

**Management of *Critically Endangered* renosterveld fragments in the Overberg,
South Africa**

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DEDICATION

This thesis is dedicated to Philip Anthony Hockey (1956 – 2013), who helped me develop the platform on which I have built my academic career, and whose friendship is sorely missed.



Drawing by Chris van Rooyen

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Overberg Lowlands Conservation Trust
Working with landowners to save renosterveld

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THESIS SUMMARY



Lowland renosterveld is a relatively fertile, shale-derived vegetation type found within the Fynbos Biome of South Africa, a biome which is recognized as one of the world's smallest, yet richest plant kingdoms. Due to the fact that renosterveld tends to be dominated by a handful of small-leaved asteraceous shrub species, it creates the illusion that it is a homogeneous habitat with low levels of alpha diversity and species turnover. This is exacerbated by the widely accepted, although not proven, hypothesis which states that current-day renosterveld is derived from a pristine C_4 grassland and that the dominance of asteraceous shrubs is solely due to more than 300 years of mismanagement in the form of overgrazing. This process of degradation is believed to have started with the arrival of the European settlers who exterminated the large herds of free-roaming ungulates and replaced them with livestock (sheep and cattle), which, through their selective feeding habits and their sedentary manner of grazing, altered the system from a grassland to a shrubland. The debate over what renosterveld actually is, combined with a dearth of knowledge as to its ecological functioning, has meant that management recommendations are largely based on a combination of guess-work and inferences from studies in adjacent and similar fynbos and karoo habitats. Additionally, renosterveld has been severely transformed for agricultural development, rendering it a *Critically Endangered* vegetation type, with 4-10 % of the original extent remaining.

In this thesis, I focus on lowland renosterveld in the Overberg (also referred to as South Coast Renosterveld), Western Cape, South Africa. I investigate, through the use of soil carbon-isotope analyses, the grassy-shrubland vs. shrubby grassland debate and assess whether or not the theory that renosterveld is merely a degraded grassland has merit. I evaluate diversity levels at the alpha, beta and gamma scales and contrast these with comparable Mediterranean-climate vegetation types, while considering the implications for conservation planning for renosterveld in the Overberg. Through the use of a simple model, I investigate whether it is possible to predict species extinction rates at the local (patch) level. I then assess responses to grazing and fire, through a combination of controlled experiments and random surveys, in order to assess management requirements.

I found that South Coast Renosterveld was more-than-likely always a grassy-shrubland, and that although data suggest slightly higher C_4 inputs historically, renosterveld was never a pure C_4 grassland. Alpha diversity was on a par, if not higher, than that of any other studied fynbos habitats and is comparable, if not richer, than its other Mediterranean-climate shrubland counterparts. Similarly, species turnover across habitat and landscape gradients was high, suggesting that multiple renosterveld

reserves will be crucial for the long-term preservation of this habitat and associated ecological processes.

Renosterveld in the Overberg responds positively to fire, through a significant increase in flowering and germination in post-burn vegetation, while older renosterveld is less productive. However, I also demonstrate that regular short burning intervals are not advisable for this relatively dry shrubland, which is better suited to fire frequencies similar to, or lower than, those in comparable fynbos habitats. Grazing impacts did not manifest on plant diversity or cover, but did affect size and productivity of species favored by livestock, suggesting potential for long-term negative impacts with continuous grazing. This study suggests that managing for the grass component alone will not have overall benefits for the biodiversity and ecosystem functioning of this severely threatened vegetation type. Thus, this study does not concur with Cowling's (1986) statement that '... the management of South Coast Renosterveld as rangeland for domestic livestock production would be entirely compatible with the conservation of this veld type and its component flora.'

The future of renosterveld in the Overberg depends on the establishment of a network of reserves which includes the full repertoire of management regimes, micro-habitats and aspects, in order to incorporate diversity at all levels. This alone, however, will not be sufficient: a strategy which ensures landowner buy-in, through tangible incentives, will be crucial for the long-term persistence of renosterveld as a functioning ecological entity at the landscape level.

CHAPTER 1: INTRODUCTION

Renosterveld: a severely threatened, misunderstood, global botanical hotspot

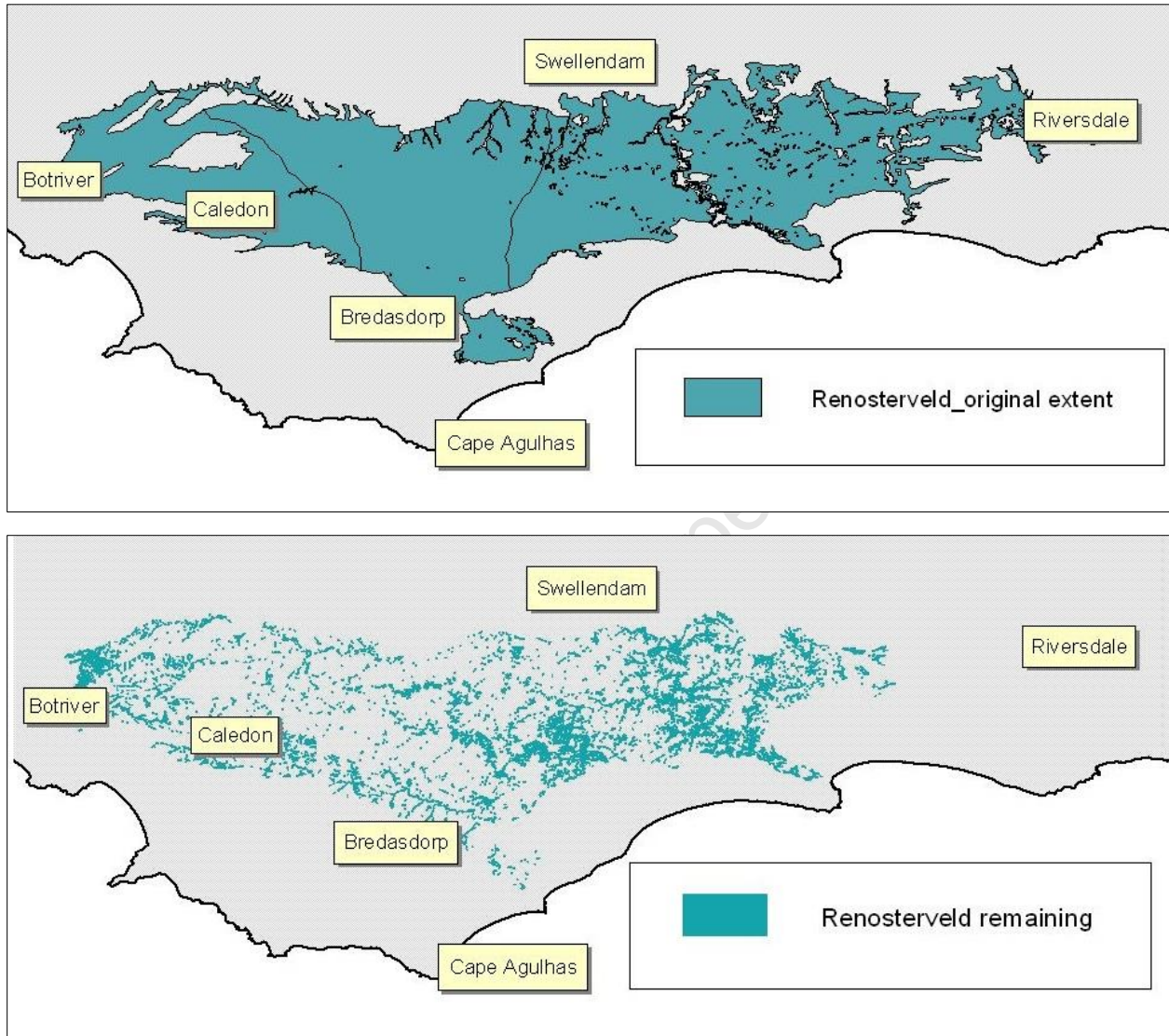
In a changing landscape, there are always winners and losers (Muthama Muasya 2011).

BACKGROUND: A THREATENED FYNBOS SYSTEM

The plight of the world's low-lying, fertile, natural habitats is a global conservation conundrum, as these have always been the most suitable for cultivation and have thus been heavily exploited since the advent of large-scale, extensive agriculture. Today, these are the most threatened ecosystems, due to the high levels of fragmentation which impose a suite of negative effects on the integrity of these systems. However, direct fragmentation effects are seldom the only negative influence on fragmented habitats. Management effects can often override these, with different species and taxa responding differently to diverse management interventions. Thus, determining appropriate management for these habitats is as crucial to reducing the direct fragmentation effects.

One fragmented system occurring in a very diverse landscape is *renosterveld*: a vegetation type found within the Fynbos Biome of South Africa, generally located on clay- and shale-based, fertile soils. Compared with adjacent fynbos habitats, it tends to have an overall grey appearance, due to the dominance of asteraceous shrubs and in particular, the renosterbos *Elytropappus rhinocerotis*. It is also a grassier habitat and is richer in forbs, annuals and geophytes than the adjacent fynbos habitats (Rebello 1995). Renosterveld is renowned for its exceptionally high levels of geophyte diversity (Cowling 1983, Paterson-Jones 1998). The name 'Renosterveld' is derived from the Afrikaans words 'renoster' (meaning rhino) and 'veld' (meaning vegetation), although the exact reasons for this choice of name are unclear. It is generally believed that the vegetation was named after the Black Rhino which occurred in the Western Cape, due to the fact that either i) the overall uniform 'grey' appearance of the vegetation resembled that of a rhino hide, or ii) that the rhinos occurred in this vegetation (Boucher 1980). Renosterveld has been severely transformed, with >90% of it ploughed for agricultural development (mostly grain and artificial pasture) (Kemper *et al.* 1999, McDowell & Moll 1992). According to the SANBI & DEAT's (2009) *Threatened Ecosystems of South Africa*, about 12% of the original extent of all renosterveld types in the Overberg still remains – although other estimates are as low as 4-6% (pers. comm. Donovan Kirkwood) (Figs. 1a and 1b). Renosterveld is listed as *Critically Endangered* and highly prone to functional extinction. The viability of renosterveld as a functioning ecosystem is influenced by a

suite of factors, from those occurring as a result of significant shifts in management regimes to those occurring as a result of significant fragmentation and habitat loss.



Figures 1a (above) and 1b (below) demonstrate the amount of renosterveld that has been lost in the Overberg over the last ± 300 years. Figure 1a denotes the original extent of renosterveld in the Overberg, while Figure 1b shows the fragments remaining to date (adapted from SANBI maps).

This thesis concerns studies of renosterveld in the Overberg region of the Cape. The 'Overberg' essentially refers to the Eastern half of the Western Cape, South Africa, and stretches from Botriver to the Heidelberg region (Figure 2). In the Southern coastal region of the Overberg, lies the 'Agulhas Plain', comprising a range of coastal, lowland and limestone-based fynbos types. In this region, farming comprises grain crops, livestock, vineyards and indigenous flower crops (mostly *Protea* species), while

commercial wildflower harvesting also provides an income for smaller local businesses. The Sonderend and Langeberg mountains straddle the northern extent of the Overberg and these are dominated by mountain fynbos vegetation types. Here, commercial forestry plantations are the major land use, while relatively large areas of fynbos are conserved by either government agencies, or private landowners. Between the coast and mountains, the soil becomes relatively fertile and rich in clay derived from shale and it is here that renosterveld habitats occurred.

Renosterveld began to be transformed for crop farming soon after the first European settlers arrived in the Cape. Today, almost all remnant renosterveld is found on privately-owned land, making it very vulnerable to the deleterious effects of management. The long-term effects of constant mis-management on these fragments are poorly understood, but it is assumed they will be significant and, in some cases, cause irreversible damage to the ecological integrity of the veld.

STATS: REMAINING RENOSTERVELD
 2021 cadastres (land parcels)
 37 527 ha renosterveld
 i.e. 6% remaining
 Spread across 12 296 fragments
 Varying in size from <1 ha to 835 ha
 72 fragments are >80 ha
 46 fragments are > 100 ha
 13 fragments are >200 ha
 Two largest remnants are ±800 ha
 (REF: SANBI GIS remnant layer).

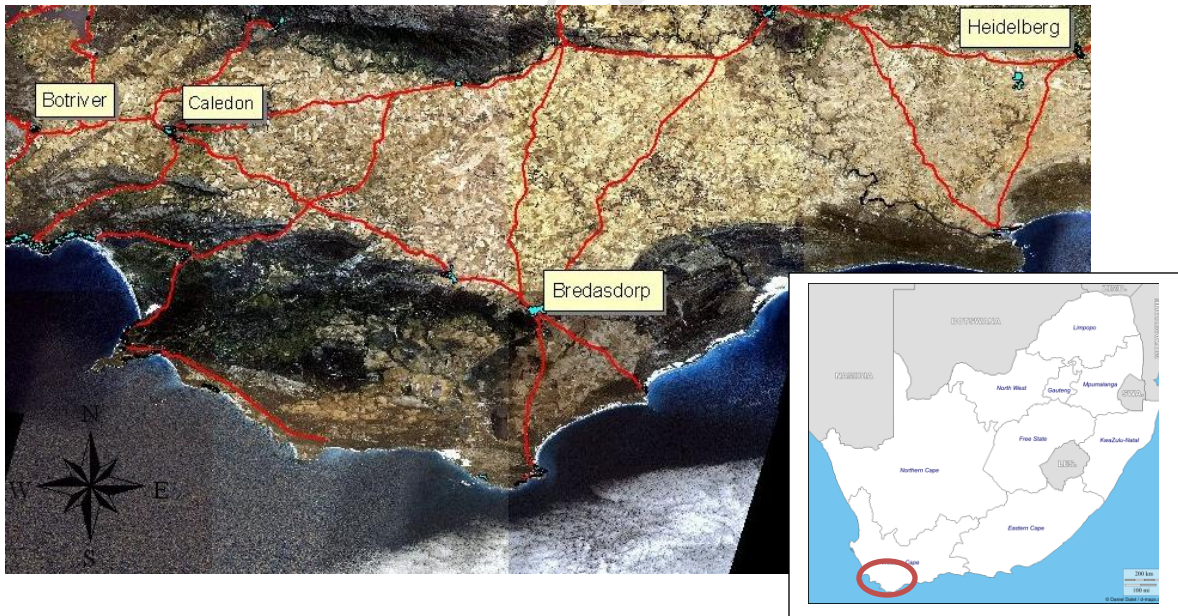


Figure 2. Map denoting the study area, Overberg, Western Cape, South Africa.

Renosterveld in the context of the Fynbos Biome

The Cape Floristic Region (CFR) is recognized as one of the World’s 34 Biodiversity Hotspots (Myers 1990, Myers 2003), is the richest of the World’s six Floral Kingdoms and is significantly threatened by a

plethora of issues, including infestations by exotic invasive plants, transformation for development and agriculture and general habitat degradation associated with mismanagement (Rebelo 1992, Rouget, *et al.* 2003, Raimondo *et al.* 2009). 'True' *fynbos* habitats tend to be concentrated in mountainous and coastal regions within the CFR and are generally associated with poor, acidic, sandy soils. These are typified by a dominance of proteas, ericas (heather) and restios (reeds) and are fire-adapted and fire-dependent systems. However, in the lowlands of the CFR, vegetation changes to *renosterveld*, in response to interactions between rainfall and a change to relatively more-fertile, clay- and shale-based soils and relatively low rainfall. Renosterveld is typified by the absence of the three main 'fynbos indicators' (proteas, ericas and restios) and tends to be dominated by Asteraceous shrubs (i.e. shrubs belonging to the daisy family, of which the 'renosterbos' is one example) (Fig. 3) and perennial grasses. It is still, however, considered part of the Fynbos Biome.



Figure 3: Renosterveld, dominated by Asteraceous shrubs.

Renosterveld is very rich in geophytes (Cowling 1990) and is most renowned for its spectacular spring (August / September) flower displays, during which a grassy shrubland resembling an American sagebrush habitat displays an exceptional array of bulb and annual diversity. In the Overberg, four types of renosterveld have been recognized (Mucina and Rutherford 2006): Western-, Central-, and Eastern-Rûens Shale Renosterveld and Rûens Silcrete Renosterveld. All are listed as *Critically Endangered* (SANBI & DEAT 2009).

Fynbos systems (including renosterveld) are exceptionally diverse, with high levels of very range-restricted, rare and endemic species. These naturally rare species are highly vulnerable to the deleterious effects of fragmentation and are often poorly represented in remnants. Thus, in contrast

with managing more homogenous systems elsewhere on the globe, management in fragmented fynbos is extremely complicated, as high levels of diversity and endemism are associated with high extinction risk and thus the need for area-specific management. Research has shown that even a fragment of only a few hectares of renosterveld can contain exceptionally high plant diversity (Curtis *et al.* 2013, Kemper *et al.* 1999.). Thus, managing lowland fragments at the farm and landscape level is essential if they are to continue functioning as ecological systems.

Background: economic and social climate in relation to climate change

Farming in the Overberg 'grain-belt' (i.e. previously renosterveld regions) comprises a variety of cash crops (wheat, barley, canola, oats) as well as livestock (mostly sheep and cattle). Essentially, food crops are planted on a rotational basis and alternated with lucerne as artificial pasture for livestock. Almost all crops depend on winter rain, while some lucerne camps are irrigated (particularly for dairy cattle) (the term 'camp' refers to a fenced-off section of the farm on which crops or pastures are grown: each farm is divided into these camps for management purposes). Increased frequency of sporadic winter drought (affecting germination and growth and therefore productivity of grain crops and artificial pastures) and late (early summer), heavy rains (sometimes having a detrimental effect on harvesting), have resulted in some farms in the region experiencing severe financial difficulties (pers. obs.). In the context of a weakening economic climate and fluctuations in the wheat price, nested in an already marginal farming area further threatened by climate change (Lumsten *et al.* 2009), landowners are anxious to maintain a hold on their farms and livelihoods. They may therefore be more prone to desperate and illegal measures, which include turning virgin land into crop farming. In addition to this, food shortages for livestock may force landowners into making poor, short-term solutions for grazing, which may involve ill-timed and frequent burning of vegetation, followed by immediate and heavy grazing. These practices could result in irreversible damage to biodiversity, and the functioning of renosterveld ecosystems.

The conservation importance of renosterveld and other lowland fynbos types has been acknowledged for many years (Cowling *et al.* 1986, Jarmin 1986, Rebelo 1995). Although very detailed and sophisticated conservation plans have been developed (e.g. von Hase *et al.* 2003), very little progress has been made in actually implementing them and securing sufficient tracts of land to meet conservation targets for critical habitats.

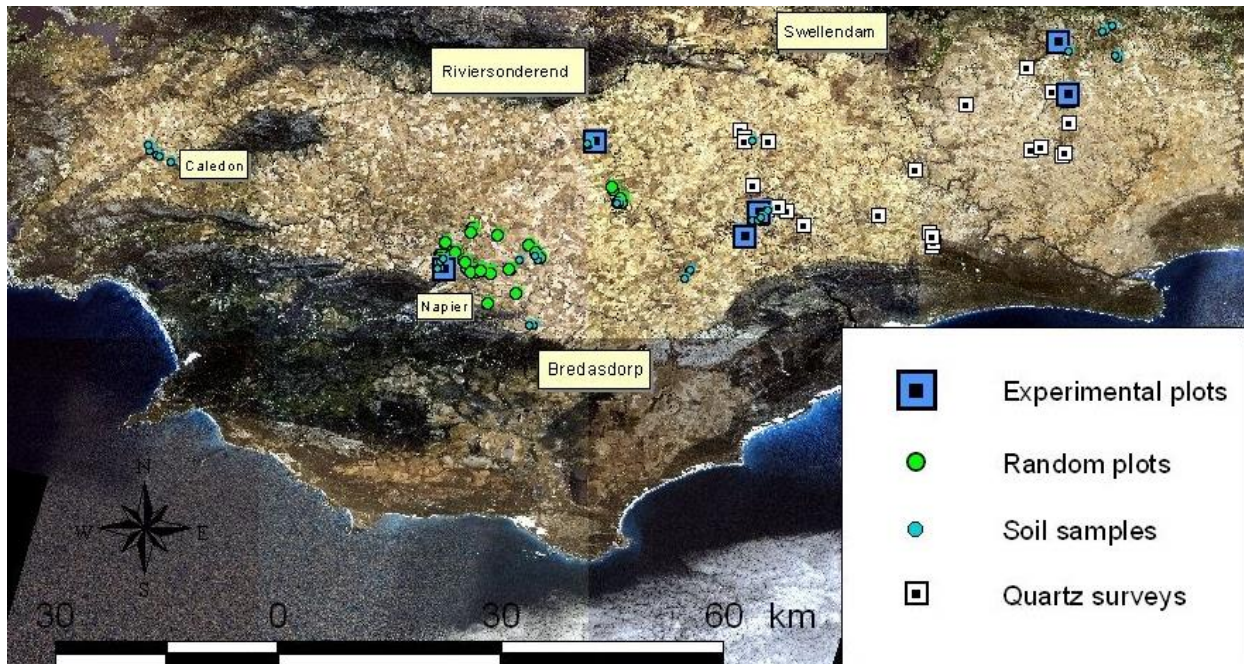


Figure 4. Map denoting the extent of the different surveys carried out in this study (experimental plots (Chapters 3, 4, 5 & 7), Random plots (Chapters 3, 4, 5 & 7), Soil samples (Chapter 3) and quartz surveys (Curtis *et al.* 2013, Appendix 1).

For example, the first maps which were intended for identifying conservation priorities in the CFR were compiled by Jarmin in 1986. Most notably, important renosterveld fragments were mapped with the following metadata: ‘largest and best remaining examples of Southwest Coast Renosterveld communities on silcrete-topped hills in the Bredasdorp-Swellendam district. Many threatened plants occur.’ And ‘grazing for sheep is the main use, but ploughing of the remaining natural veld is continuing... intensive grazing and further expansion of ploughed lands are major threats.’ Despite recognition of renosterveld as ‘a priority for conservation’ dating back 25 years, little successful conservation action has taken place since. The GIS tools for accurate conservation planning in renosterveld were developed more than 10 years ago (von Hase *et al.* 2003), and led to the generation of rather ambitious five- and twenty-year visions for the conservation of lowland renosterveld. Despite these plans, to date, only a handful of farms have had Stewardship Agreements or Conservation Easements (i.e. voluntary title deed restrictions which declare the renosterveld as Nature Reserve) placed on them, and most farms with renosterveld are not involved with conservation programmes of any sort. Current-day, management-related threats to renosterveld appear to be: i) degradation through inappropriate grazing regimes, ii) degradation through inappropriate fire regimes and iii) conversion of virgin land into cropland (Fig. 5).



Figure 5: Although spectacular at times, these ‘patchworks’ of wheat, oats, barley, canola and pasture have replaced the once diverse renosterveld systems which covered the fertile lowlands of the CFR and supported significant populations of large game and other wildlife.

Whereas fynbos has been intensively studied from diverse perspectives, renosterveld is still poorly known. This lack of knowledge hampers conservation efforts. In this thesis, I address some key questions relevant for selecting conservation areas of renosterveld and applying appropriate management. Of necessity, I also address some basic aspects of the system, including whether it was historically a grassland invaded by shrubs following heavy grazing or a shrubland system analogous to fynbos. The thesis layout is indicated in the chapter summaries that follow:

CHAPTER 3: RENOSTERVELD: GRASSY-SHRUBLAND OR SHRUBBY GRASSLAND?

What makes renosterveld management particularly challenging is that, despite the fact that this vegetation type falls within a Biome that is fairly well-studied, there is disagreement amongst ecologists about what renosterveld actually *was* (and therefore what we are managing *for*), as well as a dearth of knowledge on what factors drive renosterveld functioning (e.g. fire, grazing or neither). Newton and Knight (2004) suggested that, since the intensification of the use of domestic livestock in the Western Cape about 200 years ago, renosterveld has been severely transformed, essentially changing the system from a ‘shrubby grassland’ to a ‘grassy shrubland’ (Newton & Knight 2004). They hypothesized that two main factors contributed to this: i) the large-scale extermination of indigenous grazing and browsing herbivores and ii) the introduction of selective grazers in the form of sheep and cattle. i.e. The replacement of a suite of herbivores, of different sizes and varying grazing and browsing capacities, with two highly selective grazers (domestic sheep and cattle) resulting in a shift from a system where grasses were prominent, to a system generally dominated by unpalatable, asteraceous shrubs. An alternative hypothesis is that Overberg renosterveld was always a shrubland dominated by Asteraceous shrubs (particularly *Elytropappus*), as it is today. Current-day renosterveld is highly variable (Fig. 6).

There is considerable anecdotal evidence suggesting a shift from Poaceae to Asteraceae in the Overberg's lowlands and that this shift occurred very recently (< 200 years ago). In 1785, Sparrman published on the notable demise of the South Coast grasslands and the resultant increase in *Elytropappus*, stating, '... it is not at all likely that future ages may see this part of Africa entirely changed and different from what it is at present.' (Cowling *et al.* 1986). In 1943, Smit made reference to the lowlands of the South Coast once being known as the 'blue grassveld,' in reference to the dominance of *Themeda* (commonly known as 'red-' or 'blue-grass,' due to the hue created by extensive areas of this species) (Cowling *et al.* 1986). And Levyns (1929) viewed the Renosterbos as a potential 'problem plant' and noted, with reference to renosterveld: "Although the renoster bush is its principle constituent, several shrubs and other composites, and many geophytes are associated with it. However, these do not break the grey-green monotony of this type of plant community." Nearly 30 years later, Levyns (1956) attributed overgrazing as the likely cause for the spread of *Elytropappus* and discussed the fact that farmers were burning renosterveld in order to utilize the regrowth for grazing, but that in the long-term, this management policy only perpetuates *Elytropappus*. Several other historic accounts describing the flora of the Cape certainly suggest the existence of a grassier lowland system than that present today (Newton & Knight 2004).

Nearly three decades ago, Cowling *et al.* (1986) published a paper which should have set the scene for much-needed research on renosterveld management. Unfortunately, very little appropriate work followed this important paper. The authors made reference to their predecessors and supported the hypothesis that south-coast renosterveld (i.e. Overberg and eastwards) was historically dominated by *Themeda triandra* and that Asteraceous shrubs (particularly *Elytropappus* and *Metalasia* species) had started to dominate the landscape as a result of severe overgrazing.

These studies do suggest that the lowlands of the Overberg were richer in palatable grasses than what is seen presently. However, the European settlers (having first arrived in the 1650s) were not the first pastoralists tending livestock in the region. The Khoi-San had been present in the area for 2000 years prior to the arrival of the settlers and were already manipulating the vegetation, through frequent burning to provide fodder for livestock (Deacon 1992, Hoffman 1997). According to this argument, the Khoi-San had converted renosterveld into a grassland system to promote feed for their livestock. Thus, the argument goes, renosterveld was in fact a shrubland prior to the arrival of the Khoi-San. This argument also has merit. However, if the Khoi were regularly burning renosterveld and using the fresh new growth for grazing their cattle immediately these became available, they too might have damaged the grass component and encouraged the spread of Asteraceous species, as this is far more likely to

occur when renosterveld is continually burned and grazed, with no rest periods. If, however, the nomadic Khoi people burned extensive areas while moving through with their livestock, they may well have allowed the veld significant periods of rest and so increased, or at least, maintained the grass component. Thus, again, this issue is debatable: migrant herds versus resident persistent grazing as in present day livestock farming could have had quite different impacts on the natural vegetation (Cowling *et al.* 1986).



Figure 6: within the Overberg alone, there is variation in community structure of different renosterveld habitats: from left to right: a C_3 grass-dominated renosterveld patch in Eastern Rûens Shale Renosterveld, an Asteraceous-shrub and C_3 -grass renosterveld patch in Eastern Rûens Shale Renosterveld and a C_4 -dominated renosterveld fragment in Central Rûens Shale Renosterveld. With such an innate diversity of habitats, is it possible to make statements as to whether renosterveld 'should be' a grassy shrubland or a shrubby grassland?

Margaret Levyns was particularly interested in the Renosterbos *Elytropappus rhinocerotis* and its distribution within the Fynbos Biome and beyond, as well as the ecological constraints on its recruitment. In 1929, she published some experiments on the germination of Renosterbos under various treatments: experimental plots comparing unburned, burned and cut vegetation revealed that recruitment of renosterbos seedlings was zero in unburned plots, sparse and scattered in cut plots and very high in burned plots, suggesting that fire is crucial for renosterbos to recruit. Experiments also suggested that year-old seed had a higher probability of germinating than fresh seed (Levyns 1929).

Levyns (1929) also acknowledged the vast differences in renosterveld types and pointed out that although other less conspicuous species are able to reproduce in renosterveld in the absence of disturbance, *Elytropappus* requires disturbance (preferably fire) in order to proliferate. She concluded that renosterveld should be viewed as a *stage* in succession and not as a climax vegetation type. For this reason, she related frequent burning to the country-wide spread of *Elytropappus*, which keeps renosterveld at this stage in succession. However, in contrast to Levyns's suggestion that *Elytropappus* is encouraged by frequent burning, most ecologists will agree that, although the species is unlikely to

recruit without fire, frequent burning will result in a dramatic decrease in *Elytropappus* and an increase in perennial grasses. Cowling *et al.* (1986) suggested that because *Elytropappus* takes three years before seed is set, if the management objective is to significantly reduce the species, one should burn renosterveld every three years. The effectiveness of this tactic is affirmed by Levyns's (1926) experiments which demonstrated that *Elytropappus* seed remains viable in the soil for seven years, but that it loses a significant amount of germination capacity after four years. Of course, this research focused on only one species and did not take the effects of frequent burning on renosterveld as a *system* into account.

In this chapter, I will use stable isotope analysis (Fig. 4) of soil carbon to test the theory that, historically, renosterveld comprised a higher C₄ grass component than is seen today and that not all renosterveld, at all times, is dominated by C₃ shrubs and grasses.

CHAPTER 4: IS RENOSTERVELD A FIRE-DRIVEN SYSTEM?

Although renosterveld is included as a sub-type of the fire-prone Fynbos Biome, its fire ecology is very poorly understood (although mature veld does burn readily – Fig. 7). In contrast to fynbos, very little is known about the vegetative (sprouter vs. seeder), or reproductive responses (fire-stimulated vs. fire intolerant recruitment) of renosterveld species to burning. Crown-fire systems, such as fynbos, are known to differ in their fire-adaptive traits from surface fire regimes characteristic of grass-fuelled ecosystems (e.g. Bond & van Wilgen 1996; Pausas *et al.* 2004; Bond & Keeley 2005; Keeley *et al.* 2012). If renosterveld was originally a grassland invaded by shrubs following overgrazing, we would predict few species with fire-stimulated recruitment and very few seeders (non-sprouters) since post-burn recruitment in grasslands is inhibited by vigorous competition with grasses. If renosterveld seldom burnt because it occurs in relatively arid climates relative to fynbos, we would predict that fire-dependent recruitment and associated fire-type life histories would be rare or absent. However, if fire was a regular feature of renosterveld ecosystems, we would expect fire-stimulated recruitment to be a common feature of common species, as it is in fynbos (e.g. Le Maitre & Midgley 1992; Cowling *et al.* 1997; Keeley *et al.* 2012). If species have an obligate dependence on fire to complete their life cycles, then fire would have to be incorporated into renosterveld management. Since burning has attendant risks to people and property, it is important to establish the extent to which species are dependent on fire events for recruitment. In this chapter, I will address the question: does renosterveld need fire? I test for fire-dependence by observing vegetative responses (sprouting and non-sprouting) and reproductive responses (flowering and seedling recruitment) in response to burning. I compare regeneration

responses in burned versus unburned areas (Fig. 4) to help determine whether species have an obligate or facultative requirement for fire. In an ecosystem where the fire ecology is poorly understood, examining the extent to which fire-adapted life history traits occur in the plant communities may be useful in developing an understanding of the natural fire regimes under which that system functions best, which is essential for management purposes (Keeley *et al.* 2012).



Figure 7. Fires burn readily through renosterveld. However the extent to which plant species in the ecosystem are dependent on fire for recruitment is not known.

CHAPTER 5: UNDERSTANDING DIVERSITY IN RENOSTERVELD AT THE LANDSCAPE- AND LOCAL-LEVEL.

Currently, there are 119 vegetation types described within the Fynbos Biome (Mucina & Rutherford 2006) – of these, 29 are ‘renosterveld’ types. These comprise shale renosterveld (19 types), granite renosterveld (3), dolerite renosterveld (2) alluvium renosterveld (2), silcrete renosterveld (2) and limestone renosterveld (1). As mentioned, in the Overberg region of the southwestern Cape, there are four renosterveld types present: Western-, Central- and Eastern-Rûens Shale Renosterveld and Rûens Silcrete Renosterveld. The key question related to the conservation of fragmented systems such as this one, has always been: how many reserves are enough and do we need a few large ones, or are several small reserves equally, or more, effective? (Cowling & Bond 1991).

Southern Africa has a complex geomorphological history and there is evidence to suggest that the unparalleled floral diversity of the Cape Flora was partly determined by these historical processes. Cowling *et al.* (2009) suggest that moderate uplift during the early and late Miocene significantly

increased the topo-edaphic heterogeneity of the Cape, resulting in the formation of several 'new' habitats available for plant colonization. They surmise that these uplifts, combined with rapid climatic deterioration played a significant role in the rapid diversification of some plants in the Cape region from the late Miocene. In the Overberg region of the Western Cape, the old African Surface was capped by silcrete duricrusts, probably deposited in the early Palaeocene. Two major uplift events associated with tectonic movement occurred in the Cape: one in the early Miocene and a second in the late Miocene / early Pliocene. In the lowlands almost all the silcrete duricrusts, as well as the kaolinised soils below them, were eroded to reveal extensive tracts of shales and Cretaceous sediments, rendering a system far richer and more fertile compared with that in the adjacent mountain habitats (Cowling *et al.* 2009). Today, only small remnants of the original silcrete-capped African Surface are preserved in the Cape Lowlands, in the form of silcrete-quartz koppies (hillocks), mostly in the eastern region of the Overberg. The low-lying, clay-based, fertile soils essentially comprise the various types of lowland renosterveld. Thus, one would expect significant differences in the communities present on more ancient, silcrete-quartz outcrops and those occurring on the adjacent shale habitats. One would also expect notable differences in communities between the different renosterveld types across the Overberg (gamma diversity). These hypotheses are tested in this chapter (Fig. 4).



Figure 8. A silcrete-quartz patch in a matrix of shale –derived soils.

Until fairly recently, the renosterveld lowlands of the Overberg have been largely ignored by ecologists and most local botanists, with some exceptions. However, botanical surveys undertaken over the last ± 5 years have revealed a suite of new, endemic species within this vegetation type (Curtis *et al.* 2013).

Many of these species occur only on quartz-silcrete outcrops in ERS Renosterveld (Fig. 8). Mucina & Rutherford (2006) describe the ERS Renosterveld as occurring on 'moderately undulating hills and plains supporting cupressoid and small-leaved low to moderately tall grassy shrubland, dominated by renosterbos.' They make mention of the thin layer of calcrete found covering some parts of the veld in its southern limits, as well as the thicker deposits which support mesotrophic asteraceous 'fynbos', but make no mention of the silcrete-quartz outcrops, or their exceptional levels of endemism, which are so characteristic of this vegetation type. Here, I test whether the levels of endemism on silcrete-quartz patches within ERS Renosterveld are on a par with those found in the arid- and semi-arid regions further north in South Africa (Schmiedel & Jürgens 1999). I also explore general patterns of plant diversity within and across the Overberg renosterveld communities.

Diversity patterns have been extensively studied in fynbos (e.g. Bond 1983; Cowling 1983; Cowling 1990; Cowling *et al.* 1996, Cowling *et al.* 1998; Kruger & Taylor 1980) where the high richness of the region is attributed to high beta and gamma diversity and moderate alpha diversity. High richness on the Agulhas Plain fynbos has been attributed to high species turnover (beta diversity) across edaphic gradients. Similar studies have not been done in renosterveld although the common perception is that the vegetation is rather homogenous, overwhelmingly dominated by renosterbos *Elytropappus rhinocerotis* and a few associated Asteraceous shrubs (*Oedera* and *Metalasia* spp.) with low beta diversity and comparatively low gamma diversity (turnover along geographic gradients). I compare alpha (within community), beta (turnover across habitat gradients) and gamma diversity (turnover along geographic gradients) in Overberg renosterveld to characterize diversity patterns and then compare them with fynbos. Similar studies have been undertaken in other Mediterranean-type climate regions and are compared with renosterveld where possible. This analysis of patterns of diversity can provide useful information for conservation of the system by indicating the range of habitats that should be included in protected areas (beta diversity) and the geographic spread to preserve representative samples of the biota (gamma diversity).

CHAPTER 6: PREDICTING SPECIES EXTINCTION RISK IN RENOSTERVELD AT THE LANDSCAPE- AND LOCAL-LEVEL.

Although previous studies have demonstrated no significant effect of patch size on plant species diversity across renosterveld fragments of varying size (Kemper *et al.* 1999), the question of whether or not renosterveld is still paying its extinction debt (Tilman *et al.* 1994) is debatable (Fig. 9). As Bond (1995) emphasizes, the true measure of the extent of species losses does not lie in extensive red data

listings, but rather in the extinction or reduction of ecological *processes*. These are often overlooked, probably because they are difficult to quantify – perhaps even to identify. However, if we are to understand the real potential for a system or habitat type to become functionally extinct, we need to examine the processes that affect these systems, how threatened these processes are, and what conservation interventions can be made to reverse the downward spiral towards extinction. With a small proportion of its original extent remaining, lowland Renosterveld is an excellent model system for testing theories about extinction debts and predicting extinction risks. In this chapter, I will focus on the latter.

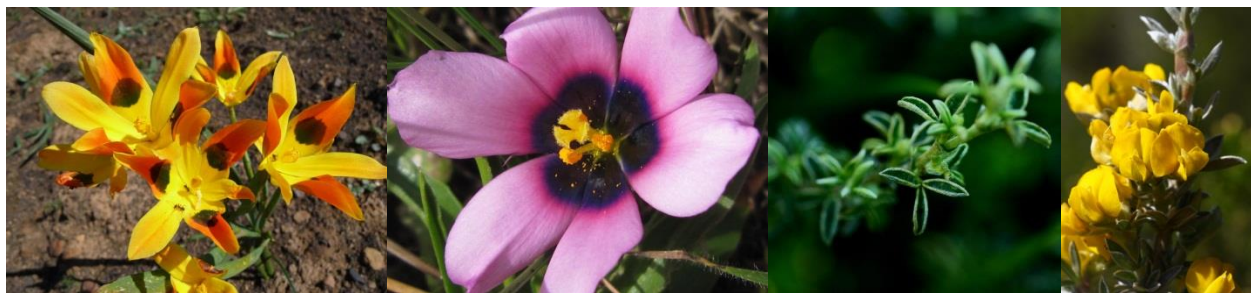


Figure 9. With less than a handful of populations remaining globally, what are the factors that determine extinction risk for these species? (left to right: *Moraea elegans*, *M. melanops*, *Polhillia brevicalyx*, *P. canescens*).

Predicting species' extinction risks, as a result of habitat loss and fragmentation has been widely discussed in the literature (Brook *et al.* 2006, Purvis *et al.* 2000, Swift & Hannon 2010, Tilman *et al.* 1994) and different investigations have reached different conclusions about what characteristics make a species resistant or vulnerable to the effects of habitat loss (Hockey & Curtis 2009). The red-listing system is based on predicting species extinction risk using theoretically determined predictors of extinction based on population viability theory. However, other means of determining species extinction risk have been developed and tested. Bond (1995) developed a model for predicting species extinction risk in plants due to loss of mutualist partners (Pauw 2007, Pauw & Bond 2011). The population consequences depend on i) risk of process failure (in terms of pollination – i.e. plants dependent on a single pollinator will be at a higher risk of extinction than those with multiple pollinators), ii) dependence on process (e.g. for pollination, degree of dependence on pollinators for seed production e.g. whether self-incompatible or capable of selfing), iii) population dependence on seed (completely dependent on seed for reproduction vs. able to propagate vegetatively or able to resprout after disturbance). This model worked well for some genera and again, draws attention to the fact that

ecological processes need closer consideration if we are to plan reserves effectively. Hockey and Curtis (2009) modified this model to predict extinction risk in birds and lemurs, using simple species' traits, including natural range size, body size, and habitat and dietary specialization. This analysis generated some simple models with high predictive power.

In renosterveld, examining the effects of habitat fragmentation and therefore predicting species' extinction risk cannot be done without considering the responses of individual species to management-associated 'threats'. For example, renosterveld systems tend to be overgrazed, which is likely to exacerbate the effects of fragmentation on species that are more sensitive to grazing (i.e. palatable species) and trampling. Likewise, fragmentation effects are often associated with pollination deficits and therefore, plants which are dependent on seed for recruitment are likely to be more sensitive to these consequences than are others which are able to resprout.

In this chapter, I explore the use of a simple model for predicting species' extinction risk in renosterveld, based on a combination of traits, whereby it may be possible to determine in what way traits are behaving synergistically to determine extinction risk.

CHAPTER 7: HOW DO FIRE AND GRAZING IMPACT RENOSTERVELD AND WHAT ARE THE IMPLICATIONS FOR MANAGEMENT?

In addition to understanding what we need to manage *towards*, it is essential that we examine the management tools available to us and how best we can apply these in a way that is practical and beneficial for farming practices as well as biodiversity. As discussed, relative to fynbos ecology and appropriate management, renosterveld is poorly understood, thus even basic management guidelines are unavailable.

'Large' patches (>80 ha) are sometimes treated as separate grazing camps (i.e. they are fenced off from productive lands), which enables the landowner to manage livestock access to the patch. However, these 'veld camps' are often grazed at an inappropriate time of year (i.e. winter and spring, when the bulbs are emerging and flowering and before the palatable grasses have set seed). Smaller patches are not managed as separate entities and are therefore managed as part of agricultural camps, meaning that livestock have constant access to the veld when, for example, they are put into a camp of lucerne or wheat stubble which is camped in with a patch of renosterveld. Thus, these patches are subject to whatever management is applied to the camp – including burning and grazing, as well as drift from herbicide and pesticide application.

In the absence of data specific to renosterveld in the Overberg, the following management-related assumptions, based on related fynbos habitats, have been made:

- i) Grazing over winter and spring months should be avoided – i.e. preferably only graze with livestock in the dry summer months between late November and late March);
- ii) Controlled burns should be carried out during late summer / early autumn months (Feb-March/April),
- iii) Veld should not be grazed directly after a fire and should preferably be rested for a minimum of 18 months to two years post-burning.

These strategies are believed to favour palatable grasses and geophytes (which generally emerge and flower in winter and spring), at the expense of less-favourable asteraceous shrubs, which is generally the objective for both conservation and agriculture. However, no experimental work has taken place in this region to test these assumptions and thereby strengthen our capacity to provide clear-cut guidelines for managers.



Figure 10. How influential are fire and grazing regimes on the integrity of renosterveld systems?

1. Is managing renosterveld for agricultural benefit (i.e. for *Themeda triandra* and other palatable species) compatible with managing for conservation objectives (i.e. overall biodiversity), as Cowling *et al.* (1986) suggest?
2. What is the appropriate fire regime for Overberg renosterveld, defined as fire return interval (frequency), season and intensity? In this study, minimum return interval could be assessed based on the youth period of the slowest-maturing shrub, *Elytropappus*. Cowling *et al.* (1986) noted that it took renosterbos three years to flower following a burn. Since these authors advocate management which focuses on eliminating or substantially reducing renosterbos in favour of palatable C₄ grasses, they suggest a management system with fire intervals of less than three years in order to prevent renosterbos from establishing and outcompeting more favourable species (Rebello 1995, Cowling *et*

al. 1986). In the present study, I explore the role of *Elytropappus* in renosterveld and whether or not these assumptions are valid.

3. Does grazing impact post-burn recovery as measured by changes in species composition, species richness or cover, as well as relative size and productivity of plants favoured by livestock grazers? Does fire promote or inhibit the main grazing grasses and does resting influence their recovery rate? (Fig. 10).
4. How does the canopy cover of Renosterbos and other unpalatable, dominant species (such as other asteraceous shrubs) and C₃ tussock grasses (i.e. *Merxmeullera* or *Pentaschistis*) influence the abundance of geophytes, forbs and annuals?
5. Are there any relationships between growth forms and particular species which can serve as indicators for the need for important management intervention? Evidence for strong correlations can infer the need for specific management actions, such as reducing shrub cover by burning or trampling to promote suppressed species. Additionally, it may be possible to identify suitable indicators of veld condition which can guide management actions.
6. What are the 'ideal' management strategies that need to be applied to renosterveld in the Overberg in order to have maximum potential for 1) conservation, 2) agriculture, and 3) both these objectives simultaneously? What are the trade-offs in managing for both conservation and agriculture and how can a 'compromise' be reached?

These questions are addressed through two sets of data: i) a set of experimental plots, placed at six sites across the Overberg and monitored pre-burning in 2007 and post-burning from 2008-2011; and ii) 40 random plots within a small range in the Napier region of the Overberg (Fig. 4). The experimental plots included fire/no fire treatments and open and fenced areas to test the effects of burning and herbivory separately and synergistically. Responses of plant communities, as well as some individual species, are compared in response to different burning and grazing regimes, in order to gauge the effects of these important management interventions on renosterveld habitats.

SUMMARY OF KEY QUESTIONS

Thus in summary, in the chapters that follow, I focus on the following key questions:

- I. What is renosterveld: a grassy shrubland or shrubby grassland?
- II. Are renosterveld species dependent on fire for regeneration?

- III. What are the patterns in alpha-, beta- and gamma diversity in renosterveld in the Overberg and how do they compare with adjacent fynbos systems?
- IV. Can we use information on species' traits and responses to fire and grazing to predict species extinction risk, using an approach suggested by Bond (1995) and Hockey and Curtis (2008)?
- V. Can we identify indicator species or guilds for renosterveld?
- VI. How does floral diversity and community composition change with increasing post-burn age?
- VII. How does renosterveld respond to fire and grazing? How can we use this information to generate appropriate management guidelines?

APPENDICES TO MAIN THESIS: papers submitted for publication during the study

Appendix 1: Paper in press (Curtis, Stirton, Muasya), Accepted by *Journal of South African Botany* 25 March 2013.

Appendix 2: Paper in prep. (Goldblatt, Manning & Curtis), sent to *Bothalia*, awaiting review.

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CHAPTER 2: SITE DESCRIPTIONS

Renosterveld in the Overberg, Western Cape, South Africa

This study took place in the Overberg, Western Cape, South Africa. The Overberg essentially lies between Grabouw and Heidelberg (west to east), and includes the Agulhas Plain in the south, with the Riviersonderend and Langeberg Mountains forming its boundary in the north.

There are 23 types of Renosterveld described in the Cape Floristic Region (Mucina & Rutherford 2006, Fig. 1) and these are broadly divided into mountain and lowland renosterveld. In the lowlands of the Cape Floristic Region are further divided into two broad types: West Coast and South Coast Renosterveld. The Overberg comprises South Coast Renosterveld, which abuts the Sandstone fynbos types on the Riviersonderend and Langeberg mountains in the north, various types of mountain (Overberg Sandstone) and lowland fynbos (Elim Ferricrete) in the south and strandveld or limestone fynbos along the eastern coastal region of the Overberg. The renosterveld now remains as isolated pockets in what is known as the Overberg's wheat-belt in the *rûens* (which comes from the Dutch word *ruggens*) and describes the gently rolling hills of the region). There are four different types of Renosterveld in the Overberg: Rûens Silcrete Renosterveld, Western Rûens Shale Renosterveld, Central Rûens Shale Renosterveld and Eastern Rûens Shale Renosterveld (Mucina & Rutherford 2006, Fig. 2). In this study, I focus on the latter three and because they are distinct from each other, here I describe their characteristics and climate attributes separately.

Distribution

Western Rûens Shale Renosterveld: from Botrivier and Villiersdorp eastwards, surrounding the Caledon Swartberg and extending to a line roughly between Napier and Genadendal. Altitude: 60-450 m a.s.l.

Central Rûens Shale Renosterveld: central rûens region, from Greyton and Stormsvlei in the north to Napier and Bredasdorp in the south, also expanding onto parts of the Agulhas Plain south of Bredasdorp. Altitude: 20-340 m a.s.l.

Eastern Rûens Shale Renosterveld: from Bredasdorp to Swellendam extending east as far as Goukou River at Riversdale, abutted by the Langeberg in the north and the coastal limestone belt in the south. Altitude: 40-320 m a.s.l. (Mucina & Rutherford 2006).

Human history and conservation status

The Western Cape was first occupied by European settlers in the mid-1600s, although evidence suggests that prior to this, the Khoi-San pastoralists had been living nomadically in the region for about 2000 years (Deacon 1992, Hoffman 1997). It did not take long for the European settlers to exterminate most large game animals; even shooting the Blue Buck and Quagga to extinction (Skinner & Smithers 1990). Initially, renosterveld was used by the settlers for livestock grazing, but due to its relatively fertile nature, renosterveld was seen as being more valuable as a ploughed land for growing grain crops (wheat, barley, oats, canola) and artificial pasture (lucerne) than as a natural pasture for livestock. Thus, land was transformed for commercial farming practices over the last century (Kemper *et al.* 1999) until all that was left were essentially those areas that were too steep, too rocky, or too wet to plough. The extant renosterveld is scattered amongst a matrix of cereal crops and lucerne pasture and it is estimated that less than 10% remains today (Kemper *et al.* 1999). All renosterveld types in the Overberg are classified as *Critically Endangered* (SANBI & DEAT 2009).

Geology and soils

Geology comprises clays and loams derived from Bokkeveld Group Shales, specifically the Ceres subgroup (Western Rûens Shale) and some Mesozoic Uitenhage Group sediments in the northeast of the Eastern Rûens Shale. Glenrosa and Mispah forms are the dominant soils in all three vegetation types.

Climate

Mean Annual Precipitation and Mean daily maximum and minimum temperature figures are summarised in the table below (from Mucina & Rutherford 2006). Rainfall tends to decline along the west-east gradient, with an increasing contribution of summer rain in the east.

	Mean Annual Precipitation	Mean daily Max. & Min Temperatures
<i>Western Rûens Shale Renosterveld</i>	490 mm (360-700), Winter rainfall	26.9 (Feb), 6.1 °C (Jul)
<i>Central Rûens Shale Renosterveld</i>	380 mm (300-480), Winter rainfall	27.3 (Jan), 5.6 (Jul)
<i>Eastern Rûens Shale Renosterveld</i>	385 (270-540), Winter & summer	26.9 (Jan), 5.9 (Jul)

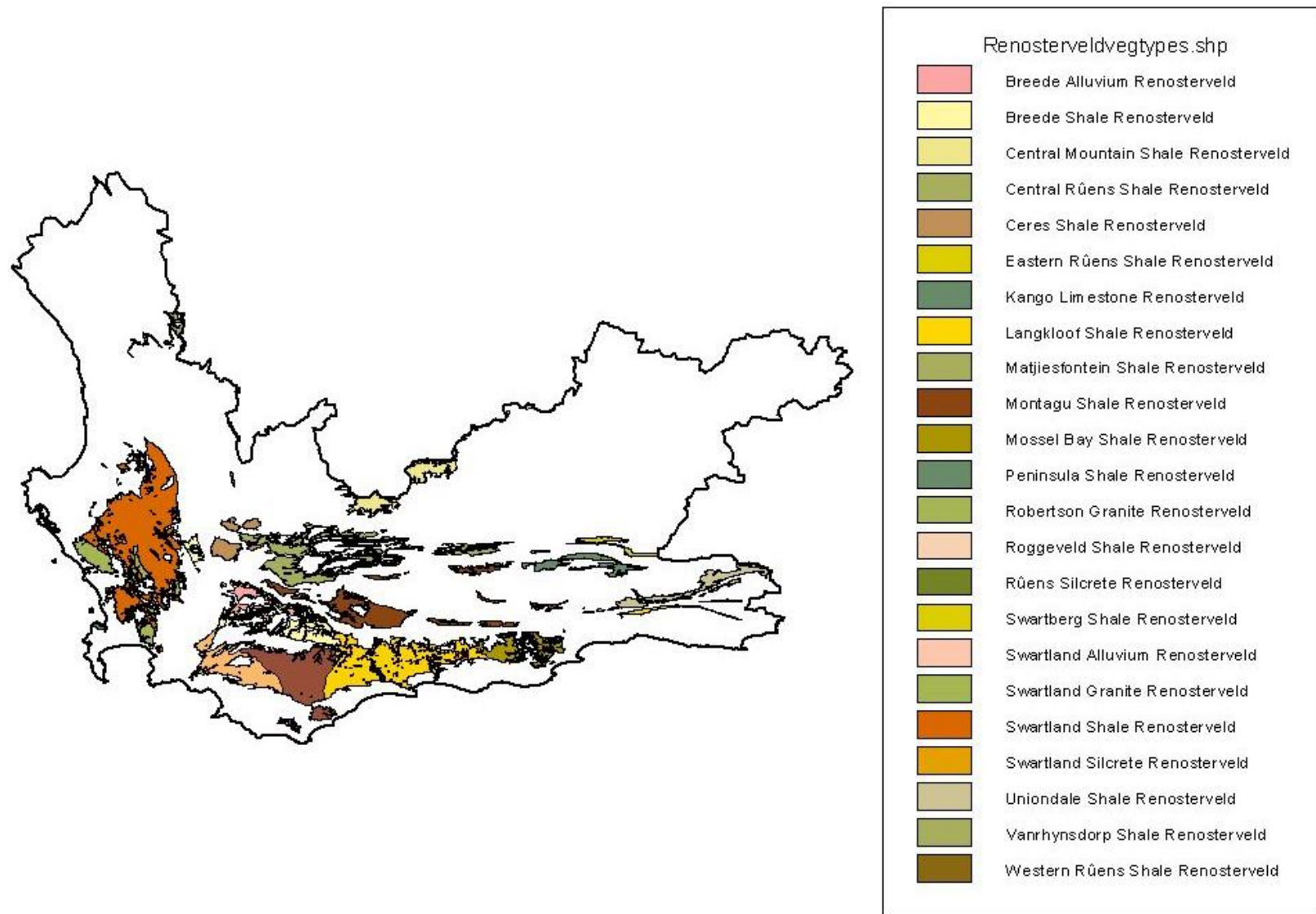


Figure 1. Map denoting the range of renosterveld types within the Cape Floristic Region, South Africa.

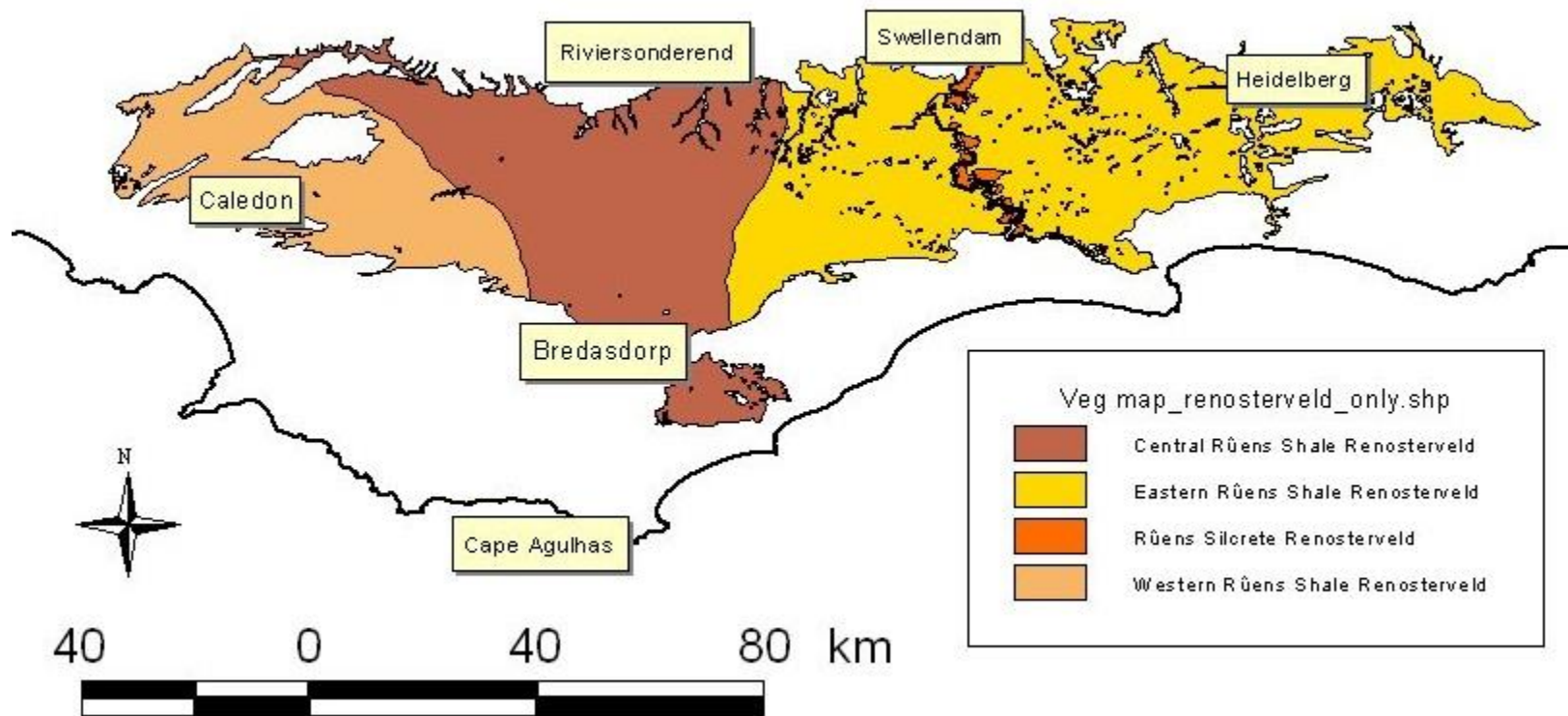


Figure 2. Map denoting the distribution of renosterveld types across the Overberg.

Vegetation and landscape features

The three vegetation types are generally described as occurring on a moderately undulating landscape supporting an open to medium dense, cuppresoid and small-leaved, low to moderately tall grassy shrubland dominated by renosterbos (Mucina & Rutherford 2006) and / or C₃ tussock grasses such as *Merxmeullera stricta* and *Pentaschistis eriostoma* (pers. obs.) Heuveltjies are very rare across the distribution of these three vegetation types (Mucina & Rutherford 2006, pers. obs.), but termitaria are present, particularly on the north-facing slopes (pers. obs.).

Western Rûens Shale Renosterveld: According to Mucina & Rutherford (2006), this type is distinguished from the other ruens renosterveld by the absence of *Hermannia flammea* and the rare occurrence of *Aloe ferox* and *Acacia karoo*. It tends to comprise a grassier component and is rich in geophytes (pers. obs). Mucina and Rutherford (2006) also claim that *Hyparrhenia hirta* (a C₄, summer rainfall species) is the most conspicuous grazing component, but I have observed this species only on road verges, while the grazing grasses comprise *Themeda triandra*, *Ehrharta* spp., and *Cymbopogon* spp.



Figure 3. Western Rûens Shale Renosterveld at Caledon, dominated by C₃ tussock grasses and *T. triandra*.

Central Rûens Shale Renosterveld: Mucina and Rutherford (2006) distinguish this type from its eastern counterpart only by the absence of *Aloe ferox*. My observations suggest that *Pteronia incana* and *Galenia africana* are also largely absent from this vegetation type, which tends to have a grassier and richer geophytic component than Eastern Rûens Shale Renosterveld. As with Western Rûens Shale Renosterveld, Mucina and Rutherford (2006) claim that *Hyparrhenia hirta* is the most conspicuous grass component, but I have observed this species only on road verges, while the grazing grasses comprise *Themeda triandra*, *Ehrharta* spp., and *Cymbopogon* spp.



Figure 4. Central Rûens Shale Renosterveld near Napier, taken from a north slope (note the termitaria), looking onto a south-facing slope, half of which was burned three years before the photograph was taken.

Eastern Rûens Shale Renosterveld: This is a very mixed vegetation type and perhaps warrants consideration for further divisions (Curtis *et al.* 2013). It is a dry shrubland with a lower grass component than its western counterparts, except in the north and eastern limits of its range against the foothills of the Langeberg Mountains where it has a high C₄ grass component (*Themeda triandra*). Dotted across this vegetation type are quartz outcrops comprising distinct plant communities with high levels of endemism and species richness (Curtis *et al.* 2013, Appendix 1), Goldblatt *et al.* in prep (Appendix 2)). Some calcrete deposits support mesotrophic asteraceous fynbos at higher altitudes (Mucina & Rutherford 2006).



Figure 5. Eastern Rûens Shale Renosterveld, dominated by *Oedera squarrosa* and C3 tussock grasses.

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CHAPTER 3:

Renosterveld: the grassy-shrubland or shrubby-grassland debate. Can this be put to rest using Carbon isotope evidence?

The debate about what 'pristine' renosterveld should consist of will no doubt continue indefinitely.

(Ian Newton 2008)

INTRODUCTION

The two Old World Mediterranean-type climate regions that contain the oldest records of human habitation are the Mediterranean region itself and the Cape region of South Africa (Deacon 1983). These regions have been occupied for hundreds of millennia, while their New World counterparts in California, Chile and Australia have only been populated by humans for tens of millennia (Deacon 1983). However, across the globe, *Homo sapiens* has been influencing the structure of landscapes and manipulating processes in order to get the maximum resources out of the system. Thus, man has evolved from being a hunter-gatherer to domesticating livestock, to manipulating natural pastures for improved grazing, to becoming more sedentary due to the development of small-scale agriculture, and finally, to developing large-scale, commercial agriculture with the aid of machinery and technology. However, in many cases across the globe, land transformation associated with man's 'development' has occurred at such a rapid rate that there are very few accounts or descriptions of what these landscapes looked like before the advent of large-scale commercial agriculture. Naturally, this presents several challenges; one of which is an ecological understanding of the systems we are attempting to conserve, so that we might make informed management decisions.

This is especially true for renosterveld, a severely fragmented habitat occurring in an exceptionally diverse landscape. Renosterveld is a vegetation type found within the Fynbos Biome of South Africa, generally located on clay-rich, shale-derived, relatively fertile soils (Cowling *et al.* 1986). Compared with adjacent fynbos habitats, it often has a uniform grey appearance due to the dominance of small-leaved asteraceous shrubs, which creates the illusion of a homogenous habitat with low diversity. This, however, is not the case: renosterveld is one of the richest plant assemblages on earth per unit of land area (Cowling 1990, Newton & Knight 2010). It is also grassier and is richer in alpha diversity than the adjacent fynbos habitats (Rebello 1995). Several types of renosterveld are recognised within the Fynbos Biome (Mucina & Rutherford 2006) and these are firstly divided up into Mountain and Lowland Renosterveld. Mountain Renosterveld occurs on less fertile soils at higher altitudes and is not as transformed, or as diverse, as its lowland counterparts. Lowland renosterveld types essentially occur in the Western Cape and are renowned

for their exceptionally high levels of geophytic diversity (Cowling 1983, Paterson-Jones 1998). The types are broadly divided into West Coast Renosterveld (the shale-derived lowlands of the ‘Swartland’ / west coast of the Western Cape) and South Coast Renosterveld (the shale-derived lowlands of the southern and southeastern Cape) (Cowling *et al.* 1986), with several unique vegetation types falling into these broad categories (Mucina & Rutherford 2006). West Coast and South Coast Renosterveld are very different systems with, for example, South Coast Renosterveld being more fertile (Schulze 1997 quoted by Newton 2008) and, particularly in the eastern-most extent of its range, receiving more summer rain and thus containing a higher proportion of C₄ grasses (Cowling *et al.* 1986).

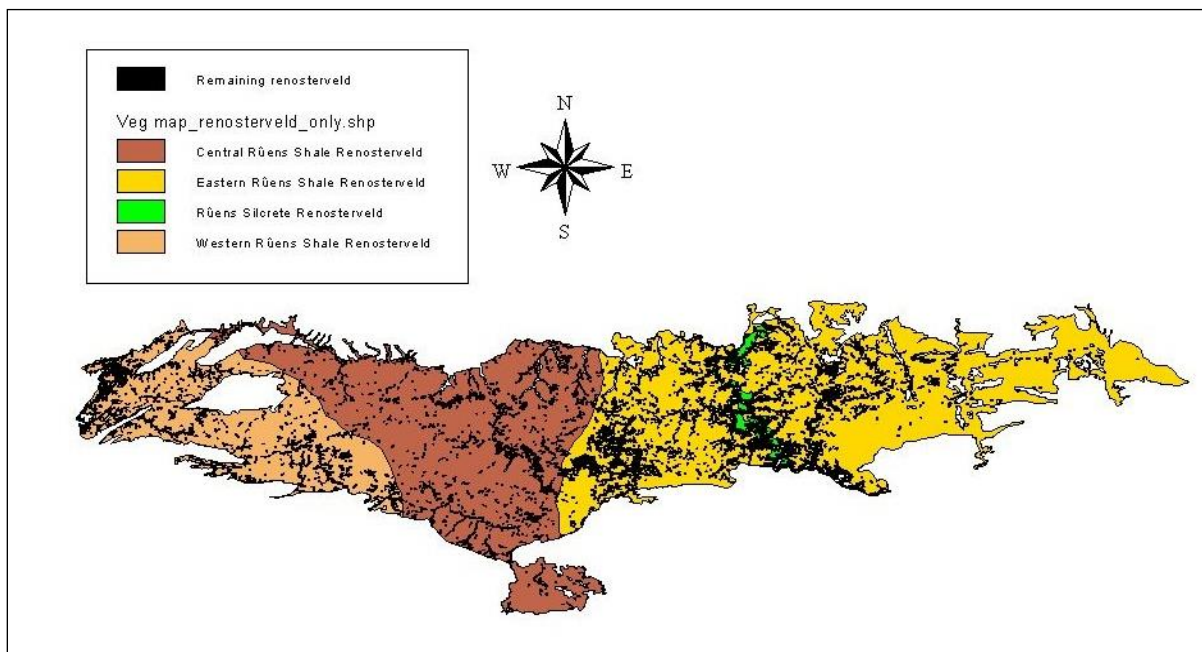


Figure 1. Map denoting the four dominant renosterveld vegetation types in the Overberg (i.e. South Coast Renosterveld) overlaid with the remaining remnants (SANBI).

Both West Coast and South Coast Renosterveld have been severely transformed, with >90% of the original extent ploughed for agricultural development (mostly grain and artificial pasture) (Boucher 1983, Kemper *et al.* 1999, McDowell & Moll 1992). Thus, most types are classified as *Critically Endangered* and are highly prone to functional extinction (Fig. 1). In the present study, I focus on South Coast Renosterveld in the Overberg, hereafter simply referred to as ‘renosterveld.’ Within this broad vegetation unit in the Overberg, there are four types of Lowland Renosterveld: Western-, Central- and Eastern-Rûens Shale Renosterveld which span the relatively fertile lowlands of the Overberg and southeastern Cape, and Rûens Silcrete Renosterveld which occurs in a thin strip along the Breede River (Fig. 1, Mucina & Rutherford 2006).

The name 'Renosterveld' is derived from the Afrikaans words 'renoster' (meaning rhino) and 'veld' (meaning vegetation), although the exact reasons for this choice of name are unclear. It is generally believed that the vegetation was named after the Black Rhino which occurred in the Western Cape, due to the fact that either i) the overall uniform 'grey' appearance of the vegetation resembled that of a rhino hide, or ii) that the rhinos occurred in this vegetation (Boucher 1983).

The viability of lowland renosterveld as a functioning ecosystem is influenced by a suite of factors, from those occurring as a result of substantial shifts in management regimes to those caused by significant fragmentation and habitat loss. Renosterveld management is particularly challenging because, despite the fact that this vegetation type falls within a Biome that is fairly well-studied, there is disagreement amongst ecologists about what renosterveld actually *was* (and thus what we are managing *for*). The suggestion that current-day renosterveld does not resemble the renosterveld communities prior to major landscape transformation, post European settlers, has been debated for several decades with no definitive conclusions being reached (Cowling *et al.* 1986, Newton 2008, Newton & Knight 2004).

Nearly three decades ago, Cowling *et al.* (1986) proposed the hypothesis that South Coast Renosterveld was historically dominated by *Themeda triandra* and that Asteraceous shrubs (particularly *Elytropappus* and *Metalasia* species) had started to dominate the landscape as a result of severe overgrazing by domestic livestock. In support of this hypothesis, Newton and Knight (2004) suggested that since the intensification of the use of domestic livestock in the Western Cape about 200 years ago, renosterveld has been severely transformed, essentially changing the system from a 'shrubby grassland' to a 'grassy shrubland'. They hypothesized that two main factors contributed to this: i) the large-scale extermination of indigenous grazing and browsing herbivores and ii) the introduction of selective grazers in the form of sheep and cattle: i.e. the replacement of a suite of herbivores, of different sizes and varying grazing and browsing preferences, with two highly selective grazers (domestic sheep and cattle) resulting in a shift from a system where grasses were prominent (if not, dominant), to a system generally dominated by unpalatable, asteraceous shrubs. An alternative hypothesis is that renosterveld was always a shrubland dominated by asteraceous shrubs (particularly *Elytropappus*), as it is today.

Several historical statements have been cited as anecdotal evidence that a shift from Poaceae to Asteraceae took place in the Western Cape's lowlands and that this shift occurred in the last two centuries (Cowling *et al.* 1986, Newton & Knight 2004, Skead 1980). In 1785, Sparrman published on what he saw as the demise of the South Coast grasslands and the resultant increase in *Elytropappus*, stating, '... it is not at all unlikely that future ages may see this part of Africa entirely changed and different from what it is at present,' (in Cowling *et al.* 1986). In 1943, Smit made reference to the lowlands of the South Coast once being known as the 'blue grassveld,' presumably in reference to the dominance of *Themeda* (commonly

known as 'red-' or 'blue-grass,' due to the hue created by extensive areas of this species) (in Cowling *et al.* 1986), although few authors acknowledge that *Ehrharta* (an important palatable C₃ grass) is also known as 'blue grass,' thus these accounts may also have been referring to this species. Levyns (1929) viewed the Renosterbos as a potential 'problem plant' and noted, with reference to renosterveld: "Although the renoster bush is its principle constituent, several shrubs and other composites, and many geophytes are associated with it. However, these do not break the grey-green monotony of this type of plant community." Nearly 30 years later, Levyns (1956) attributed overgrazing as the likely cause for what she viewed as the spread of *Elytropappus* and drew attention to the fact that farmers were burning renosterveld in order to utilize the regrowth for grazing, but that in the long-term, this management policy 'only perpetuates' *Elytropappus*. Several other historic accounts describing the flora of the Cape suggest the existence of a grassier lowland system than what is present today, as well as an increase in the spread of renosterbos, due to man-induced influences on the landscape (Newton & Knight 2004, Appendix 3.1). Although these references (Appendix 3.1) do not suggest the existence of a pure C₄ grassland, they are interesting as they provide some insights into the way in which the landscape was viewed by early settlers between the 1700s and early 1900s and they do suggest that some level of change has taken place in the Overberg – mostly in that there has been a decrease in grasses (although whether these would have been mostly C₃ or C₄ grasses is not clear), as well as an increase in renosterbos

These accounts may suggest that the lowlands of the Cape were richer in palatable grasses prior to the arrival of the settlers and that today's landscape is the result of several decades of mismanagement (Newton & Knight 2004). Alternatively, these observations were biased against unpalatable shrubs and saw the grasses as pristine and worth promoting for grazing. For example, Acocks (1953), having a bias towards grasslands preferable for cattle grazing, made the same kind of observation for the Karoo, suggesting it had been a much grassier habitat, but careful analysis (Hoffmann & Cowling 1990) and carbon isotopic evidence contradicts this hypothesis (Bond *et al.* 1994).

However, the European settlers (having first arrived in the 1650s) were not the first pastoralists tending livestock in the region. The Khoi-Khoi (also known as Khoekhoen) had been present in the area for 2000 years prior to the arrival of the settlers and were already manipulating the vegetation, through frequent burning to provide fodder for livestock (Deacon 1992, Hoffman 1997). It is surmised that the 'Khoi-Khoi' were responsible for converting renosterveld from a shrubland into a grassland system to promote feed for their livestock. Thus, the argument goes, renosterveld *was* in fact a shrubland prior to habitat manipulation by the Khoi-Khoi. This hypothesis also has merit. However, if the Khoi were regularly burning renosterveld and using the fresh new growth for grazing their cattle immediately these became available, they too might have damaged the grass component and encouraged the spread of asteraceous species, as this is far more

likely to occur when renosterveld is continually burned and grazed, with no rest periods (see Radloff 2008). If, however, the nomadic Khoi people burned extensive areas while moving through with their livestock, they may well have allowed the veld significant periods of rest and so increased, or at least, maintained the grass component. Historic accounts suggest that these rest periods would have been long and widely spread out (and were probably not even annual), implying substantial rest periods after heavy grazing and post-burning (Smith 1992, Thom 1952). While the Khoi were using the landscape for grazing their cattle, they were sharing it with the large herds of game so that a more balanced mix of grazers and browsers of various sizes would have been maintained. It was only once the European settlers had extinguished most of the wild game that the vegetation was exposed to selective grazing by livestock only. Thus again, the supposed vegetation changes are likely to be linked to the change from migrant herds to resident persistent grazing (such as with present-day livestock farming), as these two regimes would have had quite different impacts on the natural vegetation (Cowling *et al.* 1986). Again, this hypothesis is built on the assumption that indigenous game herds were migratory: there is almost no evidence in historic accounts to support this, although logically, it must have occurred. There is, however, evidence that the Khoi pastoralists were migratory and moved through the landscape with their livestock, using fire to improve pasture, but avoiding recently-burned areas for grazing (Deacon 1992).

