The Peninsula Shale Renosterveld of Devil's Peak: Phytosociology, System Drivers and Restoration Potential

By

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Declaration

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously, in its entirety or in part, submitted it at any university for a degree.

Signature……………………………… **Date**…………………………………

Dedication

This thesis is dedicated to my grandmother, Dr. Silvia Skorge, for teaching me to cherish and seek knowledge.

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Abstract

Peninsula Shale Renosterveld is a poorly understood and critically threatened vegetation type with 87% of its original extent transformed and the remaining fragments restricted to the area surrounding the Cape Town city bowl. A substantial portion of Peninsula Shale Renosterveld is situated in the Groote Schuur Estate, currently conserved within the Table Mountain National Park. Due to a history of diverse land-use impacts, what remains today is a complex mosaic of alien invasive species and indigenous vegetation in various states of degradation. As a result of the substantial transformation, it is evident that to improve the conservation value of this highly threatened vegetation type, restoration is required. However, as many restoration projects fail as a result of a poor understanding of the ecosystem dynamics in which they are operating in, it is imperative that prior to initiation data is collected from the site.

To enhance the understanding of the ecosystem drivers of Peninsula Shale Renosterveld with a view to evaluate restoration potential and inform future restoration initiatives a short-term, detailed analysis of four typical vegetation states found within the study area was undertaken. This was accomplished through a detailed land-use history analysis focusing on the practices which have brought the system to its current position; a phytosociological survey investigating the contemporary state of the study area; and an examination of the health of the seedbank through a greenhouse experiment to ascertain whether it could prove a useful asset in future restoration initiatives.

The results show how historical drivers have created a novel ecosystem with vegetation states ranging from relatively healthy Renosterveld vegetation, indigenous vegetation requiring intervention to maintain its integrity, and regions of the study area where only active restoration efforts can return the degraded vegetation to functional Peninsula Shale Renosterveld. Despite this novel ecosystem, each vegetation state broadly fits into hypothetical Renosterveld ecosystem driver models, thus providing data for future restoration requirements. The seedbank diversity was found to be poor, dominated by alien ephemeral species and unlikely to assist in restoration efforts. The results also suggest the soil-stored seedbank in Renosterveld may not be of great importance for succession post-disturbance. In addition to providing valuable baseline data and enhancing the knowledge on drivers within Peninsula Shale Renosterveld, the project recommends and provides motivation for future management actions that will enable the restoration of this critically endangered vegetation type.

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Chapter 1

Introduction, Aims & Objectives and Literature Review

1.1 Introduction

The Cape Floristic Region, situated on the southern tip of Africa, is renowned the world over for its floral diversity. An estimated 9000 species, of which 70% are endemic, can be found within its borders (Goldblatt and Manning, 2002). This ancient landscape provided evidence that modern humans occupied it at least some 117 000 years ago and ever since humans have interacted and impacted on the environment at a variety of scales (Deacon, 1992). Renosterveld, a vegetation type covering approximately 20 000 km^2 of the Cape Floristic Region, has been particularly impacted by humans due to the relatively fertile soils on which it grows with less than 15% of highly fragmented natural Renosterveld remaining. Due to the long history of alteration caused by anthropogenic actions there is a lack of reference data for pristine Renosterveld. It is this lack of knowledge which has resulted in Renosterveld being poorly defined and only recently has an effort been made to better understand the system drivers, nevertheless, many aspects of Renosterveld ecology remain poorly understood and a large proportion of the perceived knowledge is of a speculative nature.

Peninsula Shale Renosterveld, one of 29 types of Renosterveld (Mucina and Rutherford, 2006), is restricted to the area surrounding the Cape Town city bowl. This proximity to an expanding metropolis has led to 87% of the vegetation type being transformed; the remaining pockets are restricted to the mountain slopes of Signal Hill and Devil's Peak (Rebelo et al., 2006). Much of the Devil's Peak fragment lies within the Groote Schuur Estate currently protected within the Table Mountain National Park. The Estate's history is complex having been subject to plantations, game paddocks and an attempt by former owner Cecil John Rhodes to create a landscape after the European style of open parkland. The ramifications of the Estate's history have left behind a complex vegetation mosaic of alien invasive species and degraded indigenous vegetation.

Due to the substantial habitat transformation, it is not enough to simply conserve the remaining Renosterveld fragments. Restoration is an important tool in safeguarding this vegetation type and the Estate provides an ideal setting to gain further insights into the dynamics behind Peninsula Shale

Renosterveld with a view to its restoration, and in doing so contribute to a better understanding of the ecology and system drivers of this highly threatened vegetation type.

1.2 Description of Thesis and Chapter Layout

This project explores the land-use history and ecosystem drivers of the Peninsula Shale Renosterveld on Devil's Peak, a poorly defined and understood vegetation type, through a land-use history analysis, a phytosociological study of four typical vegetation states within the study area and an analysis of the seedbank dynamics within the four vegetation states. The idea is to use the information unearthed through the research to inform and assess the restoration potential of the study area and provide valuable baseline data for future restoration initiatives.

The thesis is structured into five chapters as follows: this first chapter provides a brief introduction to rationalize and set the context for the project; followed by the detailed aims and objectives of the project; a review of the relevant literature on restoration ecology, and finally the Cape Floristic Region with a specific focus on Renosterveld. The second chapter presents a description of the study area and a detailed account of the land-use history through an analysis of the ecosystem drivers such as fire, grazing, landcover change and management policies. The third chapter focuses on the current state of the study area by presenting and discussing the results of a phytosociological survey and abiotic analysis of four typical vegetation states found within the study area. The fourth and penultimate chapter addresses the state of the seedbank of the four vegetation states and the effect fire would have on the seedbank in an effort to assess its viability as an instrument for future restoration initiatives. Finally, in the fifth chapter conclusions are provided as the original aim of the thesis is revisited alongside recommendations for potential future restoration actions.

1.3 Aims and Objectives

1.3.1 *Project Aim*

The project's aim is to enhance the understanding of the ecosystem drivers of Peninsula Shale Renosterveld through a detailed analysis of four identified dominant states in one of the remaining remnants. This is carried out with a view to evaluating restoration potential and informing future restoration initiatives.

1.3.2 Project Objectives

- Understand/elucidate historical ecological drivers giving rise to current vegetation patterns though a detailed land-use history analysis of the study area.
- Develop a detailed understanding of the phytosociological status of four pre-identified typical vegetation states within the study area with a view to understand the end point of historical drivers, the status this vegetation fragment and the potential role and contribution to restoration.
- Establish the state of the seedbank in the pre-identified vegetation units with a view to understanding the impact of historical drivers on seedbanks and the potential role of fire in promoting seed bank establishment.

1.4 Literature Review

1.4.1. Prelude

This review presents contemporary thinking and debates around restoration ecology in general and the role of landscape history, current phytosociology and ecological function in informing restoration practises. Additionally, literature surrounding the Cape Floristic Region and Renosterveld is presented. The history of the study area is covered in greater detail in Chapter 2 and therefore, to avoid repetition, is only briefly touched on here. There is a dearth of literature surrounding Peninsula Shale Renosterveld, the focus of this study, but what scant information there is, is presented in Chapter 2. Finally, it should be noted that in section 1.4.2.1, due to the importance of using consistent definitions and terminology throughout the thesis, the nomenclature of Society for Ecological Restoration (an umbrella organization for many restoration ecologists) was solely utilized.

1.4.2 Restoration Ecology

1.4.2.1 Definitions and Terminology

The Society for Ecological Restoration defines ecological restoration as the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed. It is an intentional activity designed to either initiate or hasten the recovery of an ecosystem which has been impacted by humans (SER, 2004).

A degraded ecosystem is one which has been impacted for a sustained period of time, while a damaged ecosystem has been impacted on during a single event (SER, 2004). In the most basic of cases, damaged ecosystems are restored by removing or modifying a disturbance, thus passively allowing the ecosystem to restore its ecological processes. However, often ecosystem impacts are multiple and inter-related and many historical constituents of the system are missing (SER, 2004).

An ecosystem is considered successfully restored when no further manipulation is required to maintain its natural trajectory. To understand an ecosystem's natural trajectory it is important to have a reference condition or baseline to work towards. This baseline can be established through a combination of 'knowledge of the damaged ecosystem's pre-existing structure, composition and functioning, studies on comparable intact ecosystems, information about regional environmental conditions, and analysis of other ecological, cultural and historical reference information' (SER, 2004). Often it is impossible to restore the degraded ecosystem to its reference condition, in which case the desired endpoint of restoration becomes improved ecosystem health and integrity (SER, 2004).

The Society for Ecological Restoration lists various factors of a restored ecosystem. These include an ecosystem containing characteristic indigenous species with the presence of functional groups allowing for continual ecosystem development and/or stability. Additionally, the ecosystem should be resilient enough to endure normal periodical stress while being self-sustaining with potential threats eliminated or reduced. Finally, the restored ecosystem should be suitably integrated into the larger ecological matrix (SER, 2004).

A variety of other goals may result from successful restoration but these depend on the initial aims of the restoration project; for instance improved biodiversity or the ability of the restored ecosystem to provide sustainable goods and services for social benefit (SER, 2004).

1.4.2.2 Arguments For and Against Ecological Restoration

The notion of ecological restoration is swiftly entering the public policy, education and popular culture of many regions including North America, certain areas in Europe, South Africa and Australasia (Aronson et al., 2006). Despite this, opponents of the discipline argue that restoration is encroaching on the already meagre budgets that numerous countries have for conservation and rural development; thus policy and funding should focus on preservation and sustainable development rather than long-term restoration. Additionally, conservationists tend to focus on conserving what remains of 'wild' nature and writing off modified landscapes and ecosystems (Balmford et al., 2002). Other ecologists argue that the length of restoration projects makes them meaningless to necessary conservation or economic development programmes (Stephenson, 2000; Aronson et al., 2006). Finally, the high rate of failure of restoration projects has also been highlighted as a point of concern (Ehrenfield, 2000).

Aronson et al. (2006) refute these criticisms stating that ecological restoration, if done holistically, increases the economic opportunities and benefits, while also increasing the various aspects of human welfare as well as enhancing conservation. Clewell and Aronson (2006) describe five motivations for ecological restoration; namely, idealistic, technocratic, heuristic, biotic and pragmatic. However, if idealistic, technocratic, heuristic or biotic reasons for restoration are invoked alone then it is only the rich first world countries which could easily afford to invest in restoration (Aronson et al., 2006) in which case critics of the discipline have a valid point.

Within the pragmatic rationale for restoration lies the motivation to restore natural capital (Clewell and Aronson, 2006). Aronson et al. (2006) point out that the restoration of natural capital should be considered an umbrella strategy incorporating, to varying degrees, the other motivations mentioned above. In doing so, restoration becomes complementary to conservation and to sustainable socio-economic development because by restoring and enhancing the natural capital base, jobs are generated and livelihoods improved. A prime example of this restoration approach benefiting nature conservation, ecosystem service delivery and socio-economic development is the Working-for-Water programme in South Africa. This public works initiative employs over thirty thousand people to eradicate alien flora that absorb soil moisture depriving water from native vegetation, agriculture and people (Milton et al., 2003; Van Wilgen et al., 2004). While the economic and social development aspects of the programme have been a success, the enormity of the task has resulted in a failure of the initiative to significantly reduce the density of alien invasives in many parts of the country (van Wilgen et al., 2012). Despite this, the programme is an excellent demonstration of the potential for restoration to bring conservation and development ends together.

A further argument for restoration arises from the increasing acknowledgement that global climate change occurs and that it will impact on ecosystems (Harris et al., 2006). Degraded ecosystems, particularly ecosystems which have suffered from persistent human disturbance which increase their vulnerability (MacDougall et al., 2013), are hypothesized to be less resilient to climate change compared to healthy, functioning ecosystems (Harris et al., 2006). Furthermore, Hooper et al. (2012) argue that biodiversity loss is a major driver of ecosystem change globally. Thus, by holistically restoring a damaged or degraded system to one that is more ecologically sound and biodiverse, one boosts the resilience of that system which, in turn, may safeguard species within the ecosystem against the effects of rapid climate change as well as preserve the provision of ecosystem goods and services (Diaz et al., 2006; Harris et al., 2006).

1.4.2.3 Reference States, Baseline Data and Land-Use History

To facilitate the ecological restoration of degraded or damaged ecosystems, practitioners need a clear goal of what the desired endpoint of the restoration is. This baseline or reference state is often largely unknown because for most landscapes direct monitoring only goes back a few decades, if at all (Jackson and Hobbs, 2009). It is often necessary to utilise ecological history (e.g. photographs, maps, written accounts and paintings) and palaeoecological data (e.g. rodent middens, tree-ring data etc.) to gain a better understanding of the reference state of the ecosystem (Jackson and Hobbs, 2009). Despite this acknowledgement of the importance of data on the reference state, the issue is complex.

Often the desired end-point of restoration is considered to be the state of the ecosystem prior to anthropogenic impact; however the definition of what is 'natural' is not so straightforward (Hunter, 1996). There is frequently a pre-conceived notion that indigenous peoples were living in harmony with the land prior to colonization and, while this may be true relative to the large-scale degradation of the past few centuries (or decades in certain areas), it is somewhat naïve (Bush and Colinvaux, 1994; Willis et al., 2004). Indeed, the original inhabitants of areas later colonised by European settlers exerted substantial influences on ecosystems through a variety of activities (e.g. hunting, fire management and direct vegetation alteration) and few terrestrial systems escaped some effects of anthropogenic activity (Bowman, 1998; Jackson et al., 2001; Vale, 2002; Black et al., 2006). Consequently, in many parts of the globe, especially Europe, Asia and Africa where humans, or their ancestors at least, have lived for millions of years, an undisturbed landscape is too remote in time to provide meaningful baseline data (Naveh, 2005; Jackson and Hobbs, 2009). In Cazarils, situated in southern France, researchers have acknowledged this reality and set up a research station to study the response of the landscape to both past and present human uses and perturbations. The purpose of which is to approach landscape restoration planning in a complex Mediterranean-type ecosystem utilizing knowledge of the past and present (Aronson et al., 1998).

A second issue to consider when dealing with a reference state is the dynamic nature of the earth's climate system. In the last few decades the effect of anthropogenic activities on climate change has been highlighted; however, natural changes occur across a wide temporal scale (Millar and Woolfenden, 1999; IPCC, 2007; Meadows, 2012). Regardless of the cause of the change in climate, for many ecosystems restoration to a historic standard is anachronistic, thus baseline data for a site from 500 years ago may be arbitrary to contemporary restoration (Sprugel, 1991; Jackson and Hobbs, 2009).

Palaeoecological data have forced a paradigm shift in ecological thought during the last few decades as the romantic notion of 'Balance in Nature' (Egerton, 1973) has been replaced by the acceptance that the environment is in a permanent state of flux (Pickett and Ostfeld, 1995, Meadows, 2012). This 'Flux of Nature' paradigm states that ecosystems have multiple alternative 'stable' states, owing to historical contingencies effecting species migration, site colonization and extirpation (Fastie, 1995; Jackson et al., 2009). Indeed, it is rare to find major terrestrial systems older than twelve thousand years and the majority are much younger (Williams et al., 2004; Jackson and Overpeck, 2000).

The land-use history of a site is embedded in the structure and function of its ecosystems. Utilising site history adds explanatory power to our understanding of contemporary patterns and processes, while reducing uncertainty in anticipating or managing future conditions (Foster et al., 2003). Studies on environmentally homogenous sites which have different land-use histories indicate that environmental patterns are often controlled by land-use alone (Motzkin et al., 1996; Donohue et al., 1999). Many persistent physical, chemical and biological changes are imposed on soils by burning, grazing and agriculture (Milchunas and Lauenroth, 1995; Compton et al., 1998), while legacies of past land-use interact with natural disturbance regimes and may further confuse the interpretation of disturbance regimes in many ecosystems (Foster et al., 2003). Certainly, this interaction contradicts a common assumption that simply applying historically relevant disturbances such as prescribed burning will quickly restore natural processes and conditions in anthropogenically modified landscapes (Stephenson, 1999). Rayburn and Major (2008) advocate the development of a coherent site history to inform ecological restoration and guide natural resource management and planning where a landscape has been impacted on by anthropogenic land-use.

While reference sites, baseline data and land-use history still provide invaluable data for restoration ecology, the literature reviewed above warns against an over-reliance on it. Choi (2007) goes as far as advocating a paradigm shift in restoration ecology from the current past-orientated approach towards a new one with a much greater focus on the future. He describes a future-orientated approach which should focus on rehabilitating ecosystem functions with a view to sustaining the future by incorporating multiple alternative goals and trajectories for unpredictable endpoints. However, to understand the complexity surrounding the perpetual flux in nature it is often required to delve back in time as many processes span many lifetimes and are generally only validated by palaeoecological data (Gillson, 2004; Willis et al., 2004). What is required is a combination of learning from the past but preparing for the future where adaptive management is applied to restoration ecology (Du Toit et al., 2003; Schreiber et al., 2004).

1.4.2.4 Threats to Restoration Success: Alien Species, Degraded Seedbanks and Habitat Fragmentation

Invasive alien species are one of the greatest threats to biodiversity (Rouget et al., 2003a). Similarly, alien invasives provide a multitude of problems in restoration ecology (Saunders and Norton, 2001). Biological invasions can be both the cause of degradation and the driver of ecosystem change during restoration, in the worst cases resulting in irreversible changes in ecosystem structure and composition (Norton, 2009). Species invasions impose vital biotic thresholds limiting the success of restoration projects and, even when controlled, continue to exert pressure on ecosystem integrity and biodiversity (Norton, 2009). Restoration must not only address the degrading factors caused by invasives but also the altered feedbacks that lead to novel ecosystems which are different from those that would have existed prior to impact (Hobbs et al., 2006; Seastedt et al., 2008; Norton, 2009). It is clear that alien invasions pose a substantial threat to restoration ecology, often combining with other system drivers to create an even more complex hazard (Didham et al., 2005). To be successful in restoration the threats imposed by alien invaders needs to be recognised, restoration efforts need to be adaptable, and most importantly resources need to be available to enable the ongoing sustainability of the project (Norton, 2009). The ecological impact of alien trees in the Cape Floristic Region is discussed in detail in section 1.4.4.5.

The presence of a healthy seedbank is of great benefit in initiating a successful restoration project (Bakker et al., 1996). There is hardly a single area in plant ecology in which seedbanks do not play a role and a great number have direct implications for restoration ecology (Bakker et al., 1996). A review of the ecology of seedbanks is beyond the scope of this thesis (see Roberts, 1981; Leck et al., 1989; Thompson, 1992); however in many cases the reappearance of plant species in restored ecosystems depends on their persistence within the seedbank (Bakker et al., 1996). Often a disturbance such as fire is required to stimulate germination of species within the seedbank (Keeley, 1987; Keeley and Bond, 1997). If the seedbank is depleted because of activities like ploughing, species have to either naturally colonise the site again through some vector (wind, water, animals) or artificially be planted by people (Bakker et al., 1996). Often the cost of sourcing the seeds and the manual planting is a stumbling block for restoration projects with a limited budget (Holmes, 2002a).

Once restoration has been initiated and desired plant species have established, the next challenge is to maintain a functional ecosystem. This challenge is frequently hampered by habitat fragmentation where the restored ecosystem is isolated in space (Kemper et al., 1999) which can impact on pollinator ecology (Donaldson et al., 2002). Unlike in agriculture, the importance of pollinators in restoration ecology is poorly understood, yet biotically driven pollination services sustain reproductive potential and genetic resilience in many ecosystems (Dixon, 2009). In pollinator-driven systems, the ability for pollinators to re-colonize a restored area is crucial to the project's success (Donaldson et al., 2002). Due to fragmentation of habitat, non-flying pollinators are ill-fated but even flying pollinators can be placed under pressure if fragments are too isolated (Dixon, 2009). Even if fragments are of sufficient size or close enough together, a decay or shift in pollinator assemblages, for a variety of reasons, can result in lower seed-set or increased inbreeding (Lamont et al., 1993; Botes et al., 2009). It is apparent that more work needs to be done to synergise research in restoration and pollinator ecology to avoid further problems in natural and restored ecosystems (Dixon, 2009).

1.4.3 The Cape Floristic Region

1.4.3.1 Introduction

The Cape Floristic Region is situated on the south-western tip of the African continent and is completely contained within the borders of South Africa (Bond and Goldblatt, 1984). Globally, the region is recognized as a Global Diversity Hotspot (Myers et al., 2000), a Centre of Plant Diversity (Davis et al., 1994), an Endemic Bird Area (Stattersfield et al., 1998) and a Global 200 Ecoregion (Olson and Dinerstein, 1998). It has also been described as a point of endemism and diversity for mammals (Kerley et al., 2003), other vertebrates such as freshwater fish, reptiles, amphibians and numerous invertebrate groups (Skelton et al., 1995; Picker and Samways, 1996; Impson et al., 1999). The region is approximately 74 000 km^2 (Cowling and Pierce, 1999), although Cowling et al. (2003) delimit the region as 87 892 km^2.

1.4.3.2 Geological History

The landscape of the Cape Floristic Region is an ancient one, predating the emergence of the African continent from the Gondwana super-continent. The sediments known today as the Cape Supergroup were deposited between 450 and 350 million years ago in a sea that separated the two embryonic continents which would later become Africa and South America (Compton, 2004; Holmes and Meadows, 2012). The subsequent collision of the continents spanned approximately 65 million years and formed spectacularly high mountains which have since been eroded resulting in the current modest mountains of resistant quartzite. The softer shales of the Cape Supergroup have formed the undulating valleys and flats. Additionally, scattered granite outcrops, exposures of Pre-Cambrian shale, Tertiary limestone deposits, Pleistocene sands and Holocene dunes are all features of the regions landscape (Cowling and Pierce, 1999; Johnson et al., 2006; Holmes and Meadows, 2012).

1.4.3.3 Contemporary Flora

The Fynbos (Afrikaans for ‘Fine Bush’) which dominates the region today covers approximately 46 000km^2 and thrives on the nutrient-poor soils of the sandstone mountains, the shallow, nutritionally imbalanced sands associated with Tertiary limestone and the leached coastal soils (Cowling and Pierce, 1999). Fynbos vegetation is an evergreen, hard-leafed and fire-prone shrubland characterized by four major plant types; namely, Proteoids, Restioids, Ericoids and Bulbs (Low and Rebelo, 1998; Mucina and Rutherford, 2006). Aside from Fynbos and Renosterveld, of which a detailed review will be given in section 1.4.4, the Cape Floristic Region contains within its borders fragments of Afrotemperate forests. These forest fragments are essentially depauperate outliers of Afrotemperate forests of the high mountains in tropical Africa, but which also contain some relics from the mesic Tertiary times (Mucina and Rutherford, 2006). These fragments of forest tend to occur on the moist (800-2 000 mm/yr), fire-protected southern coasted forelands and lower mountain slopes (Cowling and Pierce, 1999). In addition to Afrotemperate forests, the Cape Floristic Region possesses small enclaves of Subtropical Thicket and Succulent Karoo vegetation (Proches et al., 2006).

1.4.3.4 Biotic Diversity

The Cape Floristic Region has exceptional diversity with 70% of its approximate 9000 plant species being endemic (Goldblatt and Manning, 2002). The region represents an outlier from general trends between species richness and environmental parameters (Kreft and Jetz, 2007). The reasons for these figures are debated in the literature and various hypotheses exist including the high biodiversity observed being the result of extraordinarily high environmental heterogeneity and strong gradients (Goldblatt and Manning 2000; Linder, 2003; Ellis and Weis, 2006); the exceptionally low dispersal distances and low migration rates (Cowling and Lombard, 2002; Latimer et al., 2005; Barraclough, 2006); and the relative stable nature of the region's Pleistocene climate (Sniderman et al., 2013).

The fauna of the Cape Floristic Region in contemporary times is much reduced as a result of hunting and habitat destruction. Even so, the Fynbos vegetation can only support a low density of vertebrates due to the inherent low soil fertility characteristic of this vegetation type and the subsequently poor forage quality of the flora. In contrast, the more fertile Renosterveld supported herds of various buck and associated predators at the time of European colonisation (Skead, 1980). Sadly, only 129 mammal species remain in the Cape Floristic Region today of which nine are endemic (Rebelo, 1992). Bird diversity in the region is relatively low due to the structural uniformity of the vegetation and the shortage of food (McMahon and Fraser, 1988). Excluding seabirds, approximately 300 birds have been recorded in the region, of which six are endemic (Rebelo, 1992). Despite the paucity in data, initial studies indicate high invertebrate diversity in the region. Picker and Samways (1996) found 111 endemics in 471 km^2 and Rebelo (1992) reported 234 species of butterfly in the region of which 72 were endemic.

1.4.3.5 Threats and Challenges

Biodiversity within the Cape Floristic Region faces a battery of threats generally associated with anthropogenic activities (Cowling and Pierce, 1999). Alien invasive tree species are one of the greatest threats to biodiversity (Rouget et al., 2003a); a reality shared in common with other Mediterranean-type ecosystems throughout the world (Gaertner et al., 2009). Originating from other Mediterranean climate regions, the tree species were initially introduced to supplement the paltry tree flora of the region. The impacts on local flora are catastrophic and diverse as alien invasives eliminate biodiversity, alter fire regimes by increasing fuel loads and reduce water availability (Richardson et al., 1992). The ecological impacts of alien trees are further addressed in section 1.4.4.5.

Approximately 30% of the region is currently transformed by cultivated land (including forest plantations), dense stands of alien invasive species and urban areas (Rouget et al., 2003a). Twenty-two percent of the region is assigned to reserves, however often this is in name only and the 'reserves' fail to adequately conserve biodiversity. In addition, reserves are biased towards upland areas which lead to a seriously constrained representation of biodiversity pattern and processes (Rouget et al., 2003b).

Added to this is the threat posed by climate change and the uncertainty in how indigenous, and alien species for that matter, will respond to the predicted changes in precipitation and temperature (Hannah et al., 2007).

1.4.4 Renosterveld Vegetation

1.4.4.1 Introduction

The name Renosterveld (Afrikaans for 'rhinoceros veld') has no clearly defined origin (Tansley, 1982). It has been suggested that the colour and texture of Rhinoceros (*Diceros bicornis*) hide are reflected in the vegetation (Levyns, 1956). Indeed, the name for the Swartland (Afrikaans for 'black land') region of the Western Cape originated from the black hue the Renosterveld vegetation would take on when wet (Bradlow, 1984). A further possibility is that Rhinoceros would find shelter amongst the vegetation (van der Waalt in Walton, 2006). In the first few centuries of colonial rule, Renosterveld appears to be synonymous with Renosterbos (*Elytropappus rhinocerotis*) in descriptive reports of vegetation. Renosterbos is a dominant shrub often forming monotypic stands in Renosterveld (Walton, 2006); however, Renosterveld is not always dominated by *Elytropappus rhinocerotis* (Boucher, 1980). Renosterveld is frequently confused with Fynbos by the general public as it falls alongside Fynbos within the Cape Floristic Region which is often named the Fynbos Biome (Cowling and Richardson, 1995). Despite certain overlapping species, Fynbos and Renosterveld are distinct vegetation types.

1.4.4.2 Extent and Definitions

Renosterveld, in its various forms, currently extends over approximately 20 000 km^2 of the Cape Floristic Region. This community typically comprises a low shrub layer (1-2 m tall) of predominantly ericoids, usually dominated by the Renosterbos (*Elytropappus rhinocerotis*) with a ground layer of seasonally active bulbs and grasses. Unlike Fynbos, Renosterveld generally lacks restioids, and proteoids are rare. Renosterveld is reportedly restricted to the fine-grained, shale-derived soils of the coastal plains and inland valleys, predominantly where an annual rainfall of between 300 and 650 mm falls (Boucher and Moll, 1981; Rebelo, 1998). It usually occurs on the ecotone between Fynbos and Succulent Karoo with varying proportions of perennial grasses, succulents, geophytes and re-sprouting and re-seeding evergreen shrubs (Rebelo et al., 2006). The dominant families in Renosterveld are Asteraceae, Poeaceae, Fabaceae, Malvaceae and Iridaceae, however in fire-protected areas within Renosterveld, species associated with Subtropical Thicket are present (Milton, 2007).

Renosterveld is the least well defined vegetation type in South Africa (Milton, 2007). Contemporary descriptions and definitions of Renosterveld are ambiguous or complicated and there is a lack of consensus on what its distinguishing features are (Walton, 2006). In the wake of numerous ecological studies on Fynbos in the last century, Renosterveld has often been incorrectly relegated to "transitional" (Cowling, 1984), "derived" (Boucher, 1987) or "disclimax" (Specht and Moll, 1983). The main reasons for this ambiguity surrounding Renosterveld are the lack of accurate baseline data and the considerable variation in the vegetation's composition across a gradient of rainfall quantity and seasonality (Milton, 2007). Peninsula Shale Renosterveld, the focus of this study, is described in detail in the description of the study site (section 2.2.2).

1.4.4.3 History and Variation

Due to its position in the surrounds of Table Bay, its accessibility and its relatively nutrient-rich soils, Renosterveld was the first vegetation type to be converted for agriculture by the early European settlers who first permanently settled on the shores of the Western Cape in 1652 (Rebelo et al., 2006; Newton and Knight, 2004). Even pre-Europeansettlement, the indigenous peoples of the region had influenced Renosterveld for their benefit. The Khoi-Khoi pastoralists arrived in the region approximately 2 000 years ago and they undoubtedly burnt areas of Renosterveld to promote vegetation more suitable for their cattle and sheep to graze on (Deacon, 1992). Prior to the Khoi, the San hunter-gatherers may have used fire to flush out game species from Renosterveld (Deacon, 1992). The manipulation of Renosterveld for millennia, particularly since the arrival of Europeans, has made it near impossible to know what a fully functional natural Renosterveld ecosystem looks like and how drivers interact within it. Besides the already mentioned ambiguity, this lack of baseline data creates difficulty in conservation efforts (Gillson, 2004).

The variation of Renosterveld composition falls across a gradient of rainfall quantity and seasonality (Milton, 2007). Moll et al. (1984) distinguished four Renosterveld types: West Coast Lowland, South Coast Lowland, Inland Mountain and Eastern Renosterveld. No subsequent studies on the relationships and determinants of these groupings have been undertaken (Rebelo et al., 2006). West Coast Renosterveld has the highest diversity of geophytes, whereas the South Coast Renosterveld is generally grassier. The Renosterveld on the Succulent Karoo and Subtropical Thicket ecotones tend to include more succulents than the Renosterveld types adjacent to Fynbos (Rebelo et al., 2006).

The coastal Renosterveld (incorporating both South and West Coast Renosterveld) is described by Walton (2006, pg. 8) as “a shrubland including swards of graminoids and geophytes, with some open spaces allowing for an abundance of ephemeral species”. It has been previously described as comprising of a partially open to closed 1-2 m tall matrix of small cupressoid, molliphyllous, leptophyllous, divaricately branched evergreen shrubs (Moll et al., 1984), dominated by Asteraceae (Walton, 2006). Emergent thicket species are regularly spaced throughout the Renosterveld matrix (Boucher, 1981). As alluded to previously, the South Coast Renosterveld is grassier than the West Coast variety; however grasses are still present in the West Coast Renosterveld especially in stony regions that avoided ploughing where swards of *Themeda triandra* can be found (Acocks, 1988). The different plant types within the Renosterveld have differential growth seasons: grass growth usually occurs begins in early winter to summer (Pierce, 1984), geophytes initiate growth in autumn until the end of spring, restioids from spring to summer and shrub growth occurs throughout the year but most often occurs from late winter to early summer (Walton, 2006).

1.4.4.4 Diversity and Conservation Status

The diversity in Renosterveld makes it a vital vegetation type for conservation. Renosterveld is renowned for its high diversity of spring-flowering geophytes (Milton, 2007). Indeed, on a 1000 m^2 scale, Renosterveld has higher species richness than Fynbos: circa 84 and 66 species respectively (Cowling, 1983b). While less than that of Fynbos, levels of endemism are high, especially in the Aizoaceae, Asteraceae, Fabaceae and Iridaceae (Von Hase et al., 2003). There are multiple issues facing Renosterveld conservation currently: crop cultivation over the past 150 years has led to the majority of Renosterveld being converted into agricultural land (Kemper et al., 1999), much of which is still farmed today. Conversion to agriculture is not the only threat however; and 1.4.4.5 addresses some of these in more detail. Less than 10% of the natural Renosterveld vegetation remains (Rebelo et al., 2006). Most of the remaining Renosterveld is in fragmented habitat remnants surrounded by cereal crops (Donaldson et al., 2002). Often these smaller fragments (<10 ha) have persisted because they are situated in positions where ploughing is difficult, for instance on rocky outcrops, steeper slopes and road verges. Farmers occasionally allowed larger fragments to remain to provide grazing for sheep; however these would be frequently burnt to encourage grass growth (Donaldson et al., 2002). Only a paltry 1.6% of lowland Renosterveld is conserved (Low and Rebelo, 1998).

A detailed review of vegetation within the Cape Town metropolis showed that 87% of Peninsula Shale Renosterveld, the focus of this study and one of five Renosterveld types found within the City of Cape Town, was transformed with only 11% managed for conservation (although as this project shall show this is an exaggerated figure). Swartland Alluvium and Swartland Shale Renosterveld were worse off with 100% and 92% of the original vegetation transformed, respectively, while Swartland Silcrete and Swartland Granite Renosterveld fared marginally better with 82% and 67%, respectively (Rebelo et al., 2011). All five of these units were listed as critically endangered nationally in 2004 and remained the same in 2008, except for Swartland Alluvium Renosterveld which was listed as vulnerable (Rebelo et al., 2011).

Remnant patches of Renosterveld have a high conservation value as practically all remaining habitat is required to meet a goal of 10% conservation of the pre-colonial extent of this vegetation type (Kemper et al., 1999). Despite conserved areas within the Cape Floristic Region accounting for approximately 19% of the region (Rebelo, 1992), 95% of this conserved land is restricted to mountainous areas (Cowling and Pierce, 1999). This bias is largely as a result of the *ad hoc* manner of their establishment, where reserves were constructed in areas unsuitable, or marginally suitable, to agriculture and often in the mountains to protect catchments (Rouget et al., 2003b). Renosterveld is primarily restricted to the lowlands, thus it is heavily affected by this conservation bias as only a minute amount of the original extent of

Renosterveld is conserved (Cowling and Pierce, 1999). The need for conservation of Renosterveld is apparent; however it is not simply a case of delimiting an area as a reserve.

