Assessing the vegetation and soil microbial ecology of renosterveld rangelands around Nieuwoudtville, Northern Cape Province

Gabrielle Marie Solomon

A thesis submitted in fulfilment of the requirements for the degree *Magister Scientiae*, in the Department of Biodiversity and Conservation Biology, Faculty of Natural Science, University of the Western Cape.

UNIVERSITY of the
WESTERN CAPE

May 2015

Supervisor:

Mr. Frans M. Weitz, Department of Biodiversity and Conservation Biology, University of the Western Cape

Co-supervisors:

Mr. C.F. Cupido, Animal Production Institute, Agricultural Research Council

Prof. W.J. Swart, Department of Plant Sciences, University of the Free State

Keywords

Rhizosphere, microbial ecology, plant species richness, rangelands, renosterveld, Northern Cape

Abstract

The Bokkeveld Plateau, a region hosting high plant endemism, is home to two arid mountain centre renosterveld types. One, Nieuwoudtville Shale Renosterveld, has partially been transformed into croplands and pastures, with about 40 % remaining as non-contiguous fragments on privately owned land, and is used as natural rangelands for sheep grazing. The vegetation, soil chemical parameters, and rhizosphere soil microbial ecology of a dominant plant, *Eriocephalus purpureus*, were assessed. A combination of field sampling and recording, laboratory analyses of soil samples, and interviews were used to glean data. Data were statistically analysed using multivariate techniques. Overall plant species richness did not differ among the study sites, though plant species richness and cover of the different plant growth form categories varied among the sites. Soil chemical parameters varied among sites. Soil chemical and rhizosphere soil microbial parameters co-varied, and showed different profiles among the study sites. High cover of *E. purpureus* was associated with high microbial enzyme activity, while high cover of (other, non-dominant) non-succulent shrubs was associated with high bacterial functional diversity. Cover of geophytes, *Asparagus capensis* and perennial grass was associated with high microbial biomass. The findings indicate that *E. purpureus*-dominated Niewoudtville Shale Renosterveld is heterogeneous not only in terms of vegetation, but also in terms of soil chemical and microbial parameters. The results support the conservation of *all* fragments of remaining renosterveld, as they may serve as valuable resources of not only plant genetic material but also of soil microbial communities.

UNIVERSITY of the
WESTERN CAPE

Declaration

I declare that 'Assessing the vegetation and soil microbial ecology of renosterveld rangelands around Nieuwoudtville, Northern Cape Province' is my own work, that it has not been submitted for any degree or examination at any other university, and that all the sources which I have used or quoted have been indicated and acknowledged by complete references.

UNIVERSITY of the
WESTERN CAPE

…… ……..

Gabrielle Marie Solomon Date

Acknowledgements

Without my supervisors, who provided academic, financial, and logistical support, this project would have remained an idle idea.

I was fortunate to receive a Scarce Skills bursary (number 79795) from the National Research Foundation which made pursuing this project possible.

I was helped in official, and un-official, ways by the following people, who unstintingly gave of their time and expertise. I call them my all-star cast: Lilburne Cyster and the laboratory of the Department of Biodiversity and Conservation Biology. Marieta Van der Rijst, ARC Biometry for statistical analyses. Igshaan Samuels, Melvin Swarts and Grant Birch for much advice and help in the field. In Nieuwoudtville, resident researchers and field-experts: Eugene Marinus and Colleen Rust (Hantam National Botanical Garden, SANBI), Simon Todd, Christy Bragg, and Mandy Schumann.

And, most importantly, the farmers and their families who allowed me on their land, answered my questions and pointed out the questions I *hadn't* asked. Without you there would have been no project. This is for you.

UNIVERSITY of the
WESTERN CAPE

Contents

Keywords i

Abstract i

Declaration ii

Acknowledgements iii

Table of contents iv

List of figures vii

List of tables viii

Chapter 1 General Introduction 1

1.1 Background and motivation for research 1

1.2 Objectives 3

1.2.1 Project aim 3

1.2.2 Targeted outcomes 3

1.2.3 Research questions 3

1.3 Thesis structure 4

Chapter 2 Literature review 6

2.1 Drylands 6

2.2 Agro-ecosystems, biodiversity and ecosystem services 10

2.3 Rangeland ecology 15

2.4 Renosterveld 23

2.5 Soil ecology 30

2.6 Links between vegetation and soil biota 38

Chapter 3 Study area - The Bokkeveld Plateau and Nieuwoudtville 45

UNIVERSITY of the
WESTERN CAPE

3.1 Study area 45
3.2 Study sites 52
3.3 Stocking data 53

Chapter 4 Renosterveld rangeland vegetation cover and diversity 57

4.1 Introduction 57
4.2 Materials and methods 59
4.2.1 Study area 59
4.2.2 Rapid Renosterveld Assessment Method 60
4.2.2.1 Plant surveys 60
4.2.2.2 Geographical data 61
4.2.2.3 Farmer/land manager interviews 61
4.2.3 Statistical analyses 62
4.3 Results 62
4.4 Discussion 66
4.5 Conclusion 75

Chapter 5 Rhizosphere ecology of *Eriocephalus purpureus*, a dominant shrub in renosterveld rangelands 77

5.1 Introduction 77
5.2 Materials and methods 80
5.2.1 Study area 80
5.2.2 Soil sampling 80
5.2.2.1 Soil chemical sampling 80
5.2.2.2 Soil microbial sampling, dry season 81
5.2.2.3 Soil microbial sampling, rainy season 81
5.2.3 Soil chemical analyses 82
5.2.3.1 Soil digestion 82
5.2.3.2 Cation analyses 82
5.2.3.3 Nitrogen analysis 83

UNIVERSITY of the
WESTERN CAPE

5.2.3.4 Phospate (PO_4) analysis 83
5.2.3.5 pH 84
5.2.3.6 Conductivity 84
5.2.4 Rhizosphere soil microbial analyses 84
5.2.5 Statistical analyses 85
5.3 Results 86
5.3.1 Soil chemical analyses 86
5.3.1.1 Dry season 86
5.3.1.2 Rainy season 88
5.3.2 Rhizosphere soil microbial analyses 90
5.3.2.1 Biolog EcoPlates™ 90
5.3.2.2 PLFA analysis 93
5.3.2.3 Fluorescein Diacetate (FDA) analysis 93
5.3.3 Soil chemical and rhizosphere soil microbial analyses 94
5.3.3.1 Dry season 94
5.3.3.2 Rainy season 95
5.4 Discussion 97
5.5 Conclusion 109

Chapter 6 Links between renosterveld rangelands vegetation and the soil ecology of a dominant shrub. 111

6.1 Introduction 111
6.2 Materials and methods 113
6.2.1 Study area 113
6.2.2 Rapid Renosterveld Assessment Method 113
6.2.3 Soil sampling and analyses 113
6.2.4 Statistical analyses 114
6.3 Results 114
6.3.1 Vegetation and rhizosphere soil microbial analyses, both seasons 115
6.3.1.1 Plant species richness and rhizosphere soil microbial analyses, both seasons 115

UNIVERSITY of the
WESTERN CAPE

6.3.1.2 Plant cover and soil microbial analyses, both seasons 117
6.3.2 Vegetation and soil chemical analyses 118
6.3.2.1 Plant species richness and soil chemical attributes, both seasons 118
6.3.2.2 Plant cover and soil chemical attributes, both seasons 120
6.3.3 Vegetation and all soil parameters 122
6.4 Discussion 123
6.5 Conclusion 134
Chapter 7 Summary 138
Chapter 8 References 140

UNIVERSITY of the
WESTERN CAPE

List of figures

Figure 2.1 Pre-colonial and current extent of renosterveld 27
Figure 2.2 The soil food web..... 33
Figure 3.1 Map of vegetation biomes of South Africa 46
Figure 3.2 Broad-scale geological map Bokkeveld Plateau 47
Figure 3.3 C.A.P.E broad priority areas 48
Figure 4.2 PCA plant species richness 64
Figure 4.3 PCA plant cover 65
Figure 5.1 PCA soil chemical analyses dry season 87
Figure 5.2 PCA soil chemical analyses rainy season..... 89
Figure 5.3 Bar graph of Biolog, both seasons 91
Figure 5.4 PCA both seasons Biolog carbon-source utilisation 92
Figure 5.5 PCA soil chemical and microbial, dry season 94
Figure 5.6 PCA soil chemical microbial, rainy season. 96
Figure 6.1 PCA plant species richness and soil microbial parameters 116
Figure 6.2 PCA plant cover and soil microbial parameters 118
Figure 6.3 PCA splant species richness and soil chemical measures. 120
Figure 6.4 PCA plant cover soil chemical measures 121
Figure 6.5 PLS correlation loading plot, soil (chemical and microbial) and plant variables..... 123

UNIVERSITY of the
WESTERN CAPE

List of tables

Table 3.1 Stocking data for the study plots. 55
Table 4.1 Table showing the number of plant species in each study plot. 63
Table 5.1 Results ANOVA for all soil chemical parameters..... 86

Chapter 1 General Introduction

1.1 Background and motivation for research

Drylands cover about 40 % of the world's land surface (Derner and Schuman, 2007) and 70 % of productive drylands are degraded (UNCCD, 2011). The natural capital of these regions, including biological and economic resources, e.g. freshwater sources, vegetation and soil quality, is easily damaged (MEA, 2005). These areas are characterised by temporal and spatial heterogeneity (Stafford Smith, 2008).

UNIVERSITY of the
WESTERN CAPE

Semi-arid areas can be productively used as rangelands. Varied vegetation types may be used as rangelands, including shrublands. Renosterveld is a grass- or shrub-dominated vegetation type within the fynbos biome. Renosterveld is a highly transformed and fragmented vegetation type with high plant diversity and endemism (Mucina and Rutherford, 2006; Bergh *et al*., 2014). Despite this wealth in terms of plant species richness, natural renosterveld remnants are fragmented within mostly transformed agro-ecological landscapes.

Natural renosterveld remnants can be found on the Bokkeveld Plateau, in the Northern Cape Province of South Africa. This plateau has a varied underlying geology, giving rise to different soil and vegetation types. Even within broader vegetation types, there is spatial heterogeneity in terms of the vegetation communities found here. Two sub-types of renosterveld arise from the tillite and

dolerite clay soils on the Bokkeveld Plateau, Nieuwoudtville Shale Renosterveld and Nieuwoudtville-Roggeveld Dolerite Renosterveld (Mucina and Rutherford, 2006). Both these vegetation types have been partially transformed into pastures and croplands, and the remaining natural veld fragments are used for sheep grazing. One of the most palatable sub-vegetation types of Nieuwoudtville Shale Renosterveld is dominated by an aromatic sub-shrub, *Eriocephalus purpureus* Burch.ex G.Don (wild rosemary, *kapokbos*).

Biodiversity is the sum total of living species across all kingdoms of the natural world. The biodiversity of rangelands have been well-documented, and the vegetation which supports herbivores has been extensively studied, but the biodiversity belowground which underpins rangeland productivity and stability has received less attention (Tate, 2000; Moussa *et al*., 2009).

UNIVERSITY of the
WESTERN CAPE

Belowground biota is responsible for a suite of ecosystem functions. Soil microbes are at the bottom of the soil food web and are the most numerous and diverse of all soil organisms (Wurst *et al*., 2012). Their main functions in agro-ecosystems are nutrient cycling and the maintenance of soil fertility (Wall *et al*., 2007). Soil microbes are sensitive to environmental changes and are early indicators of disturbance (Bending *et al*., 2004). Agricultural practices, including grazing, may damage these belowground organisms and affect their ability to provide ecosystem services (Sylvain and Wall, 2011). If these microbial species and their services are lost, they might only be recoverable with strong interventions, at considerable effort and expense.

1.2 Objectives

1.2.1 Project aim

To assess the vegetation and soil microbial and chemical characteristics of semi-arid renosterveld rangelands.

1.2.2 Targeted outcomes

In order to achieve this aim, the following targeted outcomes were set:

1) Assess the plant species richness and cover of *Eriocephalus purpureus*-dominated Nieuwoudtville Shale Renosterveld rangelands
2) Analyse the soil chemical profile of *E. purpureus*-dominated Nieuwoudtville Shale Renosterveld
3) Examine and describe the rhizosphere soil microbial ecology of *E. purpureus*
4) Discover whether there are any relationships among aboveground and belowground findings in *E. purpureus*-dominated Nieuwoudtville Shale Renosterveld

UNIVERSITY of the
WESTERN CAPE

1.2.3 Research questions

1) How do plant species richness and cover differ on fragments of *E. purpureus*-dominated Nieuwoudtville Shale Renosterveld rangelands?
2) How does the soil chemical profile differ among soil beneath *E. purpureus* individuals on various fragments of *E. purpureus*-dominated Nieuwoudtville Shale Renosterveld?
3) How does the soil rhizosphere microbial profile differ among the rhizosphere of *E. purpureus* individuals on various fragments of *E. purpureus*-dominated Nieuwoudtville Shale Renosterveld rangelands?
4) Are there significant relationships between aboveground and belowground measures (vegetation, soil chemical and soil microbial) from various fragments of *E. purpureus*-dominated Nieuwoudtville Shale Renosterveld rangelands?

UNIVERSITY of the
WESTERN CAPE

1.3 Thesis structure

In this project, I have made use of detailed ecological investigations. Plant and soil factors were investigated at plot level. A combination of field sampling and recording, laboratory analyses of soil samples, and interviews were used to glean data. Data were statistically analysed using multivariate techniques, including PCA.

Chapter 1 introduces the motivation for the study, including the overall aim,

targeted outcomes and research questions. Chapter 2 establishes the scope of this study with a literature review encompassing all relevant topics; drylands, agro-ecosystems, rangelands, renosterveld, soil and rhizosphere ecology, and the links between aboveground and belowground patterns and processes found in previous studies. Chapter 3 provides a detailed description of the study area. Chapter 4 presents the aboveground findings of the study; vegetation cover and diversity of untransformed renosterveld patches. Chapter 5 examines the microbial ecology of the rhizosphere soil of *Eriocephalus purpureus*, as well as the soil chemical composition. Chapter 6 links the vegetation and soil chemical and microbial parameters, and examines any relationships found. Chapter 7 summarises the study, and offers management recommendations. Chapters 4, 5 and 6 are written in journal article format, though, in order to avoid repetition, the description of the study area and study sites (Chapter 3) was not repeated in each of these chapters. Also, full terms and abbreviations are given the first time they are used, and subsequently, only the abbreviation. The results of the rhizosphere soil microbial analyses are included in both Chapter 5 and 6, but related to differing variables. The plant survey data are included in Chapters 4 and 6, but described in terms of different contexts.

UNIVERSITY of the
WESTERN CAPE

Chapter 2 Literature review

2.1 Drylands

Water is the limiting resource for life in drylands, which cover about 40 % of the world's land surface (Derner and Schuman, 2007). There is no clear definition for drylands, but they are characterised by limited supply rates of water in the form of rainfall and/or snow (UNEMG, 2011).

Drylands include hyper-arid, arid, semi-arid and sub-humid areas, and these areas are defined by the aridity index, the ratio of precipitation to potential evapotranspiration (P/PET) (Koohafkan and Stewart, 2008). Potential evapotranspiration is the maximum amount of water capable of being lost as water vapour (including transpiration from vegetation and evaporation from the soil) by a continuous stretch of vegetation in a given climate, region and time interval, when well-supplied with water (WMO, 1990).

UNIVERSITY of the
WESTERN CAPE

The P/PET ratio for the various areas are as follows: hyper-arid areas 0-0.05, arid areas 0.05-0.20, semi-arid areas 0.20-0.50, and sub-humid areas 0.50-0.65 (UNEMG, 2011). Semi-arid areas not only differ from more arid areas in that the P/PET ratio is higher, but the timing of rainfall is also more predictable. Three main types of climate occur in drylands globally; tropical, continental or mediterranean-type climates, depending on the overall normal rainfall pattern (Koohafkan and Stewart, 2008).

The lack of water in an ecosystem has several implications, the most fundamental one being the inhibition of the ability of an organism to capture and use carbon (Huxman *et al*., 2004). The availability of moisture in drylands typically is spatially and temporally heterogeneous on multiple scales (Lambers *et al*., 1998), with changes over short (hours and days) and long (seasons and years) timescales (Huxman *et al*., 2004). Low precipitation and high potential evapotranspiration are associated with overall harsh ambient conditions which dictate that organisms that live within these constraints are adapted in trait or behaviour to avoid specific conditions. For plants this includes drought deciduousness and seed dormancy (Chesson *et al*., 2004). Despite limited and patchily-available resources, arid and semi-arid areas are the habitats of unique flora and fauna (O'Farrell *et al*., 2011).

UNIVERSITY of the
WESTERN CAPE

A prominent characteristic of arid and semi-arid areas is that they display high spatial and temporal heterogeneity (Stafford Smith, 2008). Topography plays the primary role in the control of the mechanics and processes by which landscapes operate, and vegetation a secondary role. Landscape diversity and connections between diverse landscape units are integral to the biological diversity maintenance and ecosystem functioning in drylands (Schlesinger and Jones, 1984).

Landscapes in arid and semi-arid regions typically contain a mixture of different vegetation types, e.g. shrub- and grasslands, with different dominant plant

growth forms, e.g. leaf-succulent shrubs and perennial grasses. Plant communities differing in common and dominant growth forms are controlled by different ecological processes, for example how nutrients and seed are redistributed by fauna, wind and water (Peters *et al*., 2006). Subsequently, their responses to environmental drivers such as disturbance, e.g. fire and grazing, and climate also vary (Peters *et al*., 2006). In these resource-limited environments perennial plants (especially shrubs) act as important zones of nutrient accumulation, or 'islands of fertility' (Noy-Meir, 1985). Due to their structure, shrubs intercept water and wind, which carry organic matter and dust particles, contributing to the accumulation of organic matter. Shrubs control the movement and transformation of water, nitrogen and other nutrients in water-scarce systems, and the patchy distribution of soil nutrients in drylands is associated with this phenomenon (Schlesinger and Pilmanis, 1998).

UNIVERSITY of the
WESTERN CAPE

Resource availability and soil organisms dictate how intermittent water pulses affect nutrient cycling and the soil nutrient pool (Austin *et al*., 2004).The regulation of water flow and storage is dependent on plant cover, the organic matter in the soil, and soil biological activity (Swift *et al*., 2004). Soil biota in turn are limited by organic matter and moisture availability constraints (Steinberger *et al*., 1984). These organisms play key roles in the biogeochemical and ecological functioning of terrestrial ecosystems (Wardle *et al*., 2004). Many organisms that live in the soil are adapted to water stress, and display coping mechanisms that enable them to survive until conditions improve (Williams, 2007).

Although drylands, along with hillsides and rainforests, are characterised by low productivity (Scherr and McNeely, 2008), they account for two-thirds of agricultural land worldwide (Nelson *et al*., 1997). Areas with low productivity are referred to as 'marginal', and while the chief definition is economic (Schroers, 2006), the most important implication, in ecological terms, is that marginal lands are fragile and at risk of degradation (Wiegmann *et al*., 2008). The economic definition implies limitations rendering marginal lands less useful for agriculture, and constrained in delivering ecosystem services (Hart, 2001). Ecosystem services are the ecological processes and functions which underpin and better human well-being (Daily, 1997).

UNIVERSITY of the
WESTERN CAPE

The natural capital of drylands, including biological and economic resources, e.g. freshwater sources, vegetation and soil quality, is susceptible to damage through environmental changes and desertification (MEA, 2005). Through grazing, domestic livestock have significantly contributed to the degradation of drylands on a global scale (Asner and Archer, 2010). A reduced vegetation cover is one of the first signs of degradation in drylands rangelands (Hochstrasser *et al*., 2014).

Traditional agricultural systems that employ strategies like nomadic pastoralism and shifting agriculture are sensitive to the lack of resilience in dryland systems, and respond in a way that preserves ecosystem services. These practical solutions to constrained (in time and space) resources are difficult to apply in

modern times, with human settlements the norm, higher population densities, the concomitant increased demand for food, and other economic and political pressures (UNEMG, 2011).

The global human population is expected to reach nine billion by the year 2050 (Tilman *et al*., 2002; FAO, 2015), and food production should increase by 60 % by 2050 to meet demand (FAO, 2015). To meet this demand, production systems may become increasingly intensively managed (with a higher requirement of nutrients, water, and pest control), as well as expanding into previously natural areas. This expansion is anticipated to be the most pronounced in developing countries and dryland regions (Jackson *et al*., 2005).

UNIVERSITY of the
WESTERN CAPE

The human populations that live in dryland areas are often more dependent on their immediate surroundings for their livelihoods, including the use of plants for food, forage, fibre and fuel (Stafford Smith, 2008). In order to ensure food security, as well as the preservation of vegetation biomass and biodiversity, drylands must be managed sustainably (Kang *et al*., 2013).

Thus the protection of biodiversity and the sustainable production from natural resources that supports human life need to be considered, addressed, and practiced simultaneously (Tscharntke *et al*., 2012).

2.2 Agro-ecosystems, biodiversity and ecosystem services

Agriculture is an economic activity, whether for subsistence or profit. Without it humans would have little food, fibre, or medicinal compounds to provide nutrition, clothing, health care and shelter. The term agriculture usually denotes two main activities; crop production and the raising of livestock. Agro-ecosystems are natural systems that are altered by anthropogenic management in order to obtain desirable products (Swift *et al*., 1996).

Simplification of a landscape is a characteristic of agriculture (Soini and Aakkula, 2007). This simplification can be to a greater (when intensively managed) or lesser (when extensively managed) extent (Swift *et al*., 1996), but both have ecological ramifications (Scherr and McNeely, 2008). The process of agricultural intensification includes the increased use of non-renewable, purchased inputs, e.g. inorganic fertilizers and agrochemicals (Jackson, 2007). The greater the intensity of land-use, and the higher the degree of management intervention, the lower the overall species diversity (Swift and Anderson, 1993; Frison *et al*., 2011; Brussaard *et al*., *s.a*.). Lower species diversity has a negative impact on agricultural sustainability (FAO, 2011; Frison *et al*., 2011).

UNIVERSITY of the
WESTERN CAPE

An example of this is the two different methods of growing coffee (*Coffea arabica*) in Central America. In an agroforestry system, traditional coffee varieties are shade-grown beneath a canopy of native trees, fruit trees and banana (*Musa* spp.) plantations, and inter-planted with cassava (*Manihot esculenta*) and other annual crops. This system is structurally similar to a forest (Swift *et al*., 1996). The modern, intensive monoculture promoted in Central

America (Babbar, 1993) consists of a single, sun-tolerant, short coffee variety. Native trees are removed, and herbicides and fertilizers are liberally applied (ICAFE-MAG, 1989). Perfecto and Vandermeer (2002) found higher species diversity of ants in shaded agroforestry coffee plantations, compared to conventional farming with only intermittent shade in Mexico. Perfecto *et al*., (1997) found a significant loss of arthropod diversity in modern monocultures in Mexico, as compared with traditional systems.

For a continuingly healthy and productive landscape, the maintenance of biodiversity is crucial in order to ensure that renewal processes and ecosystem services, e.g. nutrient cycling, and pest and pathogen control are maintained (Swift *et al*., 1996; Jackson *et al*., 2005). These processes rely on biological components, and therefore the maintenance of biological diversity is key (Altieri, 1999; Jackson *et al*., 2005). Both the expansion and intensification of agriculture due to population growth, modern agricultural methods, globalisation of markets, and land-use changes result in the loss of biodiversity (Jackson *et al*., 2005; Jackson, 2007; Frison *et al*., 2011).

UNIVERSITY of the
WESTERN CAPE

The term biodiversity is defined by The Convention on Biological Diversity as: "…the variability among living organisms from all sources, including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part: this includes diversity within species, between species, and of ecosystems" (Heywood and Bates, 1995). South Africa became the 12th country to ratify the Nagoya Protocol (Greiber *et al*., 2012) early in 2013

(Brand South Africa, 2013). The Nagoya Protocol links the conservation of biodiversity, the sustainable use of it, and the traditional knowledge associated with it.

Biodiversity can be sub-divided into four values (Nunes and Van der Bergh, 2001). “Intrinsic” values include social, aesthetic and ethical beliefs; “utilitarian” values encompass both subsistence and commercial benefits; “serependic” (option or bequest) values denote the yet-to-be-discovered value, and finally, “functional” values. “Functional” values overlap slightly with “utilitarian” values, but differ in that they are those values which are not normally accounted for on any balance sheet, especially when it is in credit, e.g. clean air, water and uncontaminated soil.

UNIVERSITY of the
WESTERN CAPE

The term agrobiodiversity includes all plant, animal and microbial species occurring within agro-ecosystems, including predators, pollinators and decomposers, along with the various natural to transformed environments in which they interact (Jackson *et al*., 2005; Frison *et al*., 2011). Agriculture depends on agrobiodiversity, which can be sub-divided into two categories: Planned biodiversity consists of the plant and animal species chosen and managed by humans. Associated biodiversity is the ‘uneconomical’, or non-accounted for plants, e.g. weeds, cover species, and trees in agro-forestry, animals, e.g. pests, soil fauna, indigenous herbivores and predators, and microbial species, e.g. symbionts and pathogens.

Changes in faunal and microbial diversity influence ecosystem functioning, e.g. in terms of pollination, pest control, nutrient cycling, and water use efficiency (Jackson *et al*., 2005). Changes in ecosystem function influences productivity and sustainability of an agricultural ecosystem (Swift and Anderson, 1993). Both planned and associated biodiversity provide important ecosystem services in agro-ecosystems (Tscharntke *et al*., 2012). Total biodiversity in agro-ecosystems is influenced by three major factors; food resources, habitat structure and micro-climate (Swift *et al*., 1996).

In agro-ecosystems, the relationship in space and time between different species, belonging to different genera, families, and all the way to kingdoms is more important than biodiversity *per se* (Swift *et al*., 2004). The maintenance of biodiversity lies, as it should, in the hands of the landowners and farmers who spend their days and lives in close proximity to the cyclical, dynamic pattern and processes which sustain the systems that humans have put into place to produce necessary goods and services (Milton, 1997; Kaljonen, 2006), and sustain the underlying ecosystems that we have but an inkling of (Van der Heijden *et al*., 2008).

UNIVERSITY of the
WESTERN CAPE

Ecosystem functions are the minimum aggregated set of processes (including biochemical, biophysical and biological) that ensure the biological productivity, organisational integrity and perpetuation of an ecosystem (MEA, 2005). Ecosystem goods and services exist thanks to the biophysical and chemical processes performed by communities of living organisms (Swift *et al*., 2004). In

all agro-ecosystems, nutrient cycling and other ecosystem services that depend on biodiversity (both above- and belowground) need to be protected (Altieri, 1999; Sylvain and Wall, 2011). Agrobiodiversity thus constitutes the natural capital of a region, sustaining systems for crop and livestock production, and ensuring food security (Jackson *et al*., 2012).

DIVERSITAS, an international non-governmental biodiversity science research organisation, until recently hosted agroBIODIVERSITY*, a network that promotes the sustainable management of biodiversity in agricultural landscapes (Brussaard *et al*., *s.a*.). This inter-disciplinary network recommends an integrated landscape approach in order to achieve conservation and agricultural sustainability objectives. With this approach, all the multi-functional roles of biodiversity interactions within an agro-ecological matrix of natural habitats and managed areas are taken into account.

UNIVERSITY of the
WESTERN CAPE

*The Diversitas programs agroBIODIVERSITY and ecoSERVICES merged in January 2014 to become a project of Future Earth (Diversitas, 2014).

2.3 Rangeland ecology

Diverse ecosystems that are not suited to intensive agriculture due to edaphic, topographic or climatic restrictions can be productively used as rangelands (Holechek *et al*., 2004). Allen *et al*. (2011) define rangelands as “land on which the indigenous vegetation (climax or sub-climax) is predominantly grasses,

grass-like plants, forbs or shrubs that are grazed or have the potential to be grazed, and which is used as a natural ecosystem for the production of grazing livestock and wildlife". Their definition includes natural grasslands, savannas, shrublands, deserts, steppes, tundras, alpine communities and marshes.

The majority (88 %) of arid and semi-arid areas world-wide are managed as rangelands (Reynolds *et al*., 2007). Drought occurrences are common in these regions and the availability of natural resources fluctuates in time and space (Cousins, 1993). Globally, between 10-20 % of the ecosystems in arid and semi-arid lands show a degree of degradation (Reynolds *et al*., 2007). The ability of a rangeland to recuperate depends mainly on the level of grazing intensity and the variation in rainfall (Mworia *et al.,* 1997). Factors affecting rangelands include abiotic, e.g. climate and soil, and biotic factors such as grazing. Grazing is second to fire as the strongest disturbance factor worldwide in terms of plant biomass loss (Díaz *et al*., 2007). Grazing effects vary spatially at multiple scales, as herbivores graze selectively, and drylands are inherently spatially heterogeneous (Smith *et al*., 2012).

UNIVERSITY of the
WESTERN CAPE

The degradation of rangelands can be defined as a loss of productivity and diversity (Milton *et al.,* 1994), loss in terms of the cover and biomass of native perennial plants (Reynolds and Stafford Smith, 2001), or a disturbance of biological cycles, which in turn leads to a loss in economic productivity. The disturbance of biological cycles results from land use, through various processes such as erosion, loss of soil quality (physical, chemical, and biological

properties), and the loss of natural vegetation (UNCCD, 2010).

According to Scoones (1995), 59 % of livestock in Africa are based in semi-arid and arid regions. Rangelands cover 80 % of the land surface in South Africa, and sustain large amounts of livestock and game (Tainton, 1999; Hoffman and Ashwell, 2001). The grazing of domestic livestock is considered the major human-induced driver of degradation in arid and semi-arid rangelands in southern Africa (Downing, 1978; Wesuls *et al*., 2010).

Rangelands have been transformed in terms of vegetation, and large areas have been diminished in terms of productivity since the colonization of southern Africa (Roux and Vorster, 1983; Dean and Macdonald, 1994; Dean *et al*., 1995b). The consensus is that poor livestock management is the main factor for the significant changes in vegetation that have been observed in rangelands in South Africa (Roux and Vorster, 1983; Milton *et al*., 1994; Hoffman and Ashwell, 2001; Archer, 2004).

UNIVERSITY of the
WESTERN CAPE

Arid and semi-arid areas often suffer extreme climatic changes, and this exacerbates the difficulty in measuring the effects of climate and grazing (Hoffman and Cowling, 1987). Disentangling the effects of climatic patterns and stocking rates are fraught with difficulty (Dean and Macdonald, 1994; Seymour and Dean 1999; Archer, 2004), but studies have shown that the effects of heavy stocking rates are amplified by variations in rainfall (Meadows and Watkeys, 1999; Dahlberg, 2000).

Rangeland theory falls roughly into two, philosophically opposing, camps. Equilibrium theory proposes that plants and herbivores are tightly coupled, and that overgrazing leads to the degradation of rangeland resources and the ultimate collapse of a rangeland system. Non-equilibrium theory proposes that the vegetation of areas that are subjected to a high level of climatic variability (and possible ensuing droughts) is easily diminished, and consequently there may not being enough food for herbivores (Behnke and Scoones, 1993; Scoones, 1995). This causes farmers in these areas to become economically unstable, especially as they may not be able to exploit spatial heterogeneity by utilising transhumance strategies. The key assertion of non-equilibrium theory is that livestock do not affect forage resources to the degree that rangelands are diminished. The inherent spatial and temporal heterogeneity in South African rangelands creates complexity to such a degree that linear concepts are inadequate to describe or predict responses (Richardson *et al*., 2005). South African rangelands can therefore be characterised by both non-equilibrium and equilibrium aspects (Campbell *et al*., 2006; Gillson and Hoffman, 2007).

UNIVERSITY of the
WESTERN CAPE

Fully functional and regenerative rangelands are dependent on functional diversity of organisms at many spatial and temporal scales, with intact ecological processes continually regenerating ecosystem services (Kremen *et al*., 2012). Blench and Sommer (1999) propose an ecosystem approach when assessing rangeland biodiversity. This approach stresses the importance of maintaining functional diversity (Bond, 1995), including fauna and flora to the micro-

organism level, in order to attain management or economic objectives. This approach acknowledges the cyclical, continually changing and adaptive character of natural ecosystems. Rangelands offer not only natural forage for livestock, but also function as habitats for wild fauna and serve as water catchment areas (Maczko *et al.*, 2011).

In arid and semi-arid rangelands, it is impossible to disentangle those ecosystem services that the production of livestock depends on from those that sustain overall ecosystem productivity and resilience, e.g. the regeneration of plants, nutritious forage, the provision of shelter from wind and shade in summer, and the supply of clean water (Daily, 1997; Binning *et al*., 2001).

UNIVERSITY of the
WESTERN CAPE

Herbivores are recognised as drivers of ecosystem productivity and vegetation composition, as they consume varying amounts of the net primary production depending on the type of ecosystem, e.g. grassland or forest. Selective grazers and browsers (e.g. domesticated sheep and cattle) can change the plant community composition by favouring palatable plants, and potentially disrupting their reproductive cycles, and ultimately contributing to their diminishment (Díaz *et al*., 2007). Sheep will consume the flowerheads of palatable plant species, e.g. *Tripteris sinuata*, thus arresting their reproductive cycle (Milton and Dean, 1995).

Herbivore-effects on aboveground vegetation and belowground biotic communities can be divided into three categories. Effects on resource quantity:

Herbivory affects the pattern of carbon allocation in and root exudation of plants (Hamilton and Frank, 2001). Over the long-term, herbivory causes shifts in net primary production, and consequently the amount of dead organic matter that enters the soil, on which the decomposer communities feed (Bardgett and Wardle, 2003; McKeon *et al*., 2009). Effects on resource quality: Herbivory may increase the nutrient content of leaves and roots of plants, which increases the quality of the litter, and consequently that of soil organic matter (Hamilton and Frank, 2001). Conversely, herbivory may increase the production of plant secondary compounds, which lowers the litter quality (Rhoades, 1985). Effects on vegetation composition: Herbivory modifies the vegetation community in terms of functional composition by changing both plant cover and diversity (Midgley *et al*., 2010). Overgrazing of palatable plant species results in an increase in annual and unpalatable species (Todd, 1999). Riginos and Hoffman (2003) showed that shrubs decrease in abundance through reduced seed set in Namaqualand (in the succulent karoo biome) in response to heavy grazing. Changes in vegetation due to grazing in the winter-rainfall region of South Africa are well-documented, and show clear effects on both plant cover and diversity (Cupido, 2005; Kraaij and Milton, 2006; Todd and Hoffman, 2009), though these effects are not consistent. Heavy grazing in Namaqualand is further linked to a decrease in the proportion of perennial to annual plants in terms of abundance and species (Anderson and Hoffman, 2007). In general, sustained heavy grazing in the succulent karoo results in higher cover of unpalatable perennial plants, with an attendant decrease in cover and diversity of succulent and palatable non-succulent perennial plant species (Milton and Dean, 1995).

UNIVERSITY of the
WESTERN CAPE

The removal of biomass changes the capacity of vegetation patches to capture resources (Rietkerk *et al*., 2000).

Furthermore, livestock trampling causes soil compaction, increasing soil bulk density and reducing infiltration (Stavi *et al*., 2008), decreasing soil stability and structure by damaging biological soil crusts, and exposing soil aggregates to possible erosion by water and wind (Bowker *et al*., 2011; Eldridge *et al*., 2011). Herbivores contribute dung and urine to the soil organic matter pool (Frank and Groffman, 1998). These effects increase the inherent spatial heterogeneity in terms of soil resources found in water-limited environments (Wang *et al*., 2009). These influences vary in their effect on soil biological aspects, and these properties in turn affect aboveground plant production and diversity, and consequently herbivores (Bardgett, 2005).

UNIVERSITY of the
WESTERN CAPE

Changes in the plant community composition affects both the quality and quantity of litter that enters the soil food web (Chapin *et al*., 2002), consequently altering the soil decomposer community composition (Bardgett, 2005). A reduction in the litter layer on the soil surface alters the soil microclimate (Golodets and Boeken, 2006), increasing evaporation, reducing soil moisture and infiltration (Bromham *et al*., 1999).

Dryland soils typically are slow to recover post-disturbance, and areas that have been grazed long-term may show legacy effects in terms of carbon and nutrient cycling processes (Eldridge *et al.,* 2011). Furthermore, the legacies of draught

and grazing are heterogeneously arranged in space and time (Lyford *et al*., 2003).

Stocking refers to the number of animals on a specific area (normally expressed as unit per hectare). Stocking is a management decision in terms of place, timing, frequency and intensity (Sayre *et al*., 2001). Grazing is an ecological influence that flows on from stocking, and refers to the physical defoliation of plants by grazers or browsers, trampling (which may lead to soil compaction), urination and defecation (Wilson, 1990). This distinction is important. Stocking may be managed and measured per camp, but grazing in semi-arid rangelands is typically spatially heterogeneous and requires specific measurement to be fully accounted for (Samuels, 2006; Witmore, 2007; Smith *et al*., 2012). This heterogeneous use may be due to topography, forage availability and preference, and seasonality, or to other aspects of extensively managed systems, e.g. the location of water points. Rangelands are not only grazed heterogeneously, but the disturbance effects are also patchily distributed across a grazed area (Smith *et al*., 2012). Beyond a certain threshold, these effects diminish landscape functional integrity.

UNIVERSITY of the
WESTERN CAPE

Rangelands are managed in different ways depending on ownership (communal or private commercial), and the animals that they support (livestock or game). These management systems differ in terms of stocking rates, animal diversity, overall management ethos, and products (Smet and Ward, 2006). Given that commercial agricultural systems are managed for profit (realised by the maximum output of animal production), the implicit, but even more important,

goal is *sustained and continuing* livestock production at an acceptable level to the farmer.

The aim of overall rangeland health not only confers higher productivity and resilience to a rangeland ecosystem, but also affords a potentially larger income for the landowner, in addition to the delivery of ecosystem services. (Milchunas and Lauenroth, 1993; Wessels *et al*., 2007; Teague *et al*., 2009, 2011).

The health of rangeland animals is directly related to the quality of the forage available to them. Increased plant species richness equals more phytochemical variety, leading to better overall health, which confers higher immunity and more resilience to pathogens, and extreme climatic conditions (Frison *et al*., 2011; Provenza *et al*., 2013). Ranchers with access to vegetation types which host higher plant diversity benefit in running healthier herds, with lower expenditure on veterinary services.

