Vegetation change in northern KwaZulu-Natal since the Anglo-Zulu War of 1879

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ABSTRACT

Historic photographs have been successfully used to compare landscape change over time. I used photographs taken of the grassland biome during and just after the Anglo-Zulu War (1879) in KwaZulu-Natal (South Africa), which are some of the earliest known available landscape photographs. The study area encompassed Fugitives' Drift, Isandlwana and Rorke's Drift and included communal and commercial rangelands, as well as conservation areas. These fixed-point photographs showed a dramatic increase in woody cover ($< 82.5\%$) since the Anglo-Zulu War in all three land-use types. Floristic sampling showed that while vegetation structure did not differ significantly, plant species diversity and richness differed significantly for each land-use type. I also used a set of aerial photographs to give a much wider perspective of the landscape changes for the study area from 1944 to 2005. These images indicated that the increase in woody cover was progressive, with most of the woody plant recruitment occurring prior to 1964. Thereafter, the increase in woody plant cover was due to bush-clump thickening rather than recruitment into grasslands. This pattern did not occur, however, in the commercial rangeland, where recruitment into open grassland commenced in the 1980s.

Although the theory of patch dynamics is cyclical in nature, this model may fit the patterns observed in the study area. Analysis of rainfall and temperature data showed that there has been a decrease in average annual rainfall since 1902 and an increase in minimum daily temperature since 1973. However, the decrease in mean annual rainfall is not consistent with woody plant encroachment. While the increase in mean annual daily temperature appears consistent with a shift to an environment typical of savannas, woody plant encroachment started before the increase in daily temperature. A survey of long-term residents in the study area with regard to livestock numbers, grazing patterns, fire and wood harvesting was also inconclusive. I, therefore, speculate that increasing levels of atmospheric
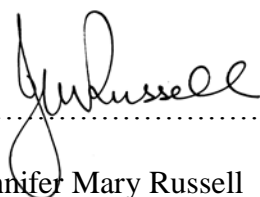
CO_2 is driving bush encroachment, with the other drivers such as rainfall, temperature, absence of intense fires, grazing patterns and land-use, playing a modifying role.

PREFACE

The work described in this thesis was carried out at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa, from January 2010 to November 2013, under the supervision of Professor David Ward.

This thesis is submitted for the degree of Master of Science in the Faculty of Science and Agriculture, University of KwaZulu-Natal, Pietermaritzburg. It represents original work by the author and has not been submitted in any form to another university. Where use was made of the work of others, it has been duly acknowledged in the text.

Chapter 2 and 3 in this thesis were formatted in the appropriate journal style to which they have been submitted.

………………………………………………

Jennifer Mary Russell

November 2013

I certify that the above statement is correct.

………………………………………………

Professor David Ward

Supervisor

26 November 2013

College of Agriculture, Engineering and Sciences

DECLARATION 1 – PLAGIARISM

I, Jennifer Mary Russell, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.

2. This thesis has not been submitted for any degree or examination at any other university.

3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.

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DECLARATION 2 – PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part of research present in this thesis.

Publication 1 – submitted to the African Journal of Range & Forage Science

Russell J M and Ward D (2013) **Vegetation change in northern KwaZulu-Natal since the Anglo-Zulu War of 1879: local or global drivers?**
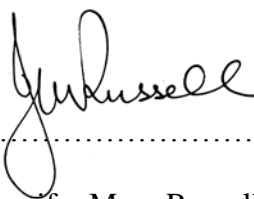
Author contributions:

JMR conceived the paper with DW. JMR collected and analysed the data and wrote the paper. DW contributed valuable comments to the manuscript and facilitated data analysis.

Publication 2 – submitted to the International Journal of Remote Sensing

Russell J M and Ward D (2013, in review) **Remote sensing provides a progressive record of vegetation change in northern KwaZulu-Natal, South Africa, from 1944 to 2005.**

Author contributions:

JMR conceived the paper with DW. JMR collected and analysed the data and wrote the paper. DW contributed valuable comments to the manuscript and facilitated data analysis.

Signed:……………………………………

Jennifer Mary Russell

26 November 2011

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Chapter 1

Literature Review

Introduction

The study of vegetation change is the study of species composition in flux (Davis *et al.* 2005). Underlying all change is the principle of succession, initiated or influenced by disturbance. The mechanisms that cause vegetation change include competition and facilitation (Callaway 1997, Davis *et al.* 2005, Prach and Walker 2011). For example, plants compete with each other for resources such as water (Davis *et al.* 1998) and light (Hoffmann *et al.* 2004, Vadigi and Ward 2013) or they may modify the environment to facilitate colonization by increasing soil moisture through hydraulic lift (Ludwig *et al.* 2003), shade (Brooker et al. 2008) or adding nutrients (Ludwig *et al.* 2001).

The potential source of disturbance leading to successional vegetation change may vary considerably, e.g. as a result of a volcanic eruption, fire, grazing or large-scale clearing for cultivation. The rate and the pattern of succession are determined by the environment (Whittaker 1953, Archer *et al.* 1988) and the changes or steps of succession may be a regular progression or irregular, oscillating back and forth and even skipping a theoretical stage (Westoby *et al.* 1989). There are several models describing succession reviewed by Connell and Slatyer (1977) (see also Pickett *et al.* 1987). The "facilitation" model states that initial colonizing species (or pioneer species) may modify the environment that enables other species to become established (Connell and Slatyer 1977). The "tolerance" model does not require that the environment is modified before the next successive species are able to become established, but each new species must be more competitive for resources than the last (Connell and Slatyer 1977). The "inhibition" model (Connell and Slatyer 1977) holds

that the pioneering species is able to inhibit further colonization by other species until some form of disturbance releases resources for further invasion. The common factor in these models is that succession is brought about by biotic actions, i.e. the modification of the abiotic environment by plants or animals (Walker 1993) and that the system moves towards a climax or equilibrium. The process of succession culminates in a purported climax (Walker 1993), which is not necessarily at maximal net primary productivity or biomass (see e.g. Whittaker 1953). Alternatively, the succession process may be interrupted by further disturbance and the potential climax never reached (Connell and Slatyer 1977). A shortcoming of these equilibrium-based models is that they do not allow for environmental variability (Breshears *et al.* 2002).

There are a number of alternatives to successional theory. Starting with Whittaker (1953), plant species are considered to be independently arranged along an environmental gradient, referred to as a continuum (see also Callaway 1997). This individualistic-continuum theory is based on the importance of the abiotic environment and on resource requirements of the plants. Following this theory, the plant community arose randomly and not through succession. The distribution of the plant species rarely overlaps (Callaway 1997). However, Callaway (1997) argued that plants interact interdependently and that plants are not distributed independently of one another, i.e. reactions are biotic and are facilitative.

Hubbell (2001) (reviewed by Alonso *et al.* 2006) proposed a neutral theory of biodiversity. The theory assumes that all species within a community are equivalent, i.e. have traits of equal strength regarding birth, death, dispersal and speciation (Alonso *et al.* 2006, Gravel *et al.* 2006). Consequently, all species within a community drift towards extinction in a stochastic manner, but extinction is prevented through random dispersal (Alonso *et al.* 2006) or immigration of propagules (Gravel *et al.* 2006). Gravel *et al.* (2006) proposed that neutral theory and niche-competition theories are not necessarily in opposition,

but are extremes on a continuum. Their simulation model, which incorporated both the regional community from which propagules dispersed and the local community into which propagules immigrated, supported their proposal (Gravel *et al.* 2006) (see also Leibold, 2008).

Westoby *et al.* (1989) suggested that the succession model, with a single-state climax, was limited in its application. It implied that vegetation trends were continuous and reversible if interrupted, but in reality this is not necessarily correct. Westoby *et al.* (1989) described a stochastic model called the state-and-transition model in which the system did not reach a single, ultimate climax. The dynamics of an ecosystem were either in a discrete "state" or in "transition" between states. Westoby *et al.* (1989) emphasized the presence of boundaries between states. Transitions were triggered by the increasing intensity of a disturbance (or the removal of the disturbance altogether) such as fire or grazing that moved the ecosystem to a different state (with regard to structure or species composition). Once the disturbance that caused the transition reverted to its previous level of intensity, the system did not revert to its previous state. Following Westoby *et al.*'s (1989) model, the system had crossed the boundary or threshold. The system, therefore, has the potential for multiple stable states (see also Dublin *et al.* 1990, Walker 1993). Westoby *et al.*'s (1989) state and transition model is not a predictive model, but is a way of describing multiple stable states (Breshears *et al.* 2002).

Richards (1952), cited by Swaine and Hall (1988), described succession in terms of a cycle of regenerating patches of trees in a forest which Richards (1952) termed the mosaic theory. When a gap, or open patch, in a plant community is created as a result of the death of an individual plant, or of a group of plants, other plants take its place which may be of the same species or may not (Grubb 1977) (see also Yeaton 1988). The composition of plant species that colonize the gap may be governed by various factors such as gap size, shade

tolerance, soil nutrients, and/or presence of propagules (Grubb 1977). In discussing patch dynamics, Wiegand *et al.* (2006) also suggested that succession could be a cyclical process. Wiegand *et al.* (2006) proposed that a plant community progresses through a series of natural changes which finally bring it back to its original state (see also Meyer *et al.* 2007). Wiegand *et al.* (2006) argued that a self-thinning process through intra-specific competition could explain the cyclical nature of arid savanna succession. Contrastingly, Adie and Yeaton (2013) describe the facilitative effect of nurse plants and natural senescence as drivers of cyclical succession in arid savannas.

Savannas

The term 'savanna' refers to mixed tree-grass communities, typified by a continuous herbaceous layer and a scattered tree layer (Knoop and Walker 1985, Scholes and Archer 1997, Lehmann *et al.* 2008, Moustakas *et al.* 2010). Savannas have strongly alternating wet and dry seasons (Skarpe 1992, Scholes and Archer 1997, Bond 2008). About one sixth of the earth's surface (Grace *et al.* 2006) and about half of Africa (Scholes and Archer 1997, Grace *et al.* 2006, Moustakas *et al.* 2010) consist of savannas. About one third of South Africa is covered by savannas (Mucina and Rutherford 2011). Of that, 84% is used for cattle, game and subsistence ranching (Grossman and Gandar 1989). Savannas are responsible for about 30% of all primary production (Grace *et al.* 2006, Lehmann *et al.* 2008) and are socioeconomically important in both tropical and temperate regions (Grossman and Gandar 1989, Scholes and Archer 1997, Twine *et al.* 2003, Ward 2005, Wigley *et al.* 2009).

There is growing concern among ecologists and rangeland managers regarding the gradual conversion of grasslands and savanna to shrublands and woodlands (Trollope 1982, Archer *et al.* 1995, Roques *et al.* 2001, Smit 2004, Kraaij and Ward 2006). As early as the 1950s, Shantz and Turner (1958) noted an increase in thorny shrubs in the grasslands of

Kenya and South Africa with a decrease in palatable grasses and forbs. The invasion of

savannas and grasslands by woody plants is a global phenomenon (see e.g. Archer *et al.*

1995, Brown and Archer 1999, Wiegand *et al.* 2006, Bond 2008). The reasons behind these

changes are hotly and widely debated and range from heavy grazing (Walker *et al.* 1981), fire

(Roques *et al.* 2001) and global climatic change (Archer 1989) to shifting human populations

(Hoffman 2011).

One of the challenges facing ecologists is the complexity of savanna dynamics (House

et al. 2003). Savannas are described as being among the most variable of terrestrial

ecosystems (Walker and Noy-Meir 1982). Any model that attempts to predict tree:grass

interactions needs to include elements of competition and facilitation which vary in time and

in space (Scholes and Archer 1997) and which may be interspecific or intraspecific (Pillay

and Ward 2013). Models also need to take into account agents of disturbance, such as fire,

climatic variability and herbivory (Scholes and Archer 1997, Sankaran *et al.* 2008), as well as

mean annual precipitation (Sankaran *et al.* 2005) as the amount and distribution of rainfall

may determine the tree:grass ratio at least at lower mean annual rainfall levels.

An overview of the dynamics of savannas

The savannas of the tropics and subtropics are dominated by C_4 grasses (Sage 2004, Bond

2008, Edwards *et al.* 2010, Ratnam *et al.* 2011). The term 'C_4' refers to a photosynthetic

pathway that arose as a supplement to the ancestral C_3 photosynthetic pathway (Sage 2004).

It is a series of biochemical and anatomical modifications to the existing C_3 pathway (Sage

2004), which concentrates CO_2 within the photosynthesizing tissue of the plant (Ehleringer *et

al.* 1991, Collatz *et al.* 1998, Morgan *et al.* 2001, Sage 2004, Bond 2008), making it more

efficient under conditions of stress. These conditions include combinations of higher

ambient temperature, low atmospheric CO_2 concentrations (see e.g. Sage 2004, Bond 2008,

Edwards *et al.* 2010), salinity, aridity and flooding (Sage 2004). C_4 plants are successful in these conditions because of better water- and nutrient-use efficiency than C_3 plants (Sage 2004). However, the CO_2 concentrating mechanism of C_4 plants require energy and if temperatures drop below 16 - 20 °C at today's atmospheric CO_2 concentrations (Cerling *et al.* 1997) or 20 - 25 °C (Osborne 2008), or if atmospheric CO_2 exceeds 500 μmol/mol, C_4 plants will lose their competitive edge over C_3 plants (Cerling *et al.* 1997).

The tree component of savannas can be described as open where the balance favours grasses or closed where the balance favours trees. Tree density may increase along a rainfall gradient, from an open state towards a closed state, until mean annual precipitation reaches ~700 mm (Sankaran *et al.* 2008) or ~820 mm (Higgins *et al.* 2010). When mean annual precipitation exceeds 700 mm, rainfall no longer limits tree density and disturbance (e.g. fire, climatic variability, herbivory) maintains the open nature of the savanna (Sankaran *et al.* 2008). Most savanna trees have the ability to coppice or resprout vigorously from an early age in response to disturbance (Scholes and Archer 1997, Bond and Midgley 2000, Higgins *et al.* 2000, Neke *et al.* 2006, Schutz *et al.* 2009). This response may enable them to survive repeated episodes of severe disturbance and maintains a viable tree component.

The dynamics of savannas and the mechanisms that maintain the balance between the tree:grass components are matters of debate. There are several proposed mechanisms that drive savanna dynamics:

1) Competition- or resource-based models

The root niche separation model is based on Walter's two-layer equilibrium model (Sankaran *et al.* 2004). In a "natural" savanna, i.e. one that is not anthropogenically derived, the structure of the savanna is determined by the competition between the roots of grasses and woody plants for soil water (Walker and Noy-Meir 1982, Eagleson and Segarra 1985, Van

Langevelde *et al.* 2003, Ward *et al.* 2013a). This implies that soil water is a limiting factor (Walker *et al.* 1981, Ward *et al.* 2013a) and that this model is not appropriate for mesic or humid savannas, where mean annual precipitation is more than 700 mm (Sankaran *et al.* 2008) or 820 mm (Higgins et al. 2010). However, even in arid regions, the root-niche-separation model does not necessarily apply. Brown and Archer (1999) found that tree seedling germination and establishment were not affected by grass competition, even in periods of drought (see also Kraaij and Ward 2006, although see Grellier *et al.* 2012). Wiegand *et al.* (2005) noted that woody plant encroachment occurred where soils are too shallow for root separation.

Another model, phenological separation, is based on separation in time (Westoby 1979, Scholes and Archer 1997, House *et al.* 2003, Sankaran *et al.* 2004). In humid savannas, trees may expand their leaves synchronously before the first rains, whereas grasses reach peak production late into the wet season (Scholes and Archer 1997). Trees may also retain their leaves after the grasses have reached senescence (Scholes and Archer 1997). The trees, therefore, have access to resources such as soil moisture much earlier and much later in the growing season than grasses (Scholes and Archer 1997, Sankaran *et al.* 2004). During the period of overlap, the grasses are the superior competitors for resources (Sankaran *et al.* 2004). However, tree leaf area index could be high enough to exclude grasses during the period of high resource-availability (Higgins *et al.* 2010), unless the grasses were shade tolerant.

The balanced competition model describes a system where competition is intraspecific (Scholes and Archer 1997, House *et al.* 2003, Sankaran *et al.* 2004) rather than interspecific. Here, the dominant competitor is self-limiting. A state of equilibrium is reached when the dominant competitor becomes self-limiting at a biomass that does not exclude the inferior competitor. Many systems comprise multiple competing tree species

(see e.g. Schleicher *et al*. 2011a) and this model would not generally be appropriate. Also, like many competition-based models, this model assumes spatial homogeneity which is unrealistic for a system such as a savanna, characterized by a heterogeneous vegetation structure (Jeltsch *et al.* 2000). Furthermore, there is limited evidence of systems at equilibrium; models based on equilibrium cannot account for the dynamic nature of ecological systems (Briske *et al.* 2003).

A hydrologically driven hierarchical competition-colonization model was proposed by Fernandez-Illescas and Rodriguez-Iturbe (2003). This models a system in non-equilibrium and expands on the competition-colonization models proposed by, for example, Tilman (1994). Tilman (1994) described a trade-off between resource utilization (competition) and reproductive fitness (colonization). Where a resource is limited, those species that are best able to utilize that resource will out-compete those that may be better seed dispersers. Tilman (1994) recognized that his model was an oversimplification of the complexities of nature. Fernandez-Illescas and Rodriguez-Iturbe (2003) added a stochastic element to this model. They proposed that, as primary production is closely related to soil moisture, competitive success is based on the plant's ability to utilize this resource (Fernandez-Illescas and Rodriguez-Iturbe 2003). However, soil moisture fluctuates throughout the growing season and between years. As a result, competitive ability will also fluctuate, thus allowing the colonizers a chance to become established (Fernandez-Illescas and Rodriguez-Iturbe 2003). Although Fernandez-Illescas and Rodriguez-Iturbe (2003) added climatic variation to the competition-colonization model, they recognized that their model remains an over-simplification.

Spatially explicit models are based on the effects of individual plants on neighbouring plants and on inherent spatial variation in abiotic factors (Wu *et al.* 1985, Scanlan 1992, Scholes and Archer 1997). An example of a spatially explicit model is Wiegand *et al.*'s

(2005) concept of patch dynamics which explains the coexistence of trees and grasses (see also Wiegand *et al.* 2006, Meyer *et al.* 2007, Moustakas *et al.* 2008, Meyer *et al.* 2009). They described a cyclical succession between open and closed savannas, driven by rainfall and inter-tree competition. Wiegand *et al.*'s (2006) honeycomb rippling model described what happens within each patch. Once woody plant encroachment has occurred (e.g. due to unique high rainfall events), certain tree seedlings with access to more resources than their neighbours, out-competes its immediate neighbours and the neighbours die off. This gives the tree seedlings beyond the ring of now dead seedlings a competitive advantage over their nearest neighbours, which in turn die off as the trees grow larger. In this way, concentric rings of dominant seedlings are formed within each patch. However, within the concentric rings of dominant seedlings, there is also competition for resources and gradually the arrangement of the trees become more regular. The self-thinning process could result in a transition back to a state of open savanna. Some evidence in support of this process is provided by Ward (2005) and Wiegand et al. (2006). Meyer *et al*. (2007) described the landscape as being made up of patches of variable sizes. In each patch, the same cyclical succession proceeds, but not necessarily at the same rate or at the same time as in the other patches. The system is, therefore, in a state of non-equilibrium within each patch. At the scale of the total landscape, however, the proportion of each successional state remains constant and, overall, the system is in equilibrium (Wiegand *et al*. 2006, Meyer *et al*. 2007, Moustakas *et al.* 2010).

The competition-based models are unable to explain all cases of tree-grass codominance in savannas. Wiegand *et al.* (2005), for example, have shown that in some areas the soils are too shallow to permit a two-layered soil differentiation and yet trees and grasses co-exist. As tree seedlings establish themselves, tree roots have to compete directly with grass roots in the upper soil zone (Ward 2005, Cramer and Bond 2013). Trees can also

have a facilitative, rather than a competitive effect, on plants under their canopies. Belsky *et al.* (1989) found that soil moisture during the rainy season and nutrients were higher under the canopies of individual savanna trees than in the open grassland beyond the canopy. Another study showed increased plant species diversity and soil nutrients under tree canopies compared to the surrounding areas (Munzbergova and Ward 2002). Ludwig *et al.* (2003) noted that hydraulic lift by trees had the potential to facilitate grass productivity, while Belsky *et al.* (1989) and Riginos *et al.* (2009) suggested that the increased grass productivity under tree canopies was the result of higher soil nutrients (see also review by Flores and Jurado 2003, Schleicher *et al.* 2011b).

2) Disturbance-based models

In many savannas, particularly mesic and humid savannas, tree-grass codominance is based on disturbance (Sankaran *et al.* 2005, Sankaran *et al.* 2008, Higgins *et al.* 2010, Murphy and Bowman 2012, Staver and Levin 2012, Ward *et al.* 2013b). Such systems are said to be in disequilibrium (Sankaran *et al.* 2004) or in non-equilibrium (Higgins *et al.* 2000) where long-term coexistence of grasses and trees would not be possible without disturbances such as fire and/or herbivory, as well as climatic variability.

Demographic-bottleneck models emphasize the role played by disturbances (reviewed by Moustakas *et al.* 2010). In the absence of disturbance, a dry savanna could turn into grassland, while a moist savanna could become a forest (Scholes and Archer 1997, Jeltsch *et al.* 2000, Sankaran *et al.* 2004). Fire is the agent of disturbance that is generally regarded as most important in moist savannas (Higgins *et al.* 2000, Jeltsch *et al.* 2000, Sankaran *et al.* 2004, Bond 2008).   In dry savannas, rainfall is generally regarded as the primary agent of disturbance (Sankaran et al. 2005).

Demographic-bottleneck models also take the life-stages of trees into account. Higgins *et al.* (2000) proposed a demographic-bottleneck model based on a storage effect where the establishment of seedlings and the recruitment from seedling to adult tree is 'stored'. Seed germination may be suppressed during years of drought and released by rare wet years. Once established, the seedlings are again suppressed as juveniles, held within the demographic-bottleneck by fire, until released by another wet season (see also Sankaran *et al.* 2004). Seedling establishment and tree recruitment is, therefore, episodic, dependent on rainfall-driven for seedling establishment and tree recruitment is limited by fire intensity. Higgins *et al.*'s (2000) model works best for mesic and humid savannas. Higgins *et al.*'s (2000) model is based on Warner and Chesson's (1985) storage effect model. Warner and Chesson (1985) assumed that competition among adult organisms did not influence adult survival, but Wiegand *et al.* (2005) and Ward (2005) have shown that competition in adult trees can be very important. This means that the mechanism behind Higgins *et al.*'s (2000) model is incorrect. Staver *et al.* (2009) proposed a similar model to Higgins *et al.* (2000), but considered the primary effects of browsing on seedlings and adult trees, with fire as a secondary influence. They found that while herbivory could suppress tree cover, fire alone could not. Browsing and fire together maintained a bottleneck by suppressing the maturation of trees. When the disturbance was interrupted, the bottleneck was removed and tree recruitment followed. Like Higgins *et al.*'s (2000) model, Staver *et al.*'s (2009) lacks general applicability, but can explain tree-grass coexistence in mesic savannas where soil water is not a limiting factor.

Jeltsch *et al.* (2000) proposed a model which focused on the boundaries of a system, rather than on equilibria or on domains of attraction. These authers called the mechanism behind the model 'ecological buffering'. Jeltsch *et al.* (2000) place their focus on what prevents a transition into grassland or woodland, rather than on what maintains a certain state.

As with other models that rely on disturbance (see e.g. Higgins *et al.* 2000, Staver *et al.* 2009, Higgins *et al.* 2010, Staver and Levin *et al.* 2012), Jeltsch *et al.* (2000) identify fire and herbivory as the buffering mechanisms which impede the transition to woodland. They also see microsites within a system as important buffering mechanisms (Jeltsch *et al.* 1998, Jeltsch *et al.* 2000). For example, a termite mound or a microdepression could protect tree seeds or seedlings from fire, thus inhibiting the transition to grassland. Jeltsch *et al.*'s (2000) model begins to address the enormous complexity of savannas by taking cognisance of disturbance as well as niche separation in terms of microhabitats.

Scholes and Archer (1997) suggested that it was unrealistic to predict tree:grass interactions with a simple model. "[Savannas] include elements of competition and facilitation, varying in complexity in space and time." They called for a model that combined niche separation, competition and disturbance to explain tree:grass coexistance (see also Briske *et al.* 2003). The model proposed by Wiegand *et al.* (2006) includes inter-tree competition as well as disturbance in their description of patch dynamics. Their model also is applicable for arid and for mesic savannas. In arid savannas, tree recruitment is trapped in a bottleneck, until sufficient rains allow for seedling establishment and recruitment. In mesic or humid savannas the bottleneck is fire-driven. Because the landscape is made up of a mosaic of patches of treees and grasses, each at a different stage in the cycle between open grassland and enclosed woodland (Meyer *et al.* 2007), the model discribes a system that has the potential to be able to withstand severe disturbances. On a landscape level, therefore, the conversion of a savanna to pure grassland or to pure forest is unlikely (Wiegand *et al.* 2006).

Potential mechanisms that determine the tree:grass ratio of savannas

It would simplify matters if one could separate the potential mechanisms that determine the tree:grass ratio of savannas and examine each in isolation. In reality, these mechanisms

interact with each other, sometimes synergistically, sometimes as opposing forces (Jeltsch *et al.* 1996, Midgley *et al.* 2010).

Climate

Soil moisture

Rainfall (soil moisture) is a potential mechanism that maintains a savanna biome (Scanlan and Archer 1991, Bond *et al.* 2003, Murphy and Bowman 2012). Sankaran *et al.* (2005) analysed data from 854 sites across Africa. They found that where mean annual precipitation was less than ~650 mm, soil water constrained woody cover and that these savannas could be regarded as "stable". In a subsequent analysis of a further 161 savanna sites across Africa, Sankaran *et al.* (2008) confirmed that, when mean annual precipitation fell between 200 mm and 700 mm, rainfall was the most important factor in bush encroachment. Higgins *et al.* (2010) suggested that the threshold might be as high as ~820 mm. Sankaran *et al.* (2005) also found that tree cover increased linearly along the rainfall gradient (see also Wiegand *et al.* 2005). In South Africa, O'Connor (1995) showed that seedling survival of *Acacia karroo,* an important woody encroacher, is much increased with increased soil moisture (see also Kraaij and Ward 2006). Where rainfall was higher than ~650 mm, disturbances such as fire and herbivory, were required to maintain an open structure to savannas (Bond *et al.* 2003, Sankaran *et al.* 2005). Lehmann *et al.* (2011) found that rainfall seasonality was the most important factor that determined the distribution of savannas. They found this to be consistent across the continents of Africa, Australia and South America, although the threshold above which savannas ceased to be affected directly by mean annual rainfall, differed across the continents (see also Murphy and Bowman 2012).

Zimmermann *et al.* (2008) emphasised that the establishment of shrub seedlings in arid savannas tends to be episodic or pulsed (see also Ellis and Swift 1988, Archer 1989,

Brown and Archer 1999, Kraaij and Ward 2006). One year of drought could trigger above-average flowering and seed set, but to ensure seed germination and seedling survival, a further two to three good rainy seasons needed to follow (O'Connor and Crow 1999, Zimmermann *et al.* 2008). Rainfall distribution within a wet season was as important as total rainfall for seed germination and seedling survival (Ward 2005, Kraaij and Ward 2006). In contrast, February *et al.* (2013) found that increasing rainfall increased competition between grasses and trees. As a result, recruitment from seedling to adult tree is more likely in drought years when there is little competition from grass for soil moisture and grass fuel loads are low (although see Ward 2009 for a contrasting view).

Temperature

Temperature may also play a role in determining the tree:grass ratio. Savannas experience higher minimum temperatures than grasslands (O'Connor and Bredenkamp 1997, Wakeling *et al.* 2012) which could favour tree recruitment. Frost has a deleterious effect on woody species (Silberbauer-Gottsberger *et al.* 1977, Brando and Durigan 2005, Holdo 2006, Coop and Givnish 2007, Wakeling *et al.* 2012). However, O'Connor and Bredenkamp (1997) noted that some savanna species such as *Acacia karroo* were frost tolerant, although frost tolerance depended on the origin of the population (see Wakeling *et al. 2012*). *A. karroo* seedlings that were grown from seeds collected in Bloemfontein, South Africa, where very low minimum temperatures are routinely experienced in winter, were frost tolerant (Wakeling *et al.* 2012), unlike seedlings grown from seeds collected from more temperate sites. Wakeling *et al.* (2012) showed that *A. karroo* from the temperate sites, along with other savanna tree species, experienced top-kill, as well as mortality (but only at the coldest site), due to frost. Wakeling *et al.* (2012) proposed that the effect of frost on savanna trees, together with fire, created a demographic bottleneck to suppress woody plant encroachment.

Fire

Fire and its effect on bush encroachment

Fire is perceived to be a major influence in maintaining the grass component in savannas (Trollope 1974, Trollope 1982, Ellery *et al.* 1995, Higgins *et al.* 2000, Kraaij and Ward 2006, Staver *et al.* 2011), particularly in mesic and humid savannas (Jeltsch *et al.* 2000, Bond *et al.* 2003, Fensham *et al.* 2003, Bond 2008, Sankaran *et al.* 2008, Ratnam *et al.* 2011). While soil moisture determines the establishment of seedlings, it is fire that limits recruitment of seedlings into adulthood (Higgins *et al.* 2000, Staver and Levin 2012) by creating a demographic bottleneck (Staver *et al.* 2009, Wakeling *et al.* 2011). Williams *et al.* (1999) noted that, among those woody species that survived a fire, flowering and fruiting was reduced. Conversely, in some circumstances, fire could exacerbate bush encroachment. Fire will also trigger germination in some species (Hodgkinson 1991, Bradstock and Auld 1995, Kraaij and Ward 2006). Many encroaching species will coppice vigorously after the above-ground portions have been killed (Van der Schijff 1957 and Pienaar 1959 cited by Trollope 1980, Wakeling and Bond 2007). Lemon (1968) suggested that apparent contradictions could be the result of differing climatic conditions and whether fire had been present within the system long enough to bring about evolutionary adaptations within the plant communities. In most cases, however, fire does not act alone on savanna dynamics and, combined with the effects of herbivory, creates a demographic bottleneck whereby saplings will persist until some event allows them to escape the fire/browse zone (see for example Trollope 1974, Dublin *et al.* 1990, Roques *et al.* 2001, Van Langevelde *et al.* 2003, Staver *et al.* 2009, Midgley *et al.* 2010).

Fire intensity and return frequency

The intensity of a fire depends on the fuel load (Trollope and Tainton 1986, Scholes and Archer 1997) and fuel moisture (Trollope *et al.* 2002), which will affect the recovery of woody plants. The greater or drier the fuel load, the more intense the fire, the higher the percentage of woody plants that experience top-kill (Trollope and Tainton 1986, Trollope *et al.* 2002) and mortality (Williams *et al.* 1999) (see also Sankaran M, Ratnam J, Hanan NP. 2004, Van Langevelde *et al.* 2003). Arid and semi-arid savannas burn only after a season of above-average rainfall and the fuel load is great enough to support a fire (Skarpe 1992, Meyer *et al*. 2005). Mesic or intermediate savannas burn frequently and more intensely because the fuel load created by grasses is generally high (Skarpe 1992, Bond *et al.* 2003, Sankaran *et al.* 2008). Fuel load will also affect fire-return frequency (Scholes and Archer 1997, Higgins *et al.* 2000). If mean annual rainfall remains high, the fuel load will build up rapidly which allows a shorter fire-return frequency (Scholes and Archer 1997, Roques *et al.* 2001, Owens *et al.* 2002) which will, in turn, inhibit woody encroachment (Hoffmann 1999, Higgins *et al.* 2000, Roques *et al.* 2001, Hudak *et al.* 2004, Sankaran *et al.* 2005, Lehmann *et al.* 2008, Gordijn *et al.* 2012).