Work done by Horn and Esler (2009) on edge effects on biodiversity in Renosterveld patches showed that all fragments over 100 m in diameter are of particularly high importance for conservation and that stepping stones and corridors should be greater than 100 m wide to ensure continued survival and mobility of all species in the matrix. A study on the effect of fragmentation on pollinator diversity and plant reproductive success in Renosterveld showed that the numbers of certain species of bee and monkey beetles were significantly affected by fragment size. Additionally, four out of the seven plant study species studied showed significant negative effects of fragment size with reduced seed or fruit set (Donaldson et al., 2002).

Due to the fact that much of the remnant Renosterveld patches occur within a matrix of agricultural land, the attitude of the landowners is an important variable in conservation. Winter et al. (2005) postulated that if landowners perceive the retention of Renosterveld on their property to provide some form of benefit, for example as an alternate grazing source in seasons of drought, they would be more willing to conserve their Renosterveld. However, Winter (2003) reported largely negative attitudes towards the conservation of Renosterveld in the Overberg region due to perceived problem plants and animals associated with Renosterveld, and because it was not economically advantageous to retain it.

1.4.4.5 Threats

The threats facing Renosterveld, both in the past and in contemporary times, are numerous and varied. Conversion to agriculture historically drastically reduced Renosterveld and a large area is still farmed today (Kemper et al., 1999). Even land which is no longer in use, so called ‘old fields’, are generally invaded by alien grasses or other weedy species (Walton, 2006). Nitrogen enrichment, associated with agricultural runoff, significantly enhances the growth of the alien grasses in Renosterveld (Stanway, 2007; Sharma et al., 2010). The issue of alien grass invading old fields is not unique to Renosterveld but is a problem identified elsewhere in Mediterranean-type ecosystems and hinders the passive return of indigenous vegetation (Cramer et al., 2008).

Unlike invasive trees and woody shrubs, there is a shortage of data on alien grass invasion and impacts in the Cape Floristic Region (Milton, 2004). Many grass species are excellent colonizers due to their production of numerous small, persistent seeds and their ability to out-compete other vegetation types in favourable circumstances such as in nutrient-enriched soil (Rejmanek and Richardson, 1996; Hunter and Omi, 2006). In South Africa, 12% of all grasses are naturalized aliens (Russell et al., 1990) although this figure may have increased. Many of these species were deliberately introduced for agricultural, restoration or horticultural reasons (Milton, 2004). Renosterveld is vulnerable to grass invasion due to the fertile soil on which it grows, particularly after a disturbance such as fire or alien plant clearing creates an opening for the grass to establish (Milton, 2004).

Perennial alien grasses do not appear to be a significant threat in the Fynbos Biome although clumps of Natal Tussock (*Nasella trichotoma*) have been reported in certain disturbed locations (Moll et al., 1991). In contrast, annual alien grasses are widespread and occasionally abundant, particularly in degraded areas in the winter rainfall region of the Fynbos Biome (Milton, 2004). Their ephemeral nature allows them to establish under favourable conditions before increasing exponentially once adapted to local conditions. Fast growing annual grasses can out-compete perennial grasses (Young and Allen, 1997), especially where the addition of nitrogen through the presence of alien invasive trees or fertilizer input increases their growth and abundance relative to perennials (Maron and Connors, 1996). Indigenous grasses of the Fynbos Biome are generally perennials of the tribe Arundinoidea and they competitively exclude annual invasives in undisturbed vegetation (Linder, 1989). Annual grasses may enter the system at a local scale following a disturbance before becoming widespread on a landscape level following fire or heavy grazing (Vlok, 1988). Their abundant seed production allows vast quantities to persist in the seedbank of disturbed vegetation (Milton, 2004) and it is believed that an increase in alien annual grass abundance is positively correlated to a decrease in indigenous perennial shrub and grass cover and herbaceous diversity (Steinschen et al., 1996; Sharma et al., 2010). It has been shown that grazing is positively correlated with alien grass presence in West Coast Renosterveld fragments (Van Rooyen, 2004).

Although typically associated as a threat to mountain Fynbos, alien tree species are a recognized threat for the entire Fynbos biome including Renosterveld (Rebelo et al., 2006). South Africa has a long history of invasion by alien plants (Richardson and van Wilgen, 2004). Key invaders are woody trees and shrubs in the *Pinus, Acacia* and *Hakea* genera (van Wilgen et al., 2012). These invasives generally spread from intentionally cultivated plantations to natural habitats (Richardson, 1998). The first record of a forestry species invading indigenous vegetation where it was noted as potentially problematic was a report of *Pinus halepensis* spreading into Fynbos in 1855 (Richardson and Higgins, 1998). By 1997, an estimated 10 million hectares of South Africa had been invaded (Le Maitre et al., 2000) and since then, despite the initiation of an extensive clearing programme, invasions have appeared to increase in many biomes (see van Wilgen et al., 2012 for an overview). The Cape Floristic Region in particular has been heavily impacted by alien invasive plants with stands of alien plants present in mountains, lowlands and along all major waterways (De Lange and van Wilgen, 2010). Many taxa in the *Pinus* and *Acacia* genera are superb colonizers with wide-ranging adaptations that allow them to become invaders (Richardson et al., 1994; Fagg and Stewart, 1994). Richardson et al. (1994) differentiated between alien species which generate freely under their own canopy but tend not to disperse long distances, and those species termed invaders, who frequently recruit copious numbers of seedlings at distances well over 100 m. Although invaders undoubtedly pose the greatest threat to indigenous ecosystems, non-invasive aliens may have severe impacts at a more localized scale.

Alien invasive trees have numerous effects on indigenous ecosystems (van Wilgen, 2012). In general, they are able to transform ecosystems altering functionality and diminishing the ability to provide goods and services in addition to greatly decreasing the biodiversity of the ecosystem (Richardson et al., 2000; Vila et al., 2010; van WiIgen and Richardson, 2012). More specifically, the above-ground biomass in alien invaded areas is 3 to 10 times higher than that found in natural Fynbos Biome ecosystems (Versfeld and Van Wilgen, 1986). This in turn impacts water dynamics and the natural fire regime. Invasive species decrease the water available to the catchment area due to an increase in transpiration and the evaporation of intercepted precipitation (Le Maitre et al., 1996). In addition to the increased biomass, alien stands change litterfall dynamics (Milton, 1981) and nutrient cycling. The change in dynamics may increase the severity of fires (Musil, 1993; Yelenik et al., 2004) which consequently may change soil structure, soil condition and induce soil repellency (Holmes, 2001). The aforementioned changes to ecosystem drivers, along with their competitive advantage through seedbank alteration and regeneration in post-fire environments, has resulted in alien invasives becoming one of the largest threats to biodiversity and one of the main causes of local extinction in the Fynbos Biome (Rebelo et al., 2006). The presence of alien invasives and their subsequent clearing often leads to increased soil erosion which is also detrimental to the indigenous vegetation and can retard natural recovery (van Wilgen and Richardson, 1985). Finally, studies have shown that changes in natural vegetation due to alien plant presence also effect indigenous fauna (Samways and Sharratt, 2010). Changes to composition and abundance of native ant species effect their ability to disperse indigenous seeds (French and Major, 2001), and the altered feeding behaviour of certain avian species due to the presence of non-indigenous species is likely to have negative effects on the dispersal of indigenous vegetation (Fraser, 1990).

Even after alien trees have been removed from an area, passive restoration is often ineffectual when attempting to return an ecosystem to a functional state dominated by indigenous plant cover (Hulme, 2006; Blackwood et al., 2010). Reasons for this failure include the likelihood of secondary invasions by alien invasives which capitalize on the disturbance of alien clearing (Le Maitre et al., 2011) and resource alteration, for example in soil chemistry or physical properties, due to alien presence or due to the management intervention (Marchante et al., 2009; Young et al., 2009).

1.4.4.6 Disturbance and Ecosystem Drivers

Only in the last few decades has there been a concerted effort to understand the drivers of Renosterveld vegetation and habitat change. Disturbances, defined as any perturbation, (either natural or caused by humans) experienced by ecosystems (Lawrence, 2005), are important influences on vegetation patterns and dynamics across a range of biomes (Sinclair and Byrom, 2006) and Renosterveld is no exception. Boucher (1983) described Renosterveld as a flora created and maintained by an intermediate level of disturbance(s). The intermediate disturbance hypothesis (Connell, 1978), which predicts that diversity is highest when vegetation is subjected to intermediate levels (both spatially and temporally) of disturbance, validates this assessment as Renosterveld is an exceptionally diverse flora (Cowling and Pierce, 1999). Schwilk et al. (1997) contest the hypothesis for Mountain Fynbos (and presumably Renosterveld too), reporting that community heterogeneity was highest at the least frequently disturbed (i.e. burnt) sites and lowest at the sites that experienced an intermediate fire frequency. On a small scale, bioturbation from mammals and termite activity associated with termitaria (locally known as *Heuweltjies*) creates local habitat heterogeneity (Moore and Picker, 1991). On a larger scale, a relative short fire interval creates a mosaic of patches of vegetation of different age. Additionally, herbivory (both grazing and browsing) acts as a disturbance, maintaining diversity in the system (Walton, 2006; Milton, 2007). Renosterveld has been described as a dynamic system with changes in the disturbance regime triggering switches between a shrub and grass- dominated state (Heydenrych, 1995; Milton, 2007).

Fire is an integral part of most Mediterranean ecosystems including the Cape Floristic Region (Gill 1981; Kruger 1983; Keeley 1986; van Wilgen et al. 1992a; Trabaud & Prodon 1993, van Wilgen, 2009). While fire has been extensively studied in Mountain Fynbos (Kruger and Bigalke, 1984; Van Wilgen, 2009), little is known, or at least documented, on the fire regime in Renosterveld (Bond et al., 2004; Curtis, 2009).

Fire frequency, season, intensity and size are all important determinants of species composition, vegetation structure and successional patterns in the Fynbos Biome (Kruger and Bigalke, 1984; van Wilgen et al., 1992a). The evolutionary responses to fire, be it for survival or reproduction, are numerous and diverse. Many species rely on the heat or chemical cues provided by fire for the release or germination of seeds (Keeley, 1987). Fire stimulates flowering in numerous geophytes, herbaceous perennials (including grasses, sedges and restios) and some shrub species (Kruger, 1983), while other species are adapted to fire and survive through persistent underground bulbs or corms. Lastly, some species have evolved to re-sprout after fire (Le Maitre and Midgley, 1992).

A change in fire frequency is one of the leading ecological concerns with respect to conservation within the Cape Floristic Region (Richardson et al., 2002). For example, the abundance and dominance of seeders is directly related to fire. Frequent burning alters community species composition by eliminating large seeding shrubs that do not have time to reach maturity and decreasing fire frequency has been reported to increase seeding Proteaceae species (Le Maitre and Midgley, 1992). Very long intervals between fires similarly eliminates larger shrubs as many species rely on canopy-stored seed banks and plants may senesce before fire allows their serotinous cones to open (Schwilk et al., 1997), thus understanding the most optimal fire regime for a system is critical to manage it for conservation. Due its grassier nature, fire frequency in Renosterveld is believed to be higher than the adjacent and compositionally similar Fynbos which has a fire frequency of 4-45 years with an average of 15 years (Van Wilgen et al., 1992b). It has been postulated that this shorter fire, interval may account for the predominance of re-sprouters in Renosterveld (Kemper et al., 1999). Due to the Renosterveld's inherent resilience and dominant species which have characteristically shorter maturation times, Boucher (1983) hypothesized a natural fire interval of 3-12 years for the vegetation type.

Kraaij (2010) reported a fire interval of four years in Renosterveld at Bontebok National Park near Swellendam between 1972 and 2004, however 70% of these burns were prescribed management burns to promote grass growth to provide grazing for the endangered Bontebok (*Damaliscus pygargus pygargus*). This was subsequently altered to a fire return period of every 8 years to promote biodiversity (Kraaij, 2010). Most of the prescribed burns were conducted during autumn, the ecologically accepted season (Bond, 1997), with accidental or natural fires peaking a few months earlier than this (Kraaij, 2010). Fire data from Renosterveld vegetation within the Table Mountain National Park (i.e. vegetation on Devil's Peak and Signal Hill) from the period 1970 to 2007 does not give much insight into the natural regime as fire management was practiced during this period (Forsyth and van Wilgen, 2008). The mean fire return period recorded for Renosterveld in 1975 was 37.4 years. This decreased to 30 years in 1985 and decreased again to 9 years in 1995 before increasing to 17.7 years by 2007 (Forsyth and van Wilgen, 2008). Approximately 90% of the fires within the park occurred during the ecologically acceptable period of summer and autumn (Forsyth and van Wilgen, 2008). Over 80% of fires were wild rather than prescribed, however only 6 of a total of 373 fires in the park during this 30 year period were attributed to natural causes (lightning strikes or rockfalls), although 244 were reported as of unknown origin (Forsyth and van Wilgen, 2008). It should be noted that the data on fire season and cause do not refer to Renosterveld areas specifically, but the general trend of human-influenced fire is consistent throughout the park due to its extensive urban boundary.

Fire and herbivory are often intrinsically linked (Van Langevelde et al., 2003). Since the Middle Stone Age, or at the latest the late Stone Age, humans in the Cape have been capable of creating fire at will (Deacon, 1992). Brown et al. (2013) reported evidence of fire usage from as early as 164 ka at Pinnacle Point on the south coast of South Africa. Both the hunter-gatherer San and Khoi herders would have used fire to stimulate grass growth, although while the San would use the grass growth to capture selective grazers the Khoi would heavily graze the grass for short periods before moving on (Smith, 1992). The use of fire by indigenous peoples was rapidly adopted in the region by early settlers and the frequency of burning increased, however overgrazing on frequently burnt ground resulted in a reduction in grass and increased shrub dominance (Walton, 2006). A number of conceptual models have been proposed by various scientists in an attempt to better our knowledge of how drivers (i.e. herbivory and fire) interact to bring about changes in Renosterveld (Milton, 2007). Cowling et al. (1986) developed a model for South Coast Renosterveld which hypothesized that a combination of spring burning with grazing prevents grasses setting seed and proliferating, benefiting the unpalatable winter-seeding shrubs. This would lead to an increase in domination by shrubs such as *Elytopappus rhinocerotis, Athanasia* spp. and *Relhania* spp. On the other hand, an autumn burn after grasses have set seed but during the flowering of shrub species would decrease shrub cover and benefit grass recruitment (Milton, 2007). Using Levyns' (1926) data which reported that *Elytropappus rhinocerotis* seeds persist in the seed bank for seven years and take three years to mature, Cowling et al. (1986) concluded that fires repeated at three year intervals would exhaust the seed bank and promote grass growth. Data from Raitt (2005) support this assertion, demonstrating that frequent burning promotes the grass *Themeda triandra* in the Renosterveld of the Overberg district. It should be noted however that many perennial grasses seldom appear to recruit but survive from underground parts after fire or grazing thus the setting of seed may not be an important part of grass dynamics in certain systems (Van Oudtshoorn, 2004).

Rebelo (1995) developed a conceptual model suggesting that intensive grazing post burn would convert grassy Renosterveld to a shrubland dominated by *Elytropappus rhinocerotis*, whereas the elimination of fire would see Renosterveld vegetation shift toward Subtropical Thicket. If this thicket were to be lightly grazed following a burn, the model hypothesizes that the vegetation would switch back to a grassier state. Data supporting this model has been produced by a number of empirical studies (Britton and Jackleman, 1995; McDowell, 1995; Raitt, 2005).

Milton (2007) combined Rebelo's (1995) model with Cowling et al.'s (1986) model and a variety of empirical data (included the effects of ploughing) to produce Figure 1.1 and Table 1.1. Figure 1.1 shows how fire and grazing may interact to change the composition of Renosterveld to a monotypic *Elytropappus rhinocerotis* stand with reduced diversity. The model suggests that autumn burning and grazing can reverse structural changes in the hypothetical system. After ploughing, Renosterveld may revert to weedy grassland dominated by *Cynodon dactylon,* and remain that way indefinitely, if fire is excluded and grazing persists (McDowell, 1995; Walton, 2006). These old fields may prevent indigenous perennial grass and shrub establishment (Midoko-Iponga et al., 2005). Active clearing of weeds and burning may facilitate a return to a more species-rich state by allowing growth and flowering of indigenous bulb species which persisted in the seed bank (Musil et al., 2005). Additionally, diversity could increase by the reintroduction of indigenous Asteraceae from adjacent Renosterveld regions via wind dispersal as Asteraceae may be dispersed up to 80 m (Shiponeni, 2002). Table 1.1 siilarly hypothesizes the effect that various management stategies have on both canopy cover and species richness for grasses, geophytes, shrubs (both re-seeders and re-sprouters) and weeds. Various other disturbances or management actions affect Milton's (2007) conceptual model. Clearly, manually reseeding old fields or degraded Renosterveld would change the composition of the returning vegetation (Holmes, 2005). Fragmentation of Renosterveld, a common occurrence in agricultural areas, in addition to an influx of fertilizer run-off from neighbouring farms has been shown to promote alien weedy grass invasion in Renosterveld (Kemper et al., 1999; Van Rooyen, 2004). Ploughing, fragmentation and nutrient enrichment may all reduce diversity in Renosterveld (Milton, 2007). Despite this, diversity counts in unploughed fragments ranging from 0.001 ha to 0.1 ha indicate that species area curves plateau at about 0.01 ha (Kemper et al., 1999).

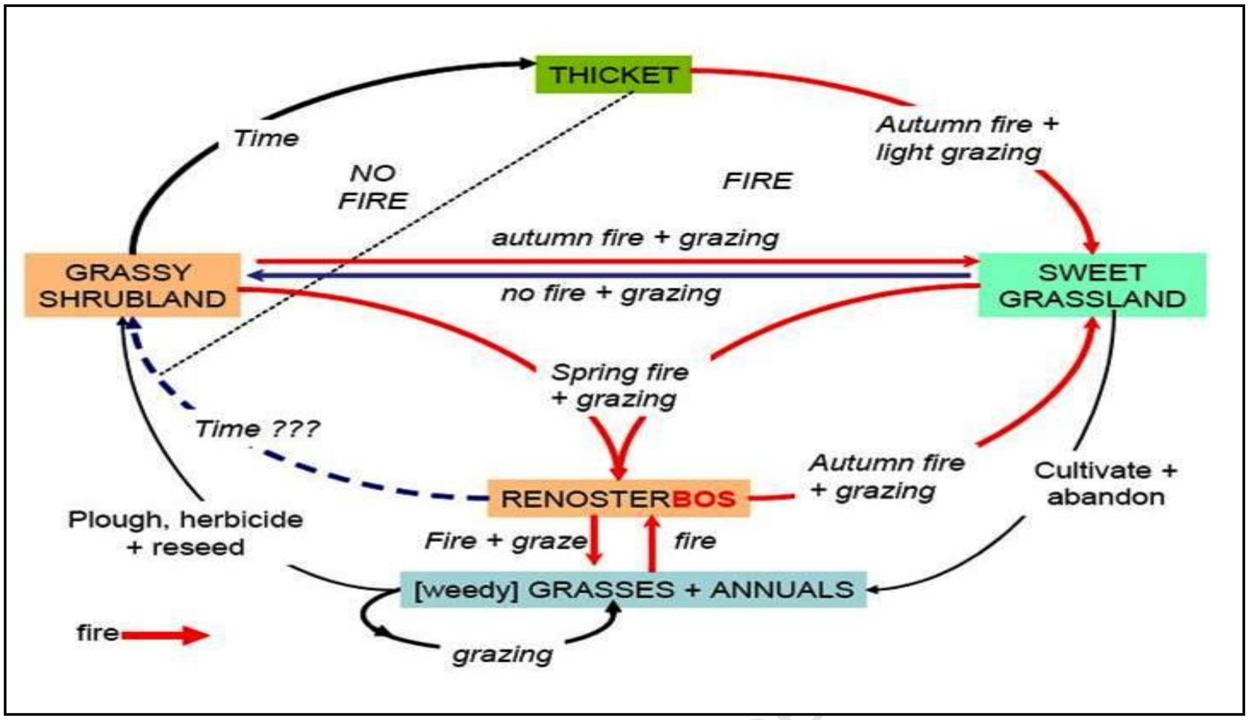

Figure 1.1: Conceptual model illustrating how fire, grazing and other disturbances may interact to change the composition of a Renosterveld ecosystem (source: Milton, 2007).

Table 1.1: Predicted effects of disturbance or management actions on Renosterveld cover composition and species richness across plant functional type. A (-) denotes decrease; (+) denotes increase and (0) denotes no change (Adapted from Milton, 2007).

Management	**Frequency**	**Grass**	**Geophyte**	**Seeder**	**Sprouter**	**Weed**
		CANOPY	**COVER**			
Succession Time	>10 years	-	-	-	+	-
Fire Alone	5-10 yearly	0	0	+	0	0
Fire Alone	3-5 yearly	+	+	0	-	+
Herbivory Alone	Low	+	+	0	0	0
Herbivory Alone	High	+	+	+	-	+
Fire+Spring Herbivory	5-10 yearly	-	-	+	-	+
Fire+Autumn Herbivory	5-10 yearly	+	+	-	-	+
Brush Cutting	>10 yearly	+	+	-	-	+
Fragmentation		0	0	0	0	+
Nitrogen input		+	-	0	0	+
		SPECIES	**RICHNESS**			
Succession Time	>10 years	-	-	-	+	-
Fire Alone	5-10 yearly	0	+	+	0	0
Fire Alone	3-5 yearly	+	0	-	-	+
Herbivory Alone	Low	+	+	0	0	0
Herbivory Alone	High	-	-	-	-	+
Fire+Spring Herbivory	5-10 yearly	-	-	+	-	0
Fire+Autumn Herbivory	5-10 yearly	+	+	-	-	+
Brush Cutting	>10 yearly	+	+	-	-	+
Fragmentation		-	0	0	0	+
Nitrogen input		-	-	-	0	+

Chapter 2

Study Area: Description and Land-Use History

2.1 Prelude

The following chapter is more detailed than a traditional study site description due to the importance of the land-use history of a study region in understanding its contemporary environmental patterns and processes. The chapter commences with a standard description of the study area including data on its location, contemporary vegetation, geology and soils, and climate. Following this, the land-use history of the area is explored and discussed by drawing on published historical works read with a view to understanding the historical use of the study area with respect to how this might inform contemporary ecosystem state and structure. Firstly, a brief précis of the importance of acquiring land-use history data is presented before a description of the methods used to generate the high resolution data for the recent fire and forestry history is given. Following that the anthropogenic history of the study area, fire and grazing history, and the history of land-cover change in the form of cultivation and forestry are explored. Finally, a brief overview of faunal introductions is given before the chapter is concluded.

2.2 Study Site Description

2.2.1 Location

The study area (~100 ha; centred at 33°56’50.51”S; 18°27’29.59”E) is located within Groote Schuur Estate, an area recently incorporated into the Table Mountain Nation Park which falls under the auspices of the South African National Parks board, on the northern slopes of Devil’s Peak above the city of Cape Town, South Africa (see Figure 2.1). The Estate contains within it three distinct natural vegetation types: small remnant patches of forest/thicket occur in the south-eastern corner and within the ravines; mesic mesotrophic proteoid Fynbos (Cowling et al., 1996) occupies the upper east-facing slopes of the slopes; and Peninsula Shale Renosterveld is distributed over the northern part of the Estate. Adding to the complexity of the vegetation in the estate is the presence, at various densities, of non-indigenous alien species. The focus of this study is the Peninsula Shale Renosterveld and the ‘study area’ refers to the Renosterveld, both contemporary and invaded, found within the Estate’s boundaries. The lower portion of the study area is fenced and bordered by the M3 freeway which links the southern suburbs and Cape Town city bowl. The upper boundary of the estate is the fairly inaccessible cliffs of the mountain face. To the north, the study area is connected with the northern slopes of Table Mountain and to the south-east the study area is adjoined to the mountain Fynbos of Groote Schuur Estate which is continuous with the eastern slopes of Table Mountain. Below the Estate lies the upper campus of the University of Cape Town.

A preliminary broad-brushed analysis of the vegetation within the Estate showed a complex mosaic of indigenous and invaded vegetation types within the study area. In an effort to investigate the role of land-use history on ecosystem drivers and elucidate the current status of the study area four different 'study sites' were chosen in which research was focused (see Figure 2.4). An Old Renosterveld site situated directly below Rhodes Memorial and adjacent to the University campus was chosen as it was considered relatively un-invaded and had not burnt for a substantial period of time. The Lightly Degraded Renosterveld site was chosen as it was dominated by indigenous vegetation and had been subjected to a recent fire. The Alien Pine stand was chosen as it was, at the time, invaded by pine trees; whereas the Game Camp site is largely covered by alien grasses and has been managed as a grazing paddock for a lengthy period of time. The four aforementioned sites were characteristic vegetation states within the study area and, as typical and distinct, were most likely to elucidate information around vegetation state shifts. They were therefore considered most relevant in inferring ecological understanding and informing future restoration efforts.

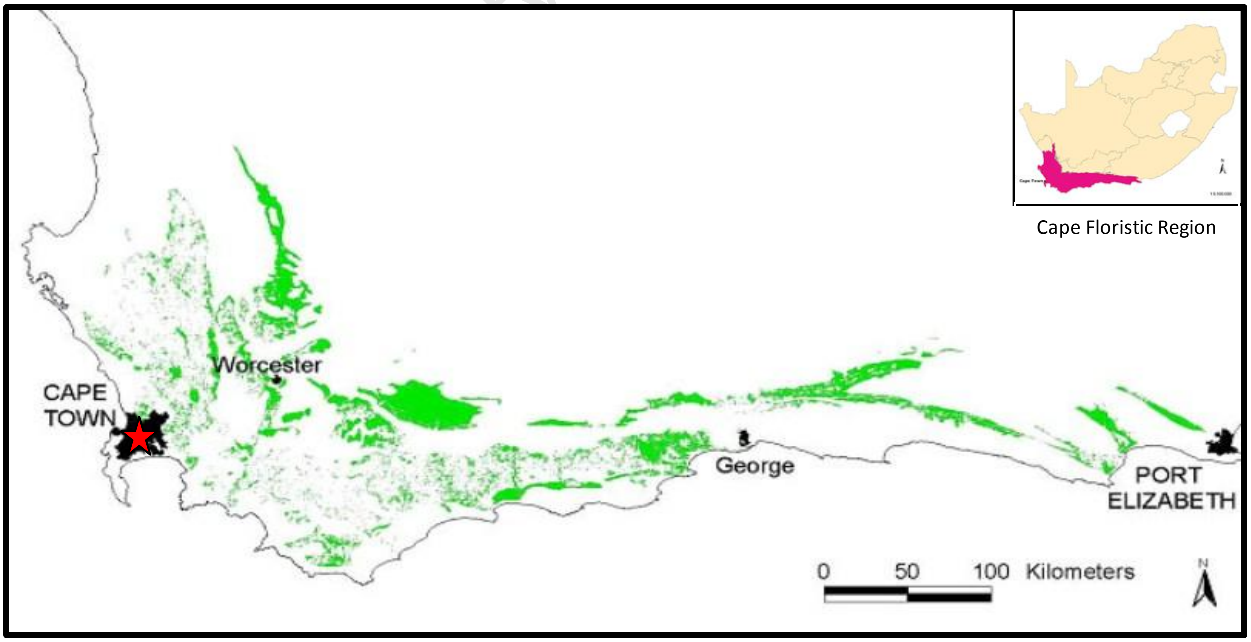

Figure 2.1: Map illustrating the location of the study site (designated by the red star) in relation to some of the remaining Renosterveld fragments in the Cape Floristic Region of South Africa (source: SANBI).

2.2.2 Vegetation

Peninsula Shale Renosterveld is found exclusively in the Western Cape. Its historical area, approximately centred on the current city bowl of Cape Town, was 2375 ha; however 87% of this has been transformed (Rebelo et al., 2011). Currently, it is restricted to Signal Hill and the lower northern slopes of Table Mountain and Devil's Peak where it is found overlying the Malmesbury Shale bedrock. Its altitudinal range extends from sea level to 350 m above sea level (Rebelo et al., 2006). According to Rebelo et al.'s (2006) description of the vegetation type, it is characterized by tall, open shrubland and grassland occurring on gentle to steep lower mountain slopes. Typically *Elytropappus rhinocerotis* is not dominant and the vegetation is described as quite grassy due to frequent fires and a lack of grazing. The early seral stages of Peninsula Shale Renosterveld are reportedly dominated by *Asparagus capensis, Haemanthus sanguineus, Hyparrhenia hirta,* various *Oxalis* species and re-sprouting *Rhus lucida*. Subsequent emergence of tussock grasses, shrubs and ferns follows and after only a year re-seeding species become more obvious. The natural fire return period is hypothesized to be 3-5 years (Rebelo et al., 2006). Peninsula Shale Renosterveld is critically endangered and highly transformed. The target of 26% of original extent conserved is unattainable as 87% has already been totally transformed, predominantly by urbanization. The majority of the remaining Peninsula Shale Renosterveld is protected within Table Mountain National Park, however a moderate proportion of the vegetation on the slopes of Devil's Peak is covered by Pine plantations (Rebelo et al., 2006) and alien grasses and even the more 'pristine' areas have been affected by centuries of human actions.

2.2.3 Geology and Soils

The gently rounded forms of the weathered shale, greywacke and phyllites of the Malmesbury Group (Tygerberg Formation) on the lower slopes contrast with the more resistant and angular quartzitic sandstone of the Table Mountain Cape Supergroup (Peninsula Formation) which comprise the cliffs of Devil's Peak (see Figure 2.2). Furthermore, a layer of siltstone and mudstone of the Graafwater Formation separates the upper Table Mountain sandstone from the base of the Malmesbury Shale. In places, the slopes are covered by mountain scree deposits which consist predominantly of gritty sand, stones and boulders (Combrink et al., 1992; Pauw and Johnson, 1999). The generally shallow clay soils underlying the Peninsula Shale Renosterveld are derived from shale of the Tygerberg Formation, Malmesbury Group. Glenrosa, Mispah and Lamotte forms are prominent and soil types are generally Fa and Ga.

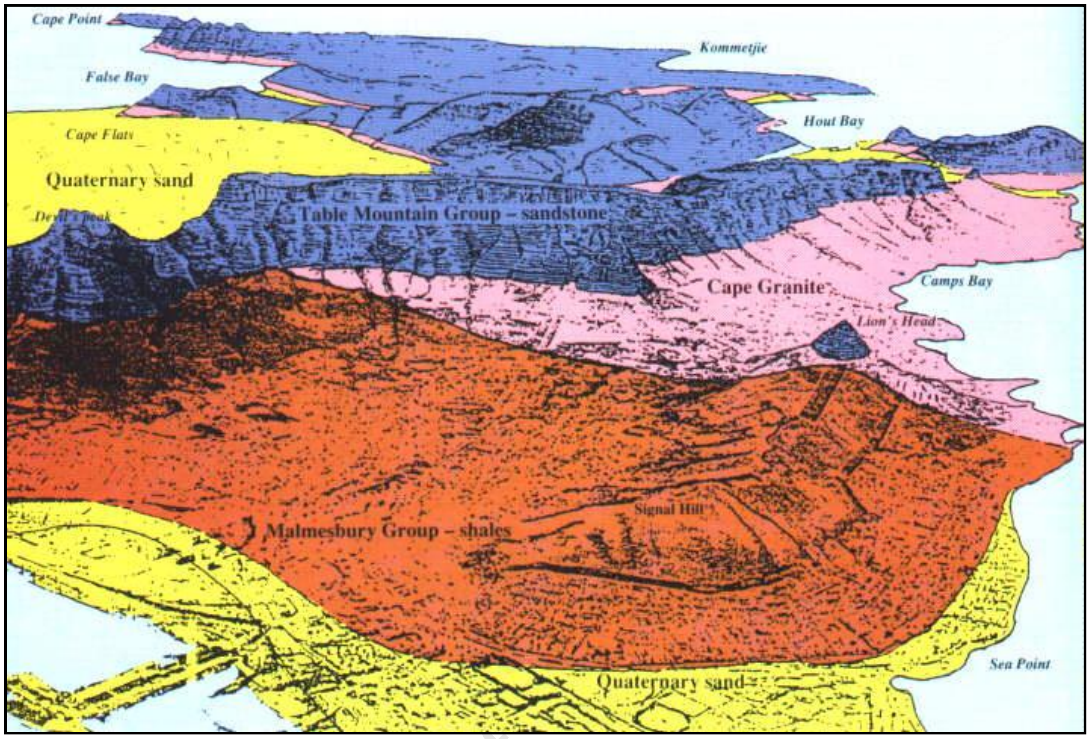

Figure 2.2. The underlying geology of the Cape Peninsula superimposed on the topography of Cape Town (source: Department of Geological Science, University of Cape Town).

2.2.4 Climate

The mean annual precipitation experienced by Peninsula Shale Renosterveld ranges from 480-870 mm (mean 720 mm) making it the wettest Renosterveld type by some margin. Like most Mediterranean-type climates, there is a marked peak in precipitation in winter (from May to August) and summer drought. The mean maximum temperatures for the region during February (taken from the Cape Town International airport, the closest weather station with an extensive climate record), the hottest month, is 26.7˚C; while the mean minimum temperature during July, the coldest month of the year, is 7.8˚C. The vegetation type only experiences 2 or 3 days of frost per year on average (Rebelo et al., 2006; CSAG, 2012). The mountain face acts like an enormous barricade, affecting the orientation and increasing the velocity of the prevailing southerly winds. More than 62% of winds experienced at the study area blow from quadrants between South and West. Wind velocities can be high, especially on the exposed ridge and the high wind speeds have a cooling effect on the ambient temperatures (Combrink et al., 1992).

