

Implications of potential biome boundary shifts for small mammal assemblages in the arid zone

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Abstract

Desertification deteriorates the landscape functionality of rangelands, affecting the resilience of biome boundaries which have a cascade effect not only in vegetation composition and characteristics but also in animal communities. The balance between plants and small mammals are essential in maintaining the functionality (i.e. nutrient cycling, soil stability, and water infiltration) of rangeland which includes the arid Steinkopf communal rangeland. However, the landscape functionality of rangelands has not been extensively studied, especially in communal areas where desertification is a serious concern since many people farm with livestock to survive. The aim of this study was to assess landscape functionality along an arid biome boundary and its relationship to small mammal assemblages. This study further aimed to provide a local landscape perspective of the current desertification process and projected expansion of the Desert Biome into more mesic biomes in South Africa.

Three replicates for three Desert Biome, ecotone and Succulent Karoo Biome sites (27 sites in total) were selected to assess landscape functionality and survey small mammal assemblages over a one-year period. The change in landscape functionality between the three areas was assessed to determine the resilience of the biome boundary to desertification. For each small mammal survey, 216 live Sherman traps were set up during the summer and winter seasons to account for breeding, mortality, and possible migration. With the data, the body condition index, population density, and diversity were quantified.

The results of this study show that the ecotone between Desert and Succulent Karoo Biomes is becoming more arid, particularly with regards to its vegetation characteristics. The soil of this region is resilient and remains closely related to that of the Succulent Karoo Biome. Out of 62 plant species recorded throughout the ecotone, 61% of these also occur within the

Desert Biome, but only 54% occurs within the Succulent Karoo Biome. Moreover, the narrow patch-interpatch characteristics of the Desert Biome relate closely to the ecotone since both have significantly small patches. The soil stability, nutrient cycling, and water infiltration of the ecotone are closely related to the Succulent Karoo Biome. This indicates that the soils of the ecotone have thus far been able to resist desertification.

Over 3204 trapping nights during winter and summer seasons, 119 small mammal captures were recorded. Three small mammal species were captured namely, *Gerbillurus paeba* (hairy-footed Gerbil), *Elephantulus rupestris* (western rock elephant-shrew) and *Desmodillus auricularis* (short-tailed gerbil). These rodents are dependent on the vegetation composition for breeding, juvenile survival, and maintaining their relative density index. The study argues that the rodents' dynamic habitat of which vegetation cover gets reduced and composition changes, might allow for *G. paeba* to replace the other two species in performing important ecosystem services like seed dispersal and nutrient cycling throughout the landscape. However, the loss of any small mammal species in a landscape can jeopardise other aspects of landscape functionality such as loss of plant species diversity, which could be particularly harmful in this communal area.

Land uses such as heavy grazing by livestock will further deteriorate vegetation cover and composition and will eventually affect soil characteristics through exposure to rainfall and thus erosion, which will lead to desertification. As such, land uses should be managed to ensure the rangeland is able to remain resilient to desertification and the small mammal assemblages remain stable.

Keywords:

Biome boundary, Body condition index, Desertification, Landscape Functionality, Livestock grazing, Namaqualand, Steinkopf Communal area, Small mammals



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Declaration

I declare that “Implications of potential biome boundary shifts for small mammal assemblages in the arid zone” is my own work, that it has not been submitted for any degree or examination in any other university, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.



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August 2019

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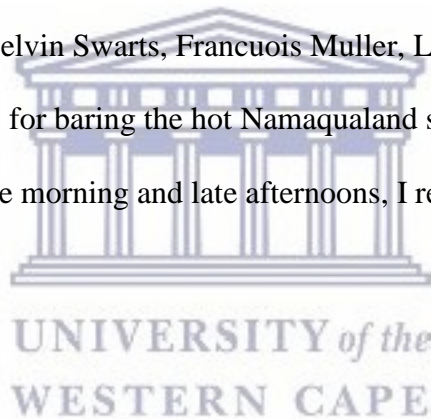


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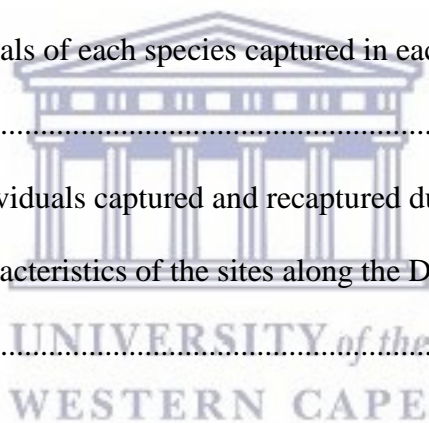
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1. Chapter 1

Literature Review and General Introduction

1.1. A global perspective of climate change and its effects on South Africa's rangelands

Climate change is an ongoing concern globally. The main characteristic of climate change is the increase in average global temperatures (UNFCCC 2017), which has increased by 0.74 °C over the past 25 years. This is the largest warming trend in history on Earth UNFCCC (2017) and has predominantly arisen as a result of human activity that has taken place since the industrial revolution.

Climate change impacts on many factors that could contribute towards desertification such as soil quality, vegetation structure, and land use (Rasmy *et al.* 2010). Desertification has been described as the continuous loss of biological and economic productivity (UNCCD 1994). However, it is also regarded as land degradation in arid and semi-arid landscapes resulting from climate and human activities (UNCCD 1994). Furthermore, land degradation has also recently been expanded to include the loss of ecosystem services in dryland ecosystems (D'Odorico *et al.* 2013).

Desertification in arid and semi-arid regions may initiate large-scale changes in vegetation community structure and composition (Tilman & El Haddi 1992; Allen & Breshears 1998; Delissio & Primack 2003). This could potentially cause a reduction in primary and secondary productivity, altered soil stability, reduced water infiltration, nutrient cycling, and a decrease in animal and plant diversity (Bollinger *et al.* 1990; Tilman & El Haddi 1992; Hanson & Weltzin 2000).

Rainfall and temperature affect a variety of processes in terrestrial ecosystems including desertification (Neilson *et al.* 1989; Ehleringer *et al.* 2001). Changes in rainfall and temperature patterns inflict various alterations in vegetation, soils, biodiversity, and ecological processes (Neilson *et al.* 1989; Ehleringer *et al.* 2001). For example, it may result in the expansion of deserts and migration of plants and animals that ultimately locate new niches to ensure their own survival. However, this is not ideal as current human-induced climate change and other global change pressures are rapid (Hewitt 1996; Anderson *et al.* 1998; He *et al.* 2003; Ackerly 2003), and as such suppresses the chances of biodiversity reaching new niche areas.

Species distributions will change drastically in the future according to climate predictions (Allen & Breshears 1998; Morin *et al.* 2008). Lafleur *et al.* (2010) suggest that soil properties, among other aspects, may restrict species migration, locally or regionally in response to climate change. Endemic species with narrow niches that are restricted to particular soils may be vulnerable to extinction under a changing climate because they have difficulty migrating to new sites (Damschen *et al.* 2010). These processes will spatially displace biomes by between 50 – 90% in response to climate change (Hufnagel & Garamvolgyi 2014). Due to its sensitivity to climate variables and the various land uses, biome boundary shifts could be imminent in South Africa (Stevens *et al.* 2015).

Arid and semi-arid ecosystems make up a third of South Africa's landscape (Milton & Dean 2015). These drylands are typically used for communal and commercial livestock farming thus climate change may put the livelihoods of people depending on these land uses at risk. Water is a scarce climatic resource that drylands depend on for agricultural purposes amongst other things (Johnston *et al.* 2016). Ultimately, climate change will reduce the amount of water available (Johnston *et al.* 2016). Furthermore, ecosystem services such as forage supply

that landscapes in the area provide are continually jeopardised when changes in climate are experienced (Johnston *et al.* 2016).

The climate change models for South Africa is in most cases largely based on bioclimatic variables over large areas and at a local spatial scale do not factor in land use. As such, Schulze (2011) suggested that climate change impacts on South Africa be modelled at a local scale to overcome the complexities of South Africa's physiography, climate, and its socio-economic environment. Moreover, few studies have focussed on the climate change projections for South Africa and the relative impacts it may have on the livelihoods of its people (Ziervogel *et al.* 2008; DEA 2013; Louw *et al.* 2017).

1.2. Impacts of climate change on South African biome boundaries

Biome boundaries are defined as a transitioning zone between vegetation types or biomes that gradually or abruptly appear in a landscape (Browsersox & Brown 2001). They are also typically defined as major geographical regions of distinctive living organisms that are physiologically well adapted to their distribution patterns and are strongly correlated with regional climate (Chakraborty *et al.* 2013). This area facilitates the movement of resources in a landscape whilst maintaining populations of plants and animals within the boundary (Wiens *et al.* 1985). Biome boundary shifts have profound ecological impacts and play a role in ecosystem feedback mechanisms by altering the resource exchange on the land surface (Allen & Breshears 1998). Increased temperatures result in the movement of biomes of a more arid affinity into more mesic biomes. Hence, the shifting will change the productivity, composition, diversity, plant dominance, plant evenness, and spatial extent of ecosystems (Suffling & Scott 2002; Kardol *et al.* 2010).

Some biome shifts may be because of bush encroachment, which could be defined as the competitive exclusion of either vegetation of a biome by another (Neilson *et al.* 1992).

Temporal or spatial shifts in biome/ecosystem types at biome boundaries are characterised by changes in dominant species or life forms (Gosz & Shape 1989). Various studies relate this shifting to changes in resource availability, such as Peters (2002), who found evidence for shifting between Chihuahuan desert and shortgrass steppe biomes following a change in climate and availability of soil water. Climate change may also decline water flow regimes and water tables which in some cases could increase flood intensity (Stromberg *et al.* 2010; Hufnagel & Garamvolgyi 2014). This reduces the amount of water absorbed by the soil where it is a limiting resource. This alteration in the water table typically affects vegetation, favouring species that are able to reach the water with adaptations such as longer roots, leading to competitive exclusion (Hufnagel & Garamvolgyi 2014).

In the arid region of South Africa, the Desert Biome is moving southward into the Nama Karoo Biome, and will likely continue to do so for the next 100 years (Driver *et al.* 2012). Together with the expansion of the Grassland Biome south-westward (Masubelele *et al.* 2015), this shift will extensively reduce the size of the Nama Karoo Biome. For the most part, the Succulent Karoo Biome will maintain its spatial extent (Fig. 1.1; Driver *et al.* 2012).

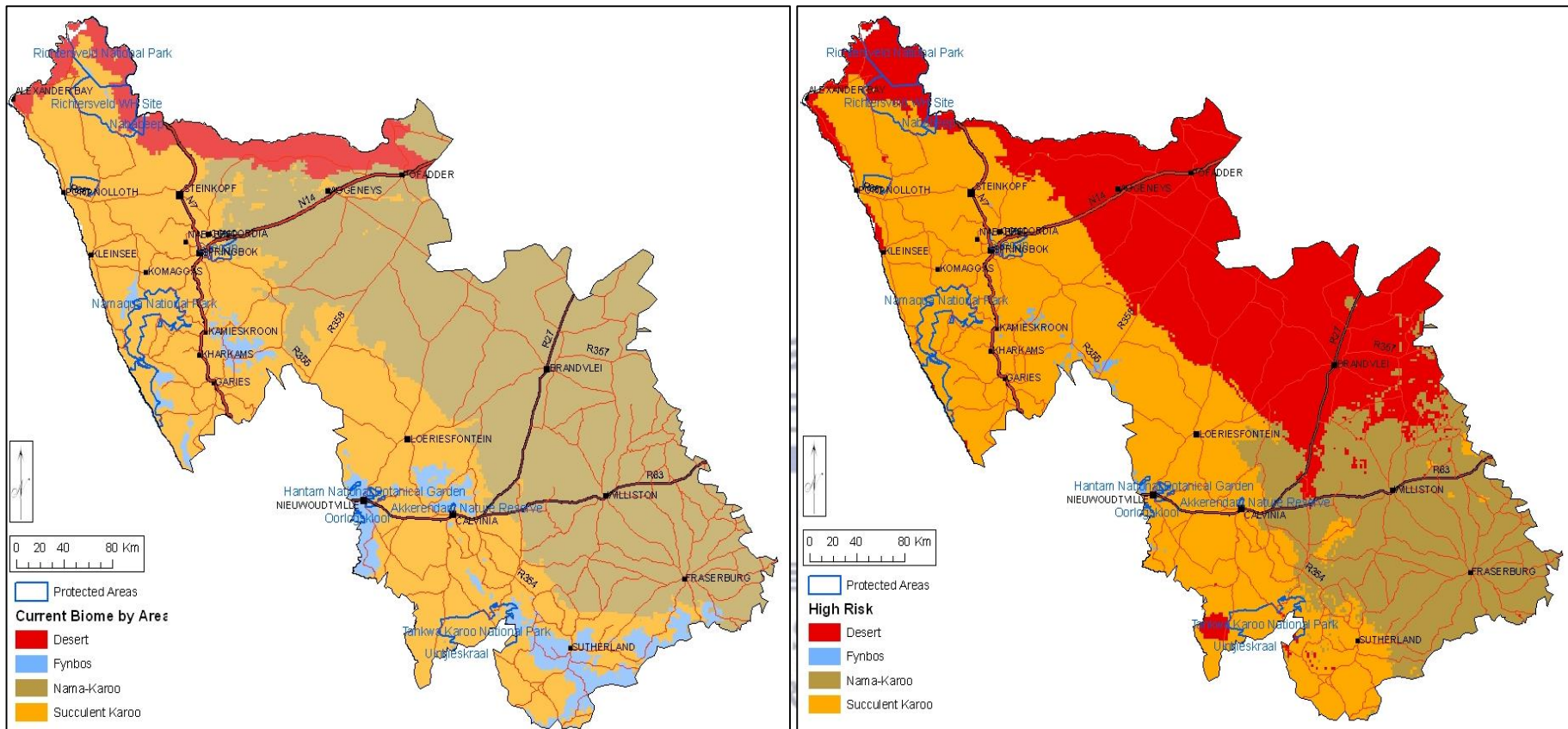


Figure 1.1: The current and high-risk scenarios for Namaqualand discussed by Holness & Midgley (2012) predicted over the next 50 years showing the increase of the Desert, Fynbos, and Succulent Karoo Biomes and decline of Nama Karoo Biome.

1.3. Landscape functional stability of biome boundaries in the face of climate change

Biome boundaries are relatively stable but predicted changes in regional precipitation patterns and soil moisture have the potential to alter interactions between vegetation types, resulting in alterations for their relative abundance and distribution (expansion or reduction; Weltzin & McPherson 2000; Chakraborty *et al.* 2013; Hufnagel & Garamvolgyi 2014). Therefore, because biome boundaries are relatively sensitive to climate change, it is ideal to assess the impacts climate change have on landscapes at these zones in ecosystems (Gosz & Sharpe 1989; Cao *et al.* 2015). The stability of a biome boundary is determined by various factors that are important for the functioning of the ecosystem. A functional ecosystem consists of an adequate scattering of vegetation patches that will facilitate the transfer of resources in the landscape, adequate water infiltration and plant diversity in order to perform various ecosystem services (Ludwig *et al.* 1994, 1997; Ludwig & Tongway 1995, 2013; Tongway & Ludwig 1997). Ludwig & Freudenberger (1997) refer to a stable system as a balanced landscape system but suggest that excessive consumption of resources will result in more losses of patches.

Climate change exacerbates this negative feedback mechanism resulting in the excessive loss of patches in an ecosystem. Patches need to adequately trap resources in order for a balanced system to persist if not productivity pulses will become smaller and the little that is produced will likely be consumed (Ludwig & Tongway 2013). Smaller feedbacks to patches will result in their functional integrity not being maintained (fewer and weaker patches; Ludwig & Freudenberger 1997; Ludwig & Tongway 2013).

The loss of patches reduces the number of refugia available for the various organisms that assist with regulating resources in these systems. Regulating organisms do this by facilitating the flow of resources (i.e. plants, soil, and other organisms) from one biome or vegetation type to another. Their movement across the ecotone allows adequate distribution of resources between the adjoining biomes. Subsequently, the ecotone provides a habitat for a wider diversity of organisms since it experiences climatic conditions of the adjacent biomes or vegetation types. Hence, Buxbaum & Vanderbilt (2007) and Hufkens *et al.* (2008) concluded that the species abundance becomes sparser as one approaches an ecotone from the core of the species range because competitive exclusion is minimal at biome boundaries, allowing a merging of species that are less competitive.

1.4. The aridity of Namaqualand in recent years

Arid regions are particularly vulnerable to climate change (De Villiers 2013; Davis *et al.* 2016). Namaqualand, as aforementioned is a well-known arid region for high biodiversity and level of endemism (De Villiers 2013; Davis *et al.* 2016), but this is at risk due to increased aridity in recent years. Adding further pressure to the situation is the high demand from the human population on the region's natural resources via livestock production and dryland agriculture (Davis *et al.* 2016).

The minimum temperatures are increasing faster than maximum temperatures, indicating that the warmer seasons will become longer negatively altering the vegetation distribution and composition (De Villiers 2013; Davis *et al.* 2016). Furthermore, changes in precipitation patterns influence species diversity through germination and seedling establishment (Lundholm & Larson 2004). Hence, the evidence is mounting especially in Namaqualand that seasonal timing of rain can hinder the ecosystem functioning.

1.5. The effects of desertification on rodent populations

It is understood that changes in the distribution of vegetation will change the distribution of animals that depend on it for their survival (Kosanic et al. 2018). Rodents are one such group that depends on vegetation, and in order to survive, rodents need to adapt to changes in environmental conditions (Hansen *et al.* 2001; Loarie *et al.* 2009). These adaptations could be physical or physiological and thus changes in vegetation composition could be detrimental and ultimately lead to the worst-case scenario, localized extinctions of rodent populations (Loarie *et al.* 2009).

Rodents and other fossorial animals are known as “ecosystem engineers” as they provide various essential ecosystem services. Their complex burrows allow water to infiltrate drylands such as arid regions. They also use their burrows as a storage space for seeds, initiating regeneration of vegetation which contributes toward nutrient cycling. Furthermore, rodent burrows also loosen up soils that are compacted by livestock, allowing seeds to penetrate the soil and establish themselves (Kinlaw 1999; Whitford & Kay 1999). These are just a few examples of the ecological benefits of ecosystem engineers that will be discussed further in Chapter Three in this thesis. Ultimately, rodents are important for the survival of the rangelands but few studies have assessed the potential effects of climate-mediated vegetation change on small mammal assemblages which this study aims to fulfil.

1.6. Small mammal activity and its relationship to the functionality of ecosystems

Patchiness is important to maintain spatial and temporal heterogeneity in ecosystems (Whitford & Kay 1999). A loss of patchiness (leaky landscapes) creates instability in a landscape, unfortunately, this phenomenon is becoming imminent in arid areas (Tongway & Ludwig 1997). Therefore, the relationship and abundance of fossorial mammals such as

rodents are increasingly important because they promote patchiness in arid ecosystems (Tongway & Ludwig 1997; Whitford & Kay 1999).

Their burrowing activity increases the porosity of soils and increasing water infiltration which is imperative in such drylands to increase the rain-use efficiency (Milton *et al.* 1994; Whitford & Kay 1999; Moreno-de las Heras *et al.* 2012). Rodent activities also enrich the soil, because they typically store seeds and other food, and defecate in their burrows (Whitford & Kay 1999). Other ground-dwelling microorganisms decompose these seeds as well as litter, plant material, and excretory material in the burrows and as a result, the burrows tend to be rich in cryptograms (Whitford & Kay 1999). The material in burrows is also transported by water and wind, providing a nitrogen-rich and high water storage site on which perennial shrubs may have higher productivity than disturbed bare soils increasing patchiness of landscape (Whitford & Kay 1999). They also directly affect the distribution of the plants in the rangelands because they feed on seeds and foliage (Whitford & Kay 1999).

