall and the rate of encroachment at the arid site does not preclude the influence of local drivers such as herbivory and other global drivers such as increased atmospheric CO_2. In fact, it is likely that at any given savanna – grassland site a combination of local and global drivers contribute to woody plant encroachment, with increased atmospheric CO_2 providing a background impetus for change (Donohue *et al.*, 2013; O'Connor *et al.*, 2014; Case & Staver, 2017; Devine *et al.*, 2017).

Historical changes

Changes in herbivory and CO_2 over the last century are also useful for explaining the recent nature of the woody cover changes at both sites. A natural cycle of high and low rainfall (every 15 to18 years) is apparent for the region (and much of summer rainfall South Africa) (MacKellar *et al.*, 2014); but periods of high rainfall (or limited drought) prior to 1950 have not resulted in the entire arid savanna region shifting to a woodland state. Fensham *et al.*(2009) showed that in Australian woodlands drought events can cause sufficient tree mortality to counteract the increases during wet years. Alternatively, it is possible that prior to 1900 high browsing pressure by large indigenous mammals (elephant & black rhinoceros in particular) would have caused high tree mortality (historical review by Skead, 2007) and moderated woody canopy cover increase (Sankaran *et al.*, 2008; Daskin *et al.*, 2016; Morrison *et al.*, 2016). At the turn of the century indigenous herbivore pressure was largely replaced by domestic stock pressure, which reached a peak between 1920 and 1960 (O'Connor *et al.*, 2014). This provides a potential explanation for the generally lower levels of woody canopy cover at the start of the study period (1953/1949). Livestock numbers, specifically sheep and goats, then declined rapidly between 1940 and 1980, potentially releasing the woody plants of the region from high herbivore pressure for the first time (O'Connor *et al.*, 2014; Stevens *et al.*, 2016) – a change that would have contributed to the increase in woody canopy cover over the last 40 years. The well documented increase in atmospheric CO_2 over the last century is likely to have contributed to increased woody canopy cover, especially over the last 30 years (Bond *et al.*, 2003; Polley *et al.*, 2003; Bond & Midgley, 2012; Buitenwerf *et al.*, 2012; Donohue *et al.*, 2013; Midgley & Bond, 2015). Fire regimes in the more mesic sites – a key influence on woody canopy cover – are also likely to have changed dramatically over the last century, driven by the fragmentation of the landscape by roads and through changes to the grazer: browser ratios of managed livestock herds.

Within a single savanna type spanning a rainfall gradient of 400–900 mm MAP, sites with mean annual precipitation of approximately 760 mm have mean and maximum rates of encroachment that are double those at sites with approximately 460 mm precipitation. Periods of high rainfall and drought have played an important role in determining the rate of woody encroachment at the arid site, but not at mesic sites. Both of these findings provide support for current conceptual models of savanna canopy cover change. The rapid and recent increases in woody canopy cover observed are consistent with changes observed regionally and globally. The changes are likely to be a result of not only rainfall / drought as I have found but of a combination of release from herbivore pressure and increased atmospheric CO_2 over the last half century.

Chapter 3: Demography of *Vachelia karroo* at an arid and mesic savanna site with histories of bush encroachment

Abstract

Field transect data were used to investigate the size class distributions and general architecture of *Vachelia karroo* in a savanna – grassland landscape in the Eastern Cape Province of South Africa. The aim was to compare the demographic profiles and allometry of *V. karroo* at the arid vs. mesic sites and determine if the demographics reflect the proposed mechanisms of encroachment. The sites were closely matched in terms of herbivore management, species composition, soil characteristics and topography. Previous research and savanna models predict seedling and sapling dominated demographics at the mesic site and adult dominated demographics at the arid site. Growth forms of *V. karroo* were predicted to be "pole-like" at the mesic site and "cage-like" at the arid site reflecting the dominant disturbances, fire and herbivory. The findings support the idea that fire has shaped both the demographics and architecture of *V. karroo* at the mesic site and conform to current conceptual models. Stunted saplings (gullivers) dominated the mesic site demographic profile and were rare at the arid site, except at stable woodland sites. The adult plants (trees) at the arid site had canopies that started significantly closer to the ground than at the mesic site (55 cm vs. 165 cm); possibly reflecting the dominant disturbance factors at the sites (sheep herbivory vs. fire). The results provide support for the use of mean annual precipitation thresholds for understanding savanna dynamics.

Introduction

Demographic models of woody plant encroachment in savannas are summarized in Table 7 and Figure 1. These models suggest that populations in arid sites will be most limited at the seedling establishment stage, an "establishment bottleneck" (Higgins *et al.*, 2000; Sankaran *et al.*, 2005); resulting in relatively low numbers of seedlings, except after an establishment pulse and a relatively flat, or in some cases, adult skewed demography (Figure 1). The potential drivers of encroachment at these sites include increased moisture availability (due to climate change or via the influence of elevated CO_2) (Polley *et al.*, 2003; Kgope *et al.*, 2010; Drake *et al.*, 2017), reduced direct browsing pressure or increased grazing which limits competition grasses (Teague, 1983; O'Connor, 1995b; Van Auken, 2009; O'Connor *et al.*, 2014). These demographic models suggest that population growth in mesic sites will be most limited by release of saplings into adult size classes, a "recruitment bottleneck"; resulting in large numbers of seedlings and many gullivers held back by disturbances (including fire and herbivory) (Figure 1). Recruitment, in this situation, is equivalent to escape from the disturbance trap and is driven by one, or an interaction between the following: i) interruption of the fire cycle (Balfour & Midgley, 2008; Wakeling *et al.*, 2011; Buitenwerf *et al.*, 2012; Case & Staver, 2017), ii) increased growth rate due to CO_2 fertilization (Bond & Midgley, 2000; Polley *et al.*, 2002; Bond, 2008; Wigley *et al.*, 2009a; Drake *et al.*, 2017), ii) reduced browsing (Staver *et al.*, 2009; O'Connor *et al.*, 2014; Staver & Bond, 2014), and iv) through increased grazing which limits fuel load, reducing fire intensity or lengthening fire return interval (Trollope, 1980; Staver *et al.*, 2009; O'Connor *et al.*, 2014).

Root niche differentiation models of woody plant encroachment focus on the competition between grasses and woody plants for soil moisture (Knoop & Walker, 1985; Kraaij & Ward, 2006; Kambatuku *et al.*, 2013). These models suggest that in arid savannas, grasses typically out-compete woody plants when their roots are in the same depth zone, resulting in low seedling establishment rates in all but the wettest years when soil moisture is not a limiting factor. The demographic profile in this situation is expected to be adult dominated.

Table 7. Key drivers of woody plant encroachment in African grassy biomes. Up arrows indicate an increase in the driver and down arrows indicate a decrease.

Primary driver	Secondary driver	Establishment / Recruitment	Arid	Mesic	Reference
↓Browsing		Both	✓	✓	(Staver *et al.*, 2009; O'Connor *et al.*, 2014; Staver & Bond, 2014)
↑Grazing	↓Fire	Recruitment		✓	(Trollope, 1980; Staver *et al.*, 2009; O'Connor *et al.*, 2014)
↑Gazing	↑Moisture Availability	Establishment	✓		(Teague, 1983; O'Connor, 1995b; Van Auken, 2009; O'Connor *et al.*, 2014)
↑CO_2	↑Moisture Availability	Establishment	✓		(Polley *et al.*, 2003; Kgope *et al.*, 2010; Drake *et al.*, 2017)
↑CO_2	↑Growth Rates	Recruitment		✓	(Bond & Midgley, 2000; Polley *et al.*, 2002; Bond, 2008; Wigley *et al.*, 2009a; Drake *et al.*, 2017)
↓Fire		Recruitment		✓	(Balfour & Midgley, 2008; Wakeling *et al.*, 2011; Buitenwerf *et al.*, 2012; Case & Staver, 2017)

The potential drivers of woody encroachment under this model are increased rainfall, which aids woody plant establishment, and heavy grazing, which suppresses the grass layer, further favouring the establishment of woody plant seedlings (Kraaij & Ward, 2006; Kambatuku *et al.*, 2013; Smit & Prins, 2015). February *et al.* (2013) on the other hand, found that juvenile tree growth was not positively influence by rainfall but by low grass biomass and that grass biomass increased with increasing rainfall. Their study straddled the rainfall threshold of ~650mm MAP (547–762mm MAP) and the results suggest that in both arid and mesic savannas high grass biomass could limit tree establishment and recruitment (February *et al.*, 2013). Sankaran *et al.* (2005) suggest that these models for savanna dynamics are complimentary and that the root niche differentiation is the mechanism that limits seedling establishment at arid sites.

Demography

Balfour & Midgley (2008) studied *V. karroo* demography at a mesic site in South Africa and concluded that woody plant encroachment was driven primarily by the release of already established individuals (due to interruption of the fire cycle) and not through the establishment of new individuals. These established individuals, which are stunted in terms of height but have substantial underground organs, have been named "gullivers" by previous researchers (Bond & Van Wilgen, 1996) and I follow this convention. Differentiating between seedlings, gullivers and saplings is therefore crucial to understanding *V. karroo* population dynamics – as illustrated by Wigley *et al.* (2013).

Previous research conducted at a site approximately 5 km from my mesic site (O'Connor & Chamane, 2012) showed a relatively large number of *V. karroo* individuals less than 50 cm in height but did not investigate underground organs and hence did not differentiate between seedlings and gullivers. Puttick *et al.*(2014a) investigated *V. karroo* plant height less than 20 km from my arid site and showed that individuals between 1.5 and 2.7 m were most prevalent in locations under commercial rangeland management (equivalent to the management at my arid site). They also found that individuals under 30 cm (likely to be true seedlings) were very uncommon. Previous research therefore shows seedling / gulliver dominated size class distributions at the mesic site and adult dominated size class distributions at the arid site. A large pool of gullivers are expected at mesic savanna sites where fires regularly damage the above ground parts of woody plants, adding successive cohorts of seedlings and saplings to the gulliver pool (Bond & Van Wilgen, 1996; Higgins *et al.*, 2000; Balfour & Midgley, 2008). Gullivers are not expected to make up a significant proportion of the woody plants at arid savanna sites due to the lack of fire (Higgins *et al.*, 2000), though heavy browsing pressure could lead to a significant gulliver pool (Staver *et al.*, 2009; Staver & Bond, 2014).

Plant architecture

The growth form and architecture of *V. karroo*, which dominates the tree layer at both sites, is strikingly differences between populations in forest (large, typical tree architecture to compete for light in forest), fire prone mesic savanna ("pole-like" architecture as an adaptation to fire) and hyper arid shrubland environments ("cage-like" architecture to defend against herbivory) (Archibald & Bond, 2003; Ward, 2011; Staver *et al.*, 2012; Taylor & Barker, 2012). This study differs from previous research in that the sites are similar in terms of climate (apart from MAP), soils, species composition and topography (Figure 6). The growth form differences between populations of *V. karroo* growing less than 120 km apart and differing only in MAP and fire regime have not been tested to my knowledge.

Key questions

In this chapter I compare *V. karroo* demographic profiles at an arid and a mesic savanna site by undertaking a transect-based census of *V. karroo* populations at locations known to have a history of woody canopy cover increase. I supplemented these transects with transects at nearby locations that were known to be stable in terms of woody canopy cover. I set out to test a selection of existing models of bush encroachment that predict that:

i. At the fire prone (mesic) site gullivers will be relatively more frequent than at the arid site where fire is largely absent;
ii. Rainfall driven seedling establishment events will have resulted in relatively even or adult dominated demographic profiles at the arid site when compared to mesic site where young plants are expected to outnumber older plants;
iii. The growth form of *V. karroo* at fire prone mesic site will be "pole-like" while the plants at the fire free arid site will be more "cage-like" in their architecture.

The history of encroachment at the sites is also a factor to be considered and I do so by comparing stable woodland transects at the arid site with transects that have shown woody cover increase.

Methods

<u>Study site</u>

Two field study sites, within *Vachelia karroo* dominated savanna-grasslands, were identified in the Smaldeel region of the Eastern Cape Province, South Africa (Figure 6). The sites are representative of the bioregion in terms of topography, management and history. One site was located in the arid portion of the region (~440 mm MAP) and one site was located in the mesic portion of the region (~760 mm MAP) (see Chapter 2 for a full site description) (Figure 6). Field work took place in 2013 and 2014.

<u>Transect data</u>

Ten 400 m x 2 m belt transects were set up on the farm Haddon (arid site, 440 mm MAP) and on the farm Killaloe (mesic site, 762 mm MAP) using GIS tools. Transects were separated by at least 100 m. I used 400 m transects in an attempt to capture the inherent variation in the landscape. On each transect all *V. karroo* individuals with stems falling within the 400 m x 2 m area were measured for a range of variables (Table 8) including height, canopy width, canopy depth, stem diameter at soil surface, stem diameter 2 cm below the soil surface and number of stems. Each transect took approximately four hours for two investigators to complete due to the time consuming task of searching for smaller *V. karroo* individuals in the grass sward and to the excavation around each stem to determine subsurface stem diameter. Derived measures included the ratio of plant height to subsurface stem diameter, basal diameter to subsurface stem diameter and canopy height to width. By combining plant height, subsurface diameter and basal diameter to subsurface diameter ratios, plants were classified into the following growth stages: seedling, gulliver, sapling and tree (Table 8). The objective was to separate true seedlings and saplings from stunted individuals (gullivers) which have large underground organs and are likely to have resprouted following disturbance (fire or herbivory) a number of times (after Bond & Van Wilgen, 1996). The wide range of measurements taken of each *V. karroo* individual allowed for an allometric comparison of tree architecture between the sites.

Following the aerial photo analysis methodology described in Chapter 2, I determined the woody canopy cover history for each transect. At the arid site five transects showed a history of woody canopy increase (referred to as woody increase transects / localities) and five showed stable woody canopy (referred to as stable woodland transects / localities). At the mesic site five transects showed woody canopy cover increase and five showed stable, low woody cover (referred to as stable grassland transects or localities). This allowed for demographic comparisons within the sites and between the sites.

Analyses

Demographic differences between the arid site and the mesic site were tested using Kruskal-Wallis tests (the size class distributions were not normally distributed) and differences between classes were tested using Dunn's *post hoc* test in conjunction with Kruskal-Wallis tests. For the allometric analyses I grouped the *V. karroo* plants into two groups: plants > 2 m in height (trees) and plants < 2 m in height (seedlings, saplings & gullivers). Using one-way analysis of covariance (ANCOVA), I tested the difference between the arid and mesic site for four measures of architecture: i) height of lowest leaf, ii) canopy depth, iii) canopy width and iv) basal stem diameter, while statistically controlling for variation caused by tree height. Plants < 2 m in height (seedlings, saplings & gullivers) were only measured for stem basal diameter and canopy width, canopy depth and lowest leaf were not measured).The requirements of ANCOVA were met in that each of the four measures of architecture, once $\log_e$ transformed (natural logarithm), were significantly correlated with tree height (Table 9). At the arid site height of lowest leaf was not significantly correlated with plant height, but since the correlation was significant when the data for the arid and mesic sites were considered together, ANCOVA remains a valid test (Field *et al.*, 2012). All the analyses were performed using RStudio interface for R v3.02 (R Core Team, 2014), with packages "reshape" (Wickham, 2007), dplyr (Wickham & Francois, 2015), "Dunn's test" (Dinno, 2016), "ggplot2" (Wickham, 2009) and "lattice" (Deepayan, 2008).

Table 8. Field measurements and derived measurements and ratios for each *V. karroo* plant.

Variable	Description and Unit
SITE	Farm on which transect was done
TRANSECT	Unique transect name
HT	Plant height (cm)
CANWIDTH	Canopy width (cm)
CANDEPTH	Canopy Depth (cm): top of canopy to lowest leaf
DIAMBASAL	Stem basal diameter (cm)
SUBSDIAM	Stem sub-surface diameter (cm) measured 2 cm below soil surface by excavating each plant (plants with diameter > 8 cm were not excavated)
TYPE	multi stemmed = m; single stemmed = s
STEMSBASE	number of stems at base (count)
R_ht:ssd	Ratio of height to sub surface diameter
R_bd:ssd	Ratio of basal diameter to sub surface diameter
R_ht:wid	Ratio of height and canopy depth; gives an indication of shape.
LOWLEAF	Height of lowest leaf of plants > 2 m (tree); calculated by subtracting canopy depth from height
SSDCL	Stem sub-surface diameter class (cm) (measured 2 cm below soil surface by excavating each plant); bins used: BIN1 = 0 to 0.5; BIN2 = 0.6 to 1; BIN3 = 1.1 to 2; BIN4 = 2.1 to 4; BIN5 = 4.1to 8; BIN6 > 8
HTCL	Plant Height class (cm); bins used: BIN1= 0 to 30; BIN2 = 31to 60; BIN3 = 61 to 100; BIN4 = 101 to 200; BIN5 = 201 to 300; BIN6 > 300
STAGE	Life history stage of the plant: Seedling, Gulliver, Sapling, Tree Formula: IF(HT < 0.6,"Seedling", IF(AND (HT < 100, BD:SSD < 0.81),"Gulliver", IF(HT < 200, "Sapling", "Tree")))

Table 9. Relationships between height and height of lowest leaf, canopy width, canopy depth & basal stem diameter for *V. karroo* trees (greater than 2 m in height) and seedlings, saplings & gullivers (less than 2 m in height). All measures were $\log_e$ transformed.

	Arid				Mesic			
Height vs.	slope	df	R^2	p	slope	df	R^2	p
lowest leaf (>2 m)	0.37	123	0.004	0.48	1.10	100	0.268	<0.001
canopy depth (>2 m)	1.14	123	0.498	<0.001	1.03	100	0.225	<0.001
canopy width (>2 m)	0.92	123	0.315	<0.001	1.23	100	0.290	<0.001
stem diameter (>2 m)	1.52	123	0.347	<0.001	1.12	100	0.364	<0.001
canopy width (<2 m)	1.35	308	0.710	<0.001	1.20	307	0.645	<0.001
stem diameter (<2 m)	0.96	308	0.739	<0.001	0.94	307	0.716	<0.001

Results

General

The density of plants in the arid woody increase transects was slightly lower than for stable woodlands; 692 ha^{-1} vs. 1082 ha^{-1} (Table 10). The density of plants on mesic woody increase transects was significantly higher than for stable grasslands; 1947 ha^{-1} vs. 167 ha^{-1} (Table 10).

Table 10. Total number and density of *V. karroo* plants at each transect

Arid site				Mesic Site			
Transect	Total	Density (ha^{-1})	Site type	Transect	Total	Density (ha^{-1})	Site type
Ha1	76	950	Woody Cover Increase	Ki1	128	1600	Woody Cover Increase
Ha2	68	850	Woody Cover Increase	Ki2	138	1725	Woody Cover Increase
Ha5	35	438	Woody Cover Increase	Ki3	145	1813	Woody Cover Increase
Ha6	28	350	Woody Cover Increase	Ki4	224	2800	Woody Cover Increase
Ha7	70	875	Woody Cover Increase	Ki5	144	1800	Woody Cover Increase
Ha3	75	938	Stable Woodland	Ki6	6	75	Stable Grassland
Ha4	83	1038	Stable Woodland	Ki7	12	150	Stable Grassland
Ha8	81	1013	Stable Woodland	Ki8	0	0	Stable Grassland
Ha9	96	1200	Stable Woodland	Ki9	27	338	Stable Grassland
Ha10	98	1225	Stable Woodland	Ki10	22	275	Stable Grassland

Demography

For many transects, the height and subsurface stem diameter size class distributions were significantly different (Appendix 1). This was particularly prevalent where stunted individuals with relatively thick stems and low height were common. The growth stage classes used in this study effectively combined these measures and provided an alternative demographic measure that highlights the number of gullivers caught in the fire or herbivore trap. At the arid site the stable woodland transects and woody increase transects shared similar demographic profiles except for gullivers which were significantly more prevalent in the stable woodland transects (Table 11 & Figure 15). At the mesic site, woody increase transects had significantly more plants than the stable grassland transects in every growth stage category and every height and subsurface stem diameter size class (Table 11 & Figure 16).

