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# Some consequences of woody plant encroachment in a mesic South African savanna

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Submitted in fulfilment of the requirements for a Master of Science Degree

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## **Abstract**

The vegetation in Hluhluwe Game Reserve is a patch mosaic of closed, forested vegetation and more open grasslands and savannas. Originally thought to be due to anthropogenic tree felling during the Iron Age, many of those habitats containing a continuous C<sub>4</sub> grassy layer are now understood to be ancient systems that predate many of the forests in the area. Over the last century woody plants have encroached into the open savannas and grasslands in the system, a trend that has been documented in open systems throughout the world. A large scale shift in land cover is likely to alter ecosystem functioning significantly, but few studies have explicitly investigated these consequences. This study investigates the diversity present in the patch mosaic of vegetation, and also investigates how woody plant encroachment is affecting ecosystem services in Hluhluwe Game Reserve, with a focus on biodiversity, carbon storage and recreation and tourism.

Savannas, grasslands and forests each contributed significantly to overall species diversity in the park. Savannas and grasslands were dominated by fire tolerant, shade intolerant species while forests were dominated by shade tolerant, fire sensitive species. Grassy systems shared few species with established forests, refuting the idea that they are seral to forests. Encroached savannas (thickets) shared many species with both savannas and forests, with older thickets more compositionally similar to forests. I therefore suggest that woody plant encroachment may eventually lead to a complete biome switch to forests, and will result in large scale savanna and grassland species losses and cascading ecosystem consequences.

Established forests contained more carbon in their soils than other vegetation types. Encroaching thickets contained only 7% more soil carbon than savannas, suggesting that afforestation in this area is unlikely to provide a major terrestrial carbon sink. I suggest the amount of soil carbon stored will vary depending on climate, and that in more arid areas woody plant encroachment may prove to be a more useful carbon sink. The main carbon gain after encroachment in my study area was due to above ground carbon, an inherently unstable sink.

Mammal distributions and densities in the park were found to decrease with an increase in forested vegetation. This was not uniform for all species; the density of smaller forest antelope such as nyala and duiker increased, while the densities of larger animals such as elephant and white rhino appeared unaffected by vegetation change. Herd sizes of all species did tend to decrease with an increase in forested vegetation. I hypothesised that as animal

densities decrease, and animals become more difficult to spot, tourist satisfaction in the park will diminish.

I surveyed tourists in an attempt to gauge their response to woody plant encroachment. My estimations suggest that the park could lose up to 30% of future visitors if woody plant encroachment is not controlled. Visitors prefer heterogeneous landscapes, and woody plant encroachment is reducing landscape heterogeneity. This highlights the fact that woody plant encroachment is not merely an environmental issue for management, but could negatively influence the economy of the park and its surrounds. Hluhluwe-iMfolozi Park contributes significantly to the revenue of Ezemvelo KZN Wildlife as a whole, so any decline in revenue will affect conservation efforts of the organisation significantly.

Hluhluwe Game Reserve is a patch mosaic of forest, grassland and highly diverse mesic savanna, which is undergoing significant woody plant encroachment. This is causing reductions in the diversity of plants, and is likely to affect mammals, insects and birds. It also threatens to reduce park revenue obtained from tourists, revenue which allows it to continue conservation efforts. Considering this is a conservation area, the effect that woody plant encroachment will have on biodiversity may be catastrophic. It is also likely to reduce runoff significantly. Future research needs to investigate woody plant encroachment on a larger scale, as well as investigate its effects on other ecosystem services, especially hydrology, and for land uses other than conservation. Intense fires may prove a useful tool in the control of woody plant encroachment. A 'firestorm' that burnt through large encroached patches in 2008 promoted plant diversity and did not cause major losses in soil carbon and nitrogen.

The widespread nature of woody plant encroachment, and the cascading ecosystem consequences that it is causing suggest that it should become a national priority comparable to the Working for Water programme which focuses on controlling alien invasives.

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# Chapter 1

## General Introduction

Grasslands and savannas are globally widespread systems, and although estimates differ, are believed to cover between 20-40% of the earth's terrestrial surface (Chapin et al. 2001; Archer et al. 2004). They are globally important systems for a variety of reasons. Much of the world's farming takes place in these open grassy systems, and they are particularly important as rangelands (Turner 1990; Scholes & Archer 1997; Sankaran et al. 2004). In Africa they have an additional value in that they are home to most of the world's last remaining megaherbivores. Megaherbivores and other African mammals have an intrinsic sentimental value to people all over the world, as well as an economic value for many African countries whose economies rely on tourists who wish to see these animals in their natural habitat (Akama & Kieti 2003). Savannas and grasslands are important to the global carbon and nitrogen cycles, contributing approximately  $19.2 \text{ PgCyr}^{-1}$  to net primary productivity (NPP), accounting for about 30-35% of total terrestrial NPP (Field et al. 1998; Archer et al. 2004; Grace et al. 2006). This is on par with tropical rainforests which contribute  $17.8 \text{ PgCyr}^{-1}$  to NPP, approximately 32% of total terrestrial NPP (Field et al. 1998; Lloyd & Farquhar 2008). Despite the global importance of these grassy systems, the focus in ecological studies has traditionally been on forests. Grasslands and savannas were originally thought to be of anthropogenic origin, formed over the last few millenia by wood clearing and fires (de La Bâthie 1936; Acocks 1953; Meadows & Linder 1993; Banerjee 1995). These open systems were thought to be seral to forests, with the only „natural' grasslands occurring in places too high or too cold for trees to grow (Axelrod 1985; Thomas & Palmer 2007).

*Many grasslands and savannas are ancient systems*

In light of palaeoecological records this view is changing (Ellery & Mentis 1992; Meadows & Linder 1993; Cerling et al. 1997; Osborne & Beerling 2006; Osborne 2008; Edwards et al. 2010). Savannas and grasslands are dominated by grasses which utilise the  $C_4$  photosynthetic pathway, a pathway that evolved 25-30Ma (Osborne & Beerling 2006; Osborne 2008). A drop in atmospheric carbon during the Oligocene resulted in the convergent evolution of the  $C_4$  photosynthetic pathway in over 45 separate lineages (Sage 2004; Osborne & Beerling

2006). However, savannas and grasslands dominated by C<sub>4</sub> grasses only became globally widespread over a very short space of time between 4 and 8Ma (Cerling et al. 1997; Osborne & Beerling 2006). The reason for this rapid expansion of C<sub>4</sub> dominated grassy systems is thought to be due to a combination of increased rainfall seasonality and increased fire frequency which allowed C<sub>4</sub> grasses to outcompete C<sub>3</sub> shrubs and trees (Bond et al. 2003; Keeley & Rundel 2005; Osborne 2008)

Indeed, these systems are highly tolerant of fire. Many non-graminoid herbaceous elements (forbs) in contemporary savannas are unable to survive without fire (Uys et al. 2004). Many of them utilise underground storage organs, which may allow them to recover rapidly after a fire has removed their above ground biomass (Simon et al. 2009; Zaloumis & Bond 2010). They are able to withstand grass competition by utilising the small seasonal gaps when grasses die back, either during the dry season or after a fire. The utilisation of underground storage organs means that many forbs are highly persistent in the face of disturbance, but the trade off is that they are poor colonisers (Zaloumis and Bond 2010).

#### *Grasslands and savannas as alternative stable ecosystem states to forests*

Many savannas and grasslands are extremely diverse systems (Overbeck et al. 2007; Sankaran 2009; Bond & Parr 2010), with many fire-tolerant herbaceous and woody species. This does not fit with the characteristics of seral landscapes, and a more appropriate way of thinking of them is as alternative stable ecosystem states to forests (Scheffer & Carpenter 2003; Warman & Moles 2009). Many grasslands and savannas exist in a patch mosaic with forests, with boundaries maintained by disturbance such as fire (Bond et al. 2005). These boundaries are fairly stable in time, but the vegetation on either side of the boundary may undergo rapid regime shifts to switch to alternative states in a fairly short space of time (Scheffer & Carpenter 2003). Indeed grasslands and savannas throughout the world are currently undergoing woody plant encroachment, a process which may eventually lead to a complete regime shift.

#### *Woody plant encroachment in savannas and grasslands*

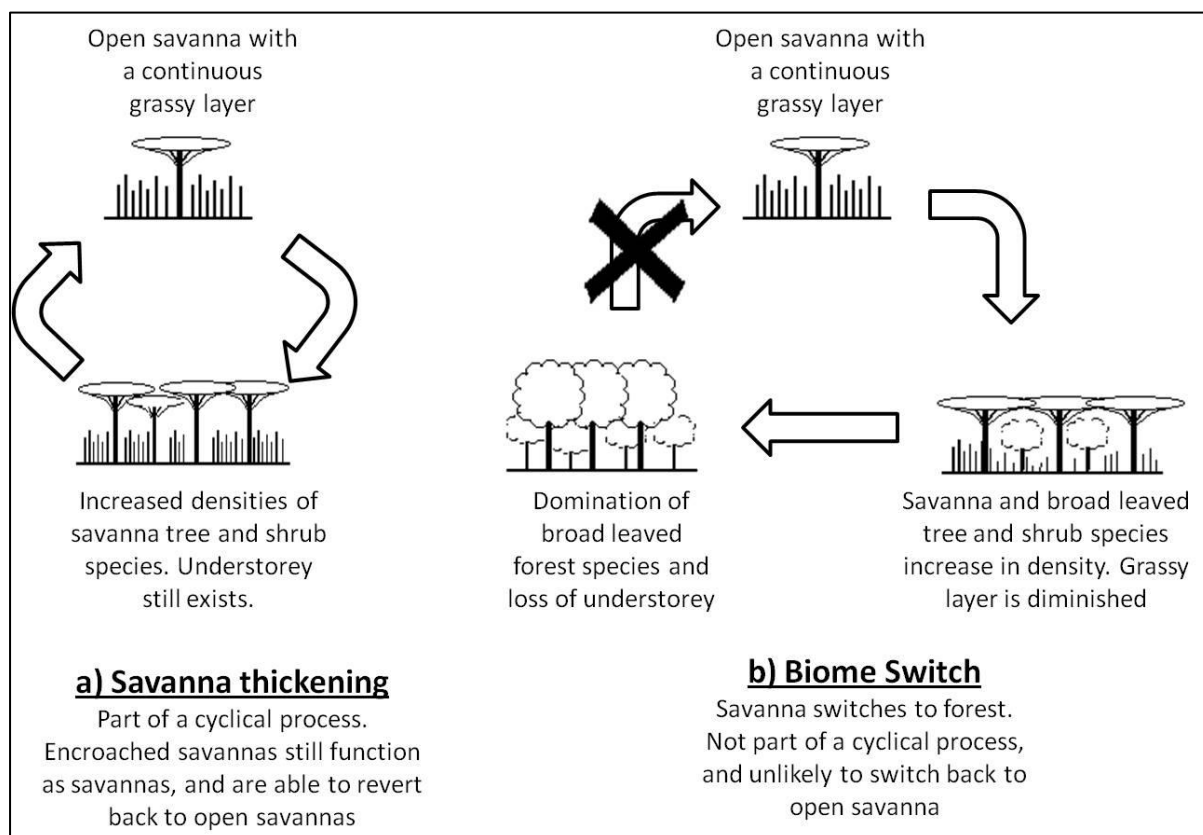
Increases in woody cover have been reported for Africa (Skarpe 1990; Hoffman & O'Connor 1999; Higgins et al. 2000; Roques et al. 2001; Moleele et al. 2002; Wiegand et al. 2006; Britz

& Ward 2007), North America (Archer et al. 1995; Van Auken 2000; Jackson et al. 2002; Asner et al. 2003) South America (Silva et al. 2001), India (Singh et al. 1990), Europe (Laiolo et al. 2004) and Australia (Burrows et al. 1990; Fensham & Fairfax 2003; Fensham et al. 2005). The reasons for this trend have been argued over in the literature. Historically, it was thought to be a local phenomenon, with intense grazing (Skarpe 1990), and altered fire regimes (Brook & Bowman 2006) the most commonly cited reasons. More recently, the global nature of the phenomenon has pointed to global-scale drivers such as changing climate (e.g. rainfall), atmospheric nitrogen deposition and elevated atmospheric carbon dioxide levels (Fensham et al. 2005; Polley 1997). The carbon dioxide hypothesis has also been supported with greenhouse trials and modelling (Bond & Midgley 2000; Hoffmann et al. 2000; Bond et al. 2003; Kgope et al. 2010).

A study by Wigley et al. (2010) in a mesic savanna in the north-east of South Africa (the same area that my study is based in) investigated driving mechanisms of woody plant encroachment across three different land-use types, namely commercial farming, communal farming and conservation. They found that although land use affected the extent of woody thickening, all three land-use types had undergone significant woody thickening between 1937 and 2004. Woody cover increased from 14-58% in conservation land, 3-50% in commercial land and 6-25% in communal lands. The fact that it was happening across different land uses, albeit at different rates, supports the hypothesis that the increased cover of woody species is driven by global-scale mechanisms such as enhanced atmospheric CO<sub>2</sub> together with local drivers.

There is ambiguity in the term woody plant encroachment, as it is a catch-all phrase which can refer to two distinct processes which are not clearly distinguished in the literature. I propose that these processes can be distinguished according to the schematic in figure 1.1. In arid and semi arid savannas woody plant encroachment most commonly refers to what can be best described as „savanna thickening’. Savanna trees and shrubs are able to establish and escape the browse and fire traps (Bond & Van Wilgen 1996), which results in a denser cover of savanna species but does not necessarily exclude the grassy layer. This is most likely part of a cyclical process which can be reversed. In mesic savannas woody plant encroachment can refer to both „savanna thickening’ and a complete „biome switch’. A biome switch can occur when broadleaved tree and shrub species are able to establish, which results in a switch in species composition to shade tolerant, fire sensitive forest species and a loss of the grassy

layer. This process may represent a shift to an alternative stable ecosystem state (Scheffer & Carpenter 2003), a shift which is not easily reversed. A biome switch is likely to cause cascading ecosystem consequences, while the effects of savanna thickening are likely to be less severe. With the encroachment of woody plants into savannas threatening a complete biome switch from savannas to forests, it is increasingly important to be able to explain and predict changes, but this is confounded by the intrinsically complex nature of these systems.



**Figure 1.1 Schematic showing two distinct woody plant encroachment processes. a) Savanna thickening which refers to increased densities of savanna tree and shrub species and is a cyclical process, and b) a biome switch which refers to increased densities of broad leaved, shade tolerant, fire intolerant forest species. This process may be difficult to reverse and is likely to alter ecosystem functioning and ecological processes significantly**

### *The implications of woody plant encroachment*

My study is less interested in the „why?“ and „how?“ of woody plant encroachment, and focuses more on the „so what?“. A global scale biome shift to tree-dominated landscapes is bound to have many consequences for ecosystem function. Ecosystems provide various goods and services, which are a form of natural capital (Costanza et al. 1997), and a change in land cover can affect services that have local, regional, or global value. Examples of such

goods and services include the quantity and quality of water supplies, the regulation of climate, air quality, soil health, carbon sequestration, and the maintenance of biodiversity (Donaldson 2003; Reyers et al. 2009). However, these ecosystem services interact in a dependent and non-linear way. Promoting one ecosystem service often results in a trade off against another ecosystem service. For example promoting production by cultivating a crop provides food, but can impair soil retention, water regulation and contribute to eutrophication of aquatic habitats (Reyers et al. 2009). The Millenium Ecosystem Assessment (2005) presented evidence of the trade-offs being made in global ecosystem services. It found that enhancement of many key ecosystem services (such as crop production, carbon sequestration, livestock production and aquaculture) has come at a cost to many other services, mostly regulating and supporting services (Reyers et al. 2009). Land cover change has been identified as one of the most important drivers of ecosystem change (Vitousek et al. 1997; Reyers et al. 2009), and a change in land cover due to woody plant encroachment is likely to affect processes such as disturbance, erosion, hydrological and biogeochemical cycling and resource competition (such as light, water, nutrients and space) (Gordon 1998) .

The effects of land cover change on ecosystem services are fairly well quantified in some southern African systems, such as the Little Karoo (Reyers et al. 2009). Many studies have focused on the effects of land cover change due to invasive plants on ecosystem processes in South Africa, which are understood to be significant (Le Maitre et al. 2002; Gorgens & Van Wilgen 2004). Woody plant encroachment is a similar process in many respects, except that the species that are encroaching are indigenous. Despite the impacts of woody plant encroachment potentially being as significant as those of invasive alien plants, I am unaware of studies focusing on the effects of woody plant encroachment on ecosystem services in southern African mesic savannas. Most existing studies took place in North America (Houghton et al. 1999; Archer et al. 2001; Pacala et al. 2001; Jackson et al. 2002; Huxman et al. 2005) with very few focusing on the southern African region, although there is a good summary of the impacts of woody plant encroachment in Namibia (De Klerk 2004). For the purposes of this study I focused on the carbon sequestration, biodiversity, and socioeconomic effects of woody plant encroachment. The promotion of either one of these services may result in a trade off against another one (Reyers et al. 2009). It is by no means an exhaustive list of the services which may be affected by an increase in tree cover but further investigations were beyond the scope of this study.

Biodiversity is an important ecosystem service of more than local significance. Many studies have shown that biodiversity is globally important as it provides systems with resilience and resistance to change, and ensures the maintenance of many other ecosystem services (Chapin et al. 2001; Loreau et al. 2001; Folke et al. 2004; Hooper et al. 2005; Balvanera et al. 2006; Tilman et al. 2006). Woody plant encroachment may have significant effects on grassy layer biodiversity (Briggs et al. 2005). My study aims to assess biodiversity in my study area, and determine the biodiversity changes that are occurring due to woody plant encroachment in a conservation area, and discusses the relevance of these changes.

In light of increasing atmospheric CO<sub>2</sub> concentrations, carbon sequestration is considered an important ecosystem service (Batjes 1998; Grace et al. 2006; Mills & Cowling 2006). Because trees are slower growing, deeper rooted and more long lived than grasses, they are expected to increase the absorption of carbon from the atmosphere (Archer et al. 2001; Jackson et al. 2002; Archer et al. 2004; Knapp et al. 2008). There is a need to reduce carbon emissions, and woody plant encroachment could prove a useful passive terrestrial carbon sink.

African savannas have a unique situation with regards to woody plant encroachment, in that they contain most of the world's remaining megaherbivores. Indeed wildlife tourists contribute significantly to the economies of many African countries (Akama & Kieti 2003). An increase in tree cover in these savannas is likely to make wildlife viewing more difficult (Prins & van der Jeugd 1993), and may even reduce animal densities. It is likely that this will affect visitor numbers to conservation areas as they would be unsatisfied with their wildlife experience, but very little data on this topic exists. Considering how economically important wildlife tourists are for the maintenance of conservation areas, I set out to explore the socioeconomic implications of woody plant encroachment by surveying tourists.

Clearly, the effect of woody plant encroachment is a complex issue, and the consequences will differ depending on land use. I focus in particular on the ecosystem consequences of woody plant encroachment in Hluhluwe-iMfolozi Park in KwaZulu Natal, South Africa (for a description of the study area see Chapter 2). Although my thesis focuses on consequences for a conservation area, I do discuss other land uses, and how it may benefit these areas differently to a conservation area.

The central questions I aim to answer are

### Chapter 3

What plant species are present in the Hluhluwe Game Reserve vegetation mosaic, what are the biodiversity implications of woody plant encroachment, and are we observing a complete biome switch to forest?

### Chapter 4

Does woody plant encroachment enhance the amount of carbon stored in savannas and grasslands, and will encroached savannas become an important terrestrial carbon sink?

### Chapter 5

Will woody plant encroachment affect the park economically, specifically by causing a reduction in visitors to the park due to difficulty in viewing wildlife?

Chapters 3 through 5 have been prepared as stand-alone papers. Each chapter has an introduction which includes some of what has already been discussed in this introduction, resulting in some repetition. Chapter 2 describes my study area, and chapter 6 is a synthesis of the conclusions from my data chapters. Appendices pertaining to the data chapters are attached at the end. I have also added a study of differences in nutrient stocks between forested and open ecosystems as an appendix, which emerged from the carbon sequestration study, but is not relevant to the central theme of my thesis. In addition, I have attached an appendix briefly investigating the ecohydrological implications of woody plant encroachment. This proved beyond the scope of my study and requires further investigation.

## Chapter 2

### Study Area

My study was conducted in the Hluhluwe-iMfolozi Park (HiP) in KwaZulu Natal, South Africa, which is situated between 28°00'S and 28°26'S and between 31°43'E and 32°09'E. HiP is a 900km<sup>2</sup> game reserve which is comprised of three smaller reserves, the Hluhluwe Game Reserve in the North East, the iMfolozi Game Reserve in the south, and the Corridor in between these two (Figure 2.1). The corridor part of the reserve was only officially incorporated into the reserve in 1982, while the Hluhluwe Game Reserve and the iMfolozi Game Reserve were both declared independently in 1895.

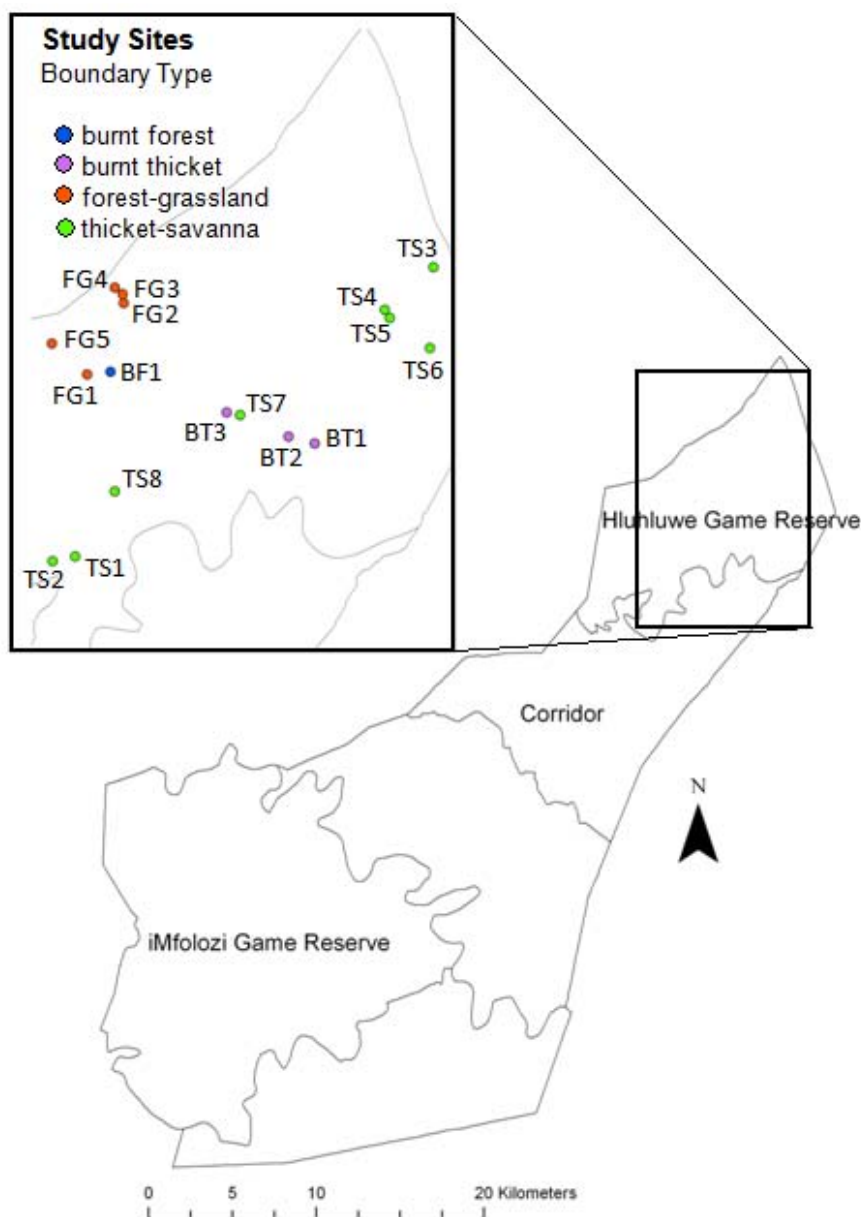
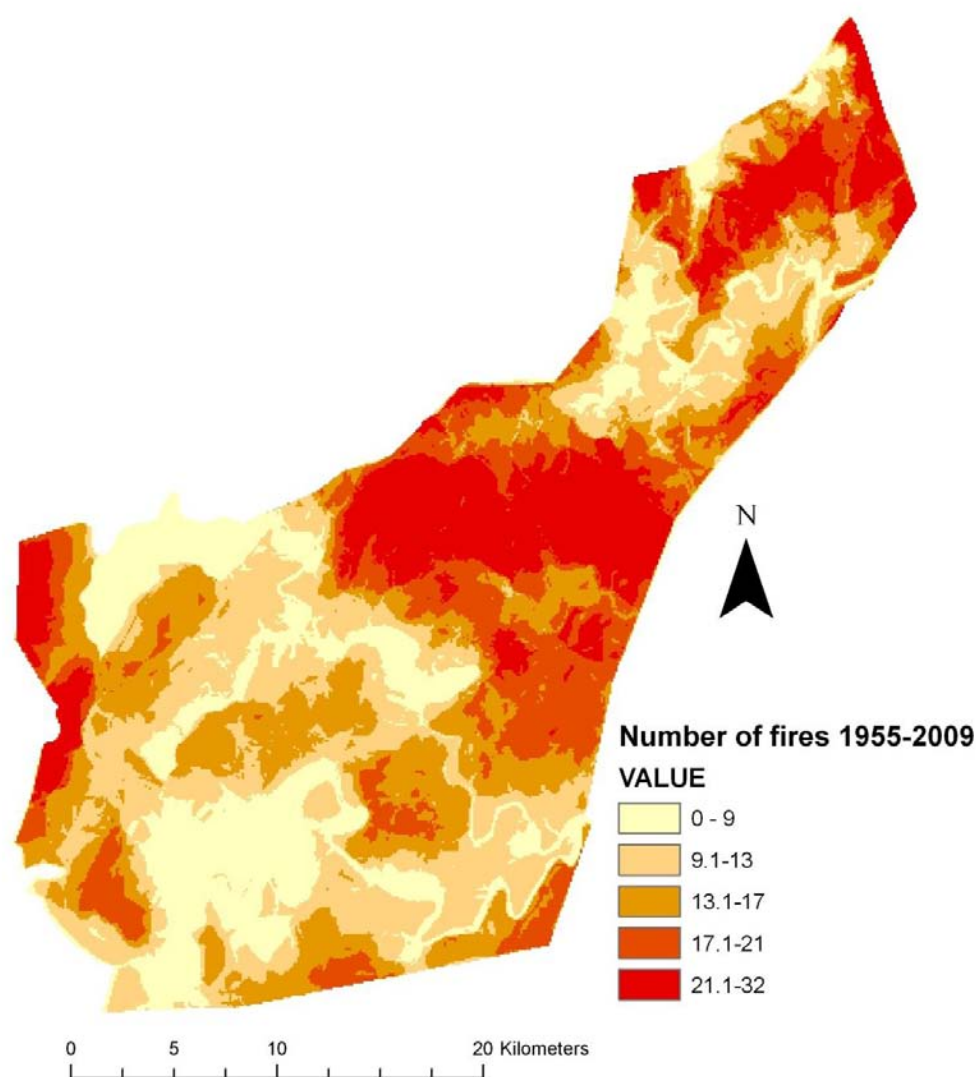


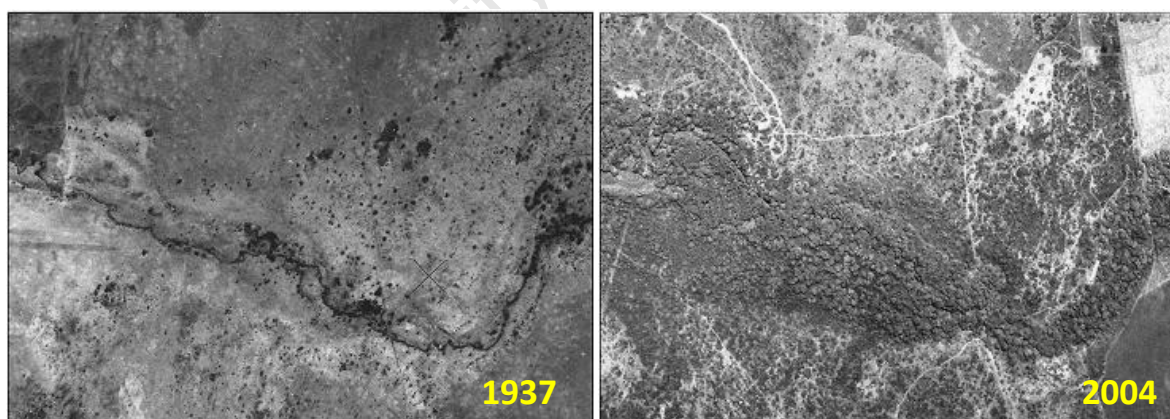
Figure 2.1 Map of Hluhluwe-iMfolozi Game Reserve indicating the location of all study sites and the type of vegetation boundary they represent

Altitude, rainfall and fire frequency (Figure 2.2) tend to decrease from Hluhluwe to iMfolozi (Balfour & Howison 2002). The altitude of the park ranges from 60m above sea level to 450m above sea level at Hilltop tourist camp in the Hluhluwe section of the park (Whateley & Porter 1983). The soils are largely derived from sandstone, shale and dolerite intrusions (King 1970; Balfour & Howison 2002). Annual rainfall ranges from above 1000mm in the high altitude regions in the north west of the park to below 635mm in the southern end (Balfour & Howison 2002). The park receives summer rainfall, which falls predominantly between October and March. All of my study sites were situated within the Hluhluwe section of the park (Figure 2.1). Between 2002 and 2007 the daily temperatures in the Hluhluwe section of the park ranged between 39°C and 15°C in the summer and between 32°C and 9°C in the winter (Zululand Tree Project data, unpublished).