Fire and the life-stages of trees

The extent of stem mortality or top-kill depends on stem height, as well as on fire intensity (Trollope 1974, Balfour and Midgley 2006) and, in general, smaller trees (< 2 - 3 m) are more vulnerable to stem mortality (Trollope 1974, Trollope and Tainton 1986, Van Langevelde *et al.* 2003, Higgins *et al.* 2007, Wakeling *et al.* 2011). There may be species-specific responses to fire. For example, while most *Acacia* species are not killed by fire, experiencing stem mortality only (Trollope 1974, Trollope and Tainton 1986, Hoffmann 1999, Higgins *et al.* 2000), adult trees of *A. mellifera* experienced a relatively higher mortality rate than *A.*

mellifera saplings (Meyer *et al.* 2005, Joubert *et al.* 2012). The resilience of species such as *A. karroo* may be due to the thickness of the stem bark and to stem diameter (Trollope and Tainton 1986, Balfour and Midgley 2006, Lawes *et al*. 2011). Meyer *et al.* (2005) suggest that the reason for the higher mortality rate in adult *A. mellifera* trees than in the saplings may be due to a limited rate of production of new cells in the apical meristem or as a result of the effects of senescence. Hanan *et al*. (2008) have proposed a "two-size-class savanna model" which separates the woody community of savannas into saplings and adult classes. The sapling class is highly sensitive to fire (mortality or top-kill), but the adult class is fire resistant (see also e.g. Trollope and Tainton 1986, Balfour and Midgley 2006, Lawes *et al*. 2011). The model demonstrates that, while sapling density fluctuates rapidly in response to fire, adult tree density remain stable until natural attrition over the long-term (20 – 100 years) causes the decline in adult tree density (Hanan *et al.* 2008).

Timing of fires

The timing of a fire will also have an impact on trees. Trollope (1982) believed that it was difficult to ascertain the season when trees would be most affected by burning because the effect could be confounded with fire intensity. Zimmermann *et al.* (2008) suggest that woody plants would be more sensitive to fire at the start of the rainy season, when stems are more sensitive and buds are exposed. A similar view is expressed by West (1965, cited by Trollope 1982). West (1965) proposed that trees would be susceptible to fire damage at the end of the dry season because: 1) the initial temperature of the plant tissue is high, 2) plant reserves are low, having just produced new leaves, 3) less protection can be gained from the bark because moisture content and thermal conductivity increased with the start of active plant growth, and 4) the newly formed buds are more easily damaged by fire. Furthermore, the fuel load will be dry at the end of the dry season, permitting a more intense fire (Trollope

and Tainton 1986, Wigley *et al.* 2010). Fires that occur early in the dry season ultimately reduce the grass layer and therefore facilitate woody plant encroachment (Zimmermann *et al.* 2008) (see also Trapnell 1959).

Effects of fire exclusion

Long-term comparative studies between different fire regimes in humid savannas, which included fire exclusion, showed greater tree and shrub density in the unburned plots (Trapnell 1959, San José and Fariñas 1983, Swaine *et al.* 1992, Woinarski *et al.* 2004), as well as a suppressed grassy layer (Trapnell 1959), compared to the burned plots. San José and Fariñas (1983) also found that where trees were sparsely scattered, tree recruitment rate was high, whereas in the woody clumps or "groves" the recruitment rate was lower (see also Roques *et al.* 2001). San José and Fariñas (1983) also found that shrub species diversity increased in the "groves". Swaine *et al.* (1992) observed an increase in tree species diversity in the fire exclusion plots, mainly resulting from forest species recruiting from the forest zone about 7 km away from the savanna plots (see also Woinarski *et al.* 2004). Hoffmann (1999) modelled the effect of fire in humid savannas. His model showed that tree density increased if fire was excluded. Field trials supported the model. Simulation modelling by Bond *et al.* (2003) predicted that exclusion of fire in arid savannas (average annual rainfall < 300 mm) would have no effect on tree cover, but that fire exclusion in semi-arid (average annual rainfall < 650 mm) and mesic savannas (average annual rainfall > 650 mm) would result in tree-dominated landscapes, i.e. an increase in tree density (see also Bond and Archibald 2003, Bond *et al.* 2005). Hudak *et al.* (2004) used satellite imagery to analyse fire patterns in semi-arid savannas. They made the assumption that fire patterns are closely related to vegetation patterns and found that fire exclusion resulted in more homogeneity in the vegetation. Higgins *et al.* (2007) found that fire exclusion in semi-arid savannas did not result in an

increase in tree density, although there was an overall increase in biomass. Midgley *et al.* (2010) suggested that there were flaws in Higgins *et al.*'s (2007) experimental design in that marked trees were not followed. As a result, it was not clear whether the changes in biomass were due to changes in recruitment, transitions or mortality, or whether the change was due to differences in growth rates (Midgley *et al.* 2010). Consequently, Higgins *et al.*'s (2007) unexpected result needs to be treated with caution.

Herbivory

Herbivory has direct and indirect effects on the tree:grass ratio of savannas (Skarpe 1991, Archer *et al.* 1995, Van Langevelde *et al.* 2003, Riginos and Young 2007, Staver *et al.* 2009). Direct effects are through consumption (Savory and Parsons 1980, Walker *et al.* 1981, Yeaton 1988, Skarpe 1991, Zimmermann *et al.* 2008, Midgley *et al.* 2010) and trampling (Savory and Parsons 1980, Walker *et al.* 1981, Skarpe 1991). Indirect effects are largely through removal of competition for resources (Scholes and Archer 1997, Kraaij and Ward 2006, Riginos 2009, Ward and Esler 2011), and through the effects on reduction of fuel load for fires (Scholes and Archer 1997, Roques *et al.* 2001, Van Langevelde *et al.* 2003, Archibald *et al.* 2005, Staver *et al.* 2009). Browsing can also prevent saplings from growing into adult trees, thereby maintaining them at a size where they are vulnerable to the effects of fire (Trollope 1974, Staver *et al.* 2009).

Direct effects of herbivory

Grazing and browsing have been shown to benefit grasses by increasing biomass (McNaughton 1979, 1984, reviewed by Skarpe 1991), palatability and ground cover (reviewed by Skarpe 1991) and shrubs by increasing production (Stuart-Hill and Tainton 1988, Skarpe 1991) respectively. There are a number of mechanisms that may be triggered

by herbivory (reviewed by McNaughton 1979) such as increased photosynthetic rates, relocation of carbohydrates, and hormonal redistribution into the residual meristems. Other mechanisms include reduced transpiration through leaf removal and, therefore, conservation of soil moisture, increased light intensity through leaf removal, increased soil nutrients from dung and urine, and growth-promoting agents in ruminant saliva (McNaughton 1979). However, grazing generally reduces the herbaceous layer, creating space and consequently permits woody plant encroachment to occur (Walker *et al.* 1981, Van Vegten 1983, Roques *et al.* 2001). Browsing, on the other hand, has the opposite effect (Grossman and Gandar 1989, Dublin *et al.* 1990, Roques *et al.* 2001, Augustine and Mcnaughton 2004, Holdo 2006, Zimmermann *et al.* 2008, Midgley *et al.* 2010) and may directly reduce woody cover. Roques *et al.* (2001) found that browsing prevented the establishment of woody seedlings, but the effect of browsing on established woody plants was not significant. The consumption of seeds and pods by large and small herbivores can either destroy reproductive potential (Or and Ward 2003, Zimmermann *et al.* 2008) or aid seed dispersal (Walker *et al.* 1981, O'Connor 1995, Brown and Archer 1999, Or and Ward 2003, Tews *et al.* 2004, Fredrickson *et al.* 2006), thereby inhibiting or facilitating woody plant encroachment.

Indirect effects of herbivory

Herbivory mostly works in concert with other factors that determine savanna dynamics. Heavy grazing may indirectly result in an increase in woody cover (Trollope 1974, Grossman and Gandar 1989, Roques *et al.* 2001, Van Langevelde *et al.* 2003, Wigley *et al.* 2010, Grellier *et al.* 2012). Browsing, on the other hand, may decrease woody cover by maintaining saplings within the fire zone where they experience extensive top-kill (Trollope 1974, Grossman and Gandar 1989, Staver *et al.* 2009). Browsing can also reduce woody cover sufficiently to allow an increase in the shade-intolerant grass cover which increases

fuel load and fire intensity (Laws 1970, Van Langevelde *et al.* 2003). Conversely, reductions in canopy cover by browsers would also permit further establishment of canopy-intolerant woody species (Ward 2005). Moderate browsing may also may stimulate canopy production, increasing the competitive ability of trees (Stuart-Hill and Tainton 1988). Ring-barking of trees by porcupines and elephants makes trees more susceptible to fire damage or results in coppicing (Yeaton 1988), thereby preventing woody plants from escaping from the fire zone. In arid and semi-arid savannas, where soil moisture limits woody plant encroachment, heavy grazing may have the effect of reducing competition between grasses and trees (Scholes and Archer 1997, Kraaij and Ward 2006, Britz and Ward 2007a, Zimmermann *et al.* 2008, Ward and Esler 2011), resulting in an increase in woody cover.

Competition and facilitation

Trees and grass compete with each other for limited resources, which may be water, light or nutrients (Scanlan 1992). Coexistence of grass with trees, which might otherwise be mutually exclusive, is modelled by niche-separation models (see e.g. Westoby 1979, Walker and Noy-Meir 1982, Sankaran *et al.* 2004, Ward *et al.* 2013a) and by spatially explicit models (Wu *et al.* 1985, Scholes and Archer 1997, Wiegand *et al*. 2006). Potential competition between intraspecifics, when trees compete with each other for the same resources, has been modelled by balanced competition models, where the superior competitor is self-limiting, (for e.g. Scholes and Archer 1997, Sankaran *et al*. 2004) and the concept of patch dynamics (for e.g. Wiegand *et al*. 2006, Moustakas *et al.* 2008). In some cases, however, there may be a positive effect of plants on the growth or establishment of other plants, known as facilitation (Callaway and Walker 1997, Holmgren *et al.* 1997). Facilitation is a common phenomenon in a wide range of plant communities (Holmgren *et al.* 1997) and may occur where light, water or nutrients are limited (House *et al.* 2003). Certain plants may

also protect others from herbivory by, for example, concealing them (Riginos and Young 2007).

Competition

Walter's (1939) two-layer hypothesis dominated the theories explaining savanna tree:grass coexistence up until the 1990s (Moustakas *et al.* 2010). Walter (1936) predicted that in any given environment, there should be a characteristic tree:grass ratio (see Scholes and Archer 1997). This would be possible if the roots of trees and grasses occupied different layers in the soil (niche or spatial separation), thereby avoiding direct competition for soil moisture. Walter's (1936, 1954, 1973) predictions also took into account the transpiration difference between grasses and trees (reviewed by Ward *et al.* 2013b) which made grasses the superior competitor for soil moisture within their rooting zone. Where soil moisture is limited, grasses are able to outcompete trees (Sankaran *et al.* 2004) by using all or most of the surface water and preventing water from percolating down to the lower soil layers (see also Riginos 2009). However, this does not always appear to hold true. Knoop and Walker (1985) noted that, in one of their study sites, tree roots and grass roots occupied the same upper soil layer, although the tree roots also penetrated into the lower layers. Brown and Archer (1999) argued that, in the semi-arid regions of north-western United States, woody plant encroachment was a continuous process and not influenced by competition with the herbaceous layer for soil moisture. Wiegand *et al.* (2005) found that the shallow soils in their study area did not allow for niche separation and tree and grass roots occupied the same soil zone. There also is a period when tree seedlings are forced to compete directly with grasses for moisture and nutrients as their roots grow through the upper layers of the soil (Ward 2005, Cramer and Bond 2013). These anomalies gave rise modifications to the two-layer hypothesis (see e.g. Knoop and Walker's (1985) 'superior competitor' proposal) or to

different models such as Jeltsch *et al.*'s (2000) ecological buffering model and the demographic bottleneck model by Higgins *et al*. (2000). However, Ward *et al.* (2013a) point out that the two-layer hypothesis is indeed applicable to arid and semi-arid savannas. There is strong evidence that in these savannas trees and grass compete with each other for water (see also Walker *et al.* 1981, Knoop and Walker 1985, Scholes and Archer 1997, Ward 2005, Kraaij and Ward 2006) , a constraint which is, to some extent, overcome by roots occupying different zones. Grasses also compete successfully with tree seedlings for light (reviewed by Bahre and Shelton 1993).

Trees also compete with each other for soil moisture (Scholes and Archer 1997), particularly in arid and semi-arid environments. Wiegand *et al.* (2005) proposed that woody plant encroachment is a cyclical succession between open and closed savannas (see also Meyer *et al.* 2006, Wiegand *et al.* 2006, Moustakas *et al.* 2008, Meyer *et al.* 2009). The patch dynamic model is a mechanism that is driven by inter-tree competition and highly variable rainfall (Wiegand *et al.* 2006). Competition may be for below-ground resources such as soil moisture (Meyer *et al.* 2008) or for light (Mohler *et al.* 1978, Ward 2005). Although Smith and Grant (1986) found there was very little interspecific competition between *Burkea africana* and *Terminalia sericea*, as their roots occupied different soil zones, studies by Schleicher *et al.* (2011)a and Pillay and Ward (2013) showed strong evidence for interspecific competition in semi-arid and humid savannas, respectively.

Many savanna trees are leguminous and are, consequently, able to fix nitrogen (Cramer *et al.* 2010). Experiments have shown that savanna grasses responded favourably to nitrogen supplements (Kraaij and Ward 2006), while nitrogen-fixing tree species did not respond to applications of nitrogen to the soil. As a result, the grasses were able to suppress tree seedling establishment, due to their increased vigour (Kraaij and Ward 2006, Britz and Ward 2007a, Sankaran *et al.* 2008). In nitrogen-poor soils, leguminous tree seedlings will be

stimulated by grass competition to fix nitrogen and survive grass competition (Kambatuku *et al.* 2013). Riginos *et al.* (2009) found that savanna trees exerted a strong negative effect on soil phosphorus, which inhibited grass productivity. Non-leguminous savanna trees competed with grasses for nitrogen and might be suppressed by grasses when competing for this resource (Cramer *et al.* 2010), but competition between grasses and trees for phosphorus inhibited both leguminous and non-leguminous savanna trees (Cramer *et al.* 2010).

Shading by tree canopies may inhibit grass productivity, particularly during the wet season (Ludwig *et al.* 2001) when soil moisture is not limited. Trees may also compete with each other for light in humid savannas (Scholes and Archer 1997, Hoffmann *et al.* 2004, Vadigi and Ward 2013), which could result in a process of self-thinning (Mohler *et al.* 1978).

Facilitation

Grass may have a facilitative effect on sapling growth, concealing saplings and thus protecting them from herbivory (Riginos and Young 2007), trapping water for the benefit of tree seedlings (Riginos and Young 2007) or by preventing the formation of soil crust and, thereby, allowing water infiltration for tree seedlings (Grellier *et al.* 2012). However, Riginos and Young (2007) noted that, in the long term, the effect of grass on tree saplings was negative.

Belsky *et al.* (1989) demonstrated that trees had a facilitative effect on grasses, particularly under the canopy, in open savannas. They found increased grass productivity as a result of increased soil fertility (from leaf litter, dung from herbivores and droppings from birds), decreased soil temperature and evapotranspiration rates due to shading, and an increase in shade-loving grass species (Belsky *et al.* 1989) (see also Riginos *et al.* 2009). Hydraulic lift by certain savanna tree species of water from the deeper soil zones has a facilitative effect on grasses growing in the rooting zone of the trees (Ludwig *et al.* 2003,

Ludwig *et al.* 2004). Schleicher *et al*. (2011b) also noted that shallow-rooted shrubs may benefit from trees such as *Acacia erioloba* having deep roots. However, the benefits could be negated by tree:grass competition for soil moisture in arid and semi-arid environments (Ludwig *et al.* 2004).

Shading of smaller tree seedlings by established saplings may also enhance survival rates (Knoop and Walker 1985) and encourage the formation of a closed woody canopy. The plant providing protection for the more tender plant is often referred to as the nurse plant (San José and Fariñas 1983, Munzbergova and Ward 2002, Rice *et al.* 2012). This nurse-plant effect between conspecific tree species was also noted by Smith and Grant (1986), but once the seedlings reached maturity, the saplings began to compete with each for resources. Ludwig *et al.* (2001) also found that shade from tree canopies could increase grass production, although only during the dry season. However, this positive effect was offset by competition for soil moisture (Ludwig *et al.* 2001).

Soils

Soil structure influences the edaphic characteristics of soil (Bronick and Lal 2005) such as water-holding capacity, pH, nutrients and the plant community growing in it. Structure is determined by the aggregation of soil particles which are held together by organic and inorganic compounds and ionic bridging (Bronick and Lal 2005).   Soil texture refers to soil particle size. Soil texture, together with soil structure, influences root distribution, as well as the ability of plants to take up water and nutrients (reviewed by Bronick and Lal 2005). Knoop and Walker (1985) found that in sandy soils of a semi-arid savanna, the grass roots dominated in the topsoil while the tree root densities were highest in the subsoil. In soils with a higher proportion of silt, the grass roots again concentrated in the topsoil, but tree roots were, generally, evenly distributed throughout the topsoil and subsoil (Knoop and Walker

1985). Sandy soils are generally low in nutrients and have poor water-holding capacity, while the reverse occurs in clay soils (Britz and Ward 2007b). Savanna trees tend to avoid soils with high sand content (Britz and Ward 2007a, Britz and Ward 2007b), as well as those with high clay content (Britz and Ward 2007a, Britz and Ward 2007b, Sankaran *et al.* 2008). In general, rocky soils favour woody vegetation (Britz and Ward 2007b, Schleicher *et al.* 2011b, Ward and Esler 2011) as rock fragments, being of coarse texture, protect the soil surface from sealing and crust formation, increase percolation and reduce evaporation. However, Ward and Esler (2011) suggested the higher density of trees in rocky areas could be the effect of lower grass density rather than soil substrate *per se*. Soils high in clay inhibit the establishment of woody species as they inhibit root growth and penetration and tend to be high in soil moisture and nitrogen, which enhances grass productivity (Sankaran *et al.* 2008).

Carbon dioxide and C_4 plants

In the last couple of decades, there has been much interest regarding escalating atmospheric CO_2 levels and its possible role in encroachment by C_3 woody plants into savanna biomes (see for e.g. Ehleringer *et al*. 1991, Morgan *et al.* 2007, Bond and Midgley 2012). There have been a number of field trials and experiments that indicate that C_3 plants will outcompete C_4 grasses at CO_2 concentrations that are higher than current concentrations (see e.g. Morgan *et al.* 2007, Kgope *et al.* 2009). Evidence suggests that C_4 plants first appeared during the Oligocene (24 – 34 million years ago), although there are suggestions that C_4 plants may have arisen earlier (Sage 2004, Edwards *et al.* 2010). C_4 grasses became dominant during the late Miocene/early Pliocene (3 – 8 million years ago) (Ehleringer *et al.* 1991, Edwards *et al.* 2010) when CO_2 levels were between 350 and 550 μmol/mol (Edwards *et al.* 2010), having initially evolved much earlier at lower atmospheric CO_2 concentrations (Ehleringer *et al.* 1991, Sage 2004). Osborne (2008) reviewed the possible reasons for the

expansion of C_4 grasses during the Miocene. These focused largely on changes of rainfall patterns (increased seasonality) and increased disturbance (fire). Atmospheric CO_2 concentrations declined again to below ~270 μmol/mol where CO_2 concentrations have remained for the last 400 000 years (Sage 2004), with the lowest levels being recorded just prior to the industrial revolution (Etheridge *et al.* 1996). Edwards *et al.* (2010) speculated that, because C_4 grasses perform best under conditions of high temperature and high light intensity, they would have risen to dominance in the tropics and then spread into the higher latitudes with declining CO_2 levels. Since the industrial revolution (late 19th century), CO_2 levels have risen to ~397 μmol/mol (Tans 2013). They are projected to rise to exceed 600 μmol/mol by the end of this century (Morgan *et al.* 2007) which would lead to an increased dominance of C_3 plants.

The effects of CO_2 enrichment have been reviewed by Bond and Midgley (2012). One of the effects of increased CO_2 concentrations is a reduction in stomatal conductance in both C_4 and C_3 plants (Polley *et al.* 1994, Morgan *et al.* 2004, Eamus and Palmer 2007). Nitrogen-use efficiency in C_3 shrubs also improved relative to C4 plants (Polley *et al.* 1994). The reduction in transpiration rates (as a result of stomatal closure) resulted in higher soil moisture (Polley *et al.* 1994, Polley *et al.* 1997, Eamus and Palmer 2007). This, in turn, could benefit tree seedling recruitment through deeper percolation of soil water to tree roots (Polley *et al.* 1997, Morgan *et al.* 2004, Eamus and Palmer 2007). Field experiments by Morgan *et al.* (2007) showed that shrubs, grown at twice the ambient CO_2 concentrations, increased 40 fold, while C_4 grasses remained unaffected.

Polley et al. (1994) found that the below-ground biomass of C_3 shrubs increased with increasing CO_2 concentrations and Ceulemans *et al.* (1995) demonstrated that above-ground biomass of poplar saplings (C_3 plants) increased under elevated CO_2 concentrations. These increases in biomass were explained by experimental work by Morgan *et al.* (2001), which

showed that leaf photosynthesis of C_3 grasses increased under CO_2 concentrations that were twice ambient concentrations, while leaf photosynthesis of C_4 grass declined. Elevated CO_2 concentrations enhanced tree shoot regrowth after injury, enabling trees to escape the fire zone more rapidly (Bond and Midgley 2000). Greenhouse experiments confirmed that *Acacia* (C_3 trees) roots and shoots responded positively to increasing CO_2 concentrations (Kgope *et al.* 2009). Kgope *et al.* (2009) noted that root starch increased as CO_2 increased, which explained the coppicing response. These authors also noted that C_4 grasses, which were grown at the same time, did not response to elevated CO_2 concentrations. Ward (2010) argued that C_3 trees, grown under elevated CO_2 concentrations, would be able to allocate more resources towards a higher growth rate. Ward (2010) added that carbon-based defence mechanisms would also be enhanced, making trees better defended against herbivory.

Nitrogen enrichment

Justus von Liebig formulated "the law of the minimum" in 1840 (Berryman 1993). Von Liebig postulated that, while plant growth was dependent upon many nutrients, maximum accumulation of plant biomass was limited by the nutrient in shortest supply. After water, nitrogen is the most important limiting factor in plant productivity (Gutschick 1981, Ting 1982, Berryman 1993, Vitousek *et al.* 1997). Most of the nitrogen (N) occurs in the atmosphere as N_2 and is made available to organisms through nitrogen fixation (Gutschick 1981, Ting 1982, Vitousek *et al.* 1997). The two natural processes that transform N_2 to biologically available forms are lightning and N_2-fixing micro-organisms, such as bacteria (Vitousek *et al.* 1997, Fisher and Newton 2002). N_2 fixation by lightning does not add significantly to the nitrogenous compounds available to plants (Fisher and Newton 2002). About 4% of the nitrogen input in Africa is the result of lightning (Boyer *et al.* 2004), whereas about 75% of the nitrogen input comes from nitrogen-fixing organisms (Boyer *et al.*

2004). Anthropogenic activity has greatly enhanced terrestrial nitrogen-fixation activity (Vitousek *et al.* 1997) *inter alia* agricultural practices and the burning of fossil fuels with resultant atmospheric pollution (Ting 1982, Vitousek *et al.* 1997, Köchy and Wilson 2001, Wenig *et al.* 2003, Collett *et al.* 2010, Josipovic *et al.* 2010, Josipovic *et al.* 2011). The South African Highveld in the province of Mpumalanga is highly industrialised and is responsible for 91% of the country's nitrogen oxide (NO_x) emissions (Held and Mphepya 2000). Plumes of industrial pollution drift across South Africa, depending on prevailing winds, and industrial nitrogen is deposited onto the land surface via wet or dry deposition processes (Collett *et al.* 2010, Josipovic *et al.* 2011), mostly as nitrogen dioxide (NO_2).

Although N enrichment has been known to stimulate carbon uptake (Vitousek *et al.* 1997), N deposition is a source of concern (Aber *et al.* 1995, Vitousek *et al.* 1997, Josipovic *et al.* 2010, Josipovic *et al.* 2011). Aber *et al.* (1995) found that long-term exposure to N enrichment caused a decline in tree growth and tree mortality and, conversely, forest expansion in the northern hemisphere is thought to be related to N deposition (Köchy and Wilson 2001). Nitrogen deposition has resulted in acidification of terrestrial and aquatic ecosystems and dramatic losses in plant diversity (reviewed by Vitousek *et al.* 1997). Experimental work in South African savannas suggests that trees are not directly affected by N enrichment, but rather that the competitive vigour of grasses is stimulated by the addition of N (Kraaij and Ward 2006, Sankaran *et al.* 2008, Cramer and Bond 2013), thus suppressing tree seedling establishment. However, current N deposition rate in South Africa is unlikely to be the primary cause of environmental change. Josipovic *et al.* (2010) found that the mean annual NO_2 concentration in South Africa was well below the international air quality standards. NO_2 deposition levels northern KwaZulu-Natal were $< 5 \ \mu g \ m^{-3}$ per annum, which is well below the critical level for all vegetation prescribed by the Convention on Long-Range Trans-Boundary Air Pollution (UNECE:CLRTAP), which was set at $30 \ \mu g \ m^{-3}$ per

annum (Josipovic *et al.* 2010). However, it is possible that occasional high levels of NO_2 could occur that, combined with long-term cumulative effects, may influence vegetation composition.

Land-use

The three main forms of land use in South African savannas are commercial ranching, game and conservation enterprises, and communal or subsistence ranching (Grossman and Gandar 1989, Higgins *et al.* 1999). Heavy grazing by domestic livestock is frequently cited as causing woody plant encroachment (Scholes and Archer 1997, O'Connor and Crow 1999, Roques *et al.* 2001, Rouget *et al.* 2006).

Garrett Hardin wrote eloquently about the 'tragedy of the commons' (Hardin 1968). He wrote that people will maximize their own profit, regardless of the cost to the rest of the community and he applied this argument to communal land ownership and animal husbandry, amongst other examples. This builds on the school of thought that communal pastoral systems are "maladaptive and destructive" (Ellis and Swift 1988) (see also Rohde *et al.* 2006). However, Ellis and Swift (1988) point out that pastoral systems in Kenya are dynamic, non-equilibrial and persistent and that there is no evidence of degradation or imminent collapse (see also Tapson 1991, Ward *et al.* 2000). Climatic variability may limit livestock numbers (Benjaminsen *et al.* 2006). During periods of drought, livestock reproductive rates decrease (Ellis and Swift 1988) and large numbers of livestock may even die (Ellis and Swift 1988, Ward 2004) which allows the communal rangelands to recover during the wet periods as livestock numbers gradually increase. Forbes and Trollope (1991) expressed a contrary view, citing heavy grazing in communal areas as being the cause of land degradation. However, they noted that once livestock were culled in these areas and rotational grazing was established, woody plant encroachment became an "alarming"

phenomenon (Forbes and Trollope 1991). Vetter and Bond (2012) referred to the dry season as a "nutritional bottleneck" when primary production was limited. They found in their study area, however, that from the 1980s onward, communal farmers were supplementing grazing by buying feed, thereby reducing livestock mortality rates, and were purchasing more livestock to replace those that did die. As a result, stocking rates exceeded the carrying capacity of the rangelands and severe environmental degradation was evident (Vetter and Bond 2012).

Ellis and Swift (1988) found that, while climate was the major force that regulated plant productivity, in the long-term, livestock altered the structure and composition of the plant community. Fynn and O'Connor (2000) came to a similar conclusion. Other studies found that herbaceous plant density and basal cover (Parsons *et al.* 1997), as well as the proportion of palatable species, was higher in communal rangelands than in commercial rangelands (Forbes and Trollope 1991, Parsons *et al.* 1997), despite the higher stocking density.

Higgins *et al.* (1999), studying the impact of land use on woody cover, found that the woody biomass and woody species composition were reduced in communal rangelands. They attributed this to wood harvesting (see also Twine *et al.* 2003, Shackleton *et al.* 2001, Puttick *et al.* 2011). Puttick *et al.* (2011) also noted that heavy utilization of woody stands by livestock resulted in an increase in the presence of grassland. This trend reversed when livestock numbers were reduced, the area fenced into camps, permitting camp rotation, and leased to commercial cattle farmers (Puttick *et al.* 2011). Other studies in mesic savannas showed that, while grass cover decreased and woody cover increased across all three different types of land use, the changes were less marked in the communal rangelands (Wigley *et al.* 2009, Wigley *et al.* 2010). Wigley *et al.* (2009) found that bush encroachment was highest in the conservation sites. In a later study, bush encroachment was found to be highest in

commercial rangelands (Wigley *et al.* 2010).   However, once mean annual precipitation increased to >250 mm, Rohde and Hoffman (2011) noted an increase in woody cover, particularly in the commercial rangelands. They ascribed the difference in woody cover to communal farmers owning more browsers (such as goats) than the commercial farmers.

Woody plant encroachment in KwaZulu-Natal grassland and savannas

As much of the vegetation in KwaZulu-Natal (KZN) is savanna or grassland, the increase in woody species has negative ramifications for rangeland management and for the economy of KZN. Many of these woody plants are *Acacia* spp. or *Dichrostachys cinerea,* which suppress grass production (O'Connor and Crow 1999), are unpalatable to herbivores because of chemical and/or physical defences (Hanley and Lamont 2002), develop into impenetrable thickets (Ward 2005), and are often fire resistant (Owens *et al.* 2002, Meyer *et al.* 2005).

A challenge that researchers face in studying the causes and effects of woody plant encroachment (known as *bush encroachment* in South Africa and Australia and *shrub encroachment* in North America), or any ecological succession process, is the timescale over which it occurs (Archer *et al.* 1995).   In South Africa, Acocks (1975) believed that most of the country was originally covered with forest or dense scrub and that the savannas and grasslands were anthropogenically derived. However, research in the Hluhlwe-iMfolozi Game Reserve of KwaZulu-Natal has indicated that, for a very long time, forests were not dominant in the KZN landscape (West *et al.* 2000). West *et al.* (2000) have shown, in soil organic carbon isotopic studies, that savanna grasses dominated the landscape, possibly as far back as 18 000 years ago, which was well before the arrival of Iron Age man in south-eastern Africa.

Long-term monitoring of vegetation change

There are a variety of methods to study vegetation over a period of time. Permanent plots (Bakker *et al.* 1996) or transects may be set up and monitored and survey data collected over a period of time may be analysed (Visser *et al.* 1999). Long-term photographic images also provide an opportunity to study vegetation change over an extended time frame. A number of studies utilize ground photographs, providing "then and now" information about landscapes (see e.g. Hoffman and O'Connor 1999, Nyssen *et al.* 2009, Ward 2011). Aerial and satellite photographs provide landscape monitoring opportunities over a much wider spatial scale than ground photographs (see e.g. Saltz *et al.* 1999, Hudak and Wessman 2001, Gordijn *et al.* 2012).

Fixed-point photography

As the name implies, repeat fixed-point photography involves retaking photographs over a period of time from the same location (Martin and Turner 1977, Kull 2005, Nyssen *et al.* 2009, Rohde and Hoffman 2010). Repeat photography can have a range of applications, such as monitoring vegetation change in ecosystems due to land use and management policies (Kull 2005, Michel *et al.* 2010), deliberate rangeland management (Howery and Sund 1998) and historical architectural studies (Ahlstrom 1992).

Historical photographs are a valuable resource to study long-term environmental changes (Bowers *et al.* 1995, Bass 2004, Bierman *et al.* 2005, Kull 2005, Boerma 2006, Nyssen *et al.* 2009) as are tourists' photographs and postcards (Pupo-Correia *et al.* 2011). During the American Civil War (1861 – 1865) landscape photography came into its own, in particular through the work of Mathew Brady and Alexander Gardner (see for e.g. Gardner 1866, Meredith 1974, Trachtenberg 1985, Griffin 1999). While photographers were depicting military scenes, they inadvertently produced images of the landscape. Photography lagged

behind in South Africa, with much of the work being done in studios. Those done out of doors were highly stilted, although by the late 1870s some South African photographers were capturing landscape scenes as well, notably James Lloyd and William Coates Palgrave. At the time of the Anglo-Zulu War (1879) James Lloyd and John Dunn (although he was not a professional) took a number of photographs of the most significant battle sites. Hardly any photographs were taken during the Anglo-Boer War of 1880-1881, but by the time the Anglo-Boer War of 1899-1902 photography was well established and many British officers even carried their own box cameras on campaign (e.g. Todd and Fordham 1980, Riall 2000).