Considering only the woody increase transects at each site (n = 5) allowed me to investigate the differences between the size classes at each site and between the sites for each size class (arid vs. mesic). Arid woody increase transects had relatively even demographic profiles when looking at height and subsurface stem diameter, but the growth stage profile revealed that seedlings were significantly less prevalent that older plants (Table 12 & Figure 15). At the equivalent mesic transects gullivers, plants with subsurface stem diameters 0.6–1 cm, and plants less than 60 cm in height dominated the demographic profiles (Table 13 & Figure 16). Comparisons between sites for each size class showed that the mesic site had far more gullivers than the arid site, but also significantly more seedlings and saplings (Table 11 & Figure 17). The sites were similar in terms of tree numbers.

Table 11. Results of Kruskal-Wallis tests of variance within and between sites for each stage, subsurface stem diameter class and height class. Significant differences indicated with *.

		Arid site			Mesic site			Transects with woody cover increase		
		Stable woodland vs. Grassland-woodland			Stable grassland vs. Grassland-woodland			Arid vs. Mesic		
		Chi	p		Chi	p		Chi	p	
Growth stage	Seedling	1.3	0.249		6.860	0.009	**	5.8	0.016	*
	Gulliver	6.9	0.009	**	6.818	0.009	**	6.8	0.009	**
	Sapling	2.2	0.142		6.988	0.008	**	4.8	0.028	*
	Tree	0.0	0.834		7.759	0.005	**	0.9	0.344	
Sub surface diameter (cm)	0–0.5	1.3	0.249		6.860	0.009	**	5.8	0.016	*
	0.6–1	1.6	0.202		6.860	0.009	**	6.9	0.009	**
	1.1–2	5.4	0.020	*	6.860	0.009	**	6.5	0.011	*
	2.1–4	2.8	0.093		7.305	0.007	**	3.2	0.074	
	4.1–8	0.0	0.834		7.813	0.005	**	0.5	0.463	
	>8	0.1	0.753		7.759	0.005	**	2.5	0.116	
Height (cm)	0–30	3.2	0.075		6.818	0.009	**	6.9	0.009	**
	31–60	2.5	0.115		6.860	0.009	**	6.8	0.009	**
	61–100	1.3	0.246		5.345	0.021	*	0.6	0.458	
	101–200	3.6	0.059		6.988	0.008	**	2.5	0.115	
	201–300	0.4	0.527		7.813	0.005	**	0.0	0.916	
	>300	0.2	0.674		7.813	0.005	**	2.5	0.115	

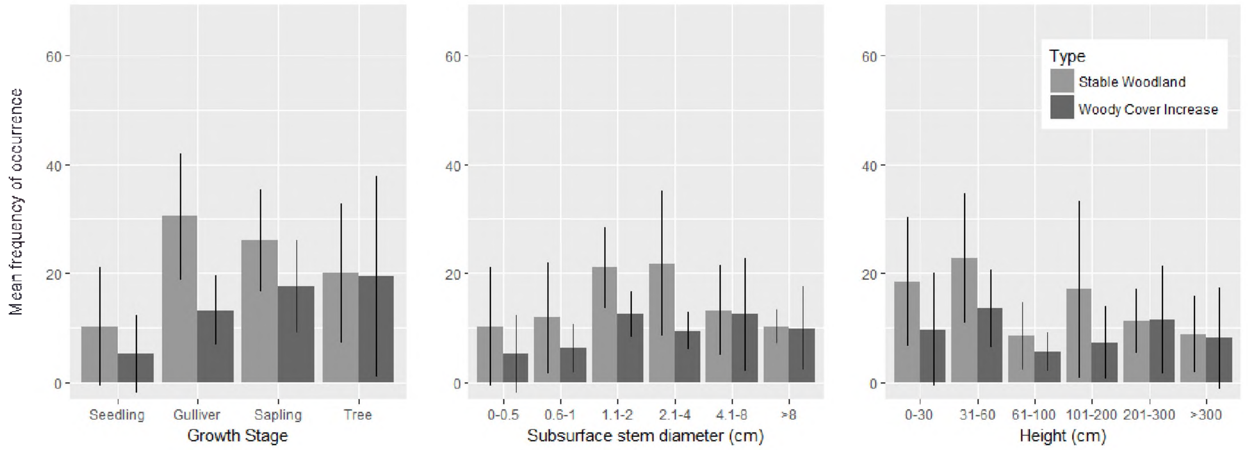

Figure 15. Demographic profiles for the arid site comparing stable woodland transects and woody cover increase transects.

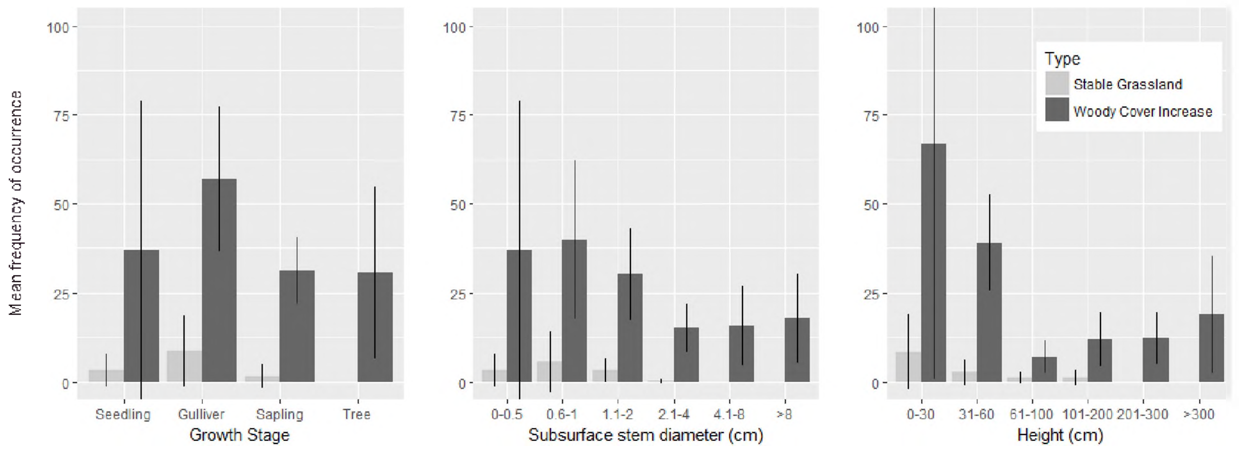

Figure 16. Demographic profiles for the mesic site comparing stable grassland transects and woody cover increase transects

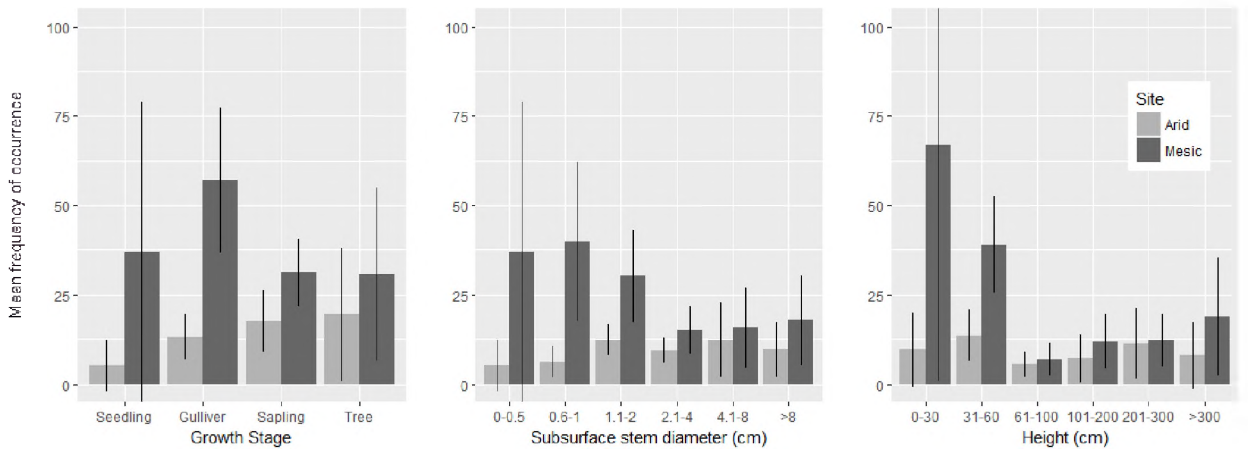

Figure 17. Demographic profiles for transects with a history of woody canopy cover increase, comparing arid and mesic sites.

Table 12. Results of Dunn's post hoc test from the arid site (based on Kruskal-Wallis test of variance) between the stage, subsurface stem diameter and height classes for transects showing woody cover increase. Dunn's test z values are shown in the matrix with p-values in brackets – significant differences indicated with *

Arid site: transects with woody canopy cover increase – comparison between classes					
Differences between growth stages (Kruskal-Wallis Chi-squared = 7.0727, df = 3, p-value = 0.07, Dunn's post hoc test)					
Growth stage	Seedling	Gulliver	Sapling		
Gulliver	-1.65 (0.048)*				
Sapling	-2.46 (0.007)**	-0.80 (0.211)			
Tree	-2.08 (0.0184*	-0.42 (0.334)	0.37 (0.353)		
Differences between subsurface stem diameter classes (Kruskal-Wallis Chi-squared = 7.7681, df = 5, p-value = 0.17, Dunn's post hoc test)					
Subsurface stem diameter class (cm)	0–0.5	0.6–1	1.1–2	2.1–4	4.1–8
0.6-1	-0.39 (0.345)				
1.1-2	-2.31 (0.01)	-1.91 (0.027)			
2.1-4	-1.46 (0.071)	-1.06 (0.143)	0.84 (0.198)		
4.1-8	-1.87 (0.030)*	-1.48 (0.069)	0.43 (0.332)	-0.41 (0.34)	
>8	-1.42 (0.077)	-1.03 (0.152)	0.88 (0.189)	0.04 (0.49)	0.45 (0.329)
Differences between height classes (Kruskal-Wallis Chi-squared = 6.1781, df = 5, p-value = 0.29, Dunn's post hoc test)					
Height class (cm)	0–30	31–60	61–100	101–200	201–300
31-60	-1.26 (0.104)				
61-100	0.84 (0.199)	2.10 (0.018)*			
101-200	0.49 (0.313)	1.74 (0.040)*	-0.36 (0.359)		
201-300	-0.65 (0.282)	0.61 (0.270)	-1.49 (0.067)	-1.14 (0.13)	
>300	0.36 (0.359)	1.62 (0.052)	-0.47 (0.313)	-0.13 (0.45)	1.01 (0.157)

Architecture

A series of one-way ANCOVAs was conducted to compare the growth form of *V. karroo* at the arid and mesic sites whilst controlling for plant height. For plants over 2 m in height (trees), there were significant differences in height of lowest leaf [$F(1,224) = 63.14$, $p < 0.001$], canopy depth [$F(1,224) = 89.23$, $p < 0.001$] and canopy width [$F(1,224) = 6.72$, $p = 0.01$] between the sites (Figure 18 & Table 14). The differences were related to magnitude of change of the dependent variable not the rate of change (i.e. there were no interactions between the dependent variable and the site) (Figure 18). Stem basal diameter of trees did not differ significantly between the sites (Figure 18).

For *V. karroo* seedlings, saplings and gullivers (i.e. height < 2 m), there were significant differences in canopy width [$F(1,616) = 131.5$, $p < 0.001$] and stem basal diameter [$F(1,616) = 15.8$, $p < 0.001$] between the sites (Table 14 & Figure 19). The differences in canopy width were related to both the magnitude and rate of change of the canopy width vs. height (i.e. there were significant interactions between the dependent variable and the site) (Figure 19). The differences in stem basal diameter of seedling/saplings/gullivers were related to magnitude only (i.e. no interactions) (Figure 19). *V. karroo* trees at the arid site have deeper canopies that start nearer to ground level than those at the mesic site (Figure 20).

Table 13. Results of Dunn's post hoc test from the mesic site (based on Kruskal-Wallis test of variance) between the stage, subsurface stem diameter and height classes for transects showing woody cover increase. Dunn's test z values are shown in the matrix with p-values in brackets – significant differences indicated with *.

Mesic site: transects with woody canopy cover increase – comparison between classes					
Differences between growth stages (Kruskal-Wallis Chi-squared = 7.0727, df = 3, p-value = 0.07, Dunn's post hoc test)					
Growth stage	Seedling	Gulliver	Sapling		
Gulliver	-2.06 (0.019)*				
Sapling	-0.21 (0.415)	1.84 (0.033)*			
Tree	0.03 (0.489)	2.09 (0.019)*	0.24 (0.405)		
Differences between subsurface stem diameter classes (Kruskal-Wallis Chi-squared = 7.7681, df = 5, p–value = 0.17, Dunn's post hoc test)					
Subsurface stem diameter class (cm)	0–0.5	0.6–1	1.1–2	2.1–4	4.1–8
0.6–1	-1.03 (0.153)				
1.1–2	-0.43 (0.333)	0.5 (0.277)			
2.1–4	1.80 (0.036)*	2.82 (0.002)**	2.23 (0.013)*		
4.1–8	1.60 (0.055)	2.63 (0.004)**	2.03 (0.021)*	0.20 (0.421)	
>8	1.19 (0.118)	2.21 (0.014)*	1.62 (0.053)	0.61 (0.271)	-0.41 (0.340)
Differences between height classes (Kruskal-Wallis Chi-squared = 6.1781, df = 5, p-value = 0.29, Dunn's post hoc test)					
Height class (cm)	0–30	31–60	61–100	101–200	201–300
31–60	0.40 (0.35)				
61–100	3.58 (0.002)**	3.18 (0.007)**			
101–200	2.71 (0.003)**	2.32 (0.010)*	-0.86 (0.19)		
201-300	2.68 (0.004)**	2.28 (0.0112)*	-0.89 (0.18)	-0.04 (0.49)	
>300	2.06 (0.019)*	1.67 (0.047)*	-1.51 (0.066)	-0.65 (0.259)	0.61 (0.27)

Table 14. Descriptive statistics for *V. karroo* growth form measures.

	Arid			Mesic		
Measure	mean	sd	n	mean	sd	n
HT tree	286.00	60.34	125	330.49	75.09	102
Canopy depth (tree)	213.46	67.10	125	166.12	71.25	102
Canopy width (tree)	288.59	90.08	125	308.62	126.68	102
Height of lowest leaf (tree)	72.59	47.95	125	164.37	66.52	102
Stem diameter (tree)	10.43	6.38	125	11.77	6.88	102
Height (seedling, sapling, gulliver)	59.49	47.44	310	47.33	43.51	309
Canopy width (seedling, sapling, gulliver)	59.14	58.14	310	25.95	39.11	309
Stem diameter (seedling, sapling, gulliver)	1.70	1.73	310	1.18	1.32	309

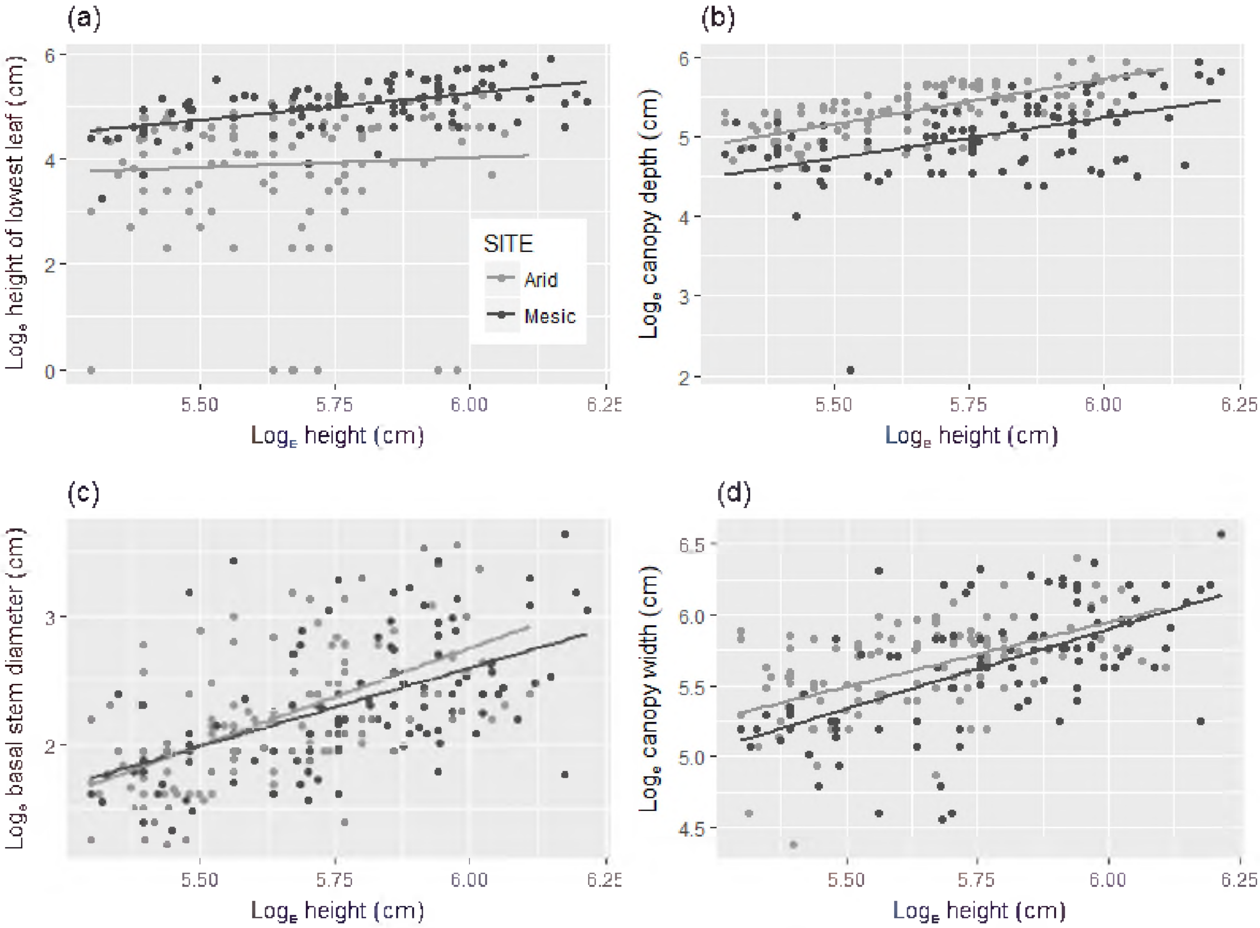

Figure 18. Allometry for *V. karroo* plants > 2m in height (trees) at the arid and mesic sites; plots show the relationship between plant height and height of lowest branch (a); plant height and canopy depth (b); plant height and stem diameter (c); and plant height and canopy width (d).