1.7. The relevance of a holistic research methodology

A Landscape Functional Analysis (LFA) is an intricate *in situ* methodology that looks at how an ecosystem functions by looking at processes related to soil surface hydrology such as infiltration, runoff, erosion, plant growth, and nutrient cycling (Tongway & Hindley 2004). The LFA is based on a conceptual framework that assesses the way in which landscapes self-organise to store, utilise, and cycle scarce resources (Tongway & Hindley 2004). This methodology takes a wide range of environmental information into consideration, namely the Trigger-Transfer-Reserve-Pulse (TTRP) conceptual framework that makes use of processes and feedback loops in an ecosystem (Fig. 1.2; Tongway & Hindley 2004).

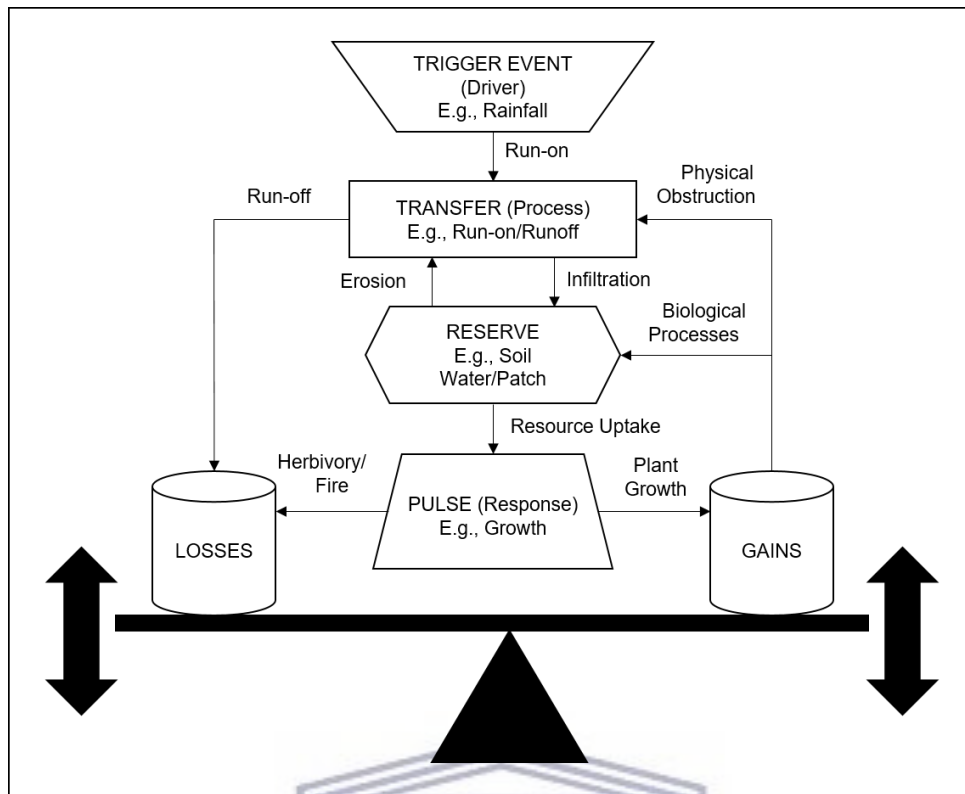


Figure 1.2: The TTRP conceptual framework representing sequences of ecosystem process and feedback loops in semi-arid and arid rangeland (Tongway & Hindley 2004; Ludwig & Tongway 1997).

The arid ecosystems in Namaqualand are fragile and excessive land use could result in ecosystem dysfunctionality within this region. This process could put various plants and animals at risk of extinction and more importantly, the ecosystem services these organisms provide which contribute to the functionality will be lost. Substantiating the importance of alleviating the impact of land uses on animals, especially small mammals that could be used as an indicator of 'healthy' or 'unhealthy' veld conditions remains a challenge. This information could potentially assist herders and other land-use managers to better understand the underlying processes occurring across the rangeland and adjust their grazing or management strategies accordingly.

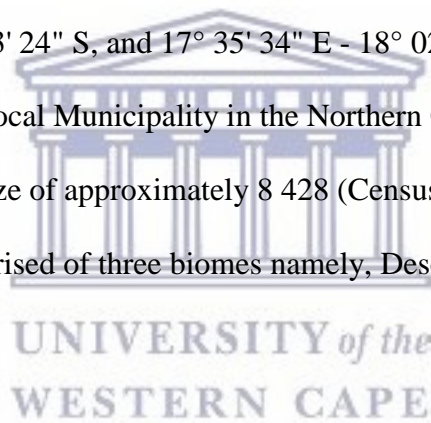
No land-based research has been carried out along the biome boundary between the Desert Biome and Succulent Karoo Biome in the Namaqualand region. More so, no previous studies have compared the landscape functionality of an arid area to an animal community.

Therefore, to fill this knowledge gap, this study aims to assess landscape functionality along the biome boundary between a semi-arid and arid biome in the Steinkopf communal area and its relationship to small mammal assemblages.

1.8. Study Area

i. Location

The Steinkopf communal area in Namaqualand is 582 634 hectares in size and is located between 29° 31' 13" S - 28° 53' 24" S, and 17° 35' 34" E - 18° 02' 55" E (Fig. 1.3). Steinkopf is a town in the Nama-Khoi Local Municipality in the Northern Cape Province of South Africa and has a population size of approximately 8 428 (Census 2011; Hoffmann *et al.* 2007). The rangeland is comprised of three biomes namely, Desert, Nama-Karoo, and Succulent Karoo.



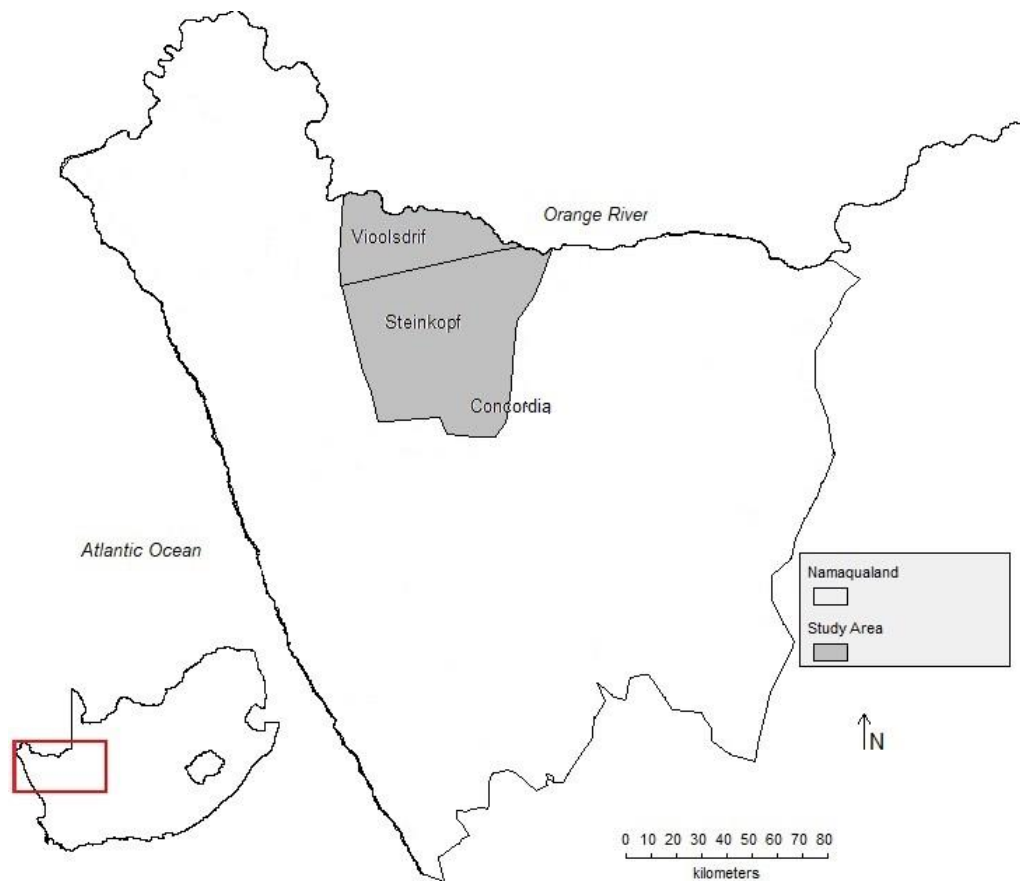
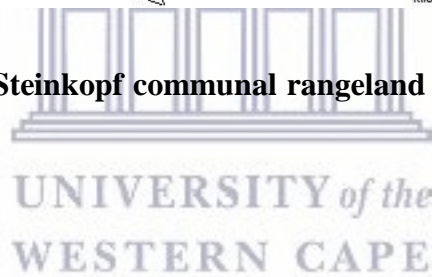


Figure 1.3: Location of the Steinkopf communal rangeland in the Namaqualand region in South Africa.



ii. Climate

Steinkopf experiences a distinct seasonality of rainfall with high average summer temperatures. It is typical of these drylands to experience an unpredictable, highly variable and patchy rainfall regime. The summer rainfall area has a mean annual temperature ranging between $-5\text{ }^{\circ}\text{C}$ in winter and $43\text{ }^{\circ}\text{C}$ in summer with a mean annual temperature of $25\text{ }^{\circ}\text{C}$ (Hines 1993; Mucina *et al.* 2006). The winter rainfall area has a mean annual temperature ranging from $14\text{ }^{\circ}\text{C}$ to $40\text{ }^{\circ}\text{C}$ with a mean annual temperature of $17\text{ }^{\circ}\text{C}$.

iii. Soil

The soils of this region are generally shallow, deep red in colour and possess a sandy texture. The dominant rock types and inselbergs are comprised of granitic and gneissic material (Mucina *et al.* 2006). The soil in the winter rainfall area has a low clay and, in most cases, it is underlain by silica or calcium (Mucina *et al.* 2006; Desmet & Marsh 2008). Conversely, the summer rainfall area consists of mostly sandy soils with scattered rocks and gravel. The summer rainfall area contains inselbergs scattered along the flat landscape. These inselbergs experience considerably greater precipitation and cooler temperatures that contribute to the more stable soil on these surfaces (Shaw 2017). It is covered with layers of durable rock that may resist erosion and increase the vegetation cover and stability of the soil in comparison to the matrices (Shaw 2017).

1.9. Description of biomes in study areas

i. Desert Biome

This biome is prevalent in the north-west region of South Africa, with a climate that is dominated by summer rainfall (DEA 2013). The annual rainfall is 10 mm in the west and 70 mm in the east. It provides grazing resources, for livestock in this area. Only 20% of it is being protected because the area is not typically regarded as economically beneficial (DEA 2013).

ii. Nama-Karoo Biome

This biome is larger than other arid biomes in South Africa (DEA 2013). It has an annual summer rainfall regime, which ranges from 60 to 400 mm and decreases from east to west.

The average temperatures range from 30 °C in January to below 0 °C in July. The biome has seasonal and perennial rivers and catchments that are useful to livestock for foraging.

iii. Succulent Karoo Biome

Only winter rainfall biome in Namaqualand, the annual rainfall varies between 20 to 290 mm and it experiences relatively high aridity during summer (DEA 2013). Only 30% of this biome is protected. However, it's economic importance in terms of livestock production could emphasize it's importance in sustaining the livelihoods of people in the area (DEA 2013).

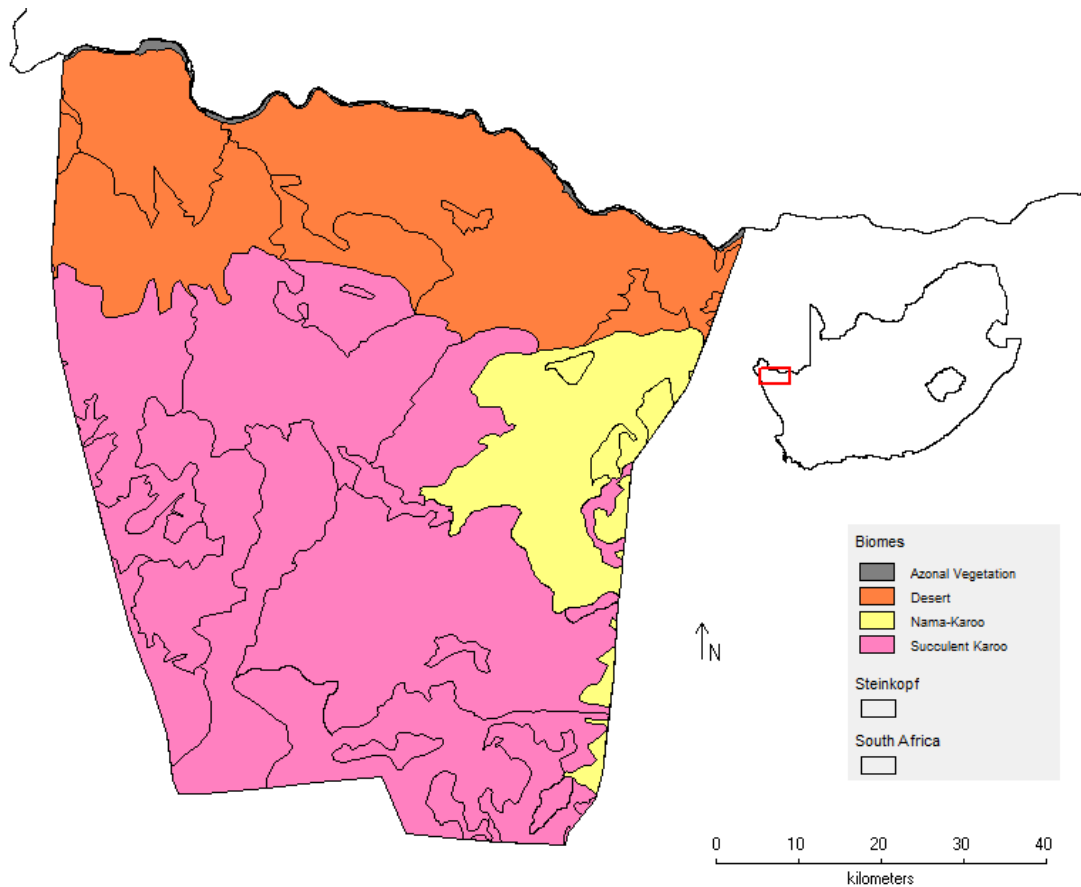


Figure 1.4: Biomes in Steinkopf communal area, the Succulent is the winter rainfall region and Nama Karoo and Desert Biome being the summer rainfall regions in the communal area.

iv. The vegetation of study areas

These biomes have an array of endemics and threatened species that have high conservation worthiness. The biomes have various vegetation types such as Namaqualand Blomveld (Succulent Karoo Biome), Bushmanland Inselberg Shrubland (Succulent Karoo Biome), Namaqualand Klipkoppe Shrubland (Succulent Karoo Biome), Umdaus Mountains Succulent Shrubland (Succulent Karoo Biome), Bushmanland Arid Grasslands (Nama-Karoo), Bushmanland Sandy Plains (Nama-Karoo Biome), and Eastern Gariiep Rocky Desert (Desert Biome), Eastern Gariiep Plains Desert (Desert Biome) and Southern Nababiepsberge Mountain Desert (Desert Biome) that have inselbergs scattered throughout its landscape along the ecotonal zones (Fig. 1.4; Mucina *et al.* 2006; Todd 2006).

In the winter rainfall area, the leaf succulent shrubs dominate sandy plains compared to the non-succulent shrubs on the rocky inselbergs (Hongso *et al.* 2009). The summer rainfall areas are dominated by perennial and annual graminoids (Hongso *et al.* 2009). The affinity of the vegetation in the ecotone alternates between Succulent Karoo Biome and the dominating Nama-Karoo or Desert Biomes, and between the Desert and Nama-Karoo biomes species depending on the land uses, geology and the climate (Fig. 1.4; Hongso *et al.* 2009).

1.10. Grazing Management Systems

Steinkopf is a communal area that forms part of approximately 30% of communal tenures in Namaqualand (Wisborg & Rohde 2004). Livestock farming is one of the primary sources of income in Steinkopf. Residents make use of commercial and smallholder livestock farming, hence approximately 90% of the land is grazed (Desmet & Marsh 2008). The communal area makes use of the kraaling system established in the 18th century, where the herders commute

with their livestock between Bushmanland (the eastern half) and Namaqualand (the western half), in accordance with the availability of water and forage (Kingston 2001).

The carrying capacity of the Karoo, in general, is estimated to be exceeded by 40% or 3 million small stock units (Dean *et al.* 1995). On average, Namaqualand, including Steinkopf have livestock numbers that are 1.85 times higher than what the estimated carrying capacity allows for (Hoffman & Ashwell 2001). Thus, communally owned rangelands are typically regarded as overgrazed due to its overstocking (Will 2003).

1.11. The rationale of the study

Overgrazing, in combination with the threat of increased temperatures and climate change in general, is likely to have cascading effects on rangeland health (Copeland *et al.* 2017).

Amongst other things, this combination will reduce soil stability, nutrient cycling status, and water infiltration capacity of the soil. Evidently, this could affect animals such as small mammals that are dependent on rangeland resources and could result in a reduction of survival rates. Thus, assessing the rangeland health and how it affects small mammals is critically important as it could contribute to the protection and longevity of the small mammals in these rangelands.

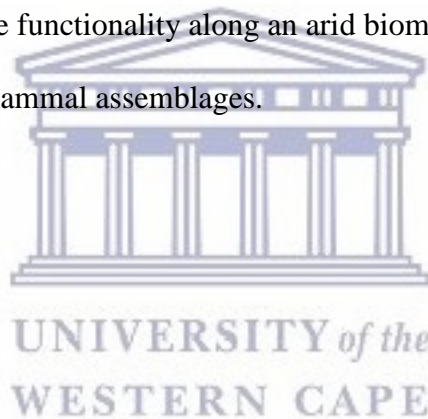
The impacts of land use on landscapes need more attention in order to protect its biodiversity. Ecologists use various methods to remedy degraded landscapes by executing research on the vegetation *in situ*. However, very few studies look at biotic and abiotic factors of the rangelands and make inferences about them as a unit as in the Landscape Functional Analysis (Tongway & Hindley 2004). Therefore, the relationship between small mammal assemblages or any animal and landscape functionality have rarely been explored.

Govender (unpublished thesis) concluded that in Namaqualand communal rangelands, small mammals have adaptations to certain environmental conditions and are occurring in areas where they are not typically expected. Areas are opening up (i.e. dysfunctional landscapes) and creating niches for small mammals that are not expected to be present there. This creates competition between different species and communities that have a negative effect on the small mammal populations. This study will assist in defining the relationship between small mammals and rangeland functionality, and ultimately providing information to assist with better management strategies with future anticipated climatic changes in mind.

1.12. Overall Study Aim

- i. To assess the landscape functionality along an arid biome boundary and its relationship to small mammal assemblages.

1.13. Specific Aims



- i. To determine whether the Succulent Karoo Biome and the ecotone of the study area are more functional than the Desert Biome of the study. Thereafter pre-empt the anticipated desertification changes due to climate change in the biome boundaries.
- ii. To assess the relationship between rangeland functionality and soil indicators (soil stability, water infiltration and nutrient cycling).
- iii. To examine the relationship between rangeland functionality and small mammal assemblages. Thereby assess the potential effects of the change in functionality from Succulent Karoo to Desert Biomes.
- iv. To determine if small mammals can be used as an indicator of rangeland health.

1.14. Research Hypotheses and Null Hypotheses

H₀: There is no significant difference in landscape functionality between the Succulent Karoo Biome, Desert Biome and the ecotone.

H₀: There is no significant relationship between landscape functionality, plant diversity and cover.