**Figure 2.2** Map indicating the number of fires occurring in each area of the park over the time period between 1955 and 2009. Highest fire frequencies are seen in the Hluhluwe and Corridor sections of the park (Source: EKZN Wildlife Dataset)

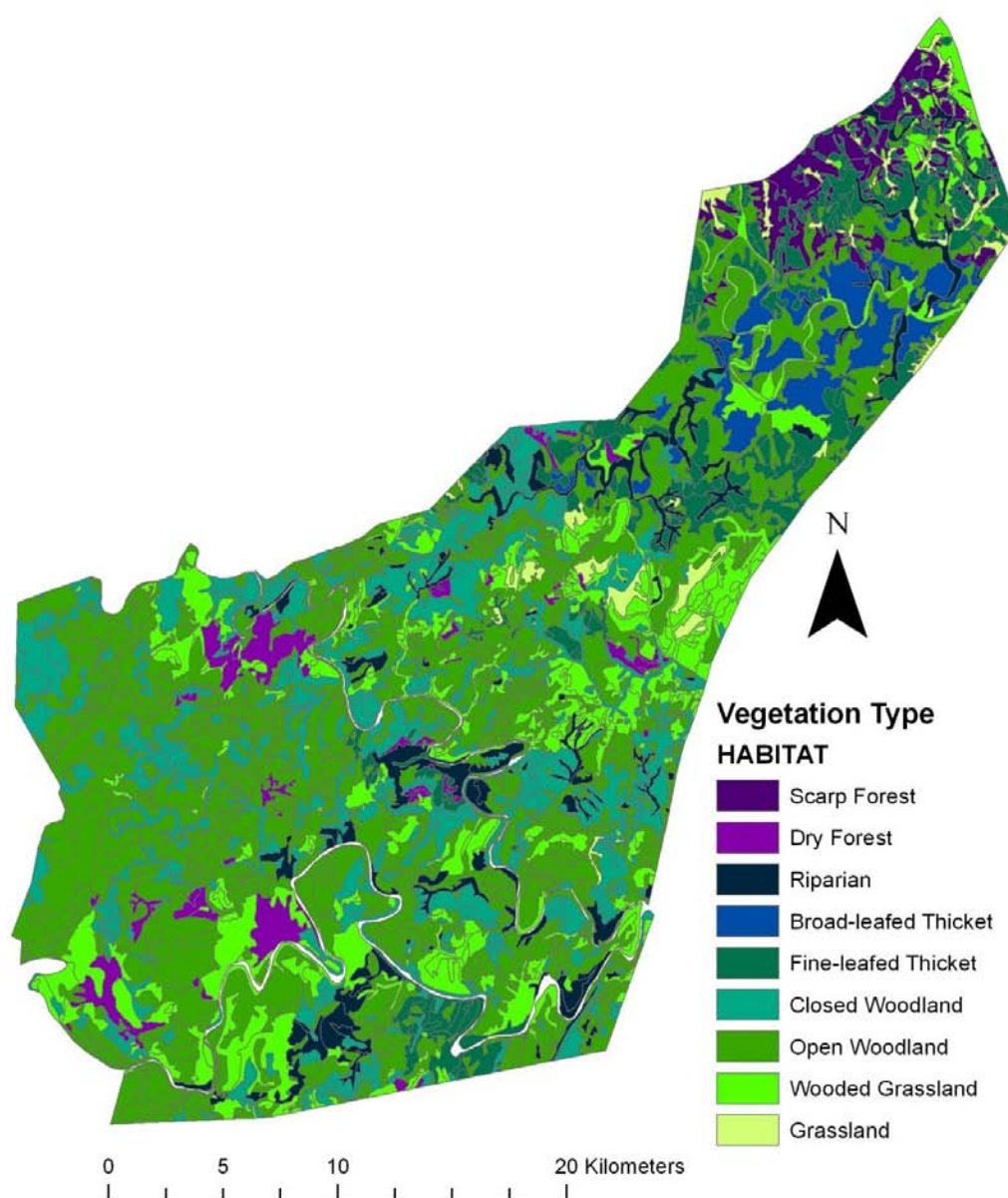
The vegetation of the park is extremely heterogeneous (Figure 2.4). The high altitude, high rainfall areas in the north end of the Hluhluwe section support forest patches (Whateley & Porter 1983). These are classified as scarp forest by Mucina & Rutherford (2006) and are often dominated by species such as *Harpephyllum caffrum* and *Celtis africana* (Mucina and Rutherford 2006). Riverine forest occur along the park's watercourses, and is normally dominated by *Ficus sycamorous* and *Schotia brachypetala* (Whateley & Porter 1983). The remainder of the park is dominated by a mixture of fine-leaved Acacia savannas and broad-leaved thicket. The Acacia savannas range from open to closed canopy patches, classified as savanna or woodland according to tree and grass cover by Whateley & Porter (1983). In Hluhluwe Game Reserve these are dominated by fine-leaved species such as *Acacia karroo*, *Acacia nilotica* and *Dichrostachys cinerea*. The broad-leaved thickets are dominated by *Euclea divinorum*, *Euclea racemosa*, *Spirostachys africana* and *Gymnosporia senegalensis*. Over the last few decades these broad-leaved thickets have encroached into previously open, grass dominated habitats, and fine-leaved savanna species have become denser (Watson & Macdonald 1983; Balfour & Howison 2002). Figure 2.3 shows two aerial photographs from 1937 and 2004 which illustrate how trees have encroached into previously open areas over time. The dominant grass species in the area is *Themeda triandra*, a highly flammable andropogonoid.



**Figure 2.3 Repeat aerial photographs from 1937 and 2004 show how the land cover has changed to become densely covered in bush and trees**

### **Study Sites**

Within the park I identified boundaries with closed, forested vegetation on one side and open, grassy vegetation on the other. These boundaries were classified as either temporally stable or



**Figure 2.4** Distribution of different vegetation types in the park according to the classification of Whateley and Porter (1983). Broad leaved thicket is already fairly dominant in the Hluhluwe section of the park even at this early stage

unstable based on repeat aerial photographs from 1937, 1960 and 2004. I then classified the vegetation in my study sites into four classes according to the stability of the boundary, rather than the species present within the habitat. „Forests’ were comprised of forested vegetation on a stable boundary. “Grasslands” were comprised of open grassy vegetation on a stable boundary. An example of a stable boundary can be seen in figure 2.5. “Savannas” were considered open grassy vegetation that contained some trees, but had a continuous grassy layer. “Thicket” patches were considered to be patches with a high density of trees whose



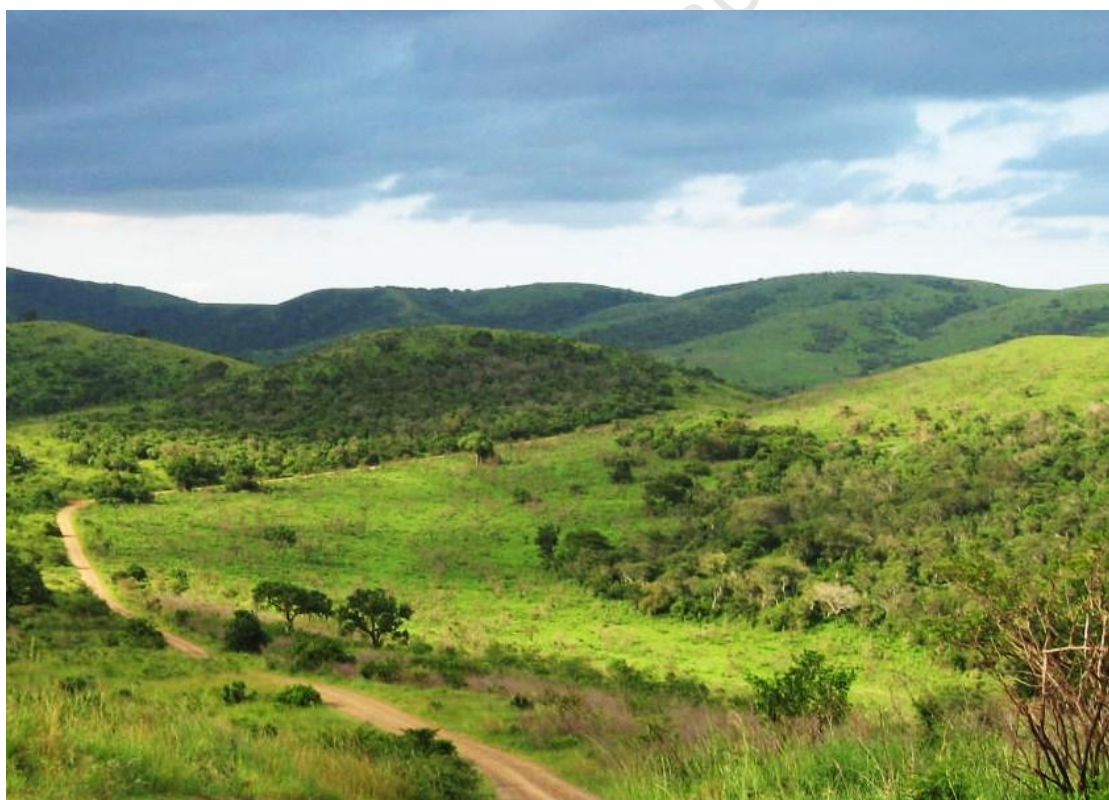
**Figure 2.5 A temporally stable boundary between forest in the background and grassland in the foreground**



**Figure 2.6 A temporally unstable boundary between thicket in the background and savanna in the foreground**

boundaries had expanded into surrounding savannas since the first aerial photograph in 1937, or patches which had not existed in the 1937 photograph but had since appeared. Because the woody patches had expanded over time I considered the boundary between savannas and thickets to be “unstable”, and an example of an unstable boundary can be seen in Figure 2.6. Thickets were different from forest in that often they still contained an herbaceous understorey with some grass cover. Both unstable and stable boundaries occur in areas where factors such as geology, aspect and slope are constant. All factors besides disturbance regimes were assessed to be uniform across the boundaries.

To reiterate what I mean by unstable boundaries, figure 2.7 shows two forested patches within a matrix of open grassy patches. We know from aerial photography that neither patch existed in a 1937 photograph, while only the one on the right existed in a 1967 aerial photograph. For this reason I consider the boundaries between these patches and their adjacent grassy vegetation to be unstable. These patches are therefore termed thicket patches.



**Figure 2.7 Photograph showing two thicket patches. The boundaries between these thicket patches and their adjacent grassy vegetation are considered unstable and changing due to aerial photographic evidence**

I identified eight unstable boundaries and five stable boundaries. Using adjacent paired boundaries allowed me to compare encroached and unencroached areas, as well as forests and

grasslands, without worrying about site differences. I used these boundaries to collect data for both Chapter 3 and Chapter 4.

The positioning of my study sites can be seen in Figure 2.1, while the geographical coordinates and soil type of each site are presented in table 2.1. I found soils to be uniform across vegetation boundaries. Common soils were oxidic soils with black, sandy clay surface layers between 30 and 60cm deep, overlying red, fine-textured subsoils of the Hutton form. Less common soils were melanic with dark, fine-textured, structured topsoils, over shallow subsoils onto rock of the Mayo or Inhoek Form (Fey 2010).

**Table 2.1 Co-ordinates and soil types of study sites**

Site code	Vegetation type	Boundary type	Latitude	Longitude	Soil Group	Soil form	Soil Series
FG1	forest-grassland	Stable	28.0792S	32.0425E	Oxidic	Hutton	Doveton
FG2	forest-grassland	Stable	28.0630S	32.0521E	Oxidic	Hutton	Doveton
FG3	forest-grassland	Stable	28.0609S	32.0518E	Oxidic	Hutton	Doveton
FG4	forest-grassland	Stable	28.0595S	32.0498E	Oxidic	Hutton	Doveton
FG5	forest-grassland	Stable	28.0721S	32.0335E	Oxidic	Hutton	Doveton
TS1	thicket-savanna	Unstable	28.1206S	32.0391E	Melanic	Mayo	
TS2	thicket-savanna	Unstable	28.1216S	32.0333E	Oxidic	Hutton	Doveton
TS3	thicket-savanna	Unstable	28.0554S	32.1318E	Melanic	Mayo	
TS4	thicket-savanna	Unstable	28.0650S	32.1192E	Oxidic	Hutton	Doveton
TS5	thicket-savanna	Unstable	28.0668S	32.1205E	Oxidic	Hutton	Doveton
TS6	thicket-savanna	Unstable	28.0738S	32.1308E	Oxidic	Hutton	Doveton
TS7	thicket-savanna	Unstable	28.0887S	32.0818E	Melanic	Mayo	Doveton
TS8	thicket-savanna	Unstable	28.1059S	32.0494E	Oxidic	Hutton	Doveton
BT1	burnt-unburnt thicket		28.0953S	32.1009E	Oxidic	Hutton	Doveton
BT2	burnt thicket		28.0937S	32.0942E	Oxidic	Hutton	Doveton
BT3	burnt thicket		28.0881S	32.0783E	Melanic	Inhoek	
BF1	burnt-unburnt forest		28.0786S	32.0485E	Oxidic	Hutton	Doveton

Although management fire policies have changed often over the last century, most areas in the Hluhluwe section have burnt at least nine times over the last 60 years (Figure 2.2) (Balfour and Howison 2002). Despite these fairly regular fires woody plant thickening has been much more prevalent in this section of the park than iMfolozi Game Reserve, which was burnt far less regularly.

## Chapter 3

### Plant Diversity and Woody Plant Encroachment in Hluhluwe Game Reserve

#### Introduction

Many grasslands exist because soils or climate make it difficult for trees to grow. However, many also occur in soils and climates which are perfectly capable of supporting forests (Bond 2010). In many of these landscapes they coexist in a patch mosaic with forests (Perez-Garcia & Meave 2006). One such system is the Hluhluwe-iMfolozi Park (HiP). Forests, grasslands and savannas co-exist in the HiP landscape to form a heterogeneous patch mosaic of open and closed vegetation. The presence of open grassland in areas that are capable of supporting forests led historians to suggest that these grasslands and savannas originated during the Iron Age when humans cleared forest trees for firewood and to make space for farming (Acocks 1953; Feely 1980). Human influence was a popular explanation for the presence of many grasslands and savannas throughout the world, which led these systems to be largely ignored by conservationists until recently (de La Bâthie 1936; Axelrod 1985; Banerjee 1995; Anderson 2006).

Recent literature has shown that a drop in atmospheric CO<sub>2</sub> about 25-30Mya resulted in the convergent evolution of C<sub>4</sub> photosynthesis in more than 45 independent lineages (Sage 2004; Osborne & Beerling 2006; Edwards et al. 2010). Many grasslands and savannas are dominated by C<sub>4</sub> grasses, and studies have shown that plants using this pathway came to dominate the global landscape between 4-8Mya (Cerling et al. 1997), when a combination of climate and increased fire occurrence are thought to have created a positive feedback promoting the spread of grasses (Keeley & Rundel 2005; Beerling & Osborne 2006; Osborne & Beerling 2006; Osborne 2008). The rapid expansion of these biomes on a global scale predates human influence on the landscape, and has been shown by numerous studies (Ellery & Mentis 1992; Meadows & Linder 1993; Cerling et al. 1997; Beisner et al. 2003; Osborne & Beerling 2006; Osborne 2008; Edwards et al. 2010). Indeed a study by West et al. (2000) using carbon isotopes as a proxy for vegetation history showed that many grasslands in the HiP forest-grassland-savanna mosaic are more ancient than their adjacent forests.

This suggests that rather than being seral to forests as has been suggested for the central grasslands of North America (Axelrod 1985; Anderson 2006), a more appropriate way of thinking of the grasslands and savannas in the HiP system are as alternative stable ecosystem states to forest (Scheffer & Carpenter 2003; Warman & Moles 2009). Alternative stable ecosystem states occur when more than one stable state is possible for the same set of environmental conditions. In the HiP mosaic of alternative stable states there are grasslands, savannas and forests. Savannas are defined as systems which have a more or less continuous C<sub>4</sub> grassy layer, with variable tree densities (Scholes & Archer 1997; Ratnam et al. 2011). These trees are generally shade intolerant, and tolerant of frequent fires, as are the grasses and herbaceous plants in their understorey. Grasslands also have a continuous C<sub>4</sub> grassy layer and are subject to similar disturbance patterns, but they contain few to no trees and often occur at higher altitudes than savannas. Forests lack a grassy understorey, and are dominated by fire sensitive, shade tolerant species (Bond & Parr 2010). The boundaries between either forest and grassland or savanna and grassland are maintained by a series of positive feedbacks in each system which are hostile to the other system. These boundaries can be relatively stable in time, such as those in Madagascar (Virah-Sawmy et al. 2009), but can undergo rapid regime shifts to the alternative state in a surprisingly short space of time (Scheffer & Carpenter 2003). Scheffer and Carpenter (2003) suggest that these shifts occur when some environmental threshold is reached, and that they may be difficult to reverse. Over the past few decades woody plant encroachment into savannas has occurred extensively in HiP. This woody plant encroachment may be evidence of a regime shift occurring.

Woody plant encroachment can refer to two processes. It can refer to a thickening of fine-leaved woody savanna species (eg. Kraaij & Ward 2006), or it can refer to an influx of broadleaved forest species into the system (eg. Brook and Bowman 2006). These two processes are distinguished in a schematic in figure 1.1 in Chapter 1. It is important to distinguish these two processes as they have very different implications. If it is just a thickening of savanna species, the implication is that it is reversible, and will not change the ecology of the system entirely. However, if it is an influx of forest species, it may eventually lead to a complete switch in community composition and a biome switch to forest. A complete switch to forest will mean a more homogenous landscape and a reduction in fire frequency as well as adjustments to other disturbance regimes.

Fire played an essential part in the expansion that led to the dominance of C<sub>4</sub> grassy biomes during the Miocene (Keeley & Rundel 2005; Osborne 2008), so it is not surprising that many species in these biomes are highly tolerant of fire and are often reliant on fire for survival (Simon et al. 2009). Many have been found to utilise underground storage organs which allow them to resprout rapidly after fire (Uys et al. 2004; Laden & Wrangham 2005; Simon et al. 2009). Although savanna grassland forbs are tolerant of many disturbances, many are entirely intolerant of shade (Uys et al. 2004). They survive being shaded out by grasses by exploiting the brief seasonal period when grasses die back, either in early growing season or after a fire (Bond & Parr 2010). Unfortunately this brief respite does not exist when trees move into a system, so many of these forbs are unable to survive in a forested environment. A study by Uys et al. (2004) in South African grasslands found that many grassland forbs disappeared from the system after fire-free intervals of 8 years or more, because there were not sufficient gaps to prevent shading out. Brazilian „Campo’ grassland forbs showed a similar dependence on fire, with diversity declining in areas where fire was kept out (Overbeck & Pfadenhauer 2007; Overbeck et al. 2007).

The changes to the fire regime and density of trees that are occurring with woody plant encroachment in HiP mean that heterogeneity in the landscape will be reduced. Savannas and grasslands contribute significantly to diversity in some systems (Perez-Garcia & Meave 2006; Overbeck et al. 2007; Sankaran 2009; Bond & Parr 2010), and the situation in HiP may be comparable. The Cerrado biome of Brazil is ranked twelfth on a list of global „hot spot’ areas (Mittermeier et al. 1998) and is extremely diverse, containing about 6000 plant species (Ratter et al. 1997). The „Campo’ biome of southern Brazil contains about 3000-4000 plant species in an area of 137 000 km<sup>2</sup> (Overbeck et al. 2007), which is highly diverse, and comparable to the Highveld grasslands of South Africa, which contain about 3800 species in 112 000 km<sup>2</sup> (Cowling et al. 1989). The Western Ghats of India are another biodiversity hotspot, and were found to contain 278 plant species in only 40 10x10m plots (Sankaran 2009). The North American tall grass prairies are one of North America’s most endangered ecosystems, and woody plant encroachment in this system has been found to reduce species richness by up to half (Briggs et al. 2005).

In this study I investigate the contribution that each vegetation type in the mosaic makes to total diversity in the HiP patch mosaic by comparing species richness of habitats and assessing the amount of overlap in species composition between habitats. I also determine

characteristic species of each habitat. Each system is currently subject to different disturbances, and therefore is likely to be floristically distinct. I also compare encroached and unencroached areas in an attempt to determine whether woody plant encroachment is likely to result in a complete biome switch to forest, or whether it is just a thickening of savanna species, in which case it may be more easily reversed. In the context of a conservation area it is extremely important to understand the relative contribution that each vegetation type makes to overall diversity. It is also important to understand the effects that woody plant encroachment will have on species diversity, so that appropriate management decisions can be made.

## **Methods**

### **Project design**

Plots were sampled over October and November 2009. Using aerial photos from 1937 and 2004 I identified adjacent encroached and unencroached savanna sites (classified as thicket and savanna respectively). Encroached sites were broadleaved thicket patches whose boundaries had expanded into savannas over the last century, identified using repeat aerial photographs. These boundaries are considered to be changing, as the thicket is actively moving into the savanna. I also identified adjacent forest and grassland sites, whose boundaries I considered to be stable, as they have not changed over the last few decades. All in all I identified 8 thicket-savanna sites, and 5 forest-grassland sites. The thicket-savanna boundaries were subsequently divided into older and newer thickets based on evidence from aerial photographs. New thickets were less than 50 years old, while old thickets were more than 70 years old. One hundred metre long transects were set up perpendicular to thicket-savanna and forest-grassland boundaries. Every ten metres along the transect 2x2m plots were marked out, to make five 2x2m plots in each habitat at each boundary. This gave me 40 plots in thicket, 40 plots in savanna, 25 plots in grassland and 25 plots in forest. All plant species within the plots were identified. Abundances were recorded for woody and herbaceous species by counting the number of individuals of each species present in each quadrat, whilst grass species were recorded as present or absent.

### *Fire*

Originally, investigations into fire effects on woody plant encroachment were not part of the project design. However, during September 2008 a fire swept through the park. This was an

unusually intense fire, and was able to burn through many encroached thicket patches. An attempt to measure how intense the fire was is made in Catherine Brown's thesis (University of Cape Town 2009). Although none of my original study sites were burnt, I decided to set out more plots in the burnt areas, in order to compare them to unburnt sites. I identified one site with adjacent burnt and unburnt thicket, one site with only burnt thicket, one site with adjacent burnt thicket and burnt savanna, and one site with adjacent burnt and unburnt forest. My intention was to use this data to determine whether grassland or savanna species were able to persist cryptically within encroached areas, and whether they were able to recover rapidly after a burn. If they were indeed persisting and able to recover rapidly, there would be scope to use intense fires as a way of reversing woody plant encroachment. I sampled these plots during November 2009, just over a year after they had been burned, using the same methods as my original plots.

## **Analyses**

### *Habitat Similarity*

The similarity in species composition between habitats was calculated using the Sørensen Index. This is calculated using the equation  $SI = \frac{2C}{A+B}$

Where  $A$  and  $B$  are the total number of species in habitats A and B, respectively, and  $C$  is the number of species shared by the two habitats.

### *Species accumulation curves*

A species accumulation curve records the total number of species revealed during the process of data collection, as additional individuals are added to the pool of all previously observed or collected samples (Gotelli & Colwell 2001). Comparing species richness without reference to a sampling curve is problematic. Communities may differ in measured species richness because of differences in underlying species richness, differences in the shape of the relative abundance distribution, or because of differences in the number of samples (Denslow 1995). Differences in numbers of individuals counted may reflect biologically meaningful patterns of resource availability or growth conditions. However, differences in abundance may also reflect differences in sampling effort or conditions for collection or observation. Comparing raw taxon counts for two or more assemblages will generally produce misleading results. Raw species richness counts can only be validly compared when taxon accumulation curves have reached a clear asymptote. The usefulness of this method is that if there has been too

little replication, so that the accumulation curves fail to reach an asymptote, the curves themselves may often be compared, after appropriate scaling. I used the EstimateS package (Colwell 2006) to estimate species richness by computing sample-based rarefaction curves. These are produced by repeatedly re-sampling the pool of N samples, at random, and plotting the average number of species represented by 1, 2,..., N samples. Sampling is generally done without replacement, within each re-sampling. Thus, rarefaction generates the expected number of species in a small collection of n samples drawn at random from the large pool of N samples (Simberloff 1978).

#### *Multi-dimensional Scaling Ordination*

The Sørensen Index takes only species presence/absence into account, so in order to compare habitats based on species abundance I used the community analysis program PRIMER to explore floristic patterns in my transect data. I used abundance scores for all species except grass species. Data from the 50m transects in each habitat were combined to get one measure for each site, to avoid pseudo-replication and ensure I had the most representative estimate of diversity. Similarity of plots was estimated using the Bray-Curtis dissimilarity index. Abundance is considered in weighing species contributions in the Bray-Curtis dissimilarity index (Bray & Curtis 1957). Data were visually presented through a multi-dimensional scaling (MDS) ordination. MDS uses rank correlations and seeks to provide an accurate visual representation of the similarity between a set of samples, on the basis of their species profiles. The stress value associated with a particular representation provides a measure of its accuracy: a stress value of above 0.2 indicates a limited ability to portray sample relationships (Clarke & Warwick 2001).

#### *Characteristic species*

Characteristic plant species of each habitat type were identified using the Indicator Value method (Dufrene & Legendre 1997). This method assesses the degree to which a species fulfils the criteria of specificity (uniqueness to a particular habitat or site) and fidelity (frequency of occurrence). A high indicator value (IndVal, expressed as %) indicates that a species has high specificity and fidelity, and the species can be considered characteristic of a particular habitat or site. This method can derive indicators for hierarchical and non-hierarchical site classifications, and is robust to differences in the numbers of sites between site groups (McGeoch et al. 2002). Indicator values for each species were calculated based on a species abundance matrix, and Dufrene & Legendre's (1997) random reallocation

procedure of sites among site groups was used to test for the significance of IndVal measures for each species. Species with significant IndVals >70 % were considered as species characteristic of the site or habitat in question (subjective benchmark, McGeoch et al. 2002). I expected that the species composition of younger thickets would show more species that were characteristic of grasslands and savannas than the older thicket patches. Indval values were determined using the following equations:

$$A_{ij} = \frac{N_{individuals_{ij}}}{N_{individuals_i}}$$

$$B_{ij} = \frac{N_{sites_{ij}}}{N_{sites_j}}$$

$$Indval_{ij} = A_{ij} \times B_{ij} \times 100$$

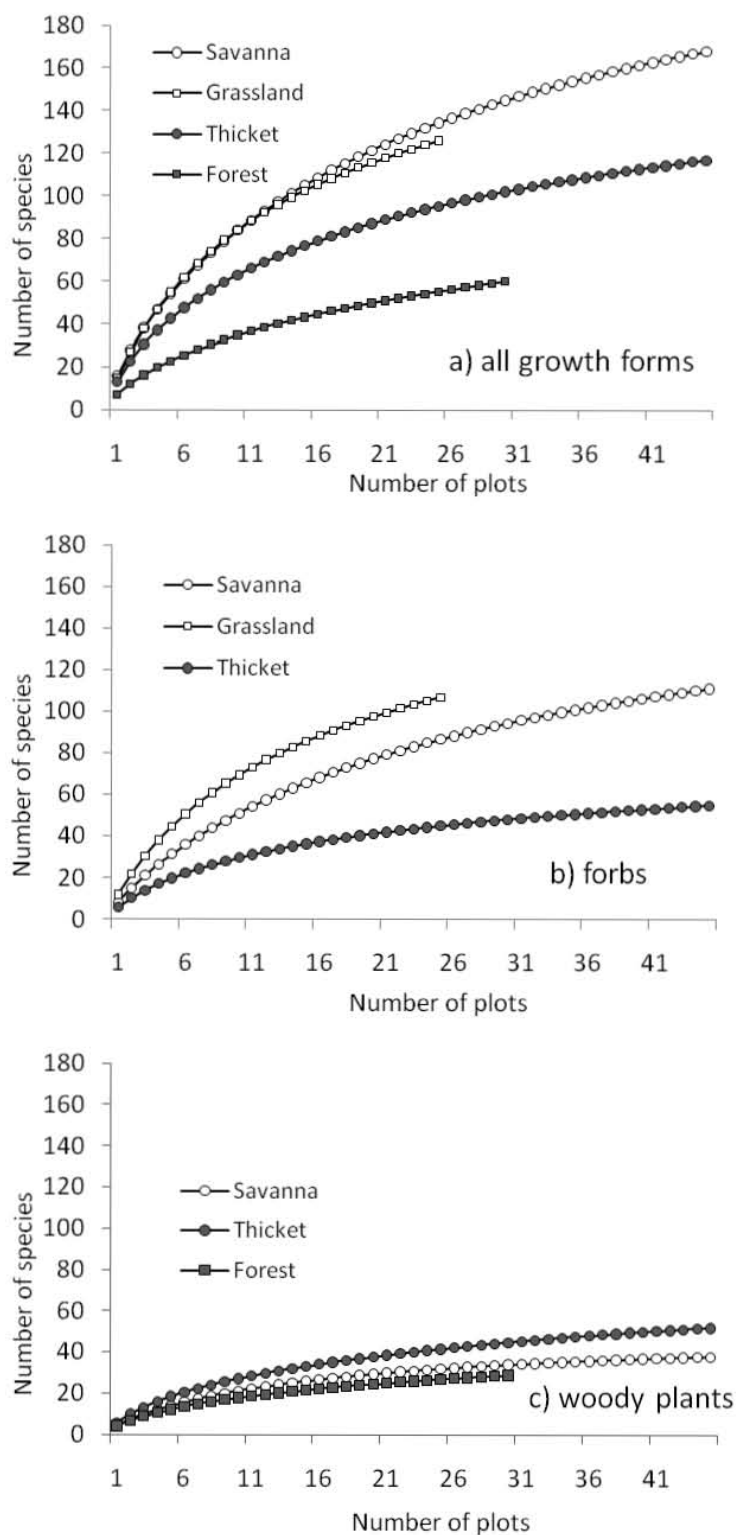
where  $IndVal_{ij}$  is the Indicator Value of species  $i$  in site cluster  $j$ . In the formula for  $A_{ij}$  (a measure of specificity),  $N_{individuals_{ij}}$  is the mean number of individuals of species  $i$  across sites of habitat  $j$ , while  $N_{individuals_i}$  is the sum of the mean numbers of individuals of species  $i$  over all habitats. I used the mean number of individuals in each habitat, instead of summing the individuals, because this removes any effect of the number of sites in the various habitats, and of differences in abundance among sites belonging to the same habitat. In the formula for  $B_{ij}$  (a measure of fidelity)  $N_{sites_{ij}}$  is the number of sites in habitat  $j$  where species  $i$  is present, while  $N_{sites_j}$  is the total number of sites in that habitat.  $B_{ij}$  is maximum when species  $i$  is present in all objects of habitat  $j$ .