In his PhD thesis, Newton (2008) builds up a hypothesis in support of the grassland hypothesis (surmising that West Coast Renosterveld is a grassy-shrubland and South Coast Renosterveld is a shrubby-grassland), based on several palaeoecological studies, which give the hypothesis substantial credibility, at least for the West Coast Renosterveld and South Coast Renosterveld in the eastern extent of its range, for which more anecdotal and palaeoecological data exist. (e.g. see Baxter 1996 in Newton 2008, Scholtz 1986).

Carbon isotopes and vegetation change

The stable carbon isotope method has been used to test ideas regarding recent shifts in vegetation communities across the globe, as well as in fynbos systems (Ambrose & Sikes 1991, Bond *et al.* 1994, Cerling *et al.* 1991, Guillet *et al.* 1988, Luyt *et al.* 2000). The method works on the premise that, because soil organic matter is derived from plant litter, the isotopic composition of soil will reflect that of the vegetation from which it stemmed (Stock *et al.* 1993). The $\delta^{13}\text{C}$ -values of C_4 and C_3 plants are very distinct, with C_4 species having a value of -12 to -14‰ and C_3 species with values of -26 to -30‰. Values between -14 and -26‰ are suggestive of a mixed C_3 - C_4 habitat (Stock *et al.* 1993). C_4 photosynthesis is common in tropical and sub-tropical grasses while most other plant species follow the C_3 pathway (Cowling 1983; Sage 2004). Plants that make use of the CAM photosynthetic pathway follow a process similar to that seen in C_4 species at night and can have a $\delta^{13}\text{C}$ -value of between -10‰ to -20‰ (O'Leary 1988). However, CAM

photosynthesis in terrestrial plants is typically restricted to succulents (O’Leary 1988) and these never dominated the surveyed sites, thus influence from CAM plants was not deemed significant in this study. Chenopodiaceae plants also have a C₄ signature (Smith & Epstein 1971), but in renosterveld these tend to be concentrated in saline bottomlands, thus these areas were avoided when sampling.

It is also assumed that present-day or more recent vegetation will be reflected in the upper parts of the soil profile, while samples from deeper in the profile will retain the carbon signature of historic vegetation cover (Stock *et al.* 1993). In the case of renosterveld, abundant C₄ grasses include *Themeda triandra* and *Cymbopogon marginatus*, while C₃ grasses include *Ehrharta calycina*, *Pentaschistis eriostoma* and *Merxmuellera stricta*.

Carbon isotopes have also been used to investigate whether the Cape’s renosterveld and Karoo lowlands were historically closer to grassland habitats. Stock *et al.* (1993) tested the ‘*Themeda* – Renosterveld controversy’ by examining three sites near the Cape Peninsula. One of these sites was a fynbos-renosterveld transition habitat and was selected because it was probably always dominated by shrubs and anthropogenic changes were likely to have been minimal. For this site, $\delta^{13}\text{C}$ values matched the current-day vegetation throughout the profile. One renosterveld site (Signal Hill) was dominated by C₄ grasses at the time of the study and the isotope results from different depths in the soil, although variable, were consistent with C₃ vegetation. The second renosterveld site, dominated by renosterbos at the time of the study, showed a consistent dominance of C₃ plants through the soil profile, although the carbon signature was variable for each sample, ranging from -21 to -28‰. The authors argue that C₃ plants had been dominant in the system historically and that the current-day dominance by C₄ grasses at some sites is the result of very recent shifts in vegetation communities. They assert that their results do not support the notion that renosterveld was a C₄-dominated habitat prior to interventions by early European settlers, but that the C₃ signature may reflect a dominance of C₃ grasses, such as *Ehrharta* spp. and not only C₃ shrubs.

Bond *et al.* (1994) undertook a study using carbon isotopes to assess the hypothesis that desertification (loss of grasses and replacement by shrubs in this case) has occurred in the arid Karoo region of South Africa as a result of overgrazing by livestock over the last 200 years since European settlement) (Acocks 1953). They found the technique to be robust and were able to demonstrate shifts from a grassy (C₄) habitat towards a shrub-dominated habitat in the northern part of the study area and that the basis for this vegetation shift is more likely to be the result of large-scale, extensive grazing by livestock, rather than a changing climate, in agreement with Acocks’s hypothesis (Acocks 1953). However, a reconstruction of pre-settlement vegetation based on rainfall/isotope relationships showed that the Central Karoo study area was a transition zone with stable shrublands in the south, grasslands in the north, and grassy shrublands in between and not the sweet grassveld, as advocated by Acocks (1953) (Bond *et al.* 1994). The authors also

found a positive linear relationship between summer rainfall and C₄ grasses, while regressions indicated negligible grass cover at sites with <100 mm summer rain.

In this chapter, I used stable isotope analysis of soil carbon to test the hypothesis that historically, renosterveld comprised a higher C₄ grass component than is seen today and that not all renosterveld, at all times, was dominated by C₃ shrubs and grasses.

STUDY AREA and METHODS

Carbon Isotope analyses

A total of 40 sites were sampled, across the Overberg, at a minimum of three positions within the soil horizon. These were generally divided into 'top' soil (5-10 cm below surface), 'lower' layer (depths varied from 30 – 75 cm) and 'middle' layer (middle of the profile, depth dependent on lowest depth). At each site, a sample of litter was collected from the general area where the soil pit was excavated, in order to assess the correlation between $\delta^{13}\text{C}$ -values in leaf litter and top soil (assuming that these should be similar). Analyses of key species were run on plant material collected from live plants in the field, in order to ascertain that the carbon signatures of these species were being read 'correctly'.

Rootlets and stones were removed from soil samples. Aggregated lumps of hardened soil were broken up, and successively smaller rootlets and stones were removed as they became exposed. The remaining material was ground in a pestle and mortar and passed through a 1.4mm sieve. Material remaining in the sieve after shaking (mainly small stones) was discarded.

Samples were weighed into tin cups to an accuracy of 1 microgram on a Sartorius micro balance. The cups were then squashed to enclose the sample. The samples were combusted in a Flash EA 1112 series elemental analyser (Thermo Finnigan, Milan, Italy). The gases were passed to a Delta Plus XP IRMS (isotope ratio mass spectrometer) (Thermo electron, Bremen, Germany), via a Conflo III gas control unit (Thermo Finnigan, Bremen, Germany). The in-house standards used were: Sucrose - "Australian National University (ANU)" sucrose, MG - Merck Gel - a proteinaceous gel produced by Merck, Lentil - dried lentils as purchased from Pick 'n Pay, Acacia - Acacia saligna leaves collected from Glencairn. All in-house standards were calibrated previously against IAEA (International Atomic Energy Agency) standards. Nitrogen is expressed in terms of its value relative to atmospheric nitrogen, while carbon is expressed in terms of its value relative to Pee-Dee Belemnite (methods pers. comm. Ian Newton, UCT Archaeology Dept.).

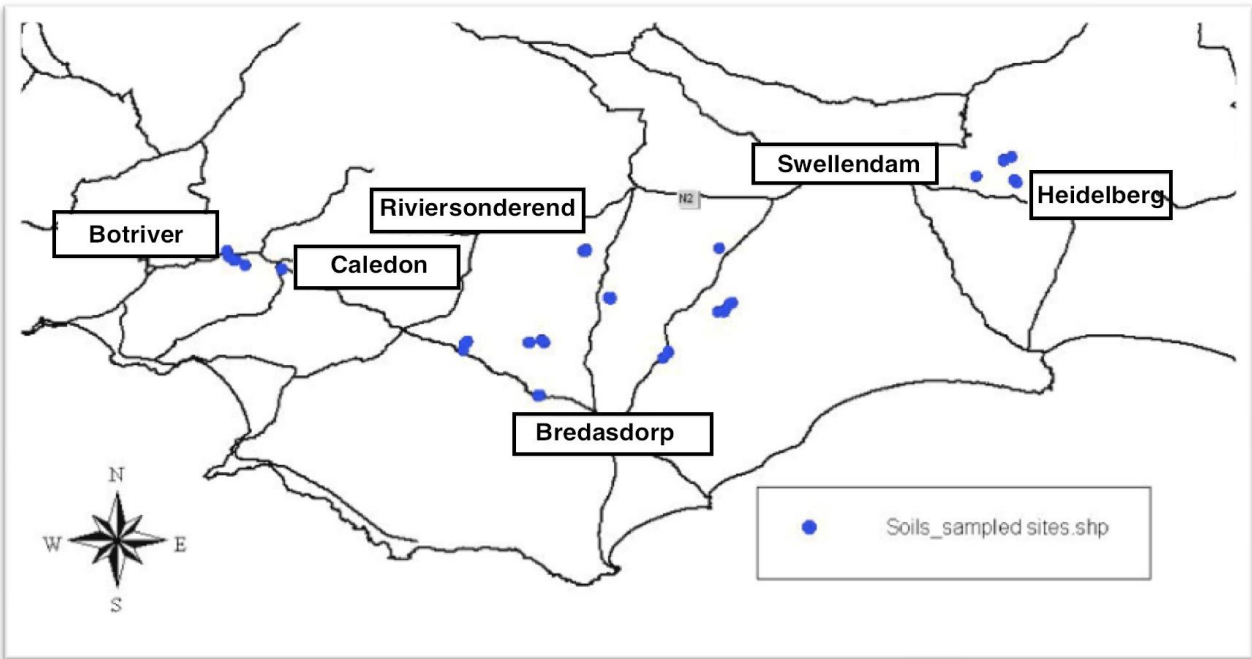


Figure 2. Map denoting sites sampled for carbon isotope analyses, Overberg, Western Cape.

Grass abundance data collected at random plots

In order to compare contemporary quantities of C_3 and C_4 grasses on different aspects in Overberg renosterveld, I used data from 47 random 10X10 m plots collected over 30 fragments, which had been sampled for alpha diversity (Chapter 5) in a relatively small study area. These data were collected in the Napier region of the Overberg in Western- and Central-Rûens Shale Renosterveld. Additionally, I used data collected from 100 m² permanent plots, spread across the three different renosterveld types in the Overberg, which were set up for long-term monitoring experiments in 2007 (Chapter 7). However, for the purposes of comparing abundance of different grasses, I used only data from the year 2011 (i.e. the 4th post-burn year).

RESULTS and DISCUSSION

Carbon Isotope analyses

$\delta^{13}C$ values across all layers and sites ranged from -28.02 to -14.15, with an average of -23.08 ± 3.06 (Appendix 3.2). According to existing literature, $\delta^{13}C$ -values for C_3 vs. C_4 plants are very distinct, with values of -12 to -16‰ for plants using C_4 photosynthetic pathways and -25 to -30‰ for C_3 species (O’Leary 1988, Stock *et al.* 1993) (d-c values are measured against PDB). In the present study, a C_4 signature is indicative of a small number of grasses (mostly palatable species such as *Themeda* or *Cymbopogon*), as well as some geophytes (Yeakel *et al.* 2007).

Analyses of key species were run on plant material collected from live plants in the field, showed that all were consistent with the photosynthetic pathways of the plants, except *Themeda* which had one of three values outside the usual range of C₄ photosynthesis (Table 1). This value of -19‰ is unexpected as, being a C₄ grass, one would expect *Themeda* to display a signature of no less than -14‰. Given these results, for the purposes of simplifying and interpreting results presented in Table 1, I allocated a C₃ value to samples with a $\delta^{13}\text{C}$ -value more negative than -23‰, while values greater than -16‰ were interpreted as C₄-dominated. Values between -23 and -16‰ were assumed to be of mixed C₃-C₄ origin. Rather disconcertingly, the top soil and leaf litter $\delta^{13}\text{C}$ -values did not consistently reflect the photosynthetic pathways of the dominant vegetation in renosterveld (Appendix 3.2).

About 58% of the virgin-land sites surveyed contained C₄ grasses (*Themeda triandra* and/or *Cymbopogon marginatus*) (Fig. 2, Table 1), but this is not reflected in most of the $\delta^{13}\text{C}$ -values for the top soil samples from virgin land, because these grasses often co-occurred with C₃ shrubs and grasses (Table 1).

Table 1. $\delta^{13}\text{C}$ values for key species in the study. The single low value for *Themeda* (-19.5) is likely to be due to sample contamination during the processing.

Species	$\delta^{13}\text{C}$ (‰)
Wheat/Barley1	-26.8
Wheat/Barley2	-27.4
<i>Pentaschistis</i>	-26.2
<i>Pentaschistis</i>	-25.1
<i>Ehrharta</i>	-27.3
<i>Cymbopogon</i>	-15.1
<i>Themeda1</i>	-12.6
<i>Themeda2</i>	-19.5
<i>Themeda3</i>	-14.9
<i>Elytropappus1</i>	-27.1
<i>Elytropappus2</i>	-25.6

Several re-runs of the samples were carried out and in most cases, results were consistent (and in these cases, an average from the different sample runs was used to assign a single result to each sample). The inconsistency between the expected C-isotope value for the dominant vegetation, the $\delta^{13}\text{C}$ -values for litter, and the top soil $\delta^{13}\text{C}$ -values could be due to two factors: i) the change to C₄-dominance is very recent, ii) the litter collected did not represent the vegetation sufficiently or iii) the influence of decomposition resulted in a variance between soil organic matter and the original plant material (see Boström *et al.* 2007,

Schweizer *et al.* 1999). Alternatively, there may have been sample contamination during processing of the litter samples.

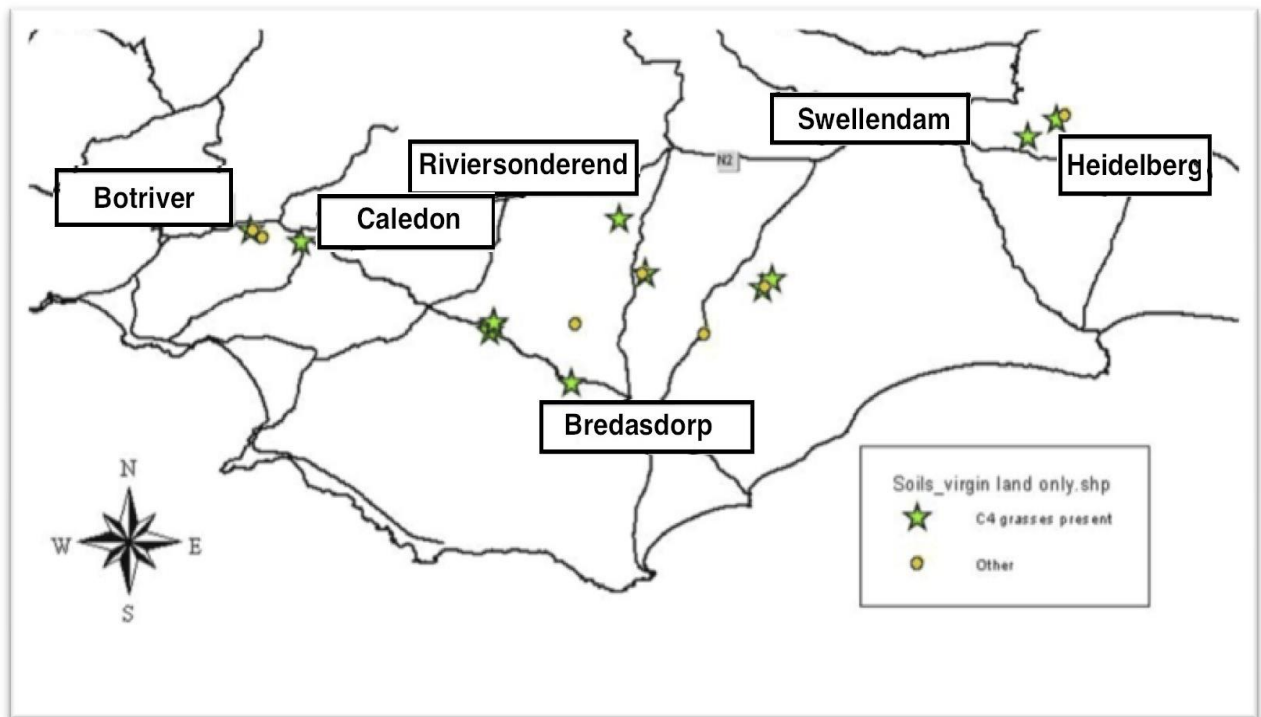


Figure 3. Map denoting occurrence of *Themeda triandra* in sampled sites of virgin land.

Despite the disagreement in results between the dominant vegetation and the top soil, where results from matched pairs were available, a T-test showed no significant differences between $\delta^{13}\text{C}$ -values for litter and top soil ($t=0.05$, $n=23$, $P=0.96$) suggesting that the methods employed here are robust-enough to understand general patterns of change over time. There was no significant difference in $\delta^{13}\text{C}$ -values for top soil on virgin vs. productive lands (Kolmogorov-Smirnov Test, *Mean Virgin* = -24 ± 2.65 ($n=14$), *Mean Productive* = -24.63 ± 1.59 ($n=12$), $P > 0.1$). Thus, all data were pooled for further analyses.

Comparisons of $\delta^{13}\text{C}$ values across Top, Middle and Lower positions in the soil profile showed a significant difference between the three positions (Friedman ANOVA & Kendall Coeff of Concordance: ANOVA Chi-Sqr ($n=34$, $df=2$)= 33.59 , $P=0.000$, Coeff of Concordance= 0.5 , rank $r=0.48$), with a gradual increase in $\delta^{13}\text{C}$ values with increasing depth in the soil profile (Figure 4 & Figure 5). In order to ascertain whether or not the effect was biased by the inclusion of samples taken from crop lands, the ANOVA was rerun using samples from virgin land only. A similar pattern remained (Friedman ANOVA & Kendall Coeff of Concordance: ANOVA Chi-Sqr ($n=19$, $df=2$)= 17.16 , $P=0.000$, Coeff of Concordance= 0.45 , rank $r=0.42$).

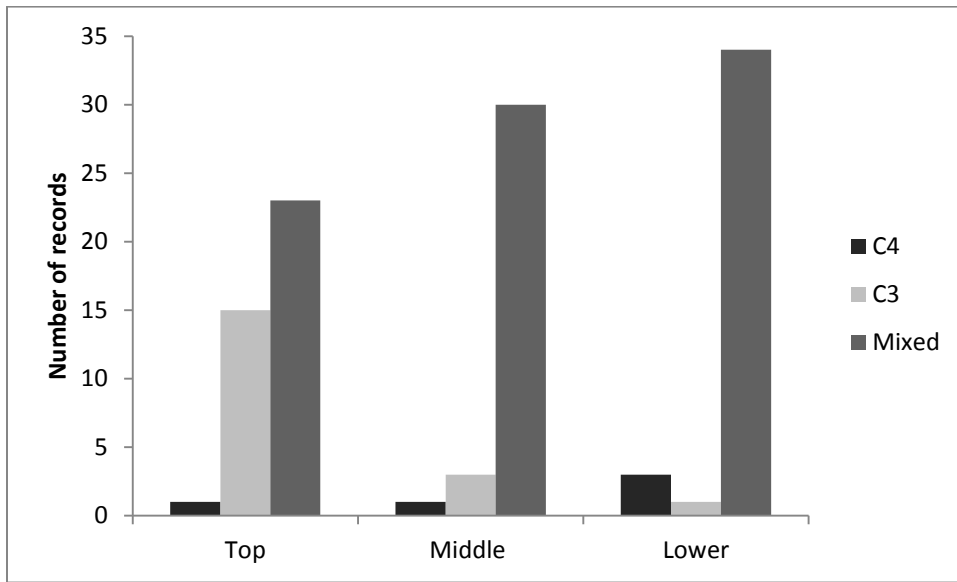


Figure 4. Bar chart showing proportions of Mixed ($\delta^{13}\text{C}$ -values of between -16 and -25 ‰), C_4 (>-16 ‰) and C_3 (<-25 ‰) isotopic values for top, middle and lower layers in the soil profile for samples collected across the Overberg.

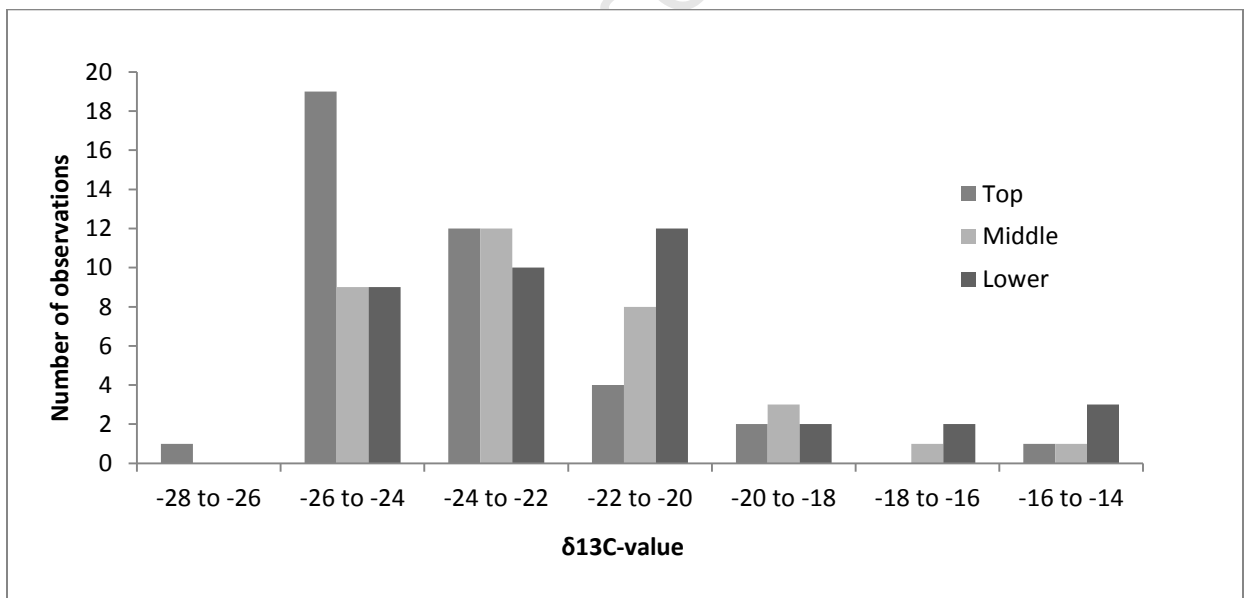


Figure 5. Histogram denoting variation in number of observations for categorised $\delta^{13}\text{C}$ -values for each of the three soil layers (top, middle and lower) from samples collected in the Overberg.

Comparisons between the different vegetation types (i.e. Western-, Central-, and Eastern-Rûens Shale Renosterveld) within each of the soil layers revealed a tendency for an increasing $\delta^{13}\text{C}$ -value from west to

east for lower soil layers (Figure 6). This result from lower layers in the soil profile suggests that the current-day pattern of C₄ grasses increasing along a west-east gradient existed historically in the Overberg (see Cowling *et al.* 1986).

The patterns in Figure 6 suggest that renosterveld is largely a mixed system, with more westerly areas tending towards a greater C₃ component and eastern areas comprising a higher C₄ component. The data suggest a slight decrease in C₄ inputs over time (i.e. that the C₄ input decreases slightly from the bottom to the top of the soil profile), with differences on the order of -4.97 to 0.35‰ between top and lower soil layers (Appendix 3.2). None of the samples fell into the C₄ range for western samples, whereas four gave a C₄ signal in the eastern range. Only three samples were pure C₃ in the east, and these were all from surface horizons, with the remaining 36 samples giving a mixed signal. The central sites comprised only one pure C₄ signal from a lower layer, eight C₃ signals on the upper and middle layers, while the remaining 25 produced a mixed signal. Western sites produced equal numbers of C₃ and mixed values, while the proportion of mixed values increased substantially with decreasing soil depth (10 mixed and only one C₃ in both middle and lower layers). The soil carbon was not radio-carbon dated so that the time scale over which these changes have taken place cannot be assessed.

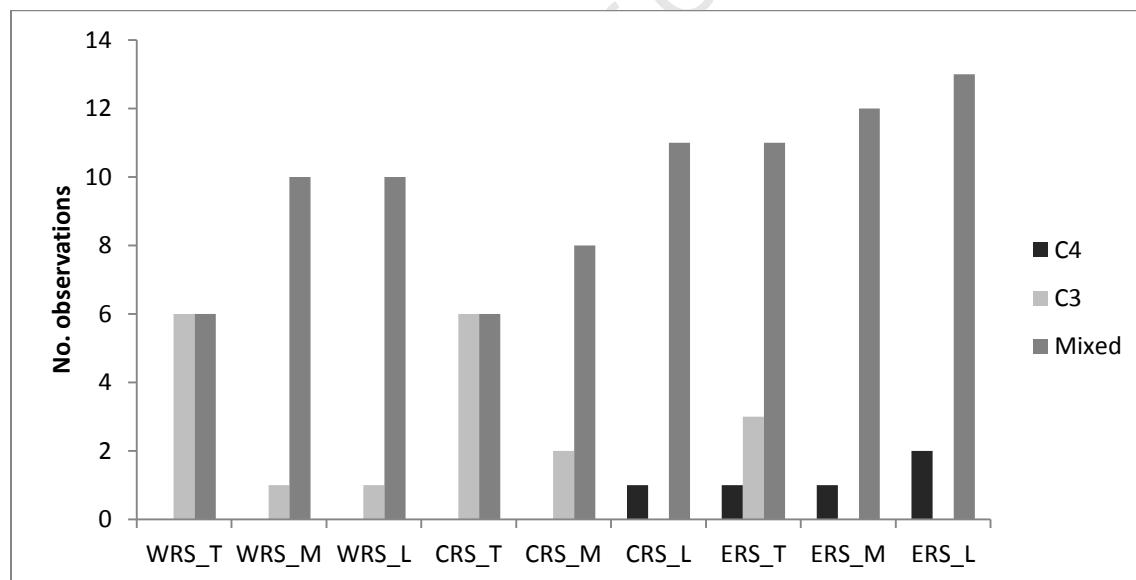


Figure 6. Comparisons of the proportions of C₄, C₃ and Mixed carbon-isotope signatures in the three different vegetation types (WRS=Western Rûens Shale Renosterveld, CRS=Central Rûens Shale Renosterveld, ERS=Eastern Rûens Shale Renosterveld) within each of the three soil profile layers (Top (T), Middle (M) and Lower (L)) for samples collect in the Overberg.

Relative grass-abundance from contemporary plots

In terms of frequency of occurrence in the 47 plots, C₃ grasses, *Merxmuellera* and *Pentascistis* both occurred on south-facing slopes, while *Merxmuellera* was absent on north-facing slopes. *Ehrharta calycina* occurred on more south plots (77%) than north (44%). Verboom *et al.* (2012) demonstrated that this species shows significant life-history variation in response to climate and substrate, being functionally perennial in the southern parts of its range and annual in the northern parts. It would be interesting to investigate whether these patterns in perenniality exist at the local level (i.e. dry north- vs. moist south-facing slopes).

With regards to C₄ species, *Cymbopogon marginatus* only occurred on north-facing plots (52%), while *Themeda* occurred on both aspects, but mostly on south slopes (95% occurrence as opposed to 44% on north-facing plots). This finding is contrary to Cowling's (1983) study which demonstrated that C₄ grasses in renosterveld in the Eastern Cape (South Africa) are more abundant on warmer, drier north-facing slopes. Here, *Themeda* appears to have a wider ecological tolerance than *Cymbopogon*, which is perhaps the result of an ability of the former to adapt to different conditions more readily.

Relative abundance, in terms of cover, of C₃ vs. C₄ grasses on north and south-facing slopes are very similar in both random plots and permanent plots (Table 2). This is in contrast to Cowling's (1983) findings in fynbos and renosterveld habitats in the Eastern Cape, where he found a higher relative cover of C₃ grasses on south-facing slopes and a higher relative cover of C₄ grasses on north-facing slopes. In the present study, *Themeda* comprised 41% of the total C₄ grass cover on north-facing slopes, with *Cymbopogon* making up the remainder of C₄ cover. Conversely, on south-facing slopes, *Themeda* accounted for 100% of the C₄ grass cover, which is unexpected, as Cowling (1983) predicts, and indeed demonstrates, that C₄ grasses are more abundant on drier, hotter north-facing slopes.

Table 2. Summary of results of total cover and proportion of cover of C₃ and C₄ grasses on north- and south-facing slopes, recorded from random and permanent plots, Western Cape.

	Random plots, Napier				Permanent plots			
	North-facing slopes		South-facing slopes		North-facing slopes		South-facing slopes	
	Total cover	%	Total cover	%	Total cover	%	Total cover	%
TOTAL C3	846	80	1010	78	125	70	179	80
TOTAL C4	206	20	282	22	52	30	45	20
Total Themeda	85	8	282	22	10	6	45	20
TOTAL C3 & C4	1052		1291		177		224	

CONCLUSIONS

This study suggests that C₃ grasses and shrubs are more prevalent in renosterveld than C₄ grasses and that renosterveld generally comprises a mixture of C₃ and C₄ shrubs and grasses. The results also confirm that renosterveld in the Overberg is unlikely to have been dominated by C₄ grasses, except in small patches, and that managing for these grasses alone could severely alter the composition, diversity, and structure of this system. The isotope results are consistent with contemporary measures of relative proportions of C₃ and C₄ plants along a west-east gradient and the increase in C₄ signals with depth suggests the presence of more C₄ grasses in the past, consistent with being grazed out more recently.

The short-comings of the carbon isotope technique warrant mentioning: i) no radiocarbon dates of the soil carbon were made so that the time periods over which vegetation shifts took place cannot be estimated and ii) nor can one distinguish between grasses and shrubs – it is merely the photosynthetic pathways that are discernible here (Bond *et al.* 1994). Nevertheless, it has proven a useful technique in piecing together the puzzle of the past and samples can be collected in diverse landscape positions compared with the constraints of pollen-based analyses restricted to wetlands.

Of concern in this study is that only 14% of the study sites dominated by C₄ plants displayed a $\delta^{13}\text{C}$ -value of litter associated with a C₄ photosynthetic pathway. The rest displayed values associated with C₃ or mixed habitats. Thus, the present-day presence of C₄ grasses is underestimated by the isotopic analyses. This may be because even when present in a plant community, C₄ grasses and bulbs may not be detected in the soil horizon, due to their root biomass and contribution to above-ground litter being much less than that of the larger C₃ shrubs and bunch grasses, resulting in a very minimal contribution of C₄ grasses towards $\delta^{13}\text{C}$ -values. Although these samples were re-run several times, they produced some inconsistent results, particularly in cases where $\delta^{13}\text{C}$ -values for litter or top soil samples did not correlate with the dominant vegetation at the site.

It is hoped that these potential problems were controlled for in this study by selecting enough sites, across a spectrum of vegetation types, and that the detection of a general trend will still be insightful, in terms of how much the C₄ component of renosterveld has been altered over the last several decades, or even centuries. Renosterveld is an extremely patchy and heterogeneous habitat, with anything from mere pockets of C₄ grasses to entire slopes dominated by *Themeda* or *Cymbopogon* (in order to illustrate the variation in renosterveld type and community structure, Appendix 3.2 comprises a series of photographs taken in Overberg renosterveld). With such high variation in community composition at the patch-level, one might encounter a large variation in $\delta^{13}\text{C}$ -values over a very small sampled area, thus it would be interesting to test how variable signatures will be within a small area (<1 ha). This variation, combined with the dynamism of renosterveld in response to disturbance factors, may partly explain the mismatches

between isotope values for top soil in relation to the vegetation covering the soil surface at the time of sampling.

The fact that the current-day trend for C₄ grasses to increase along a west-east gradient was detected suggests that the results produced by the isotope values here are valid for detecting trends. Certainly, there has been a decrease in C₄ inputs over time and it would be valuable to explore these results further, particularly in terms of the timescales over which these changes happened. Additional techniques which may be more useful for testing questions relating to the influence of historic management on vegetation communities are becoming more available and more refined. Pollen cores can be useful for determining historic presence of species (Rovner 1983), but finding suitable depositional sites is challenging. Perhaps more appropriate would be to explore the use of phytolith data, as these can be used to identify plants (and particularly grasses) to tribe, genus and sometimes even species level, allowing one to tease apart the C₃ and C₄ grasses (Fisher *et al.* 1995, Rovner 1983). For example, in Utah, USA, Fisher *et al.* (1995) use opal phytoliths to determine what vegetation was present in the study area prior to European settlement in order to determine appropriate current-day grazing regimes. They found the method to be robust and recommend it for future use. This method would be particularly useful for testing the hypothesis that palatable C₃ species (e.g. *Ehrharta*) were more common historically and that these have been severely reduced through overgrazing. It is also important that the mismatches between soil and litter carbon isotopes are a genuine result, or if these are due to contamination in the lab processing. Additionally, dating soil carbon would add a great deal of understanding regarding the time over which these changes took place. Ideally, a good depositional environment should be identified where multiple proxies can be used and compared.

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CHAPTER 4:

Is seedling recruitment and flowering in renosterveld fire-stimulated?

Like the resource it seeks to protect, wildlife conservation must be dynamic, changing as conditions change, seeking always to become more effective (Rachel Carson).

INTRODUCTION

Fynbos vegetation types are fire-dependent in the sense that most species have fire-stimulated recruitment and require fire to complete their life histories (reviews in Le Maitre and Midgley 1992; Cowling *et al.* 1997; Bond 2012). Many species (~50%) are killed by fire (seeders) and recruit only after a burn. The Proteaceae that dominate many fynbos stands are typically slow-maturing, serotinous species which require fires between ~ 8-30+ years in order to persist in the system (e.g. Bond 1997; Keeley *et al.* 2012). Fire exclusion in fynbos results in the senescence of the serotinous proteoid shrub layer, the loss of understory diversity as seedbanks gradually diminish, and, in some instances, replacement of fynbos by forest (Cowling *et al.* 1997). Alternatively, very frequent burning will result in shifts in community structure (generally towards a more grassy system) and local extinction of slow-maturing serotinous shrubs.

Renosterveld is a vegetation type found within the Fynbos Biome of South Africa, generally located on clay-rich, shale-derived, relatively fertile soils (Cowling *et al.* 1986). Compared with adjacent fynbos habitats, it often has a uniform grey appearance due to the dominance of small-leaved asteraceous shrubs, which creates the illusion of a homogenous habitat with low diversity. This, however, is not the case: renosterveld landscapes can exceed fynbos in plant species richness making them among the richest in temperate regions of the world per unit of land area (Chapter 5, Cowling 1990, Newton & Knight 2010). It is also grassier and some communities are richer in alpha diversity than the adjacent fynbos habitats (Rebelo 1995). Several types of renosterveld are recognised within the Fynbos Biome (Mucina & Rutherford 2006) and these are firstly divided up into Mountain and Lowland Renosterveld. Mountain Renosterveld occurs on less fertile soils at higher altitudes and is not as transformed, or as diverse, as its lowland counterparts. Lowland renosterveld types were most extensive in the Western Cape and are renowned for their exceptionally high levels of geophytic diversity (Cowling 1983, Paterson-Jones 1998). In the Overberg, four types of renosterveld are recognised: Western-, Central- and Eastern-Rûens Shale Renosterveld which span the relatively fertile lowlands of the Overberg and

southeastern Cape, and Rûens Silcrete Renosterveld which occurs in a thin strip along the Breede River (Mucina & Rutherford 2006).

Renosterveld is distinct from fynbos in that it is never dominated by the three characteristic groups that distinguish true fynbos from other vegetation types (i.e. it lacks proteas, ericas and restios). Serotinous shrubs, common in fynbos, are absent in renosterveld. Instead, it is typified by the dominance of Asteraceous shrubs and is described as an open to medium, dense, small-leaved, cupressoid shrubland, with a low to moderately tall grassy component (Mucina and Rutherford 2006). Renosterbos *Elytropappus rhinocerotis* is considered the dominant shrub (Mucina and Rutherford 2006), but other dominant species can also include other members of the Asteraceae, such as *Helichrysum petiolare* and *Oedera squarrosa*, as well as C₃ bunch grasses, such as *Pentaschistis eriostoma* and C₄ bunch grasses, such as *Themeda triandra* and *Cymbopogon* sp. (Kemper *et al.* 1999, pers. obs.). Another characteristic of this vegetation type is the exceptionally high geophytic component: renosterveld has a geophyte diversity comparable to or exceeding that of any other system on the globe (Cowling 1990). It also comprises a high diversity of locally endemic, range-restricted shrubs and succulents – an important feature often overlooked by ecologists.

Margaret Levyns was particularly interested in the Renosterbos and its distribution within the Fynbos Biome and beyond, as well as the ecological constraints on its recruitment. In 1929, she published studies on the germination of Renosterbos under various treatments noting that seedling recruitment was zero in unburned plots, sparse and scattered in cut plots and very high in burned plots, suggesting that fire is crucial for renosterbos to recruit. Experiments also suggested that one-year-old seed had a higher probability of germinating than fresh seed (Levyns 1929). In the 1990s, smoke-stimulated seed germination was discovered in many fynbos species but, renosterveld species, including *Elytropappus rhinocerotis*, do not seem to have been screened for smoke-stimulated germination.

Although renosterveld has been explored with great interest by botanists (albeit fairly recently), there is still significant debate as to what renosterveld actually *is* (Newton & Knight 2004); the most contentious debate being: *is renosterveld a grassy shrubland or shrubby grassland?* Lowland renosterveld is poorly studied and there is a dearth of knowledge on even the most basic ecological traits of this *Critically Endangered* system. This is probably mostly due to the fact that when the significance of the threats to renosterveld was fully appreciated (Cowling *et al.* 1986), it was already severely fragmented (Kemper *et al.* 1999, von Hase *et al.* 2003), spread across hundreds of privately-owned land parcels, and not represented in any protected areas, making experimental research complicated. Although renosterveld is included as a sub-type of the fire-prone Fynbos Biome, its fire ecology is very poorly understood, while

much research has focused on fire in fynbos. Very little is known about the vegetative (resprouter vs. seeder) or reproductive responses (fire-stimulated flowering and recruitment) of renosterveld species to fire.

Crown-fire systems, such as fynbos, are known to differ in their fire-adaptive traits from surface fire regimes characteristic of grass-fuelled ecosystems (e.g. Bond & van Wilgen 1996; Pausas *et al.* 2004; Bond & Keeley 2005; Keeley *et al.* 2012). If renosterveld was originally a grassland invaded by shrubs following overgrazing, we would predict few species with fire-stimulated recruitment and very few seeders since post-burn recruitment in grasslands is inhibited by vigorous competition with grasses. If renosterveld seldom burnt because it occurs in relatively arid climates relative to fynbos, we would predict that fire-dependent recruitment and associated fire-type life histories would be rare or absent. However, if renosterveld is a fire-driven system, we would expect fire-stimulated flowering and recruitment to be a common feature of common species, as it is in fynbos. If species have an obligate dependence on fire to complete their life cycles, then fire would have to be considered a critical component of renosterveld management. Since burning has attendant risks to people and property, it is important to establish the extent to which species are dependent on fire events for recruitment.

In this chapter, I addressed the question: is renosterveld adapted to a particular fire regime and what are the consequences of total fire absence? I tested for fire-dependence by observing vegetative responses (sprouting and non-sprouting) and reproductive responses (flowering and seedling recruitment) in response to burning. I compared regeneration responses in burned versus unburned areas to help determine whether species had an obligate or facultative requirement for fire.

STUDY SITES and METHODS

Study sites

Kykoedie farm

The study took place on the farm Kykoedie, a grain and dairy farm between Bredasdorp and Riviersonderend, about 7km east of the village of Klipdale in the Overberg, Western Cape (Fig. 1). The renosterveld type that occurs on Kykoedie is Central Rûens Shale Renosterveld (Mucina & Rutherford 2006) and mature veld is generally dominated by a combination of *Elytropappus rhinocerotis*, *Pentaschistis eriostoma* and *Themeda triandra* in the watercourses and on south-facing slopes.

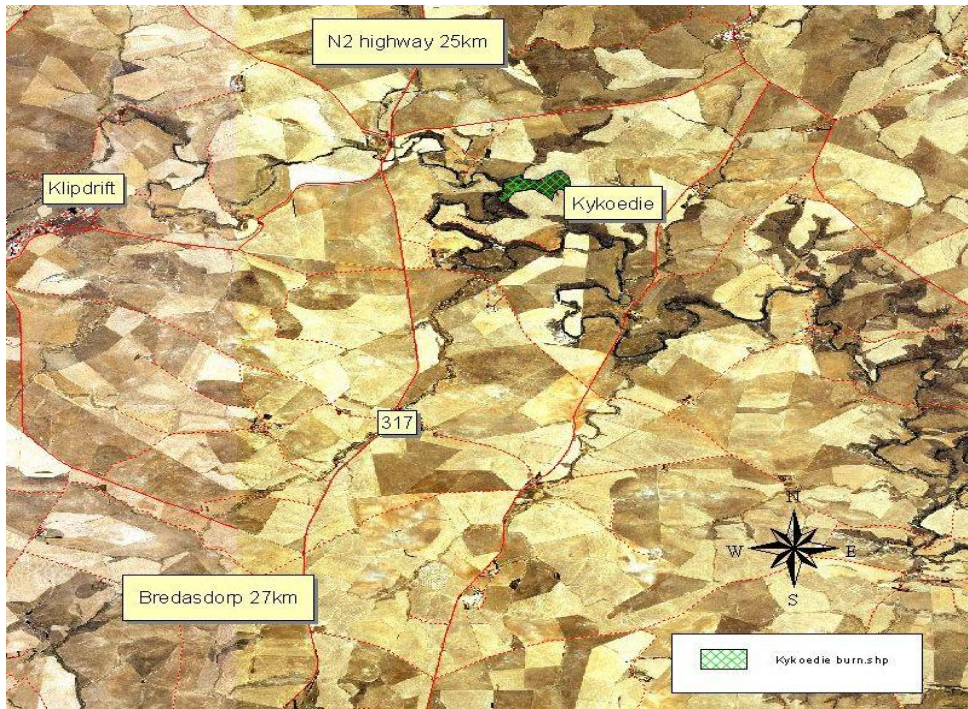


Figure 1. Map denoting the location of Kykoedie farm and the burned patch.

Annual rainfall is between 300-480 mm (mean: 380 mm), with a slight peak in winter (August). Annual temperatures range from 5.6 C (min; July) to 27.3 C (max; January) (Mucina and Rutherford 2006). The farm comprises several small renosterveld fragments – one of which partially burned in autumn (April) 2011 (Fig. 1), providing an opportunity to collect data on post-fire responses of individual species. Before the fire in 2011, the veld had not burned for about 15-20 years (pers. comm. Joshua Human, owner of Kykoedie).

Experimental plots, Overberg

Additional observations on post-fire response were made at the six study sites selected as locations for the experimental plots (see Chapter 7). These sites were chosen opportunistically, as I had to use areas where the landowners were committed to burning their renosterveld in autumn 2008. Because sites were selected opportunistically (i.e. based on landowners' commitment to burning), they were spread across a range of different lowland renosterveld types from Napier (Western Rûens Shale Renosterveld) to Riviersondered (Central Rûens Shale Renosterveld) to Bredasdorp and Swellendam/Heidelberg (Eastern Rûens Shale Renosterveld) (Fig. 2).

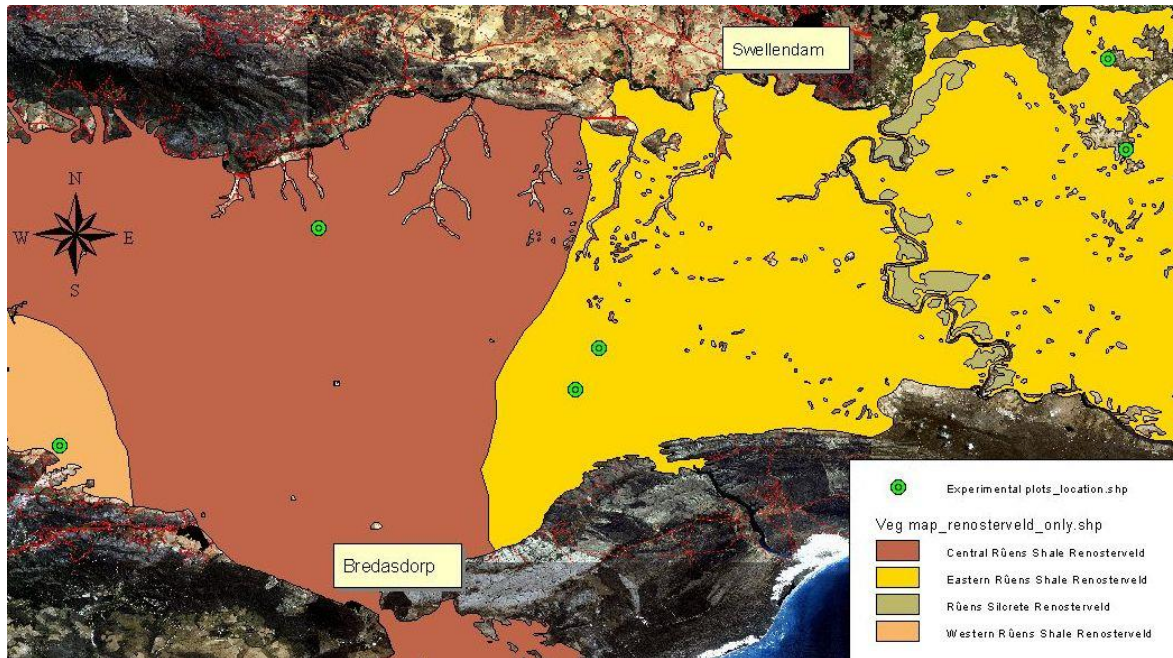


Figure 2. Map denoting location of experimental plots in relation to vegetation types.

Methods

Fire-stimulated flowering and geophyte and annual diversity

Two approaches were used for sampling plants species responses in burned and unburned areas. Firstly, 1X1 m quadrats were thrown randomly six times on burned and unburned sections on both the north- and south-facing slope of the Kykoedie fragment. The diversity (each plant recorded at least to genus level, but to species level where possible) and number (count) of geophytes and annuals were recorded in each of these quadrats; ii) random transects (± 200 m) were walked through the burned and unburned sections on both the north- and south-facing slopes at the Kykoedie study site while I recorded all observed species and noted whether or not they were flowering (this included the presence of seeds or buds).

Resprouters vs. seeders

Random transects (each ± 200 m in length, in order to ensure a similar sampling effort across all burn treatments and aspects) were walked through the burned and unburned sections on both the north- and south-facing slopes at the study site, while I recorded all observed species and noted whether they were resprouters or seedlings. The category of vegetative response was based on observations of,

typically, 10 or more pre-burn individuals per species. Surveys were conducted five months post-burning and due to time constraints, only one visit to the site was made.

Comparisons between the production of flowers in 4-year-old vs. ±20 year-old veld, using experimental plots

In 2007, a suite of 10X10m plots was set up at six sites across the Overberg in the following way: two plots on a 'burn' site, two plots in an 'unburned' site. Each pair was divided into a 'grazed' (open control) and 'ungrazed' (fenced enclosure) plot. This design was replicated on a north- and a south-facing slope, making a total of eight plots per site (i.e. a total of 48 plots). The renosterveld fragments used for these experiments varied in size from about 60 ha to 200 ha, while the extent of the burns varied from 1 ha (1 site only) to between ±20 - 60 ha.

In addition to cover (see Chapter 7), flowering data were collected in 2011, in order to test for differences in the proportion of flowering species between 'old' vegetation (unburned for ±20 years) and four-year-old vegetation. Each time a species was recorded in a quadrat, it was given a score of 1 (flowering) or 0 (not flowering). The data were divided into different guilds (annuals, geophytes, forbs, grasses, restios (including sedges), shrubs and succulents). The proportion of flowering species was taken as the number of flowering species per guild per quadrat divided by the total count of species for that guild in that quadrat.

RESULTS and DISCUSSION

Fire-stimulated flowering

Fire stimulated flowering in all guilds (transect data)

A subjective glance at the veld at Kykoedie suggests a far higher number of flowering plants in the burned section, compared with the unburned section (Fig. 3). The data confirm this expected result (Fig. 4, Table 1, $X^2=3.87$, $df=1$, $P<0.05$). Interestingly, the *percentage* of flowering species was higher on unburned sites. However, transects on burned sites comprised double the number of species (Table 1, Appendix 4.1), resulting in a higher *proportion* of flowering plants in the unburned vegetation.



Figure 3. Kykoedie renosterveld displaying a show of geophytes and annuals in the first spring after a burn, with unburned veld dominated by *Elytropappus rhinocerotis*, *Pentachistis eriostoma* and *Oedera squarrosa* in the background.

A closer look at the data shows that different guilds respond differently to fire during the first season after burning: the number of flowering forb species was higher in burned sections than in unburned sections (Table 1), while the diversity of most guilds increased after a fire (Table 1). The numbers of annuals recorded in the transects was fairly low, thus it is difficult to make inferences from these small sample sizes. This is addressed using quadrat data below. Many shrubs take longer to mature and were therefore not yet flowering on burned sites.

Table 1. Species richness, number of species flowering, and percentage of species flowering for different guilds on north- and south-facing slopes in burned and unburned renosterveld, using transect data. Transects were ± 200 m in length in order to ensure sampling effort across all sites. Data are from one site-visit only.

		North Unburned	North Burned	South Unburned	South Burned
ALL SPP	Total	39	85	39	93
	#Flowering	26	38	15	32
	%Flowering	67	45	38	34
Annuals	Total	1	3	2	9
	#Flowering	1	1	1	2
	%Flowering	100	33	50	22
Geophytes	Total	4	21	6	29
	#Flowering	4	4	1	6
	%Flowering	100	19	17	21
Forbs	Total	6	21	9	14
	#Flowering	3	11	3	6
	%Flowering	50	52	33	43
Grasses	Diversity	5	4	5	9
	#Flowering	4	2	3	5
	%Flowering	80	50	60	56
Shrubs	Diversity	21	29	16	30
	#Flowering	13	17	6	13
	%Flowering	62	59	38	43
Succulents	Diversity	2	7	1	2
	#Flowering	1	3	1	0
	%Flowering	50	43	100	0

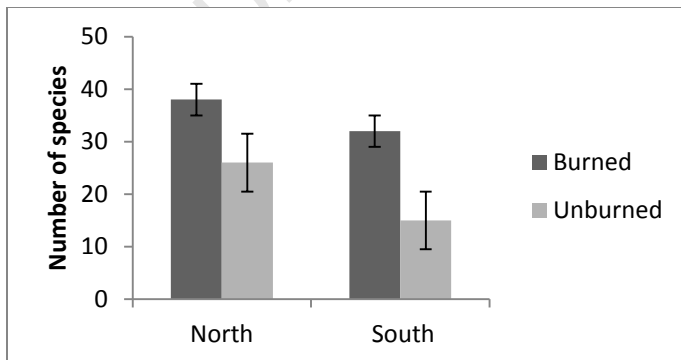
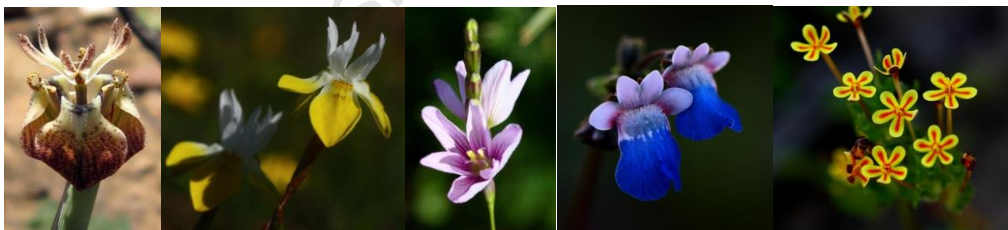


Figure 4. Differences in the total number of flowering species recorded in transects on burned and unburned slopes (with SE bars).

Fire stimulated flowering in geophytes and annuals (quadrat data)

The quadrat data for geophytes and annuals show that species diversity increased slightly with burning (Table 2) and of the 44 species recorded in the quadrats, 16 species were recorded on south slopes only, while 10 were recorded on north slopes only (Appendix 4.2). Of the 44 species recorded in total, 15 species were recorded only on burned sites, while six species were recorded on unburned sites only (Appendix 4.2). There was no difference in the proportion of flowering plants on burned and unburned slopes (T-test, $t=0.609$, $df=65$, $N=38$ burned & 29 unburned, $P=0.545$). Species' abundance, however, increased between three- and eight-fold after a burn (Appendix 4.2): burned quadrats (aspects combined) had significantly higher numbers (in terms of numbers of individual species) of geophytes and annuals compared with unburned plots (T-test, $t=3.274$, $df=86$, $n=44$, $P=0.002$).

I examined the species lists to see whether, amongst those that occurred on both aspects, there were any species whose flowering is associated only with newly-burned vegetation. There were no species recorded on south-facing slopes that were flowering in the burned section and not in the unburned part, with one exception: *Moraea fergusonii*. The trend was similar for north-facing slopes, with a few species flowering only on the burned slopes (*Babiana patula*, *Lachenalia unifolia* and a *Trachyandra* sp.). For all the exceptions, however, sample sizes were low and none of these species are known to flower exclusively after a fire (Goldblatt & Manning 2000, pers. obs.). Many species were not flowering at all at the time of the study, which is likely to be a function of the timing of data collection, as it was fairly early in the season.



Figures 5-9: some of the geophytes and annuals present only in the burned section at Kykoedie (left to right): *Moraea inconspicua*, *M. bituminosa*, *Ixia rapunculoides*, *Nemesia barbata*, *Zaluzianskya divaricata*.

In summary, the proportion of flowering individuals was only slightly increased in geophytes, but not annuals, post-burning, while species diversity increased marginally and abundance increased significantly. Thus, the apparent boom in flowering plants in the burned area, such as displayed in Fig. 10, is due to the

increase in numbers of flowering individuals, and a slight increase in species diversity, as opposed to an increase in the proportion of flowering plants within a species.

Table 2. Differences in species richness and abundance, number of flowering individuals, and proportion of flowering plants for annuals and geophytes, on burned and unburned sites, as recorded in random 1x1 m quadrats (n=6 quadrates per treatment on both north and south-facing slopes).

	BURNED	UNBURNED	BURNED	UNBURNED	BURNED	UNBURNED	BURNED	UNBURNED
SOUTH ASPECT	Richness	Richness	Abundance	Abundance	#Flowering	#Flowering	%Flowering	%Flowering
ALL	28	22	603	263	302	124	50	47
ANNUALS	8	5	222	73	222	73	100	100
GEOPHYTES	20	17	381	190	80	51	21	27
NORTH ASPECT	Diversity	Diversity	Abundance	Abundance	#Flowering	#Flowering	%Flowering	%Flowering
ALL	27	21	213	34	88	10	41	29
ANNUALS	7	3	64	8	63	8	98	100
GEOPHYTES	20	17	149	26	25	2	17	8

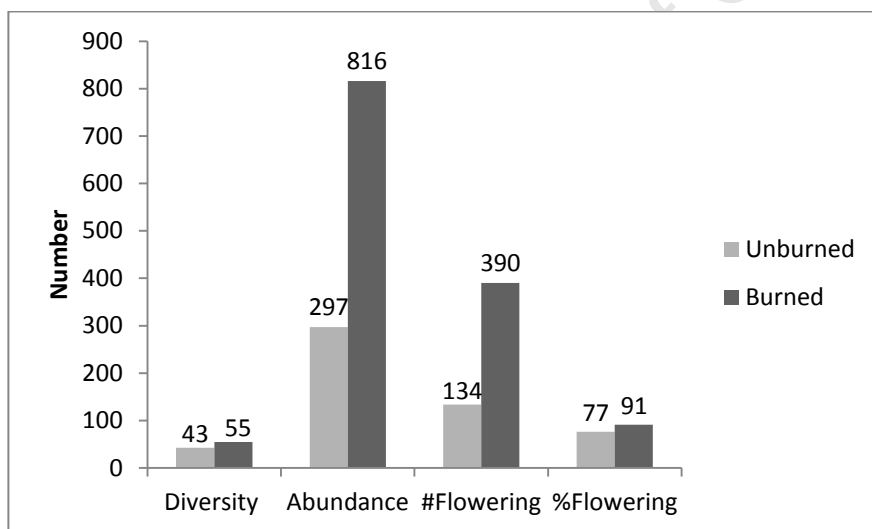


Figure 10. A summary of table 2 (north and south slopes combined), showing differences in total species richness and abundance, number of flowering individuals, and proportion of flowering plants for annuals and geophytes, on burned and unburned sites as recorded in random quadrats.

Vegetative responses: resprouters vs. seeders

Almost 62% of species resprouted in burned renosterveld, while about 30% seeded and 10% used both strategies (Table 3). If geophytes are taken out of the equation, the proportion of resprouters decreases to about 40%, while plants producing seedlings increases to 46%. Seedlings were produced by nine species on the unburned slopes which is 13% of the total species recorded in the Kykoedie study.

Table 3. Proportions of plant species recorded as resprouters (#RS), seeders (#S) and those adopting both strategies (#Both), on burned transects. The column headed ‘unburned’ indicates number of species (NS) whose seedlings were found in unburned vegetation. (Data were collected from transects).

	Burned				Unburned	
	#Species	#RS	#S	#Both	#Species	NS
Geophytes	40	40	0	0	10	0
Forbs	30	12	15	3	12	2
Grasses / sedges	10	9	1	0	10	0
Shrubs	38	13	16	9	30	3
Succulents	9	5	3	1	3	2
All (Excl. annuals)	127	79	35	13	65	7
All%		62	28	10		11
Without geophytes	87	39	35	13		7
Without geophytes (%)		45	40	15		11
Annuals	9	0	9	0	2	2

In terms of the different recruitment strategies used, 43 and 41% of resprouters flowered on north- and south-slopes respectively, while similar figures were obtained for seeders (Table 4). Eight species on north-facing slopes made use of both strategies and seven of these species flowered in the first year post-burning. For species using both strategies, it was the resprouting individuals that flowered and not the seedlings.

Table 4. Proportions of resprouters and reseeders on burned sites that flowered during the spring of 2011 at Kykoedie (RS=resprouter; S=seeder; BOTH=use both strategies), using transect data.

	North	South
TOTAL # RS	47	51
TOTAL # flowering RS	20	21
TOTAL % flower of resprouters	43	41
TOTAL # S	25	25
TOTAL # flowering S	11	9
TOTAL % flower of seedlings	44	36
TOTAL # BOTH	8	5
TOTAL # flowering BOTH	7	2
TOTAL % flower of BOTH	88	40

As is typical of fynbos, most of the dominant seeders (Asteraceae in this case) only produced seedlings in the burned veld, while only *Oedera squarrosa* readily recruited in the unburned, as well as the burned veld (Table 5). Contrary to Levyns's (1927) finding (using lab experiments) that renosterbos only germinated in the second year of seeding, seedlings in the burned veld were observed in this study, demonstrating that renosterbos can germinate in the first year after a fire.

Table 5. Asteraceous shrubs recorded at Kykoedie, showing which species produce seedlings (0=no seedlings produced, 1=seedlings produced) on burned and unburned veld. The third column indicates whether species were resprouters (RS), seeders (S) or both and a dash (-) indicates the species was not found in that treatment.

Species	Burned	Unburned	RS / S / both
<i>Chrysocoma ciliata</i>	-	0	S
<i>Elytropappus rhinocerotis</i>	1	0	S
<i>Helichrysum cf cymosum</i>	0	0	RS
<i>Helichrysum petiolare</i>	1	-	S
<i>Oedera genestifolia</i>	1	0	S
<i>Oedera squarrosa</i>	1	1	S
<i>Osteospermum sp.</i>	1	0	S
<i>Printzia polifolia</i>	1	0	Both
<i>Pteronia hirsuta</i>	0	-	RS

Comparisons between proportions of flowering plants in 4-year-old vs. ±20 year-old veld, using experimental plots

The data used to analyse proportions of flowering species were limited to those collected on grazing exclosures, in order to control for the potential effects of grazing. On south slopes, forbs flowered more prolifically on 4-year-old veld than on old veld (±20 years) (Kolmogorov-Smirnov Test, Mean unburned=23.2 (n=36), Mean burned=43.1 (n=41), $P<0.025$), while restios and sedges flowered more in mature renosterveld (Kolmogorov-Smirnov Test, Mean unburned=88.7 (n=25), Mean burned=60 (n=34), $P<0.005$). On north slopes, only asteraceous shrubs produced a higher proportion of flowers on 4-year-old veld than in the old veld (Kolmogorov-Smirnov Test, Mean unburned=42 (n=79), Mean burned=30 (n=76), $P<0.05$). Renosterbos was not recorded as flowering for any of the burned plots, while only 22% and 14% of plants recorded on north and south-slopes respectively were flowering.

CONCLUSIONS

It appears that the Central Rûens Shale Renosterveld examined in this study contains the elements of a fire-driven system, given the high proportion of non-sprouters and the many species with fire-stimulated recruitment evident from the increased diversity and abundance of plants, as well as the increase in the numbers of flowering geophytes and annuals. Further monitoring of the site is likely to reveal a steady increase in flowering across all species in the burned veld. However, this 'boom' in flowering is probably limited to the first 1-3 years after burning and is then likely to slow down, as suggested from the results of comparing 4-year-old and mature renosterveld. This is typical of post-burn recovery in Mediterranean-type with crown-fire regimes (Bond and van Wilgen 1996; Keeley *et al.* 2012). Interestingly, only about one in 10 species were flowering in the unburned vegetation.

The renosterveld studied here does not fit the model of a true C_4 grassland, as South African C_4 grasslands typically have very few seeders (Zaloumis and Bond 2011). Nor does it fit the model of an arid system seldom exposed to fire, due to the presence of numerous species with fire-stimulated seedling recruitment of fire-stimulated flowering. It does, however, compare well with Fynbos, in terms of the proportions of what appear to be fire-dependent species present in the system and the fact that most dominant shrubs are killed by fire and only produce seedlings after a burn (Le Maitre and Midgley 1992; Cowling *et al.* 1997).

The fynbos systems which abut renosterveld regularly burn and, given the readiness of mature renosterveld to burn (pers. obs. 2007), it is difficult to imagine a situation in which renosterveld (under natural conditions) would not have been exposed to fires spreading from fynbos, particularly in higher

rainfall regions close to mountains. Fires ignited in Mountain Fynbos are very likely to have spread to the lower-lying renosterveld regions and vice-versa. The proportion of resprouters is similar to what has been recorded in fynbos (le Maitre & Midgley 2004), suggesting that renosterveld will tolerate similar fire intervals to those in fynbos, although resprouting is an adaptation not only to fire, but also to grazing and other disturbances (Bond & Midgley 2001; Bradshaw *et al.* 2011). Both the patterns, and explanations for patterns of variation in proportion of resprouters and seeders along environmental gradients, have been extensively studied in Australian flammable shrublands (e.g. Pausas & Bradstock 2007; Clarke *et al.* 2005, Knox & Clarke 2005,) and fynbos *Erica* species (Bell & Ojeda 1999, Ojeda 1998). Drivers of changing proportions of resprouters include fire frequency, rainfall reliability, and nutrient availability. My study seems to be the first for renosterveld that attempts to quantify resprouter and non-sprouter proportions and fire-stimulated vs. non fire-stimulated recruitment and flowering. More geographically extensive studies of variation in resprouter/non-sprouter proportions and of fire-stimulated seedling recruitment and fire-stimulated flowering could be very informative for exploring the importance of different drivers over the full geographic range of renosterveld.

Though many species showed some evidence for fire-stimulated life histories, some showed little or no positive response to fire. Among these are what Keeley (1992) has referred to as 'obligate sprouters'. These are thicket elements (including *Rhus* spp., *Buddleja saligna*, *Acacia karoo* (Mucina and Rutherford 2006) and *Olea europaea* (pers. obs.)) in renosterveld valleys and cooler south-facing slopes) and their presence suggests that renosterveld can be invaded by thicket, in the same way that some fynbos types can be invaded by forest, in the absence of fire. However, in addition to fire, large herbivores, particularly browsing species such as Black Rhino, may also have contributed to keeping habitats more open by maintaining the thickets in small clusters.

Another group of species that are often common in renosterveld also do not appear to be dependent on fire for flowering or recruitment. They include important palatable plants that are likely to have provided the bulk of grazing biomass for large game in the past (e.g. perennial grasses, several forbs and some of the leguminous shrubs). The ability to resprout may be an important adaptation to grazing for these species. Also, geophytes make up a large percentage of the resprouters and although not classified as geophytes in the analyses, there are several forbs and succulents which have geophytic characteristics, in terms of having underground storage organs (pers. obs.). This trait also suggests adaptation to disturbance – be it fire or grazing or, more traditionally, recovery from severe drought (James 1984).

Assessing whether positive response to fire, whether through increased flowering or seedling recruitment, is indicative of a dependence on fire (= fire-driven or fire-dependent system), or other gap-creating disturbance (i.e. removal of competition, creation of light and space, increases in water and nutrient availability, etc.) requires more study. In the absence of the once prolific herds of grazing and browsing ungulates, it is difficult to determine whether some of the fire-adaptations recorded in renosterveld species have evolved in response to fire exclusively, or whether they may also (or only) have responded to gaps created by grazing pressure. At this stage it is unclear whether or not 'fire-stimulated' species were merely responding to the increased availability of light, or whether fire is critical because it introduces chemicals (smoke) or heat required to stimulate flowering and recruitment. Lamont & Downes (2011) argue that foliage removal alone is seldom sufficient to mimic the effect of fire, despite the fact that both increase light availability. They found no evidence to suggest that light was always lacking in unburned vegetation and noted that they had observed fire-stimulated flowering even in relatively open habitats where light was not lacking, suggesting that fire itself is critical for these systems to be productive (Lamont and Downes 2011). It would be interesting to determine whether gap creation by trampling, or agronomically by rolling or mowing, has similar effects to burning. In fynbos this is unlikely because of specialised fire-related cues. But in renosterveld, with its history of greater large mammal activity, gap formation may not be so explicitly related to fire.

In terms of the proportion of renosterveld species recorded in this study that appear to be fire-dependent (for flowering and/or recruitment), certainly, the most common and dominant Asteraceous shrubs are killed by fire and have fire-stimulated seedling recruitment. And across all growth forms, over 40% of species produced seedlings in the first year after burning, while only 13% produced seedlings in unburned vegetation. However, 32% of the seeders were obligate reseeders, while 10% produced seedlings facultatively.

In terms of management implications and the data presented here, it is important to remember that renosterveld across the Overberg is highly variable (Chapter 5), with substantial differences in plant communities and rainfall gradients. Thus, no sweeping statements can be made regarding appropriate fire regimes for the region, let alone the rest of the Fynbos Biome where several other types of renosterveld occur. Areas which receive high rainfall will develop biomass more quickly than dry areas and hence will develop sufficient biomass to carry a fire more frequently. For example, the grassier renosterveld habitats of the Western and Central Rûens Shale Renosterveld in the Overberg receive higher rainfall and build up a cover of tussock grasses in response to fire much more quickly than their counterparts in the drier, Karoo-like region of the Eastern Rûens Shale Renosterveld (north of De Hoop

Nature Reserve) (pers. obs.). These drier renosterveld regions have a higher diversity of succulents and are also known for their quartz outcrops, comprising rich assemblages of endemic species, most which are unlikely to be fire-adapted or dependent (Curtis *et al.* 2013). In a very different system northwest of the Overberg, Mountain Renosterveld fires in Nieuwoudtville probably at much lower frequencies than in fynbos because biomass takes a long time to build up as it is on the margin of the renosterveld aridity gradient (pers. comm. Simon Todd). I suggest that the drier regions of the Overberg require even longer (10-20 year) fire intervals.

There are several unknowns which make managing renosterveld remnants very challenging. Its grazing history and carrying capacity are poorly understood because it was not long after the first European settlers arrived in the Cape that most large game species were eradicated and replaced with livestock, while renosterveld was subsequently transformed through the large-scale conversion of virgin land for grain-crops (Cowling *et al.* 1986). It is a severely fragmented system, with altered fire regimes, enormous grazing pressure from livestock and potentially, a large extinction debt (Kemper *et al.* 1999). The data presented here suggest that Central Rûens Shale Renosterveld is a fire-adapted system, and observations suggest that other Overberg renosterveld types are likely to respond in a similar manner (Chapter 7). Although long-term studies are required in order to gauge appropriate burning frequencies, it is clear that mature renosterveld (>15-20 years) is rejuvenated by autumn burning. Conservation managers and landowners wishing to improve the long-term viability of their renosterveld should include a burning strategy in long-term management plans which involve burning mature veld, but monitoring veld recovery and key species closely before subsequent burns are initiated.

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CHAPTER 5: Plant diversity and reserve design in renosterveld

Conservation strategies may have to consider a much broader concept of 'hotspots' to adequately preserve native plant species diversity and the processes that foster persistence

(Thomas Stohlgren et al. 2005)

INTRODUCTION

Southern Africa has a rich flora with high levels of endemism, where about 80% of the *ca* 23 400 plants are endemic (Cowling *et al.* 1998). This is largely due to the diversity of the southern part of South Africa, known as the Cape Floristic Region (CFR), one of the five Mediterranean systems on the globe. The CFR, essentially comprising the Fynbos and Karoo Biomes, is renowned globally for its extraordinarily high plant diversity (Kruger & Taylor 1980), placing it amongst the world's top 34 Biodiversity Hotspots (Myers 1990, Myers 2003), and earning it the title of the richest of the six recognized Plant Kingdoms on earth. The world's five Mediterranean climates, of which the CFR is one, occupy less than 5% of the earth's surface; yet contain almost 20% of the world's vascular plants (Cowling *et al.* 1996). High levels of endemism and beta- and gamma-diversity (Cowling 1983; Cowling 1990) combined with substantial levels of habitat transformation make achieving conservation targets challenging.

Within the Fynbos Biome, there are 119 described vegetation types, of which 29 are 'renosterveld' types (Mucina & Rutherford 2006). In the Overberg region of the southwestern Cape, there are four renosterveld types present: Western-, Central- and Eastern-Rûens Shale Renosterveld which each cover roughly a third of the clay-based lowlands of the Overberg and Rûens Silcrete Renosterveld which occurs in a thin strip along the Breede River (Fig. 1). All four are listed as *Critically Endangered* (SANBI & DEAT 2009), with Eastern Rûens Shale Renosterveld comprising the largest, most intact extant remnants (Table 1). According to the SANBI & DEAT's (2009) *Threatened Ecosystems of South Africa*, about 12% of the original extent of all renosterveld types in the Overberg still remains (Table 1) – although other estimates are as low as 4-6% (pers. comm. Donovan Kirkwood). These estimates do not include the quality and ecological integrity of patches, which are often subjected to various degrees of ill-informed management, so that the proportion of viable renosterveld remaining is even smaller (pers. comm. Donovan Kirkwood, pers. obs.). Overberg renosterveld is scattered across a vast landscape of transformed lands (grain fields and artificial pasture) and almost all of it occurs on privately-owned land, with <1% falling under official protection in Nature Reserves (Table 1). The most pertinent threats facing renosterveld today are continued conversion of virgin renosterveld into ploughed croplands and inappropriate grazing and fire management of the remnants.

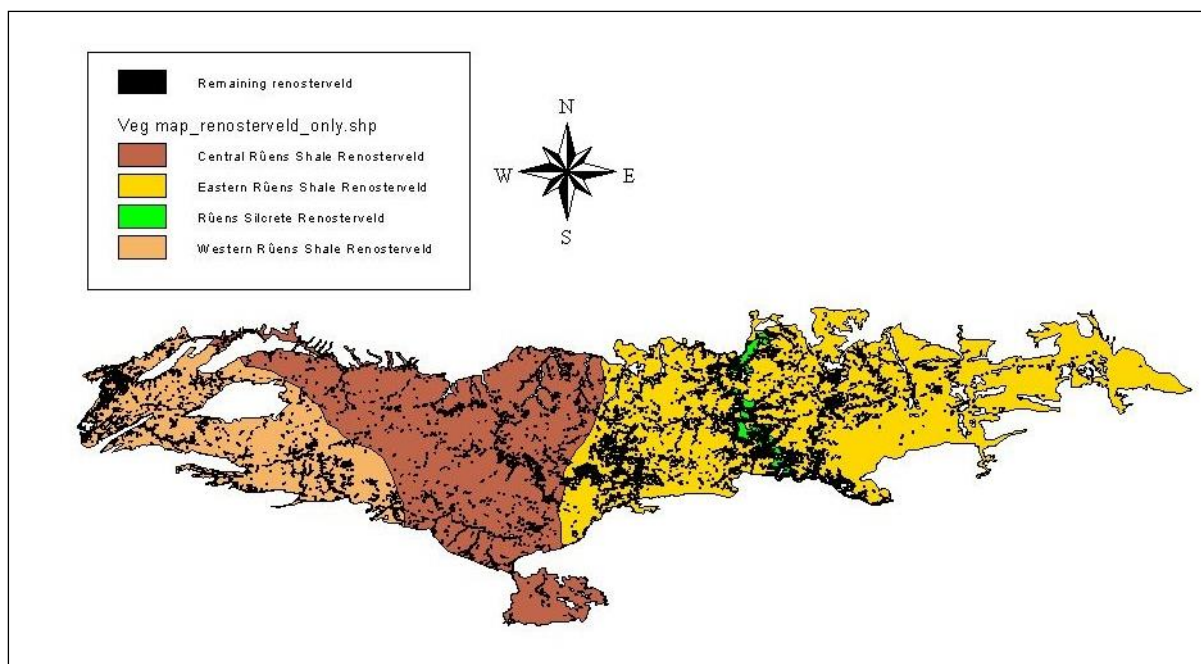


Figure 1. Map denoting the four dominant renosterveld vegetation types in the Overberg overlaid with the remaining remnants (SANBI).