In South Africa, historic photographs have been used successfully to track vegetation change (Shantz and Turner 1958, Hoffman and O'Connor 1999, Rohde and Hoffman 2010, Hoffman and Rohde 2011). Some studies have combined repeat fixed-point photographs with aerial and satellite photographs (Hongslo *et al.* 2009, Ward 2011, Ward *et al.* 2013a). Analysis of the photographs has involved delineation of land forms or catenas and the area of change manually estimated (Hoffman and O'Connor 1999, Nyssen *et al.* 2009, Rohde and Hoffman 2010, Russell and Ward 2013). In other studies, the whole photograph was evaluated (Bierman *et al.* 2005, Kull 2005, Boerma 2006).

Repeat photography is simple, relatively quick (Howery and Sundt 1998) and inexpensive (Kull 2005). Interpretation of the photographs is also relatively easy (Kull 2005) and the large scale allows for detailed analysis, such as species composition (Hoffman and O'Connor 1999, Kull 2005). However, there are limitations. Historical photographs are subject to spatial bias (Kull 2005) or compositional subjectivity (Bass 2004). Bass (2004) also noted that, in setting up a project, one is limited by what the original photographer photographed. There is the temptation to assume that any change evident between photographs is linear (Kull 2005, Hongslo *et al.* 2009). Hongslo *et al.* (2009) dealt with this by complementing the repeat photographs with a series of aerial photographs (see also Ward

et al. 2011, Ward *et al.* 2013a). Finding the correct camera position may be difficult in photographs that lack topography or identifiable objects such as large, immovable rocks (Nyssen *et al.* 2010). Photographic quality can also make interpretation difficult (Kull 2005, Pupo-Correia *et al,* 2011). Black-and-white photography is better than colour, as contrasts are more marked (Kull, 2005). Differences in season (Hongslo *et al.* 2009, Kull, 2005), obliqueness and distance of object from camera (Hongslo *et al.* 2009) can all affect interpretation.

Remote sensing

Remote-sensing techniques offer a means for monitoring environmental process and, coupled with geographic information systems (GIS), greatly enhance our understanding and predictive ability of interactions on a global scale (Wilkinson 1996). Both aerial and satellite imagery have been successfully used for these techniques (see e.g. O'Connor and Crow 1999, Manson *et al.* 2003, Britz and Ward 2007b, Wigley *et al.* 2009, Gordijn *et al.* 2012).

In some instances, manual classification proved adequate for quantifying vegetation change (O'Connor and Crow 1999, Roques *et al.* 2001, Verheyden *et al.* 2002, Corrigan *et al.* 2010, Wigley *et al.* 2010, Puttick *et al.* 2011, Ward *et al.* 2013a). Other studies have effectively used computer-based change-detection techniques (Saltz *et al.* 1999, Tottrup and Rasmussen 2004, Wang *et al.* 2004, Pillai *et al.* 2005, Levick and Rogers 2011, Adjorlolo *et al.* 2012). Some studies used aerial photographs without combining the preparation process with GIS (Scanlan and Archer 1991, Schlesinger and Gramenopoulos 1996, O'Connor and Crow 1999, Roques *et al.* 2001, Britz and Ward 2007b, Hongslo *et al.* 2009), but, generally, aerial and satellite photographs were georectified (Hudak and Wessman 1998, Hayes and Sader 2001, Pillai *et al.* 2005, Ellis *et al.* 2006, Hughes *et al.* 2006, Ward *et al.* 2013a) and, if necessary, mosaicked to produce large composite images (Hudak and Wessmann 2001,

Corrigan *et al.* 2010, Ward *et al.* 2013a). At this point, the photographs could be analysed manually by overlaying a digital grid (Wigley *et al.* 2009, Puttick *et al.* 2011). There are, however, further procedures that may be necessary as part of the preparation. It may be necessary to perform radiometric corrections to compensate for variations in reflectance (Hudak and Wessman 1998, Saltz *et al.* 1999, Hayes and Sader 2001, Hudak and Wessmann 2001) and atmospheric corrections to overcome scattering and absorption by water vapour and aerosols (Saltz *et al.* 1999, Hayes and Sader 2001). Cloud cover may also make it difficult to assess details in aerial and satellite photographs (Tottrup and Rasmussen 2004).

Computerised change detection may follow one of two routes: pixel-based classification or object-based classification. A pixel is the smallest element on a digital image. Pixel-based methods, such as textural analysis, enhance and statistically measure local pixel variance (Hudak and Wessman 1998). Object-based methods do not classify single pixels, but classify groups of homogenous pixels or an object (Laliberte *et al.* 2004, Pillai *et al.* 2005, Levick and Rogers 2011) after a filter has smoothed out excessive variation.

The study area – an historical overview

Early KwaZulu-Natal

The vegetation of KwaZulu-Natal was dominated by grasslands at least 18 000 years ago (West *et al.* 2000). Up until the arrival of Iron Age man, the grasslands and savannas would have been maintained largely through natural disturbances, viz. fire, climatic variability, herbivory. Iron Age man first arrived in modern-day KwaZulu-Natal between 260-440 CE (Common Era or Current Era) (Huffman 1982). These early arrivals appeared to be agriculturalists and metal workers who also hunted on a small scale (Maggs 1980, Huffman 1982), although Voigt (1986) described an early site in KwaZulu-Natal that yielded a few bone fragments from domestic livestock. By the 8th century CE, domestic livestock and dogs

were common in KwaZulu-Natal (Maggs 1980). Huffman (1982) suggested that this was a second group of Iron Age people who arrived about this time, who were primarily herders, although they were culturally similar to the earlier settlers. Demand for wood would have been high, being required for cooking fires, hut construction, stock pens, fences and iron smelting (Maggs 1980). This would have brought in an anthropogenic element in maintaining the open nature of the savannas and grasslands.

By the time European settlers first arrived in KwaZulu-Natal in 1824, all the individual clans had been amalgamated into the Zulu nation under one paramount chief, Shaka (Laband 1995, Wylie 2006). The Zulu people were semi-pastoralists (Jacobs 1965), famed for their love of cattle (Morris 1986, Laband 1995). Like their forebears, the Zulus hunted wild game only to a limited extent (Laband 1995, McCracken 2008). Early European explorers have described the vast herds of game of all description (Dunn 1886, Struthers 1991). However, throughout the 1800s game and domestic stock were decimated by various agents (McCracken 2008). McCracken (2008) described how excessive hunting, attempts to eradicate the effects of tsetse fly and the rinderpest epidemic (1895-1904) nearly exterminated the indigenous fauna. Domestic livestock was also severely reduced during and after the Anglo-Zulu War of 1879 (Guy 1994) and during the rinderpest epidemic of 1896 (McCracken 2008).

Study Area

The Umzinyathi River was recognised as part of the boundary between Zululand (to the north) and British colonial Natal (to the south) in 1843 (Laband 1995). In January 1879, a British column crossed the Umzinyathi River at Rorke's Drift, marking the start of the Anglo-Zulu War (see e.g. Rothwell 1989, Guy 1994, Lock and Quantrill 2002). Ten days later, the British suffered a reversal at the hands of the Zulu at Isandlwana and on the same

day, at Rorke's Drift, a small garrison of British soldiers held off a contingent of Zulus. Also on the same day, a remnant from the British camp at Isandlwana managed to escape into colonial Natal by crossing the Umzinyathi River downstream of Rorke's Drift, at what is now known as Fugitives' Drift. These three sites have become deeply entrenched into the British national psyche and are often visited. As a result these sites have been frequently photographed, from 1879 onwards. They are the focal points of this study on vegetation change.

Thesis structure and objectives:

This project uses historical ground photographs and multi-temporal sets of aerial photographs to provide insights into landscapes as they were 130 years ago and to plot vegetation change in the intervening years. Historical photographs, combined with fixed-point repeat photographic techniques, have been used successfully in the past to observe long-term environmental change (see e.g. Hoffman and Rohde 2010). Aerial photographs provide a broader view of the landscape and have been used either in conjunction with historical photographs (see e.g. Ward *et al*. 2013a) or on their own (see e.g. Britz and Ward 2007b). Plant communities are dynamic. Their composition and structure are continually being influenced by biotic drivers such as inter- or intraspecific competition and herbivory and by abiotic drivers such as climate and fire. Consequently, a comparison of a landscape over time provokes the question: why is the vegetation changing (or not changing). The objectives of this project were to: a) determine if there has been a significant increase in woody plant cover in the study area, using fixed-point repeat photographs and multi-temporal photographs, and when the changes occurred; b) identify the possible drivers behind the changes (if significant); c) ascertain community members' perceptions of environmental change.

This thesis is prepared as five chapters, two of which have been submitted for publication and which form the focus of the thesis. These are chapters two (*accepted*) and three (*in revision*). Chapter Two examines vegetation change using fixed-point repeat photographic techniques. This chapter also incorporates an analysis of the floristic sampling done in the study area. Chapter Three examines how the vegetation changed sequentially using aerial photographs. Chapter Four discusses the survey conducted with community members residing in the study area. Chapter five is the discussion, which incorporates the preceding three chapters, followed by the conclusion and an indication of the future direction.

Chapter 2

Vegetation change in northern KwaZulu-Natal since the Anglo-Zulu War of 1879: local or global drivers?

This chapter has been accepted for publication in *African Journal of Range & Forage Science* and has been formatted accordingly.

Chapter 3

Remote sensing provides a progressive record of vegetation change in northern KwaZulu-Natal, South Africa, from 1944 to 2005.

This chapter has been submitted to *International Journal of Remote Sensing* and is in revision. It has been formatted accordingly.

Chapter 4

Communal land use and community members' perceptions on vegetation change.

Chapter 5

Discussion

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Chapter 2

Vegetation change in northern KwaZulu-Natal since the Anglo-Zulu War of 1879: local or global drivers?

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Abstract: The quality of the landscape is declining in many grassland and savanna areas of Africa as a consequence of woody plant encroachment. We investigated the changes in vegetation at selected sites on the battlefields of the Anglo-Zulu War of 1879 in KwaZulu-Natal. We used fixed-point repeat photographs to compare the landscape at the time of the Anglo-Zulu War with the same landscape in 2011. Nine photo-pairs were analysed, covering three specific sites: Isandlwana, Fugitives' Drift and Rorke's Drift. A further eight photographs from these sites, taken during the intervening years, were matched and compared with the present landscape. All sites we analysed showed an increase in woody cover since 1879. We used the Whittaker plant diversity sampling method to determine current woody and grass species composition on the sites. We also investigated the effect of catena, aspect, rockiness and land-use on the bush encroachment. Rainfall and temperature data were also analysed. The observed large increases in woody cover cannot be explained by land use or by local climatic conditions only. The changes are also consistent with global climate change effects, most likely due to increasing atmospheric CO_2.

Introduction:

A number of factors have been indicated to affect vegetation succession from grasslands to tree-encroached savannas (reviewed by Ward 2005, Bond 2008). On a local level, a decrease in the numbers of indigenous herbivores (Britz and Ward 2007, Riginos and Young 2007) the confinement of their range (Skarpe 1991), an increase in domestic stock with concomitant heavy grazing (Scholes and Archer 1997, O'Connor and Crow 1999, Roques *et al.* 2001), seed dispersal by domestic stock (Schlesinger *et al.* 1990) and less frequent and less intense fires (Roques *et al.* 2001, Kraaij and Ward 2006, Gordijn *et al.* 2012) have all been cited as agents of bush encroachment. On a global scale, climate change (Kraaij and Ward 2006, Volder *et al.* 2010, Ward 2010), increases in atmospheric CO_2 concentrations (Kgope *et al.* 2009, Bond and Midgley 2012, Buitenwerf *et al.* 2012) and atmospheric nitrogen deposition (Wigley *et al.* 2010, Buitenwerf *et al.* 2012) are also cited as causing a shift to woody dominance. Carbon-based defence mechanisms used by trees, such as tannins, may also be more efficient as a result of the increase in CO_2, thereby reducing tree herbivory (Ward 2010).

Assessing the role of vegetation change by photography

Photography in South Africa was largely confined to the studio in the 1870s and 1880s (Ward *et al.* 2013a). However, there were a few photographers who documented the countryside of KwaZulu-Natal, South Africa. The battle sites of the Anglo-Zulu War of 1879 were extensively photographed immediately after the battles. The most famous of these sites are Rorke's Drift, Isandlwana and Fugitives' Drift. The photographs depicted an open grassy landscape, with a scattering of trees and aloes. As these battle sites were of considerable historical interest, visitors returned year after year. We have, therefore, a progressive record of changes in these areas.

We made the following predictions about vegetation change in the vicinity of these Anglo-Zulu War battlefields:

1. By matching historical photographs with present-day photographs, we expect to find a significant increase in woody cover in the study area.

2. We predict that the type of land-use will influence the extent of bush encroachment, with greater encroachment on communal lands due to higher stocking densities, which leads to increased tree cover because of reduced competition with grasses.

3. Tree encroachment should occur with higher annual mean rainfall (Kraaij & Ward 2006) and higher daily minimum temperatures (Wakeling et al. 2012).

4. Pollutants, such as nitrogen oxides (written as NO_x which includes both nitrogen monoxide and NO_2), from the industrial areas to the north-east of the study area, are expected to increase competition from the grass species. Trees will not benefit from increased NO_x because they are nitrogen-fixing legumes.

5. An increase in atmospheric CO_2 since the industrial revolution is expected to favour bush encroachment. Trees use C_3 photosynthesis rather than C_4, as is typical of the grasses in the study area, and will become more photosynthetically efficient and better able to defend themselves at higher levels of CO_2 than C_4 grasses (Ward 2010).

Methods

Study area

The study area covers three specific sites: Fugitives' Drift (28.23S; 30.36E), Isandlwana (28.21S; 30.39E) and Rorke's Drift (28.21S; 30.32E), which were battle fields during the Anglo-Zulu War of 1879. It is undulating countryside, with rivers and deep erosion gullies. Altitude varies between 900 m in the Umzinyathi River gorge to just over 1330 m on the summit of Isandlwana. Soils tend to be shallow and eroded (Rienks *et al.* 2000). The parent

material is sandstone and Ecca shales, with dolerite outcropping (Van der Eck *et al.* 1969). Mean annual rainfall for the area is 705 mm, as recorded by the weather station at Isandlwana which operated from 1933 to 1972. Most of the rain falls between October and March.

Fugitives' Drift study area falls within the savanna biome, Thukela Thornveld (Mucina and Rutherford 2011). The Umzinyathi River flows through the area. The south bank falls in a private game reserve. The north bank was communally held, although part is now managed by Ezemvelo KwaZulu-Natal Wildlife, a provincial conservation body. Cattle, goats and wild herbivores, such as blesbok *Damaliscus pygargus*, plains zebra *Equus quagga burchelli* giraffe *Giraffa camelopardalis*, impala *Aepyceros melampus*, kudu *Tragelaphus strepsiceros* and nyala *Tragelaphus angasii*, are present.

Isandlwana and Rorke's Drift fall within grassland biomes incorporating Northern KwaZulu-Natal Moist Grassland, KwaZulu-Natal Highland Grassland and iNcomé Sandy Grassland (Mucina and Rutherford 2011). The area around Isandlwana is managed by Ezemvelo-KwaZulu-Natal Wildlife. There is evidence of old cultivated lands which have been fallow for many years. At certain times of the year the communal ranchers are permitted to graze their livestock in the area (Ngwenya 2010). Wild herbivores, such as impala and zebra, are also present.

Most of the study area at Rorke's Drift was owned and managed by the Evangelical Lutheran Church. About 20 years ago, control of much of the land was handed over to the local isiZulu-speaking communal farmers. Under communal land ownership, all ranchers are allowed to maintain their livestock in the area. There is no restriction on livestock numbers. Often this is perceived to lead to the "tragedy of the commons" (Hardin 1968), although evidence in support of this is scant (Ellis and Swift 1988, Behnke and Abel 1996, Ward *et al.* 1998). A small part of the area falls on a privately owned commercial cattle ranch. Cattle and goats predominate among the livestock there.

Land-usage in the study area

There are a number of different land-use types in the area:

1) Communal land/farming: Communal land falls within tribal trust areas. There is no private land ownership and control over who is allowed to settle in these areas is determined by the local tribal chief. There is little or no interest in land management and householders may own as much domestic stock as they wish. Many householders undertake field cultivation. Agricultural activities are for subsistence only.

2) Commercial land/farming: Commercial land is privately owned land. The owner, generally, applies lower stocking rates in comparison with communal landholders. Agricultural activities are carried out with a profit-making motive.

3) Conservation areas: Conservation areas are either privately owned with a primary focus on ecotourism or owned by the provincial conservation body where the focus is primarily conservation of local flora and fauna.

We note that the term "encroached land" refers to any area within the above land-uses where there has been an increase in woody plant species, and "old lands" are abandoned cultivated fields.

Fixed-point, repeat photography

The use of historic photographs to assess vegetation change has been widely documented (Hoffman and Rohde 2011, Pupo-Correia *et al.* 2011, Rohde and Hoffman 2012). Some studies have made use of photographs from sight-seeing activities (Pupo-Correia *et al.* 2011, Ward *et al.* 2013a). Other studies have used photographs taken by earlier scientists (Hoffman and O'Connor 1999, Rohde and Hoffman 2012) while Nyssen *et al.* (2009) used photographs from regimental archives. Studies using fixed-point repeat photographic techniques have been able to demonstrate major patterns of change in vegetation cover, the impact of

anthropogenic influences and whether the results were consistent with projections derived from climate change studies. For example, Hoffman and O'Connor (1999) were able to use repeat panoramic photography in the Weenen and Muden areas of KwaZulu-Natal to assess change in species composition as well as the change in vegetation patterns.

We obtained archival photographs from KwaZulu-Natal Museum Services, Pietermaritzburg, and the Killie Campbell Africana Library, Durban, of the historic sites of Fugitives' Drift, Isandlwana and Rorke's Drift. Most of these photographs had been taken during or shortly after the Anglo-Zulu War of 1879. Other photographs came from the private collections of I. Knight, G. Chadwick and N. Aspinshaw.

At each photograph locality we replicated the historical photograph, matching distinctive features in the foreground and the background.   However, at some localities, bush encroachment obscured the view. When this occurred, we deliberately moved the camera to obtain a better view, albeit not a perfect match. Thereafter, the photo-pairs were matched using Adobe Photoshop CS. Nine photographs taken in 1879 were delineated into different catenal regions (Scheidegger 1986) or landforms. Scheidegger (1986) describes three fundamental catenal regions: the eluvial region is the plateau-like region of origination of material; the colluvial region is the steep incline where transport of material is substantial; and the alluvial region is at the base of the slope where deposition occurs. Seven vegetation ecologists estimated the percentage woody cover in delineated areas in the historic and current photographs. The results were pooled and the median of the estimates for each photo-pair was used. We performed a chi-squared test on the results to ascertain whether the differences in percentage woody cover between 1879 and 2011 were significant. As the data for catena and for aspect fulfilled the requirements of normality and of homogeneity, we performed single factor analysis of variance (ANOVA) on each set of data to ascertain whether either 1) catena or 2) aspect affected the increase in woody cover. We performed a

Bonferroni adjustment of α to account for the possibility of Type I error in the above-mentioned analysis.

Eight photographs that had been taken in the intervening years were also matched. No assessment of percentage woody cover in these photographs was made by the above-mentioned vegetation ecologists. However, the photographs provide insights to what happened to the vegetation between 1879 and 2011.

Floristic sampling

In addition to taking repeat photographs, we undertook floristic sampling. We used the Whittaker plant diversity sampling method (Shmida 1984) to sample species diversity and cover of woody and grass species in encroached and open areas. Fourteen sites were chosen for sampling. These largely corresponded with the catenal units examined using fixed-point photography, but included some sites outside the catenal units to obtain a more representative overview. We laid out three 20 m × 50 m plots in each of the 14 sites, following the pattern used by Ward and Olsvig-Whittaker (1993). We performed Detrended Canonical Correspondence Analysis (DCCA), a direct gradient analysis, on the species recorded at the different sites, percentage cover of the species and environmental variables. We detrended the pattern because of the problem of the "arch" effect created by random data. The environmental variables were percentage rockiness of the terrain, land-use, slope and aspect. We tested species richness and diversity, as indicated by the Shannon-Wiener diversity index, and percentage cover between the different sites for normality and for homogeneity of variance. Species richness and diversity were then assessed using Analysis of Variance (ANOVA) and Scheffe *post hoc* tests. We used a Kruskal-Wallis test to assess differences in percentage cover between sites because this variable was not normally distributed. We also performed an indirect detrended correspondence analysis (DCA) on the species recorded at

the different sites. We used a multiple regression to determine the effects of a number of

variables on the first axis values of the detrended correspondence analysis. Unstandardized

coefficients cannot be directly compared. We used standardized (beta) coefficients to

facilitate direct comparison among variables. Standardized coefficients have their variances

standardized to 1. Negative standardized coefficients indicate that there is a negative

relationship between the dependent variable and the independent variable and can thus be

compared in absolute terms with positive standardized coefficients. In this analysis the

outliers were excluded.

Rainfall trends

We used rainfall and temperature data from South African Weather Service, Talana Museum

(Dundee) and the Agricultural Research Council to investigate climatic trends over the past

100 years. All the data provided had gaps where rainfall or temperature had not been

recorded. Dundee Research Station (28.13S; 30.31E) is 35 km from Fugitives' Drift,

37 km from Isandlwana and 32 km from Rorke's Drift. Although not the closest weather

station, this station provided the longest record. Rainfall data had been collected from 1901

to 2006 and temperature data from 1973 to 2011. We therefore used this weather station's

data, combined with rainfall data from the nearby Dundee Police Station.

We performed linear regression analysis on rainfall data to establish whether there

was a long term change in mean annual precipitation. A two-tailed t-test was performed

between the amounts of rain that fell during the period covering 1901 to 1922 and the amount

that fell during the period from 1985 to 1906, having first established normality of the data

and equality of variance. The Standardized Precipitation Index (SPI) was also calculated

from the combined rainfall data. We calculated SPI by dividing the total annual precipitation

minus the long-term mean precipitation by the standard deviation in total annual precipitation

(Yurekli and Anli 2008).   SPI was developed for monitoring drought conditions (Hayes *et al.* 1999). However, it has also been successfully used for monitoring wet conditions (Seiler *et al.* 2002).

Temperature trends

Wakeling *et al.* (2012) showed that savanna trees grew more slowly in cool conditions, making them more vulnerable to fire. They also showed that frost damaged savanna tree seedlings and caused seedling mortality (see also Brando and Durigan 2005; Holdo 2006). Because we wished to ascertain whether there has been any change in ambient temperature, we performed linear regression analysis on temperature data. We extracted the number of days per year when minimum temperatures were less than 13 ^{o}C, which is the minimum required for plant growth (Wakeling *et al.* 2012) and less than freezing (0 ^{o}C).

Results

Fixed-point, repeat photography

Analysis of the 1879-2011 photo-pairs (Figures 2.1a – c; 2.2a, b, e and f; 2.4a – b and e – f; 2.5a – f) showed a marked increase in woody cover in all three study sites (Table 2.1), although the degree of increase varied. χ^2 analysis showed, in all but four of the catenal units, there were significant increases in woody cover ($p < 0.003$).   Two units at Isandlwana and one at Rorke's Drift showed increases in woody cover that were not significant ($0.055 < p < 0.197$).   One catenal unit at Isandlwana, which had 1% woody cover, showed no change. One-way ANOVA showed that the effects of catena ($p = 0.236$) and aspect ($p = 0.126$) were not significant.

Floristic sampling

Mixed, broad-leafed woody species, in particular *Euclea crispa*, as well as *Acacia ataxacantha* (alternative name *Senegalia ataxacantha*) and *Acacia karroo* (alternative name *Vachellia karroo*), were characteristic of the south- and west-facing slopes at the study site at Fugitives' Drift. The north-east facing slopes were also dominated by *A. ataxacantha* and *A. karroo* and by mixed, broad-leafed woody species, *Euclea crispa* in particular.

Acacia karroo was the dominant encroacher at Isandlwana. *Acacia karroo, Diospyros* spp*., E. crispa* and *Vitex rehmanii* were dominant encroachers at Rorke's Drift, except on the commercial rangeland at Rorke's Drift, where *A. sieberiana* was dominant.

DCA showed distinct groupings of the different sites according to species composition (Figure 2.6). Sites at Isandlwana which are a mixture of conservation and communal grazing are grouped together. Rorke's Drift sites also were grouped together with distinct species composition. These sites are largely within communal lands. The exception is the three commercial sites which form a group of outliers. Fugitives' Drift sites form the fourth group and are managed as a conservation area. These distinct groupings confirm that land-use could affect species composition.

DCCA also grouped sites according to species composition, but included the effect of environmental variables. It showed that the influence of rockiness of the terrain and the steepness (slope) was considerable (Figure 2.7). Aspect, while influential, was less important. The effect of land-use on the grouping of the sites was varied. Commercial lands had the strongest effect, followed by areas set aside for conservation. Communal land-use did not have a significant effect on the groupings, nor did the degree of encroachment by woody species. Similarly, where land-use was a mixture of communal grazing and conservation, there was little effect on the grouping of sites (Figure 2.7).

The three sites (Fugitives' Drift, Isandlwana and Rorke's Drift) had distinctive species

composition. One-way ANOVA for species richness showed there was a significant difference in species richness among sites ($F = 17.303$, error df $= 40$, $p < 0.001$). A similar result was obtained for the Shannon-Wiener diversity index among sites ($F = 10.701$, error df $= 40$, $p = 0.001$). However, the Kruskal-Wallis test comparing percentage cover on each study site indicated no significant difference among the three sites ($H = 1.227$, error df $= 40$, $p = 0.542$).

The multiple regression analysis performed on the variables on the first axis of the DCA gave an overall value that was significant ($F = 11.17$, $p < 0.001$) with a large amount of variance explained ($r^2 = 0.72$). The effect of commercial land-use ($p < 0.001$), old-lands ($p = 0.008$) and encroached lands ($p < 0.001$) was significant (Table 2.2). We focused on the significant beta (standardized) coefficients because they are directly comparable. We found that the effect of commercial farming on species composition was marginally higher than that on species composition in encroached lands, while old lands had a considerably weaker effect.

Rainfall trends

Linear regression analysis of the combined data from Dundee Research Station and Dundee Police Station showed there was an overall decrease in rainfall over time. The mean annual precipitation during the period covering 1901 to 1922 (mean 942 ± 142 mm) was significantly higher than mean annual precipitation covering the period from 1985 to 2006 (mean 754 ± 160 mm) ($t_{(40)} = 2.021$, $p = 0.0002$).

The combined SPI values indicated seven moderately wet seasons, three very wet seasons and three extremely wet seasons between 1901 and 1954. There were two moderately dry seasons, one in 1927/28 season and again in the 1932/33 season. There was only one period of extreme drought in the 1945/46 season (Figure 2.8). Between 1961 and 2006, Dundee

recorded three moderately wet seasons (1971/1972, 1974/75 and 1983/84) and one very wet season (1995/96). In contrast, nine moderately dry seasons and three very dry seasons were recorded (Figure 2.8). This confirms the results mentioned above, namely that the first part of the century was wetter than the latter part.

Temperature trends

Temperature data from Dundee Research Station suggested a marked reduction in the number of days per season when daily minimum temperatures were less than 13 ^{o}C. Two-tailed t-tests showed that the difference between the number of days between 1973 and 1999 and the number of days between 2000 and 2012 of temperatures < 13 ^{o}C was significant ($t_{(31)} =$ 14.456, $p < 0.001$) (mean number of days: 239 and 195, respectively). There was also a significant difference in the number of frost-free days between 1973 and 1999 and the number of frost-free days between 2000 and 2012 ($t_{(31)} = 3.269$, $p = 0.003$) (mean number of days: 23 and 15, respectively).

Discussion

Historical overview

In Africa, as in other tropical and subtropical regions, savannas and grasslands are dominated by C_4 grasses (Sage 2004, Bond 2008, Buitenwerf *et al.* 2012), which came into existence between 6 and 8 million years ago (Cerling *et al.* 1997, Jacobs *et al.* 1999, Bond 2008), when CO_2 concentrations were low (ca.180 parts per million; Buitenwerf *et al.* 2012). It is generally accepted that savannas are maintained by disturbance (Sankaran *et al.* 2004, Wiegand *et al.* 2006, Meyer *et al.* 2009). The disturbance can be anthropogenic or climatic in origin (Ojima *et al.* 1991, Gillson 2004, Wakeling *et al.* 2011). Herbivory and fire also play major roles in keeping savannas open (Grossman and Gandar 1989, Van Langevelde *et al.*

2003, Wiseman *et al.* 2004). Fire is particularly important in the mesic areas of South Africa (Bond *et al.* 2003). Research done in the forests of Hluhluwe, KwaZulu-Natal, suggest that grasslands dominated the landscape as far back as 18 000 years ago, long before anthropogenic activity would have had significant impacts (West *et al.* 2000). Fire (Van Langevelde *et al.* 2003, Gordijn *et al.* 2012), climate (Britz and Ward 2007) and herbivory (Grossman and Gandar 1989, Van Langevelde *et al.* 2003, Britz and Ward 2007), therefore, are the most likely agents of disturbance that have maintained the savannas of southern Africa up to the present times, rather than anthropogenic activity.

Early European explorers in KwaZulu-Natal have described the vast herds of wild herbivores of all description (Dunn 1886, Struthers 1991). However, throughout the 1800s, wild herbivores and domestic stock were decimated by various agents (McCracken 2008). McCracken (2008) describes how excessive hunting, attempts to eradicate the effects of tsetse fly and the rinderpest epidemic (1896 – 1904) nearly exterminated the indigenous fauna. Domestic livestock was also severely reduced during and after the Anglo-Zulu War (Guy 1994) and also during the rinderpest epidemic (McCracken 2008). Herbivory could cause a demographic bottleneck in tree recruitment (Sankaran *et al.* 2004, Staver *et al.* 2009, Wakeling *et al.* 2010). Once herbivore pressure is released, the bottleneck would be removed.

Indigenous herbivores in KwaZulu-Natal have not recovered since the late 19th century and have been replaced by domestic stock, a trend that has been observed throughout African savannas (Du Toit and Cumming 1999). The loss of indigenous herbivores and an increase in domestic cattle could well influence the pattern and rate of bush encroachment (O'Connor and Crow 1999, Van Langevelde *et al.* 2003). The National Herd Statistics for the area that used to be known as KwaZulu (north of the Umzinyathi and Thukela Rivers) show that between 1975 and 1988 cattle inventory fluctuated around a mean of 1 394 million

(Tapson 1991), suggesting a stable population over the long term. However, the communal famers within our study area reported stock declines varying between 100% and 50% after 1990. The reasons given for these losses are theft and natural causes. At the time of this study, these losses had not been recouped.

Fixed-point, repeat photography

The fixed-point photographs demonstrate that, overall, there has been a significant increase in woody cover in the study area (Table 2.1). Contrary to our expectations, catena and aspect did not exert a significant influence on encroachment. This apparent contradiction could be a bias resulting from the original photographs not providing adequate coverage of the overall terrain as they focussed on where specific battles occurred. Bass (2004) and Kull (2005) warn against this possibility when using historic photographs.