## Results

### The Hluhluwe Game Reserve Vegetation Mosaic

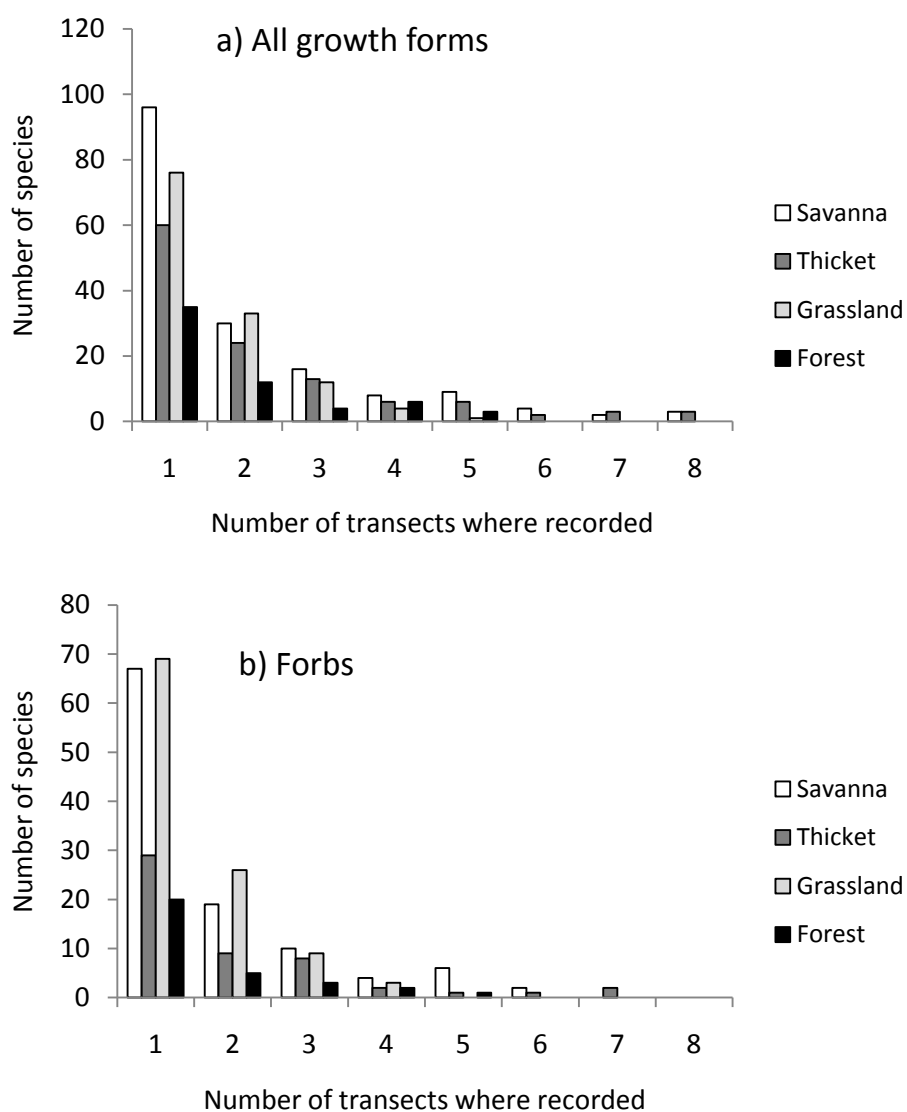
Figure 3.1 shows species accumulation curves in each habitat for all growth forms (Figure 3.1a), forbs (Figure 3.1b) and woody plants (Figure 3.1c). Savannas were the most species rich habitat overall, with 168 species in 45 2x2m plots (Figure 3.1a). Grasslands contained 126 species in 25 2x2m plots, and the species accumulation curve in figure 1a suggests that this curve would reach an asymptote just below that of savannas. Thickets contained 117 species in 45 2x2m plots, while forests contained 60 species in 30 2x2m plots. The diversity within growth forms differed between habitats. Grasslands contained 107 forb species in 25 2x2m plots, while savannas contained 111 in 40 2x2m plots (Figure 3.1b), suggesting that

grasslands are more species rich with regards to forbs than savannas. Thickets contained the least forb species (besides forests which are not shown) (Figure 3.1b). Thickets contained 52 woody species, savannas contained 38 woody species, and forests contained 29 woody species in 30 2x2m plots (Figure 3.1c).



**Figure 3.1** Species accumulation curves for a) all growth forms b) forbs and c) woody plants in different vegetation types

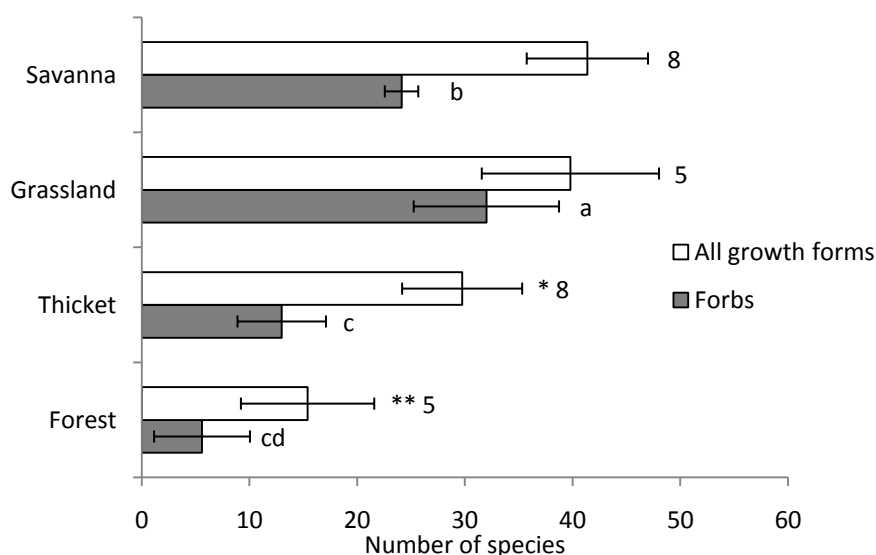
Figure 3.2 shows the number of rare species in each habitat, where a rare species is one that occurs in only one transect. Figure 3.2a shows all growth forms and figure 3.2b shows only forbs. Savannas had 96 rare species, much higher than thickets which had 60. Grasslands had 76 rare species, almost three times as many as forests which had 35. 69 of the rare species in grasslands were forbs, a higher proportion than savannas, of which 67 of 96 were forbs. Savannas contained more than double the number of rare forbs than thickets, which had 29 rare forbs. Forests contained 20 rare forb species, which although low compared to other habitats, is two thirds of all the forbs found in forests.



**Figure 3.2** Bar chart showing the number of transects each species was found in for each habitat, for a) all growth forms and b) forbs

Figure 3.3 shows the mean number of species per transect for each habitat type. Savannas and grasslands had means of  $41.4 \pm 5.6$  and  $39.8 \pm 8.2$ , which were significantly higher than forests

and thickets. Grasslands had the highest mean number of forb species in each transect ( $32.0 \pm 6.7$ ), significantly higher than other habitats. The mean number of forb species in savannas ( $24.1 \pm 1.6$ ) was significantly higher than the mean for thickets ( $13.0 \pm 4.1$ ) and forests ( $5.6 \pm 4.4$ ).



**Figure 3.3 Mean number of species ( $\pm$ s.d.) per transect in each habitat for all growth forms (white blocks) and forbs (grey blocks). Asterisks and letters indicate significant differences at  $\alpha=0.05$  using a one way ANOVA and Tukey tests. Numbers indicate number of transects**

Table 3.1 shows the number of species in each habitat, as well as the number of shared species between habitats and the Sørensen Index of similarity between these habitats. Savannas and thickets had a Sørensen Index of 0.45, indicating that they were the most similar of all the habitats. More than half of the species (55%) found in thickets were also found in savannas. In contrast, only 38% of the species found in savannas were also found in thickets. Grasslands and savannas were the second most similar, with a Sørensen Index of 0.37. Grasslands shared 43% of their species with savannas, while savannas shared 32% of their species with grasslands. Thickets and forests had a Sørensen Index of 0.35, with forests sharing 52% of their species with thickets and thickets sharing 26% of their species with forests. Forests shared very few species with savannas and grasslands. Grasslands and forests had a Sørensen Index of 0.14 and savannas and forests had a Sørensen Index of 0.13.

**Table 3.1** The total number of species found in each habitat as well as the similarity between habitats, calculated using the Sørensen Index. Numbers in parentheses indicate total number of 2x2m plots sampled

Habitat comparisons	Forest species (25)	Grassland species (25)	Thicket species (40)	Savanna species (40)	Shared species	Total species	Sørensen Index
Thicket and Savanna			117	168	64	221	0.45
Savanna and Grassland		126		168	54	240	0.37
Thicket and Forest	60		117		31	146	0.35
Forest and Grassland	60	126			13	173	0.14
Forest and Savanna	60			168	15	213	0.13
All habitats	60	126	117	168	234	336	

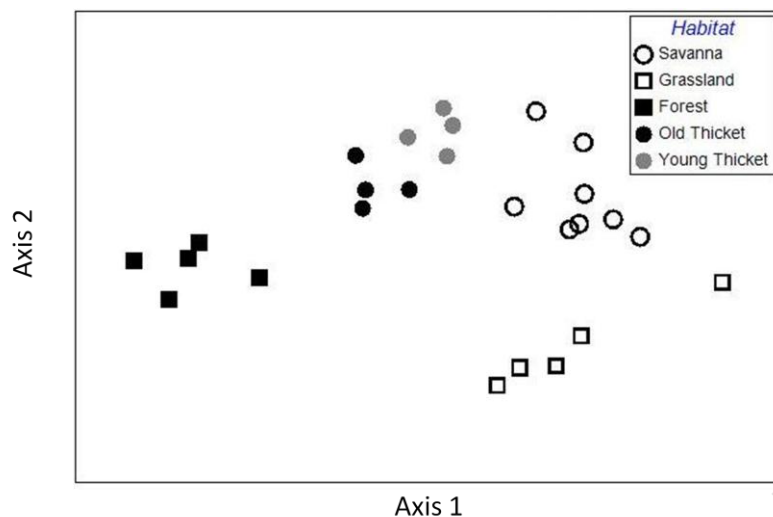
Table 3.2 shows the number of species found in older and younger thickets, separated into growth forms. It also indicates the number of shared species and the Sørensen Index of similarity between these habitats. They had a Sørensen Index of 0.49 when all growth forms were taken into account. This is only slightly higher than the similarity index of thickets and savannas, which was 0.45. Young thickets contained almost 50% more species than older thickets. Old thickets shared 59% of all their species with younger thickets, while younger thickets shared 42% of all their species with older thickets. Sørensen Indices for forbs and woody plants were much the same (Table 3.2). Old thickets had far fewer forbs than younger thickets, and shared 65% of their forbs with young thickets, while young thickets shared 37% of their forbs with older thickets. Woody plant numbers were more similar, with younger thicket species numbers marginally higher. Old thickets shared 55% of their woody plants with young thickets, and young thickets shared 45% of their woody plants with older thickets.

**Table 3.2** The total number of species found in old and young thickets as well as the similarity between them, calculated using the Sørensen Index. Numbers in brackets indicate total number of 2x2m plots sampled

	Old Thicket species (20)	Young Thicket species (20)	Shared species	Total species	Sørensen Index
All growth forms	64	91	38	117	0.49
Forbs	26	46	17	55	0.47
Woody plants	31	38	17	52	0.49

Figure 3.4 is an MDS ordination showing the compositional similarity of habitats in ordination space. This used a Bray-Curtis Similarity Index which takes species abundance as

well as richness into account. Thickets and savannas were more compositionally similar than forests and grasslands. Younger thicket patches were more similar to savannas, and older thicket patches were more similar to forests. Grasslands and savannas were compositionally similar along axis 1.



**Figure 3.4** MDS ordination of different vegetation types based on species abundances. Data were square root transformed. The ordination was run with a Bray Curtis similarity matrix. 2D stress value= 0.11

### Fire

To investigate the effect that extreme fires have on thicket diversity, I sampled three recently burnt thicket patches and compared these to unburnt thickets and savannas. Table 3.3 shows the number of species in unburnt thicket and burnt thicket, separated into growth forms, as well as the number of species that are shared between habitats. It also shows the similarity between the habitats based on the Sørensen Index. Burnt thickets shared 54% of all their species with unburnt thickets, while unburnt thickets shared 34% of their species with burnt thicket. The Sørensen Index of similarity between these habitats was 0.42. Burnt thickets were dominated by forbs, and shared 44% of these with unburnt thickets, while unburnt thickets shared 40% of their forbs with burnt thickets. Burnt thickets were sampled less intensively, and so with increased sampling their forb diversity may surpass that of unburnt thickets. Burnt thickets shared 79% of their woody species with unburnt thickets, while unburnt thickets shared 29% of their woody species with burnt thickets.

**Table 3.3 The number of species in burnt and unburnt thicket, and the number of species shared between these habitats**

	Burnt Thicket (15)	Unburnt Thicket (40)	Shared	Total	Sørensen Index
All Growth Forms	74	117	40	151	0.42
Forbs	50	55	22	83	0.42
Woody Plants	19	52	15	56	0.42

Table 3.4 shows the number of species in savanna and burnt thicket, separated into growth forms, as well as the number of species shared between habitats. It also shows the similarity between the habitats based on the Sørensen Index. Burnt thickets share 55% of all their species with savannas, while savannas share 24% of their species with burnt thicket. The similarity between these habitats was found to be 0.34. 50% of forbs found in burnt thickets were also found in savannas, while 22% of savanna forbs were also found in burnt thickets. The similarity between the habitats based solely on forbs was found to be 0.31. 68% of burnt thicket woody species were found in savannas, while 34% of savanna woody species were found in burnt thicket. The Sørensen Index between these habitats when only woody species were taken into account was much higher, at 0.46.

**Table 3.4 The number of species in burnt thicket and unburnt savanna, and the number of species shared between these habitats**

	Burnt Thicket (15)	Savanna (40)	Shared	Total	Sørensen Index
All Growth Forms	74	168	41	201	0.34
Forbs	50	114	25	139	0.31
Woody Plants	19	38	13	44	0.46

In order to take species abundances into account the MDS ordination in figure 3.5 uses the Bray-Curtis similarity Index. It shows the similarity between thickets, savannas and burnt thickets in ordination space. Along axis 1, burnt thickets appear to be midway between thickets and savannas compositionally, as the results in tables 3.3 and 3.4 suggested.

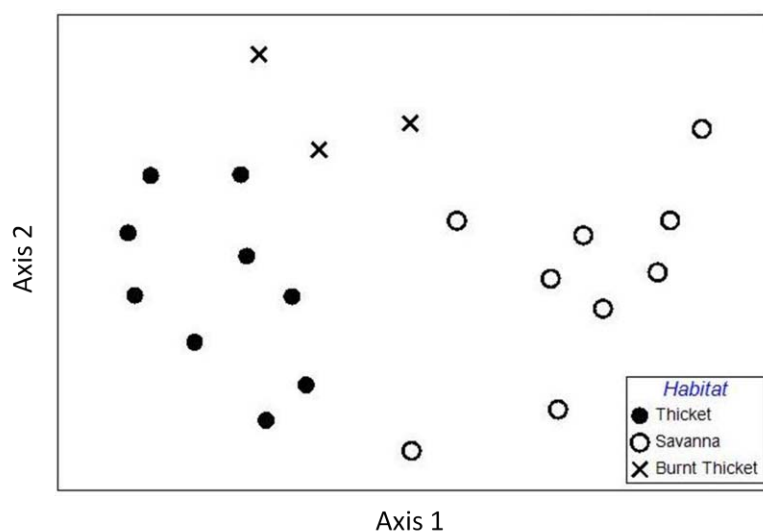


Figure 3.5 MDS ordination of savannas, thickets and burnt thickets based on species abundances. Data were square root transformed. The ordination was run with a Bray Curtis similarity matrix. 2D stress value = 0.15

### Characteristic species

Species characteristic of savannas, thickets and burnt thickets are displayed in Table 3.5. A high Indval value suggests high specificity and fidelity of that species for a particular habitat. The forb species most characteristic of thickets was *Plectranthus verticillatus* (58.1%). This species is well known for thriving in shade, and does not utilise an underground storage organ to regenerate quickly after fire. *Chromolaena odorata*, an invasive pest, was fairly characteristic of thickets (47.4%). *Euclea racemosa* was the most characteristic woody species of thickets (91.3%). This is a slow growing, broad leafed species which is tolerant of shade. It does not thrive in fire prone areas, although I did find it regenerating after fires that were not too intense. *Gerbera ambigua* was the most characteristic forb species in savannas (65.5%), which is a fast growing species. *Acacia karroo* was the most characteristic woody species in savannas (72.8%). This is a typical savanna species, which is highly tolerant of fire. Forb species that were characteristic of recently burnt thickets were *Melhania didyma* (91.3%), *Solanum panduriforme* (87.9%) and *Sida cordifolia* (76.8%). These species are known to thrive in disturbed areas, taking advantage of gaps. *Cordia caffra* (91.3%) was a characteristic woody species in burnt thickets. *Dactyloctenium australe* was the most characteristic grass species in thickets. This grass is known to thrive in shade.

**Table 3.5 Characteristic species of savannas, thickets and burnt thickets. High Indval percentages suggest high specificity and fidelity of that species for a given habitat. (\*) indicates species is not indigenous**

Growth form	Savanna	Indval (%)	Thicket	Indval (%)	Burnt Thicket	Indval (%)
<b>Forb</b>	<i>Gerbera ambigua</i>	65.5	<i>Plectranthus verticillatus</i>	58.1	<i>Melhania didyma</i>	91.3
	<i>Ruellia cordata</i>	60.3	<i>Dalechampia capensis</i>	51.5	<i>Solanum panduriforme</i>	87.9
	<i>Oxalis smithiana</i>	58.0	* <i>Chromolaena odorata</i>	47.4	<i>Sida cordifolia</i>	76.8
	<i>Sida dregii</i>	50.0			<i>Abutilon grantii</i>	50
<b>Woody</b>	<i>Acacia karroo</i>	72.8	<i>Euclea racemosa</i>	91.3	<i>Cordia caffra</i>	91.3
	<i>Dichrostachys cinerea</i>	62.9	<i>Maytenus heterophylla</i>	66.4	<i>Combretum apiculatum</i>	66.7
	<i>Sclerocarya birrea</i>	55.6	<i>Zanthoxylum capense</i>	65.5	<i>Euclea racemosa</i>	46.5
<b>Grass</b>	<i>Setaria sp.</i>	66.7	<i>Dactyloctenium australe</i>	75.0	<i>Dactyloctenium australe</i>	33.3
	<i>Eragrostis curvula</i>	60.3	<i>Panicum maximum</i>	46.4	<i>Panicum maximum</i>	26.7
	<i>Themeda triandra</i>	53.0				

Species characteristic of older thickets and younger thickets are displayed in Table 3.6. *Justicia flava* (79.3%) was characteristic of new thickets while the invasive alien *Bidens pilosa* (75.0%) was the most characteristic of older thickets. *Isoglossa woodii*, a species which only flowers every seven years, was also characteristic of older thickets. *Dalbergia obovata* (85.3%) is a woody species that was characteristic of older thickets, and can tolerate both sun and shade, although it is fairly fire sensitive. *Diospyros simii* (79.7%) and *Berchemia zeyheri* (77.3%) are woody species most characteristic of younger thicket.

**Table 3.6 Characteristic species of older thickets and younger thickets. High Indval percentages suggest high specificity and fidelity of that species for a given habitat. (\*) indicates species is not indigenous**

Growth form	Old Thicket	Indval (%)	New Thicket	Indval (%)
<b>Forb</b>	* <i>Bidens pilosa</i>	75.0	<i>Justicia flava</i>	79.3
	<i>Isoglossa woodii</i>	51.1	<i>Dalechampia capensis</i>	59.2
<b>Woody</b>	<i>Dalbergia obovata</i>	85.3	<i>Diospyros simii</i>	79.7
			<i>Berchemia zeyheri</i>	77.3
<b>Grass</b>			<i>Dactyloctenium australe</i>	34.8

Species characteristic of forests and grasslands are displayed in Table 3.7. Forests contained many species that could act as indicators (eg. the forb *Coleotrype natalensis* (100%) and the tree *Englerophytum natalense* (100%)). These species are all shade loving, slow growing

plants that are intolerant of fire. In contrast forb species indicative of grasslands were species such as *Eriosema preptum* (71.5%) and *Vernonia oligocephala* (60.1), which are sun loving, fire tolerant species. Grasslands had no woody species with high Indval values, and their grasses were not very specific to grasslands either, as they shared them with savannas.

**Table 3.7 Characteristic species of forests and grasslands. High Indval percentages suggest high specificity and fidelity of that species for a given habitat. (\*) indicates species is not indigenous**

Growth form	Forest	Indval (%)	Grassland	Indval (%)
Forb	<i>Coleotrype natalensis</i>	100	<i>Eriosema preptum</i>	71.5
	<i>Phaulopsis imbricatus</i>	62.2	<i>Vernonia oligocephala</i>	60.1
	<i>Schoenoxiphium madagascariense</i>	53.3	<i>Desmodium incanum</i>	60
			<i>Indigofera hiliaris</i>	60
			<i>Ipomoea obscura</i>	60
Woody	<i>Englerophytum natalense</i>	100	<i>Diospyros galpinii</i>	40
	<i>Celtis africana</i>	92.0		
	<i>Monanthonotaxis caffra</i>	83.3		
Grass			<i>Eragrostis superba</i>	50.6
			<i>Themeda triandra</i>	40.9

## Discussion

Each habitat supported a distinct array of species, and contributed significantly to the overall biodiversity of the system. However, in contrast to common perceptions, I found that savannas and grasslands contributed most notably to the diversity of the system. This was especially true for forb species. My results are in accordance with studies in other grasslands and savannas throughout the world (Cowling et al. 1989; Overbeck et al. 2007; Bond et al. 2008; Sankaran 2009), which have also found high forb diversity in the grassy layer of these open systems. There is a significant reduction in species numbers in encroached areas compared to open areas, a result consistent with that found by Briggs et al. (2005) after woody plant encroachment in North American tall grass prairies.

My results showed a large shift from savanna species to forest species occurring with woody plant encroachment. Species composition and abundances in thickets indicated that they contained both savanna and forest elements, and that older thickets could be considered an early successional stage to forests, as they were compositionally more similar to forests,

while younger thickets were compositionally more similar to savannas. This was not the case for savannas and grasslands, which had very little species overlap with forests, refuting the idea that they are seral to forests.

I found the species most characteristic of thicket habitats to be shade tolerant, fire intolerant species. For example, the forb most characteristic of thickets, *Plectranthus verticillatus*, does not have an underground storage organ, so it would struggle to resprout rapidly after a fire. The grass most characteristic of thickets was *Dactyloctenium australe*, a shade tolerant grass which does not burn easily, just as *Euclea racemosa*, the tree most characteristic of thickets, is a shade tolerant tree which cannot withstand intense fires. The presence of these evergreen species is likely to play a role in preventing fire from entering the system, which would then allow more shade tolerant, fire intolerant species into the system, to form a positive feedback and hasten the switch to forest. My data strongly suggest that the encroachment that is occurring in my study area is not merely a thickening of savanna species, but a change in species composition indicating a complete biome switch to forest.

With such high levels of diversity, the threat that woody plant encroachment poses to the savannas and grasslands of a conservation area such as HiP needs to be taken seriously.. In addition these grassy habitats may contain many economically important species. Many of the forb species in my study area are already known to have medicinal qualities, such as *Gerbera ambigua* which is used to treat tapeworm (Pooley 1999). It is entirely probable that there are many more waiting to be discovered so losing these grassy systems could mean the loss of many medicinal species.

But it is not only the plant species that will be affected with an invasion of woody plants. The drastic and rapid shift in species abundances and diversity which my data have shown is likely to have cascading consequences for fauna as well as flora (Skowno & Bond 2003; Andersen et al. 2006; Sirami et al. 2009). In this case it may not be the actual species loss, but the structural changes in vegetation which may have the most effect. With an increase in tall, woody, shady plants, the available habitat changes entirely. Birds have been shown to respond to changes in habitat structure associated with woody thickening in the park (Skowno & Bond 2003; Sirami et al. 2009). Insect diversity has also been shown to be fundamentally altered in the park, with species richness as well as abundance significantly reduced with woody plant encroachment (Catherine Parr, Emma Gray, William Bond,

unpublished). Habitat specificity of insects has also been shown in Australia (Andersen et al. 2006). Mammal diversity may be expected to switch from open plains adapted grazers, to forest adapted browsers.

Although I have painted a fairly dire picture of forest encroachment into savannas, the situation may not be completely out of our hands. A study by Wigley et al. (2010) showed that while woody plant encroachment is occurring across all land use types, land management practices do affect the extent of it. This suggests that the spread of thicket may be controlled with land management practices such as increased fire frequency, or use of more intense fires. The brief survey of burnt thicket patches that I did suggested that after an intense fire many savanna forbs are able to return to the system, suggesting either that their underground storage organs have allowed them to persist cryptically in thicket patches, or that they are able to re-colonise open systems rapidly. The former is more likely, for the simple reason that because many of them utilise underground storage organs which require a lot of resources, it is unlikely that they expend many resources on dispersal mechanisms. Indeed Zaloumis & Bond (2010) have shown that re-colonisation of grassland forbs into previously afforested areas is not common, possibly because it is unlikely that these forbs would be able to persist cryptically for an indefinite amount of time without a fire (Uys et al. 2004). A quick survey which I did in a burnt established forest showed no savanna grassland forbs present in the post burn area, suggesting that they do not disperse into open areas rapidly. Therefore, because savanna grassland forbs are unable to persist cryptically indefinitely, if fire is used as a method to control woody encroachment, it must be done before the thicket has been established for too long. It also needs to be burnt repeatedly to ensure that thicket species are not able to re-colonise.

## **Conclusion**

Savannas, grasslands, thickets and forests had distinct floras, with little species overlap. They coexist in a patch mosaic in the landscape and each was found to contribute significantly to total species diversity in the area. Savannas and grasslands shared very few of their species with established forests, refuting the idea that they are seral to forests. On the other hand, thickets shared many species with both forests and savannas, with younger thickets more similar to savannas and older thickets more similar to forests, suggesting that thicket encroachment may eventually lead to a complete biome switch to forest. If this switch is

allowed to progress, it may result in significant reductions in savanna and grassland species. Surveys of recently burnt thicket sites suggest that savanna forbs do persist cryptically in thicket understoreys. However, these forbs may not be able to persist cryptically for indefinite periods of time (Uys et al. 2004; Zaloumis & Bond 2010), and the restoration success of previously encroached savannas and grasslands is uncertain. Woody plant encroachment is also likely to affect bird, insect and mammal diversity and distribution in the park. Although woody plant encroachment is viewed by some as a natural process which should not be interfered with by humans, in a conservation area such as my study site, the decline in species numbers that it is causing suggests that it should be a management priority. The landscape is characterised by high heterogeneity, and it is this heterogeneity that maintains the high levels of diversity. Management needs to promote practices which maximise landscape heterogeneity in order to maximise diversity.

University of Cape Town

## Chapter 4

### The effect of woody plant thickening on carbon and nitrogen stocks

#### Introduction

Woody plant encroachment in savannas and grasslands could lead to a complete biome switch to forest. An increased presence of trees is likely to alter many ecosystem processes, with possible benefits for the carbon and nitrogen cycle (Houghton et al. 1999; Knapp et al. 2008). Savannas and grasslands in combination have been estimated to contribute about 19.2 PgCyr<sup>-1</sup> to global net primary productivity (NPP) (Field et al. 1998; Archer et al. 2004; Grace et al. 2006). This accounts for 30-35% of total terrestrial NPP (Grace et al. 2006; Archer et al. 2004; Field et al. 1998). To put this in context, tropical rainforests contribute about 17.8 PgCyr<sup>-1</sup> to NPP, which only accounts for approximately 32% of total terrestrial NPP (Field et al. 1998; Lloyd & Farquhar 2008). Clearly savannas and grasslands already play a major role in the global carbon and nitrogen cycles, so any changes to the way they cycle nutrients are likely to have global consequences.

Because woody plants are often larger, more productive, deeper rooted, longer lived and slower to decompose than grasses, a shift to their dominance may be expected to increase carbon sequestration in the soil, thereby increasing the size of the terrestrial carbon sink (Jackson et al. 2000). In recent years, there has been much emphasis on increasing possible carbon sinks to mitigate the effects of global change, and the relatively large size and long residence time of the soil carbon pool (of the order of 1,200 years) make it a potentially important sink for carbon (Post et al. 1982; Batjes 1998).

Indeed, this is the thinking behind carbon offsetting programmes such as REDD (The United Nations Collaborative Programme on Reducing Emissions from Deforestation and Forest Degradation in Developing Countries). REDD is “a mechanism to create an incentive for developing forested countries to protect, better manage, and wisely use their forest resources, thus contributing to the global fight against climate change” (UN-REDD Programme Annual Review 2009). Similar projects are happening on a smaller scale throughout the world. In the Eastern Cape of South Africa, the succulent shrub, *Portulacaria afra* („spekboom’), is being

planted to offset carbon emissions in projects such as the Spekboom Carbon and Poverty Alleviation Project. The project is based on research showing that carbon storage in areas dominated by spekboom exceeded  $20\text{kg.m}^{-2}$ , which is on par with many tropical forests (Mills & Cowling 2006; Mills & Cowling 2010). Projects such as these seem to suggest that woody plant encroachment will be beneficial to carbon stocks, but there is a need to quantify this assumption.