H₀: There is no significant difference between small mammal population density and dynamics between the Succulent Karoo Biome, Desert Biome and the ecotone.

H₀: There is no significant relationship between the landscape functionality of rangelands and small mammal assemblages.

1.15. Thesis Chapter Objectives

The objective of Chapter Two is to provide evidence for biome boundary stability or instability in arid communal areas using biotic and abiotic characteristics (i.e. soil stability,

water infiltration and nutrient cycling). This data will be obtained by executing a Landscape Functional Analysis along a Desert – Succulent Karoo gradient. The data will be compared between the Desert Biome, ecotone and Succulent Karoo Biome.

In Chapter Three, the objective is to determine how the small mammal assemblages and reproductive variables vary between the areas and between seasons. The importance of the small mammals in maintaining a healthy landscape will be defined and the consequences of diversity loss will be determined. Therefore, the data provided will be compared along the Desert – Succulent Karoo Biome gradient to assess the effect of present desertification on their populations.

In the concluding chapter, Chapter Four, the objective is to discuss the relationship and trends between the rangeland functionality and the small mammal communities in arid rangelands.



2. Chapter 2

Is land use in communal areas compromising the health of rangelands? A landscape functionality analysis of rangeland along an arid ecotone

2.1. Abstract

Arid rangelands are primarily used for livestock farming. These areas are under threat due to the combined effects of climate change and overgrazing which together can result in biome boundary shifts. This phenomenon could be a major problem for the Steinkopf communal rangeland in South Africa where the potential movement of the Desert Biome into the Succulent Karoo Biome could drastically reduce the functionality of the landscape. The aim of this chapter was to assess the landscape functionality of the arid biome boundary in the Steinkopf communal area. A landscape functional analysis was executed in 27 sites spanning across the Desert Biome, ecotone and Succulent Karoo Biome.

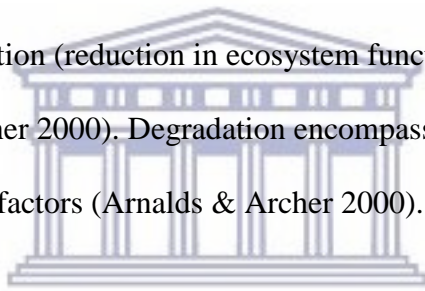
In the 27 sites, 62 different perennial plant species were recorded of which 61% is shared between the Desert Biome and the ecotone, and 54% is shared between the ecotone and the Succulent Karoo Biome. Furthermore, the overall rangeland consists on average of 66% interpatches and 34% patches substantiating its low vegetation functionality. The Desert Biome (70%) and ecotone (66%) have higher interpatch cover than the Succulent Karoo Biome (61%). The low patchiness in the landscape indicates the landscapes inability to adequately cycle nutrient and trap water, which are the two most important resources for this landscape to maintain its functionality. However, more importantly, it shows evidence for the ecotone becoming more arid in relation to its biotic environment whilst maintaining its functionality in relation to is the abiotic environment.

Furthermore, using a Non-metric Multidimensional Scaling, evidence for the desertification of the landscape was found in relation to the shrub density between the Desert Biome and ecotone showing a significant relationship. However, the relationship between the Succulent Karoo Biome and the ecotone showed a significant relationship in relation to the soil surface roughness, soil nature, soil texture, soil stability, infiltration and nutrient cycling. We argue that the change in vegetation to a more arid affinity could pave the way for changes in soils, which would make them more similar to the Desert biome.



2.2. Introduction

Drylands include arid and semi-arid ecosystems that cover 40% of Earth's land surface (MEA 2005). These areas experience high impacts of global climate change, often have low and variable rainfall as well as low nutrient availability, thereby making drylands susceptible to land degradation (MEA 2005; Reynolds *et al.* 2007). Arid rangelands represent ecosystems not suited for intensive agriculture, due to limitations imposed by climate, soils, and topography (Stoddart *et al.* 1975; Holecheck *et al.* 1989; Arnalds & Archer 2000). Livestock farming is the traditional primary use of the world's arid rangelands (Arnalds & Archer 2000). However, the ever-increasing demand for food and natural resources by a rapidly growing human population has exerted additional environmental stresses resulting in widespread rangeland degradation (reduction in ecosystem functionality and landscape heterogeneity; Arnalds & Archer 2000). Degradation encompasses a variety of processes and is driven by abiotic and biotic factors (Arnalds & Archer 2000). In drylands, land degradation often results in desertification.



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Rangelands are under threat from various land uses but also the effects of climate change. Ecotones between biomes are particularly sensitive to changing climatic conditions and are thus ideal locations to study the effects of landscape modification by regional climate (Gosz & Sharpe 1989; Cao *et al.* 2015). The typical patchiness of drylands reduces the sensitivity of rangelands by reducing the effects and risks of degradation by trapping and conserving scarce resources (Tongway & Ludwig 1997). Therefore, patchy areas in rangelands are more productive in resource-limited landscapes than non-patchy areas in the same rangeland.

The Trigger-Transfer-Reserve-Pulse (TTRP) framework assesses landscape functionality and is ideal to assess the movement of ecotones particularly in semi-arid and arid rangelands

(Ludwig *et al.* 1994). This method substantiates the importance of preserving natural patchiness if forage and animal production is to be maintained in resource-poor dryland systems. The method is used to improve the scientific assessment of land degradation at the landscape level (Warren & Agnew 1988). This is to enhance sustainable management practices of the land and to better understand the resilience of drylands (Behnke & Scoones 1993).

The biome boundary shifts in South Africa are researched extensively in relation to the threats that land uses pose to its biomes (Rutherford *et al.* 2011, Masubelele *et al.* 2014; Moncrieff *et al.* 2015; Potts *et al.* 2015). Various land uses reduces the ability of the ecosystem to respond to stress brought on by environmental fluctuations (Ludwig *et al.* 1997). Various studies have pointed out the importance of maintaining landscape functionality for the landscape to be resilient to desertification (Archer & Stokes 2013).

Very little until more recently is known about ecotones in South Africa, and no studies have been done on the ecotone between Desert Biome and the Succulent Karoo Biome, this is a huge gap in the knowledge. One of the main concerns is the moving of the Desert Biome into the Succulent Karoo Biome that will immensely reduce the productivity of the landscape (Ludwig *et al.* 1997; Potts *et al.* 2015). Since newer climate change models based on bioclimatic variables show the Succulent Karoo Biome boundary will be relatively stable, this study will assess whether Succulent Karoo Biome is stable in terms of the three ecosystem services (soil stability, nutrient cycling, and water infiltration capacity) which the LFA method focusses on. Therefore, the aim of this study is to assess the landscape health and functionality along a biome boundary in an arid region. With the aim in mind the following hypothesis was formulated;

- i. There is increased landscape heterogeneity in the Succulent Karoo Biome compared to the ecotone and Desert Biomes.
- ii. There is increased soil stability, water infiltration/runoff and nutrient cycling potential in the Succulent Karoo Biome compared to the ecotone and Desert Biome.

2.3. Materials and Methods

- i. Determining the location of ecotones

The heterogeneity of arid and semi-arid ecosystems makes it difficult to determine the width of an ecotone. Typically, it is regarded as a one-dimensional line (Fortin *et al.* 2000). Some studies have used methods such as wombing (Fortin *et al.* 2000) and fuzzy set modelling (Fisher *et al.* 2006) to determine the width of an ecotone. In this study, I instead used on-site ground-truthing to determine where the percentage of a dominant species in one biome would decrease further away from the biome. This is referred to as the sigmoid wave model (Timoney *et al.* 1993). The Succulent Karoo Biome and Desert Biome have a relatively flat topography since mountainous areas were not included in the study. Therefore, elevation or gradients were not considered in this regard as proposed by Gosz & Sharpe (1989). The initial site was identified as close as possible to the predetermined GPS locations (Succulent Karoo Biome) and gradually as sites were identified *in situ*, we assessed how the landscape and vegetation were changing to eventually that of the Desert Biome.

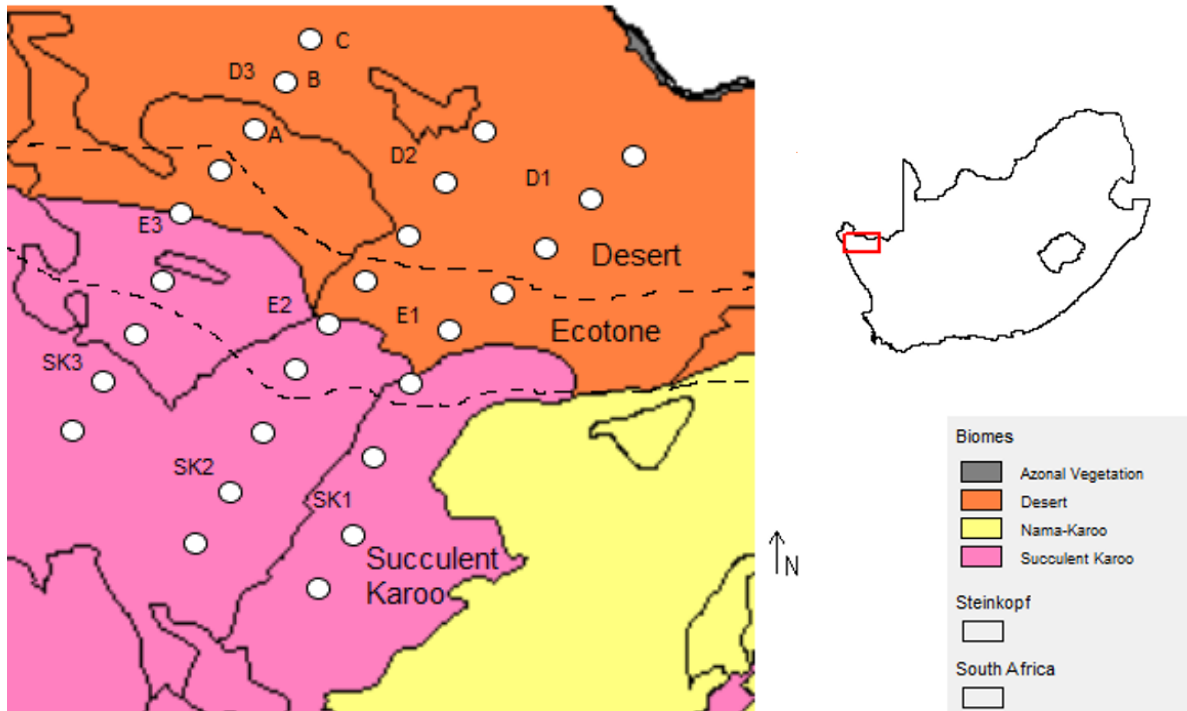


Figure 2.1: Schematic drawing depicting the distribution of sites in the study area (distances between Desert Biome and ecotone was >1000m, whereas the distance between the Desert Biome sites (D1), ecotone (E1) and Succulent Karoo Biome sites (SK1) was >500m). The broken line depicts the predicted ecotonal boundary and the circles are the sites surveyed during the study.

The data for this chapter was collected in the dry season (26 March – 2 April 2017). This is the period when the disturbance (i.e. soil erosion) is most observable, and most annual species are absent (Furniss 2009). The dry season is adequate for testing of water infiltration capacity because it enhances the speed and downward movement of water in the soil (Brouwer *et al.* 1985). All three components of the Landscape Functional Analysis were completed in each of the 27 sites to make inferences between and within the three sequences of sites (i.e. sequence constitutes all sites from SK1A – D1C; Fig. 2.1).

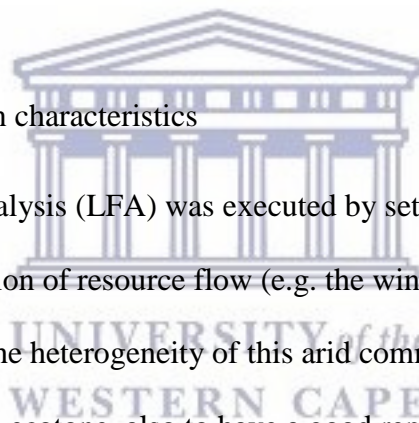
The methods of Tongway & Hindley (2004) was followed to assess the health of communal rangeland. The functionality analysis has three components to it, namely; The Geographic setting of the sampling site, Landscape organisation characteristics and Soil Surface Assessment (SSA; Tongway 1995; Tongway & Hindley 2004). Each component was completed as follows;

ii. Geographic setting of the sampling site

The site description was done by noting the position, GPS coordinates, slope, aspect, lithology, soils, evenness of site's landscape, and vegetation type and the land. The position of the sampling site in the landscape was also noted by identifying the topographic location (Tongway & Hindley, 2004).

iii. Landscape organisation characteristics

The Landscape Functional Analysis (LFA) was executed by setting up a 250m line transect downslope to assess the direction of resource flow (e.g. the wind and/or water; Fig. 2.2). A line transect was used due to the heterogeneity of this arid communal rangeland, the uncertainty of the extent of the ecotone, also to have a good representative of the landscape and vegetation present.



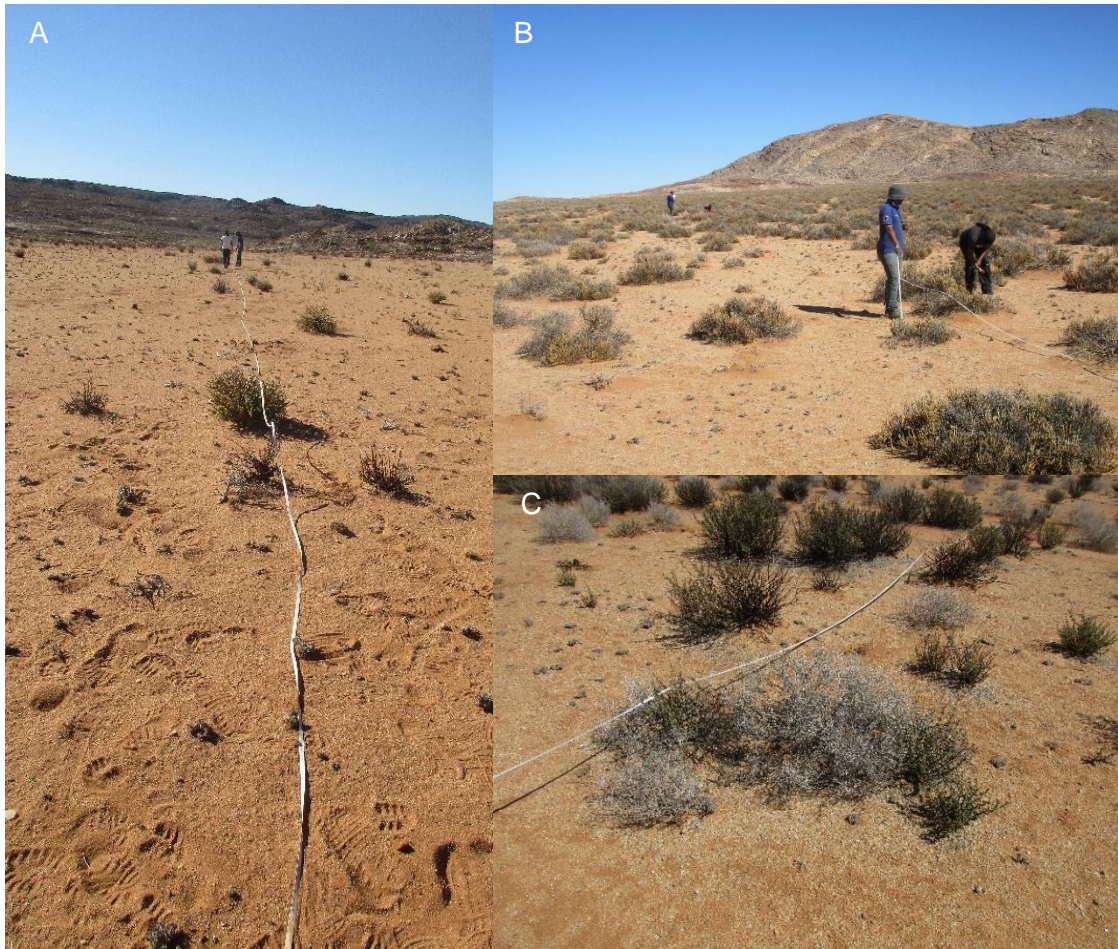


Figure 2.2: The Landscape Functional Analysis assessment in Desert Biome (A), ecotone (B) and Succulent Karoo Biome (C) on a 250m line transect.

The length and width of the obstruction that was in contact with the soil (also known as the tussock) of each patch that traps resources and inter-patch that transport resources were recorded. The type of patch was noted whether it was a complex or simple shrub and it was identified to species-level if possible. In addition, the presence of litter in the patches and inter-patches and excessive erosion was noted.

Annuals were excluded in this study and were instead recorded as litter if present. Standing perennial vegetation was taken into account because livestock primarily feeds on palatable perennial shrubs and grasses in the rangelands (Piers, unpublished thesis). They are also the

most vulnerable life form to degradation because they do not die off during the winter season for the Desert Biome and summer season for the Succulent Karoo Biome (Piers unpublished data).

In terms of the rill survey component, no extensive erosion or rills were noted along the line transects. According to Tongway & Hindley (2004), rills have to be present within 30m of each other to execute a rill survey on them. The rills were not present to this extent and thus a rill survey was not implemented at any of the sites.

For the Point Centre Quadrat (PCQ) the first 100m of the 250m line transects were used (Fig. 2.3). At every 5m point along the line, it was divided into four quarters (Fig. 2.4). In total 80 plants (20 points x 4 quarters) were assessed for each transect and the plant was identified to species level where possible. The distance of the closest plant to the 5m point was measured, its canopy breadth, canopy width, height to the canopy, total height and canopy density (% of overall canopy space occupied by foliage and stems in the quarter) were recorded.

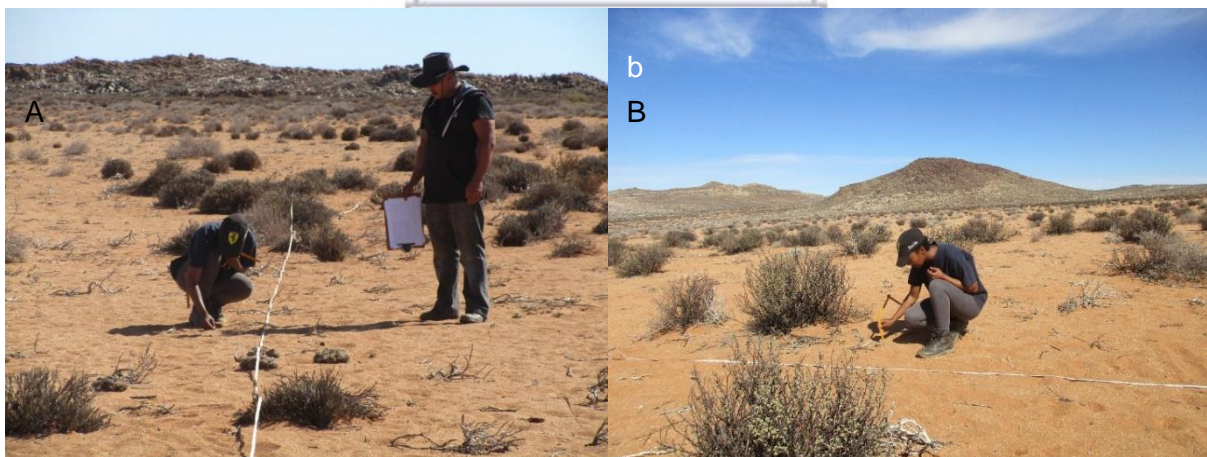


Figure 2.3: Point Centre Quadrat being assessed in the ecotone (A) and the Succulent Karoo Biome (B) along the 100m line transect.