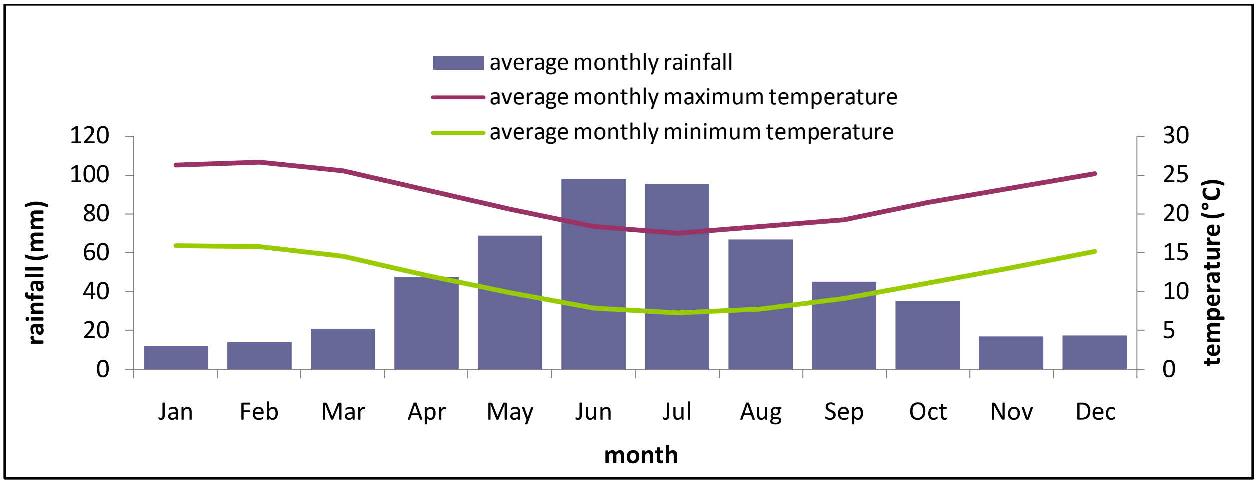

Figure 2.3: Climagraph showing the average monthly rainfall and temperature (past 21 years) data for Cape Town International Airport (courtesy of the Climate Systems Analysis Group, University of Cape Town).

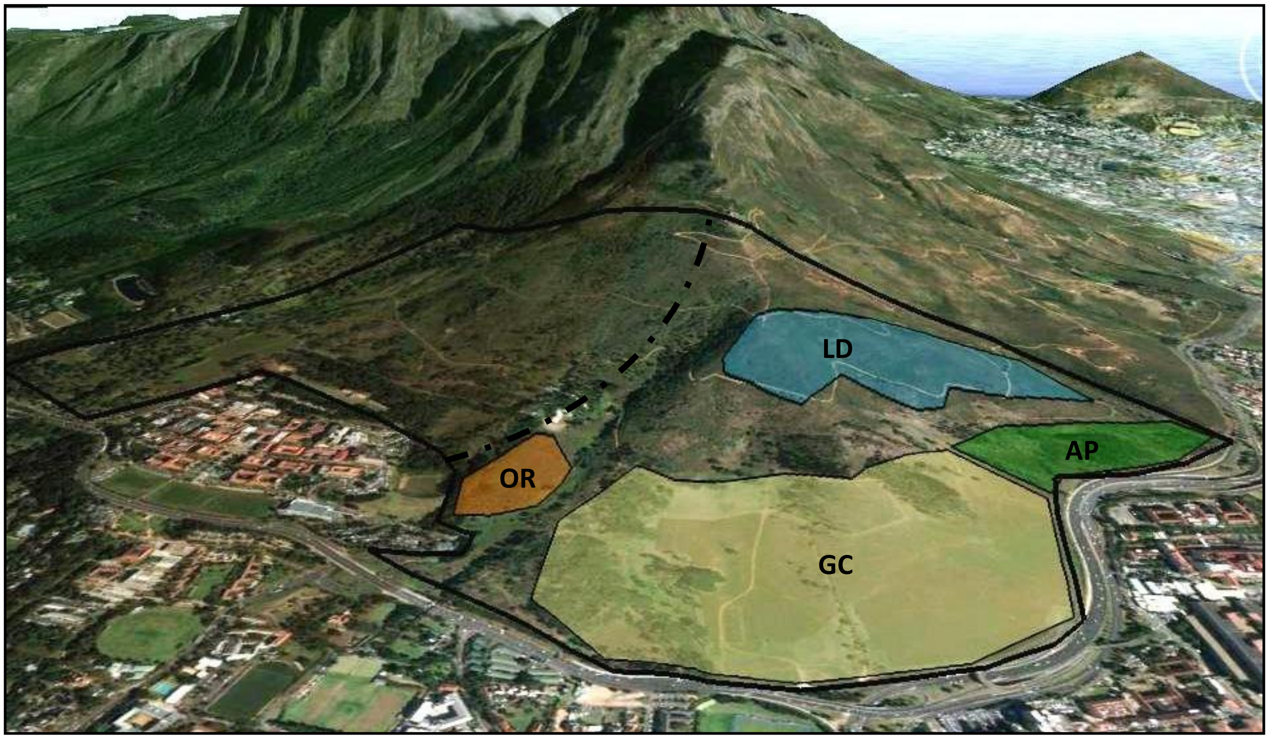

Figure 2.4: Google Earth image of Groote Schuur Estate in relation to Devil's Peak and Table Mountain showing the location of the four study sites within it. The dashed line approximates the boundary between the Renosterveld and the Fynbos. **OR**=Old Renosterveld; **LD**=Lightly Degraded Renosterveld; **AP**=Alien Pine stand; **GC**=Game Camp enclosure.

2.3 Land Use History

2.3.1 The Importance of Land-Use History in Restoration Ecology

The land-use history of a site is intrinsically linked to the structure and function of its ecosystems. For a detailed understanding of an environment's current processes and status a comprehensive account of land-use history is required (Foster et al., 2003; Szabo, 2010). Land-use legacies impact on a wide range of ecosystem factors and can create 'novel ecosystems' where species occur in combinations and relative abundances that have not occurred previously within a given biome often resulting in switches in biotic and abiotic thresholds (Hobbs et al., 2006). Past activities as diverse as grazing, ploughing, controlled and accidental burning, and species introductions all have the potential to alter ecosystems (Rayburn and Major, 2008). Ecosystem alterations can include impacts on soil properties (both chemical and physical), ecological integrity, and the corporeal physical structure of a particular area (Milchunas and Lauenrot, 1995; Compton et al., 1998; Donohue et al., 1999). Environmental variables within an ecosystem cannot be viewed in isolation, either temporally or spatially, as they interact in a multitude of ways, and to view land-use history as isolated events in time and space is erroneous (Rayburn and Major, 2008). This is particularly true of urban environments where there is a general lack of acknowledgement of the importance of temporal dynamics in the understanding of the effects of urbanization on biodiversity and ecosystem functionality (Ramalho and Hobbs, 2012). This relevance of maintaining a functional urban ecology has only recently come to the fore (Ramalho and Hobbs, 2012). With this in mind it is imperative, prior to restoration initiatives, that a thorough investigation into the history of the site is undertaken to help understand how and which land-uses have caused ecological shifts (Foster et al., 2003; Szabo, 2010) as the recognition of a novel ecosystem should be the starting point for ecosystem management efforts (Seastedt et al., 2008). A failure to do so is a common pit-fall in restoration projects and can result in a diminished understanding of an ecosystems patterns and processes (Rayburn and Major, 2008).

One of the primary objectives of this thesis is to understand and elucidate historical ecological drivers giving rise to the current vegetation patterns though a detailed land-use history analysis of the study area. Although the remainder of this chapter attempts to achieve this objective, it should be highlighted that the landscape is an integrated manifestation of all the ecological drivers discussed in this chapter;

however for the sake of clarity the remainder of the chapter is divided into separate sections for the different drivers.

2.3.2 Methods

Geospatial fire data for Table Mountain National Park was kindly provided by SANParks and was processed using Manifold System 8.0 Ultimate Edition (Manifold Software Ltd., 2012). The data was subsequently exported as an overlay onto a Google Earth (Google Inc., 2012) image of the phytosociological relevés (see Chapter 3) within the study area to establish the broad fire history of the area and, more specifically, the fire history of each specific relevé surveyed (see Figure 2.5). The geospatial fire data was also used to create a modified Gantt chart of fire occurrence through time for each relevé (see Table 2.2). It should be noted that SANParks did not have fire data for the current Game Camp site and no fire data for the site could be acquired from elsewhere.

Aerial photographs which included the study area were sourced from the South African National Geo-spatial Information Department. GIS analysis was done using Quantum GIS Version 1.5.0-Tethys. Photographs from 1944, 1953, 1968, 1977, 1989, 1996, 2000 and 2008 were geo-rectified using an ortho-rectified aerial photograph of the study area from 2010. Geo-rectification is the process of matching image data to a set of geographical co-ordinates so that each pixel of the image is assigned a geographical co-ordinate. For each photograph approximately 20 features were identified that were common to the 2010 ortho-rectified image. Only fixed features that remained inert through time were chosen. Forested areas within the study area were identified on the 2010 photograph and ground-truthed. Forested areas were delineated on all nine aerial photographs and the areas of each polygon were summed to give an estimate of total forested area for each year of interest. Finally, maps of each of the nine photographs were compiled to illustrate changes in forested areas within the study site through time (see Figure 2.6). Every effort was made to ensure accuracy, however the resolution on some of the photographs was poor, creating difficulties in identifying precise forestry boundaries.

2.3.3 Peopling of the Region

The pre-cursors of modern humans are thought to have arrived in the Cape Floristic Region during the Middle Pleistocene when *Homo erectus* dispersed beyond the tropics between 1,5 Myr and 200 000 years BP (Deacon, 1983b). Compton (2011) hypothesized that the southern coastal plain of South Africa, which is located within the Cape Floristic Region, may have served as a geographical point of origin for the evolution of humans as a result of periodic expansion and contraction (isolation) in response to glacial/interglacial changes in sea level and climate. Additionaly, paleoanthropological evidence from Pinnacle Point, situated within the Cape Floristic Region, suggests the site may a have been a point of origin for *Homo sapiens* (Marean, 2010). Regardless of their origins, fossilized footprints on the shores of Langebaan Lagoon on the West Coast suggest that anatomically modern humans were present in the Western Cape some 117 000 years BP. Since then the region has constantly been inhabited by humans (Deacon, 1992). Clans of San hunter-gatherers roamed the region until 2 000 years BP when Khoi pastoralist societies migrated down from the north with their herds of cattle and sheep (Deacon, 1983b; Sealy and Yates, 1994). The Khoi pastoralists gradually out-competed the San as their pastoralism provided them with a constant food source and fostered larger populations (Smith, 1986). Population dynamics had direct implications on environmental impacts. For the San the numbers were thought to be small with groups of 25-50 believed to be most common. On the other hand the pastoralists, due to the guarantee of food and resources, supported much larger populations (Boonzaier, 1996). The first written historical records which detailed population size come from 1652 when Van Riebeeck noted upon his arrival that the peninsula was occupied by between 4000 and 8000 Khoi organized into groups (Thom, 1952). In a later diary entry, Van Riebeeck made mention of 20 000 Khoi on the northern fringes of the peninsula (Thom, 1952). Unlike the severe environmental degradation caused by the activities of European colonialists, the indigenous inhabitants would have merely modified the environment to suit their needs (Hall, 1984). Despite this, Deacon (1992) notes that pre-historic populations may have contributed to the extinction of certain animal and plant species through over-exploitation.

Prior to 6 April 1652, the only contact the region would have had with Europeans was sporadic trading with mariners who sailed around the Cape from the 15th Century onwards (Raven-Hart, 1967). This changed when the Dutch East Indian Company (VOC) sent Johannes Van Riebeeck and three ships (two more arrived later in the year) to start a permanent settlement at what is now Cape Town (Raven-Hart, 1971). Van Riebeeck was mandated to form a way-station to provide fresh produce for VOC ships sailing between Europe and the East Indies (Guelke, 1988). In the years after his arrival, land surrounding the Company Gardens was given to free burghers, on condition that they bestowed a portion of their goods to the VOC (Raven-Hart, 1971), as the VOC were struggling to grow sufficient food (Anderson and O'Farrell, 2012). Due to the strategic nature of its geographical positioning, the Cape was an appealing piece of land to hold. After a period of conflict the Cape became a British territory in 1814 (Butlin, 2009). The change in governance saw further settlement of Europeans and an increased influx of slave labour from Asia and the rest of Africa in the subsequent century (Elphick, 1985; Anderson and O'Farrell, 2012).

2.3.4 Fire History of the Region and Study Area

Fire has been deliberately used by humans in the Western Cape for the past 160 000years (Brown et al., 2009). It has been speculated that the San hunter-gatherers would have used fire to flush out game species from Renosterveld. Additionally, the San would have used fire to stimulate grass growth to capture selected browsing species in oligotrophic environments or to promote the flowering of geophytes such as *Watsonia* species (Deacon, 1983a; Deacon, 1992). The Khoi pastoralists used fire to promote the growth of grasses more suitable for their cattle and sheep to graze (Deacon, 1976). Indeed, the maritime explorer Bartolomeu Dias reported veld burning and the presence of cattle at the Cape when he sailed around it in 1498 (Axelson, 1973). Overall, Deacon (1992) speculates that pre-historic anthropogenic environmental impacts include decreased fire intervals compared with natural regimes which resulted in decreased vegetation cover and accelerated erosion. The hypothesized regular seasonal migrations of people imply anthropogenic fires had certain regularity in terms of location and frequency from year to year (Hall, 1984).

The early European settlers would have witnessed the Khoi's use of fire and emulated it to promote better grazing conditions for their cattle (Raven-Hart, 1971). The colonialists were unaccustomed to just how flammable the indigenous vegetation really was and there were reports, within weeks of landing, of 'terrifying fires' the cause attributed to sparks from the men's pipes (Trotter, 1903). Fire frequency and intensity data from early years of the Cape Colony are scarce but by searching a variety of archived sources it is possible to create a table of recorded fires on the study site.

Table 2.1: Fire history of Devil's Peak between 1811 and 1950 from available written data sources (adapted from Rossouw, 1997).

Year	**Extent**	**Location**	**Source**
1811	No data	Upper slopes of Devil's Peak	Burchell (1822)
1891	No data	Devil's Peak to Platteklip Gorge	Mayoral Minutes (1892)
1935	No data	Devil's Peak to northern Table Mountain slopes	Shaughnessy (1980)
1936	121 ha	Devil's Peak	Shaughnessy (1980
1950	No data	Devil's Peak to northern Table Mountain slopes	Shaughnessy (1980

Geospatial fire data has been collected for Table Mountain National Park since 1962 and a fire frequency map (excluding the data for the current Game Camp which is not available) is presented below. Each polygon has a different fire frequency but Figure 2.5 is unable to display this so the fire history for each phytosociological relevé (see Chapter 3) was calculated and presented in Table 2.2 below. Of particular interest is the patchy nature of the Lightly Degraded Renosterveld relevés where relevés LD1 and LD2 burnt in 2009 and not 1988 or 1993 while relevés LD3, LD4 and LD6 burnt in each of these years. Relevé LD5 burnt in 1988 and 2009 but not in 1993 whereas relevé LD7 did not burn in 1988 but did burn in 1993 and 2009.

The accuracy of the data is questioned however as written resources and personal observations do not always agree with the recorded fire data. For instance, Moll et al. (1991) mention areas of Devil's Peak which burned three times between 1979 and 1991 but the data from SANParks used to generate Figure 2.5 and Table 2.2 do not register this. Additionally, Rossouw (1997) makes note that 'after a fire in 1974 a start was made at clearing the exotic vegetation and replacing it with indigenous plants'. There is also mention of a fire in March 1982 and in 1991 an intense fire reportedly swept through Devil's Peak (Rossouw, 1997) but all of the aforementioned fires are missing in the official data. Finally, in Shaughnessy's (1980) report on plantation history on Table Mountain she notes that after a fire on Devil's Peak in 1986 *Chrysanthemoides spp.* were planted for slope stabilization while after the 1991 fire, Namaqualand daisies (*Asteraceae spp.*) and Italian Ryegrass (*Lolium multiflorum*) were utilized to cover the bare, scorched slopes. Finally, and perhaps most significantly for analysis of later chapters, the SANParks data record a burn in the Old Renosterveld site in 2009 but judging by the current state of the vegetation and personal observation from 2009 the site remained fire free.

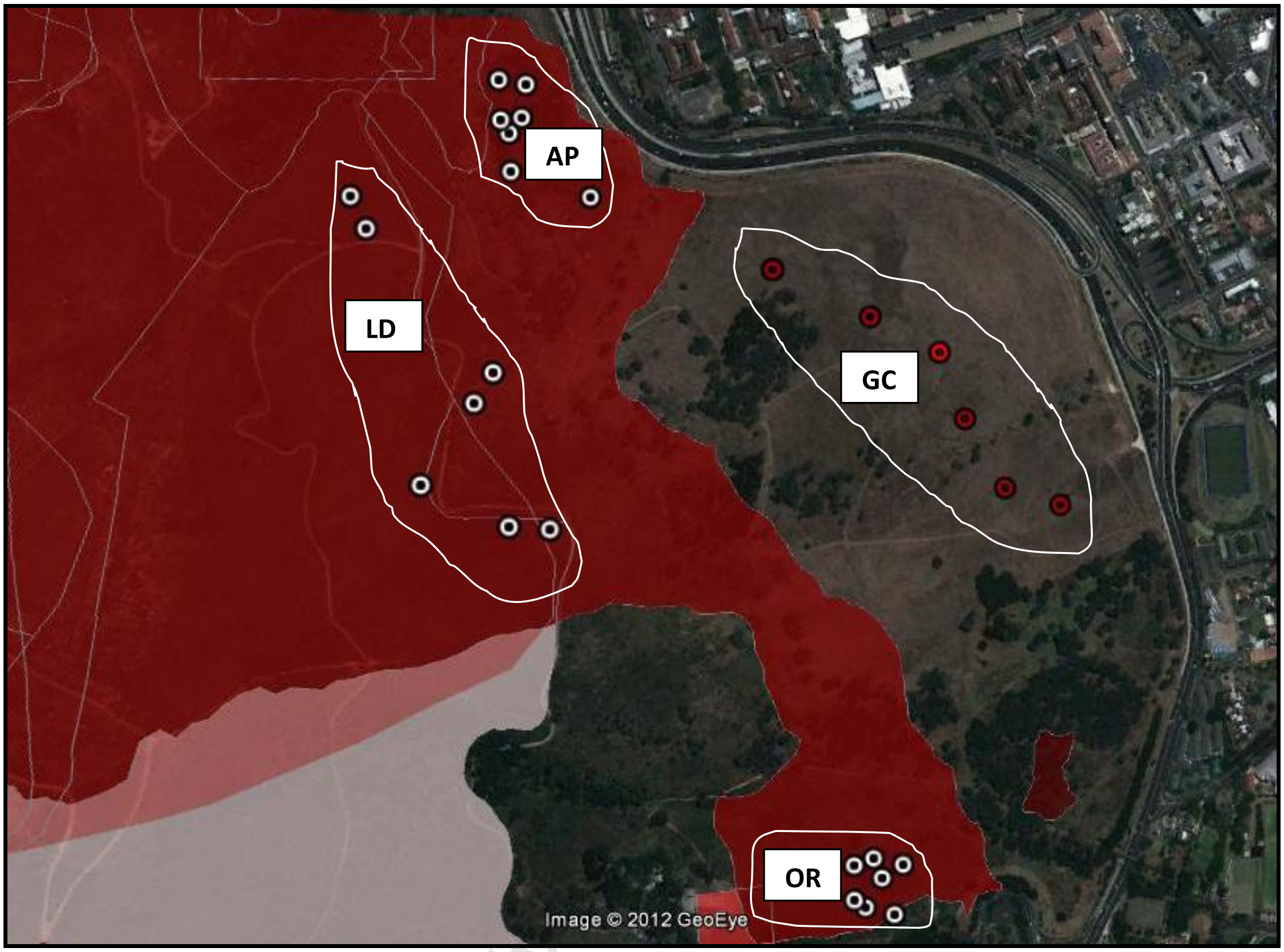

Figure 2.5: Google Earth image of the 28 relevés within the study site with vegetation age overlay. Dark red represents veld that last burned in 2009. **OR**=Old Renosterveld; **LD**=Lightly Degraded Renosterveld; **AP**=Alien Pine stand; **GC**=Game Camp enclosure.

Table 2.2: Relevé burn years from SANParks fire data (1962-Present). Shaded blocks indicate the relevé was burnt. **OR**=Old Renosterveld; **LD**=Lightly Degraded Renosterveld; **AP**=Alien Pine stand; **GC**=Game Camp enclosure.*Note: No fire data exists for GC, the current Game Camp.

Relevé	1988	1993	2009
OR1			▨
OR2			▨
OR3			▨
OR4			▨
OR5			▨
OR6			▨
OR7			▨
LD1			▨
LD2			▨
LD3	▨	▨	▨
LD4	▨	▨	▨
LD5	▨		▨
LD6	▨	▨	▨
LD7		▨	▨
AP1			▨
AP2			▨
AP3			▨
AP4			▨
AP5			▨
AP6			▨
AP7			▨

To summarize, understanding the fire history and the natural fire regime of the Peninsula Shale Renosterveld of Devil's Peak is fraught with difficulties, not least of which is the general dearth of data on fire in Renosterveld. Decoupling the impacts of humans is unwise as human-induced fires have been an integral part of vegetation dynamics for millennia. The recorded fire history (post-1962) is of interest but the likelihood of erroneous or absent data means that trusting the data implicitly would be ill-advised. It is preferable to combine the recorded fire data with logical reasoning. For instance, as is the case in the Old Renosterveld site, it is clear from the age of the vegetation that fire has been absent for an extended period of time. There is also a chance that other sections of the study area burnt too frequently, at least over a period of time, for re-seeders to set seed. Moll et al. (1991) noted that a section of Devil's Peak burned three times between 1979 and 1991; however, it is impossible to locate this area to evaluate the effect these frequent fires had on the vegetation. The patchy burn history in the Lightly Degraded Renosterveld is a further point of interest and it should be taken into account when the current vegetation of the relevés is addressed in the following chapter. The history of fire suppression, due to the proximity to human settlement, has not completely been overhauled by current management although a general trend of increased fire frequency has been observed throughout Table Mountain National Park. This is due predominantly to an increase in accidental burns, but also a shift in policy. The current policy reflects the understanding of the need for controlled burning and allowing wildfires to burn where they will not pose an ecological threat; however it acknowledges that the priority is safety for people and property (Forsyth and van Wilgen, 2008; van Wilgen et al., 2012).

2.3.5 Grazing History of the Region and Study Area

We can only estimate indigenous animal densities present in Renosterveld in pre-colonial times although estimations of current carrying capacities have been conducted (see Boshoff et al., 2002). The vegetation probably supported large herds of Zebra (*Equus quagga*), Eland (*Tragelaphus oryx*), Red Hartebeest (*Alcephalus buselaphus*) and Bontebok (*Damaliscus pygargus pygargus*). In addition, populations of African Elephant (*Loxodonta africana*), Black Rhinoceros (*Diceros bicornis*) and Hippopotamus (*Hippopotamus amphibius*) are known to have occurred in the region although whether the latter were found in the study area is doubtful. Lion (*Panthera leo*), Leopard (*Panthera pardus*), Wild Dog (*Lycaon pictus*), Cheetah (*Acinonyx jubatus*), Spotted Hyena (*Crocuta crocuta*) and Brown Hyena (*Hyena brunnea*) were all found in association where suitable prey was present (Skead, 1980; Kerley et al., 2003).

After the Khoi migrated down from the north, the Renosterveld would have been heavily utilized as grazing areas for their cattle (Deacon, 1992). Determining the number of cattle and sheep present at the time of Van Riebeeck's arrival in 1652 is possible as diary entries from December of that year note that, in their eagerness to trade, the Khoi gathered around the fort in Table Bay with an estimated 12 000 livestock (Thom, 1952). An entry from January 1653, list the number of sheep and cattle present on the peninsula at 20 000, however it is unlikely that these densities were permanent but rather transhumance was practised (Radloff, 2008). Indeed, archaeological and historic records from prior and post-European contact respectively suggest the Khoi promoted a non-selective grazing strategy made possible only by high mobility (Raven-Hart, 1971; Deacon, 1983b; Smith 1984). The early free burghers similarly allowed their cattle to graze the open veld but did not practice transhumance, limiting their grazing to land on, or in close proximity to, their farms resulting in an increase in year-round grazing intensity (Guelke, 1988).

With regards to grazing history of the study area, other than the atypical Game Camp area cordoned off by Rhodes in the early 1900s and dealt with in more detail further on, the lower slopes would have been grazed first by the Khoi's cattle and subsequently by the early settlers' livestock. It is impossible to accurately know grazing intensity or its effects on the indigenous vegetation, however for the past one and a quarter centuries livestock and the majority of indigenous grazers have been absent from the area. Grazing, as an ecological driver, has therefore been almost entirely absent from the ecosystem for an extended period of time. It is hard to know the impact this had on the study site as large tracts of the area were subject to afforestation and natural system drivers were substantially altered but according to Milton's (2007) model on Renosterveld ecosystem drivers (see Chapter 1), a lack of grazing would have encouraged an increase in grass cover. However, this does not take in the effect of fire frequency and season.

The management history of the Game Camp appears to have been lost at some point during the various management transitions. It was cordoned off from the surrounding area by Rhodes in the early 1900s and used as paddocks for an assortment of animals including grazers. Up until the latter stages of the twentieth century the paddocks were home to a herd of Wildebeest (*Connochaetes gnu*) and an assortment of other ungulates, however the majority of the animals were relocated from the area and today the enclosure is home to five Zebra (*Equus quagga*) which are remnants of the Quagga breeding project (Harlet et al., 2009). The need for fodder for the animals resulted in the probable ploughing of the land and the subsequent seeding with grasses. Another possible option is that area had been used as pasture prior to Rhodes' purchase of the land and the grass was a remnant of this. Either way the likelihood is that the area was ploughed and grasses sown just over century ago and could be considered an old field which in restoration vernacular refers to a cultivated land no longer in use (Hobbs and Cramer, 2007).

2.3.6 Land Cover Change and Species Introductions

Cultivation

One of Van Riebeeck's mandates upon arrival in 1652 was to provide fresh produce for passing ships, thus vegetable gardens were soon established. As the settlement expanded the need for provisions increased and land surrounding the company gardens was granted to free burghers provided they donated a portion of their produce to the Dutch East India Company (VOC) (Raven-Hart, 1971). The first farmers almost certainly cleared the veld to establish grazing fields and crops (Joubert, 1991); however it is particularly hard to establish the precise locations of the vineyards, cereal fields and pasture. It is likely that only the lower slopes of Devil's Peak would have been ploughed and farmed due to their accessibility with the upper slopes left untouched or afforested. Ploughing can have a dramatic effect on natural systems (Hammouda et al., 2003) and in Renosterveld ploughing has reportedly reduced geophyte numbers (Walton, 2006; Krug and Krug, 2007; Horn et al., 2011).

Major farms that were present in the immediate proximity to the study site include Welgelegen, Zorgvliet and Groote Schuur. Welgelegen was formed when Stevenz Jan Botma was granted land by Van Riebeeck in 1657 alongside the Liesbeek River. In 1676, Zorgvliet was formed when Botma's son, Cornelis, was granted land behind Devil's Peak and by 1692 the farm had over 15 000 vines. Groote Schuur was originally a piece of land owned by the VOC and housed a granary (the 'schuur' in Groote Schuur), which suggests that wheat was grown in the area, but in 1791 the VOC sold the land to Hendrick Heroldt. All three farms underwent numerous sub-divisions and changes in ownership through inheritance and transaction until 1891 when they were purchased by Cecil John Rhodes to form his Groote Schuur Estate (Chittenden, Nicks, de Villiers, 2000). By this time farming on the estate had ceased and all vines had been destroyed by the phylloxera epidemic that hit the Cape Colony in the 1880s (Royal Botanic Gardens, KEW, 1889). Nevertheless, by then over a century of cultivation had transformed the region (or atleast the lower slopes) through activities such as ploughing and the introduction of pasture grasses.

Although grass is a natural element within Renosterveld (Rebelo et al., 2006) the current study area has been subject to alien grass invasion particularly as a result of the creation of grazing paddocks. Additionally, the proximity to private gardens resulted in the colonization of common lawn grasses resulting in the presence of Kikuyu (*Pennisetum clandestinum*), Rye grass species (*Lolium spp.*), *Briza* spp., Oats (*Avena spp.*), Dallis grasses (*Paspalum spp.*) and Natal Tussock (*Nasella trichotoma*). The eradication of alien grass swards is challenging as in heavily eroded areas, such as the lower northern slopes of Devil's Peak, they are among the few plants able to colonize and their removal may be detrimental to soil integrity (Moll et al., 1991).

A further result of the history of cultivation in the study area and its proximity to a suburban environment is the issue of alien horticultural escapees, a problem recognized throughout Mediterranean vegetation worldwide (Marco et al., 2010). Their introduction to the slopes of Table Mountain and Devil's Peak probably coincided with the construction of the first homesteads on the lower slopes (Alston and Richardson, 2006) and their presence has been recorded in the study area (Gasson et al., 1992; Coetzee, 2001). However, their densities are unknown and their impacts have not been investigated.

History of Afforestation in the Region and Study Area

Trees are generally absent from Renosterveld and Fynbos vegetation therefore the only wood available to the early colonialists would have been in the Afrotemperate forests restricted to fire-free refuges and the larger Protea species which were abundant on the front slopes of Table Mountain (Moll and Campbell, 1976). The urgent need for wood meant that within half a century of colonization the degeneration of indigenous forests was well advanced (Luckoff, 1951). The provision of timber was a crucial activity for the fledgling colony and this necessity resulted in the initiation of afforestation with seeds imported from Europe and Australia (Shaughnessy, 1980), a prime example of how socio-economic factors drive environmental change. Aside from timber provision, trees were believed to provide a more aesthetic backdrop; used to stabilize dune fields and were mistakenly believed to increase rainfall (Grut, 1977; Richardson, 1998). The first *Pinus* individuals were introduced to the VOC gardens *circa* 1690 but they failed to produce viable seed (Shaughnessy, 1980). In the late 18th Century and early to mid 19th Century a variety of *Pinus* species were introduced including *P. pinaster, P. radiata, P. pinea, P.halepensis* and *P. canariensis* (Moll et al. 1991). In addition, *Acacia melanoxylon*, *A. saligna*, *A, mearnsii* were introduced *circa* 1830 (Moll and Campbell, 1976). *Pinus pinaster* and *P.pinea* were particularly popular and well suited to the landscape and by 1810 both species were prominent features of the Cape Colony (Grut, 1977). Due to the success of the aforementioned species the state and city established plantations of *Pinus pinaster* on the slopes of Table Mountain including Devil's Peak (Moll et al., 1991). An increase in afforestation occurred in the late 19th and early 20th Century; however due to limited data it is impossible to know the exact geographical position and extent of these early plantations (Shaughnessy, 1980). The importance of private afforestation should not be underestimated. During the period 1882-1893 some 34 million *P. pinaster* seeds were distributed by the Forestry Department to private entities while millions of *Acacia* seedlings were traded (Shaughnessy, 1980).

Historical forestry data is generally not at a high enough resolution to delineate the study area from Devil's Peak as a whole, thus Devil's Peak data is presented and only with data from the past seventy years is the study area explicitly referred to. While data available on the initial afforestation of Devil's

Peak in the 1700s is minimal, from the second generation of planting in the 19th century more accurate records were kept. The government's policy during the late 19th century was for private landowners to increase the density of their forests while areas as yet unafforested would be controlled by the Forestry Department (Shaughnessy, 1980). After a serious fire had burned a large portion of indigenous vegetation on Devil's Peak in 1891, the forest officer at the time proposed that forest was less flammable and an area of 105 ha was obtained by the government for the creation of a plantation. *Pinus pinaster, P. pinea, Acacia* species and *Quercus suber* seeds were sown on the slopes of Devil's Peak (Shaughnessy, 1980)**.** The plantation was also seen as an opportunity to cover the 'bare and stony slopes above Woodstock and Salt River' (Shaughnessy, 1980). *Acacia* species were often used as nurse plants for *Pinus* plantations, however in the Devil's Peak plantation it was found that *Pinus pinaster* grew sufficiently well that nurse plants were redundant thus from 1896 to 1900 the afforestation programme focused solely on this species (Shaughnessy, 1980). By 1899, the majority of the 105 ha had been afforested and in the following five years over 400 kg of *P. pinaster* seed were sown on the upper cliffs and surrounds after the area had been cleared and burnt (Shaughnessy, 1980). Following the forestry department's acquisition of 215 ha from the city's municipality, including the north-western slopes of Devil's Peak, further afforestation took place with an emphasis on *Pinus canariensis* and *Eucalyptus* species. In 1905, *P. pinaster* was sowed on 35 ha of land where the aforementioned species had failed (Shaughnessy, 1980). By the end of 1905 Devil's Peak had a reported 113 ha of its slope covered by plantation. Afforestation continued in the following decade and by 1913 plantations extended from the top of the northern slope and to the slopes above Woodstock, covering an estimated 326 ha (Shaughnessy, 1980).

At some point between 1918 and 1931 parts of the plantation on the upper slopes and cliffs of Devil's Peak plantation were abandoned for reasons unknown and in 1936 a wildfire destroyed 121 ha of the plantation (Shaughnessy, 1980). In 1962, the Devil's Peak extension plantation was handed over to the municipality of Cape Town for management (Shaughnessy, 1980). The continuation of the commercial plantation was deemed untenable and this, coupled with an increase in support for conservation of indigenous vegetation, resulted in the city beginning to clear-fell forested land especially on the north-western slopes. Most of the trees in the area had been felled by 1977 and from 1975 to 1980 most of the trees on the eastern slopes of Devil's Peak were felled (Shaughnessy, 1980). Despite the length of time that these slopes have been tree free, Terblanche (2011) showed that areas previously under alien tree canopy were less diverse, had less cover and an increased pH in comparison to control plots.