Floristic sampling

Unlike the analysis of the fixed-point repeat photographs, DCCA of the floristic survey suggests that catena (or slope) exerts a strong influence on species composition, as does the rockiness of the area. The rocks provide a refuge for tree seedlings when they would be most vulnerable to fire and would also trap moisture (Nobel *et al.* 1992, Britz and Ward 2007, Ward and Esler 2011). Steep, colluvial regions would be more vulnerable to water erosion (Scheidegger 1986), thereby exposing the rocks and removing the thin top soil, making it more difficult for the shallow-rooted grasses to establish themselves. The contrast in the ground cover between the sites at Fugitive's Drift and the commercial rangelands at Rorke's Drift is marked. The Fugitives' Drift sites were steep, colluvial regions, which, by 2011 were encroached by as much as 90% (Table 2.1; Figure 2.1a – c). The sites within the commercial rangelands at Rorke's Drift (Figure 2.5a and b, delineated region 2) were largely a series of

flat alluvial or eluvial regions. At this last-mentioned site, despite being boulder-strewn with woody encroachment starting at the large rocky outcrops, the woody cover had increased to only 15%. The catenal effect on woody encroachment is also demonstrated at Isandlwana, according to the DCCA (Figure 2.7). The old lands lie in the alluvial regions where water erosion is low. Despite the lands not having been worked since 1989 when the area was first set aside as an historic site, the grasses have managed to retain dominance in comparison to the nearby slopes. Figures 2.4a and b also show the slower rate of encroachment in the old lands which are within the catenal region 4, compared to the surrounding areas. These observations are supported by the results of the DCCA which showed that rockiness and slope affected species composition (Figure 2.7).

Herbivory and fire

Most savannas today are extensively used as grazing lands for livestock and, to a lesser extent, for indigenous herbivores (Skarpe 1991). Herbivory is frequently cited as having an impact on woody encroachment (Scholes and Archer 1997, Wiseman *et al.* 2004, Staver *et al.* 2009). It is often stated that heavy grazing by domestic livestock leads to bush encroachment (Van Vegten 1983, Adamoli *et al.* 1990, Scholes and Archer 1997), often in conjunction with the reduction of fire frequency and intensity (Roques *et al.* 2001, Van Langevelde *et al.* 2003). The removal of a vigorous grass sward would result in reduced competition for resources (Van Langevelde *et al.* 2003, Riginos 2009, Grellier *et al.* 2012) and in a reduced fuel load for hot fires (Trollope and Tainton 1986, Skarpe 1992, Higgins *et al.* 2000, Van Langevelde *et al.* 2003), permitting tree recruitment. Conversely, browsing in conjunction with fire can inhibit bush encroachment (Trollope 1974, Van Langevelde *et al.* 2003). Prins and Van der Jeugd (1993) noted that browsing alone could inhibit tree recruitment (see also Wiseman *et al.* 2004). Reduced fuel loads, such as in the communal areas where frequent

fires and a reduction in the grass sward through heavy grazing by domestic cattle occurs, result in cooler fires which are less damaging to trees.

The perception that heavy grazing by domestic livestock causes bush encroachment has been contested by authors such as Coughenour (1991), Tapson (1991) and Ward *et al.* (1998). Staver *et al.* (2009) report on grazing lawns as being the most heavily grazed components of savanna systems, yet have sparse tree cover (see also McNaughton 1984). The Zulu people of the 19th century, who lived throughout present-day KwaZulu-Natal, are described as semi-pastoralists, herding cattle, sheep and goats (Jacobs 1965, Laband 1995). Their livestock, along with the wild herbivores could have played a significant role in keeping the rangelands free of encroaching woody plants. Besides the direct effects of herbivory, Savory and Parsons (1980) suggest that hoof impact, dung and urine are important for the maintenance of a vigorous grass sward which would suppress bush encroachment.

Land use

Percentage woody cover on all the sites was not significantly affected by land-use. This similarity supports the argument that communal cattle ranching and semi-nomadic pastoralism are not necessarily the cause of land degradation and bush encroachment (Coughenour 1991; Tapson 1991; Ward *et al.* 1998). However, species richness and species diversity were significantly different among study areas (Figure 2.6) which could be related to land-use practices (Shackleton 2000, Short *et al.* 2003, Wigley *et al.* 2010). The study area at Isandlwana is managed largely as a conservation area, although restricted numbers of domestic animals are allowed to graze there at the end of summer (Ngwenya 2010). Block burning occurs every two to three years. Fugitives' Drift is also a conservation area, supporting a mixture of wild herbivores and about 20 domestic cattle. Management on the commercial rangeland is different to that in the surrounding communal areas of Rorke's Drift.

According to the landowner, Mr H. de Wet (pers. comm. 2012) camp rotation is practised and the fire return period is also less than in the surrounding areas. The commercial rangelands are burned once every three years, whereas the communal areas burn every year. DCA (Figure 2.6) and multiple regression analysis (Table 2.2) also confirm that land-use has an effect on species composition in the various sites.

Rainfall

Where water is a limiting factor, stronger competition from grasses for soil moisture is expected (Roques *et al.* 2001, Kraaij and Ward 2006, Schleicher *et al.* 2011). Walter's two-layer hypothesis (see e.g. Walker *et al.* 1981) predicts that grasses are more efficient than trees at extracting water from the top layer of soil, thereby depriving the deeper-rooted trees of adequate water (reviewed by Ward *et al.* 2013b). In this way, grasses are able to out-compete the trees (see e.g. Riginos 2009; Grellier *et al.* 2012). This hypothesis works well in arid and semi-arid environments (Ward *et al.* 2013b), although Grellier *et al.* (2012) worked in an environment with a similar rainfall to our study. Sankaran *et al.* (2005) noted that between 100 and 650 mm annual rainfall, woody cover is positively related to soil moisture (see also Sankaran *et al.* (2008)). Once mean annual precipitation exceeds ~650 mm, soil moisture is no longer limiting (Sankaran *et al.* 2005). However, Higgins *et al.* (2010) state that this threshold is above ~820 mm. Analysis of rainfall data for our study area shows that annual rainfall has decreased significantly since the start of the recorded data in 1901. However, mean annual precipitation remains above 700 mm, implying that rainfall has had no influence (or at least, very little) on the tree:grass ratio.

Temperature

Temperature change is more consistent with woody encroachment. Nemani *et al.* (2003) suggest that global plant productivity has increased with climate change, largely as a result of increased solar radiation. Our data show that there has been a significant decrease in the number of cold days.   Wakeling *et al.* (2012) found that savanna trees grew more slowly under cooler conditions. With fewer days when minimum temperatures were less than 13 ^{o}C, tree seedlings will be more robust at the end of the growing period and, as a result, be more able to survive the cold winter period (O'Connor 1995). During the winter months, trees would be subjected to top-kill when temperatures drop below freezing (Silberbauer-Gottsberger *et al.* 1977, Brando and Durigan 2005, Holdo 2006). The reduction in number of days below freezing point, combined with increased growing period during the summer months, contributes to the increased survival of the trees.

Pollution

South Africa has been identified as a major contributor to industrial pollution, particularly in the form of nitrogen oxides and sulphur dioxide (SO_2) (Wenig *et al.* 2003, Collett *et al.* 2010, Josipovic *et al.* 2010). The main source of these pollutants is the Mpumalanga Highveld, which is highly industrialized.   It is well known that nitrogen (N) deposition causes a loss of plant diversity (Vitousek *et al.* 1997, Phoenix *et al.* 2006), but the role of N in woody plant encroachment has also been under debate (Kraaij and Ward 2006, Wigley *et al.* 2010). Köchy and Wilson (2001) found that N deposition as a result of pollution led to forest expansion in the northern hemisphere. Kraaij and Ward (2006) suggest that N deposition is more likely to facilitate competition between grasses and trees in a semi-arid environment. They found that N supplementation stimulated grass growth, which, in turn, inhibited tree seedling growth (see also Cohn *et al.* 1989). However, industrial pollution, in particular nitrogen dioxide

(NO_2), is unlikely to have had an effect on plant growth in our study area. Josipovic *et al.* (2010) have found that NO_2 deposition levels in this area were < 5 $\mu g\ m^{-3}$ per annum, well below the critical level for all vegetation prescribed by the Convention on Long-Range Trans-Boundary Air Pollution (UNECE:CLRTAP), which was set at 30 $\mu g\ m^{-3}$ per annum (Josipovic *et al.* 2010).

Atmospheric CO_2

Atmospheric CO_2 concentrations have been escalating ever since the beginning of the 19th century from approximately 275 $\mu mol/mol$ air to the current concentration of ~397 $\mu mol/mol$ (Tans 2013). This figure is predicted to rise above 600 $\mu mol/mol$ by the end of this century (Morgan *et al.* 2007). An increase in CO_2 concentrations increases photosynthetic rates, more so in woody (C_3) shrubs and trees than in C_4 grasses (Polley *et al.* 1997). Experimental work by Kgope *et al.* (2009) with *Acacia* seedlings and varying CO_2 concentrations confirmed that high CO_2 concentrations favour plants that utilize C_3 photosynthetic pathways. Ambient temperatures may also play a role in modifying photosynthetic rates. Zhu *et al.* (2008) have shown that, at current CO_2 concentrations, C_3 trees are only more efficient than C_4 plants below 20 ^{o}C.

Elevated CO_2 concentrations could also result in an accumulation of carbon reserves as opposed to increased photosynthetic rates (Bond and Midgley 2000). In mesic savannas, fires are frequent, imposing a high level of disturbance. Most savanna trees are capable of resprouting vigorously after a fire (Bond and Midgley 2000, Higgins *et al.* 2000, Meyer *et al.* 2005) and high carbon reserves would enhance this ability. Ward (2010) also suggests that higher CO_2 levels not only increase the photosynthetic rates of C_3 shrubs, but also allow for the mobilization of extra carbon for increased carbon-based defences, such as polyphenols and tannins. This, in turn, would reduce herbivory (Ward 2010). In our study area, the

increase in woody cover, despite potentially inhibiting factors, is consistent with the enhancing effects of CO_2 on C_3 plants as described above.

Conclusions

Analysis of the fixed-point repeat photographs shows that there has been a significant increase in woody cover in the study area over the past 130 years. The forces that drive these changes are complex and it is likely that there are several drivers at work (Ward 2005; Bond 2008).

Herbivory combined with fire may well have had an influence on bush encroachment (see e.g. Skarpe (1991); van Langevelde *et al.* (2003)). Historical accounts detail the dramatic decline in indigenous herbivores – both browsers and grazers – which have been replaced by domestic herbivores, most of which are high bulk grazers. Grazing decreases competition between grasses and trees, allowing successful tree seedling recruitment (Scholes and Archer 1997, Riginos and Young 2007) and a reduction in fuel load necessary for hot fires (Trollope and Tainton 1986, Skarpe 1992, Higgins *et al.* 2000). The removal of the browsers, in particular, may have had a significant role in the increase in woody plant cover. It remains to be seen whether the reported decline in cattle numbers from communal lands since 1990 will have any impact on bush encroachment.

The increase in the daily minimum temperature also impacts on tree seedling recruitment and survival. The longer growing periods and a reduction in top-kill caused by freezing temperatures would favour bush encroachment. These increases in tree growth also aid tree saplings to escape the fire zone (Balfour and Midgley 2006).

It has been shown that atmospheric CO_2 levels are increasing (see for example Kgope *et al.* 2009). An increase in global CO_2 should enhance photosynthetic rates among C_3 trees and permit the mobilization of extra carbon to allow for rapid regeneration after fire as well as

increased investment in carbon-based defence mechanisms, which reduce herbivory (Ward 2010).

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Figure 2.1: Fixed-point, repeat photographs taken at Fugitives' Drift. (a, b) Photographs taken in 1879 showing the vegetation on either side of the small stream that enters the Umzinyathi River from the north-east. (c) Image taken in 2011 showing the extent of vegetation change. The photographs are not exactly matched due to encroachment at the camera site. Hence, the camera was set up *c.* 10 m west of the original camera site. Comparison of (a) and (c) shows that tree density in 2011 (c) has increased by 70% in the eluvial region (1) and by 55% in the colluvial region (2). Comparison of (b) and (c) shows that tree density has increased in the two alluvial regions (1) and (2) by 40% and 55% respectively. Tree density in the colluvial region (3) has increased by 78% and in the eluvial/alluvial region (4) by 70%. (d, e) Photographs showing vegetation change on the west-facing slope of the small stream entering the river, comparing 1936 (d) and 2011 (e) views. The photographs are not exactly matched due to bush thickening at the original camera site. Hence, the recent photograph was taken *c.* 3 m to the west of the original site. Although not assessed by vegetation experts, the dramatic increase in woody cover between 1936 and 2011 is clear. Comparison with (b) shows there has been only a small increase of woody cover between 1879 and 1936. (f, g) Photographs showing vegetation change on the west-facing slope of the small stream entering the river, comparing 1992 (f) and 2011 (g) views. The photographs were from a similar locality as those in (b) and (d). Although not assessed by vegetation experts, they show that by the early 1990s (f) the hillsides across the Umzinyathi River are heavily encroached by woody species. Historic photographs: (a) John Dunn collection, courtesy of Kwazulu-Natal Museum Services; (b) James Lloyd collection, courtesy of KwaZulu-Natal Museum Services; (d) Bowden, courtesy of KwaZulu-Natal Museum Services ; (f) Ian Knight. Recent photographs by Jennifer Russell.

Figure 2.2: Fixed-point, repeat photographs taken at Isandlwana. (a – d) Photographs taken from the east of the mountain. A comparison between 1879 (a) and 2011 (b) shows that in the foreground in the current photograph (b) bush density is low (2%) in the alluvial region (1). Tree density in the colluvial regions (2 and 3) on the south-east slopes of the mountain has increased in (b) by 39% and 11.5%, respectively. There has been no change in the eluvial/alluvial region (4), just below the summit. Photographs (c) and (d) were taken in 1992 and in 2011, respectively. These photographs have been taken from a similar locality as those in (a) and (b). Woody encroachment on the eastern slope is minimal prior to 1992, with marked increases in the next 20 years.   Photographs (e) and (f) were taken in 1879 and in 2011, respectively, from the south of Isandlwana.   In the current photograph (f), tree density has increased by 14% in the alluvial region (1) in the foreground and by 34.5% in the colluvial region (2), particularly on the western portion of the region.   Erosion gullies are evident in both photographs and do not appear to have changed much. (g, h) Photographs also from the south of Isandlwana show that little has changed on the sandstone cliffs of the mountain between 1929 (g) and 2011 (h). The southern slopes are still bare in the 1929 (g) photograph, although some evidence of woody encroachment on the skyline of the western slopes is apparent. Historic photographs: (a) John Dunn collection, courtesy of KwaZulu-Natal Museum Services; (c) Ian Knight; (e) courtesy of Killie Campbell Africana Museum; (g) courtesy of KwaZulu-Natal Museum Services. Recent photographs by Jennifer Russell.

Figure 2.3: Fixed-point, repeat photographs taken at Isandlwana show the progression of woody encroachment. (a, b) Photographs taken from the south of Isandlwana. Little has changed between 1929 (figure 2.2g) and the 1940s (figure 2.3a). By 2011 (b), *Acacia karroo* and a few *Acacia sieberiana* have encroached.   (c, d) Photographs taken in 1964 (c) and in 2011 (d) showing a similar aspect of the mountain as those in the previous figures 2.2g and

2.3a. There is evidence of woody encroachment on the western slopes (left) of the mountain

by 1964 (c), with small shrubs also evident on the eastern spur (right). Since 1964 (c) woody

encroachment has been marked, but patchy. Evidence of block burning is apparent in

photograph (c). (e, f) Photographs comparing woody cover between 1992 (e) and 2011 (f). In

1992 (e), the trees are still small, but increase in height and density over the next 20 years.

Note also the erosion gully in the foreground, which has not changed much during the

intervening 20 years. Historic photographs: (a) Mrs M. Barker, courtesy of Killie Campbell

Africana Library; (c) George Chadwick; (f) Ian Knight. Recent photographs by Jennifer

Russell.

Figure 2.4: (a – d) Fixed-point, repeat photographs of Isandlwana (west) and (e – f) Rorke's

Drift. (a, b) Photographs of Isandlwana taken from the west comparing vegetation cover

between 1899 (a) with 2011 (b). This is an unusual aspect of the mountain, as most

photographs were taken around the battle site on the eastern and southern flanks of the

mountain. Despite the historic photograph being taken 20 years later than the Anglo-Zulu

War, there is little change on the colluvial region (5) of Isandlwana between 1879 and 1899 if

compared with the historic photograph in figure 2.2e. However, when compared to the

current photograph (b), significant woody encroachment in all the delineated regions is

evident. Current human activity in the eluvial/colluvial region (2) could explain why this

region has experienced the least change. On-site inspection showed evidence of past

cultivation in the modified alluvial region (4) at the foot of the mountain. (c, d) Fixed-point,

repeat photographs of Isandlwana taken from the west, comparing vegetation cover between

2004 (c) and 2013 (d).   The photographs are not exactly matched due to encroachment at the

original site of the camera. Camera was therefore moved about *c.* 3 m south of the original

site. There has been a marked increase in woody encroachment in the foreground (d), which

is outside the historic reserve of Isandlwana. Within the historic reserve (middle- and background) tree density does not appear to have increased, although trees have increased in size (b). The difference in tree density between the foreground and the rest of the landscape may be due to a deliberate burning regime practised by the management of the reserve area. (e, f) Photographs of Rorke's Drift settlement at the foot of Shyane, taken in 1882 (e) and 2011 (f). The area has been farmed extensively since 1849. In1882 photograph, one can see cultivated lands in the middle-ground, which are still visible in the current photograph (f), although these lands are no longer cultivated. Since 1882 (e), there has been significant, although moderate, increase in woody cover. The eluvial/colluvial region (1) in the foreground is on commercial rangeland. The alluvial and alluvial/colluvial regions (2 and 3) are now communally managed by isiZulu-speaking cattle and goat ranchers. Woody encroachment has been more rapid on the northern and western slopes of the eluvial/colluvial region of Shyane (4) than on the eastern and southern slopes. Historic photographs (a): courtesy of the Killie Campbell Africana Library; 2004 photograph (c): Neil Aspinshaw; (e) courtesy of KwaZulu-Natal Museum Services. Recent photographs by Jennifer Russell.

Figure 2.5: Fixed-point, repeat photographs taken at Rorke's Drift. (a, b) Fixed-point, repeat photographs of Sinqindi from Shyane at Rorke's Drift, taken in 1879 (a) and 2011 (b). The current view (b) of Sinqindi is almost obscured by encroaching woody species on the alluvial region (1) at the foot of Shyane (25% increase). Woody encroachment on the colluvial region (2) of Sinqindi in the current photograph (b) is also significant (13% increase). The large trees in the middle-ground are exotics, namely *Pinus* sp. (c, d) Fixed-point, repeat photographs of Fort Mellvill on the hill on the banks of the Umzinyathi River, just upstream of Rorke's Drift itself, taken in 1879 (c) and 2011 (d). The historic photograph (c) shows a landscape remarkably devoid of vegetation. By 2011 (d), both the modified alluvial region

(1) and the colluvial region (2) show significant woody encroachment (increased by 39% and 60%, respectively). The central alluvial region (3) has not changed significantly. It is currently under cultivation. There has been a significant increase (25%) in the colluvial region (4) around the settlement of Rorke's Drift. Much of it is exotic vegetation, such as *Eucalyptus* spp., *Jacaranda mimosifolia* and *Pinus* spp. (e, f) Photographs of Shyane at Rorke's Drift, with the Umzinyathi River in the foreground, taken in 1879 (e) and 2011 (f). The alluvial region (1) shows significant, but moderate, woody encroachment (15%) since 1879 (e). The colluvial regions of 2, 3 and 4 all show significant woody encroachment (40%, 40% and 25%, respectively) in the current photograph (f), particularly on the northern- and north-eastern facing slopes. Historic photographs: (a) courtesy of the Killie Campbell Africana Library; (c) John Dunn collection, courtesy of KwaZulu-Natal Museum Services; (e) courtesy of KwaZulu-Natal Museum Services. Recent photographs by Jennifer Russell.

Figure 2.6: Indirect detrended correspondence analysis (DCA) shows distinct grouping of the different sites, characterised by plant species. The grouping reflects the different land-uses. At the battle site of Isandlwana (I) land-use is a combination of conservation management and communal land-use. The site is block burned every 2 – 3 years. There are a number of wild herbivores in the area, mainly impala *Aepyceros melampus* and plains zebra *Equus quagga burchelli*. Three months of the year (at the end of summer), the community members from the nearby villages are permitted to graze their cattle on the site. Rorke's Drift (R) is communal rangeland, where cattle owners all graze their cattle communally. There is no limit to how many cattle they own. Each year the area is subjected to uncontrolled fires. Within this group are three sites (RSiO) which fall within the commercial lands. They show a similar species composition to the communal lands, although subject to different management style. Fugitives' Drift (F) is a conservancy with a variety of wild herbivores as

well as a few domestic cattle. The area is block burned every two years. The three outliers (RSi) are at Rorke's Drift and part of a commercial cattle ranch. Block burning occurs every three years.

Figure 2.7: Direct detrended canonical correspondence analysis (DCCA) showing the correlation between environmental variables and sites. Percentage rock and the slope (or steepness) of the terrain exerted a strong influence on the grouping of the sites. Each study site had its own distinct composition of dominant species, which could be the result of land-use. Commercial cattle ranching had the greatest effect on species composition, while communal cattle ranching had the least effect on species composition. The diamond shapes denote sites at Fugitives' Drift (F), the inverted triangles denote sites at Rorke's Drift (R) and the square shapes denote sites at Isandlwana (I). The nominal environmental variables are denoted by large closed circles. Cons = conservation area; Comm = communal rangelands; Enc = encroached areas; Mix = areas where both conservation management and communal grazing are practised; Old = old lands that are no longer under cultivation; Coml = commercial rangelands. The other three environmental variables are indicated by arrows. Asp = aspect; rock = rockiness of the terrain; Slp = steepness of the terrain.

Figure 2.8: Standardised precipitation index (SPI) values (see Yurekli and Anli 2008). The relative amount of rainfall for each season (SPI) from 1901 to 2006 was extracted from combined rainfall data from the Dundee Research Station and Dundee Police Station. There are more years of below normal precipitation during the last 40 years than between 1901 and 1954. The events are also less extreme during the last thirty years compared to the events between 1901 and 1954. SPI values are rated as follows: extremely wet = 3; very wet = 2; moderately wet = 1; near normal precipitation = 0; moderate drought = -1;

severe drought = -2; and extreme drought = -3. The double headed arrow indicates periods where there the records were unreliable and were not included. As the wet season is over the summer period, the 12-month period was taken from the beginning of August until the end of July each year.

Table 2.1. Altitudinal range (m), aspect of catenal regions represented in Figures 2.1, 2.2, 2.4 and 2.5 showing increase in percentage woody cover between 1879 and 2011. Woody cover has increased significantly in all but four catena regions. Catenal regions are described according to Scheidegger (1986). The eluvial region is the plateau-like region of origination of material; the colluvial region is the steep incline where transport of material is substantial; and the alluvial region is at the base of the slope. % increase = increased woody cover. * = significant increase in woody vegetation cover ($p < 0.05$).

Table 2.2: Results of multiple regression analysis of the first axis of the detrended correspondence analysis (DCA) against the variances. The outliers evident in the DCA have been removed. The overall value of the multiple regression analysis is highly significant ($F = 11.17$, $p < 0.001$) and a large amount of the variance is explained ($r^2 = 0.72$). Three of the independent categories are significant: encroached sites ($p < 0.001$), old lands ($p = 0.008$) and commercial lands ($p < 0.001$). The β co-efficient was calculated. We focus on the significant β (standardized) coefficients because they are directly comparable. We found that the effect of commercial farming on species composition was marginally higher than that on areas that had undergone bush encroachment, while old lands had a considerably weaker effect. These results confirm that land-use has an effect on the species composition within the various sites. 'Mixture' refers to a combination of conservation and communal areas. 'Encroached' refers to areas within all types of land-use that have undergone bush encroachment. 'Old lands' are previously cultivated lands that are now fallow.

Figure 2.1: Fixed-point, repeat photographs taken at Fugitives' Drift.
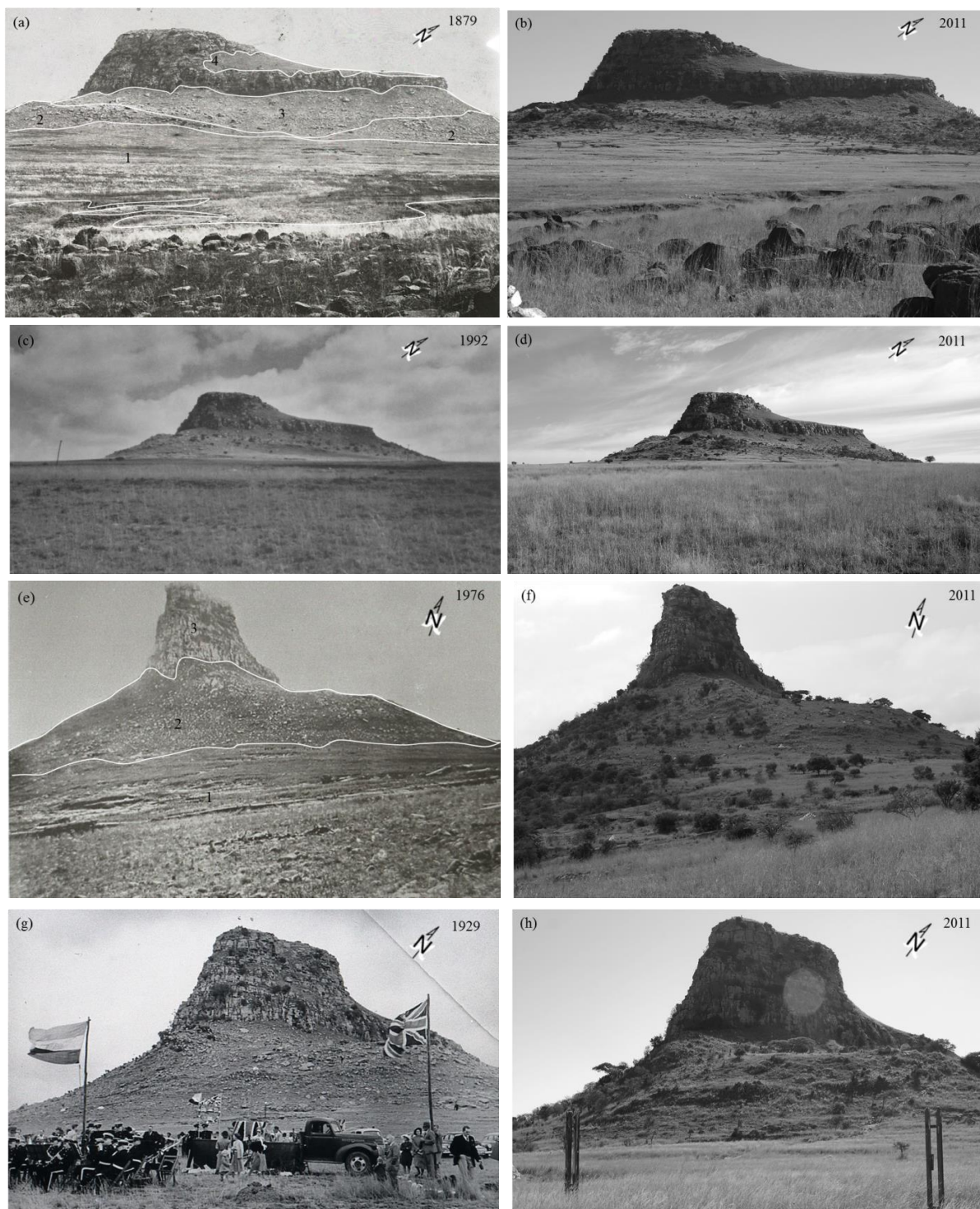
Figure 2.2: Fixed-point, repeat photographs taken at Isandlwana.
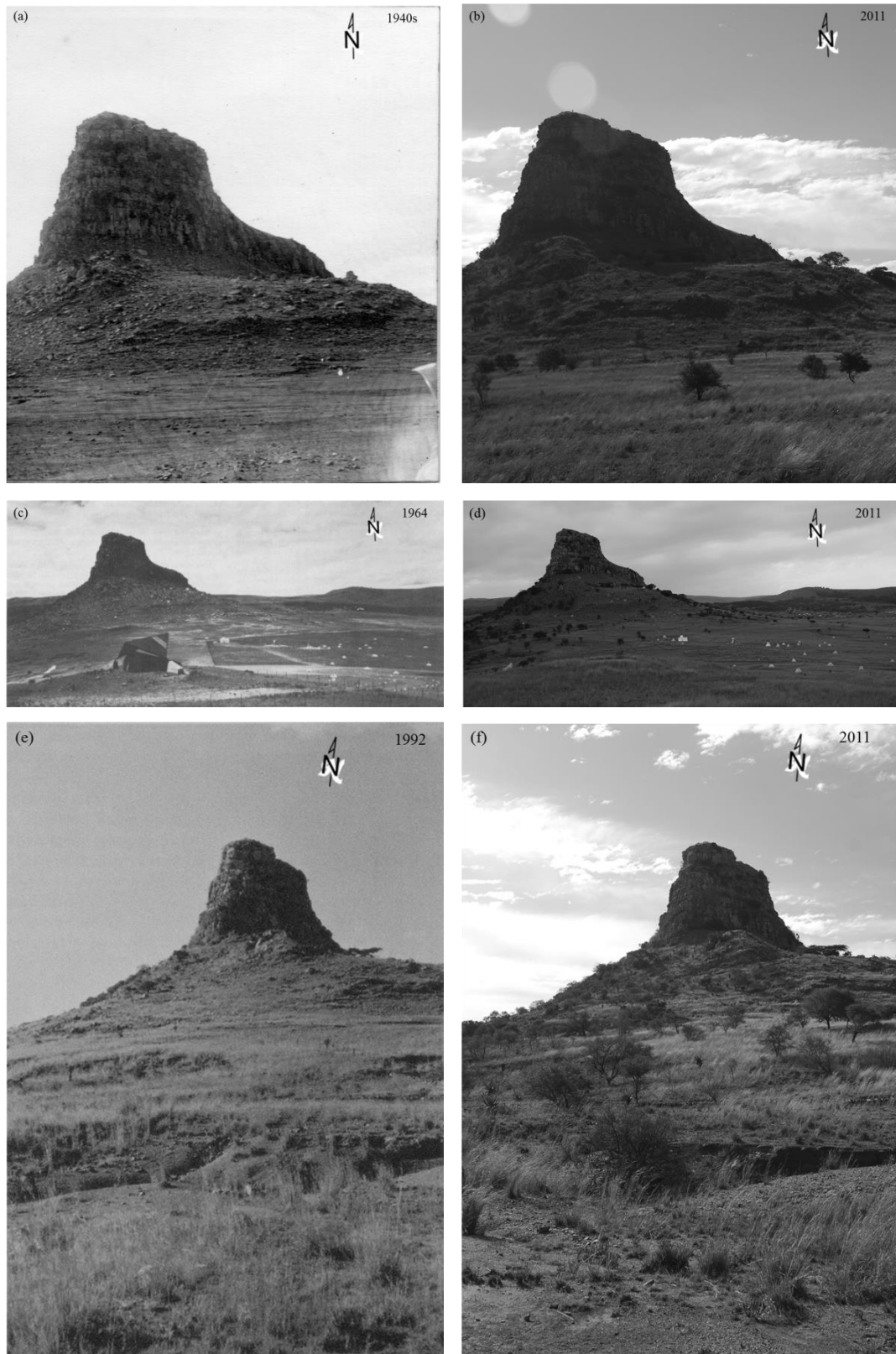
Figure 2.3: Fixed-point, repeat photographs taken at Isandlwana show the

progression of woody encroachment.
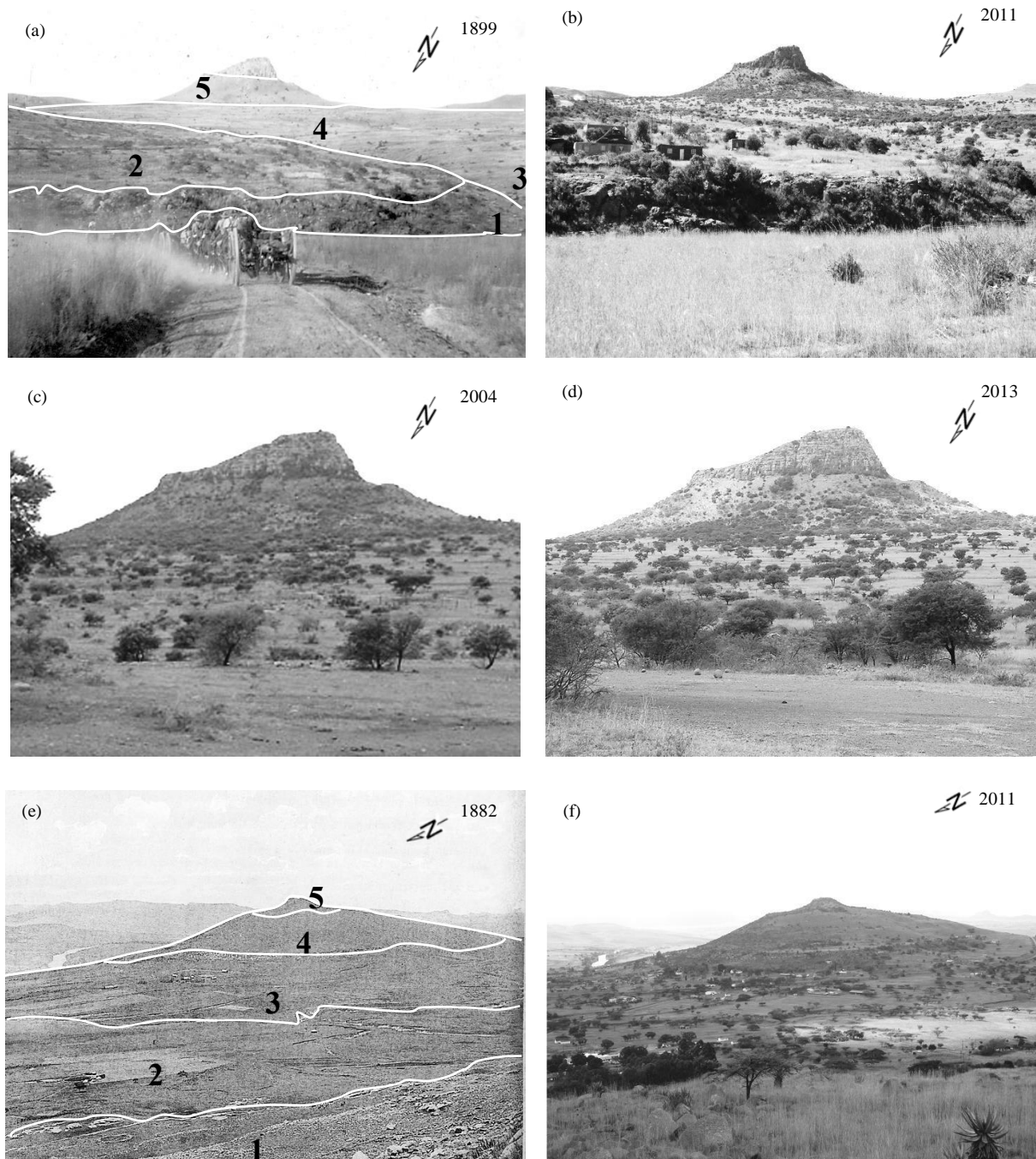
Figure 2.4: (a – d) Fixed-point, repeat photographs of Isandlwana (west) and (e – f) Rorke's Drift.