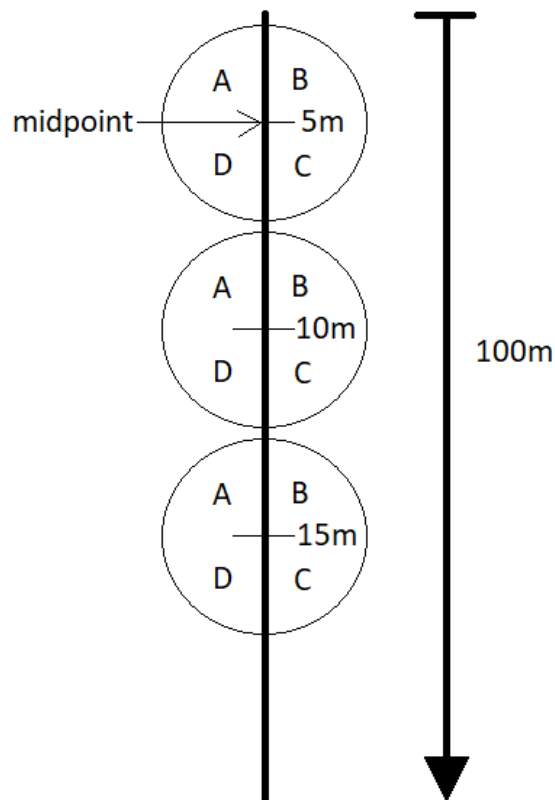


Figure 2.4: Schematic diagram of the Point Centre Quadrat method in each quadrat (i.e. A, B, C and D) the measurements of the closest shrub to midpoint was taken (radius of the circle is 1m from the midpoint).

iv. Soil Surface Assessment (SSA)

To assess the soil surface (SSA), the first 100m of the 250m LFA line transect was used. Five replicates of a simple shrub, complex shrub and inter-patch were assessed for SSA visual indicators (e.g. query zones; Fig. 2.5). At each of these features along the line, the position on the line transect was recorded on a finer scale.

Eleven indicators were noted of which the description of each is given in the manual of Tongway & Hindley (2004), namely; rain splash protection, perennial vegetation cover, litter cover, cryptogam cover, crust brokenness, soil erosion type and severity, deposited materials, soil surface roughness, surface nature (resistance to disturbance), slake test and soil texture (Table 2.2.). These 11 indicators are grouped into three indices that have a specific influence for landscape functioning monitoring, namely; soil stability, water infiltration and nutrient cycling (Tongway & Hindley 2004; Table 2.1).



Figure 2.5: Soil surface assessments were executed to determine the landscape functionality of all areas surveyed. The 11 soil indicators were determined using the methods displayed in A, the trapped resources displayed in B a simple *Ruschia pauciflora* shrub.

Table 2.1: Interpretation of soil surface indicators and functionality index allocation (Soil Stability – SS, Infiltration/Runoff – IR, Nutrient Cycling Status – NCS; Tongway & Hindley 1995; Tongway & Hindley 2004).

Indicator	Interpretation	Functionality Index
Soil cover	Assesses vulnerability to rainsplash erosion	SS
Basal cover of perennial grass	Assesses the contribution of root biomass to nutrient cycling processes	IR, NCS

Litter cover, origin and degree of decomposition	Assesses the availability of surface organic matter for decomposition and nutrient cycling	SS, IR, NCS
Cryptogam cover	An indicator of surface stability, resistance to erosion and nutrient availability	SS, NCS
Crust brokenness	Assesses loose crusted material available for wind ablation or water erosion	SS
Erosion features	Assesses the nature and severity of current soil erosion features	SS
Deposited materials	Assesses the quantity of alluvial deposits	SS
Soil surface roughness	Assesses surface roughness for water infiltration and flow disruption, seed lodgement	IR, NCS
Surface resistance to erosion	Assesses the likelihood of soil detachment and mobilisation by mechanical disturbance	SS, IR
Slake test	Assesses soil stability when wet	SS, IR
Soil surface texture	An indicator of infiltration rate and water storage	IR

2.4. Data Analysis

The data was analysed using Microsoft Excel, IBM SPSS Statistics 21 package, and PCORD 5. In all analyses, p-values less than 0.05 were considered significant. A Shapiro-Wilk test for normality was used since the data set had more than 50 but less than 2000 data entries.

The total Soil Surface Assessment indices were calculated using the three indices namely soil stability, infiltration/runoff and nutrient cycling status as follows:

$$\sum(\% \text{ of each functional zone})/100 \times \text{SSA index for each functional zone.}$$

The relationship between the 11 soil indicators was assessed using a correlation and partial correlation controlling for sites as well as its relationship to soil stability, infiltration/runoff and nutrient cycling status (SSA indices). Similarly, a partial correlation controlling areas (Desert Biome, ecotone, Succulent Karoo Biome) was used to assess the SSA indices, patch type percentages, and average patch lengths, average patch widths and the interpatch lengths.

A one-way ANOVA and Tukey Post Hoc test were used to assess the relationship between SSA indices. A partial correlation test was performed to assess the relationship between SSA indices for each patch type. The relationship between the sites and areas was assessed using a Post Hoc Test to assess its similarity in relation to the SSA indices.

i. Non-Metric Multidimensional Scaling

A Non-metric Multidimensional Scaling (NMMS) was constructed in the PCORD statistical package to assess relationships in landscape functionality along the Desert – Succulent Karoo Biome boundary. The relationship between sites were evaluated using the variables aspect, biome, slope, vegetation type, land use, lithology, soil type, topography, presence of water, runoff rate, dryness, potential of erosion, potential of water storage, species richness, vegetation cover, number of plants, and plant species present in the plots. The NMMS was run for species abundance and presence/absence of species in each of the sites. To ensure the best results, the NMMS Ordination was run 10 times for both to determine differences between these sites and the spatial distribution of sites. The NMMS was run for 500 iterations using a slow and thorough approach.

Two-dimensional plots were formulated using the joint plot method to establish the reasons for the relationships viewed in the NMMS. The axes with stress value less than 30 were used. The listed variables or plant species that were responsible for the relationships viewed in the NMMS have noted if it had a tau value of less than 0.3. These factors with a tau value less than 0.3 are regarded as having a significant effect on grouping the sites in the NMMS. To test the extent that these variables have on the outcome of the NMMS, an IBM SPSS Statistics 21 statistical package was used to test for normality and significance using

appropriate tests. A dendrogram was developed in Primer version 5 on the similarities between the different sites using presence and absence data of plant species between sites.

2.5. Results

In the 27 sites, 62 different perennial plant species were recorded of which 26 were recorded in the Desert Biome, 40 in the ecotone and 38 in the Succulent Karoo Biome (Appendix 1). The species overlap between the Succulent Karoo Biome and the Desert Biome is relatively extensive with a 38% similarity. Appendix 2 indicates the similarity between the Desert and ecotone is 61% (i.e. *Psilocaulon dinteri*; *Stipagrostis ciliata*) and the Succulent Karoo Biome and ecotone have a 54% similarity (i.e. *Cheiridopsis denticulata*). Of the overall species recorded, the most common growth form was leaf-succulent shrubs (27 spp.), grass (12 spp.), stem succulent shrubs (12 spp.), non-succulent shrubs (10 spp.), and trees (one spp.).

i. Landscape Heterogeneity

The overall rangeland consists on average of 66% interpatches and 34% patches (Table 2.2). The Succulent Karoo Biome has significantly larger patches in comparison to the Desert Biome and ecotone. The Desert Biome has the highest interpatch cover with 70%, followed by ecotone with 66%, the Succulent Karoo Biome has the lowest cover with 61%. However, the Succulent Karoo Biome interpatches are continuous and thus it has a higher average interpatch length in comparison to the Desert Biome and the ecotone (Table 2.2).

Table 2.2: Patch and interpatch measurements in each area and the relationship between the areas in relation to the vegetation characteristic measured.

Variables (m)	Desert Biome	Ecotone	Succulent Karoo Biome	Significance
Average patch width	0,501	0,609	0,629	($F = 1.690; p = 0.206$)

Average patch length	2,005	1,055	0,694	($F = 7.834; p = 0.002$)
Average interpatch length	2,058	2,016	2,639	($F = 0.223; p = 0.802$)

There is a significant correlation between the average patch width and average interpatch length ($p = 0.015$). A wide variety of patch lengths was found between the areas where the Desert Biome has the highest patch length and the Succulent Karoo Biome has the shortest. The Desert Biome has a higher average patch length because it has a high abundance of *Psilocaulon dinteri*, a broadleaf succulent shrub.

ii. Vegetation characteristics

An ANOVA showed that the average area occupied per shrub is significantly different ($F_{22,61}; p = 0.001$) where the Succulent Karoo Biome has the highest average area occupied per shrub. The distance between shrubs also show a significant difference ($F_{25,46}; p = 0.002$) the patches in the Succulent Karoo Biome are distributed further apart than the Desert Biome and ecotone. The density of shrubs per 100 m² ($F_{6,16}; p = 0.035$) was restricted to only 80 plants along the PCQ transect. This variable showed a significant relationship between areas, here again, the Desert Biome had more shrubs per 100 m². However, patch volume, the area of shrubs, and absolute density showed no significant relationship between the areas (Table 2.3).

Table 2.3: The variability in vegetation parameters derived from the Plant Centred Quadrat analysis between areas surveyed.

Variable	Desert	Ecotone	Succulent Karoo Biome
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Average distance between shrubs (m)	0,487	0,465	0,536
Average canopy volume (m³/sq. m)	0,059	0,068	0,105
Average absolute density (number of shrubs per m²)	3	3	6
Average area occupied per shrub (m²) *	0,314	0,249	0,342
Average area occupied by all shrubs (m²)	218,19	260,82	484,71

* if encountered in a 1 x 1m patch a complex shrub (more than one individual shrub) was measured as one patch.

A correlation test showed that the listed variables show no significant relationship between Desert Biome, ecotone and the Succulent Karoo Biome. However, there is a significant correlation when comparing the variables (Fig. 2.6).

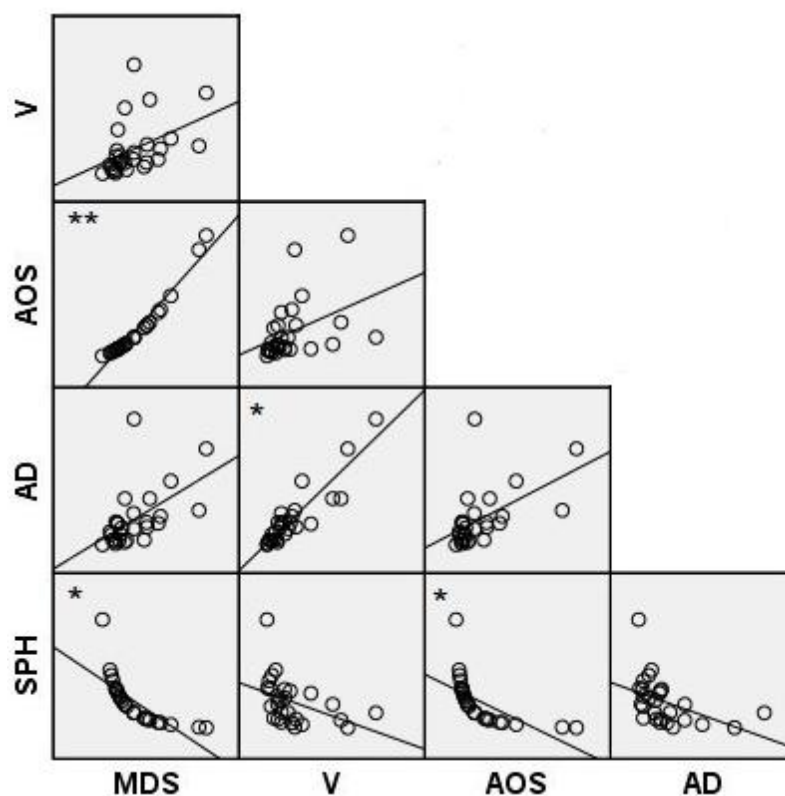


Figure 2.6: Correlation matrix depicting the relationship between vegetation characteristics (Legend: MDS – mean distance between shrubs; AOS – the average area

occupied per shrub; SPH – shrubs per 100 m; V – Volume; AD – Absolute Density; $p > 0.01$ *; $p > 0.001$ **).

iii. Soil Surface Assessment

The soil surface assessment indicates an average percentage of soil stability (39%), water infiltration/runoff (51%) and nutrient cycling status (35%) for the overall landscape (Appendix 3). There was no significant relationship found between sites in relation to the SSA indices between areas (Fig. 2.7).

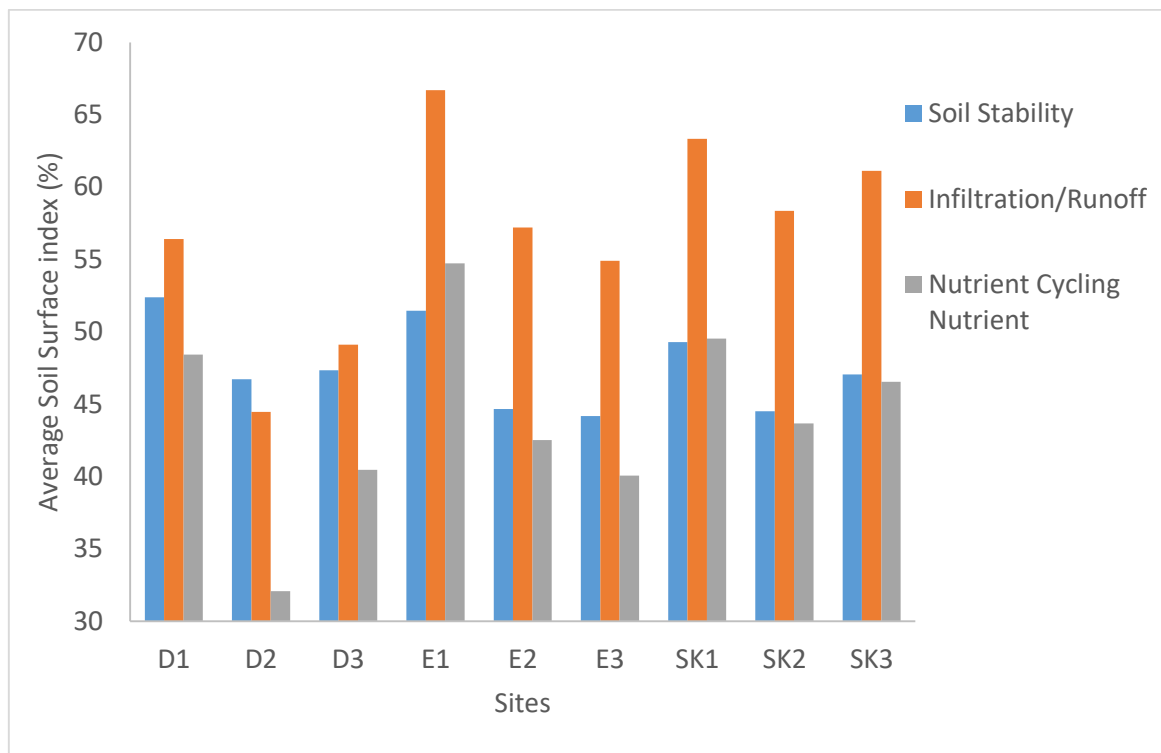


Figure 2.7: The average Soil Surface Assessment indices of the sites surveyed along the Desert – Succulent Karoo Biome gradient.

The functionality in each of the patch types are different with the interpatches having less soil stability, water infiltration and nutrient cycling, followed by the simple shrubs and lastly the complex shrubs which are more functional (Fig. 2.8).

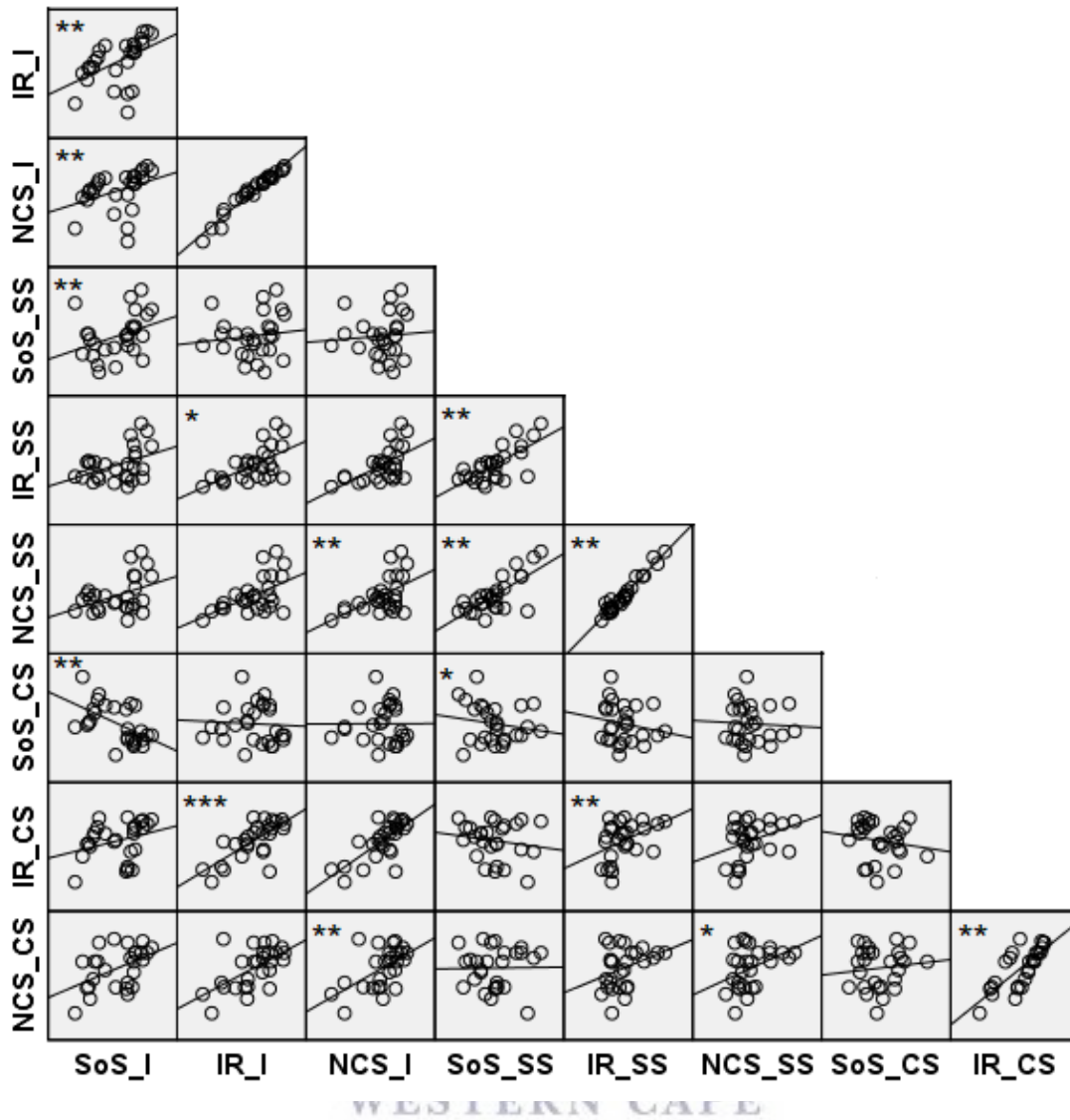


Figure 2.8: Correlation matrix depicting the relationship between vegetation characteristics (Legend: SoS – Soil Stability; IR – Infiltration/Runoff; NCS – Nutrient Cycling Status; I – Interpatches; SS – Simple Shrubs; CS – Complex Shrubs; $p < 0.0001$ ***; $p < 0.001$ **; $p < 0.01$ *).

iv. The relationship between sites using species abundance

Using an NMMS, the final stress value for axis 1 ($p = 0.004, r^2 = 0.342$) and 2 ($p = 0.004, r^2 = 0.847$) were 49.953 and 38.833, respectively (Fig. 2.9). The final stress value

was 10.907 for a 2-dimensional solution with a final instability value of 0.00. The axis 1 versus 2 explains 72.9% of the relationship between the data.