The effect of trees on soil C and N is not clear cut, and is dependent on a multitude of factors. Hibbard et al. (2001) suggest that soil C and N accumulation due to woody plant thickening may be rapid, substantial and accompanied by increased N turnover. Studies in Australia (Harms et al. 2005) and South Africa (Hudak et al. 2003; Mills & Cowling 2006) found that the presence of trees enhanced soil organic carbon (SOC), although Hudak et al. (2003) suggest that a combination of trees and grasses was optimal for carbon storage. This is in contrast to a study in southwestern USA, where Jackson et al. (2002) found a clear negative relationship between precipitation and changes in SOC when grasslands were invaded by woody vegetation, with drier sites gaining, and wetter sites losing SOC. In wetter sites, losses of SOC were substantial enough to offset increases in plant biomass carbon, resulting in a net loss of carbon following woody plant encroachment. In a study ranging the geographical extent of North America, Knapp et al. (2008) found that at a continental scale the changes to soil carbon due to woody plant encroachment were not as large as expected. In addition, it is unlikely that the rate of carbon accumulation in encroached areas would stay constant over time (Paul et al. 2002; Archer et al. 2004), and it may be that recently encroached systems promote higher rates of C storage which level off after a few years (Trumbore 1997; Hibbard et al. 2001).

The vertical distribution of soil carbon and nitrogen is expected to differ between forests and grassy systems, because differing growth forms utilise different resources. In a global study based on various soil databases, Jobbagy & Jackson (2000) found the relative contribution of SOC in the top 20cm relative to the first metre to be higher in forests than in grasslands, possibly due to the higher concentration of roots in forests. In a study using the same databases, the depth of SOC was found to be affected by climate. In arid areas SOC was distributed more deeply in grasslands, but in sub-humid areas it was distributed more deeply in shrublands (Jackson et al. 2000). Harper et al. (2005) suggest that although rainfall seems to be important in the SOC flux, it is not the amount of rainfall but rather the timing of the

rainfall that has the largest effect. These studies highlight the fact that the overall effect of woody plant encroachment on SOC is uncertain, but that there is undoubtedly an effect of climate on carbon sequestering potential. The ability of soils to absorb atmospheric CO<sub>2</sub> may not be limitless, and is complicated by many factors, including species diversity, nutrient availability and climate (Gill et al. 2002).

Despite woody plant thickening becoming widespread in savannas and grasslands throughout the world (Burrows et al. 1990; Skarpe 1990; Archer et al. 1995; Jackson et al. 2000; Van Auken 2000; Roques et al. 2001; Fensham & Fairfax 2003; Hudak et al. 2003; Wessman et al. 2004; Wigley et al. 2010; Wilcox & Huang 2010), it appears that very little is known about how it will affect the C and N cycles. In this study I compare the relative soil C and N attributes of savanna, grassland, thicket and forest soils in an attempt to fill the gap in knowledge. I also assess carbon isotope values down the soil profile in an attempt to establish the dominant vegetation of the past (O'Leary 1988; Krull & Bray 2005). The Hluhluwe-iMfolozi Game Reserve is an ideal site for this study because it is a heterogeneous landscape interspersed with large tracts of each of these habitats growing alongside each other, in an otherwise constant environment of comparable geology, climate and soils.

#### *Can we control woody plant encroachment?*

Although this chapter's main aim is to estimate carbon and nitrogen stocks due to woody plant encroachment, these are not the only ecosystem properties that land managers are interested in. In some areas woody plant encroachment is having undesirable effects on other properties, such as on biodiversity in conservation areas (Briggs et al. 2005). Because frequent fires are a natural part of savanna ecology (Shackleton & Scholes 2000; Coetsee et al. 2010), intense fires may prove to be a useful tool in controlling woody plant encroachment in these areas. However, such intense fire may cause major soil C and N losses, as well as losses to above ground carbon, an undesirable effect with respect to global change (Williams et al. 2004; Cook et al. 2005). How fire affects ecosystems is a complex issue, and is highly dependent on, amongst other things, the properties of the ecosystem, the severity and duration of the fire, and soil moisture (Neary et al. 1999). In September 2008 severe fires swept through my study area. These fires were not typical savanna fires as they were high intensity with high flame heights, burning under extreme conditions (Refer to Catherine Brown's thesis, University of Cape Town 2009). This allowed them to burn through patches of

encroached savannas and forests, many of which had not been burnt in more than half a century. I took the opportunity to sample some recently burnt soils, in an attempt to ascertain the effect of fire on soil carbon and nitrogen. It is difficult to predict how a fire will affect soil nutrients, as it depends largely on the system, and previous studies have found varying results (Debano & Conrad 1978; Rashid 1987; Neary et al. 1999; Van Der Werf et al. 2003; Williams et al. 2004; Cook et al. 2005; Coetsee et al. 2010). This brief investigation aims to determine whether extreme fires are likely to have any serious deleterious effects on the C and N stocks in encroached savannas.

## **Methods**

### **Site Selection**

I identified 5 paired forest-grassland and 8 paired savanna-thicket sites. The thicket boundaries were considered to be actively encroaching into savanna based on aerial photographs from 1937, 1960 and 2004. The forest-grassland boundaries were considered temporally stable based on aerial photographs from 1937, 1960 and 2004. In addition I identified 3 burnt thicket sites, 2 burnt savanna sites, and 2 burnt forest sites, all of which were sampled up to a year after burning. The soils were uniform across the vegetation pairs. Most soils were oxidic soils with dark surface soils 30-60cm deep over red, fine-textured, sandy-clay subsoils. Other soils were melanic with dark fine-textured, weakly structured topsoils over shallow subsoil onto rock (see table 2.1 in Chapter 2 for a classification of the study site soils).

### **Soil Sampling and bulk density**

A 1m x 2m pit was dug at each site to a depth of approximately 1.2m. Samples were taken at set depth intervals of 0-2.5cm, 2.5-7.5cm, 7.5-15cm, 15-30cm, 30-50cm, 50-75cm, 75-100cm, and where possible 100-120cm. In order to determine bulk density a known volume was removed from each layer using a core sampler. A soil auger was then used to drill to a depth of 2 metres, or until rock was hit, in order to take samples of deeper soil layers. Bulk density of deeper layers was assumed to be equivalent to the deepest layer of known bulk density.

Soil samples were dried in an oven at 70°C for 48 hours, or until constant weight. They were weighed and sieved to remove all roots and stones, the weight and volume of which were measured. To ensure accurate quantification of roots in the soil (because larger roots were avoided when taking samples) three 25cm wide transects were set out vertically down each pit. Roots were categorised into size classes of 1-2mm, 2-4mm, 4-10mm, and greater than 10mm (the diameters of these were recorded), and the number of roots in each size class in each transect was counted. We made the assumption that the roots proceeded horizontally into the soil for 25cm. In this way the volume of roots in a volume of soil of 25cmx100cmx75cm could be calculated using the equation:

$$V = \sum_{i=0}^n \left( \pi \left( \frac{d_i}{2} \right)^2 25 \right)$$

Where  $d_i$ =diameter of root  $i$ .

The volume of stones in each sample was calculated by displacement of water, unless a site had large rocks in it, in which case we employed a similar technique to that used for the roots.

The bulk density of each sample was calculated using the equation

$$BD = \frac{M}{V}$$

Where  $M$ = dry mass of soil (-roots and rocks) and  $V$ = volume of soil (-roots and rocks)

### **Soil Chemistry**

In order to determine percentage carbon and nitrogen, as well as the isotopic carbon and nitrogen ratio of each sample, a mass spectrometre was used. Samples were sorted to remove all fine roots and samples of approximately 100 micrograms were weighed into a tin cup to an accuracy of 1 microgram on a Sartorius micro balance. They were then combusted in a Flash EA 1112 series elemental analyzer (Thermo Finnigan, Italy). The gases were passed to a Delta Plus XP IRMS (isotope ratio mass spectrometre) (Thermo electron, Germany), via a Conflo III gas control unit (Thermo Finnigan, Germany). The in-house standards used were

Choc, a commercial chocolate/egg mixture, Sucrose and Merck Gel, a proteinaceous gel produced by Merck. All the in-house standards were calibrated against IAEA (International Atomic Energy Agency) standards.

I calculated the amount of C and N per square metre to a depth of one metre using the equations

$$C = \sum_{i=0-2.5}^{75-100} (BD_i \times \%C_i \times d_i)$$
$$N = \sum_{i=0-2.5}^{75-100} (BD_i \times \%N_i \times d_i)$$

Where  $BD_i$  is bulk density of layer  $i$  in  $Mg\ m^{-3}$ ,  $\%C_i$  or  $\%N_i$  is %C or %N in layer  $i$ , and  $d_i$  is depth of layer  $i$  in metres. These amounts were then converted to  $Mgha^{-1}$  by multiplying by 10 000.

### Above-ground Carbon estimate

I estimated above ground biomass using stand basal area. Although it is common practice to use basal area to determine biomass, this is usually for individual trees. I estimated stand basal area using a Bitterlich Wedge (Šálek & Zahradník 2008). At each site I walked two parallel seventy five metre transects twenty five metres apart, and every twenty five metres estimated basal area in  $m^2ha^{-1}$  using the Bitterlich Wedge. The method I used to convert stand basal area to biomass is outlined in Appendix 1. As the carbon:biomass ratio for each species was unknown, I used a generally accepted conversion factor of 0.5 to convert the biomass to a carbon value (Watson 2000). At the same time I recorded the tree species. To determine the density of wood for tree species in the stand, short branches approximately 5cm in diameter were collected from most of the species encountered. The volume of these samples was determined by water displacement. They were then dried in an oven at  $70^\circ C$  for 48 hours or until constant weight, and weighed to determine the wood density. This was done for as many species as possible in each plot. For those that it was not done for, I used an average from the entire study.

I estimated grassy biomass in the grassland and savanna sites using a disk pasture metre (DPM), a metal disk with a diameter of 45 cm and a weight of 1500 g. The height measurements were converted into biomass measurements using the equation

$$AGB = 12.6 + (26.1 \times DPM) \quad (R^2=0.73)$$

which was developed by Waldram et al. (2008) for the Hluhluwe-iMfolozi area, where DPM is measured in cm and AGB is in  $\text{g}\cdot\text{m}^{-2}$ . These AGB estimates were then converted to carbon estimates by once again using a conversion factor of 0.5.

### Effects of fire

Fire effects were not explicitly part of my project design. I took advantage of the September 2008 fire, an extreme event (Refer to Catherine Brown's thesis. University of Cape Town 2009) to obtain an estimate of the impact of an extreme fire on C and N stocks. I was able to locate one paired burnt-unburnt thicket site, a paired burnt-unburnt forest site, and a paired savanna-thicket burnt site. I also included an unpaired burnt forest site, an unpaired burnt thicket site, and an unpaired burnt savanna site (which had been sampled before it burnt) Soils were sampled and analysed in the same way as my initial sites, and above ground carbon estimates were made once again using a Bitterlich wedge, but only live trees were counted.

### Statistical analyses

The mean amount of C and N in each habitat type was calculated, and these were statistically compared using a mixed effects ANOVA, with site as a random effect, and habitat (thicket, savanna, grassland, forest) as a fixed effect. The unit of replication was each soil pit, first to 100cm, then to 30cm. Post hoc Tukey tests were performed for comparison of means. The surface (to 30cm) amount of N was compared relative to the total amount to 1 metre, as a measure of nutrient utilisation by plants. I termed this the concentration factor. With high utilisation by plants, the ratio of the top 30cm to the first metre should be high, as plants would draw nutrients upwards (Jobbagy & Jackson 2001). The C and N stocks in burnt and unburnt sites were calculated, but were only compared qualitatively as there were not enough samples to have statistical strength.

## Results

### Carbon isotope comparison

Figure 1 shows the isotopic soil profiles of each habitat. The mean  $\delta^{13}\text{C}$  value of  $\text{C}_3$  plants is approximately  $-27\text{‰}$ , and for  $\text{C}_4$  plants is approximately  $-13\text{‰}$ , with considerable variation around the means (O'Leary 1988; West et al. 2000). From figure 1 we can see that forests and thickets only exhibit a  $\text{C}_3$  signal in the top 20-40cm of the soil profile, after which they show a  $\text{C}_4$  signal. Savannas and grasslands exhibit a  $\text{C}_4$  signal all the way down to 200cm.

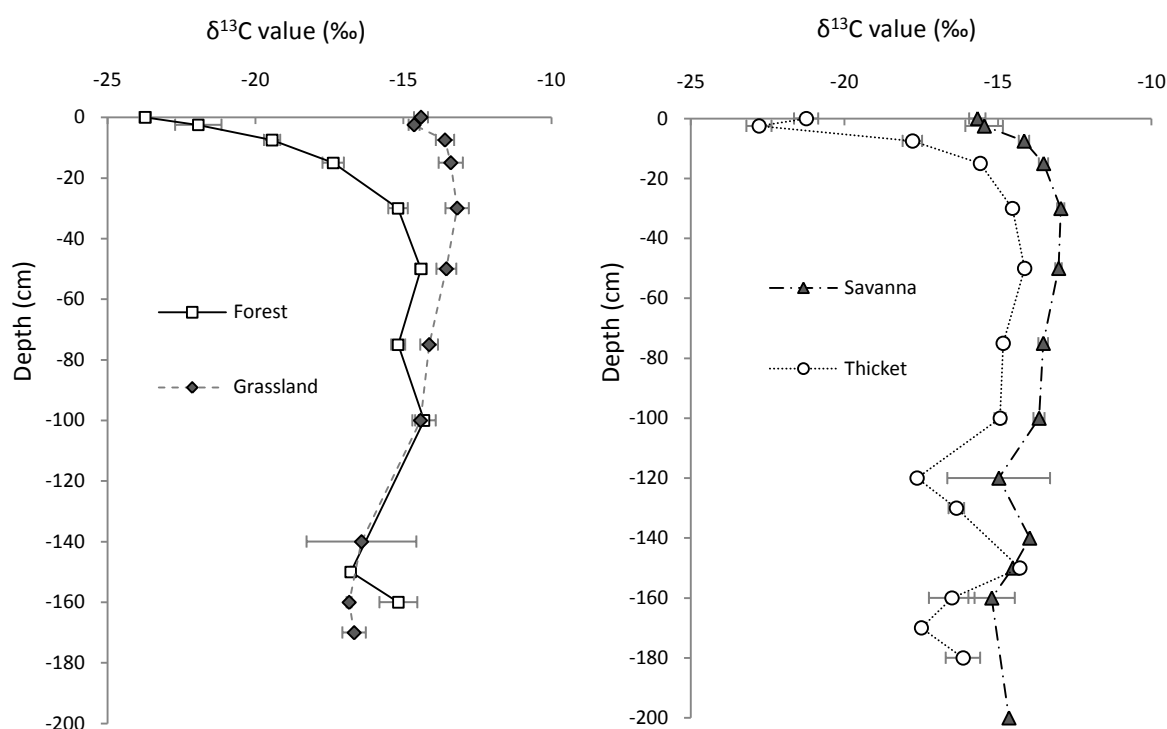


Figure 4.1  $\delta^{13}\text{C}$  isotope signatures ( $\pm$  SE) down the soil profile of each habitat type

### Carbon stocks

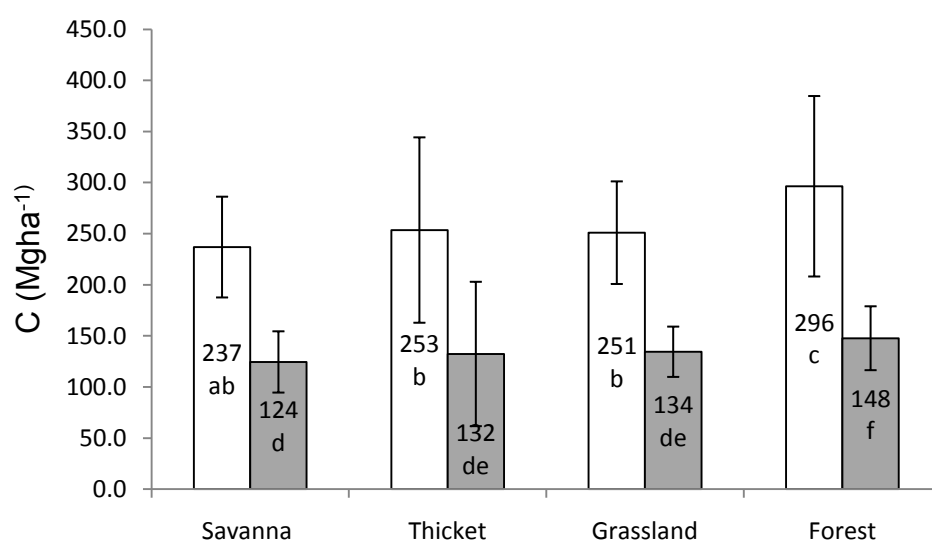
Soil and above ground carbon stocks were compared between habitats using a mixed effects ANOVA, and the results are presented in table 4.1. Most differences in carbon stocks were found to be due to random site effects, but some were attributed to habitat.

Figure 4.2 shows the soil organic carbon (SOC) stocks in each habitat, divided into the top 30cm, and below this to 100cm. Forests contained the most carbon in the top 30cm of the soil ( $147.6 \pm 31.3 \text{ MgCha}^{-1}$ ), while grasslands contained the second most ( $134.4 \pm 24.6 \text{ MgCha}^{-1}$ ).

Thickets had a mean carbon content of  $132.2 \pm 70.6 \text{ MgCha}^{-1}$  in the top 30cm of their soil, higher than savannas which had a mean of  $124.4 \pm 30.0 \text{ MgCha}^{-1}$ . These differences were found to be due mainly to random site effects (Table 4.1). When summed to a depth of 100cm, forests contained the most total soil carbon ( $296.3 \pm 75.0 \text{ MgC.ha}^{-1}$ ), but thickets contained marginally more carbon than grasslands ( $253.5 \pm 90.7 \text{ MgC.ha}^{-1}$  and  $250.9 \pm 50.2 \text{ MgC.ha}^{-1}$  respectively). Savannas contained the least carbon in their soils to 100cm ( $236.8 \pm 49.3 \text{ MgC.ha}^{-1}$ ). Although forests were significantly higher, these differences were mainly due to random site effects (table 4.1).

**Table 4.1 Mixed effects ANOVA showing habitat effects on carbon stocks**

	Effect	Df effect	MS effect	Df Error	MS error	F	p
SOC (0-30cm)	Fixed (habitat)	3	557.10	17.24	811.85	0.69	0.573
	Random (site)	11	1857.62	11.00	288.96	6.43	0.002
SOC (0-100cm)	Fixed (habitat)	3	3753.47	18.62	3252.72	1.15	0.354
	Random (site)	11	6958.10	11.00	1400.03	4.97	0.007
Above Ground C	Fixed (habitat)	3	16020.81	21.04	142.86	112.14	<0.0001
	Random (site)	11	168.56	11.00	130.00	1.30	0.3370
Total C	Fixed (habitat)	3	34328.47	19.44	3504.41	9.80	0.0003
	Random (site)	11	7165.12	11.00	1674.05	4.28	0.0117



**Figure 4.2 Soil carbon stocks ( $\pm$ SD) in each habitat type. White blocks indicate total soil stocks to 100cm, grey blocks indicate stocks from 0-30cm. Letters indicate significant differences using a mixed effects ANOVA and a Tukey test at  $\alpha=0.05$**

The most dramatic differences in carbon stocks between habitats were seen in the above ground carbon (AGC) stocks (Figure 4.3). Forests contained by far the most AGC ( $125.2 \pm 15.5 \text{ Mg Cha}^{-1}$ ), more than double what thickets contained ( $49.5 \pm 15.4 \text{ Mg Cha}^{-1}$ ). Savannas contained far less above ground carbon ( $14.3 \pm 9.6 \text{ Mg Cha}^{-1}$ ) than forests, but this was about three times the amount found in grasslands ( $4.5 \pm 1.5 \text{ Mg Cha}^{-1}$ ). Differences between habitats were all due to habitat effects rather than random site effects (Table 4.1).

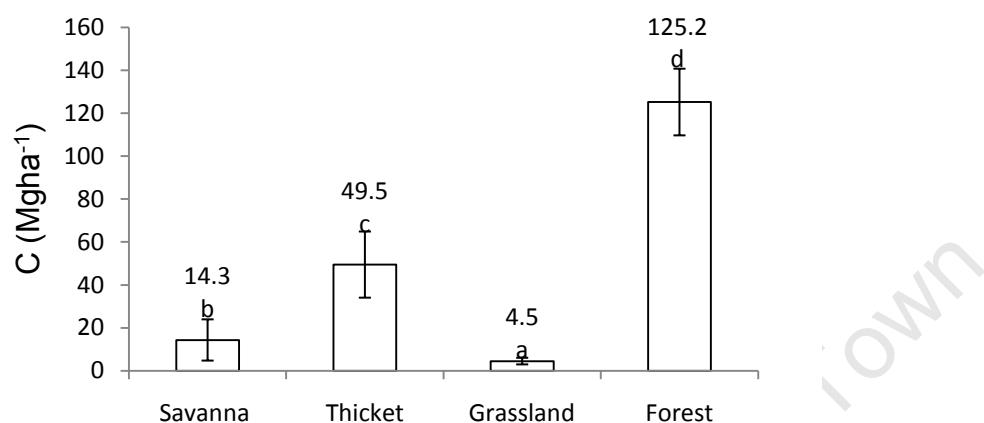


Figure 4.34 Above-ground carbon stocks ( $\pm$ SD) in each habitat type. Letters indicate significant differences using a mixed effects ANOVA and a post hoc Tukey test at  $\alpha=0.05$

Figure 4.4 combines SOC to a depth of 100cm and AGC to compare total carbon stocks in each habitat. Although significant differences were found to be due to habitat effects (Table 4.1), figures 4.2 and 4.3 highlight that these differences are mainly due to differences in AGC. Forests had a mean total carbon stock of  $421.6 \pm 88.2 \text{ MgCha}^{-1}$ , higher than thickets which had a mean of  $302.9 \pm 65.0 \text{ MgCha}^{-1}$  (Figure 4.4). Grasslands and savannas contained similar carbon stocks, with means of  $255.4 \pm 55.9 \text{ MgCha}^{-1}$  and  $251.2 \pm 51.7 \text{ MgCha}^{-1}$  respectively (Figure 4.4).

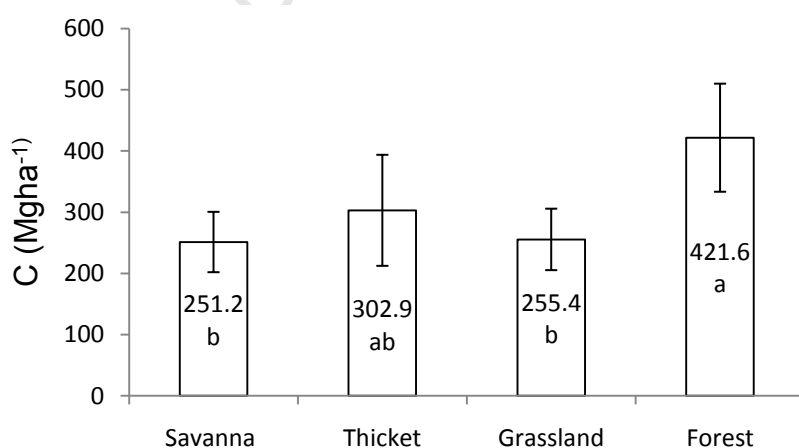
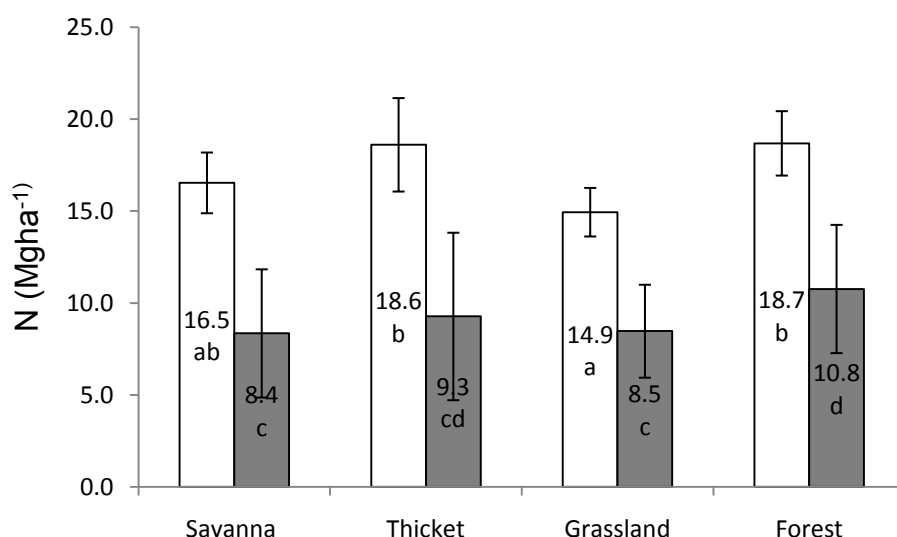


Figure 4.4 Total carbon ( $\pm$ SD) in each habitat type, including above ground carbon and soil carbon down to 100cm. Letters indicate significant differences using a mixed effects ANOVA and a post hoc Tukey test at  $\alpha=0.05$

## Nitrogen stocks

Figure 4.5 shows soil nitrogen stocks to depths of 100cm and 30cm. A similar pattern to that of carbon is seen. Forests contained significantly more nitrogen ( $18.69 \pm 3.49 \text{ MgNha}^{-1}$ ) down to 100cm than adjacent grasslands which contained  $14.94 \pm 2.53 \text{ MgNha}^{-1}$ . Savannas contained  $16.54 \pm 3.49 \text{ MgNha}^{-1}$  in soils down to 100cm, slightly less than adjacent thickets ( $18.60 \pm 4.55 \text{ MgNha}^{-1}$ ). Significant differences using a mixed effects ANOVA were found to be due to random site effects, and not habitat effects (Table 4.2).

In the top 30cm of the soil, forests had higher nitrogen levels ( $10.77 \pm 1.70 \text{ Mg N.ha}^{-1}$ ) than adjacent grasslands ( $8.47 \pm 1.55 \text{ Mg N.ha}^{-1}$ ). Thickets contained slightly more nitrogen ( $9.27 \pm 2.61 \text{ Mg N.ha}^{-1}$ ) than their adjacent savannas ( $8.35 \pm 1.92 \text{ Mg N.ha}^{-1}$ ). Once again significant differences were due to random site effects and not habitat effects (Table 4.2).

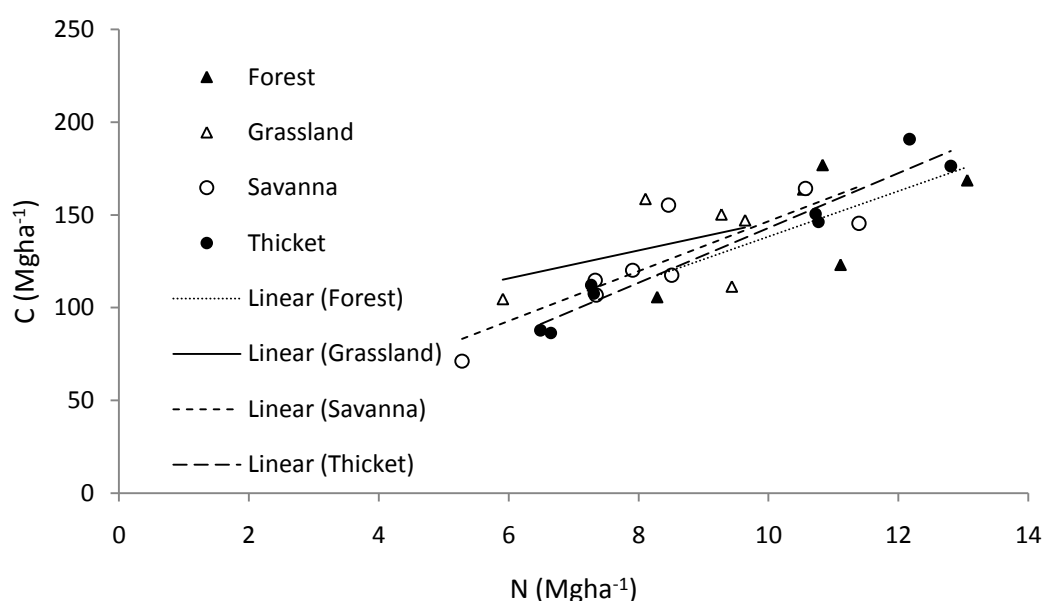


**Figure 4.5 Total nitrogen ( $\pm$ SD) in each habitat type. White blocks indicate total soil N to 100cm, grey blocks indicate soil N to 30cm. Letters indicate significant differences using a mixed effects ANOVA and post hoc Tukey test at  $\alpha=0.05$**

**Table 4.2 Mixed effects ANOVA showing habitat effects on N stocks**

	Effect	Df effect	MS effect	Df Error	MS error	F	p
N (0-30cm)	Fixed (habitat)	3	6.858	16.148	3.192	2.149	0.134
	Random (site)	11	7.670	11.000	0.953	8.049	0.001
N (0-100cm)	Fixed (habitat)	3	18.557	17.752	10.567	1.756	0.192
	Random (site)	11	23.604	11.000	4.048	5.831	0.003

Figure 4.6 shows the correlation between soil nitrogen and soil carbon in the top 30cm in each habitat. I found the slope of the grassland curve to be 7.56, almost half that of the other habitats, suggesting that for the same increase in N, there is less increase in C in grasslands than in other habitats. The  $R^2$  values were much higher in thickets and savannas (0.949 and 0.742 respectively) than in forests and grasslands (0.445 and 0.227 respectively). In addition, the thicket and savanna correlations were significant ( $p=0.00004$  and  $0.006$  respectively) whereas forest and grassland correlations were not ( $p=0.2$  and  $0.4$  respectively). This suggests that C and N are more tightly coupled in thickets and savannas than forests and grasslands.