An analysis of forestry cover change in the study area from 1944 to 2010 is displayed in Figure 2.6. There is hardly any change in total forested area between 1944 (110 ha) and 1953 (111 ha) but by 1968 the forested area had fragmented significantly and been reduced to 75 ha. In 1977 the forested area remained relatively unchanged (74 ha) which compliments Shaughnessy's (1980) assertion that the Devil's Peak plantation had been greatly reduced by 1977. In 1989 there was a significant reduction in tree cover in the north-western portion of the study area reducing the total forested area to 52 ha. Moll et al. (1991) analyzed changes in alien plant distribution on Table Mountain and Devil's Peak for the period 1976 and 1991. They reported stands of *Pinus pinaster* in and around the current Game Camp and in 1991 they reported that small pockets of *Pinus radiata* were found adjacent to the northern Game Camp border, while *Pinus pinea* were present in the vicinity of the university grounds and Rhodes Memorial. *Acacia mearnsii* was found to have spread from the lower northern slopes of Devil's Peak across Mowbray Ridge to the area above Rhodes Memorial and the university campus. *Acacia saligna* and *A. cyclops* were present in a narrow strip above Rhodes memorial, however *A. longifolia* were found in greater numbers above Rhodes memorial. Finally, a stand of *Eucalyptus* species was present directly above the university campus and on the northern boundary of Groote Schuur Estate (Moll et al., 1991). The finer details of the Moll et al. (1991) report are useful as the work conducted here cannot differentiate between different tree species and the type of alien tree present at a site impacts on the environmental effects of the plantation. There is a uniform trend of decreasing forested area and fragmentation from 1996 (38 ha) through 2000 (34 ha) and 2008 (27 ha) to 2010 (23 ha), particularly in the stand adjacent to the Game Camp. The forested area above the university campus has not changed significantly from 1996 to 2010. The reduction in forested area is a combined result of continued alien removal efforts (although as the species currently dominant is *Pinus pinea*, considered a non-invasive pine, its removal is not a high priority) and natural tree death as many of the trees are old. Additionally, certain regulations arising from Rhodes's will (Groote Schuur Devolution Act 9/19100) and the desire to maintain a sylvan backdrop and a parkland environment by a few stakeholders (Laros and Associates, 2012) have preserved substantial numbers of *Pinus* individuals in the vicinity of Rhodes Memorial and the University of Cape Town.

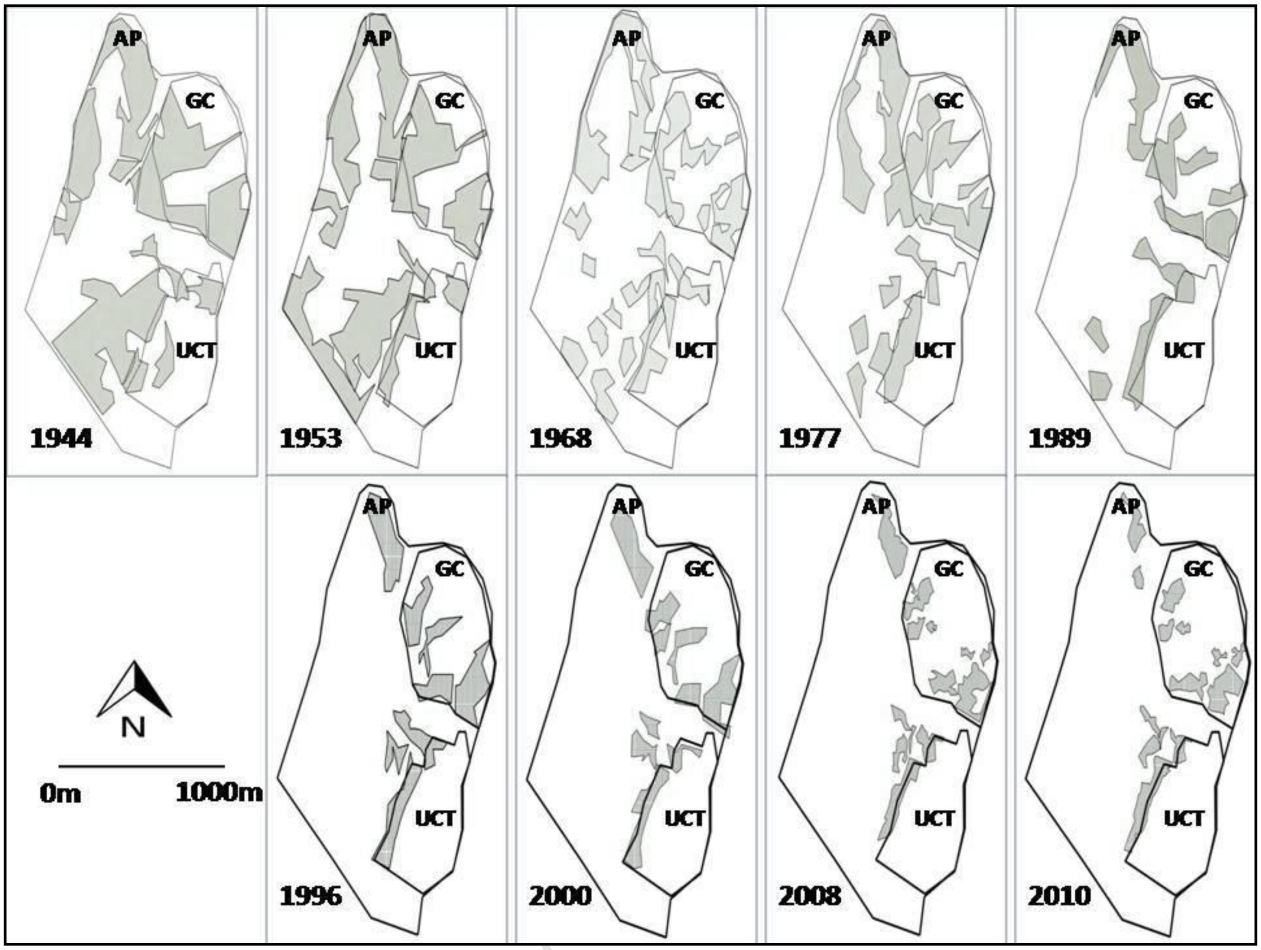

Figure 2.6: Image showing forest cover of the study area through time (1944-2010). The area labeled UCT is the upper campus of the University of Cape Town. GC is the current Game Camp and AP is the patch of forest above the M3 adjacent to the Game Camp in which the Alien Pine stand is located.

Faunal Introductions

In contrast to the severe impacts caused by introduced plants, animal introductions in the region have been relatively benign (Rebelo et al., 2011). The reasons for this are partly due to historical accident and partly to the characteristics of the indigenous vegetation which has limited the establishment of alien animals (Bigalke and Pepler, 1991). The Grey Squirrel (*Sciurus carolinensis*) is limited to forested areas where it has access to fruit/nut bearing trees. It is common among stands of pine trees, however it has failed to establish in indigenous vegetation due to the absence of a squirrel niche (Bigalke and Pepler, 1991) although it facilitates the successful burying of seeds of certain alien tree species. A pair of Himalayan Tahrs (*Hemitragus jemlahicus*) escaped from an enclosed section of Groote Schuur Estate in 1935 and established a breeding population on Table Mountain (Bigalke, 1977) leading to significant environmental impacts due to their sharp hooves and feeding habits (Rebelo et al., 2011). A culling programme was initiated in 2000 despite protests from certain quarters (Yeld, 2001). Despite the culling, Tahrs remain on the mountain but at significantly lower densities (Pers. Obs.), although numbers need to be monitored carefully so the damage to the environment is kept to a minimum. Fallow Deer (*Dama dama*) and Sambar Deer (*Rusa unicolor*) have been present on Table Mountain ever since individuals escaped from paddocks in Groote Schuur Estate in the early 1900s (Yeld, 2006), their densities and impacts are less extreme than those of the Tahr; however a programme to capture and trans-locate the populations in the early 2000s (Gosling, 2001) has been largely successful although some individuals still remained in 2011 (Pers. Obs.). Attempts have been made to re-introduce indigenous mammals and currently Klipspringer (*Oreotragus oreotragus*), Grey Rhebuck (*Pelea capreolus*), Cape Porcupine (*Hystrix africaeaustralis*) and Caracal (*Caracal caracal*) are present in low densities within Table Mountain National Park (Rebelo et al., 2011; Pers. Obs.), while five Zebra (*Equus quagga*) are currently enclosed within the Game Camp site. There have also been proposals to expand the existing game camp and add game species and numbers (Coetzee, 2001); however no final decisions have been made at the time of writing.

2.3.7 The Management History of the Study Area and the Creation of the Parkland

The history of forestry of Groote Schuur Estate is out of sync with the rest of Devil's Peak's slopes. While the initial afforestation during the 1700s and 1800s would have most likely covered the upper portions of the estate, once Cecil John Rhodes purchased the estate in 1893 he initiated his own management plans. Due to his high profile as then Governor of the Cape, much has been written about Rhodes thus we are able to glean some insight into his attitude towards his residence and its surrounds. Rhodes is quoted as saying "*I have bought this place but the jungle possesses it*" upon purchasing Groote Schuur (Chittenden, Nicks, de Villiers, 2000), suggesting a certain degree of wildness and an estate covered in dense vegetation.

A letter from Sir Herbert Baker to General Jan Smuts describes how Rhodes '*set to work to make the land a park and not a commercial forest*' (Gasson et al., 1992). In Williams' (1921) biography of Rhodes' life, he reports on Rhodes actions surrounding Groote Schuur Estate:

> *He carefully preserved all their own beauties and associations and added new ones in keeping with the mountain. He treasured a great avenue of trees as an approach from*

> *the road and the beautiful clumps of stone pines…He made a huge enclosure in his park, in which buck, zebra, ostriches and other wild animals were allowed to roam…He cut down trees here, planted new and rare ones there, always with a view to big effects and to enhance the majesty of its aspect. He made roads and paths to give access to the finest views of the mountain…His grounds were thus made beautiful, not for a morose and solitary pleasure, but that all his fellow citizens might enjoy it.*

Rhodes had a particular affection for pine trees and, on a yearly basis, walked about his estate planting or reseeding trees and it was his intention to undertake the creation of a parkland after the European style with open grassland interspersed with clumps of pine trees (Chittenden, Nicks, de Villiers, 2000). Rhodes' intention was that his estate should be a 'pleasance' accessible to the public, in which animals and humans were allowed to roam almost at will. Within this parkland, paddocks were created for Springbok (*Antidorcas marsupialis*), Kudu (*Tragelaphus spp.*), Gemsbok (*Oryx gazella*) and other unspecified antelope along with Zebra (*Equus spp.*), Wildebeest (*Connochaetes gnu*) and Tortoises (family Testudinidae). Kangaroos, Wallabies (both *Macropus spp.*), and Emus (*Dromaius novaehollandiae*) were imported in from Australia while Llamas (*Lama glama*) were brought in from Peru. Aviaries were created for an assortment of exotic birds including Golden Pheasants (*Chrysolophus pictus*), Quail (family Phasianidae), Duck (family Anatidae), Nightingales (*Luscinia megarhynchos*), Larks (family Alaudidae), Thrushes (family Turdidae) and Chaffinches (*Fringilla coelebs*) (Coetzee, 2001).

After Rhodes' death in 1902 the impetus behind the maintenance of the paddocks gradually waned until what remained were only the enclosed Game Camp and the surrounding matrix of parkland and degraded indigenous vegetation. In Rhodes' Will he made mention of what was to become of Groote Schuur Estate: the Department of Public Works was placed in charge of management of the estate but was mandated to maintain the parkland nature of the estate, thus the removal of *Pinus pinea* from the environs was prevented by law (Groote Schuur Devolution Act 9/19100). In accordance with the Will, the University of Cape Town campus was built in 1911 and in 1912 Rhodes Memorial was constructed on the middle slopes. In 1985, Rhodes' Will was modified and the upper sections of the Estate were transformed into a 'park for the people' and in 1999, the estate was integrated into Table Mountain National Park (Environmental Conservation Act 73/89). Despite the acknowledged need for the eradication of alien invasive species in recent decades, the desire for the preservation of a 'cultural landscape' (which includes the presence of *P. pinea*) around Rhodes Memorial and the Game Camp has resulted in the persistence of pine trees in the vicinity. In addition, the University of Cape Town values the vista that the presence of pines provides to its campus and until recently has been against the removal of *P. pinea* and the sylvan backdrop it affords. Recent plans have been initiated to turn the forested areas of campus into a heritage park embracing indigenous vegetation alongside the maintenance of a limited number of pines (Laros and Associates, 2012). While *P. pinea* are non-invasive and an argument can be made for a small population to be maintained near Rhodes Memorial, they alter the ecosystem directly under their canopy and there are still *P. pinaster* individuals present on the upper boundaries of the university campus and adjacent areas. These aggressive invaders need to be eliminated to prevent them acting as propagules and further degrading the Peninsula Shale Renosterveld of the study area and expanding the threat to the conservation of this highly threatened vegetation type.

Although Rhodes' intention to conserve a portion of the mountain for the public's enjoyment was noble, it was woefully inappropriate in terms of contemporary ecological and conservation understanding. In stark contrast, the management policies which were introduced post-1960 as the importance of conserving indigenous vegetation began to enter the agendas of scientists have seen a massive shift in how the natural environment is managed. The culmination of this change saw the national government, acting on the advice of scientists, implement and fund the Working for Water program in an effort to reduce alien vegetation throughout the Cape Floristic Region (including the study area and surrounds) (van Wilgen et al., 2004). In essence, this shift from Rhodes' misguided planting of pines and introduction of a menagerie to today's management policy shows that the nature of the landscape is determined essentially by the expression of political power and will, which, in turn, needs to be guided by sound scientific knowledge.

2.3.7 Conclusion

Due to the long history of human occupation, understanding the land-use history of the study area and its surrounds is essential to explain the current patterns of vegetation and ecosystem drivers. As predicted by the literature cited in the introduction, this historical analysis has shown a complex matrix of interactions, all of which operate variably both spatially and temporally which have resulted in the creation of a novel ecosystem (Hobbs et al., 2006). Surrounded by an ever-expanding urban landscape, the history of fire, land usage, species invasion, and in turn the management of these factors, are all critical elements in shaping the system that is in evidence today (Ramalho and Hobbs, 2012; van Wilgen, 2012). Furthermore, this analysis has highlighted how the management itself is a function of the socio-economic and political environment of the time (Luck et al., 2009). Where land-use history has resulted in degradation to the natural environment, the improved understanding afforded by this research, alongside a current climate where the importance of conservation is recognized, may be able to return the land in question to a more conservation-worthy state (Seastedt et al., 2008).

To conclude, the objective of this chapter was to describe the study area and understand the historical ecological drivers of the study area in an attempt to explain the current vegetation patterns present. As is often the case with historical data, managing to establish a fine-scale resolution history of forestry and fire is not always possible. Added to this is the issue of changing management regimes at the estate and the subsequent loss of information on past management policies. Despite this, general trends have been established, while certain high-resolution data were provided. In addition, the results of this historical analysis reinforce the concept, highlighted in the literature, of the importance of history in ecology and how this recognition aids the understanding of current patterns and processes. Of course, this chapter has used the past to understand how the study area has come to be in its current state, what follows in the proceeding chapter is a thorough analysis of this contemporary state through an in-depth phytosociological survey.

Chapter 3

Phytosociological Survey

3.1 Introduction

According to the Society for Ecological Restoration one of the fundamental constituents of restoration planning is the ecological description of the site designated for restoration (SER, 2004). A key component of this project is the evaluation of the restoration potential of the Peninsula Shale Renosterveld of Devil's Peak. It is therefore logical that a thorough ecological description of the current environment is provided. This chapter addresses the current state of the study site through an initial overview of the importance of acquiring knowledge of the ecosystem's contemporary state, the uncertainty surrounding baseline Renosterveld data, a systematic description of the methods employed, a presentation and analysis of the results of the phytosociological survey, and finally a discussion on how ecosystem drivers have resulted in the current environmental conditions and what bearing they will have on future restoration endeavours.

3.1.1 Importance of Baseline Data

To maximize the success and minimize the cost of restoration efforts, restoration projects require effective planning (Garbisch, 1989; Wyant et al., 1995; Hobbs and Norton, 1996; Ntshotsho et al., 2011). Baseline data analysis, here defined as the thorough understanding of an ecosystem's current characteristics, provides perspective and aids in the determination of physical and ecological design specifications for restoration initiatives. Furthermore, the availability of baseline data is a necessity if one is to evaluate changes as a result of restoration efforts (Wissmar and Breschta, 1998; Ntshotsho et al., 2011). Ideally, baseline data should provide extensive lists of fauna and flora; a description of seral or vegetation development; and include a description of habitat requirements for keystone species (Clewell and Rieger, 2008). However, provision of all of the aforementioned is not always possible. In the worst case scenarios, restoration initiatives have been unable to provide the minimum ecological drivers for the restored site due to an inadequate understanding of the ecological system being managed (Pastorok et al., 1997, Clewell and Aronson, 2007). Hobbs and Norton (1996) reiterate this need for the inclusion of the identification of the current environment and processes, and the processes which led to degradation or reduction, as an essential step in the restoration planning of an ecosystem. Without an in-depth understanding of a contemporary system, degrading influences may continue to disrupt restoration efforts and result in a failed project (Hobbs and Norton, 1996).

Plant functional types have been widely utilised to describe patterns of plant responses to the environment (Stuart et al., 1996, Powers and Tiffin, 2010) and have been used frequently and with success in bridging the gap between plant physiology and community and ecosystem processes (Diaz and Cabido, 1997; Duckworth et al., 2000). Changes in plant functional type ratio (i.e. grasses vs. shrubs) have been used successfully in Fynbos to evaluate shifts in community structure and dynamics (Cowling et al., 1994) and therefore may provide a valuable tool in analysing and understanding the study system and identifying directional change within it.

Ideally, the current state of a site is measured against a reference state, or 'pristine' example of the vegetation type in question, to establish what is required to return the degraded site to its natural trajectory. In reality, these reference states are often derived ecosystems themselves or may be one of several possible stable states (Schroder et al., 2005). Ultimately, as is the case with Renosterveld, much uncertainty exists in defining system drivers and 'natural' ecosystem processes in degraded landscapes, thus the establishment of baseline data is of paramount importance prior to the initiation of a successful restoration project.

3.1.2 The Uncertainty Surrounding Renosterveld Ecology

The current understanding of ecological processes in pristine Renosterveld, although improved in the past decade, is still very limited (Rebelo, 1995; Krug, 2004; Rebelo et al., 2006). One of the reasons behind this is the apparent inherent heterogeneity found in Renosterveld and the subsequent difficulty in describing the vegetation type ecologically (Boucher 1980, Boucher and Moll 1981, Newton and Knight 2004). A second reason is the long history of human impacts and transformation as a result of its relatively fertile nature (Rebelo, 1995; Krug and Krug, 2007). The effects of human populations on the environment prior to the arrival of colonizing Europeans in 1652 have been documented in the previous chapter. The level of impact that the herds of Khoi cattle and their seasonal migrations had on the natural vegetation is unknown (Sealy and Yates, 1994; Balasse et al., 2002), although grazing intensity would have been increased and deliberate fires would have been ignited to promote favourable grazing conditions (Smith, 1992).

The impacts that the European settlers had on ecosystem processes are better documented. Firstly, the large herds of herbivores that Renosterveld supported were hunted vigorously and were all but extinct in the region by the late 19th century (Skead, 1980). In addition, large tracts of land were converted to agriculture and fire suppression was practiced to protect these areas (Cowling et al., 1996), whereas in other areas fire was used to promote favourable grazing conditions for corralled livestock (Smith, 1992).

Herbivory and fire are speculated to be the main ecological drivers in natural Renosterveld ecosystems (Radloff, 2008). Herbivores act as dispersal and disturbance vectors, reducing grass cover and supporting the establishment of shrubs (Midoko-Iponga, 2004). Increased fire frequency, on the other hand, enhances grass and geophytes abundance while reducing shrub cover (Cowling et al., 1986; Proches et al., 2006). Because of the centuries of habitat alteration we cannot know for certain what the ecology of pristine Renosterveld systems is. The natural composition of shrubs and grasses quite possibly varied throughout the region depending on various factors and alternate stable states may have been present. Krug and Krug (2007) surmise that the fire suppression and subsequent overgrazing post-European settlement lead to the breakdown of natural processes which resulted in the dominance of the shrub *Elytropappus rhinocerotis* present in many locales today.

In conclusion, restoration endpoints for Renosterveld are hard to identify because of the uncertainty surrounding the ecology of Renosterveld prior to European settlement (Rebelo, 1995; Newton and Knight, 2004) and what drivers are required to return an ecosystem's trajectory to this unknown natural state. Peninsula Shale Renosterveld, due to its proximity to the focal point of the old Cape Colony, was one of the first ecosystems altered. This has resulted in an absence of a suitable reference state. It follows then that the establishment of a thorough description of current ecological conditions of the study area is essential to better inform us on its restoration potential and to work towards restoring those areas currently classified as Peninsula Shale Renosterveld but which are, in fact, severely degraded.

3.2 Methods

3.2.1 Field Work

To reiterate what was noted in section 1.5.2, due to the extensive study area and the specific nature of the project aims (i.e. to understand shifts between typical vegetations states to elucidate ecosystem drivers and inform restoration) the phytosociological survey was not completely randomized. Rather, an adapted approach based on an *a priori* understanding of the study area was utilized. A broad-brushed analysis of dominant vegetation types within Groote Schuur Estate was conducted and Google Earth (Google Inc., 2012) images, with delineated vegetation units, were generated and used to select regions in the Estate where analysis would most likely assist in realizing the project objectives of specifically understanding vegetation states and the shift between states. Four sites within the estate were chosen for analysis, namely, an Old Renosterveld site which had not burnt for more than 15 years; a Lightly Degraded Renosterveld site of younger and slightly invaded vegetation; an Alien Pine stand; and the current Game Camp.

At each of the four sites, seven 10x10 m relevés were semi-randomly selected and demarcated during the spring (September and October) of 2011. Relevé positions were informed by patch size, distance to features such as roads or abandoned buildings and obviously containing features such as water courses. GPS co-ordinates were recorded at each corner of the relevé. Plant species were identified and percentage cover estimated. In the Alien Pine stand, Pine tree cover was measured as percentage of trunk ground cover and sapling cover rather than canopy cover as many individuals did not have foliage. An attempt was made to identify species *in situ* with the help of field guides and personal knowledge; however where uncertainty existed, samples were collected, pressed, labelled and identified *ex situ* with the aid of records from the Bolus Herbarium and expert opinion. Experts consulted included Dr. Terry Trinder-Smith and Dr. Tony Verboom (both from the Botany Department at the University of Cape Town). In addition ISpot, a website allowing individuals to upload pictures of species for identification by fellow users, was utilized.

Once a complete species list was compiled, various literature sources were consulted in an attempt to assign each species to a height class, a functional type (adapted from Cowling et al., 1994) and biological status according to the Red List of South African Plants (SANBI, 2012). Large Shrubs/Trees were classified as species which grow higher than 2 m; Mid-high Shrubs grow to height between 1 and 2 m, while Low Shrubs are shrubs smaller than 1 m in height. Forbs and Graminoids (including grasses, sedges and restioids) were both divided according to life history (annual or perennial), while species which grew from underground bulbs or corms were designated as Geophytes.

Abiotic factors at each relevé were also measured. Total bare ground was estimated visually and recorded as a percentage of the relevé. Soil depth was measured using a modified soil depth probe at three points within each relevé and averaged. The soil depth probe was a 1.5 m steel rod which was hammered into the soil using a mallet and the length of the submerged rod was subsequently measured. Elevation was recorded using the value, in meters above sea level, given by the GPS (Garmin ETrex® 20). Slope was calculated, at the steepest gradient within each relevé, using a handheld inclinometer (Brunton Clino Master).

At each relevé a composite soil sample (approximately 500 g) was taken from four random sites at depths up to 15 cm (Bohn et al., 2001) and labelled. Soil analyses were conducted by BemLab cc in Somerset West. The following soil characteristics were measured: texture, pH (KCl; see Mclean, 1982), electrical resistance (ohms; see Richards, 1954), Hydrogen (cmol$^{(+)}$ /kg), stone volume (%), Phosphorus (Bray II) (mg/kg; see Bray and Kurtz, 1945), Potassium (mg/kg), Exchangeable Sodium, Potassium, Calcium and Magnesium cations (cmol$^{(+)}$/kg; see Chapman, 1965), organic Carbon (%; see Nelson and Sommers, 1982), Nitrogen (%), and soil moisture (%).

Additionally, for a greater macro understanding of the underlying geology of the study area and its relation to the region's soil, a 1:50 000 geology map of the Cape Peninsula incorporating the study area was overlaid onto a Google Earth Image (Google Inc., 2012).

3.2.2 Statistical Analyses

Plant diversity measures were calculated for the entire study area combined and for each of the four pre-defined vegetation states or study sites. Gamma diversity (total species richness across all sites or relevés), Alpha diversity (species richness per site or per relevé), and Beta diversity (Gamma/mean Alpha-1) were recorded (Whittaker, 1972). In addition, Shannon Diversity Index, Pielou's J as a measure of evenness, and Simpson's (1949) Dominance Index were calculated.

To show the arrangement of the relevés based on species composition and to allow comparison of the intra- and inter-site distribution, ordination was performed using the Nonmetric Multidimensional Scaling (NMS) technique (Kruskal 1964, Mather, 1976). This iterative technique ordinates based on ranked distances between sites, avoiding the assumption of data normality. "Stress" is used in NMS as a measure of departure from monotonicity in the relationship between the distance between plots in the original many-dimensional space and the distance in the reduced-dimensional space. Analysis was done using PC-ORD for Windows, v 6.0, (MjM Software, 2011). Species percentage cover data and abiotic variable data were reduced into two matrices. In order to reduce the high coefficient of variance in the species cover matrix, species which occurred in 3 or less plots were deleted. Values were then log transformed using the following formula: transformed value = log (x + 1). The second matrix contained abiotic and variables measured at each relevé. Values were log transformed using the following formula: transformed value = log (x+1). Values were then relativized by the column maximum value.

A preliminary run was made using 6-dimensional space, Sorensen distance (chosen due to the heterogeneous, zero-rich nature of the matrix), and 100 iterations. Plots of stress versus iteration were examined for instability and to find the lowest number of axes at which the reduction in stress gained by adding another axis was small. A final run of 250 iterations was made using 2 axes with a randomly selected starting configuration. A Monte Carlo simulation was included as a test whether a similar final stress could have been obtained by chance. The stress obtained with the data set was compared to the stress from 20 runs of randomized versions (data shuffled within columns) of data. Additional runs were compared to ensure that the solution was not at local minimum. Overlays of species cover data and environmental variables on the resulting ordination allowed for an examination of the correlation between these variables and the ordination axes (methods adapted from Waichler et al., 2001).

A Brown-Forsyth test for homogeneity of variances was performed on all abiotic factors to determine homoscedasticity. If data were parametric, one-way analyses of variances (ANOVAs) were performed. If not parametric, Kruskal-Wallis one-way analyses of variances were performed. Where possible a Post-Hoc Tukey HSD test was performed. All analyses of variance were done using STATISTICA (StatSoft, 2004).

3.3 Results

3.3.1 Diversity Indices

Tables 3.1 and 3.2 provide diversity indices recorded in the study area at large for all 28 relevés. For this study, Alpha diversity is defined as mean species richness and Gamma diversity is total species richness across study sites. Beta diversity, the amount of compositional variation in a collection of sample units (relevés), was calculated as Gamma diversity/mean Alpha diversity-1 (Whittaker, 1972). In addition, Evenness, Shannon Diversity Index and Simpson's Dominance Index are presented.

A total of 135 different species was encountered in the 28 relevés of which 96% were identified to species level (see Table 3.4). The mean species richness within the 28 relevés was 19.20 although the standard deviation was high, indicating high variance in species richness between relevés. The high Beta diversity value of 6.03 can be explained by the heterogeneity between the four pre-selected sites. Species evenness refers to how close in numbers each species in an environment are. The value is constrained between 0 and 1; the higher the value the more even the community. The Shannon Diversity and Simpson Dominance indices measure the heterogeneity-diversity of the study site, incorporating both species richness and species evenness/dominance. The values reported in Table 3.1 are best used for comparison with past studies and as a reference point for future work.

Table 3.1: Mean diversity indices (±SD) across the 28 relevés in the study area.

Mean Alpha (α) Diversity	Beta (β) Diversity	Gamma (γ) Diversity	Evenness	Shannon Diversity	Simpson Dominance
19.20 (8.41)	6.03	135	0.59 (0.17)	1.73 (0.73)	0.66 (0.21)

Table 3.2 breaks down the diversity indices between study sites and clearly illustrates differences between Old Renosterveld and Lightly Degraded Renosterveld when compared to the Alien Pine Stand and the Game camp. Old Renosterveld and Lightly Degraded Renosterveld shared remarkably similar values, although Alpha and Gamma diversity values are somewhat higher in the Old Renosterveld. Both the Alien Pine stand and the Game Camp have significantly lower values (the Alien Pine Beta diversity being an exception) than Old Renosterveld and Lightly Degraded Renosterveld. The Game Camp site in particular exhibited the lowest values throughout all of the diversity indices.

Table 3.2: Mean diversity indices (±SD) and number of replicates (N) across the four study sites. Index values with shared superscripts are not significantly different at the $P<0.05$ level (One-Way ANOVA). As Beta and Gamma diversity values are single values they were excluded from statistical analysis.

	Alpha Diversity	Beta Diversity	Gamma Diversity	Evenness	Shannon Diversity	Simpson's Dominance	N
Old Renosterveld	28.14 (4.45)^{a}	1.7	75	0.69 (0.09)^{a}	2.29 (0.31)^{a}	0.80 (0.09)^{a}	7
Lightly Degraded Renosterveld	24.57 (3.99)^{a}	1.8	68	0.71 (0.10)^{a}	2.26 (0.37)^{a}	0.81 (0.11)^{a}	7
Alien Pine Stand	14.43 (5.06)^{b}	1.8	41	0.54 (0.21)^{b}	1.38 (0.45)^{b}	0.54 (0.21)^{b}	7
Game Camp	9.86 (1.35)^{b}	1.2	22	0.42 (0.13)^{b}	0.97 (0.32)^{b}	0.49 (0.19)^{b}	7

Table 3.3 is provided for the purposes of comparison, where diversity indices recorded in this study can be compared to those in another Renosterveld study (see Cowling, 1983a). The relevés used for the study were the same size as the ones used in this study, although they were recorded in South Coast Renosterveld, not Peninsula Shale Renosterveld.

Alpha diversities from Table 3.3 are all higher than the highest value recorded in Table 3.1, although standard deviations are also higher. Beta diversity values for the communities where N was greater than 10 are all higher than the values reported in Table 3.2, although the value for the fourth community where N=4, is less than the values reported for the Old Renosterveld, Lightly Degraded Renosterveld and Alien Pine sites in Table 3.2. Shannon Diversity and Simpson Dominance values were uniformly less than those reported in Table 3.1.

Table 3.3: Diversity indices (±SD) and number of replicates (N) from four South Coast Renosterveld Communities (data adapted from Cowling, 1983a).

Community	Mean Alpha Diversity	Beta Diversity	Gamma Diversity	Mean Shannon-Wiener	Mean Simpson's Index	N
Themeda-Cliffortia	33.6 (8.4)	2.57	120	0.72 (0.24)	0.39 (0.17)	11
Elytropappus-Eustachys	51.5 (14.7)	2.15	162	1.11 (0.19)	0.19 (0.13)	10
Elytropappus-Metalasia	40.8 (7.8)	2.72	152	0.94 (0.19)	0.23 (0.11)	12
Elytropappus-	42.5 (11.9)	1.28	97	0.81 (0.28)	0.36 (0.21)	4

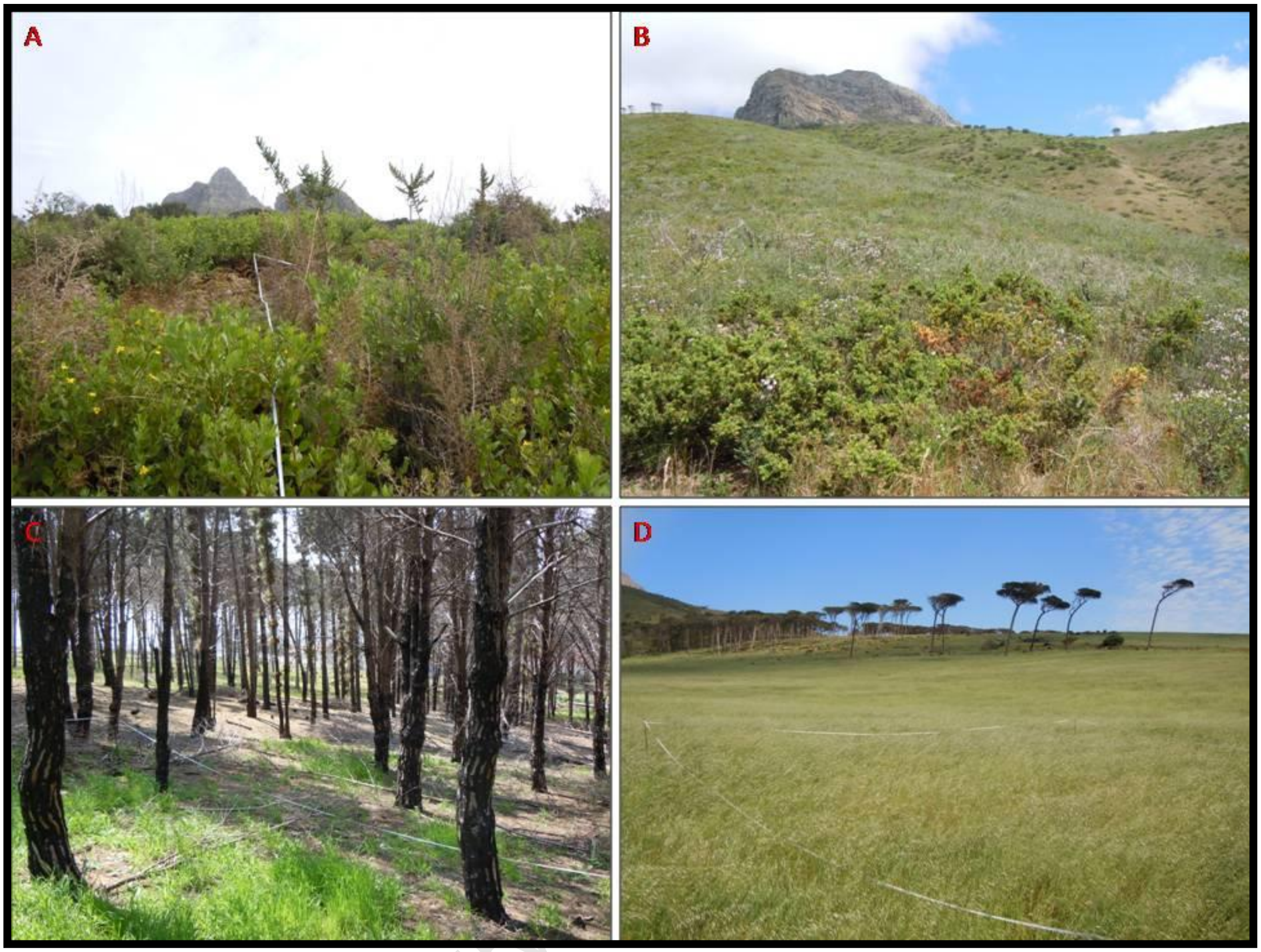

Plate 1: Photographs of the four pre-defined vegetation states found within the study area.
(A=Old Renosterveld; **B**=Lightly Degraded Renosterveld; **C**=Alien Pine Stand; **D**=Game Camp).