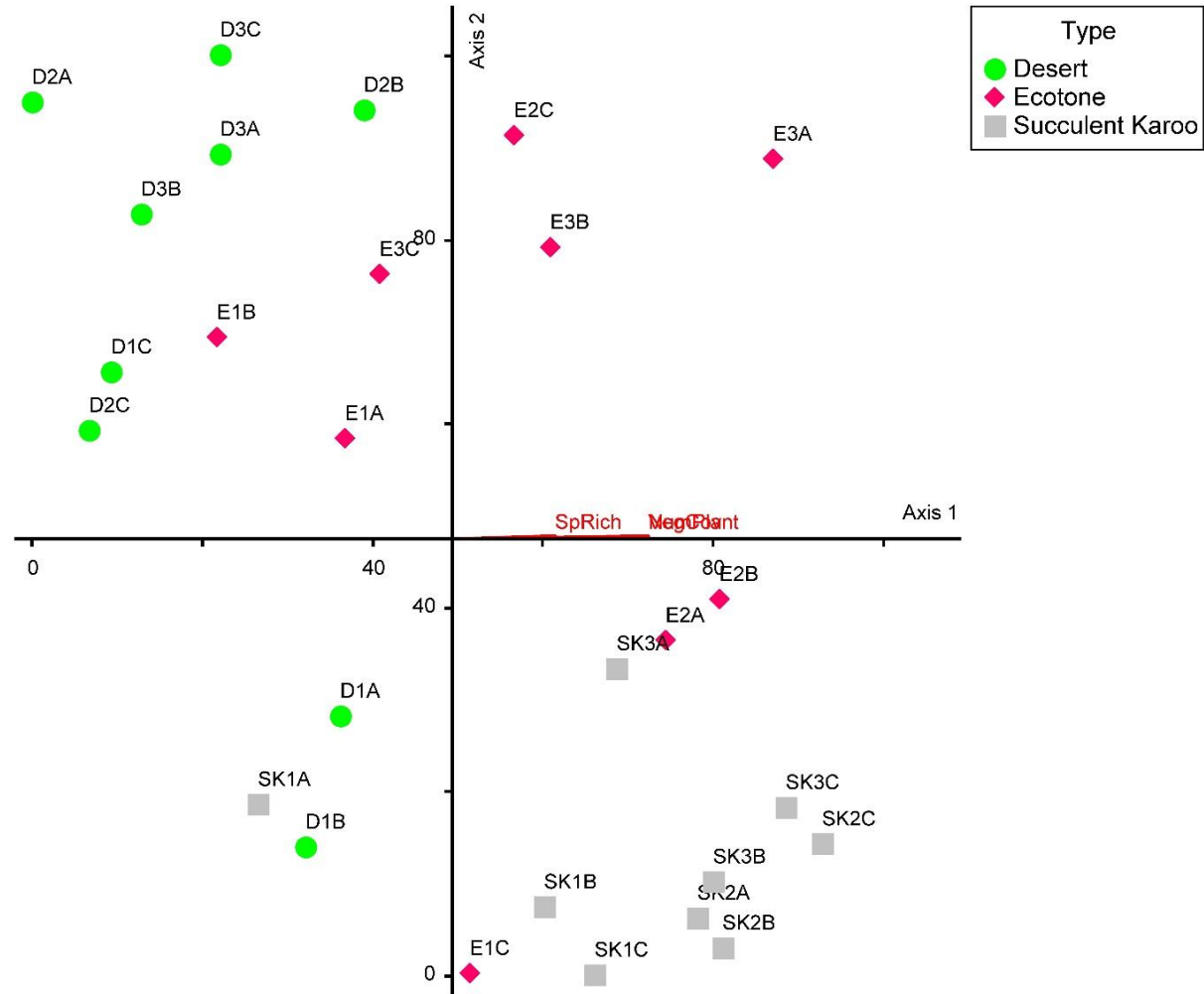


Figure 2.9: Non-Metric Multidimensional Scaling depicting the relationship between sites using species vegetation abundance data.

According to Fig 2.8 using the plant species listed in Appendix 1, the ecotone sites were more closely related to the Desert sites as it appears the ecotone vegetation is more arid.

Stipagrostis sp. is typical of the Desert Biome and is relatively abundant in ecotone sites as it composed 51% of the total vegetation cover of the ecotones. However, it is evident that vegetation cover ($r = 0.472, \tau = 0.361$) and species richness ($r = 0.652, \tau = 0.492$) is correlated to axis 1. An increase in vegetation cover indicates an increase in species richness along axis 1 indicating that Succulent Karoo sites and some ecotones have more vegetation cover and are more species rich. The NMMS analysis conducted shows that the abiotic factors (that include soil texture, soil roughness and soil nature) do not contribute significantly to the relationship between sites as their tau values were less than 0.3.

Various plant species were responsible for the relationship displayed by the Desert and Ecotone and have a strong relationship with axis 2 namely, Bees gras ($r = 0.804, \tau = 0.733$), *Mesembryanthemum* sp1 ($r = 0.623, \tau = 0.390$) and *Psilocalaon dinteri* ($r = 0.689, \tau = 0.718$). Species such as *Psilocalaon subnodosum* ($r = -0.464, \tau = -0.411$), *Ruschia pauciflora* ($r = 0.791, \tau = 0.623$) and *Stipagrostis cilliata* ($r = 0.475, \tau = -0.470$), *Zygophyllum retrofractum* ($r = 0.600, \tau = 0.513$) were most important for the relationship depicted between Succulent Karoo Biome sites and other areas.

v. The relationship between sites using soil surface indices

The final stress value for axis 1 ($p = 0.004, r^2 = 0.73$) and 2 ($p = 0.004, r^2 = 0.208$) were 40.16 and 10.98, respectively (Fig. 2.10). The final stress value was 10.32 for a 2-dimensional solution with a final instability value of 0.00026. The axis 1 versus 2 explains 74% of the relationship between the data.

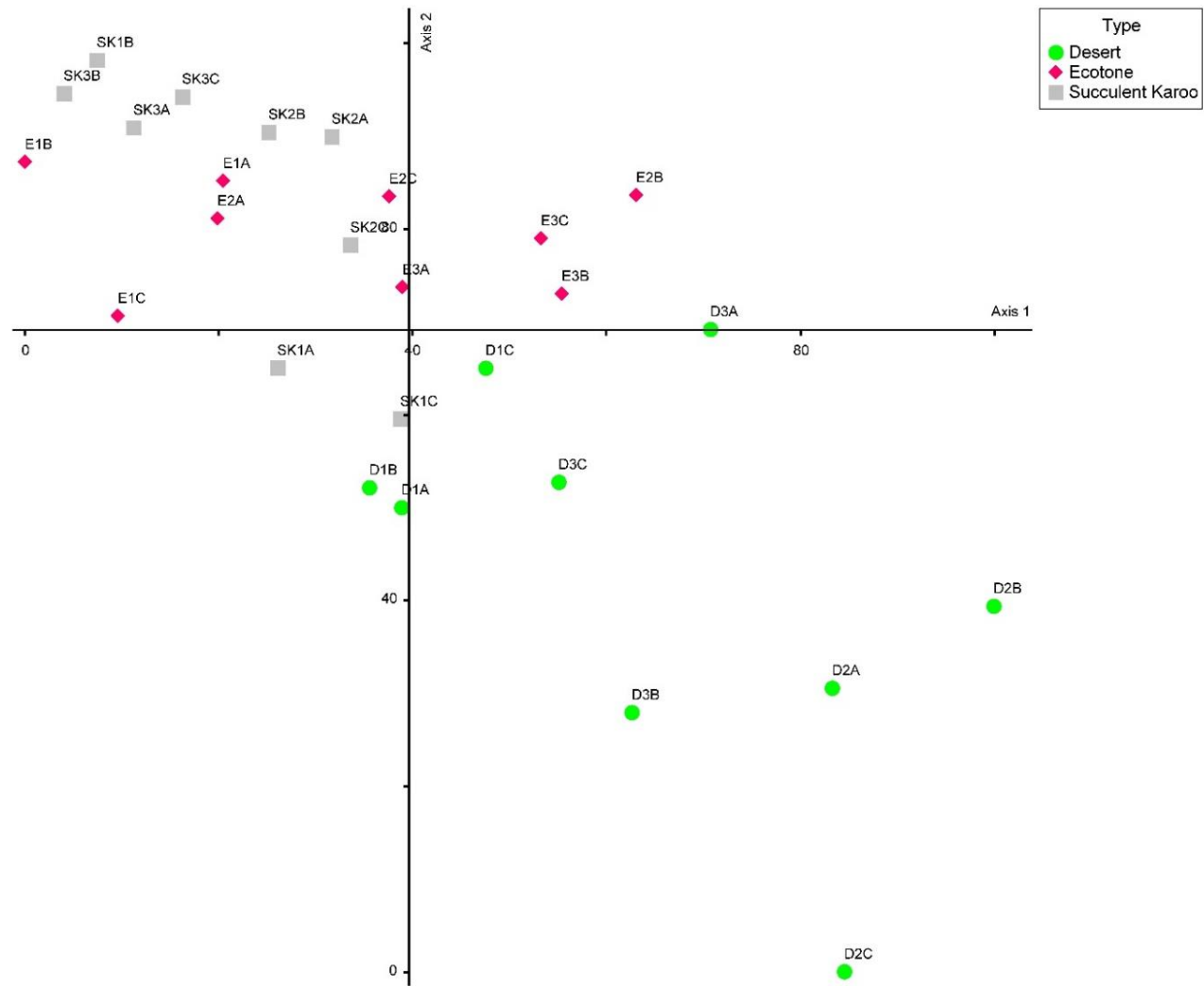


Figure 2.10: Non-Metric Multidimensional Scaling depicting the relationship between sites using only abiotic data.

Figure 2.9 displays the relationships between sites using the 11 soil indicators listed in Appendix 3. It is evident that the Succulent Karoo Biome instead of the Desert Biome is more closely related to the Ecotone sites. The NMMS showed a clear distinction between areas concerning indices measured. The abiotic factors that have a strong relationship with axis 1, litter ($r = -0.892$, $\tau = -0.832$), soil surface roughness ($r = -0.660$, $\tau = -0.345$), surface nature ($r = 0.612$, $\tau = 0.445$), soil texture ($r = 0.374$, $\tau = 0.338$) and the following with axis 2, soil stability ($r = -0.607$, $\tau = -0.530$), infiltration/runoff ($r = -0.945$, $\tau = -0.861$), and nutrient cycling status ($r = -0.928$, $\tau = -0.834$).

2.6. Discussion

The results showed that the landscape of Steinkopf communal rangeland had relatively low functionality as it consists of 66% interpatches and 34% patches. Hence, overall, the landscape is unlikely to trap resources adequately and this may worsen if the interpatches increase in length and number. Overgrazing, which is common in the study area, usually results in a decrease in vegetation cover which may subsequently increase interpatch lengths. The functionality of the overall landscape as described is relatively similar to other studies in drylands (e.g. Rezaei *et al.* 2006). According to Ludwig *et al.* (2002), a landscape with low functionality has more interpatches, low patch widths, lengths and numbers. Patches are very important in trapping resources such as water and nutrients in arid landscapes where these resources are scarce (Ludwig *et al.* 2005). Loss of patches can hinder the distribution of the resources around landscapes and diminish opportunities for nutrient cycling and water infiltration; therefore, it is an indication of functionality (Noy-Meir 1981; Holm 2000; Ludwig *et al.* 2005).

The Desert Biome has significantly longer patches that are attributed to a few complex patches in the landscape that contributes to its functionality. These patches allow the Desert Biome to trap resources and reduce the loss of resources due to erosion. Although, the ecotone is intermediary it has vegetation closely related to the Desert Biome thus it is evident that this area has a relatively higher patch length than the Succulent Karoo Biome.

The correlation analysis indicated a significant correlation between patch width and length. This is apparent because larger and wider patches increase the cohesion of soils and resistance of soil to the wind, hence the soil becomes more stable and shrubs can establish themselves enhancing plant growth (Bang *et al.* 2010; Rehacek *et al.* 2017). Wind erosion intensifies by speed and extent given there is no resistance such as geology, surface roughness and vegetation cover (Thurow 2013; Rehacek *et al.* 2017).

Perennial canopy volume is correlated to wind speed and rainfall interception (Weltz *et al.* 1998; Holm 2000; Huenneke *et al.* 2002; Ludwig *et al.* 2005; Chartier & Rostagno 2006). An increase in canopy/vegetation cover results in a reduction in wind speed hence reducing the amount of soil erosion allowing the soil to establish itself and therefore enhancing plant productivity (Ludwig *et al.* 2005; Okin *et al.* 2009; Tang *et al.* 2016). Although wind speed distributes soil and nutrients in the landscape, the canopy cover reduces the intensity of the wind preventing the topsoil from being completely lost (Van Pelt *et al.* 2010; Rehacek *et al.* 2017).

Wider patches trap more resources from interpatches and other patches (Barbosa *et al.* 2010). They have become adapted to the environment by increasing in number and size to store moisture that is a scarce resource in the landscape (Marchamalo *et al.* 2014). Grasses and shrub cover is heavily influenced by seasonal rainfall patterns (Roux 1966; Hoffman *et al.*

1990). These patches also allow litter and nutrients to be recycled and decayed more efficiently.

According to this study, the vegetation of the ecotone has a more Desert biome affinity given the current land uses are not regulated it might progress and translate to the abiotic environment and diminish the opportunity for nutrient cycling and adequate water infiltration (Johns 1983; Lang & McCaffrey 1984; Holm 2000; Huenneke *et al.* 2002; Okin *et al.* 2009). This would result in the Succulent Karoo Biome losing its patchiness and unable to retain resources which will just worsen and reduce the landscape's functionality (Bastin *et al.* 2002; Ludwig *et al.* 2005; Havstad *et al.* 2013). The significant distance between shrubs infers more energy is needed to transport resources from one patch to the next (Holm 2000). The Desert Biome spends less energy transporting resources because it has an array of small simple grass shrubs that contributes to its functionality. The ecotone is more functional in this regard because it has a low average distance between shrubs that allows it to transport resources more efficiently using less energy.

According to the study, the Desert Biome has more shrubs per 100m² because it is a grassier area and has more species such as *Stipagrostis* sp. 1 that does not adequately trap resources because it is so small. However, this also leads to a more stable soil type because patches concentrate soil from interpatches making it coarser allowing for more infiltration of water into the soil (Huenneke *et al.* 2002). The larger shrubs in the Succulent Karoo Biome is a preferred characteristic to trap resources, especially in arid ecosystems, however, small shrubs are also required in the landscape to provide other important ecosystem services (Tongway & Ludwig 1997).

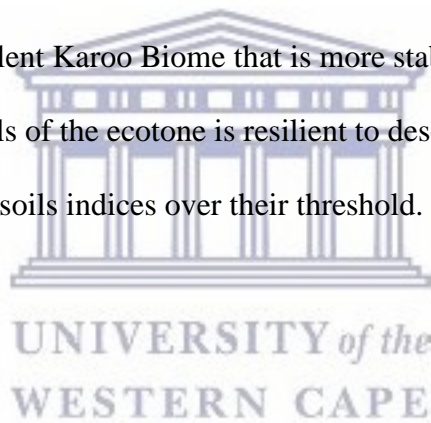
In comparison to the study by Van der Walt *et al.* (2012), the soil stability in this study does not decrease with an increase in average interpatch length. In this study, it is evident that the patch size (width and length) is positively correlated with nutrient cycling and water infiltration. These results are congruent with the finding that the infiltration/runoff rate and nutrient cycling status are the two LFA indices that has the most significant effect on the functionality of the landscape. This finding needed a more in-depth investigation hence a correlation test was performed using the 11 LFA variables measured. According to the correlation test, litter, soil surface roughness, surface nature/resistance and soil texture had a significant correlation with infiltration/runoff rate and nutrient cycling.

Desertification plays a major role in the loss of vegetation cover and ultimately an increase in interpatches. In grasslands, desertification affects ground processes before it is evident above ground (Peters 2002; Su *et al.* 2004; Tang *et al.* 2016) as previously noted. However, the soil surface assessment for this study showed that the desertification and land uses are affecting the above-ground processes more so than the below ground. The Desert Biome vegetation appears to be expanding into the ecotone thus the vegetation in this area is closely related to the Desert. Although the soil of the ecotone is functional, the biotic characteristics might gradually progress into the abiotic processes and enhance the desertification process.

Biotic responses to global climate change will not initially manifest as ecotone shifts, rather as subtle changes in ecosystem states and processes (Knapp & Smith 2001). However, once an ecosystem change has occurred, relaxation of stress and disturbance will not necessarily enable a system to return to its original state (Rapport & Whitford 1999). Therefore, continuous disturbance such as overgrazing and recurrent droughts in the study area, to an already deteriorating and sensitive landscape will result in a chronically dysfunctional landscape because it takes longer to recover from a disturbance event. As such, soil structure

(Thurow 2013), distribution and abundance of water and nutrients (Tongway & Hindley 1995; Havstad *et al.* 2013; Ludwig & Tongway 2013), and plant composition (Hobbie 1992) will eventually become affected.

The key finding of the study is that the Steinkopf communal area has a low landscape functionality due to the high proportion of interpatches. Evidently, the landscape cannot store resources such as water infiltration and nutrient cycling which is essential for this landscape's functionality according to this study. The lack of trapping resources is closely related to desertification and this is imminent in this landscape. The Desert Biome is moving towards the Succulent Karoo Biome as proven by the close relationship the ecotone and Desert Biome has in relation to its biotic characteristics. However, the ecotone has a significant similarity in its abiotic factors to the Succulent Karoo Biome that is more stable and functional. It is evident that as for now the soils of the ecotone is resilient to desertification, but continued disturbances could push these soils indices over their threshold.



3. Chapter 3

Small mammal assemblages and associated body condition along an ecotonal boundary in an arid communal rangeland

3.1. Abstract

Small mammals are typically used as biological indicators since they have rapid behavioural, dietary, and morphological responses to any biotic changes in their habitat. They are able to inhabit a variety of landscapes due to their small size, thus they are widespread, especially in disturbed and pristine ecosystems. Steinkopf communal area is in an arid area where desertification is threatening the vegetation in the landscape. The rodents depend on this vegetation for shelter and food, and in turn, their activity contributes to the health of the rangeland. Their burrows assist in water infiltration into the soil in this water-scarce landscape and they promote nutrient cycling as well by storing food in their burrows. This study aimed to determine whether the density, composition, and body condition of the rodents could be correlated to the condition of the vegetation in their habitat. Nine sites were selected to set up 216 Sherman live traps for seven consecutive nights across the Desert Biome, ecotone and Succulent Karoo Biome gradient and three replicates of each zone was done. The same sites were used to perform a 250 m line transect to assess the vegetation characteristics and compared to small mammal assemblages. It is evident that the Succulent Karoo Biome has greater plant species richness, diversity, and vegetation cover than the ecotone and Desert Biome which are relatively similar in relation to their vegetation characteristics. The three rodent species captured in this study were more abundant in the Succulent Karoo Biome with *Gerbillurus paeba* being the most abundant. The rodents are tracking vegetation condition since desertified landscapes are affecting their reproduction and

health. *G. paeba* is much smaller in comparison to the other species captured namely *Elephantulus rupestris* and *Desmodillus auricularis*. They are able to adapt much easier since they reproduce year-round, are omnivorous, and are nocturnal and prefer feeding in open areas. Essentially, *G. paeba* are able to replace the ecosystem services delivered by the other rodents in the landscape due to them being more vulnerable to desertification.