**Figure 4.6 Correlation between C and N in the top 30 cm.**

**Equations:** Forest  $y=12.25x+15.79$  ( $R^2=0.445$ ,  $p=0.2$ ), Grassland  $y=7.56x + 70.35$  ( $R^2=0.227$ ,  $p=0.4$ ), Savanna  $13.43x +12.29$  ( $R^2=0.742$ ,  $p=0.006$ ), Thicket  $y=14.78x -4.89$  ( $R^2=0.949$ ,  $p=0.00004$ )

I combined all habitat types for the top 30cm as well as below 30cm to obtain the following equations for linear regressions:

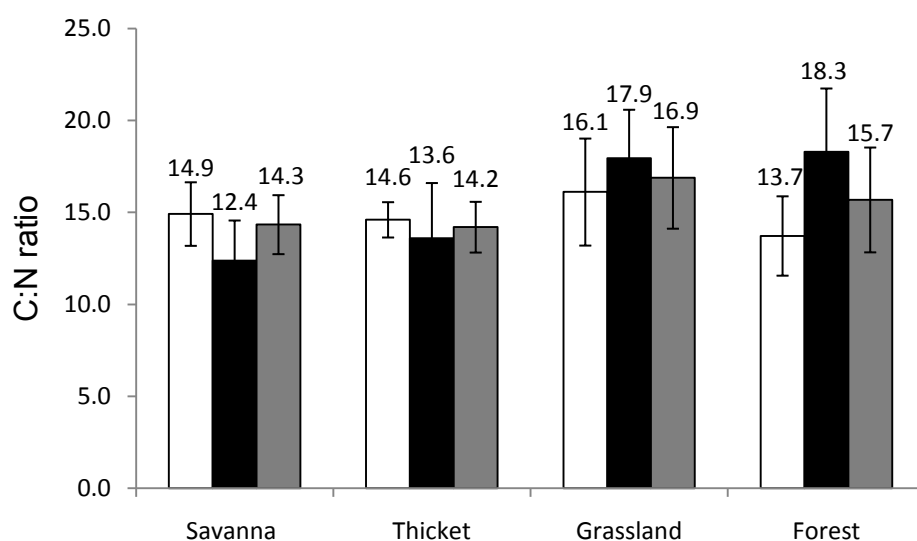
$$\text{Top 30cm} \quad N = 12.48C + 19.7 \quad (R^2=0.7063)$$

$$\text{30-100cm} \quad N = 12.59C + 20.2 \quad (R^2=0.5957)$$

Where  $N= \text{Mg. ha}^{-1}$  and  $C=\text{Mg. ha}^{-1}$

The higher  $R^2$  value for the top 30cm curve indicates that C and N are more tightly coupled in the upper soil profile.

The C:N ratio in each habitat type is shown in figure 4.7. C:N ratios are a proxy for the fertility of the soils, with low ratios suggesting more fertile soils. Forest soils had the lowest C:N ratio in the top 30cm, but below this the ratio increased drastically. Grasslands had the second highest C:N ratio in the top 30cm, and this increased slightly down the profile. Savanna and thicket soilshad lower C:N ratios in deeper soil layers than shallow soils, although thicket soils had a fairly constant C:N ratio all the way down the profile. In the top 30cm significant differences were found to be mainly due to random site effects (Table 4.3), but when the whole profile was taken into account, there were slight habitat effects (Table 4.3).



**Figure 4.7** C:N ratio ( $\pm$ SD) of soils in each habitat type. White blocks are the top 30cm of the soil, black blocks are 30cm-100cm, while grey blocks are the mean from 0cm-100cm

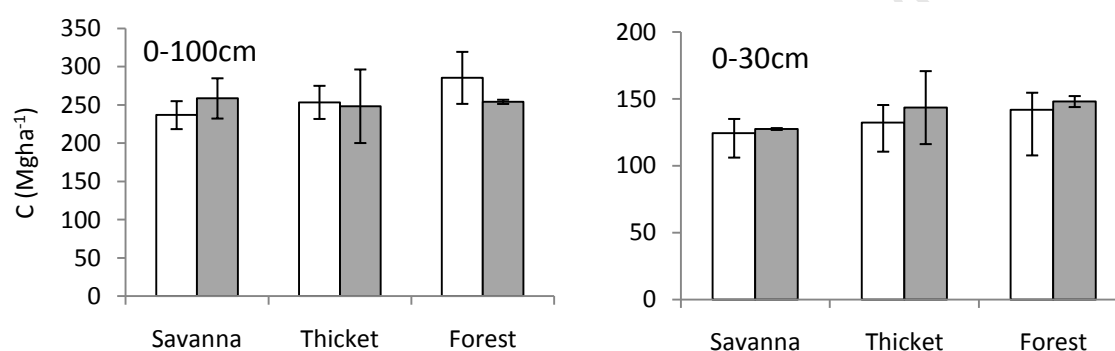
**Table 4.3** Mixed effects ANOVA results showing habitat effects on C:N ratio for soils down to 30cm and soils down to 100cm

	Effect	Df effect	MS effect	Df Error	MS error	F	p
C:N ratio (0-30cm)	Fixed (habitat)	3	5.653	18.962	2.845	1.987	0.1502
	Random (site)	11	5.976	11.000	1.280	4.669	0.0083
C:N ratio (0-100cm)	Fixed (habitat)	3	12.614	18.286	3.311	3.809	0.0279
	Random (site)	11	7.205	11.000	1.364	5.282	0.0052

### Effects of fire on carbon and nitrogen

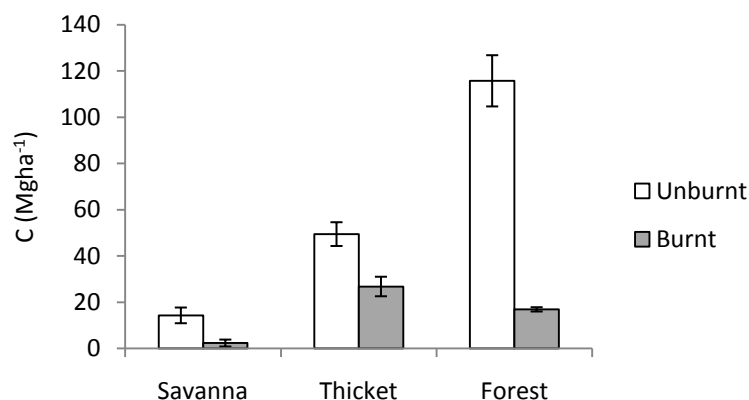
The differences between the mean amount of soil C in burnt patches and unburnt patches in savannas, thickets and forests are shown in Figure 4.8. Burnt thickets had 248.4 Mg Cha<sup>-1</sup> in

their soils to 100cm, only 2% less than unburnt thickets. In the top 30cm of their soils they had 143.5 MgC.ha<sup>-1</sup>, 8.5% more than unburnt thickets. This suggests that fires increase carbon in the top soil layers and decrease carbon in the lower layers. Savannas had 143.5 MgC.ha<sup>-1</sup> in the top 30cm of their soils, 2.5% more than unburnt savannas. In soils down to 100cm they had 258.7MgC.ha<sup>-1</sup>, 9.2% more than unburnt savannas. Forests contained 148.0 MgC.ha<sup>-1</sup> in the top 30cm of their soils, 4.5% more than unburnt forests. In soils down to 100cm they contained 254.2 MgC.ha<sup>-1</sup>, 11% less than unburnt forests. The differences between unburnt and burnt sites for all vegetation types do not seem to show any particular trend, and the differences are not large enough to be noteworthy. The small sample sizes make it difficult to draw any conclusions about the effect of fire on carbon stocks, but the fact that differences are so small suggests that spatial heterogeneity probably has a greater effect than fire.



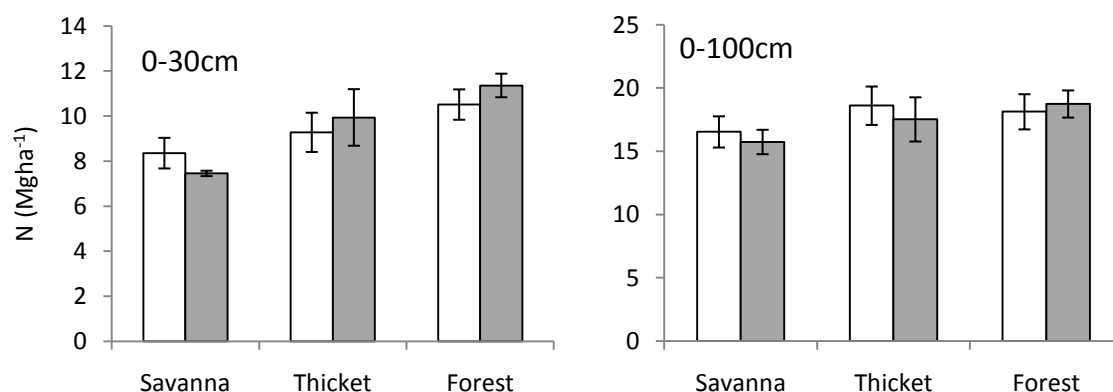
**Figure 4.8** Soil carbon stocks ( $\pm$ SE) in unburnt (white bars) and burnt patches (grey bars) for savannas, thickets and forests to a depth of 100cm (left) and 30cm (right) divided into AGC, soil carbon to a depth of 100cm and soil carbon to a depth of 30cm

Above ground carbon stocks in burnt and unburnt patches (Figure 4.9) show a far stronger trend than soil carbon. Burnt savanna patches contained 2.36 MgC.ha<sup>-1</sup> of above ground carbon, which was 83% less than unburnt savannas, although this translated into only 12 MgC.ha<sup>-1</sup> less AGC than burnt savannas. Burnt thickets contained 26.8 MgC.ha<sup>-1</sup>, 46% less than unburnt thickets. Burnt forests contained 16.9 MgC.ha<sup>-1</sup>, 85% less above ground carbon than unburnt forests, a difference of almost 100MgC.ha<sup>-1</sup>. Forest above ground carbon stocks seem to be severely affected by fires, where as thickets do not show as much of a decline. Despite savannas showing a proportionally large drop in above ground carbon, this does not convert to a large drop in actual above-ground carbon stocks, as they did not have much to begin with.



**Figure 4.9 Above ground carbon ( $\pm$ SE) in burnt and unburnt patches of savanna, thicket and forest**

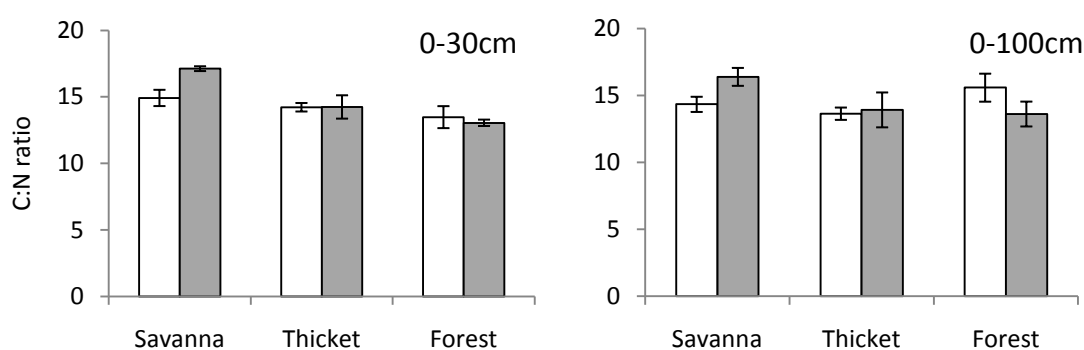
Figure 4.10 shows the difference between the mean soil N levels in burnt patches and unburnt patches in savannas, thickets and forests. Burnt savannas contained  $15.7 \text{ MgNha}^{-1}$  in their soils to a depth of 100cm, 4.8% less than unburnt savannas. In their soils to 30cm they contained  $7.5 \text{ MgNha}^{-1}$ , 2.5% less than unburnt savannas. Burnt thickets contained  $9.93 \text{ MgNha}^{-1}$  in the top 30cm of their soils, 7.1% more than unburnt thickets. They contained  $17.5 \text{ MgNha}^{-1}$  in their soils to 100cm, 5.8% less than unburnt thickets. Burnt forests contained  $11.4 \text{ MgNha}^{-1}$  in the top 30cm of their soils and  $18.7 \text{ MgNha}^{-1}$  in their soils to 100cm, 3.4% and 8.0% more than unburnt forests respectively. Once again there seems to be no discernible difference between burnt and unburnt patches of vegetation, suggesting that any differences that are seen are due to spatial heterogeneity. A larger sample size may remove some of the spatial heterogeneity.



**Figure 4.10 Soil nitrogen stocks ( $\pm$ SE) in unburnt (white bars) and burnt patches (grey bars) to a depth of 30cm (left) and 100cm (right)**

Figure 4.11 depicts the C:N ratios of soils in burnt and unburnt thicket, savannas and forest soils. Burnt thickets had a mean C:N ratio of 14.2 in the top 30cm of their soils, 0.2% higher than unburnt thickets. They had a mean C:N ratio of 13.9 in their soils to 100cm, 2.1% higher

than unburnt thickets. The differences between burnt and unburnt savannas was slightly more pronounced. They had a mean C:N ratio of 17.1 in the top 30cm of their soils, 14.8% higher than unburnt savannas. In soils down to 100cm, their mean C:N ratio was 16.4, 14.3% higher than unburnt savannas. Burnt forests had lower C:N ratios than unburnt forests. In the top 30cm of their soils the C:N ratio was 13.0, 3.2% lower than unburnt forests. In their soils down to 100cm the mean C:N ratio was 13.6, 12.6% lower than unburnt forests. Once again no discernible pattern is apparent, and the effects are probably due to spatial heterogeneity. In addition, the observed changes may not be large enough to be of consequence, even if they are not due to spatial heterogeneity.



**Figure 4.11** C:N ratio ( $\pm$ SE) in unburnt (white bars) and burnt (grey bars) patches for soils to a depth of 30 cm (left) and 100cm (right)

## Discussion

### *Grasslands are ancient systems*

Grasslands and savannas in the Hluhluwe landscape are ancient systems. I found that all habitats had a  $\delta^{13}\text{C}$  value of between -13‰ and -18‰ deeper down the soil profile, indicating a dominance of  $\text{C}_4$  plants in the Hluhluwe landscape in the past (O’Leary 1988; Krull & Bray 2005). This result is supported by the findings of West et al. (2000), and contradicts the belief that these grassy systems are seral to forests, created by the felling of forests by Iron Age humans (Acocks 1953). The use of soil carbon isotopes to describe past vegetation has been brought into question, and it is suggested that changes in  $\delta^{13}\text{C}$  signals can be attributed to soil microbes (Billings & Richter 2006; Boström et al. 2007; Lerch et al. 2010). However the changes caused by microbes appear to be on the order of around 2‰ while the variations down the soil profile that I show are on the order of 10‰. Although some of the variation in  $\delta^{13}\text{C}$  in soils in my study area may be due to microbial action, there is support for the use of

carbon isotopes as an indicator of vegetation change (O'Leary 1988; West et al. 2000; Krull & Bray 2005).

#### *Carbon storage in grassy vs. forested biomes*

Forests contained the most soil carbon as well as the most above ground carbon, so in terms of maximising carbon sequestration, the most desirable biome was forest. In a study collating global literature that report soil organic matter changes resulting from land conversion from cultivated to perennial vegetation, Post & Kwon (2000) found that annual rates of soil carbon accumulation are similar for forest and grassland establishment ( $0.338 \text{ MgCha}^{-1}\text{yr}^{-1}$  and  $0.332 \text{ Mg Cha}^{-1}\text{yr}^{-1}$  respectively). Grace et al. (2006) estimated the global mean carbon sequestration rate in savannas to be approximately  $0.14 \text{ Mg Cha}^{-1}\text{yr}^{-1}$ , although this is very variable and some savannas have much higher rates of sequestration. For example, Williams et al. (2004) estimate the carbon sequestration rate of savannas in the northern territory of Australia to be approximately  $1 \text{ MgCha}^{-1}\text{yr}^{-1}$ . In order to make a comparison with our encroaching thickets I used the following crude method of estimation. If I assume thickets in HiP have a mean age of 60 years (a reasonable assumption from aerial photographs), and assuming that carbon is accumulating at a constant rate, I estimated an annual soil carbon accumulation rate of  $0.27 \text{ MgCha}^{-1}\text{yr}^{-1}$  when savannas turn into thickets as a result of woody plant encroachment. This is coupled with an above ground carbon accumulation rate of approximately  $0.59 \text{ Mg C.ha}^{-1}.\text{yr}^{-1}$ , giving a total carbon accumulation rate of  $0.86 \text{ MgCha}^{-1}\text{yr}^{-1}$ . This is much less than the rate of  $4.2 \text{ MgCha}^{-1}\text{yr}^{-1}$  estimated by Mills and Cowling (2006) for spekboom in Eastern Cape Thicket. At this rate, it would be ~160 years before soil carbon levels in thickets reach those of established forests in Hluhluwe, and ~130 years before their above ground biomass compares to that of these forests. This is also probably an overly generous estimate, as it is unlikely that carbon accumulates at a constant rate, and as thickets get older, their carbon accumulation rate probably reduces (Trumbore 1997; Hibbard et al. 2001). Fang et al. (2001) found that from the mid 1970's until 1998 newly planted forests sequestered 450 Mg of carbon, while natural established forests lost 140 Mg of carbon, suggesting that new forest establishment provides an effective carbon sink. In the previous chapter I suggested that thickets were an early successional stage to forest, in other words, our equivalent of „new' forests. My data suggest that while these „new' forests definitely store more carbon than their adjacent unencroached savanna counterparts, most of this (~70%) is due to increases in above ground biomass, an inherently unstable and

temporary carbon sink that can be released straight back into the atmosphere with one big fire or similar event. The intense fires that burnt through thicket and forest patches in Hluhluwe in 2008 present a fine example of the impermanence of the above ground sink. This instability, coupled with the already slow rate of carbon accumulation in thickets, means that it will be centuries before thickets are able to provide the long term, relatively stable carbon sink that established forests can.

The soil carbon stocks in encroaching thickets were only 6-7% higher than savannas. Similarly, a study by Knapp et al. (2008) in North America found that woody plant encroachment only increased soil carbon by 7%. Not only were the soil carbon gains due to woody plant encroachment fairly minor in my study area, I also did not take into account the physical coupling of vegetation to climate. Gibbard et al. (2005) suggest that because trees have a lower albedo than grasses, an increase in tree density may have a net warming effect on global temperatures. In addition, both Knapp et al. (2008) and Jackson et al. (2002) suggest that climate may have a major effect on the carbon sequestering ability of woody encroached areas. Considering all the possible complexities involved in the effect of woody plants on climate and soil carbon, it becomes difficult to make any generalisations about the consequences thereof.

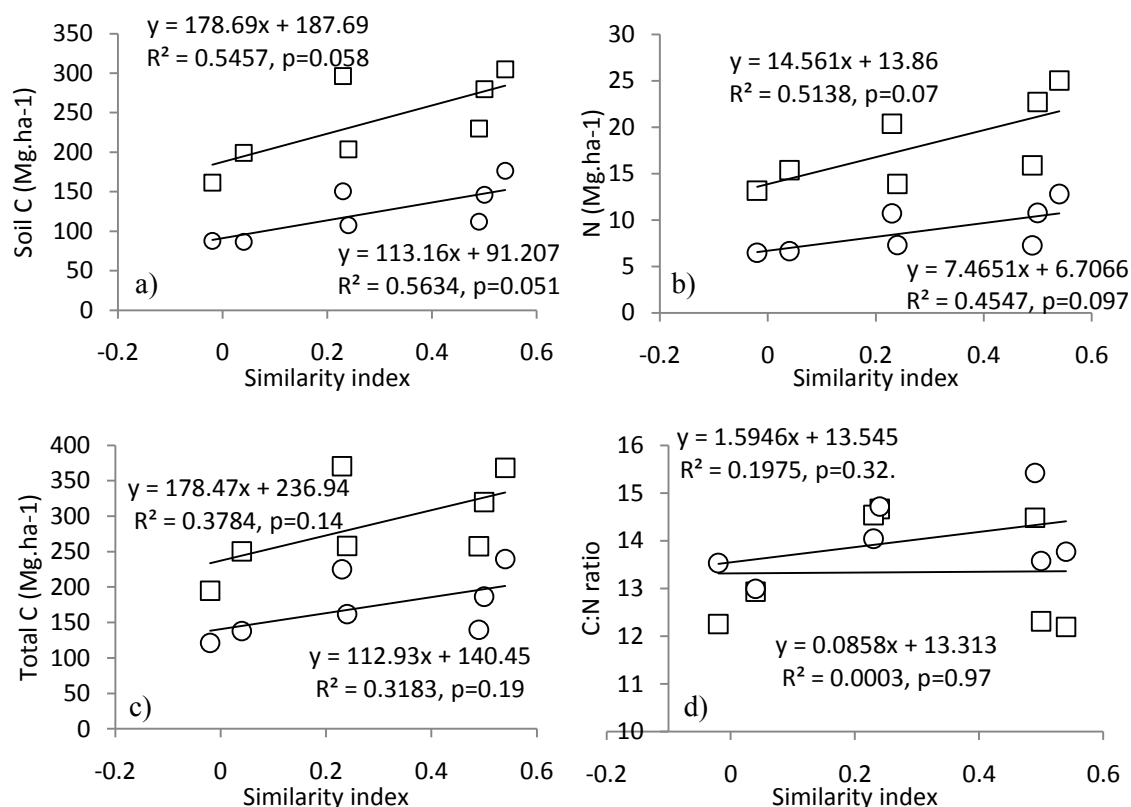
#### *Carbon and nitrogen relations are different between biomes*

Theory predicts that the amount of carbon reaching a system is tightly coupled with the amount of nitrogen in a system (Pastor & Post 1986; Neff et al. 2002), because the carbon compounds in litter control N availability, which control the rate of biomass accumulation, which would then affect the carbon cycle. Increases in plant productivity would result in greater storage of C in plants, and increased flux of C to soils through root and leaf litter (Rustad et al. 2001). However, an increase in plant productivity does not necessarily correlate directly to an increase in soil carbon, as decomposition and soil respiration rates can differ in different biomes (Neff et al. 2002). Additions of N to soils could increase decomposition rates of some soil organic matter fractions while simultaneously decreasing rates for other fractions, and so the response of soils to increased plant productivity is not clear cut (Neff et al. 2002). My results are definitely not clear cut. While grasslands had the lowest total nitrogen levels (Figure 4.5), they actually contained almost as much carbon in their soils as thickets did (Figure 4.2). Grasslands contained most of their nitrogen in the top 30cm, as well

as most of their carbon. Perhaps the shallower rooting depth of grassland species promotes C and N cycling and storage primarily higher up in the soil profile. The presence of trees in the other systems may mean that nitrogen is more limiting in these systems, and therefore more tightly coupled with carbon storage. Indeed the high  $R^2$  values and highly significant correlations for thickets and savannas in figure 4.6 supports this idea. Although forests do not show as tight a coupling, this may be an artefact of the smaller sample size for forests. Grasslands and savannas had higher C:N ratios in their topsoils than their adjacent forests and thickets, which is consistent with results from Hudak et al. (2003) who found that encroached areas had lower C:N ratios than adjacent savannas.

*Species composition may affect nitrogen and carbon storage*

I have assumed that thickets will eventually become forests, or that they are essentially a successional stage to forests. During succession, net primary productivity is thought to increase to a maximum, then decline and oscillate around a steady state, and Pastor and Post (1986) suggest that this peak in NPP will occur when the stand is composed of mature early successional trees in the overstorey (thicket species) and young late successional trees in the understorey (forest species). In our system, we could expect that thickets that had more forest (late successional) species in them would contain more carbon and nitrogen than thickets that were compositionally distinct from mature forests. I tested this theory by plotting the similarity index values from axis 1 in the MDS plots in Figure 3.4 against soil carbon, soil nitrogen, total carbon (above ground and soil) and C:N ratio of soils (Figure 4.12). Although none of these correlations are significant, a positive correlation with compositional similarity to forests is seen for all components, except for the C:N ratio, suggesting that as thickets gain more forest species, their carbon and nitrogen uptake increases. The correlation is particularly strong for soil C, with a significance level only just above the arbitrary 0.05 level.



**Figure 4.12** How a) Soil carbon, b) Soil N, c) Total C and d) C:N ratio change for soils to 100cm (blocks) and 30cm (circles) as thickets become more similar to forests. The x axis shows the similarity indices for each plot taken from figure 3.4. As the values become more positive they are more compositionally similar to forests, and as they become more negative they are more compositionally similar to savannas

Biogeochemical theory predicts that soil nitrogen scarcity may limit natural ecosystem response to elevated  $\text{CO}_2$  concentration, which would limit the  $\text{CO}_2$  fertilization effect on terrestrial plant productivity (Langley & Magonigal 2010). In other words, if  $\text{CO}_2$  fertilization promotes woody plant encroachment, systems that are nitrogen limited may not become as encroached with woody plants. In addition, the N fixing ability of the invading trees may also have a marked effect on SOC as N fixers have been found to increase SOC compared to other species (Johnson & Curtis 2001; Paul et al. 2002). Considering that savannas contain many leguminous species, woody plant encroachment by non leguminous species may have a less marked effect on soil carbon in these systems. Reich et al. (2001) found that the biomass response of systems to elevated  $\text{CO}_2$  or nitrogen is positively correlated with the species richness of assemblages. My data seems to support this, because when I divided my savanna sites into the four most species rich, and the four least species rich, thickets that had encroached into species rich savannas had accumulated far more above ground biomass than those that encroached into species poor savannas (Table 4.4). Encroached species rich savannas had also accumulated more carbon in the top 30cm of their soil, but in soils to a

depth of 100cm, encroached species poor savannas accumulated more carbon. Future work would do well to investigate the relative prevalence of nitrogen fixers in these systems, to see if they do indeed have a marked effect on carbon storage.

**Table 4.4 The changes in carbon that occurred after encroachment of species rich savannas compared to species poor savannas. Numbers in parentheses indicate standard error**

	Above ground carbon (Mg.ha <sup>-1</sup> )	Soil C to 30cm (Mg.ha <sup>-1</sup> )	Soil C to 100cm (Mg.ha <sup>-1</sup> )
Species rich savannas	+39.9 (7.8)	+10.1 (11.1)	+11.6 (21.7)
Species poor savannas	+27.3 (7.2)	+4.0 (23.6)	+25.0 (45.7)

#### *Carbon and nitrogen stocks after extreme fire events*

An obvious problem with carbon sequestration projects involving afforestation of grasslands is loss of carbon during disturbances such as fire. The September 2008 fire in Hluhluwe is a good example of an extreme event, burning through thicket and forest patches that had not burnt for 50 or more years (Refer to Catherine Brown's thesis. University of Cape Town 2009). Soil carbon contributes significantly to total carbon stocks, and in some systems, such as the peatlands in Indonesia, fires have seriously deleterious effects on soil carbon (Page et al. 2002). This makes it important to quantify possible soil carbon effects of fire in encroached thickets. My attempt to do so, however, found negligible changes in soil carbon in thickets after an intense fire, with local heterogeneity in soil carbon swamping any distinct fire effects on soil carbon losses. The only major losses were seen in above ground carbon (Figure 4.9), but these were not nearly as large as in forest plots. My results are supported by research done by Coetsee et al. (2010) in Kruger National Park who also found that regular fire over a period of 50 years had no significant negative effects on soil organic carbon or total soil N. They suggest that although fires may cause volatilization of N, this loss is balanced by inputs to the system from litter fall and root turnover. Other studies have suggested that N volatilization caused by frequent burning of savannas are balanced by N inputs in non-associative N fixation, or N deposition in rain (Frost & Robertson 1987; Holt & Coventry 1990). Overall, thicket soils were affected by fire more than savannas, but variation within thicket habitats was very high, suggesting spatial heterogeneity played a more significant role than fire. The negligible effect of this extreme fire on thicket soils implies that fire may be an appropriate method of thicket encroachment control (Fairfax et al. 2009).

## **Conclusion**

The soil attributes of encroaching thickets were not significantly different from those of savannas. My isotopic analyses suggest that grasslands in Hluhluwe are ancient systems, and the small carbon gain that woody plant thickening is causing may not be of sufficient magnitude to justify the loss of these ancient systems; especially considering the uncertainty surrounding the effectiveness of encroaching forests as a terrestrial carbon sink. It is likely to be decades if not centuries before encroached savannas sequester as much carbon as mature forests, and most of the carbon gain I found was in above ground carbon which is a temporary, unstable sink. I found that species composition and species richness had an effect on the carbon storing capacity of encroached savannas, with higher C storage in thickets more compositionally similar to forests, as well as thickets encroaching into more species rich savannas. Intense fires could prove an appropriate method of preventing and retarding woody plant thickening, and seem to have a negligible effect on soil carbon. My results suggest that woody plant thickening is not a major terrestrial carbon sink in the park. The small amount of carbon sequestered needs to be weighed up against the costs for biodiversity, water and farming practices to determine the net effects of woody plant thickening on ecosystem services.

## Chapter 5

### Socio-economic Implications of Woody Plant Encroachment

#### Introduction

Savannas and grasslands are economically important for a variety of reasons. For example they are important to the global farming community as many of the world's rangelands and much of its agriculture occur in these areas (Costanza et al. 1997; Sankaran et al. 2004). In Africa in particular savannas have a more intrinsic sentimental value because they are home to most of the world's last remaining megaherbivores. This translates into an economic significance because they attract tourists from all over the world who contribute significantly to the GDP of many African countries, not least of which is South Africa (Akama & Kieti 2003). The views of these tourists are an important source of information to guide park managers and planners (Obua & Harding 1996; Boshoff et al. 2007).

Woody plant thickening, or bush encroachment, has been extensive in both farmed and conserved savannas over the last century (Archer et al. 1995; Skarpe 1990; Van Auken 2000; Asner et al. 2003; Fensham et al. 2005; Britz & Ward 2007; Wigley et al. 2010). Besides the environmental repercussions this is causing, it is also likely to have economic consequences. On savanna rangelands stocking rates are likely to drop as access becomes more restricted by trees, and forage is reduced with declining grass cover. This would reduce the overall carrying capacity of the land (Roques et al. 2001; Moleele et al. 2002). In Namibia, cattle numbers were reduced to 36% of what they were in 1959, and woody plant encroachment is estimated to cause a loss of more than N\$700 million per annum (De Klerk 2004). What is often ignored is that in savannas under conservation in Africa there are likely to be direct consequences for wild animals, and these may translate into many unforeseeable indirect economic consequences.