UNIVERSITY of the
WESTERN CAPE

2.4 Renosterveld

At the south-western tip of Africa is the smallest of the world's six floral kingdoms (Takhtajan, 1986), the Cape Floristic Region (CFR). The CFR has the highest plant species-to-area ratio in the world (Bond and Goldblatt, 1984). About 9 000 species are found within this 90 000 km² region, of which 70 % are endemic (Goldblatt and Manning, 2000; Goldblatt *et al*., 2005). The CFR is notably richer in plant species than other mediterranean-type climate regions

(Cowling *et al*., 1996).

The majority (70 %) of the CFR is made up of the fynbos biome (Mucina and Rutherford, 2006), but this region also contains succulent karoo, forest, and thicket biomes (Bergh *et al*., 2014). The succulent karoo also hosts high plant diversity (Driver *et al*., 2003), and both fynbos and succulent karoo are considered biodiversity hotspots (Mittermeier *et al*, 2004). Floristic affinities between these two biodiversity hotspots have led to proposals of a unified Greater Cape Floristic Region (GCFR) (Jürgens, 1997; Born *et al*., 2007). The GCFR is further delineated by rainfall seasonality, it falls west of the degree 20.5ºE, distinguishing it from the all-year rainfall zone east of this longitude (Bradshaw and Cowling, 2014).

UNIVERSITY of the
WESTERN CAPE

The fynbos biome is made up of three floristically and ecologically distinct vegetation types (Bergh *et al*., 2014): fynbos, classified as a low, treeless, mediterranean heathland (Specht, 1979), and strandveld and renosterveld, both classified as mediterranean shrublands (Boucher and Moll, 1981; Mucina and Rutherford, 2006). There are more than 7 000 endemic species within fynbos, and approximately 1 000 endemic species in renosterveld (Low and Rebelo, 1996). Renosterveld has previously been described as a transitional shrubland, an 'ecotone', i.e. not a distinctive veld type (Taylor, 1978), but Bergh *et al*. (2014) have shown that renosterveld is clearly an independent, although floristically transitional, vegetation type, rather than a subtype of fynbos, succulent karoo or thicket.

Renosterveld is ecologically distinguished from fynbos in terms of soil texture and overall fertility (Bergh *et al*., 2014). Renosterveld occurs on rich, fine-grained soils derived from shale, granites, dolerites, mudstones, silcretes and limestones (Boucher and Moll, 1981). Fynbos occurs mostly on leached, sandy, nutrient-poor, acidic soils (Boucher and Moll, 1981), though there are exceptions (Mucina and Rutherford, 2006). The 29 different renosterveld units described by Mucina and Rutherford (2006) are divided according to geological subtype; there are 19 shale, five granite and dolerite, three silcrete and limestone, and two alluvium sub-types.

UNIVERSITY of the
WESTERN CAPE

The transition from renosterveld to fynbos is soil induced, but the changeover from renosterveld to succulent karoo and the other vegetation types of the CFR is most likely controlled by climate (Bergh *et al*., 2014). In general, renosterveld occurs in areas with rainfall between 250 and 600 mm per year in a typical mediterranean climate; dry, hot summers and cool, rainy winters, with the majority of precipitation falling in winter (Krug, 2004). The different renosterveld bioregions, or centres, do differ in terms of rainfall. West coast renosterveld occurs within a true mediterranean-type climate, whereas south coast renosterveld straddles the transition between winter-rainfall and a bimodal rainfall regime (autumn and spring). Mountain (inland) renosterveld types are typically too arid to be classified as truly mediterranean (Bergh *et al*., 2014).

Renosterveld is a fire-prone, evergreen, short (80-160 cm), small-leaved shrubland (Rebelo *et al*., 2006) characterized by Asteraceae, e.g. *Eriocephalus, Helichrysum, Oedera, Pteronia* and *Relhania*, though Rebelo *et al*. (2006) recognised four distinct structural categories of renosterveld; shrubland, tussock grassland, bulbland and grazing lawn. Renosterveld differs from fynbos in that it largely lacks restiods, ericoids and proteoids (Cowling, 1984; Moll *et al*., 1984; Rebelo, 1996). Renosterveld further differs from fynbos in that it harbours a higher abundance and diversity of grasses, leaf-succulent shrubs, and especially annuals (Cowling, 1990; Curtis, 2013) and geophytes (Cowling, 1990; Paterson-Jones, 1998: Procheş, 2006). Mountain renosterveld is strongly affiliated to succulent karoo in terms of floristic composition and habitat (Taylor, 1978).

Renosterveld occupied large proportions of the fynbos biome (Kruger, 1984) before it was transformed by anthropogenic pressures, e.g. urbanization, agricultural transformation, fire, and alien plant invasion (Low and Rebelo, 1996). Figure 2.1 shows the pre-colonial and current extent of renosterveld.

UNIVERSITY of the
WESTERN CAPE

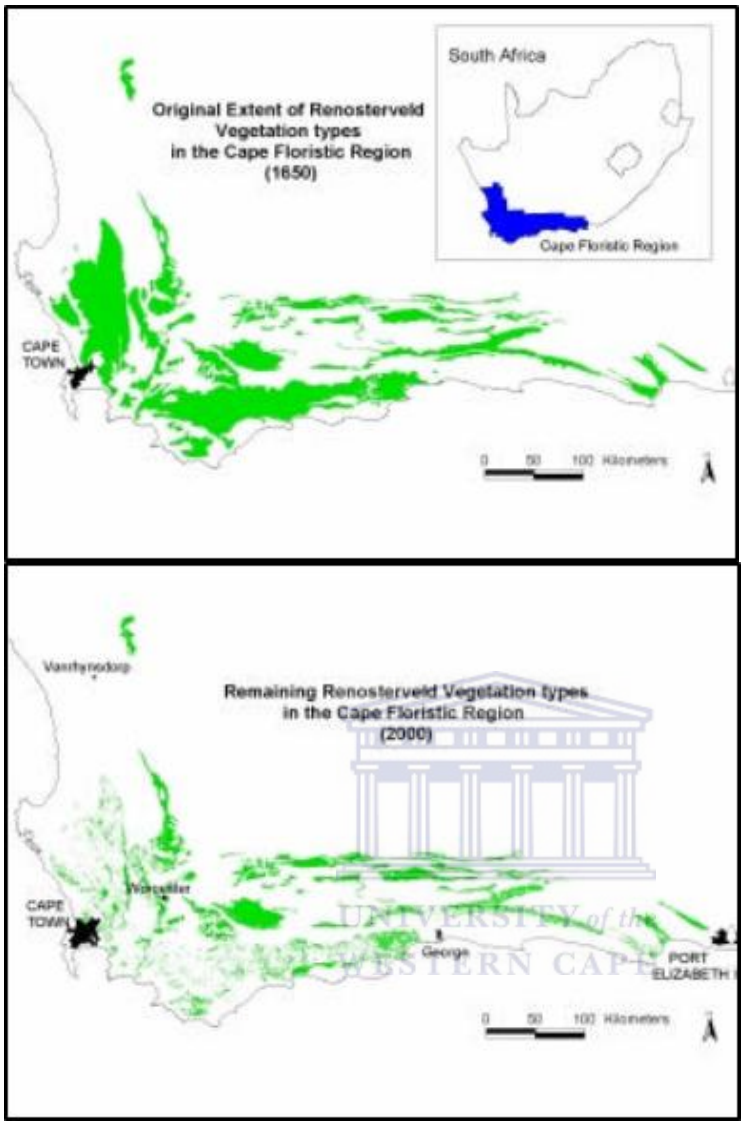

Figure 2.1 Pre-colonial and current extent of renosterveld in the Greater Cape Floristic Region (Von Hase et al., 2003)

Renosterveld is poorly conserved (Cowling *et al*., 1999) despite its global biodiversity importance (Cowling and Pierce, 1999) and regional conservation priority status (Rebelo, 1997). The various renosterveld types are allocated to lowland and mountain types, with lowland types further sub-divided into west coast and south coast centres (Mucina and Rutherford, 2006). The current status of renosterveld is *Critically Endangered* (SANBI and DEAT, 2009), with

between 4 and 10 % of the original extent remaining (Curtis, 2013).

The origin of the name renosterveld is not certain. It could be derived from the often-dominant shrub *Elytropappus rhinocerotis*, colloquially known as "*renosterbos"* (Boucher, 1980). "*Renoster*" is Afrikaans for rhinoceros and the name may be due to sightings of the black rhinoceros (*Diceros bicornis*) in this vegetation type. It is claimed that black rhinoceros were the only animals that could browse *E. rhinocerotis*, which has phenol-rich leaves (Rebelo *et al*., 2006). An alternative explanation is that the vegetation appears grey, especially in the dry summer months, resembling the hide of a rhinoceros (Boucher, 1980). This thesis uses the term renosterveld throughout, as recommended by Boucher (1980). The name renosterveld implies that this vegetation always hosts *E. rhinocerotis,* but many renosterveld sub-types do not contain *E. rhinocerotis* at all, or only in negligible numbers (Bergh *et al*., 2014).

Most natural veld renosterveld fragments occur as patches in an agro-ecological mosaic, which increases the structural diversity at a landscape level (O'Farrell *et al*., 2007). The continued presence of native plant species within this mosaic is fortunate, but to attain conservation goals these fragments should be bigger, and be protected from any further loss in terms of size and viability (Cowling and Bond, 1991; Kemper *et al*., 1999). The high conservation priority assigned to renosterveld is due to the fact that remaining renosterveld is highly fragmented, that the natural veld fragments mainly occur on privately owned land, and that they host high plant species diversity (O'Farrell *et al*., 2009).

Alien species, especially alien annual grass species, pose a well-documented threat to renosterveld (Milton, 2004; Musil *et al*., 2005). Factors such as fires, overgrazing, and nutrient enrichment create favourable conditions for the invasion of alien grass (Van Rooyen, 2003; Muhl, 2008; Sharma *et al*., 2010).

All vegetation types which are used for grazing are affected by the kind of animals (species, breed, age) and manner, e.g. timing, rotation, season, and stocking load, in which they are grazed. Grazing effects on renosterveld seem to be predominantly in terms of plant community composition (McDowell, 1994; Musil *et al*., 2005). An increase in alien annual species and weedy indigenous geophytes, and a decrease in cover of perennial grass with increasing fragmentation, which is linked to increased grazing pressure, has been noted in south coast renosterveld (Kemper *et al*., 1999). Plant diversity and cover have been shown to be largely unaffected (McDowell, 1994; Curtis, 2013), though fine-scale vegetation responses to disturbances were noted due to edaphic and landscape heterogeneity (Curtis, 2013).

Farmers benefit from the value of transformed renosterveld in terms of agriculture, with much of the original extent transformed into vineyards, wheat fields and orchards. The medicinal potential of plant species occurring in renosterveld is largely unexplored. Aromatic shrubs, e.g. *Salvi*a spp., *Eriocephalus* spp., as well as geophytes may yield valuable substances for

aromatherapy and apothecary uses. For example, *E. rhinocerotis* is used as a traditional remedy for a variety of ailments, from headaches and fever to bladder and kidney infections (Thring and Weitz, 2006). The abundance of genetic material found in renosterveld can be used for the development of new cultivars of ornamental plants, e.g. *Gladioulus* spp., *Freesia* spp., and *Babiana* spp.

Farmers further benefit from untransformed renosterveld with perennial native vegetation cover, which acts as a windbreak, protecting against wind erosion, facilitating infiltration and retaining valuable topsoil (O'Farrell *et al*., 2009).

2.5 Soil ecology

UNIVERSITY of the
WESTERN CAPE

The soil, or pedosphere, is the outermost layer of the earth. It is at the interface of, and is formed and affected by, the interactions between the lithosphere, atmosphere, hydrosphere and biosphere (Brady and Weil, 2002). Soil ecology is the study of soil biological, physical and chemical characteristics and related processes, within the context of plant-soil feedbacks (Heneghan *et al*., 2008). Soils provide ecosystem services so important that there would be no life on earth without them (Haygarth and Ritz, 2009). Ecosystem services are the regulating, supporting, cultural and provisioning services that ecosystems deliver, and that humans depend on and benefit from (MEA, 2005).

Ecosystem services depend on sound ecosystem functioning, which depends on the intact abiotic and biotic components of an ecosystem (Brussaard, 2012).

These services include amongst others; the storage and provision of water to plants; the collection, absorption and storage of water and gradual release to streams and groundwater (preventing floods); the regulation of the storage and release of gases, including oxygen and greenhouse gases; the decomposition and the cycling of nutrients and wastes; and the habitat provision for a highly biologically diverse community of organisms (Lavelle, 2012). Soil loss through erosion, desertification, incorrect farming practices and pollution affect the delivery of soil-delivered ecosystem services (Wall, 2012). The conservation and restoration of soils are therefore of critical importance, and the Food and Agriculture Organisation (FAO) has declared 2015 the International Year of Soils (FAO, 2015).

UNIVERSITY of the
WESTERN CAPE

'Soil quality' is usually defined in terms of how well the soil functions relating to a specific use (Karlen *et al*., 2003). Garbisu *et al*. (2011) propose a broader definition for soil quality, as 'the capacity of a soil to perform its ecosystem processes and services, while maintaining ecosystem attributes of ecological relevance'. The term 'soil health' is broader and more integrative: The capacity of soil, as a living system, to function; supporting biological production, promoting the health of plants and animals, and ensuring environmental quality (Doran and Zeiss, 2000). Soil health is an ecological characteristic, and is determined by soil organisms more than soil chemical properties (Van Bruggen and Semenov, 2000). Humans rely on plant production (either directly or via animals) for satisfying their nutritional needs. Plants take up nutrients from the soil, and thus soil health is inextricably linked to animal and human health

(Antunes *et al*., 2012).

The soil is a physically and chemically heterogeneous habitat, hosting organisms that have adapted to their spatially heterogeneous home (Wurst *et al*., 2012). The soil biological component, or soil food web, is the entire community of organisms that live (wholly or partly) in the soil (Beare *et al*., 1995; Ingham, 2007). Soil biota are responsible for the transfer of energy and nutrients between the abiotic and biotic components of the soil, and between trophic levels. Trophic levels are levels of the food chain. The first level consists of photosynthesisers that capture energy from the sun, e.g. plants. The second level are organisms that consume photosynthesisers, and the third level are organisms that consume the second level organisms (Figure 2.2) (Wardle *et al*., 1998; Ingham, 2007).

UNIVERSITY of the
WESTERN CAPE

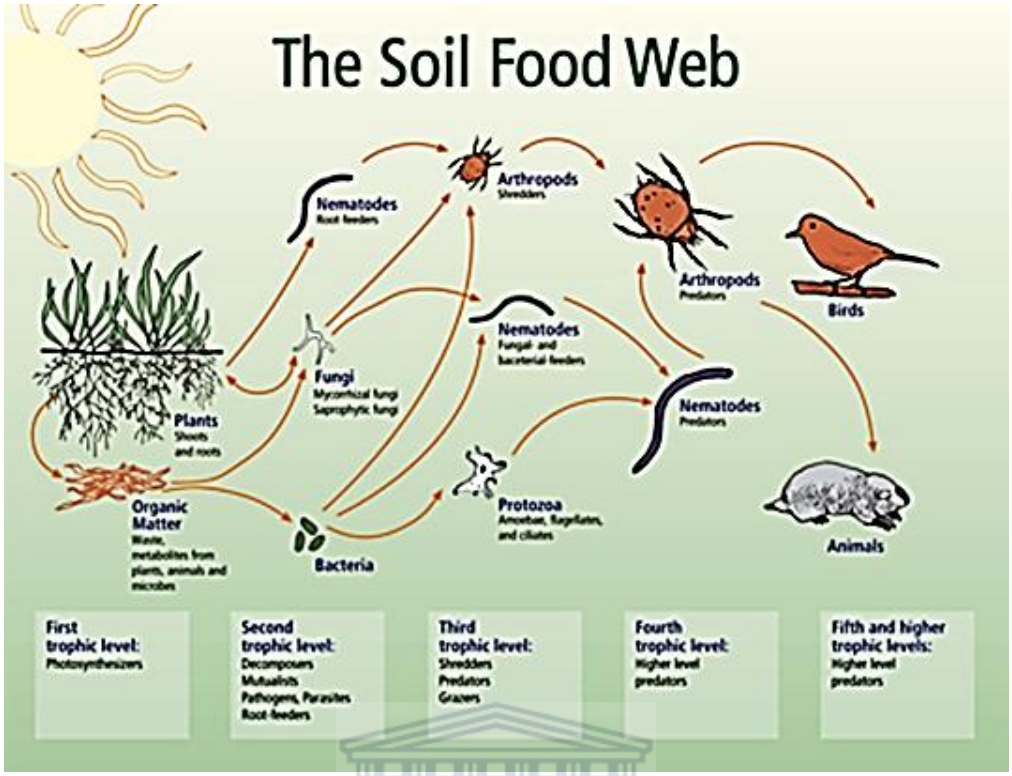

Figure 2.2 The soil food web shows the trophic levels of underground soil biota, with the arrows depicting the movement of nutrients and energy (Ingham, 2007).

UNIVERSITY of the
WESTERN CAPE

All the domains (Bacteria, Archaea and Eukarya) are contained in one teaspoonful of soil (Torsvik and Øvreås, 2002). The soil biological community can be divided into groups according to body size; macrofauna (earthworms, termites, ants, spiders), mesofauna (springtails, mites), microfauna (nematodes, protozoa) and microbes (viruses, archaea, bacteria and fungi) (Wurst *et al*., 2012).

Soil biota can be divided into different functional groups which have similar traits, and that have similar effects on soil processes. These functions are not necessarily according to size class. Organisms in the micro- meso- and macrofaunal classes act as predators, detritivores and herbivores. Only microbes

do not function outside of their size class (Wurst *et al*., 2012). This functional belowground community is taxonomically more diverse than the community that is responsible for primary production (Swift *et al*., 2004). Soil fauna mediate many soil processes, including feats of 'ecosystem engineering'; shredding and carrying of litter into the soil, developing soil porosity, and contributing to the aggregation of soil. Through these activities they shape potential habitats for, and consequently control the activity of, microbial communities (Lavelle *et al*., 2006).

Biogeochemical cycling is the "transformation and cycling of elements between abiotic and biotic matter across land, air, and water interfaces" (Madsen, 2008). Various belowground organisms perform, via direct and indirect means, biogeochemical function in the soil (Wolters, 1991). Direct means can be defined as a modification by an organism that can change the movement and transformation of elements (Beare *et al*., 1995). The soil biogeochemical and physical properties co-vary with microbial and invertebrate populations, showing how soil properties dictate habitat suitability for soil organisms (Ayers *et al*., 2009).

UNIVERSITY of the
WESTERN CAPE

The soil is not static, but biologically active, a living vault of continual dynamic change and adaptation (Wall *et al*., 2010). Identifying and monitoring the functional and structural diversity of soil biological communities can provide baseline data for agricultural practitioners and ecosystem managers. This data may be used to evaluate the effect of disturbances, treatments, management

decisions, and potential pathogens. In addition, monitoring changes in soil condition would be a useful tool in order to anticipate change in vegetation (Herrick and Whitford, 1995), as soil organisms drive vegetation change (Bardgett, 2005; Van der Putten *et al*., 2009).

Soil microbes are at the bottom of the soil food web and are the most numerous and diverse of all soil organisms (Wurst *et al*., 2012). Microbes are organisms with body widths of less than 100µm, and this group consists of fungi, bacteria, archaea, and viruses (Wurst *et al*., 2012). The hugely diverse and large contingent of microbes present in the soil have through their long evolutionary history contributed much to the wealth of belowground interactions amongst organisms (Price, 1988).

UNIVERSITY of the
WESTERN CAPE

Traditional analyses of microbial populations rely on culturing bacteria and fungi on specific substrates, but only 1 % of microbes are culturable (White *et al*., 1996). As a result, culture-based techniques of assaying microbial populations give only a limited assessment of any given microbial community. Microbial assay techniques that represent an advancement on the culture-dependent techniques can be classified into three groups: Biomass indicators, e.g. microbial biomass C and substrate-induced respiration; activity indicators, e.g. nitrification rate and enzyme activity; and diversity indicators, e.g. community-level physiological and genetic (molecular) techniques (Garbisu *et al*., 2011). Although no single technique provides a complete representation of soil microbial characteristics, each technique provides a slightly different

perspective. A polyphasic approach using different techniques and measures leads to a more complete picture of soil microbial communities.

Molecular techniques such as denaturing gradient gel electrophoresis (DGGE), terminal restriction fragment length polymorphism (T-RFLP) and quantitative polymerase chain reaction (qPCR) provide DNA analyses, so that specific species may be identified (Muyzer *et al*., 1993). Although the presence of certain genes are linked to specific functions, community-level profiles may be more useful towards understanding how microbes affect ecosystem functioning (Wurst *et al*., 2012). Functional diversity may be more important than diversity *per se* (Hooper *et al*., 2005; Reiss *et al*., 2009), as there may be considerable functional redundance in soil biological communities.

UNIVERSITY of the
WESTERN CAPE

Community-level physiological profiling (CLPP) measures microbial response to a range of carbon substrates, and so generate metabolic 'fingerprints'. Examples of these qualitative assays include Biolog EcoPlates™ (Garland and Mills, 1991). These different metabolic 'fingerprints' differentiate communities from different soil systems (Garland and Mills, 1991), and under different plant types in the same soil type (Zak *et al*., 1994). The microbes need to be metabolically active in order to establish a total view of the whole community present in the sample. But this is not an *in situ* test; and the carbon sources in each well of the test plates are not the natural food of bacteria, environmental conditions in their natural habitat are very different from these plates, and the metabolic activities of the soil communities as a whole cannot be accurately seen

(Bossio and Scow, 1995).

All living cell membranes contain fatty acids (White *et al*., 1996). Phospholipid fatty acids (PLFA's) break down very quickly on cell death, and the sum of PLFA's is a good indicator of the living, active microbial biomass (Vestal and White, 1989; Zelles *et al*., 1995; Hill *et al*., 2000). PLFA analysis gives a holistic, quantitive picture of broad-scale bacterial and fungal groups (Zelles, 1999; Kirk *et al*., 2004). When PLFA profiles are analysed with multivariate statistical methods, metabolic 'fingerprints' of the microbial community are generated (Pothoff *et al*., 2006), providing a phenotypic analysis of the community structure (Haack *et al*., 1994; Bossio and Scow, 1998). PLFA analysis may also be more sensitive than nucleic acid based methods when attempting to determine shifts in a microbial community (Ramsey *et al*., 2006). Specific PLFA's have also been used as biomarkers for the presence of certain microbial functional groups, e.g. gram-positive bacteria (Zelles, 1999), though this practice has been criticised and questioned (Frostegård *et al*., 2010).

UNIVERSITY of the
WESTERN CAPE

Fluorescein diacetate (FDA) hydrolysis assays measure microbial enzyme activity, providing an estimate of overall microbial activity. Enzymatic activity can be quantified using a spectrophotometer (Green *et al*., 2006). FDA may be particularly useful as a biological indicator in arid areas (Aseri and Tarafdar, 2006) and is one of the most frequently and consistently used measurements to distinguish between different management systems (Green *et al*., 2006).

Microbial ecology can be defined as the study of interrelationships existing between microbes and their biotic and abiotic environment (Atlas and Bartha, 1993). Investigating the microbial diversity can lead to the understanding the functional activity of microbes in their environments (Vestal and White, 1989; Garland and Mills, 1991; Zak *et al*., 1994).

Microbes are sensitive to environmental changes and are early indicators of disturbance (Wurst *et al*., 2012). Microbe populations correlate well to soil physical and chemical parameters (Mijangos *et al*., 2006). This makes them consistent and effective indicators of change (Bending *et al*., 2004), as they act as indicators of positive and negative effects of management practices in agriculture (Pankhurst *et al*., 1996; Sharma *et al*., 1998).

UNIVERSITY of the
WESTERN CAPE

2.6 Links between vegetation and soil biota

Plants generally inhabit both domains of the terrestrial ecosystem, i.e. the visible, aboveground and the hidden, belowground, connecting and integrating these two domains through two processes (Wardle *et al*., 2004).

Firstly, plants capture energy from the sun, fix carbon through photosynthesis, and exude carbon-rich compounds through their roots into the soil. These carbon-rich exudates provide food for soil-dwelling microbes, which are at the bottom of the soil food web (Wurst *et al*., 2012). Secondly, plants contribute organic matter through litter fall to the soil, providing food for soil organisms

that shred, decompose and mineralise the organic matter into inorganic mineral compounds, ready for plants to take up again (Ingham *et al*., 1985; Yeates *et al*., 1993; Bardgett and Chan, 1999). This process of nutrient cycling is one of the essential ecosystem services dependent on multi-trophic interactions (Wall *et al*., 2010).

These interactions partly occur in, and depend on, the plant-soil interface, the rhizosphere, one of the 'hotspots' of soil biological activity (Beare *et al*., 1995). The rhizosphere is the several millimetres of soil immediately adjacent to the root structure (Bais *et al*., 2006). It is the zone in the soil of primary root influence (Beare *et al*., 1995) and the interface between plant roots, soil biota, and the physical and chemical attributes of soils (Hartmann *et al*., 2009). As such it varies temporally and spatially (Beare *et al*., 1995).

UNIVERSITY of the
WESTERN CAPE

An average of 17 % (Nguyen, 2003), and up to 40 % (Bais *et al*., 2006), of photo-assimilate carbon is allocated to root exudates in the form of ions, enzymes, mucilage, and carbon-containing primary and secondary metabolites (Bertin *et al*., 2003). The rhizospere effect, first coined by Hiltner in 1904 (Hartmann *et al*., 2008) is the effect that this carbon-rich environment has, attracting more numerous microbes and generally hosting a more abundant soil microbial community than the bulk soil (Bais *et al*., 2006; Berg, 2012), although it may not be more diverse (Costa *et al*., 2006).

The amount and composition of the root exudates depend not only on the plant

species, but also climatic conditions, herbivory, and the chemical, physical and biological components of the surrounding soil (McNear, 2013). Plants can stimulate or inhibit the presence of beneficial, commensal and pathogenic microbes through root exudates (Doornbos *et al*., 2012), directly influencing the composition and activity of the microbial community, and thereby affecting the rhizosphere soil in physical, chemical and biological ways (Ayres *et al*., 2004). Roots increase soil heterogeneity on individual plant scales through their specific architecture, growth, death, and decomposition (Bardgett, 2005). Plants exude substances through their root systems, which may lower soil pH, chelate minerals, releasing essential nutrients (e.g. Fe, Ca, K, Mg, and Na) and so play a role in nutrient cycling (Likens *et al*., 1977).

UNIVERSITY of the
WESTERN CAPE

Allelopathy was originally defined as the direct plant-plant effects via allelochemicals (Rice, 1984). The current definition is broader, and includes the effects of secondary plant compounds exuded by plant parts on the biotic and abiotic soil components and processes, which then affect other plants, either directly or indirectly (Inderjit and Weiner, 2001). These secondary compounds may influence soil abiotic factors, including mineral nutrients and nutrient dynamics belowground in natural ecosystems (Wardle *et al*., 1998). These compounds influence vegetation dynamics and community structure factors (Einhellig, 1999). Ecological factors, e.g. moisture, nutrient and light regimes in turn effect the action of these compounds (Einhellig, 1996; Inderjit and Del Moral, 1997).

One hundred gigatons of plant matter is produced globally each year, and 90 % is not consumed by herbivores, becoming the bulk of dead organic matter (Cebrian, 1999). Microbes depend on plants as their major source of organic matter, which they break down and mineralise from organic to inorganic forms (Bardgett, 2005). Plant community complexity dictates the spatial and temporal heterogeneity of plant litter that enters a soil system (Beare *et al*., 1995), and the more simple (i.e. monoculture) a vegetation patch becomes, the less heterogeneous the litter that it generates. Plant species vary in terms of their chemical composition, containing varying amounts of cellulose, lignin and mineral nutrients and having different rates of growth, senescence and decomposition (Swift *et al*., 1979: Gessner *et al*., 2010).

UNIVERSITY of the
WESTERN CAPE

In addition to litter chemistry and biomass, Eviner *et al*. (2006) demonstrated that plant species affect biogeochemical cycling directly and indirectly through plant traits. Direct effects include live-tissue chemistry and biomass. Indirect effects include the alteration of soil microclimate and soil bioavailable carbon by plant species. These authors discovered that plant species affect phosphorus and, principally, nitrogen cycling, even when litter effects are excluded. Furthermore, soil decomposer communities specialise in decomposing the litter produced by the plant species above them, a phenomenon called home-field advantage (Ayres *et al*., 2009a, 2009b), which further demonstrates the tightly linked nature of these organisms.

Global climate change, ecosystem management and agricultural practices,

including grazing, all affect soil microbial communities (Bossio and Scow, 1995; Wardle *et al*., 2004). The effect of aboveground herbivores on soil biodiversity also shows idiosyncratic responses across different ecosystems. Factors that influence idiosyncratic responses include an organism's life cycle, food, reproduction rate, and how populations spread and adapt to different habitats (Siepel and Van de Bund, 1988; Scheu *et al*., 1996).

Studies on temperate grasslands in the United Kingdom have shown that sheep grazing increases soil microbial biomass and activity, nematodes and arthropods (Bardgett *et al*. 1997). Conversely, Sankaran and Augustine (2004) showed in a study in semi-arid grasslands in Kenya that removing herbivores increased soil microbial biomass in both a nutrient-rich glade and a nutrient-poor grassland. In addition, the intensity of grazing affects the fungal to bacterial ratio of decomposer communities. With heavier grazing, decomposition is dominated by bacteria, which is typical of intensively managed, high-input, fast-decomposing systems (Bardgett, 2005). With lighter grazing, the fungal decomposer system becomes stronger (Grayston *et a*l., 2004). Fungal-dominated decomposer networks are typical of extensive, low-input, slow decomposing systems (Bardgett, 2005).

UNIVERSITY of the
WESTERN CAPE

The distribution, composition and size of soil biotic communities depend on microclimate, soil structure, soil chemical composition and resource availability (Wolters, 1991). The world-wide distribution of soil microbial communities are largely explained by soil properties such as pH and organic matter quality (C:N

ratio) (Fierer *et al*., 2009). In turn, resource availability dictates the presence of plant species and plant chemical characteristics (Herms and Mattson, 1992).

Many microbes form symbiotic associations with plants, providing limiting nutrients, predominantly nitrogen and phosphorus (Chapin *et al*., 2002), and so stimulating plant productivity (Van der Heijden *et al*., 2008), nutrient cycling and plant community dynamics (Van der Heijden *et al*., 2009). These crucial functions performed by plant-associated microbial communities have earned them the name "the plant's second genome" (Berendsen *et al*., 2012). Furthermore, through their functioning they maintain the soil structure; degrade pollutants; and biologically control plant and animal pests (Bossio and Scow, 1995; Hill *et al*., 2000).

UNIVERSITY of the
WESTERN CAPE

The idea that belowground organisms help to regulate ecosystem processes, and that the relationship between aboveground and belowground organisms govern ecosystem functioning has gained increasing importance (Giller *et al*., 1997; Bardgett *et al*., 1998; Van der Putten *et al*., 2001). These functions include soil fertility and nutrient retention, water retention, and structural stability (Van Eekeren *et al*., 2009; Van der Putten *et al*., 2009). The value of relying on ecosystem self-regulation, rather than costly chemical inputs such as fertilizers and pesticides, is increasingly critical (Yeates *et al*., 1997).

If these microbial species and their services are lost, they might only be recoverable with strong interventions, at considerable effort and expense. The

more complex the community (in terms of activity and diversity), and hence the network of interactions, the better the potential for adaptation, and survival (Garbisu *et al*., 2011).

Understanding the various mechanisms that link of belowground biodiversity, ecosystem functioning, and aboveground biodiversity, is the only path to the successful maintenance and protection of soil functions. And as above- and belowground links have repercussions on the rate and direction of vegetation change, this knowledge should enhance restoration projects (Van der Putten *et al*., 2009). The understanding of ecosystem response to change will only be complete once the physiology and ecology of soil microbes are understood (Zogg *et al*., 1997; Wolters *et al*., 2000).

UNIVERSITY of the
WESTERN CAPE

Measures taken in order to protect and promote biodiversity aboveground, may not necessarily benefit belowground organisms. Sylvain and Wall (2011) recommend including 'knowledge of linkages between plant and soil biota in comprehensive biodiversity initiatives and policies' as a logical 'next step' on the research agenda. High levels of biodiversity, both above and belowground, ensure that there are many possible interactions between species and guilds, and this hierarchical interface is needed for the development and maintenance of a diversity of resource microsites in the soil (Garbisu *et al*., 2011).

Chapter 3 Study area - The Bokkeveld Plateau and Nieuwoudtville

3.1 Study area

South Africa's relatively narrow coastal zone is separated from the higher inland plateau by the Great Escarpment. The Bokkeveld Plateau is an oblong area of approximately 300 km² and forms part of the arid western edge of this geological feature at a particular degree square; 31°S, 19°E (Lemons *et al*., 2003). It is situated 300 km north of Cape Town at an altitude of 800 m.a.s.l. The Knersvlakte lies to the west, from which the Bokkeveld escarpment rises abruptly east from Van Rhynsdorp. Lower escarpments to the north and south lead to Namaqualand and the Cederberg respectively. To the east the Bokkeveld Plateau is bordered by the Hantam Mountains on the way to Calvinia (Lemons *et al*., 2003). Figure 3.1 shows the position of the plateau within the context of vegetation biomes. The map shows how the plateau forms a slim 'peninsula' of fynbos biome within a 'sea' of succulent karoo biome.

UNIVERSITY of the
WESTERN CAPE

The Bokkeveld Plateau is composed of Cape Supergroup rocks. Table Mountain Sandstone forms part of the Cape System. On top of the Cape System lies the Karoo System, represented here by sedimentary deposits of Dwyka-derived shales and tillite (Lemons *et al*., 2003; Bradshaw and Cowling, 2014). The Dwyka rocks were formed when the Karoo was covered by a glacier 300 Ma. The exposed glacier floor can still be seen south of Nieuwoudtville.

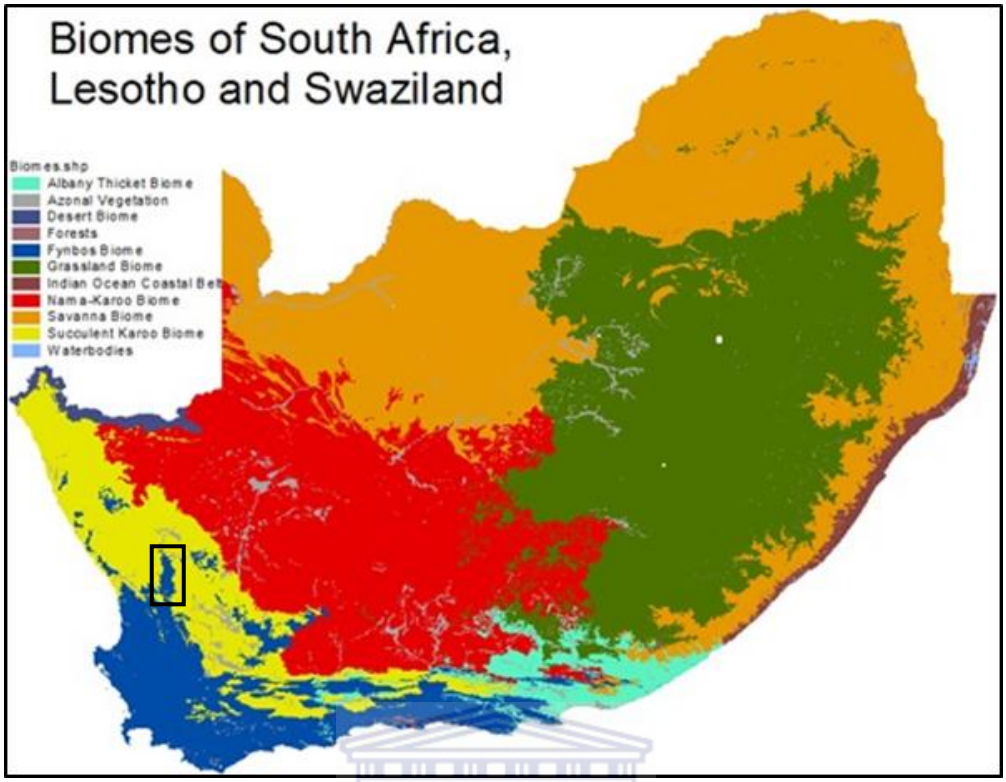

Figure 3.1 Map showing the study area and vegetation biomes of South Africa (SANBI, 2006). The Bokkeveld Plateau is indicated with a black rectangular box

UNIVERSITY of the
WESTERN CAPE

The dolerite sill was formed when molten magma was forced out between sedimentary layers, creating intrusions of igneous rock during the Jurassic Period between 180-135 Ma. The underlying geology of the Bokkeveld Plateau is shown in Figure 3.2. The underlying rock formations from west to east are: Table Mountain Sandstone, Dwyka-derived tillite, and dolerite clay. The correspondent soil types from west to east are oligotrophic sand on the Table Mountain Sandstone, fine grey/yellow tillite clay on the Dwyka-derived shales, and spongy dolerite vertisols, rocky dolerite koppies, and sandy dolerite karoo plains atop the dolerite sill (O'Farrell *et al*., 2009).

The Bokkeveld Plateau fits onto the north-eastern edge of the Cape Floristic

Region and the winter-rainfall zone. There is a steep rainfall gradient on the plateau; with 550 mm falling on average per year at the top of the Bokkeveld escarpment at Van Rhyns' Pass, 350 mm at Nieuwoudtville, 10 km further to the east, and 150 mm at Calvinia, with increasingly summer rainfall, in the Nama Karoo, 70 km further from Nieuwoudtville to the east, and slightly to the south. There is also a less sharp gradient to the south towards the Cederberg, with the average annual rainfall falling to 200 mm approximately 20 km south of Nieuwoudtville (O'Farrell *et al*., 2007).