3.2. Introduction

Small mammals, especially rodents, play an important role in ecosystems worldwide (Hart 1971). They have rapid behavioural, dietary, and morphological responses to any biotic changes in ecosystems (Pergams & Lawler 2009; Stapp 2010). They adapt easily to any habitat and are widespread in an array of landscapes where they contribute to the ecosystem functioning of those landscapes. These characteristics of rodents are essential in arid and semi-arid rangelands since the vegetation composition and landscape is closely correlated to an ever-changing climate.

Small mammals are critically important to maintaining heterogeneity in landscapes because their fossorial habits contribute to the health of these landscapes. Some small mammal burrows are close to the surface but are particularly extensive and used as a means to protect themselves from predatory animals (Eadie 1939; Jameson 1949; Kinlaw 1999). However, other burrows are as deep as possible for protection from heat, nesting and to store food (Jameson 1949; Kinlaw 1999; Louw *et al.* 2017). These burrows provide bare soil on which plant succession can commence, contributing to the diversity and vegetation cover of the rangelands amongst other things (Larrison 1942; Laycock 1958; Whitford & Kay 1999; Louw *et al.* 2017).

Rodent burrows provide a site for the establishment of vegetation that needs soils that are more porous. Their burrows loosen up the typically compacted soils and allow for adequate water infiltration. This improves the soil stability of the landscape and directly contributes to rainfall interception in water-scarce landscapes where it is essential to capture this resource as efficiently as possible. Their burrows are also storage and refuge for the seeds they collect

during winter as well as a refuge for other animals e.g. vertebrates and invertebrates (Cameron 1977).

The decomposition of plant material (e.g. litter, seeds) in the soil stored by these soil-dwelling organisms alter the chemical and physical properties of soils (Van Breemen 1993; Hoffmann & Zeller 2005; Aguilera *et al.* 2016). This contributes to the soil stability of the rangeland enhancing vegetation composition, which small mammals are dependent on indicating a vital reciprocation (Jameson 1949). Evidently, an increase in vegetation composition reduces erosion and similarly improves the soil texture and stability that accommodates their burrowing behaviour (Jameson 1949).

Various studies have categorized small mammals, especially fossorial individuals, as ecosystem engineers in an arid landscape (Kinlaw 1999; Whitford & Kay 1999; Butler & Sawyer 2012; Louw *et al.* 2017). Jones *et al.* (1994) defined ecosystem engineers as organisms that moderate the availability of resources to other species in the ecosystem. They alter the physical properties of biotic and abiotic materials leading to the creation of habitats (Jones *et al.* 1994). Their activities provide various functional roles in ecosystems such as nutrient cycling, soil stability, water infiltration, interactions with plants and modification of environments (Happold 2001). They reduce interspecific competition between plant species and thus positively influence plant diversity (Kerley 1992a; Keller & Schradin 2008).

The association between animals and plants are fundamental. Therefore, the type of plants of a given area determines what kinds of small mammals will live there (Jameson 1949).

Rodents are restricted in their distribution by their ability to access resources such as food, mating partners, shelter and protection from predators (Whithers 1983; Kotler 1984; Kerley *et al.* 1990; Hoffmann & Zeller 2005; Schradin 2005). Very little is known about the small

mammals over a landscape spatial scale in drylands and along its biome boundaries in communal rangelands especially in South Africa.

Some studies characterise the presence of certain small mammal species as indicators of poor rangeland functionality (Taylor 1936; Sieg 1987). Desertification, which poses a great threat to the vegetation composition in rangelands are related to the diversity and density of small mammals in rangelands, which could be detrimental to the ecosystem functionality (Blaum *et al.* 2007; Bosing *et al.* 2014). Apart from the change in small mammals' demographics, their overall health is also affected (Jakob *et al.* 1996; Eccard *et al.* 2000; Blaum *et al.* 2007; Hoffmann *et al.* 2010; Kok *et al.* 2012). Changes in the vegetation community composition reflect in their body condition indices since this indicates a change in resource availability and shelter making them vulnerable to predation (Hoffman & Zeller 2005; Hoffmann *et al.* 2010). In order to fill the knowledge gap, the aim of this study was to assess the effects of vegetation dynamics on small mammal population densities and body condition along arid biome boundaries. With the aim in mind the following research hypothesis was formulated;

- i. There is no difference in the body condition and other small mammal characteristics between small mammal species.
- ii. There is no difference in small mammal characteristics between seasons.
- iii. There is no difference in small mammal diversity between biomes, vegetation cover and plant diversity.

3.3. Methods and Materials

i. Site Selection

The sites of the Landscape Functional Analysis were used as a basis for the selection of this small mammal survey (Fig. 3.1). One sequence of sites was used as a representative for this study. Three of the sites in each area (i.e. Desert Biome, ecotone and Succulent Karoo Biome) were selected resulting in nine sites being surveyed.

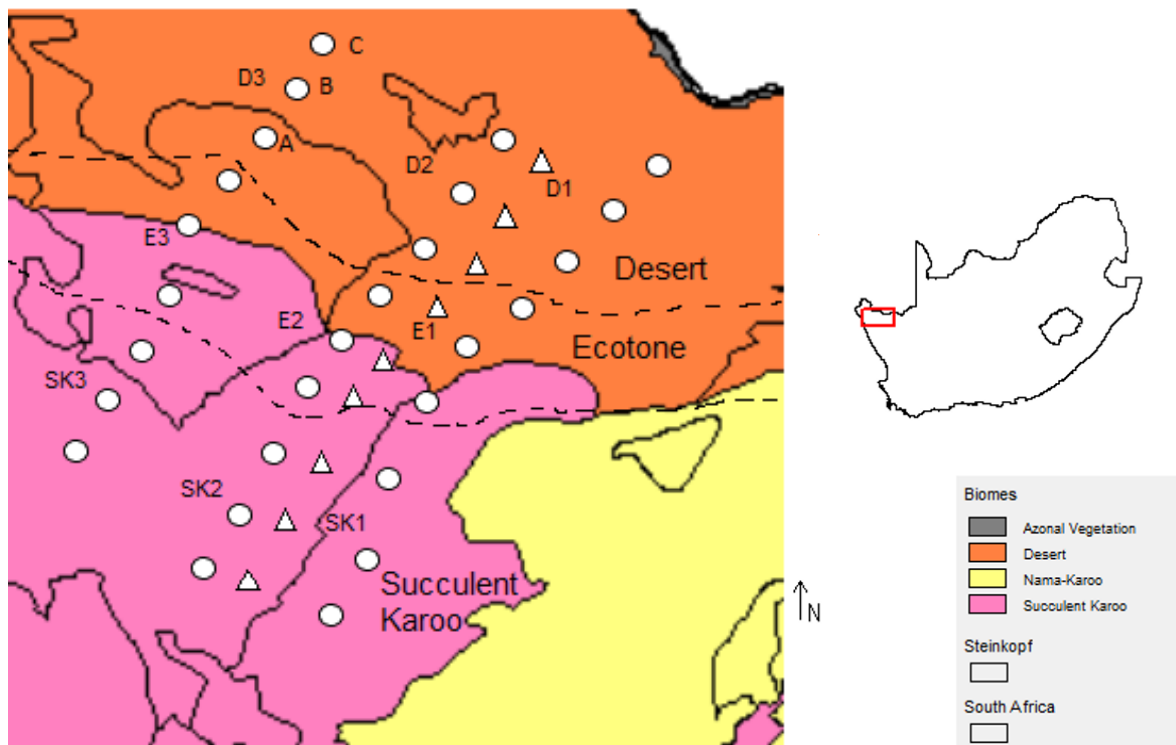


Figure 3.1: Schematic drawing depicting the distribution of sites in the study area (distances between Desert Biome and ecotone was >1000m, whereas the distance between the Desert Biome sites (D1), ecotone (E1) and Succulent Karoo Biome sites (SK1) was >500m). The broken line depicts the predicted ecotonal boundary and the circles are the sites surveyed during the study. The triangles depict the small mammal trapping sites along the Desert - Succulent Karoo Biome gradient.

ii. Data Collection

a. Small Mammal Survey

Sites were surveyed for small mammal assemblages in August 2017 (wet season) and May 2018 (dry season). The wet season trapping for the winter rainfall Succulent Karoo Biome and dry season for the summer rainfall Desert Biome took place for a duration of seven days from 20 August to 31 August 2017. The dry season trapping for the Succulent Karoo Biome and wet season for the Desert Biome took place for a duration of seven days from 3 May 2018 to 10 May 2018.

The trapping took place during both seasons because the biomes experience different rainfall seasons, to allow for unbiased trapping in each ecotone. For a duration of seven days, 24 live Sherman traps were set up each site (i.e. SK1, E1, and D1). The three replicates were set up more than 500 m apart to eliminate the possibility of an animal moving from one site to the next (Dickman *et al.* 1995).



Figure 3.2: PVC Sherman live trap next to a shrub in the ecotone.

The type of traps that were used is PVC (Poly Vinyl Chloride) Sherman live traps (Fig. 3.2; 216 x 54 x 68 mm), these traps are cheap, simple to construct, waterproof and have been proven to be effective at trapping very small mammals typical of the arid and semi-arid ecosystems (Willan 1979). Trap grids were used because it is effective since it allows area size to be determined. Furthermore, grids were used to make inferences on small mammal communities in different habitat types (i.e. Succulent Karoo Biome, ecotone and Desert Biome). Gridding is also used as a method to sample abundance and population densities of other small mammals (Cameron 1977).

The individual traps were placed 10 m apart to allow the trap grids to cover a larger home range and thus considering territoriality of the small mammals (Fig. 3.2; Meserve & Glanz 1978; Kerley & Erasmus 1992; Keller 2005). The total area covered by the traps over the three areas is approximately 7500 m² (number of traps x length x breadth x number of replicates; twenty-five traps x 10 m x 10 m x three replicates) per season. No fixed direction of the placing of the traps could be undertaken because the traps were placed downslope of the area they were placed to prevent waterlogging given an incident of rain during the study period. Traps were checked daily at 07h00 and closed to prevent any animals from being trapped throughout the day to minimize the mortality rate. The traps were opened and set again at 17h00 to allow for trapping throughout the night.

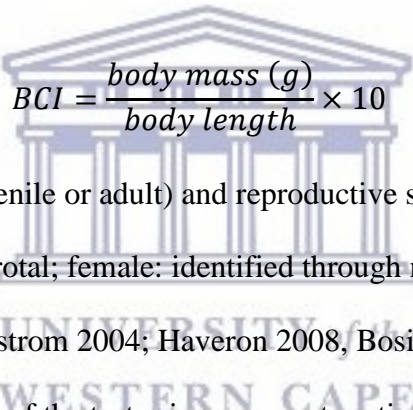


Figure 3.3: Pictures displaying vegetation composition during winter (A) and summer (B) rainfall trapping sessions in the Desert Biome (1), ecotone (2) and Succulent Karoo Biome (3).

Each trap season comprised of 1512 trap events for the study area (Fig. 3.3; 72 traps in the Desert Biome + 72 traps in the ecotone + 72 traps in the Succulent Karoo Biome x 7 nights =

1512 trap nights). The traps were baited using a mixture of peanut butter and oats (Haveron 2008). The traps were rebaited if the bait was removed, opened and eaten by a bird, or if the rodents ate it and also to reduce biases induced due to the odour of other species from previous trapping sessions (Drickamer 1995; Haveron 2008). Any species other than small mammals trapped (i.e. birds) were released immediately without harm.

The captured small mammals were identified to species level (following; Apps 2012). The following characteristics were recorded; body length using a ruler, sex, and weight using a pocket scale (Bosing *et al.* 2014). These measurements were used to assess the body condition index. The Body Condition Index (BCI) will be calculated as follows following Krug (2002) and Haveron (2008);


$$BCI = \frac{\text{body mass (g)}}{\text{body length}} \times 10$$

Furthermore, the age class (juvenile or adult) and reproductive status (male: identified by testes position abdominal or scrotal; female: identified through nipple size and perforated or imperforated; Krug 2002; Bergstrom 2004; Haveron 2008, Bosing *et al.* 2014; Jacques *et al.* 2015). The external positioning of the testes is an accurate estimate (87 – 94%) of reproductive status (McCravy & Rose 1992). This method of determining reproductive status was followed for all species except elephant shrew species because their testes remain internal. Elephant shrews reproduce throughout the year. Therefore, the female data were used to determine the reproductive status of this species (Whithers 1983). However, according to McCravy & Rose (1992), the nipple size is a less accurate estimate, therefore, the body weight and nipple size were used to determine their reproductive status.

The capture-mark-recapture method was used to assess population density and diversity in the landscape. The animals were marked by clipping their fur, which is ideal for short-term

studies because the fur will be shed during moulting (Fig. 3.4; Manville 1949; Fullagar & Jewell 1965).



Figure 3.4: Darker undercoat after fur clipping on a *Gerbillurus paeba*.

b. Vegetation Survey

The Landscape Functional Analysis (LFA) was executed by setting up a 250 m line transect and was used to assess the plant diversity, abundance, plant species richness of the vegetation. Every plant along the transect was recorded and identified to species level where possible. A 250 m line transect was used due to the heterogeneity of this arid communal rangeland, the uncertainty of the extent of the biome boundary, also to have a good representative of the landscape and vegetation present. Annuals were included in the survey as litter. The vegetation and rock cover, growth form and life form were also recorded. Merely, standing perennial vegetation was considered because livestock primarily feeds on palatable perennial shrubs and grasses in the rangelands. They are also the most vulnerable life form to degradation because they do not die off during the winter season for Desert

Biome and summer season for the Succulent Karoo Biome. The growth forms and life forms were recorded for each species to make comparisons in this regard using the Plants of South Africa website (<http://www.sanbi.posa.org.za>).

iii. Data Analysis

Species abundance was calculated as the total number of individuals captured per species and plot (excluding recaptures; Bosing *et al.* 2014) for small mammal data. Similarly, the species diversity was calculated using the Shannon Wiener index of diversity. The relative population density for the small mammal data was calculated as follows;

$$\frac{\text{number of individuals caught}}{\text{number of traps} \times \text{number of trap days}} \text{ (following Van Deventer \& Nel 2006).}$$

In all analyses, if the p-values are less than 0.05 the test is significantly different. A Shapiro-Wilk test for normality was used since the data set had more than 50 but less than 2000 data entries. The normality of all data sets was tested and where data were not normally distributed, it was log transformed.

The Body Condition Index of Krug (2002) was used to compare the body condition of small mammals between the Desert Biome, ecotone and Succulent Karoo Biome. The body condition is measured by quantifying weight and body length that is the most parameter used to assess the health of the rodents.

A partial correlation test controlling for the area was used to assess the relationship between average body condition index, reproductive status and breeding. Similarly, the variables were compared using a correlation test with other variables such as gender and trapping index. To assess the difference in small mammal variables (average body condition index, relative density index and small mammal abundance) between areas surveyed a one-way multivariate

analysis of variances (MANOVA) test was used. Similarly, to assess small variables between the species a MANOVA was used.

To assess the relationship between the average body condition index, relative density index and small mammal abundance between the areas a multivariate one-way analysis of variances (MANOVA) Post Hoc Test was used. The various small mammal population characteristics (body condition index, relative density index, abundance and species diversity) and their reproductive characteristics (gender, reproductive status, breeding) were assessed between species and season using a Multivariate General Linear Model. The relationship between species-specific small mammal variables and the vegetation characteristics was assessed using a correlation test.

iv. Non-metric Multidimensional scaling (NMMS)

A Non-Metric Multidimensional Scaling was constructed in PCORD Version 5.0 statistical package to assess relationships between small mammal assemblages and vegetation parameters between the areas surveyed. Two-dimensional plots were populated using the joint plot method to establish the reasons for the relationships. The axes with a stress value less than 30 were used. The listed variables that were responsible for the relationships were noted if it had a tau value of less than 0.3, which is significant in the grouping of sites. To test the extent that these variables have on the outcome of the NMMS, IBM SPSS Statistics 21 was used. The NMMS was run for species abundance and presence and absence of species in the sites. To ensure the best results, the NMMS Ordination was run 10 times for both to determine differences between these sites and the spatial distribution of sites. The NMMS was run for 500 iterations using a slow and thorough approach.

Two-dimensional plots were formulated using the joint plot method to establish the reasons for the relationships viewed in the NMMS. As far as possible, the axes with a stress value of less than 30 were used. The listed variables or plant species that were responsible for the relationships viewed in the NMMS have noted if it had a tau value of less than 0.3 (Martin, 2013). These factors with a tau value less than 0.3 are regarded as having a significant effect on grouping the sites in the NMMS. To test the extent that these variables have on the outcome of the NMMS.

3.4. Results

i. Trapping records over the study period

The total number of trap nights was 3024 over the study period, whereby 119 captures were made of which 34 were recaptures, some individuals several times (Appendix 4). *Gerbillurus paeba* was recaptured most often in all three areas in both seasons in a total of 61 different individuals of the three species were captured (Table 3.1). Two species of the order Rodentia and one species of the order Macroscelidea (Table 3.2) were recorded.

Table 3.1: Number of individuals of each species captured in each area over the study period (M: Male; F: Female).

Species	Desert		Ecotone		Succulent Karoo Biome	
	M	F	M	F	M	F
Order – Rodentia						
<i>Gerbillurus paeba</i> Hairy-footed Gerbil (A. Smith 1836)	5	5	11	2	8	10
<i>Desmodillus auricularis</i> Short-tailed gerbil (A. Smith, 1834)	0	0	1	1	1	0

Order – Macroscelidea

<i>Elephantulus rupestris</i>	0	0	0	1	11	5
Western rock elephant-shrew						

ii. Small mammal population density

Similarly, a significant relationship in small mammal abundance ($F_{13,103}$; $p = 0.006$) between areas where the Succulent Karoo Biome has the lowest mammal abundance. There is a significant difference in the relative density of the small mammals ($F_{13,103}$; $p = 0.006$) between the areas. The Succulent Karoo Biome has a significantly higher relative density index than the Desert Biome ($p = 0.006$) and ecotone ($p = 0.023$). The total individuals captured in winter was more than in summer in the Succulent Karoo Biome in comparison to the Desert Biome, and ecotone. A higher amount of males was captured ($p < 0.001$) and recaptured ($p = 0.005$) in winter in comparison to females (Table 3.2).

Table 3.2: The number of individuals captured and recaptured during each season.

Season	Trap Record	Females	Males
Winter	Individuals captured	17	28
	Individuals recaptured	10	17
Summer	Individuals captured	7	9
	Individuals recaptured	3	2

iii. Species-specific characteristics assessed between seasons

There is a significant difference between species in relation to their relative density index across the landscape ($F_{8,236}$; $p = 0.006$) where *G. paeba* has the highest density. Since this species has more density it is reasonable that their population contributes to the most males ($F_{6,996}$; $p = 0.002$) and females ($F_{5,953}$; $p = 0.005$) in comparison to *E. rupestris* and *D. auricularis*. They breed more in relation to the other species in the landscape ($F_{6,599}$; $p =$

0.003) and thus produce more juveniles ($F_{12.832}$; $p < 0.001$). However, *G. paeba* also has significantly more non-breeding individuals ($F_{5.782}$; $p = 0.005$) in comparison to the other species.

There is a significant difference in the relative density of each species between the seasons (Fig. 3.5; $F_{5.310}$; $p = 0.025$) where the density is more in the winter season. There is a significant difference in males ($F_{6.784}$; $p = 0.012$), juveniles ($F_{14.457}$; $p < 0.001$) and non-breeding individuals ($F_{5.704}$; $p = 0.021$). In relation to all these reproduction variables



Gerbillurus paeba had the most the males, juveniles and on breeding individuals were the most in winter in comparison to the summer trapping season (Fig. 3.5).