Table 3.4: Species list in alphabetic order including information (where available) on family, plant functional type, national red list status, occurrence and dominance (>15% cover) across study sites, and presence in seedbank study (see Chapter 4). Abbreviations used: **FT**=functionally type; **LST**=large shrub/tree; **MHS**=mid-high shrub; **LS**=low shrub; **ALS**=annual low shrub **DS**=dwarf shrub; **PF**=perennial forb; **AF**=annual forb; **PG**=perennial graminoid; **AG**=annual graminoid; **G**=Geophyte; **RB**=reproductive biology; **RSD**=re-seeder; **SPR**=re-sprouter; **ND**=no data; **LC**=least concern; **NT**=near threatened; **VU**=vulnerable; **EN**=endangered; **SA**=South Africa; **WC**=Western Cape. **OR**=Old Renosterveld; **LD**=Lightly Degraded Renosterveld; **AP**=Alien Pine; **GC**=Game Camp.

Species Name	FT	Family	Status	OR	LD	AP	GC	Seedbank
Acacia cyclops A.Cunn. ex. G.Don	LS/T	Fabaceae	Naturalized Exotic	0	2	0	0	×
Acacia pycnantha Benth.	LS/T	Fabaceae	Naturalized Exotic	0	0	2	0	×
Ageratina adenophora (Spreng.) R.M.King & H.Rob.	MHS	Asteraceae	Naturalized Exotic	1	0	0	0	×
Anagallis arvensis L. subsp. arvensis	AF	Primulaceae	Naturalized Exotic	6	4	1	2	✓
Arctopus echinatus L.	PF	Apiaceae	LC-endemic to SA	0	0	1	0	×
Aristea africana (L.) Hoffmanns,	PF	Iridaceae	LC-endemic to WC	2	1	0	0	×
Aristea pauciflora Wolley-Dod	G	Iridaceae	ND-endemic to WC	1	0	0	0	×
Aspalathus astroites L.	MHS	Fabaceae	LC-endemic to WC	1	0	0	0	×
Aspalathus cephalotes Thunb. subsp. violaceae	LS	Fabaceae	LC-endemic to WC	1	0	0	0	×
Aspalathus chenopoda L. subsp. chenopoda	MHS	Fabaceae	Rare-endemic to WC	0	3	0	0	×
Aspalathus cordata (L.) R.Dahlgren	LS	Fabaceae	LC-endemic to WC	0	6 (1)	2	0	×
Aspalathus hispida Thunm. subsp. hispida	MHS	Fabaceae	LC-endemic to SA	5	5	2	0	✓
Asparagus capensis L. var. capensis	LS	Asparagaceae	LC-not endemic to SA	1	0	0	0	×
Asparagus rubicundus P.J.Bergius	MHS	Asparagaceae	LC-endemic to SA	0	1	0	0	×
Asteraceae spp. Unknown 1	AF	Asteraceae	-	0	0	0	1	×
Asteraceae spp. Unknown 2	AF	Asteraceae	-	1	0	0	0	×
Athanasia crithmifolia (L.) L. subsp. crithmifolia	MHS	Asteraceae	LC-endemic to WC	1	5	0	0	✓
Avena fatua L.	AG	Poaceae	Naturalized Exotic	0	0	2	7 (5)	✓
Baeometra uniflora (Jacq.) G.J.Lewis	G	Colchicaceae	LC-endemic to WC	2	0	0	0	×
Berkheya rigida (Thumb.) Erwart,	PF	Asteraceae	LC-endemic to SA	1	3	0	0	×
Brachypodium distachyon (L.) P.Beauv	AG	Poaceae	Naturalized Exotic	0	0	0	5 (4)	✓
Briza maxima L.	AG	Poaceae	Naturalized Exotic	2	1	7 (5)	7 (5)	✓
Carduus pycnocephalus Curtis.	AF	Asteraceae	Naturalized Exotic	0	1	4	1	×
Cheilanthes contracta (Kunze) Mett. ex Kuhn	PF	Sinopteridaceae	LC-endemic to SA	3	0	0	0	×

Species Name	FT	Family	Status	OR	LD	AP	GC	Seedbank
Chenopodium hybrid (C. giganteum x C. album)	AF	Chenopodiaceae	Naturalized Exotic	0	0	1	0	×
Chironia baccifera L.	LS	Gentianaceae	LC-endemic to SA	3	4	0	0	×
Chrysanthemoides monilifera (L.) subsp. Monilifera	MHS	Asteraceae	LC-endemic to SA	6 (2)	7 (3)	3	0	×
Chrysocoma coma-aurea	LS	Asteraceae	Common	0	4	0	0	×
Cliffortia polygonifolia L. var. trifoliata Harv.	MHS	Rosaceae	LC-endemic to WC	4 (1)	1	0	0	×
Clutia pulchella L. var. pulchella	MHS	Euphorbiaceae	LC-not endemic to SA	0	1	0	0	×
Conyza scabrida DC.	MHS	Asteraceae	LC-not endemic to SA	3	0	0	0	✓
Cymbopogon plurinodis (Stapf.)	PG	Poaceae	LC-not endemic to SA	3	1	0	0	×
Cyphia phyteuma (L.) Willd. var. phyteuma	PF	Lobeliaceae	LC-endemic to WC	0	0	1	0	×
Diascia diffusa Benth.	AF	Scrophulariaceae	LC-endemic to WC	1	0	0	0	×
Echium plantagineum L.	ALS	Boraginaceae	Naturalized Exotic	1	0	0	7	✓
Ehrharta calycina Sm.	PG	Poaceae	LC-not endemic to SA	0	0	1	0	×
Elytropappus rhinocerotis L.f.	MHS	Asteraceae	LC-not endemic to SA	4	7	2	0	×
Erodium spp. Unknown	AF	Geraniaceae	Naturalized Exotic	1	0	0	0	×
Euclea racemosa Murray subsp. racemosa	LS/T	Ebenaceae	LC-endemic to SA	1	0	0	0	×
Euphorbia helioscopia L.	AF	Euphorbiaceae	Naturalized Exotic	0	0	0	1	×
Euphorbia peplus L.	AF	Euphorbiaceae	Naturalized Exotic	0	0	3	5	✓
Euphorbia terracina L.	PF	Euphorbiaceae	Naturalized Exotic	0	2	0	0	×
Euryops abrotanifolius (L.) DC.	LS	Asteraceae	LC-endemic to SA	0	0	2	0	✓
Felicia fruticosa (L.) G.Nicholson subsp. fruticosa	LS	Asteraceae	LC-endemic to WC	0	1	0	0	×
Ficinia filiformis (Lam.) Schrad.	PG	Cyperaceae	LC-endemic to SA	4	5	0	0	✓
Ficinia spp. Unknown	PG	Cyperaceae	-	0	0	2	0	×
Geranium molle L.	AF	Geraniaceae	Naturalized Exotic	1	0	0	1	✓
Geranium spp. Unknown	DS	Geraniaceae	-	0	0	0	1	×
Gnidia laxa (L.f.) Gilg	LS	Thymelaeaceae	LC-endemic to WC	0	0	0	1	×
Gnidia spp. unknown	LS	Thymelaeaceae	-	1	0	0	0	×
Helichrysum cymosum (L.) D.Don subsp. cymosum	LS	Asteraceae	LC-endemic to SA	5	2	0	0	×
Helichrysum patulum (L.) D.Don	LS	Asteraceae	LC-endemic to WC	7	7	0	0	×
Hermannia alnifolia L.	LS	Malvaceae	LC-endemic to SA	0	1	0	0	×
Hermannia althaeifolia L.	LS	Malvaceae	LC-endemic to SA	3	5 (1)	0	0	×

Species Name	FT	Family	Status	OR	LD	AP	GC	Seedbank
Hyparrhenia hirta (L.) Stapf	PG	Poaceae	LC-not endemic to SA	7 (1)	5 (1)	0	0	×
Hypericum canariense L.	LS/T	Hypericaceae	Naturalized Exotic	3	0	0	0	✓
Indigofera psoraloides (L.) L.	DS	Fabaceae	VU-endemic to WC	2	1	0	0	×
Indigofera spp. Unknown	PF	Fabaceae	-	6	0	0	0	×
Ischyrolepis capensis	PG	Restionaceae	LC-endemic to SA	0	1	0	0	×
Lagurus ovatus L.	AG	Poaceae	Naturalized Exotic	1	1	0	0	×
Leucadendron argenteum (L.) R.Br.	LS/T	Proteaceae	EN-endemic to WC	0	1	0	0	×
Lobostemon fruticosus (L.) H.Beuk	LS	Boraginaceae	LC-endemic to WC	0	4 (1)	0	0	×
Lythrum hyssopifolia L.	AF	Lythraceae	Naturalized Exotic	5	0	0	0	×
Melianthus major L.	MHS	Melianthaceae	LC-endemic to SA	2	0	0	0	×
Metalasia densa (Lam.) P.O.Karis	LS/T	Asteraceae	LC-not endemic to SA	1	3	0	0	×
Moraea flaccida (Sweet) Steud	G	Iridaceae	LC-endemic to WC	4	0	0	0	×
Moraea spp. Unknown	G	Iridaceae	-	0	0	3	2	×
Moraea tricuspidata (L.f.) G.J.Lewis	G	Iridaceae	LC-endemic to SA	1	0	0	0	×
Muraltia heisteria (L.) DC.	MHS	Polygalaceae	LC-endemic to SA	0	2	1	0	×
Myosotis arvensis (L.) Hill	AF	Boraginaceae	Naturalized Exotic	0	2	0	0	✓
Myrsine africana L.	MHS	Myrsinaceae	LC-not endemic to SA	0	1	0	0	×
Notobubon galbanum (L.) Magee	MHS	Apiaceae	LC-endemic to WC	0	1	0	0	×
Olea europea L. subsp. africana (Mill.) P.S.Green	LS/T	Oleaceae	LC-not endemic to SA	5	0	0	0	×
Ornithogalum thyrsoides Jacq.	G	Hyacinthaceae	LC-endemic to SA	0	0	0	3	×
Otholobium hirtum (L.) C.H.Stirt.	MHS	Fabaceae	LC-endemic to WC	0	6 (3)	1	0	×
Otholobium virgatum (Burm.f.) C.H.Stirt.	DS	Fabaceae	LC-endemic to SA	0	0	0	1	×
Oxalis caprina L.	PF	Oxalidaceae	LC-endemic to WC	3	1	1	4	×
Oxalis compressa L.f. var. compressa	PF	Oxalidaceae	LC-endemic to WC	3	2	6	7	×
Oxalis hirta L. var. hirta	PF	Oxalidaceae	LC-endemic to WC	0	2	0	0	×
Oxalis obtusa Jacq.	PF	Oxalidaceae	LC-endemic to SA	2	0	0	0	×
Oxalis pes-caprae L. var. pes-caprae	PF	Oxalidaceae	LC-not endemic to SA	1	0	0	0	✓
Oxalis purpurea L.	PF	Oxalidaceae	LC-endemic to SA	1	0	0	0	×
Oxalis tomentosa L.f.	PF	Oxalidaceae	LC-endemic to WC	0	0	1	3	×
Passerina corymbosa Eckl. ex	LS/T	Thymelaeaceae	LC-endemic to SA	7 (2)	4	0	0	×
Pelargonium capitatum (L.) L'Her.	DS	Geraniaceae	LC-not endemic to SA	3	0	0	0	×
Pelargonium cucullatum (L.) L'Her. subsp. cucullatum	MHS	Geraniaceae	LC-endemic to WC	1	2	0	0	×
Pelargonium elongatum (Cav) Salisb.	DS	Geraniaceae	LC-endemic to SA	0	1	0	0	×

Species Name	FT	Family	Status	OR	LD	AP	GC	Seedbank
Pelargonium myrrhifolium (L.) L'Her. var. myrrhifolium	DS	Geraniaceae	LC-endemic to SA	1	1	0	0	✓
Pennisetum macrourum Trin.	PG	Poaceae	LC-not endemic to SA	0	1	0	0	×
Pennisetum setaceum (Forssk.) Chiov.	PG	Poaceae	Naturalized Exotic	0	1	0	0	×
Pentaschistis curvifolia (Schrad.) Stapf	PG	Poaceae	LC-endemic to SA	1	2	0	0	×
Phylica pubescens Aiton var. pubescens	MHS	Rhamnaceae	LC-endemic to WC	2	1	0	0	×
Phytolacca octandra L.	PF	Phytolaccaceae	Naturalized Exotic	0	0	1	0	×
Picris echioides L.	AF	Asteraceae	Naturalized Exotic	5	2	7	0	✓
Pinus pinea L.	LS/T	Pinaceae	Naturalized Exotic	1	3	7 (1)	0	×
Plantago lanceolata L.	PF	Plantaginaceae	LC-not endemic to SA	4	2	0	0	×
Pseudognaphalium luteoalbum (L.) Hilliard & B.L.Burtt	AF	Asteraceae	ND	0	0	1	0	✓
Psoralea asarina (P.J.Bergius) T.M.Salter	DS	Fabaceae	NT-endemic to WC	2	0	0	0	×
Psoralea pinnata L. var pinnata	LS/T	Fabaceae	LC-endemic to WC	2	0	0	0	×
Pteridium aquilinum (L.) Kuhn subsp. aquilinum	PF	Dennstaedtiaceae	LC-not endemic to SA	1 (1)	0	0	0	×
Putterlickia pyracantha (L.) Szyszyl.	LS/T	Celastraceae	LC-endemic to SA	5 (4)	1	0	0	×
Salvia africana-caerulea L.	MHS	Lamiaceae	LC-endemic to SA	0	1	0	0	×
Searsia angustifolia (L.)	LS/T	Anacardiaceae	LC-endemic to SA	1	0	0	0	×
Searsia lucida (L.) F.A.Barkley	LS/T	Anacardiaceae	LC-not endemic to SA	0	4 (1)	0	0	×
Searsia tomentosa (L.) F.A.Barkley	LS/T	Anacardiaceae	LC-not endemic to SA	1	1	0	0	×
Selago corymbosa L.	LS	Scrophulariaceae	LC-endemic to SA	4	3	1	0	✓
Senecio pterophorus DC.	MHS	Asteraceae	LC-not endemic to SA	5	1	7	1	✓
Senecio pubigerus L.	LS	Asteraceae	LC-endemic to WC	1	3	6	4	✓
Senecio rosmarinifolius L.f.	LS	Asteraceae	LC-endemic to SA	1	1	0	2	×
Solanum marginatum L.f.	MHS	Solanaceae	Naturalized Exotic	0	1	0	0	×
Solanum nigrum L.	AF	Solanaceae	Naturalized Exotic	0	0	1	0	✓
Sonchus dregeanus DC.	PF	Asteraceae	LC-not endemic to SA	0	0	1	0	×
Sonchus oleraceus L.	AF	Asteraceae	Naturalized Exotic	0	0	2	0	✓
Stoebe cinerea (L.) Thunb,	MHS	Asteraceae	LC-endemic to SA	3	0	0	0	×
Taraxacum officinale Weber	PF	Asterceae	Naturalized Exotic	1	4	7	0	✓
Themeda triandra Forssk.	PG	Poaceae	LC-not endemic to SA	5	0	0	0	×
Torilis arvensis (Huds.) Link	AF	Apiaceae	Naturalized Exotic	0	4	2	0	×
Tribolium uniolae (L.f.) Renvoize	PG	Poaceae	LC-endemic to SA	0	0	0	2	×

Species Name	FT	Family	Status	OR	LD	AP	GC	Seedbank
Unknown annual forb 1	AF	-	-	0	2	3	0	×
Unknown annual forb 2	AF	-	-	2	0	0	0	×
Unknown annual forb 3	AF	-	-	0	4	0	0	×
Unknown annual forb 4	AF	-	-	0	1	1	0	×
Unknown Geophyte spp. 1	G	-	-	0	0	1	0	×
Unknown Geophyte spp. 2	G	-	-	1	0	0	0	×
Unknown Geophyte spp. 3	G	-	-	0	0	2	0	×
Unknown Geophyte spp. 4	G	-	-	4	0	0	0	×
Unknown Poaceae spp. 1	AG	Poaceae	-	0	1	0	0	×
Unknown Poaceae spp. 2	AG	Poaceae	-	0	0	1 (1)	0	×
Unknown Cyperaceae spp.	?	Cyperaceae	-	0	2	0	0	×
Unkown Geophyte spp. 5	G	-	-	3	0	0	0	×
Ursinia anthemoides (L.) Poir. subsp. anthemoides	AF	Asteraceae	LC-endemic to SA	0	0	1	0	×
Withania somnifera (L.) Dunal	LS	Solanaceae	LC-not endemic to SA	0	2	0	0	×
Zantedeschia aethiopica (L.) Spreng.	G	Araceae	LC-not endemic to SA	7	1	0	2	×

3.3.2 Species Composition and Characteristics

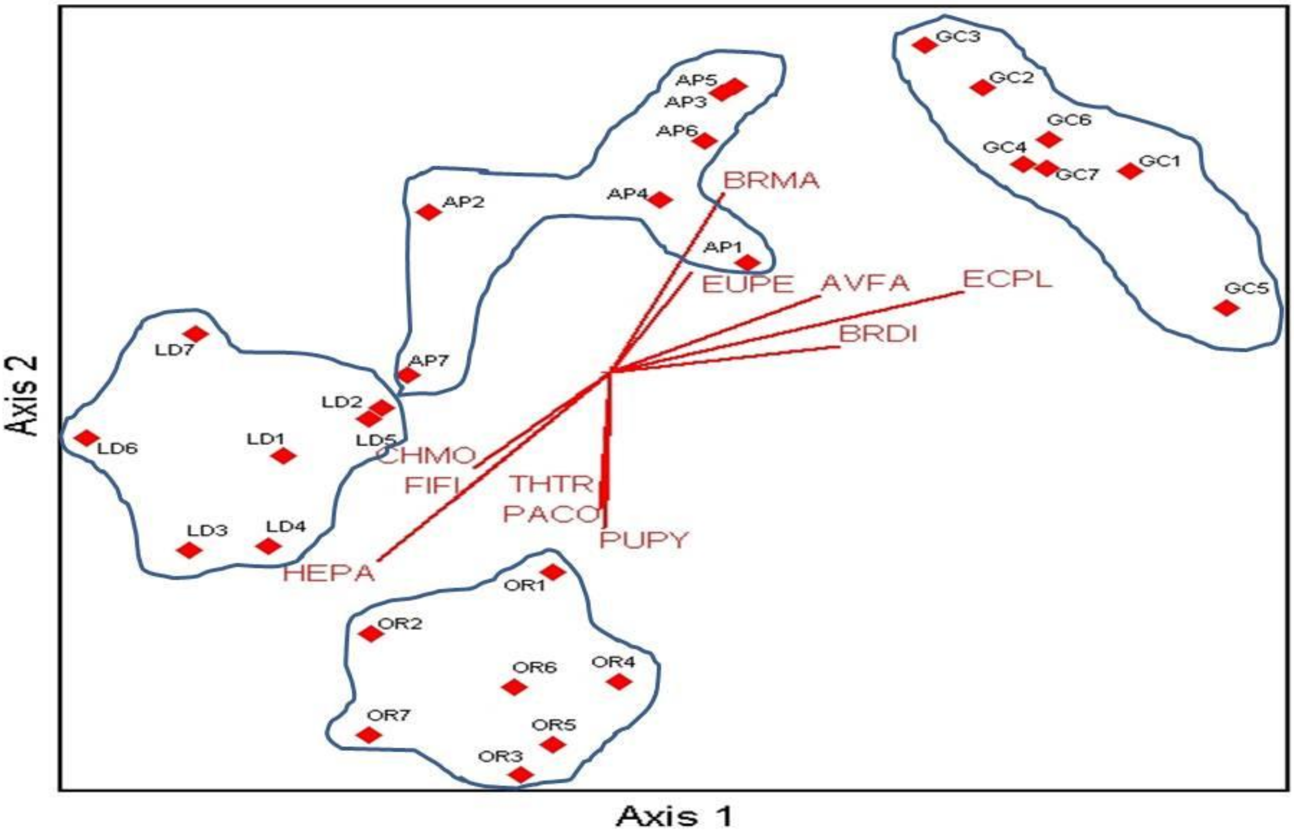

Figure 3.1: NMS Ordination of 28 relevés in species space. Axis 1 represents 31% of the variance; axis 2 represents an additional 42%. An overlay of species with $r^2 \geq 0.3$ with one or more axis is given. Vectors are sized in proportion to their correlation co-efficient. Abbreviations used: **OR**=Old Renosterveld; **LD**=Lightly Degraded Renosterveld; **AP**=Alien Pine; **GC**=Game Camp; **AVFA**=*Avena fatua*; **BRDI**=*Brachypodium distachyon*; **BRMA**=*Briza maxima*; **ECPL**=*Echium plantagineum*; **EUPE**=*Euphorbia peplus;* **CHMO**=*Chrysanthemoides monilifera*; **FIFI**=*Ficinia filiformis*; **HEPA**=*Helichrysum patulum*; **PACO**=*Passerina corymbosa*; **PUPY**=*Putterlickia pyracantha*; **THTR**=*Themeda triandra.*

The pattern of relevé ordination in Figure 3.1 was not unexpected due to the *a priori* selection of four study sites with different land-use histories. There does appear to be a continuum from the most degraded Game Camp site to the more pristine Old Renosterveld site with the Alien Pine stand and the Lightly Degraded Renosterveld sites falling between the aforementioned along both axes. The five species which are strongly associated with the Game Camp, and a lesser extent the Alien Pine stand, are all either alien annual graminoids or annual forbs. On the other hand, the six species strongly associated with the Old Renosterveld and Lightly Degraded Renosterveld are all indigenous species (two large shrubs/trees, two perennial graminoids and one low shrub). Relevé AP7 is somewhat of an anomaly but this may be a result of an unidentified grass species dominating the ground cover. It is possible that this species was *Briza maxima* and if that was the case then it would be substantially closer to the other Alien Pine relevés; however it could not be categorically identified as it was yet to flower.

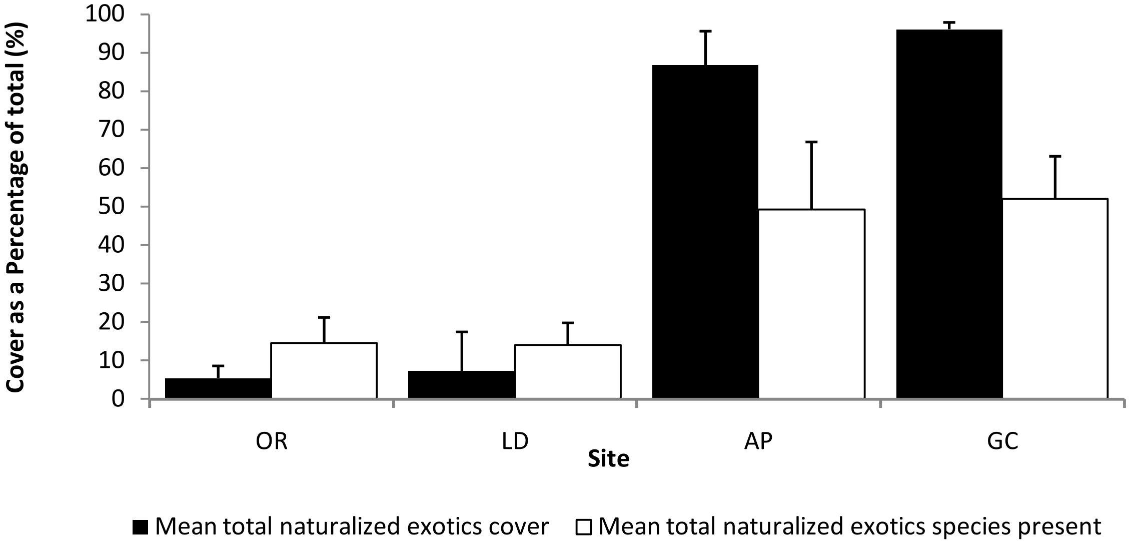

Figure 3.2: Bar graph showing mean percentage naturalized exotic cover (±SD) and mean percentage naturalized exotic species numbers (±SD) across study sites.

Figure 3.2 illustrates naturalized exotic cover in the study sites in two forms, namely the mean percent cover and percentage of total species. It is important to distinguish between the two as together they tell a more detailed story. For both Old Renosterveld and Lightly Degraded Renosterveld the mean total naturalized exotic species present is approximately 15% but the mean total ground cover is less than 10%. In contrast, the mean total number of naturalized exotic species for Alien Pine and Game Camp are approximately 50% but the ground cover percentages for both are over 80%.

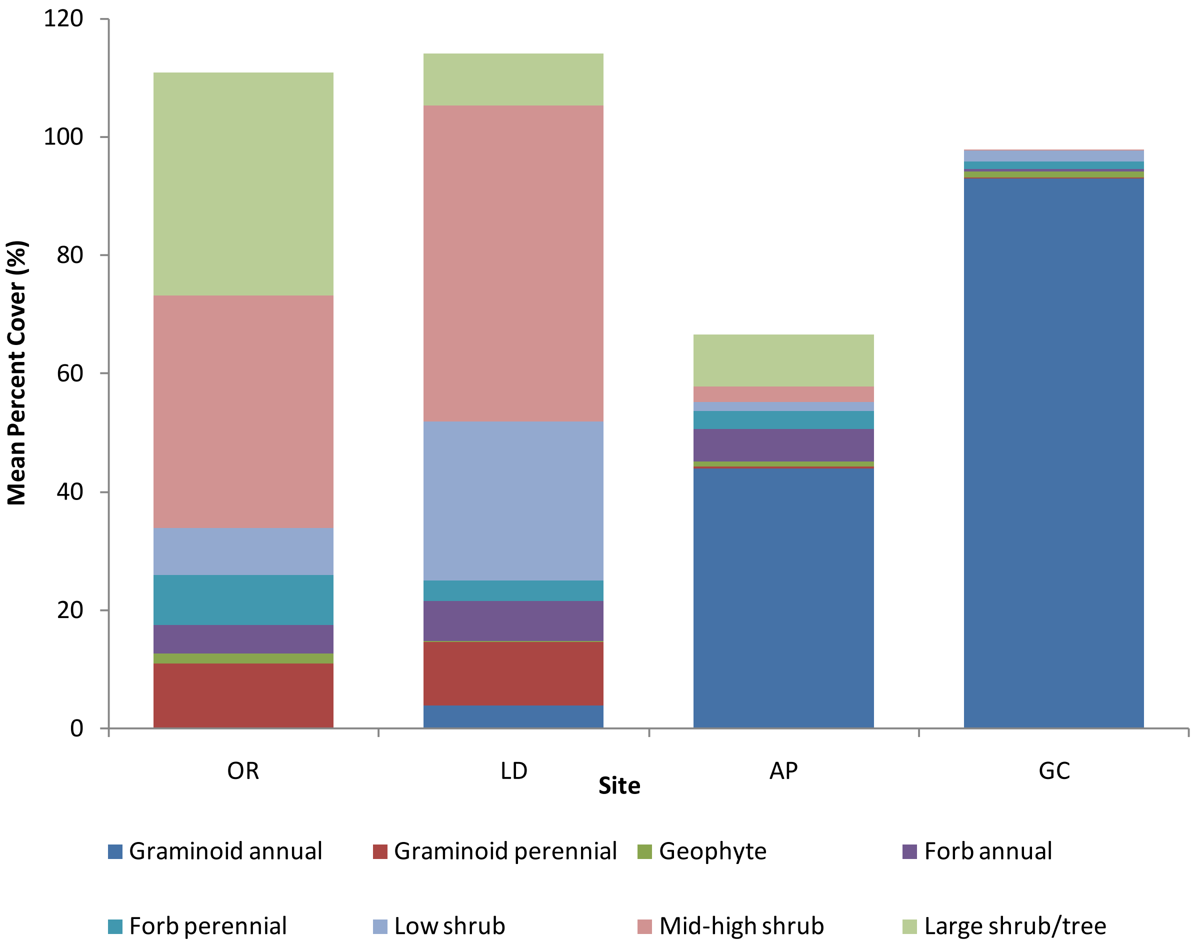

Figure 3.3: Bar graph showing mean percent plant functional type cover across study sites.

Figure 3.3 highlights the disparity in terms of plant functional type cover between Old Renosterveld and Lightly Degraded Renosterveld, when compared to the Alien Pine stand and the Game Camp with a hugely increased cover in annual graminoids in the latter two study sites. Perennial graminoids can be found in Old Renosterveld and Lightly Degraded Renosterveld (approximately 10% cover) but are lacking in the Alien Pine stand and the Game Camp. The Alien Pine relevés had a larger proportion of bare ground hence the mean percent cover does not sum to 100%. Old Renosterveld and Lightly Degraded Renosterveld exceed 100% as species cover was estimated individually and an herbaceous understory strata was often found beneath the shrub strata. Between Old Renosterveld and Lightly Degraded Renosterveld there are distinct differences with a larger proportion of Large Shrubs/Trees found in Old Renosterveld whereas a higher percentage of Low and Mid-high Shrubs were recorded for Lightly Degraded Renosterveld.

3.3.3 Abiotic Factors

Tables 3.5 and 3.6 summarize the results of the abiotic and soil analysis conducted on the study sites. The Old Renosterveld site was characterized by a generally steep slope with minimal bare ground and quite stony and sandy soil. Soil resistance was significantly higher than the other three sites while soil moisture content was highest too and Phosphorus content was comparatively low. The Lightly Degraded Renosterveld site had the highest mean elevation and the steepest mean slope although there was high variability between relevés. The stone volume of the soil was low, as was the percentage bare ground. Lightly Degraded Renosterveld exhibited the highest concentration of Potassium, Calcium and Magnesium cations in addition to significantly higher nitrogen levels.

The Alien Pine stand site was characterized by high bare ground percentage (with high variance between relevés) and quite stony, shallow soil with the lowest moisture content of the four study sites. The soil chemistry shows the Alien Pine stand having the lowest resistance but significantly higher exchangeable sodium cations. The Game Camp site has the lowest mean elevation and the gentlest slope. The bare ground cover is minimal while the soil is deepest and the least stony of the four sites. Chemically, Phosphorus amounts were uniformly low, as were the amounts of exchangeable Calcium and Magnesium cations although Potassium levels were the highest of the four study sites.

Table 3.5: Mean abiotic values (±SD) across study sites. H/F statistic and level of significance reported taken from Mann-Whitney U-test for non-parametric data or One-Way ANOVA for parametric data. Factors which share superscripts were not significantly different at the P<0.05 level (Tukey HSD). Significance levels: *** = P<0.001; ** = P<0.01; * = P<0.05.