Figure 2.5: Fixed-point, repeat photographs taken at Rorke's Drift.
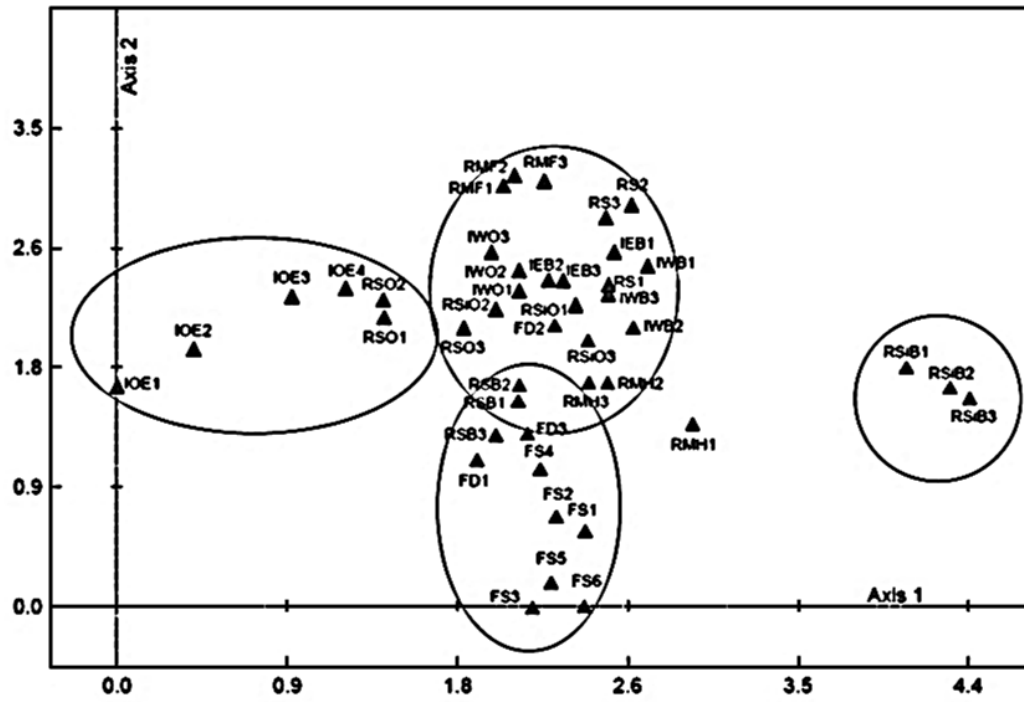
Figure 2.6: Indirect detrended correspondence analysis (DCA) shows distinct grouping of the different sites, characterised by plant species.
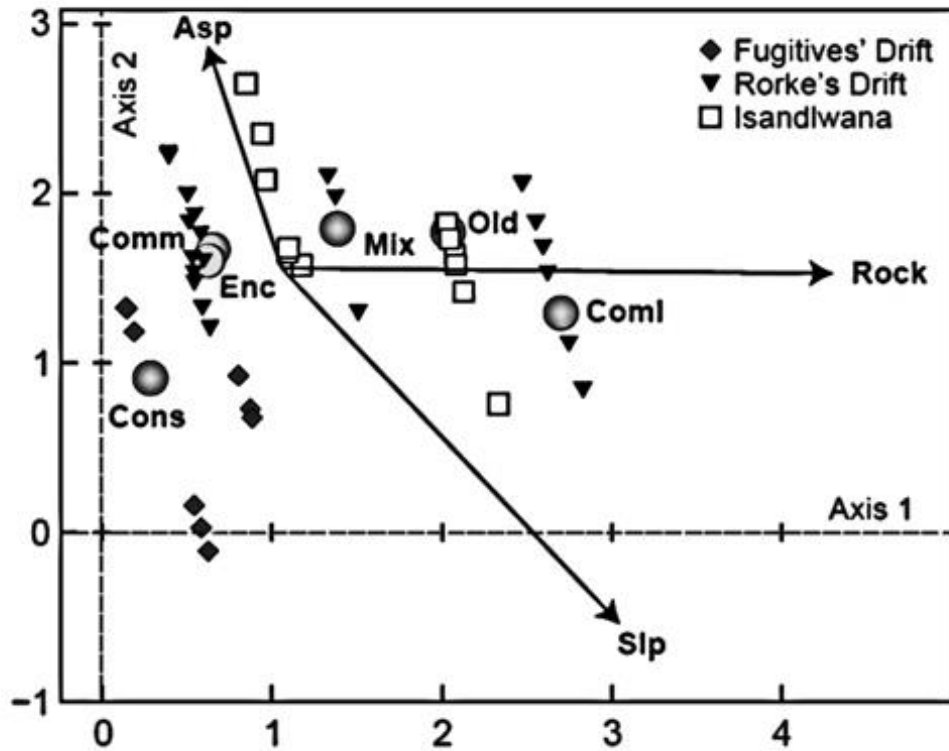
Figure 2.7: Direct detrended canonical correspondence analysis (DCCA) showing the

correlation between environmental variables and sites.

Cons = conservation area

Comm = communal rangeland

Enc = encroached areas

Mix = areas where both conservation management and communal grazing are practised;

Old = old lands that are no longer under cultivation

Coml = commercial rangelands

Asp = aspect

Rock = rockiness of the terrain

Slp = steepness of the terrain.
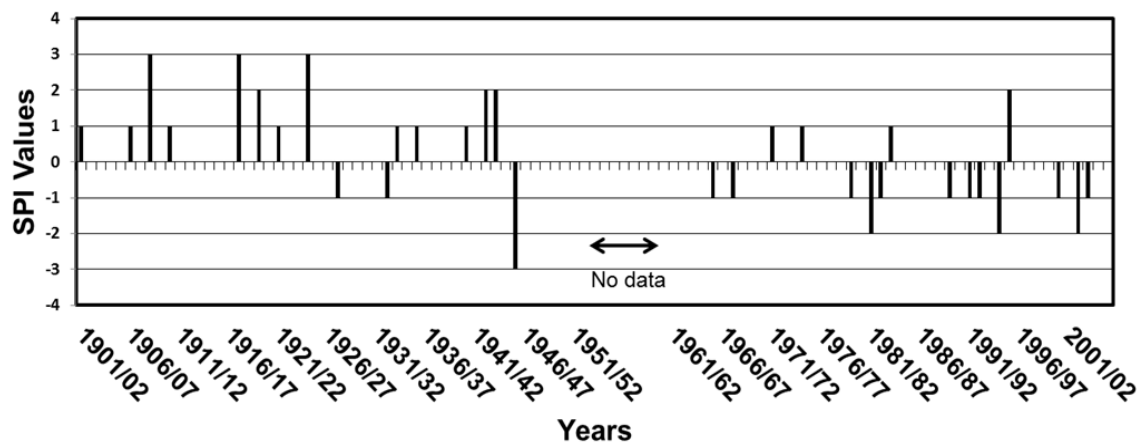
Figure 2.8: Standardised precipitation index (SPI) values.

Table 2.1: Altitudinal range (m), aspect of catenal regions represented in Figures 2.1,

2.2, 2.4 and 2.5 showing increase in percentage woody cover between 1879 and 2011.

Figure	Altitudinal range (m)	Delineated unit	Catena	Aspect	% woody cover		% increase
					1879	2011	
1a, c	960 - 1060	1	Eluvial	South	10	80	70*
		2	Colluvial	South	15	70	55*
1b,c	940 - 1060	1	Alluvial	North-east	10	50	40*
		2	Alluvial	West	20	75	55*
		3	Colluvial	West	12	90	78*
		4	Eluvial/Alluvial	West	15	85	70*
2a, b	1180 - 1310	1	Alluvial	South-east	0	2	2
		2	Colluvial	South-east	1	40	39*
		3	Colluvial	South-east	1	12.5	11.5*
		4	Eluvial/Alluvial	South-east	1	1	0
2e, f	1215 - 1330	1	Alluvial	South-west	1	15	14*
		2	Colluvial	South-west	0.5	35	34.5*
		3	Colluvial/Eluvial	South-west	5	10	5
4a, b	1090 - 1280	1	Colluvial	North-west	10	50	40*
		2	Eluvial/Colluvial	West	20	40	20*
		3	Modified alluvial	North-east	5	35	30*
		4	Modified alluvial	North-west	5	40	35*
		5	Colluvial	North-west	5	45	40*
4e, f	1140 - 1320	1	Eluvial/colluvial	East	0.5	15	14.5*
		2	Allulvial	East	1	15	14*
		3	Alluvial/colluvial	West	1	15	14*
		4	Eluvial/colluvial	West	0.5	10	9.5*
		5	Eluvial	West	1	30	29*
5a, b	1150 - 1320	1	Alluvial	North-west	5	30	25*
		2	Colluvial	East	2	15	13*
5c, d	1060 - 1140	1	Modified alluvial	East	1	40	39*
		2	Colluvial	East	0	60	60*
		3	Alluvial	East	0.5	5	4.5
		4	Alluvial	North	0	25	25*
5e, f	1060 - 1320	1	Alluvial	North	5	20	15*
		2	Colluvial	North	15	55	40*
		3	Colluvial	North	10	50	40*
		4	Colluvial	North	20	45	25*

Table 2.2: Results of multiple regression analysis of the first axis of the detrended correspondence analysis (DCA) against the variances.

ANOVA

	df	SS	MS	F	p
Regression	8	19.908	2.488	11.171	<0.001
Residual	34	7.571	0.223		
Total	42	27.481			

	Coefficients	β-Coefficient	t Stat	P-value
Intercept	0.44		1.48	0.146
Aspect	0.001	0.199	1.93	0.061
Slope	0.016	0.133	0.79	0.435
Rockiness	0.008	0.263	1.52	0.139
Commercial	1.95	0.844	5.41	<0.001
Conservation	-0.01	-0.004	-0.04	0.969
Mixture	-0.01	-0.008	-0.07	0.947
Old lands	1.07	0.34	2.83	0.008
Encroached	1.35	0.816	4.57	<0.001

Appendix 1: Plants sampled in November 2011 (woody species) and January 2012 (grass species.

List of plant species (woody and grass) found at Fugitives' Drift, a conservation area. Although site "Skubudu valley 541/7" is communal land, it was abandoned by the community in the 1980s. % aerial cover is expressed as an average cover for the replicates for each site. The number of species is the actual number.

Fugitives' Drift (woody) Species list	Skubudu valley 541/7	Skubudu valley D70/078	Fugitives' Drift D70/078
Acacia ataxacantha	3.7	2.3	18.3
Acacia karroo	1.7	3.3	1.0
Acacia nilotica	0.0	1.7	0.2
Afrocanthium mundianum	2.0	0.3	0.0
Aloe marlothi	5.7	1.7	6.3
Brachylaena elliptica	0.3	0.5	0.3
Canthium gilfillanii	5.3	3.7	0.0
Canthium inerme	0.0	0.7	0.0
Catha edulis	0.5	0.5	0.0
Chaetacme aristata	0.3	0.3	0.0
Clausena anistata	0.0	0.0	0.3
Clutia pulchella	3.7	1.8	0.0
Combretum apiculatum	0.0	0.0	1.3
Combretum erythrophyllum	0.0	0.2	0.0
Cussonia spicata	1.8	1.0	0.5
Diospyros glandulifera	0.0	0.0	2.0
Diospyros lycioides	1.3	2.3	4.2
Diospyros whyteana	4.7	2.7	0.5
Dombeya rotundifolia	0.0	0.0	0.2
Ehretia rigida	0.0	0.0	0.2
Euclea crispa	10.7	4.7	7.0
Ficus sycamorus	0.0	0.2	0.3
Grewia occidentalis	0.0	0.2	0.5
Gymnosporia heterophylla	1.0	1.0	2.7
Gymnosporia senegalensis	0.2	0.7	0.0
Gymnosporia undata	0.0	0.0	0.0
Hippobromus pauciflorus	3.0	1.2	0.8
Jasminum sp	3.7	2.7	0.3
Lantana rugosa	0.0	0.0	0.2
Lippia javanica	0.0	0.2	3.3
Meytenus umdata	1.2	0.7	0.2
Ochna arborea	0.2	0.2	0.3
Ozoroa paniculosa	0.2	0.3	0.0
Ozoroa sphaerocarpa	0.0	0.0	2.0
Pachystigma macrocalyx	0.7	0.0	0.0
Rhoicissus tridentata	0.8	0.7	0.3
Rubus sp	0.0	0.3	0.0
Schotia brachypetala	0.0	0.3	0.0
Scutia mytina	0.0	0.2	0.0
Searsia c.f. dentata	0.0	0.3	0.3
Searsia c.f. montana	1.0	1.7	0.0
Searsia pallens	1.5	2.0	0.0
Searsia c.f. pentheri	2.0	1.0	2.7
Searsia c.f. rehmanniana	0.3	0.5	0.7
Searsia c.f. tormentosa	0.0	0.0	0.8
Solanum sp	0.0	0.0	0.7
Tricalysia lanciolate	0.0	0.2	0.0
Vitex rehmannii	4.2	2.5	0.0
Zanthoxylem capense	1.5	0.7	2.2
Ziziphus mucronata	0.2	0.5	1.0
No. spp	29.0	39.0	32.0
% cover	63.2	45.7	61.7

Fugitives' Drift (grasses)

Species list		Skubudu valley 541/7	Skubudu valley D70/078	Fugitives' Drift D70/078
Aristida junctiformis		0.5	0.2	1.2
Aristida meridionalis		0.0	0.0	0.5
Bewsia biflora		0.0	0.0	0.3
Bothriochloa insculpta		0.0	0.0	0.2
Cymbopogon excavatus		0.5	0.3	2.7
Digitaria longiflora		0.2	0.0	0.0
Eragrostis curvula		0.5	0.5	3.0
Eragrostis plana		0.0	0.2	0.3
Eragrostis pseudosclerantha		0.5	0.2	0.0
Eragrostis racemosa		0.0	0.0	0.0
Eragrostis superba		0.0	0.0	13.5
Helictotrichon turgidulum		0.5	0.2	0.0
Heteropogon contortus		0.5	3.3	8.5
Hyparrhenia hirta		0.3	0.2	0.5
Melinis nerviglumis		0.0	0.0	0.3
Melinis repens		0.5	0.3	0.7
Microchloa caffra		0.2	0.0	0.2
Panicum natalensis		0.2	0.0	1.5
Schizachyrium sanguineum		0.0	0.0	0.2
Sedge		0.2	0.3	0.3
Setaria sphacelata		0.3	1.8	0.2
Themeda triandra		1.5	0.2	31.7
Trichoneura grandiglumis		0.0	0.0	0.2
	No. spp	14.0	12.0	19.0
	% cover	6.3	7.7	65.8

List of plant species (woody and grass) found at Isandlwana. The area is a mixture of conservation and communal land utilization practices. % aerial cover expressed as an average cover for the replicates for each site. The number of species is the actual number.

Isandlwana (woody)
Species list

	West slopes- bush 54/094	West slopes- open 54/094	East slopes - bush 541/2	East slopes - bush 541/2
Acacia karroo	36.7	3.3	39.3	0.2
Aloe marlothi	22.3	1.0	6.7	0.0
Aparagus sp	0.2	0.0	0.2	0.0
Brachylaena elliptica	0.0	0.0	0.7	0.0
Canthium setiflorum	2.7	0.0	0.0	0.0
Canthium spinosum	0.0	0.0	0.3	0.0
Diospyros glandulifera	0.0	0.0	0.2	0.0
Diospyros lycioides	11.3	0.8	3.2	0.0
Diospyros whyteana	0.0	0.0	0.2	0.0
Dombeya rotundifolia	0.0	0.0	0.5	0.0
Ehretia rigida	0.2	0.0	0.0	0.0
Euclea crispa	2.0	0.2	1.5	0.0
Ficus burtt-davyi	0.7	0.0	0.0	0.0
Ficus sycamorus	0.0	0.0	1.3	0.0
Grewia occidentalis	1.0	0.0	2.8	0.0
Gymnosporia heterophylla	0.0	0.0	0.3	0.0
Jasminum sp	1.0	0.0	0.0	0.0
Lantana rugosa	0.0	0.3	0.0	0.0
Lippia javanica	4.7	3.0	0.5	0.2
Obetia tenax	0.2	0.0	0.0	0.0
Premna mooiensis	0.0	0.0	0.3	0.0
Rhoicissus tridentata	0.8	0.2	0.0	0.0
Searsia c.f. dentata	0.0	0.2	0.0	0.0
Searsia c.f. montana	0.5	0.0	0.0	0.0
Searsia c.f. pallens	5.3	0.2	13.7	0.0
Searsia c.f. pentheri	0.7	0.3	0.3	0.0
Searsia c.f. rehmanniana	0.5	0.2	0.2	0.0
Searsia c.f. tormentosa	0.2	0.0	0.0	0.0
Solanum sp	0.5	0.2	0.5	0.0
No. spp	19.0	12.0	19.0	2.0
% cover	91.3	9.8	72.7	0.3

Isandlwana (grasses)
Species list

	West slopes- bush 54/094	West slopes- open 54/094	East slopes - bush 541/2	East slopes - open 541/2
Aristida junctiformis	2.0	2.7	2.3	3.0
Bewsia biflora	0.0	0.2	0.5	0.0
Bothriochloa insculpta	0.0	0.0	0.0	0.0
Brachiaria serrata	0.0	0.0	0.2	0.1
Cymbopogon excavatus	0.2	0.8	1.5	11.3
Cymbopogon pospischilli	0.0	0.0	0.3	0.3
Cynodon dactylon	1.0	0.2	1.7	0.0
Elionurus muticus	0.0	0.0	0.3	0.0
Eragrostis curvula	3.3	2.3	5.0	2.9
Eragrostis gummiflua	0.0	0.5	0.0	0.0
Eragrostis plana	9.0	0.5	2.0	2.9
Eragrostis pseudosclerantha	0.3	0.2	1.0	15.3
Eragrostis racemosa	0.2	0.0	0.0	0.4
Eragrostis superba	0.2	0.0	0.3	0.4
Heteropogon contortus	0.0	0.2	0.3	0.4
Hyparrhenia hirta	0.2	11.7	1.7	23.8
Melinis nerviglumis	0.0	0.3	0.3	0.1
Melinis repens	1.7	3.7	1.2	0.6
Microchloa caffra	0.0	0.2	0.0	0.3
Panicum natalensis	12.7	0.7	3.0	0.3
Perotis patens	0.0	2.8	0.0	0.0
Sedge	0.5	0.3	0.3	0.0
Setaria pallide-fusca	0.0	0.0	1.7	0.1
Setaria sphacelata	0.5	0.0	0.0	0.0
Themeda triandra	10.7	0.2	2.3	0.9
Trichoneura grandiglumis	0.2	0.3	0.0	0.0
No. spp	15.0	18.0	19.0	17.0
% cover	42.5	27.7	26.0	62.8

List of plant species (woody and grass) found on communal land at Rorke's Drift. % aerial cover expressed as an average cover for the replicates for each site. The number of species is the actual number also expressed as an average for the replicate plots within each site.

Rorke's Drift Communal Sites (woody)
Species list

	Shyane - bush 431/1	Shyane - open 431/1	Fort Mellvill - flood plain 541/3	Fort Mellvill - hillside 541/3	Shyane 63/005
Acacia ataxacantha	0.0	0.3	0.0	1.7	0.0
Acacia karroo	7.3	0.8	46.7	7.0	8.0
Acacia sieberiana	0.0	0.0	0.2	0.0	0.0
Afrocanthium mundianum	0.0	0.0	0.2	0.0	0.3
Aloe marlothi	2.7	2.0	0.3	3.7	6.3
Aparagus sp	0.7	0.0	0.3	0.7	0.5
Canthium setiflorum	0.0	0.0	0.0	0.0	0.7
Celtis africanis	0.0	0.0	0.0	0.5	0.0
Cussonia spicata	0.2	0.0	0.0	0.0	0.0
Diospyros austo-africana	0.0	0.0	0.0	0.3	0.0
Diospyros glandulifera	0.5	0.0	0.0	0.5	0.0
Diospyros lycioides	11.7	0.8	0.8	5.5	6.7
Diospyros whyteana	5.0	0.0	0.0	0.5	0.0
Dombeya rotundifolia	0.2	0.0	0.0	0.0	0.0
Euclea crispa	26.7	1.7	1.0	3.0	4.7
Ficus sycamorus	0.7	0.0	0.0	0.0	0.0
Grewia occidentalis	0.7	0.2	0.2	0.7	1.5
Gymnosporia heterophylla	2.3	0.3	0.0	0.5	0.0
Gymnosporia senegalensis	0.2	0.0	0.0	0.2	0.5
Heteromorpha arborescens	0.0	0.0	0.0	0.0	0.5
Hippobromus pauciflorus	0.5	0.0	0.0	0.0	0.2
Jacaranda mimosifolia	0.0	0.0	0.0	0.3	0.0
Jasminum sp	0.5	0.0	0.2	1.8	1.0
Lantan camara	0.2	0.0	0.0	0.0	0.2
Lantana rugosa	0.0	0.0	0.2	1.0	0.0
Lippia javanica	0.3	0.0	0.2	0.8	4.3
Melia azedarach	0.0	0.0	0.0	0.5	0.0
Meytenus umdata	0.0	0.0	0.0	0.2	0.0
Ochna arborea	0.2	0.2	0.0	0.3	0.2
Pittosporum viridiflorum	0.0	0.2	0.0	0.0	0.0
Premna mooiensis	0.7	0.0	0.0	0.0	13.3
Rhoicissus tridentata	1.2	0.0	0.2	0.0	0.5
Schotia brachypetala	0.3	0.0	0.0	0.0	0.0
Scolopia flanaganii	0.5	0.0	0.0	0.0	0.0
Searsia c.f. dentata	0.7	0.2	0.2	0.0	1.0
Searsia c.f. montana	1.5	0.2	0.0	0.0	0.0
Searsia c.f. pallens	2.3	0.3	0.7	2.0	0.0
Searsia c.f. pentheri	2.3	1.0	0.2	2.0	2.7
Searsia c.f. rehmanniana	0.0	0.0	0.3	1.3	0.0
Searsia c.f. tormentosa	1.2	0.0	0.3	0.7	0.0
Solanum sp	0.0	0.0	0.5	0.2	0.2
Vitex rehmannii	16.7	1.3	0.0	0.0	0.0
Zanthoxylem capense	0.0	0.0	0.0	0.3	0.0
Ziziphus mucronata	0.0	0.0	0.0	0.0	0.2
No. spp	28.0	14.0	18.0	26.0	21.0
% cover	87.7	9.5	52.5	36.2	53.3

Rorke's Drift Communal Sites (grasses)
Species list

	Shyane - bush 431/1	Shyane - open 431/1	Fort Mellvill - flood plain 541/3	Fort Mellvill - hillside 541/3	Shyane 63/005
Aristida junctiformis	0.3	1.3	2.2	0.0	0.7
Bewsia biflora	0.0	1.2	0.0	0.0	0.0
Bothriochloa insculpta	6.8	5.0	0.8	0.3	2.5
Cymbopogon excavatus	2.0	13.3	10.2	4.0	0.7
Cynodon dactylon	0.0	0.0	0.0	0.0	0.7
Digitaria sanguinalis	0.0	0.0	0.0	0.0	13.3
Diheteropogon amplectens	0.0	10.0	0.0	0.0	0.0
Elionurus muticus	0.0	0.2	0.0	0.0	0.0
Eragrostis capensis	0.2	0.2	0.0	0.0	0.3
Eragrostis curvula	0.2	0.3	0.5	0.3	4.3
Eragrostis plana	0.5	0.5	30.0	0.5	26.7
Eragrostis pseudosclerantha	5.0	0.2	0.0	0.0	0.5
Eragrostis superba	1.0	1.5	0.0	0.0	12.3
Heteropogon contortus	0.3	0.0	0.0	0.0	0.2
Hyparrhenia hirta	7.7	2.0	0.3	0.0	1.8
Melinis nerviglumis	0.0	0.7	0.0	0.0	0.0
Melinis repens	0.7	0.7	0.0	4.7	1.0
Microchloa caffra	0.0	0.0	0.2	0.0	0.0
Panicum maximum	7.0	0.0	0.0	0.0	0.2
Panicum natalensis	0.0	0.5	0.0	0.0	0.0
Paspalum dilatatum	0.0	0.2	1.2	0.0	0.0
Paspalum notatum	0.0	0.0	1.0	0.2	3.3
Sedge	0.3	1.0	0.3	0.3	0.5
Setaria pallide-fusca	1.0	0.0	0.0	0.0	0.0
Setaria sphacelata	0.0	1.5	0.2	10.0	2.0
Themeda triandra	36.7	13.3	36.7	5.7	17.3
Trachypogon spicatus	0.0	0.5	0.0	0.0	0.5
No. spp	15.0	20.0	12.0	9.0	19.0
% cover	69.7	54.0	83.5	26.0	88.8

List of plant species (woody and grass) found on commercial land at Rorke's Drift. % aerial cover expressed as an average cover for the replicates for each site. The number of species is the actual number.

Rorke's Drift Commercial Sites (woody)		
Species list	Sinqindi - bush 63/005	Sinqindi - open 63/005
	3.3	2.3
Acacia ataxacantha	58.3	0.0
Acacia karroo	0.8	0.2
Acacia sieberiana	2.2	0.8
Afrocanthium mundianum	0.3	0.0
Aloe marlothi	1.2	0.3
Aparagus sp	0.2	0.0
Canthium setiflorum	0.3	0.0
Celtis africanis	0.2	0.3
Diospyros austo-africana	6.8	1.0
Diospyros glandulifera	0.7	0.2
Diospyros lycioides	3.3	0.5
Dombeya rotundifolia	1.8	1.5
Euclea crispa	0.7	0.0
Ficus sycamorus	0.5	0.0
Grewia occidentalis	1.7	0.0
Gymnosporia senegalensis	0.2	0.0
Jacaranda mimosifolia	0.3	0.0
Jasminum sp	0.3	0.0
Lantan camara	6.3	3.0
Lantana rugosa	0.2	0.0
Meytenus umdata	0.2	0.0
Ochna arborea	4.0	0.0
Pittosporum viridiflorum	1.0	0.3
Premna mooiensis	0.7	0.0
Rhoicissus tridentata	1.7	0.0
Searsia c.f. pallens	1.7	1.7
Searsia c.f. pentheri	1.0	0.2
Searsia c.f. tormentosa	0.5	0.0
Vitex rehmannii	0.3	0.0
Zanthoxylem capense	1.0	0.0
Ziziphus mucronata	22.3	8.3
Woody 105	1.0	0.0
No. spp	33.0	14.0
% cover	102.7	12.3

Rorke's Drift Commercial Sites (grasses)
Species list

	Sinqindi - bush 63/005	Sinqindi - open 63/005
Aristida junctiformis	0.2	0.2
Bewsia biflora	0.2	0.7
Cymbopogon excavatus	0.5	3.0
Cymbopogon pospischilli	0.0	0.2
Cynodon dactylon	3.3	0.0
Diheteropogon amplectens	0.0	0.5
Eragrostis capensis	0.0	0.3
Eragrostis curvula	0.7	0.5
Eragrostis plana	0.7	0.3
Eragrostis pseudosclerantha	0.2	0.7
Eragrostis superba	0.0	0.3
Helictotrichon turgidulum	0.2	0.0
Heteropogon contortus	0.0	0.2
Hyparrhenia hirta	3.7	8.3
Melinis nerviglumis	0.0	0.7
Melinis repens	1.2	0.5
Panicum natalensis	0.5	0.7
Paspalum dilatatum	11.7	0.0
Sedge	0.3	0.7
Setaria sphacelata	0.3	0.2
Themeda triandra	0.2	0.5
Trachypogon spicatus	0.2	0.5
No. spp	16.0	19.0
% cover	23.8	18.8

Chapter 3

Remote sensing provides a progressive record of vegetation change in northern KwaZulu-Natal, South Africa, from 1944 to 2005

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Remote sensing, together with geographic information systems (GIS), provides a powerful tool for monitoring environmental processes. Aerial and satellite photographs enable the analysis of an entire landscape and, using multi-temporal sets of photographs, one is able to follow processes over time. In our study, we used multi-temporal sets of aerial photographs, taken between 1944 and 2005, to observe the phenomenon of woody plant encroachment in four neighbouring study sites in northern KwaZulu-Natal, South Africa. We also analysed rainfall and temperature trends. Woody plant encroachment was evident in all sites. We suggest possible drivers behind the bush encroachment, in particular, climatic trends. However, encroachment did not relate directly to rainfall and temperature trends. We also speculate on the effects of herbivory and fire, as well as rising atmospheric CO_2 concentrations and its effect on C_3 and C_4 plants. We suggest that increasing atmospheric CO_2 concentrations could be the overriding driver of woody plant encroachment in our study area, with other drivers, such as rainfall, temperature, fire, herbivory and land use, playing a modifying role.

Key words: Remote sensing, aerial photographs, CO_2, shrub encroachment, bush encroachment, woody plant encroachment, rainfall, temperature, land use

1.   Introduction

Remote sensing techniques offer a means for monitoring environmental process. Coupled with geographic information systems (GIS), remote sensing greatly enhances our understanding and predictive ability of interactions on a landscape scale (Wilkinson 1996; Kadmon and Harari-Kremer 1999; Browning, Archer, and Byrne 2009) and has increased in popularity and effectiveness as a tool for interpreting the environment (e.g. Saltz et al. [1999]; Hudak and Wessman [2001]; Ward [2004]; Adjorlolo et al. [2012]).