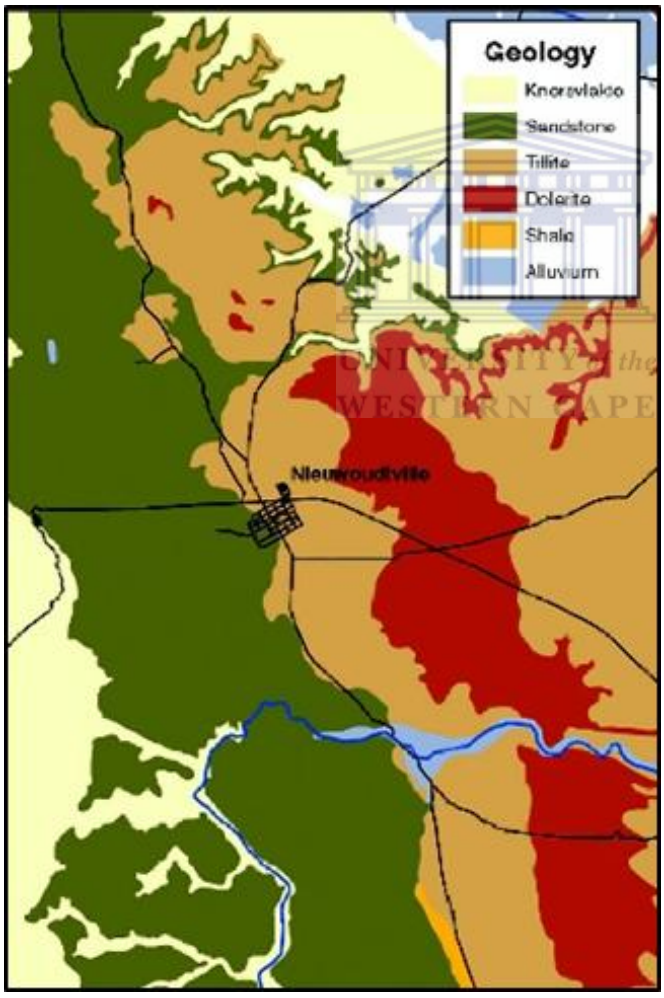

Figure 3.2 Broad-scale geological map shows the main soil types on the Bokkeveld Plateau (Conservation Farming Project, 2004).

The total annual rainfall variation can be high. Temperatures are strongly seasonal, the highest average maximum temperatures of 31°C recorded in February and the coldest temperatures occur in June reaching on average 4°C. Frost is common in winter, but it only snows infrequently.

The Bokkeveld plateau houses exceptional plant biodiversity, is a centre of endemism (Snijman and Perry, 1987; Manning and Goldblatt, 1997; Van Wyk and Smith, 2001), and has been identified as a priority area by Cape Action for People and Environment (C.A.P.E) (Pence, 2008) (see Figure 3.3). Alien grass invasion is considered to be the greatest threat to biodiversity on the Bokkeveld Plateau (Todd, 2008b). The prevalence of alien grass species is linked to disturbance (Todd, 2008a).

UNIVERSITY of the WESTERN CAPE

Figure 3.3 Cape Action for People and Environment (C.A.P.E) broad priority areas (Pence, 2008).

The sandy, nutrient-poor, sandstone-derived soils support fynbos vegetation. The nutrient-rich tillite and spongy dolerite underpin two renosterveld vegetation types (all falling within the fynbos biome), and the dolerite-derived karoo sands give rise to karoo shrublands (falling within the succulent karoo biome).

Plant species are often only found on one soil type, e.g. *Geissorhiza splendidissima* (blue pride of Nieuwoudtville) is only found on tillite-supported Nieuwoudtville Shale Renosterveld. Conversely, floristic affinities between the two renosterveld types on the plateau may be illustrated by the two sister geophyte species that are endemic to the Nieuwoudtville area, one occurs on Nieuwoudtville Shale Renosterveld, *Romulea sabulosa*, and the other on Nieuwoudtville-Roggeveld Dolerite Renosterveld, *Romulea monodelpha*. Even within sites on one soil type, there is patchiness in terms of where different plant species occur (Todd, 2010).

UNIVERSITY of the
WESTERN CAPE

The key environmental factors which influence vegetation types are geology, annual rainfall, temperature regimens and fire. In addition to soil properties, available moisture influences the plant distribution in this area, with the amount and timing of the rainfall paramount, but topography also playing a role in terms of mist and seepage (Helme, 2007).

The natural geology and vegetation lends itself to particular land uses, which fragments the landscape further - the town of Nieuwoudtville is surrounded by an agro-ecological mosaic (O'Farrell *et al*., 2007). Farms surrounding

Nieuwoudtville are predominantly large and privately owned. Livestock is mostly sheep, with some cattle. Anthropogenic influences are primarily through tillage, cropping, grazing and the application of fertilizers, herbicides, and pesticides. The sandy soils set on top of Table Mountain Sandstone are used for the cultivation of rooibos and potatoes. Tillite soils, locally known as *vaalgrond*, or dull earth, have been tilled to wheat and oat croplands and *Medicago* spp. pastures, and are used as natural veld rangelands. The dolerite vertisols, locally known as *rooigrond*', or red earth, have been partially transformed into croplands, and are grazed.

The two renosterveld types, Nieuwoudtville Shale Renosterveld and Nieuwoudtville-Roggeveld Dolerite Renosterveld (Mucina and Rutherford, 2006) form part of the mountain centre renosterveld, which stretches from Nieuwoudtville to Oudtshoorn (Mucina and Rutherford, 2006). These are arid forms of renosterveld, displaying high floristic similarity at genus level (Bergh *et al*., 2014). They typically contain varying numbers of succulent karoo species, grading into succulent karoo in the driest areas (Bergh *et al*., 2014). These two forms of renosterveld could be viewed as a mesic form of succulent karoo (Campbell, 1985; Cowling *et al*., 1992).

UNIVERSITY of the
WESTERN CAPE

More than half of the original extent of Nieuwoudtville Shale Renosterveld has been transformed into pastures planted with *Medicago* spp., or cropped with wheat and oats, with only about 40 % of the original extent remaining as natural rangelands (Rouget *et al*., 2006). This vegetation type is classified as a

Vulnerable ecosystem (SANBI and DEAT, 2009), which means that it is less threatened than those lowland renosterveld types in the west and south coast centres which have been declared *Critically Endangered* (SANBI and DEAT, 2009). However, the remaining fragments of Nieuwoudtville Shale Renosterveld are embedded in an agro-ecological mosaic of pastures and wheat fields (O'Farrell *et al*., 2007), and fragmentation in itself is a risk factor for any natural vegetation.

This vegetation type is not homogenous, and consists of three sub-types, dominated by *Merxmuellera stricta* (Schrad.), *Elytropappus rhinocerotis* (L.f.) Koekemoer and *Eriocephalus purpureus* Burch.ex G.Don, respectively. The vegetation sub-types all boast a rich understorey of annuals and geophytes (Cowling, 1990; Manning and Goldblatt, 1997). *M. stricta* is a graminoid, and typically grows on drainage lines, and on previously burnt areas (Van der Merwe and Van Rooyen, 2011; E. Marinus, pers.comm.). *E. rhinocerotis* (renosterbos), the namesake shrub of renosterveld, is a fine-leaved shrub in the Asteraceae family. *E. purpureus*, wild rosemary, is an asteraceous sub-shrub. The vegetation dominated by *E. purpureus* is considered the most useful for grazing, as *M. stricta* is only palatable when young to cattle, and *E. rhinocerotis* is not palatable.

UNIVERSITY of the
WESTERN CAPE

Landowners around Nieuwoudtville have also diversified into flower tourism, attracting thousands of eco-tourism visitors each spring. O'Farrell *et al*. (2009) have shown that natural renosterveld fragments in this region also provide

valuable ecosystem services, acting as windbreaks, reducing aeolian loads, conserving soil, and contributing to improved soil infiltrability of rainfall. It is evident that renosterveld in this region fulfils several biodiversity values: intrinsic, e.g. the aesthetic value of spring flower tourism; utilitarian, e.g. the use of natural vegetation as grazing forage for livestock; serependic, e.g. the undiscovered potential medicinal value of plant species, and functional, e.g. ecosystem services provided by untransformed renosterveld in terms of wind breaks, rain infiltration and soil retention services (O'Farrell *et al*., 2009).

3.2 Study sites

UNIVERSITY of the
WESTERN CAPE

The camps on farms in this region are usually fenced according to vegetation type, and all the study sites are situated on camps of *Eriocephalus purpureus*-dominated Nieuwoudtville Shale Renosterveld (Mucina and Rutherford, 2006), which are used solely for sheep grazing. *E. purpureus* is a palatable sub-shrub, and the veld sub-type dominated by this sub-shrub is typically grass-poor although palatable indigenous grasses, *Ehrharta calycina* and *Chaetobromus dregeanus*, are found among the shrubs. Nine study sites were chosen in four different camps. The unbalanced design was due to time and access restrictions preventing the complete surveying and soil sampling of camps on other farms. I made the decision to include all plots surveyed and sampled in full, i.e. vegetation survey in spring, and two subsequent soil samplings in summer and winter, to make use of the most replicates possible.

Three camps are situated on two privately owned farms, and one camp is located in a conservation area, Hantam National Botanical Garden (HNBG), managed by the South African National Biodiversity Institute (SANBI).

The three camps on farms are subjected to different stocking regimes, and the camp on HNBG (which used to be a farm) had not been grazed for the last five years. Overgrazed camps could not be accommodated in this study, and the camps were not located on a stocking gradient. In addition, there were not enough replicates of any one stocking regime to incorporate the stocking data into any statistical analyses, though the data were taken into account when discussing the results obtained.

UNIVERSITY of the
WESTERN CAPE

3.3 Stocking data

The camp sizes ranged from 15 hectares to 120 hectares (see Table 3.1). Season of stocking ranged from early-winter to early-spring, summer, and winter. Sheep breeds were either Merino or Letelle. Stocking was of mature sheep, or a mix of ewes and lambs, or young sheep.

The largest camp (120 hectares) is rested every two or three years. The sheep are put on it after the first rains (typically May), when lambing starts, and left there for the entire winter, until early spring (September). The total stocking period is four to five months. During the last grazing season (2013), the camp was stocked with 177 ewes and 203 lambs (see Table 3.1).

UNIVERSITY of the
WESTERN CAPE

Table 3.1 Stocking data for the study plots. Large stock units abbreviated to LSU.

Plot/ camp nr	Camp size (ha)	Sheep numbers in terms of LSU	Time of year of stocking	Stocking period as fraction of year	Stocking per annum (LSU/ ha/ stocking period per year)
1/1	120	34.93	winter	1/3	0.10
2/1	120	34.93	winter	1/3	0.10
3/2	60	0	none	none	none
4/2	60	0	none	none	none
5/2	60	0	none	none	none
6/3	15	10	summer	1/12	0.06
7/3	15	10	summer	1/12	0.06
8/4	30	8.8	winter	1/12	0.02
9/4	30	8.8	winter	1/12	0.02

UNIVERSITY of the
WESTERN CAPE

The smallest camp (15 hectares) is grazed in summer, after the spring flowering is over. One hundred lambs or young sheep are put on it for two weeks at a time, for two periods over the summer months, making a total of one month's stocking per year (see Table 3.1). This camp is mostly grass veld, with only a small component of shrub veld (dominated by *E. purpureus* and *A. capensis*), and the sheep would mostly graze the grass veld at this time of year, as the shrub component is desiccated.

One camp (the camp measures 30 hectares, but some of it has been tilled, and the natural, untilled rangeland patch is about 20 ha) is stocked with 45 ewes and 50 lambs for one month during the winter (see Table 3.1). According to the farmer it is too dry during the summer months.

The camp which is situated on what used to be a farm, but is now a conservation area, had not been grazed for five years (see Table 3.1). Unfortunately the current owner (SANBI) does not have access to the historical stocking data. No tillage to the current owner's knowledge was performed on this camp (E. Marinus pers.comm.).

UNIVERSITY of the
WESTERN CAPE

Chapter 4 Renosterveld rangeland vegetation cover and diversity

4.1 Introduction

Vegetation and soil in drylands typically exhibit spatial heterogeneity (Stafford Smith, 2008). This heterogeneity is mostly attributed to abiotic factors such as topography, erosion, rainfall, and fire (Li *et al*., 2009; Ravi *et al*., 2009). As a consequence of these factors, the vegetation in arid and semi-arid areas typically contain a mosaic of vegetation types. The relative dominance of different species and functional forms (shrub, grass, or forb) are attributed to different responses to environmental drivers like disturbance and climate. Ecological processes, such as the competition for nutrients, and the redistribution of water, exert varying degrees of control according to the plant community structure (Peters *et al*., 2006).

UNIVERSITY of the
WESTERN CAPE

The level of plant and animal biodiversity predicts the level of internal regulation of functions within an agro-ecosystem (Altieri, 1999). The insurance hypothesis of biodiversity postulates that higher species richness insures ecosystems against a decline in functioning, as many species provide greater guarantees that some will maintain functioning even if others fail (Yachi and Loreau, 1999). The maintenance of functioning confers resilience, and the ability to reorganise post-disturbance, and this is considered to be more aptly viewed from a landscape level (Swift *et al*., 2004). Landscapes that consist of well-connected fragments of natural vegetation at different seral stages have a better

chance of hosting biota that contribute to functional diversity, delivering those services that regulate and support overall production and ensure the stability of an ecosystem (Bengtsson *et al*., 2003; Swift *et al*., 2004).

Drylands are often productively used as natural rangelands. Domestic livestock graze in a non-uniform manner, especially on varied natural vegetation, as opposed to planted pastures, and thus the effects of grazing are not homogenous (Smith *et al*., 2012). A great benefit of natural, diverse forage is the rich phytochemical diversity which the livestock ingest, with a positive effect on overall health (Provenza *et al*., 2013).

UNIVERSITY of the
WESTERN CAPE

The Bokkeveld Plateau bridges the Western and Northern Cape Provinces in South Africa and is located 300 km north of Cape Town. This plateau encompasses both biomes of the Greater Cape Floristic Region - Fynbos and Succulent Karoo (Jürgens, 1997; Born *et al*., 2007). These two biomes are considered biodiversity hotspots (Mittermeier *et al*., 2004). Biodiversity hotspots are areas that contain exceptional concentrations of the world's endemic plants, and that are undergoing transformation (Myers *et al*., 2000).

Renosterveld is a diverse, fragmented and diminished vegetation type within the fynbos biome. Nieuwoudtville Shale Renosterveld (Mucina and Rutherford, 2006) is found on tillite soils around Nieuwoudtville on the Bokkeveld Plateau, with only 40 % of its original extent remaining intact in the form of non-contiguous fragments of varying sizes (Rouget *et al*., 2006).

Different patches of *E. purpureus*-dominated Niewoudtville Shale Renosterveld were investigated and assessed in terms of plant species richness and cover. The following hypotheses were formulated to guide the investigation.

Hypothesis 1: Different patches of *Eriocephalus purpureus*-dominated Nieuwoudtville Shale Renosterveld vegetation are similar in terms of overall species richness.

Hypothesis 2: Different patches of *Eriocephalus purpureus*-dominated Nieuwoudtville Shale Renosterveld vegetation are similar in terms of species richness of different plant growth form categories.

UNIVERSITY of the
WESTERN CAPE

Hypothesis 3: Different patches of *Eriocephalus purpureus*-dominated Nieuwoudtville Shale Renosterveld vegetation are similar in terms of cover of different plant growth form categories.

4.2 Materials and methods

4.2.1 Study area

Refer to Chapter 3 for a full description of the study area and study plots. The nine study plots are all located on *Eriocephalus purpureus*-dominated Nieuwoudtville Shale Renosterveld (Mucina and Rutherford, 2006) used at

present or in the past as rangelands for the grazing of sheep. The study plots are situated on different camps which are subjected to differing stocking regimes, as described in Chapter 3. Camp 2 is situated in an area where the annual rainfall is lower (200 mm p.a.) than the areas in which the other camps are situated (350 mm p.a.).

4.2.2 Rapid Renosterveld Assessment Method

The Rapid Renosterveld Assessment Method (Milton, 2007) was developed in 2007 by a team of specialists, but has to date not been tested in the field. It was developed as a method to be used by farmers and scientists, and designed to bridge the usual dichotomy between farming and conservation. Renosterveld is valuable both as an agricultural resource, and a richly biodiverse vegetation type (Milton, 2007). This method incorporates data from (1) plant surveys, (2) geographical data, and (3) interviews.

UNIVERSITY of the
WESTERN CAPE

4.2.2.1 Plant surveys

Plant surveys were conducted on the study sites during September 2012, in accordance with the Rapid Renosterveld Assessment Method (Milton, 2007). Spring is the chief flowering season in this vegetation type, starting slowly in July, peaking in August and September, and tapering off in October of each year. A 5x20 m (100 m²) plot was staked out and all plant species occurring within it were noted and added to calculate total plant species richness. In addition, a 50

m-transect was measured alongside the plot and 50, 1 m apart, canopy strikes noted with the descending-point method, in order to calculate plant cover. Plant species found were allocated to plant growth form categories. For plant species richness the categories were as follows: annual grass, perennial grass, geophytes, non-succulent shrub, leaf-succulent shrub, stem-succulent shrub, indigenous forbs, and alien forbs. For cover the categories, in addition to the above, were duff (dead plant material still attached to a plant), litter (dead plant material not attached to a plant), rock, bare (meaning bare ground), biological soil crust, and the two most commonly found non-succulent shrubs found were allocated to their own categories; *Eriocephalus purpureus* and *Asparagus capensis*. The use of broad plant growth form categories instead of species aids the discernment of general patterns in response to livestock disturbance (Wesuls *et al*., 2010).

UNIVERSITY of the
WESTERN CAPE

4.2.2.2 Geographical data

Latitude and longitude for each plot were recorded with a handheld GPS, and the slope and aspect recorded. The size and shape of the fragments of natural veld on which each study site is situated, was calculated from GIS imagery supplied by Google Earth.

4.2.2.3 Farmer/land manager interviews

Semi-structured interviews were conducted with the three farmers/land managers, using the basic questions suggested in the Rapid Renosterveld

Assessment Method (Milton, 2007). The following information was obtained for the three camps on each farm: size of the camps, stocking periods and season, and the number, age and breed of sheep. The grazing records for the conservation area had unfortunately been destroyed.

4.2.3 Statistical analyses

PCA, a multivariate analysis technique which presents high-dimensional data in a low-dimension form for simplicity and clarity, was used to analyse data. Samples which are similar (in terms of the variables measured and shown) are displayed close together, and those that are different, far apart. The factor loadings, e.g. the contribution of each variable to the factors, are calculated though not shown on the PCA graph. Pearson correlation matrices were used to reveal relationship between variables. Chi-square analysis was used to ascertain whether there were significant differences between the overall plant species richness found on the various study plots.

UNIVERSITY of the
WESTERN CAPE

4.3 Results

4.3.1 Hypothesis 1: Different patches of *Eriocephalus purpureus*-dominated Nieuwoudtville Shale Renosterveld vegetation are similar in terms of overall plant species richness.

Chi-square analysis showed no significant differences in terms of overall plant

species richness among the various study plots. The chi-square value was 1.026 (df=3, *p*=0.795). Table 4.1 shows the number of plant species found within each study plot. The plots in the same camp are depicted using the same colour (camp 1=aqua, camp 2=yellow, camp 3=green, camp 4=apricot). Plots 7 and 9 showed the highest plant species richness of all the study plots. All camps were reasonably consistent in terms of plant species richness, except for camp 4 (plots 8 and 9, with 49 and 63 species respectively).

Table 4.1 Table showing the number of plant species found within each study plot. The plots in the same camp are depicted using the same colour.

Plot number	1	2	3	4	5	6	7	8	9
Number of plant species	55	52	53	57	57	61	67	49	63

UNIVERSITY of the WESTERN CAPE

4.3.2 Hypothesis 2: Different patches of *Eriocephalus purpureus*-dominated Nieuwoudtville Shale Renosterveld vegetation are similar in terms of species richness of different plant growth form categories.

The Pearson correlation matrix (not shown) revealed only one significant (α=0.05) correlation; between the variables leaf-succulent shrubs and geophytes (-0,779). The PCA (Figure 4.1) depicts the plant species richness (allocated to plant growth form categories) found in the nine study plots. This PCA explains 54.64 % of the variation found among the nine study plots. The plots are numbered, and coloured according to the camps. The two variables with the highest factor loadings for the first PC (x-axis) are geophytes and leaf-succulent shrubs. The first PC distinguishes between plots on camp 1 (blue) from plots in camp 2 (yellow). Plots in camp 1 (plots 1 and 2) may show profiling according

to the first PC (x-axis), but not to the second PC (y-axis). This camp is the most heavily stocked (see Table 3.1). Camp 2 has not been stocked for the last five years.

The most important explaining variables along the second PC (y-axis) are annual grass and perennial grass, and this PC mainly distinguishes between plots in camp 3 (plots 6 and 7) and plots in camp 4 (plots 8 and 9), although plots within camps 1 and 2 are shown to be dissimilar in terms of these two plant growth form categories.

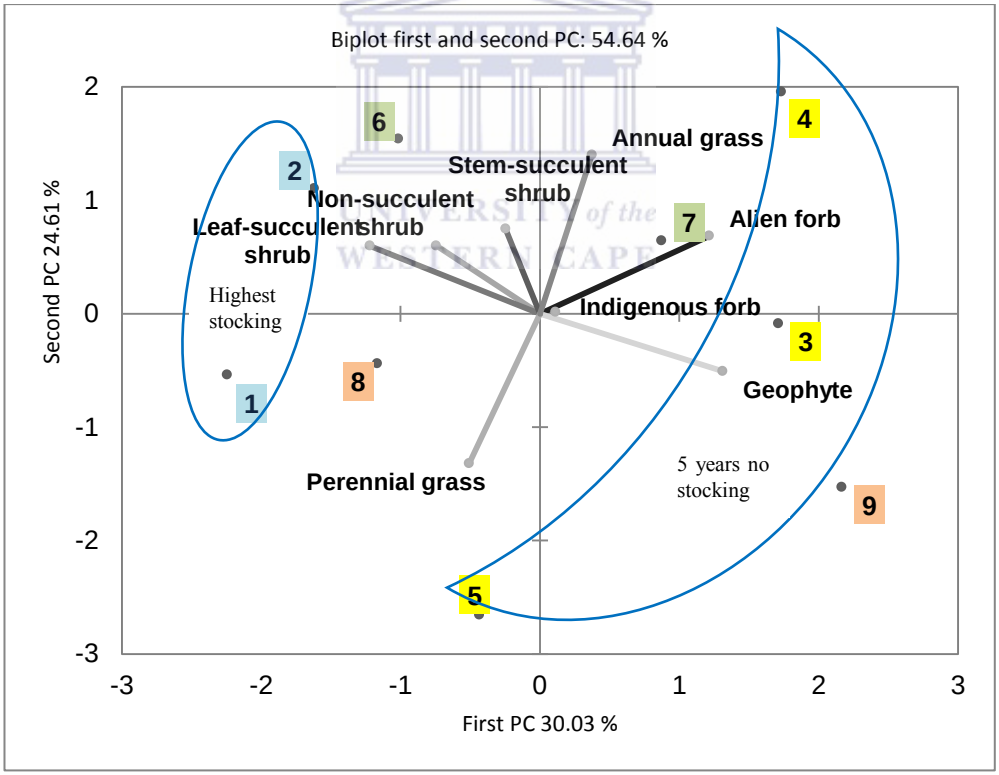

Figure 4.1 PCA showing the number of plant species according to plant growth form categories found in each plot. Plots in the same camp are shown in the same colour (camp 1=aqua, camp 2=yellow, camp 3=green, camp 4=apricot).

4.3.3 Hypothesis 3: Different patches of *Eriocephalus purpureus*-dominated

Nieuwoudtville Shale Renosterveld vegetation are similar in terms of cover of different plant growth form categories.

The Pearson correlation matrix (not shown) generated several significant correlations (α=0.05), including: Cover of the dominant shrub, *Eriocephalus purpureus* was negatively correlated to cover of both annual (alien) grass (-0,919) and alien forbs (-0,925), and these two ephemeral plant growth form categories were also positively correlated to one another (+0,959). Cover of geophytes and leaf succulent shrubs were negatively correlated (-0,851), just as plant species richness of these two categories were negatively correlated.

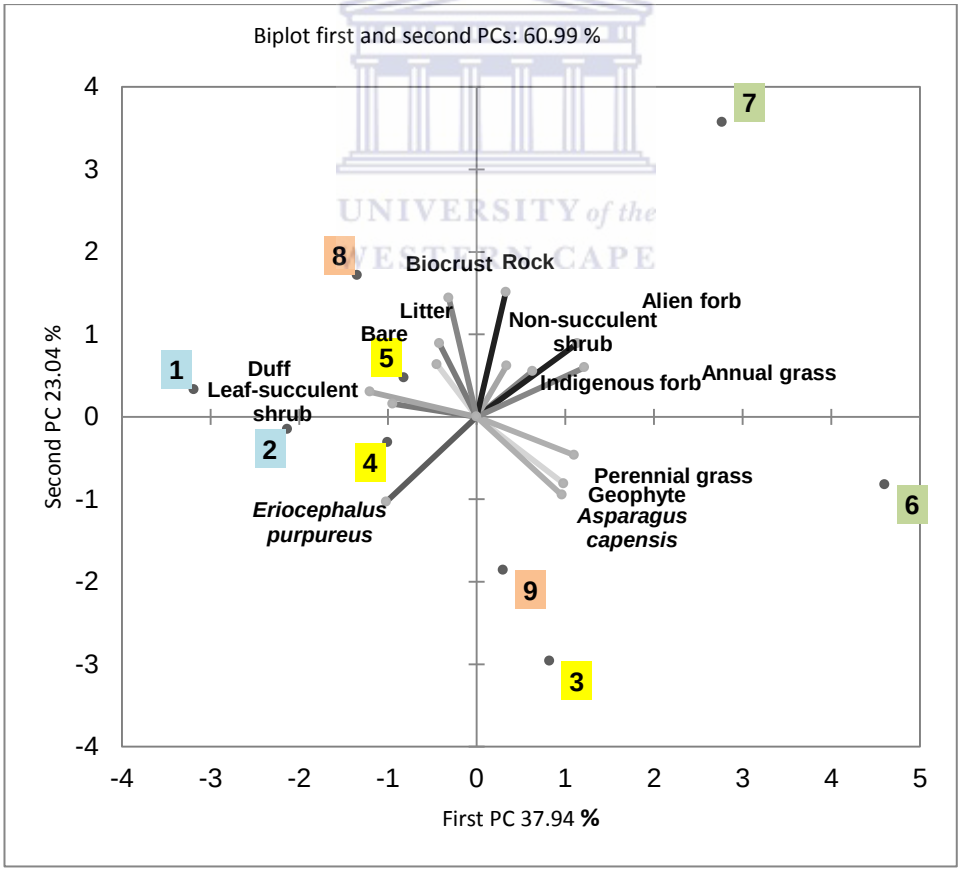

Figure 4.2 PCA showing canopy strikes, allocated to cover of the various plant growth form categories, found per 50 m-transect, which is an indication of cover (camp 1=aqua, camp 2=yellow, camp 3=green, camp 4=apricot).

The PCA shown in Figure 4.2 depicts the canopy strikes per transect (allocated to plant growth form categories) alongside each of the nine study plots. The PCA explains 60.99 % of the variation shown among the study plots. The plots are numbered, and coloured according to camp, and it shows that study plots in the same camp are not necessarily similar in terms of plant cover of the different plant growth form categories. The first PC mainly separates out the plots that had more alien (annual) grass from those that had more duff (negatively correlated in the Pearson matrix, -0,706). Plots in camp 1 (plots 1 and 2) show strong profiling according to both the first and second PCs (x- and y-axes). Plots in camp 2 (plots 3, 4 and 5), camp 3 (plots 6 and 7) and camp 4 (plots 8 and 9) show weaker profiling, and only according to the first PC (x-axis). The most important explaining variables for the second PC (y-axis) are rock and biological soil crust (positively correlated in the Pearson matrix, +0,725). This PC distinguished between plots on the same camp in terms of the absence or presence of these two positively associated variables.

UNIVERSITY of the
WESTERN CAPE

4.4 Discussion

4.4.1 Hypothesis 1: Different patches of *Eriocephalus purpureus*-dominated Nieuwoudtville Shale Renosterveld vegetation are similar in terms of overall plant species richness.

Chi-square analysis showed that the differences in overall plant species richness among the various study plots were not significant. This hypothesis is not

rejected. Todd (2010) found 42 species on same-sized plots north of Nieuwoudtville, but he contrasted these findings with the mean species richness, over 70 species in similar-sized plots, previously found south of Nieuwoudtville. The plant species richness found (between 49-67 species) in this study are thus lower than what has been previously found on Nieuwoudtville Shale Renosterveld, but higher than some other fragments of this vegetation type. The differences among the study plots could be ascribed to soil factors, which will be further discussed in Chapters 5 and 6.

4.4.2 Hypothesis 2: Different patches of *Eriocephalus purpureus*-dominated Nieuwoudtville Shale Renosterveld: vegetation are similar in terms of species richness of different plant growth form categories.

UNIVERSITY of the
WESTERN CAPE

The plant survey results in terms of plant species richness show only partial profiling according to camps. The plots are quite widely spread within the PCA (Figure 4.1), indicating that the plots were quite different in terms of the number of plant species (allocated to different plant growth form categories) found. This hypothesis is rejected. Plots were mainly distinguished on the basis of high species richness of leaf-succulent shrubs vs. high species richness of geophytes. This may be explained by the fact that more (up to five) species of leaf-succulent shrubs were found on the plots situated in the camp (1) that receives overall less rainfall (approximately 150 mm less per year) than the other camps, so this distinction may be due to climatic factors, rather than the influence of the stocking regime. Renosterveld grades into succulent karoo with increased aridity

(Bergh *et al*., 2014), and the succulent karoo biome is exceptionally rich in succulent plants, including leaf-succulent shrubs (Driver *et al*., 2003).

Plots were further distinguished on the basis of varying species richness in the categories perennial and annual (alien) grass. The study plots on camps 3 and 4 profiled according to the PC with these two variables as strongest contributing variables, with camp 3 (plots 6 and 7) most strongly associated with annual (alien) grass, and camp 4 (plots 8 and 9) most strongly associated with perennial (indigenous) grass. The difference in terms of stocking regime between these two camps were that camp 4 is only grazed in winter, and camp 3 is only grazed in summer. Only one species of annual (alien) grass was found on all the study plots, *Avena fatua,* which is palatable. Two species of perennial (indigenous) grass were found, *Chaetobromus dregeanus* and *Ehrharta calycina*, both are considered palatable.

UNIVERSITY of the
WESTERN CAPE

This is a favourable finding overall, as there are other alien grasses found on Nieuwoudtville Shale Renosterveld; *Bromus diandrus* (brome) and *Vulpia myuros* (rat's tail) (Todd, 2008). *B. diandrus* and *V. myuros* have sharp seeds (Musil *et al*., 2005), rendering them unpalatable, and they may easily increase in abundance (Todd, 1999). The prevalence of alien grass is linked to disturbance in the form of tilling and livestock presence, as the enrichment by livestock urine and dung creates soil that is conducive to the growth of these grasses (Todd, 2008). In this study, the camp which had the highest number of alien species, both grass and forb, has never been tilled, nor has it been heavily grazed, so

these results cannot be linked to overgrazing.

4.4.3 Hypothesis 3: Different patches of *Eriocephalus purpureus*-dominated Nieuwoudtville Shale Renosterveld vegetation are similar in terms of cover of different plant growth form categories.

The PCA showing transect data (Figure 4.2) accounts for a higher percentage of variance found (60.99 %), and the plots show a tighter profiling according to camp, compared to the PCA for plant species richness (Figure 4.1). This indicates that cover, rather than plant species richness, is a better indicator to account for variances in terms of vegetation among the study plots. This hypothesis is rejected. The first PC distinguishes between plots that have higher cover of annual grass, from those that had higher cover of duff. The second PC distinguishes between plots that have higher cover of both rock and biological soil crust from those that do not.

UNIVERSITY of the
WESTERN CAPE

Biological soil crust can be disrupted by grazing animals, influencing their function in terms of nutrient cycling and soil surface stabilisation (Neff *et al*., 2005). Biological soil crust and bare are in the same quadrant of the PCA, and have slightly similar factor loadings. Belnap and Eldridge (2001) found that biological soil crusts found between perennial plants were vulnerable to alien plant invasions, and that the vulnerability increased as grazing pressure increased. In this PCA, the plots separate out on the second PC, which means that the plots varied within each camp, therefore the stocking regimes cannot be

related to biological soil crust occurrence. In addition, the categories of alien forb and annual (alien) grass also loaded positively on the second PC, showing some positive association with biological soil crust, which is contrary to the findings of Belnap and Eldridge (2001). The presence of biological soil crusts is one of the factors affecting the redistribution of soil water availability, affecting water availability to plants (Schwinning and Sala, 2004). Though this does depend on the type of biological soil crust (Belnap, 2006), who found that the presence of biological soil crusts in cool and cold semi-arid areas improved rainfall infiltrability and reduced run-off. The results indicate that the presence of biological soil crusts in Nieuwoudtville Shale Renosterveld alter soil conditions, making a more favourable habitat for annual grasses and alien forbs, which may have higher water requirements than indigenous grass and forb species.

UNIVERSITY of the
WESTERN CAPE

Cover of annual (alien) grass was positively correlated to alien forbs (+0,959) and perennial grass (+0,675). The correlation between two categories of ephemerals, annual (alien) grass and alien forbs, could indicate a heavily grazed patch (Dean *et al*., 1995). But the stocking data (Table 3.1) does not support this, as the plots (1 and 2) in the most heavily stocked camp (1) are not strongly associated with cover of annual (alien) grass and alien forbs (Figure 4.2)..

Todd (2008) found that the dominance of alien grass around Nieuwoudtville is related to disturbance legacies, and current management practices. Sharma *et al*. (2010) found a significant positive relationship between the biomass of *Avena*

fatua and nitrogen in the soil in a study in south coast renosterveld. Nitrogen is often added as a soil amendment for cropped areas, and some leaching may have occurred from the surrounding farms (Van Rooyen, 2003; Muhl, 2008). The relationships that were found in this study between soil chemical elements, including nitrogen, and vegetation, are discussed in Chapter 6.

Studies in two winter-rainfall areas of South Africa situated in the Karoo and Bokkeveld regions have shown that high stocking rates and overgrazing affect the vegetation significantly, though no consistent response on different plant growth forms have been noted (Cupido, 2005; Kraaij and Milton, 2006; Todd and Hoffman, 2009). Grazing impacts interact with overall climate, and other disturbances, e.g. fire, and the response of vegetation varies according to these interactions (Curtis, 2013). Furthermore, fine-scale heterogeneity and edaphic patchiness dictate individual plant responses to disturbances (Curtis, 2013). Grazing can positively affect plants and ecosystem processes, but it plays a secondary role to soil characteristics (Todd, 2010). The soil factors measured in this study, and their interaction with the vegetation, are discussed in Chapters 5 and 6 respectively.

UNIVERSITY of the
WESTERN CAPE

This study focuses on veld which is *used for* sheep grazing, but it does not *compare* grazing, as the data are for stocking rates, and not the physical effects of grazing - defoliation, trampling, urination and defecation (Wilson, 1990), nor the patterns of movement of stock within a camp (Samuels, 2006; Witmore, 2007). The vegetation data generated supports this, as the study plots on the

different camps do not cluster tightly in the PCA's (Figures 4.1, 4.2) according to camps. There is somewhat of a stratification along the first PC (x-axis) of the PCA depicting cover (Figures 4.2), with the camps clustering loosely from left to right along the first PC (x-axis): camp 1 (most heavily stocked), 2 (not stocked for the past five years), 4 (lightly stocked in winter), and 3 (lightly stocked in summer), though there are intra-camp variations in terms of plant species richness as well as cover.

There was a limited number of study sites, which were not situated on a grazing, or climatic, gradient, and this prevents outright conclusions about rainfall or grazing effects. The different management regimes, as expressed in different stocking rates of a camp, do not translate into evenly and uniformly grazed camps (Samuels, 2006; Witmore, 2007; Smith *et al*., 2012). The lack of data for camp 2 (plots 3, 4 and 5) exacerbates the problem of assigning grazing intensity to these sites. They may not have been stocked for five years, but it is unknown how they were stocked for the decades preceding the conversion to a conservation area. The legacy of grazing persist over time, and is spatially and temporally unevenly distributed (Peters *et al*., 2006). The analysis of the specific grazing patterns within each camp was beyond the scope of this study, and no inferences could be made as to the specific effect of grazing on a certain patch of vegetation.

The two categories for cover which are normally correlated to grazing intensity are bare (positive indicator) and herbaceous litter (negative indicator) (Naeth *et*

UNIVERSITY of the
WESTERN CAPE

al., 1991; Northup *et al*., 2005; Fernandez *et al*., 2008). Although they are not significantly correlated in the Pearson correlation matrix, both variables have a similar factor loadings for the first PC (x-axis) and the second PC (y-axis) shown in Figure 4.2, though it has to be noted that no distinction was made between woody and herbaceous litter in this study. On the first PC the factor loading for bare is -0.321, and litter -0.302. On the second PC, the factor loading for bare is -0.355, and litter -0.498. Smith *et al*. (2012) found that patches of bare ground increased and litter decreased with increased grazing intensity, though litter showed a non-linear relationship with a decrease in grazing intensity. Piñeiro *et al*. (2010) showed the differences of grazing intensity from moderate to heavy had a negligible effect on litter. Schmalz *et al*. (2013) studied cattle grazing intensities on bunchgrass prairie in Oregon, and found that edaphic habitat types interacted strongly with stocking rate for the relative cover of litter, and that stocking rate also had no effect on the relative cover of bare ground. Naeth *et al*. (1991) found that the intensity and timing of grazing had the most effect on litter. The plots with the strongest association to both litter and bare were plots 5 and 8. Plot 5 is located in the camp (2) which has not been stocked for the previous five years, and the other plots (3 and 4) in this camp are not associated with these two variables. Plot 8 is located in the camp (4) which is grazed for one month in winter, and plot 9, also located in this camp, also is not associated with these two variables, indicating that, in this study, the stocking regimes certainly could not be related to relative cover of bare ground and the presence of litter.

UNIVERSITY of the
WESTERN CAPE

The camp with the highest stocking rate (camp 1; plots 1 and 2) shows consistently separate profiling, and tighter clustering on the two PCA's showing plant species richness and cover of plant growth form categories (Figures 4.1, 4.2). This may have something to do with the fact that it is in a drier area (receiving approximately 150 mm less rainfall per year than the other study areas), which would explain the higher species richness and cover of leaf-succulent shrubs on these two plots (Bergh *et al*., 2014). The non-consistent results intra-camp preclude any deductions in terms of stocking regime (and assumed grazing) effects on the vegetation.