	Elevation (m.a.s.l.)	Slope (°)	Bare Ground (%)	Stone Volume (%)	Soil Depth (cm)	Soil Type
H/F Statistic	56.34	18.57	3.75	5.05	6.09	-
Significance Levels	***	***	*	**	**	-
Old Renosterveld	93.31(16.09)^{ab}	18.86 (2.91)	3.36 (1.63)^{ab}	41.57 (12.45)^{a}	40.43 (1.81)^{a}	sandy
Lightly Degraded	183.00(20.18)	22.86(17.17)	4.07 (2.68)^{ab}	13.00(20.26)^{b}	34.95 (7.24)^{ab}	loamy
Alien Pine Stand	110.00 (5.19)^{a}	10.36 (2.19)	28.57 (35.76)^{a}	32.71 (17.21)^{ab}	25.14 (6.28)^{b}	loamy
Game Camp	83.14 (17.16)^{b}	5.93 (1.89)	0.10 (0.00)^{b}	12.14 (18.07)^{b}	42.14 (13.19)^{a}	loamy

Table 3.6: Mean soil chemical properties (±SD) across study sites. H/F statistic and level of significance reported taken from Mann-Whitney U-test for non-parametric data or One-Way ANOVA for parametric data. Factors which share superscripts were not significantly different at the P<0.05 level (Tukey HSD). Significance levels: *** = P<0.001; ** = P<0.01; * = P<0.05; NS= Not Significant.

	pH (KCl)	Resistance (Ohms)	P Bray II (mg/kg)	K (mg/kg)	Exchangeable cations: Na (cmol/kg)	Exchangeable cations: K (cmol/kg)	Exchangeable cations: Ca (cmol/kg)	Exchangeable cations: Mg (cmol/kg)	Carbon (%)	Nitrogen (%)	Moisture (%)
H/F Statistic	1.46	21.81	17.18	9.27	28.23	9.18	4.16	5.47	3.24	11.14	7.80
P sig.	NS	***	**	***	***	***	*	**	*	***	***
Old Renosterveld	4.70 (0.14)^{a}	1368.60 (224.61)	7.71 (1.11)^{a}	317.86 (59.27)^{a}	0.36 (0.08)^{a}	0.81 (0.15)^{a}	6.11 (1.86)^{ab}	2.42 (0.69)^{ab}	2.53 (0.12)^{a}	0.24 (0.05)^{a}	4.00 (1.49)^{b}
Lightly Degraded	4.91 (0.37)^{a}	790.00 (242.69)^{a}	34.71 (1.37)^{b}	441.57 (54.59)^{b}	0.64 (0.11)^{a}	1.13 (0.14)^{b}	8.27 (2.75)^{b}	3.22 (0.60)^{a}	2.24 (0.42)^{a}	0.30 (0.04)	1.24 (1.16)^{a}
Alien Pine Stand	4.64 (0.30)^{a}	444.29 (193.81)	21.43 (9.98)^{ab}	330.57 (39.41)^{a}	1.29 (0.40)	0.85 (0.10)^{a}	5.55 (1.34)^{ab}	3.03 (0.51)^{a}	2.61 (0.09)^{a}	0.19 (0.03)^{a}	2.94 (1.12)^{ab}
Game Camp	4.70 (0.16)^{a}	927.14 (202.21)^{a}	7.86 (2.91)^{a}	473.00 (99.82)^{b}	0.38 (0.11)^{a}	1.21 (0.26)^{b}	4.97 (1.05)^{a}	2.10 (0.55)^{b}	2.26 (0.34)^{a}	0.20 (0.03)^{a}	1.80 (0.76)^{ab}

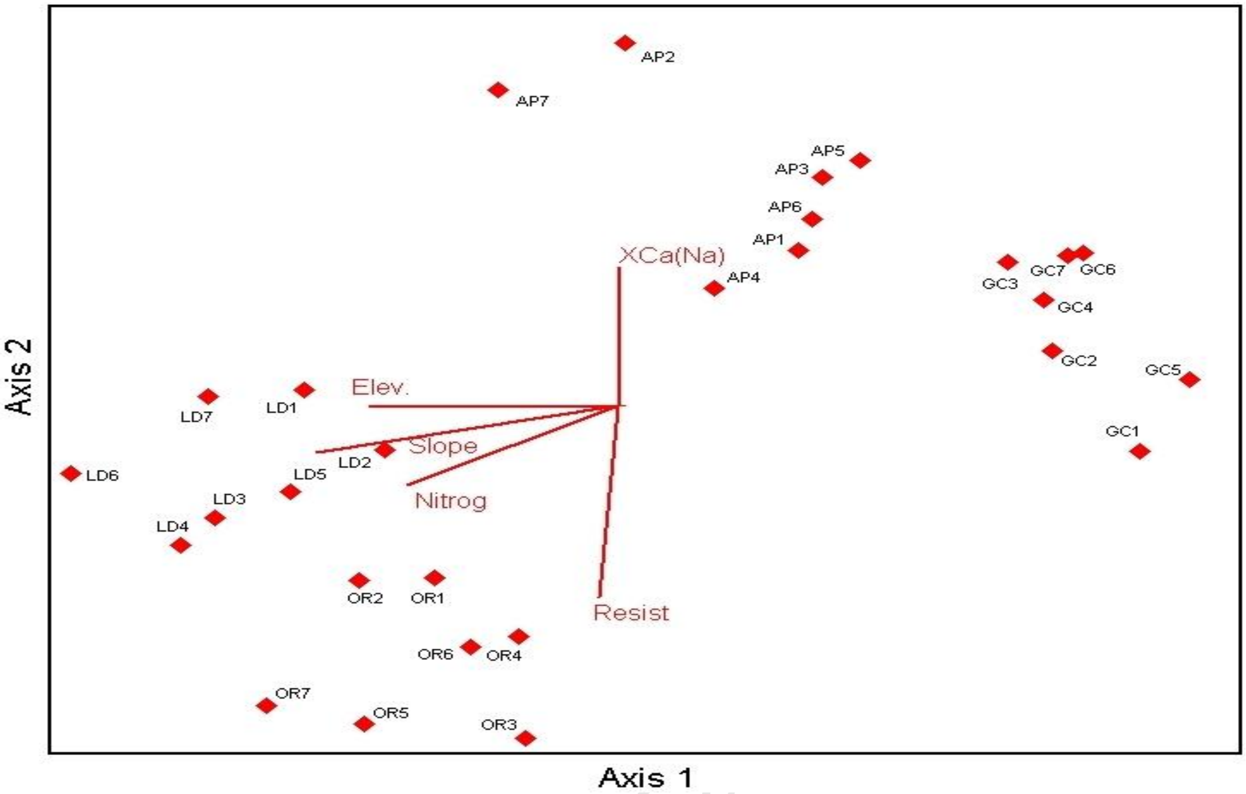

Figure 3.4: NMS Ordination of 28 relevés in species space. Axis 1 represents 31% of the variance; axis 2 represents an additional 42%. An overlay of abiotic variables with $r^2 \geq 0.3$ with one or more axis is given. Vectors are sized in proportion to their correlation co-efficient. Abbreviations: **OR**=Old Renosterveld; **LD**=Lightly Degraded Renosterveld; **AP**=Alien Pine; **GC**=Game Camp; **XCa(Na)**=exchangeable sodium cations; **Elev**=elevation; **Nitrog**=Nitrogen; **Resist**=resistance

Figure 3.4 gives a visual representation of the abiotic factors that are most strongly correlated to the ordinated relevés. Slope and elevation are strongly correlated towards the Lightly Degraded Renosterveld relevés. Increased exchangeable sodium cations are strongly correlated towards Alien Pine; conversely soil resistance is strongly correlated towards Old Renosterveld while soil Nitrogen levels are correlated towards Lightly Degraded Renosterveld and Old Renosterveld.

Figure 3.5 presents the underlying geology, and thus the soil, of the study area. The pink areas are ridges of exposed Malmesbury Group which is predominantly shale and phyllites. The lighter colour represents hill-wash from higher areas consisting of gritty, Quaternary-aged sands. Distance from the mountain face would also affect the amount of hill-wash, as would landscape features at a more localized level. The image resolution is not high enough to delineate each relevé; nonetheless the underlying geology of the four study sites has been indicated: Old Renosterveld is found over Quaternary hill-wash while the other three sites, on a macro-scale, are found over Malmesbury Group shale ridges.

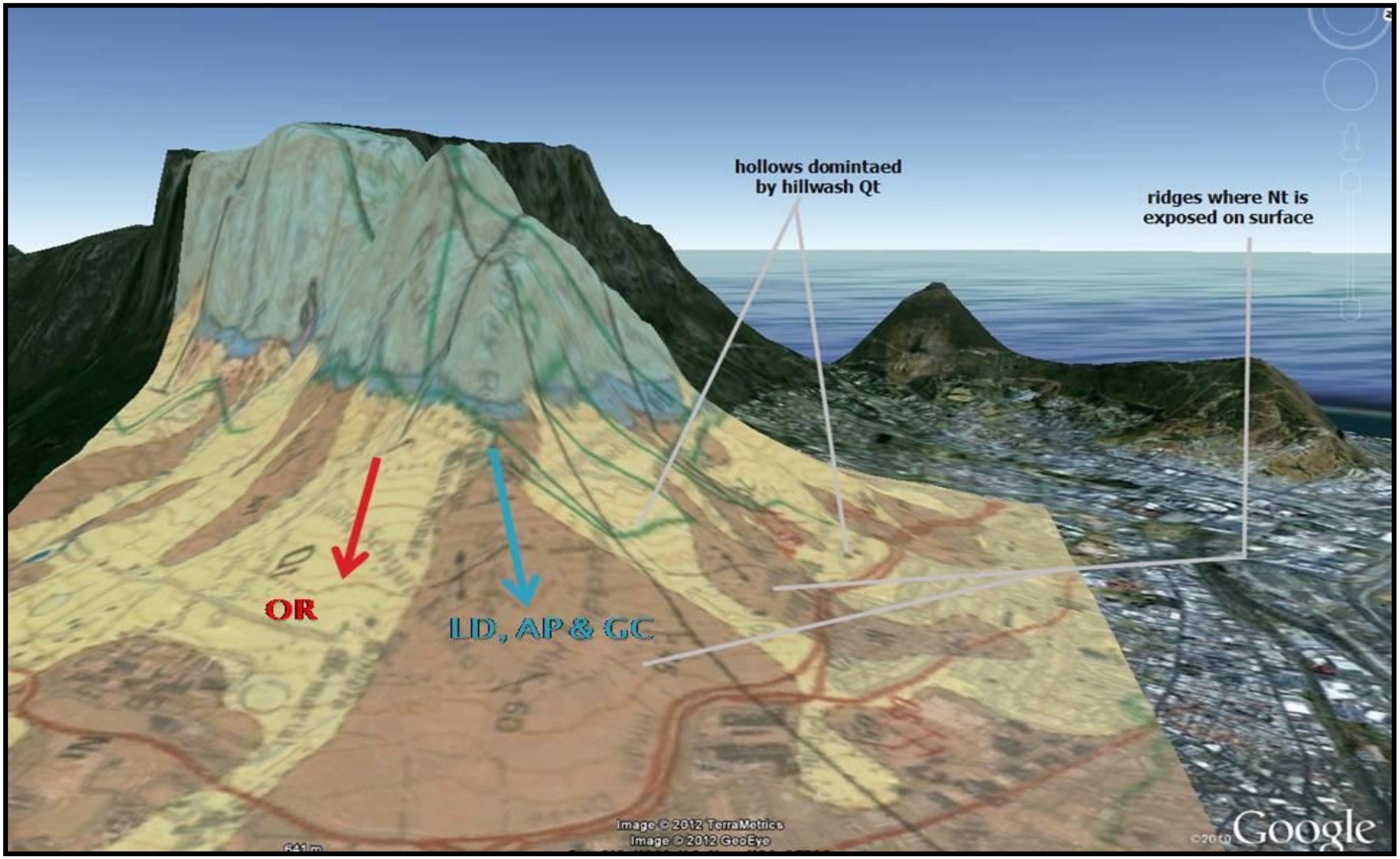

Figure 3.5: Google Earth Image of the study area with a portion of the 1:50 000 geology map of the Cape Peninsula overlaid. Locations of study sites are indicated. Abbreviations: **OR**=Old Renosterveld; **LD**=Lightly Degraded Renosterveld; **AP**=Alien Pine; **GC**=Game Camp; **Nt**=Malmesbury Group; **Qt**= Quaternary-aged sands.

3.4 Discussion

For the sake of clarity the discussion is separated into seven sections. Firstly, diversity indices recorded in the study area are discussed in relation to their conservation and restoration implications. Secondly, the phytosociology results from each of the four study sites are analysed in turn before penultimately the abiotic characteristics of the study area are considered. Finally, a conclusion is made by aggregating the most salient points from the preceding sections and reflecting on these in relation to the broad aim of this chapter which is to establish contemporary phytosociology and environmental conditions of the four dominant states in the study area with a view to inform future restoration efforts.

3.4.1 Study Site Diversity and the Implications for Conservation

Overall, the study site exhibited low diversity values. Of the 135 species recorded, the majority were identified to species level and approximately a quarter were naturalized exotics. Nearly all of the indigenous species identified were categorized as Least Concern according to the Red List of South African Plants (SANBI, 2012). This category of species is generally characterized as widespread, abundant and not facing any threat to their population sizes across the country. The high numbers of alien species and the general trend of cosmopolitan indigenous species are traits associated with disturbed landscapes and imply that the current above-ground vegetation is limited conservation value if the desired end-point of the conservation agenda is to promote and improve biodiversity and provide a refuge for endangered species.

One possible reason for the low diversity values is the dearth of geophytes recorded in the study. Renosterveld is renowned for its geophyte richness (Boucher and Moll, 1980; Cowling, 1990). The general absence of geophytes during the survey may be a product of an actual deficiency in numbers as a consequence of the complex and damaging land-use history (Horn et al., 2011). Additionally, the nature of certain geophyte species, such as short flowering duration, leaves that die back annually and flowering solely post-fire (Proches et al., 2006), may have resulted in an under-representation of geophyte populations.

A further explanation of the low diversity values is the impact of alien invasions and land degradation. Invasion of alien grasses and *Pinus* species both reduce diversity (Milton, 2004; van Wilgen and Richardson, 2012); therefore it is not surprising that the Alien Pine stand and the Game Camp exhibited such low diversity values compared to the relatively less disturbed Lightly Degraded Renosterveld and Old Renosterveld site. It should be noted that the Alien Pine stand consistantly recorded diversity values higher those from the Game Camp. This may be due to the fact that the alien grass cover in the Game Camp is extremely dense which prevents other species from establishing whereas the portions of Alien Pine stand have been cleared in recent years. The clear-felling reduced canopy cover and may have allowed the establishment of certain species. In addition, certain hardy Fynbos species have been reported to survive, albeit at low densities, under pine plantations (Holmes and Cowling, 1997).

While the Old Renosterveld and Lightly Degraded Renosterveld are relatively more diverse than the Alien Pine stand and Game Camp, they fare poorly in comparison to the diversity values reported by Cowling (1983) for South Coast Renosterveld communities. Of course, comparing two distinct Renosterveld types is problematic as they would have been subject to different historical drivers and environmental constraints; however it is likely that the long history of disturbance has resulted in an attrition of species from the study site over time. Although very little is known about the determinants of diversity in Renosterveld (Cowling et al., 1997), fire regime undoubtedly plays a part. In the adjacent Fynbos, fires occurring too frequently may reduce diversity as does the absence of fire for an extended period of time (Kruger, 1983; Van Wilgen and Forsyth, 1992). As discussed in the preceding chapter, it is not possible to know the exact fire history of the study sites but it is possible that the Lightly Degraded Renosterveld experienced fires in quick succession thus reducing diversity as obligate seeders are eliminated from the community. Conversely, the Old Renosterveld site has been fire free for over 15 years which may have contributed to the lower diversity values.

The overall Beta diversity is high and shows significant compositional heterogeneity between relevés across the study area. This is to be expected due to the *a priori* selection of the four study sites and confirms the selection of sites in different vegetation states. Individually the four study sites exhibit significantly lower Beta diversity values as a result of a more homogenous species composition. Similarly to species richness, in comparison to Cowling's (1983) values for communities where N was greater than 10, Beta diversity values from the study sites were consistently lower. It is recommended that future studies in the study area increase sample size to ensure a true estimate of diversity is captured.

Despite the obvious imperfections of comparing two different types of Renosterveld, the reduced diversity values and prevalence of alien species exhibited in the study sites suggest a study area of low current conservation value. This was, however, anticipated due to the prolonged human impact on the environment and restoration initiatives would have the ability to promote diversity. The real value in the diversity indices discussed above is, firstly to reinforce the notion that the different vegetation states are on dissimilar environmental trajectories thus confirming the need to interject with restoration efforts, but principally to provide vital baseline data for future restoration efforts. The divergent ecosystem characteristics touched on briefly here will be discussed in more detail in the proceeding section as the vegetative composition of the four study sites is explored.

3.4.2 Old Renosterveld

The Old Renosterveld site was of particular interest as it had been fire-free for an extended period of time and did not appear to be severely degraded during site selection, thus potentially providing data on Renosterveld succession in the absence of fire. Vegetation cover was dominated by indigenous species and less than quarter of the species identified were aliens. The most prevalent alien species were the herbaceous *Anagallis arvensis* and *Lythrum hyssopifolia*. *Anagallis arvensis* has been described as a potentially aggressive weed in Australia and can form dense populations in understory vegetation that exclude native species (University of Queensland, 2012). Despite the species never exceeding 10% cover, its presence should be monitored and an early intervention may maintain the relative pristine nature of the site. The benefits of an early intervention are also economical as the species will require more effort (both in terms of labour and money) to remove if it increases its dominance.

In terms of plant functional type, the Old Renosterveld site vegetation cover was dominated by Large Shrub/Trees and Mid/High Shrubs. The most dominant species were *Chrysanthemoides monilifera*, *Cliffortia polygonifolia* var. *trifoliata*, *Elytropappus rinocerotis*, *Olea europea* subsp. *africana*, *Passerina corymbosa*, *Putterlickia pyracantha* and *Senecio pterophorus*. Species were attributed a plant functional type in accordance with the literature rather than actual *in situ* plant measurements, nevertheless due to the extended absence of fire, shrubs were frequently shoulder-high or higher (see plate 1). According to Milton's (2007) model on the effect of ecosystem drivers on Renosterveld vegetation, in the absence of fire and herbivory, succession alone (>10 years) will increase shrub cover and shrub diversity (especially amongst re-sprouters) whereas grass, geophyte and weed species will decrease in cover and diversity. Similarly, Rebelo (1995) speculates that the exclusion of fire drives Renosterveld towards Subtropical Thicket. The thicket elements within the Old Renosterveld site are evidently present i.e. *Putterlickia pyracantha* and *Olea europea* subsp. *africana*; however there is still and understory of perennial graminoids and forbs while Low Shrubs such as *Selago Corymbosa*, *Pelargonium* and *Helichrysum* species were all frequently recorded. It appears that the current trajectory may be headed towards a thicket state but, at present, cannot be considered as such. An important point regarding the species composition of the Old Renosterveld site is the geographic location. Situated on the edge of the underlying Malmesbury Shale, it may be that the site is ecotonal with the adjacent Fynbos. This possibility and its implications will be explored in greater depths in the section 3.4.6.

The presence of indigenous perennial grasses such as *Themeda triandra* and *Hyparrhenia hirta* are of interest and imply that a disturbance may redirect the ecosystem trajectory from thicket towards a grassier state. Rebelo (1995) suggests that Renosterveld in a thicket state can be returned to grassy Renosterveld following a burn and application of light grazing. The grazing aspect may be absent from the site but a fire, either controlled or wild, may alter the ecosystem trajectory. The general absence of alien grasses, despite the fact that the heavily invaded Game Camp is immediately adjacent to the site, is encouraging as it suggests that the established indigenous species prevent alien grasses from colonizing the understory. The immediacy and abundance of alien grass propagules is potentially worrying as following a disturbance such as fire the grasses may gain a foothold and prevent natural succession from occurring. This threat is exacerbated by the relative isolation of the Old Renosterveld site with the Game Camp, the University of Cape Town campus and Rhodes Memorial essentially cutting it off from Lightly Degraded Renosterveld site which is prevalent above and to the north of the site.

To conclude, the lack of fire has resulted in the Old Renosterveld site shifting towards a thicket state dominated by large shrubs and trees. Despite this apparent trajectory, the presence of an understory of indigenous graminoids, forbs and geophytes means that the site still has Renosterveld elements within it. According to conceptual vegetation models, a disturbance such as fire may return the site to a grassier state although, due to its isolation and degraded neighbouring areas, the potential is there for increased presence of alien species. Thus the site needs to burn to prevent it becoming a thicket but will require close monitoring post-fire to ensure the exclusion of alien species. Finally, there is a possibility that due to the geographic location, the Old Renosterveld site may be situated on an ecotone with Peninsula Shale Fynbos; the likelihood and implications of this are dealt with in more detail further on (section 3.4.6).

3.4.3 Lightly Degraded Renosterveld

In contrast to the Old Renosterveld site, the Lightly Degraded Renosterveld has a much more recent and patchier fire history. The shorter time period since the last fire, which occurred in 2009, probably resulted in the higher proportion of Low and Mid/High Shrubs observed. Smaller shrub species are generally characteristic of shorter-lived species which are more abundant in earlier successional seres (Cowling and Pierce, 1988). *Aspalathus cordata*, *Athanasia crithmifolia, Chrysanthemoides monilifera, Elytropappus rinocerotis, Hermannia althaeifoli*a, *Helichrysum patulum, Lobostemon fruticosus* and *Otholobium hirtum* were all shrubs commonly recorded in the relevés. The majority of the larger shrubs which were abundant in the Old Renosterveld site were present in the Lightly Degraded Renosterveld and, while currently they do not account for a large proportion of the cover, as the time since the last fire increases they may grow and gradually increase in dominance.

According to Milton's (2007) summary of Renosterveld vegetation models, in the absence of grazing a fire interval of 3-5 years would increase grasses, geophytes and weeds and decrease shrub coverage. A longer fire interval of 5-10 years would increase obligate re-seeder shrubs but have no effect on the proportion of other plant functional types (Milton, 2007). The low density of mammals within the northern reaches of Table Mountain National Park means that the effect of grazing in the study site is likely to be negligible. Although the fire history data of the study site is uncertain and patchy (see Chapter 2), there had been at least 10 years of no fire prior to the burn in 2009. It is, however, possible that portions of the site experienced fire intervals of less than 3-5 years in the preceding decades. Despite the different fire histories of relevés within the study site, no discernible community patterns were observed. The extensive fire in 2009, in addition to potential shorter fire interval, may be expected to result in a grassier state than that observed in the Old Renosterveld, however this was not the case and percentage cover of perennial graminoids was comparable to that recorded in the Old Renosterveld site.

A possible reason for the unexpectedly low grass cover and consequently higher shrub cover is the potential ecosystem engineering that occurred in the early 1990s. Following issues with erosion, portions of slopes of the northern aspect of Devil's Peak were deliberately seeded in a bid to stabilize the slopes (Moll et al., 1991). Sadly there is little information on this, no doubt as a result in shifts in management and oversight. *Chrysanthemoides monilifera* was one species used and it is a ubiquitous feature of the contemporary flora. It was recorded in all seven relevés and found to be dominant in three. Due to its biology it is considered an invasive weed in Australia (Vranjic et al., 2000) and it should be monitored closely to prevent it from dominating the landscape should factors, for example increased fire frequency and disturbance, favour its spread. There are no reports of *Otholobium hirtum*, a species reportedly dominant in the first years after fire (Allsopp and Stock, 1992), being used for slope stabilization; however it was recorded in six relevés and in three of these it was the dominant species. The dominance and prevalence suggests deliberate planting, and like *C. monilifera*, it should be monitored.

Despite this site being categorized as ‘lightly degraded’, the numbers and vegetation cover of alien species were almost identical to those recorded in the Old Renosterveld site; however the composition of the alien species at the two sites were different. Herbaceous species such as *Torilis arvensis, Myosotis arvensis* and *Euphorbia terracina* were unique to the Lightly Degraded Renosterveld site as was the large shrub/tree *Acacia cyclops*. *Acacia cyclops* is a widespread and abundant invasive alien (Nel et al., 2004) and its eradication from Table Mountain National Park has been prioritized. Currently it appears limited to waterways within the park but its presence in the study site, albeit at low densities, should be monitored carefully and every effort should be made to remove them.

The presence of annual alien grasses, albeit in small amounts, in the study site is also a notable difference when compared to the Old Renosterveld site. Alien grasses often rely on a disturbance event to enter a system (Milton, 2004) and the fire in 2009 may have provided the opportunity. The low cover observed is encouraging and indicates the ecosystem is healthy enough to keep the threat of alien grass invasion at bay despite the abundance of alien grasses present in the adjacent Game Camp.

In conclusion, despite the recent fire, and the potential of too frequent fires in the past, the Lightly Degraded Renosterveld is not in a significantly grassier state when compared to the older Old Renosterveld vegetation. Nevertheless, differences in vegetation structure do exist between the two as a result of the vegetation age with the Lightly Degraded Renosterveld having a greater proportion of Low Shrubs. The effects of ecosystem engineering in the early 1990s continues to be experienced as *Chrysanthemoides monilifera* and *Otholobium hirtum* are dominant shrubs in the landscape and both should be monitored in case of further spread.

3.4.4 Alien Pine Stand

Unlike the Old Renosterveld and Lightly Degraded Renosterveld sites, the Alien Pine stand has been dominated by a pine plantation for over a century, although the tree density has undoubtedly fluctuated through time. Parts of the study site are in the process of being clear-felled, however at the time of writing many trees still remain. Pine plantations have been shown to severely reduce diversity (Richardson, 1998), therefore the reduced diversity in comparison with the Old Renosterveld and Lightly Degraded Renosterveld sites is as anticipated. The flora that is present is dominated by non-indigenous exotics. Half the species recorded were identified as aliens, however these species accounted for the majority of the vegetation cover.

Aside from the obvious presence of *Pinus pinea*, annual graminoids (predominantly *Briza maxima*) dominated vegetation cover. Annual forbs such as *Taraxacum officinale*, *Picris echioides* and *Carduus pycnocephalus* were also recorded in all of the relevés but did not account for any significant proportion of ground cover. Many of the *Pinus* individuals appeared to be in poor health and saplings, apart from in one relevé where they dominated, were infrequent. The indigenous species recorded at the site were generally weedy shrubs associated with disturbed areas such as *Senecio pubigerus* and *Senecio pterophorus* and cosmopolitan herbaceous species such as *Oxalis compressa*.

With the imminent removal of the pine trees, the site is about to enter a critical period. The abundance of aliens present and the adjacent Game Camp provides a ready source of alien species, while the indigenous species are pioneer species and weedy by nature. In all probability, without active measures taken the area will degrade towards the state of the Game Camp, an area dominated by alien grasses with a sparse cover of alien and indigenous forbs and pioneer shrubs. With this in mind the area is a perfect candidate for restoration. Despite the removal of the pine trees, the aforementioned reasons mean that passive restoration, which is in any case environmentally slow and not especially effective (Terblanche, 2011), is unlikely to shift the ecosystem trajectory towards indigenous renosterveld, rather active restoration is needed. The site falls into an area categorized and conserved as Peninsula Shale Renosterveld; however it is too degraded to be considered as such. Providing the abiotic soil chemistry has not been denigrated by the plantation (see section 3.4.6), there is an opportunity for management to increase the area of Peninsula Shale Renosterveld through a re-seeding and ecosystem management programme. The intricacies of potential active restoration are dealt with in more detail in the final chapter.

3.4.5 Game Camp

As was the case with the Alien Pine stand, approximately half of the species identified in the Game Camp were naturalized exotics but here the alien species accounted for nearly all the vegetation cover. As mentioned previously, the Game Camp exhibited the lowest diversity measures which emphasize the virulence of alien grass invasion and the manner in which it chokes the emergence and establishment of indigenous species (Milton, 2004). The site was dominated by annual graminoids, namely *Avena fatua, Brachypodium distachyon* and *Briza maxima*.

Avena fatua is a supposedly reasonably palatable grazing grass growing preferentially on sandy soils but is a serious weed throughout the world (Van Oudtshoorn, 2004) and has been shown to significantly affect the performance of indigenous Renosterveld forbs and grasses (Sharma et al., 2010), while *B. distachyon* is resilient and weedy (Opanowicz et al., 2008). *Briza maxima* is most likely a horticultural escapee and is prevalent in disturbed areas in the winter rainfall region of South Africa (Parker-Allie et al., 2009). *Avena fatua* and *B. distachyon* were possibly introduced as fodder for animals in the Game Camp approximately a century ago and in the favourable conditions soon out-competed the indigenous flora. Another possibility is the grasses are remnants from the early homesteads and prospered under management strategies which promoted grazing paddocks. The Game Camp used to house a herd of Black Wildebeest (*Connochaetes gnou*) and a number of Burchell's Zebra (*Equus burchelli*), Bontebok (*Damaliscus dorcas dorcas*) and non-indigenous Fallow Deer (*Cervus dama*) and additional fodder had to be brought in to supplement the grasses available on site. The Wildebeest herd, not indigenous to the region, was translocated out of the camp in 2009 in anticipation of the expansion of the Game Camp (SANParks, 2009), however the expansion plans stalled. Currently, only five Zebra are enclosed in the Game Camp and their numbers are insufficient to keep the alien grasses in check. The plans to enhance the Game Camp and restore indigenous Renosterveld vegetation may be resurrected in the future (see Chapter 5), however the indigenous buck likely to be introduced are not bulk feeders suited to the grass-dominated vegetation currently in place. It is thus unlikely that an increase in grazers of the type and scale planned will resolve the dominance of invasive alien grasses. Instead, the eradication of alien grass through the application of herbicide and manual removal (Milton, 2004), followed by the introduction of indigenous grasses and shrubs, will be necessary prior to the introduction of animals.

The dominance of alien graminoids may be the most pressing issue but it is not the only one. *Echium plantagineum* (Patterson's Curse) is an annual Low Shrub native to the western Mediterranean Basin, where it is a common but not dominant feature of species-rich annual grasslands (Grigulis et al., 2001). *Echium plantagineum* is a prolific seed producer and can yield up to 10 000 seeds/m^2 (Piggin, 1978). Although generally a spring-flowering annual, the species is adaptable and given favourable rainfall some plants germinate out of season and may persist for longer than a year (Sharma and Esler, 2008). In Australia, it has reportedly infested large areas of land where it can become a dominant species (Grigulis et al., 2001). It is common and widespread in South Africa and is classified as a major invader (Nel et al., 2004) especially in old fields and agricultural land. It was recorded in all of the site relevés and its eradication will need to be done concurrently with the removal of the alien grasses if restoration efforts are to prove successful.

To conclude, the Game Camp has been managed as a grazing paddock and it is likely that the withdrawal of the majority of the grazing animals that used to be corralled within the site has seen alien annual grasses dominate the site. The virulent nature of the annual grass species present has drastically reduced diversity and the site has the characteristics typical of old fields with little to no recognizable Renosterveld constituents present. Despite tentative plans to re-introduce indigenous fauna and expand the size of the enclosure, the extent of the invasion and the biology of the indigenous fauna mean that the grasses (and the potentially problematic *Echium plantagineum*) need to be eradicated and restoration efforts initiated prior to the translocation of species.

3.4.6 Abiotic Factors

Despite all the study sites occurring within a relatively small area, certain abiotic differences were evident and may in part explain vegetation differences discussed above. Elevation and slope are two variables which are known to impact ecosystem processes (Choler et al., 2001). Biophysical processes impacted include run-off, erosion, sediment accumulation and temperature. The range of elevations between study sites is only 100 m, and the difference in site aspects are similarly minimal, therefore it is unlikely temperature is affected in a significant way. Other factors such as soil depth may well be affected as topsoil washes down-slope especially in an environment, such as this, where erosion has been reported in the past (Moll et al., 1991). Other than the anomalous Alien Pine site, soil depth shares a negative relationship with elevation with the highest site, Lightly Degraded Renosterveld, having the shallowest soil profile. Similarly, steeper slopes are more prone to topsoil movement and runoff which may explain why the Lightly Degraded Renosterveld site possesses the shallowest soil depth (aside from the anomalous Alien Pine stand). A possible reason for the shallow soil profile in the Alien Pine stand site could be linked to the high bare ground percentage prevalent in the site. With less vegetation to prevent erosion, surface run-off may take top soil away from the site. In a uniform vegetation type the differences mentioned above may play a role in floral composition; however in this study the different land-use impacts have had a substantially greater impact on the observed patterns and attempting to establish whether factors such as slope, elevation or soil depth have affected community composition is impossible.

The image of the study area with the geological overlay (Figure 3.4) shows that the Old Renosterveld site is situated over Quaternary hill-wash while the other three sites, on a macro-scale, are found over Malmesbury Group shale ridges. Additionally, the soil of the Old Renosterveld Site was classified as sandy whereas the soil of the other three sites was categorized as loamy. This is probably a result of the sandier nature of the Quaternary hill-wash which is unconsolidated, newer material originating from the sandstone cliffs of the mountain. It would be expected that the soil characteristics would be affected by this; however, as shall be discussed further on, soil chemistry was remarkably similar for all of the soils. The difference in soil type and the proximity to Fynbos which extends southward on the slopes of Table Mountain may mean that the community at the Old Renosterveld site is ecotonal. The lack of typical Fynbos elements such as proteoids and restioids (Holmes and Richardson, 1999) in the community, added to the potential trajectory of the site towards a thicket state, means that the issue is complex.

There is a general trend of similarity between soil chemical values amongst the four study sites which is as expected across a relatively small area. However, some differences are evident and comparisons with other areas may highlight important aspects of the impact of land-use history on current environmental parameters. Firstly, pH values did not vary significantly between sites. In comparison with Renosterveld records, Mills and Fey (2004) reported higher pH values in West Coast Renosterveld sites although values recorded in regions invaded by alien grasses or pine trees were closer to those recorded in this study. Lechmere-Oertel and Cowling (2001) recorded a pH marginally lower than those recorded in the study site, while Vermeulen (2010) reported values similar to those reported in the results. The similarity of the results suggests that soil pH is not a limiting factor in the restoration of Peninsula Shale Renosterveld in the study area.

Fire is an ecosystem driver known to effect soil properties (Cilliers et al., 2005). The high amount of Phosphorus recorded in the Lightly Degraded Renosterveld site may be linked to its fire history. Fire is the major mineralizing agent in Renosterveld as it returns elements held in above ground biomass, such as P, to the soil (Witkowski and Mitchell, 1987). Thus the more recent burns that occurred within the site may have resulted in increased Phosphorus readings. This theory is supported by the highest soil Nitrogen content and exchangeable Calcium and Magnesium cations being found in Lightly Degraded Renosterveld. However, Cowling et al. (1997) note that mineral availability decreases rapidly post-fire as elements are incorporated into plant biomass. The Lightly Degraded Renosterveld vegetation is approximately 3 years old which may explain why the differences are not greater.

A further abiotic factor worthy of mention is the significantly higher value for exchangeable sodium cations present at the Alien Pine stand. Berthrong et al. (2009) showed how *Pinus* afforestation leads to increased Sodium levels in soils. This phenomenon is likely caused by the effect of afforestation on hydrology. Sodium is not essential to plant biochemistry therefore plants exclude it while taking up water and other cations (Marschner, 1995), resulting in the salinization of the soil under plantations. Soil Sodium levels reported by Vermeulen (2010) were marginally less than those recorded for the Old Renosterveld, Lightly Degraded and Game Camp, but significantly lower than the value recorded in the Alien Pine stand. The high Sodium levels in the Alien Pine site may require remediation if future restoration efforts are to be successful. Sodic soils can be treated through the utilization of gypsum (calcium sulphate) or limestone (calcium carbonate) or through the addition of calcium to the soil (Davis et al., 2012); however biological mediated means (e.g. the build up of organic carbon levels) are preferable since chemical additions will change the soil further.