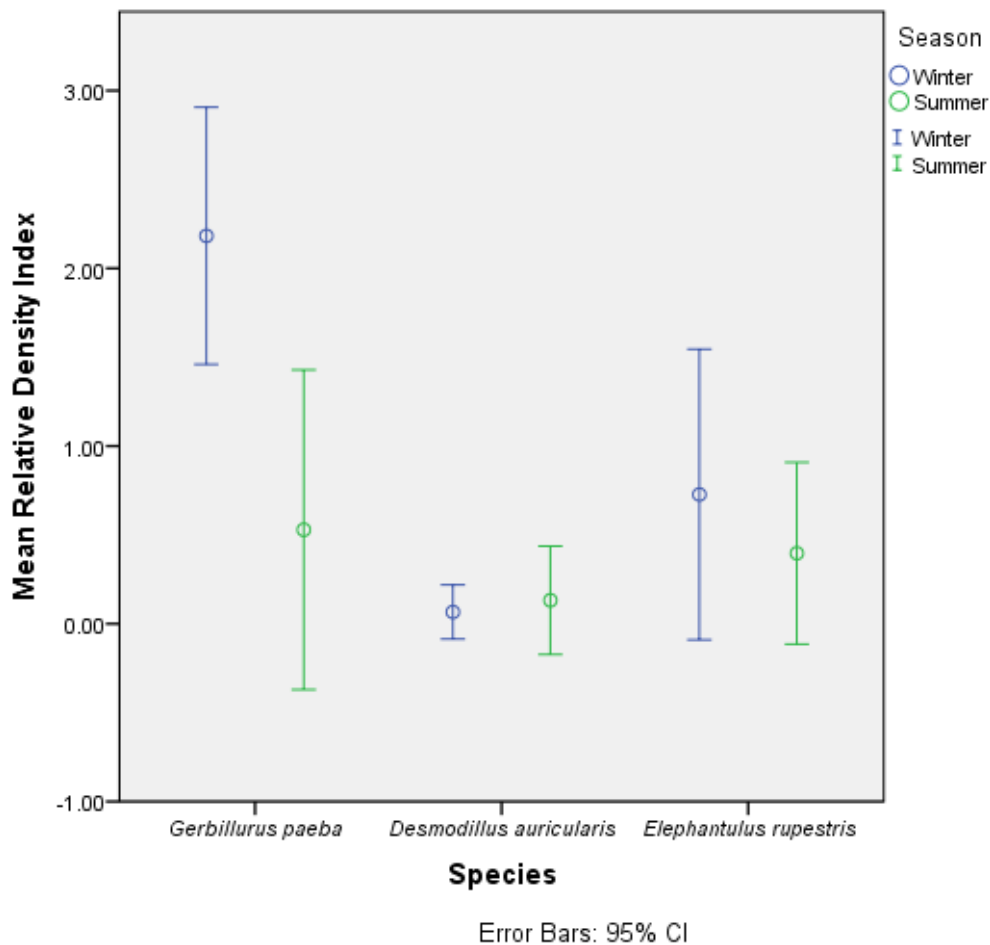


Figure 3.5: Box and whisker plot showing the relative density of each species during each season in the study area.

iv. Body condition index of small mammals across an arid biome boundary

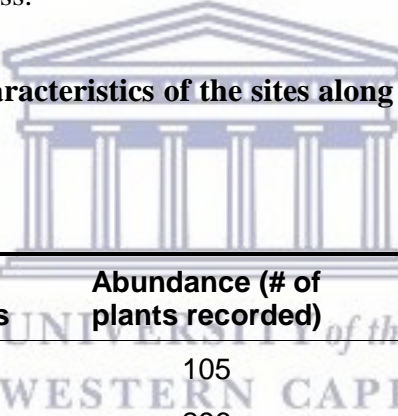
There is a significant correlation between reproductive status and the body condition index ($p = 0.007$). It is evident that the reproduction of the rodents is dependent on their health.

Adults typically have a better body condition index in comparison to juveniles hence there is a strong relationship between BCI and breeding ($p = 0.015$) because juveniles have not reached reproductive maturity. Evidently, the relative density of the population is dependent

on the breeding ($p < 0.001$), number of adults ($p < 0.001$) and juveniles ($p < 0.001$). Typically, juveniles are considered non-breeding individuals thus the strong positive relationship ($p < 0.01$) between these two variables are expected. Similarly, for the adults which are typically regarded as the breeding individuals ($p < 0.001$) in the population thus these two variables showed a strong positive correlation.

The breeding of the population is dependent on the effect of species diversity of the vegetation (Table 3.4; $p = 0.044$). The non-breeding individuals negatively correlate with the species richness of the vegetation ($p = 0.010$). Similarly, there is a significant relationship between breeding individuals ($p = 0.007$) and the number of juveniles ($p = 0.021$) and plant species richness.

Table 3.3: The vegetation characteristics of the sites along the Desert - Succulent Karoo Biome gradient.



Sites	Species Richness	Abundance (# of plants recorded)	Species Diversity (H')	Vegetation Cover (%)
D1	19	105	1,29	14
D2	30	296	1,34	39
D3	27	288	1,49	38
E1	17	184	1,69	25
E2	33	474	1,82	63
E3	43	425	1,60	57
SK1	19	160	1,56	21
SK2	36	394	1,58	53
SK3	36	455	1,56	61

A correlation test between small mammal variables and vegetation variables found a weak positive relationship between small mammal diversity and vegetation plant diversity ($p = 0.015$). A strong negative relationship was found between non-breeding individuals and non-

succulent shrubs ($p = 0.039$), vegetation species richness ($p = 0.005$) and vegetation abundance ($p = 0.045$). The only strong positive relationship was found between the leaf succulent shrubs and juveniles ($p = 0.040$) in the small mammal population.

3.5. Discussion

The ecotone has a higher plant species diversity in comparison to its adjacent biomes and thus could provide a more suitable habitat for rodent species (i.e. generalist and specialist small mammal species than the two adjacent biomes). However, on the contrary, the Desert Biome and ecotone had less small mammal species diversity and richness than the Succulent Karoo Biome. This is similar to the findings by Krystufek & Griffiths (2002) in a steppe-deciduous ecotone and contrary to the McCain & Grytnes (2010) study where according to the 'ecotone effect' in tropical mountainous forests the small mammal species peaks in diversity primarily with juveniles. Furthermore, the relative density index and small mammal abundance increase towards the Succulent Karoo Biome refuting the first hypothesis that there is no difference in small mammal population characteristics in relation to biomes. Although, the Succulent Karoo Biome does not have the highest plant species richness and vegetation cover it is providing adequate forage and habitat for the animals. This is evidence for rodent communities tracking their preferred habitat that is more mesic (Auffray *et al.* 2009; Christensen *et al.* 2018).

No small mammals were captured during the wet summer season in the Desert Biome. This barely improved during the winter trapping season where six individuals of *Gerbillurus paeba* were captured in the sites closest to the ecotone. During the winter trapping season, the biome had an abundance of annual plants which granivores such *Gerbillurus paeba* prefer since it produces more seeds than perennial plants (Abramsky & Rosenzweig 1984; Dean *et*

al. 1995). However, in this study, it had no influence on the density or abundance of the small mammals since they were caught in only one of the three Desert sites.

The small mammal population in the biome is relatively gender balanced with a healthy breeding estimate that contributes to their population having juveniles in the biome. A balanced sex ratio is essential to the persistence of a population because a male-biased sex ratio as determined for *Elephantulus rupestris* may lead to the extinction of a population (Rankin & Kokko 2007; Dreiss *et al.* 2010). More so, the absence or presence of males determines the fitness of females (Rankin & Kokko 2007; Dreiss *et al.* 2010).

The rodent density was greater in the Succulent Karoo Biome in the winter season as well, however, during the winter period two species were caught (i.e. *Elephantulus auricularis* and *Gerbillurus paeba*), and in the summer season, *Desmodillus auricularis* was caught in one of these sites. The ecotone has higher plant species diversity and vegetation cover in comparison to the other areas, thus they provide adequate resources for a higher diversity of rodents with different diversity (Table 3.4). Males dominate the small mammal population in this area hence there are fewer breeding individuals in the ecotone. However, the juveniles are abundant during winter thus the landscape may be a refuge for juveniles since it has a higher plant diversity that the juveniles are dependent on for different resources. Once the juveniles are older, they move to the Succulent Karoo Biome where they reside since this biome has more adults of all three species surveyed in the ecotone. They are outcompeted by the adults for space and resources thus they move to the ecotone.

The Succulent Karoo Biome has the greatest small mammal diversity, density, and species richness in the landscape. The species caught in this biome in winter are *Desmodillus auricularis*, *Elephantulus rupestris*, and *Gerbillurus paeba*. In summer, there was a

dominance of adults and breeding individuals in the biome, which transitioned to the dominance of juveniles in winter. The Desert Biome and ecotone has a higher cover of annual vegetation whereas the Succulent Karoo Biome has a higher perennial vegetation cover.

According to Joubert (1998), perennial vegetation is the main determinant of small mammal diversity. Perennial vegetation is essential for diurnal species since they need protection from predators when feeding, and it does not affect nocturnal species because their predators do not depend on site to look for prey (Joubert 1998).

Furthermore, the perennial vegetation constitutes a large proportion of rodent's diets especially omnivores and herbivores (Joubert 1998). The warming temperatures alongside the land uses threatens this life form especially since it survives all year round and is continually grazed on. Perennial vegetation plays a role in the distribution of small mammals and affects their physiological mechanisms (Parseman 2006). This provides more evidence for the higher small mammal diversity and abundance in the Succulent Karoo Biome due to the changes in their ecological niches driving them to areas of a more mesic environment (Myers *et al.* 2009; Gilman *et al.* 2010; Chen *et al.* 2011).

Similar to relative density and abundance, the small mammal populations' body condition index increases along the Desert – Succulent Karoo Biome gradient. The body condition index is of both health and reproductive state of and thus its measure becomes essential in conservation biology and evolutionary ecology (Moya-Larano *et al.* 2008). In order for the species captured in this study to sustain and ensure the survival of their population, they migrated to the Succulent Karoo Biome. The finding of the Desert Biome having fewer rodents indicates not only in unsuitability to provide adequate resources for rodent communities but also the ecosystem services that rodents provide are now lost.

In the Desert Biome, the animals have to travel further to get access to resources because of the patches being distributed far apart that affect their body condition and ultimately their health. The animals living there have to spend more energy searching for food making escaping from predators more difficult (Bosing *et al.* 2014). Figure 3.3 shows the comparison for the three sites throughout the winter and summer rainfall trapping seasons and it is evident why the rodents were more abundant in the Succulent Karoo. Thus given desertification does progress as is shown in the study it can evidently further reduce the space the rodents have to survive. Since the Desert Biome has sparse vegetation it may elucidate the rarity of the small mammals due to a lack of adequate shelter, protection from predators and forage. The probability of these animals breeding is at risk because it is highly dependent on them having access to resources.

A reduction in vegetation species richness will have an evident influence on the breeding of the small mammal population that plays a major role in their adaptation to environmental conditions. Essentially, the reduction of leaf succulent shrubs in this study has an influence as well since juveniles are strongly dependent on these plant growth forms for their survival. Similarly, a reduction in vegetation cover, species richness and non-succulent shrubs reduce non-breeding individuals which substantiates the importance of maintaining heterogeneity in the landscape in order to promote the persistence of populations. Rodents are small-bodied animals with a short lifespan, and they have short life histories (Auffray *et al.* 2009). Evidently, they respond rapidly to changes in the season fluctuations and the landscape (Vessey & Vessy 2007; Auffray *et al.* 2009). However, a loss of plant species richness or heterogeneity will reduce the ability of the small mammals to adequately adapt and ultimately increase the mortality rates especially specialist species (e.g. *Desmodillus auricularis*, *Elephantulus rupestris*; Rosenzweig 1981; Apps 1996; Tabeni & Ojeda 2005).

Elephantulus rufescens is strictly insectivorous (Skinner & Chimimba 2005; Apps 1996) and *Desmodillus auricularis* is primarily omnivorous where vegetation makes up 85% of their diet and insects forms a small portion of that diet (Spinks & Perrin 1995; Apps 1996).

Gerbillurus paeba, on the other hand, is omnivorous the feed on fresh vegetation and succulents as well as arthropods that make up 17% of their diet (Kerley 1992b; Apps 1996).

The diets of *Gerbillurus paeba* gives it the upper hand over other species in this study making it possible for this species to inhabit so many habitats in the landscapes which are proven by it being most abundant species in this study and others (i.e. Hoffmann & Zeller 2005; Van Deventer & Nel 2006; Bosing *et al.* 2014). Moreover, reproduction is an integral part of the survival of a small mammal population in a landscape (Rebelo *et al.* 2019). The Desert Biome is not suitable for the successful reproduction of rodents because it is becoming sparser due to disturbance (humans and environmental) and not only reducing the patches but also promoting shallow patches in order to preserve water.

The study supports the hypothesis stating a difference in small mammal characteristics between seasons. The most evident difference is the number of individuals trapped which constitutes the density and diversity of the rodents during the seasons. More rodents were trapped during the winter season. Especially in the Succulent Karoo Biome since this is its growing season although the Desert Biome has its growing season in summer the abundance of the rodents in the Succulent Karoo Biome far outweighs the other biome and the ecotone. The results are supported by studies such as Kerley (1992) where the rodents are more abundant in the winter season. The small mammal populations are more active during winter which is expected in comparison to studies such as Rowe-Rowe (1986) and Monadjem & Perrin (2003) where the rodents were more active during summer since they captured primarily insectivorous species. Whereas in this study the species are primarily herbivores

which substantiates the finding of the small mammals breeding and activity coinciding with the winter season. Also, it could be their physiology since they are small-bodied their body heat rises rapidly and thus in order to maintain their body heat they remain in burrows or underneath shrubs in order to stay cool during the summer season. Males travel more frequently in open and risky areas than females (Koivunen *et al.* 1996). Also, females remain in burrows and stores food reserves for the young during winter thus they were captured less than the males during their most active season.

The *Gerbillurus paeba* species may be able to replace the other species in this study and provide the necessary ecosystem services. It is the most abundant species recorded in this one-year study and is the only species that is able to survive in the Desert Biome although in low numbers. They are also the only species that prefer open areas when foraging at night, hence they don't need cover since their predators make use of their sense of smell (Joubert 1998). This species is the smallest of the species caught allowing them to inhabit disturbed and fragmented habitats (Merritt 2010). They are omnivorous and they are the only species that reproduce throughout the year (Apps 1996).

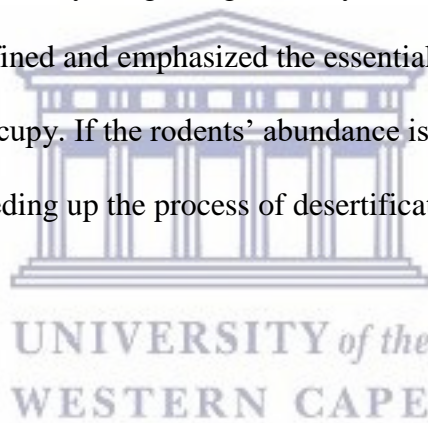
Small mammal populations adapt to the pressures of their surroundings rapidly, and thus they are typically used as indicators to monitor ecosystem responses to management (Douglass 1989, Kaufman *et al.* 1988; Olson *et al.* 1994; Dale & Beyeler 2001). In order to conserve the migratory small mammal, the farmers using the land should have a well-balanced grazing system (Haarmeyer *et al.* 2010; Bosing *et al.* 2014). Various studies found a correlation between the body condition and moderate to low grazing intensities indicating that small mammals prefer reduced grazing pressures from livestock (Parmentier & MacMahon 1983; Bosing *et al.* 2014).

This study found contradictory results to that of Horvath *et al.* (2010) in their study in Mexico that the small mammal species richness was more in the ecotone. In the Horvath *et al.* (2010) study the community composition strongly changed from the forest to the farmlands due to a reduction in vegetation and loss of shelter and food availability (Horvath *et al.* 2010). Valone & Sauter (2005) also found the same result where rodent diversity in an arid grassland in Arizona was higher in areas where it was experiencing the initial stages of desertification or recovery respectively. How does this relate to the Desert-Succulent Karoo ecotone? Various studies have documented the expansion of the Desert Biome into mesic environments (Driver *et al.* 2012; DEA 2013; Masubelele *et al.* 2015). Could this be the first signs of this shift other than the changes in vegetation composition? These studies alongside the finding of this study substantiate the use of rodent communities a biological indicator in rangelands.

Small mammals can be used as indicators of landscape functionality and ecotonal shifting. According to this study, rodents are abundant in the Succulent Karoo Biome, although the plant species richness, diversity, and vegetation cover are more in the ecotone. According to the vegetation characteristics of the ecotone, the small mammals should be more abundant in this area. However, the vegetation present in the ecotone is more of an arid affinity; thus, it is evident that the small mammals require vegetation that is more mesic. The close relationship in vegetation between the ecotone and the Desert Biome may indicate the ecotone shifting and inflicting a huge threat to the small mammal populations in these arid landscapes. A reduction in semi-arid habitat for the rodents reduces the space they have to survive. Eventually, resulting in competition for space in the Succulent Karoo Biome an increased incidence of mortality in this biome. The dominance of one species (*Gerbillurus paeba*)

which is adapted to more arid conditions reducing the animal diversity and furthermore the loss in the ecosystem services provided by the other species present in the landscape.

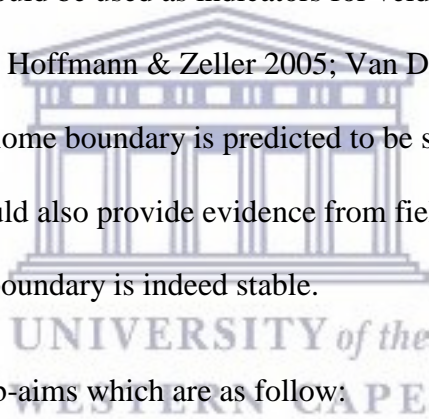
In conclusion, the Desert Biome has less overall small mammal species diversity and if this biome increases towards the Succulent Karoo Biome, it will reduce the food, shelter and burrow availability for the population. Ecotone shifting will directly affect the small mammal population density and reproduction success. Inversely, the loss of small mammals in rangelands will affect the functionality of the landscape because they provide a variety of ecosystem services through their activity that promotes landscape functionality. In order to ensure the rangeland functionality is maintained in relation to the ecosystem services that rodents provide through their activity the grazing intensity should be moderated and limited where possible. This study defined and emphasized the essential services that these animals provide to ecosystems they occupy. If the rodents' abundance is continually compromised these services will be lost speeding up the process of desertification.



4. Chapter 4: Study Synthesis

The overall aim of this study was to assess the landscape functionality of an arid biome boundary and its relationship to small mammal assemblages in the Steinkopf communal area, South Africa. The most common mammal community in these landscapes apart from the livestock is small mammals, thus the role they play in maintaining the functionality of the landscape is essential. In this study, the use of the Landscape Functional Analysis (Tongway and Hindley, 1995) was taken beyond its intended use to monitor rehabilitation as it was used to assess degradation processes in a landscape and used as a tool to provide evidence for desertification. As such, the results from this study could also provide methodological support that small mammals could be used as indicators for veld condition in arid landscapes (Govender unpublished thesis; Hoffmann & Zeller 2005; Van Deventer & Nel 2006). Since the Desert–Succulent Karoo biome boundary is predicted to be stable under future climate change scenarios the study could also provide evidence from field indicators and landscape functionality on whether this boundary is indeed stable.