Many African savannas under conservation contain megaherbivores, small herbivores and predators. A diversity of vegetation structures within the forest-grassland-savanna-thicket patch mosaic in these landscapes provides a diversity of habitats for mammals and birds

(Sirami et al. 2009). However, animals show preferences for certain habitats, due to direct (Sinclair et al. 2003) and indirect (Brown 1988, 1992, 1999; Brown et al. 1999; Laundré et al. 2001; Ripple & Beschta 2004) effects of predation and availability of grazing. Therefore an increase in tree density may be expected to affect animal distributions, both due to indirect predation pressures and direct resource pressures. All of these factors working together may result in herd sizes and animal densities decreasing with increasing woody plant encroachment. Species such as nyala and other small antelope which are adapted to forested environments may be expected to increase in number, although herd sizes should still remain fairly small as space and visibility are low.

In this chapter I am interested in the direct consequences of woody plant encroachment for wild animals in Hluhluwe-iMfolozi Park (HiP) as well as the indirect consequences that it will have on visitors to the park. Visitors to African savannas are predominantly there to see animals, and are not only an important source of income for the park, but for surrounding communities and smaller game reserves as well (Akama & Kieti 2003; Kerley et al. 2003; Lindsey et al. 2007). An increase in tree cover will reduce visibility, and as more woody plants encroach it is likely that animals will become more difficult to spot (Prins & van der Jeugd 1993), potentially affecting visitor satisfaction in the park. Whether actual animal numbers are reduced may be of less importance to visitors. If this is true would it influence park revenue?

My study is based in the Hluhluwe-iMfolozi Park (HiP) in Kwa-Zulu Natal (KZN) Province. HiP is managed by Ezemvelo KZN Wildlife (the provincial parks authority) and is a major contributor to the province's tourism industry (Aylward & Lutz 2003). The annual contribution that HiP makes to KZN Wildlife is disproportionately large for its area and expenditures (Table 5.1), so any loss in revenue that HiP suffers is likely to have repercussions for many other KZN Wildlife parks.

**Table 5.1 The relative contribution that Hluhluwe-iMfolozi Park makes to KZN wildlife's annual income (source: Aylward and Lutz 2003). (Percentages indicate the proportion of the total)**

	Hluhluwe-iMfolozi Park	Other KZN wildlife reserves	Total for KZN wildlife reserves
Land Area (ha)	96000 (14.2%)	579200 (85.8%)	675200
Revenue (millions of rand)	29.8 (31.7%)	64.2 (68.3%)	94.0
Expenditures (millions of rand)	16.8 (23.5%)	54.7 (76.5%)	71.5
Profit (millions of rand)	13.0 (57.8%)	9.5 (42.2%)	22.5

It is impossible to accurately predict how a phenomenon such as woody plant encroachment will affect the park economically, but in this chapter I attempt to make an estimate using historical animal and vegetation data, and by surveying visitors to the park. There are a few key questions I aim to answer, under the broader question of whether woody plant encroachment will affect HiP economically:

How will animal numbers, distribution, and density be affected by woody plant encroachment? Are visitors noticing woody plant encroachment? Will woody plant encroachment affect people's desire to return to the park? What proportion of tourists are regular visitors to the park, and do the perceptions of these tourists differ to once-off visitors? Do tourists think woody plant encroachment should be managed?

By answering these questions I hope to gain some insight into the economic repercussions that HiP might expect from woody plant encroachment.

## Methods

### *Vegetation preferences by animals*

To determine the impact of vegetation on animal presence, and get some idea if woody plant thickening is indeed going to affect mammal distributions I used data collected by the Earthwatch organisation every 2 years between 2002 and 2008. These observation teams walk a total of 26 fixed line transects that vary between 3.9 and 10.4 km in length (7.9 km on average). Teams of two observers walked transects just after sunrise over a 3 month period in the dry season (July to October). All herbivore observations of species larger than hare that were sighted within 500 m of both sides of each transect were recorded. The species and abundance were recorded as well as the GPS coordinates of the observer, and the distance

and bearing of the animals from the observer (Cromsigt et al. 2009). I then calculated the exact position of the animals by using the following equations

$$\text{Latitude} = \sin^{-1}(\sin \mu \cos \delta) + \cos \mu \sin \delta \cos \alpha$$

$$\text{Longitude} = \theta + \tan^{-1} \frac{\cos \delta - \sin \mu \sin \sigma}{\sin \sigma \sin \delta \cos \mu}$$

where

$\mu$ =latitude of observer

$\theta$ =longitude of observer

$\sigma$ =calculated latitude of animals

$\delta$ =distance of animals from observer

$\alpha$ =bearing of animals from observer

I overlaid the herbivore distribution data on a vegetation map developed by Modis using satellite imagery. Their vegetation classifications were used, except that I reclassified deciduous broadleaf forest as mixed forest, and evergreen broadleaf forest as old forest. I used this data to make inferences about whether animals were showing any preference for open vegetation, and if herd sizes were smaller in closed habitats. Only common animals were included in the analysis, and all small browsing antelope (except Nyala) were regarded as one species. Results were statistically compared using ANOVA and post-hoc Tukey Tests.

#### *Visitor surveys*

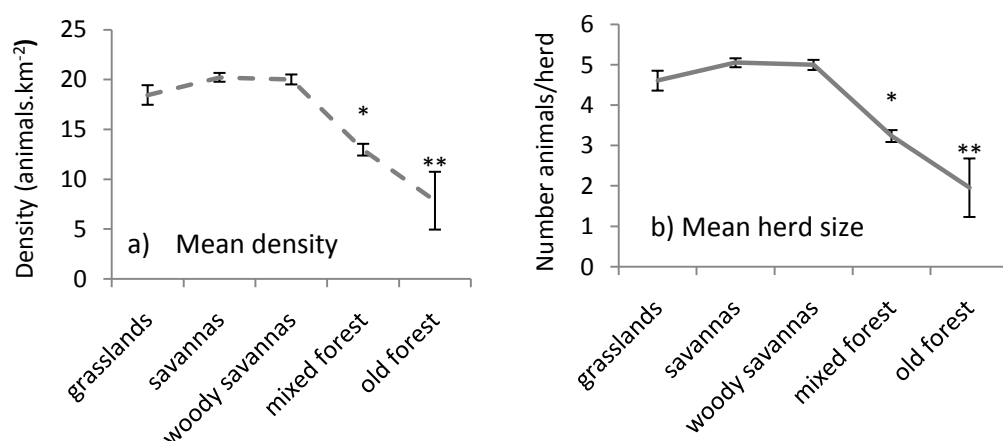
I surveyed 220 visitors to the park in July 2009 and May 2010 in tourist camps, at the entrances to the park, and in picnic areas throughout the park. The park contains two main tourist camps; Hilltop is a high budget camp in the Hluhluwe section of the park, and Mpila is a lower budget camp in the iMfolozi section of the park. Visitors were selected at random, and only one per group was selected. They were given a structured questionnaire to fill out (Appendix 2), which included both open-ended and multiple-choice questions. Open-ended questions included where they were from, why they were there, whether they had visited the park before, how often they visited, and whether they had noticed a change in vegetation since their first visit. They were also asked to indicate which animals they most wanted to see in the park. To determine if they noticed a preference in habitat by animals, they were shown photographs depicting different vegetation types and asked where they thought they had seen the most wildlife. Once they had answered these questions the woody plant encroachment phenomenon was explained, and they were asked to record how strongly they agreed with

each of a series of statements on a scale from 1 to 5 (5 being strongly agree, 1 being strongly disagree). These questions were designed to ascertain whether woody plant encroachment would indirectly cause a reduction in visitor numbers. I performed Chi-squared tests on some variables to determine if they were dependant on previous answers to questions, for example, whether visitors who stayed at Hilltop camp were more likely to be from overseas.

## Results

### Animal numbers, distribution and density

Figures 5.1 a) and b) show mean animal density and herd size for all herbivores included in the analysis in different vegetation types. There is a general trend towards increasing woodiness from left to right on the x axis, but this is not based on a quantitative measure of woodiness, and it is not a linear increase. Mean animal density and herd size showed a general decreasing trend as vegetation became more forested, although grasslands had lower means than open savannas and woody savannas. This supports the hypothesis that with an increase in woodiness there is not only a decrease in the mean number of animals per herd, but also a general decrease in mean animal densities.



**Figure 5.1 a) Mean animal density ( $\pm$ SD) and b) mean herd size ( $\pm$ SD) of animals in different habitat types. The x axis represents an increase in woodiness to the right. Asterisks indicate significant differences determined from ANOVA and Tukey tests at  $\alpha=0.05$ . Vegetation classifications are outlined in methods**

Tables 5.2 and 5.3 give the results from ANOVA tests to determine whether the mean density and herd size were significantly different between different vegetation types, first taking all

animals into account and then looking at species separately. These results are represented graphically in figures 5.2 and 5.3.

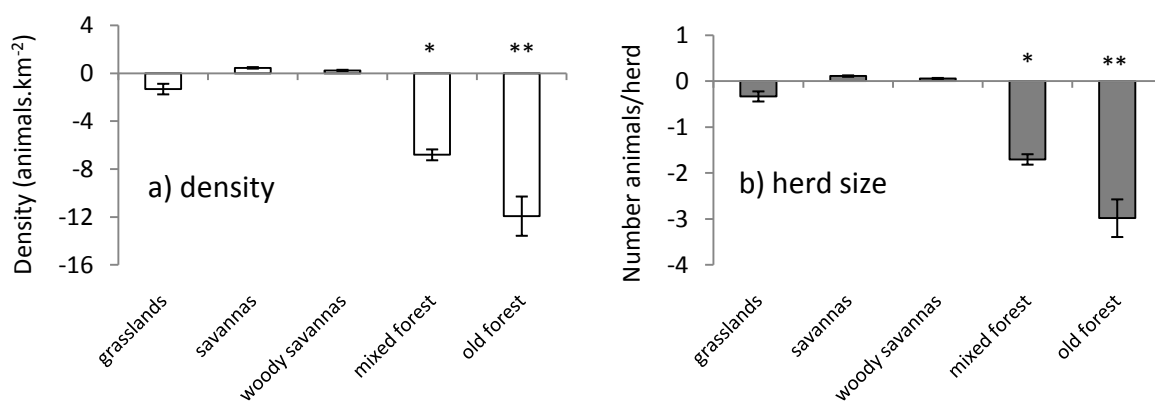
Figure 5.2 shows how different the mean density and herd size of all animals in each vegetation type is from the mean for all vegetation types. As figure 5.1 suggests, savannas and woody savannas had animal densities and herd sizes above the mean, while thicket and forest had animal densities and herd sizes well below the mean. Grassland animal densities and herd sizes were slightly below the mean. Grasslands, savannas and woody savannas did not have significantly different means, but mixed forest and old forest were significantly different from each other and the other vegetation types (Tables 5.2 and 5.3).

**Table 5.2 Results from ANOVA tests to determine whether the mean animal density was different in different vegetation types, taking all animals into account, as well as certain species in isolation. Results are significantly different at  $p < 0.05$**

	SS effect	df effect	MS effect	SS error	df error	MS error	F	p
All animals	462.50	4	115.62	37.14	15.00	2.48	46.70	<0.0001
Zebra	2.24	4	0.56	17.13	15.00	1.14	0.49	0.74
Impala	259.14	4	64.79	7.01	15.00	0.47	138.68	<0.0001
Buffalo	36.15	4	9.04	7.15	15.00	0.48	18.95	<0.0001
Giraffe	0.77	4	0.19	0.19	15.00	0.01	15.56	<0.0002
White rhino	0.17	4	0.04	3.61	15.00	0.24	0.18	0.95
Elephant	2.62	4	0.65	12.43	15.00	0.83	0.79	0.55
Small antelope	3.90	4	0.97	10.48	15.00	0.70	1.39	0.28
Nyala	11.99	4	3.00	16.33	15.00	1.09	2.75	0.07

**Table 5.3 Results from ANOVA tests to determine whether the mean herd size was different in different vegetation types, taking all animals into account, as well as certain species in isolation. Results are significantly different at  $p < 0.05$**

	SS Effect	df effect	MS effect	SS error	df error	MS error	F	p
All animals	28.91	4	7.23	2.32	15	0.15	46.70	<0.0001
Zebra	27.85	4	6.96	9.63	15	0.64	10.85	0.0002
Impala	218.59	4	54.65	5.80	15	0.39	141.22	<0.0001
Buffalo	373.21	4	93.30	304.11	15	20.27	4.60	0.01
Giraffe	18.54	4	4.63	3.09	15	0.21	22.50	<0.0001
White rhino	4.51	4	1.13	4.84	15	0.32	3.50	0.03
Elephant	35.68	4	8.92	50.67	15	3.38	2.64	0.08
Small antelope	5.65	4	1.41	12.37	15	0.82	1.71	0.20
Nyala	0.78	4	0.20	8.58	15	0.57	0.34	0.85



**Figure 5.2 a) Deviation from mean animal density ( $\pm$ SE) for all vegetation types and b) Deviation from the mean herd size ( $\pm$ SE) for all vegetation types. The x axis represents an increase in woodiness towards the right**

Figure 5.3 depicts certain species in isolation. The pattern changed depending on the species. Densities and herd sizes were below the mean in more forested vegetation for open plains species such as zebra, impala, and buffalo. I found these to be significantly different from other vegetation types at  $\alpha=0.05$ , except for zebra densities (Tables 5.2). Giraffe also showed a slight preference for savanna-like habitats, and their mean herd size and density was significantly lower in old forests (Figure 5.3d, Tables 5.2 and 5.3). Large animals such as white rhinoceros and elephant showed no particular trend in herd sizes or density with an increase in forested vegetation (Figures 5.3e and 5.3f). However, the mean herd sizes for white rhinoceros in old forest were significantly lower than the mean, and significantly higher than the mean in mixed forest (Table 5.3). Elephant showed no significant differences in mean herd size or density between vegetation types. Nyala and other small antelope showed a decreasing trend in mean herd size, but an overall increase in the number of animals per square kilometre as vegetation became more forested (Figures 5.3g and 5.3h). The means for these species were not significantly different in any vegetation type (Tables 5.2 and 5.3). These results suggest that while animal densities and herd sizes can be expected to change with woody plant encroachment, the impact will vary depending on species. The data suggest that small antelope which are already adapted to forest living, as well as larger animals such as elephant and rhino, will be unaffected or may even benefit from woody plant encroachment. On the other hand the grazing and savanna adapted species, many of which are very popular with park visitors (Figure 5.7), are likely to be affected quite severely by woody plant encroachment.

Deviation from the mean herd size (animals/herd) and mean density (animals/km<sup>2</sup>) for all vegetation types

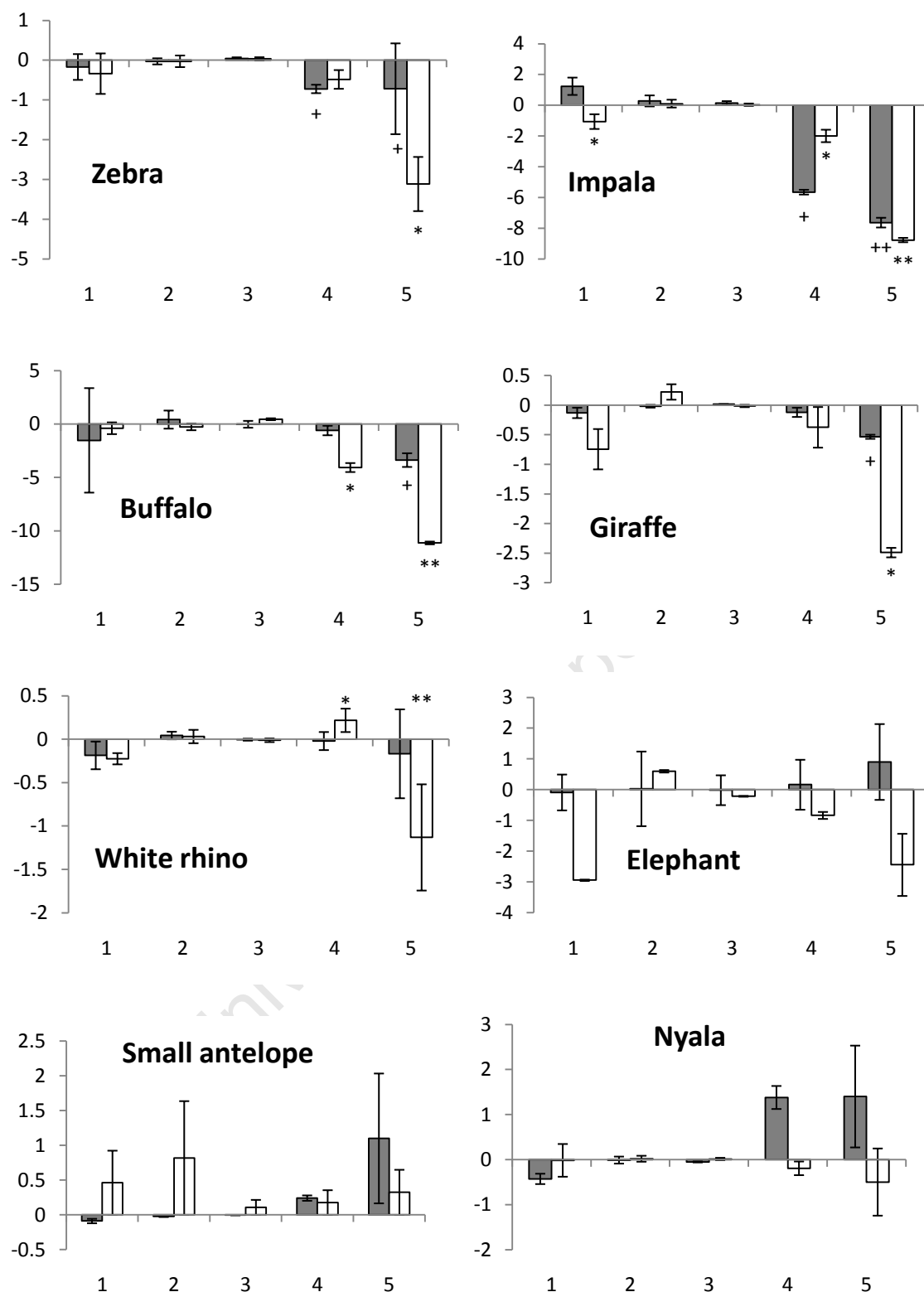
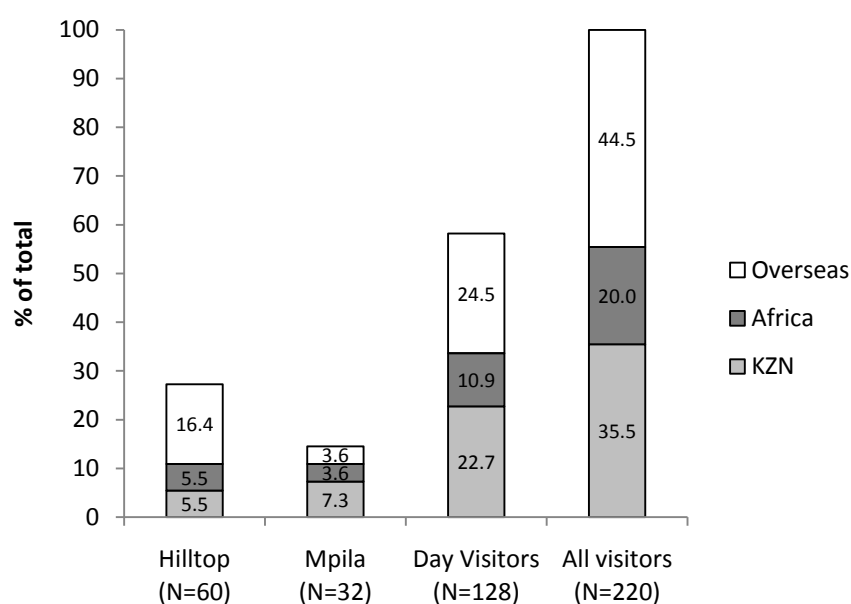


Figure 5.3 Deviation from the mean ( $\pm$ SE) for all vegetation types for herd size (white bars) and animal density/km<sup>2</sup> (grey bars) for some of the most popular herbivores in the park. The numbers on the horizontal axis represent the vegetation type: 1 grassland, 2 savanna, 3 woody savanna, 4 mixed forest and 5 old forest. \* and + refer to significant differences at  $\alpha=0.05$ , determined using ANOVA and Tukey Tests

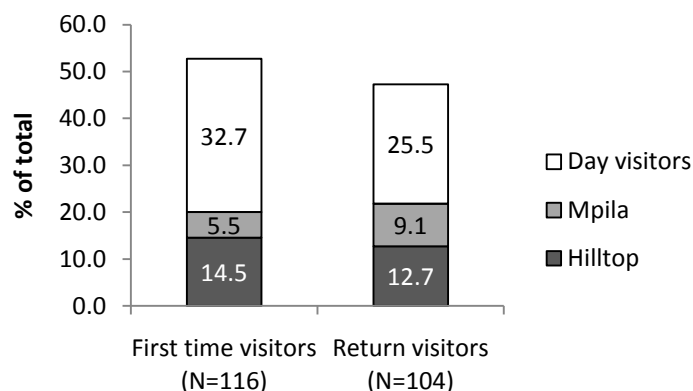
## Visitor surveys

55.5% of visitors to the park came from KZN and Africa (there were very few African visitors from outside South Africa so all Africans and South Africans were bulked together) (Figure 5.4), and 45.5% came from overseas. Most visitors were there for the day (58.1%). 27.4% of visitors were staying at Hilltop camp, and the vast majority of these were overseas visitors. A chi-squared test confirmed that tourists from KZN were less likely to stay at Hilltop while overseas visitors were more likely to stay there than would be expected by chance ( $p=0.011$ ,  $\chi^2=13.04$ ,  $df=4$ ).



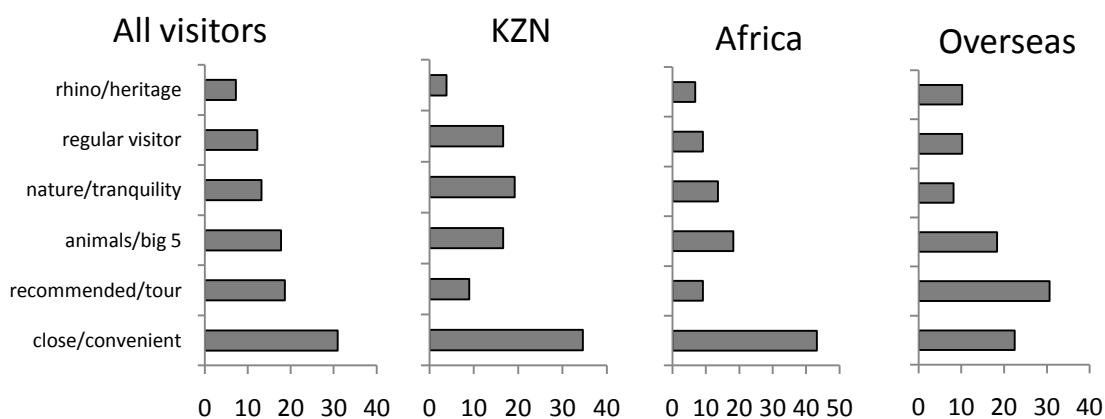
**Figure 5.4 Percentage of visitors utilising different accommodation, partitioned into where they were from**

Figure 5.5 shows the relative percentages of people who had visited the park before, and their choices of accommodation. Nearly half of the surveyed tourists had been to the park before (47.3%). 41.8% of visitors to the park had accommodation inside the park, and more than half of these were return visitors (21.8%). Most of the day visitors had not visited the park before.



**Figure 5.5** The percentage of visitors who were visiting the park for the first time and who had visited the park before, partitioned into where they were staying in the park

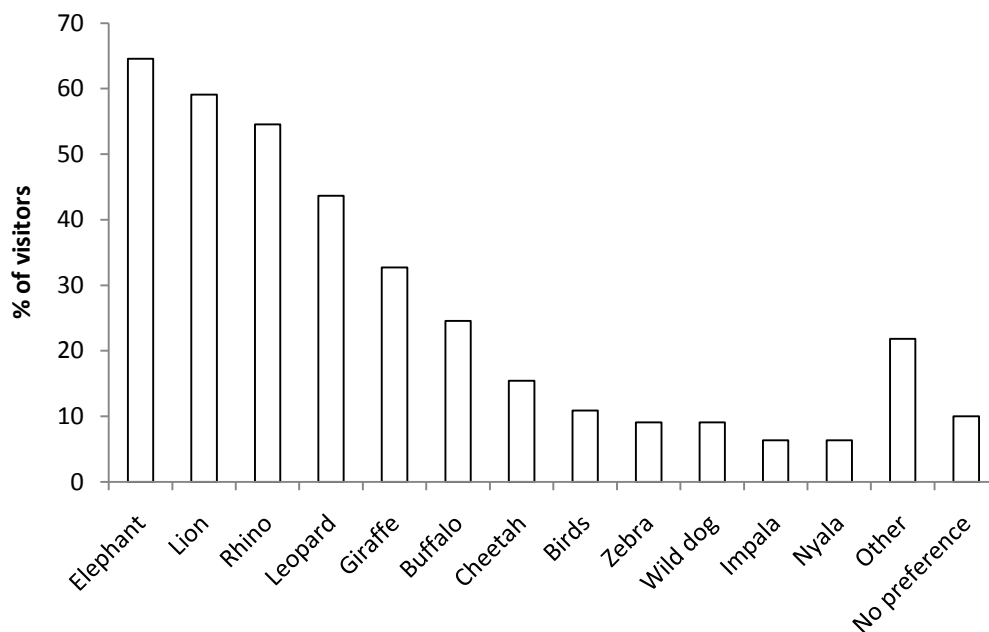
The most commonly cited reason for choosing to visit Hluhluwe-iMfolozi Park was that it was close or convenient (Figure 5.6). This was an open ended question so I have bulked the answers into categories. For overseas tourists the most commonly cited reason for visiting was that it was recommended by someone or they were on a tour. Being in nature or tranquillity was most commonly cited by people from KZN as a reason for choosing this park. Although the least commonly cited reason, the park’s heritage and the fact that it is well known for its rhino conservation efforts does attract some tourists to the park, mainly overseas tourists.



**Figure 5.6** Visitors’ reasons for choosing to visit HiP. x axis shows percentage of tourists who cite each reason

The big 5 tended to be the most popular animals (figure 5.7), except that giraffe were more popular than buffalo. The animal preferences were affected by where the visitor was from ( $p=0.002$ ,  $\chi^2=51.90$ ,  $df=26$ ), with giraffe and zebra more popular among overseas visitors, and buffalo and birds more popular among South African visitors. Whether people had been to the park before or not also affected their desire to spot certain animals ( $p=0.0098$ ,  $\chi^2=78.7$ ,

df=52). The desire to spot leopard, impala, nyala and cheetah increased if people had been before, but the desire to see zebra dropped.

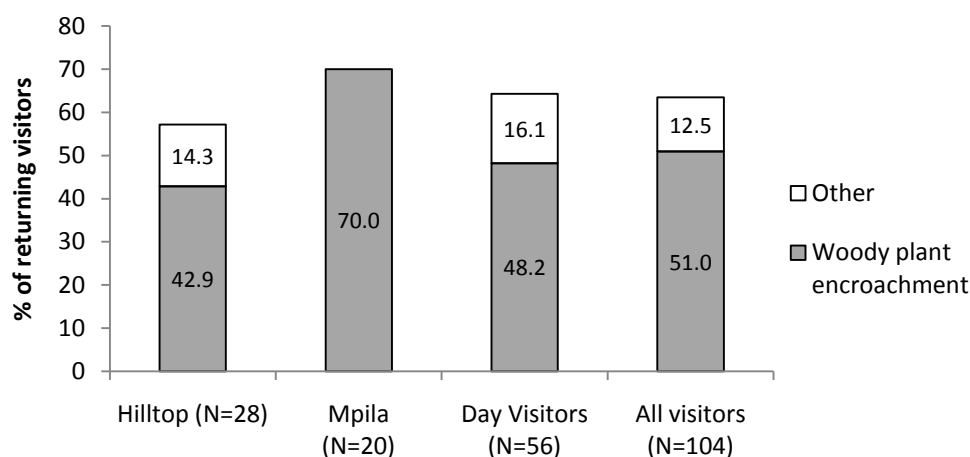


**Figure 5.7 Percentage of visitors who hoped to see each species of animal**

When asked, using photographs, which habitat they thought they had seen most animals in, 63% of visitors chose photographs showing open savannas or landscapes with both forest and savanna elements in them. Only 37% of people said they had spotted more animals in closed thicket landscapes.

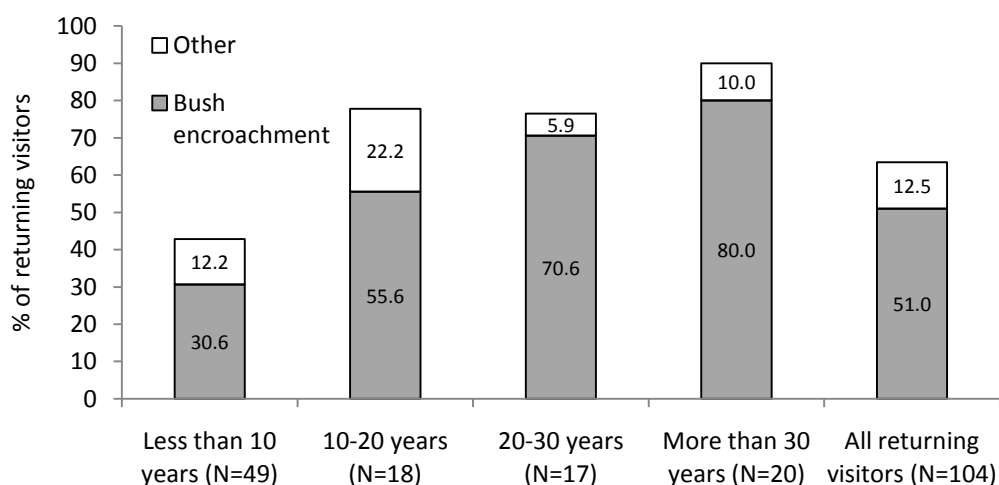
I used the same photographs to ask visitors which scenery they enjoyed most when driving through the park. 48% of visitors preferred driving through landscapes with both forest and savanna elements, 27% of people preferred open savanna landscapes, while 25% preferred closed habitats.