Table 1. Summary of the four renosterveld types found in the Overberg, with their corresponding percentage remaining and protected, as well as the number of species endemic to each of the respective veld types. Summarized from SANBI & DEAT (2009).

Renosterveld type	% remaining	% of original area protected	Number of plants of special concern
Western Rûens Shale	13%	0%	52 Red-listed, 14 endemic
Central Rûens Shale	9%	<1%	42 Red-listed, 8 endemic
Eastern Rûens Shale	14%	<1%	49 Red-listed, 15 endemic
Rûens Silcrete	14%	<1%	26 Red-listed, 13 endemic
AVERAGE ALL TYPES	12.5%		

Diversity in threatened ecosystems

The vegetation of Mediterranean climate regions is relatively rich, by global standards, when measured at the local scale (≤ 0.1 ha), with a species diversity of less than half that of tropical rainforests, but a much higher diversity than most temperate systems (Cowling *et al.* 1996). Diversity in these systems is highest on nutrient-poor soils in Australia and South Africa, where fire is an important component of the system, as well as the shrublands and woodlands of the Eastern Mediterranean basin (Israel), where grazing levels are high (Cowling *et al.* 1996, Naveh & Whittaker 1980).

Diversity patterns have been extensively studied and relatively well-quantified in fynbos (e.g. Bond 1983; Campbell & van der Meulen 1980; Cowling 1983; Cowling 1990, Goldblatt & Manning 2002; Kruger & Taylor 1980), where the high richness of the region is attributed to high beta and gamma

diversity and moderate alpha diversity. Cowling (1983) studied alpha diversity in a variety of CFR habitats including fynbos shrublands, subtropical thicket and Afromontane forest habitats and found that plant species richness was highest in lowland renosterveld and lowest in mountain fynbos and Afromontane forest. Bond (1983), in a study centered on the mountains of the southern Cape found the reverse for mountain renosterveld with just 28 species in a single 0.1 ha plot, which equated to about half the mean species recorded for fynbos, forest and thicket vegetation types in the study same area (Bond 1983).

High species richness on the Agulhas plain fynbos has been attributed to high species turnover (beta diversity) across edaphic gradients and, in these lowland landscapes, renosterveld shrublands were again the richest in alpha diversity (Cowling 1990). Later, Cowling *et al.* (1998) showed that the Succulent Karoo region of the CRR had the highest alpha diversity, relative to area, when compared to other climatically similar regions globally. For example, it had four times as many species as North American semi-arid, winter-rainfall regions over similar-sized areas. These arid regions generally displayed higher species richness than those in North Africa.

Until relatively recently, a misplaced, yet common, perception has been that renosterveld vegetation is relatively homogeneous, overwhelmingly dominated by renosterbos *Elytropappus rhinocerotis* and a few associated Asteraceous shrubs (*Oedera* & *Metalasia* spp.), with low alpha diversity and comparatively low species turnover along geographic gradients (Rebello 1995). This perception has been perpetuated despite Cowling's findings that renosterveld comprises higher levels of alpha diversity than most upland or coastal fynbos shrublands, in the eastern Cape on the fringe of the Fynbos Biome (Cowling 1983) and the Agulhas Plain (southern Overberg, Cowling 1990). More recently, Newton & Knight (2010) demonstrated that casual references to renosterveld being a homogeneous system with very few, if any, localized or rare species, are misleading. Their study on west coast renosterveld, of which an estimated <9% remains, revealed that 52% of species recorded were only found on a single site, while only three species occurred on all the sites examined. They also argue that assumptions that smaller fragments simply comprise subpopulations of larger remnants (von Hase *et al.* 2003) are incorrect and that all remaining fragments should be considered of high conservation value.

Because the Cape Floristic Region has significant levels of plant diversity, despite high levels of threat and transformation, several opportunities for conservation exist. The challenge lies in determining how best our limited resources can be exploited to maximize the biodiversity that is secured for long-term conservation.

For too long, renosterveld has been assumed to be homogenous with low species turnover, especially relative to fynbos. Thus, to conserve suitable areas it could be assumed that a few large enough reserves would suffice in order to maintain some key ecological process, such as mammal

herbivory, pollination inter-dependencies and a reasonable fire regime. However, there is much uncertainty about patterns of diversity (but see Cowling 1983 and 1990) and, in particular, turnover along habitat and geographical gradients, as these have been poorly studied in renosterveld. If turnover on habitat gradients is high, then the careful selection of reserves with the necessary habitat gradients to include habitat specialists will become all-important for the long-term preservation of this severely threatened habitat. Additionally, if geographic gradients are high, in contrast to earlier views of renosterveld monotony, then consideration has to be given to conserving many small remnants, not just large ones (Condit *et al.* 2002, Higgs & Usher 1980, Järvinen 1982, Quinn & Harrison 1988). There are challenges associated with managing small remnants and these are explored elsewhere in this thesis. Thus, the aims of this study are to explore patterns of diversity in the Overberg's lowland renosterveld in relation to intra-community diversity, turnover along habitat gradients, and turnover at the landscape scale. Since, as shown in Chapter 7, species diversity, growth form mix and abundance vary with time since fire, the sampling design included some consideration of post-burn age.

I compared alpha (within community), beta (turnover across habitat gradients) and gamma diversity (turnover along geographic gradients) (Cowling *et al.* 2004) in Overberg renosterveld to characterize diversity patterns and compare them with fynbos. Comparable studies have been done in other Mediterranean-climate regions and are compared with renosterveld where possible. This analysis of patterns of diversity can provide useful information for conservation of the system by indicating the range of habitats that should be included in protected areas (beta diversity) and the geographic spread to preserve representative samples of the biota (gamma diversity). These results are discussed in the context of reserve planning and implementation and suggestions for renosterveld conservation are offered.

STUDY AREA and METHODS

Permanent plots:

Permanent 10X10 m plots (Guo 2001) were clustered in six study areas, varying between 5 km and 98 km apart (Fig. 2). Within each study site, plots were located on north- and south-facing slopes. On each slope, half the plots were burned in 2008 and half were left as controls. Within the burned and unburned sites, half were fenced off as (livestock) grazing controls, while the other half were left open. This resulted in a total of eight plots per site (i.e. a total of 48 plots). The renosterveld fragments used for these experiments varied in size from about 60 ha to 200 ha, while the extent of the burns varied from 1 ha (1 site only) to between $\pm 20 - 60$ ha. Data were collected in the spring of 2007, prior to the autumn 2008 controlled burns and every spring thereafter from 2008-2011. Data were collected by recording all species and their relative cover within a 1 m² quadrat, placed at six

permanently marked positions in each 10X10m plot. Plants were identified to genus and / or species level where possible, although in some cases, only to family level (where seedlings were unidentifiable). Plant cover for each species was categorized in the following way: 1=<5%, 2=5-10%, 3=10-25%, 4=25-50%, 5=>50% (adapted from Braun-Blanquet 1950 in Cagnolo *et al.* 2006). Once the six quadrats were surveyed, I searched the remainder of the 10X10 m plot for any missed species and assigned these a cover value, relative to the whole plot.

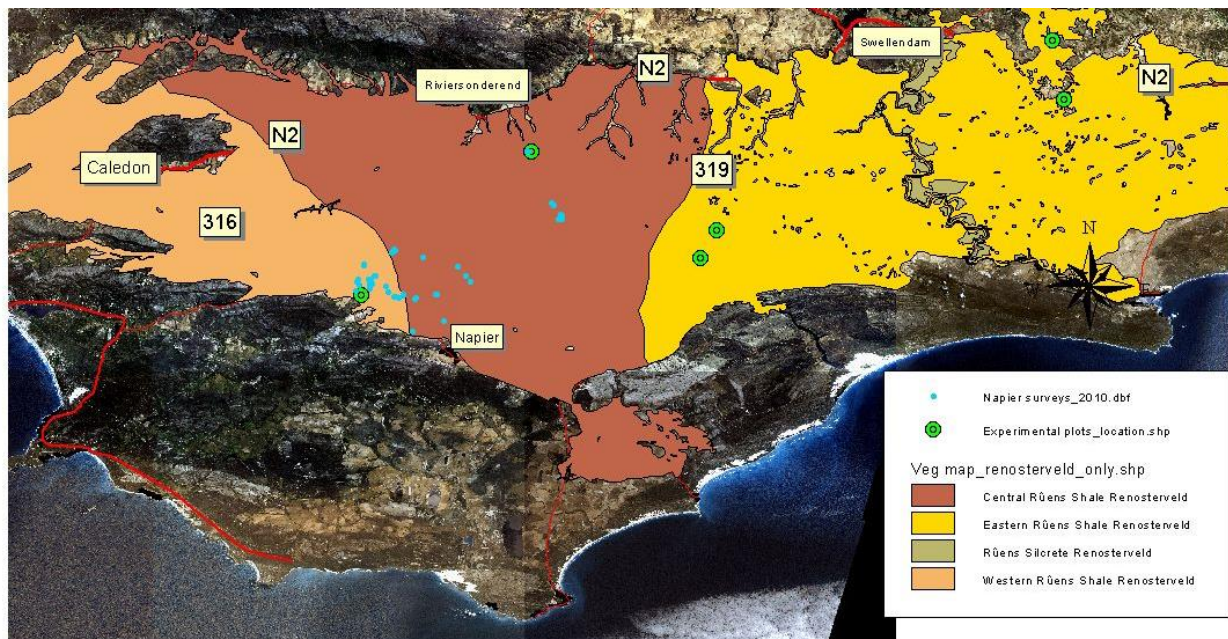


Figure 2. Map denoting study sites for both the experimental plots and the random (Napier 2010) surveys, in relation to the different renosterveld types.

Random plots

In order to examine beta and gamma diversity on a smaller scale, I also conducted random surveys within a radius of about 16 km on 47 sites within 30 fragments (Fig. 2). These comprised 22 south-facing sites and 25 north-facing sites. A temporary 10X10 m plot was set up at each site and all species within the plot were recorded and assigned a subjectively-assessed cover value (percentage cover).

Data were used to determine alpha, beta and gamma diversity in Overberg renosterveld. Thus, in keeping with similar studies, alpha diversity was simply regarded as the number of species per site (Cowling 1983). In order to compare species turnover rates over the four years post-fire, a Whittaker measure of β diversity was calculated: $\beta = \gamma / \alpha - 1$, where γ is total species richness observed over the four years post-fire and α is the mean species richness in each year (Whittaker 1972). For gamma diversity, I measured distance between plots using GIS (Arcview 2.3) and satellite imagery. I then

examined correlations between percentage similarity, generated from a Bray-Curtis similarity matrix, and distance between plots.

Soil nutrient data

Soil samples were collected for nutrient analyses were collected opportunistically while collecting samples for isotope analyses. Details on soil characteristics and nutrient analyses are not within the scope of this study, but may be useful for future research, thus the results of the nutrient analyses are attached as Appendix 5.1.

RESULTS and DISCUSSION

Experimental plots:

a) During the five-year study, a total of 466 species was recorded on south-facing slopes and 332 on north-facing slopes. These levels of alpha diversity, collated from five years of vegetation monitoring, four of which were post-burn, are exceptionally high, when compared with, for example, a similar northern hemisphere study in California chaparral, where four years of monitoring post-burn vegetation in 10X10 m plots resulted in a total of 73 species being recorded (60 on the north-slopes and 50 on the south-slopes) (Guo 2001).

b) Alpha diversity averaged 50.5 (± 12.4) for 10X10m south-facing plots and 36.5 (± 10.4) for north-facing plots. Species diversity was consistently significantly higher on south-facing slopes (t-test: $t=-4.54$, $df=8$, $P=0.002$ (Fig. 3) over the five-year period. A similar pattern was observed in California chaparral, where northern hemisphere north-facing slopes, which tend to be cooler and wetter than south-facing slopes (being the counterparts of south-facing slopes in the southern Hemisphere), displayed higher species richness (Guo 2001).

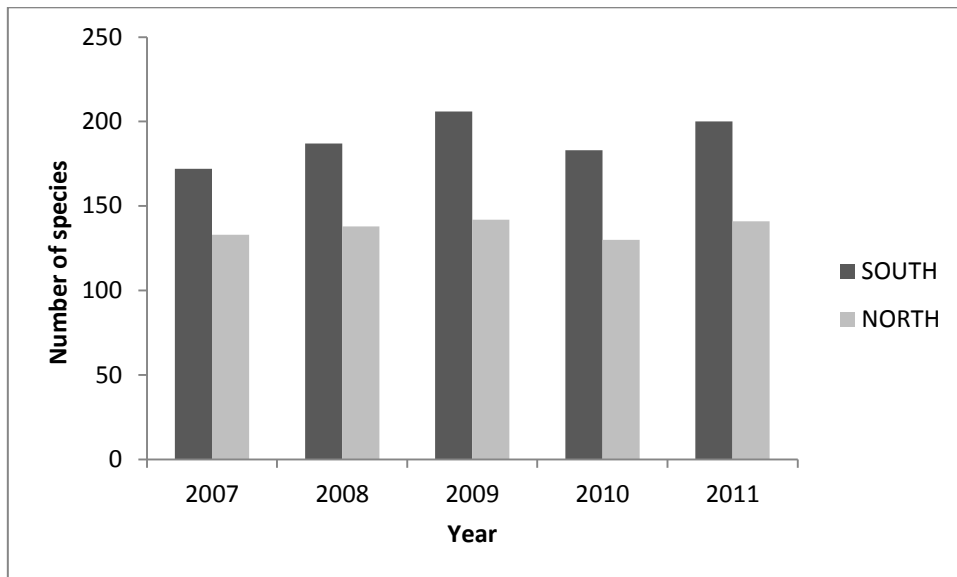


Figure 3. Species diversity (total number of species) on north and south -facing slopes across six sites over the five-year study period (2007: pre-burning; 2008-2011: post-burning). Data is total number of species tallied in all of six 10x10m plots at each site each year’.

c) In terms of the different growth forms, south-facing slopes had, on average, a higher diversity of annuals, asteraceous shrubs, other woody shrubs, bulbs, grasses and restios, while north-facing slopes had a slightly higher number of forb and succulent species (Fig. 4).

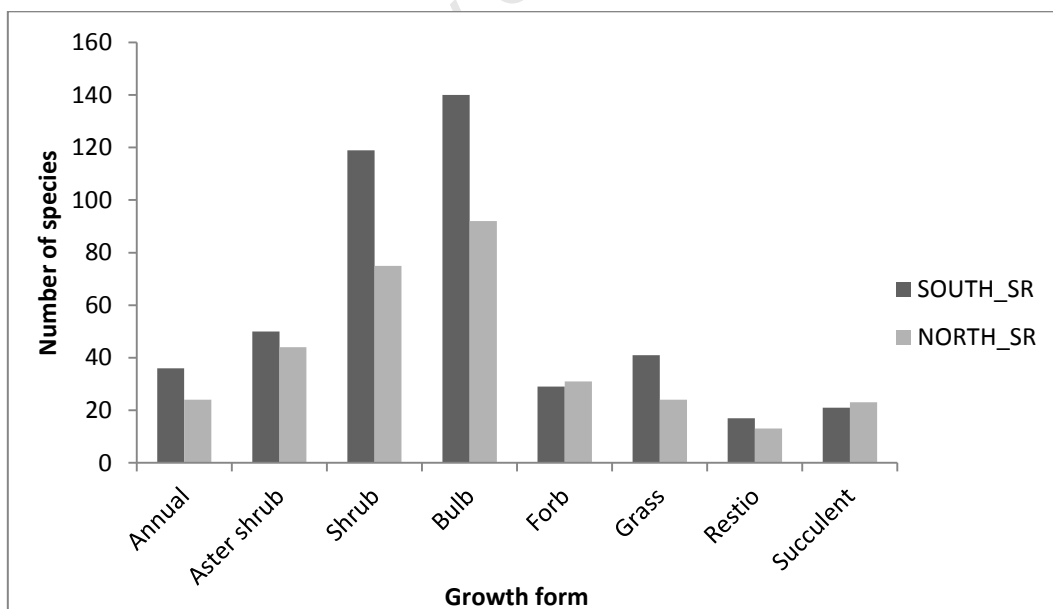


Figure 4. Species richness of different growth forms on north- and south-facing slopes.

d) In order to generate comparable data, species turnover rates for only exclosures in post-burn years (i.e. 2008-2011) were calculated using Whittaker’s β -diversity Index (Guo 2001). In contrast to chaparral, temporal species turnover rates in renosterveld on north and south-facing

slopes did not differ dramatically, although south-facing sites had a slightly higher β -value, with β -diversity values of 0.5 and 0.61 on north and south-slopes respectively. These were slightly higher than those in chaparral, which were 0.21 for south and 0.48 for north slopes (Guo 2001).

Species diversity, when averaged for burned exclosure plots across the six experimental sites, did not change substantially after burning on north slopes, while it increased gradually (although not consistently) on south slopes, as demonstrated in Figure 5. There are several confounding variables which may have influenced this pattern. Firstly, species diversity does change in response to fire, but this response is different for different growth forms in different years (see Chapter 7), thus while diversity increases for some growth forms (e.g. annuals, geophytes and forbs) and decreases for others (e.g. shrubs) in one year, these contrasting responses result in a very low overall change. This pattern is confirmed by the high rates of temporal species turnover in following a burn. Secondly, fires across the six experimental sites varied in intensity (pers. obs.), thus responses across sites were highly variable (Fig. 6 and Fig. 7). Additionally, it is likely that annual variation in some growth forms (particularly annuals and geophytes) varied in response to other climatic factors, such as rainfall, as demonstrated in a similar study by Keeley *et al.* (2005).

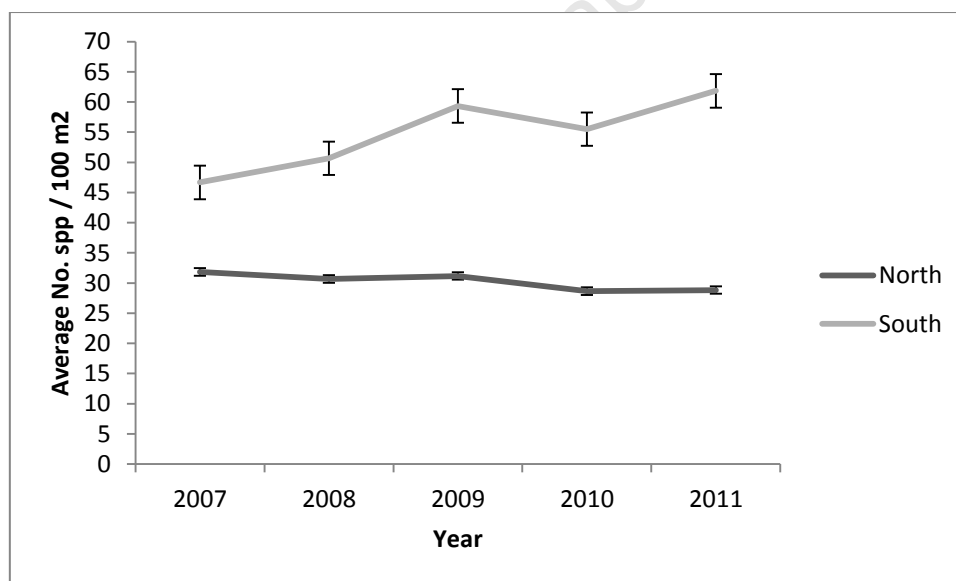


Figure 5. Changes in average species richness measured from 100 m² plots in renosterveld from pre-burning (2007) over four years post burning (2008-2011) at six experimental sites (n=2 plots per site).

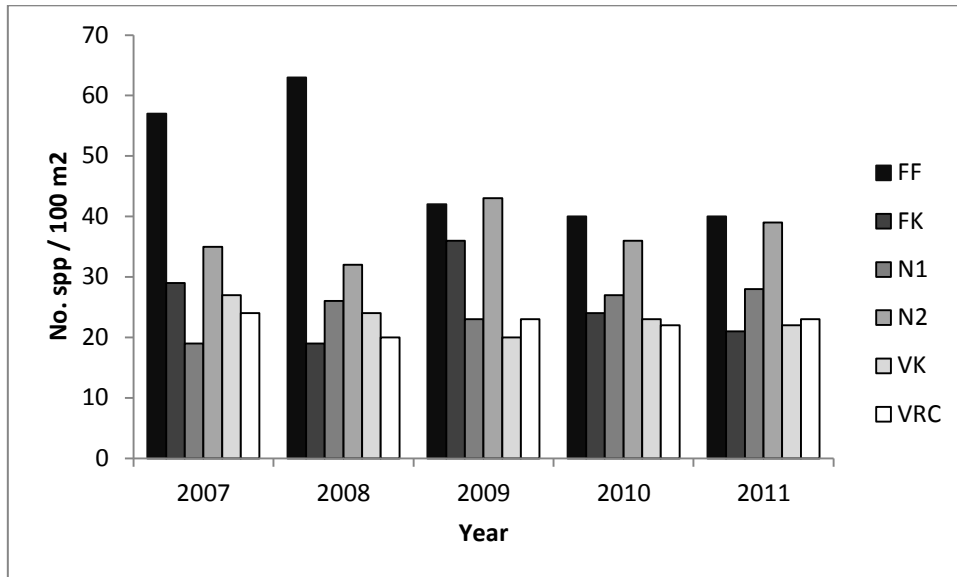


Figure 6. Changes in average species richness on north-facing slopes in renosterveld from pre-burning (2007) over four years post burning (2008-2011) at six experimental sites (FF=Fairfield, FK=Fonteinskloof, N1=Nysty1, N2=Nysty2, VK=Voorstekop, VRC=Van Rheenen's Crest) in the Overberg (n=2 X 100m² plots per site).

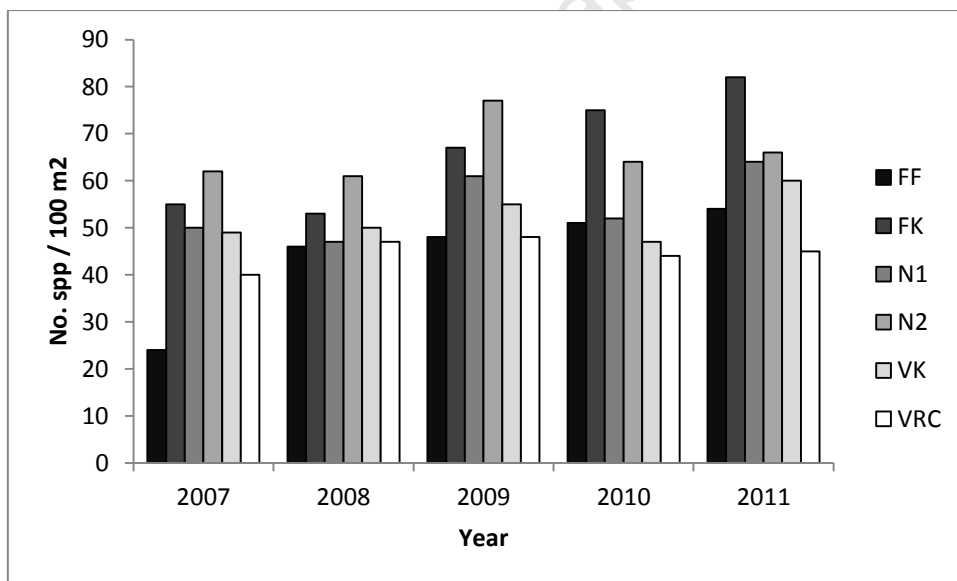


Figure 7. Changes in average species richness on south-facing slopes in renosterveld from pre-burning (2007) over four years post burning (2008-2011) at six experimental sites (FF=Fairfield, FK=Fonteinskloof, N1=Nysty1, N2=Nysty2, VK=Voorstekop, VRC=Van Rheenen's Crest) in the Overberg (n=2 X 100m² plots per site).

e) Gamma diversity: Gamma diversity was relatively high. A Bray-Curtis similarity coefficient showed that turnover of species increased significantly with distance for plots from south slopes (Spearman R, R=-0.863, t(N-2)=-6.174, n=15, P=0.00003), with a distance of 5km having a mean

similarity of 59% and a distance of 96km having a mean similarity of only 38% (Fig. 8). However, diversity on north slopes was less variable along a geographic gradient (Spearman R, $R=-0.493$, $t(N-2)=-2.04$, $n=15$, $P=0.062$) and plots were more similar overall; even between the furthest plots (i.e. nearly 100km) a similarity of 49% was maintained (Fig. 8). South slopes averaged 44.5% similarity (range 37-59%), while north slopes averaged 45.5% (range 33-55%).

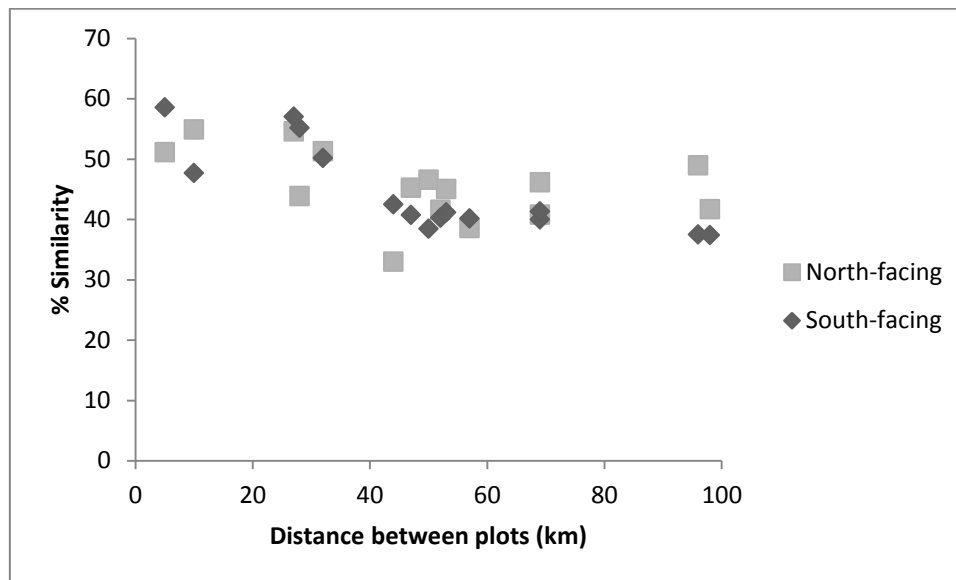


Figure 8. Correlation between distance between plots and percentage similarity in species composition, measured by the Bray-Curtis similarity coefficient, for experimental plots on north- and south-facing slopes across the Overberg (using data from all years and burned and unburned plots).

f) When similarity coefficients were compared only for burned plots from the 2008 census, the first year post-burn when all fire ephemerals had emerged and the number of species in the analysis was maximal, a stronger relationship with distance (decreasing similarity with increasing distance) was found for both north- and south-facing slopes (Fig. 9).

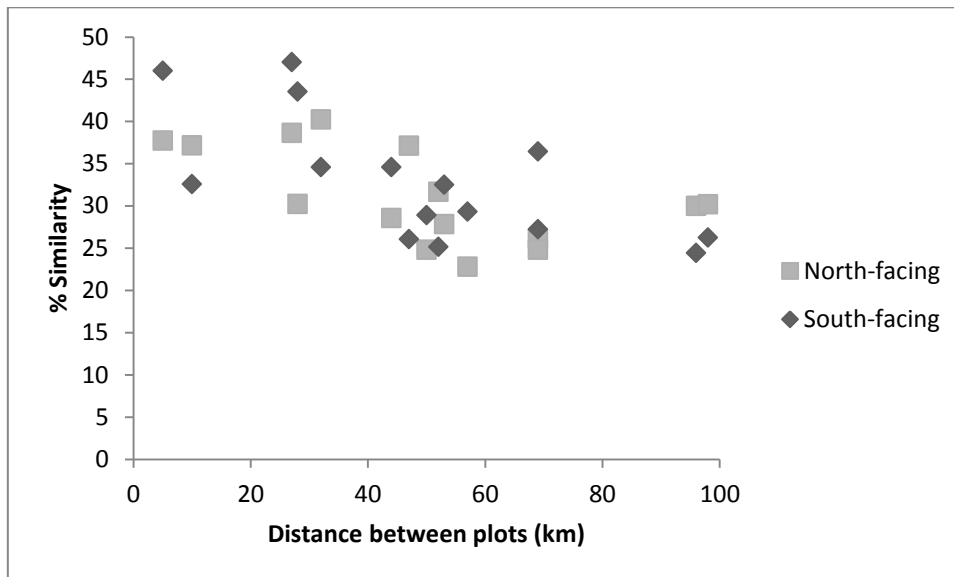


Figure 9. Correlation between increasing distance apart and percentage similarity in species composition, measured by the Bray-Curtis similarity coefficient, for experimental plots on north- and south-facing slopes across the Overberg, using only post-fire data for first season after burn (year 2008).

g) Temporal species turnover was calculated for the four post-fire years (2008-2011) using Whittaker's beta diversity index for the six study sites, on north- and south-facing slopes. There were no differences in beta diversity between the two aspects (Kolmogorov-Smirnov, Mean S=0.86, Mean n=0.73 P>0.1), or across the different renosterveld types (Kruskal-Wallis, H (2, n=12)=0.2, P=0.9) (Table 2).

Table 2. Temporal species values for the six experimental plot sites in the Overberg, using data from the four post-fire years, calculated using Whittaker's beta diversity index.

Site name	Aspect	Veg type	Whittaker's Beta index
Fairfield	S	Western Rûens Shale Renosterveld	0.97
Fonteinskloof	S	Central Rûens Shale Renosterveld	0.72
Nysty1	S	Eastern Rûens Shale Renosterveld	0.86
Nysty2	S	Eastern Rûens Shale Renosterveld	0.67
Voorstekop	S	Eastern Rûens Shale Renosterveld	1.04
Van Rheenen's Crest	S	Eastern Rûens Shale Renosterveld	0.93
Fairfield	N	Western Rûens Shale Renosterveld	0.70
Fonteinskloof	N	Central Rûens Shale Renosterveld	0.75
Nysty1	N	Eastern Rûens Shale Renosterveld	0.55
Nysty2	N	Eastern Rûens Shale Renosterveld	0.83
Voorstekop	N	Eastern Rûens Shale Renosterveld	0.71
Van Rheenen's Crest	N	Eastern Rûens Shale Renosterveld	0.86

h) Comparable data were available from 1X1 m quadrates in Keeley *et al.* (2012). Thus, in order to place renosterveld alpha diversity in the broader context, I generated a table (Table 3) based on Table 11.2 in Keeley *et al.* (2012), incorporating data from this study and Cowling (1990). Species diversity at the 1 m² quadrat level averaged between 21 to 24 on south-facing slopes and 13 to 16 on north-facing slopes in veld from one to four years old (using data from burned exclosures only (i.e. 12 plots across the six study sites). These figures are higher than what Keeley *et al.* (2005) reported in chaparral (average between 3 to 12) and sage scrub (5 to 15) in 1 m² quadrats in the same range of vegetation age. However, species numbers at the 100 m² level were substantially higher than, in some cases double, those reported for the same habitats in the same study (i.e. 29 to 32 on north-facing slopes and 47 to 62 on south-facing slopes in renosterveld compared with 10 to 25 in chaparral and 13 to 27 in sage scrub) (Keeley *et al.* 2005). Mature (i.e. pre-burn) renosterveld in 100 m² plots in the present study averaged 47 species (range 24-62) on south slopes and 36 species (range 24-53) on north slopes, comparable with diversity in mature chaparral and coastal sage (Keeley & Fotheringham 2003) and figures for renosterveld in the southeastern Cape, reported by Cowling (1983) (in Keeley *et al.* 2005). Interestingly, however, these figures were substantially higher than those recorded by Bond (1983) (in Keeley *et al.* 2005) mountain renosterveld systems in much larger (1000 m²) plots, reiterating the variability in species richness even within different renosterveld types across the Fynbos Biome.

Furthermore, in the context of the Mediterranean systems, Cowling *et al.* 1996 summarised alpha diversity for 1m² plots in the five Mediterranean regions of the world as follows (highest to lowest): Cape: 16 ±6 (n=54), Mediterranean Basin: 14 ±10 (n=29), SW Australia: 13 ±10 (n=33), Central Chile: 8 ±2 (n=3), California 7 ±6 (n=13). Taking the averages obtained in this study, renosterveld scored a slightly higher average than the average Cape system to which it belongs: 72 1x1m plots monitored over 5 years had an average species richness of 18 ±7. Thus, on this scale, on average, lowland renosterveld in the Overberg displayed a species richness exceeding some of the richest Mediterranean shrublands measured in similar studies.

Table 3. Summary of comparison of results of alpha diversity obtained from 1m² quadrats in this study and several others in Mediterranean-shrublands.

Country, vegetation type	Veld age / description	average	max	min	# sites	Source
SOUTH AFRICA						
Renosterveld, S-facing	Mature	18.2	32.0	7.0	6	This study
	1	21.1	34.0	10.0	6	This study
	2	23.8	38.0	9.0	6	This study
	3	21.0	38.0	6.0	6	This study
	4	24.1	36.0	11.0	6	This study
Renosterveld, N-facing	Mature	12.1	26.0	5.0	6	This study
	1	13.6	24.0	5.0	6	This study
	2	16.5	34.0	7.0	6	This study
	3	14.4	29.0	4.0	6	This study
	4	15.5	25.0	6.0	6	This study
Fynbos	6	9.5	-	-	3	Keeley <i>et al.</i> 2012
	8	11.0	-	-	3	Keeley <i>et al.</i> 2012
	8	16.6	-	-	3	Keeley <i>et al.</i> 2012
	Mature	15.2	26.0	9.8	20	Keeley <i>et al.</i> 2012
	Mature	16.1	24.5	12.8	9	Keeley <i>et al.</i> 2012
	Mature	13.7	24.1	3.8	17	Keeley <i>et al.</i> 2012
Renosterveld	Mature	6.2	-	-	-	Bond 1983 in Keeley <i>et al.</i> 2005
Renosterveld	Mature	13.6	-	-	-	Cowling 1983 in Keeley <i>et al.</i> 2005
Swartberg: tall open proteoid shrubland	Mature	14.8	18.6	10.2	7	Bond 1983
Arid fynbos / renosterveld	Mature	10.2	10.6	9.8	2	Bond 1983
Baviaanskloof: tall open proteoid shrubland	Mature	17.8	26.6	13.2	3	Bond 1983
Baviaanskloof: low grassy heathland	Mature	16.0	-	-	1	Bond 1983
Outeniquas: proteoid shrubland	mature	17.0	18.0	13.0	4	Bond 1983
Outeniquas: open arid fynbos	mature	10.4	-	-	1	Bond 1983
Tsitsikama open shrubland-heath	mature	15.6	-	-	1	Bond 1983
Tsitsikama shrubland grassy-heath	mature	20.0	-	-	1	Bond 1983
CALIFORNIA						
California chaparral	2	9.5	22.1	2.9	250	Keeley <i>et al.</i> 2012
	2	12.2	20.6	4.8	28	Keeley <i>et al.</i> 2012
	4	6.6	3.0	11.4	28	Keeley <i>et al.</i> 2012
	mature	5.5	-	-	10	Keeley <i>et al.</i> 2012
	mature	1.8	-	-	1	Keeley <i>et al.</i> 2012
CHILE						
Chilean matorral	20-25	7.7	-	-	3	Keeley <i>et al.</i> 2012
ARIZONA						
Arizona chaparral	2 (yearly total)	7.8	12.0	3.1	40	Keeley <i>et al.</i> 2012
	2 (spring)	4.0	8.1	2.0	40	Keeley <i>et al.</i> 2012
	2 (autumn)	5.3	10.9	2.4	40	Keeley <i>et al.</i> 2012
AUSTRALIA						
Australian Heathland	mature	12.9	-	-	30	Keeley <i>et al.</i> 2012
	mature	13.3	-	-	7	Keeley <i>et al.</i> 2012
Australian Banksia Woodland	mature	15.5	19.0	11.0	9	Keeley <i>et al.</i> 2012
ISRAEL						
Woodlands, grazed		22.0				Naveh & Whittaker 1980
Open shrubland		25.0				Naveh & Whittaker 1980
Closed shrubland		4.0				Naveh & Whittaker 1980
Batha, Mt. Carmel		14.0				Naveh & Whittaker 1980
Western garrigue	2	6.7	7.8	5.6	2	Keeley <i>et al.</i> 2012

Random plots:

a) The total species count across all 47 random plots was 311, which is markedly higher than any of the total counts within 100m² plots in South Coast Renosterveld in Cowling (1983), although sample sizes in the present study are higher. Alpha diversity in 100m² plots varied between 28-57 (average 43.1) species for south-facing plots and 15-67 (average 35.2) for north-facing plots, in line with Cowling's (1983) findings for renosterveld. In concurrence with Cowling (1983), and in the context of the Fynbos Biome, Overberg renosterveld generally has higher species diversity than mountainous and coastal fynbos – this is particularly true for the richer south-facing slopes.

Comparisons of species diversity present several challenges, particularly due to problems of scale (Rice & Westoby 1983). Nevertheless, it is interesting to compare results with other studies; for example: Campbell & van Meulen (1980) recorded average diversity-values of 27.2 in mountain fynbos (calculated from the 10X5 m plots in their study); Valencia *et al.* (2004) reported 473 species in a 1 ha plot in Amazonian Ecuador; Cagnolo *et al.* (2006) recorded 253 species in 500m² plots in Argentinian Woodland; while Stohlgren *et al.* (2005) found 550 species in 1000m² plots in mixed habitats in Utah. Rice & Westoby (1983) examined species richness in a suite of Australian habitats at the 0.1 ha scale and found ranges from <50 species for temperate closed forests, to 50-100 species in temperate sclerophyll shrub-dominated habitats, to 140 species in tropical rainforest. Different forces act on different habitats and therefore influence the species-area curve (Keeley & Fotheringham 2003) and species diversity can be highly variable within one plot in response to a suite of habitat characteristics and abiotic impacts (such as fire) (Keeley *et al.* 2005). Thus when comparing data across multiple habitats using once-off species counts, one should be mindful of the fact that these figures are not always absolute and that they can change with time.

b) As with the permanent plots (and Guo 2001), species richness on random plots was significantly higher on wetter, cooler south-facing slopes than on the north-facing slopes (Kolmogorov-Smirnov: Mean North=35.3, Mean South=43.1, P<0.01,).

c) When species turnover between north- and south-facing slopes was compared, Whittaker's beta diversity index was 0.65.

d) Gamma diversity: Similarity percentages ranged from 2.5 – 64.4%, with an average of 28.5%. The minimum distance between plots was 0.1 km, while the maximum was 32 km, but there was no relationship between similarity indices and distances between plots (Fig. 7). To rephrase: sites within a relatively small radius were, on average, 70% dissimilar from each other, displaying exceptional levels of gamma diversity on a localised scale. Kruger and Taylor (1980) found a 50-70% change in species composition between Fynbos sites within 75 km of each other. Condit *et al.* (2002) found a strong negative correlation between similarity in tropical forests and distance apart, at three study sites for distances under 5km. After 5 km, similarity in Central American plots continued to decrease

with increasing distance (up to 100 km), while similarity barely changed over the same distance for the two Amazonian study sites. Their study demonstrates that different factors influence beta and gamma diversity at different scales and that it is not likely to be speciation and dispersal limitation only that affect species turnover, but that habitat structure and heterogeneity, as well as species life-history traits also require investigation. The reasons why the relationship between similarity and distance apart is so different for the Napier random plots, when compared with the experimental plots, are unclear but may be a result of the different scales of the two sets of data. For the experimental plots, the data were collected from paired plots at six distinct sites across the Overberg with a maximum distance of 100km between the sites while the random plots were located between <1-30 km from each other, across a range of aspects and different management practices. The lack of response to distance within a smaller area emphasises the high levels of local heterogeneity.

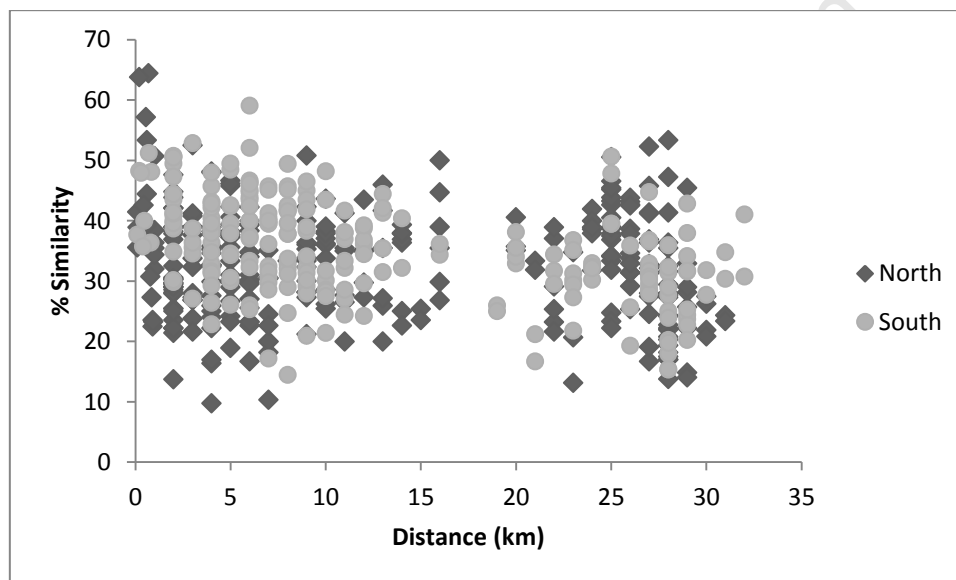


Figure 7. Graph denoting the relationship between similarity indices and distance (km) between plots on north- and south-facing slopes in random plots in the Napier area.

e) Table 4 presents a summary of the frequency of species occurrence across the 47 plots examined here and is comparable with Table 2 in Newton and Knight (2010). In terms of frequency of occurrence, about 85% of species occur in a quarter of the plots surveyed. Only one species, *Pentaschistis eriostoma*, occurred in all 47 plots. The second most-frequent species present was *Asparagus capensis* (in 34 plots), followed by *Themeda triandra* (Poaceae, 32 sites), *Anthospermum galiodes* (Rubiaceae, 30 plots) and *Elytropappus rhinocerotis* (Asteraceae, 29 plots). Most notably, 23% of species occurred at only one site (Table 4). Perhaps surprisingly, *Elytropappus* was not the most common species in renosterveld observed in this study. Similarly, Newton & Knight (2010) found the dominant species in west coast renosterveld to be *Eriocephalus africanus* (Asteraceae), but this only occurred on 63.2% of the 114 sites surveyed in their study. They also identified an

extraordinary number of species (1025) that were only found on one site. However, their study was based on collation of a suite of publications and anecdotes and covered a much larger region, resulting in a longer list of species. Nevertheless, as with the present study, Newton & Knight (2010) clearly demonstrate the exceptional levels of plant diversity present in lowland renosterveld.

f) Alpha diversity was not influenced by patch size ($R=-0.2$, $t(N-2)=1.36$, $P=0.18$).

Table 4. Table denoting the number of species and corresponding percentage figures common to random plots in the Napier area.

No. sites	No.	%
Species common to all 47 sites	1	0.35
Species common to > 30 sites	4	1.42
Species common to >20-30 sites	12	4.26
Species common to 13-20 sites	25	8.87
Species common to 12 sites	5	1.77
Species common to 11 sites	9	3.19
Species common to 10 sites	6	2.13
Species common to 9 sites	13	4.61
Species common to 8 sites	9	3.19
Species common to 7 sites	14	4.96
Species common to 6 sites	18	6.38
Species common to 5 sites	14	4.96
Species common to 4 sites	15	5.32
Species common to 3 sites	28	9.93
Species common to 2 sites	43	15.25
Species occurring at only 1 site	66	23.40

CONCLUSIONS

Newton and Knight (2010) describe the findings of their study on west coast renosterveld as follows: ‘... although from a gross overview the landscape is dominated by a few shrubs, within which are dispersed a variety of grasses and geophytes, there is a great variation in how these are distributed, and micro-habitat and disturbance play a much greater role than thought.’ Thus, although at a first glance, renosterveld often has the appearance of a homogeneous habitat, with little to offer, in terms of rare and endemic species, or any measure of species diversity, it is clear that this vegetation type requires far greater conservation attention than it has received to date.

Here I discuss the key findings in this chapter and the implications for renosterveld conservation and planning.

Alpha diversity:

Although less than 10 species dominate the cover across the Overberg, alpha diversity (at the 1X1 m scale) is high, even relative to species-rich fynbos systems. Both sets of data have demonstrated that renosterveld diversity in the Overberg region is, at the very least, on a par with other studied fynbos types and often supersedes that of these habitats (see Campbell & van der Meulen 1980, Cowling 1983, Cowling *et al.* 1996, Keeley *et al.* 2005, Keeley *et al.* 2012, Kruger & Taylor 1980). None of the data from other Mediterranean regions, as listed in Table 3, matched the high alpha diversity of south-facing slopes in the renosterveld studied here. North-facing slopes were on a par with results from fynbos studies of equivalent quadrat size. These data cannot be used to extrapolate species diversity values across the range of renosterveld vegetation types, but high levels of diversity and local endemism have also been demonstrated for other lowland renosterveld (e.g. West Coast Renosterveld, Newton & Knight 2010), while southern Cape mountain renosterveld has substantially lower species richness (Bond 1983 in Keeley *et al.* 2005).

Diversity along habitat- and geographic-gradients:

In keeping with findings in comparable northern hemisphere habitats, south-facing slopes display higher levels of alpha diversity than their north-facing counterparts, while species turnover rates between aspects are substantial. Thus, when selecting reserves, it is imperative that a multitude of aspects are included in the reserve network, in order to ensure that conservation areas will be representative of the entire renosterveld system. Geographic gradients were surprisingly high, with a great deal of species turnover between each of the six experimental sites (Fig. 6). Gamma diversity across the landscape, as measured by the six experimental sites along a 100km gradient, was high, while data from random plots within a moderately restricted part of the Overberg (with a maximum distance of 35 km between plots) showed that fragments only shared, on average, 30% similarity, demonstrating that even within a relatively small area, beta diversity across remnants was high. Additionally, Curtis *et al.* (in press, Appendix 1) describe a distinct vegetation community restricted to quartz/silcrete outcrops in Eastern Rûens Shale Renosterveld and propose the need to revise our thinking in terms of classifying vegetation types and defining microhabitats which tend to exist as specialised communities on specific substrates, nested within a broader vegetation type. Excluding these specialised habitats when defining vegetation types could lead to these species-rich communities being undermined in reserve networks in future. Again, these data emphasize the importance of creating multiple reserves across the matrix of remnants in order to capture the greatest amount of plant diversity.

Fire and temporal species turnover:

Although overall species richness did not change substantially in response to fire, renosterveld displayed high levels of species turnover measured over four post-fire years. Fire can increase the abundance (or appearance) of geophytes and annuals (Chapter 4), as well as influencing the species richness and cover, either positively or negatively, of other growth forms (Chapter 7), demonstrating that fire too plays an important role in determining the species richness (Keeley *et al.* 2005). Bond *et al.* (1988) demonstrated that in fragmented fynbos habitats, species loss is often linked to deterministic rather than stochastic extinctions – i.e. changes in the disturbance (i.e. management) regime can play a bigger role in extinction rates than reduction in population sizes associated with insularisation of smaller fragments. Management of remnants is critical as it can determine the persistence or disappearance of species and growth forms from habitat remnants (also see Chapter 6).

Conservation strategy for renosterveld in the Overberg

Species-area studies addressing the SLOSS (single Large or Several Small) debate have tended to conclude in favour of several small reserves as opposed to single large ones (e.g. Condit *et al.* 2002, Higgs & Usher 1980; Järvinen 1982, Quinn & Harrison 1988), but such conclusions have received criticism as they do not address the critical issue of differences in species susceptibility to extinction (Diamond *et al.* 1976), nor do they address the suite of issues associated with fragmentation, such as dispersal, decreases in population size, genetic isolation, etc., which affect different species in different ways. Also, species-area studies are often ‘snapshots’ of species numbers and abundance and do not consider temporal changes and disturbance effects (grazing, fire seasonality and post-fire succession) (see Keeley & Fotheringham 2003), which is partly why there remains disagreement regarding the SLOSS debate. Diamond *et al.* (1976) argued that small reserves often lose sedentary species threatened by human activities, while retaining the quick-dispersing successional and edge species that do not require protection. Thus, using ‘species diversity’ as the sole means for determining the appropriate sizes of nature reserves can be misleading and should be treated with caution. This argument holds true for renosterveld, where smaller fragments tend to be subjected to increased levels of disturbance which is often associated with an increase in species diversity, albeit the more ‘weedy’ annuals and geophytes (Kemper *et al.* 1999). However, conservation opportunities for renosterveld in the Overberg are severely limited by the extent of transformation that has already occurred, thus there are relatively few options: the establishment of ‘large’ renosterveld reserves is severely impeded by the fact that there are only 46 remnants of >100 ha remaining in the Overberg, and only 13 of these are over 200 ha (calculations based on SANBI maps). Nevertheless, the present study has demonstrated the need for multiple reserves across habitat, geographical and

management gradients in order to maximise the biodiversity and thereby, preserve associated processes across as wide an area as possible within the constraints of a severely fragmented system. The remnants of the four renosterveld types that occur in the Overberg represent completely different communities and associations from the other 25 renosterveld types which are recognised in the Cape Floristic Region. These are all likely to display their own endemic communities, but alpha diversity and turnover along habitat gradients may either be equivalent to, higher than (e.g. West Coast Renosterveld) or lower than (e.g. Mountain Renosterveld types) those reported here. However, these high levels of diversity at the regional, landscape and localised scales make conserving representative amounts of all these vegetation types critical for preserving biodiversity on a global scale. The most recent classification of vegetation types in the Fynbos Biome forms part of an account of the 3773 vegetation types in South Africa, thus it cannot by nature be detailed enough to inform conservation planning at anything more than the regional scale (Mucina & Rutherford 2006). However, it provides a guide as to where to start investigating the need for more detailed planning. Much work has gone into conservation planning initiatives in the Cape Floristic Region and some fine-scale plans have been generated (e.g. von Hase *et al.* 2003), but these are based on GIS-mapping of the remnants of natural vegetation according to Mucina & Rutherford's vegetation map. This study shows that merely conserving a few large remnants within each of the four renosterveld types in the Overberg will not be sufficient to retain the species richness within the region, due to the extraordinarily high rates of species turnover along aspects, microhabitats (Curtis *et al.* 2013, Appendix 1) and vegetation types within the region. Thus, a conservation strategy for lowland renosterveld in the Overberg needs to include a mechanism for maximising the numbers of protected areas across the landscape.

Extant renosterveld is distributed as scattered remnants across privately-owned farmland and one fragment is often spread across more than one cadastral boundary. And perhaps most importantly, landowner willingness is extremely variable (O. Curtis pers. obs.), which is a critical aspect in securing habitat for conservation on privately-owned land (Knight & Cowling 2007). As suggested by Kemper *et al.* (2000), within the Overberg, there is potential for 'large' reserves and corridors in the east, while only small fragments remain in the west (Fig. 1). Given the extent of transformation, every single piece of renosterveld is now essentially viewed as being worthy of conservation attention (Kemper *et al.* 1999, Newton & Knight 2010), although the proportion of remnants that are ecologically intact is far smaller than their physical range (Donovan Kirkwood, pers. comm., O. Curtis, pers. obs.). Not only is the system severely fragmented and altered, but the remnants are spread across four substantially different renosterveld types (Mucina & Rutherford 2006) meaning that conserving remnants in only one type of renosterveld will not conserve alpha, beta, or gamma diversity across the Overberg sufficiently. Renosterveld conservation planners no longer have the luxury of 'picking and choosing', and with these limitations, one has to ask whether remnant

renosterveld has the potential for conserving *retention and persistence* (as termed by Cowling *et al.* 1999), or whether it is merely the 'living dead' that are being protected for a limited time (e.g. Tilman *et al.* 1994, Bond 1995). Thus, along with the establishment of several protected areas across the Overberg, the intricacies of inter- and intra-species interactions and dependencies need further exploration and opportunities for mitigation against fragmentation, should any exist, require investigation as a matter of priority.

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CHAPTER 6:

Predicting species responses to habitat loss using simple models: can global assessments of threat status be misleading at local levels?

“Extinction from habitat loss is the signature conservation problem of the twenty-first century”

(He & Hubbell 2011)

INTRODUCTION

The large-scale transformation and fragmentation of natural landscapes to make way for agriculture is a global conservation conundrum and much work has gone into trying to understand the long-term viability of severely fragmented ecosystems. It is important for conservation managers to understand what constitutes a viable ecosystem and how to maintain this system in a functioning state across the landscape, as opposed to pouring resources into systems that are essentially functionally extinct. What complicates matters is that different taxa respond differently to the ‘new’ landscape brought about by fragmentation and this may be influenced by a suite of characteristics, including fragment size and quality, isolation, edge effects and the nature of the surrounding matrix (Tscharrntke *et al.* 2002). In addition to this, inherent species’ traits (including rarity [man-induced vs. natural], population variability [stabilized vs. fluctuating], trophic position, body size, specialization, dependence on mutualists and dispersal ability) also determine how successful a species will be in a fragmented landscape (Tscharrntke *et al.* 2002).

The importance of conserving large tracts of connected fragments in a fragmented landscape has been established (Püttker *et al.* 2011). However, many fragmented systems can no longer afford this luxury, as they are already too transformed and fragmented, with little or no opportunity for restoration. This begs the question of whether these systems are doomed for inevitable extinction due to loss of process and gradual species extinctions (as Extinction Debt theory predicts – Loehle & Bai-Lian 1996, Tilman *et al.* 1994), or whether some species or systems are more resilient than others to fragmentation and habitat loss, enabling them to continue to function in transformed landscapes. Again, these are difficult questions to answer because of the multitude of confounding variables that affect different species on different levels. It has been suggested, however, that several small fragments may continue to thrive where the overall landscape is more heterogeneous (Tscharrntke *et al.* 2002) – i.e. that not all fragmented systems are paying extinction debts. The Extinction Debt Theory essentially hypothesizes that where the large-scale fragmentation of habitats is a relatively recent occurrence, more species are

present in a habitat patch then can be sustained. Thus, with time, species will be lost from a fragment until the 'debt is paid' and the number of species is in equilibrium with the area of the fragment. Thus we have not yet seen the full effects of fragmentation. These effects have not yet manifested themselves and are thus still in the process of affecting islands of remnant vegetation – i.e. although many plant species are still present in fragments, the breakdown in ecosystem functioning (e.g. loss of pollinators due to pesticide drift, too little or too much fire, etc.) will eventually result in species extinctions, as recruitment processes fail and essential processes are halted (Loehle & Bai-Lian 1996, Tilman *et al.* 1994).

He and Hubbell (2011) note that extinction rates are typically estimated by reversing the species-area accumulation curve and extrapolating backwards to smaller areas to predict expected species extinctions (known as the Species-Area Relationship (SAR)). The authors show that this method of calculating extinction rates almost always substantially overestimates species losses and that a far greater area of habitat than previously thought must be lost before extinctions start occurring. However, the authors emphasize that, although the SAR is an unreliable predictor of extinction risk, this does not negate the possibility of the existence of extinction debts. Furthermore, they demonstrate that an alternative curve, termed the Endemic-Area Relationship (EAR), is far more effective in predicting species losses and may be better at predicting the probability of imminent extinctions. Testing the extinction debt theory presents several challenges and He and Hubbell (2011) note that testing this theory will require dynamic modeling. The fact that the EAR curve was more effective in predicting extinction rates emphasizes the need for a more complex approach and this would certainly apply to heterogeneous habitats with high levels of endemism, such as renosterveld.

The Fynbos Biome in South Africa comprises the smallest, yet richest, plant kingdom in the world. Within the Fynbos Biome, about 24% of the described vegetation types fall under 'renosterveld' – a shrubby habitat, usually lacking the three 'typical' fynbos elements (i.e. Proteaceae, Ericaceae and Restionaceae) and dominated by a mixture of C₃ shrubs and C₄ and C₃ grasses. In the Overberg, four distinct Lowland Renosterveld types are scattered across a vast landscape of transformed lands (grain fields and artificial pasture) and almost all extant vegetation occurs on privately-owned land, with <1% falling under official protection in Nature Reserves. The most pertinent threats facing renosterveld today are continued conversion of virgin renosterveld into ploughed croplands and inappropriate grazing and fire management of the remnants. Less than 10% of the original extent of renosterveld remains in the Overberg (and across the remaining range of lowland renosterveld vegetation types). In the Overberg, these fragments vary in size from <0.1 to 835 ha, but the average size, based on all remnants on the GIS

database (from SANBI, in von Hase *et al.* 2003) is 3 ± 16 ha, with fewer than 50 fragments being larger than 100ha. Within these remnants are a plethora of rare, endemic and severely threatened plants, about which very little is known (Raimondo *et al.* 2009).

Although previous studies have demonstrated no significant effect of patch size on plant species diversity across renosterveld fragments of varying size (Kemper *et al.* 1998), the question of whether or not renosterveld is still paying its extinction debt is debatable. The same study demonstrated community-level changes in response to fragmentation and this is concerning. As Bond (1995) emphasizes, the true measure of the extent of species losses does not lie in extensive red data listings, but rather in the extinction or reduction of ecological *processes*. These are often overlooked, probably because they are difficult to quantify – perhaps even to identify. However, if we are to understand the real potential for a system or habitat type to become functionally extinct, we need to examine the processes that affect these systems, how threatened these processes are, and what conservation interventions can be made to reverse the downward spiral towards extinction. With an estimated 4-6% of its original extent remaining, lowland renosterveld is an excellent model system for testing theories about extinction debts and predicting extinction risks. In this chapter, I will focus on the latter.

Predicting species' extinction risks, as a result of habitat loss and fragmentation has been discussed extensively in the literature (Bommarco *et al.* 2010, Brook *et al.* 2006, Purvis *et al.* 2000, Swift & Hannon 2010, Tilman *et al.* 1994) and different studies have reached different conclusions about what characteristics make a species more resistant or more vulnerable to the effects of habitat loss (Hockey & Curtis 2009). It has also been demonstrated recently that species-area relationships tend to overestimate rates of extinction resulting from habitat loss (He & Hubbell 2011) – i.e. patch size alone cannot determine the persistence of species. The red-listing system used by Raimondo *et al.* (2009) is based on predicting species extinction risk using theoretically determined predictors of extinction based on population viability theory. However, other means of determining species extinction risk have been proposed. For example, Bond (1995) developed a model for predicting species extinction risk in plants due to loss of mutualist partners. The population consequences depend on i) risk of process failure (in terms of pollination – i.e. plants dependent on a single pollinator will be at a higher risk of extinction than those with multiple pollinators), ii) dependence on process (e.g. for pollination, degree of dependence on pollinators for seed production e.g. whether self incompatible or capable of selfing), iii) population dependence on seed (completely dependent on seed for reproduction vs. able to propagate vegetatively or able to resprout after disturbance). This model worked well for some genera and again, probably most importantly, highlighted the fact that ecological processes need closer consideration if

reserves are to be effectively planned. Hockey and Curtis (2009) modified this model to predict extinction risk in birds and lemurs, using simple species' traits, including natural range size, body size, and habitat and dietary specialization. This analysis generated some simple models with high predictive power.

Most extinction-risk theories relating to fragmentation predict that species' traits will determine how vulnerable they are to fragmentation. For example, high-risk species are predicted to have low dispersal ability and be highly specialized in terms of pollinator requirements. However, Bond *et al.* (1988) found that although islands of fynbos had significantly lower species diversity than large, 'mainland' patches, none of these factors contributed towards this difference. Instead, they found that disturbance regime played the biggest role in determining species richness in a fire-dependent system. Islands of fynbos are less likely to be exposed to fire through natural processes (i.e. lightning strikes) than are large, extensive tracts of fynbos. In keeping with this trend, extensive tracts of fynbos also contained a higher ratio of reseeders to resprouters, as they are more exposed to natural disturbances (fire) than are islands. Kemper *et al.* (1999) found similar results in their renosterveld study: although overall species diversity (a weak representation of fragmentation effects) did not change with decreasing patch size, community composition was altered significantly and it was suggested that this was related to disturbance regimes. However, in renosterveld, disturbance (particularly grazing and fire) is generally greater in smaller fragments, as these form part of agricultural camps and are therefore subject to some of the same disturbances (e.g. grazing) as the surrounding farmlands.

In renosterveld, examining the effects of habitat fragmentation and therefore assessing species' extinction risk cannot be done without considering the responses of individual species to management-associated 'threats'. For example, renosterveld systems tend to be overgrazed, which is likely to exacerbate the effects of fragmentation on species that are more sensitive to grazing (i.e. palatable species) and trampling. Likewise, other factors such as fire management or management of the surrounding matrix are likely to act synergistically on different species in different fragments.

Here, I explore the use of a simple model for predicting species' extinction risk in renosterveld, based on a combination of traits, whereby it may be possible to determine in what way traits are behaving synergistically to determine extinction risk.

METHODS

The main objectives of generating these simple extinction risk models were to assess what aspects of a plant's biology are associated with extinction risk, as well as to determine how species respond to the

identified threats within this severely threatened system. The aim was to keep the models as simple as possible, so that they could be replicated and tested for other species in different systems.

As a starting point, a database comprising 73 species, recorded in renosterveld as part of ongoing research and monitoring, was generated. The database was then populated with the following variables for each species and allocated a score between 0 and 1: i) palatability index (0=low palatability, 1=very palatable to livestock); ii) habitat specialization (0=occurs in many habitats across the Fynbos Biome, or across South Africa, 1=very specialized (e.g. only grows on quartz hilltops in Eastern Rûens Shale Renosterveld)); iii) range size (0=a large range (e.g. occurs across South Africa), 1=a very limited range (e.g. only grows in a 50 km radius); iv) pollination specialization (0=generalist and/or able to self-pollinate, 1=dependent on only one or two pollinators); and v) dependence on seed (0=not dependent on seed, capable of vegetative growth and/or resprouts after disturbance, 1=totally dependent on seed for recruitment). Appendix 6.1 provides the full list of species and continuous data scores for each variable. These traits were unknown for many species and a subjective 'expert opinion' approach had to be taken where this was the case. These scores were generated using either existing data for similar taxa (e.g. palatability indices for similar species as listed by Esler *et al.* (2006)), or flower morphology (which can be used to determine pollinator specialization). Scores for range size and habitat specialization were determined from information in Goldblatt & Manning (2000). Thus, one could predict that, for example, a species that is highly palatable to livestock and has a very restricted range or very specialized habitat requirements will be at a higher risk of extinction than a plant which is unpalatable and a widespread habitat generalist. Alternatively, a species that is very specialized in terms of pollinator requirements or is totally dependent on seed production and dispersal will be at a higher risk than a plant that has multiple pollinators or is capable of resprouting and vegetative reproduction. However, a species that is highly palatable, yet is able to reproduce and/or resprout after fire or heavy grazing is far less likely to go extinct than a palatable species which can only reproduce from seed.

Following the allocation of these scores, a suite of models using the above-mentioned traits, were generated by plotting two traits against each other at a time and broadly dividing the model into three categories of probability of extinction risk: high-, medium- and low-risk (following Bond (1995) and Hockey & Curtis (2009)).

As with Hockey and Curtis's models (2009), I first assessed which of the variables used in these models best predicted the species threat status, by testing the model against the species' Red Data status, as listed by Raimondo *et al.* (2009). The Red List for South African Plants (Raimondo *et al.* 2009) lists all South African plants and uses the following categories: *Extinct*, *Extinct in the Wild*, *Critically Endangered*

and Possibly Extinct, Critically Endangered, Endangered, Vulnerable, Near-Threatened, Least Concern, Critically Rare, Rare, Declining, Data Deficient and Threatened. For the purposes of testing these models, I focused only on 'threat categories' (i.e. *Critically Endangered, Endangered and Vulnerable*), as well as the *Near-Threatened* and *Least Concern* categories. Table 1 provides a summary of the Red List criteria used by Raimondo *et al.* (2009) for separating species into the three threat categories. A species is considered *Near-Threatened* if it almost meets any of the five criteria for *Vulnerable* and of *Least Concern* if it meets none of the requirements for these four categories.

Table 1 A summary of the criteria used by Raimondo *et al.* (2009) for assessing the categories of threat – i.e. *Critically Endangered, Endangered and Vulnerable*.

Biological Indicator	Quantitative thresholds
Rapid population decline in relation to life history of taxon in the past, present or projected future	Proportion by which population is reduced
Small geographic range, decline and few locations or fragmentation or population fluctuation	i) Size of geographic range ii) Number of locations
Small population size, decline and fragmentation or population fluctuations	i) Total number of individuals in global population ii) Number of individuals in largest sub-population iii) Proportion by which population is reduced
Very small population size or very restricted distribution	i) Total number of individuals in global population ii) Size of geographic range iii) Number of locations
Quantitative analyses of extinction risk	Probability of extinction over a specific time period

Secondly, I identified some known threats to plants in renosterveld systems and listed these. These included: over-grazing by livestock, inappropriate burning regimes (i.e. too much or too little fire), further habitat loss and loss of pollinators from fragments. The plant traits that would determine how species respond to these threats include: habitat specialisation, palatability to livestock, dependence on seed (as opposed to being able to resprout or reproduce vegetatively) and pollinator specialization requirements.

Analyses by Raimondo *et al.* (2009) for assessing Red Data status essentially use range size and population size as input variables. Thus, apart from the use of range size, the variables used in the models generated in the present study are different from those used by Raimondo *et al.* (2009) to determine threat status, preventing the models from becoming circular. It is important to note that

habitat specialisation is not a surrogate for range size or population size, although it may be closely tied with these variables for some species. Habitat specialisation was determined by assessing the range of habitats that a species is able to occupy; for example, a species which only occurs in renosterveld was allocated a higher score than one which occurs throughout the fynbos biome, while a plant that only grows on quartz outcrops in renosterveld, or on a specific aspect within renosterveld was allocated a higher score than one that grows throughout renosterveld.

These models were therefore used to identify which traits are important when assessing a species' ability to persist not only in a landscape context, but also on a local scale (e.g. identifying useful indicator species within patches). For example, a highly palatable grass such as *Themeda triandra*, which is capable of seeding and resprouting and has an extensive range across the continent, as well as India and Australia, and is therefore unlikely to ever be considered a threatened species, but over-grazing may result in significant localised population declines (Heady 1966). Thus, there are two objectives to these models: i) assessing which species traits are most likely to predict a species' *global* threat status and ii) identifying traits which can be used to predict *localised* extinction risk within renosterveld fragments, with the understanding that these traits may differ at these two scales.

Most extinction theory is based on statistical principles of stochasticity in small populations. 'Deterministic extinctions' are those happening for a reason, such as overgrazing, harvesting, or too much or too little fire (Shaffer 1981). Thus, these models are an attempt to identify how different species may become threatened at different scales, where localised threats are identified. Here, I carry out an assessment of whether Red-listing threat categories are useful in assessing local population viability, in an attempt to address the question: can global assessments of threat be misleading in the local context?

RESULTS AND DISCUSSION

Extinction Risk Models

The models achieved varying degrees of success, in terms of nesting species with similar Red Data statuses together, but overall, this method appears to have potential and may indeed be useful in drawing attention to species currently listed as *Least Concern* whose conservation status may be more tenuous. In the first model (Fig. 1), I plotted the Range Size Index against the Habitat Specialization Index. Here, none of the *Near-Threatened* species fall into the High Risk area of the model, while one *Endangered* species falls into medium risk. This model is effective, but could be improved upon. Overall,

about 84% of threatened plants were correctly predicted, while about a quarter of the species classified as *Least Concern* were predicted to be at medium risk.

One *Endangered* species, *Otholobium pungens*, fell into the medium-risk zone. This species is recorded as being an endemic to the limestone ridges of the southern Overberg coast. However, recent surveys have revealed that this species is fairly widespread in Eastern Rûens Shale Renosterveld and should probably be down-listed to *Vulnerable* (C. Stirton and O. Curtis unpubl. data). Two Near-threatened species, *Agathosma foetidissima* and *Peucedanum striatum* fell into the High Risk zone, suggesting that these species may be deserving of a higher threat status. Interestingly, a species previously misidentified and recorded as *Aspalathus incompta*, is currently being described as a new species by C. Stirton (Curtis *et al.* 2013) as *A. quartzicola*. This species is a quartz specialist within the Eastern Rûens Shale Renosterveld and its minimum proposed Red Data status will be *Endangered*, due to significant habitat loss. Currently, it is lumped with *A. incompta* as *Near Threatened*, but in this model it fell into the high threat category. A few *Least Concern* species, e.g. *Cymbopappus adensolen* and *Erica karoica*, fell into the medium threat category, but there is no apparent reason to be concerned about these species (pers. obs.). Several other species currently of *Least Concern* were borderline cases for inclusion in a higher risk category.

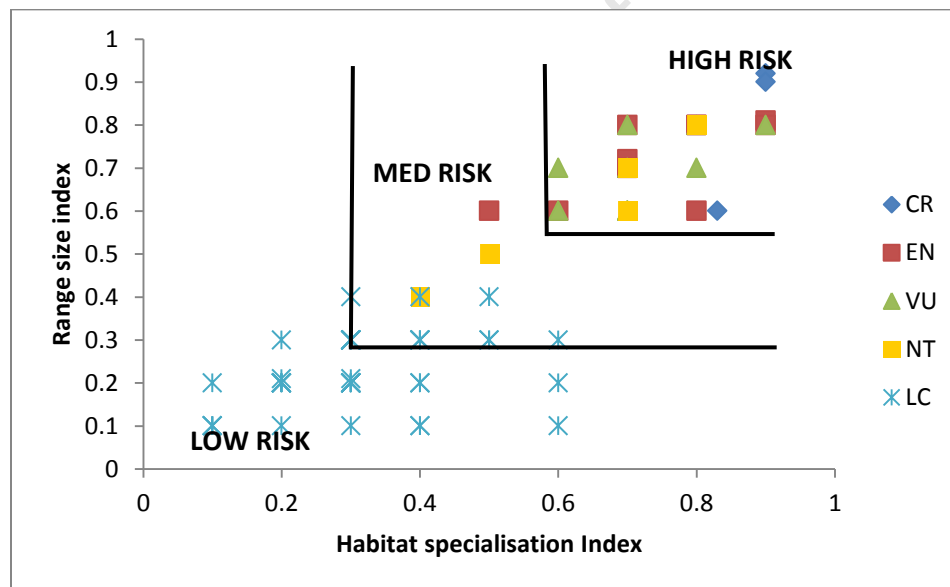


Figure 1. The simplest model using Habitat Specialization and Range Size indices to predict species extinction risk (High, Medium and Low), tested against the Red Data status of the species used in the study (CR=Critically Endangered, EN=Endangered, VU=Vulnerable, NT=Near-Threatened, LC=Least Concern).

Because of using range size data, there is a risk that the this model could become circular, since the Red Data listing uses this trait, amongst others, to determine a species' threat status. Therefore, I opted to test the usefulness of the model by adding and combining these traits with others completely unrelated to those used for the Red Listing process and eliminating the Range Size Index from the model. This would also help determine whether the model works for predicting species' extinction risk within fragments, while the first model essentially determines global risk.

In the second model (Fig. 2) I plotted Palatability Indices against the Habitat Specialisation Index, the idea being that a highly habitat-specific species would be at a lower risk of local extinction if it were less palatable to livestock, while a more palatable species would be at a greater risk. As expected, the result compared poorly with the species' Red Data status, as palatability is not taken into account for Red Listing purposes. Only two threatened species remained in the High Risk zone (*Trichodiadema pygmaeum* and *Peucedanum striatum*), while several others fell into the Medium-Risk and Low-Risk zones. One *Critically Endangered* species, *Polhillia curtisiae* (Curtis *et al.* 2013) of which there is only one known extant population, is unpalatable to livestock and is thus not at risk of extinction from overgrazing. Two *Endangered* succulents (*Gibbaeum haaglenii* and *Brownanthus fraternus*) fell into the Low Risk zone because, despite their very specialized habitat requirements, they too are not grazed by livestock. Being succulents, they are, however, very vulnerable to trampling and are damaged where livestock have been present (pers. obs). This model, although seemingly not as robust as the one based on range size and habitat specialisation, could assist in predicting which already-threatened species may be at a higher risk under heavy grazing regimes. It also highlights some species which are 'globally' of *Least Concern*, but locally, may be the first to suffer significantly losses in systems with poorly managed grazing regimes. These species, when present, may be useful indicators of over-grazing, as their populations can be monitored and used as indicators for when over-grazing is taking place (i.e. they can be the 'warning system' which alerts managers to remove livestock or game from fragments). Sue Milton (pers. comm. 2008) notes this in her general guidelines for renosterveld management, but focuses mostly on *Themeda* as an indicator. This model highlights some additional species which may be useful, as *Themeda* does not occur in all fragments. Such species include *Hermannia flamula*, *Aspalathus submissa* and *Ischyrolepis capensis*.