Woody plant encroachment (also known as shrub or bush encroachment) into grasslands and savannas has become a global phenomenon (Archer, Schimel, and Holland 1995; Moleele et al. 2002; Kraaij and Ward 2006). Communities that rely on wood for their everyday needs may regard this as beneficial (Shackleton, Shackleton, and Cousins 2001; Dovie, Shackleton, and Witkowski 2002; Twine 2005). However, woody plant encroachment into savannas with the concomitant loss of biodiversity has great socio-economic implications (Grossman and Gandar 1989; Wigley, Bond, and Hoffman 2009; Ward 2011).

There are a number of possible causes of bush encroachment.

1. The most widely cited cause is heavy grazing, which may reduce tree:grass competition for soil moisture (Kraaij and Ward 2006; Ward and Esler 2011) and will also reduce fuel loads, resulting in bush encroachment (Roques, O'Connor, and Watkinson 2001; Archibald et al. 2005).

2. An increase in annual rainfall may reduce competition between woody plants and grasses for soil moisture (see e.g. O'Connor [1995]; Kraaij and Ward [2006]), enhancing tree recruitment. It has also been noted that, in arid and semi-arid savannas, an increase in rainfall events or intensity (Kraaij and Ward 2006; Kulmatiski and Beard 2013) without a corresponding change in annual

rainfall may also enhance seedling establishment

3. The absence of fires may also promote bush encroachment (Higgins, Bond, and Trollope 2000). Contrastingly, fires may create space for trees to establish which may result in increased tree encroachment (Ward 2005). A decrease in mean annual rainfall may result in reduced grass cover, thereby reducing the fuel load necessary for the hot fires that inhibit bush establishment (see e.g. Trollope [1974]; Higgins, Bond, and Trollope [2000]; Staver and Levin [2013]). Another factor that may cause a change in the probability of bush encroachment is the presence of roads. Roads may be considered effective firebreaks (see e.g. Syphard, Clarke, and Franklin [2007]). By interrupting the spread of fires, roads may indirectly be a factor in bush encroachment. However, fires may jump roads, even major motorways (Syphard, Clarke, and Franklin 2007). In South Africa, roads do not necessarily inhibit the spread of fires (pers. obs.).

4. Increasing ambient temperatures may also increase woody plant growth rates and recovery rates after fire damage (Wakeling, Cramer, and Bond 2012). Similarly, absence of frost may increase survival of tree seedlings and lead ultimately to encroachment (Ben-Shahar 1993; Holdo 2006).

5. Soil nutrients, which are often linked with soil structure (see e.g. Britz and Ward [2007a]) also play a part in the tree:grass ratio of savannas. Low nitrogen levels reduce grass biomass which in turn benefits tree seedling recruitment (see e.g. Kraaij and Ward [2006]; Sankaran et al. [2008]; Cramer and Bond [2013]).

6. Land use patterns may also affect encroachment by trees. For example, Hardin (1968) considered that when land is held communally (where no

individual privately owns land), individuals will exploit the land to his/her maximum profit, regardless of the cost to the rest of the community. It is, therefore, considered that under communal pastoralism, bush encroachment may be exacerbated by the heavy stocking rates frequently employed there. This view is, however, contested by authors such as Ellis and Swift (1988), Ward et al. (1998) and Benjaminsen et al. (2006).

7. The increase in atmospheric CO_2 concentrations is attracting much attention with regard to bush encroachment. It has been shown that higher CO_2 concentrations enhance photosynthetic rates of C_3 plants (shrubs and trees) (see e.g. Ehleringer et al. [1991]; Morgan et al. [2007]; Bond and Midgley [2012]). With a predicted increase of atmospheric CO_2 to 600 μmol/mol by the end of this century (Morgan et al. 2007), one could expect an increase in C_3 shrubs as a result of improved photosynthetic rates and of allocation of extra carbon to roots (Kgope, Bond, and Midgley 2009) or to carbon-based defence mechanisms (Ward 2010).

In our study, we investigated the change in vegetation in northern KwaZulu-Natal, South Africa. The region has been classified as grassland and open savanna (Mucina and Rutherford 2011) and is extensively used for cattle and game ranching. Immediately after the Anglo-Zulu War of 1879, photographs were taken of the battle sites, in particular Fugitives' Drift, Isandlwana and Rorke's Drift. These photographs, when compared with the same landscape today, demonstrate how the land cover has modified from open savanna and grassland to closed and encroached savanna and grassland (See Figure 3.1(*a*), (*b*) and (*c*)). We wished to measure the changes in the intervening years and to ascertain whether this had occurred at the landscape scale. To this end, we used multi-temporal sets of aerial photographs taken of the area between 1944 and 2005. After processing the photographs, we

classified the observed changes manually as percentage woody cover (see also O'Connor and Crow [1999]; Roques, O'Connor, and Watkinson [2001]; Verheyden et al. [2002]; Corrigan et al. [2010]; Wigley, Bond, and Hoffman [2010]; Ward, Hoffman, and Collocott [2013]). We predicted the following: 1) there is a unidirectional trend towards increased woody cover between 1944 and 2005; 2) the phenomenon occurred over a large scale; 3) we expect the driver/s of this phenomenon to be a consequence of a change in rainfall, temperature trends and land use.

2.   Study area

The study area is in northern KwaZulu-Natal, South Africa, 35 km south-east of Dundee (28.10° S; 30.24° E). The four study sites or areas of interest are about 6 160 ha in extent: Fugitives' Drift (28.23° S; 30.36° E), Isandlwana (28.21° S; 30.39° E) and two sites at Rorke's Drift (28.21° S; 30.32° E). The terrain is rugged, with river gorges and deep erosion gullies. The Umzinyathi River flows through the area with several tributaries draining into it. Altitude varies from 900 m to just over 1330 m. The soils are generally shallow and eroded (Rienks, Botha, and Hughes 2000). Parent material is sandstone and Ecca shales, with dolerite outcropping (Van der Eck, MacVicar, and de Villiers 1969). Rainfall is seasonal, with most of the rain falling during the summer months (October – March). Mean annual precipitation is 705 mm, as recorded by the weather station at Isandlwana, which operated from 1933 to 1972. Average daily maximum temperature is 25°C, with January and February being the hottest months. Average daily minimum temperature is 9°C. June and July are the coldest months.

The study site at Fugitives' Drift is 77 ha in extent and is on the north bank of the Umzinyathi River, within the Skubudu valley. It falls within the savanna biome known as Thukela Thornveld (Mucina and Rutherford 2011). The altitude ranges from 900 m to 1060 m. The area is partly managed by Ezemvelo KwaZulu-Natal Wildlife, a provincial conservation body. As at Isandlwana, burning is carried out every two to three years, depending on fuel load. The rest of the area is communally used by isiZulu-speaking

subsistence (communal) farmers. Fires are generally accidental and at no set timing. In the
mid-1980s, the community was removed from the entire valley, ostensibly to be closer to
amenities such as schools and clinics. Cattle, goats and wild herbivores, such as plains zebra
Equus quagga burchelli, impala *Aepyceros melampus*, kudu *Tragelaphus strepsiceros* and
red hartebeest *Alcelaphus buselaphus* are present in small numbers.

The site at Isandlwana is described as KwaZulu-Natal Highland Grassland (Mucina
and Rutherford 2011). The area of study is 108 ha in extent. Altitude of the study site ranges
from 1200 m to 1330 m. A large free-standing sandstone outcrop, from which the area
derives its name, runs north-south across the centre of the study site and rises to 1330 m.
There is evidence of old cultivated lands in the western portion of the site which have been
fallow since the mid-1980s. In 1985 the area was declared a reserve and was fenced. It is
managed by Ezemvelo KwaZulu-Natal Wildlife. Block burning is practised every two to
three years, depending on fuel load (Ngwenya 2010). Community members are still
permitted to graze their livestock there, but only at the end of summer (Ngwenya 2010).
There is no control as to how many livestock use the area. Wild herbivores, such as impala
and zebra, are also present.

At Rorke's Drift we studied two areas: a) the communally held rangeland farmed by
isiZulu-speaking subsistence (communal) farmers (231 ha); and b) commercial rangeland
(142 ha). Altitude ranges from 1060 m (communal rangelands) to 1240 m (commercial
rangelands). In the communal rangelands, the grasslands are classified as KwaZulu-Natal
Highland Thornveld and iNcomé Sandy Grassland (Mucina and Rutherford 2011). There is
no restriction on the number of animals that graze on land under communal ownership. The
area is burned every year. The commercial rangelands are considered Northern KwaZulu-
Natal Moist Grassland (Mucina and Rutherford 2011). Burning occurs every three years on a
rotational basis (H. de Wet, pers. comm. 2012).

3.   Data acquisition and preparation

Aerial reconnaissance flights have been conducted in the area since 1944 at approximately 10-year intervals. Six sets of panchromatic aerial photographs taken during these flights were obtained from the Chief Directorate of National Geo-spatial Information, Mowbray, South Africa. The flights were flown in winter (May-August), which is the dry season. The scale of the photographs varied between 1:20 000 and 1:50 000 (see Table 3.1). Most of the photographs had been captured on film, except for those taken in 2005, which were digital.

The set of photographs taken in 2005 was supplied already processed and georeferenced, using a 1:50 000 topographical map (2830BC South Africa). Hence, no further preparation of these photographs was required. This composite set was, therefore, used to georeference the remainder of the photographs. There was a large degree of variation in brightness and contrast among the other photographs, even among those taken during the same flight. Using Adobe Photoshop CS$^{®}$, a photographic editing suite, we achieved limited success in smoothing out the variation. We further processed the photographs, using ArcGIS Desktop 10$^{®}$. We mosaicked each set of photographs to create a single composite image for each time set. Each composite set of images was then resampled to equalize pixel size. All the images were georeferenced using the composite 2005 satellite image as the base layer (see Hughes *et al.* [2006]). Greatest accuracy was achieved when using the spline transformation method. This meant a minimum of 10 ground control points (GCPs). We found there was an optimum number which varied for each image and which was between 40 and 100 GCPs, depending on the degree of the original distortion of the image. If too many GCPs were used, the positional error increased, resulting in further distortion.   Because we had visited the area frequently, we could recognise permanent features on the images – such as distinctive rocks, buildings (e.g. the corner of the church that had been built in 1882) and stone cattle pens. These features were chosen as GCPs.   We then clipped areas of interest

from the composite images for analysis.

We were interested in percentage change in woody cover and not in absolute values. Thus, we used manual classification based on vegetation structure, i.e. a comparison of percentage woody cover present. Generally, the changes were in the form of increases or decreases in bush clump size, which were clearly discernible from the herbaceous layer. We placed 50 m $\times$ 50 m grids over the areas of interest and estimated percentage woody cover within each grid cell, based on pixel darkness and shape of object. The percentage difference in woody cover between sequential composite photographs was ranked (Table 3.2) (see Scanlan and Archer [1991]; Wigley, Bond, and Hoffman [2009]; Ward, Hoffman, and Collocott [2013]). We expressed the number of each ranked value of each grid cell in each area of interest as a percentage of the total number of grid cells within that area of interest. We determined that the threshold for shrub size detection in our aerial photographs was 2.9 m^2. We identified 11 small shrubs in the 2005 images and located and measured the shrubs in the field. We found that the mean minimal detectable size was 2.88 m^2 (SD = 1.09). Robinson, Van Klinken, and Metternicht (2008) and Browning, Archer, and Byrne (2009) determined the threshold to be 2.9 – 3.3 m^2 and 3.8 m^2 respectively. As our measurements were done eight years after the last aerial photographs had been taken, detection threshold may well be slightly lower than 2.9 m^2.

Rainfall and temperature data for the area were obtained from South African Weather Service, Talana Museum (Dundee) and the Agricultural Research Council. As none of the data received from the various weather stations were complete, we combined the data from Dundee Police Station and Dundee Research Station which gave us the longest rainfall record that was available for the area: 1901 to 2006, albeit with a 7-year gap from 1954 to 1961. Temperature data ran from 1973 to 2011.

We performed a linear regression analysis on rainfall data to establish whether there

was a long-term change in mean annual precipitation. To ascertain whether there had been any change in mean annual precipitation, we compared the amount of rain that fell during the period from 1901 to 1922 with that which fell during the period from 1985 to 2006 by performing a two-tailed t-test, having first established normality of the data and equality of variance. We believed this was meaningful because there is a 20-year quasi-periodic oscillation in South African rainfall patterns (Dyer and Tyson 1977; Gertenbach 1980; Tyson 1980). The Standardized Precipitation Index (SPI) was also calculated from the combined rainfall data (see Gordijn, Rice, and Ward [2012]; Russell and Ward [2013]). SPI was developed to monitor drought conditions (Hayes et al. 1999), but was also successfully used for wet conditions (Seiler, Hayes, and Bressan 2002). This formula is obtained by dividing the total annual precipitation minus the long-term mean precipitation by the standard deviation in total annual precipitation (see Yurekli and Anli [2008]). We extracted the number of days per year when minimum temperatures were less than 13°C (non-growth days), which is the minimum required for plant growth (Wakeling, Cramer, and Bond 2012). We also extracted the number of days per year that were less than freezing (0°C) as frost can have a deleterious effect on woody species (Silberbauer-Gottsberger, Morawetz, and Gottsberger 1977; Brando and Durigan 2005; Holdo 2006; Coop and Givnish 2007; Wakeling, Cramer, and Bond 2012). We performed two-tailed t-tests on non-growth days between 1973 – 1999 and 2000 – 2012 and on frost days between 1975 – 2000 and 2000 – 2012 (Russell and Ward 2013).

4.   Results

Bush recruitment and increased canopy cover were evident at all the study sites except between 1973 and 1981 (Figures 3.4 (*a*) – (*d*)) when there was a marked decrease. Maximum equilibrium woody cover is reached when tree density reaches 40% in mesic savannas (Roques, O'Connor, and Watkinson 2001) and 31% in semi-arid savannas (Meyer et

al. 2007) (see also Staver, Archibald, and Levin [2011]). Where woody cover exceeded 40% in our study sites, we deemed the area encroached (see also Meyer et al. [2007]) and rate of recruitment will be low.

At Fugitives' Drift, 38% of the area was already encroached by 1944 (Figure 3.3) i.e. shrub cover was > 40%. Woody recruitment and canopy cover increased dramatically between 1944 and 1964 (Figure 3.2 (a) (i) – (ii) and Figure 3.4(*a*)). Although woody cover continued to increase in subsequent years, the aerial photographs (Figure 3.2 (a) (iii) – (vi)) showed that most of the change was the result of bush thickening (= increased density) within the bush clumps (an increase in size and number of shrubs), rather than from further recruitment into open spaces. The increases in bush clump size gradually decreased as bush clump density increased (see also Roques, O'Connor, and Watkinson 2001). By 2005, 74% of the area was encroached.

At Isandlwana, encroachment was slow, with only 2% encroached in 2005 (Figure 3.3) where shrub-cover was > 40%, although there has been a gradual increase in woody cover since 1944, particularly between 1944 and 1964 and again between 1981 and 1991 (Figure 3.4(*b*)). Most of the changes occurred on the western side of the mountain. On the eastern side of the mountain, aerial photographs showed that, from 1964 (Figure 3.2 (*b*) (ii)) onwards, small increases of woody invasion occurred only along the steep lower slopes of the mountain. Once the trees were established, most of the increase was due to thickening of bush clumps, rather than further recruitment into the grassy plain below the mountain (Figure 3.2 (*b*) (ii) – (vi) and Figure 3.4 (*b*).

About 6% of the communal rangelands at Rorke's Drift were encroached in 1944 (Figure 3.3), followed by a slow steady increase in woody cover (Figure 3.4(*c*)). By 2005, 20% of the area was encroached. The aerial photographs (Figure 3.2 (*c*) (i) – (vi)) showed a steady increase in thickening of bush clumps in the study sites, rather than further recruitment

into open grassy areas. The earlier aerial photographs of the commercial rangeland show only small patches of shrubs, particularly in the stream beds (Figure 3.2 (*d*) (i) – (iii)). Woody recruitment into the open grassland was slow, but steady. From 1981 onwards (Figure 3.2 (*d*) (iv – vi)), the increases in woody recruitment were dramatic (Figure 3.4(*d*)). Woody encroachment (where shrub cover was > 40%) increased from 0 to 9% of the study site between 1981 and 2005 (Figure 3.3).

Rainfall

Regression analysis of rainfall figures showed a decrease in mean annual precipitation. The two-tailed t-test confirmed that the reduction in mean annual precipitation between the periods 1901 to 1922 and 1985 to 2006 was significant ($t_{(40)} = 2.021$, p = 0.0002). Mean annual precipitation for the two periods was 942 ± 142 mm and 754 ± 160 mm, respectively. SPI also demonstrated that the first half of the 1900s was wetter than the second half (Figure 3.5). There were three extremely wet years and three very wet years between 1901 and 1952 and one year of extreme drought. Between 1961 and 2006, there was one very wet year and three years of severe drought. There were no extreme events during this period (see Russell and Ward [2013]).

Temperature

The mean ambient temperatures increased between 1973 and 2012. Two-tailed t-tests on the temperature data showed a significant decrease in non-growth days (minimum temperature < 13°C) between 1973 and 1999 and between 2000 nd 2012 ($t_{(31)} = 14.456$, p < 0.001) (mean number of days: 239 and 195, respectively). Frost days also decreased significantly ($t_{(31)} = 3.269$, p = 0.003) from a mean number 23 to 15 days per annum (see Russell and Ward [2013]).

5.   Discussion

Landscape ecology has a temporal dimension (Gillson 2009) and a knowledge of the past helps predict the future. Historical aerial photographs have been successfully used to monitor environmental change and they provide a valuable source of long-term patterns and rates of change (Kadmon and Harari-Kremer 1999). Initially, aerial photographs were merely examined for general information. However, geographic information systems (GIS) software has made aerial photographs more accessible. Using GIS, images can be preprocessed before being manually delineated for analysis (see e.g. Johnston and Naiman [1990]; Simpson et al. [1994]; Turner et al. [1996]). Many studies now use computerized classification of vegetation based on pixel darkness (see e.g. Carmel and Kadmon [1998]; Hudak and Wessman [1998]; Corrigan et al. [2010]), although for certain applications, manual delineation and vegetation classification are still appropriate (see e.g. Eckhardt, Van Wilgen, and Biggs [2000]; Britz and Ward [2007a]; Puttick, Hoffmann, and Gambiza [2011]). Remote sensing has been successfully used in the South African context to study bush encroachment (e.g. Hudak and Wessman [1998]; Britz and Ward [2007a]; Puttick, Hoffman, and Gambiza [2011]).

The success of change detection techniques depends on the accuracy of the preprocessing of the photographs. Hughes, McDowell, and Marcus (2006) found that only eight GCPs were necessary to accurately georeference aerial photographs. They do, however, make the point that the landscape in their study was relatively flat. We found that the number of GCPs required was much higher and depended on relief and radial tilt of the camera (see Kadmon and Harari-Kremer [1999]). Geometric accuracy was not good due to the heterogeneity of the topography in our study area and the degree of distortion as a result of radial tilt in the images. This could not be corrected by increasing the number of GCPs as this created further distortion. Consequently, pixels in one image did not always correspond

to the same ground area in the corresponding image. Deep shadows or patches of burned vegetation also obscured detail.

Preprocessing also required correction for excessive brightness and contrast between aerial photographs and also within the same photograph (see e.g. Carmel and Kadmon [1998]; Hudak and Wessman [1998]). Our aerial photographs were highly variable with regard to the levels of brightness, with patches of high reflectance and areas of deep shadow which were difficult to smooth out without losing detail or to avoid altogether. Burned patches also presented similar problems. This, together with the difficulties we experienced with geometric accuracy, made it impracticable to use change detection techniques and we, therefore, used manual inspection and classification of the images. Despite these limitations, the patterns and rates of changes in woody cover were clearly observed and quantified.

Rainfall

Gordijn, Rice, and Ward (2012) have demonstrated that woody cover increases with increased rainfall (see also Bond, Midgley and Woodward [2003]; Murphy and Bowman [2012]). Gordijn, Rice, and Ward (2012), working at a site close to our study area, also showed that, while the intensity of low-magnitude rainfall events decreased, the increase in average annual rainfall was the result of an increase in the intensity of high-magnitude rainfall events (> 20mm). Kulmatiski and Beard (2013) describe a similar phenomenon in their study, although overall average annual rainfall did not increase. Roques, O'Connor, and Watkinson (2001) have also noted that, at high mean annual rainfall, the rate of woody plant recruitment was high when woody cover was initially low and that the rate of recruitment declined as cover increased. This, initially, appears be the case in our study area. From 1901 to 1953 there were a number of years of above-average rainfall and there was woody recruitment and increased canopy cover in all our study sites. Thereafter, woody cover continued to increase, but at a reduced rate, except in the commercial rangelands at Rorke's

Drift, where dramatic woody recruitment continued, despite the reduction in mean annual rainfall. Although Isandlwana is no longer under communal ownership, the area is still heavily grazed by domestic livestock, as are the communal rangelands at Rorke's Drift. There is only limited woody recruitment at both these study sites, although an increase in canopy cover is evident.

From the 1960s onwards, mean annual precipitation decreased significantly throughout the study area. The reduction in soil moisture should inhibit woody recruitment (Sankaran, Ratnam, and Hanan 2008) and, in drought years, even cause shrub mortality (Scanlan and Archer 1991; Roques, O'Connor, and Watkinson 2001). Sankaran, Ratnam, and Hanan (2008) stated that bush encroachment was driven by soil moisture availability when the average annual rainfall ranged between 200 mm and 650 mm. Once mean annual rainfall exceeded 650 mm, disturbances such as fire and herbivory were required to maintain an open structure to savannas (see also Bond, Midgley, and Woodward [2003]; Sankaran et al. [2005]). Higgins, Scheiter, and Sankaran (2010) suggested that the threshold below which soil moisture controls bush encroachment is a mean annual rainfall of ~820 mm. In our study area, from 1964 onwards, average annual rainfall declined from 942 mm to 754 mm. This amount is very close to the threshold for African savannas that marks the transition from a soil moisture-driven to a disturbance-driven tree:grass ratio (Sankaran et al. 2005; Higgins, Scheiter, and Sankaran 2010). Because there was a decline and not an increase in mean annual rainfall, this suggests that soil moisture was not the overall driver of the observed increases in woody cover in our study area.

Disturbance can take the form of extreme climatic events, such as extremely wet seasons or as seasons of extreme drought, in addition to fire or herbivory (e.g. Denny et al. 2009). Tree recruitment in arid and semi-arid savannas tends to be episodic (Archer 1989; Kraaij and Ward 2006), often in response to a drought followed by several very wet seasons

(Zimmermann, Joubert, and Smit 2008). February et al. (2013) showed that growth rates of tree saplings grown with grass were retarded with increasing soil moisture because of the increasing competitive pressure from grasses. By implication, saplings recruit into adult trees at a time of drought, when competition from the herbaceous layer is low (February et al. 2013). In our study area much of the bush encroachment was a result of bush clump thickening where grasses are limited by shading (Ludwig et al. 2001) or occurred where the soil was rocky (see e.g. Breebaart et al. [2001]; Britz and Ward 2007b]) and where the herbaceous cover was already low. Where new bush clumps had formed, ground inspection suggested that isolated trees had established in rocky outcrops. Once established, trampling of the surrounding area by animals and competition for light may have prevented a dense layer of grass from establishing. It seems, therefore, unlikely that extreme climatic events were driving the observed bush encroachment.

Between 1973 and 1981, the aerial photographs (Figure 3.2 (*a*) (iii) – (iv), (*b*) (iii) – (iv), (*c*) (iii) – (iv) and (*d*) (iii) – (iv) showed a marked reduction in woody cover at all the sites, although the decrease was less marked at Fugitives' Drift (see also Figure 3.4 (*a*) – (*d*)). Mean annual precipitation for the seasons of 1978/79 and 1980/81 was within the 'near normal' range (Figure 3.5), although below the overall mean annual precipitation. The 1979/80 season was a dry season and ranked as a 'moderate drought' (Figure 3.5). This would account for the dramatic reduction in woody cover in the 1981 photographs. While the drought may not have been severe enough to result in shrub morality, shrubs may have lost sufficient above-ground biomass to be inconspicuous from the air. Conditions at Fugitives' Drift may have been less severe, being sheltered in the Umzinyathi River gorge and, therefore, the reduction in woody cover was less dramatic.

Nutrients

Soil structure influences nutrient availability (Breebaart et al 2001; Britz and Ward 2007a).
The effect of an increase in soil nutrients is to suppress tree seedling establishment through
an increase in grass biomass because additional nutrients do not affect savanna tree growth
rates (Kraaij and Ward 2006; Britz and Ward 2007b; Van der Waal et al. 2009; Cramer and
Bind 2013). However, in our study site the increase in woody cover suggests that soil
nutrients were not affecting the tree:grass ratio.

Temperature

Wakeling, Cramer, and Bond (2012) speculated that temperature may determine the
boundary between savanna and grassland. The observed decrease in the number of non-
growth days and frost days in our study area was consistent with an increase in woody cover
(O'Connor 1995; Nemani et al. 2003; Wakeling, Cramer, and Bond 2012). More robust and
taller tree seedlings would be more resistant to frost damage (Silberbauer-Gottsberger,
Morawetz, and Gottsberger 1977; Holdo 2006) and would aid these plants in escaping the
fire/browse trap (Trollope 1974; Van Langevelde et al. 2003; Midgley, Lawes, and
Chamaillé-Jammes 2010). The longer growing period and milder winters could mitigate the
below-average annual rainfall. The Fugitives' Drift study site differed from the other sites,
being at a lower altitude and sheltered in the gorge. Ambient temperature may, therefore, be
slightly higher, which might have been the reason woody cover was highest at this site. A
localized effect of temperature on vegetation at Isandlwana is also possible. It is possible that
the western flanks of Isandlwana mountain are drier and warmer than the eastern flanks (see
e.g. Breebaart et al. [2001]). All the aerial photographs of Isandlwana (Figure 3.2 (b) (i) –
(vi)) show scattered woody cover on the steep western slopes of the mountain and no shrubs
to the east of the mountain. However, the dramatic increases in woody cover and
encroachment in the commercial rangelands started well before the reduction in non-growth

and frost days (see Ward, Hoffman, and Collocott [2013 submitted]), which suggests that the increase in ambient temperature has not had a major influence on bush encroachment.

Effects of livestock density

Herbivory by domestic livestock appears to have had little impact on bush encroachment in the study area. It is probable that there were far more livestock at Fugitives' Drift prior to the 1980s. Heavy grazing could have encouraged woody recruitment by reducing competition between grasses and shrubs for soil resources, such as water (Walker et al. 1981; Van Langevelde et al. 2003; Ward, Wiegand, and Getzin 2013). The reduction in the number of livestock with the relocation of community members at Fugitives' Drift, combined with decreasing rainfall should, therefore, have resulted in a decrease in woody cover. This was not the case. At Isandlwana, earlier field cultivation in the western portion of the study site would have kept the area clear of shrubs. There is no evidence of field cultivation on the eastern side, but being grassy, open countryside it is likely that most of the livestock grazed here. Yet, despite heavy grazing, there has been very little woody recruitment on the eastern side of the mountain, contrary to prevailing theories of the connection between heavy grazing and initiation of bush encroachment (e.g. Walker et al. [1981]). Once the area was fenced off from the community in the 1980s, the human activity to the west ceased and may account for the relatively rapid increase in woody cover sometime between 1981 and 1999. The communal rangelands at Rorke's Drift also exhibit a steady increase in bush clump thickening in the study sites, rather than further recruitment into open grassy areas, despite heavy grazing. Fence-line contrasts have demonstrated the effect of heavy grazing on vegetation cover (see e.g. Todd and Hoffman [1999]; Roques, O'Connor, and Watkinson [2001]), but the few fences that have been erected in our study area do not hamper the movement of livestock to any great extent.

Land use and wood harvesting

In arid areas, very little difference in plant cover between communal and commercial rangelands was recorded (Ward et al. 1998, Hoffman and Rohde 2007; 2011), except in areas where there had been previous cultivation (Hoffman and Rohde 2007; 2011). Other studies in mesic savannas showed that, while grass cover decreased and woody cover increased across all three different types of land use, the changes were less marked in the communal rangelands (Wigley et al. 2009, Wigley et al. 2010). Our study showed that there was bush encroachment across all three land uses: commercial rangelands, communal rangelands and conservation areas, although species composition changed with land use (Russell and Ward 2013) (see e.g. Higgins et al. [1999]). Besides the potential impact of their livestock on the vegetation, rural communities make extensive use of natural resources (Higgins, Shackleton, and Robinson 1999; Twine et al. 2003; Twine 2005). An average rural household uses 3 − 5 tons of fuel wood per annum (Dovie, Shackleton, and Witkowski 2002; Twine et al. 2003). The collection of fuel wood in our study area is declining, not only because community members have been excluded from the Fugitives' Drift and Isandlwana sites, but also because many community members are placing more reliance on paraffin and electricity for their energy needs (pers. obs.). It is likely that, while harvesting of wood had some impact on shrub density (Higgins, Shackleton, and Robinson 1999; Wigley, Bond, and Hoffman 2010; Puttick, Hoffman, and Gambiza 2011), it was probably not significant in our study area. This observation is suggested by the earlier aerial photographs. At a time when community members would have been largely reliant on wood for their fuel needs, woody recruitment was highest.

Fire

Burning regimes in the study sites are not consistent throughout the area. Communal areas are burned every year, while commercial and conservation areas are block-burned every two

to three years. Despite these differences in fire regimes, woody encroachment has occurred in all the sites.

Atmospheric CO_2

Increases in atmospheric CO_2 and the effects on shrub recruitment into grasslands and savannas have attracted much attention (e.g. Polley et al.1997; Bond and Midgley 2000; Kgope, Bond, and Midgley 2009; Ward 2010; Buitenwerf 2012). Atmospheric CO_2 concentrations have risen from pre-industrial concentrations of ~270 μmol/mol at the end of the 1800s (Etheridge et al. 1996) to the current concentration of ~397 μmol/mol (Tans 2013). Savanna grasses in the tropics and subtropics are typically C_4 grasses (Sage 2004; Bond 2008; Ratnam et al. 2011), while the woody component of savannas has a C_3 photosynthetic pathway (Archer, Schimel, and Holland 1995; Ward 2010). The C_3 pathway becomes more efficient with increasing atmospheric CO_2 concentrations (Ceulemans, Jiang, and Shao 1995; Morgan et al. 2007). C_3 plants also respond to higher CO_2 concentrations with an increase in growth rate and in carbohydrate reserves (Ceulemans, Jiang, and Shao 1995; Bond and Midgley 2000; Kgope, Bond, and Midgley 2009; Ward 2010) and enhanced carbon-based structural and chemical defence mechanisms (Kgope, Bond, and Midgley 2009; Ward 2010). These positive responses in shrubs and trees aid post-disturbance recovery, such as after fire (Bond and Midgley 2000; Bond, Midgley, and Woodward 2003), and assist trees in escaping the fire/browse trap (Schutz, Bond, and Cramer 2009; Wakeling, Staver, and Bond 2011).

6.   Conclusions

Multi-temporal sets of aerial photographs have provided a long-term overview of vegetation change in northern KwaZulu-Natal. There has been a widespread and steady increase in woody cover over 61 years. Less obvious are the causes of the change. Each study site has different parameters, such as vegetation type, altitude, land-use, herbivory and fire regime. However, these local drivers do not appear to have had a significant effect on woody

encroachment or increases in canopy cover. Initially, the response of woody cover to higher-than-average rainfall was as expected, but when average annual rainfall dropped to below the long-term mean, woody cover continued to increase. The response of woody cover to the increase in ambient temperature is as expected, although the timing of the response does not synchronise with this increase, as observed in the commercial rangelands. There must, therefore, be an additional driver. Rising atmospheric CO_2 concentrations have been shown to have a significant impact on the vigour and survival of savanna trees and shrubs (Kgope, Bond, and Midgley 2009). While above-average rainfall may have been the initial driver of bush encroachment into our study area, it is possible that rising CO_2 concentrations may well be the overriding driver, with local drivers tempering the effects of CO_2 to a greater or lesser extent at the various study sites.