Plant species richness in renosterveld does not seem to be adversely affected by grazing, though functional composition of plant communities are altered (McDowell, 1995; Musil *et al*., 2005). The criticism of livestock grazing in renosterveld includes the promotion of alien annuals and 'weedy' indigenous geophytes (Kemper *et al*., 1999), e.g. *Ornithogalum conicum,* which is toxic to livestock (Watt and Breyer-Brandwijk, 1962). In addition, the perennial grass component normally diminishes with increased grazing pressure, and the asteraceous shrub component increases (McDowell, 1995). Curtis (2013) found that grazing affected the size and productivity of the most palatable plant species in her study area of south coast renosterveld, but had no effect on plant diversity and cover. Furthermore, she found varied responses of vegetation to grazing and burning, due to edaphic patchiness and landscape heterogeneity. Radloff *et al*. (2014) found in a study on three structurally distinct south coast renosterveld types that grazing had a significant effect on lawn and tussock grassland

UNIVERSITY of the WESTERN CAPE

biomass, and that the exclusion of grazing from shrublands resulted in a palatable shrubland with a grass understorey. Palatability of any one plant species can differ from place to place, and this phenomenon, coupled with the complex effects of grazing, explains the highly varied responses of vegetation to grazing (McDowell, 1995).

4.5 Conclusion

The results show that although Nieuwoudtville Shale Renosterveld is homogenous in terms of plant species richness, it is not homogenous in terms of plant species richness and plant cover of plant growth form categories, which concurs with previous studies (Helme, 2007; Todd, 2010). These authors ascribed the variation in vegetation to soil and habitat differences. Although there was no significant difference among the study plots in terms of overall plant species richness, the species richness and cover of the different plant growth form categories differed among plots.

UNIVERSITY of the
WESTERN CAPE

This study does support the findings from previous studies, by Musil *et al*. (2005), O'Farrell *et al*. (2010), and Curtis (2013). O'Farrell *et al*. (2010) recommended that conservation efforts should focus on agro-ecological landscapes, embracing the 'non-conservation' activities that occur in them, in order to attain conservation targets (Pence, 2008; O'Farrell *et al*., 2009). These authors found that on-farm conservation of even the smallest fragment of natural renosterveld has positive landscape and plot-level effects - for overall

biodiversity, the integrity of the landscape, and animal health. Musil *et al*. (2005) suggest that fragments of natural renosterveld can be viewed as valuable seed and propagule sources, which would serve as irreplaceable resources for any future rehabilitation and restoration efforts. The study plots in this study hosted different species, and are rich in varying plant growth form categories, so they are clearly not replicas of one another, nor interchangeable in terms of the genetic material retained within them. The maintenance of biodiversity on all levels is needed for the continued viable existence of (south coast) renosterveld (Curtis, 2013). She proposes a network of reserves, encompassing *all management styles and micro-habitats*, in order to ensure conservation.

UNIVERSITY of the
WESTERN CAPE

The findings in this study do not indicate over-grazing of this vegetation type, and farmers should continue to utilise Nieuwoudtville Shale Renosterveld for sheep grazing in order to reap the benefits of the rich phytochemical diversity in terms of satiety and overall animal health (O'Farrell *et al*., 2007; Provenza *et al*, 2013). The results of this study demonstrate the variability in vegetation cover and diversity of an arid mountain centre renosterveld sub-type: *Eriocephalus purpureus*-dominated Nieuwoudtville Shale Renosterveld. The astonishing diversity that the CFR region and the Bokkeveld Plateau are known for is further portrayed, within the context of an agro-ecological matrix.

Chapter 5 Rhizosphere ecology of *Eriocephalus purpureus*, a dominant shrub in renosterveld rangelands

5.1 Introduction

Dryland areas cover about 40 % of the land surface of Earth (Derner and Schuman, 2007) and ecosystems in these areas may be the most vulnerable to the effects of climate change (Körner, 2000). The predicted increase in temperature (Solomon, 2007) may reduce the functioning of biogeochemical cycles in drylands (Maestre *et al*., 2012). Characteristically displaying spatial and temporal heterogeneity (Stafford Smith, 2008), dryland areas are often water- and nitrogen-limited (Whitford, 1989).

UNIVERSITY of the
WESTERN CAPE

South African soils generally have a low humus content, and this, coupled with aridity, makes them vulnerable to degradation, compared to soils found in more temperate climates (Du Toit, 1938). Overall low levels of organic matter in South African soils have been further lowered by overgrazing, which has caused significant losses of soil organic matter, mostly resulting from lower biomass production (Du Preez *et al*., 2011a)

Soils are living and adaptive systems, but their resistance to perturbation has limits (Ritz and Van der Putten, 2012). Soils are heterogeneous, formed by the legacies of geology, climate, vegetation and soil biota, all operating at different scales (Sylvain and Wall, 2011). The biodiversity of animals, plants and

microbes in the soil contribute to the functioning of this living 'skin' of the earth. It is the biota which live in the soil which support Earth's provisioning of ecosystem services, e.g. nutrient cycling, carbon sequestration and the production of plants for the creation of food, clothing and shelter (Wall *et al*., 2010). Soil biota play crucial roles in biogeochemical cycles (Wardle *et al*., 2004; Gessner *et al*., 2010). The important role that they play emphasises the need to understand the physiology and ecology of these organisms in their natural habitat in order to better understand them (Zogg *et al*., 1997; Wolters, 2001).

Soil biological communities are shaped by factors such as soil solution chemistry, microclimate, soil structure and resource availability (Wolters, 1991). Soil type plays a large role in microbial community composition (Garbeva *et al*., 2008; Berg and Smalla, 2009). Spatial heterogeneity in soil resources in terms of millimetres will affect habitat suitability for microbes. Organisms are influenced by the chemical composition of their environment, and influence their environment in turn (Barrett *et al*., 2007). Soil chemical parameters have been shown to co-vary with soil biological parameters (Mijangos *et al*., 2006; Pallarès Vinoyles, 2008). All biota require nitrogen for growth (Bardgett, 2005), and in natural systems, it can limit growth and activity of many organisms (Jackson *et al*., 2008).

The effect that soil microbes and invertebrate organisms have on ecosystem functioning is the key to understanding the way in which biogeochemical cycles

UNIVERSITY of the
WESTERN CAPE

are altered by human-driven system perturbations, and may aid us in protecting the integrity of the soil (Wall *et al*., 2010), in order to maintain the production of needed goods and services (Smith and Powlson, 2003). When analysing soil in a management context, it is important to use a variety of analyses, to ascertain the effect of actions on soil management quality, and microbial analyses may be more consistent than biochemical analyses in this regard (Bending *et al*., 2004).

The present study aims to assess the soil, in terms of chemical and rhizosphere microbial characteristics, of natural veld fragments of *Eriocephalus purpureus*-dominated Nieuwoudtville Shale Renosterveld (Mucina and Rutherford, 2006) which is used for sheep grazing. The objective is to investigate the soil microbial ecology, linking soil microbial with soil chemical parameters. Three hypotheses were formulated to guide this investigation.

UNIVERSITY of the
WESTERN CAPE

Hypothesis 1: Different patches of *E. purpureus*- dominated Nieuwoudtville Shale Renosterveld are similar in terms of soil chemical composition.

Hypothesis 2: Different patches of *E. purpureus*- dominated Nieuwoudtville Shale Renosterveld are similar in terms of soil microbial activity and diversity.

Hypothesis 3: Soil chemical composition and rhizosphere soil microbial communities co-vary in different patches of *E. purpureus*-dominated Nieuwoudtville Shale Renosterveld.

5.2 Materials and methods

5.2.1 Study area

Please refer to Chapter 3 for a full description of the study area and study plots. The nine study plots are all located on *Eriocephalus purpureus*-dominated Nieuwoudtville Shale Renosterveld (Mucina and Rutherford, 2006) used at present or in the recent past as rangelands for the grazing of sheep. The study plots are situated on different camps which are subjected to differing stocking regimes, as described in Chapter 3.

UNIVERSITY of the
WESTERN CAPE

5.2.2 Soil sampling

5.2.2.1 Soil chemical sampling

Soil was collected on 5 February and 19 June 2013 for the dry season and rainy season sampling respectively. The same five *E. purpureus* individuals chosen for the rhizosphere sampling, were used for the soil chemical sampling (45 plants/samples per season in total).

As each individual plant was dug up for the rhizosphere sample, 1 litre of the surrounding, loosened root-depth soil was taken for the chemical analyses and put into a large Ziploc® bag. Large stones and pieces of plant litter were picked out by hand. After collection the soil was placed on newspaper in a closed room,

allowed to air dry for two weeks, and then passed through a 1 mm sieve.

5.2.2.2 Soil microbial sampling, dry season

Five *E. purpureus* individuals were randomly chosen per study site (45 samples in total) and rhizosphere soil was collected from each one. The plants were dug up, the root-zone soil adhering to the roots shaken off, and the rhizosphere (Yanai *et al*., 2003) soil remaining on the roots carefully brushed into a specimen vial with a small paint brush, and immediately put into a cool box with dry ice. The samples were transported over dry ice. As not enough rhizosphere soil adhered to the roots of the *E. purpureus* individuals when dug up (the soil, and roots, were extremely dry), there was only enough soil to conduct Biolog Ecoplates™ (Biolog, Inc. Hayward, CA.) analyses on each plant.

UNIVERSITY of the
WESTERN CAPE

5.2.2.3 Soil microbial sampling, rainy season

The same procedure was followed as for the dry season, and soil was collected on 19 June 2013. During the rainy season collection, the soil adhered well to the roots, and enough soil could be collected to, in addition to the Biolog EcoPlates™, also run Fluorescein Diacetate (FDA) analysis (a quantitative measure of enzymatic activity), as well as Phospholipid Fatty Acid (PLFA) analysis (a quantative measure of microbial biomass and diversity). The five rhizosphere samples from individual *E. purpureus* plants in each plot were pooled for the Biolog EcoPlates™ analyses, as the dry season results showed a

remarkably consistent profile per plot. The rhizosphere samples were also pooled for the PLFA analyses to save on costs, though the FDA analyses were performed on each individual sample.

5.2.3 Soil chemical analyses

5.2.3.1 Soil digestion

A macro-Kjeldahl acid-digest on one gram from each sample with a sulphuric-peroxide mixture (Allen *et al*., 1986) was carried out. The soil was wrapped in cigarette paper (Rizla brand, red) and placed in the bottom of a Kjeldahl flask. Five ml of the sulphuric-peroxide mixture was added and the flasks placed in a Gerhardt Block Digestion System. The digestion started at a low temperature of 150^{0}C for half an hour. Thereafter, the temperature was raised consecutively to 250^{0}C, 350^{0}C, 380^{0}C at half-hour intervals and finally to 395^{0}C until a colourless solution was obtained. The samples were removed from the digestion block and allowed to cool. The digest was then diluted with deionised water and quantitively transferred into a 100 ml volumetric flask after filtering through Whatman no. 42 filter paper. It was then made up to volume using deionised water. Each sample solution was then transferred and stored in a 100 ml plastic bottle, and refrigerated.

UNIVERSITY of the
WESTERN CAPE

5.2.3.2 Cation analyses

The samples were analysed for Ca, Mg, K and Na using a Unicam Solaar M Series Atomic Absorption Spectrophotometer (AAS) with the flame system. K and Na were analysed using an air/acetylene flame, while Ca and Mg were analysed using a nitrous oxide/acetylene flame.

5.2.3.3 Nitrogen analysis

Total Nitrogen (N) concentration was determined using the Kjeldahl method with a K-350 Büchi Distillation Unit. Thirty ml of the sample solution was placed in a Büchi digestion tube. Excess of a 32 % Sodium Hydroxide (NaOH) solution was added to the sample and processed for 30 seconds. The distillate was collected in a 100 ml Erlenmeyer flask containing five ml 4 % Boric Acid. Five drops of methyl red indicator solution was added to the resultant mixture. The mixture was titrated with 0.01 M standardized hydrochloric acid (HCl) solution until a pale pink colour was obtained. The concentration of N was calculated using the following formula:

$$\text{N (mg/kg)} = \frac{\text{(ml standard acid – ml blank) x N of acid (0.01) x 1.4007 x 100}}{\text{weight of sample in grams (10 000) x 30 ml}}$$

(Expotech USA, 2011).

5.2.3.4 Phospate (PO_4) analysis

Five ml of a ten-times diluted version of each soil sample was taken with an auto-pipette and put into a 15 ml ‘Cellstar’ tube (Greiner Bio-One). Five drops of PO4 -1 reagent and 1 scoop of PO4 -2 reagent were added, shaken to dissolve,

and left for five minutes. The solution was poured into a ten mm cell and inserted into the spectrometer (Spectroquant® Pharo 300M), and a reading taken.

5.2.3.5 pH

The pH of each soil sample was determined using the 'sticky point' method. The samples of sieved and air-dried soil were used (as for the cation analyses). A standard amount (100 grams) was weighed from each sample and placed in a 250 ml beaker. The soil was moistened with deionised water to 'sticky point', forming a homogenous mass, with no separate water layer, before waiting for ten minutes and then measuring with an Orion 2 Star Benchtop pH meter, calibrated with buffers to pH 4, 7 and 10 (Cyster *et al*., 2010).

UNIVERSITY of the
WESTERN CAPE

5.2.3.6 Conductivity

The same moistened soil of each sample was used to test for conductivity (after the pH readings had been taken). A soil cup was filled with the wetted soil, and a reading taken with a YSI model 35 Conductance Meter. The resultant reading (micro Siemens, μS) was multiplied with 0.301 (the cell constant, $cm^{-1)}$ to obtain micro Siemens per centimetre, $\mu S.cm^{-1}$.

5.2.4 Rhizosphere soil microbial analyses

All microbial analyses were carried out in the Plant Sciences laboratory at the University of the Free State following standard practices. Biolog EcoPlates™ were used to characterise the bacterial community in the dry and rainy seasons. PLFA and FDA analyses were also carried out in the rainy season. Average well colour development (AWCD) and carbon utilisation patterns (of the 31 carbon sources on the Biolog EcoPlate™) were recorded (Garland and Mills, 1991). AWCD is the mean of the absorbance values for the whole EcoPlate™ (31 carbon sources), read on a spectrometer, and averaged (Stefanowicz, 2006). The AWCD value represents the total potential metabolic activity of the bacterial community found in a particular sample. Carbon substrate utilisation patterns are a measure of diversity (Mele and Crowley, 2008).

UNIVERSITY of the
WESTERN CAPE

PLFA 18:2ω6 was used as an indicator for fungal biomass, and the sum of the following PLFA's were used as an indicator of bacterial biomass: 15:0, *i*15:0, *α*15:0, 16:1ω7*t*, 17:0, *i*17:0, *cy*17:0, 18:1ω7 and *cy*19:0 (Frostegård and Bååth, 1996). The presence of gram negative bacteria was calculated as the sum of cy17:0, 18:1ω7 and cy19:0 and the presence of gram positive bacteria was calculated as the sum of i15:0, α15:0, *i*16:0 and *i*17:0 (Bardgett, 2001)

5.2.5 Statistical analyses

The soil chemical and microbial results were statistically analysed with Pearson correlation matrices and PCA. ANOVA (General Linear Model) was carried out to check for significant differences among the soil samples in terms of soil

chemical parameters. Linear regression was carried out to ascertain whether there were any relationships between certain variables. Descriptive statistics (bar graphs) were used to further illustrate results.

5.3 Results

5.3.1 Soil chemical analyses

Table 5.1 showed that all soil chemical parameters varied significantly (α=0.05) among the study sites.

Table 5.1 Results from GLM-ANOVA for all soil chemical parameters

Variable	F-value	*P*-value
K	57.01	<.0001
Na	131.09	<.0001
Ca	2.78	0.0015
Mg	39.57	<.0001
N	2.44	0.0047
P	38.83	<.0001
pH	6.65	<.0001
conductivity	17.19	<.0001

UNIVERSITY of the
WESTERN CAPE

5.3.1.1 Dry season

The Pearson correlation matrix generated various significant (α=0.05) correlations: Potassium was positively correlated to magnesium (+0,883) and to

phosphorus (+0,526). Further significant positive correlations included; magnesium and phosphorus (+0,538) and nitrogen and conductivity (+0,507).

The PCA showing the dry season soil chemical analyses (Figure 5.1) accounts for 52.08 % of the variation found among the plots. The three most important factor loadings for the first PC (x-axis) were magnesium (+0,915), potassium (+0,889) and phosphorus (+0,723). The two most important factor loadings for the second PC (y-axis) were conductivity (+0,810) and nitrogen (+0,766).

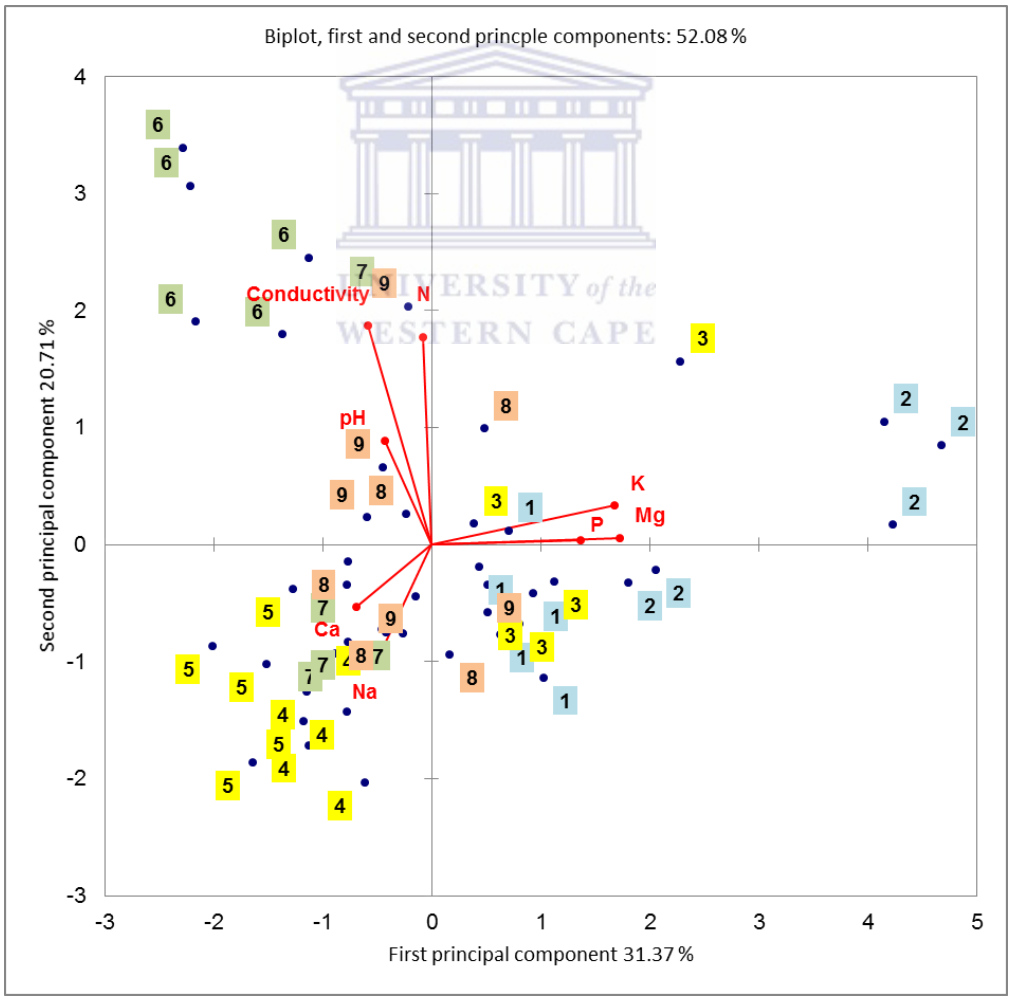

Figure 5.1 PCA of soil chemical analyses dry season, per plant sample. Total variation explained by this PCA is 52.08 %. The samples are numbered per plot, and coloured according to camp (camp 1=aqua, camp 2=yellow, camp 3=green, camp 4=apricot).

The PCA separates plots that had high readings of magnesium, potassium and phosphorus from those that did not along the first PC. The second PC mainly separated plots that showed high readings of nitrogen and conductivity from those that had higher readings of sodium and calcium. The forty-five samples cluster somewhat according to plot and camp (plots are numbered, and coloured according to camp: camp 1=aqua, camp 2=yellow, camp 3=green, camp 4=apricot). Plots in camp 1 (plots 1 and 2) cluster mostly according to the second PC, though all samples from these plots are positively placed on the first PC, showing that they had the highest readings of magnesium, potassium and phosphorus. Plots in camp 2 (plots 3, 4, and 5) are spread diagonally over the PCA, but plot 4 and 5 cluster according well in the third quadrant (positioned negatively on both PCs), showing that they had high readings of sodium and calcium. Plots in camp 3 (plots 6 and 7) and camp 4 (plots 8 and 9) cluster according to first PC, but also separate intra-plot on the second PC, showing that these plots were not homogenous in terms of soil chemical attributes measured, especially in terms of conductivity, nitrogen and sodium and calcium.

UNIVERSITY of the
WESTERN CAPE

5.3.1.2 Rainy season

The Pearson correlation matrix generated various significant (α=0.05) correlations. Potassium was positively correlated to magnesium (+0,556), phosphorus (+0,378), and pH (+0,331). Sodium was positively correlated to calcium (+0,337), and negatively to nitrogen (-0,330). Further significant

correlations included: Magnesium and nitrogen (-0,381); magnesium and phosphorus (+0,452); nitrogen and conductivity (+0,400); and phosphorus and conductivity (-0,412). There were more significant correlations in the rainy season Pearson correlation matrix compared to that of the dry season.

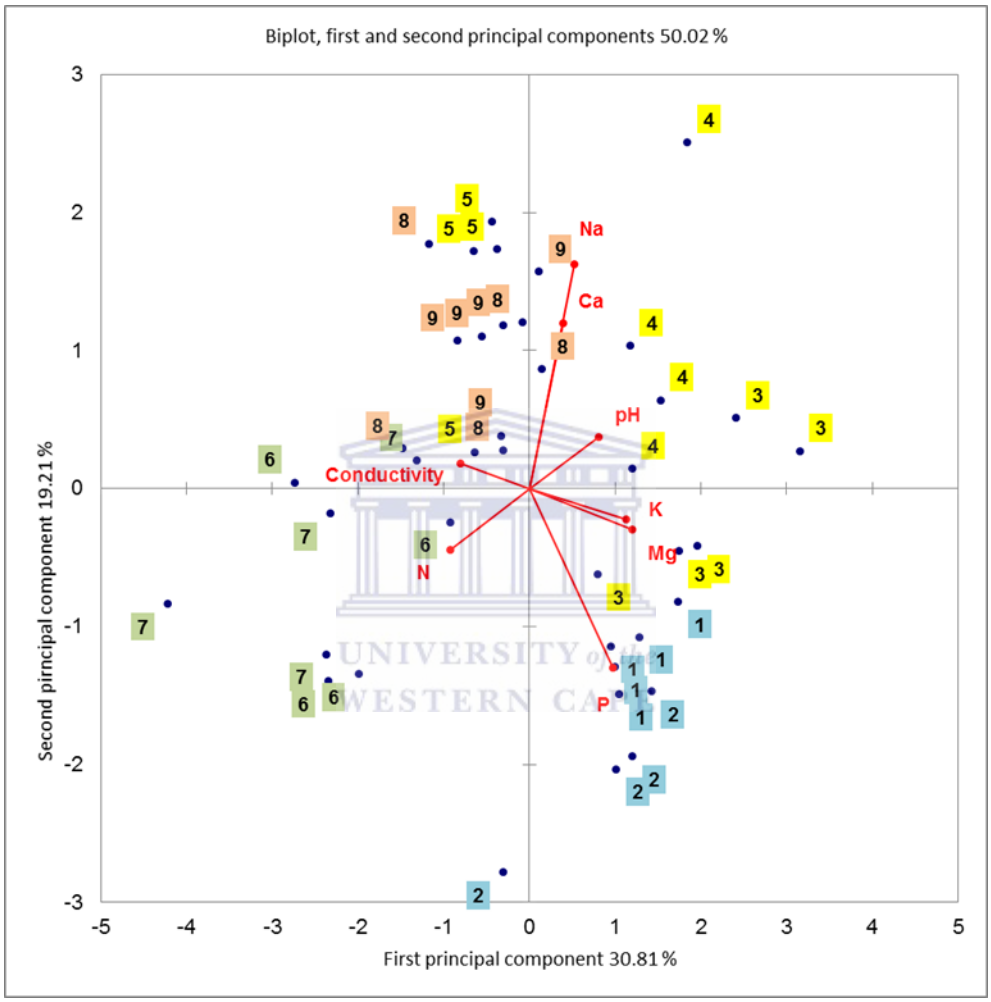

Figure 5.2 PC Analysis (PCA) of soil chemical analyses rainy season, per plant sample. The total variation accounted for is 50.02 %.

The PCA of soil chemical analyses rainy season (Figure 5.2) accounts for 50.02 % of the variation shown, which is similar to the dry season results (Figure 5.1). The two most important factor loadings for the first PC (x-axis) were magnesium (+0,754) and potassium (+0,709), which were also the two most

important factor loadings in the dry season. The three most important factor loadings for the second PC (y-axis) were sodium (+0,805), phosphate (-0.644) and calcium (+0,592), which were completely different from the most important dry season factor loadings on the second PC.

Plots on camp 1 and 4 show clearer profiling, whereas plots on camp 2 and 3 were more loosely arranged. The plots separate according to the first PC, distinguishing plots that had high readings of magnesium and potassium from those that had higher readings of conductivity and nitrogen. The second PC separated those plots that had higher readings of phosphorus form those that had high readings of sodium and calcium. Plots 1 and 2 (camp 1) were strongly associated with phosphates. Plots 6 and 7 (camp 3) were strongly associated with nitrogen and conductivity. Plots 3, 4, 5, 8 and 9 (camps 2 and 4) were strongly associated with sodium and calcium.

UNIVERSITY of the
WESTERN CAPE

5.3.2 Rhizosphere soil microbial analyses

5.3.2.1 Biolog EcoPlates™

The results from both seasons are only combined in terms of the Biolog EcoPlates™ results, as this analysis was the only one carried out on the samples from both the dry and the rainy seasons. The Discriminant Analysis (DA) (not shown) indicates how well the five dry season samples in each plot profile according to plot, with a 99.3 % fit according to the pre-assigned groupings, i.e.

plots, and the individual samples were therefore pooled per plot in the rainy season.

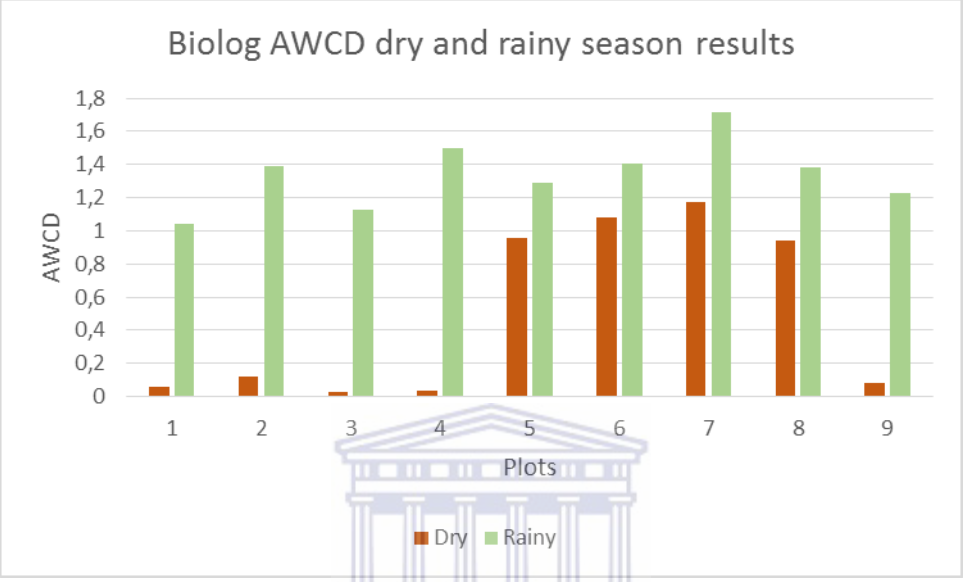

Figure 5.3 Bar graph of Biolog analyses results for both dry and rainy season, shown as Average Well Colour Development (AWCD) for the samples for each plot.

UNIVERSITY of the
WESTERN CAPE

Figure 5.3 shows a bar graph of Biolog AWCD results for both dry and rainy seasons. Rainy season results were all high, and dry season results show very low readings for plots 1-4 and 9, and very high readings for plots 5-8. The plots with the highest readings in the dry season (5, 6, 7, and 8) did not necessarily have the highest readings in the rainy season, though there is some inter-seasonal overlap (plots 6, 7 and 8), the plots with the highest readings in the rainy season were 2, 4, 6, 7, and 8.

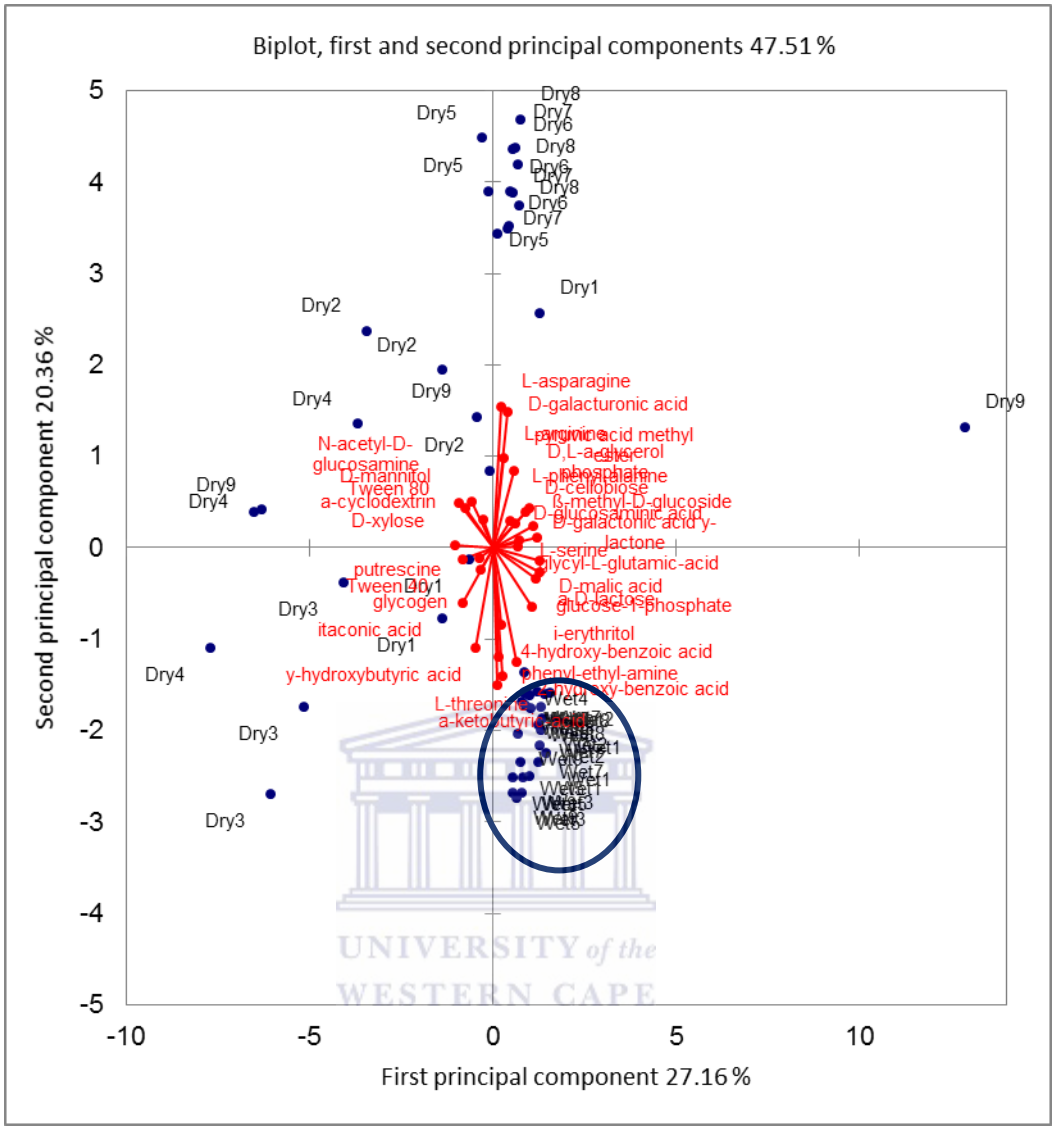

Figure 5.4 This PCA shows both the dry and rainy season Biolog results in terms of carbon-source utilisation, with days 4, 5 and 6 shown. The cluster of rainy season samples are emphasized with a blue oval shape.

Figure 5.4 shows the PCA depicting the differences in potential bacterial metabolic functioning, as measured by Biolog carbon-source utilisation patterns, among study plots and between seasons. The total variation accounted for was 47.51 %. This PCA shows that the rainy season results were similar (clustered in the fourth quadrant, within the blue oval). The dry season results showed a much looser arrangement, with more differences intra-camp, though there is a clear profiling by the plots with the highest dry season AWCD values (plots 5, 6, 7

and 8) on both axis. The plots with the highest AWCD values in the rainy season showed clear clustering according to the first PC. The strongest explaining variables for the first PC (x-axis) were D-malic acid (+0,873), a-D-lactose (+0,870), and D-galactonic acid y-lactone (+0,831). This PC distinguished between all rainy season samples (which were all high) and the dry season samples with high readings, from the dry season samples which showed low readings. The variables with the highest factor loadings for the second PC (y-axis) were L-asparagine (+0,921), L-threonine (-0,896), and D-galacturonic acid (+0,886). The plots with the highest dry season readings were separated on the second PC from the plots in the rainy season along this PC.

5.3.2.2 PLFA analysis

UNIVERSITY of the
WESTERN CAPE

Most fatty acids were not well represented within the samples. The only fatty acids with readings over 200 nmol/g were: 14:0, 16:0, 18:0 and 18:1ω9*c*. The bacterial to fungal ratios for the nine study plots showed no clear pattern per camp. Across all plots, gram negative bacteria were far more numerous. Gram positive bacteria were entirely absent in plots 1, 2, 3, 4, and 7.

5.3.2.3 Fluorescein Diacetate (FDA) analysis

FDA results were disparate intra- and inter-plot, indicating variation among the study plots in terms of microbial enzymatic activity.

5.3.3 Soil chemical and rhizosphere soil microbial analyses

The results from the soil chemical and rhizosphere soil microbiological analyses are presented together, according to season.

5.3.3.1 Dry season

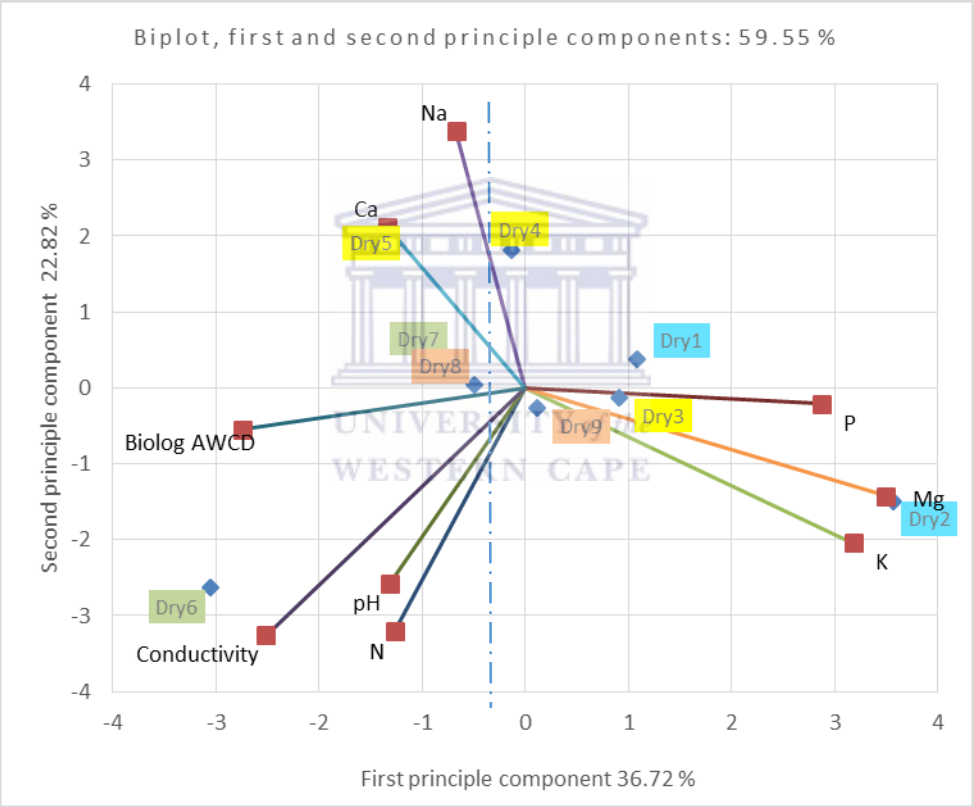

Figure 5.5 Dry season soil chemical analyses and rhizosphere soil microbial (AWCD) results. The vertical dashed blue line parallel and to the left of the y-axis separates those plots that showed high AWCD readings from those that showed low readings. Plots are numbered and coloured according to camp (camp 1=aqua, camp 2=yellow, camp 3=green, camp 4=apricot).

Figure 5.5 Dry season soil chemical analyses and rhizosphere soil microbial (AWCD) results. The vertical dashed blue line parallel and to the left of the y-axis separates those plots that showed high AWCD readings from those that

showed low readings. Plots are numbered and coloured according to camp (camp 1=aqua, camp 2=yellow, camp 3=green, camp 4=apricot). The first two PCs explain 59.55 % of the variation found among the study plots. The three variables with the highest positive eigenvector loadings for the first PC (x-axis) were magnesium (+0,495), potassium (+0,449) and phosphate (+0,405). The first PC (x-axis) mainly separated plots with higher readings from those with lower readings of these elements. The highest negative eigenvector loadings for the first PC (x-axis) were AWCD (-0,388) and conductivity (-0,356). Thus, plots with high magnesium, potassium and phosphorus had low AWCD readings, and plots with high conductivity had high AWCD reading. The vertical blue line separates those plots that showed high AWCD readings (plots 5, 6, 7 and 8), from those which showed low readings (1, 2, 3, 4, and 9). The variables with the highest eigenvector loadings along the second PC (y-axis) distinguishes between plots with high sodium (+0,478) from plots with high conductivity (-0, 461) and nitrogen (-0,454).