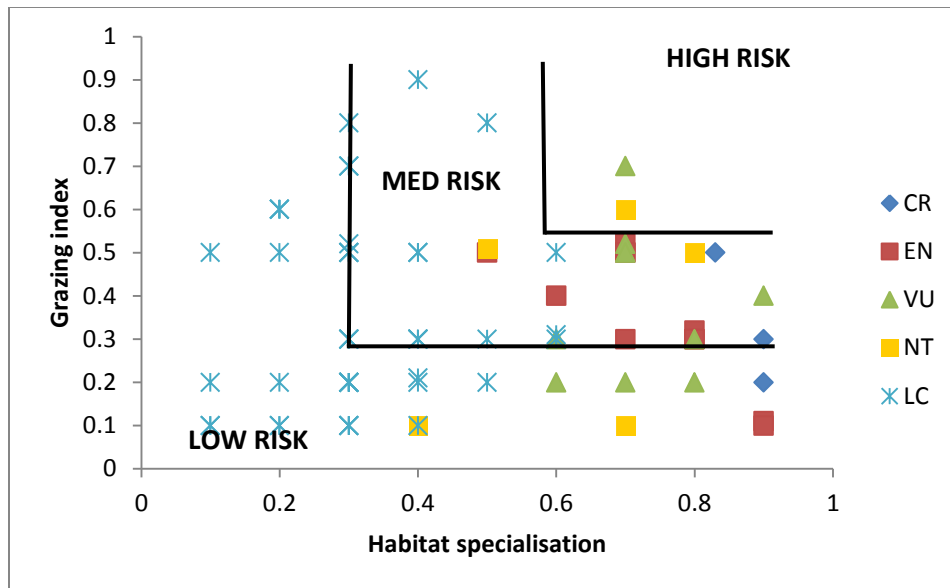


Figure 2. Model incorporating the Palatability Index and the Habitat Specialization Index to predict species extinction risk (High, Medium and Low), tested against the Red Data status of the species used in the study (CR=Critically Endangered, EN=Endangered, VU=Vulnerable, NT=Near-Threatened, LC=Least Concern).

In the third model, I plotted an index of Dependence on Seed against the respective Habitat Specialisation Indices. A species which relies solely on seed production to reproduce was allocated a high score, while those capable of resprouting, or both seeding and resprouting, were given a lower score. This model produced a better fit to the Red List classifications than did the Palatability model. Again, several *Least Concern* species fell into the Medium-High Risk zone, as a result of being highly dependent on seed production and these may warrant monitoring at localized sites. These species were *Cymbopappus adensolen*, *Freylinia undulata*, *Erica karooica*, *Gladiolus permeabilis*, *G. stellatus*, *Hermannia flamula*, *H. saccifera*, *H. alnifolia*, *H. hyssopifolia*, *Printzia polifolia*, *Berkheya barbarta*, *Clutia tomentosa*, *Conyza scabrida*, *Eucomis regia*, *Ischyrolepis capensis* and *Aspalathus submissa*.

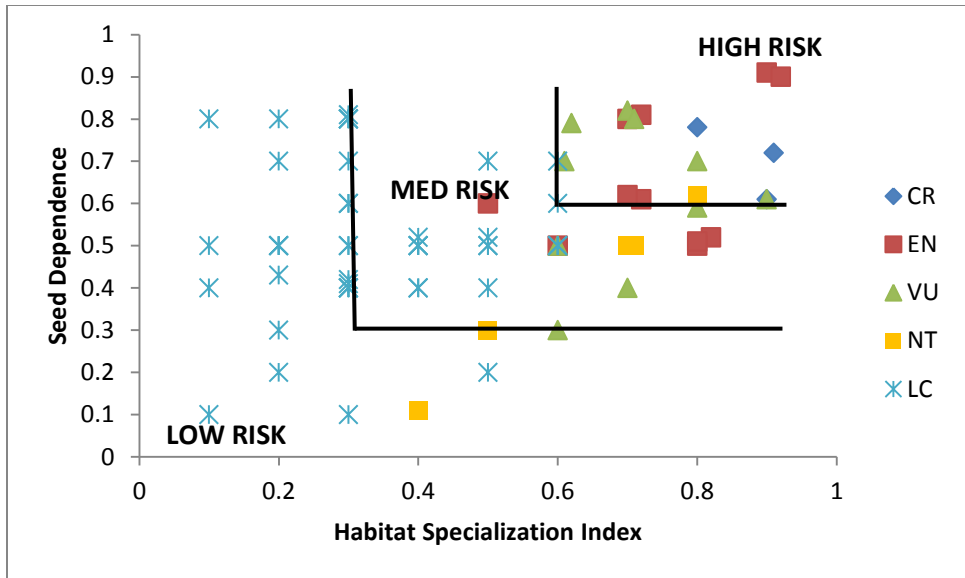


Figure 3. Extinction Risk Model with an index of Seed Dependence plotted against the Habitat Specialization Index to predict species extinction risk (High, Medium and Low), tested against the Red Data status of the species used in the study (CR=Critically Endangered, EN=Endangered, VU=Vulnerable, NT=Near-Threatened, LC=Least Concern).

In the fourth model, I plotted Pollination Specialization against Habitat Specialization, but this did not produce as good a fit with the Red Data status as did the Dependence on Seed model. The threatened species that remained in the High Risk zone include *Gladiolus acuminatus*, *Gladiolus vandermerwei*, *Haworthia mirabilis*, *H. mutica*, *H. floribunda* and *Relhannia garnotii*.

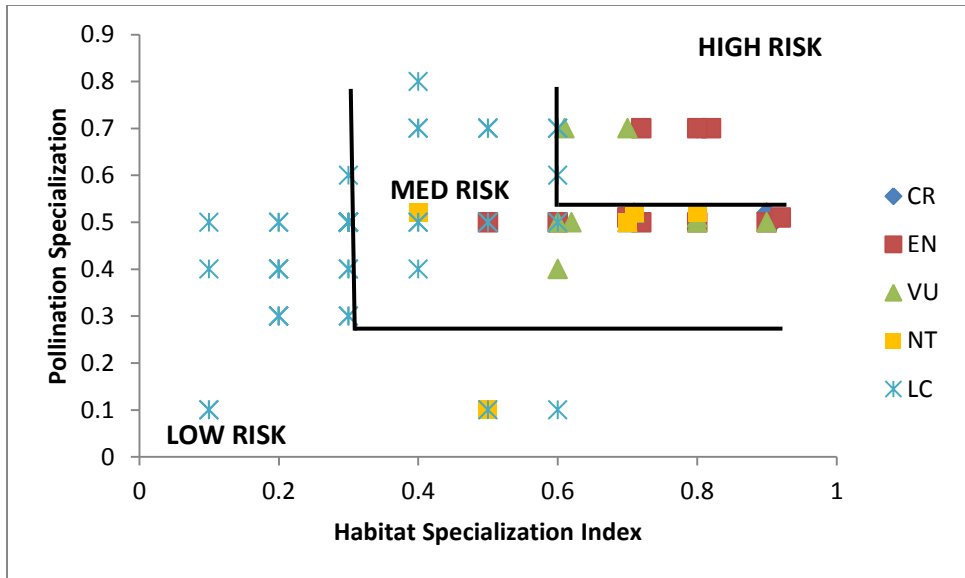


Figure 4. Extinction Risk Model with an index of Pollination Specialization plotted against the Habitat Specialization Index to predict species extinction risk (High, Medium and Low), tested against the Red Data status of the species used in the study (CR=Critically Endangered, EN=Endangered, VU=Vulnerable, NT=Near-Threatened, LC=Least Concern).

In the fifth model, I tested whether removing habitat specialisation from the model would strengthen or weaken the results, in terms of comparisons with the species' Red Data status. Overall, there does not appear to be much of a difference between the fourth and fifth models, although more *Least Concern* species are found in the higher risk regions of the model in the latter.

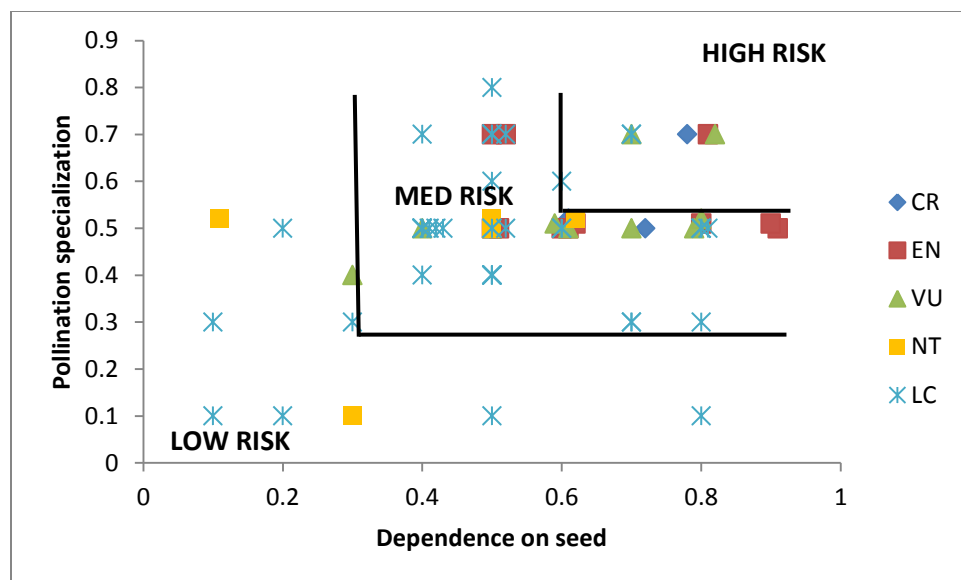


Figure 5. Extinction Risk Model with an index of Pollination Specialization plotted against the Dependence on seed Indices to predict species extinction risk (High, Medium and Low), tested against the Red Data status of the species used in the study (CR=Critically Endangered, EN=Endangered, VU=Vulnerable, NT=Near-Threatened, LC=Least Concern).

Classification and Regression Trees

In order to give statistical value to the models and determine their viability, I generated some standard Classification and Regression Trees (Breiman *et al.* 1984). These trees determined which variables (indices) have the most predictive power for predicting terms Red Data status. The categorical predictor was the species Red Data status and the predictors were the indices generated for the models – i.e. Range Size, Habitat Specialization, Palatability, Pollination Specialization and Seed Dependence. The Gini Measure Goodness of Fit was used, with FACT-Style Direct Stopping set at 0.05 (STATISTICA Version 10). The first classification and Regression Tree showed that Range Size is the most important variable in predicting a species' known Red Data status. Using this tree, the following key could be used: If a species has a Range Size Index of greater than 0.45, it will have a Red Data status of *Endangered* and upwards. If the Range Size is greater than 0.86, the species is likely to be *Critically Endangered*. However, if the plant has a Range Size Index less than or equal to 0.45, it will be *Least Concern*. These remaining species are then divided further by their Dependence on Seed.

The importance plot generated from the Classification and Regression Trees confirmed that Range Size is most important in determining Red Data Status, with Habitat Specialization also being a critical

determining factor. Dependence on Seed registers as being less than half as important as Habitat Specialization, while Pollination Specialization and Palatability appear insignificant in predicting a species threat status, based on comparisons with the SA Red List (Raimondo *et al.* 2009).

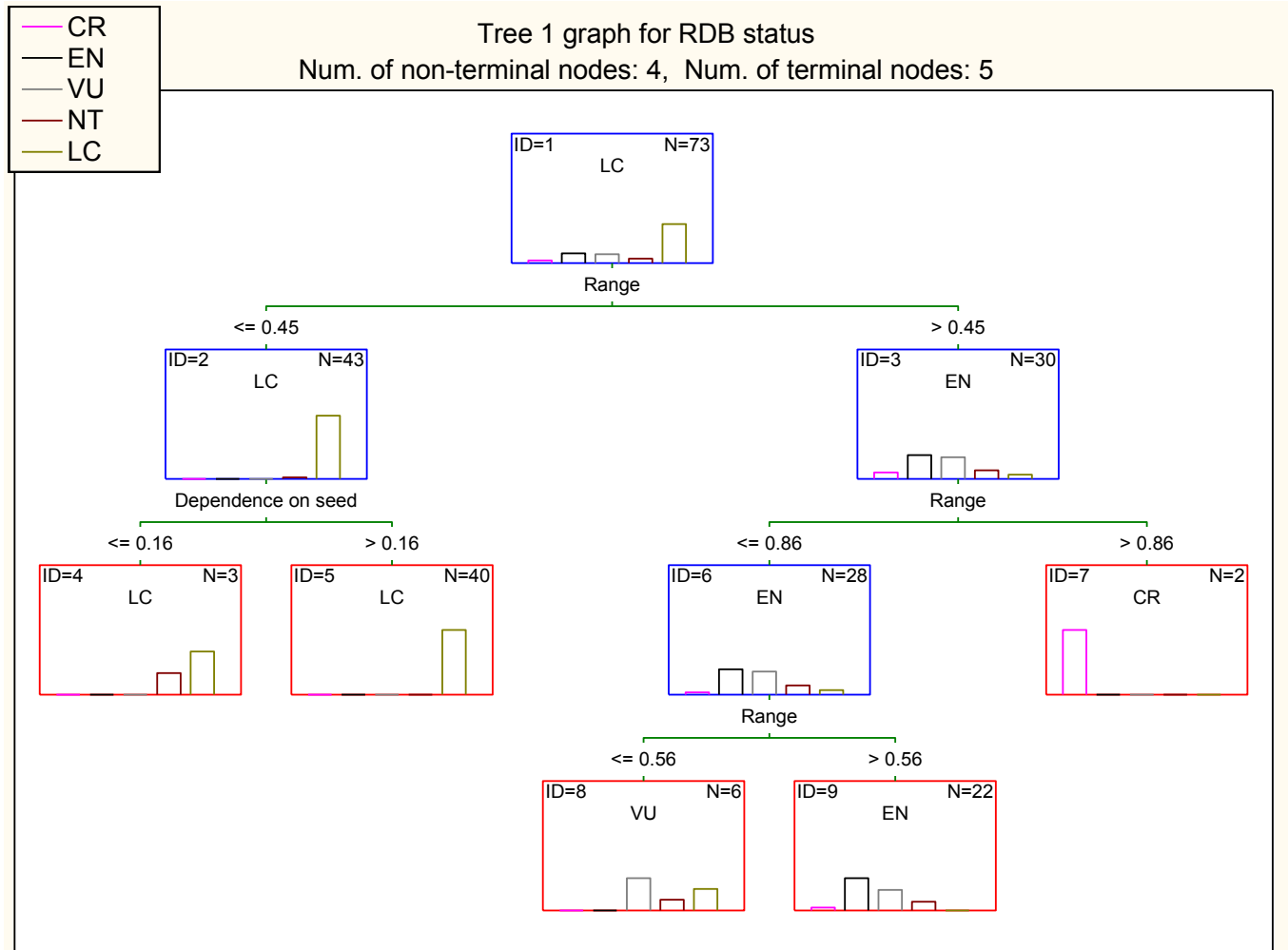


Figure 6. Classification and Regression Tree, with all indices used in the Extinction Risk Models generated above (Figs. 1-5) included as predictors. The legend refers to the Red Data categories (i.e. (CR=Critically Endangered, EN=Endangered, VU=Vulnerable, NT=Near-Threatened, LC=Least Concern). The individual bar charts indicate the number of species in each Red Data class, ID is an identifier (for each bar graph), N is number of species, and the symbol (i.e. CR, EN, V, NT, LC) the most frequent class for that position in the classification tree. For example, chart ID=7 has CR as the only class containing two species.

When Range Size Index is removed from the Tree, a different result is produced: habitat specialization becomes most important and is the determining factor in separating threatened species (i.e. *Endangered* and *Vulnerable* species) from *Least Concern* species, with the cut-off point being 0.61 and again, in separating *Endangered* from *Vulnerable* (where the cut-off is 0.72). Dependence on seed is only identified as separating some *Least Concern* species.

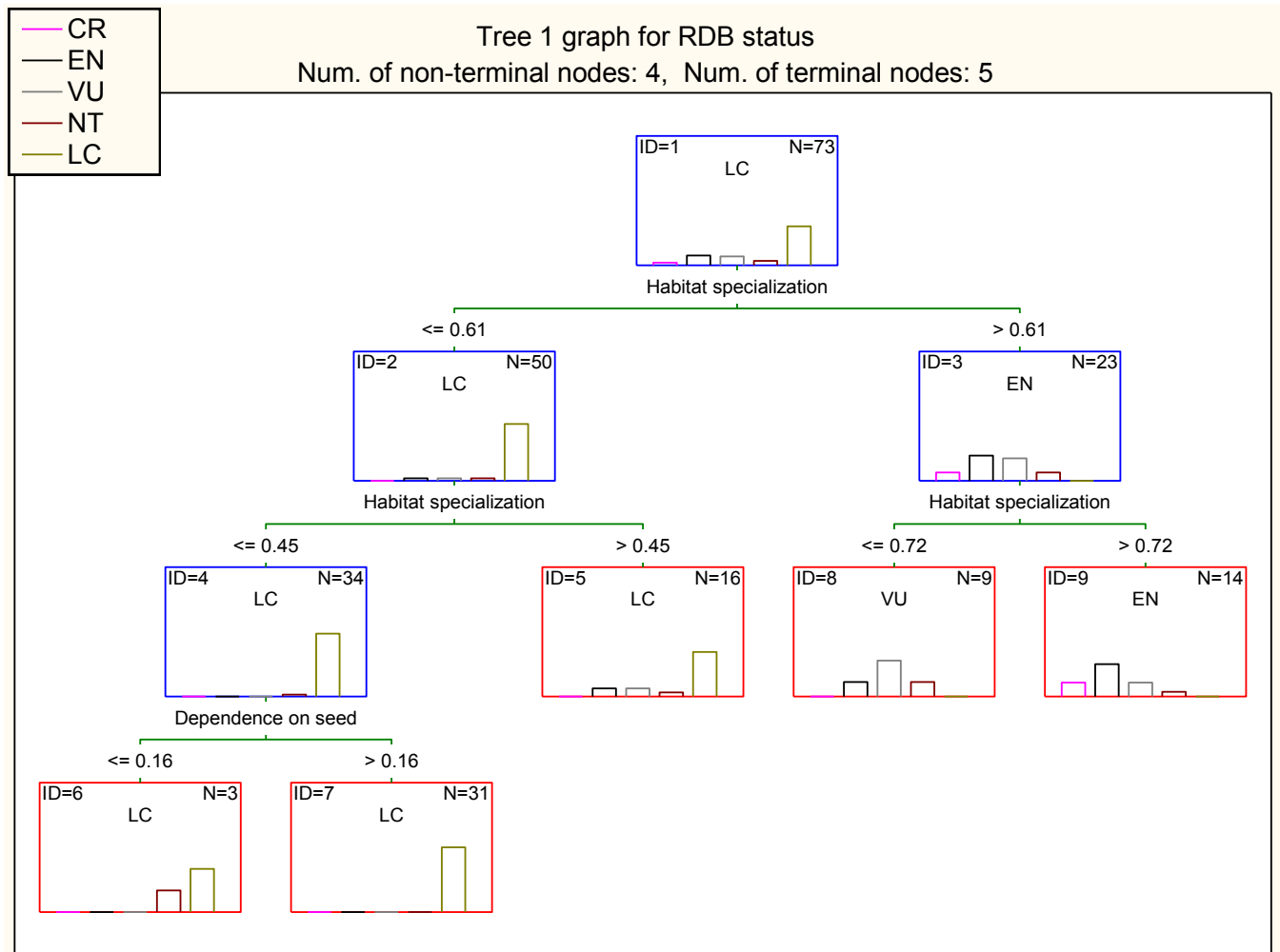


Figure 7. Classification and Regression Tree generated by excluding Range Size Index and including the following indices: Habitat Specialization, Palatability, Pollination Specialization and Seed Dependence.

CONCLUSIONS

The initial model which only took range size and habitat specialisation into account proved to be fairly accurate in predicting species' extinction risk across the entire renosterveld system, in relation to the existing Red Data status of the species used in the model. However, this model borders on circular

reasoning, due to the fact that the red-listing process incorporates similar (although not the same) variables for assessing a species status. Although subsequent models were not as accurate in predicting existing threat status of species, these may well be useful in highlighting potential indicators of localised threat (e.g. overgrazing or the loss of pollinators).

The ecological plant traits modelled in this study generally correlated poorly with species threat status, as identified in the Red Listing process (Raimondo *et al.* 2009). This is not surprising, as the Red List uses population viability data, rather than ecological traits, to assess species global threat status. At a global scale, this is appropriate. However, when one is assessing species' viability within remnants, it is clear that the generation of a different set of tools may be more appropriate, as some species may experience significant population declines at the local level as a result of process change (e.g. loss of pollinators, loss of specialised habitat, changes in fire and/or grazing regimes), irrespective of threat status. Population monitoring could therefore benefit from including some of the species identified as 'High-Medium Risk' by the models, but considered *Least Concern* by the Red List. These species may prove to be important indicators within a fragmented landscape, subject to suite of different management regimes. Honnay *et al.* (2005) caution against drawing any general conclusions regarding fragmentation and extinction risk, as the effects on population fitness are difficult to disentangle and these appear to vary across habitats and species (e.g. Bommarco *et al.* 2010, Brook *et al.* 2006, Donaldson *et al.* 2002, Purvis *et al.* 2000, Swift & Hannon 2010). This is particularly true for the heterogeneous renosterveld systems in this study, where beta and gamma diversity is high (Chapter 5, Newton & Knight 2010). Thus, using site-specific species to assess the integrity of a patch could be useful.

The Classification and Regression Trees (C&R T) provided results consistent with those from the models, but one must be mindful of the fact that in both cases, the 'validity' of variables was tested against the Red Data status of the species. Thus, although some of the variables do not appear to predict Red Data status, this should not undermine their usefulness in predicting species loss at a local level. It would be most useful to test the validity of the extinction risk models for local loss from habitat fragments by testing their predictions against the results of long term monitoring data. This would be particularly useful in areas of contrasting management (e.g. heavy vs. light grazing). Unfortunately such data is very rare in renosterveld, if it exists at all (but see Kemper *et al.* 1999 & 2000).

In terms of grazing, one could predict that palatable plants will be adapted to grazing and therefore would be more likely to be resprouters. However, there is likely to be a threshold above which highly palatable plants are no longer able to sustain prolonged or continuous grazing (e.g. Walton 2006). Today, these plants may be at risk from overgrazing, due to the fact that livestock often spend extended

periods in a small piece of renosterveld and are therefore 'forced' to forage in relatively unsuitable habitats, driving them to plant refuges, such as rocky outcrops. Another factor that should be considered when assessing a plant's vulnerability to grazing is not only the effect of being grazed or browsed, but the effect of being trampled (as is the case for many small, endemic succulents – pers. obs.).

Many studies have focused on the effects of fragment size on species extinction risk, with mixed conclusions. For example, Bommarco *et al.* (2010) found that species richness in wild bees increased with increasing patch size. Also, species composition was altered by fragmentation, but this differed due to variation in life-history traits (particularly diet niche breadth and dispersal capacity) (Bommarco *et al.* 2010). Cagnolo *et al.* (2009) showed that response to fragment size was not uniform across insects in South American dry forest fragments, nor did species body size affect responses to fragment size. However, while larger insects were unaffected by patch size, smaller species declined with decreasing patch size, apparently attributable to the limits placed on them by their smaller wing span (Cagnolo *et al.* 2009). Also, rare species were lost from fragments of decreasing size at a faster rate than common species, while food-web traits (i.e. trophic level and trophic breadth) interacted synergistically to determine species extinction rates in relation to fragmentation. Püttker *et al.* (2011) examined immigration rates for a small marsupial (Grey Slender Mouse Opossum) in relation to fragment size and overall habitat availability in Brazilian forests and showed that population densities were analogous for large and small patches. They conclude that this is due to the high overall proportion of remaining habitat and relatively short distances between fragments, which result in high levels of dispersal to smaller fragments. Thus, populations in small fragments are effectively 'rescued' from local extinction (Püttker *et al.* 2011). He and Hubbell (2011) caution against the use of species-area relationships for predicting extinction rates, as these tend to be overestimated and demonstrate that extinction resulting from habitat loss requires a much greater loss of habitat than previously predicted.

Pollinator (bees, butterflies and flies) diversity in Lowland Renosterveld in the Overberg was not adversely affected by fragment size, but individual species (particularly some Monkey Beetles) responded differently to fragment size, some showing a preference for small fragments, others preferring large ones (Donaldson *et al.* 2002). Distance to large patches, however, was important for many species, suggesting that larger patches are still critical for pollinator populations. However, vegetation cover had a significant impact on overall insect diversity, with high vegetation- and high grass-cover being associated with low species richness. Conversely, when individual species were examined, again there was discrepancy, with some favouring high vegetation cover and low grass cover

and others preferring high percentage grass cover and rockiness (Donaldson *et al.* 2002). Pauw (2007) found that the presence of an important pollinator, an oil-collecting bee, was determined by soil type and at what stage of succession the vegetation was, while it was absent from smaller fragments in an urban matrix. This finding emphasises the importance of habitat management within fragments and, as Donaldson *et al.* (2002) conclude, the difficulties associated with predicting plant species extinction risk are not insignificant.

I argue that unless habitats are particularly homogeneous, one cannot examine patch-size effects in isolation. This is especially true for an extraordinarily heterogeneous system such as renosterveld, where the occurrence of particular species is often dependent on the availability of specific microhabitats. For example, a specialist plant community comprising several quartz-specialists has recently been described in renosterveld (Curtis *et al.* 2013) and these specialists tend to occur wherever these are remnants of quartz hillocks, irrespective of patch size. Likewise, there are rare species that only occur on certain aspects, such as *Gladiolus acuminatus* (*Endangered*) which only occurs on north-facing slopes in the Napier district (Raimondo *et al.* 2009) and there are common species, such as *Printzia polifolia* which only grows on south-facing slopes (pers. obs.). In most cases, very little is known about these species life-history traits or pollination requirements.

The Black Harrier *Circus maurus*, an endemic and *Vulnerable* raptor, has shown a preference for nesting in large renosterveld fragments, although reasons for this are not entirely clear (Curtis 2005). Harriers, however, do not use all large fragments and a study comparing large patches with and without harriers revealed that patches associated with breeding harriers also had a higher abundance of both birds and small mammals (Jenkins *et al.* 2012), suggesting a sensitivity to habitat quality. Cape Spurfowl *Pternistis capensis* are associated with grassier patches of renosterveld (i.e. patches with a higher proportion of perennial grasses), irrespective of patch size (O. Curtis unpubl. data). Thus, in addition to patch size, there are other factors influencing a species capacity to make use of a habitat patch, and these may be indicative of the inherent availability of microhabitats, and /or the past and present management regimes. Clearly, life-history traits are important determinants of how species are distributed in the landscape and thus their responses to fragmentation and ultimately, their extinction risk. But these tend to act synergistically, thus predicting species loss as a direct result of habitat loss is extremely challenging.

Diamond argued that unless a species can be proven to be extant and secure, it should be considered extinct or *Endangered* (Diamond 1987). Because this approach is not always adopted, the percentage of threatened species is often underestimated by Red Data Lists (Diamond 1987). The South African Red

Data List for plants (Raimondo *et al.* 2009) has gone a long way to improve the red-listing approach by including all South African plants and separating threatened species which are well-known (i.e. status from *Near-Threatened* to *Endangered*) from those which may only be known from a single location, but for which no immediate threats have been identified (these plants are classified as *Rare* or *Critically Rare*).

Brook *et al.* (2006) draw attention to the potential disparity between the conservation interventions required for managing local risks for small populations in jeopardy at the local level versus those needed to reduce global population declines. Furthermore, the variation in minimum viable population sizes across species tends to be dwarfed by anthropogenic effects that often result in the decline of once-abundant species (Brook *et al.* 2006). A species' risk of extinction is influenced by many compounding factors – which may act synergistically to either exacerbate or reduce the risk. These compounding influences should always be considered when planning for new reserves and formally protected areas. As Bond (1995) concludes' we need to carefully consider the risks of a dysfunctional system, whereby what remains is effectively the 'living dead,' where ecological functioning has effectively been halted. Certainly, if conservation efforts do not address the importance appropriate management in order to conserve ecological *processes*, as opposed to species, these systems may be paying their extinction debts at an alarming rate.

Experimenting with these models has emphasized the importance of having access to simple biological data, which rather perturbingly, is not available for many of the species found within this highly threatened ecosystem (a similar problem was encountered by Hockey & Curtis (2009)). There are several other traits that could have been built into these models, had the data been available. These include, but are not restricted to, seed size, number of seeds produced, age at first flowering and dependence on fire. Also, these models were tested on a sample of renosterveld species and can be expanded by increasing the number of species used in the database and expanding the database to include other fynbos habitats. Imperfect vs. perfect trade-offs warrant further investigation, as do predation and dispersal capacity (Banks 1997) across various taxa within renosterveld.

It is critical that one considers not only the inevitable impacts associated with fragmentation (e.g. edge effects, possible extinction debts), but also the management effects, which have the potential to steer a system, or an individual species, either way. This is particularly true for dynamic systems which are exposed to natural and man-induced disturbance regimes such as fire and grazing. Understanding how life-history traits influence a species response to these impacts could provide some guidance as to what mitigation strategies to implement.

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CHAPTER 7: Fire and grazing in renosterveld: an experimental approach

*Thank God men cannot fly, and lay waste the sky as well as the earth.
(Henry David Thoreau)*

INTRODUCTION

The study of lowland renosterveld systems in order to inform management decisions, presents several challenges. Firstly, there is only an estimated 4-6% of the original extent of renosterveld remaining, scattered in a matrix of transformed agricultural land, across a landscape with varying climatic conditions and therefore different vegetation types and plant communities. In addition to the natural variation in renosterveld type, there are several localized microhabitats containing range-restricted, endemic species: alpha-, beta- and gamma-diversity are all high (Chapter 5). Thirdly, there is the influence of management, which makes renosterveld fragments extremely variable in terms of how similar they are to the original pre-agricultural state and how degraded they have potentially become through mismanagement. And innate characteristics of individual species, such as pollinator-dependence, seed dispersal mechanisms, recruitment strategies (e.g. resprouter vs. seeder), and how palatable the plant is to livestock, can determine the persistence of different species (Tscharntke *et al.* 2002). Often these innate characteristics influence communities and individuals, irrespective of fragmentation and other anthropogenic effects. Thus teasing these factors apart and examining them more closely is essential for understanding ecosystem processes in a system that is threatened with functional extinction. Because almost all lowland renosterveld remnants in the Overberg are found on private land, the future of renosterveld conservation lies in the hands of the private landowner. However, because of the lack of management-related information available to landowners and conservation managers, very little active management of remnants occurs (Winter *et al.* 2007).

Although the need for improving our understanding of renosterveld management requirements has been recognised for several years (e.g. Low & Jones 1995), very few experimental investigations have been undertaken. Despite a relatively good understanding of processes driving adjacent fynbos habitats (e.g. Cowling 1992, Keeley *et al.* 2012), there remains a dearth of knowledge on the primary drivers of lowland renosterveld systems (Walton 2006). Fire and grazing are two major processes that influence the structure and composition of renosterveld. Fire has been studied extensively in fynbos and fire regimes that are compatible with conservation objectives have been developed. Grazing is rare in fynbos and a

minor consideration in its management and it has been largely ignored as a management tool or a threat. In contrast, renosterveld responses to both grazing and fire are poorly known and management recommendations are poorly grounded in published experimental and/or observational studies. Renosterveld management is further confounded by mixed objectives of both conservation and livestock farming when these may not necessarily be compatible.

As regards fire management, most literature on fynbos management recommends burning fynbos at frequencies of 8-15 years or more, yet some authors (e.g. Cowling *et al.* 1986, Rebelo 1995) advocate higher burning frequencies in renosterveld, and suggest that fire intervals as frequent as every three years would be acceptable for this vegetation type. This assumption is based on the hypothesis that lowland renosterveld was originally grassland and therefore should be managed for palatable C₄ grasses (Cowling *et al.* 1986). Also, it is assumed that the apparent absence of slow-maturing species provides an indication of an adaptation to frequent burning (Boucher 1983, Forsyth & van Wilgen 2008). Forsyth & van Wilgen (2008) showed that fynbos and renosterveld habitats had been subjected to increasingly shorter fire-return intervals (37 to 18 years in renosterveld) and that more frequent fires were being experienced across a wider area on the Cape Peninsula. Although this raised concern about the long-term effects on fynbos in the region, the authors surmise that increased burning is unlikely to affect species diversity in renosterveld, based on the assumption that renosterveld can safely burn more frequently than fynbos, due to the dominance of species with relatively short maturation times. Conversely, Hoffman *et al.* (1987) found plant species richness and cover increased from one to three years post-fire in Sand Plain Lowland Fynbos, with species richness reaching a peak at five years, where it was significantly higher than in 19-year old communities.

In a study on natural fire regimes, Seydack *et al.* (2007) demonstrated that for fynbos and renosterveld habitats in the Swartberg region of the semi-arid little Karoo, fire frequencies are higher (15 – 30 years) in mid-high altitude, more mesic fynbos habitats and are much lower (30 - 55 years) in xeric lowland (renosterveld / karoo) shrublands. They also demonstrated that fire frequencies are inversely proportional to fuel load (vegetation biomass), which accumulates faster in the higher-altitude proteoid environments. Applying this principle to Overberg renosterveld (while keeping in mind that it is not as dry as the Swartberg vegetation), one would infer that much longer fire frequencies than those advocated by Cowling *et al.* (1996) and Rebelo (1995) would be appropriate for renosterveld.

Renosterveld, being a clay-based vegetation type is comparable with its northern counterpart, California chaparral, which occurs on similar substrate, does not contain serotinous seeders and has the overall appearance of a homogeneous vegetation type (Keeley 1992b, Keeley *et al.* 2012). California chaparral

which has not been burned for >50 years has been described as ‘decadent’, ‘senescent’, ‘senile’, ‘trashy’ and ‘unnatural’ (Keeley 1992b), although studies have demonstrated that productivity in this system is unaffected by time-since-burn (Keeley 1992a, Keeley 1992b). Like its northern counterpart, ‘old’ renosterveld (>20 years) is referred to by many early explorers and current-day landowners in a derogatory manner (pers. obs.) and is commonly referred to as ‘uitvalgrond’ (essentially translated as ‘wasteland’) by farmers (pers. comm. Overberg landowners). Fire is an integral part of the ecology of most Mediterranean shrublands, yet little is known about the effects of keeping fire out of these systems (but see Bond *et al.* 2005), although Keeley (1992b) found no evidence for a decline in species diversity and very little change in productivity in old chaparral vegetation and concluded that successional replacement of this habitat due to lack of fire was not a threat—contrary to what had previously been hypothesized. On the other end of the scale, Zedler *et al.* (1983) found that very short fire intervals (one year) in chaparral had significant negative impacts on the vegetation, with even the most common resprouting shrubs being dramatically reduced. A common pattern in all fire-prone shrublands is that species diversity decreases with increasing veld age as a result of decreasing understory cover due to increasing over-storey of tall shrubs and restioids (Bond and van Wilgen 1996; and e.g. for fynbos, Campbell & van der Meulen 1980). The effects of repeated burns at different fire frequencies in fynbos was studied by Schwilk *et al.* (1997). They showed that although higher species richness in fynbos was associated with higher fire frequencies at most scales, older fynbos had higher levels of heterogeneity than younger veld. They conclude that frequent burning may reduce heterogeneity in fire-prone fynbos habitats and therefore reduce species richness at the community level. On the other hand, fynbos can become invaded by forest or thicket in the absence of fire, resulting in a total change in the vegetation community over time (Cowling *et al.* 1997, Manders & Richardson 1992). Masson & Moll (1987) show that over fifty years of fire-protection in a fynbos-forest reserve resulted in the forest doubling in size. Renosterveld often contains thicket elements (e.g. *Buddleja saligna*, *Chrysanthemoides monilifera*, *Olea capensis*, *Acacia karroo* – pers. obs. O. Curtis, Mucina & Rutherford 2006) and observations have suggested that, particularly on cooler, south-facing slopes, in the absence of fire, thicket can become dominant (such as witnessed at Tygerberg Nature Reserve, outside Cape Town – pers. comm., Pat Holmes).

Due to the severely transformed and fragmented state of current-day renosterveld, grazing impacts are very different from what they would have been 300 years ago (Cowling *et al.* 1986, Newton & Knight 2004). While herds of ungulates would have roamed large areas and foraged in a nomadic way, livestock tend to aggregate in particular favoured spots and forage on favoured species, which can lead to over-trampling (resulting from heavy hoof action, which damages the soil crust, affecting water retention,

causing erosion, etc.) and over-exploitation of palatable species which puts these species at a competitive disadvantage, reducing their productivity and leading to an increase in unpalatable ('unwanted') species and a reduction in overall diversity. Results from work done in comparable winter-rainfall habitats in the Karoo and Bokkeveld revealed that high stocking rates and overgrazing can have a significant negative impact on the vegetation (Cupido 2005, Kraaij & Milton 2006, Todd & Hoffman 2009). Contrary to most predictions, there was no consistent response by the different growth forms to grazing pressure, despite predictions by, for example, Milton *et al.* (1994) for dry rangelands such as South African Karoo habitats that the proportion of shrubs relative to grasses will increase with increased grazing. The authors conclude that grazing impacts are seldom manifested through grazing alone, but that it is the interactions between climate, fire and grazing that determine the impacts on the vegetation. Because the significance of most responses varied with changes in humidity and the duration of grazing history, predictions and response 'rules' for different plant functional types need to be area-specific in order to be applicable.

Livestock grazing in the Overberg area varies substantially as it tends to be opportunistic because farmers rely on artificial pastures through much of the year and make use of 'opslag' (weed) forage on stubble lands in summer. Farms vary in size and stocking rate with some farmers focusing more on grain crops and others on livestock (sheep and /or cattle). Most combine cropping and livestock in order to maximise profit and use of the land. On average, a landowner may run 500 sheep or 200 cattle on about 200 ha, rotating them between varying amounts of artificial pasture and grain fields in different years. 'Large' patches (>80 ha) are sometimes treated as separate grazing camps (i.e. they are fenced off from productive lands), which enables the landowner to manage livestock access to the patch. However, these 'veld camps' are often grazed at an inappropriate time of year (i.e. winter and spring, when the bulbs are emerging and flowering and before the palatable grasses have set seed). Smaller patches are not managed as separate entities but are included as part of agricultural camps. When livestock are put into, a camp of lucerne or wheat stubble, for example, which is camped in with a patch of renosterveld, the sheep and cattle have constant access to the veld. Thus, these patches are subject to whatever management is applied to the camp – including burning and grazing, as well as drift from herbicide and pesticide application.

In addition to understanding what we need to manage *towards* (Chapter 3), it is necessary to examine the management tools available and how best to apply these in a way that is practical and beneficial for farming practices, as well as biodiversity. In the absence of data specific to renosterveld in the Overberg, the following assumptions, based on related fynbos habitats and work in the Karoo (e.g. Milton & Todd 2007), are made:

1. Grazing over winter and spring months should be avoided – i.e. preferably only graze with livestock between late November and late March. This is because during winter and spring the vegetation is at its flowering and growth peak so that production is likely to be impacted negatively if animals are foraging on flowering and seeding plants.
2. Controlled burns should be carried out during late summer / early autumn months (Feb-March/April). This also makes ecological sense, as this is the driest time of the year, when fuel loads will be high and lightning-ignited fires would have spread with ease historically.
3. Veld should not be grazed directly after a fire and should preferably be rested for a minimum of 18 months to two years post-burning. This strategy allows for reseederers to set seed (as long as they do it within the first year), for important (palatable) grasses and shrubs to resprout and set seed and for fire-stimulated flowerers to flower at least once. Of course, before renosterveld was so severely fragmented, it was grazed by large free-roaming herbivores and these animals would have moved onto the burned areas to forage on sprouting forbs and grasses. However, because renosterveld is fragmented and fires are restricted to small areas, sedentary livestock are likely to have higher impacts on the veld.

These strategies are believed to favour palatable grasses and geophytes (which generally emerge and flower in winter and spring), while reducing 'less-favourable' asteraceous shrubs. However, no experimental work has taken place in this region to test these guidelines or the consequences for overall biodiversity of using them.

In this study, I attempt to address some of the important fire- and grazing-related questions in renosterveld, through an experimental approach. In order to address these management issues, the following key questions are addressed in this chapter:

1. Is managing renosterveld for agricultural benefit (i.e. for *Themeda triandra* and other palatable species) compatible with managing for conservation objectives (i.e. overall biodiversity), as Cowling *et al.* (1986) suggest?
2. What is the appropriate fire regime for Overberg renosterveld, defined as fire return interval (frequency), season and intensity? In this study, minimum return interval could be assessed based on the youth period of the slowest-maturing shrub, *Elytropappus*. In proteas, the youth period can be as long as 5 to 7+ years (Bond & van Wilgen 1996), thus a burn before the plants have flowered will eliminate proteas from a stand, so that they will then only be able to recolonize the stand from surviving populations. Cowling *et al.* (1986) noted that it took renosterbos three years to flower following a burn. Since these authors advocate management which focuses on eliminating or

substantially reducing renosterbos in favour of palatable C₄ grasses, they suggest a management system with fire intervals of less than three years in order to prevent renosterbos from establishing and outcompeting more favourable species (Rebello 1995, Cowling *et al.* 1986). In the present study, I explore the role of *Elytropappus* in renosterveld and whether or not these assumptions are valid.

3. Does grazing impact post-burn recovery as measured by changes in species composition, species richness or cover, as well as relative size and productivity of plants favoured by livestock grazers? Does fire promote or inhibit the main grazing grasses and does resting influence their recovery rate?
4. How does the canopy cover of Renosterbos and other unpalatable, dominant species (such as other asteraceous shrubs) and C₃ tussock grasses (i.e. *Merxmeullera* or *Pentaschistis*) influence the abundance of geophytes, forbs and annuals? For example, burning could promote grasses by temporarily removing taller shrubs which may otherwise shade out shade-intolerant species. Alternatively, dense shrubby cover may also suppress growth forms such as geophytes, succulents and annual and perennial forbs. Or, there may be more complicated interactions at play: for example, Vlok and Yeaton (1999) showed that higher pre-fire densities and cover of overstorey proteas result in increased alpha diversity of understorey species and that this pattern held true for all growth forms. Thus, they argue, proteas play an important role in reducing competitive understorey resprouting plants (such as graminoids), thereby enabling a greater diversity of species richness to occupy the understorey. Subsequently, the authors (Vlok & Yeaton 2000b) found evidence for competitive interactions between the overstorey seeders and the understorey sprouters: vegetative growth and seed production of understorey species was reduced under a protea canopy, while fecundity of overstorey proteas was compromised where plants grew near understorey sprouters as opposed to open habitats.
5. Are there any relationships between growth forms and particular species which can serve as indicators for the need for important management intervention? Evidence for strong correlations can infer the need for specific management actions, such as reducing shrub cover by burning or trampling to promote suppressed species. Additionally, it may be possible to identify suitable indicators of veld condition which can guide management actions.
6. What are the 'ideal' management strategies that need to be applied to renosterveld in the Overberg in order to have maximum potential for 1) conservation, 2) agriculture, and 3) both these objectives simultaneously? What are the trade-offs in managing for both conservation and agriculture and how can a 'compromise' be reached?

STUDY AREA AND METHODS

The renosterveld of the Overberg comprises four distinct types: Western, Central and Eastern- Rûens Shale Renosterveld and Rûens Silcrete Renosterveld (Mucina & Rutherford 2006). In this study, I focus on the first three, which are broadly described as being moderately undulating plains, with open to medium, dense, cuppresoid and small-leaved, low to moderately tall grassy shrubland, usually dominated by renosterbos (Mucina & Rutherford 2006). These habitats have soils which are clay-rich, shale derived and relatively fertile when compared with their fynbos counterparts which occur on poorer, sandier soils. Mean annual rainfall is higher in the Western Rûens Shale Renosterveld than the Central and Eastern types (490 mm for the former and about 380 for the two latter) (Mucina & Rutherford 2006), resulting in grassier habitats in the west and a higher succulent component in the east.

Experimental plots

Six sites were selected as locations for the experimental plots. These sites were chosen opportunistically, as I had to use areas where the landowners had committed to burning their renosterveld in autumn 2008. This meant that the six sites were spread across a wide range of lowland renosterveld habitats from Napier/Riviersondered to Bredasdorp to Swellendam/Heidelberg. Thus, there is a notable variation in veld type (Fig. 1). The most westerly sites, on Fairfield and Fonteinskloof farms, are found in Western Rûens and Central Rûens Shale Renosterveld respectively. The two sites at Nysty farm are located in the driest region of the Eastern Rûens Shale Renosterveld, where recent studies have demonstrated high levels of endemism on quartz outcrops within this habitat (Curtis *et al.* 2013). The two most eastern sites, Voorstekop and van Rheenen's Crest, are located in a transitional habitat of Eastern Rûens Shale Renosterveld and Swellendam Silcrete Fynbos (a lowland fynbos type often dominated by *Themeda triandra* – Raitt (2005)). Because site selection was opportunistic, grazing pressure differed substantially between sites, with heaviest grazing at Nysty1, Voorstekop and van Rheenen's Crest, moderate grazing at Fonteinskloof and light and almost no grazing at Fairfield and Nysty2 respectively. Grazing was continuous with very few rest periods at van Rheenen's Crest, while at Nysty1, Fonteinskloof and Voorstekop, animals tended to be on the veld for relatively short (a few weeks), intense periods (about 100 sheep or cattle at a time) at different times of the year. Grazing at Fairfield was infrequent and restricted to summer months. In 2007, a suite of 10X10m plots was set up at each site in the following way: two plots on a 'burn' site (to be burned in 2008), two plots in an 'unburned' site (to remain a control plot) (Fig. 2 & 3). Each pair was divided into a 'grazed' (open control) and 'ungrazed' (fenced enclosure) plot (Fig. 4 & 5). This design was replicated on a north- and a south-facing slope, making a total of eight plots per site (i.e. a total of 48

plots). The renosterveld fragments used for these experiments varied in size from about 60 ha to 200 ha, while the extent of the burns varied from 1 ha (1 site only) to between ± 20 - 60 ha.

Data were collected by recording all species and their relative cover within a 1x1m quadrat, placed at 6 permanently marked positions in each 10X10m plot. Plants were identified to species level where possible. Plant cover for each species was categorized in the following way: 1= $<5\%$, 2=5-10%, 3=10-25%, 4=25-50%, 5= $>50\%$. Once the six quadrats were completed, I searched the remainder of the plot for any missed species and assigned these a cover value, relative to the whole plot.

The first data were collected from the plots in spring (August / September) 2007, prior to the experimental burns, which were carried out in autumn (March/April) 2008. Post-burn data were collected each spring for four seasons: from 2008-2011. Because all the fires were burnt in the same year and season, the community composition data is not complicated by comparing different stages of post-burn succession.

In this study, minimum return interval could be assessed based on the youth period of the slowest maturing shrub (renosterbos). Data from pre-burn plots (which were all at least 20 years old) were used to compare species richness for 'old' vegetation and that of newly-burned and progressively aging (over 4 years) vegetation.

Guo (2001) found that nitrogen-fixing species increased steadily after fire and that although species-richness of nitrogen-fixers was similar on north- and south-facing slopes, biomass was significantly higher on north-facing aspects. In order to test for comparable relationships, I investigated the change in nitrogen-fixing *Aspalathus* species over time-since-burn and compared changes in *Aspaalthus* cover with species-richness.

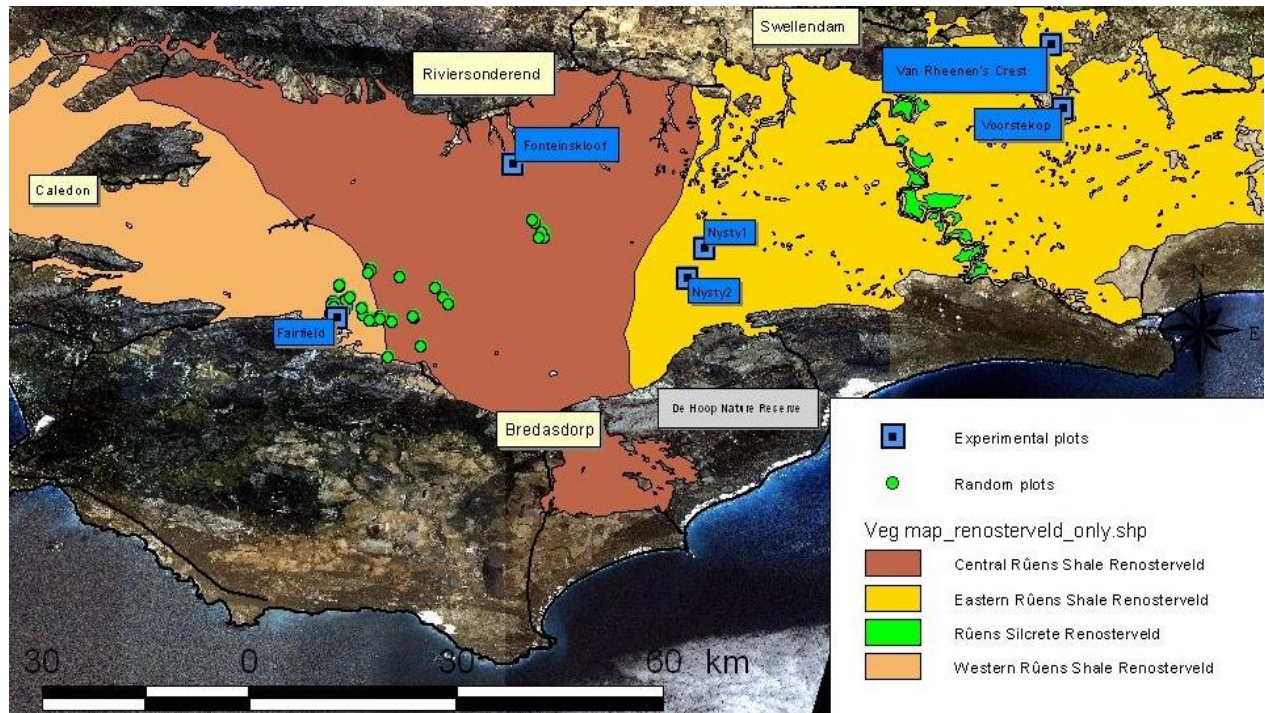
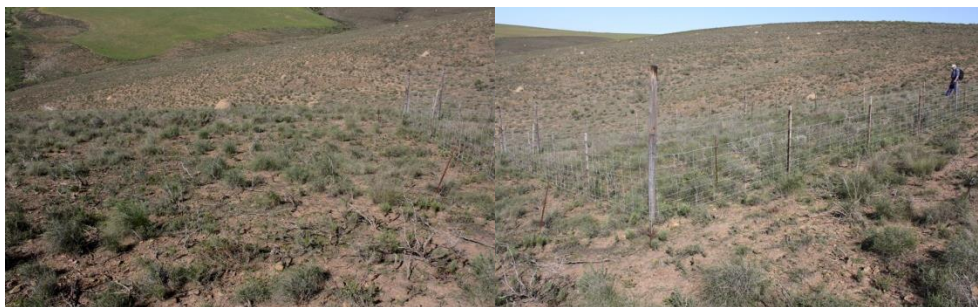


Figure 1. Map denoting study sites for both the experimental plots and the random (Napier 2010) surveys, in relation to the different renosterveld types.



Figures 2 & 3: (left): enclosure plot at Fairfield, Napier; (right): burn at Fonteinskloof, Riviersonderend



Figures 4 & 5: Grazed (left) and enclosure (right) plots at the Riviersonderend site (Fonteinskloof).

Random plots (Napier)

To extend the results of the burning / grazing experimental plots, I added a set of random surveys to the study in order to explore correlations between species and growth forms as a preliminary indication of species and guild interactions. In order to minimize the effect of variation in veld type, this study (which took place in 2010) was restricted to the Napier-Riviersonderend area (within a radius of about 16 km – see Fig. 1). Landowners were interviewed in order to identify fragments for which the approximate time-since-last-burn was known. Thus, a total of 47 sites were selected in 30 fragments. These comprised 22 south-facing sites and 25 north-facing sites. A random temporary 10X10 m plot was set up on each site and all species within the plot were recorded and assigned a cover value (percentage cover). Physical variables recorded at each plot included: grazing index (1-3: 1=lightly grazed or not grazed, 2=moderately grazed, 3=heavily grazed), overall percentage cover, estimated veld age (i.e. time since last burn), average vegetation height and patch size (calculated from GIS maps). Analyses comprised ordinations and Spearman Rank Correlations.

In order to determine whether certain species influence, or are associated with, overall species richness, as well as the abundance of other growth forms, I generated correlation matrices for all growth forms and physical variables, as well as 1) dominant species and 2) dominant perennial grasses for the two aspects.

Statistical analyses

Experimental plot data were subjected to ordinations in order to test for general trends and assess how data were clustered. Plants were identified to at least genus level and to species level, where possible. Several grasses were not identifiable at the time of the study and were thus given a temporary name, which was used consistently throughout the study. Thus, analyses relating to grass abundance focus on the most common species, as the unidentifiable species were scattered and not common on any site. Growth forms were divided into annuals, annual grasses, asteraceous shrubs, other woody shrubs (excluding Asteraceae), forbs, perennial grasses, geophytes, restios / sedges and succulents. I applied ANOVA (Kruskal-Wallis), Kolmogorov-Smirnov, and Spearman Rank tests in STATISTICA (version 11) to test for relationships between species richness and cover in the various growth forms, as well as between growth forms and habitat variables. In order to test for temporal changes in community structure, ordinations of species composition at different sampling times were produced using Bray-Curtis similarity indices. The data were then subjected to ordination by non-metric multidimensional scaling (NMDS) using the Bray-Curtis distance coefficient (Bray & Curtis 1957). The NMDS ordination was produced using multiple runs and following the stress and stability criteria described in detail by McCune & Grace (2002).

Community composition change was analysed by generating Bray-Curtis similarity matrices for each treatment year (i.e. 2007-2008, 2008-2009, 2009-2010 and 2010-2011).

Due to the size of the correlation matrices generated, there were many 'false' results, with low R-values. Therefore, a Bonferroni adjustment was made to the α -values, thus ensuring the results were robust. However, as the Bonferroni correction may also result in the loss of information on less significant, but important trends (Zar 1999), I examined those results that were highlighted before Bonferroni adjustment and tested the relationships graphically.

RESULTS

Experimental plots

Composition analysis

An NMDS ordination with two axes was sufficient to explain the majority of the variance in the data set. The stress of the final 2-D solution was 10.21 and the instability 10^{-5} , indicating acceptable levels of stress and stability (McCune & Grace 2002). The cumulative R^2 of the correlation between distance in the ordination space and distance and the original n -dimensional space was 0.989 for the two axes of the ordination. The first axis accounted for 0.6 and the second 0.389 of the cumulative R^2 .

The results of an ordination of the plots across the different sites are illustrated in Figures 6 and 7. The plots are clustered within sites and the sites are clearly differentiated from one another, indicating that the vegetation composition at each site is unique and that no two sites have highly similar vegetation composition. Furthermore, even after fire, this differentiation remained. An independent ordination of each site was also produced (Appendix 7.1). In general, the results were similar for north and south aspect plots. Several pertinent patterns emerge from this analysis. Firstly, burnt plots showed a large amount of change relative to unburned plots. However, unburned plots showed a directional change in composition over time indicating that vegetation composition was not stable, and that shifts from year to year were not random as might be expected if such change was driven by rainfall variability alone. The directional shift in composition is most likely indicative of a post-fire successional development of the vegetation and indicates that vegetation shifts persist for a long time after fires and that a stable vegetation composition is not likely to occur within short to medium time frames (10-30 years). In burned plots, shifts in composition were progressively less in each year post fire. This is also as expected since change is rapid in the immediate post fire period and slows down over time as perennial vegetation cover increases again.

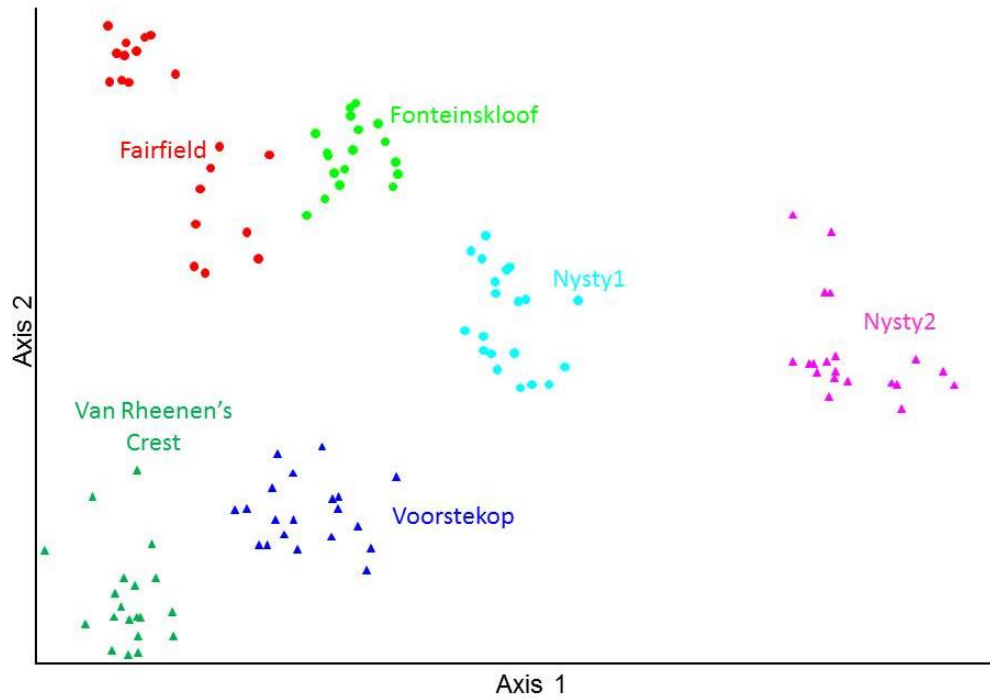


Figure 6. NMS ordination of the various treatments involved in the fire and grazing experiment on north aspect plots. The six sites are clearly differentiated from one another.

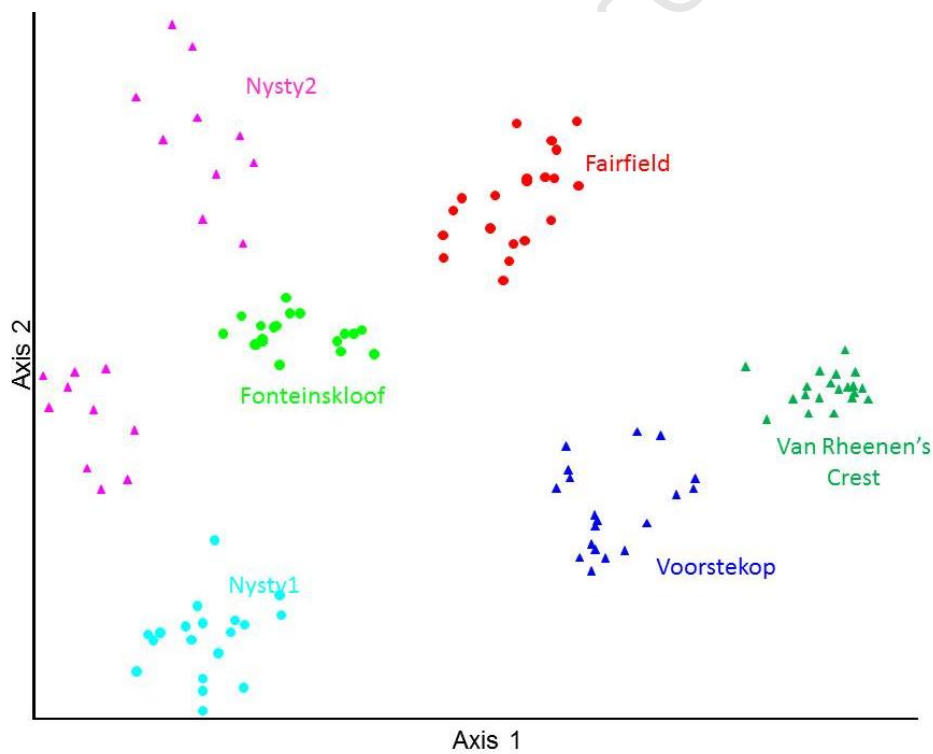


Figure 7. NMS ordination of the various treatments involved in the fire and grazing experiment on south aspect plots. The six sites are clearly differentiated from one another.

One would have expected a grazing effect to manifest as an impact on either the direction or extent of change in the grazed plots as compared to the enclosure plots over time. However there appear to be no consistent differences in either the magnitude or direction of change between years between grazed and ungrazed plots. Overall, the results indicate that the primary driver of vegetation composition in the post-fire environment was the impact of the fire itself, while grazing had only a secondary and subordinate effect. However, this conclusion is contingent on the range of grazing intensities experienced in the study area and more severe grazing could clearly produce a different outcome.

Growth form analysis and species richness

The degree of influence of burning, vs. grazing vs. year-effects on the different growth forms were compared using ANOVA (Kruskal-Wallis) analyses and results of the *P*-values are tabulated in Table 1. Species richness and cover changes were most influenced by burning, followed by census year. There were no significant differences between grazed and ungrazed plots. Species richness of annual, forb, perennial grass and restio/sedge growth forms were all affected significantly by burning on both north and south-facing slopes (Table 1, Fig. 8, Fig. 9). Species richness of asteraceous shrubs decreased after burning on south-facing slopes, while cover of Asteraceae was significantly reduced on both slopes. Diversity and cover of other shrubs (i.e. all shrubs excluding Asteraceae) were not as impacted by fire or year as the Asteraceae. Both species richness and cover of geophytes were only affected on south slopes with total species richness strongly increasing after burning on south slopes, but not on north-facing aspects (Table 1, Fig. 8, Fig. 9).

Table 1. Results of an ANOVA showing P-values after testing for differences between species richness (SR) and vegetation cover in different growth forms (Kruskal-Wallis ANOVA), over grazed treatments (grazed vs. ungrazed), burn treatments (burned vs. unburned) and years (2007-2011). Significant results are highlighted.

Variable	Growth form	South-facing slopes			North-facing slopes		
		Effect			Effect		
		Burn	Graze	Year	Burn	Graze	Year
SR	Annual	0.004	0.311	0.002	0.005	0.941	0.005
	Annual grass	0.180	0.324	0.000	0.693	0.202	0.062
	Forb	0.000	0.226	0.087	0.002	0.800	0.019
	Geophyte	0.003	0.078	0.090	0.358	0.809	0.993
	Perennial grass	0.002	0.605	0.123	0.012	0.925	0.740
	Restio / sedge	0.006	0.749	0.012	0.010	0.599	0.141
	Asteraceous shrub	0.000	0.932	0.087	0.061	0.461	0.163
	Other shrub (excluding Asteraceae)	0.100	0.201	0.545	0.010	0.725	0.063
	All shrub	0.577	0.361	0.351	0.074	0.668	0.040
	Succulent	0.880	0.538	0.648	0.373	0.955	0.924
	Total SR	0.002	0.087	0.119	0.380	0.671	0.192
Cover	Annual	0.015	0.465	0.002	0.000	0.929	0.038
	Annual grass	0.656	0.793	0.000	0.802	0.314	0.056
	Forb	0.000	0.234	0.085	0.002	0.381	0.164
	Geophyte	0.006	0.321	0.226	0.303	0.927	0.675
	Perennial grass	0.801	0.467	0.161	0.050	0.165	0.154
	Restio / sedge	0.001	0.660	0.050	0.000	0.720	0.211
	Asteraceous shrub	0.000	0.361	0.001	0.000	0.233	0.011
	Other shrub (excluding Asteraceae)	0.702	0.361	0.042	0.039	0.539	0.091
	All shrub	0.000	0.293	0.001	0.032	0.519	0.001
	Succulent	0.023	0.912	0.177	0.377	0.564	0.939
	Total cover	0.513	0.264	0.000	0.740	0.500	0.000
	Total cover of 6 dominant spp.	0.001	0.598	0.137	0.003	0.921	0.248

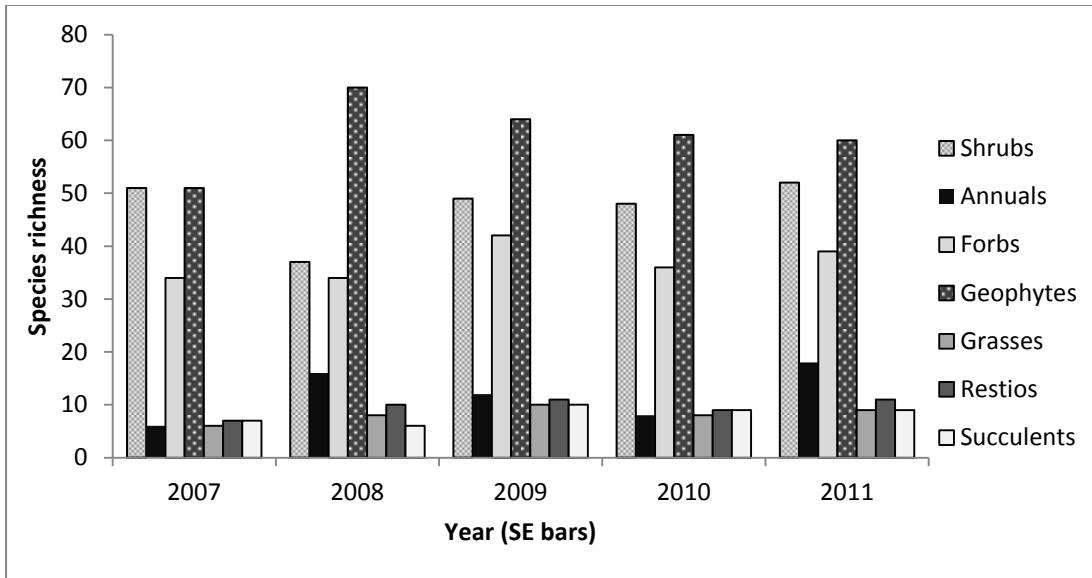


Figure 8. Total species richness of different growth forms on south-facing slopes from 2007 (pre-burn), over four post-burn years, from data collected from experimental plots in the Overberg.

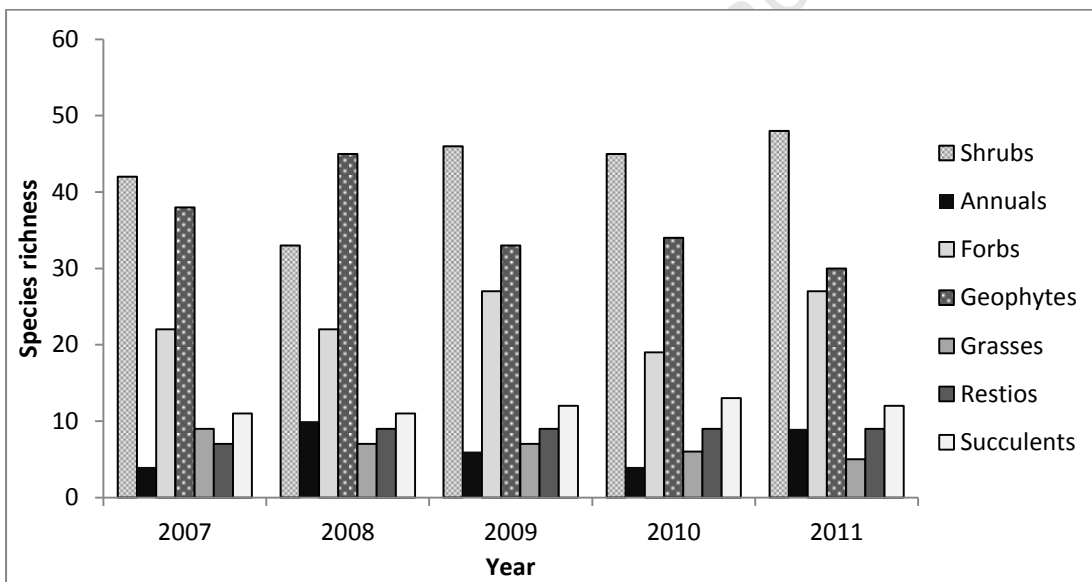


Figure 9. Total species richness of different growth forms on north-facing slopes from 2007 (pre-burn), over four post-burn years, from data collected from experimental plots in the Overberg.

Contrary to what was expected, although total overall species richness varied with fire treatment for south slopes, a correlation of species richness with year since fire showed no significant relationships between time-since burn and species richness on either south- ($R=0.62$, $T(N-2)=1.35$, $n=5$, $P=0.269$), or north-facing slopes ($R=0.38$, $t(N-2)=0.56$, $n=5$, $P=0.614$) (Fig. 10). This is probably due to the variation in

responses to burning by the different growth forms, with some growth forms increasing either immediately post-burn (annuals and geophytes), or gradually (forbs) in response to burning and others declining (woody shrubs) and then gradually increasing two-three years post-burning (Figures 8 & 9).

Thus, as demonstrated by results from the ANOVA in Table 1, although the species richness of certain growth forms was significantly affected on both aspects, overall species richness was only significantly affected on south-facing slopes (Fig. 10). Both experienced a drop in species richness in 2010, for unknown reasons.

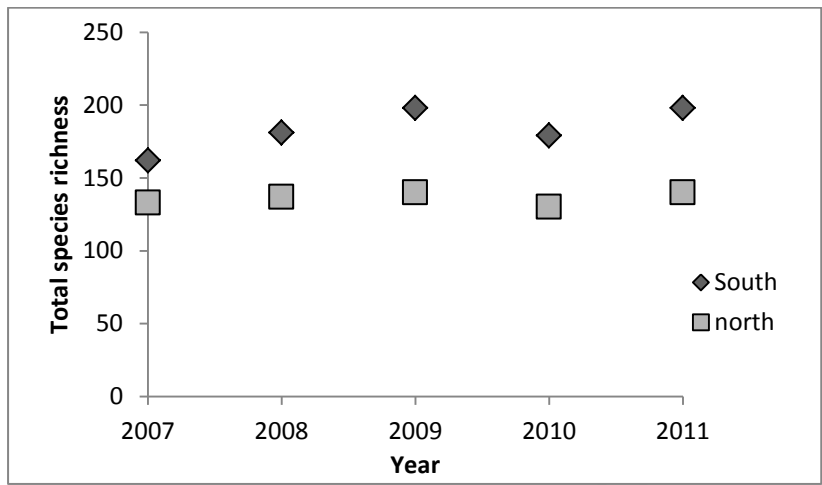


Figure 10. Graph denoting the change in species richness over time, from 2007 (pre-burn), over four post-burn years, from data collected from experimental plots in the Overberg on south-facing (Kruskal-Wallis H (4, N=60)=9.4, P=0.052) and north-facing slopes (Kruskal-Wallis H (4, N=60)=4.17, P=0.38).

It is interesting to note the yearly fluctuation in cover of annual plants in the unburned plots on both aspects (Fig. 11, Fig. 12) suggesting a rainfall or temperature effect. This is overridden by the effects of fire in the burned plots.

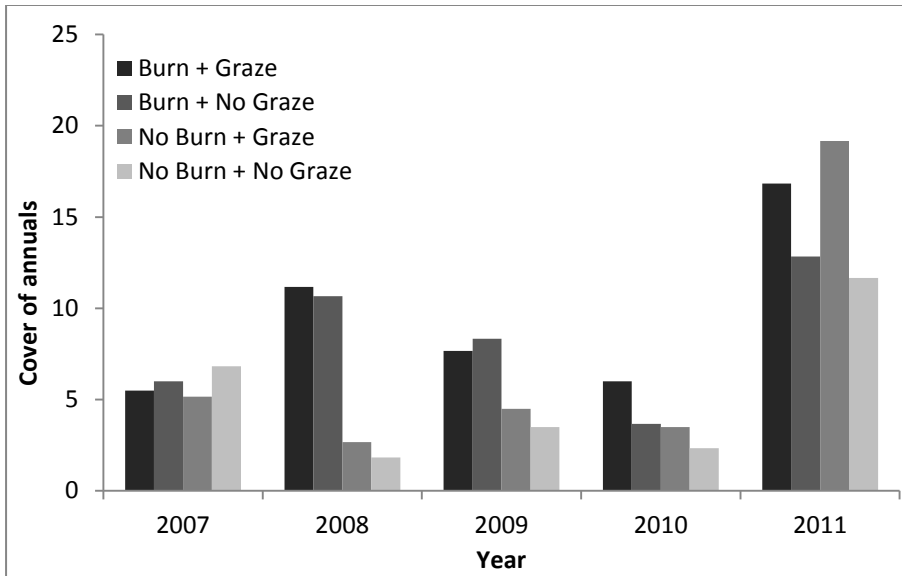


Figure 11. Variation in cover of annual plants on south aspects, in relation to different treatments from 2007-2011, averaged from six sites across the Overberg (4 treatment plots per site).