Figure 5.8 illustrates the percentage of returning visitors who had noticed woody plant encroachment over the years. 51% of returning visitors had noticed woody plant encroachment specifically, while an extra 12.5% of visitors had noticed vegetation changes of some sort, but did not explicitly identify it as woody plant encroachment. Visitors staying at Mpila noticed woody plant encroachment more than visitors to Hilltop or day visitors.



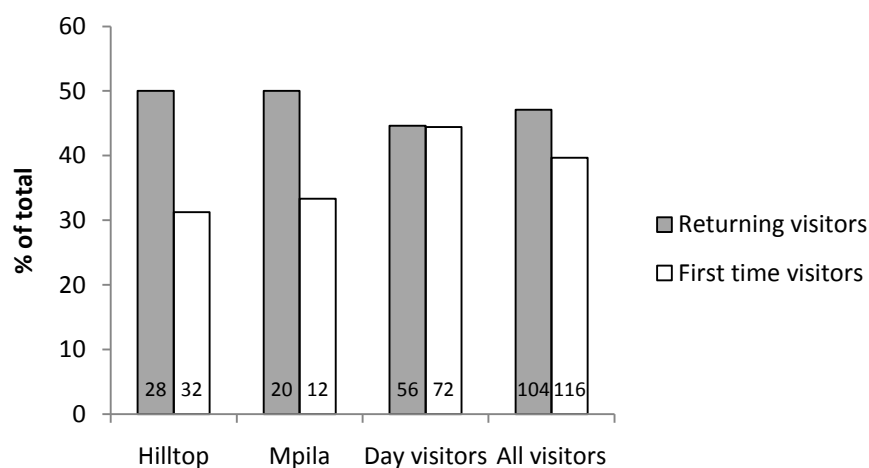
**Figure 5.8** Percentage of returning visitors who have noticed woody plant encroachment over the years. The x axis indicates their accommodation in the park, N refers to the total number of returning visitors

Figure 5.9 illustrates the percentage of returning visitors who had noticed woody plant encroachment, according to when they first visited. Visitors that had been visiting for longer were more likely to have noticed woody plant encroachment; 80% of visitors who had been visiting the park for more than 30 years had noticed woody encroachment, while a further 10% had noticed some change in the vegetation, not explicitly identified as woody plant encroachment. This was in contrast to visitors who had been visiting for less than 10 years, of which only 30.6% had noticed woody plant encroachment, and a further 12.2% had noticed a change in vegetation.



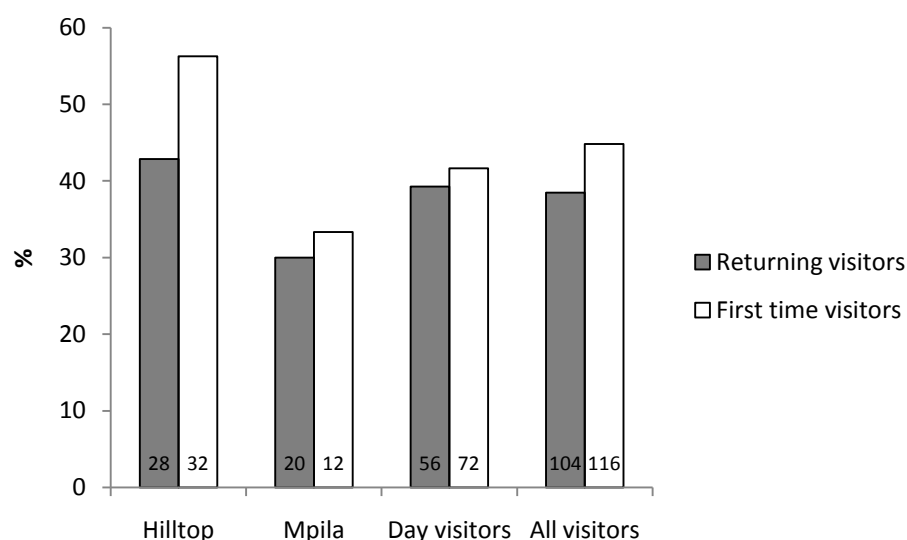
**Figure 5.9** Percentage of returning visitors who had noticed woody encroachment over the years (grey blocks) or some other shift in the vegetation which they did not explicitly identify as woody plant encroachment (white blocks). The horizontal axis indicates how long they have been visiting the park for. N refers to the total number of returning visitors in each category

Visitors were asked to rate how much they agreed with certain statements, with 5 being strongly agree and 1 being strongly disagree. I considered those who answered either 4 or 5 to be in agreement with the statement. Figure 5.10 illustrates the response to the statement that woody plant encroachment *should* be controlled. Grey blocks indicate the response of returning visitors while white blocks indicate the response of first time visitors. In all cases those who had visited before were more inclined to want to control woody plant encroachment than those who had not. Returning visitors who were staying inside the parks were also more inclined to want to control woody plant encroachment.



**Figure 5.10 Percentage of first time visitors who thought woody plant encroachment should be controlled compared to the percentage of returning visitors who thought woody plant encroachment should be controlled. Numbers indicate total sample size**

With regards to the statement “I would not visit the park again if game became more difficult to spot”, in which visitors were once again asked to rate how much they agreed to the statement on a scale from 1 to 5 (5 being strongly agree), the mean response was  $3.0 \pm 1.29$ , and the mode was 4. Figure 5.11 illustrates the percentage of tourists that circled either 4 or 5. Percentages were highest for Hilltop visitors, and lowest for Mpila visitors. They were also lower for returning visitors than first time visitors. When first time and returning visitors are combined, these results suggest that Hilltop would lose 50% of their visitors, and 20% of these would be regular visitors, if animals became more difficult to spot.



**Figure 5.11** Percentage of visitors who would not return to the park if animals became more difficult to spot. White shows first time visitors, while grey shows return visitors. Numbers indicate total sample sizes

Table 5.4 shows visitors who would not return to the park if animals became more difficult to spot as a percentage of all the visitors in the park. If we consider returning visitors as *definite* future visitors, the park would lose 18.2% of their definite future visitors to woody plant encroachment, and 5.5% of these were visitors to Hilltop. Combine this with a return rate of 47.8% for first time visitors (figure 5), and they would lose an additional 11.2% of *potential* future visitors. This combines to a total loss of 29.4% of potential future visitors if animals become more difficult to spot.

**Table 5.4** The percentage of the total number of visitors who would not return if animals became more difficult to spot due to woody plant encroachment, divided into those who have been to the park before and first time visitors

		Hilltop	Mpila	Day visitors	All visitors
Would return if animals became more difficult to spot	Returning visitors	7.3	6.4	15.5	29.1
	First time visitors	6.4	3.6	19.1	29.1
Would not return if animals became more difficult to spot	Returning visitors	5.5	2.7	10.0	18.2
	First time visitors	8.2	1.8	13.6	23.6
Total		27.3	14.5	58.2	100

## Discussion

*Woody plant encroachment is likely to cause mammal species composition and densities to shift*

Animal numbers, distributions and densities are likely to be impacted by woody plant encroachment, although the direction and magnitude of the change is dependent on the species of animal. Impala appear to be most strongly negatively influenced by woody plant encroachment, and they are the most abundant herbivore in the park (KZN wildlife census data). As the most abundant prey item it would follow that they contribute a significant amount to predator diets. If their density dropped, prey densities may not be high enough to maintain predator populations, which would also drop, as suggested by Brown (1992). This is significant for the park because many of the most popular species for visitors are predators. This has also been found by studies in Addo Elephant National Park (Lindsey et al. 2007). Although predator-prey relationships would likely eventually stabilise, the overall reduction in prey densities that woody plant encroachment is likely to cause may lead to a decline in predator numbers. In addition, predators which require space to hunt such as cheetah, which are already rare in the park, would be very restricted in their hunting range. The dominant prey species is likely to switch to something that is better suited to forests, such as nyala. However, currently there are about four times the number of impala in the park than the number of nyala. Whether predator populations suffer or not, we can say with some degree of certainty that herbivore community composition would shift from being dominated by open plains species such as impala, zebra, buffalo and giraffe to smaller, forest tolerant antelope and larger herbivores which are less affected by encroachment, such as elephant and rhinoceros. However, white rhinoceros may eventually also be limited by resource availability, as grass cover would be significantly reduced.

*Heterogeneity in the landscapes is important to visitors*

Whether mammal populations are affected or not, visibility is likely to decrease as tree density increases, and so visitors will be less likely to spot animals (Prins & van der Jeugd 1993). Most visitors noticed that more animals were spotted in open and heterogeneous habitats. Perhaps of greater consequence to park revenue is that the most popular habitats from an aesthetic standpoint were diverse landscapes which still contained some of the

typical savanna characteristics, such as open plains and single trees. With an influx of trees into the system, the park is in danger of becoming too homogeneous and uninteresting for tourists.

Visitor's reasons for choosing HiP over other game reserves may be important in predicting their response to woody plant encroachment. The most commonly cited reason for visiting the park was that it was close or convenient (Figure 5.6), except for overseas visitors, who were most often in the park because of recommendations or with a tour. Mmopelwa et al. (2007) found that in Botswana overseas visitors were more willing to pay higher rates for wildlife tourism, which is mirrored by my results which found that overseas tourists often stayed in the more expensive accommodation. These visitors may be more likely to be put off visiting by woody plant encroachment, because tour operators are unlikely to take tourists to a game reserve where their wildlife viewing success is minimised, and the same can be said for guide book recommendations. This suggests that the park may lose a large portion of their overseas visitors (and therefore biggest spenders) because of woody plant encroachment. I would postulate that woody plant encroachment is less likely to put off visitors that are in the park because it is close or convenient, as the convenient location of the park and its proximity to other areas will not change. Other visitors who are unlikely to be put off by woody plant encroachment are those who have come because of the park's heritage and its rhino conservation efforts, as well as those who have come just to escape city life and experience the tranquillity of nature.

#### *Many regular visitors have noticed woody plant encroachment*

More than half of returning visitors had noticed woody plant encroachment since their first visit to the park. This was posed as a completely open-ended question asking whether they had noticed any changes in the vegetation over the years, so we can assume that the change has been drastic enough for uninformed individuals to notice it. Unsurprisingly, as it is a slow process, visitors who have been visiting the park for two or more decades were more likely to have noticed woody plant encroachment (Figure 5.9). Just under half (47.8%) of the visitors surveyed had been to the park at least once before, suggesting that the opinions of returning visitors are fairly important to the park, as returning visitors contributed quite significantly to visitor numbers. Returning visitors were also more likely to stay in park accommodation which means they contributed more to park revenue. Very few studies have looked explicitly

at how park visitors perceive woody plant encroachment and other vegetation changes, so comparison of these results to previous studies is problematic.

#### *Woody plant encroachment may reduce visitor numbers*

62% of visitors thought that management should attempt to control the spread of woody plants in the park, but only a third of these were returning visitors. 41.8% of visitors would not return to the park if game became more difficult to spot (Figure 5.11), and as table 5.4 highlights, this translates to an approximate loss of 30% of potential future visitors if I assume that visitors who have been before are all likely to return and approximately half of first time visitors are likely to return in the absence of woody plant encroachment. These results suggest that not only are tourists noticing woody plant encroachment, but that their decision to visit the park again may be negatively impacted by it. The lack of literature on the topic suggests that it has not been considered a major issue in the past, but my results suggest it should be more thoroughly investigated.

#### **Conclusion**

These survey results highlight the fact that woody plant encroachment is not merely an environmental issue for management, but could negatively influence the economy of the park. HiP contributes significantly to the revenue of KZN wildlife as a whole (Aylward & Lutz 2003), and so any drop in revenue will affect the organisation significantly. In addition, KZN wildlife employs many members of the local community (Aylward & Lutz 2003), so many livelihoods would be affected. It is not only HiP which would be affected by a drop in visitor satisfaction, but also the many smaller businesses and private game reserves, as well as local ecotourism ventures, which benefit from being in close proximity to such a large tourist attraction (Bookbinder et al. 1998; Kiss 2004).

Visitor demand for viewing large animals is unlikely to disappear, so the overall number of wildlife tourists in Africa is unlikely to drop (Obua & Harding 1996; Goodwin & Leader-Williams 2000; Boshoff et al. 2007; Lindsey et al. 2007; Mmopelwa et al. 2007). Rather we may see a shift in visitor numbers to different parks as tourists may be inclined to choose parks where they are more likely to have the experience they are looking for. In order to ensure success of the park in the future, managers need to make decisions based first and

foremost on conservation, but with an understanding that conservation will be facilitated by the revenue that is brought in by visitors (Kiss 2004; Boshoff et al. 2007; Lindsey et al. 2007; Mmopelwa et al. 2007). In previous chapters I have shown that woody plant encroachment is affecting ecosystem processes such as carbon cycling (Jackson et al. 2002; Hudak et al. 2003; Archer et al. 2004), as well as community composition and species richness of birds and plants (Skowno & Bond 2003; Sirami et al. 2009). I have now shown that it is also likely to affect mammal community composition as well as visitor satisfaction in the park. This suggests that it may be prudent for managers to consider strategic management of the phenomenon using fire and other management tools.

University of Cape Town

# Chapter 6

## Synthesis

This thesis set out to determine what the ecosystem consequences of woody plant encroachment are for Hluhluwe-iMfolozi Park, with an emphasis on biodiversity, carbon and tourism. Because an increase in tree densities affects many and varied processes, it becomes difficult to easily weigh up costs and benefits, and the outcome is heavily dependent on the land use in question. There are inevitable trade-offs with respect to ecosystem services (Jackson et al. 2005; Reyers et al. 2009). For example, while biodiversity is important to a conservation area, in an area less geared towards conservation it may be more beneficial to maximise carbon storage. However, maximising carbon storage with an influx of trees may cause significant reductions in stream flow, causing a trade off between water and carbon (Jackson et al. 2005; Jackson et al. 2007). With this amount of complexity, it is difficult to say whether the net effects of woody plant encroachment are positive or negative in general, but it is possible to make value judgements based on certain aspects. In the next few paragraphs I summarise my findings with respect to the biodiversity, carbon and socioeconomic implications of woody plant encroachment in a conservation area.

There is a common perception that forests are the primary cover of humid tropical regions, and that grasslands are secondary, produced by burning and felling of forests. It is now clear that C<sub>4</sub> grasslands are millions of years old and have their own distinct biodiversity (Cerling et al. 1997). Past research has shown that C<sub>4</sub> dominated biomes became widespread about 8Ma (Cerling et al. 1997; Osborne & Beerling 2006; Osborne 2008). My isotopic profiles suggested that in all cases the grasslands and savannas in my study sites were older than the woody habitats. I found the alpha and beta diversity in these grasslands and savannas to be very high, a pattern seen in other grassy ecosystems in the world (Cowling et al. 1989; Ratter et al. 1997; Mittermeier et al. 1998; Overbeck et al. 2007; Sankaran 2009). The alpha diversity was in fact much higher than in adjacent woody habitats. The herbaceous component of grassy systems was dominated by shade intolerant, fire tolerant plants that utilise underground storage organs. These were almost absent in forests, and very rare in encroached savannas („thickets”). Characteristic species in encroached areas were shade tolerant, fire sensitive species, although they did contain both savanna and forest elements. Older thickets were more compositionally similar to forests than savannas, suggesting that

thickets are seral to forests. In contrast, savannas and grasslands shared very few species with forests, refuting the idea that they are an early successional stage to forest.

It became clear that the shift occurring in Hluhluwe Game Reserve was not merely a thickening of savanna species, but rather a complete switch to forest adapted species, which is likely to eventually cause a complete biome switch from savannas and grasslands to forest. The prevalence of shade tolerant, fire sensitive species in encroached areas is likely to cause a positive feedback loop as they hinder the movement of fire into the system, which then allows more slow growing, shade tolerant species into the system, which further hinder the progress of fire into the system. This is likely to hasten the switch to forest. Woody plant encroachment appears to be causing dramatic species loss in Hluhluwe Game Reserve and, considering that it is a conservation area first and foremost, management needs to consider that woody plant encroachment may currently be one of the biggest threats to the park.

Possible methods of controlling woody plant encroachment, which is essentially a biome switch, include the use of intense fire (“firestorms”) (Refer to Catherine Brown’s thesis. University of Cape Town 2009). I looked briefly at the efficacy of intense fires in restoring savannas in Hluhluwe Game Reserve. The intense fire of September 2008 caused a reduction in woody cover, and encouraged many herbaceous species to return to the system. However, many of the herbaceous species were weedy annuals. In contrast, the grassy layers of pristine savannas and grasslands were dominated by long lived forbs with underground storage organs. Though these plants persist in the face of regular fires and herbivory, they are unable to persist in long term shaded environments (Uys et al. 2004). Predictably, due to the heavy shading, I found many of these forbs to be missing in unburnt thickets. Zaloumis and Bond (2010) have shown that South African grasslands that were restored after afforestation contained fewer species, and less than half the number of forb species, than pristine grasslands (144 vs 221 species; 73 vs 163 forb species). This suggests that forbs are not able to easily recolonise a system after being removed. Similarly, although recently burnt thicket patches contained many herbaceous species, very few of these were long lived forbs with underground storage organs. It will likely take many years before savannas recovering from woody plant encroachment contain forb numbers comparable to their pristine, unencroached counterparts. There is a scarcity of similar studies in a southern African context, but studies in the Brazilian Cerrado and in Mexico have shown that open vegetation supports distinct plant communities to forest (Perez-Garcia & Meave 2006; Overbeck & Pfadenhauer 2007),

and a study in Australia has shown that insect communities switch to domination by forest-tolerant species as savanna switches to forest (Andersen et al. 2006).

I have shown that woody plant encroachment is negatively impacting biodiversity. My results are specific to my study area, but the globally widespread nature of woody plant thickening suggests it would be important to extend such studies elsewhere. Biodiversity is considered globally important for the maintenance of ecosystem services (Diaz & Cabido 2001; Tilman et al. 2006), as the genetic diversity provides a system with resilience and resistance to change. Despite the negative impacts of woody plant thickening on biodiversity, it is often championed as a good terrestrial carbon sink (Hibbard et al. 2001; Hudak et al. 2003; Harms et al. 2005), and to some stakeholders this is arguably a more important ecosystem service than biodiversity, considering the growing need to mitigate carbon dioxide emissions.

Indeed, I did find that encroached areas contained more carbon than savannas, but two thirds of the gain was due to above ground carbon increases. Above ground carbon is an inherently unstable sink, and is easily lost to large disturbance events such as fire. I estimated the mean rate of carbon accumulation in encroached thicket areas to be  $\sim 0.86 \text{ MgCha}^{-1}\text{yr}^{-1}$ , which was far below the  $4.2 \text{ MgCha}^{-1}\text{yr}^{-1}$  estimated in spekboom rehabilitation projects in Eastern Cape Thickets (Mills and Cowling 2006). It was also below the  $1.0 \text{ MgCha}^{-1}\text{yr}^{-1}$  estimated for savannas in Australia's Northern Territory by Williams et al. (2004). Despite this, it is higher than the mean rate of carbon accumulation for savannas globally, estimated by Grace et al. (2006) to be  $0.14 \text{ MgCha}^{-1}\text{yr}^{-1}$ . As encroached savannas became more similar to forests, their carbon storage increased, suggesting that older thickets store more carbon. The carbon storage was tightly linked to nitrogen storage (Figure 4.6), but I did not investigate whether the presence of nitrogen fixers affected carbon storage at all. They may have a pronounced effect on carbon sequestering potential in the soils (Johnson & Curtis 2001; Paul et al. 2002), and this should be investigated further.

To summarise, I found only a small increase in carbon as woody plants encroached, a result mirrored by Knapp et al. (2008) in North America. This increase was dependent on many factors, such as species richness of the savannas that were encroached, as well as the age of the encroached area. In addition, past research has shown that climate has an influence on the amount of carbon stored in a system, and Jackson et al. (2002) suggest that the relative increase in carbon storage will be greater in more arid areas, possibly due to reduced

decomposition rates. It is important, therefore, to broaden the scale of these investigations to ensure that climatic variability as well as geological differences are taken into account when estimating changes in carbon stocks following woody thickening. What I did not take into account was the physical coupling of vegetation to climate. Trees have a much lower albedo than grasses, and (Gibbard et al. 2005) suggest that a global replacement of current vegetation by trees would have a net warming effect on global temperatures. They suggest that this may be more pronounced at higher latitudes than at the tropics, where evapotranspiration by trees is likely to have a net cooling effect. However, savannas are complex systems, and there are various other contributing factors, such as fire, which may also affect the net temperature effect of trees (Beerling & Osborne 2006). This makes it difficult to accurately estimate the effect of increased tree cover on global temperatures, but if their net effect is to warm the earth, then this may counteract the soil carbon gains that they promote.

In the fifth chapter of my thesis I moved away from the physical and biological environmental effects of woody plant encroachment, and focused on the direct and indirect socio-economic consequences it would have on the park. The park's mission statement is "To ensure effective management and sustainable use of KwaZulu Natal's biodiversity in collaboration with the community". In addition their strategic conservation goal is "To conserve the indigenous biodiversity of KwaZulu-Natal both within and beyond protected areas" ([www.kznwildlife.com/index.php?/Wildlife-management.html](http://www.kznwildlife.com/index.php?/Wildlife-management.html)). Considering that the goals of the reserve are so centred around biodiversity, the loss in plant diversity that woody plant encroachment is causing should be considered catastrophic by management. In addition, plants are not the only organisms affected by woody plant thickening. I found that mammal numbers, densities and distribution were impacted by habitat, but that the direction and magnitude of this impact were dependent on the species of animal. Grazers such as impala and zebra were negatively affected by woody plant thickening, while forest adapted browsers such as nyala were positively impacted. Other studies have shown that insect and bird communities are also affected by stand structure, with a switch in community composition observable in encroached savannas or forested areas (Skowno & Bond 2003; Andersen et al. 2006; Sirami et al. 2009). Larger mammals and birds were cited as one of the main reasons that visitors came to the park (Figure 5.6, Chapter 5), and visitors are the main source of revenue for the park (Aylward & Lutz 2003); the revenue from these visitors is in turn what allows the park to continue conservation efforts. This means that any significant

changes to mammal or bird populations and distributions in the park are likely to have cascading consequences for conservation efforts in the park.

Visitors prefer to drive through heterogeneous landscapes, and an influx of trees into the landscape threatens not only to make animals difficult to spot, but also to make the landscape less appealing to visitors. Many surveyed visitors had noticed woody plant encroachment in the park, and 62% of visitors were of the feeling that it should be managed. My research suggested that the park could potentially lose ~30% of its future visitors to the park if animals and birds became more difficult to spot due to woody plant thickening. In addition, the economic implications of woody plant thickening would not be restricted to the park. Tourists facilitate the presence of many communities, private game lodges and other ventures in the surrounding areas of the park due to the revenue they bring in. Smaller conservation areas in the province, which rely on HiP revenue to supplement their own, may also be sidelined if revenue reduced. Woody plant encroachment is not restricted to KZN. Savannas throughout Africa are experiencing woody plant encroachment, and much of this is occurring in conservation areas. Tourism is the backbone of many African economies (Akama & Kieti 2003), and my research suggests that conservation area revenue will suffer if visitors are not able to view the wildlife they expect to.

### **Future Research**

*Investigate the impact of woody plant encroachment on other ecosystem services*

My research looked at three aspects of woody plant encroachment, but this is only the tip of the iceberg. There are many other ecosystem processes that are likely to be affected by woody plant encroachment (Archer et al. 2001; Huxman et al. 2005), and future research needs to investigate these. Arguably one of the most important of these is hydrology. Over the last decade in South Africa there has been a lot of focus on the effects of invasive alien trees on ecosystem processes, with an emphasis on hydrological impacts (Le Maitre et al. 2002; Gorgens & Van Wilgen 2004). “Working for Water” is a nationwide government implemented programme to remove alien plants from catchment areas in an attempt to increase runoff (Le Maitre et al. 2002; Gorgens & Van Wilgen 2004). It has been hugely successful, and since its inception in 1995 has cleared more than one million hectares of invasive alien plants providing jobs and training to approximately 20 000 people from among

the most marginalized sectors of society per annum. Of these, 52% are women (<http://www.dwaf.gov.za>). There has been considerable research into both the extent and the effects of invasive alien plants, and most of the costs and benefits have been analysed as well as quantified. The basic assumption is that increased tree cover reduces streamflow by greater uptake of water, higher evapotranspiration, and more interference by leaves, thereby reducing water resources (Gorgens & Van Wilgen 2004). Woody plant encroachment is essentially the same process except with indigenous species rather than non-indigenous species. It is therefore surprising that there is so little understanding of the ecohydrological implications of woody plant encroachment in a southern African context.

In other regions people have explored the ecohydrological impacts of woody plant encroachment (Farley et al. 2005; Huxman et al. 2005; Jackson et al. 2005; Wilcox et al. 2005; Wilcox & Huang 2010). A global synthesis by Farley et al. (2005) on the effects of afforestation on water yield found that annual runoff was reduced by 31% and 44% when shrublands and grasslands were afforested respectively. Jackson et al. (2005) are less conservative and estimate that plantations cause a 52% reduction in global stream flow, with 13% of streams drying completely for at least one year. However, in more arid areas the effects of woody plant encroachment may be less severe, as research in Texas has shown (Wilcox et al. 2005; Wilcox & Huang 2010). The ecohydrological effects of woody plant encroachment will differ depending on the climate and the flow regime, and are difficult to predict (Huxman et al. 2005). Base flow in the dry season is likely to be most affected by woody plant encroachment, but this may be brushed off as insignificant because dams are filled during flood events in the wet season. However, alterations to base flow will have significant effects on communities living alongside rivers as well as other stakeholders who abstract water directly from streams. I briefly investigated the ecohydrological implications of woody plant encroachment in Hluhluwe Game Reserve, and the results can be seen in appendix 4.

#### *Determine the regional extent of woody plant encroachment*

While the various impacts of woody plant encroachment can be identified and compared, it is difficult to extend these findings to a large enough scale without accurate knowledge of the regional extent of woody plant encroachment. More than 20 years ago it was estimated that 13 million hectares of savanna in South Africa had been subject to thorn bush encroachment

(Trollope et al. 1989). This estimate did not include the proliferation of broadleaved trees such as is seen in my study area. Grossman & Gandar (1989) were less conservative, and estimated that more than 28 million hectares of a total of 43 million hectares of savanna vegetation in South Africa were under threat from woody plant encroachment. It is important to get up to date, accurate and large scale estimates of woody plant encroachment to inform national policy responses. Without an accurate understanding of the extent, the impacts of woody plant encroachment on South African economy and ecology remain speculation.

#### *Understand woody plant encroachment impacts across a range of climates*

It is also important to understand spatial variation in ecological responses in different climates. My results are for a high rainfall savanna (1000mm MAP). The processes involved are likely to differ with rainfall (Jackson et al. 2002, Knapp et al. 2008), so it is important to sample effects over a rainfall gradient. The dominant disturbance regimes change with climate, and in arid savannas fire plays a far less important role in the maintenance of vegetation boundaries. The absence of fire, as well as the reduction in rainfall is likely to alter the biogeochemical consequences of woody plant encroachment, and it is possible that carbon benefits in these landscapes will be much higher than in mesic savannas (Jackson et al. 2002). In addition, biodiversity losses may not be as severe, because in arid savannas woody plant encroachment often represents an increase in savanna tree densities rather than a complete switch to forest species, and may therefore seldom lead to complete exclusion of the grassy layer by shading, as the canopy generally remains more open (Kraaij & Ward 2006; Wiegand et al. 2006). This is in contrast to a mesic savanna such as Hluhluwe Game Reserve, where woody plant thickening refers to both savanna thickening as well as complete compositional shift to forest species. The appropriate management decisions would be different depending on the dominant processes and can only be made with a clear understanding of the drivers behind the phenomenon.

#### **Conclusions**

In Hluhluwe Game Reserve woody plant encroachment is negatively affecting biodiversity, and may cause a reduction in visitors to the park, thereby damaging conservation efforts in the process. On a positive note, it may be increasing carbon sequestration slightly. However, in a conservation area this is not as valuable as it could be elsewhere. Different land users

will view different effects of woody plant encroachment as either positive or negative depending on their objective. While reduced forage availability may negatively affect stock farmers, they may be able to trade in the carbon credits that woody plant encroachment could provide them with if policy allowed it. The climate and rainfall of a system is likely to affect the consequences of woody plant encroachment, and the negative effects may not be as severe in more arid areas. However this is speculation, and a more widespread investigation of the ecosystem consequences of woody plant encroachment is necessary. Hydrological impacts must be investigated more thoroughly, and awareness of the potential threat of natural woody plant encroachment needs to be spread. The causes and potential environmental consequences involved in woody plant encroachment need to be thoroughly investigated, so that well informed management decisions can be made. Without understanding why something is happening it is impossible to know how to control it effectively.