Unlike Sodium levels, plantations tend to decrease the amount of Potassium, Calcium and Magnesium cations in the soil as the trees have a greater cation uptake than shrubs and grasses consequently redistributing the cations from the soil to biomass pools (Jobbagy and Jackson, 2003). This pattern of decreased cations is not evident in the results; although the fact that the other sites beside the Alien Pine stand were subject to afforestation at some point may have reduced the expected differences. Vermeulen's (2010) values for the aforementioned cation showed great variation making a comparison futile; however it suggests that the values recorded in the study sites are in fact very similar and should not be over-read in terms of statistically significant differences.

Generally, the abiotic soil factors measured showed little variation between study sites. The pH, Carbon, Nitrogen and exchangeable cations (with the exception of Sodium), while on occasion being statistically significantly different, showed much less variation when compared to other studies. The higher Sodium levels found in the Alien Pine stand may require addressing prior to restoration but on the whole there does not appear to be any abiotic factors which may impede the restoration of the study area.

3.5 Conclusion

The current ecological status of the study area is complex. Centuries of human impacts and a substantial urban interface (see Chapter 2) has resulted in a multifarious mosaic of indigenous vegetation (some of which has been deliberately introduced), remnants of *Pinus* plantations, pastures and alien shrubs and annuals. Currently the vegetation of the entire study area is classified, and indeed conserved, as Peninsula Shale Renosterveld, however the phytosociological results show that there is a substantial degree of degradation among the sites. The overall trend of abiotic similarity between sites suggests that different land-use histories, rather than variable abiotic properties, have resulted in the vegetation patterns witnessed today. The two sites with more recent human impacts, namely the Game Camp and Alien Pine stand, are clearly in a worse-off state than Old Renosterveld and Lightly Degraded Renosterveld.

An analysis of historical drivers of change demonstrates that Peninsula Shale Renosterveld is readily degraded by poor management practices and that to return it to a functional Renosterveld state is evidently complicated. Currently the Game Camp is almost completely covered by alien grasses due to the site historically being managed as a grazing paddock. In addition, the relatively recent reduction in grazing animals has seen the grasses increase their domination unchecked. Plans to expand the Game Camp and increase the numbers of indigenous grazers and browsers will remain unattainable unless management actively eradicate the alien grasses and introduce indigenous palatable grass species, such as *Themeda triandra*, and shrubs. Similarly, the Alien Pine stand vegetation bears little resemblance to a Renosterveld community; however here the cause of this, the pine trees, is currently being removed. Despite this, the saline soil and the adjacent source of alien grasses means that active management will be required to switch the ecosystem trajectory towards the Lightly Degraded Renosterveld and prevent the site turning into a highly degraded grass state.

Evaluating the current health and conservation value of the more pristine Lightly Degraded and Old Renosterveld site is not straight forward. Both sites have vegetation cover dominated by indigenous species yet a proportion of the species identified were non-indigenous. It is encouraging that indigenous vegetation in both young and old vegetation is holding its own, as is the evidence of natural succession. Despite this, simply having indigenous plant cover does not necessarily equate to a healthy ecosystem. Determining the state of these two sites is hard as there is a lack of reference data for which to compare. The general trend of cosmopolitan and early successional plants may be a result of the historical degradation of the environment (and the potential ecosystem engineering of planting certain species to prevent erosion) or it may be a result of nutrient limitations. Soil chemistry recorded in the study area was broadly comparable to studies in other Renosterveld communities therefore I hypothesize that the patterns witnessed today are the result predominantly of land-use history. Depending on the conservation agenda practiced by management, action such as controlled burning and species introduction may need to be taken to increase diversity within these two sites.

A more in-depth analysis of restoration potential will be undertaken in the final chapter therefore it will suffice, for the conclusion of this chapter, to note the precarious ecological position the study area is in. Depending on management actions or lack thereof, the study area has the potential to be restored to a healthy, functional ecosystem, although perhaps not as species rich as a pristine site; or it may become a degraded region dominated by alien grasses, shrubs and annuals with the indigenous shrubs present cosmopolitan and weedy. In addition, the variable states observed within the study area may require variable management interventions. A key factor in determining this is the potential of natural recolonisation of indigenous species currently lying dormant in the seedbank and it is thus the focus of the following chapter.

Chapter 4

Seedbank Analyses

4.1 Introduction

The term seedbank can be defined here as all viable seeds lying on the surface or buried in the soil (Ferrandis et al., 2001) rather than those held aloft in the canopy. There is scarcely an area in plant ecology in which seedbanks do not play a role and a great number have direct implications for restoration ecology (Bakker et al., 1996). In degraded sites where restoration is required, the biota above-ground is not always analogous to the seeds present in the soil. Many species' seeds have evolved to persist in the soil for extensive periods of time; thus while the parent plants may have disappeared, a 'memory' (Cavers, 1995) of the original community remains below ground (Bakker et al., 1996). This has considerable implications for restoration ecologists because, if this pristine, or at least more original, community can be resurrected from resources available on-site, the project's costs (both monetary and labour-wise) can be greatly reduced (Holmes, 2002a). Additionally, the fear of introducing seeds from an external source, which may be genetically unsuitable and hybridize with indigenous and endemic species (Rebelo et al., 2011), is negated.

In practice, it is seldom as simple as removing alien plants then watching as a healthy community emerges from the soil. Often the activity which led to the degradation of the original pristine community corrupts the seedbank (Buhler et al., 1997). Ploughing is a particularly damaging activity (Joubert et al., 2009) and, as large tracts of Renosterveld have been converted to agriculture and subjected to ploughing, this has led to the degradation of many seedbank reserves in the Western Cape (Kemper, 1997). Many alien species, soon after establishment, dominate the seed rain and subsequently the seedbank (Holmes and Cowling, 1997; Holmes, 2002b). Thus, even after their above-ground removal, their physiology allows them to regenerate and out-compete the indigenous seeds.

Different seeds persist for varying amounts of times and in different soil layers (see Bakker, 1989; Thompson, 1992). Long-term persistent seeds, which remain viable in the seedbank for longer than five years, are the only seeds likely to contribute to the regeneration of degraded areas in need of restoration (Bakker et al., 1996). The duration and/or frequency of disturbance also impacts on the seedbank. In regularly disturbed habitats above and below-ground species composition is often similar, whereas in less disturbed areas there is frequently a lack of correspondence between the two as shorter-lived species are lost from the above-ground community but their seeds remain in the seedbank (Warr et al., 1993). In this way a seedbank can also be diagnostic of the health of environment through which one could 'read' ecosystem trajectories and inform management policies (Fenner and Thompson, 2005).

Many species have seeds stored in the seedbank which rely on a variety of specialized cues to synchronize germination (Bond, 1997). Often a disturbance such as fire is required to stimulate germination of species within the seedbank (Keeley, 1987; Keeley and Bond, 1997). The ecology behind this phenomenon is complex with some species receiving germination cues from the chemical constituents of smoke (Brown, 1993), although the ecological significance is unclear as research has shown smoke to stimulate germination in taxa from habitats that are not fire-prone (Pierce et al., 1995). Other fire-induced cues include fluctuating soil temperature, elevated oxygen levels and heat pulses (Cowling et al., 1997).

There is a dearth of data on Renosterveld seedbanks (Heeleman et al., 2013). Myrmecochores (ant dispersed) species are virtually absent (Cowling et al., 1997) and there are a larger proportion of re-sprouters in comparison to Fynbos (Kemper et al., 1999). Some species in the Fynbos Biome accumulate seeds in a seedbank stored in the canopy of the plant. The protective structures which protect the seeds open and release *en masse* after fire in a condition known as serotiny (Bond, 1997). Serotiny occurs in a variety of unrelated families and genera (Kruger, 1983; Lamont et al., 1991); however its occurrence, and the potential of fire in general to stimulate the seedbank in Renosterveld, has not been investigated (Heeleman et al., 2013). Heeleman et al. (2013), comparing the seedbanks of pristine Renosterveld to that of an old field and a pine plantation, found that the old field displayed a depleted seedbank ostensibly unsuited for restoration whereas the pine plantation had a seedbank more similar to that of the pristine Renosterveld. From their results the authors concluded that the pine plantation had a high recover potential in comparison to the abandoned field which had a low restoration potential. Similarly, Shiponeni (2003) reported a dominance of annual forbs and grasses in the seedbank of Renosterveld old fields at Elandsberg Nature Reserve with highest densities furthest away from natural vegetation. Geophytes were identified across her study area; however they are poorly dispersed and are thought to have survived in the soil as bulbs and only one shrub species was identified from the seedbank (Shiponeni, 2003). Terblanche (2011) investigated the effectiveness of passive restoration after the clearing of aliens in Peninsula Shale Renosterveld and found that a history of afforestation reduced species cover and diversity generally while favouring graminoids and annuals. Of course, this cannot only be attributed to seedbank dynamics as other factors would impact on the colonization of the cleared land, nevertheless it may be indicative of a depleted seedbank. The scant picture suggests a vulnerable seedbank that shifts rapidly towards a low diversity state dominated by annual alien grasses (Terblanche, 2011).

The third and final objective of this thesis is to establish the state of the seedbank in the different pre-defined vegetation states within the study area. The results presented in this chapter will not only contribute to the sparse knowledge on Renosterveld seedbanks, but will better inform us on the role of historical drivers on the seedbank; its current health and, in turn, likely trajectory shifts in communities; and the potential for re-establishment of indigenous species with a view to restoration.

4.2 Methods

4.2.1 In Situ Collection

At each of the four pre-defined study sites (Old Renosterveld, Lightly Degraded Renosterveld, Alien Pine Stand and Game Camp) ten duplicated soil samples were taken during the late winter/early spring (August, September) of 2011. As seed density is highest in the top 5 cm of soil (Roberts, 1981; Ferrandis et al., 2001), soil samples never exceeded a depth of 10 cm and each sample of approximately 500 g was labeled with its study site, number and future off-site treatment (i.e. unburnt or burnt). Additionally, corresponding above ground biomass was collected for each sample labeled to burn. The vegetation, both litter and living plants, was taken from the vicinity of each soil sample in an attempt to imitate the fuel that an *in situ* fire would use. Standardizing the amount of biomass was not possible but every effort was made to ensure parity by using identically sized plastic bags. All soil and vegetation samples were taken to a sterile laboratory and allowed to dry.

4.2.2 Ex Situ

It was unfeasible to perform burn experiments *in situ* due to the risk of the fire spreading, thus, in a safe and sheltered environment a small open-topped outdoor enclosure suitable for burning was fashioned using bricks. Soil samples labelled to burn were placed in large trays (42x20x9 cms) and placed in the enclave. The corresponding vegetation was placed on top of the baking tray and ignited. An attempt was made to measure the temperature of the soil with a heat probe, however the apparatus broke during the burning process and the data was insufficient to include in the results. Once all vegetation had burnt the trays were removed from the enclave and allowed to cool before the soil was transferred to a labelled punnet (23x16x5 cms). Control samples were concurrently transferred to punnets and labelled. All 80 punnets were placed in an irrigated greenhouse and monitored weekly for 6 months. The irrigation system was set so that the punnets received 10 minutes of light sprinkling twice a day at 6am and 6pm. Seedlings, once identified, were recorded and removed. Where numerous seedlings of a single unidentified species occurred, most were given a temporary name, recorded and removed while a few were allowed to grow to an identifiable size. While every attempt was made to limit contamination, the fast-natured life cycles typical of certain alien annuals may have resulted in the contamination of other punnets from these few mature individuals.

Once the species list had been created and seedling occurrence numbers recorded, various literature sources were consulted in an attempt to assign each species to a functional type which included the species growth form and height class (i.e. what height they may grow to; not their height in the greenhouse) and biological status according to the Red List of South African Plants (SANBI, 2012). Large Shrubs/Trees were species which grow higher than 2 m; Mid-High Shrubs grow to a height between 1 and 2 m while Low Shrubs are shrubs smaller than 1 m in height. Forbs and Graminoids (which included grasses, sedges and restioids) were both divided according to life history (e.g. annual or perennial).

4.2.3 Statistical Analysis

Alpha diversity (mean species richness for the ten punnets of each study site/treatment) and Gamma diversity (total species richness for the ten punnets of each study site/treatment) were calculated. A Brown-Forsyth test for homogeneity of variances was performed on the Alpha diversity data to determine homoscedasticity. Subsequently, a one way analysis of variance (ANOVA) was performed and a Post-Hoc Tukey HSD to determine whether any of the sites and treatments were significantly different to each other. All statistical analysis was performed using STATISTICA (StatSoft, 2004).

Plate 2: Photographs showing the chronology of the seedbank study: (a) The burn; (b) allowing the soil to cool; (c) placing the punnets in the greenhouse; and (d) the punnets one month later.

4.3 Results

A total of 54 species emerged from the seedbank, 46 of which were identified to species level. Twenty-seven of the identified species were indigenous species. The mean number of species per punnet was 6 (±2.54). Table 4.1 displays the mean species richness (Alpha diversity) and total species (Gamma diversity) recorded for the two treatments of the four study sites. No significant differences between study sites or treatments were found at the p<0.05 significance level. In terms of species richness, there were no significant differences between study sites or treatments. The highest number of species recorded (32) was found in Lightly Degraded Renosterveld soils in the unburnt treatment, while the lowest (15) was observed in the Alien Pine stand soils in the burnt treatment. Higher Gamma diversity was observed in unburnt treatments for Lightly Degraded Renosterveld, the Alien Pine stand and the Game Camp but not the Old Renosterveld site. Diversity should not in this case be mistaken for a healthy seedbank as in this measure no distinction was made between alien species and indigenous species. As Figure 4.1 illustrates, alien seeds are dominant in the seedbank. Only Old Renosterveld had a higher percentage of indigenous individuals germinate in the punnets and even there only marginally so. The Game Camp recorded the highest proportion of alien individuals, while Lightly Degraded Renosterveld and the Alien Pine stand both reported percentages of alien individuals between 60 and 70%. Old Renosterveld and the Game Camp showed increased alien numbers in unburnt treatments, whereas the opposite was true for Lightly Degraded and Alien Pine, although none of these differences were statistically significant.

Table 4.1: Mean Alpha diversities (±SD) and Gamma diversities across study sites and by treatment. OR=Old Renosterveld; LD=Lightly Degraded Renosterveld; AP=Alien Pine Stand; GC=Game Camp.

	Alpha Diversity (± SD)	Gamma Diversity
F Statistic	2.74	N/A
Significance level	P<0.05	N/A
OR Unburnt	6.30 (1.16)	16
OR Burnt	8.30 (2.16)	23
LD Unburnt	8.00 (2.36)	32
LD Burnt	5.40 (2.72)	20
AP Unburnt	5.10 (1.73)	18
AP Burnt	5.10 (1.45)	15
GC Unburnt	6.80 (3.00)	23
GC Burnt	6.40 (2.17)	21

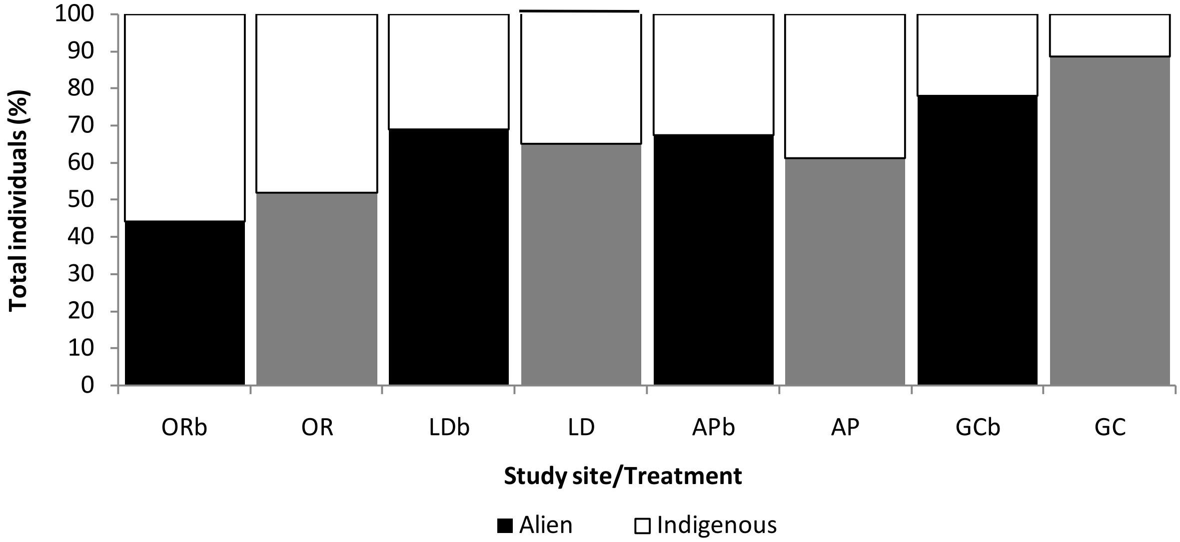

Figure 4.1: Bar graph showing mean proportion of alien and indigenous individuals counted for the two treatments of the four study sites.**OR**=Old Renosterveld; **LD**=Lightly Degraded Renosterveld; **AP**=Alien Pine stand; **GC**=Game Camp enclosure; **b**=burnt treatment.

Table 4.2: Species list in alphabetic order including information (where available) on family, species functional type, national red list status, number of occurrences in punnets, and whether the species was recorded in the phytosociological survey of the standing crop (see Chapter 3). Abbreviations used: **FT**=functionally type; **LST**=large shrub/tree; **MHS**=mid-high shrub; **LS**=low shrub; **ALS**=annual low shrub; **PF**=perennial forb; **AF**=annual forb; **PG**=perennial graminoid; **AG**=annual graminoid; **ND**=no data; **LC**=least concern; **SA**=South Africa; **WC**=Western Cape; **OR**=Old Renosterveld; **LD**=Lightly Degraded Renosterveld; **AP**=Alien Pine; **GC**=Game Camp; **b**=burnt; **phyto.=**presence in phytosociology standing crop.

Species Name	Family	FT	Status	OR	ORb	LD	LDb	AP	APb	GC	GCb	Phyto.
Anagallis arvensis L. subsp. arvensis	Primulaceae	AF	Naturalized Exotic	28	8	9	0	1	0	20	0	✓
Anthospermum spp. Unknown	Rubiaceae	MHS	indigenous	0	0	0	0	0	0	1	0	×
Aspalathus hispida Thunm. subsp. hispida	Fabaceae	MHS	LC-endemic to SA	0	0	1	3	0	0	0	0	✓
Athanasia crithmifolia (L.) L. subsp. crithmifolia	Asteraceae	MHS	LC-endemic to WC	0	0	1	0	0	0	0	0	✓
Avena fatua L.	Poaceae	AG	Naturalized Exotic	0	0	0	0	0	0	11	7	✓
Brachypodium distachyon (L.) P.Beauv	Poaceae	AG	Naturalized Exotic	0	0	0	0	0	0	24	12	✓
Briza maxima L.	Poaceae	AG	Naturalized Exotic	0	0	3	0	5	2	8	5	✓
Briza minor L.	Poaceae	AG	Naturalized Exotic	0	1	2	0	0	0	3	6	×
Centella asiatica (L.) Urb.	Apiaceae	AF	LC-not endemic to SA	0	0	12	2	0	0	0	0	×
Conyza bonariensis (L.) Cronquist	Asteraceae	AF	Naturalized Exotic	14	10	8	7	5	21	15	12	×
Conyza scabrida DC.	Asteraceae	MHS	LC-not endemic to SA	14	9	1	0	1	0	0	0	✓
Cotula turbinata L.	Asteraceae	AF	LC-endemic to SA	0	0	0	0	0	2	0	0	×
Crassulaceae spp. unknown	Crassulaceae	LS	Indigenous	1	0	0	0	0	0	1	1	×
Cynosurus echinatus L.	Poaceae	AG	Naturalized Exotic	0	2	32	0	2	0	0	0	×
Cyperaceae spp. Unknown	Cyperaceae	AG	Indigenous	423	231	39	0	1	2	1	1	-
Diascia capensis (L.) Britten	Scrophulariaceae	AF	LC-endemic to WC	0	0	14	0	0	0	0	0	×
Echium plantagineum L.	Boraginaceae	ALS	Naturalized Exotic	0	0	0	0	0	0	2	0	✓
Euphorbia peplus L.	Euphorbiaceae	AF	Naturalized Exotic	0	0	0	11	2	1	0	1	✓
Euryops abrotanifolius (L.) DC.	Asteraceae	LS	LC-endemic to SA	0	0	9	0	2	0	0	1	✓
Ficinia filiformis (Lam.) Schrad.	Cyperaceae	PG	LC-endemic to SA	0	0	4	0	0	0	0	0	✓
Geranium molle L.	Geraniaceae	AF	Naturalized Exotic	0	17	0	40	0	3	0	0	✓
Hypericum canariense L.	Hypericaceae	LS/T	Naturalized Exotic	357	82	0	0	0	0	0	0	✓
Isolepis levynsiana Muasya&D.A.Simpson	Cyperaceae	AG	LC-endemic to SA	0	1	0	0	0	0	0	0	×
Isolepis marginata (Thunb.) A.Dietr	Cyperaceae	AG	LC-not endemic to SA	9	29	0	0	0	1	0	0	×
Lactuca serriola L.	Asteraceae	AF	Naturalized Exotic	1	4	1	0	3	0	0	0	×
Lobelia anceps L.f.	Lobeliaceae	PF	LC-not endemic to SA	0	2	3	0	0	1	5	1	×
Lolium perenne L.	Poaceae	AG	Naturalized Exotic	0	0	1	0	0	0	58	1	×
Lotononis cf. prostrata	Fabaceae	LS	Indigenous	0	0	3	3	0	1	0	0	×
Lotus angustissimus	Fabaceae	AF	Naturalized Exotic	0	1	4	8	0	0	0	0	×

Species Name	Family	FT	Status	OR	ORb	LD	LDb	AP	APb	GC	GCb	Phyto.
Myosotis arvensis (L.) Hill	Boraginaceae	AF	Naturalized Exotic	0	12	0	0	0	0	0	0	✓
Oxalis compressa L.f. var. compressa	Oxalidaceae	PF	LC-endemic to WC	3	0	10	0	12	0	0	4	✓
Oxalis corniculata L.	Oxalidaceae	AF	Naturalized Exotic	35	64	58	34	6	69	86	40	×
Oxalis pes-caprae L. var. pes-caprae	Oxalidaceae	PF	LC-not endemic to SA	0	0	1	0	0	0	0	0	✓
Pelargonium myrrhifolium (L.) L'Her. var. myrrhifolium	Geraniaceae	LS	LC-endemic to SA	0	0	0	2	0	0	0	0	✓
Pelargonium spp. Unknown (hybrid)	Geraniaceae	LS	Indigenous	0	0	1	3	0	0	0	0	×
Pennisetum clandestinum Hochst. Ex Chiov.	Poaceae	AG	Naturalized Exotic	0	3	3	2	0	0	8	0	×
Picris echioides L.	Asteraceae	AF	Naturalized Exotic	33	8	4	39	11	2	5	22	✓
Poaceae spp. Unknown	Poaceae	AG	-	0	0	0	0	18	3	2	43	-
Pseudognaphalium luteoalbum (L.) Hilliard & B.L.Burtt	Asteraceae	AF	ND	2	68	3	8	29	48	7	26	✓
Pseudognaphalium undulatum (L.) Hilliard&B.L.Burtt	Asteraceae	AF	LC-not endemic to SA	0	0	0	0	2	0	0	0	×
Pteris dentata Forssk.	Pteridaceae	PF	LC-not endemic to SA	0	0	0	0	7	0	0	0	×
Restionaceae spp. Unknown	Restionaceae	PG	Indigenous	1	0	0	0	0	0	0	0	-
Selago corymbosa L.	Scrophulariaceae	LS	LC-endemic to SA	0	0	1	6	0	0	0	0	✓
Senecio pterophorus DC.	Asteraceae	MHS	LC-not endemic to SA	6	2	11	0	0	0	13	2	✓
Senecio pubigerus L.	Asteraceae	LS	LC-endemic to WC	0	0	0	0	0	0	2	6	✓
Solanum nigrum L.	Solanaceae	AF	Naturalized Exotic	0	1	0	0	0	0	0	0	✓
Sonchus oleraceus L.	Asteraceae	AF	Naturalized Exotic	10	24	11	8	8	18	8	12	✓
Taraxacum officinale Weber	Asteraceae	PF	Naturalized Exotic	0	0	0	1	4	0	12	2	✓
Trifolium angustifolium L. var. angustifolium	Fabaceae	AF	Naturalized Exotic	0	0	4	0	1	0	0	0	×
Trifolium dubium Sibth.	Fabaceae	AF	Naturalized Exotic	1	6	10	11	0	0	3	10	×
Trifolium glomeratum L.	Fabaceae	AF	Naturalized Exotic	0	7	36	1	0	0	0	0	×
Uknown Species 1	-	AF	-	0	0	1	0	0	0	0	0	-
Unknown Shrub 2	-	-	Naturalized Exotic	0	0	0	2	0	0	0	0	-
Unknown Species 3	-	AF	-	0	0	0	1	0	0	0	0	-

In terms of seedbank density, Figure 4.2 illustrates the disparity in total amounts of seedlings recorded in Old Renosterveld compared to the other three sites. The Old Renosterveld, Lightly Degraded Renosterveld and the Game Camp all exhibited higher seedling emergence in unburnt treatments, whereas the reverse was recorded in the Alien Pine stand. It should be emphasized that none of these differences were significant.

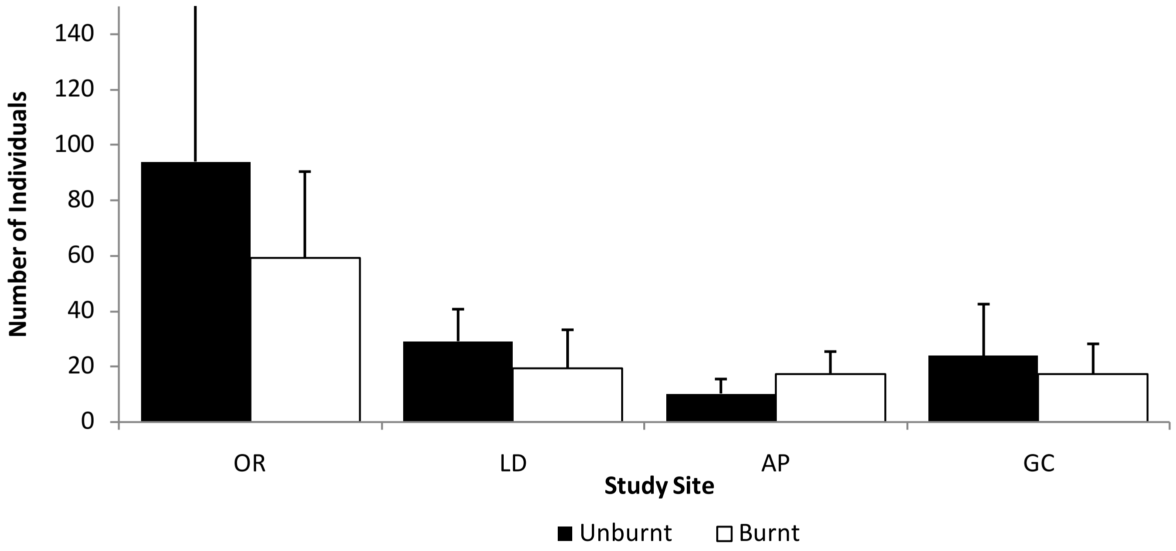

Figure 4.2: Bar graph showing mean total number of individuals (± SD) for two treatments of the four study sites. **OR**=Old Renosterveld; **LD**=Lightly Degraded Renosterveld; **AP**=Alien Pine stand; **GC**=Game Camp enclosure.

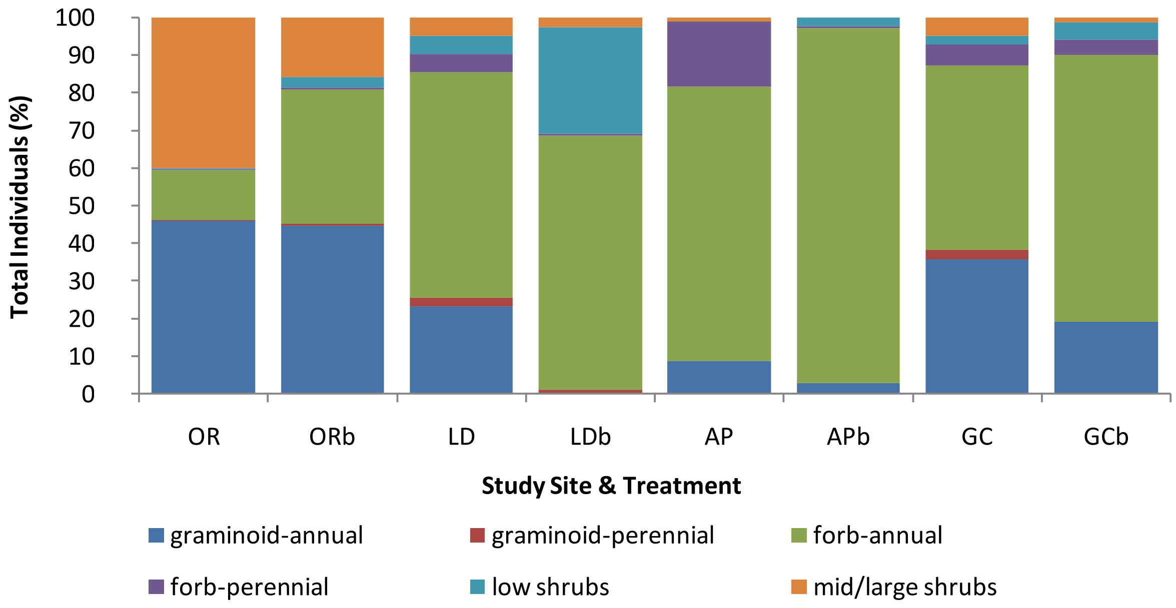

Figure 4.3: Bar graph showing mean percentage plant functional type for the two treatments (b signifies burnt treatment) of the four study sites. **OR**=Old Renosterveld; **LD**=Lightly Degraded Renosterveld; **AP**=Alien Pine stand; **GC**=Game Camp enclosure; **b**=burnt treatment.

As illustrated by Figure 4.3, annual forbs dominated the identified seedlings in the Lightly Degraded Renosterveld, Alien Pine stand and Game Camp, while annual gramminoids dominated in the Old Renosterveld site. Mid/large shrubs were found in greatest numbers in the Old Renosterveld site; however the majority of these individuals were the alien Canary St. Johns Wort (*Hypericum canariense*).

4.4 Discussion

The discussion is divided into four sections for the sake of clarity. Firstly, the effect of the burn treatment on the seedbank is appraised. Secondly, the variation in alien and indigenous species seedling emergence is discussed before thirdly, the differences between the above-ground communities and the corresponding seedbank communities are explored. Finally, the results are discussed in relation to the restoration potential of the study area.

4.4.1 Treatment

Overall, there were no statistically significant differences between unburnt and burnt treatments, a result in common with Heeleman et al.'s (2013) experiment using a smoke primer on Renosterveld seedbanks. Despite this, certain trends were evident and are worthy of further discussion. Only the Old Renosterveld site exhibited an increase in Gamma diversity in the burnt treatment, whereas the Lightly Degraded Renosterveld, the Alien Pine stand and the Game Camp all displayed a decrease in Gamma diversity in the burnt treatments. Burning decreased total seedling emergence in Old Renosterveld, Lightly Degraded Renosterveld and the Game Camp but not in the Alien Pine stand which had a marginal increase in seedling emergence in the burnt treatment. The relatively dense seedbank exhibited in the Old Renosterveld site is predominantly a result of the abundance of an unidentified Cyperaceae species and *Hypericum canariense* (Canary St. Johns Wort). It is possible that the Cyperaceae species was *Isolepis marginata* that did not flower in the six month greenhouse germination period as this species was also recorded in the Old Renosterveld seedbank. *Hypericum canariense* is an alien shrub native to the Canary Islands. A single plant can produce hundreds of flowers, and individual fruits can yield thousands of minuscule seeds (Dlugosch and Parker, 2008). The general trend of fire reducing seedling emergence suggests that, in areas within the study site dominated by alien species (such as the Alien Pine stand and Game Camp), burning post-clearing may be a policy that will actively reduce the total number of aliens that re-emerge from the seedbank.

With regards to the composition of the seedbank in terms of the alien and indigenous constituents, burning did not have a significant effect. There was however a reduction in proportion of alien species in the Old Renosterveld and Game Camp; however the opposite trend was recorded in the Lightly Degraded Renosterveld and Alien Pine stand. Burning the soil reduced annual graminoid percentage in Lightly Degraded Renosterveld, the Alien Pine stand and the Game Camp. In Old Renosterveld the percentage remained constant between burnt and unburnt treatments although the graminoid element in Old Renosterveld consisted predominantly of Cyperaceae rather than annual grasses which make up the majority of the graminoid element in the other three sites. This apparent reduction in annual grass seed viability following fire could be of use for conservation purposes if the reduction of alien grass is required. It should be noted that although it appears that fire reduced grass seedling emergence, the grass life form is adapted for rapid recovery following a fire as there is little above-ground structural tissue and grasses frequently re-sprout vegetatively (D'Antonio and Vitousek, 1992) therefore burning my hinder the removal of grasses. Conversely, burning increased the percentage of annual forbs across all of the sites although this trend was less pronounced in Lightly Degraded Renosterveld and the Alien Pine stand.