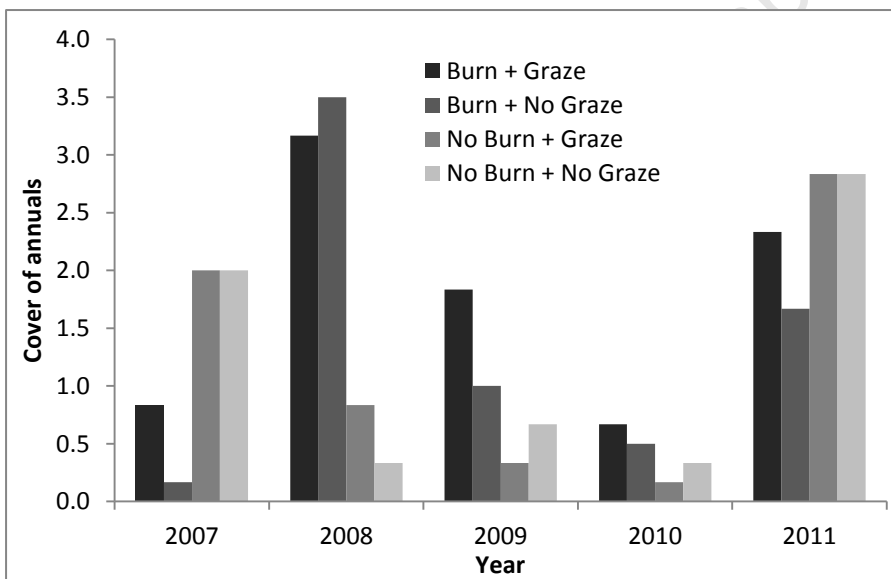


Figure 12. Variation in cover of annual plants on north aspects, in relation to different treatments from 2007-2011, averaged from six sites across the Overberg (4 treatment plots per site).

Comparisons between the six study sites

As indicated by the ordinations, each study site was unique from the other, thus one would expect some community-level differences between the sites which may be useful for extrapolating into management recommendations for the respective vegetation types. In order to examine species diversity change over

time-since-burn, I analysed only data from burned plots. There was no significant difference between species richness in control and exclosure plots (Kolmogorov-Smirnov Two-sample Test, Mean Control=45.68, Mean Exclosure=46.88, $P > 0.1$) so data from these were pooled. However, species diversity was significantly higher on south-facing slopes (Kolmogorov-Smirnov Two-sample Test, Mean South=53.82, Mean North=38.75, $P < 0.001$) thus data were analysed separately by aspect. On south-facing slopes, species richness varied significantly across sites (Kruskal-Wallis H (5, N=60)=37.82, $P=0.000$), while an equally strong variation was detected for north-facing slopes (Kruskal-Wallis H (5, N=60)=45.44, $P=0.000$) (see Fig. 13 for an illustration of the relationship between species richness and study site for north- and south-facing slopes combined).

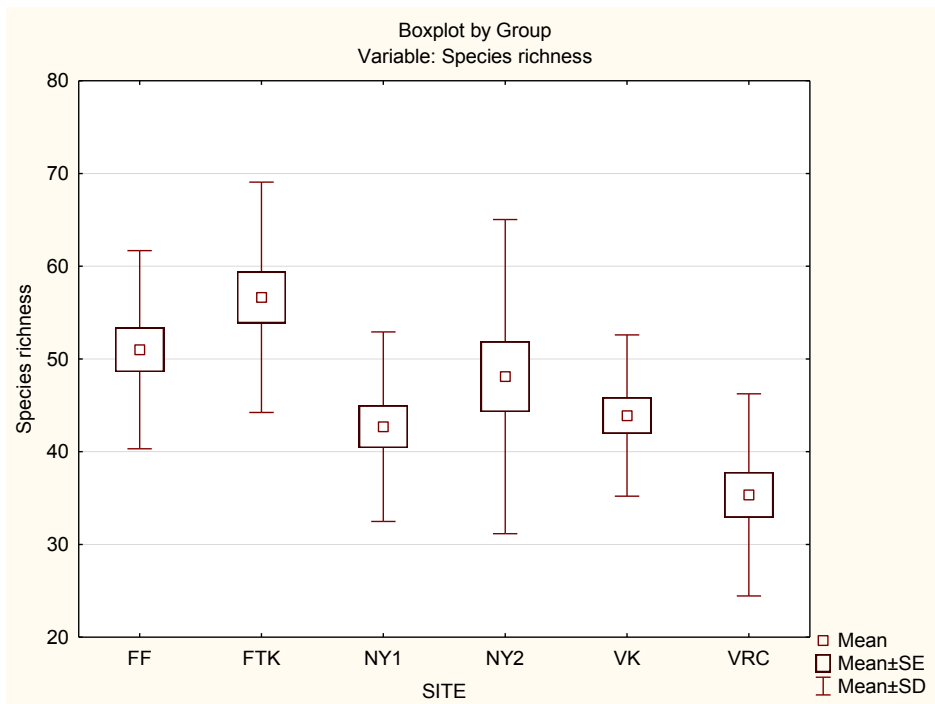


Figure 13. Box and Whisker plot comparing species richness (on north- and south-facing slopes combined) across the six sites in the Overberg where permanent plots are located, using data from all plots and treatments (i.e. 8 plots per site).

Community change in relation to fire and grazing

Changes in community structure were generally highest after the first year of burning (i.e. between 2007 and 2008). On south slopes, community change was on average much higher than on north slopes, with the greatest amount of change taking place in geophytes (7-13%) (Fig. 14), followed by shrubs (5-12%),

asteraceous shrubs (3-9%) and grasses (3-8%). Community change in annuals, forbs, restios and succulents never exceeded 5%.

On north slopes, annuals displayed the greatest levels of community change (25-46% - see Fig. 15) with a gradual decline in change over the study period, followed by asteraceous shrubs (4-13%), other shrubs (5-10%) and geophytes (5-10%), forbs (3-6%) and grasses (2-4%). Percentage change for restios and succulents never exceeded 3%. Similarly, Guo (2001) found that annuals displayed the highest temporal levels of species turnover on both north- and south-facing slopes in California chaparral.

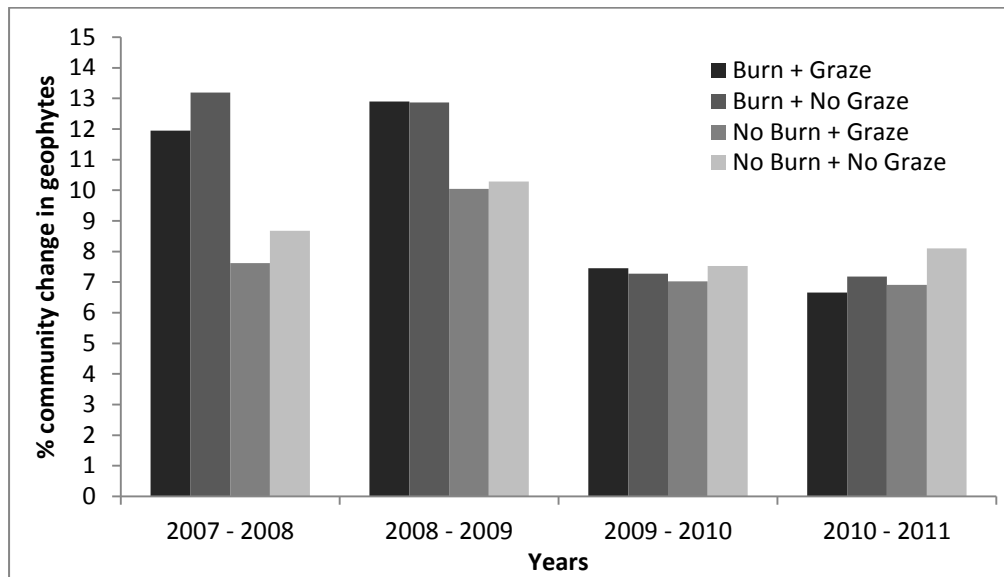


Figure 14. Percentage community change for geophytes on south slopes for different treatments over the study period averaged from six sites across the Overberg (4 treatment plots per site).

Community change over years for paired sites (i.e. burned enclosure and controls and unburned enclosures and controls) was determined using Bray-Curtis analyses (Appendix 7.2). These data were summarised in order to detect overall patterns of change. For north-facing plots (Fig. 16), the temporal trend in all four treatments is similar, with unburned plots showing less overall change, but proportionally similar changes over the study period.

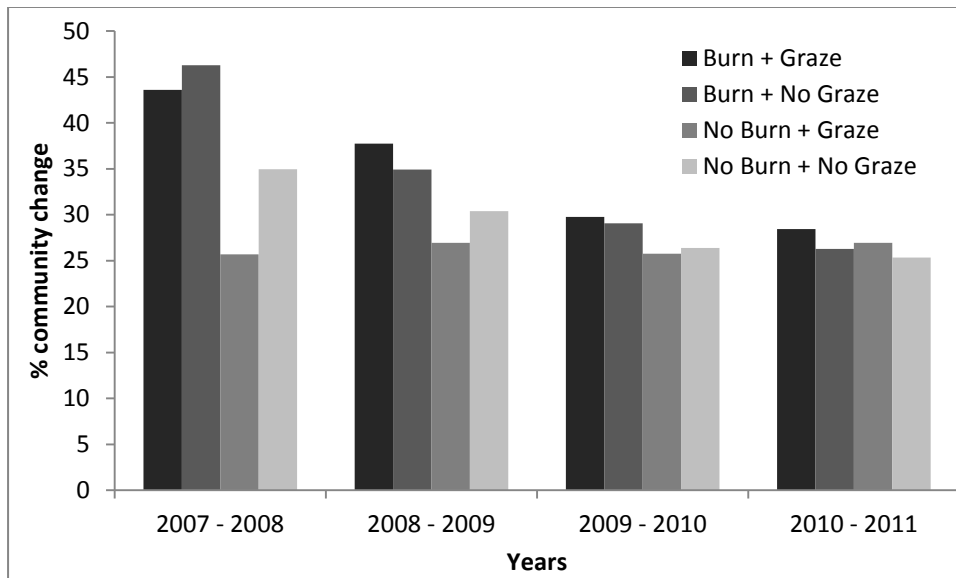


Figure 15. Percentage community change for annuals on north slopes for different treatments over the study period, averaged from six sites across the Overberg (4 treatment plots per site).

However, for south-facing plots (Fig. 17), this pattern is not consistent and, unexpectedly, in some years, the percentage change is slightly higher in unburned plots than in burned ones. However, closer inspection of the individual sites (Appendix 7.2, south sites) shows that community change is higher in unburned exclosures for sites that were the most heavily grazed (i.e. Nysty 1, Voorstekop and Van Rheenen's Crest), suggested that grazing (or the release from grazing) accounts for some of the temporal changes, in both the burned and unburned plots. It appears that in several cases the exclosures experienced the highest levels of change which may be the result of being rested following a history of heavy grazing. As discussed above, these changes are also suggestive of an additional overriding factor such as rainfall, which is likely to have influenced changes in annuals and geophytes, irrespective of treatment (Fig. 14 and Fig. 15).

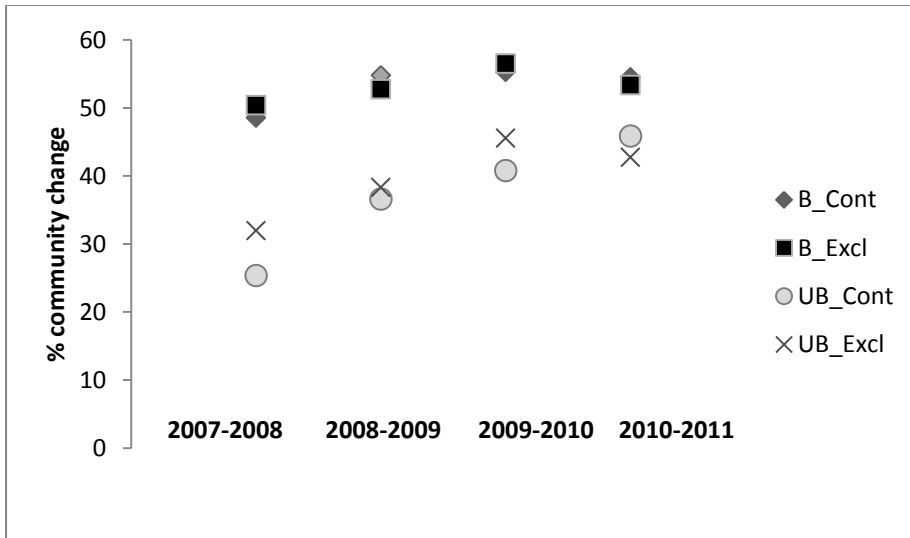


Figure 16. Percentage change in plant communities over the four years for north-facing plots (B_Cont=Burned Control, B_Excl=Burned Exclusion, UB_Cont=Unburned Control, UB_Excl=Unburned Exclusion).

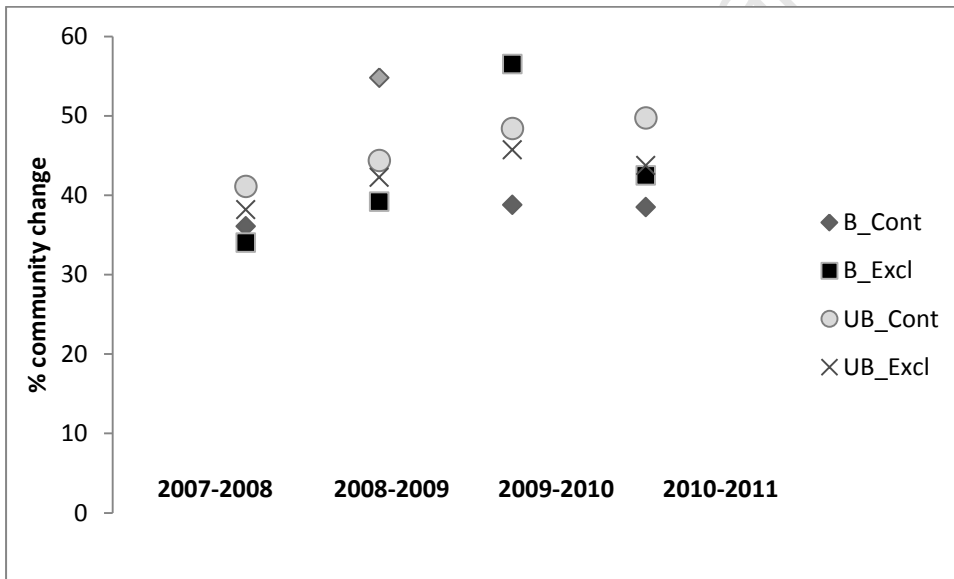


Figure 17. Percentage change in plant communities over the four years for south-facing plots (B_Cont=Burned Control, B_Excl=Burned Exclusion, UB_Cont=Unburned Control, UB_Excl=Unburned Exclusion).

Diversity relationships

Total mean cover across all sites was calculated for each species recorded in the study and used to identify the five dominant shrubs, as well as the dominant grasses on each slope, in order to gauge their responses to burning. For south slopes, shrubs were *E. rhinocerotis*, *Helichrysum petiolare* and *Oedera squarrosa* (three reseeding Asteraceae) *Aspalathus nigra*, *Aspalathus alpestris* (two resprouting Fabaceae) (Fig. 18a) and grasses *Pentaschistis eriostoma* / *Merxmeullera stricta* (C_3 bunch grasses, Poaceae, treated as a single species because they are very similar in form), *Themeda triandra* (C_4 grass, Poaceae) and two *Ehrharta* species (C_3 palatable species, also combined into one) (Figure 18b). For north slopes, the dominant shrubs were *E. rhinocerotis*, *Helichrysum cymosum* (reseeding Asteraceae), *Asparagus capensis* (a resprouting Asparagaceae), *Aspalathus submissa*, and *Aspalathus spinosa* (two resprouting Fabaceae) (Fig. 19a), while *Pentaschistis eriostoma*, *Themeda triandra* and *Cymbopogon marginatus* (19b) were the dominant grasses.

Reseeding shrubs were dramatically reduced by fire and increased gradually over the four-post burn years, while the resprouters were able to almost regain pre-burning cover by the first growth season (Figures 18a and 19a).

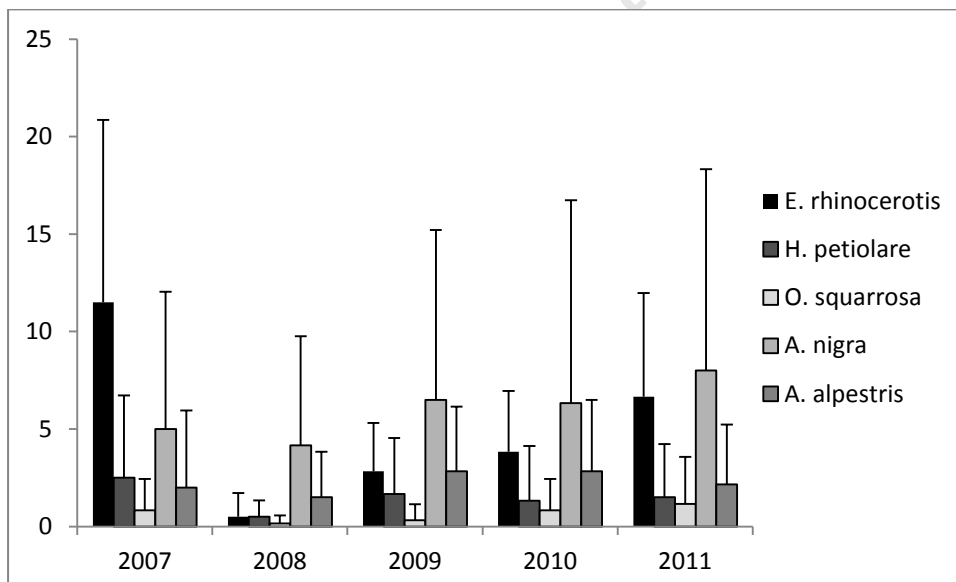


Figure 18a. Changes in average cover of the five dominant shrubs (*E. rhinocerotis*, *Helichrysum petiolare*, *Oedera squarrosa*, *Aspalathus nigra* and *Aspalathus alpestris*) on south-facing slopes, using data from only the burned exclosures across the six study sites ($n=6$) (2007 is pre-burn, 2008-2011 is post-burn, SE bars shown).

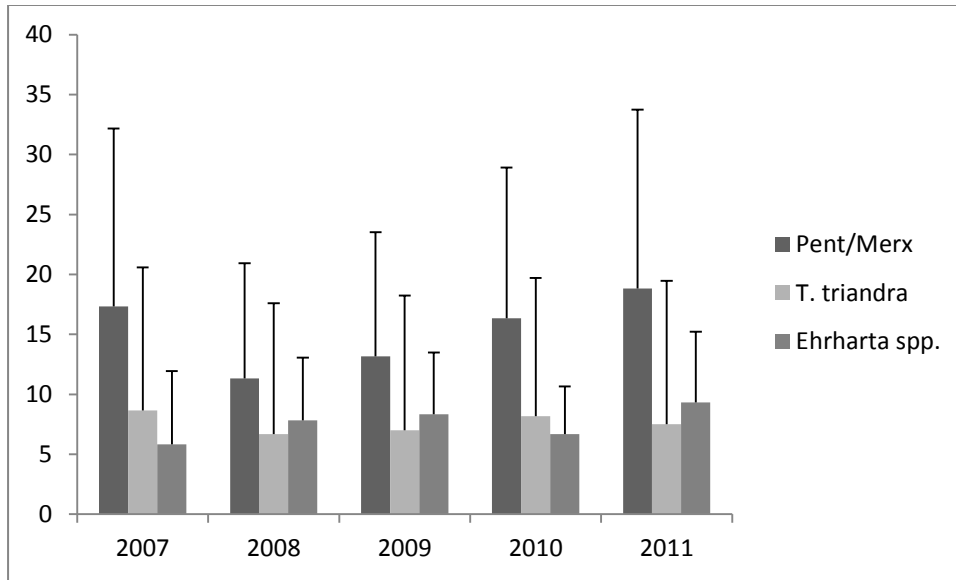


Figure 18b. Changes in average cover of the dominant grass species (*Pentaschistis/Merxmeullera* combined, *Themeda triandra* and combined *Ehrharta* species) on south-facing slopes using data from only the burned exclosures across the six study sites (n=6) (2007 is pre-burn, 2008-20011 is post-burn, SE bars shown).

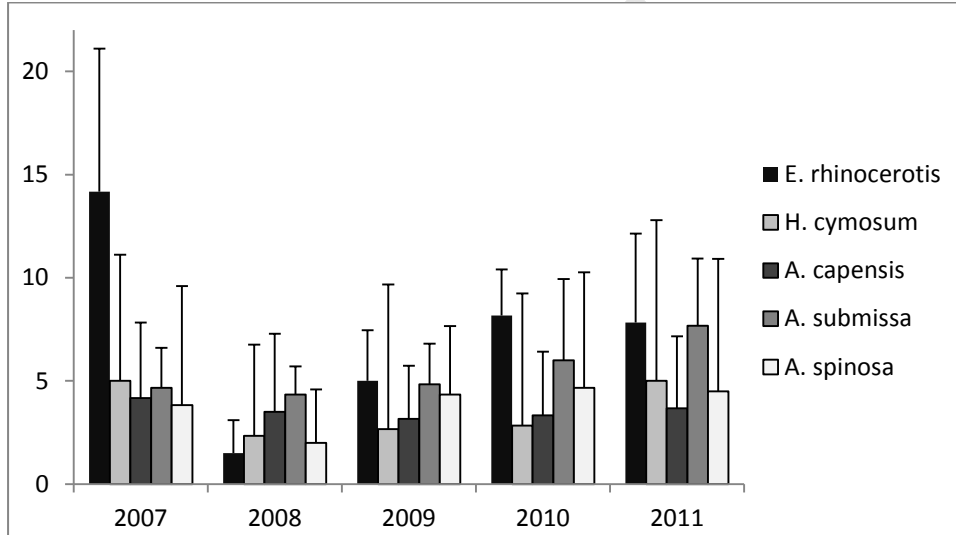


Figure 19a. Changes in average cover of the five dominant shrubs (*E. rhinocerotis*, *Helichrysum cymosum* *Asparagus capensis*, *Aspalathus submissa*, and *Aspalathus spinosa*) on north-facing slopes, using data from only the burned exclosures across the six study sites (n=6) (2007 is pre-burn, 2008-20011 is post-burn, SE bars shown).

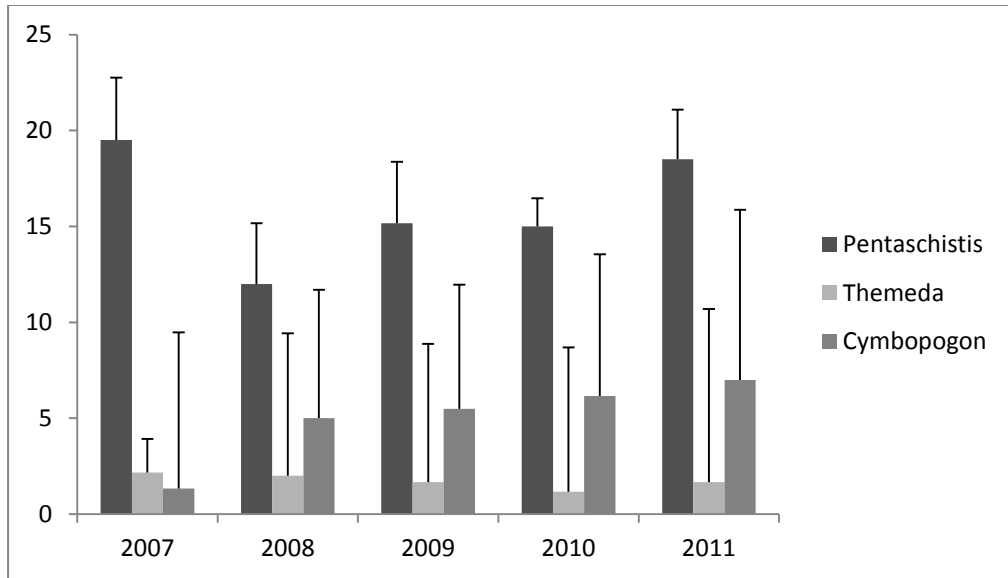


Figure 19b. Changes in average cover of the dominant grass species (*Pentaschistis eriostoma*, *Themeda triandra* and *Cymbopogon marginatus*) on north-facing slopes, using data from only the burned exclosures across the six study sites (n=6) (2007 is pre-burn, 2008-2011 is post-burn, SE bars shown).

In order to test the effects of cover of different growth forms as well as dominant species on species richness and cover of the respective growth forms, I generated a Spearman Rank Correlation matrix on these data. I tested for correlations between i) cover of the dominant grasses, ii) cover of the three dominant asteraceous shrubs, iii) total cover (all species), iv) total cover of the five dominant shrubs species and v) overall species richness against the Appendix 7.3 summarises these results. Despite having applied a Bonferroni correction to the analyses, many of the substantially low R-values were returned as significant at the $P < 0.001$ level. Therefore, only correlations with an R-value of greater than 0.5 were investigated further.

South slopes

The highlighted results (i.e. results where $R > 0.5$) from the Spearman Rank Correlations are listed in Table 2, while the entire Correlation Matrix is attached as Appendix 7.3. Total cover was positively correlated with geophyte, forb, shrub and *Aspalathus* cover, as well as forb species richness (Fig. 21) on south facing slopes (Table 2).

Table 2. Significant correlations between growth forms and dominant species identified in a Spearman Rank Correlation Matrix (Appendix 7.3) for experimental plots on south-facing slopes (24 plots, all treatments).

Pair of variables	R-value	P-value
Overall cover & geophyte cover	0.569	P<0.001
Overall cover & forb cover	0.550	P<0.001
Overall cover & forb diversity	0.605	P<0.001
Overall cover & Aspalathus cover	0.501	P<0.001
Pentasthisis/Merxmeullera cover & Themeda/Ehrharta cover	-0.510	P<0.001
Cover 3 dominant Asteraceae & shrub diversity	-0.518	P<0.001

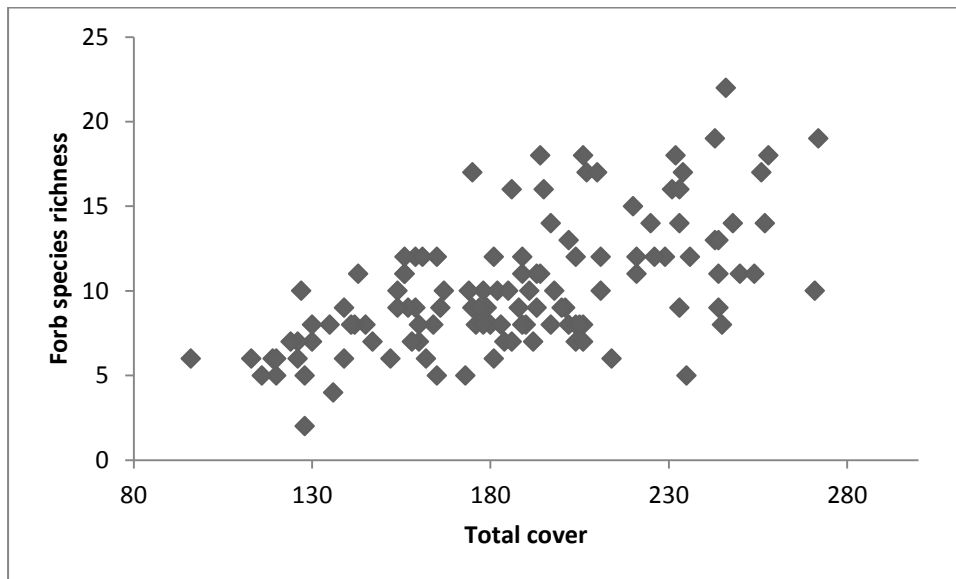


Figure 21. Positive correlation between total cover (all growth forms) and forb species richness on south-facing slopes ($R=0.605$, $P<0.000$) in experimental plots from all treatments in all years; $n=24$ plots sampled annually over five seasons.

An increasing cover of the two C_3 tussock grasses, *Pentasthisis* and *Merxmeullera*, was correlated with a decrease in cover of the two important palatable grasses, *Themeda* and *Ehrharta* (Fig. 22). Shrub diversity tended to decline with increasing cover of dominant asteraceous shrubs (Fig. 23). There were no significant relationships between dominant asteraceous shrubs and C_3 tussock grasses (Appendix 7.3).

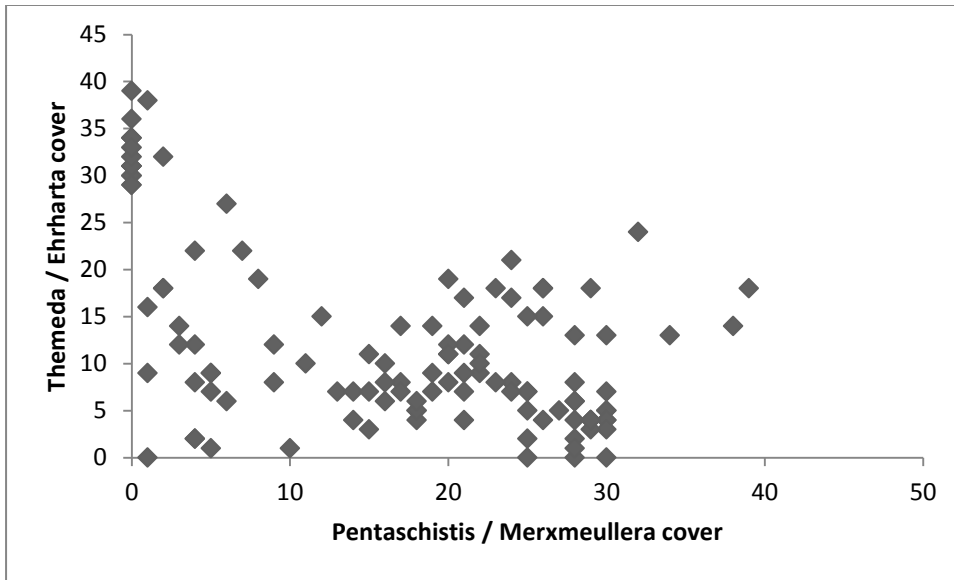


Figure 22. Negative correlation between cover for *Themeda* and *Ehrharta* combined and *Pentaschistis* and *Merxmeullera* combined cover on south-facing slopes in experimental plots from all treatments in all years; n=24 plots sampled annually over five seasons.

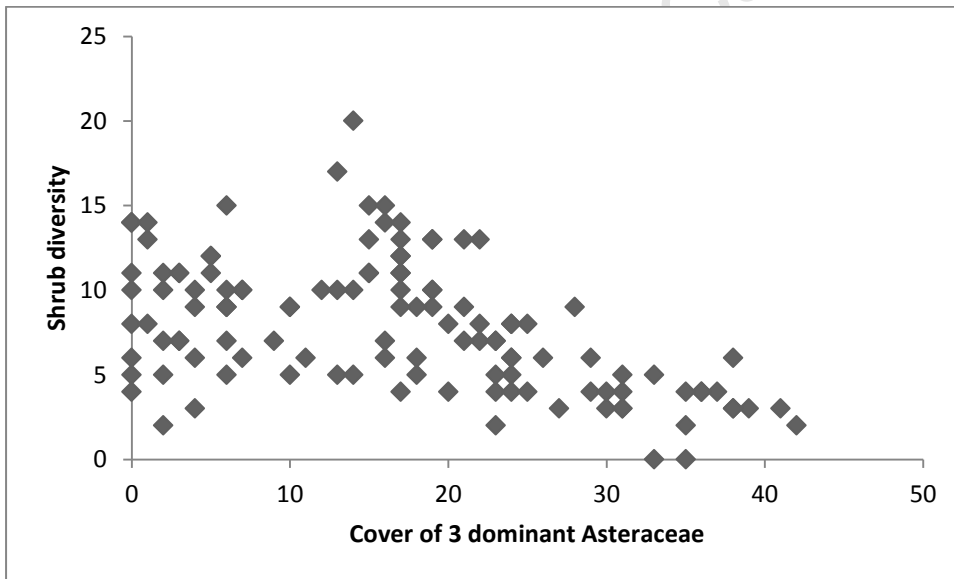


Figure 23. Negative correlation between shrub diversity and the combined cover of the three dominant Asteraceous shrubs (*Elytropappus rhinocerotis*, *Helichrysum petiolare* and *Oedera squarrosa*) on south-facing slopes in experimental plots from all treatments in all years; n=24 plots sampled annually over five seasons.

North slopes

The significant results from the Spearman Rank Correlations are listed in Table 3, while the entire Correlation Matrix is attached under Appendix 7.3. Total cover was positively correlated with cover and diversity of grasses and shrubs and in particular cover of *Themeda* and *Cymbopogon* (Table 3). Total species richness was positively correlated with cover of annuals, geophytes and restios and diversity of annuals, forbs and geophytes (Table 3). Increasing cover of *Themeda* was associated with increasing overall diversity (Fig. 24) and specifically species richness of geophytes and grasses. Cover of the five dominant shrubs was positively correlated with grass cover, but had a negative influence on forb diversity (Fig. 25), as well as succulent cover (Fig. 26) and diversity. Cover of the three dominant asteraceous shrubs negatively impacted forb diversity and succulent cover (Table 3). As with south slopes, there were no significant relationships between dominant asteraceous shrubs and C₃ tussock grasses (Appendix 7.3).

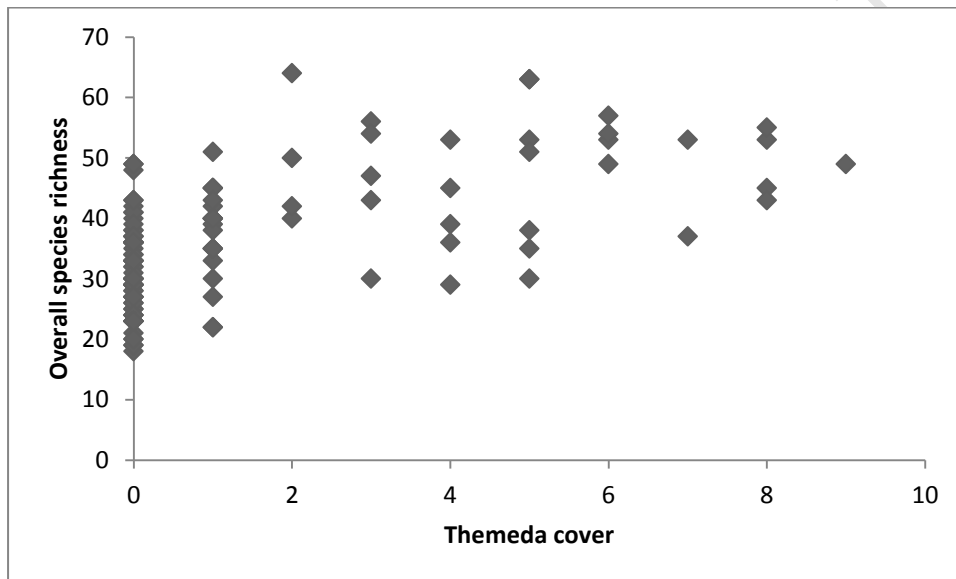


Figure 24. Positive correlation between overall species richness and *Themeda* cover on north slopes ($R=0.60$, $P<0.000$), in experimental plots from all treatments in all years; $n=24$ plots sampled annually over five seasons.

Table 3. Significant correlations between growth forms and dominant species identified in a Spearman Rank Correlation Matrix (Appendix 7.3) for experimental plots on north-facing slopes (24 plots, all treatments).

Pair of variables	R-value	P-value
Overall cover & Themeda cover	0.517	<0.001
Overall cover & Cymbopogon cover	0.511	<0.001
Overall cover & grass diversity	0.640	<0.001
Overall cover & shrub diversity	0.553	<0.001
Overall diversity & annual cover	0.576	<0.001
Overall diversity & geophyte cover	0.761	<0.001
Overall diversity & resio cover	0.613	<0.001
Overall diversity & annual diversity	0.622	<0.001
Overall diversity & forb diversity	0.607	<0.001
Overall diversity & geophyte diversity	0.782	<0.001
Themeda & geophyte cover	0.500	<0.001
Themeda & grass diversity	0.703	<0.001
Themeda & overall diversity	0.617	<0.001
Dominant shrub cover & grass cover	0.518	<0.001
Dominant shrub cover & succulent cover	-0.743	<0.001
Dominant shrub cover & forb diversity	-0.511	<0.001
Dominant shrub cover & succulent diversity	-0.712	<0.001
Cover of 3 dominant Asteraceae & forb diversity	-0.427	<0.001
Cover of 3 dominant Asteraceae & succulent diversity	-0.310	<0.001

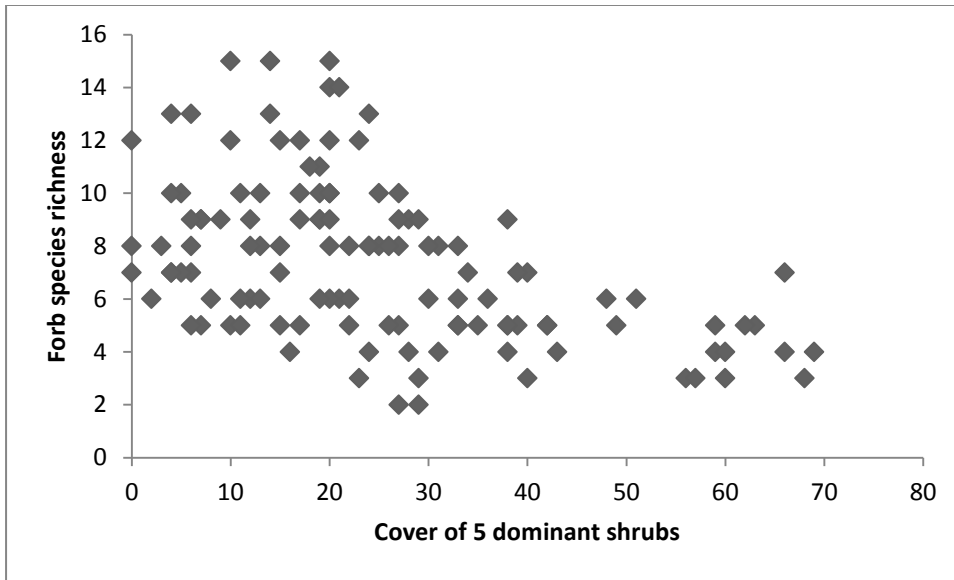


Figure 25. Negative correlation between cover of the five dominant shrubs (*E. rhinocerotis*, *Helichrysum cymosum*, *Asparagus capensis*, *Aspalathus submissa* and *Aspalathus spinosa*) and forb species richness on north-facing slopes ($R=-0.51$, $P<0.000$), in experimental plots from all treatments in all years; $n=24$ plots sampled annually over five seasons.

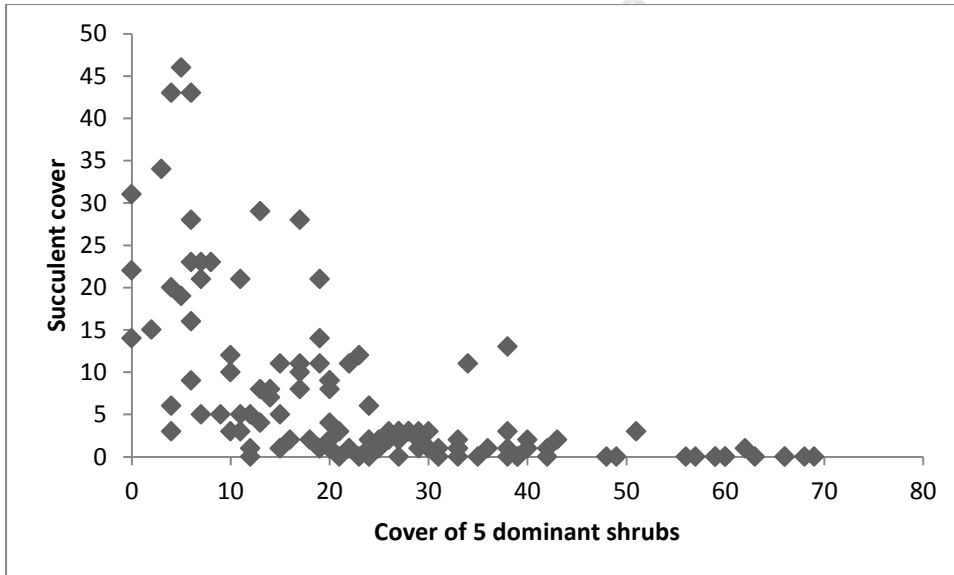


Figure 26. Negative correlation between cover of the five dominant shrubs (*E. rhinocerotis*, *Aspalathus submissa*, *Helichrysum cymosum*, *Asparagus capensis* and *Aspalathus spinosa*) and succulent cover on north-facing slopes ($R=-0.564$, $P<0.000$), in experimental plots from all treatments in all years; $n=24$ plots sampled annually over five seasons.

Temporal changes in cover of Nitrogen-fixing species

Cover of Nitrogen-fixing *Aspalathus* (Fabaceae) species decreased in the first year post-fire, but steadily increased in the three consecutive years after the fire (Fig. 27), showing a strong relationship with increasing time since burn on north and south-facing slopes, with equal R values for both ($R=0.9$, $t(N-2)=3.58$, $n=4$, $P=0.037$). Cover of the *Aspalathus* species did not differ significantly between the slopes (T-test, $t=0.22$, $df=118$, $P=0.82$), but on north-facing slopes, *Aspalathus spinosa* and *A. submissa* were the dominant species, while on south-facing slopes *A. nigra*, *A. alpestris* and *A. hispida* subsp. *albiflora* were dominant. Species diversity across all sites and treatments on south-facing slopes was positively correlated with *Aspalathus* cover (Fig. 28, $R=0.64$, $n=120$, $P<0.000$).

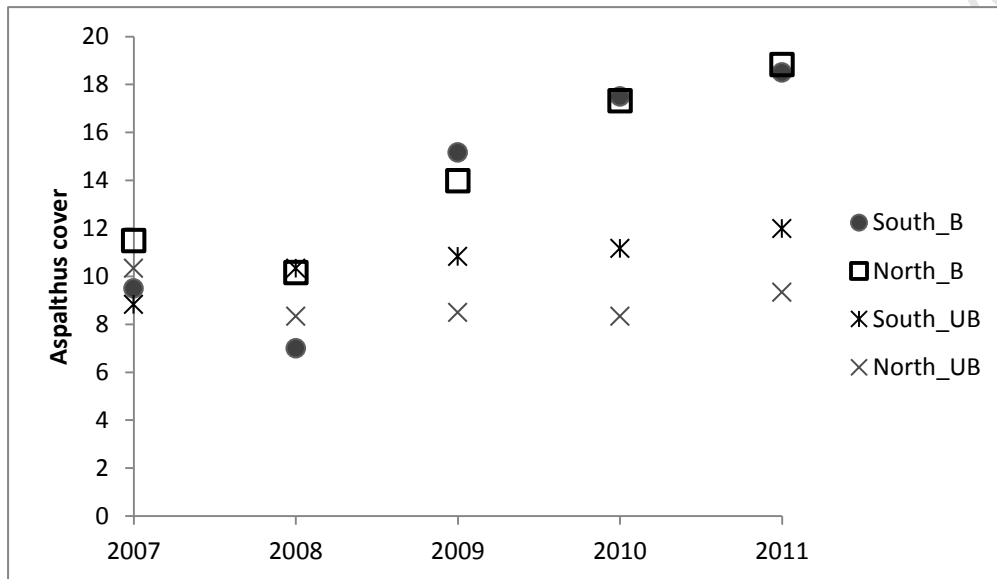


Figure 27. Change in cover of Nitrogen-fixing *Aspalathus* species four years post-burning (2008-2011), using averages taken across all sites from burned exclosure plots only, on north and south-facing slopes respectively. A logarithmic regression was fitted to post-burn averages, demonstrating a significant correlation between *Aspalathus* cover and time since burn (Spearman R, $R=0.9$, $t(N-2)=3.58$, $n=4$, $P=0.037$). Unburned averages are included on this graph for comparison.

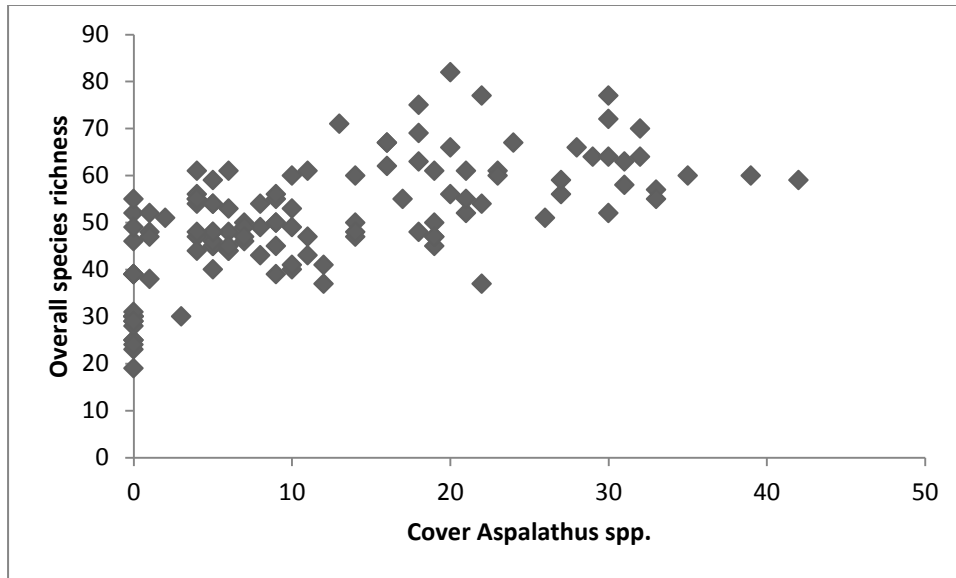


Figure 28. Positive correlation between the combined cover of all *Aspalathus* species and overall species richness on south-facing slopes ($R=0.64$, $P<0.000$) from experimental plots (from all treatments in all years; $n=24$ plots sampled annually over five seasons).

Grazing impacts on height, flowering and plant size (diameter)

In order to detect the more subtle effects of grazing, data on plant size and productivity were collected from a selection of plants within the control and exclosure plots (Appendix 7.4). Initially, the species that were obviously grazed in the controls were listed and where there were a minimum of four individual plants of a particular species available within a paired plot (i.e. in both the exclosure and the control), measurements of the plant height, plant diameter and the approximate number of flowers on the individual were noted for between 4-6 of the individuals present.

Comparisons between plant height, plant diameter and number of flowers present in grazed and ungrazed plots revealed that these three measurements were always significantly higher in ungrazed plots vs. grazed plots (Table 5). These results confirm that those species that are targeted for grazing / browsing by livestock are significantly impacted by grazing. Thus, one could assume that continuous grazing with no rest will have detrimental impacts on the plant community – where unpalatable species are given a competitive advantage over palatable species.

Table 5. Comparisons of mean plant height and diameter and number of flowers per plant in grazed and ungrazed treatments on burned and unburned plots for north- and south-aspects combined, using a Matched-Pairs T-test. See Appendix 7.4 for a list of the species used.

Variable	Mean_not grazed	Mean_grazed	t-value	df	P-value
Burned					
Height	18.2	7.3	13.7	640	0.000
Flowering	13.3	2.2	7.3	637	0.000
Diameter	22.7	14.3	8.0	633	0.000
Unburned					
Height	24.2	9.7	10.0	408	0.000
Flowering	16.3	1.3	4.0	408	0.000
Diameter	27.4	17.3	6.7	398	0.000

The influence of aspect on growth form

South-facing slopes had a higher cover of annuals, shrubs, geophytes, perennial grasses and restios / sedges, while north slopes tended to have a greater proportion of asteraceous shrubs, forbs and succulents (Fig. 29). The woody shrub component is quite similar for both slopes in this dataset and this is probably due to the inclusion of recently burned plots, which will have a lower-than-average proportion of woody shrubs. However, when average species richness was compared between the two slopes, south-facing slopes demonstrated a higher diversity for all growth forms (Fig. 30).

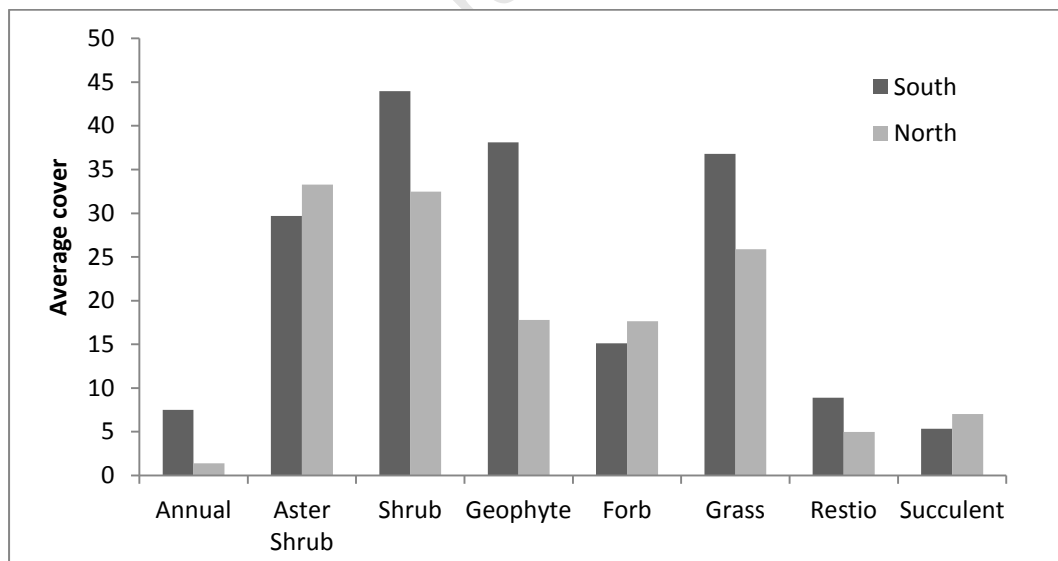


Figure 29. Bar chart demonstrating the differences in cover of growth forms on north- and south-facing slopes, based on average cover data from the full set of experimental plots.

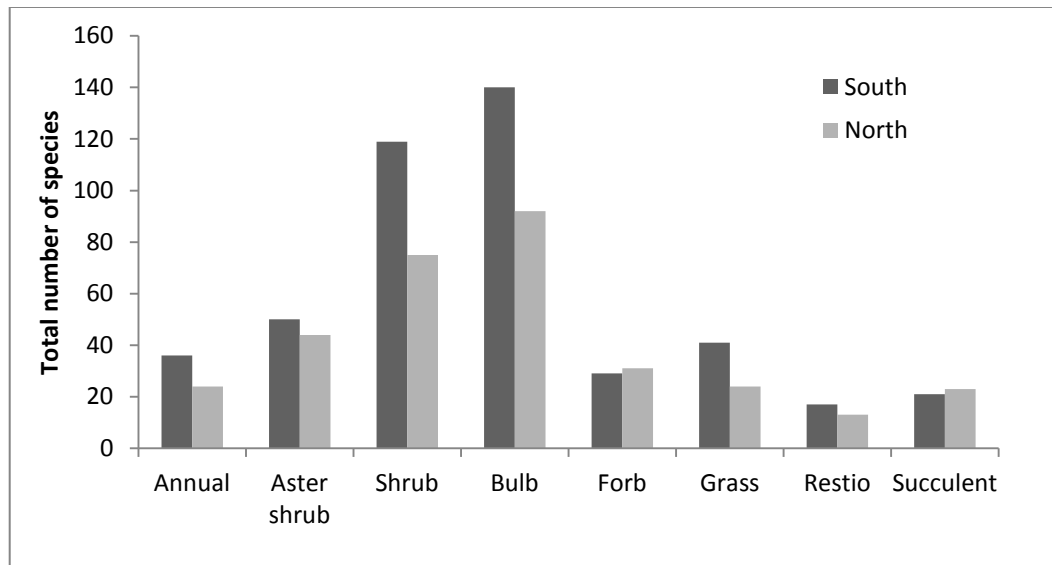


Figure 30. Bar chart demonstrating the differences in *species richness* of growth forms on north- and south-facing slopes, based on data from the collective set of experimental plots.

Correlations between average cover and species richness of the growth forms were significantly positively correlated for south-facing slopes (Spearman R, $R=0.83$, $t(N-2)=3.69$, $n=8$, $P=0.01$), while the trend was similar on north slopes, but not significantly so (Spearman R, $R=0.66$, $t(N-2)=2.14$, $n=8$, $P=0.08$).

Random plots, Napier

Relationships between physical variables, growth forms, dominant species and diversity

South-facing slopes

Six dominant species (measured by percentage cover) were identified on south slopes: *M. stricta* / *P. eriostoma* (these two species were treated as one for analyses as they have a similar form), *Themeda triandra*, *Elytropappus rhinocerotis*, *Helichrysum petiolare*, *Printzia polifolia* and *Ischyrolepis capensis* (Restionaceae). *Ehrharta calycina* was included in the rank correlations, as it ranked close to *I. capensis* and is regarded as an important perennial grazing grass and may be associated with 'better quality' (richer) habitats. *Merxmeullera* and *Pentascistis* are similar in form and function and are considered mostly unpalatable (unless resprouting directly after a fire) and a dominance of these species was therefore expected to be associated with less diverse habitats, due to over-shading and suppression of less vigorous or palatable species (e.g. Cowling 1983). Important palatable grasses on south slopes included *Ehrharta* and *Themeda*.

Table 6. Summary of significant results from correlation matrix of habitat variables, cover of dominant shrubs and grasses and cover and diversity of growth forms on south-facing slopes (n=22 plots). See Appendix 7.5 for all results.

Combination of variables	R-Value	P-value
Total cover & grass species richness	0.815	<0.001
Total cover & grass cover	0.764	<0.001
Height & forb cover	-0.703	<0.001
Height & Ehrharta cover	-0.641	<0.01
Species richness & forb cover	0.725	<0.001
Species richness & forb diversity	0.806	<0.001
Species richness & geophyte diversity	0.696	<0.001
Themeda cover & Elytropappus cover	-0.590	<0.01

Species richness and cover of different growth forms for south-facing slopes was not correlated with any of the dominant species listed above (Appendix 7.5). There were significant correlations between overall species richness and cover and diversity of forbs and geophyte diversity, while overall cover was associated with higher overall diversity and cover of perennial grasses (Table 5).

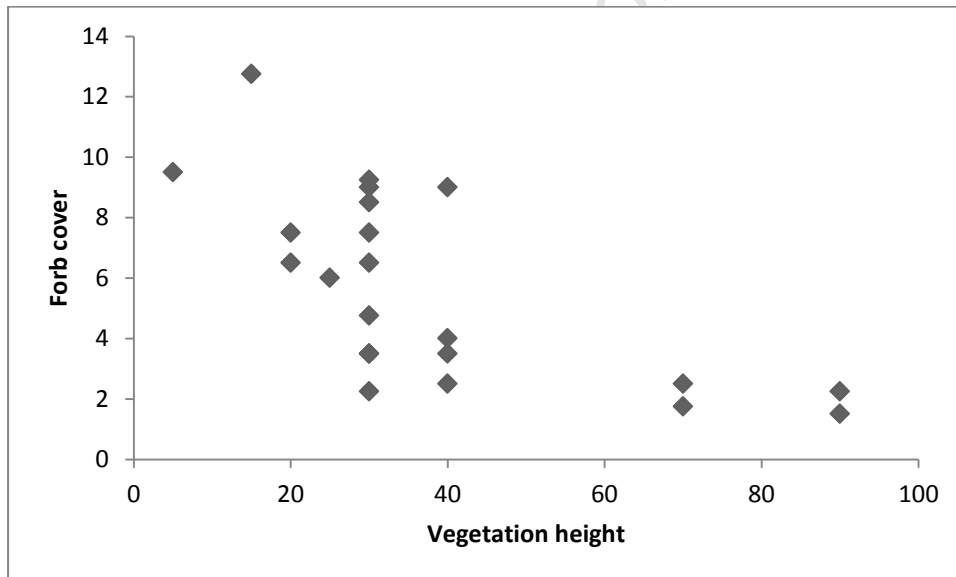


Figure 31. The negative correlation between vegetation height and forb cover ($R = -0.70$, $n = 22$, $P = 0.000$) on south-facing slopes.

Vegetation height had a negative impact on forb cover (Fig. 31) and *Ehrharta* cover. Although not statistically significant at the α level of 0.001, it is interesting to note the negative relationship between *Elytropappus* cover and *Themeda* cover ($R = -0.59$, $n = 22$, $P = 0.004$, Fig. 32) which indicates that within the 22 south-facing plots studied here, *Themeda* did not occur where percentage cover of *renosterbos* was over 6%.

Ehrharta calycina was negatively correlated with vegetation height ($R = 0.64$, $n = 22$, $P = 0.001$), and was weakly positively correlated with overall species richness ($R = 0.55$, $n = 22$, $P = 0.009$) and forb cover ($R = 0.67$, $n = 22$, $P = 0.001$) (Appendix 7.5).

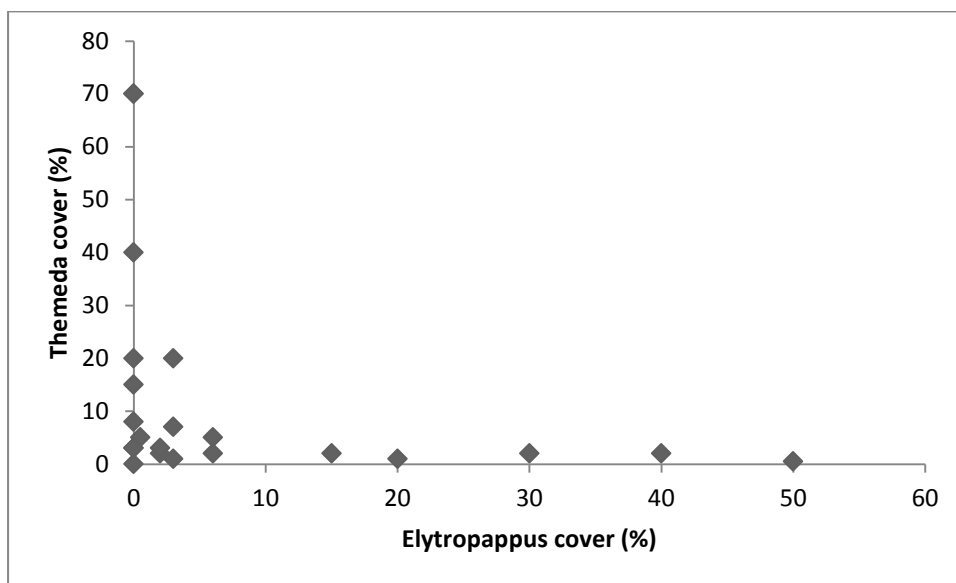


Figure 32. The negative relationship between cover (%) of *Elytropappus rhinocerotis* and *Themeda triandra* on south-facing slopes ($R = -0.59$, $P = 0.004$).

North-facing slopes

The six dominant species identified on north-facing slopes were: *P. eriostoma*, *E. rhinocerotis*, *C. marginatus*, *Aspalathus steudeliana* (Fabaceae), *Asparagus capensis* (Asparagaceae) and *C. marginatus*. Important palatable genera on these slopes were *Themeda*, *Ehrharta* and *Cymbopogon*.

The palatable C_4 grass *Cymbopogon* displayed some interesting associations: being positively correlated with both annual and geophyte cover and species richness (Table 7). Combined cover of important palatable grasses was also positively correlated with both annual and geophyte (Fig. 33) species richness and cover (Table 7) and weakly, but positively with overall species richness ($R = 0.52$, $n = 25$, $P = 0.007$, Table

7). Additionally, the results indicate that species richness was associated with geophyte, forb and annual cover and/or diversity (Table 7).

Table 7. Summary of significant results from correlation matrix of habitat variables, cover of dominant shrubs and grasses and cover and diversity of growth forms on north-facing slopes (n=25 plots). See Appendix 7.5 for all results.

Combination of variables	R-Value	P-value
Annual diversity & geophyte cover	0.626	<0.001
Annual diversity & geophyte diversity	0.652	<0.001
Cymbopogon cover & annual cover	0.653	<0.001
Cymbopogon cover & annual diversity	0.652	<0.001
Cymbopogon cover & geophyte cover	0.652	<0.001
Cymbopogon cover & geophyte diversity	0.645	<0.001
Overall species diversity & annual diversity	0.670	<0.001
Overall species diversity & forb cover	0.754	<0.001
Overall species diversity & forb diversity	0.768	<0.001
Overall species diversity & geophyte cover	0.819	<0.001
Overall species diversity & geophyte diversity	0.804	<0.001
Overall species diversity & shrub diversity	0.686	<0.001
Dominant perennial palatable grasses & annual cover	0.673	<0.001
Dominant perennial palatable grasses & annual diversity	0.678	<0.001
Dominant perennial palatable grasses & geophyte cover	0.673	<0.001
Dominant perennial palatable grasses & geophyte diversity	0.668	<0.001
Dominant perennial palatable grasses & overall species richness	0.520	<0.01

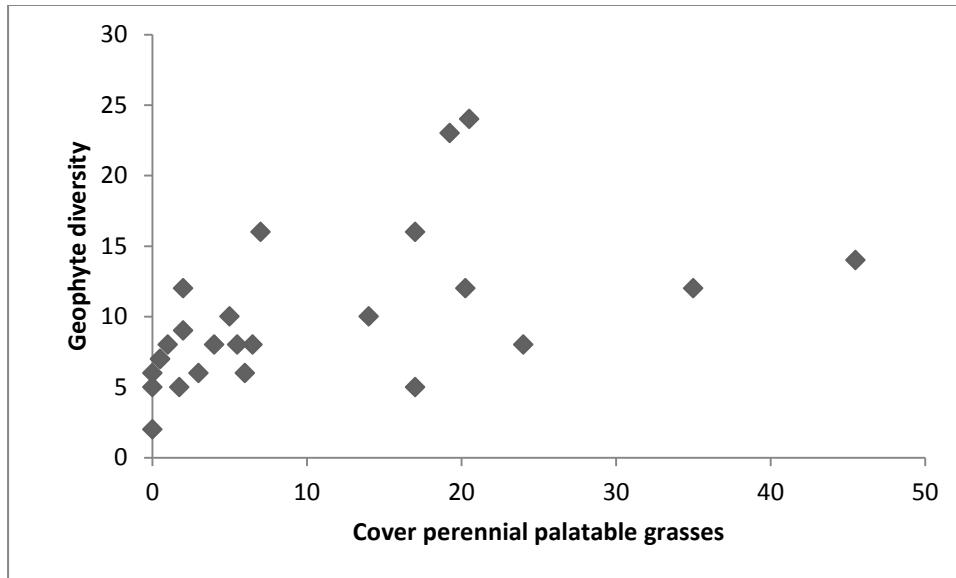


Figure 33. Positive correlation between the cover of palatable grasses (*Ehrharta* spp., *Themeda* & *Cymbopogon*) and geophyte species richness on north-facing slopes.

The influence of aspect on growth form

As expected, cooler, wetter south slopes had a significantly higher percentage cover (Table 9), as well as a higher overall species richness. Specifically, south slopes had a higher diversity of forbs and geophytes, while north slopes displayed a greater diversity of succulents (Table 9). Cover of bulbs, grasses and restios is also higher on south-facing slopes, while north facing slopes have a higher proportion of cover by succulents (Table 9).

Table 9. Summary of results from Kolmogorov-Smirnov tests (STATISTICA) comparing cover and species richness of the different growth forms on south- (n=22) and north-facing slopes (n=25).

Variable	Mean South	Mean North	Std.Dev. South	Std.Dev. North	p-value
Total cover	86.18	70.80	12.28	8.98	p < .001**
Overall species richness	40.09	32.96	7.03	10.99	p < .005**
Height (cm)	37.95	35.80	22.34	13.20	p > .10
Annual cover	4.18	0.85	7.31	1.12	p < .10
Annual diversity	3.18	1.72	1.94	1.77	p < .10
Forb cover	5.64	3.58	3.16	2.21	p > .10
Forb diversity	9.36	6.40	2.85	2.87	p < .005**
Geophyte cover	6.08	3.00	2.07	2.26	p < .001**
Geophyte diversity	15.86	9.88	4.19	5.36	p < .001**
Perennial grass cover	59.73	42.17	24.42	15.93	p < .025*
Perennial grass diversity	0.73	0.72	0.55	0.54	p > .10
Restio / sedge cover	3.85	0.77	6.69	0.87	p < .05*
Restio / sedge diversity	1.59	1.20	1.14	0.87	p > .10
Succulent cover	0.39	2.44	0.51	2.20	p < .001**
Succulent diversity	0.91	2.88	0.75	1.81	p < .001**
Asteraceous shrub cover	19.42	17.73	18.87	20.41	p > .10
Asteraceous shrub diversity	3.59	4.24	1.71	1.74	p > .10
Shrub cover (excl. Asteraceae)	9.68	17.32	8.63	13.77	p > .10
Shrub diversity (excl. Asteraceae)	4.86	5.92	2.66	1.80	p > .10
Overall shrub cover	29.10	35.05	18.68	22.38	p > .10
Overall shrub diversity	8.45	10.16	3.26	2.58	p > .10

DISCUSSION and CONCLUSIONS

The clustering of the six experimental sites in the ordination serves to emphasize the fine-scale heterogeneity and edaphic variability of renosterveld within the study area and thus cautions against the use of broad generalizations regarding renosterveld communities. These vegetation types are substantially variable within- and between- different veld types, soil types, rainfall regimes and aspect, thus management guidelines cannot be uniform across the landscape. Renosterveld is a broad term within the Fynbos Biome and currently, 29 types of renosterveld are recognised (Mucina & Rutherford 2006). These vary in terms of the altitude (i.e. mountain vs. lowland renosterveld), rainfall and substrate (e.g. dolerite vs. clay) on which they occur (Mucina & Rutherford 2006, Todd 2010) and consequently, their responses to fire and grazing will differ substantially. Thus, the findings of this study can be used only to extrapolate management recommendations for the Overberg's lowland renosterveld, while similar comparable studies should be encouraged in other regions where renosterveld occurs.

The results from the collective datasets are summarised in Table 10, where some patterns are consistent: species richness and cover of forbs and annuals is increased with fire. Shrub cover is reduced immediately by fire, but since many species are resprouters, and those that are reseederers are able to re-establish quickly, this is followed by a steady increase in shrub cover.

Is managing renosterveld for agricultural benefit (i.e. for *Themeda triandra* and other palatable species) compatible with managing for conservation objectives (i.e. overall biodiversity), as Cowling et al. (1986) suggest?

This study demonstrates that renosterveld is a complex system, displaying high levels of diversity, with some rare and endemic species that are particularly long-lived and unlikely to be fire-adapted (Chapters 5 and 7). Data presented here show that renosterveld habitats are not compatible with management required for promoting *Themeda* pasture, as this would require frequent burning-intervals of about three years (as suggested by Cowling *et al.* 1986 and Rebelo (1995)). Ordinations and community-change analyses show that vegetation is not stable at three-years post-burning and there is no indication that it will reach stability within another few years. There is some indication of a positive relationship between the presence of *Themeda* and species richness on north-facing slopes, suggesting that *Themeda* may well be a useful indicator of habitat 'quality' on north slopes. However, *Themeda* is much more common on south-facing slopes, where the same relationship with species diversity does not exist. I therefore conclude that managing lowland renosterveld in the Overberg should not be based on promoting a single

palatable grass species, but that it should take cognisance of the suite of species occurring here, particularly while patterns of process are so poorly understood.

Table 10. Summary of the effects of time-since-last-burn (i.e. veld age) on cover of the different growth forms, comparing results from random and experimental plots (SR=species richness).

Note: ↑= increase with increasing veld age; ↓=decrease with increasing veld age; ↑↓=immediate increase in response to fire, followed by gradual decrease; ↓↑=immediate decline after a fire, followed by a gradual increase.

	North-facing	South-facing
Random plots	↓ overall SR	
	↓ annual SR	
	↓ forb SR & cover	↓ forb SR & cover
	↑ perennial grass cover	↑ woody shrub cover
Experimental plots	↑↓ annual SR & cover	↑↓ annual SR & cover
	↑↓ forb SR & cover	↑↓ forb SR & cover
	↓↑ shrub cover	↓↑ shrub cover
		↓↑ succulent cover

What is the appropriate fire regime for Overberg renosterveld, defined as fire return interval (frequency), season and intensity?

For decades, renosterbos has been referred to as a ‘problem plant’ (Levyns 1929), described by early Cape farmers as ‘punishment for their sins’ (Sparrman 1786 in Adamson 1938) and described as ‘wasteland’ on current-day farm plans. Furthermore, it is seen by several ecologists as unfavourable and to quote Cowling *et al.* (1986): ‘... Fire stimulates the germination of *E. rhinocerotis* seeds... considerable recruitment of this species can be expected after an autumn burn... Follow up burns should be carried out every three years in an attempt to exhaust the seed bank of these species...’ This was a recommendation made on the basis that managing the system as a grassland for livestock grazing would act as an incentive to landowners to use their veld for grazing as opposed to ploughing it for grain crop expansion. It was also assumed that South Coast Renosterveld was derived from a *Themeda* grassland, thus both conservation and farming objectives would be met using this management approach (Cowling *et al.* 1986, Forsyth & van Wilgen 2008, Rebelo 1995). This, however, is contradictory to what one might expect from a vegetation type that typically receives less rainfall than fynbos (which is generally montane and therefore receives more rainfall). Burning frequencies are generally determined by the accumulation of fuel biomass, which tends to happen faster in wetter climates (Seydack *et al.* 2008). Hence, one could argue

that biomass accumulation in renosterveld will be slower and therefore, renosterveld will burn less frequently than its fynbos counterparts. Alternatively, despite receiving lower rainfall than fynbos, renosterveld might accumulate fuel more rapidly because of the predominance of resprouting C_3 tussock species and C_4 grasses. Thus, an assessment of fuel accumulation rates would be useful future research. Vlok & Yeaton (2000a) demonstrated that frequent fires in fynbos increased cover and size of resprouters at the expense of seeders, while cover of resprouters was shown to have a direct negative impact on species richness. These results serve to caution against the frequent use of fire in adjacent renosterveld habitats, where similar effects may manifest and where little is known about the role that dominant Asteraceae might play.

In addition to a fairly large component of resprouting species (Chapter 4), there is also a fairly large part of the renosterveld community that relies on seed production for recruitment and it is this component which is likely to be the best indicator of appropriate burning frequencies. Cowling *et al.* (1986) observed that it takes renosterveld three years to flower after a burn. Very little is known about age of first flowering for many of the other large reseeding shrubs that occur in renosterveld across the Overberg. An exceptional case, *Relhannia garnotii*, a silcrete / quartz specialist found in Eastern Rûens Shale Renosterveld, is reported to take about 20 years to reach flowering age (Raimondo *et al.* 2009), which may be indicative of the low fire return intervals in the habitat on which it grows. This species is linked with a unique assemblage of rare and endemic plants that grow only on quartz outcrops in Eastern Rûens Shale Renosterveld. Amongst these species are slow-maturing shrubs, including some recently-discovered species, which, surprisingly, are believed to be fire-stimulated flowerers, such as *Xiphotheca rosemarinifolia* (Schutte-Vlok 2011) and *Otholobium curtisiae* (Curtis *et al.* 2013). These contradictions in fire-adaptations, even within a small community assemblage, make inferences about fire-dependency and appropriate frequencies complicated.

Does grazing impact post-burn recovery, as measured by changes in species composition, species richness, or cover? Does fire promote or inhibit the main grazing grasses and does resting influence their recovery rate?

At face value, it appears that the grazing as measured in this study is compatible with renosterveld conservation: there were no apparent consistent differences in either the magnitude or direction of change between years between grazed and ungrazed plots. This result should however be interpreted with caution as the ordination is driven by the dominant species present. A grazing impact may still be present, but if rare or small species are affected then this may not be apparent from the ordination. This

study does, however, suggest that continuous grazing, with no rest periods, would ultimately have a detrimental effect on the fitness of species favoured by livestock, which is likely to favour unpalatable, competitive species, as observed by several authors (e.g. Beukes & Ellis 2003, Bond *et al.* 1994, Cowling *et al.* 1986, Jeffrey 2005, Levyns 1956, Todd & Hoffman 2000, Todd & Hoffman 2009).

The experimental design of the present study was such that instead of testing the effects of grazing by, for example, comparing areas of known and measurable grazing regimes, I essentially tested the effects of resting renosterveld from grazing, over a four-year period. Results from this treatment may manifest themselves with further monitoring, but the challenge still remains that each site is subjected to varying grazing regimes.

How does the canopy cover of Renosterbos and other unpalatable, dominant species (such as other asteraceous shrubs) and C₃ tussock grasses (i.e. Merxmeullera or Pentaschistis) influence the abundance of geophytes, forbs and annuals?

There was no relationship between species diversity, or abundance of focal dominant species and time-since-burn across random plots of varying vegetation ages. Cowling (1983) found that C₃ grasses are positively correlated with vegetation age. Additionally, increasing vegetation age also resulted in increased shading by overstorey shrubs, reducing soil surface temperatures and further supporting growth conditions for C₃ grasses (Cowling 1983). On the other hand, Vlok and Yeaton (1999) demonstrated that post-fire diversity and recovery was higher when a stand of vegetation was dominated by reseeding (proteoid) shrubs before burning. They maintain that non-sprouting overstorey shrubs contribute to high alpha diversity of fynbos. It would be interesting to explore their hypothesis but with non-sprouting asteraceous shrubs playing the role of protea overstoreys in renosterveld, by competing with vigorous resprouters, such as the C₃ tussock grasses which may suppress diversity in the absence of competition from reseeding shrubs. However, asteraceous shrubs and C₃ tussock grasses may not necessarily be in competition throughout the succession period (barring the first few years after fire) and their differences in abundance at different sites may purely be a function of different climate or soil variables which favour one and not the other.