Acknowledgements

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Figure 3.1: (*a*). Repeat ground photographs taken at Fugitives' Drift indicate the degree of vegetation change. By 2011, the increase in woody cover had obscured the grave and rocks that were visible in 1879. Bush had also encroached extensively on the opposite hillside. (*b*). Repeat ground photographs taken at Isandlwana. Bush recruitment to the west of the mountain and along the eastern slope is clearly discernible in the photograph taken in 2011. (*c*). Repeat ground photographs taken at Rorke's Drift. Bush recruitment on the northern and western slopes of Shyane is clearly visible. In the foreground there is a mix of *Acacia* and exotic trees. Historic photographs: (*a*) James Lloyd collection, courtesy of KwaZulu-Natal Museum Services; (*b*) courtesy of the Killie Campbell collection; (*c*) John Dunn Collection, courtesy of KwaZulu-Natal Museum Services. Recent photographs: Jennifer Russell

Figure 3.2: (*a*) Aerial photograph of the area of interest at Fugitives' Drift. Location at centre point of photograph: 28° 22′ 38″ S; 30° 36′ 6″ E. Woody plant encroachment (dark pixels) is evident between (i) 1944 and (ii) 1964. From (iii) 1973 bush clumps thicken with only small amounts of recruitment into the open spaces. Total area 77 ha. (*b*) Aerial photographs of the area of interest at Isandlwana. Location at centre of the photograph: 28° 21′ 38″ S; 30° 39′ 01″ E. Gradual bush recruitment (dark pixels) is evident on the western side, while the eastern side of the mountain remained open (light pixels). However, between (iii) 1973 and (iv) 1981 woody cover appears to have reduced, possibly as the result of a prolonged dry period prior to 1981 (see Figure 3.5). Total area 108 ha. (*c*) Aerial photographs of the area of interest within Rorke's Drift communal rangelands. Location at centre of photograph: 28° 20′ 59″ S; 30° 32′ 27″ E. Most of the increase in woody cover in the communal rangelands is due to increases in tree canopy cover (dark pixels). Total area 231 ha. (*d*) Aerial photographs of the area of interest within Rorke's Drift commercial rangelands. Location at centre of photograph: 28° 22′ 04″ S; 30°31′ 19″ E. The increase in woody cover in the

commercial rangelands is due to both increased canopy size and recruitment (dark pixels). Total area 142 ha.

Figure 3.3: A comparison of the increase in bush encroachment (> 40% cover) between 1944 and 2005 in all the areas of interest. Bars represent the percentage change in shrub cover per 50 m × 50 m grid once the cover exceeds 40%.

Figure 3.4: (*a – d*). Increase in woody cover at Fugitives' Drift, Isandlwana, Rorke's Drift (communal rangelands) and Rorke's Drift (commercial rangelands), respectively, from 1944 to 2005 over five intervals. Tree growth and recruitment was negatively affected by a dry period just prior to 1981. Bars represent percentage change per 50 m × 50 m grid cell.

Figure 3.5: Standardised Precipitation Index (SPI) Values (see Data acquisition and preparation). There are significantly more years of below-average precipitation during the last 40 years than between 1901 and 1954. The events are also less extreme during the last 30 years compared with the events between 1901 and 1954. SPI values are rated as follows: extremely wet = 3; very wet = 2; moderately wet = 1; near normal precipitation = 0; moderate drought = -1; severe drought = -2; extreme drought = -3. The double-headed arrow indicates periods where the records were unreliable and were not included. Because the wet season is over the summer period, the 12 month period was taken from the beginning of August until the end of July each year.

Table 3.1: A list of aerial photographs obtained from the Chief Directorate of National Geo-spatial Information, giving year, month and time of day when the photographs were taken, as well as the original scale. Because this is a summer rainfall area, annual rainfall was calculated from August to July of the following year. The values for rainfall status refer to SPI values. See figure 3.5.

Table 3.2. A summary of the numerical rankings given to the observed percentage change in woody cover between each 50 m $\times$ 50 m grid cell in sequential aerial photographs.

(*a*)

(*b*)

(*c*)

Figure 3.1: Repeat ground photographs taken at Fugitives' Drift, Isandlwana and Rorke's Drift

N

(i) 1944

(iv) 1981

(ii) 1964

(v) 1991

(iii) 1973

(vi) 2005

| 0 | 0.25 | 0.5 | 1 | 1.5 | 2 |
km

Figure 3.2 (*a*): Aerial photograph of the area of interest at Fugitives' Drift.

(i) 1944

(ii) 1964

(iii) 1973

(iv) 1881

(v) 1991

(vi) 2005

N

0   0.25   0.5   1   1.5   2
km
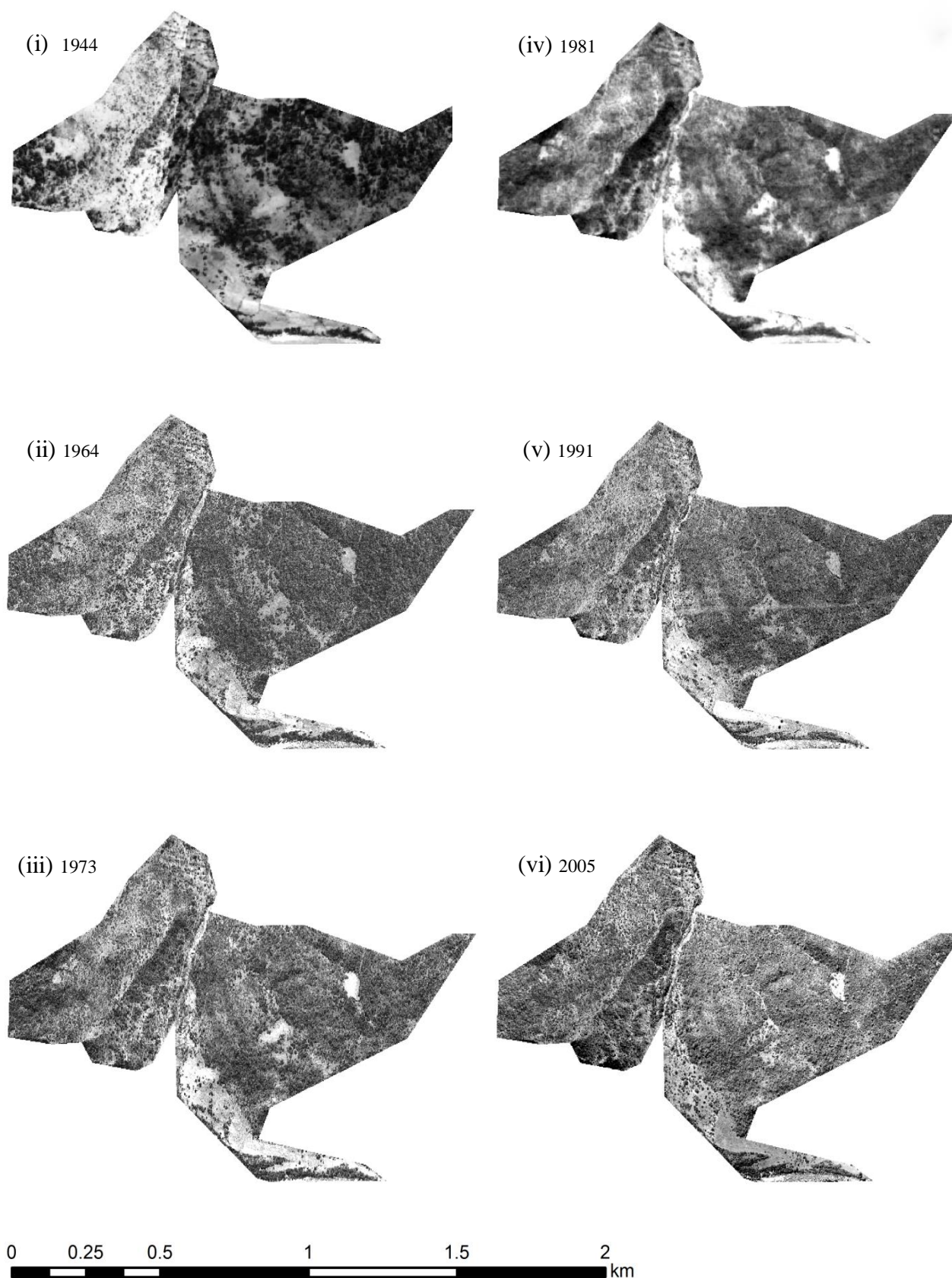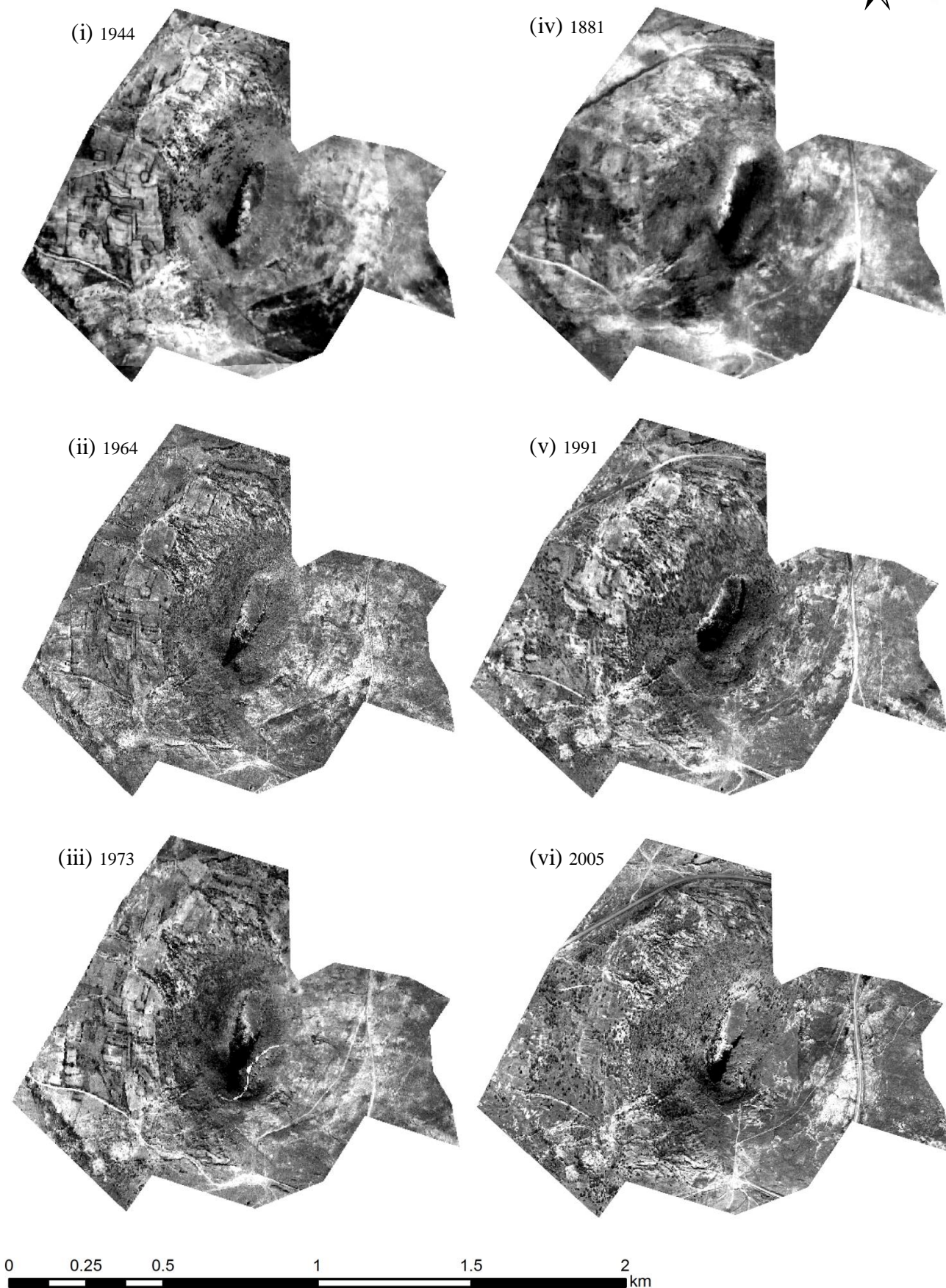
Figure 3.2 (*b*): Aerial photographs of the area of interest at Isandlwana.

N

(i) 1944

(iv) 1881

(ii) 1964

(v) 1991

(iii) 1973

(vi) 2005

0   0.25 0.5   1   1.5   2
km
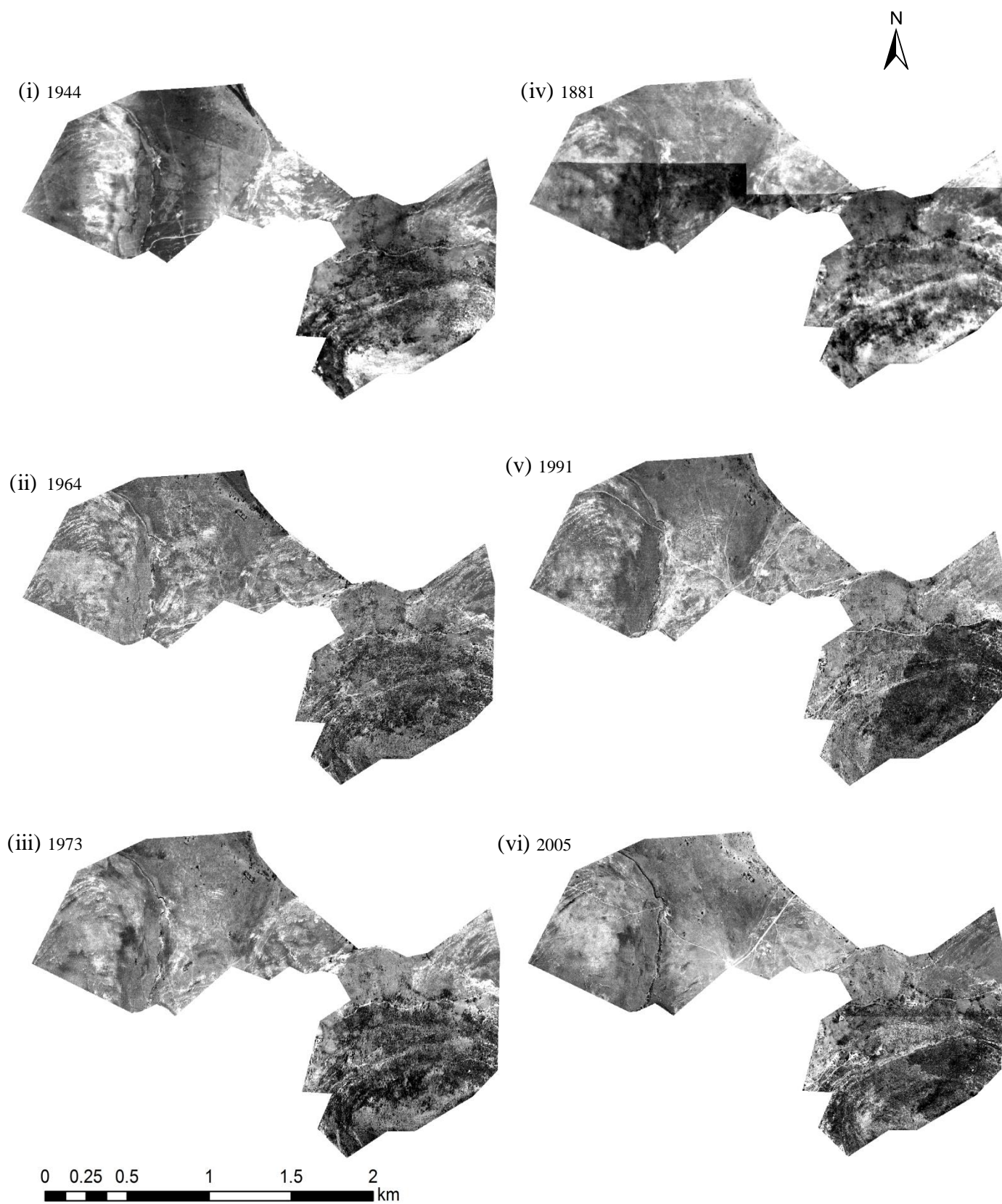
Figure 3.2 (*c*): Aerial photographs of the area of interest within Rorke's Drift communal rangelands.
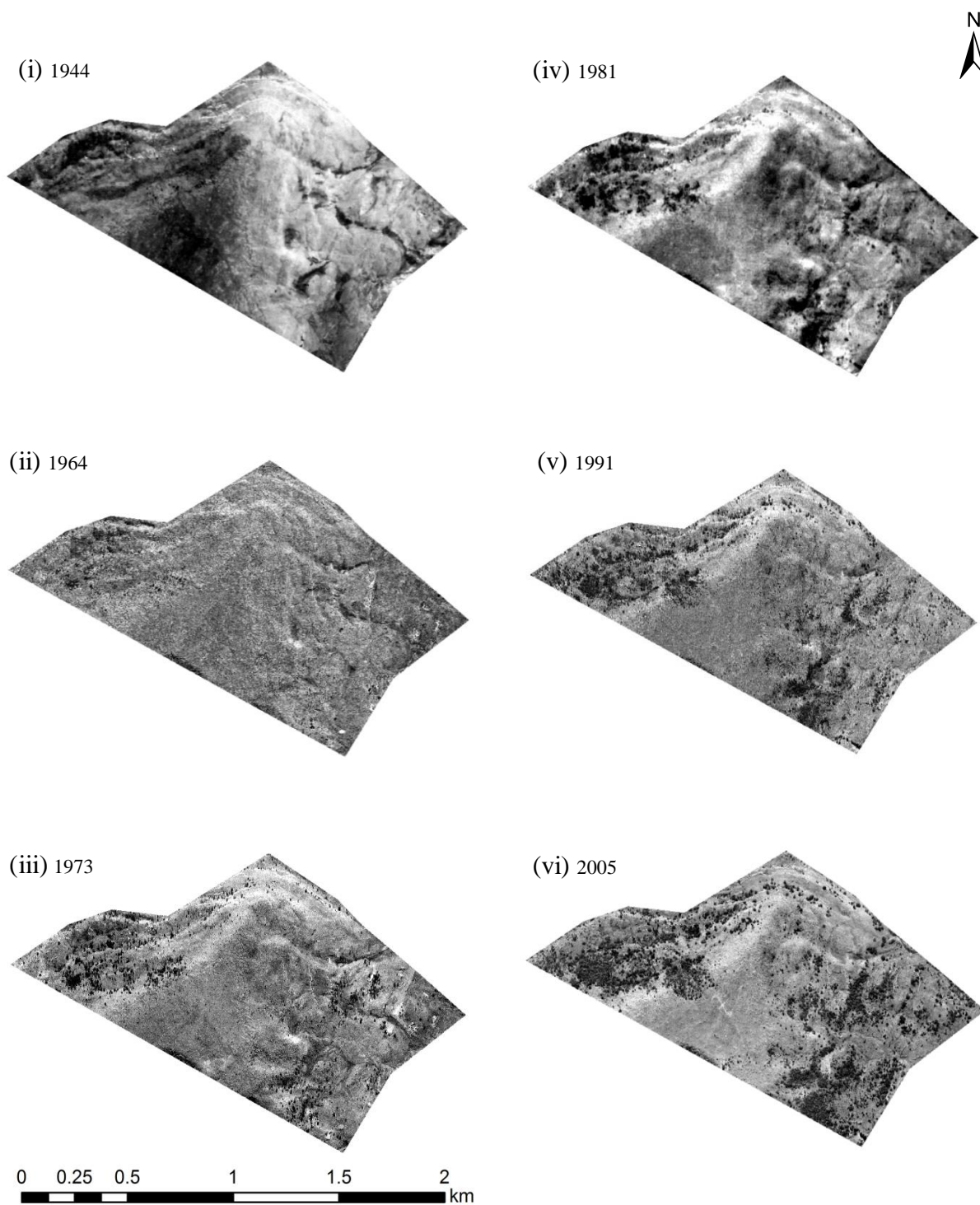
Figure 3.2 (*d*): Aerial photographs of the area of interest within Rorke's Drift commercial rangelands.
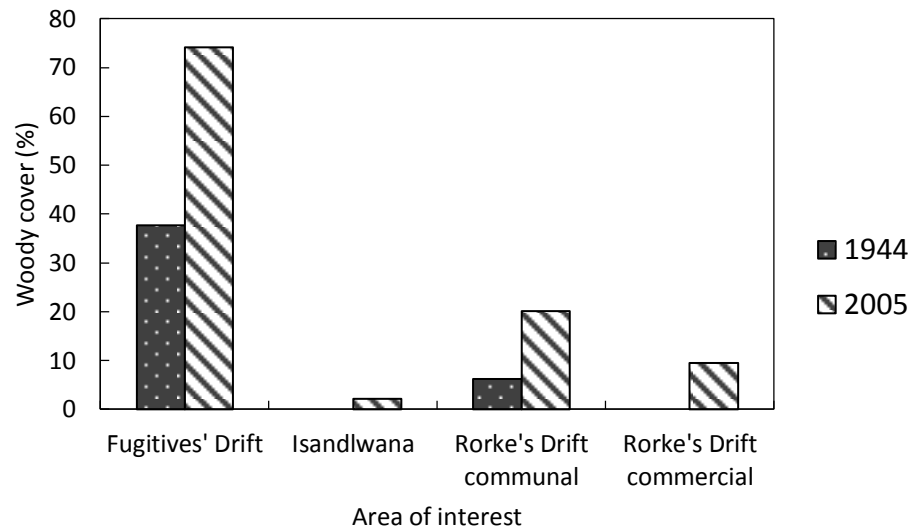
Figure 3.3: A comparison of the increase in bush encroachment (> 40% cover) between 1944 and 2005 in all the areas of interest.

(a)

(b)

Decrease

No change

1-25% increase

26-50% increase

51-75% increase

76-100% increase

(c)

(d)
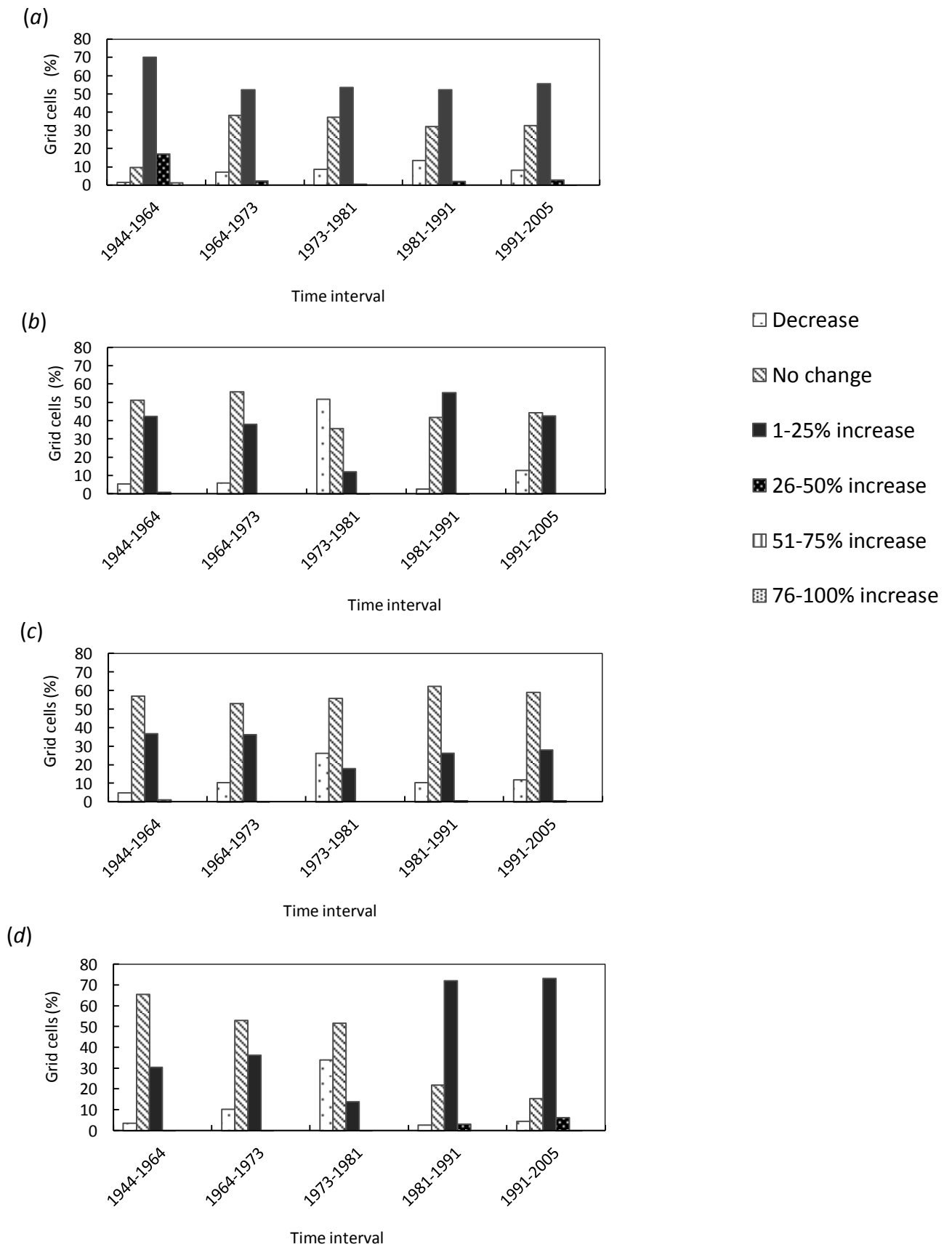
Figure 3.4: Increase in woody cover at Fugitives' Drift, Isandlwana, Rorke's Drift (communal rangelands) and Rorke's Drift (commercial rangelands), respectively, from 1944 to 2005 over five intervals.
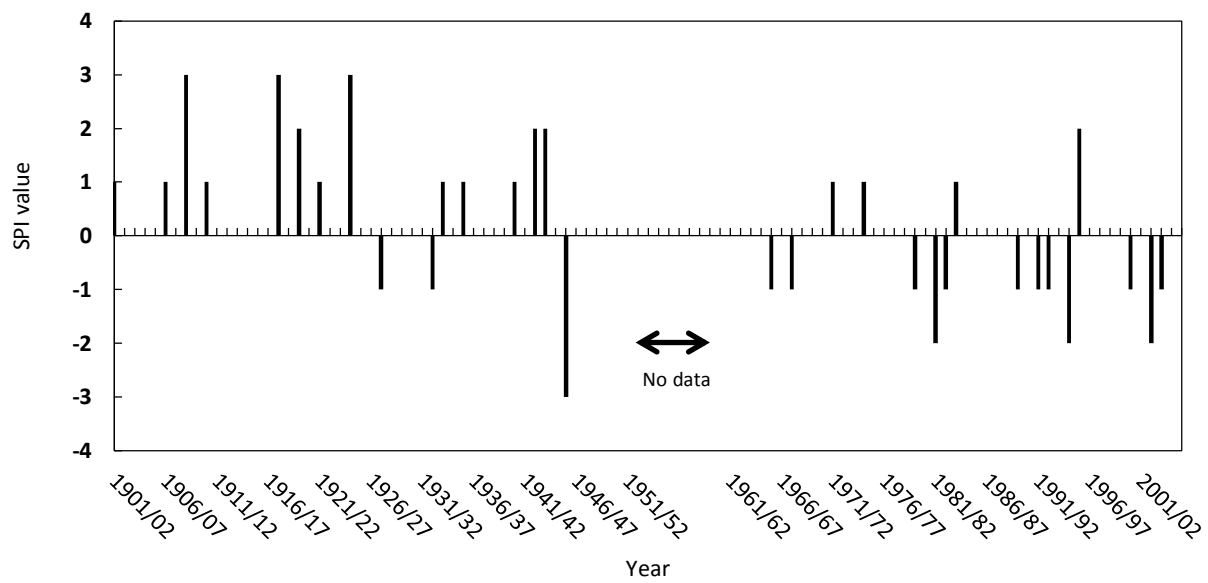
Figure 3.5: Standardised Precipitation Index (SPI) Values.

Table 3.1: A list of aerial photographs obtained from the Chief Directorate of National Geo-spatial Information, giving year, month and time of day when the photographs were taken, as well as the original scale.

Date of photography		Time of day	Scale	SPI value of
year	month	photograph taken	of photography	rainfall status for the year
1944	N/A	N/A	1:20 000	2
1964	April	Mid/late morning	1:40 000	0
1973	June	Early/mid morning	1:50 000	0
1981	July	Midday	1:30 000	0
1991	Aug/Sept	Midday	1:50 000	-1
2005	N/A	N/A	N/A	0

Table 3.2. A summary of the numerical rankings given to the observed percentage change in woody cover between each 50 m $\times$ 50 m grid cell in sequential aerial photographs.

Change in woody cover in each grid cell between sequential aerial photographs	Numerical rank of woody cover change assigned per grid cell
Decrease in woody cover	-1
No change	0
1 - 25 % increase	1
26 - 50 % increase	2
51 - 75 % increase	3
76 - 100 % increase	4

Chapter 4

Communal land use and community members' perceptions on vegetation change

Introduction

Anthropogenic activity plays as much of a role in shaping the landscape as does natural

processes (Nash *et al.* 2006, Hoffman and Rohde 2007). Environmental processes that shape

landscapes include long-term climate change, natural disturbance such as fire, wind, floods,

herbivory, pathogens and pests. In the past, and increasingly so in recent years, ecological

systems have changed under anthropogenic impacts (Foster 2002). Agricultural activity,

such as deforestation (Nash *et al.* 2006), grazing (Foster 2002, Nash *et al.* 2006), cultivation

and terracing (creating step-like platforms for field crops on steep slopes) (Gillson 2009) and

the use of fire and water management (Erickson 2006), have had a massive impact on the

landscape at a local and regional scale. As a result of a history of disturbance, some species

have disappeared (either locally or globally), new species have arrived from other regions,

and the diversity and abundance of organisms have been altered (Foster 2002, Erickson

2006).

In southern Africa, extensive anthropogenic influence on the landscape appears to

have been limited to fires (see e.g. Hall 1984, Bird and Cali 1998) until the arrival of Iron

Age man 1 600 to 1 800 years ago (Maggs 1980, Voigt 1986, West *et al.* 2000). The Iron

Age settlers were semi-pastoralists who arrived in present-day KwaZulu-Natal in two

successive waves from the north (Huffman 1982). They settled in semi-permanent villages in

alluvial flood plains where soils were suitable for the cultivation of crops (Maggs 1980, Voigt

1986). Their need for wood for building, fencing, stock pens and iron-smelting kilns (Maggs

1980) along with grazing needs for their livestock, would have begun to modify their

environment, if only on a local scale (West *et al.* 2000). During the Late Iron Age, human

communities expanded into mixed bushveld and thornveld, as well as the grasslands of the

higher altitudes (Maggs 1980). It is likely that these people would have practised

transhumance, following the seasonal grazing with their flocks and herds (Maggs 1980).

Hardin (1968) proposed a concept which he termed 'the tragedy of the commons'.

The tragedy of the commons occurs when a resource is held in common, such as communal

grazing lands. Each individual will exploit that resource to his/her maximum profit,

regardless of the long-term consequences (Hardin 1968). African pastoral systems have been

strongly criticized as being unproductive, poorly managed and degraded (see e.g. Ellis and

Swift 1988, Rohde *et al.* 2006). They have been described as being maladaptive and

destructive (Ellis and Swift 1988) and as leading to the 'tragedy of the commons'. In the

context of communal rangelands, this will lead to overstocking, overgrazing, bush

encroachment (Rohde *et al.* 2006) and soil erosion (Tapson 1991, Rowntree *et al.* 2004). The

criticism of this paradigm is that it is based on the assumption that African rangelands are at

equilibrium (Ellis and Swift 1988, Benjaminsen *et al.* 2006, Rohde *et al.* 2006). These

potentially stable systems are destabilized by disturbance, such as grazing pressure, but will

return to equilibrium once the destabilizing influences are removed. The paradigm is also

based on the succession model which suggests a predictable and successional trend as plants

replace each other until a climax is reached (Rohde *et al.* 2006). The equilibrium paradigm

also assumes that every system has a certain carrying capacity, based on predictable

biophysical characteristics (Vetter 2003). The assumption is that adherence to a carrying

capacity permits sustainable off-take which maintains the balance between the resource and

resource utilization (Benjaminsen *et al.* 2006, Rohde *et al.* 2006). Ellis and Swift (1988),

Benjaminsen *et al.* (2006), Rohde *et al.* (2006) suggest otherwise: that African rangelands are

non-equilibrial, but persistent. The imposition of a carrying capacity upon such a system is

inappropriate (Benjaminsen *et al.* 2006), because of the unpredictability of the environment. Herd mortality during several years of drought reduces grazing pressure and permits primary productivity on the rangelands to recover (Ward 2003). Pastoralists also, where possible, practice transhumance, removing their livestock from areas which can no longer support them, again allowing the rangeland to recover after heavy utilization (see e.g. Ward 2003, Rohde *et al.* 2006).