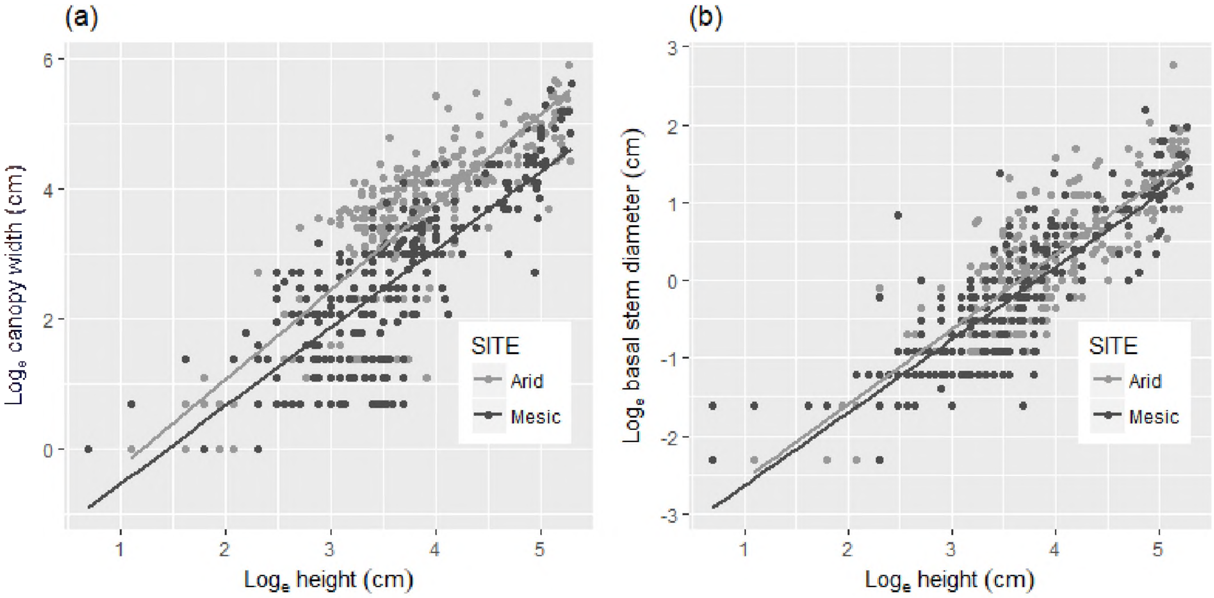

Figure 19. Allometry for *V. karroo* plants < 2 m in height at the arid and mesic sites; plots show the relationship between height and canopy width (a); height and stem basal diameter (b).

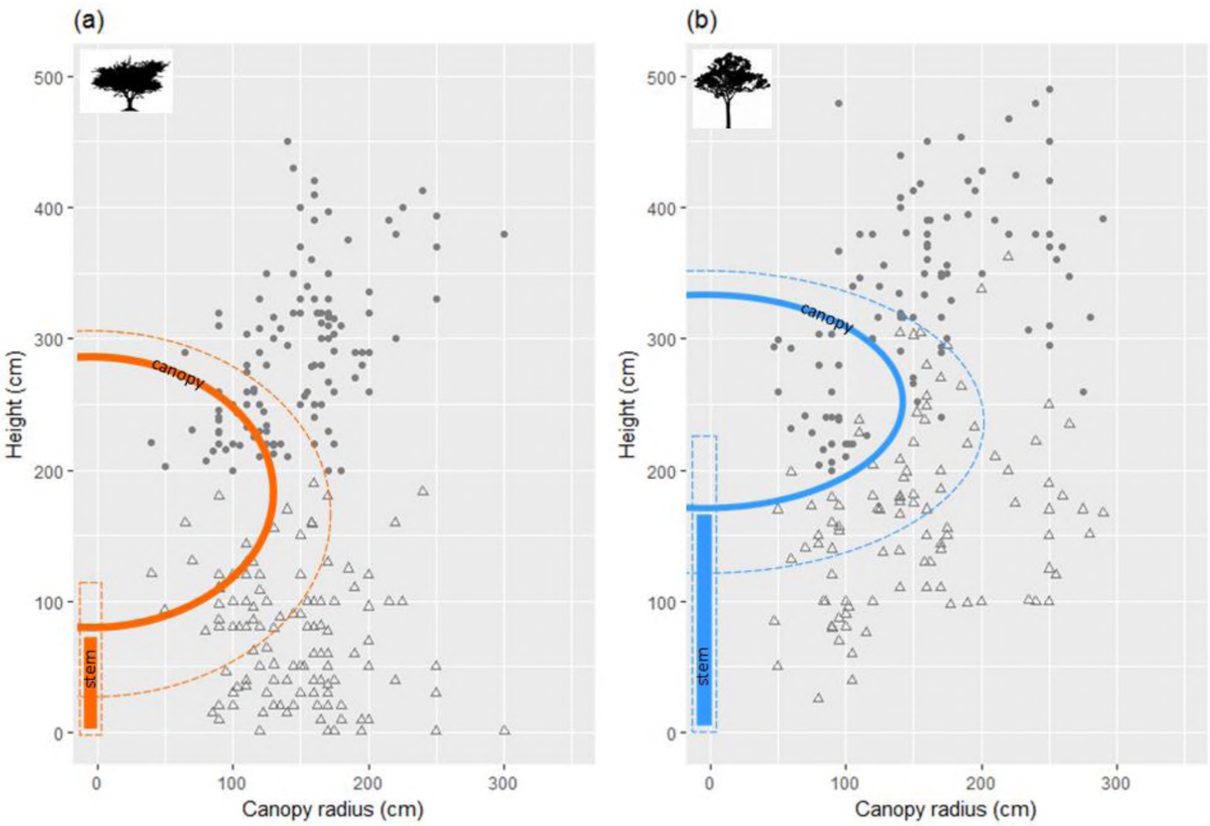

Figure 20. Canopy profile of *V. karroo* trees (> 2 m height) at the arid (a) and mesic (b) sites. The grey dots represent tree height and the grey triangles represent the height of the lowest leaf. Overlaid on the scatter plot are schematic diagrams of mean tree dimensions with the arid site in orange and mesic site in blue. The solid oval represents the mean canopy radius and depth. The solid vertical bar is the mean height of lowest leaf. The dashed lines represent the standard deviations of the values.

Discussion

Demography

The different demographic profiles of the arid and mesic sites lend support to the idea of distinctive savanna dynamics on either side of a moisture availability threshold (Higgins *et al.*, 2000; Sankaran *et al.*, 2008; Lehmann *et al.*, 2011). On the mesic side of the threshold seedling establishment is high (due to high moisture availability) and disturbance shapes the demographic profile of *V. karroo*, resulting in large number of gullivers. The absence of fire on the arid side of the threshold may result in lower numbers of gullivers and the lower moisture availability limits *V. karroo* seedling establishment.

The low number of seedlings and gullivers at arid locations with a history of woody cover increase suggests that establishment is the limiting step for *V. karroo*, a finding well aligned with previous studies and with existing models of savanna demography (Higgins *et al.*, 2000; Midgley & Bond, 2001; O'Connor *et al.*, 2014; Puttick *et al.*, 2014a). However, stable woodland locations at the arid site showed a demographic profile similar to that of the mesic site, with dominance by gullivers. This is difficult to explain but could be a result of unmeasured variables such as subtle differences in livestock utilization or through shading by tree canopies. The stable woodland and woody increase locations at the arid site had very similar tree density and the mesic site had 50% higher tree density, suggesting that maximum tree density may be linked to MAP, a finding that is well aligned with previous global and local work (Sankaran *et al.*, 2005, 2008; Lehmann *et al.*, 2011; Staver *et al.*, 2011b; O'Connor *et al.*, 2014).

From a methodological point of view the comparison of growth stage, subsurface stem diameter and plant height based profiles highlights the shortcoming of using height alone as a measure in demographic profiles. Figure 16c, based on plant height suggests that seedlings were the dominant individuals at the mesic sites, while mid-sized individuals were scarce. Figure 16a, on the other hand, tells a different story; showing that true seedlings were outnumbered by stunted mid-aged gullivers that dominate the profile. The short gullivers (< 50 cm) are far more likely to survive fire and herbivory and become adult trees than true seedlings of the same height and need to be considered separately when studying demography or managing a rangeland (Wigley *et al.*, 2013).

Architecture

The results show striking differences in *V. karroo* growth form between the sites. For plants < 2 m in height (including seedlings, saplings and gullivers) plants at the mesic site had narrow canopies and slender stems when compared to the plants at the arid site – matching previous research comparing growth forms (Archibald & Bond, 2003). The assumption here is that the presence of fire at the mesic site acts as a selective pressure favouring genotypes of *V. karroo* that pass through the fire zone as rapidly, by committing resources to vertical growth rather than horizontal growth (Higgins *et al.*, 2000; Archibald & Bond, 2003; Staver *et al.*, 2012). Balfour & Midgley (2006) showed that stem width was another important factor in determining *V. karroo* sapling fire survival in a similar mesic savanna.

For plants > 2 m in height (trees) vertical canopy shape was the key difference between the arid and mesic site. At the mesic site tree canopies started on average 165 cm above the ground. At the arid site many trees had canopies starting at ground level and on average the lowest leaves were 55 cm above the ground (Figure 20). These height differences correspond well with main sources of disturbance at each site. The expected flame heights at the mesic site are close to 165 cm (Trollope, 1974, 1980; Trollope & Tainton, 1986); and sheep, the main mixed feeder at the arid site, feed predominantly in the 0–50 cm range (du Plessis *et al.*, 2004). Previous research has compared *V. karroo* populations from very different biomes (Karoo shrubland, savanna & forest), separated by large distances. This study, in contrast, compares populations separated by only 120 km and occupying very similar environments (but not in terms of rainfall and fire). The genetic basis for the clear morphological differences between these sites remain to be tested (Taylor & Barker, 2012).

Implications for managers

The low number of *V. karroo* individuals encountered at the stable grasslands locations at the mesic site suggests that these areas are unlikely to see significant canopy cover increases in the next 5–10 years. However, given the rapid and recent encroachment in the region, revealed in the aerial photograph analyses (Chapter 2), managers should remain vigilant to the invasion of these areas by seedlings if they hope to maintain them in a low canopy cover state. The high numbers of recruits (seedlings, saplings and gullivers) at the mesic woody cover increase transects suggest that canopy cover may increase in future, or is unlikely to decline naturally. The high number of gullivers at these mesic sites also indicates that clearing programmes are likely to require extensive follow up treatment to deal with resprouting plants. In contrast, the arid woody increase sites have relatively few new recruits and gullivers are rare. Rapid future canopy cover increases are therefore unlikely and clearing programmes are more likely to succeed in these arid areas.

There is also mounting evidence that anthropogenic CO_2 enrichment is a key driver of woody plant encroachment in both arid and mesic African savannas (Bond & Midgley, 2012; Devine *et al.*, 2017; Stevens *et al.*, 2017). Higher atmospheric CO_2 may promote seedling establishment in arid savannas, due to increased water use efficiency, thus facilitating woody encroachment (Polley, 1997; Polley *et al.*, 2003; Eamus & Palmer, 2007; Devine *et al.*, 2017; Drake *et al.*, 2017). In mesic savannas higher atmospheric CO_2 may drive woody plant encroachment by enhancing allocation of carbon to roots, thus increasing the plants ability to resprout after disturbance, allowing a higher proportion of gullivers and seedlings to grow through the “fire trap” or “browser trap” (Wigley *et al.*, 2009b; Bond & Midgley, 2012; Devine *et al.*, 2017). At a local scale, fire and herbivore management may still dominate rangeland management decisions, but in many regions managers now need to adapt to and contend with these on-going global trends in savanna vegetation change (Case & Staver, 2017; Stevens *et al.*, 2017).

Chapter 4: Woodland expansion in South African grassy biomes based on satellite observations (1990–2013): general patterns and potential drivers[8]

Abstract

Increases in woody plant cover in savanna-grassland environments have been reported on globally for over 50 years and are generally perceived as a threat to rangeland productivity and biodiversity. Despite this, few attempts have been made to estimate the extent of woodland increase at a national scale; principally due to technical constraints such as availability of appropriate remote sensing products. In this study I aim to measure the extent to which woodlands have replaced grasslands in South Africa's grassy biomes. I use multi-season Landsat data in conjunction with satellite L-band radar backscatter data to estimate the extent of woodlands and grasslands in 1990 and 2013. The method employed allows for a unique, nation-wide measurement of transitions between grassland and woodland classes in recent decades. I estimate that during the 23 year study period woodlands have replaced grasslands over ~57 000 km^2 and conversely that grassland have replaced woodlands over ~30 000 km^2; a net increase in the extent of woodland of ~27 000 km^2 and an annual increase of 0.22%. The changes varied markedly across the country; areas receiving over 500 mm mean annual precipitation showed higher rates of woodland expansion than regions receiving less than 500 mm (0.31% y^{-1} & 0.11% y^{-1} respectively). Protected areas with elephants showed clear loss of woodlands (-0.43% y^{-1}) while commercial rangelands and traditional rangelands showed increases in woodland extent (> 0.19% y^{-1}). The woodland change map presented here provides an opportunity to test the numerous models of woody plant encroachment at a national / regional scale.

[8] This chapter was published in 2017 in the journal Global Change Biology (Skowno *et al.*, 2017). I was the lead author of the paper and conceptualized and executed the analyses and wrote the manuscript. William Bond, Adam West and Brad Ripley helped conceptualise the study and provided guidance and assistance with interpreting the results. Mark Thompson and Jens Hiestermann provided guidance in the remote sensing analyses.

Introduction

A number of localised studies have shown woody plant increase over the last century in southern Africa. The methods used include repeat photographs (e.g. Puttick et al., 2011; Ward et al., 2014; Masubelele et al., 2015), aerial photo interpretation (O'Connor & Crow, 1999; Wigley *et al.*, 2010; Stevens *et al.*, 2016), repeat surveys of field plots (e.g. Buitenwerf et al., 2012) and satellite image analysis (e.g. Ringrose et al., 1997 reported in Moleele et al., 2002; Samimi & Kraus, 2004; Wessels et al., 2011).

In a recent review, O'Connor *et al.* (2014) conclude that there are no reliable estimates of the extent of encroachment for South Africa, though experts have suggested that up to 13million ha may have been affected by "thorn tree encroachment" (Trollope *et al.*, 1989 as cited by Wigley *et al.*, 2009). Remote sensing based estimates were published for neighbouring Botswana, indicating that up to 37 000 km^2 had become encroached by 1995 (Ringrose *et al.*, 1997 as cited by Moleele *et al.*, 2002).

In Chapter 2, historical aerial photographs were used to quantify changes in woody plant cover at two sites over a 60 year period. The horizontal resolution (~2 m) and depth of the time series (approximately decadal time steps) were the strengths of using the aerial photograph approach to land cover change detection. The key drawback of the approach is the limited spatial extent (~20 to 200 km^2) that it allows (Howard, 1970; Morgan *et al.*, 2010). Satellite imagery, on the other hand, can be used to measure changes in woody cover over millions of km^2 and allows for the investigation of landscape and regional patterns, and rates of change (Franklin & Wulder, 2002; Gómez *et al.*, 2016). The trade-off for this large spatial extent is a limited (though growing) historical record of between two and four decades (for MODIS and Landsat products respectively) and horizontal resolution of between 30 m and 500 m (for Landsat and MODIS respectively).

In this study I attempt the first spatially continuous measurement of changes in woodland and grassland extent, based on satellite images, for South Africa's grassy biomes. To do this I used a recent Landsat based land cover product in combination with L-band Synthetic Aperture Radar (SAR) data to estimate the extent of woodlands and grasslands in 1990 and 2013. I then quantify the changes in woodland and grassland extent across the country and illustrate the potential links with rainfall, land tenure and presence of mega-herbivores using a simple spatial analysis.

Methods

Study area

The savanna and grassland biomes of South Africa occupy the northern and eastern portions of the country, making up over 2/3^{rds} of the surface area (Figure 21). South African savannas fall in the lower end of the rainfall envelope described for savannas globally (180–2500 mm MAP) (Lehmann *et al.*, 2011, 2014; Staver *et al.*, 2011a) occurring between 180–1200 mm MAP; with 50% of their extent receiving less than 500 mm MAP. Fire is infrequent in the arid savannas in the west of the country but is frequent in mesic savannas receiving more than 600 mm MAP.

There are three broad land use types in the savanna-grasslands of the region. These are livestock farming in commercial rangelands, livestock and mixed farming in communally owned areas (Meadows & Hoffman, 2002; Puttick *et al.*, 2014a) and conservation in protected areas where indigenous mammals predominate (Eckhardt *et al.*, 2000; Balfour & Midgley, 2008). Land use categories, such as urban and rural settlements, mining, intensive agriculture and plantation forestry are not considered in this study.

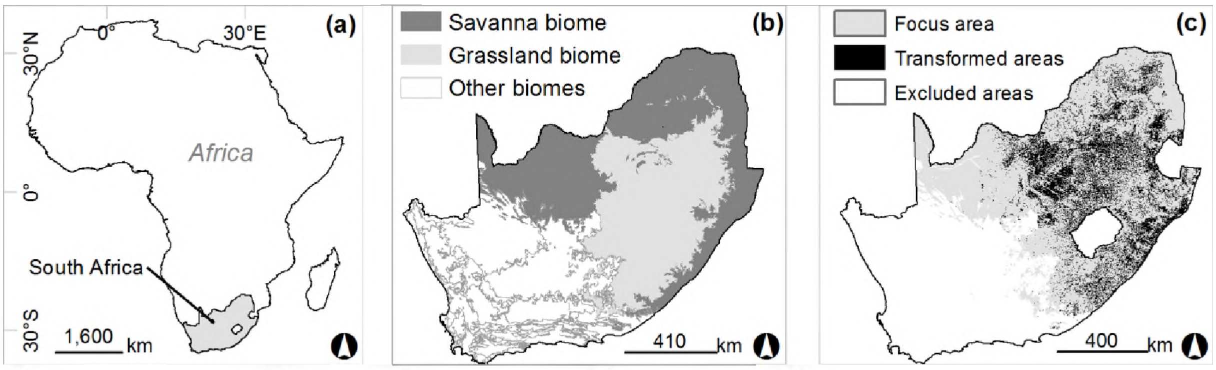

Figure 21. (a) South Africa; (b) Biomes of South Africa; (c) Area of interest and focus area of the study. The excluded areas to the south and south-west are the semi desert Karoo shrublands of the interior, the Fynbos biome in the extreme south west and the Albany thicket biome in the south-east. Areas with no natural vegetation remaining are referred to as "transformed areas" in this study.

Mapping approach

The development of the national woody cover change map followed a three-step process: i) developing maps of woodland and grassland extent by extracting and reclassifying information from available Landsat derived national land cover / use products for 1990 and 2013; ii) adjusting the 2013 woodland-grassland map using L-band SAR data to improve the classification accuracy; and iii) combining the 1990 map and adjusted 2013 map to produce a map of changes in woodland-grassland extent for the country. I used ARCGIS 10.3 (ESRI, Redlands, California) for all GIS processes and cartography in this study.

Refining the area of interest

The national vegetation map of South Africa (Mucina & Rutherford, 2006) was used to select the focus area for this study (Figure 21a,b). The entire savanna biome (including the Indian ocean coastal belt) was included in the study as this biome is defined as having mixed tree and grass dominance (Scholes & Archer, 1997; Mucina *et al.*, 2006b; Rutherford *et al.*, 2006b). In addition, all grassland bioregions were included even though woody encroachment is likely to be limited in montane regions (Mucina *et al.*, 2006a; Wakeling *et al.*, 2012). Other South African biomes were excluded since grasses are not a dominant component of the vegetation (e.g. Fynbos, Karoo shrublands, Albany thicket and forest). The grassy biomes selected contain isolated pockets of forest vegetation and areas dominated by woody shrubs which is typical of savanna-dominated landscapes in Africa (Rutherford *et al.*, 2006a).

The resulting area of interest (AOI) (Figure 21a) comprises 63% (795 547 km^2) of South Africa. The broad AOI includes natural and near-natural areas in which at least plant species composition, structure and function are largely intact and transformed areas, such as cultivated lands, urban developments and mines, in which all natural habitat has been lost (Figure 21c). In this study extensive rangelands, where indigenous herbivores have been replaced by domestic stock and top predators have been extirpated, are considered to be near-natural. I include degraded rangelands in this near-natural category as no reliable map of ecological condition / degradation exists for the country at an appropriate scale.

Landsat based national land cover / land use maps of South Africa

Landsat multi-spectral data is widely used in land-cover change mapping (reviewed by Hansen & Loveland, 2012) with numerous studies aimed specifically at detecting woody plant changes (Gasparri *et al.*, 2010; Barger *et al.*, 2011; Favier *et al.*, 2012). In this study I use the grassland and woodland classes from a national land cover / land use product generated for 1990 and 2013/4 by Geo Terra Image (Pty Ltd) (http://egis.environment.gov.za). The product uses multi season Landsat 5 (TM) data acquired between 1989 and 1993 and multi season Landsat 8 (OLI) data acquired in 2013 and 2014 in a hierarchical, rule-based classification system; and was purchased by the National Department of Environmental Affairs of South Africa and made publically available in 2015.