Are there any relationships between growth forms and particular species which can serve as indicators for the need for important management interventions?

Differences in species and growth form composition recorded for different aspects may be accounted for by the difference in soil depth (south slopes have deeper soils – O. Curtis pers. obs.), temperature (south slopes are cooler – Cowling 1983) and moisture (south slopes tend to be wetter, as they are cooler and not as exposed to the sun). However, whether the response of the growth forms to these differences are innate, or whether they are induced by management, is unclear. North slopes often appear to be more heavily grazed, more scarred by mismanagement (inappropriate grazing and fire) and have more compacted soil than south slopes (pers. obs.), which suggests they are more sensitive to the long-term effects of mismanagement through overgrazing, trampling and inappropriate burning regimes. Because of the deeper soil and less exposure to direct sun, south slopes may be more resilient to disturbance, as suggested by Guo (2001) for north-facing slopes in chaparral. Some landowners have noticed this difference and have suggested applying separate management to the two slopes and where necessary, fencing them off separately. However, it would be more advisable to note where north and south slopes occur in the same fragment, north slopes are used as the indicators of what management should be applied to the whole fragment: splitting fragments into smaller management units by erecting internal fences is not likely to have overall biodiversity benefits.

Total cover was correlated with forb species richness on south facing slopes (Fig. 18), which could either be attributed to the fact that greater cover simply implies more plants and hence, more diversity, or that cover is higher in wetter places where forbs tend to be more abundant. The negative correlation between cover of the five dominant shrubs and forb species richness on north-facing slopes suggests that greatest richness exists at intermediate cover. The fact that *Ehrharta* is correlated with species richness is interesting: *Ehrharta* is a palatable species and is often more common or abundant than *Themeda* in renosterveld. The link between overall species richness and *Ehrharta* suggest that this species may be a useful indicator of biodiversity-rich renosterveld. Low to moderate grazing intensity promotes *Ehrharta* (pers. comm. Simon Todd) and is therefore likely to promote overall biodiversity. Conversely, *Ehrharta* tends to decline under high grazing pressure or continuous grazing (Rossiter 1952), which, according to results here, would infer a decline in overall species richness.

In concurrence with what Guo (2001) found for chaparral, nitrogen-fixing species increased significantly in response to burning, suggesting that fire plays an important role in the maintenance of these species. Guo (2001) maintains that nitrogen may be a limiting resource in early-succession chaparral (as nutrient leaching is common in Mediterranean climates) and will thus be a strong determinant of post-fire recovery and succession. The fact that overall species richness was positively correlated with *Aspalathus* cover lends credibility to this theory.

What are the trade-offs in managing for both conservation and agriculture and how can a 'compromise' be reached?

In terms of meeting the objectives for both agriculture and conservation, it appears that there would be some differences in how the veld would be managed: agriculture would be focused on more regular burning in order to reduce the woody shrub component and increase palatable grasses, while conservation or biodiversity management would be aimed at maintaining a functioning system, where all species and growth forms are given the opportunity to compete and reproduce. This suggests the potential for conflict between these two management objectives. However, extensive communication with landowners suggests that although the idea of burning renosterveld is appealing to them, very few actually have the resources, or even the inclination, to carry out a burn. With the restrictions on burning permits and seasons, the high risk of escaping fires, and the complications involved with constructing fire breaks to protect fences and wheat stubble from runaway fires, very few farmers actually burn their renosterveld.

Observations suggest that renosterveld habitats are burned infrequently, due to the fact that i) they are not generally viewed as a fire hazard, because they no longer burn under natural conditions (due to being extremely fragmented and isolated, they are seldom ignited by lightning; see Leach & Givnish 1996), ii) they are not managed as separate entities as most landowners are unwilling or unable to put resources into managing small remnants of renosterveld, and iii) they are not positioned adjacent to high density human populations, where ignition incidences tend to be higher (Keeley *et al.* 1999, van Wilgen *et al.* 2010). Thus unlike related fynbos and European-Mediterranean habitats (Van Wilgen *et al.* 2010, Pausus & Vallejo 1999 respectively) which in some areas have experienced exceptionally high fire frequencies, renosterveld is unlikely to be threatened by too-frequent fires. This has resulted in a high proportion of older veld (> 20 yrs old) in the landscape (O. Curtis, pers. obs). Therefore, I predict little conflict around high burning frequencies *per se*.

Fire management is, however, compounded by the effects of livestock grazing. As discussed in this chapter, most renosterveld is not fenced as a separate camp and therefore, grazing management is often non-existent. Those landowners who do burn their renosterveld generally do not follow-up with appropriate rest from grazing (pers. obs) and in doing this, potentially do more harm to the veld than good. After a burn, veld should be rested for as long a period as possible (at least 2 years) and then grazed only lightly in the summer months. However, if the veld is not fenced, it is not possible to control livestock access, thus sheep and cattle have constant access to the veld if they are put into an adjacent artificial

pasture. Additionally, in the Overberg, the least amount of pasture available on the arable lands is during winter and spring. This means that farmers are often forced to make use of their renosterveld for grazing during this critical growth and flowering time. Herein lies the conflict. It is critical that solutions to this problem are identified and implemented, so that these landscapes can be managed with benefits for both agriculture and ecological functioning, which must work hand-in-hand, if either one is to be sustained.

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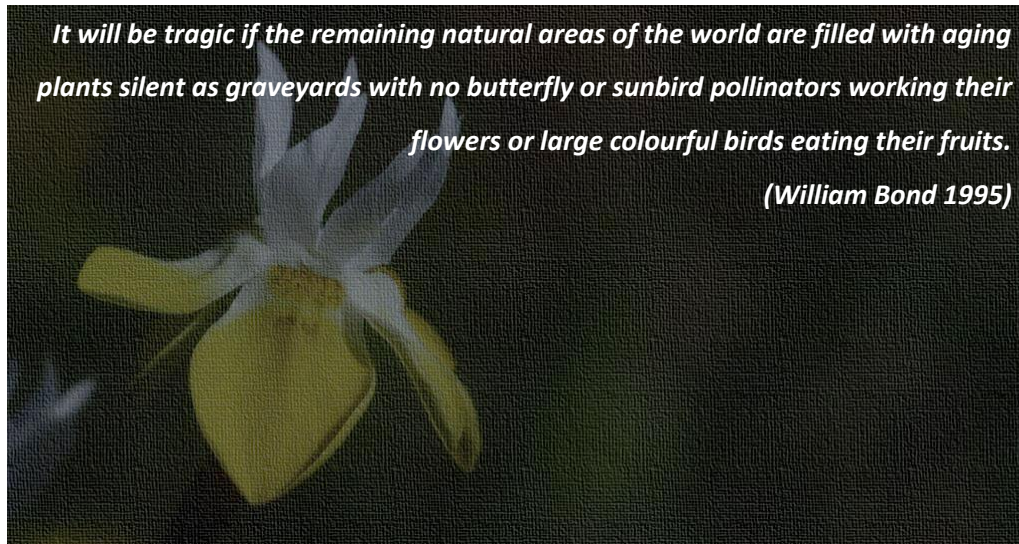
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SYNTHESIS:

Implications for renosterveld conservation and management in the Overberg and priorities for further research



Following on from the key questions set out in the introductory chapter, in this thesis I have demonstrated that:

- South Coast Renosterveld was more-than-likely always a grassy-shrubland, but that it may have had a higher grass component historically and that this component included palatable C₃ and C₄ grasses.
- Renosterveld in the Overberg responds positively to fire, showing a marked increase in flowering and germination in immediate post-burn vegetation.
- Older renosterveld is less productive, in terms of flowering and seedling production.
- Alpha diversity in lowland renosterveld in the Overberg is on a par, if not higher, than that of any other studied fynbos habitat and is comparable, if not richer, than its other Mediterranean-climate shrubland counterparts.
- Beta and Gamma diversity is high across habitat and landscape gradients, suggesting that multiple renosterveld reserves will be crucial for the long-term preservation of this habitat and associated ecological processes.
- A simple model using basic biological data has some accuracy in predicting red data status for renosterveld plants, but most importantly, these models may assist with identifying high-risk species at the patch scale.

- It is unlikely that managing renosterveld as a *Themeda* pasture will have benefits for the overall integrity of the vegetation. Thus, this study does not concur with Cowling's (1986) statement that '... the management of South Coast Renosterveld as rangeland for domestic livestock production would be entirely compatible with the conservation of this veld type and its component flora.'
- Regular short burning intervals are not advisable for this dry shrubland, which is likely to have fire frequencies equivalent to, or lower than, adjacent fynbos habitats.
- Grazing, as applied in this study, did not have an effect on the diversity or cover of plants, as measured in the treatments. It did, however, have a significant negative impact on size and flowering of individual plants targeted by livestock, suggesting that continuous grazing would have a negative impact on the veld.
- Plant community structure was significantly different on north- and south-facing slopes, with more mesic south-facing slopes being more species rich than their northern counterparts.
- No indicator species were identified that could be used across all renosterveld types in the Overberg. However, forb species richness was negatively impacted by cover on both aspects, suggesting that the proportion of forbs is a useful indicator of readiness to burn. *Ehrharta* may be a useful grazing grass to monitor for signs of overgrazing.
- In order for renosterveld to be retained in the Overberg as a functioning ecological system, a network of reserves is needed across the Overberg, which incorporates all habitats, aspects and micro-habitats. But this is unlikely to be enough. Landowners need to understand the importance of what they own and be given the knowledge and tools to manage their renosterveld remnants appropriately. Without buy-in from landowners across the landscape, securing a few reserves will not ensure the long-term survival of this vegetation type.



Othobium curtisiae



Polhillia curtisiae



Hesperantha kiaratayloriae

Above: three new species discovered by the author during the study period.

What is South Coast Renosterveld?

South Coast Renosterveld in the Overberg is a unique grassy-shrubland habitat, with exceptional levels of endemism with several new species having been discovered in the last few years (Curtis *et al.* 2013, Goldblatt *et al.* in press), as well as remarkable levels of diversity on all scales. Most importantly, this abundance of plant life is still extant in the meager 4-6% that remains. One can't help but wonder how much richer the system might have been when it covered the entire lowlands of the Western Cape. There is no evidence to suggest that renosterveld is a 'transitional' habitat, or that it is merely a grassland invaded by C₃ shrubs. The system is a dynamic one, shifting from 'grassland' to 'shrubland' states and to transitions between the two, depending on disturbance, slope, soil and rainfall regimes.

Carbon isotope results in this study suggest a very slight shift towards more C₃ plants, over an unknown time period. They do not, however, support the hypothesis that South Coast Renosterveld was a C₄ grassland prior to European settlement, or even prior to habitat manipulation by the Khoi-San people over a 2000 year period pre-European arrival. The Carbon isotope results also support the idea of a natural shift towards an increasing abundance of C₄ grasses from west to east, as is apparent today (Cowling *et al.* 1986).

Most ecologists assume that the 'grassy shrubland vs. shrubby grassland' debate intimates that those in the 'shrubby grassland' camp argue that '... renosterveld has been derived in historical times from a *Themeda triandra*-dominated grassland.' (Cowling 1984). However, it may be that many of the earlier accounts of renosterveld were in fact referring not only extensive fields of C₄ grasses, but also to an abundance of palatable C₃ species such as *Ehrharta*, which occur in renosterveld throughout the Overberg (O. Curtis pers. obs, Chapter 7). Cowling's (1986) reference to Smit's (1943) account of the 'blue grassveld' could also have been misinterpreted as referring only to *Themeda*, as other palatable grasses, such as *Ehrharta* are also known as 'blue grass'. Such interpretations may have underestimated the possibility that although the habitat was indeed

grassier, it was in fact due to the abundance of palatable C₃ grasses. Therefore, I interpret the debate as being centered on the historic abundance of *palatable* grasses and whether or not the present-day absence of these grasses from extensive parts of remnant renosterveld is innate, or whether this is the result of many years of mismanagement. And this is something we may ponder into perpetuity.

I support the hypothesis that there has been some decline in C₄ grasses in renosterveld in more recent times. Conversely, I also propose that the common beliefs that renosterveld was a true C₄-grassland system, or that it is a transitional vegetation type – which implies that it is not a unique vegetation type (Cowling *et al.* 1986, Taylor 1978) – are wrong. In concurrence with the findings of Bond *et al.* (1994) in the Karoo, and within the time-frame in question (i.e. the last 2000 years), this lowland system is most likely to have been a grassier system, but never a pure C₄ grassland, prior to European settlement in the mid- to late-1600's.

Historic accounts (Appendix 3.1) suggest that the renosterbos has spread across the renosterveld and into other areas of South Africa over the last 200-300 years. However, it has not been possible to establish whether in fact it was merely the regular burning of renosterveld being carried out by the Khoi-San that convinced early settlers of its status as a verdant grassland. Many ecologists concur that since the early European settlers, renosterveld was more than likely to have been grazed immediately post-burning, weakening the palatable species and allowing for the unpalatables, such as

renosterbos, to out-compete favourable species. However, I propose that although the renosterbos can increase under certain disturbance regimes, and that this may have happened to some extent, this does not mean that the renosterbos does not play a pivotal role in the ecology of the vegetation which derives its name from this plant. Renosterbos is a widespread and successful species (Bergh *et al.* 2007) and it is perhaps time that we start to investigate what it contributes towards the overall biodiversity of renosterveld, as opposed to how we can eliminate it in favour of plants more appealing to the eye.

'The endless succession of luxuriant plants and shrubs of the most novel and singular appearance and manifold hues, gave me the idea that I was wandering through a vast garden of rare exotics... not a foot of ground is lost or unproductive of something belonging to the vegetable kingdom, adapted to the soil or situation, and if we believe that nothing was created in vain, what an ample and delightful field for reflection does a journey through a country like this afford.'
Description of (renoster)veld from Genadendal eastwards towards Riviersonderend
J.W.D. Moodie 1835, in Skead 1980



Figures above show the enormous variety of renosterveld habitats that occur in the Overberg: from (top) succulent-rich rocky habitats to grassy, geophyte-rich grassy shrublands (recently burned) to quartz outcrops with their own distinct plant communities to dry shrublands with *Aloe ferox*.

Is lowland renosterveld in the Overberg fire-dependent?

It appears that lowland renosterveld contains the elements of a fire-driven system, given the high proportion of non-sprouters, the increase in diversity and abundance of plants post-burning, the increase in the numbers of flowering bulbs and annuals, as well as high species turnover along temporal gradients after burning. We are certainly closer to understanding what renosterveld actually is, in terms of whether it functions more like a shrubland or a grassland: it has a fire ecology more representative of woody ecosystems with crown fire regimes (Bond and van Wilgen 1996; Pausas *et al.* 2004; Keeley *et al.* 2012). Therefore, although I concur with Cowling *et al.*'s (1986) suggestion that renosterveld is a grassier system than its adjacent fynbos habitats and that the long absence of fire will result in a species-poor, shrub-dominated system, I do not support the same authors' suggestion that South Coast renosterveld should be managed like a grassland and burned every three years in order to reduce the asteraceous shrub component and promote the more 'favourable' (i.e. palatable, in terms of livestock grazing) grasses, as i) our understanding of the role that these obligate reseeder play in the renosterveld ecosystem is poor, and ii) the effects of high burning frequencies on slow-maturing, rare species are not known.

Diversity in renosterveld and comparisons with other Mediterranean habitats

Renosterveld is a unique system, comprising exceptional levels of endemism and threat (Curtis *et al.* 2013). Local and regional diversity is high (Chapter 5), placing it amongst the richest of the world's Mediterranean-type shrublands. Newton and Knight (2010) noted that, for west coast renosterveld : '... although from a gross overview the landscape is dominated by a few shrubs, within which are dispersed a variety of grasses and geophytes, there is a great variation in how these are distributed, and micro-habitat and disturbance play a much greater role than thought.' At a first glance, renosterveld often has the appearance of a homogeneous habitat, with little to offer, in terms of rare and endemic species, or any measure of species diversity. However, this study, as well as other recent research (e.g. Newton & Knight 2010, Walton 2006), has clearly demonstrated that this vegetation type requires far greater attention than it has been given to date. Despite the fact that several local professional- and hobby-botanists, CREW (Custodians of Rare and Endangered Wildflowers) volunteers and local conservation agencies have been well-aware of the biodiversity value and threat status of renosterveld, very few scientists have paid it much attention.

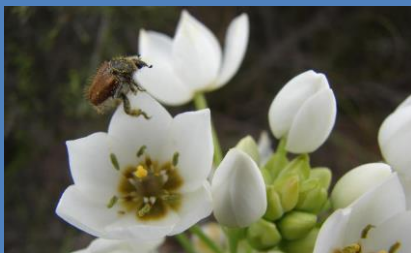
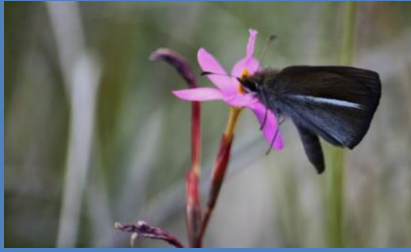
Renosterveld diversity in the Overberg region is, at the very least, on a par with other fynbos types and often supersedes fynbos (see Campbell & van der Meulen 1980, Cowling 1983, Keeley *et al.* 2012, Kruger & Taylor 1980). It is a dynamic system, the appearance and functioning of which is determined

strongly by disturbance, primarily in the form of fire and grazing (Chapters 4 & 7). It fluctuates between an open, 'grassy shrubland', a 'shrubby grassland' and a superficially homogeneous asteraceous shrubland (Chapter 3, Walton 2006). Although less than 10 species dominate the cover across the Overberg, alpha diversity is high, even relative to species-rich fynbos systems, while beta and gamma diversity are also relatively high. This has important implications for conservation planning and prioritization.

Burning and grazing in renosterveld

It appears that lowland renosterveld in the Overberg is not only tolerant of fire, but that it responds positively to burning, although at this stage, it is difficult to speculate on appropriate fire frequencies; long-term monitoring is required to assess this thoroughly. Interestingly, *Elytropappus* did not flower until at least four years after burning and even at this age, it did not flower prolifically (or at all on some north-facing slopes), suggesting that this species may be one of the slowest-maturing, re-seeding shrubs in renosterveld. In the case of fynbos, it is the serotinous proteas that are slowest to reach maturity. Vlok and Yeaton (1999, 2000) have argued that reseeder proteas are important in maintaining alpha diversity in fynbos. They suppress graminoids which rapidly suppress small shrubs and forbs recruiting from seedbanks after fire. Thus proteas provide a post-burn 'gap' free of graminoid competition. Could *Elytropappus* be the 'protea' of renosterveld? Is it possible that this shrub suppresses vigorous graminoids, such as perennial C₃ and C₄ grasses, creating recruitment gaps for less competitive shrubs and forbs?

Until more information is available, regular burning for achieving conservation objectives in renosterveld should be approached with great caution. Due to the substantial variability in renosterveld habitats, one should consider the variance in rainfall and community structure when determining burning regimes. For example, renosterveld in the Western and Central Rûens of the Overberg fall into a higher rainfall regime than renosterveld in the east, suggesting the former are more prone to higher fire frequencies because fuel accumulation happens at a faster rate. Conversely, the drier Eastern Rûens Shale Renosterveld has vegetation communities resembling Karoo habitats, including unique quartz outcrops (Curtis *et al.* 2013) comprising several rare and threatened endemic succulents and shrubs, which are unlikely to be adapted to frequent burning. Thus, I propose maintaining a precautionary principle and applying a minimum burning frequency of 8-10 years in higher rainfall regions of Overberg renosterveld and longer between-fire intervals, similar to Fynbos, in drier, Karoo-like renosterveld (15-20 years or more).



Pollinators in renosterveld: from top to bottom: *Tsitana* sp. on *Hesperantha* sp. nov. (Goldblatt *et al.* in prep), Honey Bee on *Aspalathus submissa*, moth on *A. submissa*, butterfly on *Statys* and Monkey Beetle on *Ornithogalum thyrsoides*.

(Photos: Odette Curtis)

Continuous grazing, with no rest periods, would ultimately have a detrimental effect on the fitness of species favoured by livestock, through excessive trampling and grazing which reduce the size and productivity of plants), which is likely to favour unpalatable, competitive species, resulting in a dominance of unpalatable asteraceous shrubs (Todd & Hoffman 2000) and tussock grasses (pers. obs.). I concur that, due to the fragility of this fragmented system and its high levels of endemism, light and limited summer grazing is appropriate as suggested by Milton & Todd (2007). It is also important to caution landowners and managers against the use of renosterveld for grazing at the critical growth and flowering periods for geophytes, forbs, annuals and grasses (i.e. winter and spring).

It is crucial, however, that managers understand that the most significant negative impacts on renosterveld are likely to be caused by the synergistic effects of grazing and burning, which if managed incorrectly can have detrimental impacts on renosterveld.

Summary of recommendations for future research

Recommendations for further research in Overberg renosterveld and other similar lowland habitats are briefly summarized below:

Extinction debts in renosterveld: how much time have we got?

Extinction debt theory predicts that transformed and fragmented habitats are still undergoing the extinction processes associated with fragmentation, thus we have not yet witnessed the full effects of fragmentation (Tilman *et al.* 1994). This relatively slow response to fragmentation may be the result of a delayed break-down in ecological functioning, including the loss of pollinators and dispersers, which will affect the fitness of isolated plant populations (Bond 1995). This impact is not always immediately detectable, as many plants are either resprouters or have persistent seed banks and therefore do not disappear from the system immediately. However, empirical studies have resulted in varying levels of support for the extinction debt hypothesis (e.g. Banks 1997, Hanski & Ovaskainen 2002, Honnay *et al.*

2005, Loehle & Bai-Lian 1996, Vellend *et al.* 2006). Linked with the hypothesis is the assumption that the more specialised a plant is, in terms of its pollination requirements, the more vulnerable it will be to fragmentation. However, in a comprehensive review, Aizen *et al.* (2002) found no difference in the proportion of generalist vs. specialist plants and pollinators that were affected by fragmentation – both exhibited a reduction in pollination and breeding success. Ashworth *et al.* (2004) hypothesised that this is due to the asymmetric nature of plant-pollinator webs. Many ecologists have presumed that a specialist plant is dependent on a specialist pollinator and vice-versa. However, recent studies have demonstrated that this is not always the case and that, in fact, specialist plants tend to be pollinated by generalist animals, while generalist plants are pollinated by both specialist and generalist animals (Ashworth *et al.* 2004). Thus, the authors conclude that the fitness of specialist plants may not necessarily be as detrimentally affected by fragmentation as previously assumed. It is therefore critical that plant specialisation is not examined in isolation from specialisation in pollination partners if one is to make accurate predictions about extinction risk in responses to fragmentation. This has relevance to renosterveld, which we presume is paying significant extinction debts. Very little is known about mutualistic relationships in this system, making this a priority for further investigation (Pauw 2007, Pauw & Bond 2011). Thus two critical areas for future research include: i) Pollination webs and specialisation in renosterveld fragments and ii) effects of fragmentation on diversity, breeding and movement of insect pollinators.

Fire-stimulated responses in renosterveld plants:

Fire-stimulated responses warrant further investigation across a wider suite of renosterveld fragments, habitats and aspects. Key questions include: i) of the species that appeared to flower or germinate in response to being stimulated by fire, how many would do so under other disturbances, such as grazing or mowing and how many are dependent on the heat of the fire itself, or the chemicals produced by the smoke (REF), inferring a total dependence on fire? ii) Why does geophyte abundance increase in response to fire? Do these plants lie dormant for decades awaiting a burn and why? lii) What role does renosterbos play in renosterveld? Does it function as a nurse plant? Does it suppress resprouting understorey species in the way that proteas do in fynbos (Vlok & Yeaton 1999, 2000)? Does this mean that loss of renosterbos and other reseeding shrubs will result in lower alpha diversity post-burning because of the release of highly competitive graminoids, as Vlok and Yeaton (1999, 2000) found for proteas in fynbos?

Fire frequencies: the effects of very short, and very long, intervals between fires on plant communities and their diversity, in order to establish guidelines for fire management.

In California chaparral frequent fires result in a decrease in some key shrub species, the conversion of a shrub-dominated vegetation type to an herbaceous habitat and a significant increase in non-indigenous weeds (Haidinger & Keeley 1993). I predict the same will happen in renosterveld, if exposed to short fire intervals. Conversely, it is unclear what risks are associated with leaving renosterveld unburned for several decades. One would predict that species with transient seed banks (i.e. seeds that do not lie dormant, but either germinate or die within a year - Keith *et al.* 2007) will not persist in very old or senescent vegetation. One would also predict that a proportion of species would have more persistent seed banks and that these are able to germinate after a fire (Keith *et al.* 2007). Thus, the persistence of seed banks in different species would be a useful avenue for further research. In fynbos, serotinous proteas senesce in the long absence of fire and these and other species with soil-stored seedbanks are lost from the system (Keeley *et al.* 2012). However, although very old renosterveld habitats appear homogeneous and unproductive, there is no evidence that they reach senescence, in the sense that dominant species die and plant diversity declines. They are therefore more comparable with chaparral habitats, for which there is no evidence that productivity declines with very long fire free intervals (Keeley 1992).

Very little is known about the recruitment strategies, fire-responses and age-of-first-flowering in many large renosterveld shrubs. Certainly, none of them are serotinous. There are several species of conservation concern that require further research in this respect and it is important that basic biological information on these species is expanded. *Relhania garnotii*, an asteraceous shrub classified as *Vulnerable*, is believed to have a minimum generation length of 20 years (Raimondo *et al.* 2009). There are other species which are slow-maturing and associated with older vegetation, such as *Printzia polifolia*, *Leucadendron coriaceum* (Proteaceae), *Polhillia* spp. (Fabaceae), whose life-histories are poorly known. Conversely, several newly-discovered legumes have been described in renosterveld recently and it is believed that at least two of them, namely *Xiphotheca rosemarinifolia* (Schutte-Vlok 2011) and *Otholobium curtisiae* (Curtis *et al.* 2013), only flower after a fire. However, research on individual species' responses to fire, or dependence thereon, is fundamentally lacking and insights into the life-histories of key species would prove invaluable.

The potential of other disturbances, including heavy grazing, trampling, or mechanical cutting or rolling, as alternatives to burning in sensitive areas.

Experimental research which focuses on the effects of managed grazing or mechanical means of reducing the dominant plant cover would help to clarify whether the vegetation responds in a similar manner to trampling and grazing as it does to fire, i.e. whether the role that fire plays can be substituted by other disturbances (for example, see Musil *et al.* 2005).

Season of burn and season of grazing effects and their interaction.

Seasonality of disturbance in renosterveld would have been negligible when the entire lowlands of the Overberg were ecologically intact. Large herds of grazing and browsing ungulates would have moved across the landscape in search of the best forage and when an area burned, they would have targeted it in order to take advantage of the new green shoots from resprouting grasses. However, given the sedentary nature of today's grazers, combined with the severely fragmented nature of renosterveld (which makes it vulnerable to edge effects and population crashes associated with decreasing fragment size), it follows that grazing will require active management. The greatest need for farmers to make use of grazing in renosterveld happens in winter and spring, when croplands are growing (i.e. there are no stubble lands to be used for grazing) and there is pressure on dry-land artificial pastures which generally become overstocked at this time of the year. At this time, farmers have a choice between bringing in forage for livestock (which is costly), or, if it is available, using their renosterveld for grazing. This coincides with peak growing and flowering season for most renosterveld species, thus is likely to cause long-term damage. Landowners are very hesitant to burn renosterveld at the 'ecologically correct' time of year (i.e. late summer), as this is the 'least safe' time, from a fire-management perspective. Therefore, some landowners prefer to burn in winter, which is also likely to have negative impacts on the plant communities. And what exacerbates these risks to renosterveld is that it is very seldom that grazing and burning, whether intentional or not, are implemented in a way that they do not have synergistic effects on the vegetation. Very few landowners camp their renosterveld separately, thus a burn is seldom followed-up by sufficient rest before grazing is allowed. Research which compares the effects of these management practices in a way that can be shared with landowners and managers will not only inform science, but also act as a tool for convincing landowners to change their management practices, if and where necessary.

Tests of the grazing guidelines of Milton & Todd (2007) on how communities and species diversity are impacted by different stocking rates, livestock type, season of grazing, etc.

Ideally, a long-term experimental study, where the precise number of animals, grazing season and grazing frequencies can be controlled and measured, should be undertaken. Here, the impacts on individual plants, in terms of biomass and productivity, should be measured, as well as effects on diversity and community composition over time.

Grazing and burning effects on the fauna, and especially those components that interact with the plants such as pollinators and herbivores, also needs attention.

There is a dearth of knowledge on animal ecology in relation to fire in fynbos (Parr & Chown 2003) and inter-dependencies are poorly understood. For example, the effects of short vs. long fire-return intervals on small mammal requirements (Willan & Bigalke 1982), threatened birds that make use of renosterveld for foraging or breeding (e.g. Black Harrier (Curtis 1995), Black Korhaan, Cape Francolin, Denham's Bustard (O. Curtis pers. obs)) and medium-large mammals that depend on renosterveld fragments as refugia, have not been investigated. Also, in addition to understanding the direct effects of fragmentation on pollinators (Donaldson *et al.* 2002), it is critical that the impacts of management on insects and other pollinators, both inside fragments and on the surrounding matrix, are understood, as this is likely to be the strongest determinant of future extinctions.

Conservation and management of renosterveld on private land: the challenges

South Africa has been acknowledged as a 'leader' in conservation planning (Balmford 2003) and fynbos ecologists have produced world-class conservation strategies for fynbos and renosterveld conservation (e.g. von Hase *et al.* 2003). However, despite these extraordinary accomplishments in the planning sector, the implementation of these plans has been disappointing: after nearly three decades of refining maps and plans (Jarman 1986, von Hase 2003), less than 0.1% of the Overberg's remaining lowlands (calculated from CapeNature's Stewardship layer and SANBI's fragment map) have been formally conserved and a substantial amount of additional, mostly illegal transformation of renosterveld habitats has taken place (pers. obs.). South Africa, and in particular the Western Cape, may be leaders when it comes to conservation planning, but we have a long way to go before we can turn these plans into actions and realise these goals.

Some authors (e.g. Diamond *et al.* 1976, Quinn & Harrison 1988) recommend that where choices are extremely limited, the ideal conservation plan would include a combination of as many large reserves as possible combined with a network of smaller reserves. I concur that this approach should be adopted for

renosterveld. However, due to the extraordinary levels of endemism (Curtis *et al.* 2013) and high species turnover along habitat gradients, the establishment of many small reserves is equally important. Considering the fact that i) there is already less renosterveld intact than the conservation target required for the vegetation type (Rouget *et al.* 2003), ii) most remnants are species-rich (Kemper *et al.* 1999), iii) that capacity for undertaking an effective conservation initiative at the landscape scale is severely restricted, and iv) that landowner buy-in is currently very limited, there is a need to be opportunistic under these exceptionally dire circumstances (Knight & Cowling 2007).

As discussed previously, most renosterveld is not fenced as a separate camp and therefore, grazing is not actively managed. Those landowners who do burn their renosterveld seldom follow-up with appropriate rest from grazing (pers. obs) and in doing this, potentially do long-term damage to the vegetation. However, if the veld is not fenced, it is not possible to control livestock access, thus sheep and cattle have constant access to the veld if they are put into an adjacent camp. But, at a cost of about \$3000 per km for standard stock fencing, this is an expense most landowners cannot incur.

Conservation on private land can be achieved by setting up a series of private renosterveld refuges across the Overberg, through conservation easements and partnerships with landowners. Entrenched in this approach must be management agreements and plans which not only address the management of renosterveld remnants themselves, but also the surrounding agricultural matrix, in order to reduce edge effects and facilitate dispersal, migration and pollination across the landscape. Here, it is imperative that the 'human factor' (Knight & Cowling 1997) is strongly considered, as landowners do not have the resources to manage renosterveld at their disposal - it is a costly undertaking with little or no economic return. Thus, incentives for conservation easements are the backbone for making these negotiations with landowners successful (Pence *et al.* 2003, Rouget *et al.* 2003). Without incentives (preferably in the form of hard cash or assistance with costly management interventions), there will be no conservation on private land on the scale necessary to prevent renosterveld from becoming functionally extinct. This approach is by far the most feasible means to ensuring that renosterveld will be conserved at the landscape- and process- level (Rouget *et al.* 2003). With the possibility of 'payment' of extinction debts looming (Tilman *et al.* 2004) and the uncertainty regarding the viability of these systems as functioning ecological entities, it has become even more apparent that there is an urgency regarding conservation action for this *Critically Endangered* vegetation. Enough plans have been drawn. Until these plans are brought to fruition and hectares of renosterveld are actually conserved, under law, and into perpetuity, we will not have achieved anything tangible.

To this end, the Overberg Lowlands Conservation Trust (www.overbergrenosterveld.org.za) was established in April 2012 and it is hoped that sufficient funds will be raised in order to address these critical issues. These habitats are eroding rapidly and, like so many rare and threatened habitats and taxa, not nearly enough is being done to halt this downward spiral.



Moraea elegans, Endangered, known from a handful of farms in the central & western Overberg
(Photo: Odette Curtis)

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APPENDIX 1: Published paper (*South African Journal of Botany* 87: 99-111):

A conservation and floristic assessment of poorly known species rich quartz-silcrete outcrops within Rûens Shale Renosterveld (Overberg, Western Cape), with taxonomic descriptions of five new species

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Abstract

Quartz fields are islands of distinct vegetation in southern Africa. Such habitats differ from surrounding shale substrate in geomorphological and climatic attributes, and are dominated by a predominantly succulent flora with between 14% and 91% endemism. Previous studies have identified and surveyed quartz fields within the Succulent Karoo biome, but little is known about the Overberg quartz-silcrete fields located in the Renosterveld vegetation (Fynbos biome). This study maps the occurrence of quartz-silcrete fields in the Overberg (Eastern and Central Rûens Shale Renosterveld) and investigates if such fields support distinct vegetation compared with surrounding shales. Forty-seven plant species were recorded, 19 of which are endemic to the quartz-silcrete patches, including several newly discovered species in vascular plant families Cyperaceae (*Ficinia*), Iridaceae (*Hesperantha*) and Fabaceae (*Aspalathus*, *Otholobium*, *Polhillia*, *Xiphotheca*). Five species among these are described in this paper: *Aspalathus quartzicola* C.H.Stirt. & Muasya, *Aspalathus microlithica* C.H.Stirt. & Muasya, *Ficinia overbergensis* Muasya & C.H.Stirt., *Otholobium curtisiae* C.H.Stirt. & Muasya, *Polhillia curtisiae* C.H.Stirt. & Muasya. Detailed floristic composition of 25 quartz fields are surveyed, together with their conservation status. The Overberg Quartzveld is a critically endangered vegetation type that is the sole locality for 18 Red Listed plant species; which include seven new taxa. It is a distinct vegetation unit embedded within Rûens Shale Renosterveld in the eastern Overberg region of South Africa. These quartz patches have been overlooked in the past and we emphasize the need for further research and conservation attention of these habitats.

Keywords: *Aspalathus*; Cyperaceae; Fabaceae; *Ficinia*; New species; *Otholobium*; *Polhillia*; Quartz, Renosterveld; Taxonomy.

1. Introduction

Renosterveld is the broad term used to describe one of the distinct vegetation types found within the Fynbos Biome. It is very distinct from Fynbos – the main difference being that it generally lacks, with some exceptions, the three distinctly fynbos elements (proteas, ericas and restios) and that it tends to be dominated by a combination of asteraceous shrubs and C₃ grasses (Rebello, 1995). It occurs on relatively fertile soils and is one of the richest plant communities in the world, due to its extraordinary bulb diversity (Cowling, 1983) and high levels of endemism. However it is a severely threatened vegetation type (Kemper et al., 1998, von Hase et al., 2003), facing a very real risk of functional extinction, due to severe levels of transformation and fragmentation.

Mucina and Rutherford (2006) recognized 119 vegetation types within the Fynbos Biome – of which 29 are ‘renosterveld’ types. These comprise shale renosterveld (19 types), granite renosterveld (3), dolerite renosterveld (2), alluvium renosterveld (2), silcrete renosterveld (2) and limestone renosterveld (1). In the Overberg region of the Western Cape, there are four renosterveld types: Western-, Central- and Eastern-Rûens Shale Renosterveld and Rûens Silcrete Renosterveld. The word ‘rûens’ is derived from the Dutch word ‘ruggens,’ meaning ‘hilly,’ which was used to describe the undulating, fertile lowlands of the Overberg. All four of these vegetation types are listed as *Critically Endangered* (SANBI & DEAT, 2009), with Eastern Rûens Shale (ERS) Renosterveld comprising the largest, most intact extant remnants (about 10% of the original extent remains). The Overberg renosterveld is scattered across a vast landscape of transformed lands (grain fields and artificial pasture) and almost all of it occurs on privately-owned land. Thus, the biggest threats facing renosterveld today are continued (illegal) conversion of virgin land into productive farm camps and poor management (particularly grazing and fire management) of the remnants.

Southern Africa has a complex geomorphological history and there is evidence to suggest that the unparalleled floral diversity of the Cape Flora was in fact determined by these historical processes. Cowling et al. (2009) suggest that moderate uplift during the early and late Miocene significantly increased the topo-edaphic heterogeneity of the Cape, resulting in the formation of several ‘new’ habitats available for plant colonization. In the Overberg region, the old African surface was capped by silcrete duricrusts, probably deposited in the early Palaeocene. Two major uplift events associated with tectonic movement occurred in the Cape: one in the early Miocene and a second in the late Miocene / early Pliocene. In the lowlands almost all the silcrete duricrusts, as well as the kaolinised soils below them, were eroded to reveal the extensive tracts of shales and Cretaceous

sediments, rendering a far richer and more fertile soil system compared with that of the abutting mountain habitats (Cowling et al., 2009). Today, only small remnants of the original silcrete-capped African surface are preserved in the Cape Lowlands, in the form of quartz-silcrete koppies (hillocks), mostly in the eastern region of the Overberg. The low-lying, clay-based, fertile soils essentially comprise various types of renosterveld, while the silcrete outcrops may be present in some areas. However, these systems have been significantly transformed for agriculture, with less than a tenth of the original system being represented in the landscape today.

Until fairly recently, the renosterveld lowlands of the Overberg have been largely ignored by local botanists, with some exceptions (e.g. Chris Burgers, Bruce Beyers, Nick Helme). However, botanical surveys undertaken over the last 5 years have revealed a suite of undescribed endemic species within this vegetation type. Many of these species occur only on quartz patches on silcrete outcrops in ERS Renosterveld. Mucina and Rutherford (2006) describe this veld type as occurring on 'moderately undulating hills and plains supporting small-leaved low to moderately tall grassy shrubland, dominated by renosterbos.' They make mention of the thin layer of calcrete found covering some parts of the veld in its southern limits, as well as the thicker deposits which support mesotrophic asteraceous 'fynbos', but make no mention of the quartz-silcrete outcrops which are so characteristic of this vegetation type.

In their paper which examined the community structure on quartz patches in the Succulent Karoo biome, Schmiedel and Jürgens (1999) state that quartz fields are clustered into six main regions in arid- to semi-arid southern Africa and that these are characterized by 'dwarf and highly succulent growth forms, which contrast strongly with the shrubby vegetation of the surroundings.' In her PhD thesis, Schmiedel (2002) makes reference to some quartz patches occurring in a transformed landscape south of the Langeberg mountains (which is the most northeastern extent of the ERS Renosterveld), which are characterized by *Gibbaeum haagei*, but states that, 'the quartz fields south of the Langeberg can be regarded as (relicts of) a fairly species-poor quartz field phytochorion.' Here, we challenge this statement and test whether the levels of endemism on quartz-silcrete patches within ERS Renosterveld are on a par with those found in the arid- and semi-arid regions further north.

Despite being more extensive and detailed than ever before, current-day vegetation maps are still relatively broad, when one considers local microclimates, and thus micro-habitats, which are present in so many vegetation types. For example, a particular fynbos type may also contain wetland, thicket, and/or riparian vegetation, but this is difficult to capture on a vegetation map, due to the small-scale mapping that would be required to achieve this. In the eastern part of the Overberg region, the remnant renosterveld is dotted with quartz-silcrete outcrops, containing several rare and

endemic plants, including some recently-discovered species (described in this paper). These quartz habitats have not been formally described, although their high levels of endemism and rarity are increasingly recognized amongst local botanists (pers. obs. O. Curtis). Observations suggest that the communities on the quartz-silcrete patches within ERS Renosterveld appear distinct, begging the question: do these patches warrant being recognized as a distinct vegetation unit and if so, at what level? We have undertaken a systematic botanical inventory of the ERS Renosterveld to identify and characterize the floristic composition of the quartz-silcrete patches. In this study, we map location of the quartz patches, investigate the levels of endemism, and describe five new species found on these patches. This has relevance for conservation planning and development applications.

2. Materials and methods

2.1 Study site

We conducted our field work in the Eastern Rûens Shale Renosterveld of the eastern Overberg, restricting our surveys to the renosterveld fragments located north of Bredasdorp, south of Swellendam, east of Riviersonderend and west of Heidelberg. Eastern Rûens Shale Renosterveld is found between the coastal limestone and sandstone belt in the south and the southern foothills of the Langeberg Mountain in the north, from Bredasdorp and the Breede River area near Swellendam to the Heidelberg region (Mucina and Rutherford 2006).

Quartz-silcrete patches are restricted to the silcrete outcrops on the Bokkeveld Group Shale-derived clay and loam within ERS Renosterveld, between the Bredasdorp and Swellendam/Heidelberg regions. While ERS Renosterveld has an altitudinal range of 40-320 m a.s.l., quartz patches within this are restricted to >180 m a.s.l. Average rainfall for ERS Renosterveld is 384 mm per annum, with an essentially even distribution, apart from a slight low from December to February (Mucina and Rutherford 2006), while mean daily temperatures range from 5.9°C (min, July) to 26.9°C (max, January) (Mucina and Rutherford 2006). Quartz patches fall within a similar climate, although these tend to occur within the drier parts of the ERS Renosterveld.

2.2 Vegetation surveys

We used GIS and satellite mapping to assist in selecting quartz patches and surveyed a representative and even spread sample. We recorded all vascular plants present, with particular emphasis on taxa which from our reconnaissance visits showed predominant presence on quartz, namely: i) succulents (including Aizoaceae and Crassulaceae), ii) legumes (Fabaceae) iii) sedges (Cyperaceae) and iv) restios (Restionaceae). We noted whether or not these were growing on quartz-silcrete outcrops only, or whether they were present on both the quartz-silcrete patches and

the lower slopes of ERS Renosterveld. We also recorded any additional rare or endemic species, as well as some dominant, common species, present on the quartz-silcrete outcrops.

2.3 Taxonomy

Field plant identification was done using reference taxonomic literature and confirmed with reference to well curated herbaria (BOL, NBG). Voucher specimens for all species encountered were prepared in the field and deposited at BOL. For the five taxa in Cyperaceae and Fabaceae new to science, a comparative morphological study was undertaken of available herbarium specimens (BOL, K, NBG, and PRE; acronyms follow Index Herbarium, <http://sciweb.nybg.org/science2/IndexHerbarium.asp>). Taxonomic descriptions are made following standard approaches and naming in accordance to the Melbourne Code of 2012.

3. Results

3.1 Vegetation surveys

We surveyed 25 quartz-silcrete patches (Fig. 1). Species in each patch were recorded and assessed whether they either occurred across a suite of other habitats ('generalists') or were restricted to the quartz-silcrete outcrops (Table 1). The Red Data Status of all species including the new species described in this paper was also assessed (Raimondo et al. 2009) (Table 1).

A distinct community is present on quartz-silcrete outcrops in the Eastern Rûens Shale Renosterveld of the Overberg, and typically comprises *Gibbaeum haagei*, *Elegia verreauxii*, *Mesembryanthemum longistylum*, *Acrodon deminutus*, *Amphithalea violacea*, *Relhania garnotii*, *Ficinia overbergensis*, *Otholobium curtisiae*, and *Aspalathus quartzicola* (the latter three are described under 3.2 as new species). In addition to this community, other quartz-silcrete specialists occur at less regular intervals (Table 1). Out of the 47 species recorded, 19 occur on quartz-silcrete patches only.

We selected a point on the map which represented the highest levels of species richness (GRS, PK1, PK2, NY1, NY2, HWK; Table 1) and most 'typical' quartz-silcrete habitats and measured the distance from this 'core' to each of the surveyed patches. The number of species recorded (with emphasis on quartz-silcrete patches) declined significantly, with increasing distance from the core, when all 47 species were used in the analysis (Fig. 2) ($R=-0.55$, $t(N-2)=-3.17$, $N=25$, $P=0.004$), as well as when only the species listed as 'threatened' (23 species) were used ($R=-0.47$, $t(N-2)=-2.53$, $N=25$, $P=0.02$), although this result was weaker. This suggests that levels of species richness are highest at the core, which centres on the renosterveld cluster north of the limestone ridge in De Hoop Nature Reserve (Fig. 1), hereafter referred to as the 'De Hoop-Rûens Cluster'.

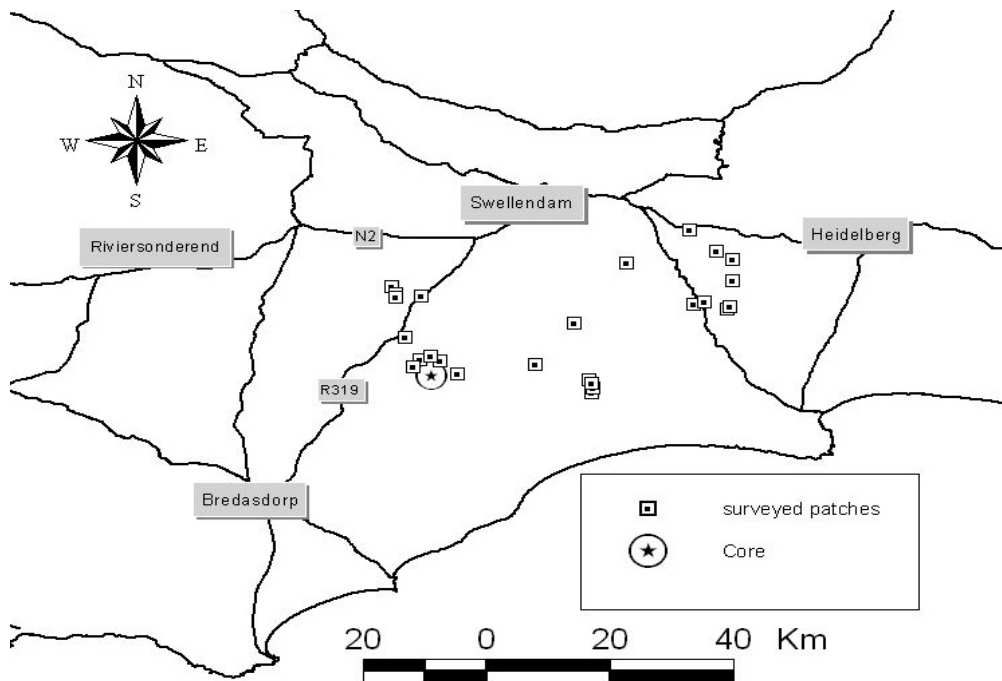


Figure 1. Map denoting the quartz-silcrete patches surveyed. The ‘core’ area comprises the highest levels of species richness recorded in this study.

The De Hoop-Rûens Cluster also contains several species new to science (included in these analyses) which, to date, have only been recorded on one site within this core and were described recently or are in press (e.g. *Xiphotheca rosmarinifolia* Schutte-Vlok (2011), *Hesperantha* sp. nov. Goldblatt & Porter 13729 (NBG, holo.; K, MO, PRE, iso.) (P. Goldblatt, pers. comm.), and *Polhillia curtisiae* (described under 3.2)). Thus, from a conservation-planning perspective, this area is pre-eminent on conservation priority. Of the 47 species recorded, the cluster lacks only four species, two of which appear to have a restricted range northeast of this cluster (*Polhillia* sp. nov. cf. *pallens* (Vulnerable) and *Liparia striata* (Endangered)). This strengthens the arguments for conservation planning based on GIS- mapping, which is currently being used as a guide for conservation authorities and NGOs in the region (von Hase et al., 2003).

Table 1. List of species recorded in the study (arranged alphabetically according to family), with corresponding Red Data status (CR=Critically Endangered, En=Endangered, VU=Vulnerable, NT=Near-Threatened, LC=Least Concern – Raimondo et al., 2009), as well as whether they are quartz specialists (*). Numbers in the top row indicate the site number. Key to farm names: AB=Aandblom, D=Dipka, GRS=Goereesoe, GK=Grootkloof, HWK=Haarwegskloof, K=Koppies, NKH=Niekerkshek, NKM=Napkysmond, NY=Nysty, OK=Oudekraal, PB=Potteberg, PK=Plaatjieskraal, UIT=Uitvlugt, UVS=Uitvlugt school, VST=Voorstekop, WGM=Welgemoed, ZK=Zandkraal.

Species	Family	Status	AB	D1	GK	GRS	HWK	K1	K2	NKH	NKM	NY1	NY2	OK1	OK2	PB1	PB2	PB3	PB4	PK1	PK2	UIT1	UIT2	UVS	VST	WGM	ZK
<i>Acrodon deminutus</i> Klak	Aizoaceae	VU*	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0	0	1	0
<i>Brownthanthus fraternus</i> Klak	Aizoaceae	EN*	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0
<i>Delosperma asperulum</i> (Salm-Dyke) L.Bolus	Aizoaceae	LC	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	0	1	1	1	1	1	1
<i>Drosanthemum parvifolium</i> (Haw.) Schwantes	Aizoaceae	LC	1	0	0	1	1	1	0	0	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	0	1
<i>Drosanthemum quadratum</i> Klak	Aizoaceae	EN*	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0
<i>Gibbaeum haagei</i> Schwantes	Aizoaceae	EN*	1	1	1	1	1	1	1	0	0	1	0	1	0	0	0	0	0	1	1	0	1	0	1	1	0
<i>Glottiphyllum cf. depressum</i> (Haw.) N.E.Br.	Aizoaceae	LC	1	0	1	0	0	0	1	0	1	0	0	1	1	0	0	0	0	1	1	1	1	1	1	0	0
<i>Mesembryanthemum longistylum</i> DC.	Aizoaceae	LC	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	1	0	1	0
<i>Trichodiadema gracile</i> L.Bolus	Aizoaceae	LC	0	0	0	0	1	1	0	0	1	1	1	0	1	0	1	0	0	1	0	0	1	0	0	0	0
<i>Notobubon striatum</i> (Thunb.) Magee	Apiaceae	NT*	0	0	1	1	1	0	0	1	0	1	0	0	1	0	0	1	1	0	0	0	0	1	0	0	0
<i>Asparagus capensis</i> L.	Asparagaceae	LC	1	0	0	0	1	0	0	0	0	1	0	0	0	1	1	1	1	1	0	1	1	1	0	0	0
<i>Cymbopappus adenosolen</i> (Harv.) B.Nord.	Asteraceae	LC	0	1	1	0	0	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	0	0	1	1	0
<i>Elytropappus rhinocerotis</i> (L.f.) Less.	Asteraceae	LC	0	1	1	0	1	0	1	0	1	0	1	1	0	1	1	1	1	1	1	1	1	1	0	0	0
<i>Metalasia acuta</i> Karis	Asteraceae	LC	0	1	1	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	0	0	0	1	0	0
<i>Oedera squarrosa</i> (L.) Anderb. & Bremer	Asteraceae	LC	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
<i>Oedera uniflora</i> (L.f.) Druce	Asteraceae	LC	0	0	0	1	0	1	1	0	1	1	0	1	1	1	1	1	1	0	0	0	0	1	0	0	1
<i>Relhania gamotii</i> (Less.) Bremer	Asteraceae	VU*	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1
<i>Triperis tomentosa</i> (L.f.) Less.	Asteraceae	LC	0	0	0	0	1	0	0	0	0	1	1	0	0	1	1	0	0	1	0	0	0	1	0	0	0
<i>Adromischus triflorus</i> (L.f.) Berger	Crassulaceae	LC	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
<i>Crassula muscosa</i> L.	Crassulaceae	LC	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
<i>Crassula nudicaulis</i> var. <i>platyphylla</i> L.	Crassulaceae	LC	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	1
<i>Crassula tetragona</i> L.	Crassulaceae	LC	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Ficinia gordongrayae</i> Muasya & C.H.Stirt.	Cyperaceae	NT*	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0

Species	Family	Status	AB	D1	GK	GRS	HWK	K1	K2	NKH	NKM	NY1	NY2	OK1	OK2	PB1	PB2	PB3	PB4	PK1	PK2	UIT1	UIT2	UVS	VST	WGM	ZK
<i>Erica venustiflora</i> subsp. <i>glandulosa</i> E.G.H.Oliv.	Ericaceae	VU	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
<i>Clutia govaertsii</i> Radcl.-Sm.	Euphorbiaceae	LC*	1	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	1	1	0	1	0
<i>Amphithalea ericifolia</i> (L.) Eckl. & Zeyh.	Fabaceae	LC	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Amphithalea violacea</i> (E.Mey.) Benth.	Fabaceae	LC	0	0	0	1	1	0	0	0	0	1	0	1	1	1	1	1	1	1	1	0	0	0	0	1	0
<i>Aspalathus incurvifolia</i> Vogel ex Walp.	Fabaceae	LC	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
<i>Aspalathus microlithica</i> C.H.Stirt. & Muasya	Fabaceae	VU*	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Aspalathus mundiana</i> Eckl. & Zeyh.	Fabaceae	LC	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0
<i>Aspalathus quartzicola</i> C.H.Stirt. & Muasya	Fabaceae	VU*	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	1	1	0	0	0
<i>Aspalathus smithii</i> R. Dahlgren	Fabaceae	EN*	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0
<i>Liparia striata</i> A.L.Schutte	Fabaceae	EN*	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
<i>Otholobium curtisiae</i> C.H.Stirt. & Muasya	Fabaceae	EN*	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0	1	0
<i>Polhillia cf. pallens</i> C.H.Stirt.	Fabaceae	EN	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Polhillia curtisiae</i> C.H.Stirt. & Muasya	Fabaceae	CR*	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Xiphotheca guthrei</i> (L.Bolus) A.L.Schutte & B.-E.van Wyk	Fabaceae	EN	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0
<i>Xiphotheca rosemarinifolia</i> A.L.Schutte	Fabaceae	CR*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Bobartia longicyma</i> subsp. <i>microflora</i> J.B.Gillett	Iridaceae	NT	1	0	0	1	1	0	0	1	0	1	1	0	0	0	0	0	0	1	1	1	1	1	0	1	0
<i>Hesperantha</i> sp. nov. Goldblatt & J.C.Manning	Iridaceae	CR*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Hermannia trifoliata</i> L.	Malvaceae	LC	0	0	1	1	1	1	1	0	0	1	1	1	0	0	1	0	1	1	1	0	0	0	0	0	0
<i>Merxmuellera</i> sp.	Poaceae	LC	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
<i>Pentaschistis eriotoma</i> (Nees) Stapf	Poaceae	LC	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	0	1	1
<i>Leucadendron coriaceum</i> E.Phillips & Hutch.	Proteaceae	EN*	1	0	1	1	0	0	0	1	0	1	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0
<i>Elegia recta</i> (Mast.) Moline & H.P.Linder	Restionaceae	NT	0	0	0	1	1	0	1	0	0	1	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0
<i>Elegia verreauxii</i> Mast.	Restionaceae	VU*	0	0	1	1	1	0	0	1	0	1	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1
<i>Acmadenia macropetala</i> (P.E. Glover) Compton	Rutaceae	VU*	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0

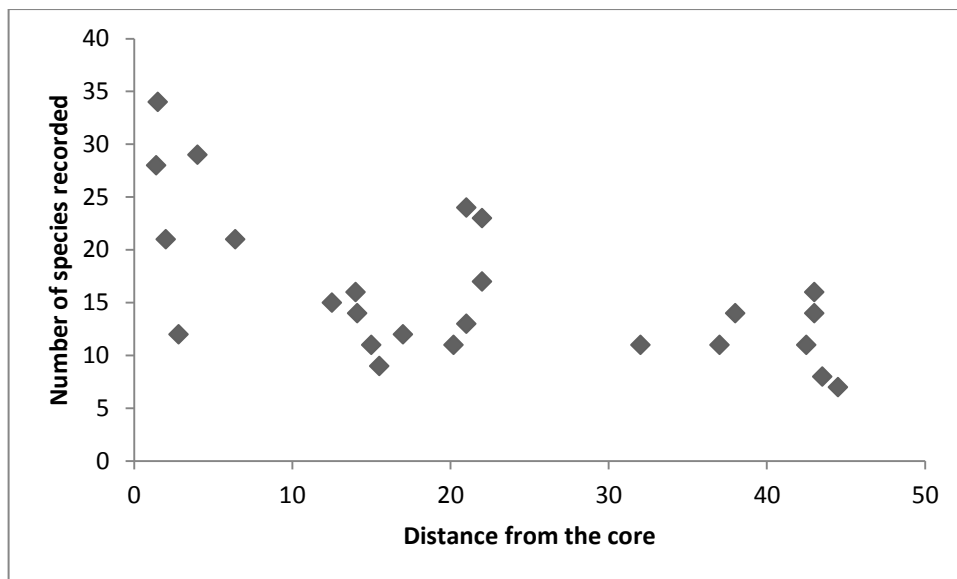


Figure 2. The negative correlation between the number of sampled species recorded on quartz-silcrete outcrops and the distance from the core site ($R=-0.55$, $t(N-2)=-3.17$, $n=25$, $P=0.004$).

A Bray-Curtis resemblance matrix demonstrated that similarity varied between 15% and 89%, reiterating the highly variable floristic composition of these habitats (Appendix 1.1). This trend appears typical across renosterveld in the Overberg, where current research using 10×10 m plots has shown that similarity indices can vary between 3% and 64%, where the maximum distance apart is only 32 km (O. Curtis, Unpublished results). The six sites (Potteberg 2 & 4, Nysty 1, Plaatjieskraal 1 & 2 and Haarwegskloof) forming the cluster with the highest number of species recorded in the study share between 57 to 89% similarity (Appendix 1.1).

3.2 Taxonomy

3.2.1 *Otholobium curtisiae* C.H.Stirt. & Muasya, *sp. nov.*, is similar to *O. pictum* C.H.Stirt., but differs in its resprouting habit (with multiple low stems vs. shrubs in *O. pictum*), terminal leaflet shorter than laterals (vs. leaflets equal in length), straight mucro (vs. recurved mucro), pediculate inflorescences with 6–9 flowers per shoot (vs. densely spicate inflorescence with 20–30 triplets of flowers), oblong flower triplet bracts (vs. broadly ovate bracts), and warty fruits. Type: South Africa, Western Cape Province, Bredasdorp Dist., Plaatjieskraal farm, upper slopes of Sonderkoskop (3420 AD), S 34°18'39.15" E20°17'52.29", 7 Dec 2012, *Curtis 57* (BOL, holol!; K, NBG, PRE, iso!).

Mounded to spreading shrubs up to 50–100 (200) mm tall, resprouter. Stems erect off basal rhizomes, branched near base, 5–10 mm thick, brown, bark split vertically encrusted with old urn-shaped pustules and thickened persistent stipule scars. Young shoots purplish green, hispid (mixture of short and long hairs). Flowering shoots clustered in the upper two axils of the new season's

growth, densely white hispid, with large urn-shaped pustules concentrated below leaves. Leaves digitately trifoliolate. Stipules 1.5–1.7 × 1.0 mm, narrowing and shortening up the shoot, scarcely fused to the base of the petiole, subulate, glabrous, margins scarcely ciliate, densely encrusted with orange glands especially at the base. Leaflets (5) 7–12 × 2.5–3.0 mm, flat, veins and areoles clearly visible; oblanceolate to oblong, somewhat falcate, apex acuminate, base cuneate; mucro straight in older leaves, recurved mucronate in basal leaves; laterals glabrous, margins sparsely appressed scabrid, longer than terminal leaflet, slightly asymmetrical, glands denser on lower surface, raised; petioles 0.5–1.0 mm long, gland encrusted. Inflorescences 1 or 2 axillary, capitate, with 1 or 2 triplets of flowers; each triplet subtended by a single 4 × 2 mm, oblong, pubescent, glandular bract; pedunculate, 2–3 mm long. Flowers 10 mm long, white; pedicel 2–3 mm long; bract filiform, densely hairy, 1 mm long. Calyx 9 mm long; upper four teeth equal, 5 × 2 mm, keel tooth 7 × 3 mm; vexillar teeth scarcely connate, teeth covered in small and large glands, densely white pilose outside; tube 2 mm deep. Standard 10 × 6.0 mm, blade elliptic, white with a large central 4 × 2 mm wide purple nectar guide, slightly auriculate, apex acute, appendages absent; claw 0.5 mm long. Wing petals 9 × 2.5–2.6 mm, longer than the keel, auriculate, cultrate but tips billowy and incurving, midline of blade sharply upcurved; claw 3 mm long; sculpturing upper basal, upper central and upper left distal comprised of 30–55 irregularly parallel lamellae. Keel blades 7 × 4 mm, apex rounded, apex purple on inner face; claw 3 mm long. Androecium 7 mm long; vexillar stamen 6.0–6.5 mm long, attached at base only. Pistil 7 mm long; ovary 2.5 mm long, papillose, glabrous; gynophore 0.5 mm long; style glabrous, 0.5 mm thick at point of flexure, height of curvature stigma 1.5 mm, incurved. Fruits 4 × 2 mm, glabrous, densely glandular, papery thin; seeds unknown. Fig. 3.

Etymology

The specific epithet honours Odette Curtis (1978) from Napier who has done much to champion the protection of the rare and threatened Overberg Renosterveld, and who first discovered this species.

Diagnostic characters

Othobium curtisiae can be diagnosed by its resprouting habit; seasonal shoots blackish on upper surface covered in urn-shaped pustules; leaflets digitately trifoliolate, sub-petiolate, flat, dark green, glabrous, veins clearly visible, terminal shorter than laterals; inflorescence pedunculate, 3–9-flowered, axillary, each triplet subtended by a broadly oblong bract; flowers white with a large purple nectar guide, bracts filiform, hairy; standard elliptic; calyx shaggy, white haired, accrescent; fruits glabrous, glandular. *O. pictum* C.H.Stirt. is distinguished from *O. curtisiae* by its erect 2 m tall shrubby habit with flat, densely nigro-punctate leaflets; densely spicate inflorescences with 20–30

triplets of white flowers, each triplet subtended by a broadly ovate bract; broadly elliptic standards, and shaggy calyces.



Figure 3. *Otholobium curtisiae*: (A) habit; (B) flowering shoot; (C) leafy shoot; (D) fruiting shoot; (E) flower; (F) fruit; (G) stem; (H) branching pattern.

We are including an anomalous specimen in *O. curtisiae* collected at Fouriesberg in the Outeniqua Mountains (*Jan Vlok 367*, PRE), that requires further investigation in the field. The specimen has similar leaves and accrescent calyces but lacks petals. It matches no other species in the genus and may represent a distinct species.

Distribution and habitat

Otholobium curtisiae, a distinctive endemic of the Overberg quartzveld (Fig. 4), was first collected in 2010. Given the inaccessibility of the terrain and the scattered remnants of ERS Renosterveld it is not surprising that no previous collections had been made. *Otholobium curtisiae* occurs at an altitude of 250–300 m on quartzitic outcrops within a fragmented landscape of ERS Renosterveld. Flowering takes place during August and September.

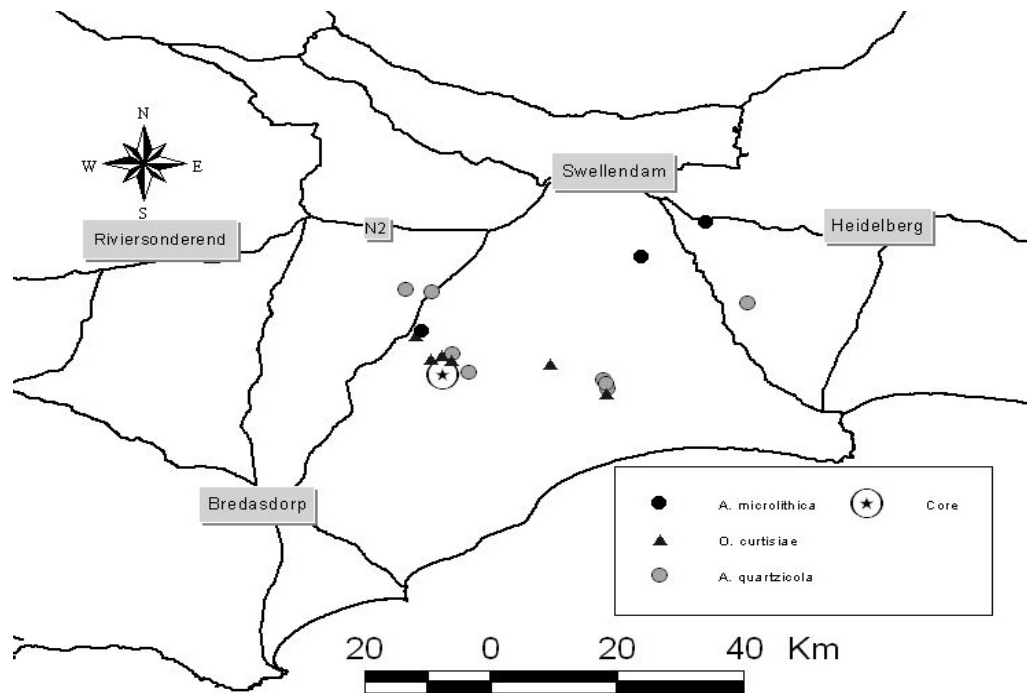


Figure 4: Distribution map of *Otholobium curtisiae*, *Aspalathus quartzicola* and *A. microlithica*, based on surveys in this study.

Conservation status

Otholobium curtisiae is locally uncommon and none of its known distribution occurs in a protected area and thus far, it has only been recorded from six sites. Its distribution is tied to that of the quartz patches and, as discussed, these patches occur within a habitat type listed as Critically Endangered. Thus, as with most quartz-silcrete endemics within the ERS Renosterveld, this species is not immune to the deleterious effects of fragmentation. We therefore assess this species to be Endangered under the South African Red list categories and criteria (Raimondo et al., 2009).

Additional specimens examined

3420 (Bredasdorp): Goeresoe Farm (–AD), 26 Nov 2011, *Stirton, Muasya & Curtis 13565* (BOL, NBG); 7 Dec 2011, *Stirton, Muasya & Curtis 13587* (BOL, NBG); Sonderkoskop, Plaatjieskraal Farm, (–AD), 7 Dec 2011, *Stirton, Muasya & Curtis 13595* (BOL, NBG).

3.2.2 *Aspalathus quartzicola* C.H.Stirt. & Muasya, *sp. nov.*, is similar to *A. incompta* Thunb. and *A. acutiflora* Dahlg., but differs in its spreading mat-like habit, glabrous leaves, white flowers with pink tips, subulate linear calyx teeth, splayed white wing petals, white keel with dark purple to violet tips, four ovules and glabrous ovary. Type: South Africa, Western Cape Province, Bredasdorp Dist. 16 Sep.1979, *Burgers 2262* (NBG, holo!).

A prostrate mat-like shrub to 20 mm tall, with a gnarled stem up to 30 mm thick; resprouter. Branches closely packed, dense, hugging the ground; young branches minutely and sparsely scabrous. Leaflets linear, tubular, 3.5–4.0 × 0.2–0.3 mm, succulent, erect, glabrous, arranged in dense clusters on short brachyblasts. Inflorescences 1- or 2-flowered, terminal on short shoots arising along each branch. Flowers 8–9 mm long, white, standing proud of leaf clusters, pedicel 1 mm long; bract 0.7–0.8 × 1 mm, tooth-like, at base of peduncle, tip black-haired; bracteoles 1 × 0.5 mm, at top of peduncle, tip black-haired. Calyx campanulate, glabrous; teeth sharply demarcated from tube, subulate-linear, terete, 1 mm long, stiff, green; tube 2 mm long, longer than teeth, pale yellow. Petals white. Standard blade broadly ovate, 4 × 3–5 mm, glabrous with acute somewhat incurved and thickened apex, auricles prominent; remains attached in fruit; claw 1.5 mm, broad, straight. Wing blades 4 × 2 mm, glabrous, white, held erect like fairy wings, upper margin inrolled; petal sculpturing present, indistinct, lamellate along upper inrolled thickened edge; claw 3 mm, straight. Keel petals 3.5 × 1.8–2.0 mm, blades fused, claw 3 mm long, ribbon-like; white, tips purple to violet; blade glabrous, auriculate, pocketed, upper margin almost straight, lower convex. Hypanthial disk present, 2 mm high, prominent. Androecium 6 mm long, 5 basifixed anthers, 5 versatile. Pistil 4.5 mm long; ovary 1.5 mm long, glabrous, stipe 0.5 mm long, ovules 4; style upcurved 1.6 mm near end from point of flexure. Fruits 7–8 × 3 mm, borne erect, obliquely ovate, glabrous, glossy, apex acute, reticulately veined, bright green when young, pale brown when mature; seeds 2.0–2.3 × 1.8–2.0 mm, tan with dark brown blotches. Fig. 5.

Etymology

The specific epithet alludes to its restriction to quartzitic outcrops in ERS Renosterveld.

Diagnostic characters

Aspalathus quartzicola is a very distinctive species that falls into Dahlgren's (1988) Group 22: *Pingues*. The species is characterised by its spreading mat-like habit, glabrous leaves, white flowers with pink keel tips, subulate linear calyx teeth, splayed erect white wing petals, glabrous ovary with four ovules, and glabrous fruits. It is most similar to *Aspalathus acutiflora* Dahlg. and *A. incompta* Thunb., which also occur in the Overberg region. *Aspalathus acutiflora* is distinguished from *A. quartzicola* by its erect or ascending habit to 1 m tall, short-villous young shoots, lack of bracteoles, densely puberulous calyx, light yellow petals with a purple standard midrib, sericeous ovary with 2 ovules, and sericeous pods. *A. incompta* differs in its procumbent habit, pubescent leaves, light or bright yellow petals, hairy ovary with 2 ovules, cultrate wing petals with lunate petal sculpturing, and short partly pubescent ovary with 2 ovules.



Figure 5. *Aspalathus quartzicola*: (A, B) habit; (C) abaxial surface of shoot; (D) adaxial surface of shoot; (E) flowering shoot; (F) fruiting shoot; (G) flower.

The following key helps distinguish these three species which have been commonly misplaced in herbaria.

1. Plants mat-like, up to 1 m across; leaves glabrous; flowers white with purple to violet keel tips; ovary glabrous, with 4 ovules *A. quartzicola*
- 1*. Plants procumbent to erect; leaves pubescent; flowers yellow; ovary partly sericeous, with 2 ovules 2
 2. Young branches short pubescent; bracteoles tooth-like; calyx sericeous; standard puberulous on upper half of back *A. incompta*
 - 2*. Young branches short villous; bracteoles lacking; calyx densely subglabrous or sparsely puberulous; standard glabrous *A. acutiflora*

Distribution and habitat

Aspalathus quartzicola is restricted to flat areas on white quartz pebble patches in Eastern Rûens Shale Renosterveld between 170–300 m (Fig. 4). Flowering is from August to September. *Helme* 1759 reports that the flowers are sweet-smelling and pollinated by honey-bees.

Conservation status

Aspalathus quartzicola is locally common, but none of its distribution occurs in a protected area. However, the species is a habitat specialist, occurring exclusively on quartzitic outcrops. Although these are uncultivated, over-grazing remains a real threat which could be mitigated by fencing off some of the areas as a means of controlling livestock access to these sensitive habitats. We therefore assess this species to be *Vulnerable* under the South African Red list categories and criteria (Raimondo et al., 2009).

Additional specimens examined

— 3420 (Bredasdorp): Swellendam, after road to Protem (—AB), 11 Feb 2010, *Tyambetyu & Stoll 4258* (NBG); Vreda farm, 40km from Bredasdorp to Swellendam (—AC), 21 Oct 1976 (NBG); Saddle WNW of Spitzkop, hills E of Vrede, Bredasdorp – Swellendam road (—AD), 22 Aug 2000, *Oliver 11582* (NBG); Sonderkoskop, Plaatjieskraal farm (—AD), 7 Dec 2011, *Stirton, Muasya & Curtis 13596* (BOL, NBG, PRE); Plaatjieskraal (—AD), 1 Oct 2011, *Stirton & Curtis 13726* (BOL); Nysty farm, Bredasdorp region (—AD), 27 Nov 2011, *Muasya, Stirton & Curtis 6340* (BOL); Goereesoe Farm (—AD), 7 Dec 2011, *Stirton, Muasya & Curtis 13586* (BOL); Farm Luipardskop 53, about 12 km NW of Wydgelee, slopes between Suikerkankop, Kraaiheuwel and Rooikop Trig. Beacon 157, 10 Sept 2000, *Helme 1759* (NBG); De Hoop Nature Reserve, Potberg (—BC), 1 Nov 1984, *Scott 472* (NBG).