UNIVERSITY of the
WESTERN CAPE

The study plots in the same camp are not necessarily similar in terms of soil chemical composition or rhizosphere soil potential bacterial metabolic functioning, as shown by the AWCD. Plots in camp 4 (plots 8 and 9) show clustering on both PCs (x- and y-axes), but plots in camps 2 (plots 3, 4, and 5) and 3 (plots 6 and 7) show only loose clustering on the first PC (x-axis), and plots on camp 1 (plots 1 and 2) only show loose clustering on the second PC (y-axis).

5.3.3.2 Rainy season

Figure 5.6 shows the PCA of soil chemical means and FDA, PLFA and AWCD measurements for the rainy season.

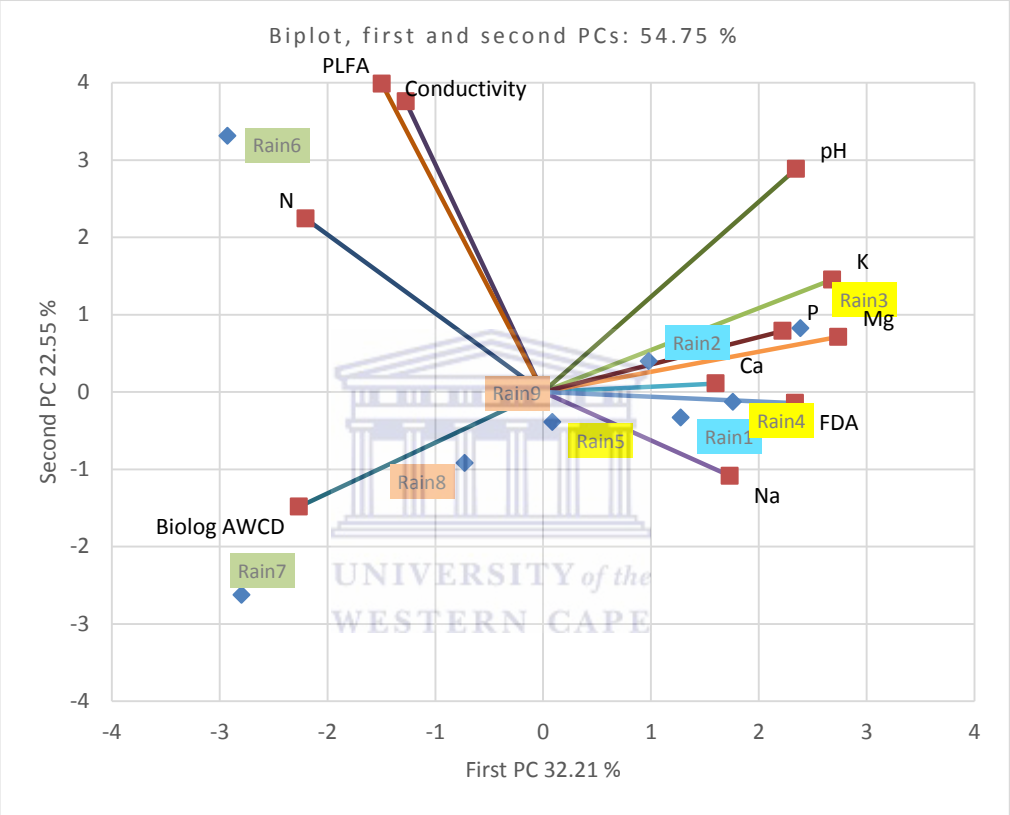

Figure 5.6 PCA of soil chemical analyses and rhizosphere soil microbiological, i.e. FDA, PLFA and AWCD analyses for the rainy season. Plots are numbered and coloured according to camp (camp 1=aqua, camp 2=yellow, camp 3=green, camp 4=apricot).

The three variables with the highest positive eigenvector loadings for the first PC (x-axis) were magnesium (+0,387), potassium (+0,379) and pH (+0,332). The highest negative eigenvector loadings for the first PC (x-axis) were AWCD (-0,321) and nitrogen (-0,311). The variables with the highest positive eigenvector loadings along the second PC (y-axis) distinguishes between plots

with high PLFA (+0,563) and high conductivity (+0,531) from plots with high AWCD (-0,210) and sodium (-0,153) readings.

The plots are numbered, and coloured according to camp. The study plots in the same camp are not necessarily similar in terms of soil chemical composition or rhizosphere soil microbial communities, though the plots show better profiling according to the first PC compared to the PCA for the dry season (Figure 5.5). Plots in camp 1 (plots 1 and 2) and camp 4 (plots 8 and 9) show clustering on both PCs (x- and y-axes), but plots in camps 2 (plots 3, 4, and 5) profile well on the second PC (y-axis) and profile loosely on the first PC (x-axis), and plots on camp 3 (plots 6 and 7) shows profiling on the first PC (x-axis).

5.4 Discussion

UNIVERSITY of the
WESTERN CAPE

The results will be discussed relating to the three hypotheses introduced in Section 5.1.

5.4.1 Hypothesis 1: Different patches of *E. purpureus*-dominated Nieuwoudtville Shale Renosterveld are similar in terms of soil chemical composition.

The Pearson correlation matrix for the rainy season showed more significant correlations between variables, compared to that of the dry season. The PCA for the rainy season (Figure 5.2) depicts the plots and camps also showing similar profiling as for the dry season (Figure 5.1), and with plots per camp grouping

slightly closer together, indicating that the soil chemical readings were more similar intra-camp in the rainy season.

The association of different plots with differing elements varied between seasons. High readings of phosphate was strongly associated with plots 1 and 2 in both seasons, and also 3 in the rainy season. High readings of potassium and magnesium were strongly associated with plots 1, 2, and 3 in the dry season, and the same plots, with the addition of 4, in the rainy season. High readings of nitrogen were strongly associated with plots 6, 8 and 9 in the dry season and 6 and 7 in the rainy season. And whereas plots on camp 4 (8 and 9) did not show any strong associations with elements in the dry season sampling, they showed strong associations with sodium and calcium in the rainy season. The ANOVA showed significant differences ($p<0.05$) for all chemical parameters, and this hypothesis is rejected.

UNIVERSITY of the
WESTERN CAPE

These results demonstrate how the soil in fragments of Nieuwoudtville Shale Renosterveld used as rangelands is not homogenous in terms of soil chemical characteristics, and that variation is evident even within camps. Grazing supports fine-scale, i.e. < 25 cm, heterogeneity in the soil (Augustine and Frank, 2001), through scattered dung and urine inputs (Piñeiro *et al*., 2010) and trampling (Stavi *et al*., 2008). The soil chemical composition is not static over time, and changes occur within a relatively short space of time (4 months in this study). Chemical elements in the soil are in constant flux, relating to biogeochemical processes that occur on varying spatial and temporal scales (Beare *et al*., 1995;

Bodelier, 2011). The composition and activity of microbial communities govern biogeochemical cycling, recycling organic matter and ensuring continuing fertility of soils (Bååth and Anderson, 2003). The availability of mineral nutrients is not only fundamentally linked to the soil microbial community, but also to the plant, and ultimately faunal, community which it supports. These links will be explored later in this chapter and in Chapter 6.

5.4.2 Hypothesis 2: Different patches of *E. purpureus*-dominated Nieuwoudtville Shale Renosterveld are similar in terms of soil microbial activity and diversity.

Similar utilisation of the various groups of carbon-sources in Biolog EcoPlates™ indicate similar metabolic profiles within bacterial communities (BushawNewton *et al*., 2012). The fact that high AWCD readings in the dry season were associated with similar carbon-source utilisation profiles, and low AWCD readings in the dry season were associated with disparate carbon-source utilisation profiles, may point to a loss of functional stability in those samples with low AWCD readings (Pallarès Vinyoles, 2008).

UNIVERSITY of the
WESTERN CAPE

The striking result is that the specific carbon-source utilisation echoes the AWCD result. The samples with the highest AWCD dry season results are similar, as the rainy season AWCD results (which are all high) are similar. This shows that the carbon-source utilisation differed seasonally, and that certain carbon sources, notably L-asparagine, a-D-galacturonic acid, L-arginine, and pyruvic acid methyl ester were used more in those samples with high AWCD in

the dry season, whereas the samples with high AWCD in the rainy season showed stronger utilisation of L-threonine, a-ketobutyric acid, 2-hydroxy-benzoic acid, phenyl-ethyl-amine and 4-hydroxy-benzoic acid. These results indicate that microbial communities function differently according to the season. The lack of potential function in the dry season was alleviated in the rainy season, showing seasonal resilience.

Bacteria and fungi form cysts and spores in order to survive unfavourable environments (Lavelle, 2012). Active microbes are more vulnerable to water stress (Williams, 2007), and, at any one time, most of the microbial community may be physiologically dormant in order to protect themselves from environmental stress (Chen and Alexander, 1973), and surviving until conditions improve (Bardgett, 2005).

UNIVERSITY of the
WESTERN CAPE

Within bacterial communities, gram-positive bacteria are more resistant to desiccation (Williams, 2007). The sum of PLFA's (not shown) used as indicators of gram-positive bacteria were highest in plots 5, 6, 8, and 9, which overlap mostly with the plots which showed the highest dry season AWCD (plots 5, 6, 7, and 8). The highest readings for PLFA gram-negative bacteria (not shown), were plots 5, 6, 7, and 8 which corresponds perfectly with the highest readings of the dry season AWCD. Gram-negative bacteria were far more abundant than gram-positive bacteria, and contribute more to the total bacterial communities on the various plots. Although the PLFA analyses were only carried out in the rainy season, the result, that all plots showed high gram-negative numbers, as

compared to gram-positive, and that gram-negative bacteria are more sensitive to drought conditions, may explain the low readings of the AWCD for those plots that had low readings of gram-negative bacteria. It may be that the communities in the soil of *E. purpureus*-dominated Nieuwoudtville Shale Renosterveld are characteristised by the presence of gram-negative bacteria, with strong seasonal dormancy within the bacterial community, as the vegetation is also largely dormant during the dry summer.

Soil communities are not static, and change on daily, seasonal, and successional terms (Bardgett, 2005). Temporal changes in the soil biological community are confounded further by long periods of inactivity when resources, particularly water, are scarce. Bacteria that live in areas that experience seasonal variation in water availability have been shown to be more resilient to water stress (Fierer and Schimel, 2003), and the results concur with these previous findings. Further investigation would be useful, perhaps over the course of a rainy season, coupled with specific soil moisture measurements, in order to gain a fuller understanding of these results.

UNIVERSITY of the
WESTERN CAPE

The vegetation in the rainy and dry seasons could be classified as two differing systems, i.e. high- and low-productivity respectively. Soil communities are either predominantly bacterial-based, and characteristically inhabit fast-growing, short-lived, fast-decomposing vegetation stands, or predominantly fungal-based and characteristically inhabit slow-growing, long-lived, slow-decomposing vegetation stands (Wardle *et al*., 2004). Nieuwoudtville Shale Renosterveld in

winter and spring may be characterised by the former, and in summer and autumn by the latter. The shrub component, including stem-, non- and leaf-succulent shrubs, remains throughout the year, in addition to perennial grass. Possible links among the vegetation and the soil microbial community will be further explored in Chapter 6.

The PLFA result shows poor representation of many fatty acids (not shown). Of the 26 fatty acids measured, ten showed zero values for all the samples, and twelve fatty acids had low readings. Of the four PLFA's with the highest readings, three of the PLFA's with the highest readings are normal saturated fatty acids; 14:0, 16:0 and 18:0, and 18:1ω9*c* is a mono-unsaturated fatty acid. Normal saturated acids are found in prokaryotic and eukaryotic organisms. A relative increase has been shown to correlate with decreased diversity of the microbial community (Microbial Insights, 2009), which corresponds with the overall poor representation of the PLFA's measured.

UNIVERSITY of the
WESTERN CAPE

The ratios of bacterial to fungal biomass (not shown) often changes in response to management actions (Bossio *et al*., 1998; Frostegård *et al*., 2010). The ratios of the nine study plots were extremely diverse, and did not profile per camp, further emphasising the heterogeneous nature of the semi-arid landscape in which the study was conducted (Smith *et al*., 2012). Furthermore, these ratios could not be used to distinguish between different camps, i.e. stocking regimes, which was contrary to expectations. Heavier grazing tends to lead to systems dominated by bacteria, and lighter grazing often results in a fungal-dominated

decomposer system (Grayston *et al*., 2004). This result indicates that the stocking data is inadequate to account for grazing effects on the belowground microbial community, and that any future studies should include specific measurements of grazing effects, e.g. defoliation and trampling.

High bioturbation of the soil is another characteristic of a bacterial-based soil decomposer community (Wardle *et al*., 2004). Previous studies (Bragg *et al*., 2005; O'Farrell *et al*., 2007) have shown that there are many ecosystem engineers found in natural patches of Nieuwoudtville Shale Renosterveld. Porcupines, gerbils and earthworms all contribute to the bioturbation of the soil in this vegetation type. Furthermore, most of the study plots are used for winter-grazing. The presence of livestock would increase the labile faecal deposits, which would also contribute to a more bacterial-based decomposer channel (Wardle *et al*., 2004).

UNIVERSITY of the
WESTERN CAPE

As there were no 'pristine' *E. purpureus*-dominated Nieuwoudtville Shale Renosterveld fragments with which to compare the fragments used as rangelands, it is not possible to surmise the original state of these fragments in terms of fungal vs. bacterial dominance of the decomposer web. If models from mull and mor systems (normally used to characterise forests) are used, renosterveld would be classified as more mull, i.e. more fertile, and fynbos would be an example of mor soils, i.e. less fertile and more acidic. The microbial decomposer networks in mull soils are characteristically dominated by bacteria, and those of mor soils, by fungi (Ponge, 2003). The result, that there was very

little fungal presence in the various samples, as indicated by PLFA analyses, may not necessarily indicate any perturbation in the decomposer system, but may be typical of renosterveld. Although nitrogen enrichment has been linked to shifts from fungal to bacterial dominance in hardwood forests (Frey *et al*., 2004), the bacterial to fungal ratios in the study plots do not show overall clear relationships in terms of linear regression (not shown) with soil nitrogen content across the study plots, nor with overall nutrient content (not shown).

5.4.3 Hypothesis 3: Soil chemical composition and soil microbial community composition co-vary in different patches of *E. purpureus*-dominated Nieuwoudtville Shale Renosterveld.

UNIVERSITY of the
WESTERN CAPE

Processes of mineral nutrient mineralization and immobilization are sensitive to microbial community composition (Schimel *et al*., 2005). The results support co-variation among soil chemical and microbial variables, and this hypothesis is not rejected. The PCA depicting soil chemical and microbial variables for the dry season (Figure 5.5) shows significant co-variation (78.56 %). This result corresponds with previous studies done in various ecosystems (Steenwerth *et al*., 2002; Barrett *et al*., 2006; Pallarès Vinyoles, 2008). The study plots show an extremely varied association with the soil variables. Despite the varied profiles, the first PC distinguishes between plots with the highest AWCD readings (plots 5, 6, 7, and 8) from those that showed low readings.

The PCA showing the rainy season results (Figure 5.6) shows that the three

measures for microbial biomass, activity, and potential bacterial metabolic functionoing (PLFA, FDA and AWCD) are located in three different quadrants of the PCA, and are associated with different mineral elements. High enzyme activity (FDA) is closely associated with the variables phosphate, magnesium and potassium. The results in both seasons show that potential bacterial metabolic functioning (AWCD), and to some extent microbial biomass (PLFA, rainy season only), were negatively associated with high readings of these two elements, and that the highest readings of these two elements were in the camp (1) that was subjected to the longest stocking period.

Of all the elements, phosphorus is the most important for continued animal health (Underwood, 1981). The presences of this chemical element in the soil is thus a positive indicator, as it may be taken up by plants, and may eventually be ingested by animals. If phosphorus is abundant in the soil, plants do not benefit much from allocating resources to supporting mutualistic relationships with mycorrhizal fungi (Treseder, 2004) which facilitate the uptake of phosphorus by most plants (Vance, 2001).

UNIVERSITY of the
WESTERN CAPE

The results show no relationship between soil microbial measures, and overall nutrient content. Nutrient accumulation in managed systems is associated with an increased ratio of bacterial to fungal markers, as shown in a PLFA analysis (Bardgett and McAllister, 1999). More natural systems are associated with a lower bacterial to fungal ratio (Bardgett, 2005). Overall nutrient value, nitrogen and phosphorus all showed no relationship in linear regressions (not shown) with

the bacterial to fungal ratio in the study plots. The bacterial to fungal ratio (Frostegård and Bååth, 1996) was extremely varied for all study plots, showing no profiling per camp, further emphasising the heterogeneity in the soil of these natural rangelands, and the fine-scale heterogeneity promoted by grazing livestock (Augustine and Frank, 2001).

Temporal changes due to plant seasonal growth may affect nitrogen partitioning (Schadt *et al*., 2003). Plants and microbes compete for nitrogen, which is one of the most limiting mineral nutrients, in addition to phosphorus, in terrestrial ecosystems (Chapin *et al*, 2002). Nitrogen was lower in the rainy season (the growing season), which may indicate that plants have taken up more nitrogen, leaving less nitrogen in the soil accessible to microbes (Bardgett, 2005). The conservation and replenishment of nitrogen is important in order to retain humus in the soil, and maintain soil quality (Du Preez *et al*., 2011b), which may explain the result of nitrogen being strongly associated with plot 6, which also showed high values for dry and rainy season AWCD, as well as PLFA's.

UNIVERSITY of the
WESTERN CAPE

Heterogeneity in terms of nitrogen and phosphorus can drive the patchy distribution of soil organisms (Swift *et al*., 1979; Bardgett, 2005; Berg and Bengtson, 2007). In turn, rhizosphere bacteria, through the production of enzymes, can change the availability of different forms of nitrogen and phosphorus in the soil (Reynolds *et al*., 2003; Ehrenfeld *et al*., 2005). Phosphate was one of the strongest explaining variables in the PCA's depicting the variation in the different samples for soil chemical and soil microbial variables

measured (Figures 5.5 and 5.6). Phosphorus was negatively associated with potential bacterial metabolic functioning (AWCD) in both seasons, and microbial biomass (total PLFA) in the rainy season, but positively associated with enzyme activity (FDA).

In a model of soil organic matter decomposition, Fontaine and Barot (2005) postulate that when nitrogen is abundant in the soil, the mineralization rate of soil organic matter is low, and the pool of soil organic matter increases. With a decrease in nitrogen in the soil, it is predicted that the soil decomposer community, including microbes, will increase, with an increase in soil organic matter mineralization and a reduction in the soil organic matter pool. This model fits with findings of Waldrop *et al*. (2004), who found that an increase in nitrogen availability changes the structure of the microbial community. The results show that FDA is negatively associated with nitrogen and Biolog and PLFA measures, meaning that the microbial enzymatic activity was highest in those plots that had the lowest readings of nitrogen, which fits with the above theory and previous findings (Carreiro *et al*., 2000).

UNIVERSITY of the
WESTERN CAPE

Effects of pH on soil microbial communities are considered strong (Frostegård *et al*., 2010). For example, Steenwerth *et al*. (2002) found significant negative correlations between pH and PLFA-defined soil microbial communities, across systems under different management regimes in California. In this study pH did not have strong effects on any of the three microbial measures used. Soil samples measured pH values between 5.9 and 6.9 which falls into the slightly

acid category, which is optimum for most plant species (Amacher *et al*., 2007).

5.5 Conclusion

Chemical elements in the soil are in constant flux, relating to biogeochemical processes that occur on varying spatial and temporal scales (Beare *et al*., 1995; Bodelier, 2011). The composition and activity of microbial communities govern biogeochemical cycling, recycling organic matter and ensuring continuing fertility of soils (Bååth and Anderson, 2003). The availability of mineral nutrients is thus fundamentally linked to the soil microbial community. In this study, there was no overall relationship between high readings of soil chemical elements and soil microbial community composition or activity, though the various soil microbial measures showed co-variation with certain soil mineral elements.

UNIVERSITY of the
WESTERN CAPE

There is considerable variation within *E. purpureus*-dominated Nieuwoudtville Shale Renosterveld fragments in terms of soil chemical composition, and soil microbial activity and diversity, and these measures co-vary. Therefore the first two hypotheses are rejected, and the third hypotheses is accepted. The chemical analyses in both seasons show remarkable profiling according to different plots, and camps.

The dry and the rainy season combined soil chemical and rhizosphere soil microbial analyses show that the different microbial measures are associated with different soil chemical elements. The most salient finding is that there is remarkable profiling of the samples per plot with the AWCD results, and

carbon-source utilisation per season in those plots that showed high AWCD readings. Another important finding is that high FDA readings are associated with high readings of phosphate, magnesium and potassium. The PLFA results show extremely poor representation of fatty acids overall, and thus indicate a possible loss of microbial diversity.

The heterogeneous nature of soil in terms of chemical, physical and biological characteristics may be the biggest factor in the diversity of soil organisms (Wurst *et al*., 2012). The results in this study show that the microbial and chemical measures co-vary, and that within this vegetation sub-type, there are differing patterns of soil chemical composition and soil microbial communities (Berg, 2012).

UNIVERSITY of the
WESTERN CAPE

Interactions among soil organisms have been shown to be linked to particular locations (Porazinska *et al*., 2003), and particularly within a heterogeneous vegetation type, and in a heterogeneous landscape such as the Bokkeveld Plateau (Helme, 2007), this may be the most likely explanation for the varying results obtained in this study.

Chapter 6 Links between renosterveld rangelands vegetation and the soil ecology of a dominant shrub.

6.1 Introduction

Drylands, including arid, semi-arid, and dry sub-humid ecosystems, cover about 40 % of the earth's land surface (Derner and Schuman, 2007). Rangelands which are situated in drylands are sensitive to degradation by domestic livestock. This degradation happens through direct (e.g. altering plant cover and diversity) and indirect (e.g. trampling increases soil bulk density and compaction) processes (Asner and Archer, 2010). These processes vary spatially at varying scales (Lyford *et al*., 2003). Livestock graze selectively, increasing the inherent spatial heterogeneity of the soil and vegetation in dryland areas (Smith *et al*., 2012).

UNIVERSITY of the
WESTERN CAPE

South African rangelands have been diminished in terms of productivity since colonization of this region (Dean and McDonald, 1994). Degraded rangelands are characterised by vulnerability to soil erosion, reduced ability to buffer soil temperatures and receive rainfall infiltration, and changes in soil organism communities (Whitford *et al*., 1989; Du Preez *et al*., 2011 b; Mills *et al*., 2012). Due to aridity and a lack of organic matter, soils in South Africa are delicate and vulnerable compared to those in more temperate zones (Du Toit, 1938). Organic matter loss is attributed to vegetation removal and erosion, whether that happens through tillage, heavy grazing or burning (Du Preez *et al*., 2011b).

Plants are connectors between the aboveground and belowground domains, and integrate these two subsystems (Wardle *et al*., 2004). Plants influence soil biota through two paths; decomposition and production (Wardle *et al*., 2004; De Deyn *et al*., 2007). The communities of soil organisms recycle the plant-produced organic matter, underpinning plant productivity (Sylvain and Wall, 2011), and positively affecting soil fertility, plant growth, soil structure and carbon storage (Coleman, 2008).

Microbes are sensitive and respond quickly to change, providing information that integrates varying factors (Mijangos *et al*., 2006). The quantity and community composition of microbes in the soil affects the ability of a plant to access nutrients, affecting resource competition between plants (Bais *et al*., 2006). Human activities influence soil biological communities, but the response is variable, and depends on a range of biological factors (Wall *et al*., 2010).

UNIVERSITY of the
WESTERN CAPE

Renosterveld is a diverse, fragmented and diminished vegetation type within the fynbos biome. Untransformed fragments of Nieuwoudtville Shale Renosterveld (Mucina and Rutherford, 2006) are found on tillite soils around Nieuwoudtville, on the Bokkeveld Plateau, and are used as natural forage for sheep.

For the purpose of this study the following hypothesis has been tested:

Hypothesis 1: Patches of *Eriocephalus purpureus*- dominated Nieuwoudtville Shale Renosterveld are similar in terms of aboveground and belowground

biological measures: plant species richness, vegetation cover, and soil chemical and microbial profiles.

6.2 Materials and methods

6.2.1 Study area

Refer to Chapter 3 for a full description of the study area and study plots. The nine study plots are all located on *Eriocephalus purpureus*-dominated Nieuwoudtville Shale Renosterveld (Mucina and Rutherford, 2006) used at present or in the past as rangelands for the grazing of sheep. The study plots are situated on different camps which are subjected to differing stocking regimes, as described in Chapter 3.

UNIVERSITY of the
WESTERN CAPE

6.2.2 Rapid Renosterveld Assessment Method

The Rapid Renosterveld Assessment Method (Milton, 2007) is described in brief in Chapter 4.2.

6.2.3 Soil sampling and analyses

The rhizosphere soil sampling for the microbial analyses, as well as the soil sampling for the soil chemical analyses are described in Chapter 5.2. In this chapter, the microbial parameters are; total PLFA (indicating microbial biomass),

Biolog AWCD, an indicator of potential metabolic functioning of the bacterial community, and FDA, a measure of microbial enzyme activity.

6.2.4 Statistical analyses

The vegetation and soil chemical and rhizosphere soil microbial results were statistically analysed with Pearson correlation matrices and PCA. Partial least squares (PLS) regression was carried out with soil parameters as independent and vegetation parameters as dependent variables. PLS is used to find primary relationships between two sets of variables, and is well suited when the number of observations are fewer than the number of variables.

UNIVERSITY of the
WESTERN CAPE

6.3 Results

The aboveground data gleaned from the vegetation surveys are divided into plant species richness and cover of all plant growth form categories. Section 6.3.1.1 and Section 6.3.2.1 show the combined results of plant species richness with soil microbial and soil chemical results respectively. Section 6.3.1.2 and Section 6.3.2.2 show cover of all plant growth form categories (including rock, litter, duff, biological soil crust, and separate categories for the two most common non-succulent shrubs found: *Eriocephalus purpureus* and *Asparagus capensis*) combined with soil microbial and soil chemical results respectively.

6.3.1 Vegetation and rhizosphere soil microbial analyses, both seasons

6.3.1.1 Plant species richness and rhizosphere soil microbial analyses, both seasons

The Pearson correlation matrix (not shown) generated only two significant (α=0.05) correlations, but only one set of correlations relates an aboveground to a belowground measure: Species richness within the category non-succulent shrubs was positively correlated to AWCD results in the dry season (+0,824).

The PCA depicting the vegetation survey results in terms of plant species richness and soil microbial parameters - AWCD (both seasons), PLFA and FDA (rainy season only) is shown in Figure 6.1. The PCA explains 49.23 % of the variation found among the nine study plots. The highest eigenvector scores on the first PC (x-axis), are for the variables non-succulent shrubs (+0,535), AWCD in the dry season (+0,456), leaf-succulent shrubs (+0,387), FDA (-0,350) and PLFA (+0,340). The first PC mainly separated plots with more non-succulent and leaf-succulent shrub species and that showed higher readings of AWCD and PLFA, from those that had higher readings of FDA.

UNIVERSITY of the
WESTERN CAPE

The highest eigenvector scores on the second PC (y-axis), are for the variables annual (alien) grass (+0,488), alien forbs (+0,466), AWCD rainy season (+0,441), and perennial grass (-0,386). This PC distinguishes between plots intra-camp on camps 1 and 2, demonstrating that these plots were not similar in

terms of plant species richness of the above plant growth form categories, despite being situated on the same camp.

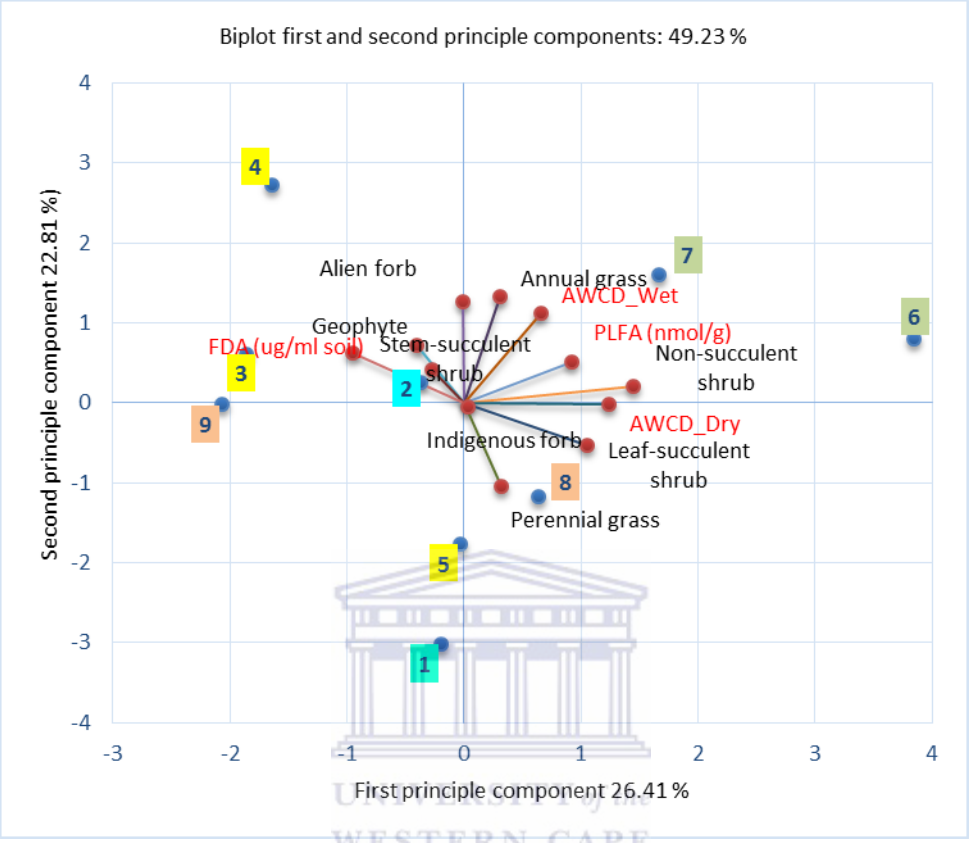

Figure 6.1 PCA depicting vegetation survey results in terms of plant species richness, and soil microbial parameters recorded in both seasons; AWCD (both seasons), PLFA and FDA (rainy season only). Plots are numbered, and coloured according to camps (camp 1=aqua, camp 2=yellow, camp 3=green, camp 4=apricot).

The plots were chiefly distinguished intra-camp by the plant species richness in terms of perennial (indigenous) vs. annual (alien) grass growth form categories. This PC also distinguishes between plots situated on camps 3 (plots 6 and 7) and 4 (plots 8 and 9), and these plots profile according to the second PC, showing that they were similar in terms of plant species richness of the above plant growth form categories.

6.3.1.2 Plant cover and soil microbial analyses, both seasons

The significant (α=0.05) aboveground-belowground correlations generated by the Pearson correlation matrix (not shown) included the following: Dry season AWCD results was positively correlated to cover of rock (+0,749), alien forbs (+0,689), and alien grass (+0,680), and negatively correlated to cover of *E. purpureus* (-0,786). Rainy season AWCD results was also negatively correlated to *E. purpureus* (-0,701), and PLFA was positively correlated to cover of perennial grass (+0,817).

The PCA depicting the vegetation survey results in terms of plant cover and soil microbial parameters - AWCD (both seasons), PLFA and FDA (rainy season only) is shown in Figure 6.2. This PCA explains 60.31 % of the variation found among the nine study plots.

UNIVERSITY of the
WESTERN CAPE

The highest eigenvector scores for the first PC (x-axis) are for the variables alien grass (+0,362), alien forbs (+0,345), *E. purpureus* (-0,303), perennial grass (+0,291), and duff (-0,288). The first PC mainly separated plots with higher cover of annual (alien) grass and alien forbs from those that had higher cover of *E. purpureus* and duff. The plots show remarkable profiling per camp according to the first PC.

The highest eigenvector scores on the second PC (y-axis), are for the variables biological soil crust (+0,427), rock (+0,398), and *A. capensis* (-0,315). This PC

distinguishes between plots intra-camp situated on camps 2, 3, 4, and very slightly 1, demonstrating that there was considerable variation intra-plot in terms of cover of these three variables.

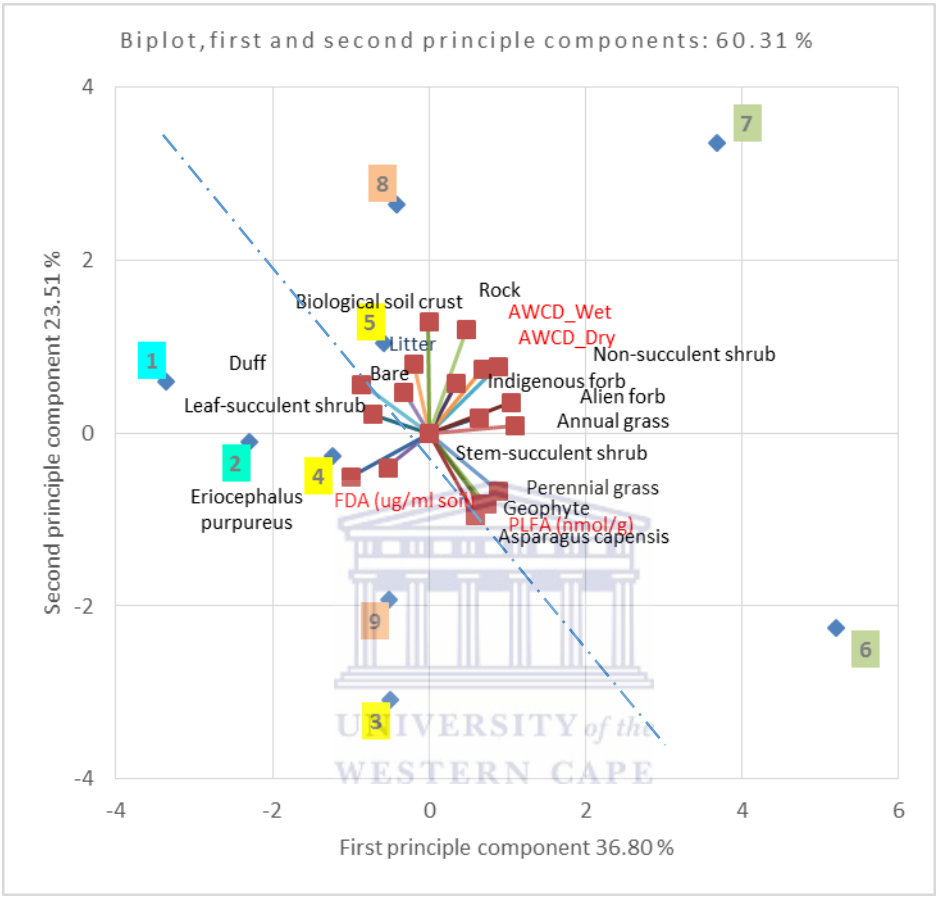

Figure 6.2 PCA depicting vegetation survey results in terms of plant cover and soil microbial parameters; AWCD (both seasons), PLFA and FDA (rainy season only). The dotted blue line separates those plots with high readings of AWCD in the dry season, from those that showed a low reading. Plots are numbered, and coloured according to camps (camp 1=aqua, camp 2=yellow, camp 3=green, camp 4=apricot).

6.3.2 Vegetation and soil chemical analyses

6.3.2.1 Plant species richness and soil chemical attributes, both seasons

The Pearson correlation matrix (not shown) of plant species richness allocated to plant growth form categories and soil chemical parameters sampled over both

seasons showed a few significant correlations between variables, but the highest correlations between vegetation and soil chemical variables include: leaf-succulent shrubs and sodium (-0,733), and non-succulent shrubs and sodium (-0,612). Figure 6.3 shows the PCA depicting plant species richness allocated to different plant growth form categories per plot, and soil chemical measures in both dry and rainy seasons. The plots are numbered (1-9) and coloured per plot. The PCA explains 41.56 % of the total variation found among the study plots.

The variables with the strongest eigenvectors on the first PC are geophytes (+0,446), sodium (+0,408), leaf-succulent shrubs (-0,381) and magnesium (-0,380). The first PC mainly separated plots with more geophyte species and that had higher readings of sodium, from those that had more species of leaf-succulent shrubs and higher readings of magnesium. The variables with the highest eigenvector scores on the second PC were non-succulent shrubs (+0,414), potassium (-0,351), stem-succulent shrubs (-0, 325) and leaf-succulent shrubs (0,322).

UNIVERSITY of the
WESTERN CAPE

Plots in camp 1 (plots 1 and 2) and 2 (plots 3, 4, and 5) separate intra-camp along this PC. The plots in camps 3 (plots 6 and 7) and 4 (plots 8 and 9) show neater profiling than those plots in camp 1 (plots 1 and 2) and 2 (plots 3, 4, and 5). The soil chemical attributes of each plot in both seasons were very similar, with the dry season and rainy season version of each plot clustering close together. The plots situated on different camps cluster in different quadrants of the PCA, with the exception of plots in camp 2, with plots 3 and 4 clustering,

and plot 5 separate.