The 1990 national land cover / land use product used 646 Landsat 5 images and the 2013 product used 616 Landsat 8 images (GeoTerraImage, 2015, 2016). The Landsat data was downloaded from the GLOVIS web portal (http://glovis.usgs.com) and the standard top of atmosphere reflectance corrections were applied using ERDAS Imagine software (Hexagon Geospatial). The Landsat data set includes between seven and nine images for each of the 76 Landsat scenes covering the country, ensuring that seasonal variations were included in the landscape interpretations. Terrain effects were dealt with by including slope and multi-season solar illumination data in the classification models (based on 90 m resolution SRTM digital elevation model; http://srtm.csi.cgiar.org).

A standardised set of spectral indices were identified from which the required foundation cover classes; tree dominated, bush dominated, grass dominated, water and bare ground could be modelled (Table 15). Generic threshold values were determined for each foundational class and each spectral index by iterative testing over multiple sites within each biome. All modelling was undertaken on an individual image frame by image frame basis – each set of seasonal acquisition dates was processed as a separate exercise.

Given the use of indices (that rely on the ratio between bands), and the broad descriptive nature of the output classes targeted by the spectral modelling, it was deemed acceptable to use the same spectral threshold values on Landsat 5 imagery as for the Landsat 8 imagery. This approach was validated by comparing modelled outputs using the same thresholds for both Landsat 5 and 8 over sample areas known to have suitable landscape characteristics. Since no single index was found to work well in all landscapes and all seasons, the final geographic extent of each foundation class was generated from the combined use of several different spectral indices, for which all threshold conditions had to be met.

Table 15. Indices used in the modelling of foundational land cover classes. Bands referred to in the formula column: NIR = Near Infrared; R = Red; G = Green; SWIR1 = Shortwave Infrared 1; SWIR2 = Shortwave Infrared 2.

Index	Acronym	Formula
Normalised Difference Vegetation Index	NDVI	(NIR - R) / (NIR + R)
Normalised Difference Wetness Index 1	NDWI1	(G - NIR) / G + NIR)
Normalised Difference Wetness Index 2	NDWI2	(NIR - SWIR1) / (NIR + SWIR1)
Modified Normalised Difference Wetness Index	MNDWI	(G - SWIR1) / (G + SWIR1)
Bare Soil Index	BSI	(SWIR2 - G) / (SWIR2 + G)
Burnt Index	BI	(1.6*SWIR1 - 2.2*SWIR2) / (1.6*SWIR1 + 2.2*SWIR2)

The modelling and generation of each foundation cover class was undertaken as a separate modelling exercise (e.g. water was modelled separately from bare ground, which was modelled separately from tree and bush cover). This approach simplified the modelling steps and facilitated easier desk-top quality control of outputs; compared to attempting to model all foundation cover types simultaneously within a single model workflow. Further details are available in Geo Terra Image (2015, 2016).

Developing woodland and grassland maps from the national land cover / land use data

The 1990 and 2013 land cover / land use datasets were clipped to the AIO for this study. The [woodland & open bushland], [dense bush & thicket] and [grassland] classes were retained in their original form. The non-natural classes were reclassified into a single [transformed] class and the other natural classes, such as wetlands, were excluded from the area of interest. This resulted in a refined Focus Area for the study comprising 43% of South Africa (548 143 km^2) (Figure 21c). A small portion of transformed areas in 1990 recovered in the 23 year period (24 174 km^2) and an approximately equal portion of natural areas were lost during the period (24 794 km^2); to simplify the assessment, these areas were excluded from the study.

Achieving the desired level of accuracy in remotely sensed land cover products is a well described problem but the challenge is even more apparent in change detection studies where the errors are compounded (Foody, 2002, 2010; Pontius & Millones, 2011). One way of improving the accuracy of land cover products and the change detection analyses which are based on them, is to reduce the number of classes considered at each time point (Pontius *et al.*, 2008; Foody, 2010). The developers of the national land cover / land use products warn that transitions between the [dense bush & thicket] class and the [woodland & open bushland] class should be treated with caution because the models do not consistently separate the classes and that these classes have low accuracy when compared to the [grassland] class. To this end, the [dense bush & thicket] class was merged with the [woodland & open bushland class]. This resulted in simplified 1990 and 2013 woodland and grassland extent maps where the [woodland] class is defined as having > 20% canopy cover and canopy height 2–5 m and the [grassland] class is defined as having bush and or tree canopy cover < 20% (GeoTerraImage, 2015, 2016).

The woodland-grassland maps were then resampled from 30 m pixels to 120 m pixels (using majority interpolation) in order to: a) improve the confidence in the change analysis, b) reduce the impact of geo-referencing inaccuracies and c) facilitate integration with the satellite L-band radar data. The projection system of the original downloaded data was retained (UTM35S).

Adjustment of 2013 map using satellite L-band radar data

In open savanna woodlands optical remote sensing approaches to land cover mapping tend to classify grassland and open woodlands into the same category, due primarily to the dominance in reflectance of the grass layers (Asner *et al.*, 2003; Mitchard *et al.*, 2011). This is especially true when sparse canopied trees and shrubs such as microphyllous acacias are the dominant woody species (Asner *et al.*, 2003; Turner *et al.*, 2003; Lehmann *et al.*, 2008). Synthetic aperture radar sensors on the other hand measure backscatter relative to the wavelength of its active senor, the resulting data contains information on surface roughness and soil moisture (Woodhouse, 2006). L-band SAR has a wave length of 15–30 cm making it sensitive to vegetation structure, tree stems and main branches in particular. Because of this, ALOS PALSAR data (and other L-band SAR sensors) have been successfully applied to biomass estimation studies in the savanna biome in Africa (Mitchard *et al.*, 2009, 2011; De Grandi *et al.*, 2010; Taylor *et al.*, 2011; Ryan *et al.*, 2012; Carreiras *et al.*, 2013). Several authors have noted that combining optical and SAR remote sensing products holds promise for woody cover change studies at a range of scales (Hellwich *et al.*, 2000; Hudak & Brockett, 2004; Mitchard *et al.*, 2009, 2011).

ALOS PALSAR Fine Beam Dual mode collects HV (horizontal transmit vertical receive) and HH (horizontal transmit and horizontal receive) backscatter intensity data which have recently been terrain corrected, geo-referenced, radiometrically calibrated; and provided for download in 1°x 1° tiles with horizontal resolution of 25 m for 2007– 2010 (Shimada & Ohtaki, 2010; Shimada *et al.*, 2014). The 2010 dated tiles covering South Africa were downloaded from the JAXA EOS website (www.eos.jaxa.jp), mosaicked to a single raster, re-projected (to UTM35S) and resampled to 120 m pixels (using bilinear interpolation). The resampling / resolution reduction step served to reduce some of the speckle inherent in the PALSAR data and to ensure the optical data and SAR could be matched to a common reference grid. A small amount of spatial error is introduced in this resampling process. The data was then converted from digital numbers to $\gamma 0$ (gamma nought) values following Shimada et al. (2014). I tested the relationship between HH and HV polarizations and found them to be closely correlated in the study area ($R^2 = 0.921$, $P < 0.001$). In this study I used only the HV polarisation as it has been shown to be more sensitive than HH polarization to the lower biomass of savanna systems (relative to forest systems) and has been particularly effective in savanna biomass estimation studies (Mitchard *et al.*, 2009; De Grandi *et al.*, 2011; Ganguly *et al.*, 2012; Ryan *et al.*, 2012). Since the mosaic data obtained from JAXA is effectively terrain-corrected it was unnecessary to combine the HH and HV polarizations to reduce terrain effects as suggested by Kellndorfer et al., 2014. The mean and standard deviation for HV $\gamma 0$ values were calculated for grassland and woodland areas by first reversing the log transformation process, then calculating the arithmetic mean and standard deviation (SD) and converting back to $\gamma 0$ (dB). A t-test based on 20 000 random samples showed that the mean HV $\gamma 0$ in the grassland class vs. the woodland class were significantly different ($t = -93.54$, $df = 3591$, p-value < 0.01). Low HV backscatter intensity was associated with grasslands (mean $\gamma 0 = -23.60$dB, SD = 4.25) and high HV backscatter intensity was associated with woodlands (mean $\gamma 0 = -17.52$, SD = 3.58). These means and standard deviations were used to set thresholds for adjusting the 2013 woody cover map. The HV $\gamma 0$ upper threshold for the grassland was set to -15.72 (this is equal to the mean HV for the woodland class + ½ SD) and HV $\gamma 0$ lower threshold for woodland was set to -23.73 (this is equal to the mean HV $\gamma 0$ for the grassland class -½ SD). In this way I focused the adjustment on the pixels which were most likely to have been misclassified by the 2013 national woodland-grassland map. These “suspect regions” include mesic grasslands with dense and tall grass layer which are likely to be incorrectly classified as woodland, and arid woodlands with narrow canopied, microphyllous tree species which are likely to be misclassified as grasslands by 2013 map. This approach attempts to improve the 2013 map by adjusting only a small proportion of the pixels. Unfortunately this type of adjustment could not be applied to the 1990 map as no suitable L-band SAR data could be found for that time period. While this is a significant drawback, the overall accuracy of the change map will still improve as a result of the adjustment.

Accuracy assessment

In this study I follow the components of disagreement method (Pontius & Millones, 2011; Pontius & Santacruz, 2014) for assessing the accuracy of the maps (using reference data) and for quantifying the degree of change between 1990 and 2013. Overall disagreement (%) is equal to the sum of "quantity disagreement" (%) and "allocation disagreement" (%) and can be calculated from any square contingency table / population matrix. I used the spread-sheet based tool developed by R.G. Pontius (http://www2.clarku.edu/~rpontius/PontiusMatrix41.xlsx) for all components of disagreement calculations, including the conversion of sample matrices to population matrices. In this study there are only two land cover classes, woodland vs. grassland, which great simplifies both accuracy assessment and change detection processes.

For the accuracy assessment; quantity disagreement is driven by differences in the relative proportions of woodland and grassland when comparing the reference data (observations) and the land cover map (Zhou *et al.*, 2014). For example, if both the reference data and land cover had a 50:50 mix of woodland and grassland pixels then quantity disagreement would be 0%, if the reference data were all grassland and the land cover were all woodland then quantity disagreement would be 100%. Allocation disagreement is driven by the spatial mismatches in woodland and grassland pixels between the reference data and the land cover map, given the proportion of woodland and grassland in each data set (Zhou *et al.*, 2014). For example, if all the woodland pixels in the reference data were grassland pixels in the land cover data, but the ratio of grassland to woodland remained the same in both datasets, the allocation disagreement would be 100%, if none of the pixels switched classes then the allocation disagreement would be 0%.

Accuracy assessment of the Landsat derived land cover maps

Accuracy assessment for the 2013 map was based on 1500 randomly selected reference points from a 1minute x 1minute sampling frame, stratified by bioregion. Using a sampling frame ensured that the sample sites were evenly distributed throughout each bioregion and were at least eight km apart. At each point I assessed the woody cover % in a desk top GIS by inspecting a square support region equal to the pixel size of the woodland-grassland map (120m x120m), on screen at a scale of 1:1000, using a backdrop of 50 cm ground resolution, ortho-rectified, colour digital aerial photographs (circa 2011–2013) (images obtained from the Chief Directorate: National Geospatial Information, www.ngi.gov.za). I overlaid a quadrant grid on the square support area to assist in estimating the percentage cover. No verification of the historical 1990 land cover dataset was undertaken due to the lack of comparable high resolution geo-referenced imagery for the period, a common problem for historical remote sensing analyses (Foody, 2010). I investigated the use of independent reference points from previous woody encroachment studies (that include areas of known woodland loss or gain) but found that very few studies recorded woody cover in and around 1990 with most focussing on earlier (1940–1970) and later dates (2000–2014). Since both the 1990 and 2013 land cover maps were derived from equivalent resolution Landsat imagery, using the same modelling procedures, the accuracy results determined for the 2013 map are assumed to be representative of the likely accuracies for the 1990 map.

Accuracy assessment of the PALSAR adjustment of 2013 land cover

To test the impact of the PALSAR adjustment on the accuracy of the 2013 land cover I computed the components of disagreement, between the PALSAR adjusted 2013 land cover and a second reference dataset. This dataset was generated by randomly selecting a further 1000 reference points, stratified by bioregion, where half the points were selected from unadjusted regions of the map and half were from adjusted regions. This step was necessary because, in change detection studies, cases of change are typically very rare (Foody, 2002; Strahler *et al.*, 2006), and the PALSAR adjustment process only influenced a small number of pixels in the 2013 map.

Change detection over the 23 year time period

The 1990 woodland-grassland map and the adjusted 2013 map were combined to create a change map (Figure 22). Using the resulting population matrix I computed the components of disagreement between the 1990 map and the adjusted 2013 map. In the context of change detection with only two map categories, quantity disagreement is driven by the overall increase of category A at the expense of category B. For example, if there are substantially more woodland pixels in the 2013 map than in the 1990 map then the quantity disagreement will be higher than if the number of woodland pixels does not change over time. High quantity disagreement would suggest a directional change in woody cover over the 23 year period. Allocation disagreement in this context, also referred to as "exchange" (Pontius & Santacruz, 2014), is driven by spatial mismatches in grassland and woodland pixels between 1990 and 2013. Substantial allocation disagreement (exchange) would indicate that two opposite processes may be working at various places in this dynamic savanna landscape (Pontius & Santacruz, 2014).

While the use of Landsat and PALSAR data allows me to estimate changes over a large area, it also limits the study to the last two decades (23 years). Studies of earlier patterns of woody plant increase cover small regions and typically use aerial photographs or matched photo pairs. These have shown that in many South African localities the maximum rate of woody cover increase occurred after 1990 (summarised by O'Connor *et al.*, 2014; page 70). In order to facilitate comparison with other studies I report on both the total extent of change (km^2) and the annual percentage changes in woodland extent assuming linear change between the two census dates. Positive values indicate increases in woodland extent cover and negative values decreases in woodland extent.

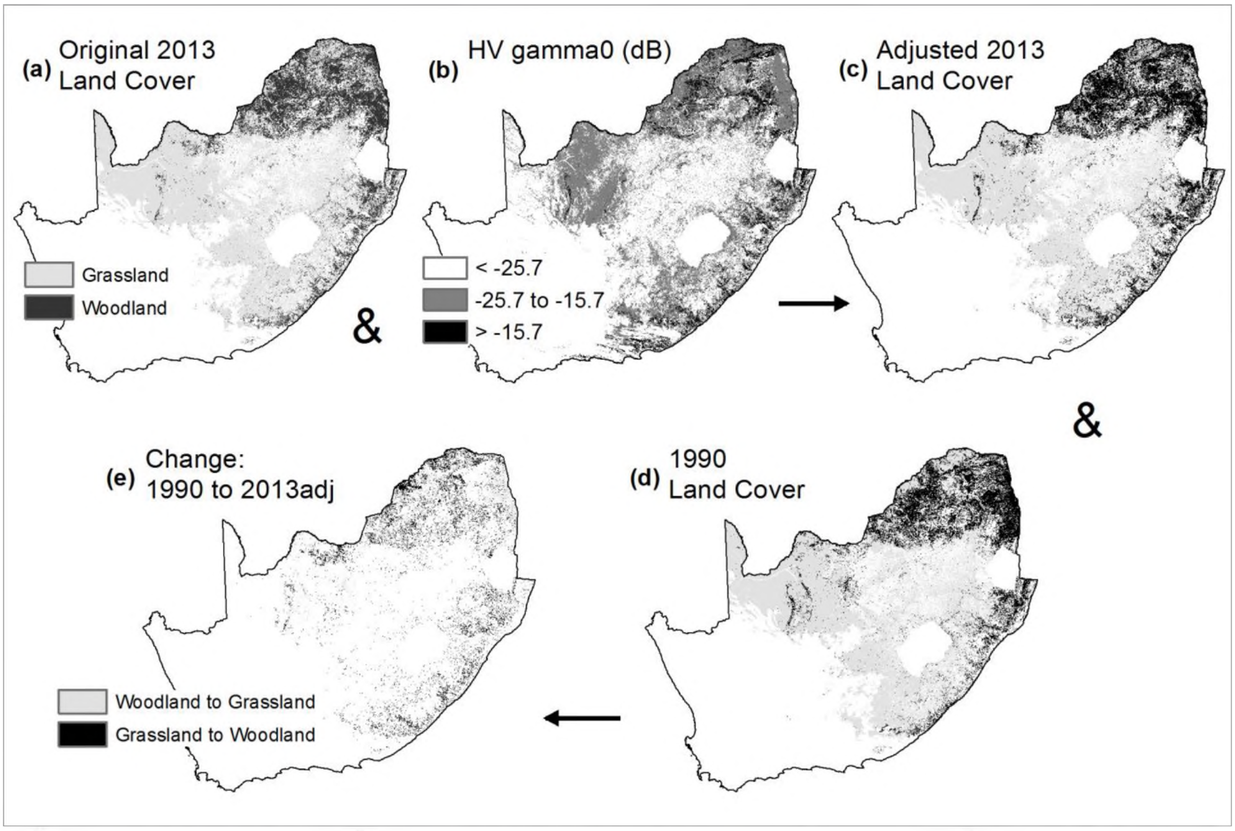

Figure 22. Process of developing a woodland-grassland change map for South Africa: The 2013 Landsat derived map (a), was combined with the 2010 PALSAR data (b), to produce an adjusted 2013 map (c), which was then combined with a 1990 map to produce a change map (e).

Assessment of influence of the PALSAR adjustment on the change map

The final step was to assess the extent to which the PALSAR adjustment process influenced the change detection analysis. To do this I combined the 2013 map, the adjusted 2013 map and the change map and calculated i) the proportion of the pixels that shifted from grassland to woodland that were adjusted from grassland to woodland by the PALSAR process; and ii) the proportion of the pixels that shifted from woodland to grassland that were adjusted from woodland to grassland by the PALSAR process.

Patterns of woodland-grassland change

In order to describe the general patterns of change in woodland-grassland extent in the country I used the bioregions described in the national vegetation map (Mucina & Rutherford, 2006), a mean annual precipitation surface (Schulze *et al.*, 2008) and a land tenure / land use map developed for this study. The mean annual precipitation surface was binned into nine categories representing 100 mm increments between 200 mm and 1100 mm. The land tenure map was developed by combining the South African protected area database (SAPAD version 201504; http://egis.environment.gov.za) with existing maps of traditional / communal owned areas (www.ngi.gov.za) and commercial farming areas (www.agis.agric.za). The protected area map was combined with elephant distribution data contained in the South African wild elephant database (supplied by the Elephant Specialist Advisory Group; www.esag.co.za). The resultant map had the following land tenure / land use map categories: i) traditional rangelands; ii) commercial rangelands; iii) protected areas with elephants; and iv) protected areas without elephants. I report the annual change in woodland extent as a percentage for each bioregion and for each rainfall and land tenure zone.

Results

Accuracy assessment of the 2013 land cover and adjusted 2013 land cover

The overall level of disagreement for the 2013 land cover map was 28%, with 17% quantity disagreement and 11% allocation disagreement. Grassland is over estimated in the 2013 map and woodland is underestimated. This can be considered as the baseline for the accuracy assessment (Table 16).

Table 16. Estimated population matrix for the unadjusted 2013 map based on 1500 reference sites. Values are shown as proportions of total population, which in this case is the total number of pixels in 2013 map.