3.2.3 *Aspalathus microlithica* C.H.Stirt. & Muasya, *sp. nov.*, is similar to *A. retroflexa* L. but differs in its dense spreading mat-like habit, strigo-villous vestiture, prostrate woody stems, stiff leaves, condensed floriferous branches, bright yellow sessile flowers turning orange to red, purple-veined calyx, obtuse keel, and linear oblong wing petals with infolded thickened upper edge and well-developed sculpturing. Type: South Africa, Western Cape Province, Bredasdorp Dist., Goereesoe Farm (3420AB), 7 Dec 2011, *Muasya, Stirton & Curtis 6301* (BOL, holo!; NBG, iso!).

Prostrate mat-like shrub, 10–20 mm tall, with a gnarled stem 5–8 mm thick; resprouter. Branches closely packed, dense, hugging the ground; young branches appressed short white strigo-villous. Leaflets 3.1–3.5 × 0.5–0.7 mm, linear-subulate, terete, apiculate, succulent, bright green, erect to spreading, glabrous, arranged in dense clusters of 9–12 leaflets on short alternately arranged brachyblasts. Inflorescences 1(2)-flowered, terminal on short shoots. Flowers 5–6 mm long, sessile, dark yellow, standing proud of leaf clusters; pedicel absent; bract 1 × 0.5 mm, naviculate, green, acuminate, densely villous inside; bracteoles 0.5 mm × 0.3 mm, pale green, situated just above bracts on base of tube. Calyx campanulate, strigo-villous; teeth 2.5 mm long, linear-subulate, terete, carnosose, bright green, distinctly demarcated from tube, acuminate, identical to leaflets; tube 2.5 mm long, same length as teeth, pale yellowish green and purple veins with white appressed strigose

hairs. Petals bright yellow, turning orange to red with age. Standard blade broadly ovate, 5.0 × 5 mm, glabrous with acute somewhat incurved and thickened purple apex, yellow turning orange, auricles absent; claw 1.5 mm, broad and flattish, straight. Wing blades 4.0 × 0.5 mm; blade 3.0–3.5 mm long, glabrous, yellow, upper margin inrolled with a thickened edge; claw 1.5 mm, upcurved; petal sculpturing present, distinct, lamellate near auricles becoming lunate towards centre, lamellate, upper basal and upper left central, comprised of 3–4 rows of up to 9 lunate pockets. Keel petals 5.0–5.5 × 2.5 mm, blades fused, scarcely auriculate, micropapillate along margin towards the claw, pocketed, lunate, upper margin concave-convex, lower convex, obtuse, hyaline below becoming pale yellow in upper parts, turning reddish brown with age; claw 1.0–1.5 mm long. Hypanthial disk present. Androecium 4 mm long, 5 basifixed anthers, 5 versatile. Pistil 4.5 mm long; ovary 1.5 mm long, strigose on upper margin of straight part of style, ovules 2; style upcurved, height of flexure 2 mm. Pods and seeds unknown. Fig. 6.

Etymology

The specific epithet *microlithica* alludes to the white strigose hairs on the purple stripes of the calyces, which is a unique feature in *Aspalathus*. However, the idea for the name came from seeing pictures of Late Pleistocene microlithic silcrete assemblages (Orton, 1988) that looked similar to the calyx hairs and also echoed the many small quartzite pebbles that cover the silcrete outcrops in which the species inhabits.

Diagnostic characters

Aspalathus microlithica is a very distinctive species that falls into Dahlgren's (1988) Group 32: *Teretilobae*. The species is characterised by its dense spreading mat-like habit, strigo-villous vestiture, thick twisted prostrate woody stems, stiff leaves, condensed floriferous branches, bright yellow sessile flowers turning orange to red, purple-veined calyx, obtuse keel, linear oblong wing petals with infolded thickened upper edge and well-developed sculpturing. It is most similar to *A. retroflexa* L. which occurs more to the west. *A. retroflexa* is distinguished from *A. microlithica* by decumbent or procumbent to semi-erect sparingly branched habit, white villous, tomentose or puberulous vestiture, long floriferous branches with dispersed internodes, tomentose calyx, light yellow petals with a purple standard midrib, green calyces, sericeous ovary, and sericeous pods. *A. incompta* differs in its procumbent habit, pubescent leaves, light or bright yellow petals, cultrate wing petals with lunate petal sculpturing, and short partly pubescent ovary with 2 ovules.

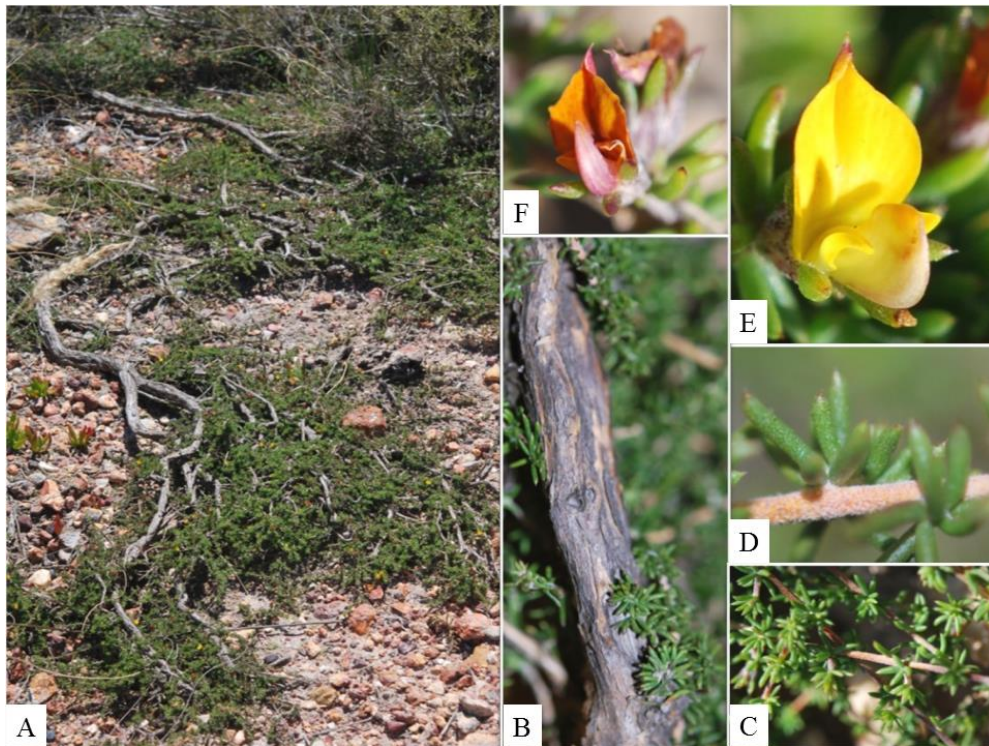


Figure 6. *Aspalathus microlithica*: (A) habit; (B) stem; (C) leafy shoot; (D) leaves; (E) young flower; (F) old flower.

Distribution and habitat

Aspalathus microlithica was only recorded in three of the 25 studied outcrops of silcrete and quartz patches in Eastern Rûens Shale Renosterveld between 170–300 m (Fig. 4), although it was found subsequently at other sites further northeast. Flowering takes place during October and November.

Conservation status

Although *A. microlithica* is locally common, none of its distribution occurs in a protected area. However, the species is a habitat specialist, occurring exclusively on quartzitic outcrops. Although these are uncultivated, over-grazing remains a threat which could be mitigated by fencing off some of the areas as a means of controlling livestock and ostriches access to these sensitive habitats. We therefore assess this species to be *Vulnerable* under the South African Red list categories and criteria (Raimondo *et al.*, 2009).

Additional specimens examined

— 3420 (Bredasdorp): Swellendam, after road to Proteem (—AB), 11 Jan 2010, *Tyambetyu & Stoll* 4358 (NBG); Vreda farm, 40km from Bredasdorp to Swellendam (—AC), 21 Oct 1976 (NBG); Saddle WNW of Spitzkop, hills E of Vrede, Bredasdorp – Swellendam road (—AD), 22 Aug 2000, *Oliver 11582*

(NBG); Farm Luipardskop 53, about 12 km NW of Wydgelee, slopes between Suikerkankop, Kraaiheuwel and Rooikop Trig. Beacon 157, 10 Sep 2000, *Helme 1759* (NBG); Goeresoe Farm (—AD), 7 Dec 2011, *Stirton, Muasya & Curtis 13588* (BOL); Goeresoe Farm en route to Bredasdorp, 26 Nov 2012, *Muasya, Stirton & Curtis 13564* (BOL); 26 Nov 2011, *Muasya, Stirton & Curtis 6301* (BOL); Sonderkosp, Plaatjieskraal, 7 Dec 2012, *Stirton, Muasya & Curtis 13600* (BOL); De Hoop Nature Reserve, Potberg (—BC), 1 Nov 1984, *Scott 472* (NBG); Skeiding Farm (—DD), 3 Feb 2013, *Stirton & Curtis 13796* (BOL).

3.2.4 *Polhillia curtisiae* C.H.Stirt. & Muasya, *sp. nov.*, is similar to *P. pallens* C.H.Stirt., but differs in its more open habit, yellowish green branchlets turning brown with age, broader partly conduplicate obovate leaflets with densely hairy margins and green upper leaf blades, patently hairy calyces, and shorter more pilose 5–7-seeded shaggy pods. Type: South Africa, Western Cape Province, Bredasdorp Dist., Haarwegskloof Farm (3420AB), 12 Oct 2011, *Stirton, Muasya & Curtis 13361* (BOL, holo!; NBG, iso!).

Erect, multi-stemmed shrubs up to 500 mm high, resprouter. Leaflets 5–7 x 3 mm wide, obovate but usually partly conduplicate giving an open tubular appearance, flatter in younger plants, straight sometimes arcuate, densely villous-sericeous, terminal leaflet same size as laterals or slightly longer. Stipules 25–30 mm long, fused, villous with longer patent pilose hairs. Inflorescences 1- or 2-flowered. Flowers 10–11 mm long, yellow, ebracteolate; pedicel 2.5 mm long, tapering. Calyx 5 mm long, including tube 3 mm long, vexillar teeth broadly triangular, 1.5 mm long, almost equally broad at base, lateral and keel lobes mutually coherent to a lip, fused for two thirds of their length, smaller and shorter than vexillar teeth, densely villous, glabrous inside. Standard 10 × 10 mm; blade emarginate, sericeous on back, glabrous inside; claw 3 mm long, narrow. Wing petals 10 × 4 mm wide, blade 7 mm long, curved, strongly auriculate, broadly cultrate, widest in middle, thickened with upper margin inrolled, longer than keel petals; sculpturing upper basal and left central, strongly lamellate-lunulate, claw 4 mm long. Keel petals 8–9 × 2.5–3.0 mm long, auriculate, pocketed, hairy in bottom half; claw 4 mm long. Androecium 9 mm long, stamens sheathed, open on upper side, anthers dimorphic, 5 alternately elongate and basifixed plus 5 short and versatile. Pistil 7 mm long, ovary 5 mm long, linear, flattened, sessile; ovules 5–7; golden shaggy; style forward sloping to erect, height of curvature of style 2.5 mm. Fruits 20–28 × 5–7 mm, undulating, densely covered in long patent silver shaggy hairs, upper margin purplish in fresh state; indehiscent; seeds 10–15 × 8–10 mm, brown. Fig. 7.

Etymology

The specific epithet honours Odette Curtis (1978) from Napier who has greatly increased our knowledge on the distribution of *Polhillia* in Renosterveld and who first discovered this species.

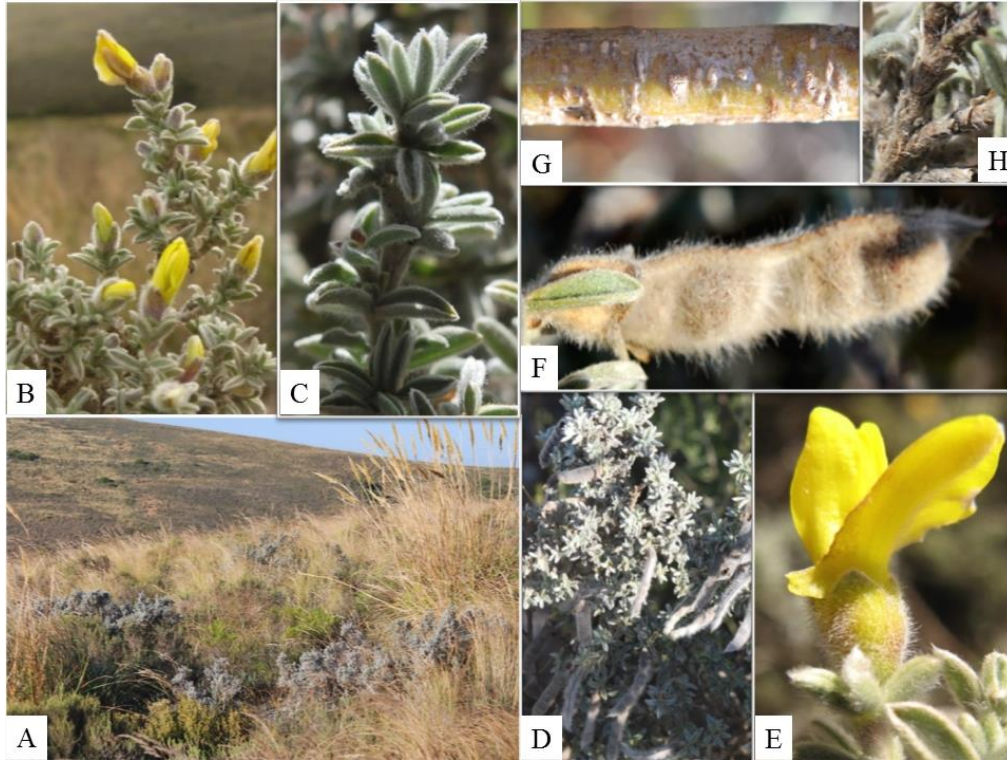


Figure 7. *Polhillia curtisiae*; (A, B) habit; (C) leafy shoot; (D) stem; (E) inflorescence; (F) flower; (G) calyx; (H) fruit.

Diagnostic characters

The species is characterised by its looser more spreading habit, yellowish green upper branchlets turning brown with age, broader (5–7 x 3 mm) partly conduplicate obovate leaflets with densely hairy margins and green upper leaf blades, patently hairy pale green to pink flushed calyces, and with shorter (4x length of leaflets) more pilose 5–7 seeded shaggy fruits. It is most similar to *P. pallens* which is a more compact, multi-stemmed shrub with greyish brown branchlets turning charcoal grey with age, conduplicate narrowly arcuate leaflets with evenly haired silvery leaf margins and leaf blades, mostly appressed hairy yellowish green calyces, and with longer (6x length of leaflets), 8–10 seeded less shaggy pods.

Distribution and habitat

Polhillia curtisiae is restricted to a single locality on a dry north-facing aspect on a white quartz pebble patch at Haarwegskloof Farm in Eastern Rûens Shale Renosterveld between 230–242 m (Fig.

8). Powdery kaolinitic soils are particularly deep on this site. Flowering takes place from May to July with fruit shed in August to September.

Conservation status

This species is only known from one site, despite concerted efforts to find more populations. We therefore assess this species to be *Critically Endangered* under the South African Red list categories and criteria (Raimondo et al., 2009). Only 28 individuals of various ages were counted in November 2012. It appears from the age of the individual resprouting plants that there is limited recruitment following fires.

Additional specimens examined

— 3420 (Bredasdorp): Haarwegskloof Farm (—AB), 2 Dec 2011, *Stirton, Muasya & Curtis 13461* (BOL, NBG).

3.2.5 *Ficinia overbergensis* Muasya & C.H.Stirt. *sp. nov.*, similar to *F. quartzicola*, differing in leaves (with well-developed blades vs. blades reduced to lobes), and involucral bracts (leafy vs. culm-like). Type: South Africa: Western Cape: Bredasdorp Dist., Plaatjieskraal (3420AD), S34°18'38" E20°17'48", 30 Sep 2012, *Stirton, Muasya & Curtis 13727* (BOL, holo!; K, NBG, PRE, iso!).

Perennial, forming clumps to 300 mm diameter, base hardened, without obvious rhizome. Culm 50–160 mm tall, 0.3–0.6 mm thick, glabrous. Leaf sheath 7–19 × 1.5–2.2 mm, glabrous, not papery, wine-red, sticky. Leaf blade 26–55 × 0.3–0.9 mm, channelled, glabrous except for scabrid margins towards apex. Involucral bract 2 or 3, leaf-like, 10–29 × 0.4–0.6 mm, margin scabrid towards apex. Inflorescence capitate, 4–8 × 2.4–5.7 mm, with 3–6 spikelets. Spikelets 3.9–6.4 × 1.6–2.5 mm, terete, dark brown. Glumes 2.7–3.8 mm long, acute, with a mucro to 0.3 mm long; margins entire. Style trifold. Stamens 3, anthers crested. Nutlets 1.5–2.0 × 0.8–1.0 mm, brown, minutely papillose; hypogynous disk to 0.8 mm long, cupular, 3-lobed. Fig. 9.

Etymology

The specific epithet refers to the Overberg region where the taxon is endemic.

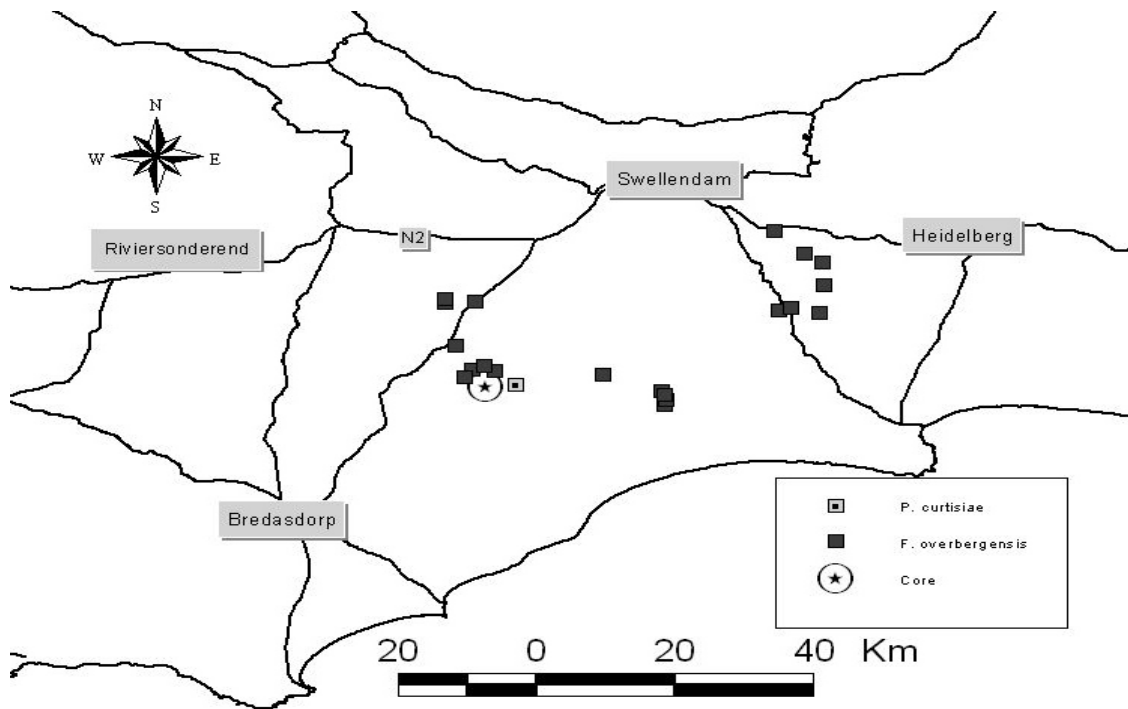


Figure 8. Distribution map of *Ficinia overbergensis* and single location for *Polhillia curtisiae*, based on surveys in this study.

Diagnostic characters

Ficinia overbergensis has morphological and ecological similarity to *F. quartzicola* Muasya & N.E.Helme. Both taxa grow in quartz substrate but are geographically separated with *F. quartzicola* only known from the Knersvlakte (Muasya et al. 2012), where it forms tufts of similar size. Morphologically, the species share sticky leaf sheaths, but *F. quartzicola* forms tough tufts (stuck together tightly) with rigid culms that lack leaf blades. The inflorescence of *F. overbergensis* is capitate with 2 or 3 leafy involucre bracts and 3–6 spikelets whereas *F. quartzicola* has a pseudolateral to capitate inflorescence with 5–10 spikelets and where the involucre bract is stem-like.

Distribution and habitat

F. overbergensis is currently known from the Eastern Rûens Shale Renosterveld occurring on quartz-silcrete patches (Fig. 8). It also grows on silcrete substrates where quartz is not strongly exposed, and extends to lower altitudes (to 10 m above sea level).

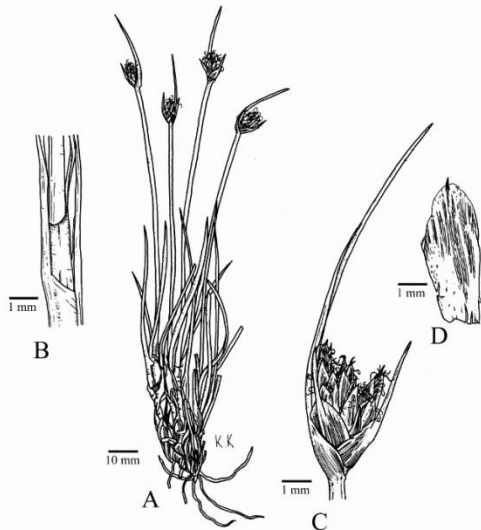


Figure 9. *Ficinia overbergensis*: (A) habit; (B) leafy culm; (C) inflorescence; (D) glume. All drawn from Von Witt CR6010 by K-L Kilian.

Conservation status

This taxon is currently known from scattered localities in the Overberg, all under private ownership, with several currently used as grazing for sheep. Although there are no threats evident at any site, overgrazing could be a potential threat, and it is estimated to comprise fewer than 100 tufts at each site, and it is thus very likely that the total area of occupancy is less than 1 km². We therefore assess this taxon as Near Threatened (Raimondo et al., 2009).

Additional specimens examined

3420 (Bredasdorp): Haarwegskloof, N of Plaatjieskraal, near San Souci, 29 Aug 2008, Von Witt 6010 (BOL, NBG); Cape Agulhas - Elim Murram road, 24 Jan 2009, Muasya & Muthama 4354 (BOL); Goereesoe, off Bredasdorp-Swellendam road, 7 Dec 2011, Muasya, Stirton & Curtis 6333 (BOL); Goereesoe, 30 Aug 1962, Acocks 22669 (BR, PRE); Rooi Vlei, off Bredasdorp-Swellendam Road, 30 Sep 2012, Muasya, Stirton & Curtis 6596 (BOL); Swellendam Road, 30 Sep 2012, Muasya, Stirton & Curtis 6596 (BOL); Plaatjieskraal, 7 Dec 2011, Muasya, Stirton & Curtis 6342 (BOL); Plaatjieskraal, 30 Sep 2012, Muasya, Stirton & Curtis 6599 (BOL); Nysty Farm, 40 km N. of Bredasdorp, along San Souci Road, 2 Dec 2011, Stirton & Curtis 13450 (BOL).

4. Discussion

4.1 *Is Overberg Quartzveld a hotspot of endemism and should it be recognised as a distinct vegetation unit?*

From the data we have presented it is clear that the quartz patches occurring on silcrete outcrops in ERS renosterveld comprise distinct plant communities and are hotspots of endemism. This was not recognised by Schmiedel (2002) although she did recognise *Gibbaeum haagei* as an endemic and characteristic species of the quartz habitats. A relatively small number of surveys within these patches have revealed a suite of new species and it is likely that further surveys will reveal more new discoveries. With up to 19 endemic species, quartz-silcrete patches in ERS Renosterveld display higher levels of endemism than the quartz fields of the Little Karoo (10 endemic species), but lower than in the Knersvlakte which displays exceptionally high levels of endemism (39 endemic species) (Schmiedel and Jürgens, 1999). Unlike the quartz fields of the Succulent Karoo which are dominated by nanochamaephytes (succulent dwarf shrubs <5 cm - Schmiedel and Jürgens, 1999) and contain no shrubs or trees >50cm tall, the Overberg's quartz patches comprise a high diversity of species from different family groups, including a notable number of legumes (Fabaceae), as well as several grasses and asteraceous shrubs over 50cm in height. This may be due to the more fertile soils and higher rainfall to which the Overberg's patches are subject, when compared with their Karoo counterparts. *Clutia govaertsii* is currently described as occurring between Albertinia and Brak River on stony gravel slopes (Goldblatt & Manning 2000) and is listed as Least Concern (Raimondo et al. 2009). However, our study has demonstrated that this species appears to be a quartz / silcrete endemic within ERS Renosterveld. We therefore recommend that the ecology and threat status of this *Clutia* be investigated further and considered for listing as Near Threatened or Vulnerable in the near future.

4.2 How to deal with microhabitats within broad vegetation types

Currently, routine vegetation classification methods (Mucina and Rutherford, 2006) do not include vegetation anomalies or microhabitats within existing vegetation types. While we acknowledge that revising the system to include the many different micro-vegetation types might be a lengthy and complicated process, it is important that we at least acknowledge these distinct habitats that are currently lumped under the same description as the more wide-spread habitat in which they occur. Quartz-silcrete patches are not the only micro-vegetation types within ERS Renosterveld: this system also contains thicket, fynbos and riparian systems – all currently not recognised within this vegetation type. We therefore recommend that a different and more detailed approach to vegetation mapping is considered in future, so that these area-specific vegetation types can be recognised when describing vegetation at the landscape-level. This is of particular relevance when generating conservation plans where the maintenance of biodiversity at the landscape level is the primary objective. If this approach is taken, we further recommend that the quartz-silcrete patches

in ERS Renosterveld are recognised as a distinct vegetation type, namely *Overberg Quartzveld*, and that this is listed as *Critically Endangered*, given that this vegetation is completely restricted to outcrops within an existing *Critically Endangered* vegetation type, is vulnerable to poor livestock management, and is not represented in any Protected Area. However, we stress that it is the nature of their distinctness, size and location that makes it possible to identify and manage them practically. While it is clear that Overberg Quartzveld is a distinct plant community, it is still uncertain at what level it might be recognized. Further studies are needed of all of the quartzveld patches, as well as other distinct vegetation types which occur in a scattered fashion within a broader habitat, in the Cape Floristic Region before this question can be resolved. Also, if this community were to be recognized as a separate vegetation type, it would not be difficult to map, as the quartz patches are fairly easy to identify from satellite imagery. However, this approach might not be a viable one for all 'micro-habitats' or special vegetation units within broader vegetation units, as mapping habitats that are less distinguishable on available satellite imagery may not be as viable.

4.3 Management of Overberg Quartzveld

Although very few palatable species occur in Overberg Quartzveld, many of the endemics are highly susceptible to the deleterious effects of heavy trampling by livestock (sheep, cattle & ostriches) and therefore, livestock management is an essential component of keeping these patches intact. This essentially involves fencing remnants off from productive lands. However, this management intervention is important for the maintenance of lowland renosterveld generally but is an expensive outlay for a landowner and most are unable to carry these costs (O. Curtis pers. obs). Inappropriate fire regimes will also be detrimental to the future of these patches, which probably would have escaped fire due to their more open, rocky habitat and they are therefore not as fire-adapted as the grassier renosterveld surrounding the outcrops. Certainly, some species are slow maturing, such as *Relhania garnotii*, which is believed to require 20 years to reach maturation (Raimondo et al., 2009) and thus we caution against the use of frequent fires within this renosterveld region. Conversely, some species, such as *Xiphotheca rosmarinifolia*, only flower after a fire (Schutte-Vlok 2011) and we suspect this might also be the case for *Otholobium curtisiae*.

It is important to remember that these quartz patches are part of a bigger system and that they should not be managed in isolation, from either the natural habitats in which they are nested, or from the matrix of transformed land surrounded them. There is a dearth of knowledge with regards the life-histories of many renosterveld plants and their pollinators – and this applies particularly to the specialists and the endemics. Thus reserve design and management should be as inclusive as possible, as without conserving processes and inter-dependencies, we may merely be prolonging

extinctions debts (Tilman et al. 1994). Additional studies on the ecology of these plants and their respective pollinators should be a priority for future renosterveld research. Also, as the surveys carried out in this study were limited due to time constraints, a more detailed examination of alpha, beta and gamma diversity across the renosterveld in which the quartz-silcrete hillocks occur would be invaluable.

4.3 Protecting the last remnants of Overberg renosterveld

Despite a heightened awareness about the levels of threat which renosterveld faces (e.g. von Hase et al. 2003), conservation efforts to conserve renosterveld across the Overberg landscape have been largely fruitless, with some rare exceptions. The $\pm 30,000$ ha that remain today represent less than 6% of the original extent of this vegetation type. Only four of these remnants are larger than 500 ha and 30 are larger than 100 ha. About 30% of these 'large' (i.e. >100 ha) fragments contain quartz patches. We reiterate that these quartz patches have been overlooked in the past and emphasize the need for further research and conservation attention in these habitats. These areas are relatively small in a global context, but comprise some of the richest plant diversity in the world, within the smallest, but richest Plant Kingdom, thus any successful attempts to secure these fragments for long-term conservation will certainly be of significant conservation and biodiversity value. By focusing on a small component of this rich ecosystem our study has highlighted the urgency for conservation organizations to urgently re-prioritize some of their efforts within the Fynbos biome.

We have presented data that shows that the quartz fields south of the Langeberg are not relicts of a fairly species-poor quartz field phytochorion as previously thought, but instead are a rich and distinct assemblage of species on an old landscape. The distinctive Overberg Quartz-silcrete patches, just one of a number micro-vegetation types within ERS Renosterveld, are a challenge to broader landscape and vegetation mapping, particularly given their conservation importance. They do stand apart though in that they are easier to identify than the other micro-vegetation units and have a better potential to be managed and protected. Finally, this study has shown that there is still urgent work needed to fully document the plant diversity of the much-neglected renosterveld and that, given its threatened existence, it deserves a higher priority from conservation bodies and biodiversity NGOs.

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Appendix 1.1 (Curtis *et al.* 2013). Summary of Bray-Curtis Similarity Matrix generated for plant communities on quartz-silcrete outcrops on renosterveld in the Overberg, Western Cape. Key to farm names: AB=Aandblom, D=Dipka, GRS=Goereesoe, GK=Grootkloof, HWK=Haarwegskloof, K=Koppies, NKH=Niekerkshok, NKM=Napkysmond, NY=Nysty, OK=Oudekraal, PB=Potteberg, PK=Plaatjieskraal, UIT-Uitvlugt, UVS=Uitvlugt school, VST=Vorstekop, WGM=Welgemoed, ZK=Zandkraal

	GORS	NY1	NY2	PL1	PL2	HWK1	UVS	NKM1	WGM1	UIT1	UIT2	AB	K2	ODK1	ODK2	GK	D1	VST	ZK	K1	NKH	PB1	PB2	PB3	PB4
GORS																									
NY1	78																								
NY2	44	55																							
PL1	63	66	52																						
PL2	67	57	50	77																					
HWK1	61	60	49	73	70																				
UVS	51	50	52	49	42	59																			
NKM1	39	44	44	31	31	35	46																		
WGM1	61	54	50	60	55	58	45	37																	
UIT1	35	40	57	42	38	37	58	50	48																
UIT2	47	46	54	54	43	56	69	56	53	70															
AB	52	44	35	44	36	40	62	36	52	60	80														
K2	47	51	46	46	48	42	41	48	47	44	43	32													
ODK1	47	51	46	50	48	42	48	48	47	44	50	32	79												
ODK2	31	42	25	30	30	29	30	35	29	19	15	17	39	46											
GK	56	60	43	48	50	40	39	52	38	40	47	44	60	67	36										
D1	36	41	50	38	39	32	35	42	50	47	46	32	64	73	20	67									
VST	30	36	32	29	29	22	27	22	44	25	29	33	48	57	32	52	80								
ZK	39	38	26	27	31	35	39	73	37	40	40	36	48	40	26	44	32	22							
K1	52	63	61	40	36	40	39	55	52	40	48	36	72	72	44	52	63	56	46						
NKH	52	56	44	36	31	35	39	27	44	40	32	36	40	40	44	59	53	56	46	46					
PB1	55	59	48	51	44	48	64	50	55	46	52	42	44	59	24	41	57	40	42	50	33				
PB2	59	71	50	76	58	64	51	46	55	36	47	34	53	58	39	50	44	32	40	51	40	65			
PB3	54	58	41	55	44	57	63	50	61	46	52	36	52	65	35	55	56	42	50	50	50	73	78		
PB4	65	68	40	67	63	65	58	41	51	38	43	35	49	60	40	56	45	33	41	47	47	61	89	80	

APPENDIX 2: Co-authored paper in prep. (awaiting review)

A new species of *Hesperantha* Ker Gawl. (Iridaceae: Crocoideae) from the Overberg, Western Cape, with observations on a novel strategy for pollen transfer in the genus and family by a hesperid butterfly

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Keywords: Iridaceae, *Hesperantha*, Hesperidae, new species, pollination, southern Africa, *Tsitana*, taxonomy

ABSTRACT

Hesperantha kiaratayloriae is a new species from the Rûens Hills northeast of Bredasdorp, Western Cape. It is distinguished by its diurnal, small pink flowers with stamens tightly surrounding the exerted style, which divides near the apices of the anthers. The three style branches are erect and loosely coiled around one another well above the mouth of the perianth tube. The arrangement of the stamens, exerted style and erect style branches are unique for the genus. The bell-shaped corms with an oblique flat base and floral bracts united basally around the spike are consistent with sect. *Radiatae*, and the twisted style branches and short leaves clasping the flowering stem are shared with white-flowered *H. muirii* (L.Bolus) G.J.Lewis, putatively its closest ally in the genus. The flowers begin to open at about 06:00 and close after 12:30, reopening the next day. At its only known site, open flowers were visited by the small butterfly *Tsitana* cf. *tulbagha* (Hesperidae), which effected pollen transfer to stigmatic surfaces. Although it is not yet established that this butterfly is the sole pollinator of the species or

whether it is part of a more generalist pollination system, this is nevertheless the first record of a hesperid butterfly as a pollinator in any sub-Saharan Iridaceae. The unscented flowers and perianth tube 13–16 mm long containing nectar are consistent with pollination by small butterflies, which is an uncommon strategy for pollen transfer in Iridaceae.

INTRODUCTION

Plants of an unknown species of *Hesperantha* Ker Gawl. discovered in the Rûens Hills northeast of Bredasdorp, Western Cape, South Africa present some unusual features in the genus. *Hesperantha*, a sub-Saharan African genus of some 85 species of Iridaceae subfamily Crocoideae Burnett, extends from Western Cape to Ethiopia and Cameroon (Goldblatt 2003, Goldblatt & Manning 2007, Goldblatt & Manning in prep.). The genus is recognized by \pm woody corm tunics and a spicate inflorescence of radially symmetric flowers with the style branches dividing close to the mouth of the perianth tube into long, spreading style branches. The new species, *H. kiaratayloriae*, has diurnal, small pink, salver-shaped flowers that are remarkable for the erect stamens tightly enclosing the exerted style. The style divides well above the mouth of the perianth tube near the apices of the anthers, thus unlike any other species in the genus, and the three style branches, which are loosely twisted or coiled around one another, are held well above the mouth of the perianth tube. Although the exerted style and erect style branches are unique for the genus, the bell-shaped corms with an oblique flat base and floral bracts united basally around the spike are consistent with sect. *Radiatae* Goldblatt. Three days of observation for pollinators have shown that the flowers, which begin to open at about 6:00 and close after 12:30, are visited and pollinated by the small butterfly *Tsitana tulbagha* (Hesperidae), not before recorded as an agent for pollen transfer in any sub-Saharan species of Iridaceae (Goldblatt & Manning 2006). We describe the new species here, discuss its relationships within *Hesperantha*, and present evidence for this novel pollination system within Iridaceae.

TAXONOMY

***Hesperantha kiaratayloriae* Goldblatt & J.C.Manning, sp. nov.**

TYPE.—Western Cape, 3420 (Bredasdorp): Rûens Hills, northeast of Bredasdorp, Farm Plaatjieskraal, upper slopes of ridge in stony quartzite gravel over shale, (–AC), 8 Nov. 2011, *Goldblatt & Porter 13729* (NBG, holo.; K, MO, PRE, iso.).

Plants mostly 150–200 mm high, rarely to 300 mm, erect, unbranched. *Corm* obliquely bell-shaped, 6–8 mm diam. at base, tunics \pm woody, dark grey, fragmenting from lower margins into tile-like segments.

Leaves several, dry at flowering time, sheaths imbricate, blades linear, mostly 10–60 × 1.0–1.5 mm, margins smooth, uppermost 2 or 3 leaves sheathing for entire length. *Spike* 2–4(–7)-flowered, flexuose; bracts dry and pale brown at flowering, outer mostly 12–15 mm long with margins connate near base for 1–2 mm and sheathing spike axis, inner slightly shorter than outer and forked apically. *Flowers* diurnal, pink with white throat, unscented, anthers bright yellow and prominently displayed; perianth tube cylindric, slightly expanded at apex, 13–16 mm long, distal half exerted from bracts; tepals subequal, spreading horizontally, elliptic, ± 12 × 4–5 mm, outer slightly larger than inner. *Stamens* symmetrically disposed, erect; filaments 2.5 mm long, exerted ± 1 mm from mouth of tube; anthers ± 5 mm long, yellow, remaining coherent around style. *Ovary* ovoid-oblong, ± 6 mm long; style exerted and dividing just below anther apices, branches ± 5 mm long, remaining erect, slightly twisted and often interlaced. *Capsules* subcylindric, 7–8 mm long. *Seeds* angular, ± 0.7 × 0.4 mm, with membranous raphal ridge expanded into a wing at micropylar end, surface cells colliculate. *Flowering time*: (late October) November. Figure 1.

Distribution & ecology: known from a single south-facing ridge in Eastern Rûens Shale Renosterveld (Mucina & Rutherford 2006), ± 40 km northeast of Bredasdorp, *Hesperantha kiaratayloriae* grows among silcrete-quartzite stones over a shale substrate among tufts of the graminoids *Pentachistis* and *Merxmeullera* (Poaceae) and *Bobartia* (Iridaceae), and the shrubs *Elytropappus rhinocerotis* (L.f.) Less. (Asteraceae), *Amphithalea violacea* (E.Mey.) Benth and *Aspalathus mundiana* Eckl. & Zeyh. (Fabaceae). It shares this unique habitat with several threatened quartz-specialists, including *Gibbaeum haagei* Schwantes (Aizoaceae: *Endangered*), *Elegia verreauxii* Mast. (Restionaceae: *Vulnerable*) (*Notobubon striatum* (Thunb.) Magee (Apiaceae: *Near Threatened*), *Otholobium curtisiae* C.H.Stirt. & Muasya ined. (Fabaceae, proposed status *Endangered*), as well as the recently described *Xiphotheca rosemarinifolia* A.L.Schutte (Fabaceae: *Critically Endangered*), which is known only from this single locality.

Although there is thus a good probability that *H. kiaratayloriae* may likewise be restricted to this single locality, additional surveys are required to establish this. Silcrete-quartz outcrops are restricted to Eastern Rûens Shale Renosterveld, a *Critically Endangered* vegetation type, with <12% remaining (SANBI & DEAT 2009). Renosterveld remnants are vulnerable to mismanagement, including inappropriate use of fire and over-grazing and trampling by livestock (Schutte-Vlok 2011, O. Curtis pers. obs.). Given the evident rarity of the species and the threats from agriculture to single known locality, which remains unprotected, we suggest a conservation status of *Critically Endangered* (CE).

The leaves of *Hesperantha kiaratayloriae* are dry and withered at flowering, a feature not known elsewhere in the genus and evidently associated with its late spring/early summer flowering. The pink,

unscented flowers last three days (determined by maintaining cut stems in water in the laboratory), and open early in the morning each day, \pm 06:00, beginning to close after 12:30 and are fully closed by 13:30.

Diagnosis and relationships: a small plant, *Hesperantha kiaratayloriae* has small pink flowers with a relatively long perianth tube, 13–16 mm long and slightly longer than the tepals, erect stamens with the anthers connate around the style, and an erect style that divides opposite the anther apices into three erect, slightly twisted branches. The short, linear leaves are \pm dry at flowering and the floral bracts are united for 1–2 mm around the spike axis. The general aspect of *H. kiaratayloriae* is that of sect. *Radiata*, diagnosed by the flat-based corms with hard tunics fragmented at the base, and the partial union of the outer floral bract margins around the spike axis (Goldblatt 2003). A well developed perianth tube is common in the genus and not unusual in sect. *Radiata* but pink flowers are otherwise known in the section only in *H. elsiae* Goldblatt from the southern Cedarberg, which in other features, including a long perianth tube, is very different to *H. kiaratayloriae* (Goldblatt 1984). The southern Cape *H. muirii* (L.Bolus) G.J.Lewis is most like *H. kiaratayloriae* in the twisted style branches (although spreading in the former) and we see the two as a species pair within the section.

The relatively long style enclosed by the erect stamens and dividing well above the mouth of the perianth tube close to the anther apices significantly expands the circumscription of *Hesperantha*.

The species is named for Kiara May-Leen Taylor in honour of the generous donation to renosterveld conservation by her father, Oren Taylor.

POLLINATION

Only a single insect species, the skipper butterfly *Tsitana*, cf. *T. tulbagha* (Hesperiidae), was seen visiting flowers of *Hesperantha kiaratayloriae* over two days of observations. The bright pink flowers evidently lack floral odour as determined from open flowers held indoors in a warm, still room. Several (<10 individuals) *Tsitana* butterflies were observed visiting the flowers after 6:30, soon after the perianth expanded fully, moving directly from one opened flower to another. On alighting on a flower, the frons of the insect first contacted the style branches, the surfaces of which are sticky and stigmatic throughout the lifespan of a flower. The insect then inserted its proboscis into the floral tube, evidently foraging for nectar present in the lower part of the perianth tube (nectar concentration and chemistry not examined) but we confirm the presence of nectar, sweet to the taste. During foraging activity the frons of the insects became visibly covered with a dense accumulation of bright orange pollen from contact with the anthers. Stigmas that were devoid of pollen before visits by *T. cf. tulbagha* were seen to bear heavy deposits of pollen after visits by the butterfly.

Our observations show that this butterfly is an active and effective agent for pollen transfer *H. kiaratayloriae*. We also note that we observed no other insect visitors to the flowers either in the early morning or later (several hours of observation on different days). From this we then infer that *Tsitana* cf. *tulbaghia* is at least one but possibly the sole pollinator of the species at this locality.

Butterfly pollination is evidently rare among southern African Iridaceae apart from the guild of species with large red flowers, mostly species of *Gladiolus* and *Tritoniopsis*, pollinated predominantly by *Meneris tulbaghia* (Satyridae) (Goldblatt & Manning 2002, 2005, 2006), a very different system to that reported here. Pollination by the Painted Lady *Cynthia cardui* (Pieridae) has been observed in yellow-flowered *Ixia acaulis* Goldblatt & J.C.Manning and *Nivenia parviflora* Goldblatt & J.C.Manning and this butterfly is the only recorded visitor to *I. acaulis* (Goldblatt & Manning 1993, 2006, 2011). Several other species of Iridaceae are visited by butterflies as part of a generalist pollination system also involving nectar-feeding bees and sometimes hopliine beetles. These include *I. orientalis* L.Bolus, reported as pollinated by the butterfly *Colias electo* (Pieridae) (Goldblatt *et al.* 2000), and *Micranthus* spp., visited by *Pieris helice* (Pieridae) and *Belenois aurata* (Pieridae), but these plants are generalists and are also visited and pollinated by hopliine beetles and large anthophorine bees (Goldblatt & Manning 2006). *Colias electo* has also been captured while visiting flowers of *Geissorhiza foliosa* Baker and *G. heterostyla* L.Bolus but its role in the pollination of these relatively short-tubed species is uncertain (Goldblatt & Manning 2009).

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Appendices to thesis

APPENDIX 3.1. Quotes from early settlers / explorers / authors referring to the vegetation of the Overberg.

From: C. J. Skead 1980 (*Historical mammal incidence in the Cape Province*, Volume 1, the Western and Northern Cape. Zone 9: The Overberg)

Sparrman, 1775

Bot River and environs: "Rode on horseback over plains, hills and dales. The whole of this extensive tract was, by reason of the default of water, left uncultivated and uninhabited." (Sparrman saw for the first time large herds of plains-game and ostriches and mentions them – Skead).

Lichtenstein, 1803

Zoetemelks valley (Soetmelksvlei), just east of Riviersonderend, 60 km E. Caledon: "The valley of Zoetemelk is a place which in earliest times, on account of its **excellent grass**, had been used by government for resting and recruiting cattle bought of the distant Hottentot tribes and destined for slaughter in the town."

Burchell, 1811

From Caledon to Genadendal, round the western end of the Swartberg: "The face of the country was open and its surface varied with smooth hills covered almost exclusively with a neat, pale bushy shrub of the height of 3 or 4 feet called Rhinoster bosch (Rhinoceros bush) (Fn. Stoebe rhinocerotis) and said to have formally been the food of the huge rhinoceros till those animals fled before the colonists as they gradually advanced over the country where the shrub grows."

Riviersonderend: "Firewood is an article generally very scarce in the vicinity of a Hottentot settlement, and in all the grazing parts of the colony it is rendered much more so by the **wasteful and destructive practice of annually setting fire to the old withered grass as the means of clearing the pastures.**"

La Trobe, 1816

At Sergeant's River, Caledon District: "... surrounded by the same dreary country as before. Very few shrubs and low bushes enclose the Sergeant's River in the valley."

J.W.D. Moodie, 1819/20

Western Caledon District: "The surface of the country from the time we left Hottentots Holland Kloef had been gradually improving and **was better covered with grass**. There were more springs... **the sombre hue of the grass** which was still of dry and coarse quality and closely eaten by the numerous cattle and flocks of sheep."

Bunbury 1848

From Houw Hoek Pass to the Zonder-Einde River (Riviersonderend): "... wide plains and low round hills uniformly covered with stunted bushes, without trees or cultivation. There is little grass and most of the shrubs which make up the great mass of the vegetation have either leaves so minute, and of substance so dry and juiceless, that they give no verdant effect to the landscape, or else are covered with a whitish wool or down which entirely hides their green. In this latter class is to be ranked the prevailing Rhinosterbosch or Rhinoceros bush, Stoebe rhinocerotis, which literally covers leagues and leagues together in the districts of Zwellendam and George. It is a low, half-shrubby, grey, cottony plant, in form resembling a miniature cypress or juniper."

Between the Kars- and Breede Rivers: "I also found waterless hills of slate-clay with a sort of aloe growing about 5-6 ft high, the sap of which is collected. There were mimosas (*Lycium kraussii*) and other sorts of karroo plants as well. As I was in a hurry I travelled on that day until nearly midnight and had to outspan in the open veld without having found grass or water." (10 Dec. 1938).

Between Swellendam and Buffeljagsrivier: "... I again had the strange experience of seeing a bushfire... in the fields and on the slopes of the mountains the farmers set fire to the dead bushes and the dry, sour Restiacean grass to make way for fresh grass to grow again. It was lovely to watch the strips of fire running in all directions into the ravines of the mountains."

From C. G. Botha 1924 (read at the Symposium on Veld Burning: *Note on early veld burning in the Cape Colony*)

"There are many farmers to-day who consider it advantageous to burn their grasslands which have become depastured by cattle so that there may be a better crop after the rains. Kolbe, in his 'Beschryving van de Kaap de Goede Hoop' (1727) informs us that the Cape Farmers learnt the practice from the Hottentots, who burnt the grass when it became too old and the cattle could not pasture there.... From the early days of the settlement, the government set its face against this practice and we find repeated prohibitions in the law against it... In 1687 a law was passed imposing the severest penalties for contravention, namely, a severe scourging for the first offence and death by hanging for the second... Regardless of the law, veld burning went on..."

In discussions following this presentation, the following are recorded: "Mr. Malleson said that, speaking as a farmer, veld burning was a terrible menace... That perpetual burning had also done away with useful grasses. They must stop that veld burning. Riversdale, instead of being a good grass district, had Rhenoster bush, and the value of the land had been reduced to £2 per morgen." Also, "Mr J. Smuts contended that the manner in which the habit should be eradicated by means of the education of the younger generation; it was, he said, a deeply-rooted habit amongst their farmers. **The result was that the finer grasses were destroyed, and the coarser kinds remained.**"

From Muir 1929 (Muir, J. 1929. The vegetation of the Riversdale area, Cape Province. Botanical Survey of South Africa, Memoir no. 13: 1-82. In: Supplement VII: British Empire Vegetation Extracts: Titles and Abstracts of Publications on the Vegetation and Ecology of the Overseas Empire and on Related Topics. *Journal of Ecology* 19(2): 103-125).

The Renosterveld: This lies between the Strandveld and the Langebergen in the middle of the district: it is characterised by gently undulating hills and valleys, and is fairly well watered. The vegetation contrasts strongly with that of the Strandveld, the Proteaceae, Ericaceae and Restionaceae becoming scarcer as one goes northwards and *Sideroxylon inerme* almost entirely disappearing. The vegetation is of a sclerophyllous type with *Elytropappus Rhinocerotis*, a xerophytic shrub belonging to the Compositae, dominant. In the Rhenoster- veld area proper *Relhania genistaefolia* and the grasses *Cynodon dactylon* and *Themeda forskalii* are often sub-dominant, and the three great geophytic families of Monocotyledons are well represented owing to centuries of veld burning. The Aloe Scrub, confined to the hill slopes of the eastern half of the Division, is being rapidly cleared away, except on rocky ground. The characteristic species are *Aloe ferox*, *A. arborescens* and *A. Salmdyckiana*, while *Sideroxylon inerme* and *Cussonia spicata* are common trees in the scrub. Species of *Rhus* and several Celastraceae are represented, also several succulents and such climbers as *Asparagus* spp. and *Sarcostemma viminale*. A marked feature is the number of species with thorns. *Acacia karoo* occurs in the river valleys of the Renosterveld.

From Levyns, 1929 (*The Problem of the Rhenoster Bush*, South African Journal of Science XXVI: 166-169).

"Sparrman, one of the most distinguished of the early South African travellers, refers to the **spread of Rhenoster bush as long ago as 1775**. To-day the plant is still regarded as a pest by the farming community and it is therefore a matter of some importance to have a detailed knowledge of its habit and life-history."

“Veld on which the rhenoster bush is firmly established is useless to pasture and farmers resort to burning in order to induce a temporary growth of other plants suitable for grazing. Recent experiments... have rendered it obvious that this is a shortsighted policy and only serves to perpetuate the rhenoster bush.”

“Ecologically, therefore, rhenosterveld must be considered a stage, though probably a protracted stage, in succession and not a climax. Burning is undoubtedly responsible for the wide spread of the rhenoster bush over large areas of the country, as this practice tends to keep the plant community in this particular stage in succession.”

From Newton & Knight (2004) (Newton, I. P. & Knight, R. 2004. The matrix: the evolutionary development of coastal renosterveld. *Veld & Flora* (Dec): 162 – 165).

Levyns 1936

Before renosterveld is once more established there is a series of successional changes distributed over several years... (referring to south coast renosterveld).

R.S. Adamson in 1929

..owes presence to man’s disturbance... (referring to both south and west coast renosterveld)

From R. S. Adamson, 1938 (*The Vegetation of South Africa*, Chapter V: Bush (Sclerophyll) vegetation)

“Alterations of the vegetation as a result of man’s activity are probably more widespread and general in the Sclerophyll than in any other type in the country. The main agent has been fire, which has affected all but the very driest portions... one of the commonest and most extensive is completely dominated by *Elytropappus rhinocerotis*, Rhenosterbush. This forms extensive tracts of secondary vegetation. It covers most of the clay-like soils on the lower grounds. Such soils have been much cultivated and over large areas the original vegetation has disappeared; all uncultivated areas are now covered by Rhenosterbush... **All farmers and others connected with the land are agreed that the plant is much more abundant than it once was, and there is some evidence that its range has increased... Continued disturbance helps to perpetuate the plant.**”

Omer-Cooper & Shiff, 1955

“The renosterbos *Elytropappus rhinocerotis* (Linn.) Less., is a very unusual plant, for it is not only a Western Cape endemic belonging to an endemic genus, but it is a dominant organism which has been spreading for more than 200 years and was in already in 1786, when Sparrman wrote about it, described by the farmers of the Cape Province as a ‘punishment for their sins’.”

Appendix 3.2. Summary of $\delta^{13}\text{C}$ results from soil samples. Note the disagreement in $\delta^{13}\text{C}$ values for top soil and litter for several samples.

Sample name	Vegetation type	Aspect	Slope	Dominant vegetation at soil pit	Expected signature for dominant vegetation	Litter $\delta^{13}\text{C}$	Top $\delta^{13}\text{C}$	Signature of Top	Middle $\delta^{13}\text{C}$	Signature Middle	Lower $\delta^{13}\text{C}$	Signature Lower
BK1	WRS Rveld	W	low-lying	Clover, weeds	C3	-26.27	-23.71	Mixed	-22.00	Mixed	-20.77	Mixed
BK2	WRS Rveld	N	low-lying	Wheat	C3	-15.30	-23.26	Mixed	-24.12	Mixed	-23.39	Mixed
BK3	WRS Rveld	N	slope	Themeda, Cymbopogon	C4	-18.03	-19.85	Mixed	-18.19	Mixed	-17.20	Mixed
BK4	WRS Rveld	N-NW	slope	Merxmuellera, Elytropappus	C3	-26.48	-25.41	C3	-24.72	Mixed	-24.85	Mixed
BK5	WRS Rveld	S	slope	Aspalathus, Ehrharta calycina	C3	-26.48	-25.45	C3	-24.72	Mixed	-24.71	Mixed
BK6	WRS Rveld	S-SW	slope	Clover, mixed grasses	C3	-26.27	-25.87	C3	-22.71	Mixed	-22.29	Mixed
CC	WRS Rveld	S	slope	Themeda, Cymbopogon	C4	-19.27	-23.01	Mixed	-21.48	Mixed	-21.99	Mixed
EC	CRS Rveld	-	flat	Cymbopogon	C4	-19.43	-24.41	Mixed				
	WRS Rveld	S	slope	Merxmuellera, Elytropappus,	Mixed							
FF1				Themeda		-28.02	-23.41	Mixed				
FF2	WRS Rveld	N	slope	Merxmuellera, Cymbopogon	Mixed	-26.00	-24.43	Mixed	-23.72	Mixed	-23.71	Mixed
FF3	WRS Rveld	S	slope	Merxmuellera, Helichrysum	C3	-27.04	-25.17	C3	-25.35	C3	-25.04	C3
FF4	WRS Rveld	-	hilltop	Wheat	C3	-16.79	-26.59	C3	-23.98	Mixed	-22.78	Mixed
FF5	WRS Rveld	SE	slope	Themeda, Elytropappus	Mixed	-27.96	-25.09	C3	-20.87	Mixed	-23.68	Mixed
	CRS Rveld	S	slope	Themeda, Merxmuellera,	Mixed							
FTK1				Elytropappus		-21.72	-23.72	Mixed	-22.33	Mixed	-19.38	Mixed
FTK2	CRS Rveld	-	hilltop	Themeda	C4	-22.63	-24.97	Mixed	-23.74	Mixed	-22.26	Mixed
FTK3	CRS Rveld	W	hilltop	Lucerne	C3	-24.06	-25.42	C3	-21.90	Mixed	-21.34	Mixed
FTK4	CRS Rveld	W	slope	Lucerne	C3	-24.06	-25.01	C3	-23.17	Mixed	-21.97	Mixed
	CRS Rveld		hilltop	Cynodon, Eragrostis curvula,	C3							
FTKR				Sporobolus		-24.65	-22.72	Mixed	-22.67	Mixed	-23.08	Mixed
GVB1	ERS Rveld	E	slope	Merxmuellera	C3	-26.96	-23.40	Mixed	-14.35	C4	-23.02	Mixed
GVB2	ERS Rveld	N	slope	Themeda	C4	-25.78	-15.54	C4	-24.05	Mixed	-14.15	C4
GVB3	ERS Rveld	S	slope	Bobartia, Diosma	C3	-26.49	-25.16	C3	-20.35	Mixed	-24.20	Mixed
KK1	CRS Rveld	-	low-lying	Themeda, Elytropappus, Oedera	Mixed	-21.38	-22.04	Mixed	-25.10	C3	-18.73	Mixed
KK2	CRS Rveld	N	slope	Themeda	C4	-25.99	-25.33	C3			-24.27	Mixed
KK3	CRS Rveld	S	slope	Pentaschistis, Ehrharta calycina	C3	-26.55					-24.59	Mixed
N1	ERS Rveld	S	low-lying	Forage & weed	C3	-27.44	-23.83	Mixed			-20.79	Mixed
N2	ERS Rveld	S	slope	Themeda, Polhillia, Pentaschistis	Mixed	-22.61	-20.98	Mixed	-20.47	Mixed	-20.60	Mixed
N3	ERS Rveld	N	slope	Pentaschistis, Elytropappus	C3	-24.50	-23.00	Mixed	-22.25	Mixed	-21.47	Mixed
	ERS Rveld	E	slope	Pentaschistis, Cymbopogon,	C3							
N4				Ehrharta		-26.84	-25.58	C3	-24.76	Mixed	-24.19	Mixed
N5	ERS Rveld	S-SE	slope	Polhillia, Elytropappus	C3	-27.33	-24.46	Mixed	-21.40	Mixed	-21.73	Mixed
Q1	CRS Rveld	-	low-lying	Cynodon, clover	C3	-27.54	-25.43	C3	-23.06	Mixed	-22.14	Mixed
Q2	CRS Rveld	S-SE	slope	Cynodon, clover	C3	-27.54	-20.85	Mixed	-19.19	Mixed	-15.88	C4

Sample name	Vegetation type	Aspect	Slope	Dominant vegetation at soil pit	Expected signature for dominant vegetation	Litter $\delta^{13}C$	Top $\delta^{13}C$	Signature of Top	Middle $\delta^{13}C$	Signature Middle	Lower $\delta^{13}C$	Signature Lower
Q3	CRS Rveld	-	hilltop	Merxmeullera, Ehrharta, Elytropappus	C3	-26.50	-25.72	C3	-25.33	C3	-24.66	Mixed
Q4	CRS Rveld	S-SW	slope	Fallow pasture	C3	-25.35	-25.25	C3	-23.85	Mixed	-22.09	Mixed
RV1	ERS Rveld	S	slope	Pentaschistis, Elytropappus	C3	-26.83	-25.58	C3	-24.59	Mixed	-24.13	Mixed
RV2	ERS Rveld	E	slope	Wheat	C3	-25.81	-22.28	Mixed	-19.57	Mixed	-20.16	Mixed
RV3	ERS Rveld	N	slope	Pasture	C3	-21.38	-23.63	Mixed	-22.63	Mixed	-20.43	Mixed
SK1	ERS Rveld	NW	slope	Wheat	C3	-16.52	-21.02	Mixed	-20.23	Mixed	-16.70	Mixed
SK2	ERS Rveld	W	hilltop	Coriander	C3	-25.96	-21.58	Mixed	-16.93	Mixed	-20.05	Mixed
UV1	ERS Rveld	N	low-lying	Cynodon	C3	-14.28	-24.53	Mixed	-20.91	Mixed	-20.49	Mixed
VRC1	ERS Rveld	NW	slope	Themeda	C4		-19.06	Mixed			-15.81	C4

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APPENDIX 3.3. Photographs of different renosterveld habitats in the Overberg, showing the variation in grass occurrence and mixtures in communities.



Themeda-dominated renosterveld on south-facing slope and seepage are in the foreground (2 years old), with old *Elytropappus*-dominated renosterveld in the background (Riviersonderend district, Central Rûens Shale Renosterveld).



Themeda-dominated south-facing slope (recently burned), with river and unburned C_3 -dominated patches in the background, between a matrix of grain fields (Napier district, Central Rûens Shale Renosterveld).



North-facing slope dominated by *Cymbopogon* and C_3 shrubs and grasses (Napier district, Central Rûens Shale Renosterveld).



A mixed C₃-C₄ grassy renosterveld (with *Themeda* and *Ehrharta*), rich in geophytes (Napier district, Western Rûens Shale Renosterveld).



C₃-dominated renosterveld with legumes in the foreground and asteraceous shrubs in the background. C₃ grasses are present throughout (Swellendam district, Eastern Rûens Shale Renosterveld).



C₃-dominated renosterveld with *Oedera squarrosa* (Asteraceae) and *Pentaschistis* in the foreground, as well as *Gladiolus vandermerwei*, an *Endangered* Iris (Raimondo *et al.* 2009) (Bredasdorp district, Eastern Rûens Shale Renosterveld).

APPENDIX 4.1. Species recorded on transects at Kykoedie in burned and unburned renosterveld on north- and south-facing slopes. Vegetative response=resprouter (RS), seeder (S), both; Reproductive response=flowered (1), did not flower (0). Those marked with an asterisk represent species with large underground storage organs, in addition to those classified as 'geophytes'.

Species	Guild	North burned		North unburned	South burned		South unburned
		Vegetative response	Reproductive response	Reproductive response	Vegetative response	Reproductive response	Reproductive response
<i>Briza maxima</i>	Annual					1	1
<i>Cotula</i> sp.	Annual					0	
<i>Crassula capensis</i>	Annual						0
<i>Crassula</i> tiny annual	Annual					0	
<i>Diascia capensis</i>	Annual		0	1		0	
<i>Heliophila</i> sp.	Annual		0				
<i>Hemimmaris racemosa</i>	Annual					0	
<i>Isolepis maginata</i>	Annual					0	
<i>Lessertia</i> tiny creeper	Annual					1	
<i>Sebaea aurea</i>	Annual					0	
<i>Zaluzianskya divaricata</i>	Annual					0	
<i>Zaluzianskya villosa</i>	Annual		1				
<i>Albuca</i> sp.	Geophyte	RS	0	1			
<i>Albuca spiralis</i>	Geophyte	RS	0				
<i>Amaryllis belladonna</i>	Geophyte	RS	0				
Apiaceae geophyteous, flat leaves	Geophyte	RS	0		RS	1	
<i>Babiana patula</i>	Geophyte	RS	0		RS	0	
<i>Cyanella lutea</i>	Geophyte	RS	1		RS	0	
<i>Disa bracteata</i>	Geophyte				RS	1	
<i>Drimia capensis</i>	Geophyte	RS	0				
<i>Drimia</i> sp.	Geophyte	RS	1				
<i>Drimia</i> wavy leaves	Geophyte						0
<i>Empodium plicatum</i>	Geophyte	RS	0		RS	0	0
<i>Eriospermum</i> sp.	Geophyte	RS	0	1			
<i>Eucomis regia</i>	Geophyte				RS	0	
<i>Freesia caryophyllaceae</i>	Geophyte				RS	0	
<i>Freesia refracta</i>	Geophyte				RS	0	
<i>Geissorhiza parva</i>	Geophyte				RS	0	
<i>Gethyllis</i> cf <i>grandiflora</i>	Geophyte				RS	0	
<i>Gethyllis villosa</i>	Geophyte				RS	0	
<i>Haemanthus coccineus</i>	Geophyte				RS	0	
<i>Hesperantha fulcata</i>	Geophyte	RS	0		RS	0	
<i>Holothrix schlechteriana</i>	Geophyte			1	RS	0	

<i>Ixia</i> sp.	Geophyte				RS	1	
<i>Lachenalia</i> sp.	Geophyte	RS	0	1			
<i>Laperousia pyramidalis</i>	Geophyte	RS	0				
<i>Massonia echinata</i>	Geophyte				RS	0	
<i>Micranthus</i> sp.	Geophyte				RS	0	
<i>Moraea ciliaris</i>	Geophyte	RS	0				
<i>Moraea fergusoniae</i>	Geophyte				RS	0	
<i>Moraea inconspicua</i>	Geophyte				RS	0	
<i>Moraea</i> spp	Geophyte	RS	0				0
<i>Ornithogalum</i> cf <i>hispidum</i>	Geophyte				RS	1	
<i>Ornithogalum dubium</i>	Geophyte	RS	1		RS	1	0
<i>Ornithogalum thyrsoides</i>	Geophyte	RS	1				1
<i>Oxalis</i> spp.	Geophyte	RS	0		RS	0	
<i>Pelargonium</i> geophytic (fern leaves)	Geophyte				RS	0	
<i>Pterygodium</i> sp.	Geophyte				RS	0	
<i>Romulea rosea</i>	Geophyte				RS	0	
<i>Satyrion neglectum</i>	Geophyte	RS	0		RS	1	
<i>Spiloxene capensis</i>	Geophyte				RS	0	
<i>Spiloxene ovata</i>	Geophyte						0
<i>Syringodea longituba</i>	Geophyte	RS	0				
<i>Trachyandra</i> sp.	Geophyte	RS	0		RS	0	
<i>Wurmbea</i> sp.	Geophyte				RS	0	
<i>Anthospermum galioides</i>	Forb	S	0		S	0	
<i>Arctopus echinata</i>	Forb	S	0				
<i>Arctotis</i> sp.	Forb	S	0		S	1	0
<i>Berkheya barbata</i>	Forb						0
<i>Geophyteine foleyi</i>	Forb	RS	1				
<i>Geophyteine succulenta</i>	Forb				S	0	
<i>Centella</i> sp.	Forb	S	1				
<i>Cyphia</i> sp.	Forb	RS	0		RS	0	
<i>Dianthus</i> sp.	Forb*	RS	1	1	RS	1	1
<i>Dicoma</i> sp.	Forb	Both	1				
<i>Doder</i> sp.	Forb	S	1				
<i>Falkia repens</i>	Forb	S	0				
<i>Fern</i> sp.1	Forb				RS	0	0
<i>Fern</i> sp.2	Forb				RS	0	
<i>Galenia</i> creeper	Forb	S	1				
<i>Gazania krebsiana</i>	Forb*	RS	0	0			
<i>Hermannia</i> red stem	Forb	S	0				
<i>Hibiscus pusilis</i>	Forb*	RS	1		RS	1	
<i>Hibiscus</i> sp2	Forb*	RS	1				
<i>Indigofera porrecta</i>	Forb*	RS	1	1	RS	1	
<i>Lotononis</i> sp.	Forb				S	0	

Microlooma sagittatum	Forb	RS	0				0
Muraltia mualtoides	Forb	S	0				
Pelargonium black ring	Forb				Both	0	
Pelargonium sp grey crinkled	Forb	S	1		S	1	
Polygala garcinii	Forb						1
Scabiosa sp.	Forb				S	1	
Stachys sp.	Forb						0
Sutera sp.	Forb	RS	0		RS	0	
Tephrosia capensis	Forb	S	0				
Thesium sp.	Forb	Both	1	1			1
Zygophyllum sp.	Forb			0			
Chlorus sp.	Grass			1			
Cymbopogon sp.	Grass			0	RS	1	
Ehrharta cf calycina, geophytic	Grass	RS	1		RS	1	1
Ehrharta red oats	Grass						0
Festuca scabra	Grass				RS	0	
Ficinia indica	Sedge				RS	1	
Ficinia sp.	Sedge	RS	0	1	RS	0	0
Isolepis capensis	Sedge				RS	0	
Pentachistis eriostoma	Grass	RS	1	1	RS	1	1
Schoenoxiphium ecklonii	Sedge				RS	0	
Themeda triandra	Grass	RS	0	1	RS	1	1
Anthospermum spathulum	Shrub			0			0
Aspalathus alpestris	Shrub	Both	1	1	Both	1	0
Aspalathus millifolia	Shrub				RS	1	0
Aspalathus creeper	Shrub	RS	1		RS	0	
Aspalathus large white	Shrub			0	S	0	
Aspalathus nigra	Shrub			0			
Aspalathus sp.	Shrub				S	0	
Aspalathus spinosa	Shrub	Both	1	1	RS	1	1
Aspalathus submissa	Shrub	RS	1	0	RS	1	
Asparagus capensis	Shrub	RS	0	0	RS	0	0
Asparagus long thorns	Shrub	RS	0				0
Chrysocoma ciliata	Shrub			1			
Daisy cf Cymbopappus	Shrub	S	1	1			
Elytropappus rhinocerotis	Shrub	S	0	0	S	0	0
Freylinia undulata	Shrub	S	0				
Gnidia soft	Shrub					RS	0
Gnidia squarrosa	Shrub	RS	0		S	0	0
Helichrysum cf cymosum	Shrub	RS	1	1			
Helichrysum cf petiolare	Shrub				S	0	
Helichrysum petiolare	Shrub				S	0	

Hermannia carrot	Shrub				RS	0	
Hermannia crinkled creeper	Shrub	S	1	1	Both	1	
Hermannia flamula	Shrub	S	1		S	1	
Hermannia grey shiney	Shrub	S	1		S	1	
Hermannia saccifera	Shrub	RS	0	0	Both	0	0
Hermannia trifoliata	Shrub	RS	0				
Lessertia large shrub, flat pods	Shrub			1			
Lobostemon echioides	Shrub	Both	1		RS	1	
Lotononis sp. (large shrub)	Shrub			1			1
Lycium sp.	Shrub				S	0	
Metalasia acuta	Shrub				S	0	
Montinia caryophyllaceae	Shrub				RS	0	
Oedera genestifolia	Shrub	S	0	1			1
Oedera squarrosa	Shrub	S	0	1			1
Osteospermum sp.	Shrub	Both	1	0			0
Polygonum sp.	Shrub	RS	1		RS	0	
Printzia polifolia	Shrub				Both	0	1
Pteronia hirsuta	Shrub	RS	1		RS	1	
Rhus rosmarinifolia	Shrub	RS	0		RS	0	0
Rhus sp.	Shrub	RS	0				
Selago (long leaves)	Shrub	RS	1		RS	1	
Selago (short fleshy leaves)	Shrub			1			
Selago (tiny leaves)	Shrub	S		0	S	0	
Walhenbergia sp. Large blue flower	Shrub	RS	1		S	1	
Walhenbergia sp. Tiny p & w flower	Shrub	Both	1	1	RS	1	1
Crassula thin leaves	Succulent	S	1				
Drosanthemum cf hispidum	Succulent	S	1	1	S	1	
Drosanthemum sp (very glossy)	Succulent	S	0		S	0	
Drosanthemum sp.	Succulent	RS	0				
Glottiphyllum	Succulent*	RS	1	0			
Mesemb box leaves	Succulent	S		1			1
Mestoklema tuberosum	Succulent*	RS	1				
Ruschia rigida	Succulent	Both	0		RS	0	
Trichodiadema pygmaeum	Succulent*	RS	0				

APPENDIX 4.2. Numbers of annuals (A) and geophytes (B) recorded in quadrats at Kykoedie on both north- and south-facing slopes, in burned and unburned vegetation.

Species	Guild	North-facing		South-facing		Both slopes	
		Burned	Unburned	Burned	Unburned	Burned	Unburned
<i>Cotula</i> sp.	A	11	5	43	50	54	55
<i>Diascia capensis</i>	A	23	0	43	0	66	0
<i>Felicia</i> tiny yellow daisy	A	0	2	-	-	0	2
<i>Heliophila</i> sp.	A	3	0	12	1	15	1
<i>Nemesia barbata</i>	A	-	-	12	0	12	0
<i>Sebeae</i> sp.	A	1	0	1	11	2	11
<i>Ursinia</i> sp.	A	3	1	3	10	6	11
<i>Zaluzianskya divaricata</i>	A	13	0	28	0	41	0
<i>Zaluzianskya villosa</i>	A	10	0	80	1	90	1
<i>Aristea africana</i>	B	2	0	-	-	2	0
<i>Babiana patula</i>	B	1	1	4	0	5	1
<i>Cyanella</i> sp.	B	7	0	5	5	12	5
<i>Empodium plicatum</i>	B	-	-	15	0	15	0
<i>Eriospermum</i> (heart) sp.	B	1	5	1	0	2	5
<i>Eriospermum</i> large heart	B	-	-	0	2	0	2
<i>Eriospermum paradoxum</i>	B	-	-	0	2	0	2
<i>Freesia refracta</i>	B	-	-	0	2	0	2
<i>Gessorhiza parva</i>	B	1	0	7	3	8	3
<i>Hesperantha fulcata</i>	B	-	-	18	0	18	0
<i>Ixia rapunculoides</i>	B	-	-	16	0	16	0
<i>Gladiolus permeabilis</i>	B	2	1	-	-	2	1
<i>Lachenalia unifolia</i>	B	2	2	0	2	2	4
<i>Lapeirousia pyramidalis</i>	B	0	1	-	-	0	1
<i>Ledebouria</i> sp.	B	1	0	-	-	1	0
<i>Moraea inconspicua</i>	B	2	0	-	-	2	0
<i>Moraea</i> sp.	B	43	2	49	13	92	15
<i>Moraea fergusoniae</i>	B	-	-	8	3	8	3
<i>Moraea gawleri</i>	B	-	-	5	9	5	9
<i>Ornithogalum</i> cf <i>dubium</i>	B	16	0	0	10	16	10
<i>Ornithogalum suavelens</i>	B	5	0	0	3	5	3
<i>Ornithogalum</i> 'tree geophyte'	B	-	-	8	0	8	0
<i>Oxalis</i> bunny tail	B	-	-	1	0	1	0
<i>Oxalis</i> cf <i>polyphylla</i>	B	5	0	-	-	5	0
<i>Oxalis depressa</i>	B	39	6	10	10	49	16
<i>Oxalis</i> hairy	B	-	-	48	51	48	51
<i>Oxalis</i> hairy umbrella	B	-	-	106	31	106	31

Species	Guild	North		South		Total	
		Burned	Unburned	Burned	Unburned	Burned	Unburned
<i>Oxalis purpurea</i>	B	3	0	55	26	58	26
<i>Oxalis red under</i>	B	1	0	-	-	1	0
<i>Oxalis thin umbrella</i>	B	8	2	14	0	22	2
<i>Oxalis tiny leaves, large pink flower</i>	B	8	5	0	17	8	22
<i>Trachyandra</i>	B	2	1	3	0	5	1
<i>Trachyandra sp. (broad leaf)</i>	B	-	-	2	0	2	0
<i>Wurmbea cf variabilis</i>	B	-	-	6	0	6	0
<i>Wurmbea marginata</i>	B	-	-	0	1	0	1

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APPENDIX 5.1. Summary of soil-nutrient data collected and analysed during the present study.