Certain species had clear responses to burning. The annual alien forb, *Anagallis arvensis*, was reduced by burning across all four sites while the unknown Cyperaceae species was significantly reduced by burning in Old Renosterveld and Lightly Degraded Renosterveld (only a few individuals emerged in the other two sites). The invasive alien shrub *Hypericum canariense*, found exclusively in the Old Renosterveld site, was also reduced by fire as was *Senecio pterophorus* an indigenous but weedy species associated with disturbed areas (Garcia-Serrano et al., 2004). In the Game Camp site the annual alien grass, *Lolium perenne*, was significantly reduced by burning. This corresponds with data from Valbuena and Trabaud (2001) who investigated the seedbank of a Mediterranean ecosystem following a fire. The authors found that *Lolium perenne* and two *Senecio* species, although present at the site in the standing crop, did not grow from the scorched seedbank.

There was a pattern of increased seedling emergence after burning in two species. The alien forb, *Geranium molle,* was not present in any of the unburnt treatments but was recorded in the burnt treatments of Old Renosterveld, Lightly Degraded Renosterveld and the Alien Pine stand. Additionally *Pseudognaphalium luteo-album*, an annual forb increased in burnt treatment across all four sites. Both are pioneer weedy species associated with disturbed landscapes, however there are no known records of them dominating an area and are most probably relatively short lived (De Lillis and Federici, 2009; Saayman and Botha, 2008).

Fire is an integral component of Renosterveld dynamics (Milton, 2007). However, due to its increased graminoid component in comparison to the adjacent Fynbos, and the higher proportion of re-sprouters in relation to re-seeders (Kemper et al., 1999), it may be that the subterranean seedbank is not as essential in post-fire recruitment as has been observed in Fynbos which has a high proportion of species which re-seed (Cowling et al., 1997). It is hard to draw any rigid conclusions on the role of fire on Renosterveld seedbanks due to the degraded nature of the study area. Additionally, the off-site burning may not have replicated a natural wild fire. In particular, the isolated nature of the burn experiment may have resulted in a cooler fire. Fire intensity is a known factor in seed germination in Fynbos (Cowling et al., 1997) and heat-stimulated germination of certain species can fail if the fire is to cool (Bond, 1997).

4.4.2 Alien vs. Indigenous Species

Of the 54 species that were identified, precisely half were naturalized exotics. The majority of these alien species were annual grasses and forbs whereas indigenous species had a higher representation of low and mid-high shrubs. All of the sites and treatments, with the exception of the Old Renosterveld burnt treatment, had a higher percentage of alien seedlings emerge from the soil. Old Renosterveld exhibited the lowest percentage of alien seedling emergence and the Game Camp site had the highest percentage. The Lightly Degraded Renosterveld and the Alien Pine stand had similar percentages of alien seedlings and fell between the two extremes. The high proportion of alien plants do not come as a surprise for the Alien Pine stand and Game Camp which have both been dominated by alien species for an extended period of time; however it surprising and somewhat disconcerting to see such high numbers for the less degraded Old Renosterveld and Lightly Degraded Renosterveld sites. The link between the above-ground community and seedbank will be addressed in further detail in the following section. To re-iterate the observation made from the treatment section, burning did not have a significant effect on alien and indigenous species percentages across the four study sites, nor was there a uniform response of either an increase or decrease in alien seedling emergence.

There was a general trend of alien species being ubiquitous throughout the four study sites. Species which are examples of this include *Anagallis arvensis*, *Conyza bonarienses*, *Oxalis corniculata*, *Picris echioides*, *Sonchus oleraceus*, *Briza* species, *Trifolium* species and *Pseudognaphalium luteo-album*. *Pseudognaphalium luteo-album* is an interesting species as its origins are uncertain (SANBI, 2012) therefore it cannot be confidently described as alien or indigenous. Regardless, it is a weedy, pioneer species associated with disturbed environments (Saayman and Botha, 2008) thus it was included in the aforementioned list. There were some notable exceptions to the ubiquitous alien pattern. The alien grasses *Avena fatua*, *Brachypodium distachyon* and *Lolium perenne* were found solely in the Game Camp while the large shrub *Hypericum canariense* (Canary St. Johns Wort) was found exclusively, but in abundance, in the Old Renosterveld site. This suggests that these alien grass species are fairly localized, constrained to a site where the species are found within the standing crop. Similarly, *H. canariense* seeds are abundant but limited to where adult plants are present and it is recommended that efforts to eradicate the species are performed while it is still localized. A second option is that *H. canariense* is favoured by the lack of fire which is a distinctive feature of the Old Renosterveld site and that an increase in fire frequency is a useful mechanism of control.

The Lightly Degraded Renosterveld had the most occurrences of indigenous species occurring in one site only which may be an indication that more regular burning favours a healthier seedbank. Species included the shrubs *Athanasia crithmifolia*, *Lotononis* cf. *prostrata*, *Selago corymbosa* and the annual forbs *Centella asiatica* and *Diascia capensis*. Two indigenous shrubs, *Aspalathus hispida* and *Senecio pubigerus*, were found exclusively in the Game Camp site while the indigenous forbs *Cotula turbinata* and *Pteris dentata* were present solely in the Alien Pine stand seedbank. Interestingly, the only indigenous species to be found exclusively in the Old Renosterveld seedbank was *Isolepis marginata* although the unknown Cyperaceae species and *Conyza scabrida* were abundant in the Old Renosterveld seedbank in comparison to their scant presence in the other three sites. The lack of fire experienced by the Old Renosterveld site appears to have negatively affected the indigenous seedbank. It may be better for the site's long term viability for it to burn as the re-seeding component of its standing crop may senesce if fire remains absent.

The study area has a long history of environmental degradation, which included periods of alien invasion. Indeed, the Alien Pine stand and the Game Camp should be considered currently to be invaded environments. Alien invasion has been shown to significantly reduce seedbank density and diversity in the Fynbos Biome (Holmes and Cowling, 1997; Holmes, 2002b). In addition, Holmes (2002b) reports that invasion also effects seedbank species composition. The shift in composition was not uniform across sites or vegetation type although in one particular site invaded seedbanks had a lower proportion of shrubs and a higher proportion of graminoids and forbs (Holmes, 2002b). Shiponeni (2003) reported a seedbank dominated by annual forbs and grasses with minimal shrub species in Renosterveld old fields. In general, Holmes (2002b) found that ephemeral and short-lived species were dominant in the seedbanks at invaded sites which is indicative of the long-term persistence of their propagules. This corresponds with Dreber and Esler's (2011) assertion that areas with a long history of degradation favour small-seeded annuals and Jones and Esler's (2004) description of seedbanks in degraded regions in Southern Africa which are characterized by a dearth of palatable and perennial species. As the literature demonstrates, the seedbank of the study area is consistent with seedbanks from degraded regions elsewhere in the region. This is unsurprising for the sites currently invaded (Alien Pine stand and Game Camp) but more unexpected for the more indigenous Old and Lightly Degraded Renosterveld sites.

The general observation of a dominant alien ephemeral seedbank may only translate into a few alien adults as the few, more resilient indigenous shrub species out-shade or out-compete the more transient alien species. Re-sprouters may also out-compete the transient alien species. Additionally, seeds may enter the system from a source other than the seedbank for example via wind transport or in the spoor of animals (Shiponeni, 2003). Only a longer term study could shed light on whether this hypothesis is accurate, however it is encouraging that, following the 2009 fire in the Lightly Degraded Renosterveld, the site returned to a state dominated by indigenous species which suggests that the state of seedbank may not play such an important role in successional ecology in Peninsula Shale Renosterveld. The link between the above-ground community and corresponding seedbank is discussed in more detail below.

4.4.3 Seedbank Communities vs. Above-Ground Communities

Less than half the species recorded in the seedbank were identified during the phytosociological survey conducted on the above-ground communities. Of the indigenous species recorded there was a pattern of shrubs tending to occur in both the seedbank and the above-ground community while more indigenous forb species were found solely in the seedbank. The only shrubs found exclusively in seedbank were an *Anthospermum* species, a *Crassulaceae* species and *Lotononis cf. prostrata* whereas *Aspalathus hispida*, *Athanasia crithmifolia*, *Euryops abrotanifolius*, *Pelargonium myrrhifolium*, *Selago Corymbosa*, *Senecio pterophorus* and *Senecio pubigerus* were all also found in the above-ground community. In addition, all the aforementioned species, with the exception of *Euryops abrotanifolius*, were found within the seedbank of the corresponding study site i.e. there were no instances of a species occurring in the Game Camp seedbank that were not recorded during the phytosociological study in the Game Camp.

In contrast to shrub species, there were many indigenous forb species that fell into the seedbank-only category. These include *Centella asiatica*, *Cotula turbinata*, *Diascia capensis*, *Lobelia anceps*, *Pseudognaphalium undulatum* and *Pteris dentata*, whereas *Oxalis compressa* and *Oxalis pes-caprae* were the only indigenous forbs also found in the above-ground community. These results are not unexpected as pioneer forb species will gradually be succeeded by larger shrub species in natural conditions. In addition, the transient life history of annuals means that they may have been absent from the community during the phytosociological survey and the smaller herbaceous species, when not in flower, may have been overlooked.

Nine of the alien species identified in the seedbank were absent from the phytosociological survey. These included grasses such as *Briza minor*, *Cynosurus echinatus*, *Lolium perenne* and *Pennisetum clandestinum* and the annual forbs *Conyza bonarienses*, *Lactuca serriola*, *Lotus angustissimus*, *Oxalis corniculata* and three *Trifolium* species. As discussed earlier, the ephemeral life history of annual species means that individuals may have been missed due to the timing of the phytosociological survey. There are particular alien species worthy of discussion. *Conyza bonarienses* and *Oxalis corniculata* were both ubiquitous and relatively abundant in the seedbank. Both are pioneer weedy species characterized by small seeds and annual life histories occurring world-wide in old fields (Lovett-Doust et al., 1985; Pieur-Richard et al., 2000). It is possible that after a disturbance event they may proliferate in the study site; however it is more likely that after emerging from the seedbank to colonize an area, they will gradually be out-competed by an influx of more hardy indigenous species. Nevertheless, their ability to become pests should be noted and their population post-disturbance monitored particularly in the more degraded Alien Pine stand and Game Camp.

A potentially troublesome species is *Hypericum canariense*. *Hypericum canariense* is a listed environmental weed in Australasia (University of Queensland, 2011) and the USA (Cal-IPC, 2006) and it appears that it has established itself in the seedbank of the Old Renosterveld stand. It was observed in low densities in the Old Renosterveld site during the phytosociological survey but its dominance in the emerging seedlings is a cause for concern as a disturbance at the site may provide an opening for the species to further establish itself. The burning treatment did significantly reduce seedling emergence in the seedbank which is encouraging as the most likely disturbance event in Old Renosterveld would be a fire which would hopefully reduce the establishment of seedlings.

Holmes and Cowling (1997) conducted an in-depth study on above-ground communities and corresponding seedbanks in invaded and uninvaded Fynbos vegetation sites. Similarly to the results from this study, they found that indigenous species detected exclusively in the seedbank tended to be forbs and annuals, whereas shrub species were more likely to be found in both the seedbank and the standing crop. Warr et al. (1993) noted that in disturbed areas seedbank composition is often similar to above-ground communities. This was not case in the study area overall, however the two more degraded sites, the Alien Pine Stand and Game Camp, did have a slightly higher percentage of species in the seedbank which were recorded in the corresponding phytosociological survey compared with the overall figure.

A further determinant of seedbank size and composition that has not been addresses is that of seed predation by rodents. Seed predation is considered an important determinant of seedbank size in fire-prone shrublands (Parker and Kelly, 1989). Rodent data from the study area recorded densities ranging from 102 individuals/ha in the Game Camp to 206 individuals/ha in the Old Renosterveld stand (Dreyer, 2012). The high numbers, particularly in the less degraded Old Renosterveld site, suggests that seed predation could impact on seedbank dynamics, potentially favouring small seeded species (such as annuals) and partly explain the relatively small proportion of many of the longer-lived species.

4.4.4 Implications for Restoration

Reduced diversity, density and a domination of ephemeral species in the seedbank are all indicative of a degraded ecosystem. It is perhaps surprising that the relatively undisturbed Old Renosterveld site and, to a lesser extent, the Lightly Degraded Renosterveld have seedbanks with similar compositions to the degraded Alien Pine stand and the Game Camp. This may be a result of the relatively low persistence of long-lived species in the seedbank (Holmes and Cowling, 1997) in addition to an increased seed predation by rodents and a general skew towards a resprouting community in Renosterveld. It may be that the most recent year’s seed inputs are the most important determinant of recruitment post-disturbance for longer-lived indigenous species (Pierce and Cowling, 1991). It is worth reiterating that despite a fire three years ago, the Lightly Degraded Renosterveld is not currently dominated by species prevalent in its seedbank. Re-growth of re-sprouters, influx of indigenous seeds from other vegetated areas or the presence of an indigenous seedbank not accurately represented during this experiment prevented an ecosystem ‘threshold change’ (Hobbs and Norton, 1996) from a shrubland to system dominated by annual forbs and grasses. Shiponeni (2003) demonstrated that the return of wind and dung dispersed indigenous plant species to old fields in Renosterveld are not limited by seed availability. However, it has also been reported that indigenous seedlings in recovering Renosterveld compete for resources with grasses and the competition negatively affected seedling growth and survival (Midoko-Iponga et al., 2009).

The seedbank study also highlights areas of concern and attention regarding the presence of certain alien species. *Hypericum canariense*, while currently limited to the Old Renosterveld site, has been shown to be a pest species elsewhere and it is advisable to eradicate it as soon as possible to prevent it from further gaiming a foothold in the study area. The recommended method is a burn followed by manually clearing any emerging seedlings or the application of herbicides. Fortunately, the site requires a burn regardless of the presence *H. canariense* however the post-fire clearing will be vital to prevent re-establishment.

Compared to the healthier Old and Lightly Degraded Renosterveld sites, the future of the Alien Pine stand and Game Camp is less certain. It is less likely that following the removal of the current alien species the systems will return to a lightly degraded state as observed in the Lightly Degraded Renosterveld as the sites have been too damaged for too long. After the removal of the standing crop of alien species, it will be necessary to reduce the re-emergence from the seedbank of alien grasses and forbs as the reduction of herbaceous competition significantly accelerates shrubland recovery in old fields in Renosterveld (Midoko-Iponga et al., 2009). Concurrently, it will be necessary to reintroduce longer-lived indigenous species through a seed collecting and sowing programme. It is likely that the re-sowing initiative will need to be accompanied by rodent exclusion strategies as a result of the high rodent densities reported (Dreyer, 2012) and constant monitoring if the restoration of the area is to be a success.

Chapter 5

Conclusions

5.1 Introduction

During the two years of researching, conducting fieldwork and writing up this thesis countless people have enquired about the nature of my topic. Upon hearing my answer they invariably respond animatedly asking about the fate of the animals which they remember inhabiting the lower slopes of Devil's Peak. Indeed, family from overseas have remarked that the first impression they had of Cape Town was driving from the airport towards the city centre and seeing herds of animals within a few hundred meters of the freeway. My study area truly has been, and has the potential to be, a landmark feature of the Cape Town metropolis. Unfortunately, in its current state, what exists is vegetation in various degrees of degradation and a paltry number of Zebra enclosed in the Game Camp. There is hope for the area though as it is conserved within the Table Mountain National Park and with sufficient funding and will-power it has the potential to be restored and reclaim its position as one of the city's most cherished landmarks. To achieve this however, the vegetation of the study area will require intervention and restoration. The results of my thesis have made this clear and elucidated key points of entry and concern while simultaneously shedding some light on the ecological functioning of Peninsula Shale Renosterveld. This final chapter provides a brief overview of the key results from the previous chapters and considers them in relation to the broader literature, such as their implications towards understanding the ecological drivers of Peninsula Shale Renosterveld and how these inform restoration options.

5.2 Overview of Key Results

It is clear that certain activities have had specific effects on the environment and the historical analysis most certainly revealed significant factors in driving the system to what we see today. The use and control of fire by humans has seen changes to the fire regime throughout the area. In some areas, such as the Old Renosterveld site, fire has been absent for decades whereas in the Lightly Degraded Renosterveld site there is a strong possibility that for periods in the last half-century fires have occurred at a higher frequency than the hypothesized natural fire regime. Fire is a key ecosystem driver in Renosterveld (Bond et al., 2004) and its absence has resulted in a larger proportion of longer-lived, large shrub species being present at the Old Renosterveld site in comparison to the Lightly Degraded Renosterveld site. The fire return period of the Lightly Degraded Renosterveld site is more frequent and patchy and too frequent fires, along with ecosystem engineering in the early 90s, may have resulted in the elimination of certain re-seeding species from the community contributing to the relatively poor (in comparison with other Renosterveld sites) diversity indices.

The effects of the afforestation programmes of the previous century are still evident today with the Alien Pine stand situated within a remnant of an earlier plantation. The literature is explicit in the impact afforestation has on indigenous flora (Richardson et al., 2000; Vila et al., 2010; van Wilgen and Richardson, 2012) and the effects on the site are obvious with large amounts of bare ground present and the vegetation dominated by annual alien grasses resulting in low species richness and a high Sodium soil content. Although the plantations have generally been eradicated from the rest of the study area, their impacts are still in evidence today in their legacy of reduced diversity. Importantly, the results of the abiotic analysis of the study site, with the exception of the saline Alien Pine stand soil, show that the soil chemistry is comparable to the results recorded in other Renosterveld sites. This indicates that abiotic variables, so often a stumbling block in restoration efforts (Bakker and Berendse, 1999) should not be an issue in restoring the vegetation of the study area.

The effects of management strategy are most obvious in the Game Camp site where for decades it has been managed as a grazing paddock or parkland. This has resulted in a drastic reduction in diversity as virulent alien annual grasses have come to dominate and have excluded indigenous species. With the recent removal of the majority of the grazing animals the grasses have proliferated and the site bears all the characteristics of an old field (Cramer and Hobbs, 2007). As a result the Game Camp is the site worst off in terms of floral diversity. Compared to the alien-dominated Alien Pine stand and Game Camp sites, the Lightly Degraded and Old Renosterveld sites are much more diverse and are dominated by indigenous species. However, they fare poorly in comparison with other Renosterveld studies and the majority of the indigenous species are common cosmopolitan species. As such, the study area currently has little conservation value in terms of promoting biodiversity within the region. Nevertheless, the maintenance of the functional indigenous Renosterveld ecosystems recorded in the Old Renosterveld and Lightly Degraded Renosterveld sites is of importance and has a multitude of benefits such as the maintenance of environmental integrity (Diaz et al., 2006) and increased resilience in the face of global climate change (Harris et al., 2006).

The seedbank of the study area was investigated to assess its potential role in future restoration initiatives as the literature reports that seedbanks have been critical elements in successful restoration work elsewhere (Bakker et al., 1996; Holmes and Richardson, 2002). Unfortunately the results revealed a degraded seedbank dominated by alien annuals with little value for restoration projects. The consequence of this is that if sites such as the Game Camp and Alien Pine stand are to be restored, indigenous seeds will have to be sourced from elsewhere and sown manually which increases the expense of the restoration effort (Holmes 2002a). There is a possibility however, that the soil seedbank in Renosterveld ecosystems may not play as important a role compared to that of Fynbos. This is potentially due to the relative abundance of re-sprouting shrub species (Kemper et al., 1999) and the ability of many species which utilize a wind dispersal mechanism to re-colonize an area from adjacent vegetation (Shiponeni and Milton, 2006). However, even if the role of the seedbank is reduced, without a standing crop of appropriate diversity seeding would still be necessary in a successful restoration project.

5.3 Implications: Understanding Ecological Drivers and Informing Future Restoration Work

There is a severe lack of data surrounding the ecosystem drivers of Peninsula Shale Renosterveld, however this project has shown that, by and large, the ecosystem drivers of the vegetation type fit in broadly with Milton's (2007) model for general Renosterveld drivers. Figure 5.1 is an annotated version of Milton's (2007) model on which the four vegetation states of the study area have been superimposed. The figure provides a useful illustration as I discuss the ecological drivers that have brought the study sites to their current position and what management actions can be taken to restore them towards a healthier state.

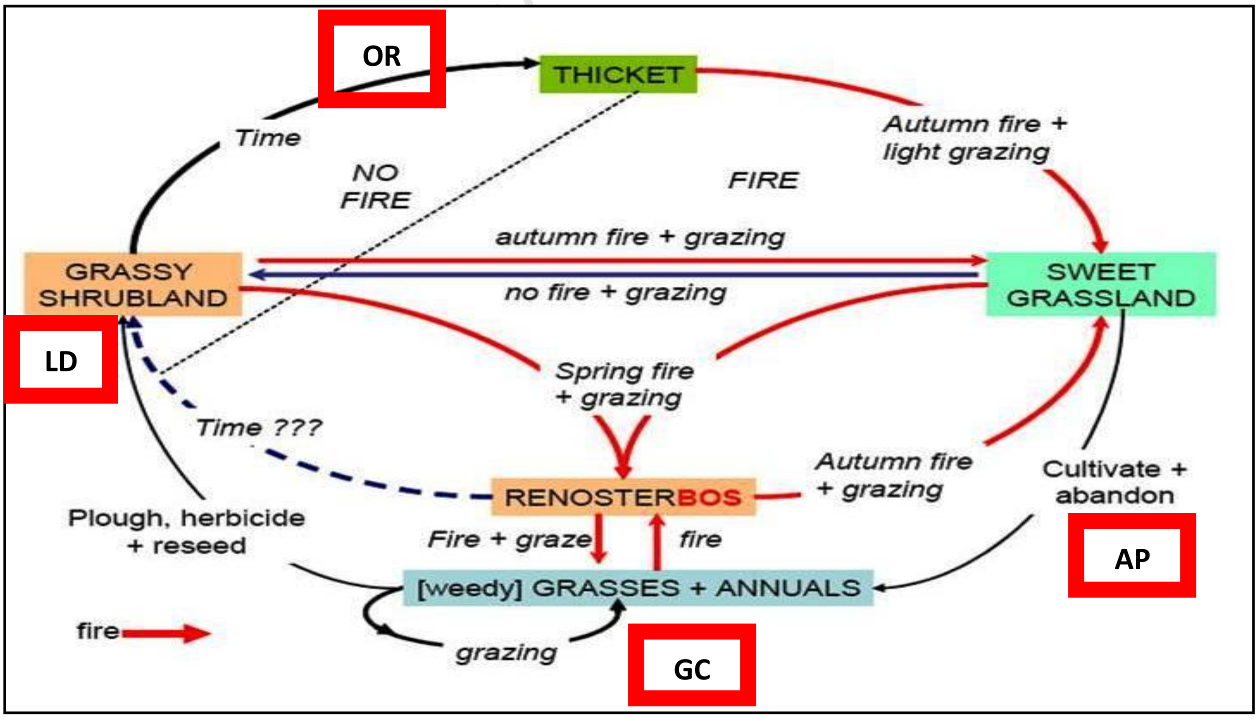

Figure 5.1: Conceptual model illustrating how fire, grazing and other disturbances may interact to change the composition of a Renosterveld ecosystem. The four vegetation states of the study area have been added in the position which best describes their current position. **OR**=Old Renosterveld; **LD**=Lightly Degraded Renosterveld; **AP**=Alien Pine stand; **GC**=Game Camp enclosure (Adapted from Milton, 2007).

The current nature of each of the four vegetation states can be ascribed to a specific land-use history and management policy. By recognizing this and utilizing Milton's (2007) model it is possible to intervene and alter the current ecosystem trajectories if restoration endeavours require this. The Old Renosterveld site, as a result of remaining fire-free for an extended period of time, is on a trajectory towards a thicket. Although the thicket would be dominated by indigenous shrubs and trees, the understory diversity found in Renosterveld would be lost and as the total area occupied by Peninsula Shale Renosterveld is so small this is undesirable. Additionally, the seedbank study showed the dissimilarity between the standing community and the seedbank and the general poor health of the seedbank. If the site continues to remain fire-free, large shrubs may senesce and the community will be unable to rejuvenate itself. Although the need to burn the Old Renosterveld site is clear, the implementation is fraught with difficulties due to the site's proximity to the university campus. Nevertheless, if SANParks wishes to conserve this fragment of Peninsula Shale Renosterveld a controlled burn needs to be performed in the near future. As the natural fire season for Renosterveld is autumn, it is advised that the burn takes place in April and May. Additionally, the burn treatment used in the seedbank experiments was potentially not hot enough therefore ideally any controlled burn would be hotter than that of the seedbank trial. Conversely, it could be argued that due to its proximity to the university campus, to have a fire-prone Renosterveld patch here is undesirable and by keeping fire out the thicket state may eventually become a low woodland. However, when the site does burn, as it may every century or so, the fire would be much hotter than a Renosterveld fire. The final decision would lie with the management who would be advised to consult with university authorities.

The Lightly Degraded Renosterveld is probably the site closest to the desired state as frequent fires have maintained the grassy shrubland of Milton's (2007) model. Despite the length of time since the area was last subjected to plantations, the site appears less diverse than other Renosterveld sites (Cowling, 1983a). Additionally, the ecosystem engineering which occurred in the early 1990s through the planting of *Chrysanthemoides* (Moll et al., 1991) may have further contributed to the reduced diversity observed. Nevertheless, the community structure following the latest fire in 2009 suggests that the site is relatively healthy. Obviously the presence of alien species is not ideal and they need to be continually monitored and, in the best case scenario, removed completely. Despite this, the Lightly Degraded Renosterveld is the most easily manipulated of the four sites depending on what management deems desirable. If the plan to increase the current Game Camp and re-stock it with indigenous fauna is resurrected (discussed in section 5.4), the Lightly Degraded Renosterveld site can be manoeuvred towards a grassier state through frequent autumn burning and light grazing (see figure 5.1) which will benefit the reintroduced game. If the plans for the expansion remain suspended and grazing continues to be nearly negligible, then fire becomes the most important ecological driver and tool in controlling the ecosystem trajectory. To maintain and hopefully increase ecosystem resilience and improve diversity it is recommended that a patchy fire return period varying from between three and eight years is implemented and every precaution is taken to avoid too frequent fires (i.e. more than two within a five year period).

There is no afforestation disturbance included in Figure 5.1 but I took the liberty to insert the Alien Pine stand site next to the closest option - that of cultivation followed by abandonment. The remnants of the pine plantation are currently in the process of being removed; however the length of time of their presence has resulted in a site with saline soil and a community dominated by bare ground and unrecognizable as Peninsula Shale Renosterveld. Once the entire site has been clear-felled the community will enter a critical phase. Milton's (2007) model, supported by research done by Terblanche (2011), shows that passive restoration will see the flora become dominated by weedy, annual grasses and forbs and this is most likely the trajectory the study site will head towards without intervention. The removal of the pines does however provide an excellent opportunity to increase the conservation value and extent of the Peninsula Shale Renosterveld on Devil's Peak. Soil remediation to decrease the soil salinity (for example through the application of Gypsum or Limestone (Davis et al., 2012)), followed by a re-seeding programme, has the ability to intervene in the sites natural degeneration into a weedy wasteland and redirect it back towards Peninsula Shale Renosterveld.

Despite different drivers acting on it, the ecological endpoint of the Alien Pine stand, if there is no intervention, may be that of the current Game Camp site. The Game Camp, while avoiding substantial afforestation, has been in all likelihood ploughed, overgrazed, managed as a grazing paddock and parkland and at present the recent removal of the majority of grazers has seen virulent alien annual grasses proliferate. The five zebra individuals currently housed within the Game Camp enclosure are not adequate in keeping the alien grasses in check and, regardless, Figure 5.1 suggests that grazing alone is not sufficient in shifting the ecosystem trajectory. As a result the vegetation is akin to that of an old field and not Peninsula Shale Renosterveld. Milton's (2007) model advocates that to transform the ecosystem to a grassy shrubland management need to plough the area, apply herbicide and re-seed the site. This may be a costly initiative; however at present the site offers little in conservation value and its relatively large area means, if successfully restored, it would significantly increase the total footprint of protected Peninsula Shale Renosterveld.

5.4 Towards the Future: Rationale for Restoration and Potential Management Actions

A key factor in the future of the study area is the point of entry of any restoration initiative and, unsurprisingly, this depends on the funding available. The cheapest option is to preserve what we already have by maintaining the Lightly Degraded Renosterveld and burning the Old Renosterveld site, and in so doing redirect its trajectory from a thicket back towards Peninsula Shale Renosterveld. This option neglects the future of the Alien Pine stand and Game Camp which will remain land dominated by aliens with no conservation value and unable to increase the natural resilience of the landscape. There may be merit in maintaining an alternate land cover at these sites as the resources necessary for their restoration may be better utilised in maintaining areas of natural vegetation currently under threat. However, the Alien Pine stand and Game Camp sites, if left unattended, will act as a persistent source of alien seed to any adjacent Peninsula Shale Renosterveld remnants which could lead to further degradation. In addition, due to limited area of healthy Peninsula Shale Renosterveld currently present, restoration of the degraded regions will greatly enhance its conservation status. The benefits of a larger restoration effort utilizing seeding, the use of herbicides and tilling are multiple. Firstly, restoration can increase biodiversity and improve ecosystem resilience, an important factor in the face of global climate change (Harris et al., 2006; Diaz et al., 2006). Indeed, in light of predicted climate change in the Cape Floristic Region, Hannah et al., (2007) highlighted the need to establish and maintain the functionality and health of protected areas in the region. Additionally, the location of the study area at the wild-urban interface means that the restoration of the vegetation towards a healthy, functional ecosystem creates an important buffer against the threat of invasive species, loss of habitat and general degradation of the natural environment (Alavalapati et al., 2005).

A final point of consideration is the role that restoration has in the proposed expansion of the Game Camp (Coetzee, 2001). It is beyond the scope of this chapter to discuss the intricacies of such an expansion but restoration is a common theme for each of Coetzee's (2001) three expansion options. The expanded Game Camp would see indigenous animals such as Eland, Red Hartebeest, Grey Rhebok, Common Duiker, Steenbok, Grysbok and Bontebok re-introduced at an appropriate stocking rate and live sustainably on the indigenous Peninsula Shale Renosterveld of the study area. If implemented, this would bring back one of the critical elements missing from the system, grazing, and would surely have significant ecological implications and work in tandem with restoration efforts to good effect. Clearly, this project would require substantial investment. Nevertheless, the tourism opportunities it would afford are immense as a game park situated at the base of the world-renowned Table Mountain, within a stone's throw of the city of Cape Town, would become a landmark attraction and a feature few cities could boast of.

5.5 Conclusion

This thesis has met the initial objective of enhancing the understanding of the ecosystem drivers of Peninsula Shale Renosterveld with a view to restoration through the demonstration of the value of a historical lens in understanding contemporary vegetation states; provided valuable baseline data through a strategic phytosociological survey of specific vegetation states; and demonstrated the potential (in this case poor) of the existing seedbank in understanding contemporary vegetation states. While the thesis has shown potential management actions to redirect the trajectories of the typical vegetation states within the complex study area, it would be imprudent to act without acquiring more empirical data. The initiation of seeding trials in the Alien Pine stand and Game Camp sites is an essential step prior to any widespread seeding. The establishment of a database on the success or otherwise of various indigenous seeds is important and will ultimately save money, time and increase the likelihood of a successful restoration programme (Pretorius et al., 2008). Seeding and treatment experiments have already begun in the Game Camp (Waller, unpublished data) and the results will be vital in creating a list of indigenous species to be used for reseeding. Hopefully similar investigations can be expended to the Alien Pine stand in the near future and with sufficient funding and will-power, the study area can be restored to a landmark feature of the Cape Town landscape and a valuable asset to the region as a whole.

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Appendix I

Example of field sheet used during phytosociological survey:

Releve code: GC4

Surveyor: Oliver Cowan Dimensions: 10x10m Time & Date: 11 October 2011; start@9am

Site Information

Elevation: 55m asl **Aspect**: ~ East **Slope** (%): 4.9 **Slope Position**: lower

Successional status: ploughed in past-grassland /old field **Last Fire**: ?

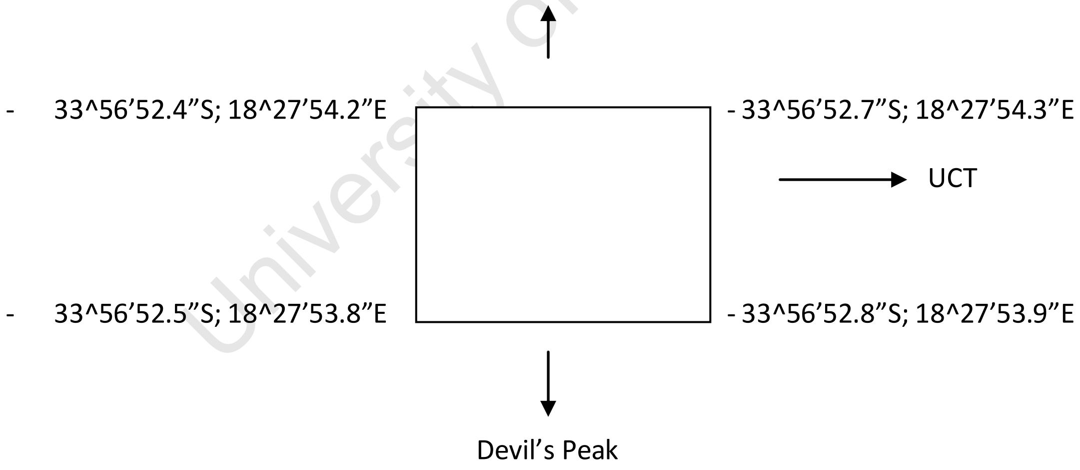
Erosion: no **Animal Activity**: rodents, insects

Soil Depth: 42cms

Additional Notes:

Bare ground= r

Location and co-ordinates m3



r = rare, solitary with small cover **+** = few with small cover

Species Name	**B-B Cover**	**Collected?**	**Additional Notes**
Grass Species 1-Avena fatua?	90%	Yes	
Grass Species 2-Briza maxima	5%	Yes	Possibly female of spp1…unlikely
Grass species 3-?	+	Yes	Similar to Grass species 1
Zantedeschia aethiopica	+	No	
Lobostenum argenteus-Patterson's curse	+	No	
Oxalis compressa	+	no	
Green flower/weed	r	yes	Euphorbeaeceae spp.?