Accuracy of the 2013 map		Observed 2013		
2013 map		grassland	woodland	Total
	grassland	0.48	0.22	0.70
	woodland	0.05	0.21	0.26
Disagreement: Overall = 28%, Quantity = 17%, Allocation = 11% Population size: grassland = 26694568, woodland = 10161313				

The effect of the PALSAR adjustment on the accuracy of the 2013 map was assessed using the reference data where half the points were selected from the adjusted areas (3% of focus area or 17 417 km^2) and half from the unadjusted areas (97% of the focus area or 530 726 km^2). The overall level of disagreement for the PALSAR adjusted 2013 map was 26%, with 14% quantity disagreement and 12% allocation disagreement. This suggests that, despite influencing only 3% of the focus area, the PALSAR adjustment improved the overall classification accuracy (Table 17). While this improvement in accuracy helps to justify the use of the adjusted 2013 map in the change detection analysis, I acknowledge that this is only a partial solution and that performing a similar accuracy assessment and adjustment on the 1990 woodland-grassland map should be a research priority.

Table 18 shows that the overall disagreement (in this case equivalent to a measure of change) between the 1990 and the adjusted 2013 map is 16%, with 5% quantity disagreement (increase in woodland at the expense of grassland) and 11% allocation disagreement (exchange between grassland and woodland).

Table 17. Estimated population matrix for the adjusted 2013 map based on 1000 reference sites. Values are shown as proportions of total population, which in this case is the total number of pixels in adjusted 2013 map. Note 500 reference sites were selected from the adjusted regions of the map and 500 from the unadjusted regions of the adjusted 2013 map.

Accuracy of PALSAR adjusted map		Observed 2013		
		grassland	woodland	Total
Adjusted 2013 map	grassland	0.51	0.20	0.71
	woodland	0.06	0.23	0.29
Disagreement: Overall=26%, Quantity=14%, Allocation=12% Population size: grassland = 26952717, woodland =11112802				

Table 18. Population matrix showing the 1990 map compared to the adjusted 2013 map. Values are shown as proportions of total population, which in this case is the total number of pixels in 1990 map.

Degree of Change		Adjusted 2013 map		
		grassland	woodland	Totals
1990 map	grassland	0.65	0.10	0.76
	woodland	0.05	0.19	0.24
Disagreement (change): Overall = 16%, Quantity = 5%, Allocation = 11% Population size: grassland = 28830972, woodland = 9234513				

I calculate that 15% of woody cover increase can be attributed to the PALSAR adjustment of grassland to woodland (9 430 km^2/ 57 194 km^2) and 5% (1 471 km^2/ 30 147 km^2) of woody cover decrease can be attributed to the PALSAR adjustment of grassland to woodland. Figure 23 shows the estimated woody cover change for the country at a ground resolution of 120m.

General woodland-grassland change statistics

I estimate that woodlands increased across 57 194 km^2 (10.4%) of the focus area and decreased across 30 147 km^2 (5.5%) of the focus area– a net increase of 27 047 km^2 (4.9%) of the focus area (Figure 23). Expressed as annual increase in woodland extent for the focus area, the rate is 0.22% (1 175 km^2 y^{-1}). In relative terms woodlands covered 24% of the focus area in 1990 and 29% in 2013; a 20% increase in woodland extent over the 23 year period.

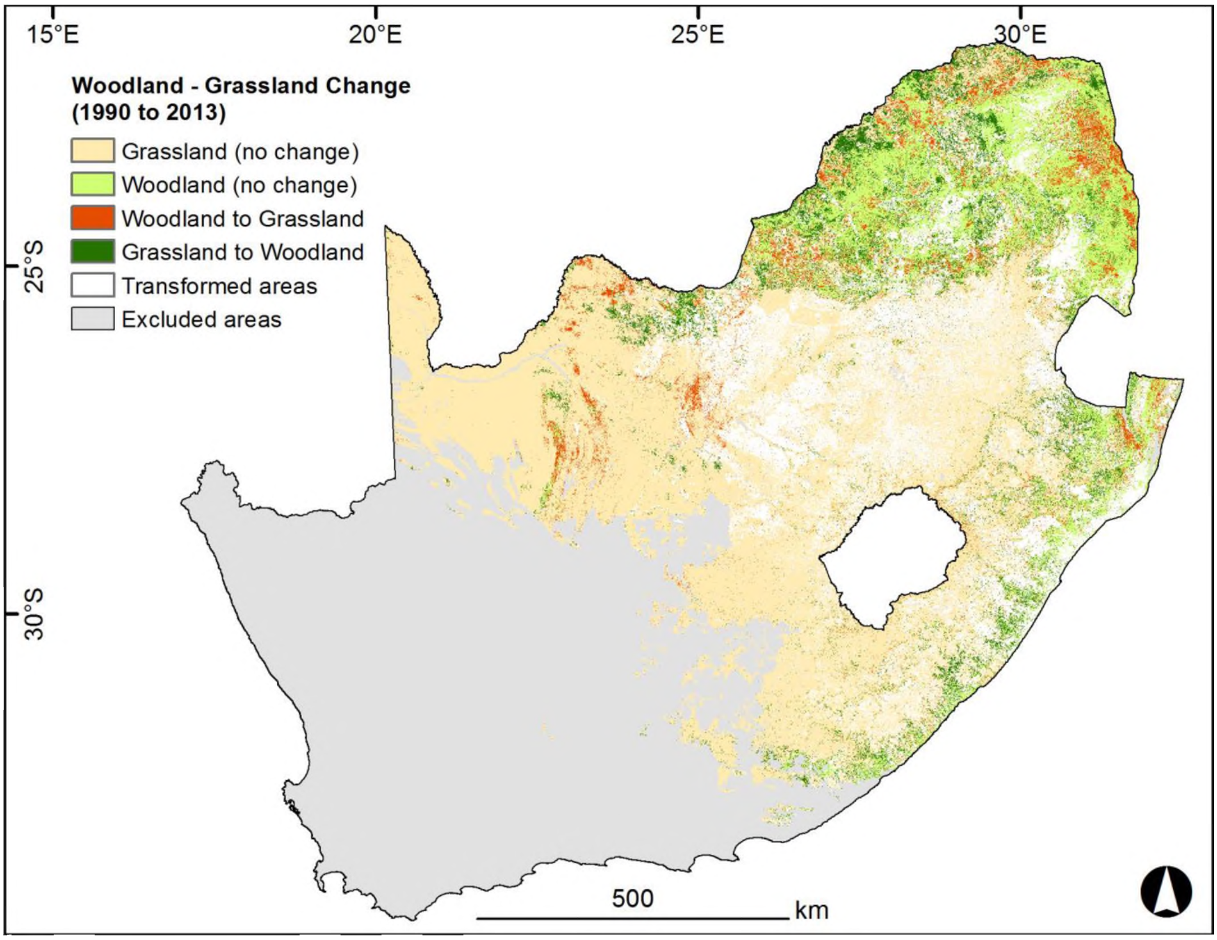

Figure 23. Estimated change in woodland and grassland extent between 1990 and 2013 in the grassy biomes of South Africa.

The annual percentage change in woodland extent per mean annual precipitation (MAP) bin, land tenure category and bioregion are shown in Figure 24, Figure 25 and Table 19. Low rainfall areas had lower rates of woodland expansion than high rainfall areas – the maximum rate of change (0.62% y^{-1}) was found between 900 mm and 1000 mm MAP and the minimum rate of change (-0.002% y^{-1}) was found between 100 mm and 300 mm MAP (Figure 24). The country's arid savanna-grasslands, receiving less than 500 mm MAP and making up approximately half the area, showed woodland increase of 0.11% y^{-1}. Those areas receiving more than 500 mm MAP showed an average increase of 0.31% y^{-1}.

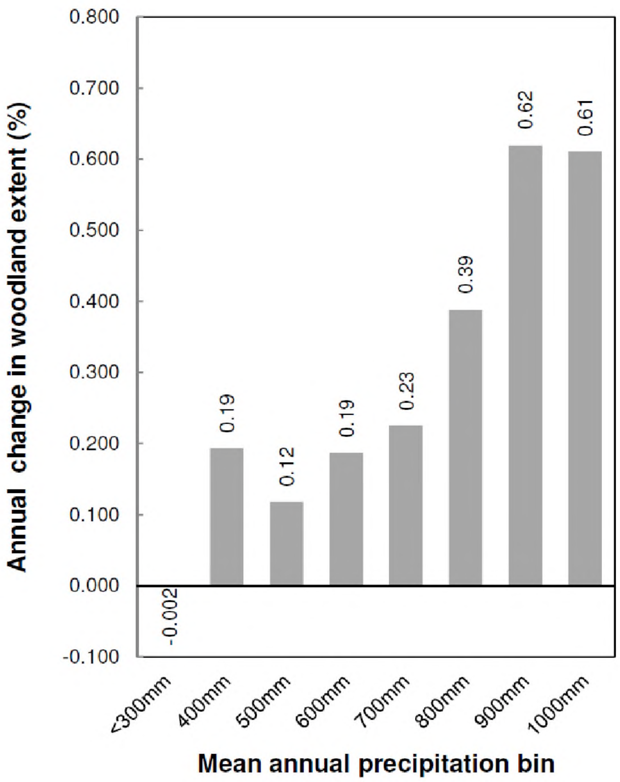

Figure 24. Annual change in woodland extent (%) per rainfall category (MAP bins of 100 mm). Positive values indicate increase in woodland extent, negative values indicate decrease.

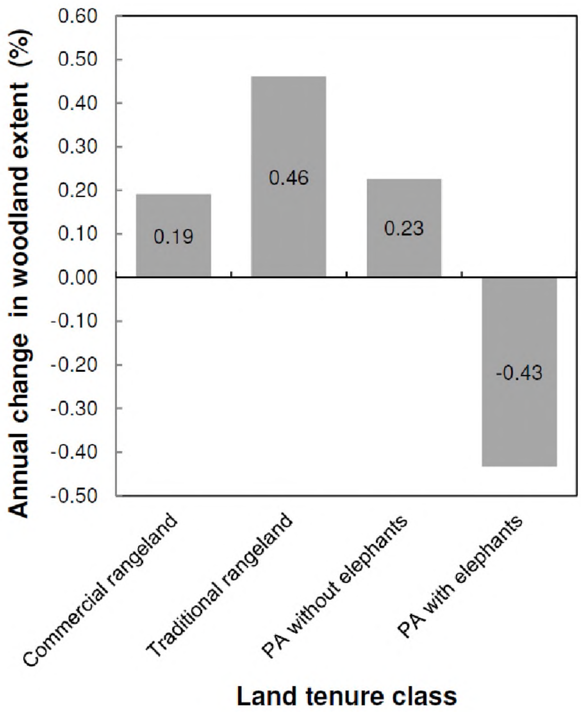

Figure 25. Annual change in woodland extent (%) per land tenure category. PA = protected areas (both private and state run). Positive values indicate increase in woodland extent, negative values indicate decrease.

Table 19 summarises the considerable variability in the rates of woodland expansion across between bioregions. The central bushveld bioregion is a key contributor to woodland expansion, while the mopane bioregion and the two Kalahari bioregions show overall loss of woodland. The savanna bioregions generally had higher rates of woody cover increase than grassland bioregions; the sub-escarpment savanna bioregion had the highest rate of increase (1.1% y^{-1}) but covers only 4% of the focus area, and the mopane bioregion (found mostly within the Kruger National Park) had the lowest rate of increase (-0.09% y^{-1}).

Table 19. Changes in woodland extent (expressed as % per year) for each bioregion. The MAP (mm), % with elephants, % of the focus area (FA), total extent (km^2), extent of woodland (km^2) and % in natural state are shown for each bioregion.

Bioregion	Wood-land change (% y^{-1})	MAP (mm)	% PA with elephant	% of FA	Total Extent (km^2)	Woodland Extent (km^2)	% Natural
Savanna Bioregions							
Mopane Bioregion	-0.09	423	39%	4%	24645	13871	94%
Eastern Kalahari Bushveld	-0.04	348	0%	20%	110293	7692	87%
Kalahari Duneveld	-0.01	183	0%	8%	42574	165	96%
Lowveld	0.13	702	25%	7%	40018	31921	74%
Indian Ocean Coastal Belt	0.43	970	11%	1%	7593	5370	46%
Central Bushveld	0.58	532	2%	17%	93985	68798	79%
Sub-Escarpment Savanna	1.11	805	0%	4%	24612	13879	69%
Grassland Bioregions							
Dry Highveld Grassland	0.02	481	0%	14%	75492	2102	64%
Mesic Highveld Grassland	0.16	690	0%	11%	59498	6750	53%
Drakensberg Grassland	0.22	729	0%	3%	19109	2154	91%
Sub-Escarpment Grassland	0.32	737	0%	9%	50298	7312	67%

Approximately 70% of the focus area is commercial rangeland, 20% is traditional rangeland and 10% is protected area – half with elephants and half without. Woodland extent declined in protected areas with elephants (-0.43% y^{-1}) and increased the most in traditional (communal) rangelands (0.46% y^{-1}) (Figure 25). Protected areas without elephants and commercial rangelands showed similar rates of woodland change (0.19% y^{-1} & 0.23% y^{-1} respectively).

Discussion

This study, focused on the last two decades, provides the first spatially continuous, national scale estimate of woodland expansion in South Africa. The allocation disagreement of 11%, which indicates exchange between the classes over the 23 year period, is consistent with the predicted and observed shifts between woody and grassy states in dynamic biomes such as savanna. In these biomes, disturbances such as fire and herbivory, can switch an area from woodland to grassland, and their absence can do the opposite (Higgins *et al.*, 2000; Scholes, 2003; Sankaran *et al.*, 2008). The quantity disagreement of 5%, which indicates a change in overall extent of one class at the expense of another, would not be unexpected or particularly noteworthy in a localized study where specific land use activities or management goals drive change in a particular direction. However, in this national scale study, covering over

0.5 million km^2 a ~27 000 km^2 increase in woodland at the expense of grassland suggests that regional or global drivers linked to climate and atmospheric changes are worth considering in addition to local drivers such as fire and herbivory.

Regional or national drivers that could be responsible include temperature trends (Warburton *et al.*, 2005), changes in rainfall seasonality, variability and amount (Hewitson *et al.*, 2005), changes in evaporation rates (Roderick & Farquhar, 2002), nitrogen deposition (Josipovic *et al.*, 2010) and increased atmospheric CO_2 (Bond & Midgley, 2000, 2012; Devine *et al.*, 2017). Of these, CO_2 has received considerable attention in studies of woody plant increase (Polley *et al.*, 2003; Higgins *et al.*, 2007; Wigley *et al.*, 2009b; Kgope *et al.*, 2010; Buitenwerf *et al.*, 2012; Russell & Ward, 2014b; Devine *et al.*, 2017). The estimates of woodland expansion presented in this study will allow some of these national drivers to be tested in a spatially explicit manner for the first time.

Our estimates of the rate of woodland expansion for the different bioregions (-0.091 to 1.1% y^{-1}) are similar in range to site specific estimates from a number of African studies conducted between 1940 and 2014 (-0.13 to 1.25% y^{-1}) (reviewed by O'Connor *et al.*, 2014). The fact that this national scale remote sensing approach produces similar estimates of woodland change to detailed localised studies is noteworthy and provides some support for the method employed and for the potential influence of regional drivers.

Our spatial analysis showed that there has been limited woodland expansion in the arid half of South Africa's savanna-grassland biome (< 500 mm MAP). Above this 500 mm MAP threshold, the rate of woodland expansion increases as rainfall increases, reaching a maximum in the mesic areas receiving over 900 mm MAP. This pattern has been noted by other investigators (Higgins *et al.*, 2007; Buitenwerf *et al.*, 2012) but is at odds with research focussed on the arid regions of the country (review by O'Connor *et al.*, 2014; Ward *et al.*, 2014) where woody cover was shown to be increasing below the 500 mm MAP threshold. The bioregional analysis showed that woodland expansion occurred in a wide range of settings across markedly different soil types, vegetation types and bioclimatic envelopes. The dry western savannas of the Kalahari and the mopane bioregion stand out in that no net woodland expansion was observed there. Why is there such limited woodland expansion the arid savannas of South Africa? From a technical point of view it is possible that, despite the PALSAR adjustments, the method I have used is not sensitive enough to detect woodland expansion in arid savannas. This highlights the potential weakness of remote sensing approaches which rely mostly on tree canopy cover and do not detect changes in the density of stems or the proliferation of saplings. Alternatively, if I accept the finding that woodland expansion is limited in arid regions, it is possible that tree growth rates in arid areas are simply too low to expect (and detect) landscape-level changes in woodland vs. grassland extent over a 23 year period.

Woodland expansion was less pronounced in the grassland bioregions than the savanna bioregions. Grassland bioregions generally occupy the high altitude central plateau of the country. In these bioregions woody plant increases may be limited by lack of source populations of woody plants and seed and the effect of low temperatures on seedling growth rates (Wakeling *et al.*, 2012).

The land tenure summary showed that woodland extent decreased substantially in protected areas which contain elephants but increased in other protected areas, commercial rangelands and traditional rangelands. These protected areas with elephants cover only 5% of the savanna-grassland biome but include the Kruger National Park, where this pattern of woodland loss has been linked to increasing mega-herbivore densities and increased fire frequency (Eckhardt *et al.*, 2000; Asner *et al.*, 2009; Asner & Levick, 2012). The land tenure and rainfall findings together suggest good agreement with a study by Stevens *et al.* (2016) which found that sites with mega-herbivores and with mean annual precipitation of less than 650 mm, showed lower levels of woody cover increase than sites without mega-herbivores (regardless of rainfall). The high rates of woodland expansion in traditional rangelands is surprising as, unlike commercial ranches, trees are used for building and fuel-wood and browsers (goats) are typically present along with cattle. Until recent decades, communal areas have generally been shown to have low rates of woody cover increase when compared to commercial rangelands (Wigley *et al.*, 2009b; Puttick *et al.*, 2011, 2014a). Recent work by Russell & Ward (2014) suggest declining fuel wood collection (due to increased electrification of rural areas) may be contributing to woodland expansion in traditional rangelands but this has been specifically ruled out by other investigators (Matsika *et al.*, 2013) and further work is required before this pattern is understood.

Many models of woody cover change have been proposed based on site specific studies (Bond & Midgley, 2000; O'Connor *et al.*, 2014; Devine *et al.*, 2017) and using dynamic vegetation models (DVGMs) at a biome or continental scale (Bond *et al.*, 2003; Scheiter & Higgins, 2009; Moncrieff *et al.*, 2015). The woodland change map presented here provides a unique opportunity to test the numerous site specific models at a national / regional scale and could aid in efforts to validate DGVMs for this region, ultimately allowing investigators to untangle the local and global drivers of land cover change: fire frequency and intensity (Ryan & Williams, 2011; Archibald *et al.*, 2013), mega-herbivore and browser influences (Sankaran *et al.*, 2008; Staver *et al.*, 2009), climate change and increasing atmospheric CO_2 (Polley, 1997; Bond & Midgley, 2012; Donohue *et al.*, 2013; Moncrieff *et al.*, 2015; Devine *et al.*, 2017), topographic position (O'Connor & Crow, 1999), soil properties (Belsky, 1994; Lehmann *et al.*, 2011; Wigley *et al.*, 2013), nitrogen deposition (Kraaij & Ward, 2006) and socio-economic factors such as fuel wood usage (Hoffman & Todd, 2000; Wessels *et al.*, 2004).

The results show that the PALSAR adjustment step improved the accuracy of the 2013 map and the resulting change analysis. While uncertainties about the 1990 map remain, I propose that this is a potentially useful way to combine SAR and optical data when the optical classification has already been completed. However, combing optical data and SAR data during the classification process remains the preferred approach where it is feasible (Hellwich *et al.*, 2000; Mitchard & Flintrop, 2013).

Technical issues have typically impeded the development of national level datasets that have the potential to further our understanding of the impacts of global change on land cover and ecosystems (McManus *et al.*, 2012; Mitchard & Flintrop, 2013). While this medium resolution, national scale remote sensing approach produces less detail (and lower accuracy outputs) than localised *in situ* or aerial photography approaches, the broad spatial coverage provides a crucial link between global scale models of land cover change and research on savanna dynamics.