Soil nutrient data from randomly-selected renosterveld sites across the Overberg, Western Cape, South Africa for top soil (T), middle (M) and lower (L) levels in the soil profiles. Results in bold and italics present the two quartz outcrops. Averages exclude samples from quartz outcrops.

Sample	Level in profile	pH	Ca	Mg	P	Na	K	Total K	Total N
		(KCl)	(cmol/kg)	(cmol/kg)	(mg/kg)	(mg/kg)	(mg/kg)	(mg/kg)	%
BK3	T	5.2	2.45	3.24	3	100	117	77.25	0.12
BK4	T	4.3	1.87	1.2	13	46	131	106.05	0.12
BK5	T	5.4	5.75	2.94	21	46	257	113.96	0.19
CC	T	4.6	1.86	1.85	5	46	122	168.64	0.09
EC	T	4.3	5.25	2.2	24	45	170	160.7	0.21
FF1	T	5.2	6.38	3.71	12	224	492	161.34	0.22
FF2	T	4.8	2.98	4.75	13	626	149	79.93	0.2
FF3	T	4.4	2.12	1.98	11	146	191	30.9	0.14
FF5	T	5.4	7.12	5.23	37	210	353	279.85	0.36
FTK1	T	5.4	5.65	3.35	13	120	280	133.21	0.2
FTK2	T	5.9	4.96	4.46	10	74	363	247.52	0.19
GVB1	T	4	1.03	2.35	6	122	49	162.06	0.12
GVB2	T	4.8	3.25	4.22	9	184	131	105.17	0.23
GVB3	T	4.1	1.3	2.46	18	99	98	183.52	0.21
N2	T	5.4	4.69	4.71	6	203	183	210	0.2
N4	T	4.7	7.33	5.23	41	87	315	1243.54	0.49
N5	T	5.1	4.31	3.6	13	169	278	191.41	0.23
Q3	T	5.2	4.03	2.35	15	166	163	143.75	0.17
VR1	T	4.7	2.05	3.36	7	253	49	124.71	0.14
Average		4.89	3.91	3.33	14.58	156.11	204.79	206.50	0.20
<i>P1</i>	<i>T</i>	<i>6.8</i>	<i>0.63</i>	<i>10.35</i>	<i>7</i>	<i>1928</i>	<i>38</i>	<i>310.09</i>	<i>0.09</i>
<i>UVQ2</i>	<i>T</i>	<i>4.3</i>	<i>1.29</i>	<i>3.36</i>	<i>15</i>	<i>1106</i>	<i>99</i>	<i>118.91</i>	<i>0.13</i>
BK3	M	5	2.14	4.08	2	202	55	110.22	0.11
BK4	M	4.4	0.54	0.82	6	59	69	38.89	0.04
BK5	M	5.1	1.6	1.91	3	63	101	94.64	0.07
CC	M	4.6	1.44	1.8	4	93	65	136.12	0.08
FF2	M	4.8	1.38	2.51	4	723	94	13.24	0.08
FF3	M	4.1	1.28	1.6	7	182	139	30.42	0.13
FF3	M	4.1	1.05	1.45	3	272	88	34.07	0.11
FTK1	M	5.5	4.54	3.3	7	157	213	168.6	0.17
FTK2	M	5.6	3.67	3.51	9	74	260	312.47	0.17
GVB2	M	4.9	1.59	4.42	3	537	24	94.6	0.12
GVB3	M	4.3	0.49	2.26	18	140	25	217.72	0.13
N2	M	5.3	2.9	3.89	8	232	162	272.09	0.18
N5	M	5.5	4.5	3.98	7	167	235	236.51	0.17
Q3	M	4.6	2.62	2.06	10	159	150	131.97	0.1
Average		4.84	2.12	2.69	6.50	218.57	120.00	135.11	0.12
<i>P1</i>	<i>M</i>	<i>6.2</i>	<i>0.53</i>	<i>5</i>	<i>3</i>	<i>2106</i>	<i>22</i>	<i>189.86</i>	<i>0.07</i>
<i>UVQ2</i>	<i>M</i>	<i>3.8</i>	<i>0.77</i>	<i>2.73</i>	<i>3</i>	<i>1726</i>	<i>91</i>	<i>60.37</i>	<i>0.07</i>

Cont...

Sample	Level in profile	pH	Ca	Mg	P	Na	K	Total K	Total N
		(KCl)	(cmol/kg)	(cmol/kg)	(mg/kg)	(mg/kg)	(mg/kg)	(mg/kg)	%
BK3	L	5.2	2.02	4.49	2	278	42	176.04	0.1
BK4	L	4.4	0.57	1.03	6	78	75	52.21	0.08
BK5	L	4.8	1.2	1.73	2	65	72	118.21	0.06
FF2	L	5.4	0.97	2.04	2	1325	46	37.52	0.07
FF3	L	4.4	0.78	1.39	1	514	27	20.59	0.09
FF5	L	4.8	1.41	2.23	2	149	193	211.68	0.1
GVB1	L	4.5	1.02	3.02	4	168	38	136.69	0.11
GVB2	L	6	1.78	5.82	2	1265	24	113.74	0.12
GVB3	L	4.4	0.68	2.59	21	165	27	216.83	0.12
N4	L	4.5	2.35	2.81	13	104	201	274.32	0.18
N5	L	5.4	3.24	3.53	6	199	193	274.17	0.17
Q3	L	4.7	1.39	1.35	5	83	104	58.8	0.05
VR1	L	5	2.08	5.19	3	629	23	212.48	0.13
Average		4.88	1.50	2.86	5.31	386.31	81.92	146.41	0.11
P1	L	7	0.55	6.3	2	2055	20	156.27	0.09
UVQ2	L	4	0.68	1.65	3	882	113	32.13	0.07

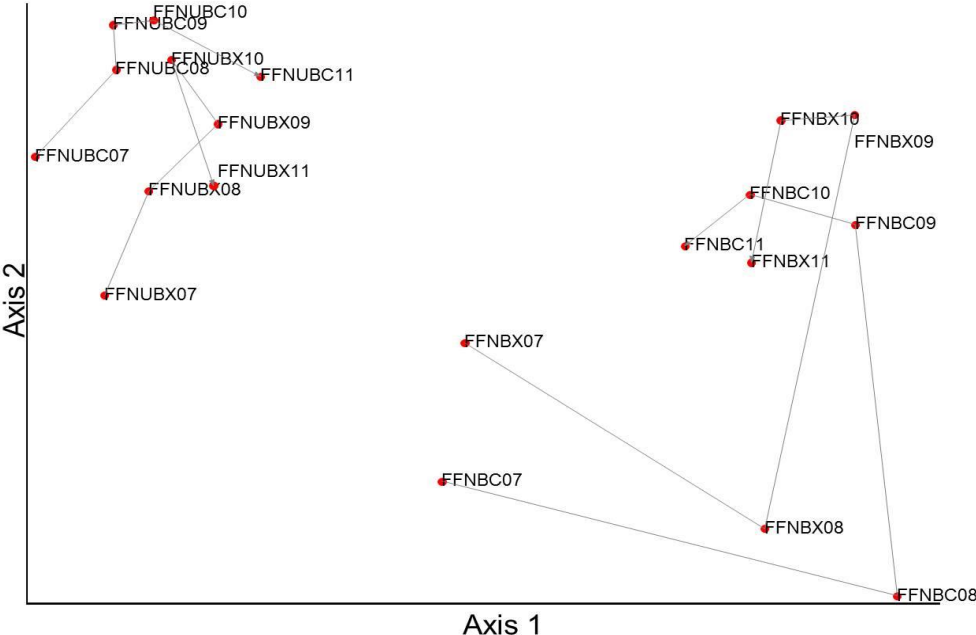
APPENDIX 6.1. Database of the species used in this study, with their Red Data Book status (RDB status) and their relative palatability, habitat specialisation, range size, pollination and dependence on seed indices. The latter are ranked subjectively from 0, no concern, to 1 which is highly vulnerable. Indices with two decimal places are for graph purposes only to avoid complete overlap with other species.

Species	RDB status	Grazing index (palatability)	Habitat specialisation	Range	Pollination	Dependence on seed
<i>Haworthia floribunda</i>	CR	0.5	0.8	0.6	0.7	0.78
<i>Polhillia brevicalyx</i>	CR	0.52	0.91	0.9	0.5	0.72
<i>Polhillia connata</i>	CR	0.4	0.9	0.92	0.52	0.61
<i>Aspalathus grobleri</i>	EN	0.5	0.72	0.8	0.5	0.61
<i>Aspalathus joubertiana</i>	EN	0.52	0.7	0.7	0.51	0.62
<i>Brownanthes fraternus</i>	EN	0.11	0.9	0.81	0.5	0.91
<i>Gibbaeum haaglenii</i>	EN	0.1	0.92	0.8	0.51	0.9
<i>Gladiolus acuminatus</i>	EN	0.32	0.82	0.8	0.7	0.52
<i>Gladiolus vandermerwei</i>	EN	0.3	0.8	0.6	0.7	0.5
<i>Haworthia mirabilis</i>	EN	0.5	0.72	0.72	0.7	0.81
<i>Leucadendron coryacium</i>	EN	0.3	0.7	0.7	0.51	0.8
<i>Liparia striata</i>	EN	0.3	0.8	0.8	0.5	0.51
<i>Otholobium pungens</i>	EN	0.5	0.5	0.6	0.5	0.6
<i>Xiphosiphon guthrei</i>	EN	0.4	0.6	0.6	0.5	0.5
<i>Acrodon deminutus</i>	VU	0.3	0.8	0.7	0.5	0.7
<i>Aloe brevifolia</i>	VU	0.2	0.61	0.7	0.7	0.7
<i>Drosantheum striatum</i>	VU	0.5	0.62	0.52	0.5	0.79
<i>Elegia vereauxii</i>	VU	0.52	0.6	0.5	0.4	0.3
<i>Haworthia mutica</i>	VU	0.5	0.7	0.6	0.7	0.82
<i>Lobostemon capitatus</i>	VU	0.3	0.6	0.6	0.5	0.5
<i>Polhillia canescens</i>	VU	0.5	0.9	0.8	0.5	0.61
<i>Polhillia pallens</i>	VU	0.38	0.8	0.8	0.51	0.59
<i>Relhannia gamotii</i>	VU	0.2	0.71	0.5	0.52	0.8
<i>Trichodiadema pygmaeum</i>	VU	0.7	0.7	0.7	0.5	0.4
<i>Agathosma foetidissima</i>	NT	0.1	0.7	0.72	0.5	0.5
<i>Aspalathus quartzicola</i>	NT	0.5	0.8	0.8	0.52	0.62
<i>Bobartia longicyma</i>	NT	0.1	0.4	0.4	0.52	0.11
<i>Elegia recta</i>	NT	0.51	0.5	0.5	0.1	0.3
<i>Peucedanum striatum</i>	NT	0.6	0.71	0.7	0.52	0.5
<i>Aloe ferox</i>	LC	0.2	0.3	0.1	0.6	0.6
<i>Aspalathus angustifolia</i>	LC	0.1	0.2	0.2	0.5	0.43
<i>Aspalathus nigra</i>	LC	0.52	0.3	0.3	0.5	0.41
<i>Aspalathus pinguis</i>	LC	0.5	0.3	0.3	0.5	0.42
<i>Aspalathus submissa</i>	LC	0.5	0.5	0.5	0.5	0.4
<i>Athanasia trifurcata</i>	LC	0.1	0.3	0.2	0.3	0.7
<i>Berkheya barbata</i>	LC	0.7	0.4	0.4	0.5	0.52
<i>Chrysocoma ciliata</i>	LC	0.2	0.2	0.2	0.3	0.7
<i>Clutia tomentosa</i>	LC	0.3	0.4	0.4	0.5	0.4
<i>Conyza scabrida</i>	LC	0.1	0.4	0.1	0.4	0.5
<i>Cymbopappus adenosolen</i>	LC	0.2	0.6	0.4	0.5	0.6
<i>Cymbopogon cf prolixus</i>	LC	0.6	0.2	0.3	0.3	0.3
<i>Delosperma asperulum</i>	LC	0.2	0.1	0.2	0.4	0.5
<i>Drimia capensis</i>	LC	0.1	0.1	0.1	0.5	0.4
<i>Ehrharta calycina</i>	LC	0.6	0.2	0.2	0.4	0.5
<i>Elytropappus rhinocerotis</i>	LC	0.1	0.1	0.1	0.1	0.8
<i>Erica karoica</i>	LC	0.21	0.5	0.5	0.7	0.7
<i>Eucomis regia</i>	LC	0.3	0.4	0.3	0.7	0.4
<i>Freylinia undulata</i>	LC	0.5	0.6	0.4	0.7	0.7
<i>Gazania krebsiana</i>	LC	0.6	0.2	0.1	0.5	0.2
<i>Gladiolus permeabilis</i>	LC	0.31	0.6	0.1	0.7	0.5
<i>Gladiolus stellatus</i>	LC	0.3	0.6	0.2	0.6	0.5
<i>Gnidia squarrosa</i>	LC	0.3	0.3	0.21	0.5	0.5

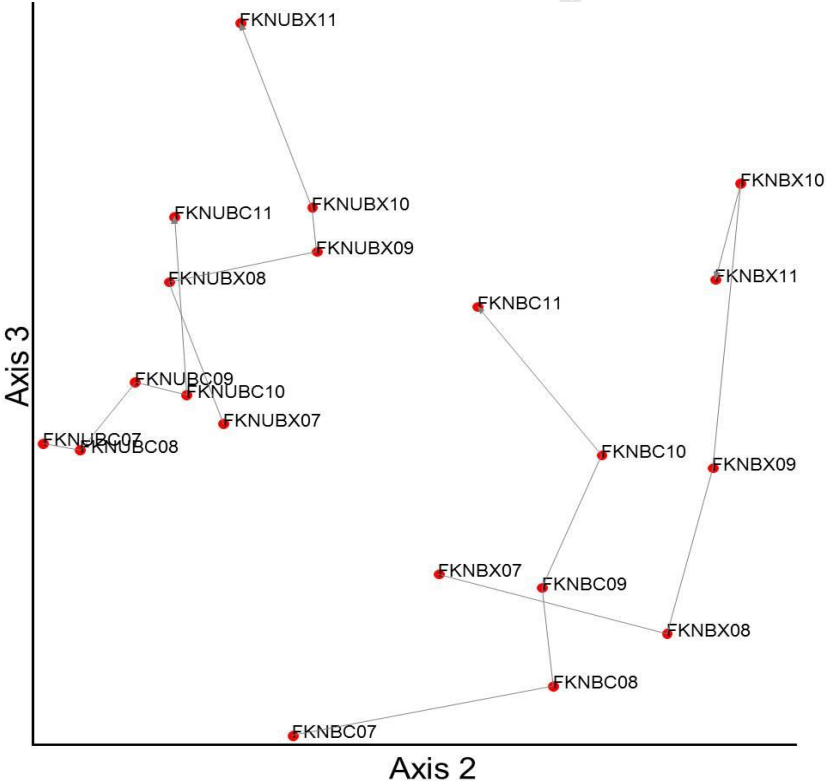
Species	RDB status	Grazing index (palatability)	Habitat specialisation	Range	Pollination	Dependence on seed
<i>Helichrysum petiolare</i>	LC	0.2	0.3	0.2	0.5	0.8
<i>Hermannia cf alnifolia</i>	LC	0.2	0.4	0.4	0.8	0.5
<i>Hermannia flamula</i>	LC	0.8	0.5	0.3	0.7	0.5
<i>Hermannia hyssopifolia</i>	LC	0.3	0.4	0.3	0.7	0.5
<i>Hermannia saccifera</i>	LC	0.7	0.5	0.4	0.7	0.52
<i>Ischyrolepis capensis</i>	LC	0.5	0.6	0.3	0.1	0.5
<i>Jamesbrittenia albomarginata</i>	LC	0.3	0.3	0.4	0.4	0.4
<i>Lobostemon echioides</i>	LC	0.2	0.3	0.3	0.5	0.4
<i>Merxmüllera stricta</i>	LC	0.5	0.1	0.1	0.1	0.1
<i>Metalasia acuta</i>	LC	0.2	0.3	0.4	0.5	0.8
<i>Oedera genistifolia</i>	LC	0.1	0.3	0.3	0.5	0.81
<i>Oedera squarosa</i>	LC	0.1	0.3	0.3	0.5	0.8
<i>Pelargonium triste</i>	LC	0.3	0.3	0.2	0.5	0.4
<i>Pentaschistis eriostoma</i>	LC	0.5	0.3	0.2	0.3	0.1
<i>Printzia polifolia</i>	LC	0.3	0.5	0.3	0.5	0.5
<i>Pteronia incana</i>	LC	0.1	0.2	0.2	0.3	0.8
<i>Rhus rosemariifolia</i>	LC	0.2	0.3	0.2	0.4	0.5
<i>Stachys aethiopica</i>	LC	0.5	0.2	0.21	0.4	0.5
<i>Themeda triandra</i>	LC	0.9	0.5	0.1	0.1	0.2
<i>Tripteris tomentosa</i>	LC	0.5	0.3	0.4	0.5	0.6
<i>Walhenbergia tenella</i>	LC	0.6	0.2	0.2	0.4	0.5

APPENDIX 7.1. Individual ordinations for north & south sites

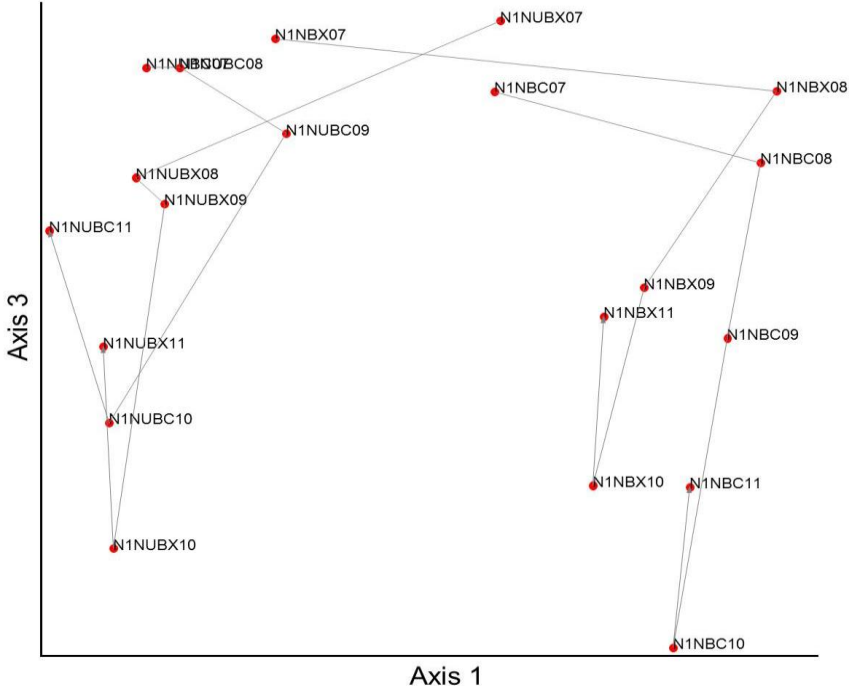
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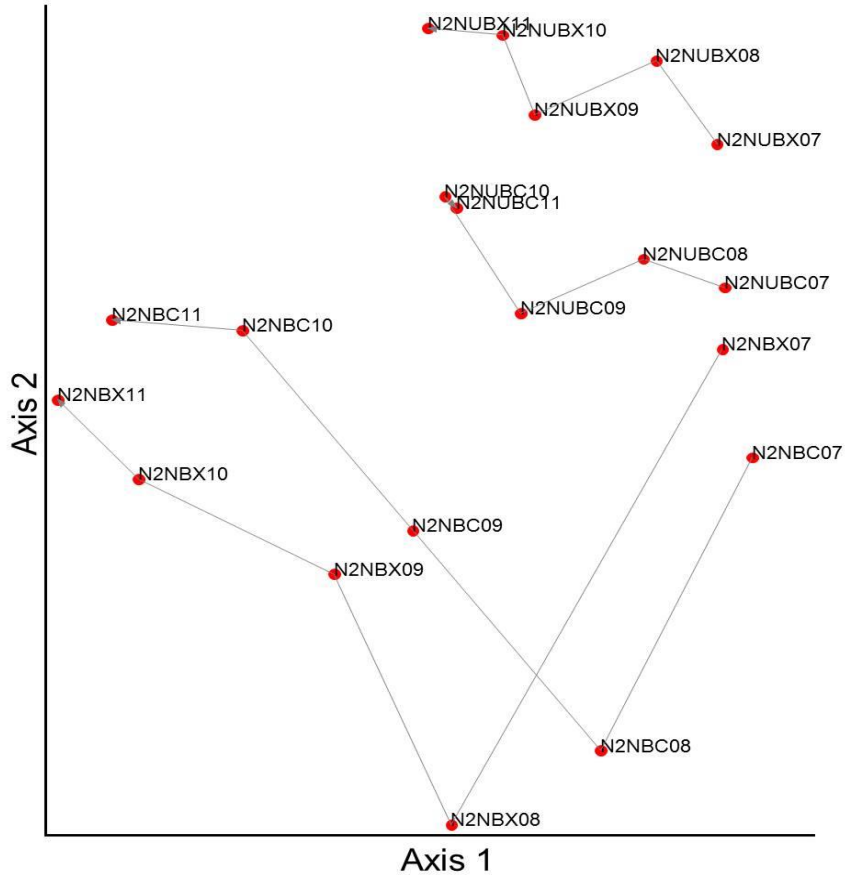
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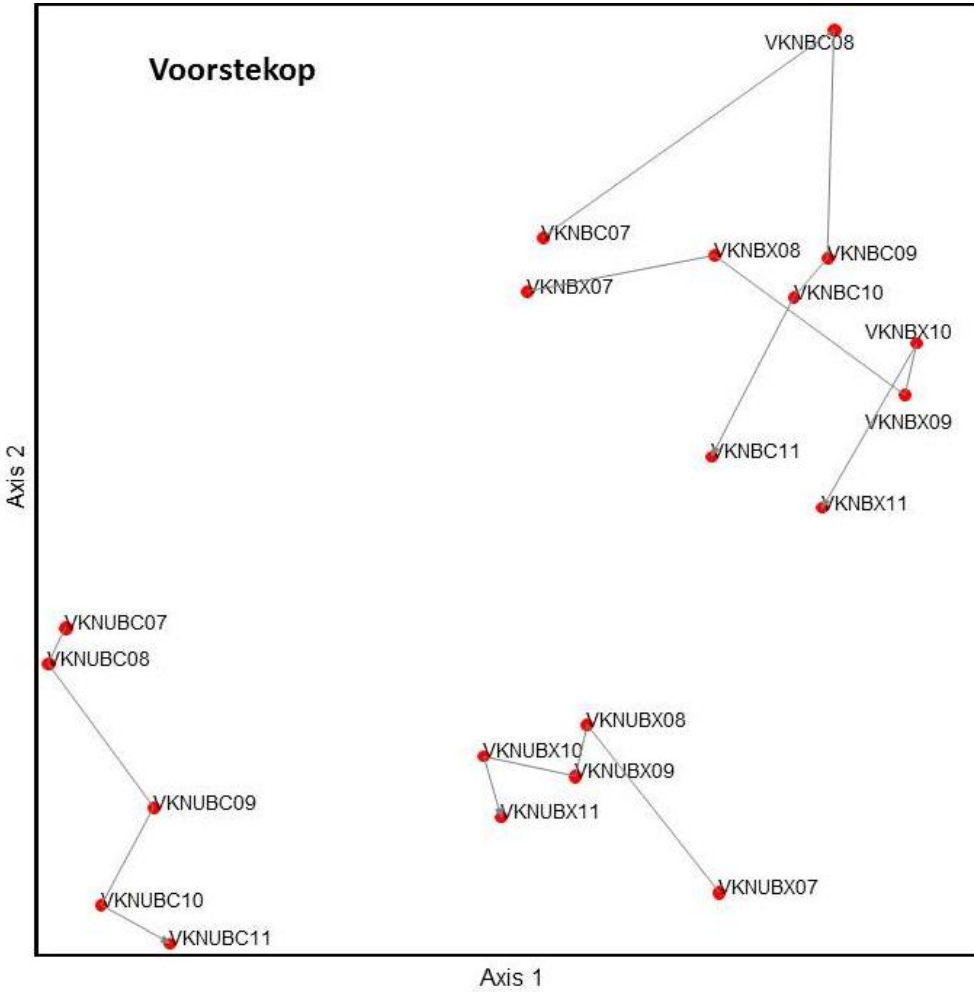
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NORTH SITE: NYSTY2

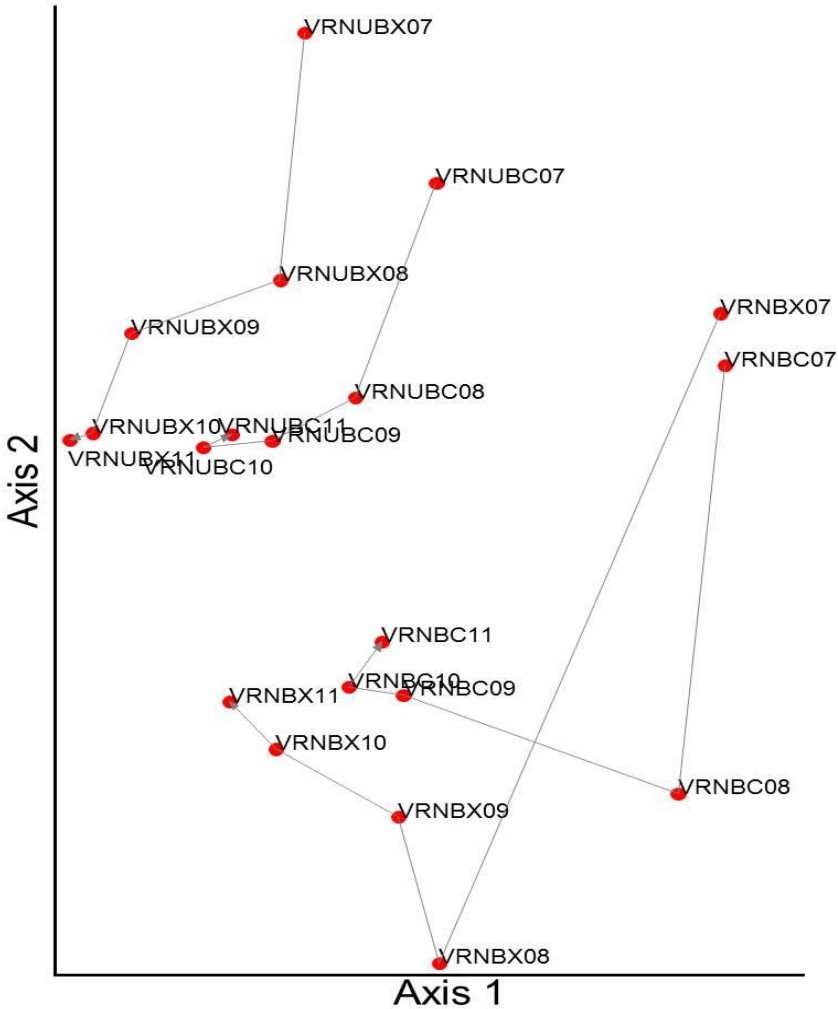


NORTH SITE: VOORSTEKOP

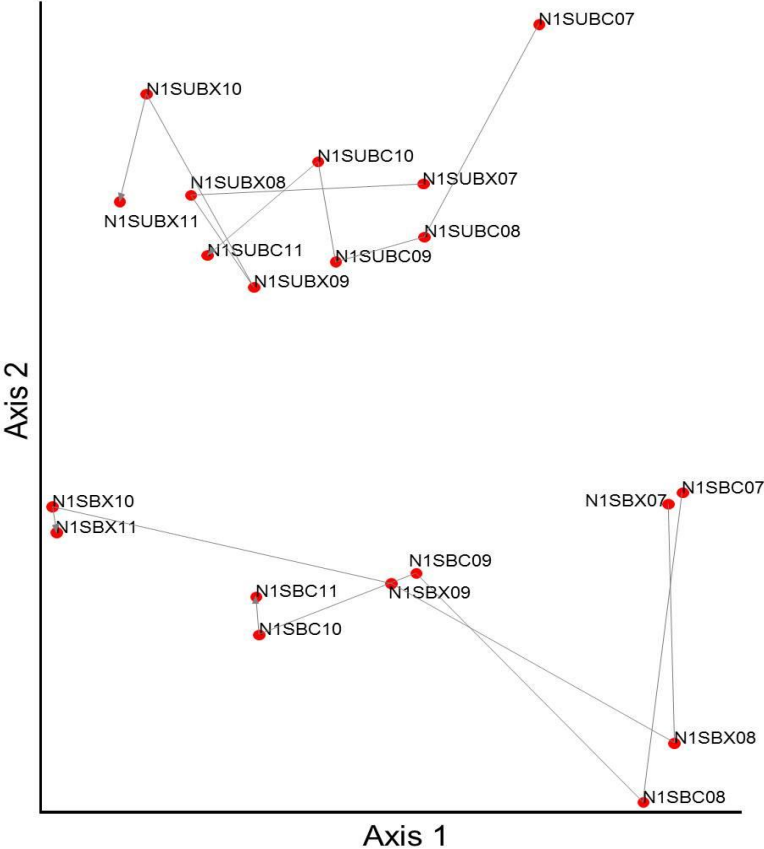


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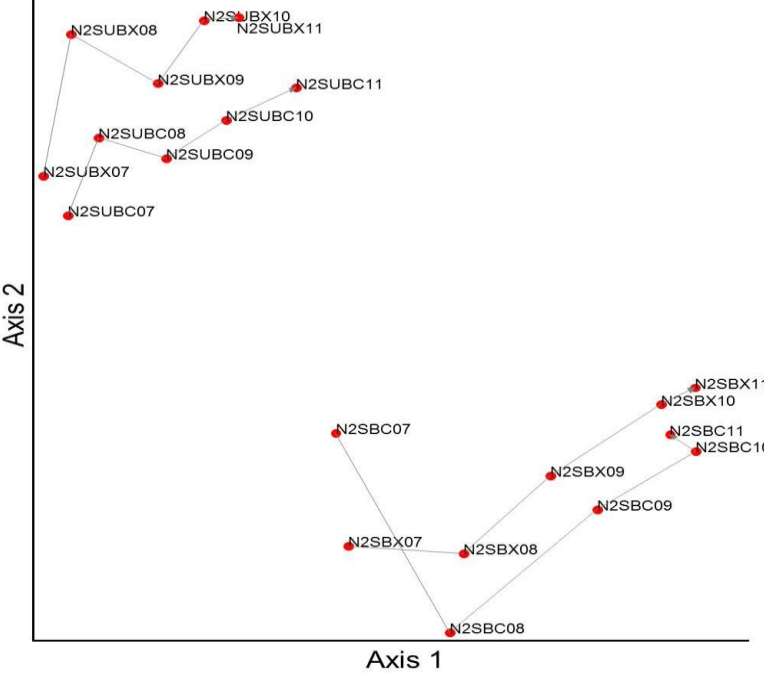
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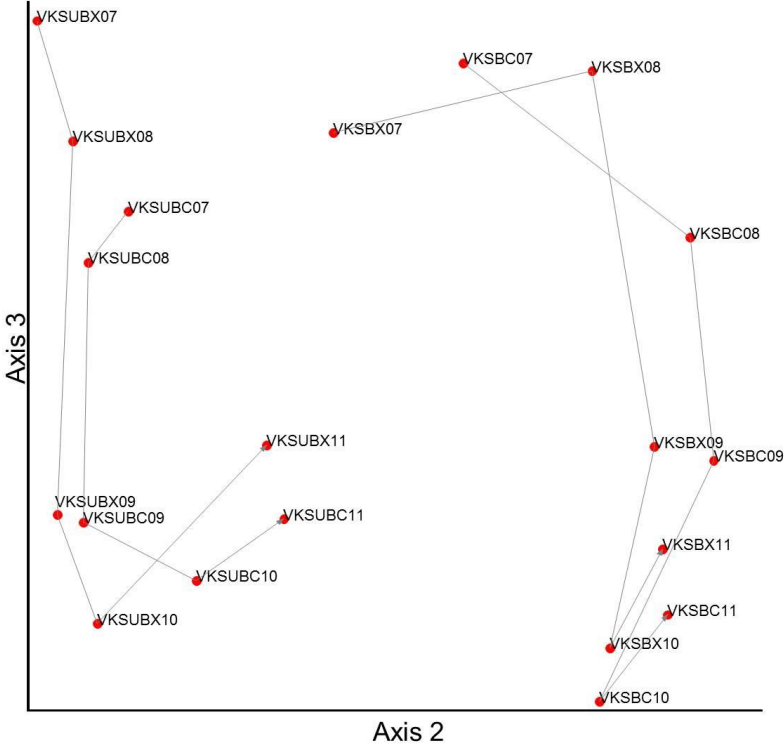
SOUTH SITE: NYSTY1



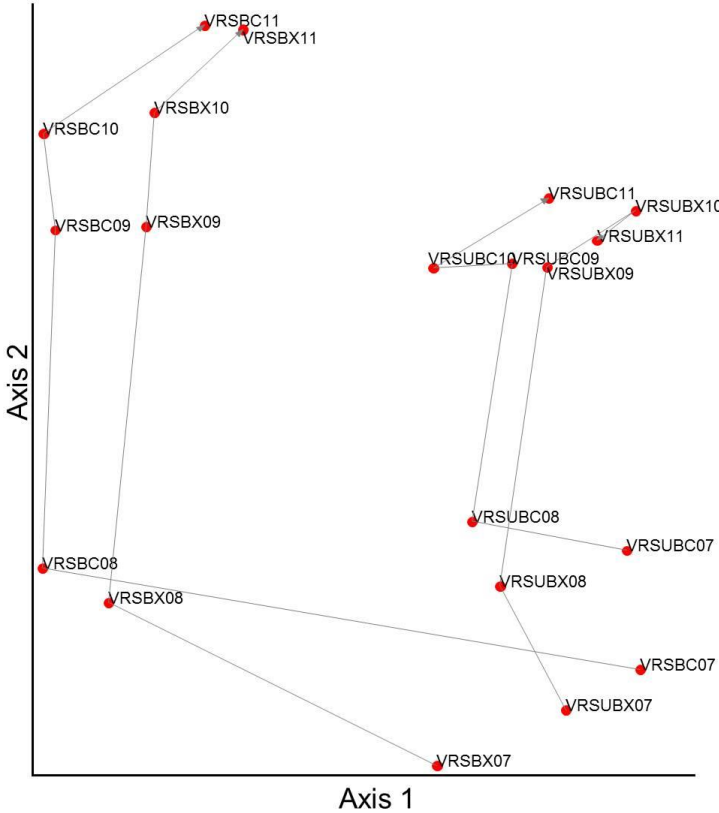
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SOUTH SITE: VOORSTEKOP

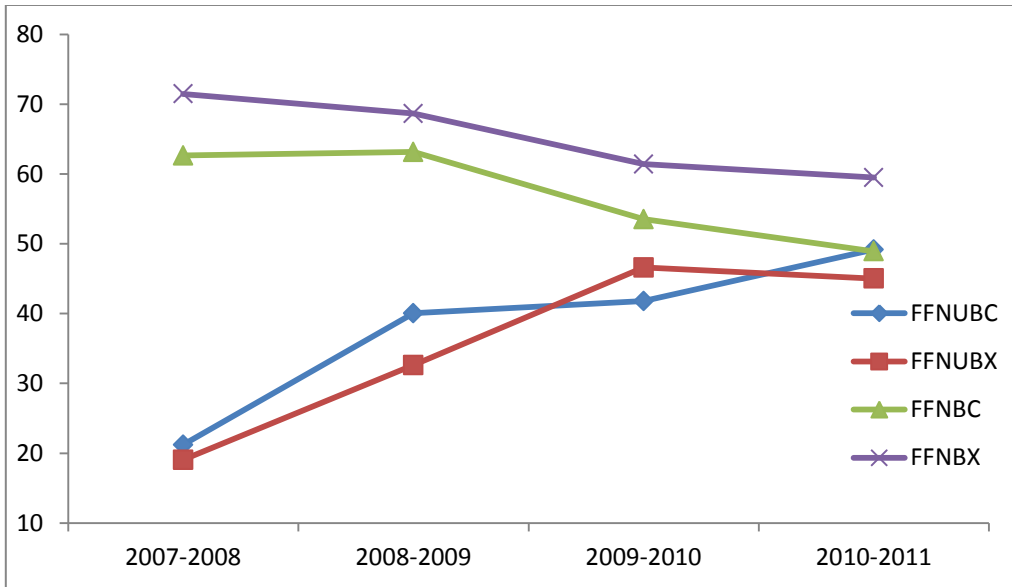


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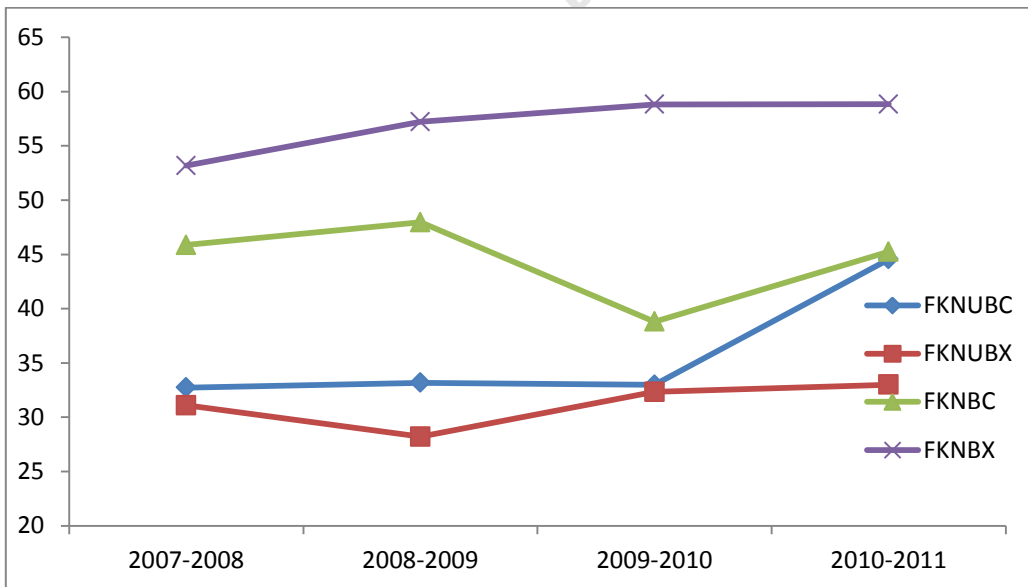


APPENDIX 7.2. Percentage change over years in burned and unburned plots

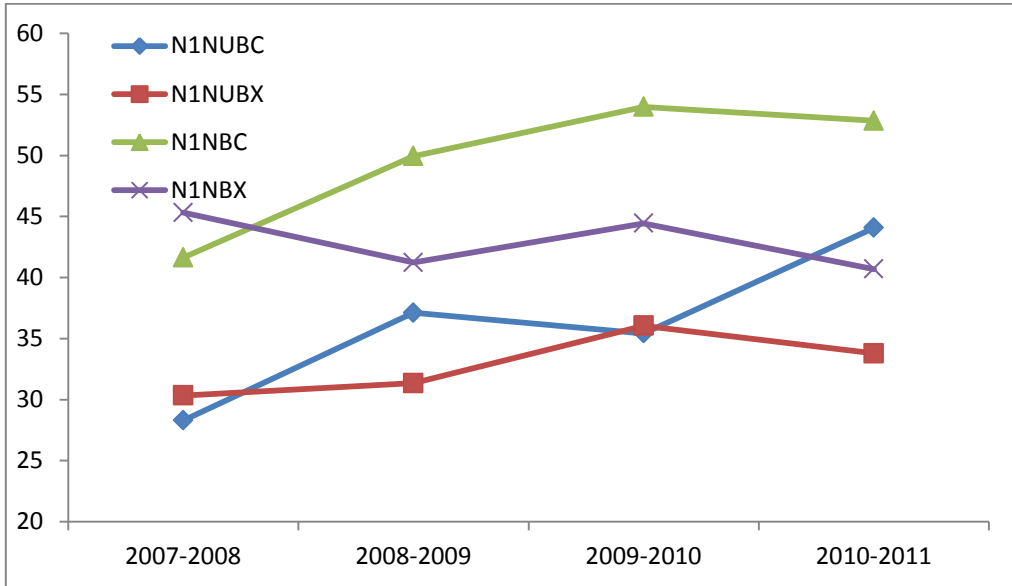
NORTH SITE: FAIRFIELD



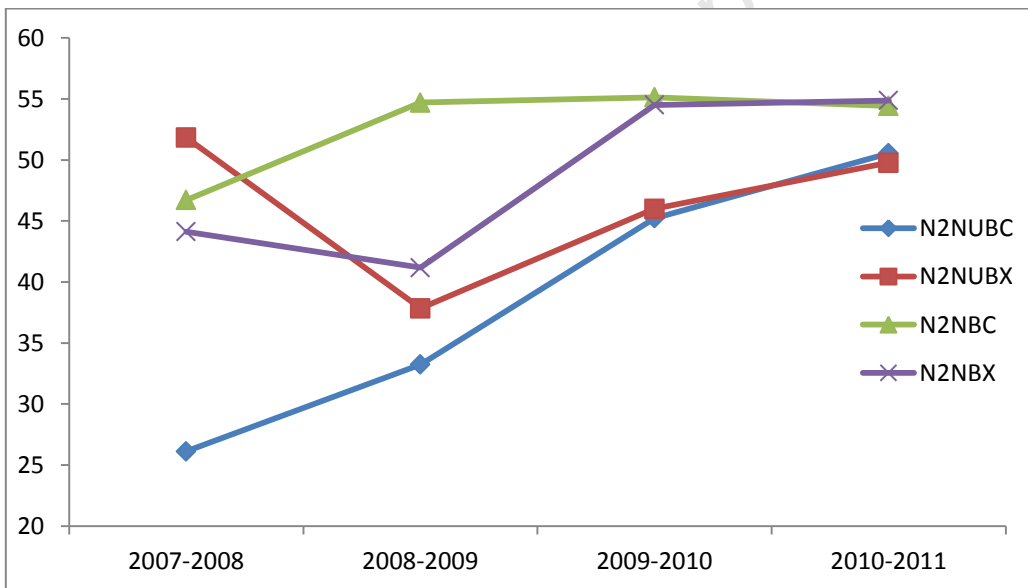
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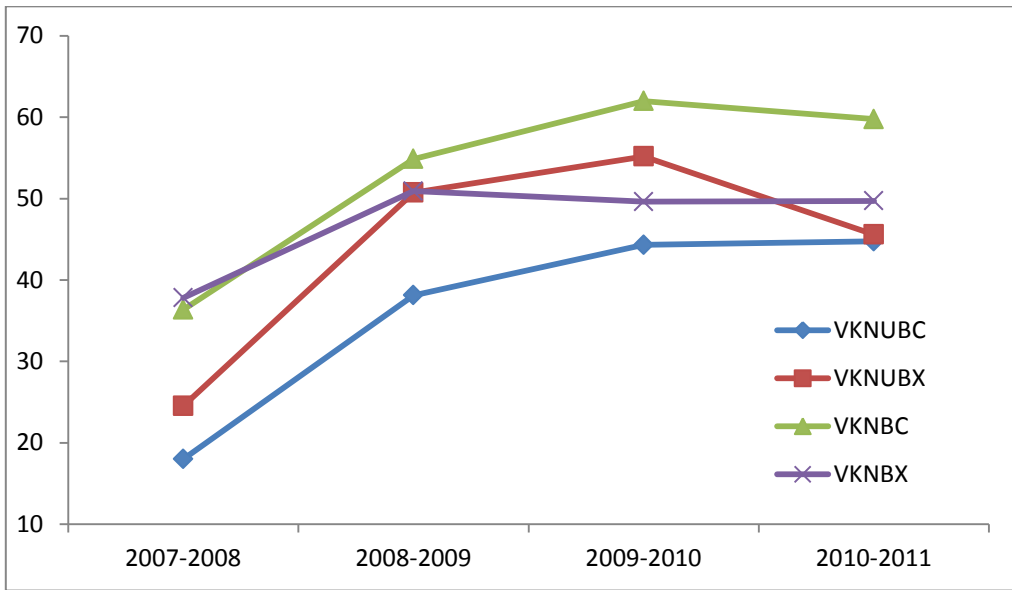
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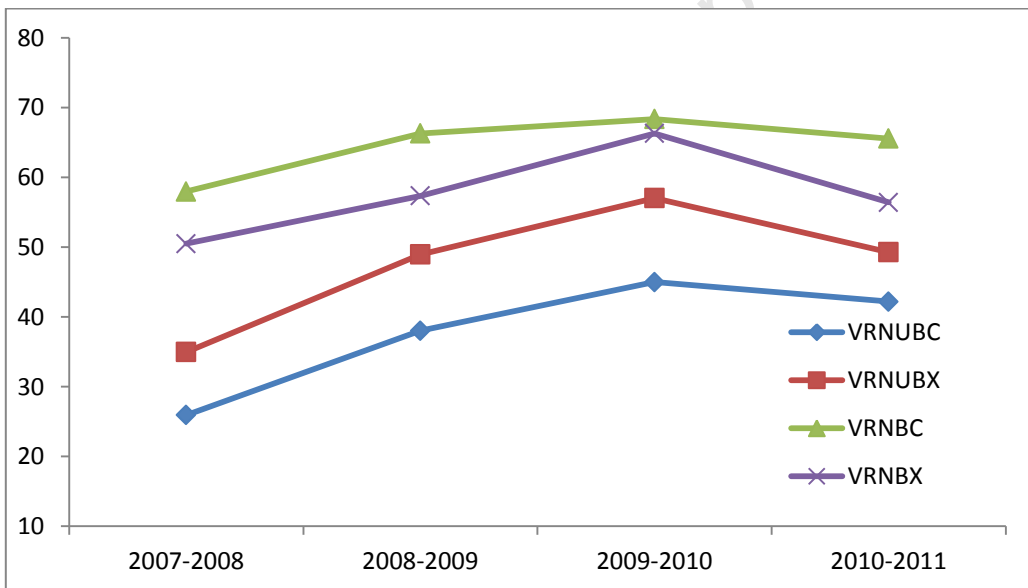
NORTH SITE: NYSTY2



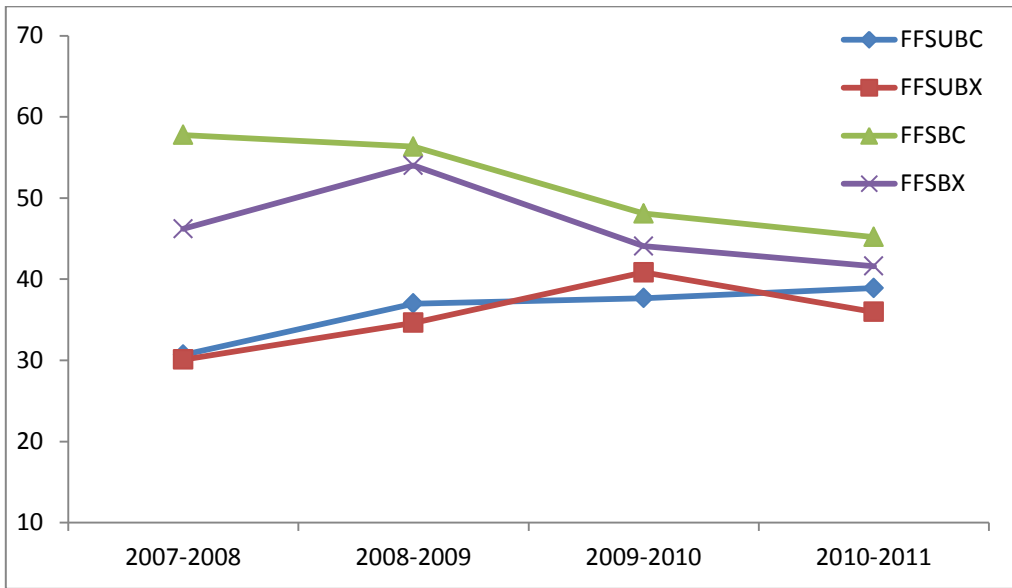
NORTH SITE: VOORSTEKOP



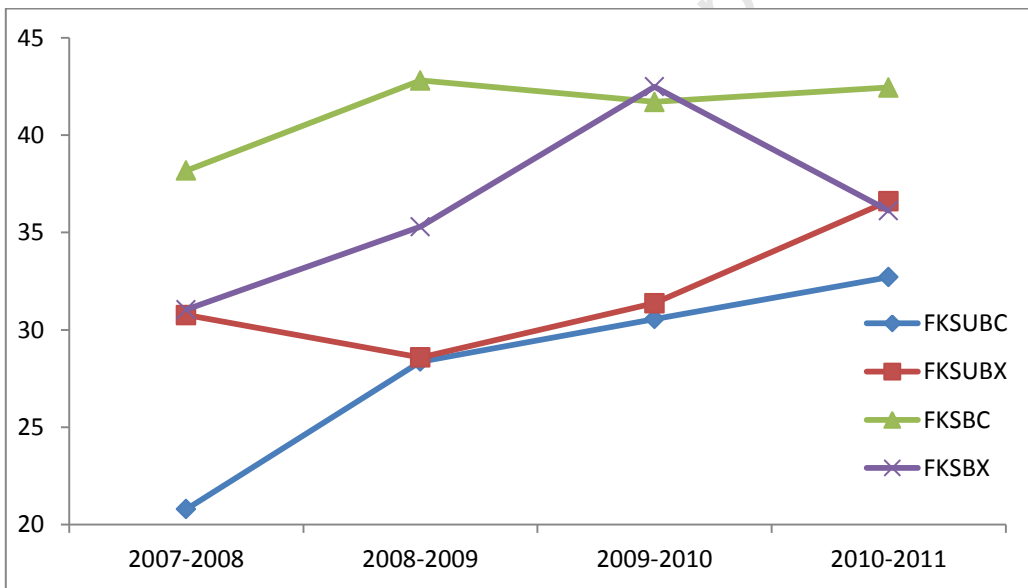
NORTH SITE: VAN RHEENEN'S CREST



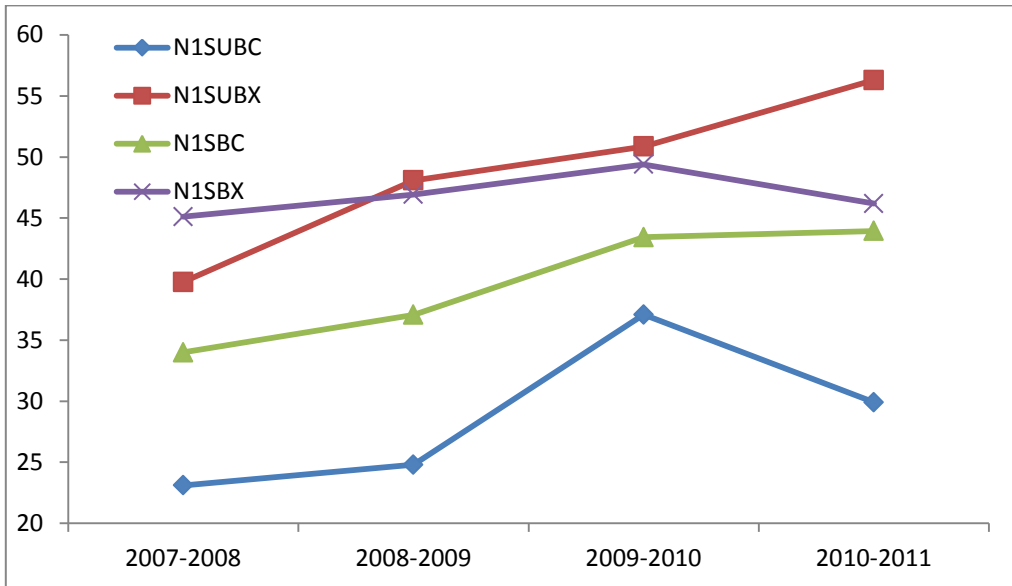
SOUTH SITE: FAIRFIELD



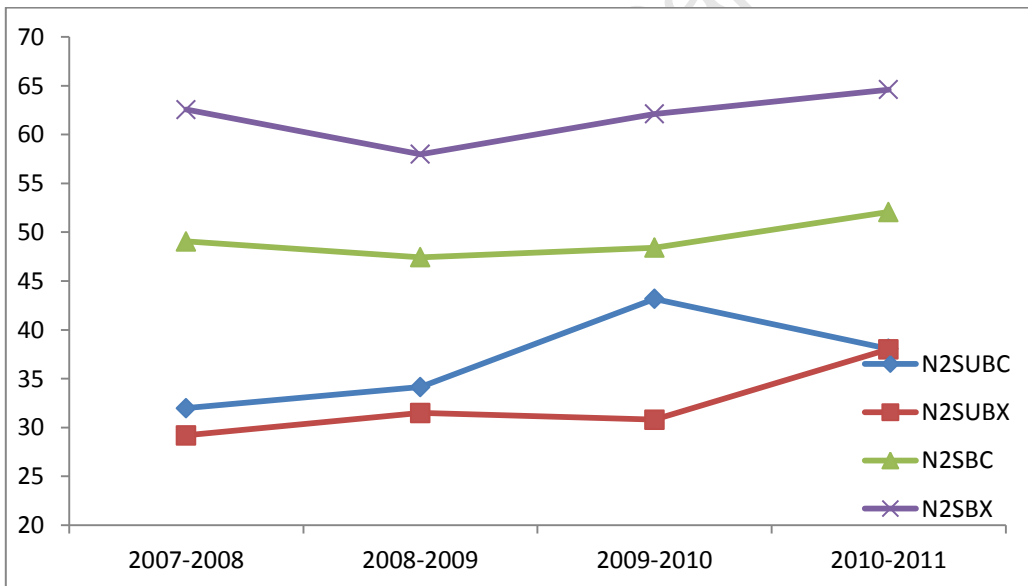
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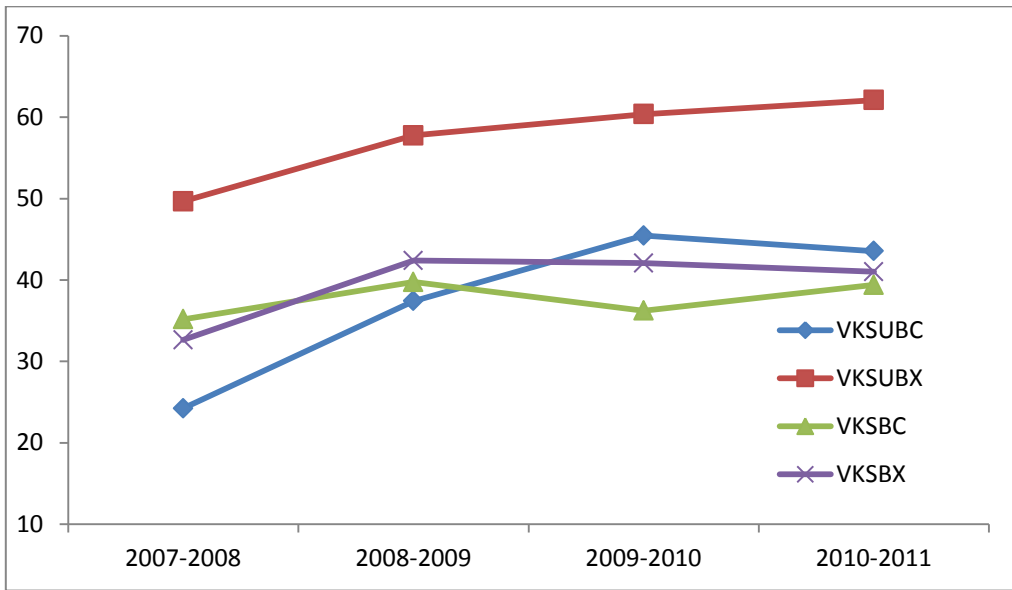
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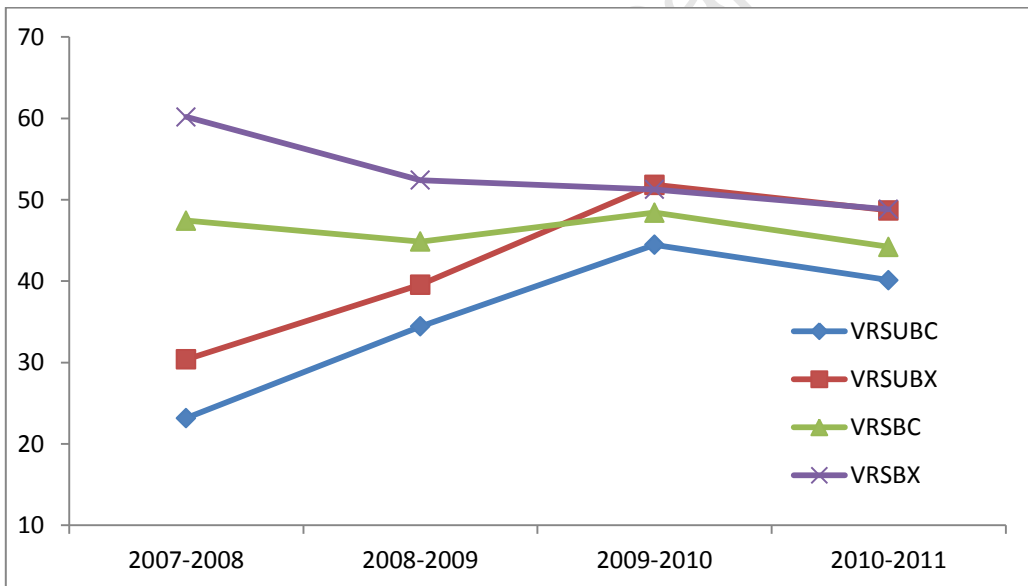
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SOUTH SITES: VOORSTEKOP



SOUTH SITES: VAN RHEENEN'S CREST



APPENDIX 7.3. Spearman Rank Correlations between species richness and cover of various growth forms, as well as cover of dominant, or potentially important species for permanent plots in the Overberg (six sites, with four plots per aspect (n=24 plots per aspect)).

SOUTH-FACING SLOPES

	Cover overall	Diversity overall	Cover Dom. Shrubs	Cover Dom. Grasses	C_Themeda / Ehrharta	C_Pentastichis / Merxmeullera	Cover Dom. Asteraceae
C_Annuals	0.228	0.340	0.006	-0.228	-0.051	-0.209	-0.029
C_Annual grasses	0.037	0.029	-0.039	-0.102	0.088	-0.103	-0.041
C_Asteraceous shrubs	0.051	-0.255	0.623	-0.026	-0.205	0.113	0.817
C_Forbs	0.569	0.558	-0.178	-0.268	0.185	-0.334	-0.157
C_Geophytes	0.550	0.697	-0.313	0.166	0.049	0.096	-0.361
C_Grasses	0.282	0.058	-0.091	0.896	0.479	0.328	-0.111
C_Restios	0.355	0.327	-0.498	0.177	0.229	0.069	-0.484
C_Shrebs	0.631	0.521	-0.124	0.100	0.335	-0.149	-0.411
C_Succulents	0.070	-0.036	0.225	-0.346	-0.272	-0.031	0.427
C_Overall	1.000	0.762	-0.143	0.213	0.305	0.022	-0.179
C_Dom. Shrubs	-0.143	-0.249	1.000	-0.150	-0.367	0.217	0.834
C_Dom. Grasses	0.213	-0.056	-0.150	1.000	0.400	0.476	-0.049
C_Themeda & Ehrharta	0.305	0.037	-0.367	0.400	1.000	-0.510	-0.371
C_Pentastichis / Merxmeullera	0.022	0.021	0.217	0.476	-0.510	1.000	0.294
C_Dom. Asteraceae	-0.179	-0.364	0.834	-0.049	-0.371	0.294	1.000
SR_Annuals	0.280	0.412	-0.010	-0.257	-0.015	-0.245	-0.073
SR_Annual grasses	0.027	0.040	0.038	-0.114	0.054	-0.077	-0.003
SR_Asteraceous shrubs	0.212	0.086	0.178	-0.085	0.325	-0.419	0.060
SR_Forbs	0.605	0.721	-0.179	-0.169	0.146	-0.183	-0.217
SR_Geophytes	0.453	0.771	-0.257	0.088	-0.119	0.239	-0.303
SR_Grasses	0.402	0.594	-0.311	-0.087	0.234	-0.164	-0.378
SR_Restios	0.391	0.402	-0.431	0.149	0.209	0.057	-0.472
SR_Shrebs	0.448	0.412	-0.281	0.098	0.396	-0.199	-0.518
SR_Succulents	0.173	0.264	0.205	-0.334	-0.425	0.174	0.291
SR_Overall	0.762	1.000	-0.249	-0.056	0.037	0.021	-0.364
C_Aspalathus spp.	0.501	0.668	0.072	-0.115	-0.068	0.028	-0.277

NORTH-FACING SLOPES

	Cover overall	Diversity overall	C_Themeda triandra	C_Cymbopogon sp	C_Pentachistis eriostoma	C_Dominant shrubs	Cover_3 dominant Asteraceae
C_Annuals	0.11	0.58	0.23	-0.17	-0.07	-0.22	-0.16
C_Asteraceous shrubs	0.07	-0.19	-0.15	-0.25	-0.13	0.16	0.77
C_Forbs	0.11	0.49	0.33	-0.21	-0.12	-0.43	-0.36
C_Geophytes	0.39	0.76	0.50	0.05	0.31	0.09	-0.16
C_Grasses	0.79	0.24	0.46	0.60	0.50	0.52	0.23
C_Restios	0.38	0.61	0.35	0.23	0.47	-0.08	-0.38
C_Shrebs	0.67	0.01	0.11	0.57	0.09	0.61	0.11
C_Succulents	-0.38	0.17	0.04	-0.48	-0.21	-0.74	-0.27
C_Dominant grasses	0.66	0.19	0.32	0.70	0.70	0.36	-0.04
C_Themeda triandra	0.52	0.62	1.00	0.19	0.18	0.11	0.00
C_Cymbopogon sp	0.51	-0.03	0.19	1.00	0.12	0.36	-0.07
C_Pentachistis eriostoma	0.40	0.29	0.18	0.12	1.00	0.23	0.03
C_Dominant shrubs	0.64	-0.11	0.11	0.36	0.23	1.00	0.58
Cover_3 dominant Asteraceae	0.30	-0.19	0.00	-0.07	0.03	0.58	1.00
C_Overall	1.00	0.41	0.52	0.51	0.40	0.64	0.30
SR_Annuals	0.19	0.62	0.27	-0.11	0.04	-0.14	-0.11
SR_Asteraceous shrubs	-0.05	-0.12	-0.17	0.04	-0.25	-0.16	0.29
SR_Forbs	0.01	0.61	0.31	-0.24	0.06	-0.51	-0.43
SR_Geophytes	0.32	0.78	0.48	-0.05	0.37	0.05	-0.17
SR_Grasses	0.64	0.49	0.70	0.38	0.08	0.47	0.26
SR_Restios	0.24	0.36	0.16	0.16	0.27	0.20	-0.19
SR_Shrebs	0.55	0.42	0.27	0.47	0.27	0.34	0.10
SR_Succulents	-0.31	0.30	0.16	-0.46	-0.12	-0.71	-0.31
SR_Overall	0.41	1.00	0.62	-0.03	0.29	-0.11	-0.19
C_Annual grasses	-0.01	0.14	0.02	-0.19	-0.26	-0.04	0.06

APPENDIX 7.4. A summary of the grazed species used for comparing size and proportion of flowering plants in grazed and ungrazed plots.

Species	North plots	South plots
<i>Anthospermum galioides</i>	*	
<i>Aspalathus creeper</i>	*	
<i>Aspalathus nigra</i>		*
<i>Aspalathus spinosa</i>	*	
<i>Aspalathus submissa</i>	*	*
<i>Aspalathus yellow</i>		*
<i>Athanasia sp</i>		*
C4 grass		*
<i>Cymbopogon sp.</i>	*	
<i>Dicoma sp.</i>	*	
<i>Ehrharta calycina</i>	*	*
<i>Ehrharta red oats</i>	*	*
<i>Elegia verreauxii</i>		*
<i>Erica karooica</i>		*
<i>Erica sp.</i>		*
<i>Ficinia sp.</i>	*	
<i>Gnidia squarrosa</i>		*
<i>Helichrysum cymosum</i>		*
<i>Hermannia creeper</i>	*	*
<i>Hermannia flamula</i>		*
<i>Hermannia flat leaves</i>	*	
<i>Hermannia saccifera</i>	*	*
<i>Ischyrolepis capensis</i>		*
<i>Passerina sp.</i>		*
<i>Pelargonium sp.</i>	*	
<i>Pentaschistis eriostoma</i>	*	*
<i>Peucedanum striatum</i>	*	
<i>Phyica sp.</i>		*
<i>Stachys sp (pink)</i>		*
<i>Themeda triandra</i>	*	*
<i>Thesium sp.</i>		*
<i>Walhenbergia sp.</i>	*	*

APPENDIX 7.5. Correlation matrix generated to identify relationships amongst growth forms and between growth forms and physical variables for data collected from random plots in the Overberg.

SOUTH-FACING SLOPES

	Cover overall	Diversity overall	Veld age	Height	Patch size	Cover Themeda	Cover Ehrharta	Cover 3 Dom. Asteraceae	Cover Elytropappus
Cover overall	1.000	0.080	0.246	0.194	-0.163	0.212	-0.047	0.098	-0.287
Diversity overall	0.080	1.000	-0.231	-0.357	-0.034	0.147	0.546	-0.313	-0.289
Veld age	0.246	-0.231	1.000	0.484	-0.083	-0.326	-0.216	0.512	0.338
Height	0.194	-0.357	0.484	1.000	0.150	-0.165	-0.641	0.396	0.127
Patch size	-0.163	-0.034	-0.083	0.150	1.000	-0.513	-0.210	0.121	0.506
Cover Themeda	0.212	0.147	-0.326	-0.165	-0.513	1.000	0.005	-0.444	-0.591
Cover Ehrharta	-0.047	0.546	-0.216	-0.641	-0.210	0.005	1.000	-0.174	-0.122
Cover 3 Dom. Asteraceae	0.098	-0.313	0.512	0.396	0.121	-0.444	-0.174	1.000	0.543
C_Annual	0.020	0.403	-0.199	-0.448	-0.537	0.394	0.348	-0.354	-0.375
D_Annual	-0.122	0.478	-0.205	-0.352	-0.466	0.285	0.369	-0.150	-0.305
C_Forbs	-0.196	0.725	-0.457	-0.703	0.055	0.195	0.668	-0.268	-0.090
D_Forbs	-0.046	0.806	-0.410	-0.582	0.214	-0.012	0.620	-0.242	-0.034
C_Bulb	0.493	0.315	-0.300	-0.219	-0.147	-0.081	0.325	-0.005	-0.270
D_Bulb	0.386	0.696	-0.254	-0.338	-0.157	0.141	0.394	-0.419	-0.465
C_Grass	0.764	0.357	0.050	-0.171	-0.033	0.252	0.190	0.008	-0.187
D_Grass	0.815	0.158	0.387	0.147	-0.126	0.072	0.005	0.206	-0.119
C_Restio	0.437	0.123	0.061	0.192	-0.237	0.234	-0.088	-0.105	-0.290
D_Restio	0.348	-0.095	0.279	0.464	-0.126	0.257	-0.252	0.173	-0.061
C_Succulent	-0.087	0.133	-0.125	0.002	-0.051	0.558	-0.076	-0.397	-0.240
D_Succulent	-0.063	0.074	-0.117	0.032	-0.036	0.562	-0.211	-0.433	-0.301
C_AsterShrub	0.125	-0.294	0.583	0.398	0.163	-0.474	-0.254	0.940	0.574
D_AsterShrub	-0.117	0.133	0.417	0.147	0.325	-0.354	-0.034	0.330	0.447
C_Shrub	-0.135	0.057	-0.029	0.259	0.346	-0.163	0.007	-0.043	-0.035
D_Shrub	-0.360	0.165	0.001	0.150	0.293	-0.128	0.124	0.041	0.173
C_All Shrubs	0.152	-0.304	0.527	0.501	0.279	-0.565	-0.225	0.901	0.588
D_All Shrubs	-0.351	0.241	0.211	0.149	0.341	-0.250	0.183	0.266	0.408
Cover Elytropappus	-0.287	-0.289	0.338	0.127	0.506	-0.591	-0.122	0.543	1.000

NORTH-FACING SLOPES

	Cover overall	Diversity overall	Veld age	Height	Patch size	Cover Pentaschistis	Cover Themeda	Cover Cymbopogon	Palatable grasses	Cover Elytropappus	Cover 3 Dom. Asteraceae
Cover overall	1.000	-0.375	0.571	0.332	-0.286	0.297	-0.086	0.057	0.067	0.141	0.304
Diversity overall	-0.375	1.000	-0.505	-0.400	-0.238	-0.474	0.128	0.488	0.522	-0.101	-0.196
Veld age	0.571	-0.505	1.000	0.545	-0.201	0.215	0.179	-0.018	-0.148	0.303	0.480
Height	0.332	-0.400	0.545	1.000	-0.226	0.196	-0.239	-0.076	-0.300	0.282	0.457
Patch size	-0.286	-0.238	-0.201	-0.226	1.000	0.146	-0.261	-0.652	-0.606	0.130	-0.006
C_Annual	-0.164	0.580	-0.460	-0.340	-0.290	-0.358	0.263	0.653	0.673	-0.220	-0.183
D_Annual	0.015	0.670	-0.395	-0.222	-0.443	-0.241	0.183	0.652	0.678	-0.231	-0.117
C_Forab	-0.128	0.754	-0.530	-0.448	-0.036	-0.281	-0.111	0.277	0.274	0.082	-0.157
D_Forab	-0.215	0.768	-0.491	-0.574	-0.072	-0.288	-0.014	0.235	0.317	0.017	-0.256
C_Bulb	-0.293	0.819	-0.285	-0.287	-0.338	-0.472	0.449	0.652	0.673	-0.129	0.029
D_Bulb	-0.269	0.804	-0.297	-0.217	-0.388	-0.378	0.411	0.645	0.668	-0.192	-0.024
C_Grass	0.498	-0.217	0.289	0.000	-0.218	0.751	-0.056	0.111	0.139	-0.251	-0.036
D_Grass	0.350	-0.255	0.355	-0.019	0.204	0.643	-0.188	-0.067	-0.242	0.032	0.191
C_Restio	-0.296	0.518	-0.085	-0.152	-0.159	-0.348	0.406	0.301	0.314	-0.283	-0.083
D_Restio	-0.412	0.515	-0.130	-0.023	0.001	-0.291	0.236	0.253	0.225	-0.295	-0.074
C_Succulent	-0.143	0.047	-0.280	-0.076	0.029	-0.032	-0.359	-0.277	-0.339	0.000	-0.357
D_Succulent	-0.596	0.455	-0.493	-0.240	0.028	-0.092	-0.312	-0.017	-0.146	-0.144	-0.517
C_AsterShrub	0.160	-0.094	0.223	0.351	0.264	-0.251	-0.096	-0.333	-0.389	0.756	0.683
D_AsterShrub	-0.154	0.295	0.026	0.207	-0.032	-0.511	-0.057	0.002	-0.067	0.301	0.173
C_Shruh	-0.062	0.250	-0.160	-0.170	-0.112	-0.464	0.168	0.181	0.347	-0.245	0.018
D_Shruh	-0.391	0.686	-0.564	-0.478	0.185	-0.369	-0.009	-0.014	0.253	-0.068	-0.191
C_All Shrubs	0.172	0.045	0.144	0.198	0.161	-0.439	0.048	-0.218	-0.154	0.521	0.633
D_All Shrubs	-0.386	0.603	-0.387	-0.236	0.158	-0.597	-0.017	-0.120	0.094	0.213	0.007
Cover Pentaschistis	0.297	-0.474	0.215	0.196	0.146	1.000	-0.469	-0.357	-0.466	-0.052	-0.054
Cover Themeda	-0.086	0.128	0.179	-0.239	-0.261	-0.469	1.000	0.272	0.522	-0.048	0.131
Cover Cymbopogon	0.057	0.488	-0.018	-0.076	-0.652	-0.357	0.272	1.000	0.729	-0.239	-0.005
Palatable grasses	0.067	0.522	-0.148	-0.300	-0.606	-0.466	0.522	0.729	1.000	-0.458	-0.233
Cover Elytropappus	0.141	-0.101	0.303	0.282	0.130	-0.052	-0.048	-0.239	-0.458	1.000	0.741
Cover 3 Dom. Asteraceae	0.304	-0.196	0.480	0.457	-0.006	-0.054	0.131	-0.005	-0.233	0.741	1.000