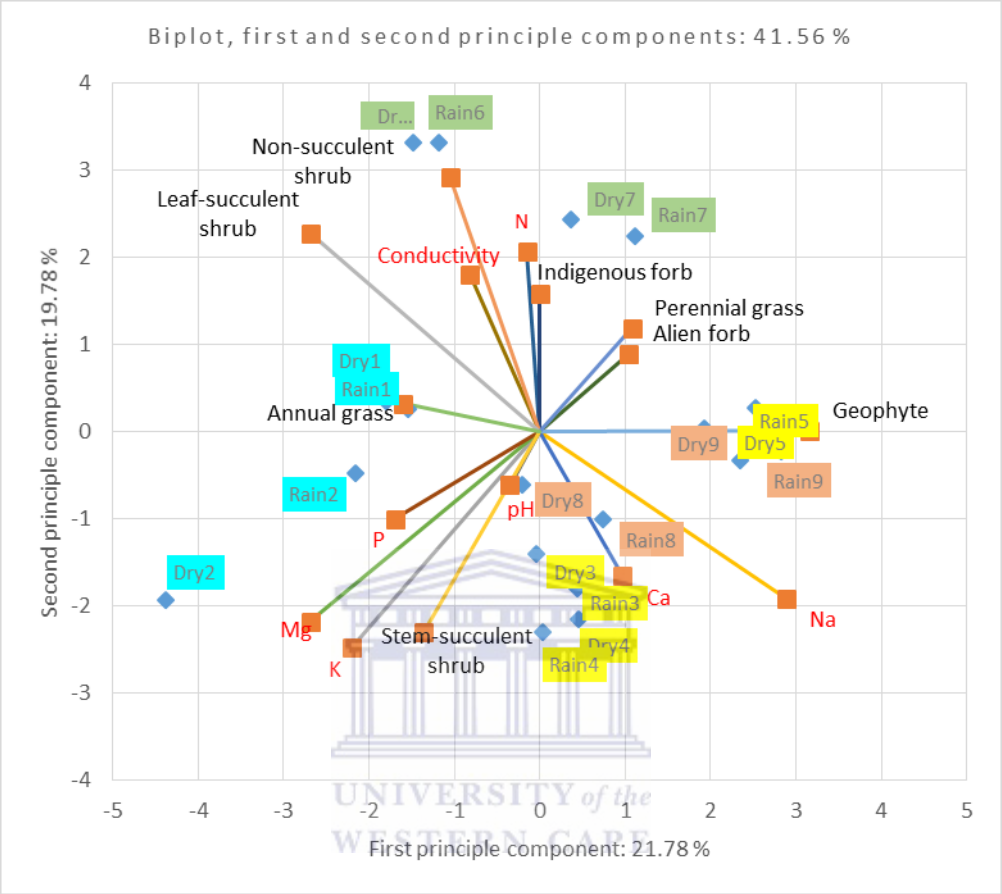

Figure 6.3 PCA showing plant species richness per plot in the different plant growth form categories, and soil chemical measures in both dry and rainy seasons. Plots are numbered, and coloured according to camps (camp 1=aqua, camp 2=yellow, camp 3=green, camp 4=apricot).

6.3.2.2 Plant cover and soil chemical attributes, both seasons

The Pearson correlation matrix of cover of the different plant growth form categories and soil chemical parameters sampled over both seasons (not shown) displayed many significant (α=0.05) correlations between variables, but the highest correlations between plant cover categories and soil chemical parameters include: perennial grass and conductivity (+0,707), rock and pH (-0,687),

perennial grass and nitrogen (+0,677) and biological soil crust and pH (-0,612), and annual grass and sodium (-0,618).

The PCA depicting plant cover in the various study plots and the soil chemical profiles for both the dry and rainy seasons is shown in Figure 6.4. Plots are numbered, and coloured according to camps. The PCA explains 50.86 % of the variation found among the study plots, which is higher than the PCA depicting plant species richness and soil chemical attributes (Figure 6.4).

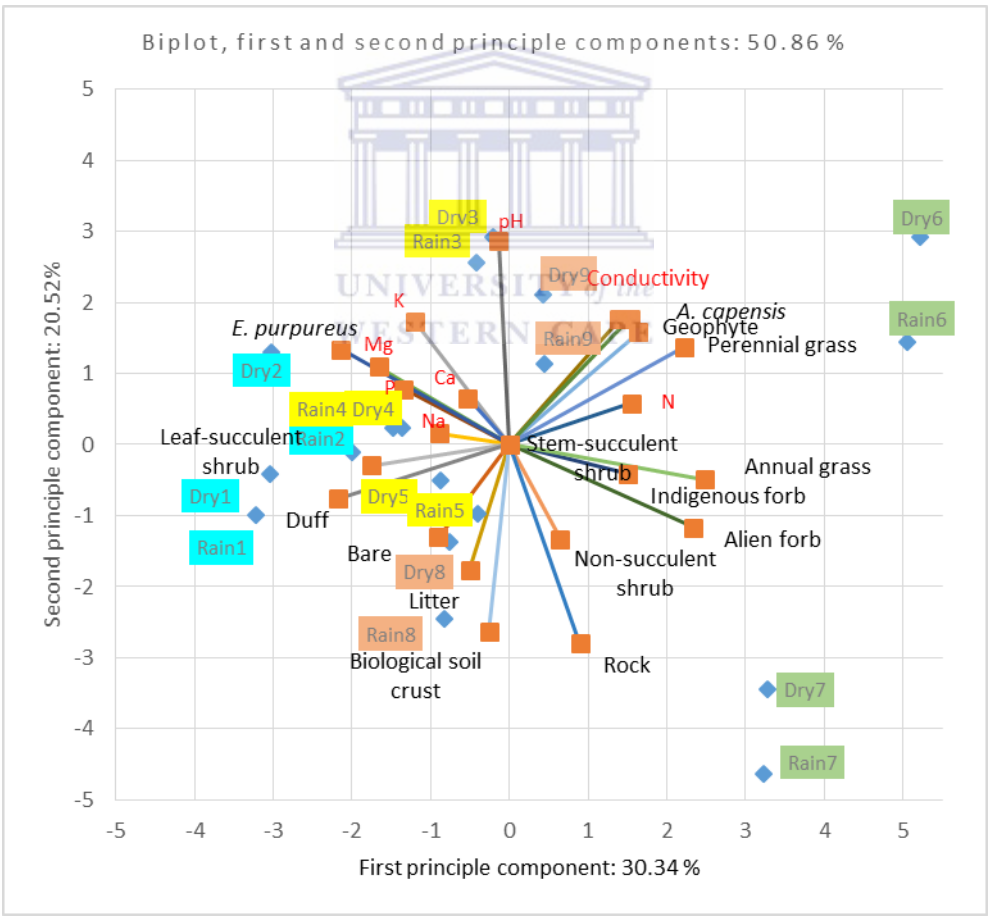

Figure 6.4 PCA depicting plant cover in the various study plots and the soil chemical profiles for both the dry and rainy seasons. Plots are numbered, and coloured according to camp (camp 1=aqua, camp 2=yellow, camp 3=green, camp 4=apricot).

The variables with the strongest eigenvectors on the first PC are annual grass (+0,351), alien forbs (+0,330), perennial grass (+0,314), duff (-0,309) and *E. purpureus* (-0,303). The plots all show neat profiling, and are distinguished by camp along the first PC (x-axis). Furthermore, the plots are distinguished on the first PC according to high N readings and cover of many plant growth form categories on the one side; and high readings of soil chemical elements Mg, K, P, Ca and Na, and cover of leaf-succulent shrubs and *E. purpureus*, on the other.

The variables with the strongest eigenvectors on the second PC are pH (+0,405), rock (-0,396) and biological soil crust (-0,373). The second PC mainly separated plots with higher cover of rock and biological soil crust from those that had higher pH readings, and the plots separated out intra-camp along this PC. The soil chemical attributes of each plot in both seasons were very similar, with the dry season and rainy season version of each plot clustering close together.

UNIVERSITY of the
WESTERN CAPE

6.3.3 Vegetation and all soil parameters

Figure 6.5 shows a partial least square (PLS) regression correlation loading plot showing soil (chemical and microbial; AWCD) as independent variables (x) and plant variables (diversity and cover) as dependent variables (y). Observations (Obs) are written in green, but the plots are coloured according to camp as before. The PLFA and FDA variables were excluded, as they were only taken in the rainy season. The plots cluster according to camp, and are associated with cover and species richness of different plant growth form categories, as well as

soil (chemical and microbial) variables.

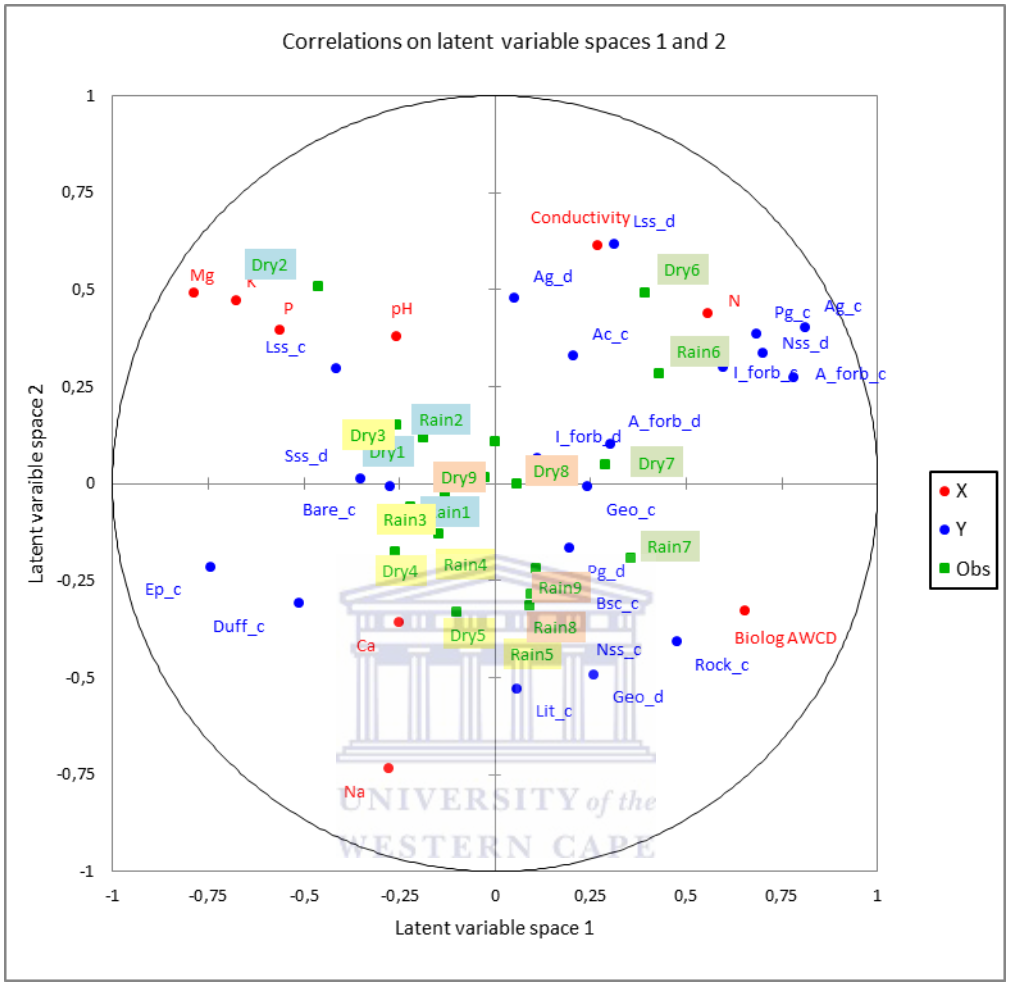

Figure 6.5 Partial least square regression (PLS) correlation loading plot showing soil (chemical and microbial; AWCD) as predictor variables (x, red) and plant variables (diversity and cover) as dependent variables (y, blue). Observations (Obs) are shown in green, but the plots are coloured according to camp as before (camp 1=aqua, camp 2=yellow, camp 3=green, camp 4=apricot).

6.4 Discussion

The results show covariance between plant species richness within and cover of different plant growth form categories, and soil microbial community characteristics. The hypothesis, that different patches of *E. purpureus*-

dominated Nieuwoudtville Shale Renosterveld are similar in terms of aboveground and belowground biological measures: plant species richness, vegetation cover, and soil microbial and chemical profiles, is rejected.

Bardgett and Wardle (2010) found consensus in over 300 studies that plant diversity does not affect soil organisms. But Eisenhauer *et al*. (2011, 2013) found that increased plant diversity in terms of species and functional group richness had a positive effect on the density and diversity of soil organisms (soil microorganisms, microarthropods and nematodes). It was shown in Chapter 4 that the differences in terms of overall plant species richness among the study plots were not significant, though the different study plots differed in plant species richness in terms of different plant growth form categories. In this chapter, the microbial parameters are associated with this variation in plant species richness when allocated to the different plant growth form categories.

UNIVERSITY of the
WESTERN CAPE

Zak *et al*. (2003) related an increase in soil microbial biomass as measured by total PLFA to increased plant production associated with an increase in plant species richness, and not an increase in diversity *per se.* Plant species effects that alter ecosystem processes, such as nutrient cycling, may differ from season to season. Biogeochemical cycling is affected by plant species traits through direct and indirect influences, and these influences are altered by the seasons (Eviner *et al*., 2006).

The vegetation in the rainy and dry seasons could be classified as two differing

systems, i.e. high- and low-productivity respectively. Renosterveld in winter and spring hosts fast-growing, short-lived, fast-decomposing plant species, e.g. annual forb *Senecio cakilefolius*, but the vegetation that remains in the hot dry summer months and through autumn until the rains start consist of slow-growing, long-lived, slow-decomposing perennials, mostly shrubs.

In a study of fynbos and renosterveld plant species, Bengtsson *et al*. (2011) found differences in litter decomposition rates among litter from three different plant species. Their study concurs with previous studies where plant species effects on soil microbial communities can be observed (Saetre and Bååth, 2000; Ettema and Wardle, 2002). On a small-patch scale, these effects were mostly related to plant growth (Ettema and Wardle, 2002), but also to the quality of soil organic matter (Saetre and Bååth, 2000), which is related to both above- and belowground plant inputs, e.g. litter and root exudates respectively, into the soil. These authors found no support for the home field advantage (HFA) theory, ie. soil communities are adjusted to decompose litter that they most often contend with (Ayres *et al*., 2009a, 2009b). A more diverse plant community generates more diverse litter for return to the soil, and specialised use of resources by soil organisms contributes to niche partitioning, maintaining soil microbial diversity (Hooper *et al.* 2000).

UNIVERSITY of the
WESTERN CAPE

Active and growing microbes may be more vulnerable to water stress (Williams, 2007). The largest part of the microbial community may be inactive at any one time, which protects them against environmental stress (Chen and Alexander,

1973). Inactive microbes can survive inhospitable conditions by forming cysts and spores (Lavelle and Spain, 2001) until they improve, tolerating austere conditions (Bardgett, 2005). Plots with more diverse non-succulent and leaf-succulent shrub components measured higher microbial biomass (total PLFA) in the rainy season, and higher potential bacterial metabolic functioning (AWCD) in both seasons, while plots with a more diverse geophyte component showed higher microbial enzyme activity (FDA). The increased diversity in the non-succulent and leaf-succulent shrub component may offer more varied, and better (increased shading, less evaporation, lower temperatures, and less temperature fluctuations) soil conditions providing a refuge for the soil microbial community, although *cover* of these plant growth form categories are not significantly correlated to the microbial measures. The 'fertile island effect' (Noy-Meir, 1985) is a function of both shrub size and age, thus this effect differs according to the shrub component present, creating patchiness in vegetation and soils at a range of spatial scales (Throop and Archer, 2008).

UNIVERSITY of the
WESTERN CAPE

In a global study on natural dryland ecosystems, Maestre *et al*. (2012) related abiotic factors and plant species richness to multifunctionality, referring to functions such as carbon storage, nutrient cycling and productivity. These ecosystem functions are linked to a healthy soil microbial community (Wall *et al.,* 2010). In drylands, plant species richness of perennial plants show a positive and significant relationship to multifunctionality (Maestre *et al*., 2012). The authors suggest that plant species richness offers a buffering against the negative effects of climate change and desertification. An increase in plant diversity has a

beneficial impact on ecosystem function, as measured by soil respiration, water infiltration capacity, compaction, and enzyme activity related to the carbon, nitrogen and phosphorus cycles (Maestre *et al*., 2012).

In the PCA showing the soil microbiological data and cover of the various plant growth form categories (Figure 6.2), variation is better explained (60.39 %) than in the PCA depicting plant species richness and soil microbiological profiles (Figure 6.1), and there is stronger profiling of the study plots according to camp on the first PC. However, the variables that carry the highest eigenvalues are all plant growth form categories, and not soil microbial variables. This points to tighter co-variance between plant species richness within the different plant growth form categories to soil microbial parameters, compared to cover of plants allocated to the different plant growth form categories.

UNIVERSITY of the
WESTERN CAPE

Although the various measures of soil biological activity were spread over three quadrants of the PCA, they were associated with cover of different plant growth form categories. High microbial enzyme activity (FDA) and cover of *E. purpureus* cover were associated, high microbial biomass (total PLFA) was associated with increased cover of perennial grass, geophytes and *A. capensis*, and high potential bacterial metabolic functioning (AWCD) was associated with cover of rock and non-succulent shrubs.

This suggests that the shrub canopies may cast valuable shade in the dry summer, thus creating a refuge for soil microbes by protecting the soil from losing moisture. The perennial presence of vegetation (e.g. shrubs) buffers the

physical stress of soils through the wet/dry cycles (Van Bruggen and Semenov, 2000) and where vegetation becomes sparser in cover, abiotic factors supersede biotic factors in their effect on soil parameters (Bardgett, 2005; Delgado-Baquerizo *et al*., 2013). Shrubs moderate ecosystem services, micro-climate, reduce erosion and nutrient loss, increase soil water-holding capacity, maintain the structure of the soil, offering a habitat for numerous organisms (Peters *et al*., 2006).

In the PCA depicting plant species richness and soil microbial measures (Figure 6.1), plots were distinguished on the basis of those that hosted annual (alien) grass and alien forbs, and which were associated with high potential bacterial metabolic functioning in the rainy season, and the other plots, which only hosted perennial (indigenous) grass species. The only annual grass species found at the study sites was *Avena fatua*, a palatable alien grass. The perennial grass species found were both palatable and indigenous; *Chaetobromus dregeanus* and *Ehrharta calycina*. *A. fatua* loaded heavily (+0,808) on the second PC, clearly separating out the plots on which it was found: 2, 3, 4, 6 and 7. Perennial grass species were found on all plots, which accounts for the lower factor loading (-0,639) that this variable has on the second PC.

Annual and perennial grass favour the same habitats (Van Rooyen, 2003), but the results show clear separation among plots on the basis of the presence or absence of *A. fatua*. The reason for this is unclear, but Steenwerth *et al*. (2002) found in a Californian study that alien grasses are associated with a unique

microbial community, and it has been shown that invasive alien plants, such as alien grasses, can alter the composition of the soil microbial community (Klironomos, 2002; Duda *et al*., 2003; Mele and Crowley, 2008). Todd (2008) ascribed the presence of alien grass around Nieuwoudtville to current and historical disturbances. The plots on camp 3 (plots 6 and 7) may be more susceptible to disturbance from surrounding croplands and pastures, as they have the highest fragmentation level of all plots, though they are not subjected to heavy grazing. Plots 3 and 4 are situated in the camp where livestock has been excluded for the previous five years, though they are situated closer to the homestead, and a historical water point, compared to plot 5, situated in the same camp (2). Plot 2 is situated in the camp which is subjected to the longest stocking period, and is in a more sheltered position compared to plot 1 on the same camp (1).

UNIVERSITY of the
WESTERN CAPE

The Pearson correlation matrix of cover of plant growth form categories and soil microbial parameters showed significant negative correlations between cover of *E. purpureus*, and the AWCD results in both dry (-0,786) and rainy (-0,701) seasons. The relative dominance of the dominant plant species, i.e. *E. purpureus*, is negatively correlated with potential bacterial metabolic functioning in the rhizosphere of the dominant shrub. This links with the PCA depicting plant species richness and soil microbial community data (Figure 6.1), where high species richness within the category non-succulent shrubs was correlated with a high potential bacterial metabolic functioning in the dry season. In Chapter 4, it was shown how the cover of *E. purpureus* and other non-succulent shrub species

loaded oppositely on both the first and second PCs of the PCA (Figure 4.2), showing that plots varied in terms of relative cover of *E. purpureus* and other species of non-succulent shrubs. Woody plant diversity may affect the decomposer food web in that litter composition differs between plant species, and require differing decomposer guilds to transform it (Hanson *et al*., 2008; Ayres *et al*., 2009b). A high diversity of woody plant species would thus contribute to a more diverse decomposer community.

The dotted vertical line on the PCA depicting cover of the various plant growth form categories and soil microbial measures shown in Figure 6.2 separates the four plots that measured high potential bacterial metabolic functioning in the dry season (plots 5, 6, 7 and 8) from those that measured extremely low. The plots that measured low potential bacterial metabolic functioning in the dry season are also those that were more strongly associated with high enzyme activity (in the rainy season), and cover of *E. purpureus*. This result also points to functionally differing soil microbial communities among the different study plots.

UNIVERSITY of the
WESTERN CAPE

Although enzyme activity was associated with cover of *E. purpureus*, potential bacterial metabolic functioning was associated with cover of other species of non-succulent shrubs. In proposing an alternate decomposition model, Fontaine and Barot (2005) emphasise that the quantity of enzymes is the limiting factor for the decomposition rate of recalcitrant litter, and not the quantity of substrate available. This may indicate that *E. purpureus*-rhizosphere soil microbial communities in renosterveld patches with increased relative dominance of *E.*

purpureus produce more enzymes, and are therefore more efficient in decomposing litter produced by *E. purpureus*. Despite this model, these authors emphasise that the presence of several microbial types, i.e. high diversity (as measured by, for example, Biolog carbon-source , and the fingerprint of individual PLFA's) is critical for primary productivity and sound ecosystem functioning. The three soil microbial measures, and their varying associations with plant growth form categories in terms of both plant species richness and cover may then point to enzymatic activity depending more on plant community characteristics, and not the microbial community in the rhizosphere soil of the dominant plant, *E. purpureus*.

UNIVERSITY of the
WESTERN CAPE

Patterns of soil biodiversity are related to the spatial patterns of vegetation in semi-arid ecosystems (Bardgett, 2005), which are characteristically patchy in these resource-limited ecosystems (Noy-Meir, 1985; Peters *et al*., 2006). The diversity of soil biota is dictated to a large degree by effects modulated by plants, e.g. plant-derived organic matter (quality and quantity), and disturbances. Livestock preferentially graze certain plants, and the soil community below palatable plants may be more affected than those that are less palatable. The soil samples in this study were all taken from the rhizosphere of *E. purpureus* individuals, a palatable sub-shrub. The distance from those individuals that were sampled to other plants, and their identities, were not recorded. The influence of plant species diversity on belowground biota in the vicinity of a dominant plant species has been shown, and constitutes an alternative paradigm to accepted belowground community ecology (Bliss *et al*., 2010). Other studies have shown

that the relative dominance of a dominant plant species is the most important factor influencing the soil biotic community (De Deyn *et al*., 2004; Viketoft *et al*, 2005; Bezemer *et al*., 2010).

The direct presence, and identity of, litter under the shrub canopy was not recorded, although little litter was observed underneath the shrub canopy of *E. purpureus* individuals in general (personal observation). Litter was only recorded if it was a canopy-strike on the 50 m-transect. The relative cover of duff and litter, which is associated with soil organic matter (SOM), as this is the available plant material that breaks down and becomes available to the soil food web (Peters *et al*., 2006; Smith *et al*., 2012), is in the PCA-quadrant where *none* of the soil microbiological measures appear. The cover of litter has a strong loading on the second PC (y-axis) in Figure 6.2, but plots separate within camps on this component, except camp 1 (plots 1 and 2), which emphasises the fact that camps display spatial heterogeneity and are grazed heterogeneously (Lyford *et al*., 2003).

UNIVERSITY of the
WESTERN CAPE

An increase in grazing intensity is associated with a decrease in relative cover of litter, and an increase in bare patches (Northup *et al*., 2005; Fernandez *et al*, 2008; Schmalz *et al*., 2013). In this study however there was no significant relationship (in the Pearson correlation matrix), nor close association in the PCA between bare ground and all soil microbial parameters. The factor loading for the category bare was -0,281 for the first PC and +0,327 for the second PC, indicating that it did not have a strong influence on the amount of variability

found among study plots, compared to other factors. The plant surveys were conducted in spring, when most plant species are present in renosterveld. Indigenous and alien forbs, annual grasses and geophytes all disappear from late-spring onwards, only starting to appear again in early autumn, when the first rains start.

The management measure in this study, stocking regime, is inadequate to account for the differences found in this study that are possibly related to grazing disturbances. Camps are grazed heterogeneously, as livestock graze selectively, and semi-arid areas are typically heterogeneous (Smith *et al*., 2012). Grazing affects both plant cover and diversity (Midgley *et al*., 2010). Grazing affects the litter input into the soil, as species preferred by grazers (palatable, non-woody) are consumed, and other species (woody, unpalatable, or toxic) are left to become litter (Díaz *et al*., 2007). With an increase in grazing intensity, or even at moderate grazing intensities, litter diminishes (Peters *et al*., 2006; Smith *et al*., 2012).

UNIVERSITY of the
WESTERN CAPE

Cover of rock and biological soil crust were negatively associated with high pH (Figure 6.4). Biological soil crusts exude organic acids, which facilitates the weathering of rock (Belnap, 2003). This may explain the lower pH (i.e. higher acidity) in those plots that had higher cover of rock and biological soil crusts.

The varied nature of the vegetation as well as soil characteristics were supported by the PLS correlation loading plot shown in Figure 6.5. The variability and

heterogeneity of Nieuwoudtville Shale Renosterveld is illustrated through the association of study plots with different soil and vegetation factors, supporting the conservation of all fragments of remaining untransformed renosterveld, as they are not uniform.

Porazinska *et al*. (2003) noted that relationships between biotic and abiotic soil variables, and plant community traits showed no clear patterns. Bardgett (2005) emphasised that generalisations about complex interactions are misguided, as idiosyncratic effects can be seen in plant and soil biotic communities. Plant community composition affects the decomposer food web, including the soil microbial community, but it appears that these effects are context-dependent (Wardle *et al*., 2004). Berg (2012) points out that the drivers affecting soil organism diversity differ in their spatio-temporal aspects, and that the spatial scales are nested, i.e. global (e.g. climate), landscape (topography), plot and individual (chemical heterogeneity). Interactions amongst these drivers are complicated due to the different scales and time-frames in which they operate.

UNIVERSITY of the
WESTERN CAPE

6.5 Conclusion

The focus in this study was on the first level of the two food webs, production and decomposition, involved in nutrient cycling in *Eriocephalus purpureus*-dominated Nieuwoudtville Shale Renosterveld used as extensive rangelands. The vegetation, soil chemical characteristics, and the rhizosphere soil microbial community were assessed, in order to glean how aboveground and belowground

phenomena relate to one another (Wall *et al*., 2010; Sylvain and Wall, 2011).

The findings show that vegetation communities, soil chemical characteristics, and soil microbial communities differ among sites, and are site-specific, though there were some similarities within camps. The soil microbial parameters displayed different associations with plant species richness and cover of the various plant growth form categories. Plots with higher cover of non-succulent shrubs measured higher potential bacterial metabolic functioning, while plots with higher *E. purpureus* cover showed more microbial enzyme activity. Plots with high cover of perennial grass and *A. capensis* (a monocotyledon shrub), and geophytes (mostly monocotyledon) showed overall higher measures of soil microbial biomass. The identification of soil biological 'hotspots', which are responsible for providing the bulk of soil-based ecosystem services, should be integrated in local landscape knowledge (Barrios, 2007). Native plants as indicators of soil health is a key tool for decision making in farming landscapes in South America and Africa (Barrios *et al*., 2006). This would be an appropriate addition to the management toolbox of farmers and land managers of the remaining fragments of renosterveld.

UNIVERSITY of the
WESTERN CAPE

Overall high measures of mineral elements magnesium, potassium, phosphate, calcium and sodium were associated with high cover of *E. purpureus*, and plots that associated strongly with these variables were distinguished (on the PCA in Figure 6.4) from those plots that showed high readings of nitrogen and were associated with high cover of annual and perennial grass. These results show that

soil chemical attributes do play a role in plant community composition.

A recommendation for future studies would be to take multiple samples over a period, including dry and rainy seasons, and then assessing patterns that emerge (if any) of how the different measures relate to one another, as well as to their environment.

Plants, symbionts, decomposers and herbivores interact at different trophic levels to maintain a dynamic balance (Swift *et al*., 2004). The patterns and relationships found may all be important, as the numerous factors and idiosyncratic responses (Bardgett, 2005) of the biotic communities confer resilience on the vegetation type, as well as the agro-ecological matrix in which it is embedded. Since it was found that the different fragments of Nieuwoudtville Shale Renosterveld harbour differing soil microbial communities, the importance of conserving *all*, including the smallest, fragments is emphasised, supporting recommendations of previous studies (e.g. Kemper *et al*., 1999). Soil biota not only regulate organic matter turnover and nutrient cycling, they affect (positively or negatively) vegetation change in terms of biodiversity and productivity (Bardgett, 2005), and aboveground and belowground interactions affect both the rate and direction of vegetation change (Van der Putten *et al*., 2009). Heneghan *et al*. (2008) suggest that enriched soil ecological knowledge may be needed to restore complex interactions post-disturbance. Natural renosterveld fragments are not just repositories for plant species but also for the microbial species that live belowground. Re-inoculation of beneficial microbes

UNIVERSITY of the
WESTERN CAPE

is a way to revitalise and rehabilitate soil (Rowe *et al*., 2009). In this context, soil heterogeneity is important, providing refugia for the recolonization of soil biota.

The study context was completely realistic (*sensu* Provenza *et al*., 2013), with a complete lack of control of all variables, and thus the aim was to describe what was found, and to point out any potentially significant relationships. As the parameters measured in this study represent biological components at different spatial scales and organisation levels (Noss, 1996; Pence, 2008), the results underline the fact that the relationship between a landscape and the organisms that inhabit it is reciprocal, with all 'components' reliant on each other for continual and concurrent change and adaptation (Pringle and Tinley, 2003).

UNIVERSITY of the
WESTERN CAPE

Chapter 7 Summary

The aim of this study, to assess the vegetation and soil chemical and microbial characteristics of semi-arid renosterveld rangelands, was achieved.

The vegetation survey showed that despite no significant difference in overall plant species richness among the study plots, the study plots differed in terms of plant species richness within, and cover of, the various plant growth form categories.

Soil chemical profiles differed significantly among the study plots. Potential bacterial metabolic functioning differed between the dry and rainy seasons, but study plots with lower potential bacterial metabolic functioning showed high potential bacterial metabolic functioning in the rainy season, indicating seasonal resilience.

UNIVERSITY of the
WESTERN CAPE

Soil microbial parameters co-varied with cover of different perennial plant growth form categories, but the three soil microbial analyses did not support one another, indicating that a further, more detailed investigation into the soil microbial ecology of *Eriocephalus purpureus*-dominated Nieuwoudtville Shale Renosterveld is warranted.

7.1 Management implications and recommendations

Farmers should continue to benefit from utilizing Nieuwoudtville Shale Renosterveld as natural forage for grazing sheep. The results support the conservation of all fragments of remaining renosterveld, as the study plots differed in all parameters measured, and may serve as valuable resources of not only plant genetic material but also soil microbial communities for any future rehabilitation or restoration efforts.

7.2 Further research/lessons learnt

The extreme dryness of the soil in the dry season sampling made it impossible to collect enough soil to conduct all the planned-for analyses. It would be recommended to sample right after the first rain, at the start of the rainy season, and again at the end of the rainy season, although this may make field work difficult to plan.

UNIVERSITY of the
WESTERN CAPE

Not all historical stocking data were obtainable from all landowners/managers, and it was not possible to find a statistically significant amount of sites subjected to different stocking regimes. Future studies would be enlightening if sites were chosen along a stocking gradient. Furthermore, taking the grazing effects, e.g. the physical defoliation, trampling, urination and dunging, into account may shed light on the variable results obtained.

Chapter 8 References

Allen, S.E., Grimshaw, H.M., Rowland, AP., 1986. Chemistry analysis, in: Moore, P.D., Chapman, S.B. (Eds.), Methods in Plant Ecology, second ed. Blackwell Scientific Publications, London, pp. 302-303, 331-332.

Allen, V.G., Batello, C., Berretta, E.J., Hodgson, J.M., Kothmann, M., Li, X., McIvor, J., Milne, J., Morris, C., Peeters A., Sanderson M., 2011. An international terminology for grazing lands and grazing animals. Grass and Forage Science 66, 2-28.

Altieri, M.A., 1999. The ecological role of biodiversity in agroecosystems. Agriculture, Ecosystems and Environment 74, 19-31.

UNIVERSITY of the
WESTERN CAPE

Amacher, M.C., O'Neill, K.P., Perry, C.H., 2007. Soil Vital Signs: A new soil quality index (SQI) for assessing forest soil health. USDA Forest Service Research Paper, RMRS-RP-65WWW. Rocky Mountain Research Station.

Anderson, P.M.L., Hoffman, M.T., 2007. The impacts of sustained heavy grazing on plant diversity and composition in lowland and upland habitats across the Kamiesberg mountain range in the Succulent Karoo, South Africa. Journal of Arid Environments 70, 686-700.

Antunes, P.M., Franken, P. Schwarz, D., Rillig, M.C., Cosme, M., Scott, M.,

Hart, M.M., 2012. Linking soil biodiversity and human health: Do Arbuscular Mycorrhizal Fungi Contribute to Food Nutrition? in: Wall, D.H., Bardgett, R.D., Behan-Pelletier, V., Herrick, J.E., Hefin Jones, T., Ritz, K., Six, J., Strong, D.R., Van der Putten, W.H. (Eds.), Soil Ecology and Ecosystem Services. Oxford University Press. Oxford, pp. 153-172.

Archer, E.R.M., 2004. Beyond the "climate versus grazing" impasse: using remote sensing to investigate the effects of grazing system choice on vegetation cover in the eastern Karoo. Journal of Arid Environments 7, 381-408.

Aseri, G.K., Tarafdar, J.C., 2006. Fluorescein Diacetate: A potential biological indicator for arid soils. Arid Land Research and Management 20(2), 87-99.

UNIVERSITY of the
WESTERN CAPE

Asner, G.P., Archer, S.R., 2010. Livestock and the global carbon cycle, in: Steinfeld, H., Mooney, H., Schneider, F., Neville, L. (Eds.), Livestock in a changing landscape: drivers, consequences, and responses. Island Press, Washington, D.C., pp. 69-82.

Atlas, R.M. and Bartha, R., 1993. Microbial Ecology: fundamentals and applications, third ed. Benjamin Cummings Publishing Company, Redwood City.

Augustine, D.J., Frank, D.A., 2001. Effects of migratory ungulates on spatial heterogeneity of soil nitrogen properties on a grassland ecosystem. Ecology 82,

3149-3162.

Austin, A.T., Yahdjian, L., Stark, J.M., Belnap, J., Porporato, A, Norton, U., Ravetta, D.A, Schaeffer, S.M., 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141, 221–235. Doi: 10.1007/s00442-004-1519-1.

Ayres, E., Heath, J., Possell, M., Black, H.I.J., Kerstiens, G., Bardgett, R.D., 2004. Tree physiological responses to above-ground herbivory directly modify below-ground processes of soil carbon and nitrogen cycling. Ecology Letters 7,469-479.

Ayres, E., Steltzer, H., Berg, S., Wall, D.H., 2009a. Soil biota accelerate decomposition in high-elevation forests by specializing in the breakdown of litter produced by the plant species above them. Journal of Ecology 97, 901-912.

Ayres, E., Steltzer, H., Simmons, B.L., Simpson, R.T., Steinweg, J.M., Wallenstein, M.D., Mellor, N., Parton, W.J., Moore, J.C., Wall, D.H., 2009b. Home-field advantage accelerates leaf litter decomposition in forests. Soil Biology and Biochemistry 41, 606-610.

Bååth, E., Anderson, T.-H., 2003. Comparison of soil fungal/bacterial ratios in a pH gradient using physiological and PLFA-based techniques. Soil Biology and Biochemistry 35, 955-963.

UNIVERSITY of the
WESTERN CAPE

Babbar, L.I., 1993. Nitrogen cycling in shaded and unshaded coffee plantations in the Central Valley of Costa Rica. PhD thesis, University of Michigan.

Bais H.P., Weir, T.L., Perry, L.G., Gilroy, S., Vivanco, J.M., 2006. The role of root exudates in rhizosphere interactions with plants and other organisms. Annual Review of Plant Biology 57, 233-266.

Bardgett, R.D., 2005. The Biology of Soil: A community and ecosystem approach. Oxford University Press, Oxford.

Bardgett, R.D., 2005. The Biology of Soil: A Community and Ecosystem Approach. Oxford University Press, Oxford.

UNIVERSITY of the
WESTERN CAPE

Bardgett, R.D., Chan, K.F., 1999. Experimental evidence that soil fauna enhance nutrient mineralization and plant uptake in montane grassland ecosystems. Soil Biology and Biochemistry 31, 1007-1014.

Bardgett, R.D., Jones, A.C., Jones, D.L., Kemmitt, S.J., Cook, R., Hobbs, P.J., 2001. Soil microbial community patterns related to the history and intensity of grazing in sub-montane ecosystems. Soil Biology and Biochemistry 33, 1653-1664.

Bardgett, R.D., Leemans, K.K., Cook, R., Hobbs, P.J., 1997. Seasonality of the

soil biota of grazed and ungrazed hill grasslands. Soil Biology and Biochemistry 29, 1285-1294.

Bardgett, R.D., McAllister, E., 1999. The measurement of soil fungal: bacterial biomass ratios as an indicator of ecosystem self-regulation in temperate meadow grasslands. Biology and Fertility of Soils 29, 282-290.

Bardgett, R.D., Wardle, D.A., 2003. Herbivore mediated linkages between aboveground and belowground communities. Ecology 84, 2258-2268.

Bardgett, R.D., Wardle, D.A., 2010. Aboveground–belowground linkages, biotic interactions, ecosystem processes, and global change. Oxford University Press, New York.

UNIVERSITY of the
WESTERN CAPE

Bardgett, R.D., Wardle, D.A., Yeates, G.W., 1998. Linking above-ground and belowground food webs: how plant responses to foliar herbivory influence soil organisms. Soil Biology and Biochemistry 30, 1067-1078.

Barrett, J.E., Virginia, R.A., Wall, D.H., Cary, S.C., Adams, B.J., Hacker, A.L., Aislabie, J.M., 2006. Co-variation in soil biodiversity and biogeochemistry in northern and southern Victoria Land, Antarctica. Antarctic Science 18(4), 535-548.

Barrett, J.E., Virginia, R.A., Lyons, W.B., McKnight, D.M., Priscu, J.C., Doran, P.T., Fountain, A.G., Wall, D.H., Moorhead D.L., 2007. Biogeochemical

stoichiometry of Antarctic Dry Valley ecosystems, Journal of Geophysical Research 112, G01010. Doi: 10.1029/2005JG000141.

Barrios, E., 2007. Soil biota, ecosystem services and land productivity. Ecological Economics 64, 269-285.

Barrios, E., Delve, R.J., Bekunda, M., Mowo, J., Agunda, J., Ramisch, J., Trejo, M.T., Thomas, R.J., 2006. Indicators of soil quality: A South-South development of a methodological guide for linking local and technical knowledge. Geoderma 135, 248-259.