Because of the history of land use in northern KwaZulu-Natal and because of the debate regarding the condition of communal rangelands, I interviewed a number of community members living at Fugitives' Drift, Isandlwana, and Rorke's Drift. The object of the survey was to a) determine whether the community members still placed importance on animal husbandry; b) ascertain community members' dependence on woody plants; and c) gain insights into the perceptions of community members with regard to environmental change.

Methods

Study site:

The general study site is in northern KwaZulu-Natal and includes the three battle sites of the Anglo-Zulu War (1879): Fugitives' Drift (28.23^o S; 30.36^o E), Isandlwana (28.21^o S; 30.39^o E) and Rorke's Drift (28.21^o S; 30.32^o E). The Umzinyathi River flows through the study site and marks the boundary between the historic entities of Zululand and Natal. On either side of the river are undulating grasslands and savannas which are scored by deep erosion gullies and tributaries to the Umzinyathi River. Parent material is sandstone and Ecca shales, with dolerite outcropping (Van der Eck *et al.* 1969). Sandstone outcrops rise some 300 m up out of the plains as extensive plateaus. The terrain is rocky and dolerite boulders dominate. Altitude varies between from 900 m to just over 1330 m. Rain falls predominantly in the

summer months, October to March, and the mean annual rainfall is 705 mm. Winters are cool and dry. Winter frost and occasional light snowfalls occur. Average daily maximum temperature is 25 ^{o}C, with January and February being the hottest months. Average daily minimum temperature is 9 ^{o}C. June and July are the coldest months.

The people of the area

The country north of the Umzinyathi River is communal land. In a communal system, land is held by a group of householders, under the authority of a hereditary tribal chief. Individual households have certain non-negotiable rights (Grossman and Gandar 1989, Adams *et al.* 2000). These rights include *inter alia* the right to occupy a homestead, to use land for crops, to graze animals, to have access for gathering fuel, fruits and grass (Adams *et al.* 2000).

The people living in communal areas of KwaZulu-Natal are the descendants of the Iron Age people. Early in the 1800s, Shaka kaSenzangakhona of the Zulu tribe amalgamated the surrounding tribes in, what is now called, KwaZulu-Natal, into a loose political entity (see for e.g. Wylie 2006), which became the Zulu nation. The tribal chiefs were answerable to Shaka and to subsequent Zulu paramount chiefs. By the late 1840s, the Zulu kingdom had been reduced to less than half its original extent by the colonising activities of the European settlers. The British colony of Natal was south of the Umzinyathi and Tugela Rivers and Zululand was to the north. After 1994, Zululand and Natal became one political entity, KwaZulu-Natal, but the historic political structures have, to some extent, remained.

Extensive cattle ranching is still practised on both sides of the Umzinyathi River. The rationale behind maintaining livestock would have been, and still is, for cultural reasons, rather than for financial gain (Grossman and Gandar 1989). Rangeland management is opportunistic (Rohde *et al.* 2006). Drought drastically reduces stock numbers from time to time. In the past, transhumance would have been practised, but now the movement of flocks

and herds is greatly reduced. Goats and, to a lesser degree, sheep are also present. There is

agricultural activity in the form of dry-land crop farming and small hand-irrigated garden

plots. There is limited mechanization in the communal areas and most communal farmers

rely on oxen to plough the soil. Since 1994, electricity has been brought into many

communities. South of the Umzinyathi River, the land is privately owned by commercial

cattle and game ranchers, although at Rorke's Drift, the land owned by the Evangelical

Lutheran Church of South Africa (ELCSA) is managed as communal rangeland.

Survey approach

I interviewed 23 communal farmers living close to the three battle sites and the only

commercial farmer at Rorke's Drift. One member per household was interviewed. The

interviews were semi-structured. Each person interviewed was over 50 years old and had

lived in the area all his/her life. The questions explored issues regarding: 1) number of

animals per household, 2) the benefits derived from keeping stock, 3) the strategies farmers

adopted at times of drought, 4) the requirements for wood, 5) the practice of crop cultivation,

and 6) whether the respondent had noticed any changes in his/her environment (see appendix

1 for detailed survey sheet).

Results

All respondents, but one (who had arrived with his family as a small child), had been born in

the area. Two respondents had never owned livestock and two used to own livestock, but all

had been stolen or had died. The 15 out of 22 respondents reported significant reductions in

numbers of stock (> 50%), mostly due to theft within the last 20 years, or they had simply

"died". All those who owned livestock, kept them "according to customs": as status symbols,

as gifts for children as they come of age, as *lobola* (bride price), for slaughter for special

events, and for *maas* (curdled milk). Hides were used for making thongs. Oxen were used for ploughing. Cattle were only sold in times when cash was urgently required. Herd size for cattle ranged between one and 40; flocks of goats ranged between two and 25. Only one respondent owned sheep. None of the respondents owned donkeys, although donkeys were used as draught animals by other community members.

At Isandlwana, a system of camps (also known as "paddocks") had been introduced in the 1980s. While there was no restriction on the number of cattle kept, restriction was placed on where they were grazed. Some of the respondents from Isandlwana (n = 2/9) noticed that since the adoption of controlled access to grazing, woody shrubs were appearing in what was previously open grassland. Goats and sheep ranged freely, as they were not easily restricted by fencing. At Rorke's Drift, animals wandered at will and respondents said that the number of livestock were originally limited to a maximum of seven beasts per household by the ELCSA. This restriction was lifted in the late 1970s and householders run as many animals as they could manage. Here, too, community members were concerned about the increase of woody shrubs. At Isandlwana and at Rorke's Drift there is a heavy reliance on rainfall to water and feed livestock. In times of drought the springs and water courses dry up, there is no longer any forage and the cattle simply die. No attempt is made to move livestock to areas where there may be resources and no food brought in for the cattle. With the Umzinyathi River nearby, water is always available, even if only stagnant, for those with access to the river. Only one communal livestock owner brought in fodder and licks for his cattle. He was also the only person who owned cattle as a commercial enterprise as well as for cultural reasons. At Fugitives' Drift, very few cattle were evident, either in the communal area or in the conservation area. The respondent interviewed at Fugitives' Drift lived in a private conservancy where he was allowed (by the owner) to keep 12 head of cattle, but no sheep or goats. Most of the herbivores in this area were wild ungulates, including giraffe (*Giraffa*

camelopardalis), and plains zebra (*Equus quagga burchelli*). In the past the area was stocked with up to 200 head of cattle and "many" goats (Mr Mpanza: respondent). In 1991 the area became a conservation area and all of the domestic livestock was removed, except for those that the single respondent was permitted to retain.

Eighteen of the 22 respondents had extensive fields for cultivating maize, ground nuts and pumpkins. Oxen were used to prepare the fields. All of the 18 respondents relied on rainfall, so they planted in the spring and summer only. All said they had not planted extensive field crops during 2012, because of late and insufficient rains, although six respondents also said that the lack of draught animals prohibited planting as they would not have been able to hire a tractor. Four of the six women interviewed had a share in a community garden at Rorke's Drift where vegetables were grown all year round. Water was stored in tanks which came from the nearby stream.

All the respondents used wood for cooking and heating – including those who had electricity (n = 4/22), although electicity was available in all three study sites. One respondent used paraffin in preference to electricity. At Isandlwana some householders (n = 2/9) bought wood from vendors from Isibindi valley (28.25 S; 30.33 E). Candles and paraffin were used for lighting (n = 11/22). Six of the 13 respondents at Rorke's Drift had solar panels, which were used for lighting. The preferred fire wood was *Acacia karroo* and *A. ataxacantha*. *Erythrina latissima* was also used. Two respondents (n = 2/9) at Isandlwana said that there were restrictions on tree cutting, imposed by the local chief. They were only allowed to cut the exotic (Australian) *A. mearnsii* (wattle) in nearby wood lots and not the indigenous trees. However, they could still use *A. sieberiana* for stockades for cattle pens. At Rorke's Drift there were no such restrictions on cutting wood. All wood was harvested nearby by family members. *A. ataxacantha* and *E. latissima* could also be bought from farmers in the Isibindi valley. *A. mearnsii* from a nearby woodlot, that was no longer being

managed and was spreading, was also used by community members at Rorke's Drift, particularly for rafters, fence posts, but also for fire wood. Some of the men (n = 5/22) also used wood for craftwork, such as spoons, meat platters and stools, which were sold as curios. Although wood was still being used for construction of homes, mostly as rafters, the requirement for wood for this purpose was greatly reduced. In the past, a traditional Zulu beehive hut used approximately 2000 saplings for construction (Mr Magubane and Mr Tyler: respondents). However, this style of construction is no longer used, except in very rare instances. Some of the preferred trees for building beehive huts were *Ziziphus mucronata*, *Dombeya rotundifolia*, *Catha edulis*, *Euclea crispa* and *Sclerocarya birrea*. At Fugitives' Drift, no wood harvesting occurred and woody cover had increased. The single respondent at Fugitives' Drift believed that the increase in woody cover was the result of the removal of goats from the area. Although indigenous herbivores had been introduced, most of them were grazing ungulates.

Communal areas around Isandlwana and Rorke's Drift were burned every year, but mostly as a result of vandalism or carelessness. These fires happened during the winter, well before the arrival of the first rains. Two respondents (n = 2/21) burned grazing lands that had escaped the accidental fires, being careful to burn after the first of the spring rains only. In the past, grazing lands were burned every two to three years at Rorke's Drift, until control was given to the community members in the 1970s by the ELCSA.

All the respondents commented that the climate was drier and warmer. They were all concerned about the reduction in available surface water, which they ascribed to reduction in rainfall, although two respondents also expressed a concern about woody encroachment into the drainage lines, which would have a severe negative impact on stream flow (Huxman *et al.* 2005). Springs that had flowed throughout the year now only flowed in the summer. Most of the respondents (n = 20/22) said that there has been noticeable increase in trees and a

reduction in grass cover. Four respondents (n = 4/13) cited *A. sieberiana* as the dominant encroacher at Rorke's Drift and two respondents (n = 2/9) from Isandlwana cited both cited *A. sieberiana* and *A. karroo* as the dominant encroaching species. One respondent saw no increase in trees and another respondent noted that when he was a boy there were lots of tree seedlings, which have now grown into big trees, although these trees were now at a lower density.

The commercial farmer, who was born in the Rorke's Drift area, endorsed much of what the communal farmers had said about the changing environment. Only the Umzinyathi River flowed all year round; the other streams flowed during the summer only. The commercial farmer ascribed this to woody encroachment into the catchment areas and river sources. Most of the encroaching species in the stream catchment areas were broad-leaved species, while the fine-leaved *A. sieberiana* was encroaching into the rangelands. In an attempt to eradicate the encroaching trees, he encouraged the community members to cut fire wood on his land and he burned his camps every three years on a rotational basis. He believed that the winters were less harsh than in the past, with fewer frost days. This perception is supported from temperature data obtained from the Dundee Research Station (Russell and Ward 2013a).

Discussion

Historically, Zulu culture was intimately entwined with the keeping of livestock, especially cattle (see e.g. Laband 1995). Although much of the traditional Zulu lifestyle has been eroded since the colonisation of KwaZulu-Natal by Europeans, cattle remain a source of cultural significance (see also Shackleton *et al.* 2001). I found that the community members still placed a great deal of importance in being cattle owners. Cattle not only had a practical function, but also bestowed status upon the owner. Those who had lost cattle also faced

economic hardship. The inability to plough their fields and the loss of by-products such as *maas* (curdled milk) meant an increased reliance on commercially produced products. Cattle as gifts or as *lobola* would need to be purchased. This placed a further financial burden on the individual, whereas the cost of raising one's own livestock was negligible. The attitude towards these losses and financial hardships seemed to be one of stoic fatalism. All the respondents had access either to some form of employment and/or to social welfare benefits. As a result, community members in the study area were less reliant on subsistence farming and their livestock for survival.

The traditional institutions of communal rangeland management influenced grazing patterns to some extent at Isandlwana. Fences had been erected, creating extensive, but contained, grazing areas, which replaced the practice of herding. However, several community members noted that shrubs were invading the camps since the introduction of rotational grazing. Forbes and Trollope (1991) and Puttick *et al.* (2011) observed a similar phenomenon in the Eastern Cape. At Rorke's Drift there was no rangeland management (except on the commercial rangeland) and all community members had open access to all the grazing. At both Isandlwana and Rorke's Drift, opportunistic management was still practised. Livestock numbers were still largely dictated by climatic variation and no attempt was made to feed or move livestock in times of drought. Animals simply died, giving the vegetation opportunity to recover with the onset of rains. As no information was available on the floristic composition in the past, one cannot determine whether species composition has changed. However, analysis of fixed-point repeat photographs and multi-temporal aerial photographs shows a dramatic change in vegetation structure from open to closed savannas over 130 years (see Russell and Ward 2013a, Russell and Ward 2013b). This confirms community members' perceptions that woody plants are indeed increasing. The multi-temporal aerial photographs also confirm the commercial farmer's observations that his

rangelands are also becoming encroached (Russell and Ward, 2013b), not only by *A. sieberiana* in the rangelands, but also mixed woody species in the drainage lines.

The requirement for wood per household has probably reduced with access to modern building materials and wire for fencing. Grass huts, which required about 2000 saplings to construct, are rare and modern homes, built of concrete blocks, are favoured. However, all community members still rely on wood for heating and for cooking. Dovie *et al.* (2002) and Twine *et al.* (2003), working in Bushbuckridge Lowveld, Limpopo province and Mametja Traditional Authority, Limpopo province respectively, estimate that each household consumed 3 – 5 tons of wood for fuel per annum. However, as many of the encroaching species (such as *A. sieberiana, Diospyros spp.* and *Euclea crispa*) at Rorke's Drift and Isandlwana were not considered to be good fire wood, little is harvested for fuel. At Fugitives' Drift, the predominance of grazing ungulates would increase grazing pressure, resulting in reduced tree:grass competition as well as a reduced fuel load when the rangelands were burned. This could well lead to an increase in woody species (see also Skarpe 1991, Roques *et al.* 2001, Van Langevelde *et al.* 2003).

The frequency of grass fires varied in the different areas within the study area. Nonetheless, both communal and commercial areas experienced an increase in woody cover. One pair (out of 17 pairs) of fixed-point repeat photographs (Figure 3.4 c and d in Russell and Ward 2013a) taken of the reserve area at Isandlwana shows that woody biomass has decreased between 2004 and 2011. The area where there was a decline is managed by Ezemvelo KwaZulu-Natal Wildlife, a provincial conservation body. The burning regime in this area is flexible, being based on fuel load rather than a fixed time period (Ngwenya 2010). It is possible that fire in this area is an effective management tool in dealing with bush encroachment when return frequency is managed according to fuel load, which, in turn,

determines fire intensity (Trollope and Tainton 1986, Higgins *et al.* 2000, Gordijn *et al.* 2012).

Often farmers' perceptions of climate change do not always correspond to the records from weather monitoring stations (Maddison 2007). However, the observations of all the respondents in the study area corresponded well with the climatic records. Analysis of mean annual rainfall between 1901 and 2004 confirmed that the study area is currently experiencing less rainfall (Russell and Ward, 2013a). This trend should increase competition between grasses and trees for soil moisture, but woody cover has increased. However, the overall increase in temperature (Russell and Ward, 2013a) would favour woody encroachment.

Conclusions

Cattle still form a significant part in the cultural identity of the community members in the study area. The emphasis on cattle may become diluted over time if stock theft continues and as the economy becomes increasingly cash-based. A cash-based economy also removes community members' reliance on resources available to them, such as wood, allowing them to prefer the convenience of buying building material and energy in the form of electricity and solar energy from solar panels. However, community members are aware of the changes in their environment and are greatly concerned about the long-term prognosis. Differing rangeland management approaches appear to have little effect on vegetation structure, except with regard to burning regimes where burning based on fuel load appears to be effective in controlling woody cover.

The survey targeted only the older generation, who may still be hankering after a life-style that is being eroded. However, it would be of interest to learn of the perspectives of the young people, who had not been interviewed as they would have had less concept of the

history of the area and its land use. Their views may be helpful for long-term planning if planners could anticipate community needs in the future.

Acknowledgements

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Appendix 1: Questionnaire used as the basis for the community survey. The interviewer completed the sheet during the interviews.

Interview number:
Date: Name of interviewer: Contact details:
Name of respondent: Age of respondent:
Place of residence :
How long has respondent lived in the area?   How long his/her family lived here before him/her?

Does the respondent own:	Cattle	yes/no	How many?	When was there the most and how many?
	Goats	yes/no	How many?	When was there the most and how many?
	Sheep	yes/no	How many?	When was there the most and how many?
	Donkeys	yes/no	How many?	When was there the most and how many?

What are the benefits to the respondent in keeping stock?   Social status
                                                                  Cultural identity
                                                                  Draught
                                                                  Gifts for children
                                                                  Labola
                                                                  Meat
                                                                  Milk
                                                                  Hides
                                                                  Cash income (sale of animals or produce)
                                                                  Other

What happens to livestock at times of dought?
What happens if drought lasts for more than a year?
Are animals moved to better grazing/water?

Do tribal/community leaders control how many animals a respondent may own?
Do tribal/community leaders control where animals may graze?

What does the respondent use for cooking?	Wood	Electricity	Paraffin	Battery	Generator	Other
What does the respondent use for lighting?	Wood	Electricity	Paraffin	Battery	Generator	Other

If the respondent uses wood, what trees does he/she prefer to use?
Where does the wood come from?
How does he/she obtain it?
Does the respondent use wood for anything else - fencing, building, crafts…?
What wood does the respondent use of other uses as mentioned above?

Does the respondent cultivate crops?   yes/no   What is the most important crop grown?
                                                         How big an area is cultivated?
                                                         When is the most cultivation done?
                                                         Does the respondent rely only on rain for water for the crops?

Does the respondent think there are any changes in:	Amount of grass	yes/no	When did the changes happen?
	Amount of trees	yes/no	When did the changes happen?
	Amount of rain	yes/no	When did the changes happen?
	Number of animals that can live off the land	yes/no	When did the changes happen?

Can the respondent say how, why, where the changes, if any, have occurred?

How have these changes, if any, have effected the respondent?

Chapter 5

Discussion

The combination of fixed-point repeat photographs and multi-temporal aerial photographs has provided a useful overview of changes in the landscape since the Anglo-Zulu War of 1879. The historic photographs have provided a rare opportunity to compare vegetation over a 130 year period. The use of aerial photographs in the intervening years have avoided the pitfall, pointed out by Kull (2005) and Hongslo *et al.* (2009), of making a possibly invalid assumption that observed changes in the repeat photographs are linear. Analysis has shown that there has, indeed, been dramatic change in the vegetation in the study area since 1879. Woody plant cover has increased markedly. Although the pattern and rate of change have varied in the three different study sites within the study area, the changes are progressive rather than part of an oscillating system that will eventually revert back to grassland (Archer 1989). It is not clear what may be driving the changes. It appears that some drivers may be superseded by others or may be modifying an over-arching trend.

Heavy grazing is frequently cited as the cause of bush encroachment (see e.g. Van Vegten 1983, Scholes and Archer 1997, Ward *et al.* 2012). Trees and grasses compete with each other for resources, such as soil moisture (Van Langevelde *et al.* 2003, Ward *et al.* 2012) and light (Bush and Van Auken 1987, Vadigi and Ward 2013). Tree seedlings would be particularly vulnerable to grass competition because their roots still occupy the upper layers of the soil (Sankaran *et al.* 2004, Riginos 2009), presuming that grasses are the superior competitors (Knoop and Walker 1985). With the removal of grass competition, the seedlings would be more successful in establishing themselves. Dynamics of African rangelands are frequently modelled on succession models which assume that rangelands are potentially at equilibrium and form the basis for the criticism of communal land tenure

systems (Rohde *et al.* 2006). Heavy grazing (also called 'overgrazing') in communal land tenure is seen to lead to the 'tragedy of the commons' (Hardin 1968), which inevitably leads to environmental degradation, such as bush encroachment. Authors such as Ellis and Swift (1988), Ward *et al.* (1998), Ward (2004) and Rohde *et al.* (2006) contest this perception, although, as Rohde *et al.* (2006) point out, as new, 'modern' management strategies are introduced and transhumance is no longer possible, communal rangelands are becoming degraded (see also Vetter and Bond 2012). In our study area, communal and commercial rangelands, as well as the conservation areas, were undergoing bush encroachment, i.e. degradation, despite different grazing strategies, although the rate of encroachment may differ with land-use. Wigley *et al.* (2009) have made similar observations (see also Wigley *et al.* 2010). Other studies have noted that communal rangelands that have been set aside for commercial cattle ranching with lower stocking rates have also become encroached (Forbes and Trollope 1991, Puttick *et al.* 2011, Rohde and Hoffman 2012), possibly as a result of the reduction in the number of browsers such as goats (Rohde and Hoffman 2012). Removal of domestic livestock from the study area at Fugitives' Drift should have resulted in the reversal of the trend towards bush encroachment, if the proponents of the tragedy of the commons are correct. This reversal has not occurred (Russell and Ward 2013a). While bush encroachment has occurred at all the study sites regardless of land-use, species composition has been affected by different land uses because species richness was significantly different across the three study sites (Russell and Ward 2013b) (see also Ellis and Swift 1988, Benjaminsen *et al.* 2006).

With a mean annual rainfall of 705 mm, the study area is either just within the category of savanna where the tree:grass ratio is controlled by disturbance (threshold of ~650 mm, see e.g. Sankaran *et al.* 2008) or the study area is at the upper limits of the continuum where the tree:grass ratio is controlled by rainfall (threshold ~820 mm, see Higgins *et al.*

2010). Consequently, the natural trend in the study area is towards increasing tree density (see e.g. Sankaran *et al.* 2005, Murphy and Bowman 2012). However, analysis of rainfall data for the area (Russell and Ward 2013b) shows that mean annual rainfall is decreasing. This is not consistent with the observed trend of increasing woody cover. Bahre and Shelton (1993) also noted an increase in shrub density in their study site, despite decreasing mean annual rainfall. Analysis of temperature trends suggests that ambient temperatures are increasing (Russell and Ward 2013b) which is more consistent with the expectations of bush encroachment as savannas typically have higher temperatures than grasslands (see e.g. O'Connor and Bredenkamp 1997, Wakeling *et al.* 2012).

Fire, together with herbivory (see e.g. Higgins *et al.* 2000, Gordijn *et al.* 2012), influences tree:grass dynamics. Coupled with browsing, which maintains woody shrubs within the fire trap, fire can maintain an open savanna (Trollope 1974). Conversely, heavy grazing may reduce fuel loads resulting in cooler fires, which favours bush encroachment (Roques *et al.* 2001). Fire return frequency is also important with regard to its effect on bush encroachment (Gordijn *et al.* 2012). Trollope (1980) suggests that in moist savannas, fire return frequency should be between every 3-4 years. Fire, however, has little effect on arid and semi-arid savannas (Kraaij and Ward 2006) as fires are neither sufficiently frequent nor sufficiently intense. Fire return frequencies in the study area are variable. Some areas are burned every year, some every three years. Yet all areas are experiencing bush encroachment. There is one possible exception. One pair (out of 17 pairs) of fixed-point repeat photographs in Russell and Ward 2013b (Figure 2.4 c and d) suggests that fire may be limiting bush encroachment at Isandlwana between 2004 and 2011. There appears to be no further recruitment in this area, although tree size has increased (see Hanan *et al.* 2008). Analysis of the aerial photographs (Russell and Ward 2013a) shows a reduction in the rate of increase in woody cover at Isandlwana between 1991 and 2005 (see Figure 3.4 (b)). This

supports the observation that bush encroachment reduced in this area. The area is burned every 2-3 years, but the final decision when to burn rests on the fuel load (Ngwenya 2010). This may be a more appropriate long-term strategy to limit bush encroachment (see Trollope and Tainton 1986, Hanan *et al.* 2008).

Wood harvesting within the study area is decreasing. Community members who were interviewed during the survey (see chapter 4) were either employed locally or drew social benefits (pers. obs.). As the community moves towards a purely cash-based economy, individuals prefer to use commercially produced commodities such as building materials, fencing and household utensils. Wood was still used for heating and cooking, but much of it was not harvested locally and wood from woodlots was used for general requirements. Many of the encroaching woody species, such as *Euclea crispa, Diospyros* spp. and *Acacia sieberiana*, were not considered suitable for fuel or fencing by the communal pastoralists that I interviewed and were, therefore, not harvested. Another factor was that most of the young people from the community were either in school or were employed in urban areas and were not available to assist with manual labour, such as wood collection.

Since the industrial revolution there has been a steady increase in atmospheric CO_2 (Etheridge *et al.* 1996). Current CO_2 concentrations are ~397 μmol/mol (Tans 2013), which is an increase of almost 50 μmol/mol since 1960. Much has been written about the effects of CO_2 concentrations on the photosynthetic rates of C_3 and C_4 plants (see e.g. Ehleringer and Monson 1993, Collatz *et al.* 1998, Edwards *et al.* 2010). It appears, however, that photosynthetic benefits of increased CO_2 are rare (Körner 2006). Many of the responses to elevated CO_2 incorporate water saving (Morgan *et al.* 2004) which would benefit both C_3 (woody species) and C_4 (tropical savanna grasses), and an accumulation of carbon reserves (Bond and Midgley 2000) and enhanced carbon-based defence mechanisms (Ward 2010), both of which benefit woody species. However, I note that nutrient availability sets the

ultimate limit to the benefits that may be attained by the increased growth rates of C_3 plants due to the increased availability of carbon from CO_2 (Finzi *et al*. 2002, Hungate *et al*. 2006, Körner 2006).

Conclusions

The fixed-point repeat photographs, together with the multi-temporal aerial photographs, have shown that progressive bush encroachment is occurring in the study area. The interactions of the agents of change are complex and it is likely that there are several drivers at work (Ward 2005, Bond 2008). In the past, African grasslands and savannas were maintained through fire, herbivory (see e.g. Skarpe 1992) and possibly high demand for wood (Maggs 1980). However, the removal of wild herbivores and the increase of grazing livestock in KwaZulu-Natal since the mid-1800s have led to the increase in woody shrubs and trees. Increased grazing has also reduced the effectiveness of fire in maintaining grasslands. It appears, however, that in more recent years, livestock numbers are decreasing and, combined with decreasing annual rainfall, woody plant density should likewise decrease. This, however, has not occurred and woody cover continues to increase in the study area. Increasing atmospheric CO_2 concentrations are likely to be the overriding driver of bush encroachment in the study area. Initially, the effects of increasing CO_2 concentrations were enhanced by heavy grazing by domestic livestock and relatively high rainfall and by increasing ambient temperature. However, these changes have been tempered by a reduction in grazing pressure and reduced annual rainfall in recent years.

Future directions

Measurement of changes in woody cover over time has resulted in conclusive evidence that bush encroachment is occurring in the study area. The reasons cited as driving the changes

are, however, largely speculative. Communal and commercial ranchers have all expressed concern regarding bush encroachment. It would be useful to further investigate drivers of bush encroachment in the study area, which may aid the formulation of a management strategy. African savannas and grasslands are dynamic and unpredictable systems (Ellis and Swift 1988, Skarpe 1992, Rohde *et al.* 2006) and need to be managed in a flexible and innovative manner.

There is much evidence that fire is an important agent of disturbance in maintaining the open nature of savannas and grasslands (see e.g. Trollope 1974, Roques *et al.* 2001). In the study site at Isandlwana, fire management is based on fuel load. Observations regarding the rate of encroachment suggest that this is successful in controlling encroachment (Russell and Ward 2013a, Russell and Ward 2013b). Long-term monitoring of the site would be desirable and trials on fire return frequency based on fuel load (Trollope and Tainton 1986, Trollope *et al.* 2002), as well as timing of fire occurrence (Trollope and Tainton 1986, Zimmermann *et al.* 2008, Wigley *et al.* 2010), should be encouraged in the other study sites.

The effects of grazing and browsing in the study area bear closer examination. Cattle census figures used in this project end in 1988 (Tapson 1991). More recent livestock census figures from dip tanks in the study area would give an indication whether domestic livestock are indeed decreasing in number, as indicated in the community survey. The census figures would also indicate the proportion of browsers to grazers. Browsing not only removes above-ground biomass that may otherwise compete with grass for light (Laws 1970, Van Langevelde *et al.* 2003), but, together with fire (Trollope 1974, Staver *et al.* 2009), may even reverse bush encroachment. It may, therefore, be beneficial to encourage greater diversity in stock keeping and game ranching.

Cramer *et al.* (2010) showed that grasses competed successfully for nitrogen with non-nodulating tree seedlings, whereas those seedlings that were able to fix nitrogen

(nodulating seedlings) were unaffected by limited nitrogen. Many of the encroaching tree species at the study sites were non-nodulating trees, such as *Euclea crispa* and *Diospyros spp.* Nitrogen enrichment of the soil would, therefore, be beneficial to such trees. While grasses would also benefit from the extra nitrogen (Kraaij and Ward 2006, Cramer and Bond 2013), heavy grazing would reduce the competitiveness of the grasses. A potential source of nitrogen enrichment would be derived from nitrogen deposition from the industrial town of Newcastle about 90 km away. Although Josipovic *et al.* (2010) have noted that deposition of nitrogen dioxide was well below the critical level for vegetation, closer monitoring of nitrogen deposition in the study area would be desirable. Another source of nitrogen is from the dung of large mammals (Belsky *et al.* 1989), such as cattle. If cattle numbers are in fact decreasing, this source of nitrogen should reduce. Grasses, being superior competitors for nitrogen (Cramer *et al.* 2010), would benefit and the densities of non-nodulating trees may subsequently decrease in density.

The structure and composition of plant communities of savannas are influenced by topo-edaphic conditions (see e.g. Witkowski and O'Connor 1996, Breebaart *et al.* 2001, Clegg and O'Connor 2012). Heavy-textured clay soils generally support a well-developed grass layer, with few trees (Clegg and O'Connor 2012), whereas light-textured soils are favoured by woody shrubs and trees (Britz and Ward 2007b, Clegg and O'Connor 2012). Parent material of the soils was noted in this project, but no soil sampling was undertaken. A survey of the soils in the study area should be undertaken to further understand the dynamics of bush encroachment.

The use of repeat fixed-point photographs based on historic images has proved to be a successful means of monitoring vegetation change (see also Rohde and Hoffman 2012; Masubelele *et al*. 2013). The progressive nature of the change was demonstrated by incorporating the more recent ground photographs with the historic images, as well as by

using aerial photographs. Continued monitoring of the sites would be relatively easy and inexpensive by setting up permanent photo-stations at the same localities from which the photographs were taken for this project (see Howery and Sundt 1998, Kull 2005, Masubelele *et al*. 2013). Any experimental studies set up to ascertain factors involved with bush encroachment should be set up with this in mind.

Although I have ascribed the changes observed in the study area, primarily, to increasing atmospheric CO_2 (see e.g. Kgope *et al*. 2009), herbivory and fire are modifying influences. The decimation of the megaherbivores and indigenous browsers, the substitution of these indigenous herbivores with cattle, and the suppression of fire have had a major impact on the landscape (e.g. Rohde and Hoffmann 2012). An innovative approach towards range management may maximize the potential impact of herbivory (particularly browsing) by introducing more browsers and the impact of fire by basing fire-return frequency on fuel load. In this way it may be possible to reverse the current trend towards bush encroachment.

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