Chapter 5: A spatial model of the potential contributing factors to woodland increase and woodland decrease across South Africa

Abstract

A wide range of global, regional and local drivers have been proposed to explain the phenomenon of woody plant increase in grassy biomes of southern Africa. These include climatic variables, disturbance regimes (herbivory and fire), soil properties, topographic position, land tenure / land use and elevated atmospheric CO_2. Only a small portion of South Africa has been sampled for the occurrence of bush encroachment, limiting investigators ability to evaluate the potential drivers of change in a quantitative and spatially explicit way. The high resolution woodland-grassland change map developed in Chapter 4 provides a high resolution, dataset with which to explore the factors contributing to woodland expansion and woodland decline in South Africa. In this study a machine-learning approach (boosted regression trees) was used to model the relationship between woodland expansion or woodland decline and a suite of 11 environmental variables. Despite an imbalanced class distribution in the data set for each model, testing on a holdout set showed useful predictive performance. Woodland expansion occurred close to existing woodlands and in rugged terrain (with typically wooded valleys), reflecting a potential spatial constraint on woody encroachment linked to seed dispersal. Woodland expansion was dependent on temperature in the range 15 to 20 ˚C, which is well aligned with previous studies. Rainfall also showed the expected strong link with woodland expansion. These environmental variables have the potential to positively influence seedling establishment and recruitment of woody plants in grass dominated systems and the models provide a novel and quantitative confirmation of their influence on grassland to woodland shifts. Woodland decline occurred predominantly in areas with relatively low rainfall and terrain ruggedness, short fire return intervals and low temperatures. The importance of these predictors highlights the pivotal role of rainfall and fire in savanna dynamics. Overall, the models provided new insights into the patterns and potential drivers of change in South African savanna-grasslands. Future efforts should consider comparing alternative spatial modelling approaches and should focus on including additional / improved environmental predictor data (e.g. herbivory intensity & fire intensity).

Introduction

A wide range of drivers have been proposed for woody plant increase in savanna-grassland biomes. These global, regional and local factors have been described in preceding chapters and include climatic variables, disturbance regimes, soil properties, topographic position, land tenure / land use and elevated atmospheric CO_2 (Scholes & Archer, 1997; Sankaran *et al.*, 2005; Van Auken, 2009; Devine *et al.*, 2017; Stevens *et al.*, 2017). Most studies of woody cover change in savanna-grassland either ignore spatial elements or refer to spatially implicit models of savanna change (Higgins *et al.*, 2000; Staver *et al.*, 2011b; Bond & Midgley, 2012; DeAngelis & Yurek, 2016; Devine *et al.*, 2017). Perhaps as a consequence, only a small portion of South Africa has been sampled for the occurrence of bush encroachment (O'Connor *et al.*, 2014), limiting investigators ability to examine drivers of change in a spatially explicit way. Recently, spatial models of savanna change, such as dynamic global vegetation models (Bond *et al.*, 2003; Higgins & Scheiter, 2012; Moncrieff *et al.*, 2014, 2015) and remote sensing based tree cover models have emerged; exploring the drivers of change across regions and continents (e.g. Donohue *et al.*, 2013; Hall & Scanlon, 2015). While these models address spatial elements of woody cover change, the scale of analysis is generally better suited to continental scale work; with input data in the 1 to 30 km horizontal resolution range. High resolution (e.g. Landsat derived) global forest monitoring tools have been developed and used to investigate the drivers of deforestation (Hansen & Loveland, 2012), but these global tools have not been widely applied to land cover change studies in grassy biomes.

The woodland-grassland change map developed in Chapter 4 (Skowno *et al.*, 2017) provides a useful dataset with which to explore the drivers of woodland expansion (and decline) in South Africa's grassy biomes in a spatially explicit manner. The key strengths of this data set are that it is spatially continuous (covers the all of South Africa's grassy biomes) and that it has a relatively high spatial resolution (120 m pixel size). The key draw back for the data set is that it divides the continuum of tree cover into two distinct classes based on the 20% tree canopy cover threshold – due to limitations in the remote sensing methods applied.

Many of the proposed drivers of woodland increase and decrease can be represented using existing, spatially-continuous data sets (e.g. mean annual rainfall surfaces, mean fire return interval). Some global drivers, such as elevated atmospheric CO_2, do not vary significantly in space and act through interactions with other drivers. Despite the availability of a wide range of relevant spatial datasets, some key drivers such as herbivory (intensity and grazer : browser ratio) cannot be represented spatially at an appropriate scale at this time (Robinson *et al.*, 2014). In this study I constructed simple spatial models of a) woodland increase and b) woodland decrease using a suite of 11 environmental variables, for which national scale data was available. I aimed to characterise the environmental envelope in which woodland increase and woodland decrease occurred and gain ecological insights into the causal drivers of the observed changes. The basis of this approach is that if models can be trained to predict the changes they will provide novel quantitative evidence of at least some of the environmental contributors to woodland increase and decrease in South Africa (Guisan & Zimmermann, 2000). To achieve this aim I used a machine learning algorithm known as boosted regression trees (BRTs) (Elith *et al.*, 2008a) which have recently risen to prominence in spatial ecology for examining the relationship between multiple environmental variables and species / habitat occurrence (Elith *et al.*, 2008a; Sankaran *et al.*, 2008).

Rainfall, drought, fire return interval, herbivory and elevated atmospheric CO_2 are the main drivers of change in tropical grassy biomes discussed in preceding chapters of this thesis. Recent conceptual models of woody plant increase in Africa (Bond & Midgley, 2012; Devine *et al.*, 2017) highlight these drivers and propose different mechanisms of encroachment in arid vs. mesic regions (Figure 1). Rainfall is therefore expected to be a key factor in the predictive models of woodland expansion. Closely related to this is the average fire return interval and its direct influence on woody cover (Sankaran *et al.*, 2008; Archibald *et al.*, 2010b) which is expected to influence woodland decline (or limit woodland expansion). Herbivory is a key driver of woody cover change (Sankaran *et al.*, 2008; Staver *et al.*, 2009; Wigley *et al.*, 2010) that is not well represented in the models developed here, and therefore represents a potential source of unexplained variance in both the woodland increase and woodland decrease models. Other potential drivers of woodland increase mentioned in the literature include, soil properties (texture and depth) (Kraaij & Ward, 2006), topographic position and slope (O'Connor & Crow, 1999), temperature (Wakeling *et al.*, 2012) and proximity to woody vegetation (Skarpe, 1991) (Table 20). Elevated atmospheric CO_2 acts as a global driver of woodland increase and it is not represented in the spatial models. While some authors have argued that the occurrence of woody plant encroachment across rainfall, fire and herbivory gradients is evidence of the importance of a global driver (such as CO_2) (Buitenwerf *et al.*, 2012), others have pointed out that the effect of any global driver will only be evident if local drivers are not strong (Stevens *et al.*, 2017).

In this chapter, I set out to quantitatively explore some of the factors that may have contributed to woodland increase and woodland decrease across South Africa between 1990 and 2014. This is a spatially explicit approach, made possible by the woodland change map developed in the previous chapter. This investigation of woodland – grassland change at a national scale will allow many assumptions to be tested for the first time.

Methods

The remote sensing based observations of woodland-grassland change between 1990 and 2013, presented in Chapter 4 (Skowno *et al.*, 2017), has four categories: 1) stable grassland (GG), 2) stable woodland (WW), 3) woodland increase (GW) and 4) woodland decrease (WG). The map was divided into two subsets: one for grassland pixels in 1990 (time point one) and one for woodland pixels in 1990. A binary classification model was then trained for each. For the "woodland expansion" model the response levels were stable grasslands (GG) or woodland increase (GW), and for the "woodland decline" model the response levels were stable woodland (WW) or woodland decrease (WG). ARCGIS 10.3 was used to prepare all the maps in raster format in the UTM35S projection.

Environmental variables

A range of environmental predictor variables were selected; including four climatic variables, one terrain derived variable, two soil linked variables, fire frequency, broad land tenure / land use, and proximity to woodland. Fire return interval data, soil data and terrain ruggedness were obtained from Professor Michael Cramer (Cramer & Hoffman 2015; Cramer & Verboom 2016). The climatic variables were obtained from the South African Atlas of Climatology and Agrohydrology (Schulze *et al.*, 2008) and the rainfall anomaly layer was developed for this study using monthly rainfall data downloaded from the Global Precipitation Climatology Centre (GPCC) data portal (www.esrl.noaa.gov). The global 0.5° gridded monthly rainfall data 1901–2015 (precip.mon.total.v7.nc; downloaded June 2016) (Schneider *et al.*, 2013) was converted to monthly rainfall grids using ARCGIS 10.3 multidimensional toolbox. The proportional difference between the long term mean annual precipitation (MAP) (Schulze *et al.*, 2008) and the MAP between 1990 and 2013 was calculated; resulting in an additional climatic variable referred to as "rainfall anomaly" (MAPANOM). Land tenure data (described in Chapter 4) was added as an additional variable and included the following four classes:

commercial rangelands, traditional rangelands, protected areas and protected areas with elephants. The "distance to woodland" (DIST2W) grid was generated in ARCGIS 10.3 using the Euclidean distance tool with the 1990 woodland pixels as the input grid. This variable was only used in the woodland expansion model since all sites in the woodland decline model have a distance to woodland of 0 m. A significant gap in the input data was information on levels of herbivory over time. While modelled livestock densities are available globally (Robinson *et al.*, 2014), I did not include them in this study due to accuracy concerns. Further investigation of the various forms and formats of this important variable is required. Unlike generalised linear models and generalised additive models, BRTs are not unduly influenced by collinear environmental variables (Elith *et al.*, 2008b). However, to aid in the interpretation of the BRT results, the variance inflation factor (VIF) was calculated using the R package "usdm" (Naimi, 2015) and no significant colinearities were detected among the input variables.

Sampling framework

A 4 km by 4 km sampling frame was used to generate a vector (ESRI shapefile format) of points covering the natural, non-wetland portion of the savanna and grassland biomes of South Africa (see Chapter 4 for full description of Area of Interest). I used the Extract Multiple Values tool in ARCGIS 10.3 Spatial Analyst to extract the value for each environmental variables and the appropriate response variable at the sample locations. This process resulted in two model input datasets: the woodland increase dataset had 24 809 data points and the woodland decrease dataset had 7 865 points.

Table 20. Environmental variables used in the models – with key references and summary of the basis for inclusion.

Variable code	Variable	Unit	Description	Basis for inclusion in the models
FIREFREQ	Prob. of fire (fire freq.)	proportion	A measure of the fire return interval ("fire frequency"). Probability of fire between 2000 and 2015 as measured by MODIS active fire sensor. Zero indicates no fire during the period and one indicates annual fires (Cramer & Verboom, 2017).	High fire frequency could limit recruitment of woody plants and influence the woodland expansion model negatively and the woodland decline model positively (Higgins *et al.*, 2000).
BROCPRB	Prob. of shallow soil	proportion	A measure of soil depth. Probability of occurrence of an R-horizon (bedrock) within the first 120 cm of soil. Obtained from SoilGrids 1 km global soil data (Hengl *et al.*, 2014).	Shallow soils could constrain woody plant root extension and limit access to soil moisture and negatively influence the woodland expansion model (Kraaij & Ward, 2006).
SAND	Sand	%	Soil sand content (gravimetric) from SoilGrids 1 km global soil data (Hengl *et al.*, 2014).	High sand fraction could promote water infiltration and promote deep rooted woody species and positively influence the woodland expansion model (Britz & Ward, 2007).
MAP	Mean annual precipitation	mm.y^{-1}	Mean annual precipitation based on station data (1900 – 2006) with interpolation based on elevation (Schulze *et al.*, 2008).	High MAP could promote woody plant establishment and recruitment and positively influence the woodland expansion model (Sankaran *et al.*, 2008).
MAPANOM	Rainfall anomaly	%	Rainfall anomaly: % above (+) or below (-) the long term mean (1900–2006) measured in the period 1990–2013. Based on GPCC data records (Schneider *et al.*, 2013).	Higher than average rainfall in the period 1990–2013 could promote woody plant establishment and recruitment and have a positive influence on woodland expansion model or a negative influence on the woodland decline model (Hall & Scanlon, 2015).
MAT	Temperature	° Celsius	Mean annual temperature based on station data (1900 – 2006) with interpolation based on elevation (Schulze *et al.*, 2008).	Low temperatures could negatively influence the woodland expansion model through frost impacts (Wakeling *et al.*, 2012).
PETMON	Mean monthly potential evapo transpiration	mm	Mean monthly potential evapotranspiration (Trabucco & Zomer, 2009).	High evapotranspiration could increase water stress and have a negative influence on the woodland expansion model and positive influence on the woodland decline model (Eamus & Palmer, 2007).
RAINCON	Rainfall concentration	%	Rainfall concentration calculated as the proportional spread of MAP across the years: where 100% represents MAP falling within one month and 0 representing MAP evenly spread across 12 months (Schulze *et al.*, 2008).	High rainfall concentration could increase water stress and limit woody plant establishment and have a negative influence on the woodland expansion model.
RUGGED	Terrain ruggedness	meters	Standard deviation in elevation within a moving widow of nine cells and based on ASTER 30 m resolution global digital elevation model (Cramer & Verboom, 2017).	High ruggedness could reduce burnt area and promote recruitment and positively influence the woodland expansion model (Archibald *et al.*, 2009). Rugged terrain with incised, wooded valleys could provide a better source of seed and promote woody plant establishment and positively influence the woodland expansion model (Skarpe, 1991).
TENURE	Tenure/ Landuse class	Four categories	Four category "land tenure / land use": 1) protected areas with elephants; 2) protected areas without elephants; 3) traditional rangelands; and 4) commercial rangelands (Skowno *et al.*, 2017).	The land tenure classes typically have different herbivore regimes; grazing dominated commercial rangelands may have higher woody plant establishment and recruitment due to suppression of the grass layer, which may have a positive influence on the woodland expansion model.
DIST2W	Distance to woodland	meters	Distance to nearest woodland pixel observed in 1990. Used only in grassland model as this variable = 0 for all sites in woodland model. Developed for this study.	Low distance to woodland may increase the probability of seedling establishment and positively influence woodland expansion model.

Modelling procedure

Woodland expansion and woodland decline were modelled independently using the suite of environmental predictor variables described in Table 20. The woodland expansion model constitutes a binary classification of grassland sites that remain stable (0) or undergo transition to woodland (1). The woodland decline model constitutes an equivalent binary classification of woodland sites that remain stable (0) or undergo a transition to grassland (1). Boosted Regression Tree models, as implemented by the "dismo" package (Elith *et al.*, 2008a; R Core Team, 2014; Hijmans *et al.*, 2015), were built on previously prepared data in Table 20. Model training and evaluation was conducted using a train (64%) / validate (16%) / test (20%) stratified split of the data.

Both data sets were imbalanced: 14% of observations in the woodland expansion model were of woodland increase (1's) and 22% of observations in the woodland decline model were of woodland decrease (1's). These figures illustrate a problem that is common in land cover change studies; change is relatively rare and the majority of the landscape tends to remain stable (Foody, 2010). The imbalanced nature of the class distributions meant that overall measures of accuracy were not useful (i.e. the respective naïve models have an accuracy of 86% and 78%). Therefore, in addition to accuracy, model recall (sensitivity or true positive rate), precision (positive predictive value) and F_1 score measures (Powers, 2011) were used to compare model performance against a random predictor.

Recall: $\frac{True\ Positive}{True\ Positive\ + False\ Negative}$

Precision: $\frac{True\ Positive}{True\ Positive\ + False\ Positive}$

F1 Score: $2\ x\ (\frac{Recall\ x\ Precision}{Recall + Precision})$

Accuracy: $\frac{True\ Positive + True\ Negative}{True\ Positive + True\ Negative + False\ Positive + False\ Negative}$

The initial model selection process involved a grid search over the key parameters: learning rate, bag fraction and tree complexity (as described in Elith *et al.*, 2008a). The optimal number of trees was determined for each combination of hyper-parameters using dismo's step function. The models were evaluated on the validate split and ranked according to deviance and AUC. The model with the optimal parameters was then retrained on the combined train/validate data and evaluated on the test split that had not been seen in the training process.

In a situation where the environmental predictors are not correlated with the response variable the models would not be expected to outperform a random model (in this case, a model where the class is predicted independently of the features and with probability equal to the underlying class distribution). Models with useful predictive power, on the other hand, imply that the predictor variables are worth further consideration in terms of importance and interactions with the responses. The most important variables that emerge from the models are then explored further, as potential drivers of change. As an additional test, BRTs were trained on data where the response variables were randomly assigned; but even with a very small learning rate these BRT models failed to converge on a solution.

The R package "caret" (Kuhn, 2008) was used to produce a confusion matrix and calculate the performance measures for the final models and the random models. Standard dismo functions were used to produce a table of the relative influence of each predictor variable and a table of interactions between variables in each model. Partial dependence plots were produced for the four most influential variables. These plots show the effect that a particular variable has on the response after accounting for the average effects of all other variables in the model. Despite ignoring interactions between variables, they provide a useful basis for interpreting the model results (Friedman, 2001 as cited by Elith *et al.*, 2008a).

Results

The hyper-parameter optimization process revealed that the learning rate, tree complexity and tree number settings recommended in Elith *et al.(*2008b) were close to optimal. While the training and test score for the woodland expansion model are close (Table 21), the larger disparity in the woodland decrease model, indicates that some over-fitting may have occurred. The final model settings and the results of the training and testing scores are presented in Table 21. The confusion matrices from the test of the final woodland expansion model and the test of the random model are presented in Table 22. Table 23 contains the same confusion matrices for the woodland decline models.

Model performance

The woodland expansion and woodland decline models performed reasonably well, with F1 scores of 0.58 and 0.54 respectively. The F1 scores for the random models were far lower, 0.14

and 0.25 respectively (Table 22 & Table 23). For both the models overall accuracy exceeded that of the naïve model (0.90 vs. 0.86 & 0.82 vs. 0.78). Precision and recall (which contribute to the F1 score) were quite similar in the woodland expansion model due to the fact that the model produced a similar number of false positives, false negatives and true positives (Table 3). In the woodland decline model recall was double precision because the model produced substantially more false positives than false negatives and true positives (i.e. the model generally over-predicts woodland decrease). Overall, the models were able to predict both woodland increase and woodland decrease with reasonable power; indicating that the most influential variables in the models should be viewed as potentially important drivers of change, thus warranting further investigation and discussion.

Table 21. Optimal parameter settings and key output metrics for the validation and testing steps of the grassland and woodland models.

	Woodland Expansion Model	Woodland Decline Model
Response variable (binary)	**Woodland increase (1); Stable grassland (0)**	**Woodland decrease (1); Stable woodland (0)**
Total trees	6800	6550
Learning rate	0.004	0.0024
Tree complexity	5	5
Bag fraction	0.6	0.6
Training AUC	0.9440	0.8825
Training deviance	0.4045	0.6826
Test AUC	0.9160	0.7895
Test deviance	0.4660	0.8483
Variables in final Model	11	10

Table 22. Confusion matrix and performance measures for the final testing step of the woodland expansion model. The test measures of the random model are included for comparative purposes.

Test of final woodland expansion model		Reference		
Prediction		Stable grassland	Woodland increase	Total
	Stable grassland	4093	197	4290
	Woodland increase	298	373	671
	Total	4391	570	
Recall (sensitivity):	0.654			
Precision (positive predictive value):	0.556			
F1 score:	0.601			
Test of random woodland expansion model		Reference		
Prediction		Stable grassland	Woodland increase	Total
	Stable grassland	3689	601	4290
	Woodland increase	576	95	671
	Total	4265	696	
Recall (sensitivity):	0.136			
Precision (positive predictive value):	0.141			
F1 score	0.139			

Table 23. Confusion matrix and performance measures for the final testing step of the woodland model. The test measures of the random model are included for comparative purposes.