Beare, M.H., Coleman, D.C., Crossley Jr, D.A., Hendrix, P.F., Odum, E.P., 1995. A hierarchical approach to evaluating the significance of soil biodiversity to biogeochemical cycling. Plant and Soil 170, 5-22.

Behnke, R.H., Scoones, I., 1993. Rethinking range ecology: Implications for rangeland management in Africa, in: Behnke R.H., Scoones I., Kerven, C. (Eds.), Range Ecology at Equilibrium and Dis-equilibruim. New models for natural variability and pastoral adaptation in African Savannas. Overseas Development Institute, London.

Belnap, J. 2003. The world at your feet: desert biological soil crusts. Frontiers in Ecology and the Environment 1, 181-189.

UNIVERSITY of the
WESTERN CAPE

Belnap, J. 2006. The potential roles of biological soil crusts in dryland hydrologic cycles. Hydrological Processes 20, 3159-3178.

Belnap, J., Eldridge, D.J., 2001. Disturbance and recovery of biological soil crusts, in: Belnap, J., Lange, O.L. (Eds.), Biological soil crusts: structure, function and management. Springer, Berlin, pp. 363-383.

Bending, G.D., Turner, M.K., Rayns, F., Marx, M.C., Wood, M., 2004. Microbial and biochemical soil quality indicators and their potential for differentiating areas under contrasting agricultural management regimes. Soil Biology and Biochemistry 36, 1785-1792.

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F., Nystrom, M., 2003. Reserves, resilience, and dynamic landscapes. Ambio 32, 389-396.

Bengtsson, J., Janion, C., Chown, S.L., Leinaas, H.P., 2011. Variation in decomposition rates in the fynbos biome, South Africa: the role of plant species and plant stoichiometry. Oecologia 165(1), 225-235.

Berendsen, R.L., Pieterse, C.M.J., Bakker, P.A.H.M. 2012.The rhizosphere microbiome and plant health. Trends in Plant Science 17(8), 478-486.

Berg, G., Smalla, K., 2009. Plant species and soil type cooperatively shape the

UNIVERSITY of the
WESTERN CAPE

structure and function of microbial communities in the rhizosphere. FEMS Microbiology Ecology 68, 1-13.

Berg, M.P., 2012. Patterns of biodiversity at fine and small spatial scales, in: Wall, D.H., Bardgett, R.D., Behan-Pelletier, V., Herrick, J.E., Hefin Jones, T., Ritz, K., Six, J., Strong, D.R., Van der Putten, W.H. (Eds.), Soil Ecology and Ecosystem Services. Oxford University Press. Oxford, pp. 136-152.

Berg, M.P., Bengtsson, J., 2007. Spatial and temporal variation in food web composition. Oikos 116, 1789-1804.

Bergh, N.G., Verboom, G.A., Rouget, M., Cowling, R.M., 2014.Vegetation types of the Greater Cape Floristic Region, in: Allsopp, N., Colville, J.F., Verboom, G.A. Cowling, G.M. (Eds.), Fynbos: Ecology, Evolution, and Conservation of a Megadiverse Region. Oxford University Press, Oxford, pp. 1-25.

Bertin, C., Yang, X.H., Weston, L.A., 2003. The role of root exudates and allelochemicals in the rhizosphere. Plant and Soil 256, 67-83.

Bezemer, T.M, Fountain, M.T., Barea, J.M., Christensen, S., Dekker, S.C., Duyts, H., Van Hal, R., Harvey, J.A, Hedlund, K., Maraun, Mikola, J.,Madelove, J.G., Robin, C., De Ruiter, P.C., Scheu, S., Setala, H., Milauer, S., Van der Putten, W.H., 2010. Divergent composition but similar function of soil food webs of individual plants: plant species and community effects. Ecology 91(10),

UNIVERSITY of the WESTERN CAPE

3027-3036.

Binning, C.E., Cork, S.J., Parry, R., Sheldon, D., 2001. Natural Assets: An Inventory of Ecosystem Goods and Services in the Goulburn Broken Catchment. CSIRO, Canberra.

Blench, R., Sommer, F., 1999. Understanding rangeland biodiversity. Working Paper 121, London. Available at: http://www.odi.org/sites/odi.org.uk/files/odi-assets/publications-opinion-files/2531.pdf. Date accessed: 20 August 2013.

Bliss, T., Powers, T.O., Brassil, C.E., 2010. The spatial influence of aboveground diversity on belowground communities. Ecosphere 1(2/3), article 7.

UNIVERSITY of the
WESTERN CAPE

Bodelier, P.L., 2011. Toward understanding, managing, and protecting microbial ecosystems. Frontiers in microbiology 2(80), 1-8.

Bond, P., Goldblatt, P., 1984. Plants of the Cape flora. South African Journal of Botany. Supplementary volume 13.

Bond, W. J., 1995. Assessing the risk of plant extinction due to pollinator and disperser failure, in: Lawton, J.H., May, R.M. (Eds.), Extinction rates. Oxford University Press, New York, pp. 131-146.

Born, J., Linder, H.P., Desmet, P., 2007. The Greater Cape Floristic Region. Journal of Biogeography 34(1), 147-162.

Bossio, D.A., Scow, K.M., 1995. Impact of carbon and flooding on the metabolic diversity of microbial communities in soils. Applied and Environmental Microbiology 61, 4043-4050.

Bossio, D.A., Scow, K.M., 1998. Impacts of carbon flooding on soil microbial communities: phospholipid fatty acid profiles and substrate utilization patterns. Microbial Ecology 35, 265-278.

Bossio, D.A., Scow, K.M., Gunapala. N., Graham, K.J. 1998. Determinants of soil microbial communities: effects of agricultural management, season, and soil type on phospholipid fatty acid analysis. Microbial Ecology 36, 1-12.

UNIVERSITY of the
WESTERN CAPE

Boucher C., Moll E.J., 1981. South African mediterranean shrublands, in: Di Castri, F., Goodall, D.W., Specht, R.L. (Eds.), Ecosystems of the World, vol. 11, Mediterranean Type Shrublands. Elsevier, Amsterdam, pp. 233-248.

Boucher, C., 1980. Notes on the use of the term ‘Renosterveld’. Bothalia 13, 237.

Bowker, M.A., Mau, R.L., Maestre, F.T., Escolar, C., Castillo-Monroy, A.P., 2011. Functional profiles reveal unique ecological roles of various biological soil crust organisms. Functional Ecology 25, 787-795.

Bradshaw, P.L., Cowling, R.M., 2014. Landscapes, rock types, and climate of the Greater Cape Floristic Region, in: Allsopp, N., Colville, J.F., Verboom, G.A. Cowling, G.M., (Eds.), Fynbos: Ecology, Evolution, and Conservation of a Megadiverse Region. Oxford University Press, Oxford, pp. 26-46.

Brady, N.C., Weil, R.R., 2002. The soils around us, in: Brady, N.C., Weil, R.R., The Nature and Properties of Soils, 17th ed. Pearson Education, Upper Saddle River, pp. 9-11.

Bragg, C.J., Donaldson, J.D., Ryan, P.G., 2005. Density of Cape porcupines in a semi-arid environment and their impact on soil turnover and related ecosystem processes. Journal of Arid Environments 61, 261-275.

UNIVERSITY of the
WESTERN CAPE

Brand South Africa, 2013. South Africa Information portal on the internet. Available at: http://www.southafrica.info/about/sustainable/biodiversity-050213.htm#.U32hyvmSz9U#ixzz32QSpL9BH. Date accessed: 20 October 2014.

Bromham, L., Cardillo, M., Bennett, A.F., Elgar, M.A., 1999. Effects of stock grazing on the ground invertebrate fauna of woodland remnants. Austalian Journal of Ecology 24, 199-207.

Brussaard, L., 2012. Ecosystem services provided by soil biota, in: Wall, D.H.,

Bardgett, R.D., Behan-Pelletier, V., Herrick, J.E., Hefin Jones, T., Ritz, K., Six, J., Strong, D.R., Van der Putten, W.H. (Eds.), Soil Ecology and Ecosystem Services. Oxford University Press. Oxford, pp. 45-58.

Brussaard, L., Jackson, L., Pulleman, M., Bawa, K., Cardoso, I., Barrios, L.G, Brown, G., Lavelle, P., Ouedraogo, E., Pascual, U., Perrings, C., De Ruiter, P., Tscharntke, T., Van Noordwijk, M. *Sino anno*. Biodiversity in support of sustainable agricultural landscapes and rural livelihoods - the agroBIODIVERSITY research agenda. Poster-pdf. Diversitas. Available from: http://www.diversitas-international.org/activities/research/agrobiodiversity/resources/agroBIODIVERSITYResearchAgendaPoster.pdf. Date accessed: 15 October 2014.

UNIVERSITY of the WESTERN CAPE

Bushaw-Newton, K.L., Ewers, E.C., Velinsky, D.J., Ashley, J.T.F., MacAvoy, S.E., 2012. Bacterial community profiles from sediments of the Anacostia River using metabolic and molecular analyses. Environmental Science and Pollution Research 19(4), 1271-1279. Doi: 10.1007/s11356-011-0656-4.

Campbell, B.M., 1985. A classification of the mountain vegetation of the Fynbos Biome. Memoirs of the Botanical Survey of South Africa 50, 1-21.

Campbell, B.M., Gordon, I.J., Luckert, M.K., Petheram, L., Vetter, S., 2006. In search of optimal stocking regimes in semi-arid grazing lands: One size does not fit all. Ecological Economics 60, 75-85.

Carreiro, M.M., Sinsabaugh, R.L., Repert, D.A., Parkhurst, D.F., 2000. Microbial enzyme shifts explain litter decay responses to simulated nitrogen deposition. Ecology, 81, 2359-2365.

Cebrian, J., 1999. Patterns in the fate of production in plant communities. The American Naturalist 154, 449-468.

Chapin, F.S., Matson, P.A., Mooney, H.A., 2002. Principals of Terrestrial Ecosystem Ecology. Springer Science and Business Media, New York.

Chen, M., Alexander, M., 1973. Survival of soil bacteria during prolonged desiccation. Soil Biology and Biochemistry 5, 213-221.

UNIVERSITY of the
WESTERN CAPE

Chesson, P., Gebauer, R.L., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S.K., Sher, A., Novoplansky, A., Weltzin, J.F., 2004. Resource pulses, species interactions and diversity maintenance in arid and semi-arid environments. Oecologia 141, 236-253. Doi: 10.1007/s00442-004-1551-1.

Coleman, D.C., 2008. From peds to paradoxes: linkages between soil biota and their influences on ecological processes. Soil Biology and Biochemistry 40(2), 271-289.

Conservation Farming Project, 2004. Nieuwoudtville. A Biodiversity 'Hotspot'.

National Botanical Institute, South Africa.

Costa, R., Götz, M., Mrotzek, N., Lottmann, J., Berg, G., Smalla, K., 2006. Effects of site and plant species on rhizosphere community structure as revealed by molecular analysis of microbial guilds. FEMS Microbiology Ecology 56, 236-249.

Cousins, B., 1993. Debating Communal Tenure in Zimbabwe. Journal of Contemporary African Studies 12 (1), 29-39.

Cowling, R.M., 1984. A syntaxonomic and synecological study in the Humansdorp Region of the Fynbos Biome. Bothalia 15, 175-227.

UNIVERSITY of the
WESTERN CAPE

Cowling, R.M., 1990. Diversity components in a species-rich area of the cape floristic region. Journal of Vegetation Science 1, 699-710.

Cowling, R.M., Bond, W.J., 1991. How small can reserves be? An empirical approach in Cape fynbos, South Africa. Biological Conservation 58(3), 243-256.

Cowling, R.M., Esler, K.J., Rundel, P.W., 1999. Special issue editorial: the plant ecology of Namaqualand, South Africa. Plant Ecology 142, 1-2.

Cowling, R.M., Holmes, P.J., Rebelo, A.G., 1992. Plant diversity and endemism, in: Cowling, R.M. (Ed.), The Ecology of Fynbos: Nutrients Fire and Diversity.

Oxford University Press, Cape Town, pp. 62-134.

Cowling, R. M., Pierce, S.M., 1999. Cape Floristic Province, in: Mittermeier, R.A., Myers, N., Mittermeier, C.G. (Eds.), Hotspots. Earth´s biologically richest and threatened terrestrial ecoregions. CEMEX Mexico City and Conservation International, Washingtion DC, pp. 218-227.

Cowling, R.M., Rundel, P.W., Lamont, B.B., Arroyo, M.K., Arianoutsou, M., 1996. Plant diversity in mediterranean-climate regions. TREE 11(9), 362-366.

Cupido, C.F., 2005. Assessment of veld practices and veld condition in the Little Karoo. MSc thesis, University of Stellenbosch.

UNIVERSITY of the
WESTERN CAPE

Curtis, O.E., 2013. Management of Critically Endangered renosterveld fragments in the Overberg, South Africa. PhD thesis, University of Cape Town.

Cyster, L.F., McLaren, P.M., Raitt, L.M., 2010. Plant ecophysiology practicals. Unpublished, University of the Western Cape, Bellville, pp. 25-26.

Dahlberg, A.C., 2000. Vegetation diversity and change in relation to land use, soil and rainfall: a case study from North-East District, Botswana. Journal of Arid Environments 44, 19-40.

Daily, G., 1997. Nature's services: societal dependence on natural ecosystems. Island Press. Washington, DC.

De Deyn, G.B., Raaijmakers, C.E., Van Ruijven, J., Berendse, F., Van der Putten, W.H., 2004. Plant species identity and diversity effects on different trophic levels of nematodes in the soil food web. Oikos 106, 576-586.

De Deyn, G.B., Van Ruijven, J., Raaijmakers, C.E., De Ruiter, P.C., Van der Putten, W.H., 2007. Above- and belowground insect herbivores differentially affect soil nematode communities in species-rich plant communities. Oikos 116, 923-930.

UNIVERSITY of the
WESTERN CAPE

Dean, W.R.J., Hoffman, M.T., Meadows, M.E., Milton, S.J., 1995. Desertification in the semi-arid Karoo, South Africa: review and assessment. Journal of Arid Environments 30, 247-264.

Dean, W.R.J., Macdonald, I.A.W., 1994. Historical changes in stocking rates of domestic livestock as a measure of semi-arid and arid rangeland degradation in the Cape Province, South Africa. Journal of Arid Environments 26, 281-298.

Dean W.R.J., Milton, S.J., Du Plessis, M., Siegfried, W.R., 1995. Dryland Degradation: Symptoms, Stages, and Hypothetical Cures, in: Roundy, B.A., Durant, M.E., Haley, J.S., Mann, D.K. (Eds.), Proceedings: wildland shrub and

arid land restoration symposium, October 19-21 1993, Las Vegas.

Delgado-Baquerizo, M., Maestre, F.T., Gallardo, A., Bowker, M.A., Wallenstein, M.D., Quero, J.L., Ochoa, V., Gozalo, B., García-Gómez, M., Santiago Soliveres, S., García-Palacios, P., Berdugo, M., Valencia, E., Escolar, C., Arredondo, T, Barraza-Zepeda, C., Bran, D., Carreira, J.A., Chaieb, M., Conceição, A.A., Derak, M., Eldridge, D.M., Escudero, A., Espinosa, C.I., Gaitán, J., Gatica, M.G., Susana Gómez-González, S., Guzman , E., Julio R. Gutiérrez, J.R., Florentino, A., Hepper, E., Hernández, R.M., Huber-Sannwald, E., Jankju, M., Liu, J., Mau, R.L., Miriti, M., Monerris, J., Naseri, K., Noumi, Z., Polo, V., Prina, A., Pucheta, E., Ramírez, E., Ramírez-Collantes, D.A., Romão, R., Tighe, M., Torres, D., Torres-Díaz, C., Ungar, E.D., Val, J., Wamiti, W., Wang, D., Zaady, E., 2013. Decoupling of soil nutrient cycles as a function of aridity in global drylands. Nature 502, 672-688.

Derner, J.D., Schuman, G.E., 2007. Carbon sequestration and rangelands: a synthesis of land management and precipitation effects. Journal of Soil and Water Conservation 62, 77-85.

Díaz, S., Lavorel, S., McIntyre, S.U.E., Falczuk, V., Casanoves, F., Milchunas, D.G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W.E.I., Clark, H., Campbell, B.D., 2007. Plant trait responses to grazing - a global synthesis. Global Change Biology 13, 13-341.

UNIVERSITY of the
WESTERN CAPE

Diversitas, 2014. AgroBIODIVERSITY highlights webpage. Available at: http://www.diversitas-international.org/activities/research/agrobiodiversity. Date accessed: 20 October 2014.

Doornbos, R., Van Loon, L.C., Bakker, P.A.H.M., 2012. Impact of root exudates and plant defense signaling on bacterial communities in the rhizosphere. A review. Agronomy for Sustainable Development 32, 227-243.

Doran, J.W., Zeiss, M.R., 2000. Soil health and sustainability: managing the biotic component of soil quality. Applied Soil Ecology 15, 3-11.

Downing, B.H., 1978. Environmental consequences of agricultural expansion in South Africa since 1850. South African Journal of Science 74, 420-422.

UNIVERSITY of the
WESTERN CAPE

Driver, A., Desmet, P.G., Rouget, M., Cowling, R.M., Maze, K.E., 2003. Succulent Karoo ecosystem plan. Cape Conservation Unit, Botanical Society of South Africa, Cape Town.

Du Preez, C.C., Van Huyssteen, C.W., Mnkeni, P.N.S., 2011a. Land use and soil organic matter in South Africa 1: A review on spatial variability and the influence of rangeland stock production. South African Journal of Science, 107(5/6), Art. #354.

Du Preez, C.C., Van Huyssteen, C.W., Mnkeni, P.N.S., 2011b. Land use and soil

organic matter in South Africa 2: A review on the influence of arable crop production. South African Journal of Science, 107(5-6), 35-42.

Du Toit, A.L., 1938. Geological and soil characteristics in relation to deterioration and conservation of natural resources, etc., in the Union. South African Journal of Science 35, 470-476.

Duda, J.J., Freeman, D.C., Emlen, J.M., Belnap, J., Kitchen, S.G., Zak, J.C., Sobek, E., Tracy, M., Montante, J., 2003. Differences in native soil ecology associated with invasion of the exotic annual chenopod, Halogeton glomeratus. Biology and Fertility of Soils 38, 72-77.

Ehrenfeld, J.G, Ravit, B., Elgersma, K., 2005. Feedback in the plant-soil system. Annual Review of Environment and Resources 30, 75-115.

Einhellig, F.A., 1996. Interactions involving allelopathy in cropping systems. Agronomy Journal 88, 886-893.

Einhellig, F.A., 1999. An integrated view of allelochemicals amid multiple stresses, in: Inderjit, Dakshini, K.M.M., Foy C.L. (Eds.), Principals and Practices in Plant Ecology: Allelochemical Interactions. CRC Press, Boca Raton, pp. 479-494.

Eisenhauer, N, Dobiesc, T., Cesarza, S., Hobbie, S.E., Meyer, R.J., Worm, K.,

UNIVERSITY of the WESTERN CAPE

Reich, P.B., 2013. Plant diversity effects on soil food webs are stronger than those of elevated CO_2 and N deposition in a long-term grassland experiment. PNAS 110 (17), 6889-6894.

Eisenhauer, N., Milcu, A., Sabais, A.C.W., Bessler, H., Brenner, J., Engels, C., Klarner, B., Maraun, M., Partsch, S., Roscher, C., Schonert, F., Temperton, V.M. Thomisch, K., Weigelt, A., Weisser, W.W., Scheu, S., 2011. Plant diversity surpasses plant functional groups and plant productivity as driver of soil biota in the long term. PLoS ONE 6(1), e16055.

Eldridge, D.J., Val, J., James, A.I., 2011. Abiotic effects predominate under prolonged livestock-induced disturbance. Austral Ecology 36, 367-377,

UNIVERSITY of the
WESTERN CAPE

Ettema, C.H., Wardle, D.A., 2002. Spatial soil ecology. Trends in Ecology and Evolution 17, 177-183.

Eviner, V.T., Chapin III, F.S.C., Vaughn, C.E., 2006. Seasonal variations in plant species effects on soil N and P dynamics. Ecology 87(4), 974-986.

Expotech USA, 2005. A guide to Kjeldahl nitrogen determination methods and apparatus. An industry service publication. LABCONCO. Available at: http://www.ExpotechUSA.com. Date accessed: 15 November 2011.

Fernandez, D.P., Neff, J.C., Reynolds, R.L., 2008. Biogeochemical and

ecological impacts of livestock grazing in semi-arid southeastern Utah, USA. Journal of Arid Environments 72, 777-791.

Fierer, N., Schimel, J.P., 2003. A proposed mechanism for the pulse in carbon dioxide production commonly observed following the rapid rewetting of a dry soil. Soil Science Society of America Journal 67, 798-805.

Fierer, N., Strickland, M. S., Liptzin, D., Bradford, M. A., Cleveland, C. C., 2009. Global patterns in belowground communities. Ecology Letters 12, 1238-1249.

Fontaine, S., Barot, S., 2005. Size and functional diversity of microbe populations control plant persistence and long-term soil carbon accumulation. Ecology Letters 8, 1075-1087.

UNIVERSITY of the
WESTERN CAPE

FAO, 2011. Food and Agriculture Organization of the United Nations. Biodiversity for Food and Agriculture. Contributing to food security and sustainability in a changing world. Outcomes of an expert workshop held by Food and Agriculture Organization of the United Nations (FAO) and the Platform on Agrobiodiversity Research (PAR) from 14–16 April 2010 in Rome, Italy.

FAO, 2015. Food and Agriculture Organization of the United Nations. Healthy soils are the basis for healthy food production. Available at: www.fao.org/soils-

2015. Date accessed: 27 February 2015.

Frank, D.A., Groffman, P.M., 1998. Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park. Ecology 79, 2229-2241.

Frey, S.D., Knorr, M., Parrent, J.L., Simpson, R.T., 2004. Chronic nitrogen enrichment affects the structure and function of the soil microbial community in termperate hardwood and pine forest. Forest Ecology and Management 196, 159-171.

Frison, E.A., Cherfas, J., Hodgkin, T., 2011. Agricultural biodiversity is essential for a sustainable improvement in food and nutrition security. Sustainability 3, 238-253.

UNIVERSITY of the
WESTERN CAPE

Frostegård, A, Bååth E., 1996. The use of phospholipid analysis to estimate bacterial and fungal biomass in soils. Biology and Fertility of Soils 22, 59-65.

Frostegård, A., Tunlid, A., Bååth, E., 2010. Use and misuse of PLFA measurements in soils. Soil Biology and Biochemistry 43(8), 1621-1625.

Garbeva, P., Van Elsas, J.D., Van Veen, J.A., 2008. Rhizosphere microbial community and its response to plant species and soil history. Plant and Soil 302, 19-32.

Garbisu, C., Alkortab, I., Epelde, L., 2011. Assessment of soil quality using microbial properties and attributes of ecological relevance. Applied Soil Ecology 49, 1-4.

Garland, J.L., Mills, A.L., 1991. Classification and characterization of heterotrophic microbial communities on the basis of patterns of community-level sole-carbon source utilization. Applied and Environmental Microbiology 57, 2351-2359.

Gessner, M.O., Swan, C.M., Dang, C.K., McKie, B.G., Bardgett, R.D., Wall, D.H., Hättenschwiler, S., 2010. Diversity meets decomposition. Trends in Ecology and Evolution 25(6), 372-380.

UNIVERSITY of the
WESTERN CAPE

Giller, K.E., Beare, M.H., Lavelle, P., lzac A.-M.N., Swift, M.J., 1997. Agricultural intensification, soil biodiversity and agroecosystem function. Applied Soil Ecology 6, 3-16.

Gillson, L., Hoffman, M.T., 2007. Rangeland ecology in a changing world. Science 315, 53-54.

Goldblatt, P., Manning, J.C., 2000. Cape plants. A conspectus of the Cape flora of South Africa. Strelitzia 9, National Botanical Institute, Pretoria.

Goldblatt, P., Manning, J.C., Snijman, D., 2005. Cape plants: corrections and

additions to the flora. 1. Bothalia 35, 35-46.

Golodets, C., Boeken, B., 2006. Moderate sheep grazing in semi-arid shrubland alters small-scale soil surface structure and patch properties. Catena 65, 285-291.

Grayston, S.J., Campbell, C.D., Bardgett, R.D., Mawdsley, J.L., Clegg, C.D., Ritz, K., Griffiths, B.S., Rodwell, J.S., Edwards, S.J., Davies, W.J., Elston, D.J., Millard, P., 2004. Assessing shifts in soil microbial community structure across a range of grasslands of differing management intensity using CLPP, PLFA and community DNA techniques. Applied Soil Ecology 25, 63-84.

Green, V.S., Stott, D.E., Diack, M., 2006. Assay for fluorescein diacetate hydrolytic activity: optimization for soil samples. Journal of Soil Biology and Biochemistry 38, 693-701.

UNIVERSITY of the
WESTERN CAPE

Greiber, T., Moreno, S.P., Åhrén, M., Carrasco, J.N., Kamau, E.C., Jorge Cabrera Medaglia, J.C., Oliva, M.J., Perron-Welch, F., Ali, N., Williams, C., 2012. An Explanatory Guide to the Nagoya Protocol on Access and Benefit-sharing. IUCN, Gland, Switzerland. Available at: https://cmsdata.iucn.org/downloads/an_explanatory_guide_to_the_nagoya_protocol.pdf. Date accessed: 20 October 2014.

Haack, S.K., Garchow, H., Odelson, D.A., Forney, L.J., Klug, M.J., 1994. Accuracy, reproducibility, and interpretation of fatty acid methyl ester profiles of

model bacterial communities. Applied and Environmental Microbiology 60, 2483-2493.

Hamilton, E.W., Frank, D.A. 2001. Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. Ecology 82, 2397-2402.

Hanson, C.A., Allison, S.D., Bradford, M.A., Wallenstein, M.D., Treseder, K.K., 2008. Fungal Taxa Target Different Carbon Sources in Forest Soil. Ecosystems 11, 1157-1167.

Hart, J.F., 2001. Half a century of cropland change. Geographical Review 91, 525-543.

UNIVERSITY of the
WESTERN CAPE

Hartmann A., Rothballer M., Schmid, M., 2008. Lorenz Hiltner, a pioneer in rhizosphere microbial ecology and soil bacteriology research. Plant and Soil 312, 7-14.

Hartmann, A., Schmid, M., Van Tuinen, D., Berg, G., 2009. Plant-driven selection of microbes. Plant and Soil 321, 235-257.

Haygarth P. M., Ritz, K., 2009. The future of soils and land use in the UK: Soil systems for the provision of land-based ecosystem services. Land Use Policy 26, 187-197.

Helme, N.A., 2007. Botanical report: Fine scale vegetation mapping of the Bokkeveld Escarpment. Report for CapeNature. Available at: http://bgis.sanbi.org/fsp/bokkeveldvegetationreport.pdf. Date accessed: 19 October 2014.

Heneghan, L., Miller, S.P., Baer, S., Callaham Jr., M.A., Montgomery, J., Pavao-Zuckerman, M., Rhoades, C.C., Richardson, S., 2008. Integrating soil ecological knowledge into restoration management. Restoration Ecology 16, 608-617.

Herms, D. A., Mattson, W. J., 1992. The dilemma of plants: to grow or defend. Quarterly Review of Biology 67, 283-335.

UNIVERSITY of the
WESTERN CAPE

Herrick, J.E., Whitford, W.G., 1995. Assessing the quality of rangeland soils: challenges and opportunities. Journal of Soil and Water Conservation 50(3), 237-242.

Heywood, V.H., Bates, I., 1995. Introduction, in: Heywood, V.H., Watson, R.T. (Eds.), Global Biodiversity Assessment. Cambridge University Press, Cambridge, pp. 1-21.

Hill, G.T., Mitkowski, N.A., Aldrich-Wolfe, L., Emele, L.R., Jurkonie, D.D., Ficke, A., Maldonado-Ramirez, S., Lynch, S.T., Nelson, E.B., 2000. Methods for assessing the composition and diversity of soil microbial communities. Applied

Soil Ecology 15, 25-36.

Hochstrasser, T., Millington, J.D.A., Papanastasis, V.P., Parsons, A.P., Paolo, P., Roggero, R.E., Farina, A., Puttock, A., 2014. The Study of Land Degradation in Drylands: State of the Art, in: Mueller, E., Wainwright, J., Parsons, A., Turnbull, L. (Eds.), Patterns of Land Degradation in Drylands: Understanding Self-Organised Ecogeomorphic Systems. Springer, pp.13-54.

Hoffman, M. T., Cowling, R. M., 1987. Plant physiognomy, phenology and demography, in: Cowling, R.M., Roux, P.W. (Eds.), The karoo biome: a preliminary synthesis. Part 2. Vegetation and history. South African National Scientific programmes, Pretoria, pp.1-34.

UNIVERSITY of the
WESTERN CAPE

Hoffman, M.T., Ashwell, A., 2001. Nature Divided – land degradation in South Africa. University of Cape Town Press, Cape Town.

Holechek, J.L., Pieper, R.D., Herbel, C.H., 2004. Range Management, Principals and Practices, fifth ed. Prentice Hall, Upper Saddle River, New Jersey.

Hooper, D.U., Bignel, D.E., Brown, V.K., Brussaard, L., Dangerfield, J.M., Wall, D.H., Wardle, D.A., Coleman, D.C., Giller, K.E., Lavelle, P., Van der Putten, W.H., De Ruiter, P.C., Rusek, J., Silver, W.L., Tiedje, J.M., Wolters, V., 2000. Interactions between aboveground and belowground biodiversity in terrestrial ecosystems: Patterns, mechanisms, and feedbacks. BioScience 50(12), 1049-

1061.

Hooper, D.U., Chapin, F.S., Ewel, J.J., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75(1), 3-35.

Huxman, T.E., Snyder, K.A., Tissue, D., Leffler, A.J., Ogle, K., Pockman, W.T., Sandquist, D.R., Potts, D.L., Schwinning, S., 2004. Precipitation pulses and carbon fluxes in semiarid and arid. Ecosystems. Oecologia 141, 254-268.

ICAFE-MAG, 1989. Manual de Recommendaciones para el cultivo del café. Programa Cooperatives ICAFE-MAG, San José, Costa Rica.

UNIVERSITY of the
WESTERN CAPE

Inderjit, Del Moral, R., 1997. Is separating resource competition and allelopathy from allelopathy realistic? Botanical Review 63, 221-230.

Inderjit, Weiner, J., 2001. Plant allelochemical interference or soil chemical ecology? Perspectives in Plant Ecology, Evolution and Systematics 4(1), 3-12.

Ingham, E.R., 2007. Soil food web. Available at: http://soils.usda.gov/sqi/concepts/soil_biology/soil_food_web.html. Date accessed: 9 May 2014.

Ingham, R.E., Trofymow, J.A., Ingham, E.R., Coleman, D.C., 1985. Interactions of bacteria, fungi, and their nematode grazers: effects on nutrient cycling and

plant growth. Ecological Monographs 55, 119-140.

Jackson, L.E., 2007. Biodiversity in agricultural landscapes: Investing without losing interest. Agriculture, Ecosystems and Environment 121, 193-195.

Jackson, L., Bawa, K., Pascual, U., Perrings, C., 2005. agroBIODIVERSITY: A new science agenda for biodiversity support of sustainable agroecosystems. DIVERSITAS Report number 4. Available at: http://www.agrobiodiversity-diversitas.org/documents/Jackson%20et%20al%20Science%20plan%20agroBIODIVERSITY.pdf. Date accessed: 23 May 2013.

Jackson, L.E., Burger, M., Cavagnaro, T.R., 2008. Roots, nitrogen transformations, and ecosystem services. Annual Review of Plant Biology 59, 341-363.

UNIVERSITY of the
WESTERN CAPE

Jackson, L.E., Pulleman, M.M., Brussaard, L., Bawa, K.S., Brown, G.G., Cardoso, I.M., de Ruiter, P.C., García-Barrios, L., Hollander, A.D., Lavelle, P., Ouédraogo, E., Pascual, U., Setty, S., Smukler, S.M., Tscharntke, T., Van Noordwijk, M., 2012. Social-ecological and regional adaptation of agrobiodiversity management across a global set of research regions. Global Environmental Change 22, 623-639.

Jürgens, N., 1997. Floristic biodiversity and history of African arid regions. Biodiversity and Conservation 6, 495-514.

Kaljonen, M., 2006. Co-construction of agency and environmental management. The case of agri-environmental policy implementation at Finnish farms. Journal of Rural Studies 22(2), 205-216.

Kang, S., Post, W.M., Nichols, J.A., Wang, D., West, T.O., Bandaru, V., Izaurralde, R.C., 2013. Marginal Lands: Concept, Assessment and Management. Journal of Agricultural Science 5, 129-139.

Karlen, D.L., Andrews, S.S., Weinhold, B.J., Doran, J.W., 2003. Soil quality: humankind's foundation for survival. Journal of Soil and Water Conservation 58, 171-179.

UNIVERSITY of the
WESTERN CAPE

Kemper, J., Cowling, R.M., Richardson, D.M., 1999. Fragmentation of South African renosterveld shrublands: effects on plant community structure and conservation implications. Biological Conservation 90, 103-111.

Kirk, J.L., Beaudette, L.A., Hart, M., Moutoglis, P., Klironomos, J.N., Lee, H., Trevors, J.T., 2004. Methods of studying soil microbial diversity. Journal of Microbiological Methods 58, 169-188.

Klironomos, J.N., 2002. Feedback to the soil community contributes to plant rarity and invasiveness in communities. Nature 417, 67-70.

Koohafkan, P., Stewart, B.A., 2008. Water and Cereals in Drylands. Food and Agriculture Organisation of the United Nations (FAO). Earthscan, London.

Körner, C.H. 2000 Biosphere responses to CO_2-enrichment. Ecological Applications 10, 1590-1619.

Kraaij, T., Milton, S. J., 2006. Vegetation changes (1995-2004) in semi-arid Karoo shrubland, South Africa: Effects of rainfall, wild herbivores and change in land use. Journal of Arid Environments 64(1), 174-192.

Kremen, C., Iles, A., Bacon, C., 2012. Diversified farming systems: an agroecological, systems-based alternative to modern industrial agriculture. Ecology and Society 17(4): 44.

UNIVERSITY of the
WESTERN CAPE

Krug, C.B., 2004. Practical Guidelines for the Restoration of Renosterveld. University of Stellenbosch. Available at: http://academic.sun.ac.za/consecol/RenosterveldRestorationProject/index.htm. Date accessed: 20 June 2013.

Kruger, F.J., 1984. Patterns of vegetation and climate in the mediterranean zone of South Africa. Bulletin de la Société Botanique de France 131, 213-224.

Lambers, H., Chapin III, F.S., Pons, T.L., 1998. Plant physiological ecology. Springer, Berlin.

Lavelle, P., 2012. Soil as a Habitat, in: Wall, D.H., Bardgett, R.D., Behan-Pelletier, V., Herrick, J.E., Hefin Jones, T., Ritz, K., Six, J., Strong, D.R., Van der Putten, W.H. (Eds.), Soil Ecology and Ecosystem Services. Oxford University Press. Oxford, pp. 7-27.

Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P., Rossi, J-P., 2006. Soil invertebrates and ecosystem services. European Journal of Soil Biology 42, S3-S15.

Lavelle, P., Spain, A., 2001. Soil Ecology. Springer Science and Business Media.

Lemons, J., Victor, R., Schaffer, D., 2003. Conserving Biodiversity in Arid Regions: Best Practices in Developing Nations. Springer Science and Business Media.

Li, J., Okin, G.S., Epstein, H.E., 2009. Effects of enhanced wind erosion on surface soil texture and characteristics of windblown sediments. Journal of Geophysical Research: Biogeosciences, 114 (G2).

Likens, G.E., Bormann, F.H., Pierce, R.S., Eaton, J.S., Johnson, N.M., 1977. Biogeochemistry of forested ecosystems. Springer, New York.

Low, A.B., Rebelo, A.G., 1996. Vegetation of South Africa, Lesotho and

UNIVERSITY of the WESTERN CAPE

Swaziland. A companion to the vegetation map of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria.

Lyford, M.E., Jackson, S.T., Betancourt, J.L., Gray, S.T., 2003. Influence of landscape structure and climate variability on a late Holocene plant migration. Ecological Monographs 73, 567-583.

Maczko, K., Tanaka, J. A., Breckenridge, R., Hidinger, L., Heintz, H. T. Fox, W. E. Kreuter, U. P., Duke, C. S., Mitchell, J. E., McCollum, D.W., 2011. Rangeland ecosystem goods and services: values and evaluation of opportunities for ranchers and land managers. Rangelands 33(5), 30-36.

Madsen, E. L., 2008. Microbial biogeochemistry: A grand synthesis, in: Environmental Microbiology: From Genomes to Biogeochemistry. Blackwell Publishing, Malden, pp. 281-299.

Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., García-Gómez, M., Bowker, M.A., Soliveres, S., Escolar, C., García-Palacios, P., Berdugo, M., Valencia, E., Gozalo, B., Gallardo, A., Aguilera, L., Arredondo, T., Blones, J., Boeken, B., Bran, D., Conceição, A.A., Cabrera, O., Chaieb, M., Derak, M., Eldridge, D.J., Espinosa, C.I., Florentino, A., Gaitán, J., Gatica, M.G., Ghiloufi, W., Gómez-González, S., Gutiérrez, J.R., Hernández, R.M., Huang, X., Huber-Sannwald, E., Jankju, M., Miriti, M., Monerris, J., Mau, R.L., Morici, E., Naseri, K., Ospina, A., Polo, V., Prina, A.,

UNIVERSITY of the WESTERN CAPE

Pucheta, E., Ramírez-Collantes, D.A., Romão, R., Tighe, M., Torres-Díaz, C., Val, J., Veiga, J.P., Wang, D., Zaady, E., 2012. Plant species richness and ecosystem multifunctionality in global drylands. Science 335 (6065), 214-218.

Manning, J., Goldblatt, P., 1997. Nieuwoudtville, Bokkeveld Plateau and Hantam. Botanical Society of South Africa, Cape Town.

McDowell, C., 1994. Grazing and renosterveld management, in: Low, A.B., Jones, F.E. (Eds.), Symposium on the sustainable use and management of renosterveld remnants in the Cape Floristic Region, FCC Report 95/4. Botanical Society of South Africa, Cape Town. pp. 63–71.

McDowell, C., 1995. Grazing and renosterveld management, in: Low, AB., Jones, F.E. (Eds.), The sustainable use and management of renosterveld remnants in the Cape Floristic Region. FCC Report 1995/4. Botanical Society of South Africa, Cape Town, pp. 63-80.