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# Appendix 1

## Above Ground Carbon Estimate

In order to make rapid assessments of terrestrial carbon stocks it is necessary to develop a quick method of estimating above ground biomass, and one way of doing this is to find a way to convert stand basal area to biomass, as stand basal area can be determined quickly and easily using a Bitterlich wedge. Basal area is widely used to estimate the biomass of trees, but the only allometric relationships that exist for this region are for individual trees. I followed two methods to convert stand basal area to biomass. Firstly, I followed Midgley & Seydack's (2006) approach using an equation developed for neotropical forests (by Baker et al. (2004) to estimate woody biomass. Baker et al. (2004) estimated above ground biomass (AGB) of single trees using the equation

$$AGB = \frac{\rho}{0.67} e^{[0.33(\ln dbh) + 0.933(\ln dbh)^2 - 0.122(\ln dbh)^3 - 0.37]}$$

where dbh is diameter at breast height. The equation was taken from Chambers et al. (2001) (in Baker et al. 2004). I then regressed the stand basal area against stand biomasses reported in Tables 1 and 5 in Baker et al. (2004) to get the equation

$$AGB = \frac{\rho}{0.67} \times (11.19 \times \text{Stand Basal Area}) + 2.118 \quad (R^2 = 0.96)$$

shown in Figure A1.1, where  $\rho$  is the average wood density of the stand in our study, and 0.67 is the average wood density for the neotropical study. This standardisation was done in order to remove possible inaccuracy due to the fact that the average wood density in our study was  $0.86\text{g.cm}^{-3}$ , which is far higher than the wood density of the neotropical study. This equation has not been verified for the Hluhluwe area, so it must be used with caution.

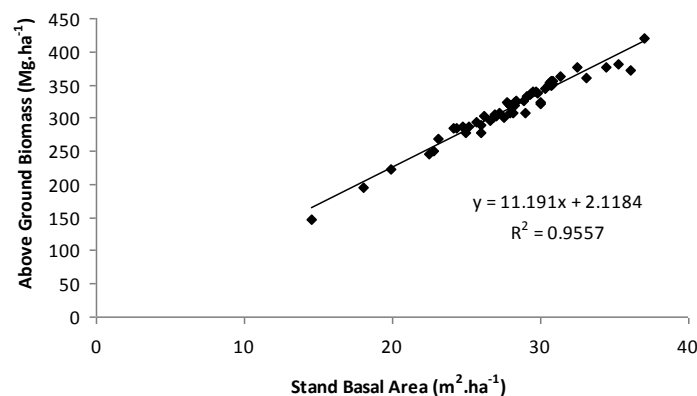


Figure A1.1: Regression of stand basal area against AGB using data taken from Baker et al (2004)

# Appendix 2

## Visitor Surveys



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### Hluhluwe-iMfolozi Game Reserve Visitor Survey

Please take 5 minutes to answer the questions below

1. Where are you from? \_\_\_\_\_
2. Are you staying inside the park? If so, which camp?  
\_\_\_\_\_
3. How long will you be staying in the park, or are you just a day visitor?  
\_\_\_\_\_
4. Have you been to a game reserve before? Which one?  
\_\_\_\_\_
5. Why did you choose to come to this game reserve?  
\_\_\_\_\_  
\_\_\_\_\_
6. Which part of the park did you enjoy the most?  
\_\_\_\_\_
7. Which animals do you enjoy seeing, or want to see, in the park? (Please list 5)  
\_\_\_\_\_
8. Using the pictures provided, with respect to vegetation which 2 landscapes do you enjoy driving through the most?  
\_\_\_\_\_  
Using the pictures provided, which 2 landscapes do you think you have seen the most animals in?  
\_\_\_\_\_
9. If you have been to this park before, when did you first come to the park, and approximately how often do you visit?  
\_\_\_\_\_  
Have you noticed any change in the vegetation or scenery in the park since you first came? If so please describe it.  
\_\_\_\_\_  
\_\_\_\_\_

Tree densities have increased in savannas throughout the world, a process termed **BUSH ENCROACHMENT**. Simply put, savannas are slowly turning into forests. Bush encroachment is generally understood to be occurring due to changing land management as well as changes in the atmosphere. Whether bush encroachment is affecting animals and environmental processes is not well understood, and this is what we are investigating.

**10. Rate how strongly you agree with each of the statements below by circling the number which best describes your feelings. Remember, there are no right or wrong answers.**

**Rating:** 1-strongly disagree    2-disagree    3-neutral    4-agree    5-strongly agree

We should not attempt to control bush encroachment	1	2	3	4	5
We should attempt to control bush encroachment	1	2	3	4	5
The main reason I am visiting this park is to see animals	1	2	3	4	5
I am only interested in seeing the Big 5	1	2	3	4	5
I have enjoyed my experience in the park	1	2	3	4	5
I would visit the park again if I had the chance	1	2	3	4	5
I would not visit the park again if game became more difficult to spot	1	2	3	4	5
Game viewing is the most important service that a game reserve provides	1	2	3	4	5
Conservation is the most important service that a game reserve provides	1	2	3	4	5
Fires in the park do not worry me	1	2	3	4	5

**11. Do you have any general comments you would like to add about your experience in the park, or your opinions on any matter?**

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Thank you so much for your time.

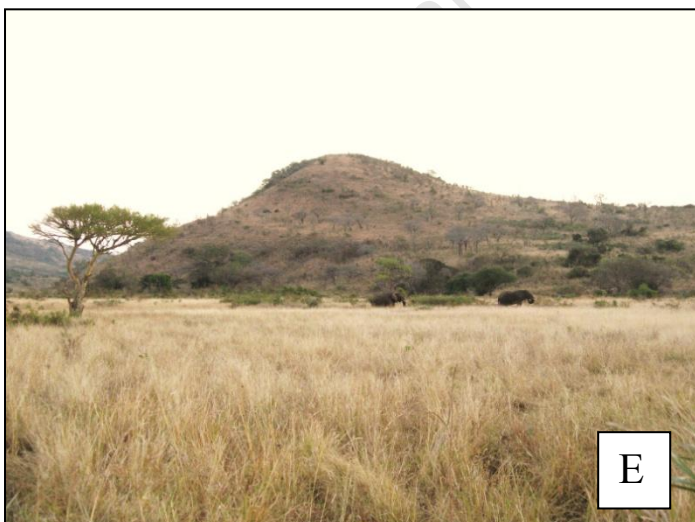
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## Appendix 3

### Soil nutrient stocks in different habitats

It is often argued that forests are only capable of establishing on nutrient rich soils (for examples see Bond (2010)), and low nutrient soils are often called upon to explain the presence of grasslands in climates that appear suitable for forest growth. However Bond (2010) has questioned the validity of this assumption. There is a general shortage of literature pertaining to soil nutrient stocks on forest-grassland boundaries, particularly in an African context (Jobbagy & Jackson 2001; Bond 2010). The few studies I have found do not give a decisive answer to the debate. Some studies have found no noticeable changes in soil properties along a forest grassland gradient (Dezzeo et al. 2004; Dezzeo & Chacón 2005), while others have found that forests are higher in some nutrients, but not all (Kellman 1979; Belsky et al. 1989; Johnson & Wedin 1997; Laurance et al. 1999; Folster et al. 2001; Bond 2010). Billore & Mall (1976) found that grasslands generally take up more nutrients than they release, barring Ca, although these grasslands were not compared to forests. In a comparison of secondary and primary forests in Brazil, Ca and Mg concentrations decreased with increasing stand age, being higher in secondary forests than primary forests (Johnson et al. 2001). Biological cycling generally moves nutrients upwards in the soil profile due to litter fall and decomposition. This is in contrast to leaching, which if acting in isolation would increase nutrient concentrations with depth (Jobbagy & Jackson 2001). Therefore the relative contribution of nutrients in the topsoil compared to the total soil pool is indicative of the role that plants play in the system. In a global synthesis, nutrients known to be cycled more intensively by plants (like P, K and Ca) were found to be more shallowly distributed than Mg and Na (Jackson et al. 2000; Jobbagy & Jackson 2001). The varying results in these studies do not lend themselves to making predictions of land cover with respect to soil nutrient stocks.

### Methods

I used soils from the soil pits dug for analysing carbon and nitrogen stocks to also explore soil nutrient stocks in grassy and forested ecosystems. Soil samples were air dried and sieved through a 2 mm sieve prior to analysis. Available [P] was determined by extracting 2 g of soil in Bray II solution (Bray & Kurtz 1945) which was filtered through Whatman No.2 filter paper. The filtrate was analyzed colorimetrically using the Malachite Green method (Motomizu et al. 1983). Total [P] was determined according to Bray & Kurtz (1945) using

ICP-AES analysis. Exchangeable cations were displaced from 10 g of sample with 25 mL of 0.2M ammonium acetate. The samples were filtered through Whatman No. 2 filter paper and made to 200 mL before the concentrations of Ca, K, Mg and Na were determined using ICP-AES analysis. The concentrations of these cations along with the concentration of H<sup>+</sup> ions were used to calculate soil T-value, a measure of CEC. The concentrations were converted to amount per square metre using the bulk density values determined in chapter 4.

The mean amount of each element in each habitat type was calculated, and these were statistically compared using a mixed effects ANOVA, with site as a random effect, and habitat as a fixed effect. Total [P] rather than available [P] was used. The surface (to 30cm) concentrations were compared relative to the total amount to 1 metre, and converted to a percentage to determine how much each nutrient was utilised by plants. If the element is well utilised by plants, the relative contribution of each element in the top 30cm relative to the first metre should be high, as nutrient levels would be expected to decrease with depth.

## Results

Figures A3.1 to A3.5 show the amount of K, Mg, Ca, Na and P in soils down to 100cm in each habitat type, as well as down to 30cm, and how much the topsoil contributes to the total. In soils down to 100cm, thicket and savanna contained more K, Mg, Ca, and Na than forest and grassland, while forest and grassland contained more P than savanna and thicket. Thicket contained slightly more K, Ca and Na than savanna, but statistical analyses using mixed effects ANOVA tests (Table A3.1) indicated that these differences were due only to random site effects, rather than due to explicit differences between habitats. Savanna contained slightly more Mg than thicket, but again differences were due to random site effects. P was not significantly different between savanna and thicket. Grasslands contained just over half the amount of K, Mg, Ca and Na that was found in forest, and differences in Na were found to be due to habitat effects as well as random site effects (Table A3.1), while the amount of P in forest and grassland was not significantly different.

Thicket and savanna contained the most K, Mg and Ca in soils to a depth of 30cm. Forest, thicket and savanna all contained similar levels of Na (0.03 kg m<sup>-2</sup>), while grassland only contained about half this amount (0.016 kg m<sup>-2</sup>). Grassland, savanna and thicket all contained similar levels of P (approximately 0.05 kg m<sup>-2</sup>), while forest contained more than this (0.08

kg m<sup>-2</sup>). Savanna and thicket showed no significant differences in topsoil amounts for any of the nutrients. The topsoil concentration factors of K and Ca were much higher in grassland and forest, while for Mg and Na they were very similar in all of the habitats. Topsoil concentration factors of P were highest in savanna, thicket and forest.

**Table A3.1: Mixed model ANOVA showing habitat effects on each nutrient, at depths of 0-30cm and 0-100cm**

Nutrient	Depth	Effect	Df	MS	Df	MS	F	p
			effect	effect	Error	error		
K	0-30cm	Fixed (habitat)	3	0.007	14.49	0.0037	2.042	0.1526
		Random (site)	11	0.009	11.00	0.0007	12.266	0.0001
	0-100cm	Fixed (habitat)	3	0.0596	12.72	0.0324	1.840	0.1907
		Random (site)	11	0.090	11.00	0.0035	25.489	<0.0001
Mg	0-30cm	Fixed (habitat)	3	0.145	19.82	0.0683	2.121	0.1298
		Random (site)	11	0.136	11.00	0.0343	3.983	0.0153
	0-100cm	Fixed (habitat)	3	2.649	19.78	1.1382	2.327	0.1057
		Random (site)	11	2.279	11.00	0.5679	4.012	0.0149
Ca	0-30cm	Fixed (habitat)	3	0.839	15.61	0.3054	2.747	0.0779
		Random (site)	11	0.751	11.00	0.0824	9.116	0.0005
	0-100cm	Fixed (habitat)	3	7.683	14.91	2.3945	3.209	0.0536
		Random (site)	11	6.069	11.00	0.5571	10.894	0.0002
Na	0-30cm	Fixed (habitat)	3	0.0002	17.92	0.0001	3.848	0.0274
		Random (site)	11	0.0001	11.00	0.0001	0.708	0.7118
	0-100cm	Fixed (habitat)	3	0.008	20.34	0.0013	6.527	0.0029
		Random (site)	11	0.002	11.00	0.0007	3.602	0.0220
P	0-30cm	Fixed (habitat)	3	0.001	21.65	0.0002	2.715	0.0698
		Random (site)	11	0.001	11.00	0.0001	2.587	0.0650
	0-100cm	Fixed (habitat)	3	0.006	19.10	0.002	2.663	0.0772
		Random (site)	11	0.005	11.00	0.001	4.553	0.0093

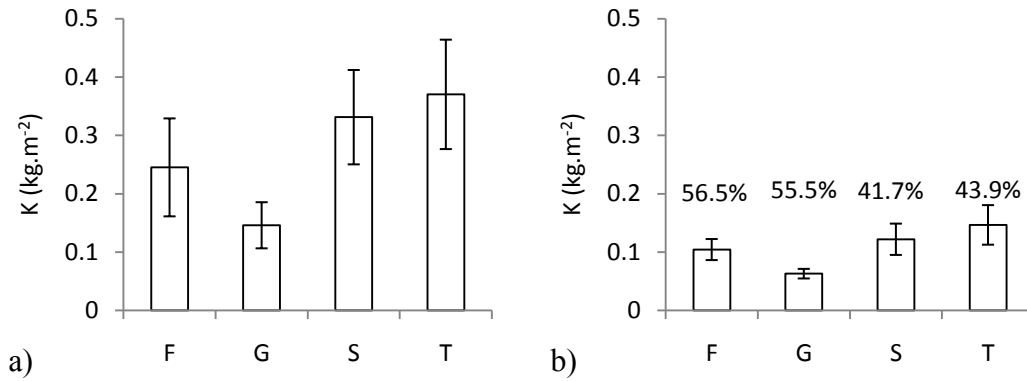


Figure A3.1a) Amount of K in each habitat ( $\pm$ SE) to a depth of 100cm (F-Forest, G-Grassland, S-Savanna, T-Thicket)

b) Amount of K in each habitat ( $\pm$ SE) to a depth of 30cm

Percentages indicate how much the top 30cm contributes to the total amount in (a)

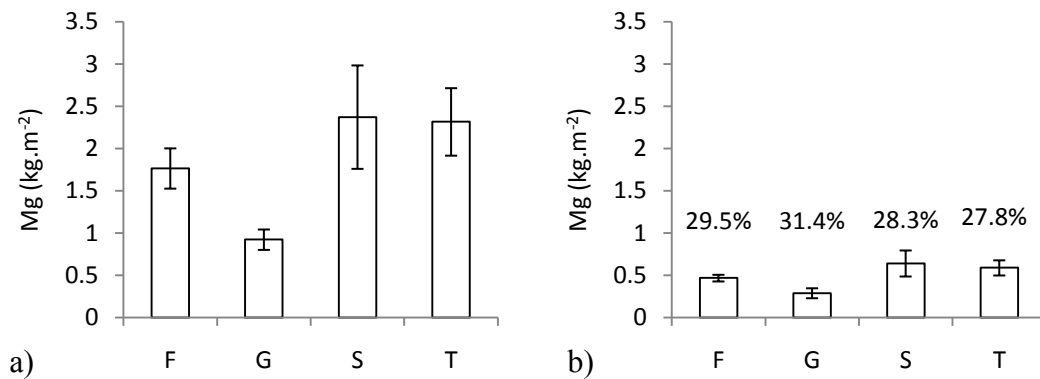


Figure 5a) Amount of Mg in each habitat( $\pm$ SE) to a depth of 100cm (F-Forest, G-Grassland, S-Savanna, T-Thicket)

b) Amount of Mg in each habitat ( $\pm$ SE) to a depth of 30cm

Percentages indicate how much the top 30cm contributes to the total amount in (a)

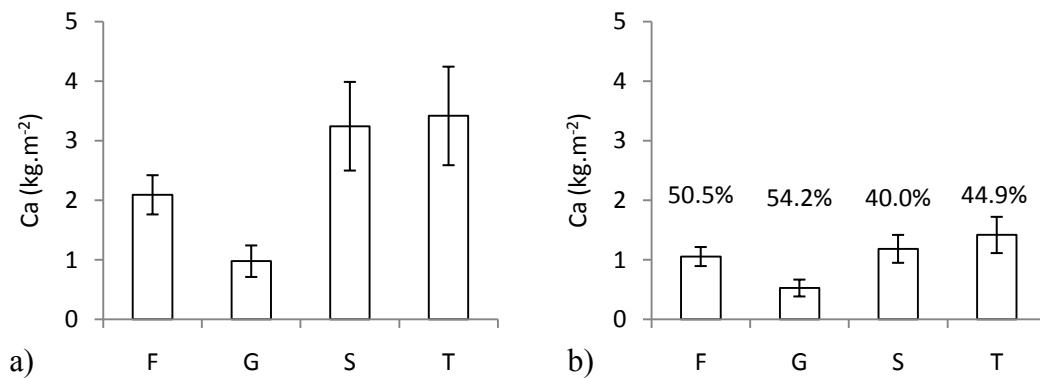
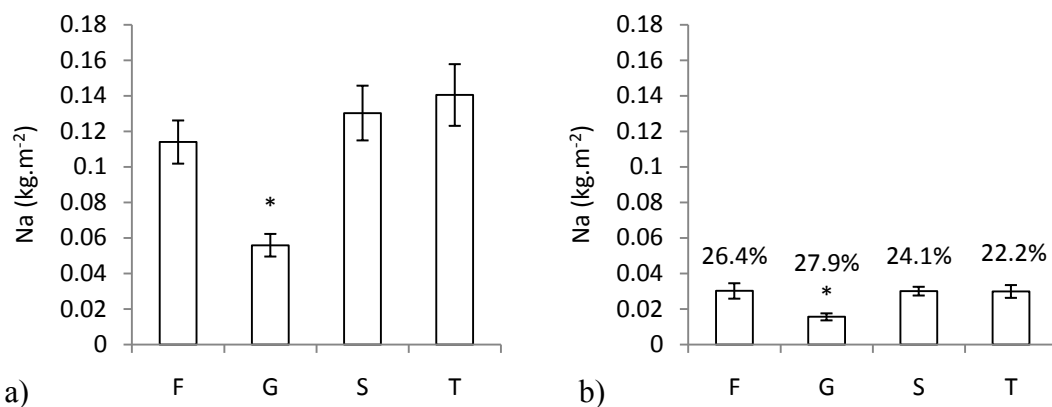


Figure A3.3a) Amount of Ca in each habitat( $\pm$ SE) to a depth of 100cm (F-Forest, G-Grassland, S-Savanna, T-Thicket)

b) Amount of Ca in each habitat ( $\pm$ SE) to a depth of 30cm

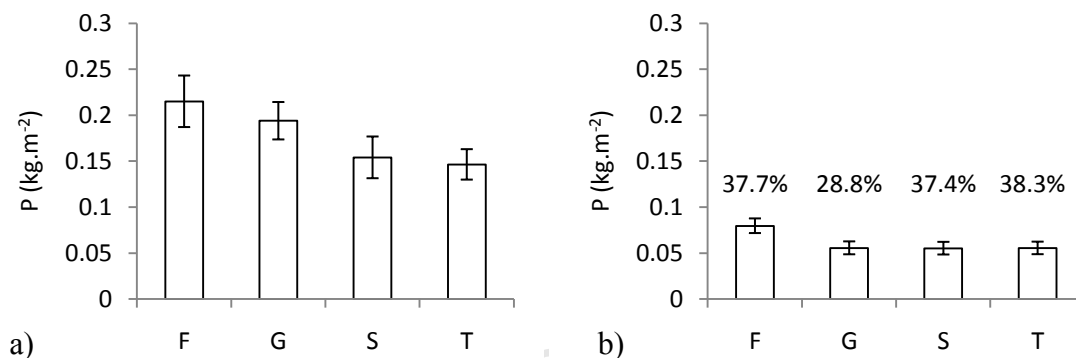
Percentages indicate how much the top 30cm contributes to the total amount in (a)



**Figure A3.4a) Amount of Na in each habitat ( $\pm$ SE) to a depth of 100cm (F-Forest, G-Grassland, S-Savanna, T-Thicket)**

**b) Amount of Na in each habitat ( $\pm$ SE) to a depth of 30cm**

Percentages indicate how much the top 30cm contributes to the total amount in (a). Asterisks indicate significant difference due to fixed habitat effects at  $\alpha=0.05$



**Figure A3.5a) Amount of P in each habitat( $\pm$ SE) to a depth of 100cm (F-Forest, G-Grassland, S-Savanna, T-Thicket)**

**(b) Amount of P in each habitat ( $\pm$ SE) to a depth of 30cm**

Percentages indicate how much the top 30cm contributes to the total amount in (a)

Forest contained more soil nutrients than grassland not only in their topsoils, but also down to 100cm. In other studies nutrients known to be cycled more intensively by plants (like P, K and Ca) have been found to be more shallowly distributed than Mg and Na (Jackson et al. 2000; Jobbagy & Jackson 2001). In my plots K, Ca and P all had topsoil concentration factors above 30%, while Na and Mg had fairly low topsoil concentration factors, suggesting that K, Ca and P are cycled slightly more by plants.

The soil nutrient stocks in my study area were found to be higher than those in a primary forest in Brazil (Johnson et al. 2001) as well as soils in South-Western Australia (McArthur et al. 1991). My analysis also showed overwhelmingly that nutrient stocks in thicket were not very different from savannas. This suggests that soil nutrients in savannas are not limiting for plant growth. Bond (2010) estimated the threshold minimum soil nutrient requirements for forest establishment to be 0.002-0.003kg m<sup>-2</sup> for P, 0.03-0.06 kg m<sup>-2</sup> for Ca, 0.0055-0.0065

kg m<sup>-2</sup> for Mg and 0.02-0.035 kg m<sup>-2</sup> for K. All soils in my study area contained more nutrients than these minimum thresholds, suggesting that even in grassland sites soil nutrients do not constrain forest development. The isotopic profiles in Figure 4.1 (Chapter 4) suggested that all forested landscapes were previously dominated by C<sub>4</sub> grasslands. These results suggest that nutrient stocks would not have limited forest development these open areas, lending support to the isotopic results. The high nutrient content in forests, savannas and thickets in comparison to grasslands (for all nutrients besides P) suggests trees may enhance nutrient storage in soils.

University of Cape Town

## Appendix 4

### Measuring ecohydrological effects of woody plant encroachment

I looked briefly into whether woody plant encroachment in HiP was affecting stream flow, using runoff and rainfall data, as well as evapotranspiration data (Huxman et al. 2005). Initially I investigated whether runoff had reduced over the last few decades using rainfall and runoff data from Hluhluwe Dam. The results from this study are shown in Figure A4.1 and A4.2. The expected pattern of decreasing runoff with the same rainfall over time is not seen. I expected the residuals from the line plotted in Figure A4.1 to become more negative as time passed, but they did not (Figure A4.2). However, the weir that the runoff data came from was below the dam, which meant that the dam may have been confounding runoff measurements, due to abstractions and other activities. For this reason I attempted a different method, using remotely sensed evapotranspiration estimates obtained from the CSIR (Meijninger, Wouter and Jarman, unpublished).

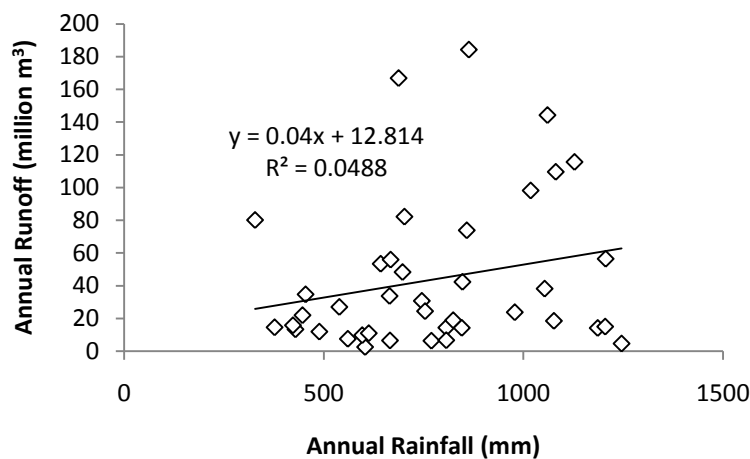


Figure A4.1 Regression of runoff in Hluhluwe River against rainfall, using data from 1965 until present

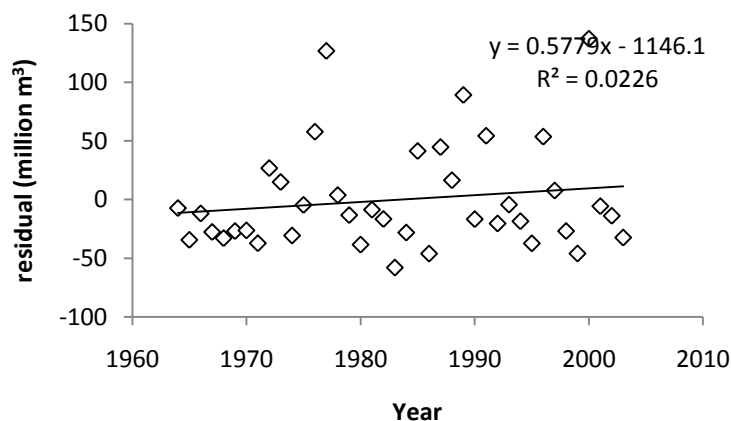


Figure A4.2 Residuals from the regression in Figure A4.1, plotted against time

## Methods of estimating evapotranspiration through remote sensing

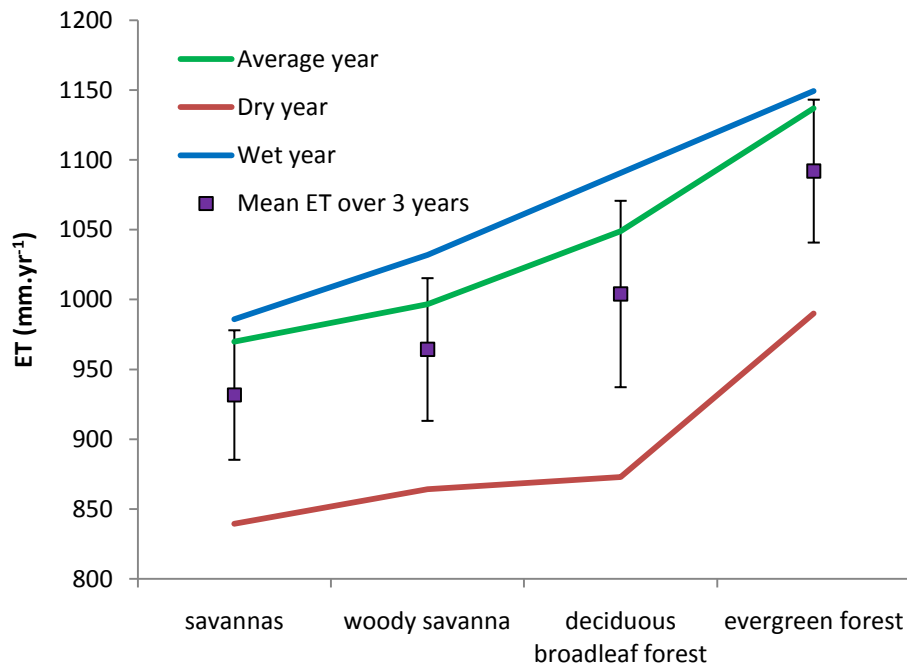
Meijninger, Wouter and Jarman (unpublished) used the SEBAL model to estimate actual total evapotranspiration (ET) for the Hluhluwe area. This model is described in depth by Bastiaanssen et al. (2005), but in short SEBAL combines the broadband surface albedo, NDVI and surface temperature with spatially gridded weather data (air temperature ( $T$ ), relative humidity ( $RH$ ) and wind speed ( $u$ )) using Meteolook (Voogt 2006), a digital elevation map (DEM) and a land cover map to determine ET. Solar radiation ( $K^{\downarrow}$ ) were estimated using the DEM, the solar radiation model of Tasumi et al. (2005) in combination with atmospheric transmissivity ( $\tau$ ) data from either ground stations or the remote sensing products of the Land Surface Analysis Satellite Applications Facility. The surface roughness ( $z_o$ ) and zero-displacement height ( $d$ ) were derived from the land cover map and NDVI data to incorporate seasonal changes in  $z_o$  and  $d$ . Total evapotranspiration refers to the sum of water lost from a surface, and was considered a measure for plant water use, as Meijninger et al. (unpublished) considered the loss from soil and interception as negligible. They used rainfall data from the Tropical Rainfall Measurement Mission (TRMM), and selected 2000-2001 as an average year, 2003-2004 as a dry year and 2006-2007 as a wet year. 70 cloud free MODIS (Moderate Resolution Imaging Spectrodiometre) images were used in the study, one image per two week period. ET was estimated at a 250m resolution.

I then overlaid this evapotranspiration data on a MODIS vegetation map to determine mean annual evapotranspiration for each habitat type. The results of this are shown in Figure A4.3.

## Results

These results suggest a trend of increasing evapotranspiration with increasing woody plant cover. This cover does not increase linearly across the x axis, the categories are determined by Modis vegetation classifications. The results suggest that a biome switch from grassland and open savannas to thicket could result in a local reduction of stream flow. These effects are well studied for afforestation in South Africa (Le Maitre et al. 2002; Gorgens & Van Wilgen 2004). There are some studies from Texas, and some global studies which investigate the hydrological impacts of natural woody thickening (Farley et al. 2005; Huxman et al.

2005; Jackson et al. 2005; Wilcox et al. 2005; Wilcox & Huang 2010), but as far as I am aware, none from South Africa.



**Figure A4.3 Annual evapotranspiration in different habitats in HiP for a dry year, a wet year and an average year, as well as the mean of these three years. There is an increase in woody cover from left to right on the x axis**

Though the remote sensing approach of estimating evapotranspiration looks very promising, the values generated in my results have exceeded annual precipitation by a considerable margin. This is not physically possible. Clearly, further refinements are necessary before this approach can be used to estimate the hydrological consequences of woody plant encroachment. Despite this, it is likely to become a useful tool for estimating the hydrological consequences of woody plant thickening at various scales.