Test of final woodland decline model		Reference		
Prediction		Stable woodland	Woodland decrease	Total
	Stable woodland	1179	58	1237
	Woodland decrease	234	150	384
	Total	1413	208	
Recall (sensitivity):	0.721			
Precision (positive predictive value):	0.391			
F1 score	0.506			
Test of random woodland decline model		Reference		
Prediction		Stable woodland	Woodland decrease	Total
	Stable woodland	962	275	1237
	Woodland decrease	290	94	384
	Total	1252	369	
Recall (sensitivity):	0.254			
Precision (positive predictive value):	0.244			
F1 score	0.250			

Woodland expansion model

The woodland expansion model attempted to predict woodland increase using 11 environmental predictor variables. The most influential variable (by a substantial margin) was distance to woodland (36%), followed by mean annual temperature (16%), mean annual rainfall (8%) and topographic ruggedness (7%). The relative influence of the remaining variables is shown in Figure 26 and their contribution to the model was limited. Weak interactions between ruggedness and annual rainfall were detected. The partial dependence plots showed that woodland increase tended to occur within 1.5 km of stable woodland (Figure 27a), beyond which distance to woodland had no effect. The model predicted a strong increase in woodland above a mean annual temperature 15 °C, with the maximum influence reached at 20 °C (Figure 27b). Woodland increase showed a non-monotonic dependence on mean annual precipitation (Figure 27c). Between 250 and 500 mm MAP woodland increase was dependent on rainfall, from 500 to 750 mm rainfall had little influence, from 750 mm to 1000 mm woodland increase was influential again, and above 1000 mm rainfall again had little influence. In general, the model predicted higher levels of woodland increase in rugged terrain than in flat or gentle terrain (Figure 27d). Woodland increase showed a surprising negative partial dependence on rainfall anomaly (i.e. locations that were relatively dry in the study period 1990–2014 showed the highest levels of woodland increase), though the relative importance of the variable was only 5%.

Woodland decline model

Four variables stood out in the woodland decline model which attempted to predict woodland decrease using 10 environmental variables. The most influential of which was mean annual rainfall (16%), followed by terrain ruggedness (14%), fire frequency (12%) and mean annual temperature (11%). The relative influence of the remaining variables is shown in Figure 26. Weak interactions between soil sand fraction & rainfall, temperature & rainfall, and temperature and ruggedness were detected. The partial dependence plots for the woodland model (Figure 28) showed that woodland decrease occurred predominantly in arid regions that received less than 500 mm MAP (Figure 28a). Woodland decrease occurred mostly in flat terrain with low ruggedness (Figure 28b). In the model, frequent fires were associated with woodland decrease non-monotonically (Figure 28c). Fire-free areas were predicted to be stable, as the fires became more frequent the model predicted woodland decrease. When the probability of fire exceeded 0.5 (annual or biennial fires) the model predicted no further dependence of woodland decrease on fire frequency. Woodland decrease also showed a negative dependence on mean annual temperature (Figure 28d). The model predicted woodland stability above a threshold of 15 °C. Below this temperature threshold the model predicted marginal woodland decrease. As for the woodland expansion model, rainfall anomaly showed an unexpected influence on the woodland decrease model – woodland decrease occurred in areas which received above average rainfall in the period 1990–2014.

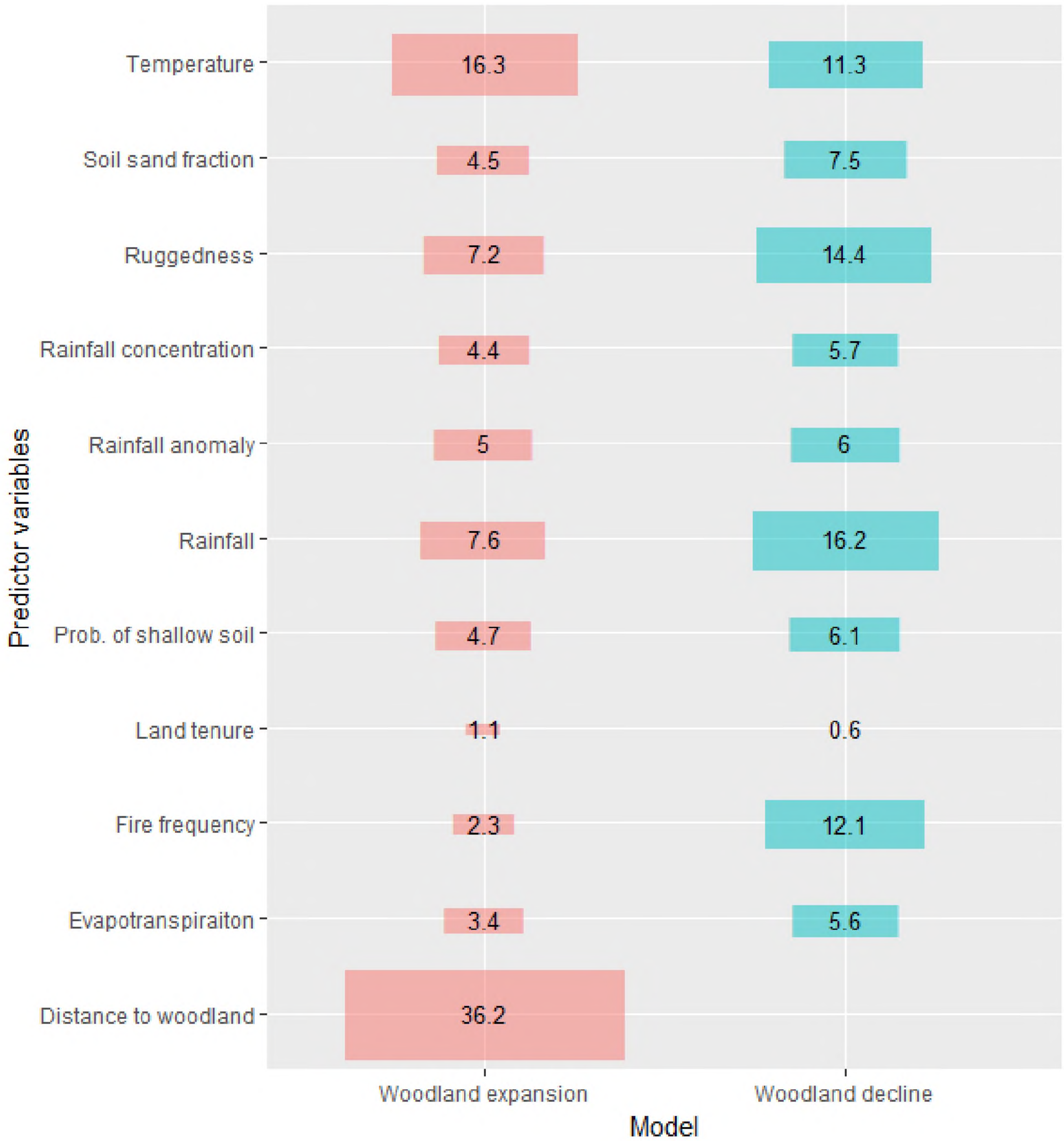

Figure 26. Relative influence of each predictor variable on the final models. The size of the bar indicates the percentage influence of the variable on the final model. The woodland expansion model focused on woodland increase in pixels classified as grasslands in 1990. The woodland decline model focused on woodland decrease in pixels classified as woodlands in 1990. More information on the predictor variables can be found in Table 20.

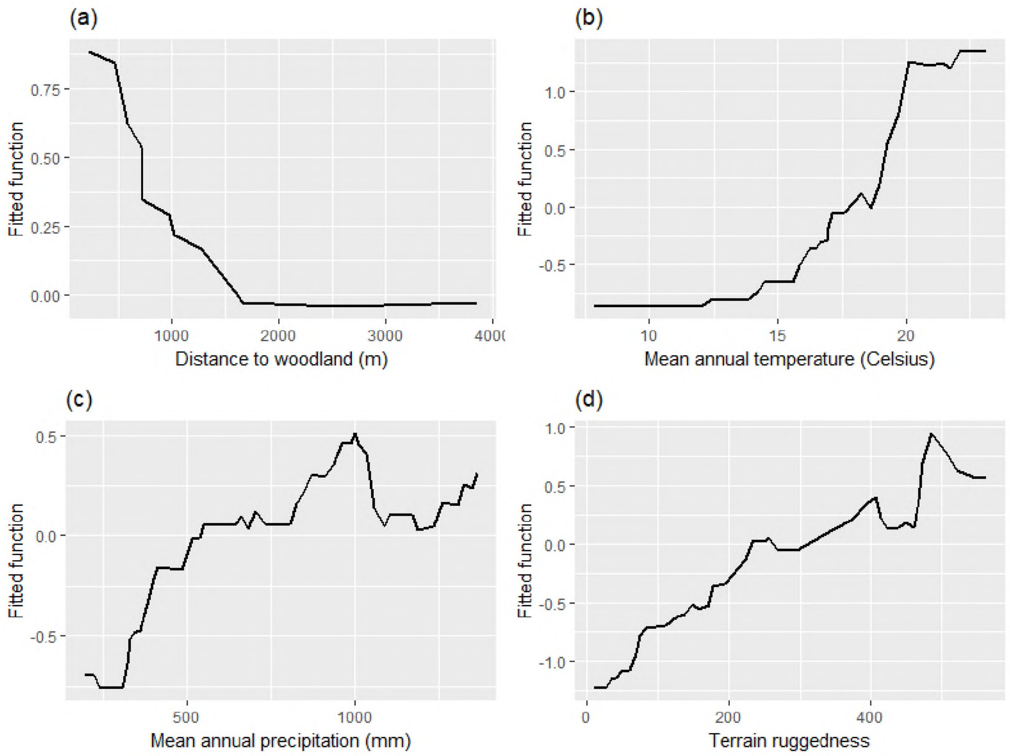

Figure 27. Partial dependence plots for the four most influential predictor variables in the woodland expansion model. The model aims to predict woodland increase (1) vs. grassland stability (0).

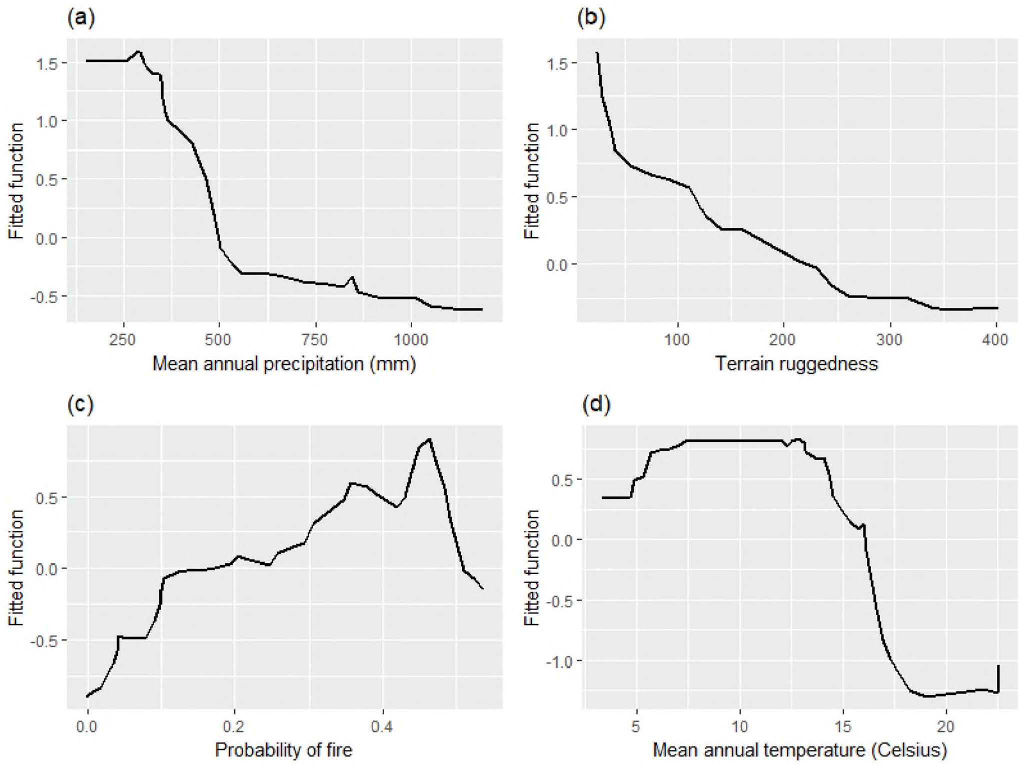

Figure 28. Partial dependence plots for the four most influential predictor variables in the woodland decline model. The model aims to predict woodland decrease (1) vs. woodland stability (0).

Discussion

Woodland expansion

Overall, both models were robust enough in their predictive power to warrant further consideration of the most influential contributing factors. The key finding from the woodland expansion model was that woodland increase tends to occur in grassy sites that are in close proximity to persistently woody sites. This suggests woodland expansion occurs incrementally along an advancing "tree front" and that seed dispersal of encroaching woody species may be a limiting factor in extensive, treeless landscapes that are located more than 1.5 km from woodland patches. Since it is unlikely that seed dispersal distances for woody encroaching species have changed significantly over the last 50 years, this strong correlation does not point to a possible driver of change (O'Connor *et al.*, 2014). Rather, the implication of this spatial correlation is that environmental drivers of woody encroachment may only be operating within a certain distance (~1.5 km) of this tree front. *Vachelia karroo,* for example, is thought to be primarily autochorous with some herbivore dispersal (O'Connor, 1995b; Milton & Dean, 2001), and the herbivores are mostly livestock that are confined to management camps (fenced parcels of land ~50–200 ha in extent); the distance to which these herbivores could disperse *V. karroo* is therefore constrained to approximately one km. This aspect of the model should be investigated at a finer scale with links to dispersal mechanisms of the dominant encroaching species.

In a similar vein, rugged and incised landscapes, which generally have woody communities in their valleys, saw higher levels of woodland increase than flatter areas, a pattern observed by previous investigators who also used a "distance to seed source" explanation (Skarpe, 1991; O'Connor & Crow, 1999) – densely wooded incised valleys are seed sources for encroaching species and encroachment close to these valleys is expected as they are within the dispersal range of many woody species and large amounts of seed. Rugged landscape are also less likely to burn which could indirectly make them prone to woodland increase (Archibald *et al.*, 2009, 2013).

The influence of temperature on the woodland expansion model is well aligned with a comprehensive field studies by Wakeling *et al.* (2012, 2015). These authors showed that temperature had a strong influence on the growth rate of woody encroachers (through an interaction with fire and with grass competition) and identified a so called savanna "tree line" in the ~15 °C mean annual temperature range (Wakeling *et al.*, 2012, 2015).

Rainfall is an important factor in the woodland expansion model. The thresholds in the partial plot of woodland increase and MAP are reasonably well aligned, though somewhat lower than the thresholds proposed previously (Sankaran *et al.*, 2005; Hirota *et al.*, 2011; Lehmann *et al.*, 2011; Staver *et al.*, 2011a; Devine *et al.*, 2017). The positive relationship between woodland increase and rainfall anomaly is difficult to explain. The expectation is that negative rainfall anomaly would indicate a prolonged period of drought, which in-turn could lead to tree death and woodland decline (Fensham *et al.*, 2009). While it is possible that above-average-rainfall could interact positively with fire (promoting grass production / fuel load), the more likely explanation is that the rainfall anomaly of the full 24 year period contains more than one drought cycle. This warrants further investigation. These models were not designed to gauge the influence of global drivers, such as elevated CO_2, which could act to moderate or modify the influence of the regional and local drivers; as demonstrated by Donohue *et al.* (2013) in a study of Australian tree cover.

<u>Woodland decrease</u>

In contrast to woodland expansion, woodland decline is not expected to have a global driver. Other drivers, such as regional drought (Fensham *et al.*, 2009), local disturbance (Asner & Levick, 2012; Devine *et al.*, 2017) and land use activities (Ryan *et al.*, 2012; Mograbi *et al.*, 2015) have been the focus of previous studies. Overall the woodland decline model was weaker than the woodland expansion model and results should be interpreted with more circumspection. The model suggests that arid savannas (< 500 mm MAP) have seen more woodland decrease than mesic savannas, but that over 500 mm MAP the models partial dependence on rainfall declined. Woodland decrease was not correlated with prolonged regional droughts, with the rainfall anomaly variable having little influence on the model. The strong link between woodland decrease and short fire return interval is easier to explain as fire can act as a direct driver on the tree grass balance (Bond & Van Wilgen, 1996). Fires can limit new woody recruits, potentially preventing recovery of woodlands that have declined for other reasons (such as wood collection or elephant damage). The partial dependence of woodland decline on low terrain ruggedness and low mean annual temperatures are more difficult to explain and require further investigation.

Interestingly, long fire return interval (low fire frequency), was not correlated with woodland increase, while short fire return interval (high fire frequency) was influential in the models of woodland decrease. Case & Staver (2016) recently showed that "higher-than-historical" fire frequencies were required to limit woody plant increase in a mesic South African savanna-grassland; providing a potential explanation for this observation. The link between elephant herbivory and woodland loss, highlighted in Chapter 4, was not supported by the models – tenure (particularly protected areas with elephants) was not an influential variable in any of the models. Protected areas with elephants cover a very small fraction of savanna – grassland biome, so even a strong relationship between the presence of elephants and woodland decrease would contribute very little to a model covering a whole biome.

Like all models of complex ecological systems, there is scope to improve both the modelling approach and the input data used. In this study the key data weakness was the lack of herbivory intensity information. Efforts should be made to develop appropriate spatial data, perhaps downscaling or refining the global datasets that have proved so useful in broad scale analyses (Robinson *et al.*, 2014), or working with agricultural scientists to develop new data sets. It is worth investing further in fire mapping, focused on intensity rather than frequency alone (Hawbaker *et al.*, 2008; Ryan & Williams, 2011; Giglio *et al.*, 2016). The commonly used MODIS derived fire data sets have their limitations in terms of detection and spatial scale (Roy & Boschetti, 2009; Randerson *et al.*, 2012) and improved fire data using high resolution sensors such as Landsat should be pursued (see Schroeder *et al.*, 2016). The tree front idea should be further investigated at a finer spatial scale using the pixel level data on woodland expansion and distance from established woodland rather than a coarse sampling grid.

Chapter 6: Conclusion

The local studies of historical canopy cover change and contemporary *V. karroo* demographics in the Eastern Cape Province, South Africa, provided high resolution insights into canopy cover change and *V. karroo* population structure and growth form on either side of an important savanna rainfall threshold. The results provided clear spatial, temporal and demographic tests of recent conceptual frameworks of change in arid vs. mesic savannas, without the confounding effects of climatic zones or differences in species composition and phylogeny (Bond & Midgley, 2012; Devine *et al.*, 2017; Stevens *et al.*, 2017). The national scale map of grassland-woodland shifts was the first estimation of the extent of canopy cover change in South Africa's grassy biomes and allowed for a unique model-based investigation of the potential drivers of woodland increase and decrease. Overall, the models provided new insights into the patterns and potential drivers of change in South African savanna-grasslands.

Summary of findings

Local studies of woody plant encroachment

Local-scale changes in an Eastern Cape savanna landscape were assessed for a 60 year time period and showed that woody canopy cover increased significantly at both arid and mesic sites. Mesic sites showed a fourfold increase in woody cover and arid sites a twofold increase. The rate and timing of the changes at the arid site suggests woody canopy cover increase may have occurred during periods of relatively high moisture availability when seedling establishment by encroaching V. karroo was more likely (Figure 1). At the mesic site, where seedling establishment is not thought to be limited by water availability, links between rates of encroachment and rainfall were not evident. Although I was unable to assess fire as a driver, existing evidence from the region suggests that fire is absent at the arid site and is a key disturbance limiting recruitment at the mesic site. The acceleration in woody canopy cover increase at both the arid and mesic site over the last 30 years suggests that a background driver such as increased atmospheric CO_2 plays a significant role in facilitating woody plant encroachment.