McKeon, G.M., Stone, G.S., Syktus, J.I., Carter, J.O., Flood, N.R., Ahrens, D.G., Bruget, D.N., Chilcott, C.R., Cobon, D.H., Cowley, R.A., Crimp, S.J., Fraser, G.W., Howden, S.M., Johnston, P.W., Ryan, J.G., Stokes, C.J., Day, K.A., 2009. Climate change impacts on northern Australian rangeland livestock carrying capacity: a review of issues. The Rangeland Journal 31, 1-29.

McNear Jr., D. H., 2013. The Rhizosphere - Roots, Soil and Everything In

UNIVERSITY of the WESTERN CAPE

Between. Nature Education Knowledge 4(3):1. Available at: http://www.nature.com/scitable/knowledge/library/the-rhizosphere-roots-soil-and-67500617. Date accessed: 20 January 2014.

Meadows, M. E., Watkeys, M. K., 1999. Palaeoenvironments, in: Dean, W. R. J., Milton, S.J. (Eds.), The Karoo: Ecological Patterns and Processes. Cambridge University Press, United Kingdom, pp. 27-41.

Mele, P.M., Crowley, D.E., 2008. Application of self-organizing maps for assessing soil biological quality. Agriculture, Ecosystems and Environment 126, 139-152.

Microbial Insights, 2009. PLFA overview. Available at: http://www.microbe.com/wp-content/uploads/2015/01/plfa-mic.pdf. Date accessed: 20 April 2013.

Midgley, G.F., Bond, W.J., Kapos, V., Ravilious, C., Scharlemann, J.P.W., Woodward, F.I., 2010. Terrestrial carbon stocks and biodiversity: key knowledge gaps and some policy implications. Current Opinion in Environmental Sustainability 2, 264-270.

Mijangos, I., Pérez, R., Albizu, I., Garbisu, C., 2006. Effects of fertilization and tillage on soil biological parameters. Enzyme and Microbial Technology 40, 100-106.

UNIVERSITY of the WESTERN CAPE

Milchunas, D.G., Lauenroth, W.K., 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63, 327-366.

MEA, 2005. Millennium Ecosystem Assessment. Ecosystems and Human Well-being: Biodiversity Synthesis. World Resources Institute, Washington, DC.

Mills, A.J., Birch, S.C., Stephenson, J.D., Bailey, R.V., 2012. Carbon stocks in fynbos, pastures and vineyards on the Agulhus Plain, South Africa: a preliminary assessment. South African Journal of Plant and Soil, 29 (3-4), 191-193.

UNIVERSITY of the
WESTERN CAPE

Milton, K., 1997. Nature, culture and biodiversity, in: Arler, F., Svennevig, I. (Eds.), Cross-Cultural Protection of Nature and the Environment. Odense University Press, Odense, pp. 71-83.

Milton, S.J., 2004. Grasses as invasive alien plants in South Africa. South African Journal of Science 100, 69-75.

Milton, S.J., 2007. Rapid Assessment Method for Renosterveld. Renosterveld Assessment Workshop, unpublished report.

Milton, S.J., Dean, W.R.J., 1990. Seed production in rangelands of the southern

Karoo. South African Journal of Science 86, 231-233.

Milton, S.J., Dean, W.R.J., Du Plessis, M. A., Siegfried, W.R., 1994. A conceptual model of arid rangeland degradation. The escalating cost of declining productivity. Bioscience 44, 70-76.

Mittermeier, R.A., Gil, P.R., Hoffmann, M., Pilgrim, J.D., Brooks, T.M., Mittermeier, C.G., Lamoreux J.F., Da Fonseca, G.A.B., 2004. Hotspots revisited: earth's biologically richest and most endangered terrestrial ecoregions. Cemex, Mexico City.

Moll, E.J., Campbell, B.M., Cowling, R.M., Bossi, L., Jarman, M.L., Boucher, C., 1984. A description of major vegetation categories in and adjacent to the Fynbos Biome. CSIR, Pretoria, pp. 12-14.

Moussa, A.S., Van Rensburg, L., Kellner, K., Bationo, A., 2009. Soil microbial biomass in semi-arid-communal sandy rangelands in the Western Bophirima district, South Africa. Applied ecology and environmental research 5(1), 43-56.

Mucina, L., Rutherford, M.C., (Eds.), 2006. The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19, South African National Biodiversity Institute, Pretoria.

Muhl, S.A., 2008. Alien grass invasion of Renosterveld: Influence of soil

UNIVERSITY of the
WESTERN CAPE

variable gradients. MSc thesis, University of Stellenbosch.

Musil, C.F. Milton, S.J. Davis, G.W., 2005. The threat of alien invasive grasses to lowland Cape floral diversity: an empirical appraisal of the effectiveness of practical control strategies. South African Journal of Science 101, 337-343.

Muyzer, G.E., De Waal, C., Uitterlinden, A., 1993. Profiling of complex microbial populations by denaturating gradient gel electrophoresis of polymerase chain reaction-amplified genes encoding for 16 S rRNA. Applied Environmental Microbiology 59, 695-700.

Mworia, J.K., Mnene, W.N., Musembi, D.K., Reid, R.S., 1997. Resilience of soils and vegetation subjected to different grazing intensities in a semi-arid rangeland of Kenya. African Journal of Range and Forage Science 14, 26-31.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403(6772), 853-858.

Naeth, M.A., Bailey, A.W., Pluth, D.J., Chanasyk, D.S., Hardin. R.T., 1991. Grazing impacts on litter and soil organic matter in mixed prairie and fescue grassland ecosystems of Alberta. Journal of range management 44(l), 7-12.

Neff, J.C., Reynolds, R.L., Belnap, J. Lamothe, P., 2005. Multi-decadal impacts

UNIVERSITY of the
WESTERN CAPE

of grazing on soil physical and biogeochemical properties in southeast Utah. Ecological Applications 15, 87-95.

Nelson, M., Dudal, R., Gregersen, H., Jodha, N., Nyamia, D., Groenwald, J.-P., Torres, F., Kassam, A., 1997. Report of the studies of CGIAR research priorities for marginal lands. Technical Advisory Committee, Consultative Group on International Research and FAO, Rome.

Nguyen, C., 2003. Rhizodeposition of organic C by plants: mechanisms and controls. Agronomie 23, 375-396.

Northup, B.K., Brown, J.R., Ash, A.J., 2005. Grazing impacts on spatial distribution of soil and herbaceous characteristics in an Australian tropical woodland. Agroforestry Systems 65, 137-150.

UNIVERSITY of the
WESTERN CAPE

Noss, R.F., 1996. Ecosystems as conservation targets. Trends in Ecology and Evolution 11, 351.

Noy-Meir, J., 1985. Desert Ecosystem structure and function, in: Evenari, M., Noy-Meir, I., Goodall, D.W. (Eds.), Hot deserts and arid shrublands. Elsevier Scientific Publishers, Amsterdam, pp. 93-103.

Nunes, P.A.D, Van der Bergh, J.C.J.M., 2001. Economic valuation of biodiversity: sense or nonsense? Ecological Economics 39, 203-222.

O'Farrell P.J., De Lange, W.J, Le Maitre, D.C, Reyers B., Blignaut J.N, Milton S.J., Atkinson D., Egoh B., Maherry A., Colvin C., Cowling, R.M., 2011. The possibilities and pitfalls presented by a pragmatic approach to ecosystem service valuation in an arid biodiversity hotspot. Journal of Arid Environments 75, 612-623.

O'Farrell, P.J., Donaldson, J.S., Hoffman, M.T., 2007. The influence of ecosystem goods and services on livestock management practices on the Bokkeveld plateau, South Africa. Agriculture, Ecosystems and Environment 122, 312-324.

O'Farrell, P.J., Donaldson, J.S., Hoffman, M.T., 2009. Local benefits of retaining natural vegetation for soil retention and hydrological services. South African Journal of Botany 75, 573-583.

O'Farrell, P.J., Donaldson, J.S., Hoffman, M.T., 2010. Vegetation transformation, functional compensation, and soil health in a semi-arid environment. Arid Land Research and Management 24(1), 12-30.

Pallarès Vinyoles, G., 2008. Effects of land use on soil microbial community function in western Kenya highlands. MSc thesis, Swedish University of Agricultural Sciences.

UNIVERSITY of the
WESTERN CAPE

Pankhurst, C.E., Ophel-Keller, K., Doube, B.M., Gupta, V.V.S.R., 1996. Biodiversity of soil microbial communities in agricultural systems. Biodiversity and Conservation 5, 197-209.

Paterson-Jones, C., 1998. Renosterveld's Floral Treasure: Headed for extinction. Africa- Environment and Wildlife 6, 27-32.

Pence, G.Q.K., 2008. C.A.P.E. Fine-Scale Systematic Conservation Planning Assessment: Technical Report. CapeNature, Cape Town.

Perfecto, I., Vandermeer, J., 2002.Quality of agroecological matrix in a tropical montane landscape: Ants in coffee plantations in southern Mexico. Conservation Biology 16(1), 174-182.

UNIVERSITY of the
WESTERN CAPE

Perfecto, I., Vandermeer, J., Hanson, P., Cartín, V., 1997. Arthropod biodiversity loss and the transformation of a tropical agro-ecosystem. Biodiversity and Conservation 6, 935-945.

Peters, D.P.C, Bestelmeyer, B.T., Herrick, J.E., Fredrickson, E.L., Monger, H.C., Havstad, K.M., 2006.Disentangling complex landscapes: New insights into arid and semiarid system dynamics. BioScience 56(6), 491-501.

Piñeiro, G., Paruelo, J.M., Oesterheld, M., Jobbágy, E.G., 2010. Pathways of grazing effects on soil organic carbon and nitrogen. Rangeland Ecology and

Management 63, 109-119.

Ponge, J.F., 2003. Humus forms in terrestrial ecosystems: a framework to biodiversity. Soil Biology and Biochemistry 35, 935-945.

Porazinska, D.L., Bardgett, R.D., Blaauw, M.B. Hunt, H.W., Parsons, A.N., Seastedt, T.R., Wall, D.H., 2003. Relationships at the aboveground-belowground interface: Plants, soil biota and soil processes. Ecological Monographs 73(3), 377-395.

Pothoff, M., Steenwerth, K.L., Jackson, L.E., Drenovsky, R.E., Scow, K.A., Joergensen, R.G., 2006. Soil microbial community composition as affected by restoration practices in California grassland. Soil Biology and Biochemistry 38, 1851-1860.

UNIVERSITY of the
WESTERN CAPE

Price, W.P., 1988. An overview of organismal interactions in ecosystems in evolutionary and ecological time. Agriculture, Ecosystems and Environment 2, 369-377.

Pringle, H., Tinley, K.L., 2003. Are we overlooking critical geomorphic determinants of landscape change in Australian rangelands? Ecological Management and Restoration 4, 180–186.

Procheş, S., Cowling, R.M., Goldblatt, P., Manning, J.C., Snijman, D.A., 2006.

An overview of the Cape geophytes. Biological Journal of the Linnean Society 87, 27-43.

Provenza, F., Pringle, H., Revell, D., Bray, N., Hines, C., Teague, R., Steffens, T., Barnes, M., 2013. Complex Creative Systems. Principals, processes, and practices of transformation. Rangelands 35(5), 6-13.

Provenza, F., Pringle, H., Revell, D., Bray, N., Hines, C., Teague, R., Steffens, T., Barnes, M., 2013. Complex creative systems. Principals, processes, and practices of transformation. Rangelands 35(5), 6–13.

Radloff, F.G.T., Mucina, L., Snyman, D., 2014. The impact of native large herbivores and fire on the vegetation dynamics in the Cape renosterveld shrublands of South Africa: insights from a six-year field experiment. Applied Vegetation Science 17(3), 456-469.

Ramsey, P.W., Rillig, M.C., Feris, K.P., Holben, W.E., Gannon, J.E., 2006. Choice of methods for soil microbial community analysis: PLFA maximizes power compared to CLPP and PCR-based approaches. Pedobiologia 50, 275-280.

Ravi, S., D'Odorico, P., Wang, L., White, C., Okin, G., Macko, S., Collins, S., 2009. Post-fire resource redistribution in desert grasslands: a possible negative feedback on land degradation. Ecosystems 12, 434-444.

UNIVERSITY of the
WESTERN CAPE

Rebelo, A.G., 1996. South and South-west Coast Renosterveld, in: Low, A.B., Rebelo, A.G. (Eds.), Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs and Tourism, Pretoria, p 67.

Rebelo, A.G., 1997. Conservation, in: Cowling, R.M., Richardson, D.M., Pierce, S.M. (Eds), Vegetation of Southern Africa. Cambridge University Press, Cambridge, pp. 571-590.

Rebelo, A.G., Boucher, C., Helme, N., Mucina, L., Rutherford, M.C., Smit, W.J., Powrie, L.W., Ellis, F., Lambrechts, J.J., Scott, L., 2006. Fynbos biome, in: Mucina, L., Rutherford, M.C. (Eds), The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute, Pretoria, pp. 53-219.

UNIVERSITY of the
WESTERN CAPE

Reiss, J., Bridle, J.R., Montoya, J.M., Woodward, G., 2009. Emerging horizons in biodiversity and ecosystem functioning research. Trends in Ecology and Evolution 24, 505-514.

Reynolds, H.L., Packer, A., Bever, J.D., Clay, K., 2003. Grassroots ecology: plant-microbe-soil interactions as drivers of plant community structure and dynamics. Ecology 84, 2281-2291.

Reynolds, J.F., Stafford Smith, D.M., 2001. Do humans cause deserts?, in:

Reynolds, J.F., Stafford Smith, D.M., (Eds.), Global desertification: do humans cause deserts? Dahlem University Press, Berlin, pp. 1-22.

Reynolds, J.F., Stafford Smith, D.M., Lambin, E.F., Turner II, B.L., Mortimore, M., Batterbury, S.P.J., Downing, T.E., Dowlatabadi, H., Fernández, R.J., Herrick, J.E., Huber-Sannwald, E., Jiang, H., Leemans, R., Lynam, T., Maestre, F.T., Ayarza, M., Walker, B., 2007. Global desertification: building a science for dryland development. Science 316, 847-851.

Rhoades, D.F., 1985. Offensive-defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. American Naturalist 125, 205-238.

UNIVERSITY of the
WESTERN CAPE

Rice, E.L., 1984. Allelopathy. Academic Press, Orlando.

Richardson, F.D., Hahn, B.D., Hoffman, M.T., 2005. On the dynamics of grazing systems in the semi-arid succulent Karoo: the relevance of equilibrium and nonequilibrium concepts to the sustainability of semi-arid pastoral systems. Ecological Modelling 187, 491-512.

Rietkerk, M., Ketner, P., Burger, J., Hoorens, B., Olff, H., 2000. Multiscale soil and vegetation patchiness along a gradient of herbivore impact in a semi-arid grazing system in West Africa. Plant Ecology 148, 207-224.

Riginos, C., Hoffman, M.T., 2003. Changes in population biology of two succulent shrubs along a grazing gradient. Journal of Applied Ecology 40, 615-625.

Ritz, K., Van der Putten, W.H., 2012. The living soil and ecosystem services, in: Wall, D.H., Bardgett, R.D., Behan-Pelletier, V., Herrick, J.E., Hefin Jones, T., Ritz, K., Six, J., Strong, D.R., Van der Putten, W.H. (Eds.), Soil Ecology and Ecosystem Services. Oxford University Press. Oxford, pp. 5-6.

Rouget, M., Jonas, Z., Cowling, R.M., Desmet, P.G., Mohamed, B., Mucina, L., Rutherford, M.C., Powrie, L.W., 2006. Ecosystem status and protection levels of vegetation types, in: Mucina, L., Rutherford, M.C. (Eds.), 2006. The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute, Pretoria.

UNIVERSITY of the
WESTERN CAPE

Roux, P.W., Vorster, M., 1983. Vegetation changes in the Karoo. Proceedings of the Grassland Society of Southern Africa 18, 25-29.

Rowe, H.L., Brown, C.S., Paschke, M.W., 2009. The influence of soil inoculums and nitrogen availability on restoration of high-elevation steppe communities invaded by *Bromus tectorum*. Restoration Ecology 17, 686-694.

Saetre, P., Bååth, E., 2000. Spatial variation and patterns of soil microbial community structure in a mixed spruce-birch stand. Soil Biology and

Biochemistry 32, 909-917.

Samuels, M.I., 2006. Patterns of resource use by livestock during and after drought in a communal rangeland in Namaqualand. MSc Thesis, University of the Western Cape.

SANBI, 2006. South African National Biodiversity Institute. Vegetation map of Lesotho, Swaziland and South Africa. Available at: http://bgis.sanbi.org/vegmap/biomes.asp. Date accessed: 13 October 2014.

SANBI and DEAT, 2009. South African National Biodiversity Institute and Department of Environmental Affairs and Tourism. Threatened Ecosystems in South Africa: Descriptions and Maps. Draft for Comment. South African National Biodiversity Institute, Pretoria, South Africa. Gazetted: Threatened Ecosystems National Environmental Management: Biodiversity Act: National list of ecosystems that are threatened and in need of protection.

Sankaran, M., Augustine, D.J., 2004. Large herbivores suppress decomposer abundance in a semiarid grazing ecosystem. Ecology 85, 1052-1061.

Sayre, N.F. 2001. The new ranch handbook: a guide to restoring western rangelands. Quivira Coalition, Santa Fe.

Schadt, C.W., Martin, A.P., Lipson, D.A., Schmidt, S.K., 2003. Seasonal

UNIVERSITY of the WESTERN CAPE

dynamics of previously unknown fungal lineages in tundra soils. Science 301, 1359-1361.

Scherr, S.S., McNeely, J.A., 2008. Biodiversity conservation and agricultural sustainability: Towards a new paradigm of 'ecoagriculture' landscapes. Philosophical Transactions of the Royal Society 363, 477-494.

Scheu, S., Schulz, E., 1996. Secondary succession, soil formation and development of a diverse community of oribatids and saprophagous soil macro-invertebrates. Biodiversity and Conservation 5(2), 235-250.

Schimel, J.P. Bennet, J., Frierer, N., 2005. Microbial community composition and soil nitrogen cycling: is there really a connection?, in: Bardgett, R.D., Usher, M.B., Hopkins, D.W. (Eds.), Biological Diversity and Function in Soil. Cambridge University Press, Cambridge.

Schlesinger, W. H., Jones, C. S., 1984. The comparative importance of overland runoff and mean annual rainfall to shrub communities of the Mojave Desert. Botanical Gazette 145, 116-124.

Schlesinger, W.H., Pilmanis, A.M., 1998. Plant-soil interactions in deserts. Biogeochemistry 42, 169-187.

Schmalz, H., 2011. Soil spatial heterogeneity and measured soil responses:

UNIVERSITY of the
WESTERN CAPE

factors in an ecological grazing experiment on a bunchgrass prairie. Thesis, University of Idaho.

Schmalz, H.J., Taylor, R.V., Johnson, T.N., Kennedy, P.L., DeBano, S.J., Newingham, B.A., McDaniel, P.A., 2013. Soil morphologic properties and cattle stocking rate affect dynamic soil properties. Rangeland Ecology and Management 66(4), 445-453.

Schroers, J. O., 2006. Towards the development of marginal land use depending on the framework of agricultural market, policy and production techniques. University of Giessen, Germany.

Schwinning, S., Sala, O.E., 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia 141(2), 211-220.

Scoones, I., 1995. New directions in pastoral development in Africa, in: Scoones, I., Living with uncertainty: new directions in pastoral development in Africa. Intermediate Technology Publications, London, pp. 1-36.

Seymour, C.L., Dean, W.R.J., 1999. Effects of heavy grazing on invertebrate assemblages in the succulent karoo, South Africa. Journal of Arid Environments 43, 267-286.

Sharma, G.P., Muhl, S.A., Esler, K.J., Milton, S.J., 2010. Competitive

UNIVERSITY of the
WESTERN CAPE

interactions between the alien invasive annual grass Avena fatua and indigenous herbaceous plants in South African Renosterveld: the role of nitrogen enrichment. Biological Invasions 12, 3371-3378.

Sharma, S., Rangger, A, Von Lutzow, M., Insam, H., 1998. Functional diversity of soil bacterial communities increases after maize litter amendment. European Journal of Soil Biology 34, 53-60.

Siepel, H., Van de Bund, C. F., 1988. The influence of management practises on the microarthropod community of grassland. Pedobiologica 31, 179-185.

Smet, M., Ward, D., 2006. Soil quality gradients around water-points under different management systems in a semi-arid savannah, South Africa. Journal of Arid Environments 64, 251-269.

UNIVERSITY of the
WESTERN CAPE

Smith, J.G., Eldridge, D.J., Throop, H.L., 2012. , Landform and vegetation patch type moderate the effects of grazing-induced disturbance on carbon and nitrogen pools in a semi-arid woodland. Plant and Soil 360(1-2), 405-419.

Smith, P., Powlson, D.S., 2003. Sustainability of soil management practices - a global perspective, in: Abbott, L.K., Murphy, D.V. (Eds.), Soil biological fertility - a key to sustainable land use in agriculture. Kluwer Academic Publishers, Amsterdam.

Snijman, D., Perry, P., 1987. A floristic analysis of the Nieuwoudtville wild flower reserve, Northwestern Cape. South Arican Journal of Botany 53(6), 445-454.

Soini, K., Aakkula, J., 2007. Framing the biodiversity of agricultural landscapes: The essence of local conceptions and constructions. Land Use Policy 24, 311-321.

Solomon, S., (Ed.), 2007. Climate Change: The physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

UNIVERSITY of the
WESTERN CAPE

Specht, R.L. (Ed.), 1979. Heathlands and related shrublands. Ecosystems of the World. Vol. 9A. Descriptive Studies. Elsevier, Amsterdam.

Stafford Smith, M., 2008. Foreword, in: Galvin, K.A., Reid, R.S., Behnke, R.H. Jr, Hobbs, N.T. (Eds.), Fragmentation in semi-arid and arid landscapes. Springer, Dordrecht, pp. ix-x.

Stavi, I., Ungar, E.D., Lavee, H., Sarah, P., 2008. Grazing-induced spatial variability of soil bulk density and content of moisture, organic carbon and calcium carbonate in a semi-arid rangeland. Catena 75, 288-296.

Steenwerth, K.L., Jackson, L.E., Calderón, F.J., Stromberg, M.R., Scow, K.M., 2002. Soil microbial community composition and land use history in cultivated and grassland ecosystems of coastal California. Soil Biology and Biochemistry 34, 1599-1611.

Stefanowicz, A., 2006. The Biolog plates technique as a tool in ecological studies of microbial communities. Polish Journal of Environmental Studies 15(5), 669.

Steinberger, Y., Freckman, D.W., Parker, L.W., Whitford, W.G., 1984. Effects of simulated rainfall and litter quantities on desert soil biota; nematodes and microarthropods. Pedobiologia 26, 267-274.

UNIVERSITY of the
WESTERN CAPE

Swift, M.J., Anderson, J.M., 1993. Biodiversity and ecosystem function in agricultural systems, in: Schulze, E.D., Mooney, H. (Eds.), Biodiversity and Ecosystem function. Springer, Berlin, pp. 15-41.

Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in terrestrial ecosystems. University of California Press, Berkeley.

Swift, M.J., Izac, A.-M.N., Van Noordwijk, M., 2004. Biodiversity and ecosystem services in agricultural landscapes - are we asking the right questions? Agriculture, Ecosystems and Environment 104, 113-134.

Swift, M.J., Vandermeer, J., Ramakrishnan, P.S., Anderson, J.M., Ong, C.K., Hawkins, B.A., 1996. Chapter 11: Biodiversity and Agroecosystem function, in: Mooney, H.A., Chushman, J.H., Medina, E., Sala, O.E., Schulze, E.-D. (Eds.), Functional Roles of Biodiversity: A Global Perspective. John Wiley and Sons, New York, pp. 261-298.

Sylvain, Z.A., Wall, D.H., 2011. Linking soil biodiversity and vegetation: Implications for a changing planet. American Journal of Botany 98(3), 517-527.

Tainton, N.M., 1999. Veld management in South Africa. University of Natal Press. Pietermaritzburg.

Takhtajan, A., 1986. Floristic regions of the world. University of California Press, Berkeley.

UNIVERSITY of the
WESTERN CAPE

Tate, R.L., 2000. Soil microbiology, second ed. John Wiley and Sons, New York.

Taylor, H.C., 1978. Capensis, in: Werger, M.J.A. (Ed.), Biogeography and ecology of southern Africa. Dr. W. Junk, The Hague, pp. 171-229.

Teague, W.R., Dowhower, S.L., Baker, S.A., Haile, N., DeLaune, P.B., Conover, D.M., 2011. Grazing management impacts on vegetation, soil biota and soil chemical, physical and hydrological properties in tall grass prairie. Agriculture, Ecosystems and Environment 141, 310-322.

Teague, W.R., Kreuter, U.P., Grant, W.E., Díaz-Solis, H., Kothmann, M.M., 2009. Economic implications of maintaining rangeland ecosystem health in a semiarid savanna. Ecological Economics 68, 1417-1429.

Thring, T.S.A., Weitz, F.M., 2006. Medicinal plant use in the Bredasdorp/Elim region of the Southern Overberg in the Western Cape Province of South Africa. Journal of Ethnopharmacology 103, 261-275.

Throop, H.L., Archer, S.R, 2008. Shrub (Prosopis velutina) encroachment in a semi-desert grassland: spatial-temporal changes in soil organic carbon and nitrogen pools. Global Change Biology 14, 2420-2431.

UNIVERSITY of the
WESTERN CAPE

Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R., Polasky, S., 2002. Agricultural sustainability and intensive production practices. Nature 418, 671-677.

Todd, S. W., 1999. Patterns of seed production and shrub association in two palatable Karoo shrub species under contrasting land use intensities. African Journal of Range and Forage Science, 17, 22-26.

Todd, S.W., 2008a. Options for Invasive Grass Management in the Nieuwoudtville Wildflower Reserve. Indigo Development and Change, Nieuwoudtville.

Todd, S.W., 2008b. Final report on the results and analysis of the Wild Oats control experiment in the Nieuwoudtville Wildflower Reserve. Indigo Development and Change, Nieuwoudtville.

Todd, S.W., 2010. Vegetation and Plant Communities Associated with the Tillite and Dolerite Renosterveld Types of the Avontuur Conservation Area, Nieuwoudtville, South Africa. A Drynet Science and Technology Expertise.

Todd, S.W., Hoffman, M.T., 2009. A fence-line in time demonstrates grazing-induced vegetation shifts and dynamics in the semiarid Succulent Karoo. Ecological Applications 19(7), 1897-1908.

UNIVERSITY of the
WESTERN CAPE

Torsvik, V., Øvreås, L., 2002. Microbial diversity and function in soil: from genes to ecosystems. Current Opinion in Microbiology 5, 240-245.

Treseder, K.K., 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO_2 in field studies. New Phytologist 164, 347-355.

Tscharntke, T., Clough, Y, Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., Whitbread, A., 2012. Global food security, biodiversity conservation and the future of agricultural intensification. Biological Conservation 151, 53-59. Doi:10.1016/j.biocon.2012.01.068

Underwood, E.J., 1981. The mineral nutrition of livestock. Commonwealth Agricultural Bureaux, Slough.

UNCCD, 2010. United Nations Convention to Combat Desertification. Drylands Soil Brochure. United Nations Environment Programme, Geneva. Available at: http://www.unccd.int/Lists/SiteDocumentLibrary/Publications/DrylandsSoilUNCCDBrochureFinal.pdf. Date accessed: 12 February 2013.

UNCCD, 2011. United Nations Convention to Combat Desertification. Factsheet number 5. United Nations Environment Programme, Geneva. Available at: http://www.unccd.int/publicinfo/factsheets/pdf/factsheets-eng.pdf. Date accessed: 10 October 2011.

UNIVERSITY of the
WESTERN CAPE

UNEMG, 2011. United Nations Environment Management Group. Global Drylands: A UN system-wide response. Available at: http://www.unccd.int/Lists/SiteDocumentLibrary/Publications/Global_Drylands_Full_Report.pdf. Date accessed: 16 October 2014.

Van Bruggen, A. H. C., Semenov, A. M., 2000. In search of biological indicators for soil health and disease suppression. Applied Soil Ecology 15, 13-24.

Van der Heijden, M. G. A., Bardgett, R.D., Van Straalen, N.M., 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in

terrestrial ecosystem. Ecology Letters 11, 296-310. Doi: 10.1111/j.1461-248.2007.01139.x.

Van der Heijden, M.G.A., Horton, T. R., 2009. Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. Journal of Ecology 97(6), 1139-1150.

Van der Merwe, H., Van Rooyen, M.W., 2011. Vegetation trends following fire in the Roggeveld, Mountain Renosterveld, South Africa. South African Journal of Botany 77(1), 127-136.

Van der Putten, W.H., Bardgett, R.D., De Ruiter, P.C., Hol, W.H.G., Meyer, K.M., Bezemer, T.M., Wardle, D. A., 2009. Empirical and theoretical challenges in aboveground–belowground ecology. Oecologia, 161(1), 1-14.

Van der Putten, W.H., Vet, L.E.M., Harver, J.A., Wackers, F.L., 2001. Linking above and belowground multitrophic interactions of plants, herbivores, pathogens and their antagonists. Trends in Ecology and Evolution 16, 547-554.

Van Eekeren, N., Van Liere, D., De Vries, F., Rutgers, M., De Goede, R., Brussaard, L., 2009. A mixture of grass and clover combines the positive effects of both plant species on selected soil biota. Applied Soil Ecology 42(3), 254-263.

UNIVERSITY of the
WESTERN CAPE

Van Rooyen, S., 2003. Factors affecting alien grass invasion into Renosterveld fragments. MSc thesis, University of Stellenbosch.

Van Wyk, A.E., Smith, G.F., 2001. Regions of Floristic Endemism in southern Africa: a review with emphasis on succulents. Umdaus Press, Hatfield, South Africa.

Vance, C.P., 2001. Symbiotic nitrogen fixation and phosphorus acquisition: plant nutrition in a world of declining renewable resources. Plant Physiology 127, 390-397.

Vestal, J.R., White, D.C., 1989. Lipid analysis in microbial ecology: quantitative approaches to the study of microbial communities. BioScience 39, 535-541.

UNIVERSITY of the
WESTERN CAPE

Viketoft, M., Sohlenius, B., Palmborg, C., Huss-Danell, K., Bengtsson, J., 2005. Plant species effects on soil nematode communities in experimental grasslands. Applied Soil Ecology 30, 90-103.

Von Hase, A., M., Maze, K., Helme, N., 2003. A fine-scale conservation plan for Cape lowlands renosterveld. Report No. CCU 2/03. Cape Conservation Unit: Botanical Society of South Africa, Cape Town.

Waldrop, M.P., Zak, D.R. Sinsabaugh, R.L., 2004. Microbial community response to nitrogen deposition in northern forest ecosystems. Soil Biology and.

Biochemistry 36, 1443-1451.

Wall, D.H., 2012. Introduction, in: Wall, D.H., Bardgett, R.D., Behan-Pelletier, V., Herrick, J.E., Hefin Jones, T., Ritz, K., Six, J., Strong, D.R., Van der Putten, W.H. (Eds.), Soil Ecology and Ecosystem Services. Oxford University Press. Oxford, pp. 1-2.

Wall, D.H., Bardgett, R.D., Kelly, E., 2010. Biodiversity in the dark. Nature Geoscience 3(5), 297-298.

Wall, D.H., Behan-Pelletier, V., Covich, A.P., Snelgrove, R., 2007. Hidden assets: Biodiversity below-surface. UNESCO-SCOPE, Paris. Available at: http://unesdoc.unesco.org/images/0015/001539/153945e.pdf. Date accessed: 16 October 2014.

UNIVERSITY of the
WESTERN CAPE

Wang, L., D'Odorico, P., Manzoni, S., Porporato, A., Macko, S., 2009. Carbon and nitrogen dynamics in southern African savannas: the effect of vegetation-induced patch-scale heterogeneities and large scale rainfall gradients. Climatic Change 94, 63-76.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setala, H., Van der Putten, W.H., Wall, D.H., 2004. Ecological linkages between aboveground and belowground biota. Science 304, 1629-1633.

Wardle, D.A., Nilsson, M.C., Gallet, C., Zackrisson, O., 1998. An ecosystem level perspective of allelopathy. Biological Reviews 73, 305–319.

Watt J.M., Breyer-Brandwijk M.G., 1962. Medicinal and poisonous plants of southern and eastern Africa. E and S Livingstone, Edinburgh.

Wessels, K.J., Prince, S.D., Carroll, M., Malherbe, J., 2007. Relevance of rangeland degradation in semiarid northeastern South Africa to the nonequilibrium theory. Ecological Applications 17, 815-827.

Wesuls, D., Strohbach, M., Horn, A., Kos, M., Zimmermann, J., Hoffmann, J., Geldenhuys, C., Dreber, N., Kellermann, L., Van Rooyen, M.W., Poschlod, P., 2010. Plant functional traits and types as a tool to analyse landuse impacts on vegetation, in: Schmiedel, U., Jürgens, N. (Eds.), Biodiversity in southern Africa. Volume 2: Patterns and processes at regional scale. Klaus Hess Publishers, Göttingen and Windhoek, pp. 222–232.

White, D.C., Stair, J.O., Ringelberg, D.B., 1996. Quantitative comparisons of in situ microbial biodiversity by signature biomarker analysis. Journal of Industrial Microbiology 17(3-4), 185-196.

Whitford, W.G., Aldon, E.F., Freckman, D.W., Steinberger, Y., Parker, L.W., 1989. Effects of organic amendments on soil biota on a degraded rangeland. Journal of Range Management 42(1), 56-60.

UNIVERSITY of the
WESTERN CAPE

Wiegmann, K., Hennenberg, K.J., Fritsche, U.R., 2008. Degraded land and sustainable bioenergy feedstock production. Joint International Workshop on High Nature Value Criteria and Potential for Sustainable Use of Degraded Lands, Paris, France. Öko-Institut, Darmstadt. Available at: http://np-net.pbworks.com/f/OEKO,%20RSB,%20UNEP%20et%20al%20%282008%29%20Degraded%20land%20and%20sustainable%20bioenergy%20feedstock%20production.pdf. Date accessed: 20 October 2014.

Williams, M.A., 2007. Response of microbial communities to water stress in irrigated and drought-prone tallgrass prairie soils. Soil Biology and Biochemistry 39, 2750-2757.

Wilson, A.D., 1990. The effect of grazing on Australian ecosystems. Proceedings of the Ecological Society of Australia 16, 235-44.

Witmore, B., 2007. The behavioral timeline of sheep on semiarid rangelands and its inference using GPS and pedometry. IALC Peace Fellowship Final Report. New Mexico State University.

Wolters, V. 1991. Soil invertebrates – Effects on nutrient turnover and soil structure – a review. Journal of Plant Nutrition and Soil Science 154, 389-402.

Wolters, V., 2001. Biodiversity of soil animals and its function. European

UNIVERSITY of the WESTERN CAPE

Journal of Soil Biology 37, 221-227.

Wolters, V., Silver, W.L., Bignell, D.E., Coleman, D.C., Lavelle, P., Van der Putten, W.H., De Ruiter, P., Rusek, J., Wall, D.H., Wardle, D.A., Brussaard, L., Dangerfield, J.M., Brown, V.K., Giller, K.E., Hooper, D.U., Sala, O., Tiedje, J., Van Veen, J.A., 2000. Effects of global changes on above- and belowground biodiversity in terrestrial ecosystems: implications for ecosystem functioning. Bioscience 50, 1089-1098.

WMO, 1990. World Meterological Organisation. Glossary of terms used in agrometeorology. CAgM No. 4. WMO/TD-No. 391. WMO, Geneva. Available at: http://www.wmo.int/pages/prog/wcp/agm/publications/cagm_reports.php. Date accessed: 16 October 2014.

UNIVERSITY of the
WESTERN CAPE

Wurst, S., De Deyn, G.B., Orwin, K., 2012. Soil Biodiversity and Functions, in: Wall, D.H., Bardgett, R.D., Behan-Pelletier, V., Herrick, J.E., Hefin Jones, T., Ritz, K., Six, J., Strong, D.R., Van der Putten, W.H. (Eds.), Soil Ecology and Ecosystem Services. Oxford University Press. Oxford, pp. 28-44.

Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. Proceedings of the National Academy of Sciences 96(4), 1463-1468.

Yanai, R.D., Majdi, H., Park, B.B., 2003. Measured and modelled differences in

nutrient concentrations between rhizosphere and bulk soil in a Norway spruce stand. Plant and Soil 257(1), 133-142.

Yeates, G.W., Bardgett, R.D., Cook, R., Hobbs, P.J., Bowling, P.J., Potter, J.F., 1997. Faunal and microbial diversity in three Welsh grassland soils under conventional and organic management regimes. Journal of Applied Ecology 34, 453-471.

Yeates, G.W., Bongers, T., De Goede, R.G.M., Freckman, D.W., Georgieva, S.S., 1993. Feeding habits in soil nematode families and genera - an outline for soil ecologists. Journal of Nematology 25, 315-331.

Zak, D.R., Holmes, W.E., White, D.C., Peacock, A.D., Tilman, D., 2003. Plant diversity, soil microbial communities, and ecosystem function: are there any links? Ecology 84(8), 2042-2050.

Zak, J.C., Willig, M.R., Moorhead, D.L., Wildman, H.G., 1994. Functional diversity of microbial communities: a quantitative approach. Soil Biology and Biochemistry 26, 1101-1108.

Zelles, L., 1999. Fatty acid patterns of phospholipids and lipopolysaccharides in the characterisation of microbial communities in soil: a review. Biology and Fertility of Soils 29, 111-129.

UNIVERSITY of the
WESTERN CAPE

Zelles, L., Bai, Q.Y., Rackwitz, R., Chadwick, D., Beese, F., 1995. Determination of phospholipid- and lipopolysaccharide-derived fatty acids as an estimate of microbial biomass and community compositions in soils. Biology and Fertility of Soils 19, 115-123.

Zogg, G.P., Zak, D.R, Ringelberg, D.B., MacDonald, N.W., Pregitzer, K.S., White, D.C., 1997. Compositional and functional shifts in microbial communities due to soil warming. Soil Science Society of America Journal 61, 475-481.

UNIVERSITY of the
WESTERN CAPE

Personal communication

Eugene Marinus, Hantam National Botanical Garden, South African National Biodiversity Institute (SANBI).