The field transect data showed that *V. karroo* demographic structure and growth form reflect the principal dichotomy between the arid and mesic sites: fire-prone vs. not fire-prone. The large number of seedling and gullivers suggest that at the mesic site seedling establishment is not limited by water availability and that disturbances (fire and browsers) suppresses woody plants causing the demography to be dominated by gullivers (Figure 1). At the arid site the low number of seedlings and gullivers suggest that opportunities for seedling establishment are infrequent and are likely to be linked to high rainfall periods highlighted in Chapter 2. *V. karroo* growth form also differs significantly between the sites. The fire prone, mesic site had taller *V. karroo* with canopies that start high off the ground (possibly driven by average flame height) compared to the arid site where *V. karroo* plants have canopies that extend to near ground level.

National models

Measuring canopy cover changes for the whole of South Africa with the same spatial and temporal resolution as that achieved for the local study is not possible with current remote sensing techniques. As a result only very broad estimates of the extent of change have been made nationally (Hoffman & Ashwell, 2001). The grassland-woodland change map produced as part of this thesis is the first attempt at a national-scale, spatially explicit, remote sensing driven estimate of change. However, the trade-off for the large focus area of this study (548 000 km^2) was that the estimates were restricted to 'gross' changes; shifts between grassland and woodland states. As a result the invasion of grasslands by shrubs and densification of woodlands were not detected. The results show that in South Africa's grassy biomes woodland replaced grassland over 57 000 km^2 and grassland replaced woodland over 30 000 km^2. Higher rainfall regions saw more extensive increases in woodland than arid regions. Protected areas with elephants showed a clear decrease in woodland when compared to other land use systems (protected areas without elephants, commercial rangeland and traditional rangelands). The local (aerial photo based) and regional (Landsat and PALSAR based) estimates of the rates of woody cover change presented in this thesis are remarkably similar when one considers the different scale and resolution of the studies. Both studies revealed rates of change that were well aligned with continental and regional means presented in the literature (~2.5% y^{-1}) (generally lower than for South American savannas and higher than for Australian savannas) (Stevens *et al.*, 2017). Both studies also indicated that the rate of woody cover increase in mesic savannas was approximately double that found in arid savannas.

The national scale spatial models suggest that woodland increase occurred close to existing woodlands and in rugged terrain (which typically has wooded valleys), reflecting a potential spatial constraint on woody encroachment linked to seed dispersal. Woodland increase was partially dependent on temperature in the range 15 to 20°C mean annual temperature, which is well aligned with previous studies. Rainfall also showed a strong but complex link with woodland increase in the expected range of 500 to 1000 mm MAP. These environmental variables have the potential to positively influence seedling establishment and recruitment of woody plants in grass dominated systems and the models provide a novel and quantitative confirmation of their influence on grassland to woodland shifts (Figure 1). Woodland decrease occurred predominantly in areas with relatively low rainfall and terrain ruggedness, short fire return intervals and low temperatures. The importance of these predictors lends support to previous work on fire as a direct driver of woodland decline and highlights the pivotal role of rainfall in savanna dynamics (Figure 1). Overall, the models provide new insights into the patterns and potential drivers of change in South African savanna-grasslands.

A global change perspective

While herbivore and fire management regimes remain key factors in woody plant expansion at a local scale, the widely predicted global changes in temperature, atmospheric CO_2 and rainfall patterns are likely to influence woody plant encroachment patterns across the rainfall gradient (Stevens *et al.*, 2017). Higher temperatures could result in higher evapotranspiration rates and lower moisture availability; limiting seedling establishment and reducing woody plant encroachment in arid regions (but see Stevens *et al.*, 2014). Sites that are only slightly above the MAP threshold of ~650 mm may shift from recruitment / disturbance limited system to an establishment / moisture-limited system. Increasing atmospheric CO_2 concentrations work in opposition to this and can reduce woody plant water stress, potentially promoting seedling establishment and woody encroachment (Polley, 1997; Devine *et al.*, 2017). In more mesic regions, where moisture is not limiting, higher CO_2 concentrations are likely to promote woody plant encroachment by enhancing carbon allocation to the roots and increasing the ability of woody plants to make it through the herbivore or fire trap (Bond & Midgley, 2012). The future trends for rainfall are less well understood than temperature and CO_2, but it is possible that the predicted increases in rainfall seasonality in arid regions could reduce woody plant encroachment by decreasing moisture availability and further limiting seedling establishment. In mesic regions increased rainfall seasonality could increase fire intensity (by allowing the grass sward to dry out more thoroughly) and limit woody plant expansion (Staver *et al.*, 2011b). These diverging predictions present a number of interesting future research questions that should be tested in arid and mesic grassy biomes.

Future research directions

A major shortcoming for multi-temporal canopy cover change studies (and the studies of demography and architecture) is a poor understanding of savanna tree growth rates (Higgins *et al.*, 2012); which makes interpreting the observed patterns of change difficult. Long-term, field-based growth experiments focussed on key encroaching species are required. The highly localised studies presented here should also be expanded to cover all the important bioregions in South Africa and the analysis of historical changes should be fused with the demographic data, growth rate data and fire history data; eventually enabling rangeland managers to predict where encroachment is likely to occur and the rate at which it could occur.

There are emerging, cloud based, remote sensing platforms (such as Google Earth Engine) that are lowering the barriers for researchers to conduct multi-temporal, continental-scale burnt area mapping and woody cover change mapping at moderately high resolution (i.e. using the Landsat platforms with 30 m ground resolution) (e.g. Hansen *et al.*, 2013; Pekel *et al.*, 2016); which will be invaluable to savanna ecologists. Consequently, the methods applied in Chapter 4 could already be described as "dated". In the hands of savanna ecologists these new techniques will allow for the development of pixel level observations of woody cover change and fire history, providing far more information than the binary woodland change map presented in Chapter 4. Future efforts to refine the models should focus on including additional and/or improved input data (e.g. herbivory intensity & fire intensity) and on comparing the outcomes of contrasting modelling approaches. There is also scope to investigate the "advancing tree front" idea at finer spatial scales and link this with dispersal ecology and traits of the key encroaching species.

Conclusion

Patterns and trends in woody plant cover change in savannas may vary and the local drivers may differ, but the observations from this study provide a novel test of recent conceptual models of woody plant encroachment in arid vs. mesic savannas (Bond & Midgley, 2012; Moncrieff *et al.*, 2014; Devine *et al.*, 2017; Stevens *et al.*, 2017). In some situations the global CO_2 enrichment driver may override the local drivers such as fire, herbivory and management activities and the regional drivers such as rainfall and drought. The implications of this are that management strategies to address the proliferation of woody plants in savanna-grasslands need to expand to include adaptation rather than focusing on mitigation alone (Case & Staver, 2017). Environmental policies and regulations may also need to change in order to better address land cover change of this nature since the desired ecological state of rangeland managers (usually an open savanna) is becoming progressively more difficult to attain. Given the socioeconomic and conservation importance of tropical grassy biomes worldwide – and the potential impacts of land cover change in these biomes – it follows that quantifying and predicting woody plant encroachment at a scale useful to rangeland managers should continue to receive the attention of ecologists and remote sensing scientists.

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Appendix

Appendix 1.

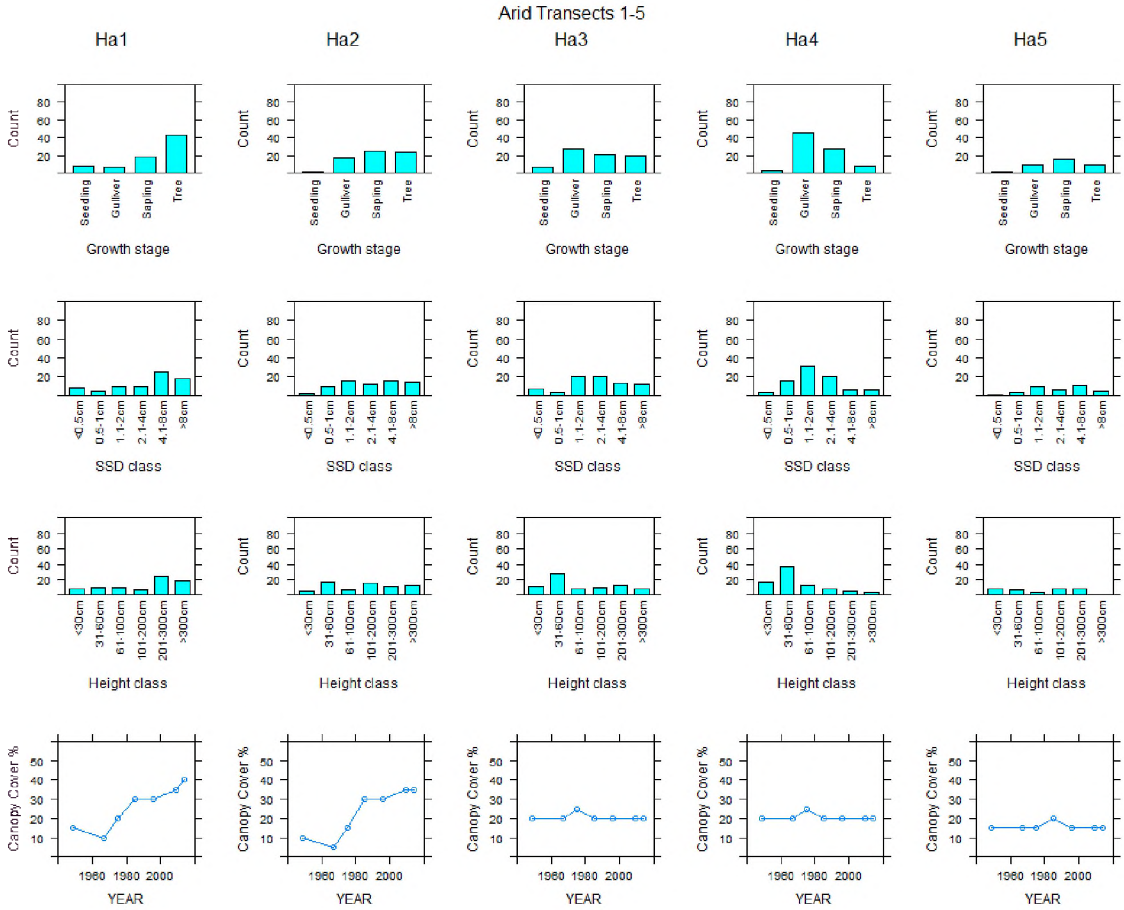

Figure A1. Summary of all demographic measures for arid site transect 1-5

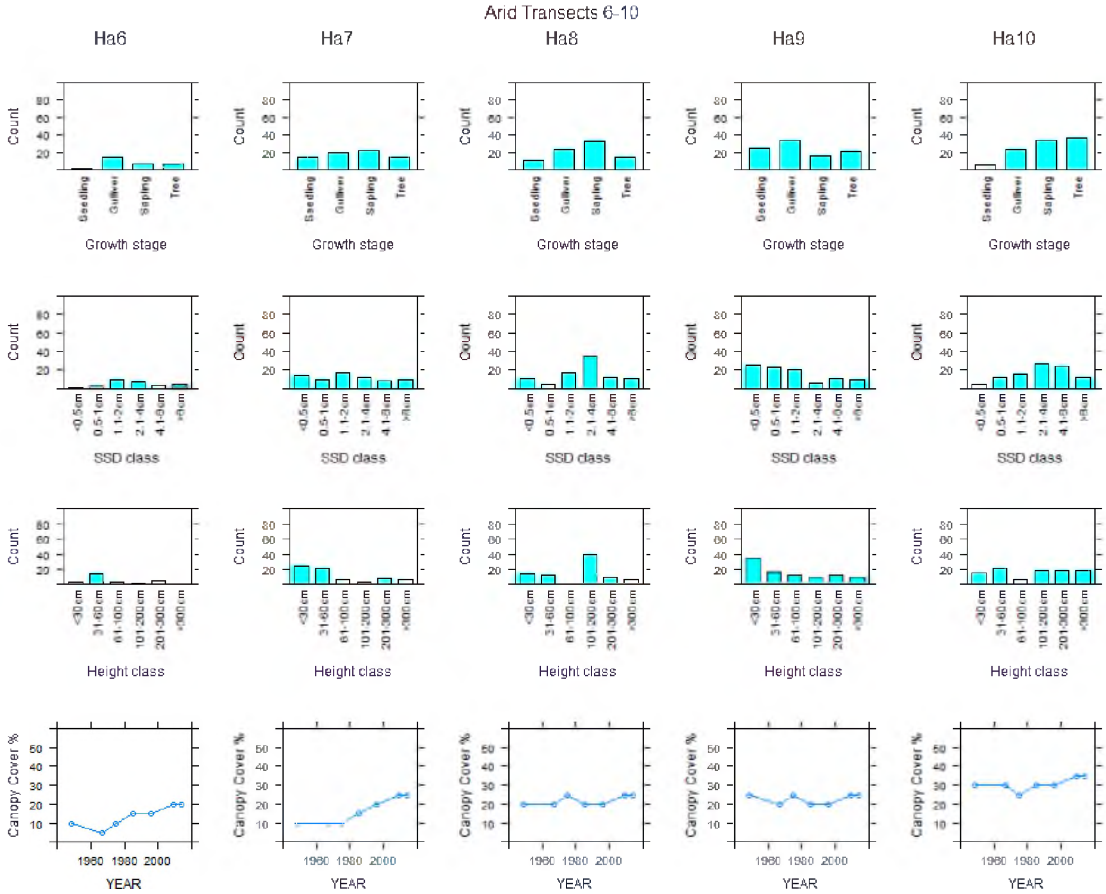

Figure A2. Summary of all demographic measures for arid transects 5-10.

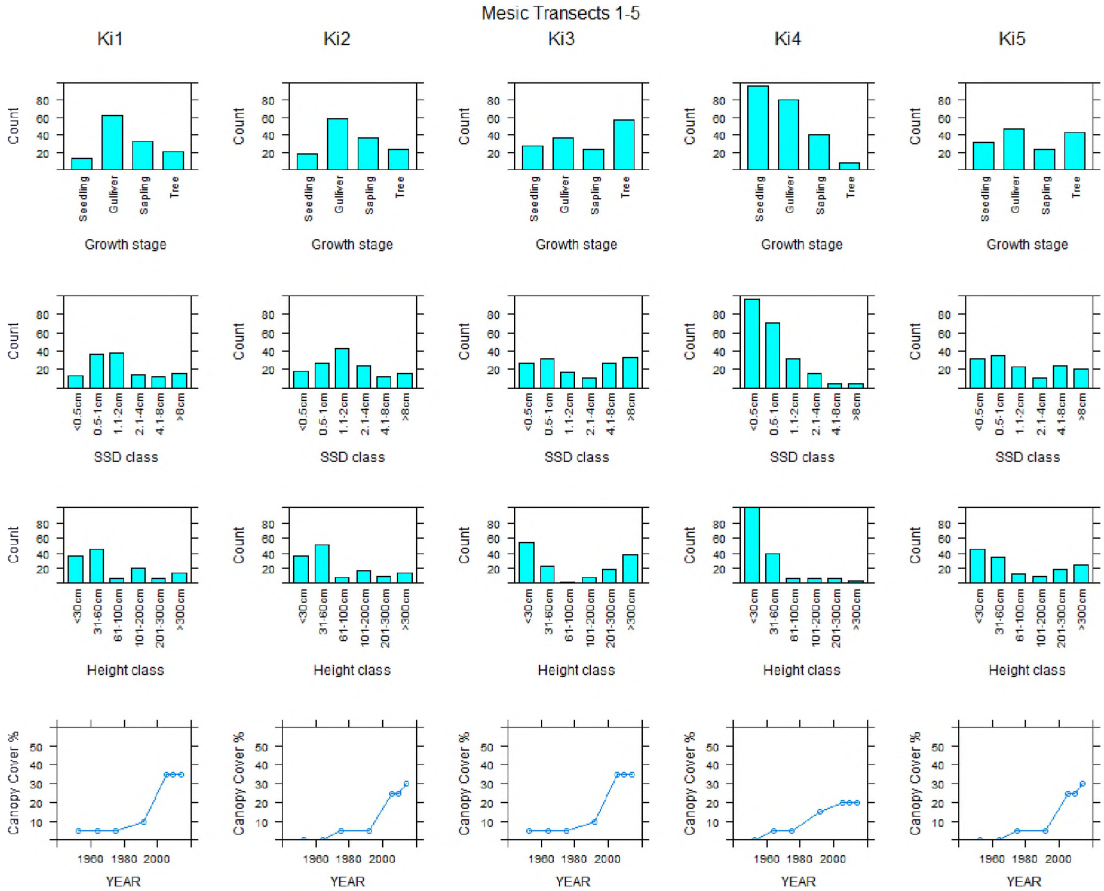

Figure A3. Summary of all demographic measures for mesic transects 1-5

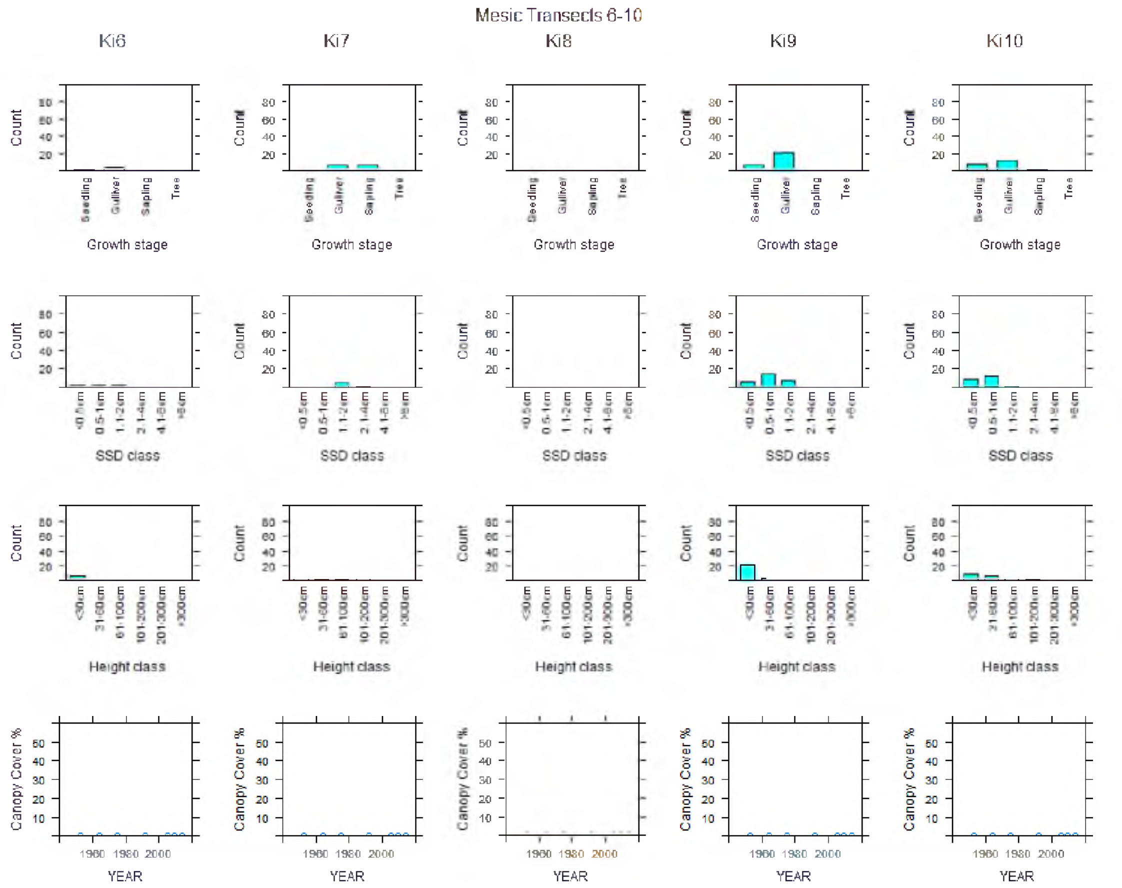

Figure A4. Summary of all demographic measures for mesic transects 5-10