This study set four specific sub-aims which are as follow:



- i. To determine whether the Succulent Karoo Biome and the ecotone of the study area are more functional than the Desert Biome of the study. Thereafter pre-empt the anticipated desertification changes due to climate change in the biome boundaries.
- ii. To assess the relationship between rangeland functionality and soil indicators (soil stability, water infiltration and nutrient cycling).
- iii. To examine the relationship between rangeland functionality and small mammal assemblages. Thereby assess the potential effects of the change in functionality from Succulent Karoo to Desert Biomes.
- iv. To determine if small mammals can be used as an indicator of rangeland health.

In addressing specific Aim (i), Chapter 2 showed that the vegetation of the ecotone between the Desert and Succulent Karoo Biomes is becoming more arid as it has a closer affinity to the Desert biome. The soils of the ecotone, on the other hand, is showing a closer relationship with the Succulent Karoo Biome as it is showing signs of stability and resilience to desertification. However, this may change given the land uses in the communal area continue to deteriorate the Succulent Karoo Biome vegetation making it more arid. Although the soil is stable, the lack of protection from the vegetation from environmental elements including rain splash will eventually result in the soil becoming eroded speeding up the process of desertification in the rangeland.

When investigating specific aims (ii), the study found evidence indicating nutrient cycling and water infiltration are the most important determinants of landscape functionality in this arid landscape. Loss of vegetation in a landscape understandably affect its functionality because there will be a lack of nutrient cycling. Similarly, water infiltration is also lacking more so in the ecotone and Desert Biome because of a lack of patches to trap the water. The

continued loss of patches will exacerbate the dysfunctionality and enhance the movement of the Desert Biome into the Succulent Karoo Biome.

Patches affect the distribution and abundance of generalist small mammal herbivores and granivores by creating spatial variability in resources, vegetation cover and interaction with other small mammals (Schnurr *et al.* 2004). Similarly, the rodents determine the distribution of the patches through variation in seed predation and survival (Schnurr *et al.* 2004). This substantiates the importance of the conservation of the small mammals in the landscape since they are so closely related to the vegetation composition and plant diversity. Simultaneously they determine the functionality of the landscape with their foraging activity and in part controlling the distribution of vegetation in the landscape.

The preference for one species of rodent, according to this study, particularly the *G. paeba* is imminent with the climatic changes and landscape functionality in the arid zone. Although it is resulting in reducing the important microhabitats for other species the presence of one generalist species that are able to assist the landscape to restore itself is adequate. The nutrient cycling and water infiltration processes of *Elephantulus rupestris* and *Desmodillus auricularis* will be lost however it will be provided by the *G. paeba* population although less prominent.

Evidently, the rodents can be used as indicators for veld conditions since they likely respond to changes in landscape functionality. According to this study, the abundance of *G. paeba* indicates low veld condition since they all migrating to the Succulent Karoo Biome indicating that this biome is becoming open and sparse in relation to the vegetation composition. The soil indicators of the ecotone were relatively stable and closely related to the Succulent Karoo Biome. The loss of rodent abundance in this area can speed up the soil degradation process

alongside the loss of vegetation cover to that of a more arid affinity. In order to support this process, the landscape needs to be supported by land users by implementing sustainable management practices.

The small mammals are diverse and are adapted to different biomes and thus reduce competition due to resource partitioning. However, because of desertification, the small mammal abundance is greater in the Succulent Karoo Biome. This supports studies by other researchers such as Grant *et al.* 1982 and Manson *et al.* 1999 who in their studies found that rodents are dominant in a landscape with more vegetation cover which is to be expected since they require the vegetation for various resources. In this study, the increased density of the rodents in the Succulent Karoo Biome provides evidence for this notion since it has a higher vegetation cover and density in comparison to the other areas. This biome also supports a higher diversity of rodents and thus it is essential in order to ensure the persistence of the small mammal community for the future.

The concentration of rodents in one area results in more competition for resources and mates further reducing their population and density. The gene exchange in small mammal communities are essential for the persistence of the population, however, climate change, and land-use practices are affecting the home range by decreasing them significantly. Gene exchange occurs when juveniles are dispersed from their place of birth at the approach of sexual maturity (Blair 1953), this will significantly affect their reproduction and breeding. The reduced abundance of rodents in the Desert Biome could affect the ecosystem services that they provide and reduce the functionality of this biome. One species (*Gerbillurus paeba*) is dominant in the landscape as this species is typically adapted to open habitats and biotic environments of a more arid affinity. The dominance of one species in the landscape can be detrimental since the ecosystem services provided by the other species will be lost. The

question remains how detrimental is the loss of the other species or can the landscape be optimally functional with the dominance of one species? Further research needs to be done on this topic to ascertain the extent of loss in functionality with the dominance of one species.

The dominant species typically show no change in dominance over the landscape and seasons, as in Manson *et al.* (1999) the voles which are the competitive dominant in their three-year study showed a consistent variation in comparison to the inferior species, the white-footed mouse. The Jones & Longland (1999) and Manson *et al.* (1999) study supports this research in that a species which is more adaptable such as *Gerbillurus paeba* who was the most dominant species in all the areas and thus it is evident that it will be reasonable to suggest that the *G. paeba* species will persist in the landscape. *G. paeba* prefers open patches both for feeding and habitat (Apps 2012; Govender unpublished thesis) and thus they are most likely going to expand their range further than the other two species trapped during this study.

The study found evidence for desertification in the landscape since the ecotone is currently more closely related to the Desert Biome in relation to its vegetation and this will support the *G. paeba* spread. In a tropical forest in Australia, a one-year study by Laurance (1994) the same results were found where a few small mammal species (i.e. *Melomys cervinipes*, *Rattus leucopus* and *Antechinus falvipes*) favoured fragmented and disturbed forest habitats and thus they increased in those fragments. Similar results were found by Pardini *et al.* (2005) in a fragmented Atlantic forest landscape where a small mammal species prefers small isolated fragments. Although, these species are prone to being in disturbed and dysfunctional habitats they play an important role in the rehabilitation of these landscapes. Evidently, they are one of few species recorded in these landscapes that can survive in these fragments and thus they should be considered key species for conservation.

The body condition of the small mammals is directly affected by the functionality of the landscape. Thus, the body condition also increases from the Desert Biome into the Succulent Karoo Biome. Furthermore, the loss of functionality will be detrimental to the small mammal populations since it will affect their reproduction, breeding and survival due to a lack of resources in the landscape. However, in order to mitigate the reduction in body condition in the changing landscape of the arid areas globally, habitat generalists may be the most successful species since they are able to make use of resources in the neighbouring areas as well. Since *G. paeba* is the only cosmopolitan species caught in this study and a habitat generalist they could dominate since they can use the Desert Biome ecotone as well.

Essentially, small mammals can be used as an indicator of landscape functionality. They adapt rapidly to any environmental conditions as well as land uses in the landscape. Their overall health, distribution, density and reproduction will be affected if the desertification persists. The land uses exacerbate desertification, however, if these land uses are alleviated in any way the rodents may be an essential part of rehabilitating the landscape. Although water infiltration, nutrient cycling and soil stability are important in landscape functionality, only the two former processes are essential in the biome boundary in Steinkopf communal area. The activities of the small mammals in this regard can contribute positively. Their burrows allow infiltration of water into the soil in this water-scarce rangeland. Furthermore, their forage, defaecation in their burrows as well as the space they provide for more shrubs to occupy contributes to the nutrient cycling. Thus, the land uses should be monitored in order to regulate the rangeland health and contribute to the conservation of small mammals in the arid rangelands.

The study refutes the use of climate modelling, vegetation composition and diversity solely as a method to assess and track desertification. It has to be expanded to include the landscape

functionality (i.e. water infiltration, soil stability and nutrient cycling) as well as small mammal abundance and density. This study showed evidence of the advancement of desert biome vegetation the ecotone further than expected into the Succulent Karoo Biome upon ground-truthing. The vegetation map of South Africa needs to be updated in order to account for these changes to ensure adequate management decisions for the benefit of the land users and conservation.

The research was a snapshot of what was present in the study area, therefore, it is providing evidence for possible desertification at the study area. Previous findings and research in the area could be helpful in order to map and track the ecotone over time in order to support this research. Future research should be done to explore the landscape functionality and process of desertification in the Desert Biome and Nama Karoo Biome gradient. Similarly, the relationship between functionality to small mammals and extend it to other animals in the landscape. In this study, the overall abundance of the small mammals was assessed against the landscape functionality. However, this is not adequate in order to ensure the conservation of the small mammal communities in the Steinkopf communal area, follow up surveys should be performed to monitor the population over time since the area is primarily used for livestock farming. Furthermore, the type of patches (i.e. simple or complex) and plant species that the small mammals are most likely burrowing under and feeding (assessing stomach or faeces content) on should be included in the assessment in order to verify which species are a priority for the conservation of the small mammals. Burrows should be included as well in order to assess the abundance more so, as well as the effect grazers may have on the quantities of the burrows.

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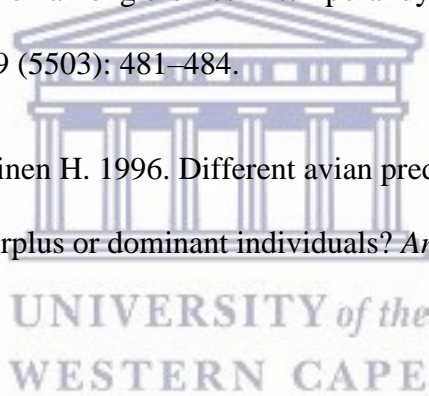
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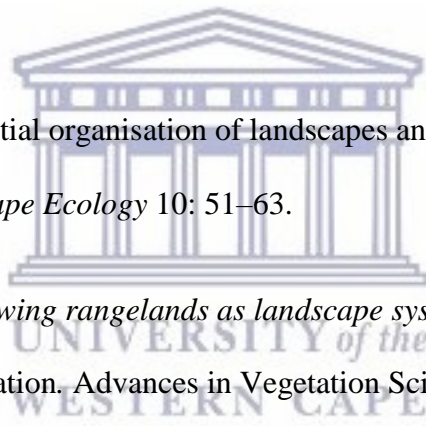
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6. Appendix

Appendix 1: Plant species list including growth and life form.

Number	Species	Growth Form	Life Form
1	<i>Asparagus suaveolens</i>	Perennial	Non-Succulent Shrub
2	<i>Psilocalon subnodosum</i>	Perennial	Stem Succulent Shrub
3	Non-Succulent sp. 1	Perennial	Non-Succulent Shrub
4	<i>Sisyndite spartea</i>	Perennial	Non-Succulent Shrub
5	<i>Stipagrostis</i> sp. 1	Perennial	Grass
6	<i>Monsonia ciliatum</i>	Perennial	Stem Succulent Shrub
7	<i>Cheiridopsis denticulata</i>	Perennial	Leaf Succulent Shrub
8	<i>Mesembryanthemum</i> sp. 3	Perennial	Leaf Succulent Shrub
9	<i>Mesembryanthemum</i> sp. 2	Perennial	Leaf Succulent Shrub
10	<i>Euphorbia mauritiana</i>	Perennial	Stem Succulent Shrub
11	<i>Euphorbia gregaria</i>	Perennial	Stem Succulent Shrub
12	<i>Mesembryanthemum</i> sp. 1	Perennial	Leaf Succulent Shrub
13	<i>Mesembryanthemum nodiflorum</i>	Perennial	Leaf Succulent Shrub
14	<i>Stipagrostis obtusa</i>	Perennial	Grass
15	<i>Galenia fruticosa</i>	Perennial	Leaf Succulent Shrub
16	Stem Succulent sp. 1	Perennial	Stem Succulent Shrub
17	<i>Aptosimum spinescens</i>	Perennial	Non-Succulent Shrub
18	<i>Hermannia</i> sp. 1	Perennial	Non-Succulent Shrub
19	Non-succulent sp. 2	Perennial	Non-Succulent Shrub
20	<i>Hoodia gordonii</i>	Perennial	Stem Succulent Shrub
21	<i>Aridaria</i> sp. 1	Perennial	Leaf Succulent Shrub
22	<i>Eriocephalus namaquensis</i>	Perennial	Non-Succulent Shrub
23	<i>Tylecodon wallichi</i>	Perennial	Stem Succulent Shrub
24	<i>Lycium amoenum</i>	Perennial	Leaf Succulent Shrub
25	<i>Lycium cinereum</i>	Perennial	Leaf Succulent Shrub

26		Perennial	Stem Succulent Shrub
27	<i>Crassula muscosa</i>	Perennial	Leaf Succulent Shrub
28	<i>Lycium bosciifolium</i>	Perennial	Non-Succulent Shrub
29	<i>Psilocaulon dinteri</i>	Perennial	Leaf Succulent Shrub
30	<i>Polymita albiflora</i>	Perennial	Leaf Succulent Shrub
31	<i>Euphorbia rhombifolia</i>	Perennial	Stem Succulent Shrub
32	<i>Ruschia</i> sp. 1	Perennial	Leaf Succulent Shrub
33	Leaf Succulent sp. 1	Perennial	Leaf Succulent Shrub
34	<i>Mesembryanthemum lepratarthron</i>	Perennial	Leaf Succulent Shrub
35	<i>Astridia</i> sp. 1	Perennial	Leaf Succulent Shrub
36	<i>Lampranthus</i> sp. 2	Perennial	Leaf Succulent Shrub
37	<i>Ruschia pauciflora</i>	Perennial	Leaf Succulent Shrub
38	<i>Ruschia</i> sp. 2	Perennial	Leaf Succulent Shrub
39	Non-succulent sp. 3	Perennial	Non-Succulent Shrub
40	<i>Salsola tuberculata</i>	Perennial	Leaf Succulent Shrub
41	<i>Stoeberia beetzii</i>	Perennial	Leaf Succulent Shrub
42	<i>Vachellia karoo</i>	Perennial	Non-Succulent Shrub
43	<i>Stipagrostis</i> sp. 2	Perennial	Grass
44	<i>Leipoldita schultzei</i>	Perennial	Leaf Succulent Shrub
45	<i>Stipagrostis</i> sp. 3	Perennial	Grass
46	<i>Searsia</i> sp. 1	Perennial	Tree
47	<i>Drosanthemum ramosissimum</i>	Perennial	Leaf Succulent Shrub
48	<i>Stipagrostis</i> sp. 1	Perennial	Grass
49	<i>Lampranthus</i> sp. 1	Perennial	Leaf Succulent Shrub
50	Non-succulent sp. 4	Perennial	Non-Succulent Shrub
51	Non-succulent sp. 5	Perennial	Non-Succulent Shrub
52	<i>Stipagrostis ciliata</i>	Perennial	Grass
53	Non-succulent sp. 6	Perennial	Non-Succulent Shrub
54	<i>Zygophyllum retrofractum</i>	Perennial	Leaf Succulent Shrub

Appendix 2: The similarity matrix between sites using plant species and abundance.

	D1 A	D1 B	D1 C	D2 A	D2 B	D2 C	D3 A	D3 B	D3 C	E1 A	E1 B	E1 C	E2 A	E2 B	E2 C	E3 A	E3 B	E3 C	SK 1A	SK 1B	SK 1C	SK 2A	SK 2B	SK 2C	SK 3A	SK 3B	SK 3C	
D1 A	10	0																										
D1 B	57	10																										
D1 C	73	46	10																									
D2 A	31	53	33	10																								
D2 B	22	50	24	53	10																							
D2 C	35	32	50	33	43	10																						
D3 A	50	44	53	35	45	67	10																					
D3 B	40	47	29	50	67	50	53	10																				
D3 C	43	38	46	53	60	63	67	71	10																			
E1 A	62	67	83	43	32	33	59	38	53	10																		
E1 B	80	50	89	36	25	40	57	31	50	73	10																	
E1 C	50	43	55	15	11	24	38	13	29	62	60	10																
E2 A	48	43	40	27	30	23	40	25	35	55	42	29	10															



E2 B	35	42	25	22	61	36	57	50	42	33	27	24	46	100													
E2 C	62	67	67	43	42	33	59	38	53	86	73	46	64	44	100												
E3 A	50	44	53	35	36	48	70	42	44	71	57	38	48	38	71	100											
E3 B	40	37	33	31	32	47	48	50	44	38	35	24	29	27	38	55	100										
E3 C	40	36	42	38	38	56	75	43	55	48	44	30	34	40	48	58	55	100									
SK 1A	50	57	36	31	22	47	63	40	29	46	40	33	29	35	46	63	48	50	100								
SK 1B	53	47	29	25	19	20	32	33	24	38	31	27	33	40	38	32	29	26	53	100							
SK 1C	80	33	67	18	13	27	43	15	33	55	75	60	42	40	55	43	26	33	40	46	100						
SK 2A	40	47	29	25	19	20	32	33	24	38	31	27	42	40	38	32	36	43	53	44	31	100					
SK 2B	53	35	29	13	19	20	21	33	12	25	31	27	33	50	25	32	36	26	40	44	46	56	100				
SK 2C	33	38	17	16	20	14	21	22	15	24	18	17	48	41	32	29	27	31	33	44	27	67	44	100			
SK 3A	60	45	42	29	23	32	42	35	36	57	44	30	55	40	57	50	42	36	40	43	44	43	43	38	100		
SK 3B	47	53	38	33	35	36	38	50	42	44	40	24	38	45	44	48	53	40	47	50	27	60	60	48	48	100	
SK 3C	47	42	25	22	17	18	29	30	21	33	27	35	38	45	33	29	33	32	47	60	40	60	70	55	48	64	100

Appendix 3: The 11 soil surface assessment variables and the resultant indices for the study sites along the Desert biome and Succulent Karoo biome boundary.

	D1 A	D1 B	D1 C	D2 A	D2 B	D2 C	D3 A	D3 B	D3 C	E1 A	E1 B	E1 C	E2 A	E2 B	E2 C	E3 A	E3 B	E3 C	SK 1A	SK 1B	SK 1C	SK 2A	SK 2B	SK 2C	SK 3A	SK 3B	SK 3C
Rainsplash Protection (1-5)	1	1	2	3	2	1	2	2	2	2	2	1	3	1	2	2	2	2	1	2	2	2	2	2	2	2	3
Perennial veg. Cover (1-4)	1	1	1	2	2	1	2	2	2	2	1	1	3	1	2	2	2	2	1	2	1	2	2	2	2	2	2
Litter (1-10)	4	4	4	3	3	2	3	3	4	5	6	5	5	3	4	4	3	4	4	6	3	5	5	4	5	6	5
Cryptogam / Cover (0-4)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crust brokenness (0-4)	4	4	1	2	1	3	1	4	3	3	3	4	2	1	1	2	2	1	4	3	3	1	1	2	3	3	2
Soil erosion / Type	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
Deposited materials (1-4)	1	1	4	3	1	2	2	3	2	2	1	1	2	1	2	2	2	2	1	2	1	2	2	2	2	2	2
Soil surface roughness (1-5)	5	5	4	1	1	1	4	3	2	4	5	5	3	5	4	4	4	4	5	4	5	4	4	4	4	4	4
Surface nature/resistance (5-1)	1	1	1	2	2	1	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Slake test (0-4)	2	1	1	2	1	2	1	1	1	1	1	1	2	1	1	2	1	1	2	2	2	1	2	2	2	2	3
Texture (1-4)	3	3	3	3	3	3	3	2	3	2	3	2	2	3	2	3	3	3	3	2	3	3	2	3	3	3	2
Soil Stability	16	16	16	18	14	15	13	17	17	17	18	17	17	12	15	16	14	13	17	19	16	15	16	16	18	18	18
Calc. of origin of litter / Cryptogam (located/transported)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Calc. of decomposition / Cryptogam degree	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Calc. of Litter	8	9	10	8	7	5	8	7	10	12	14	12	11	8	10	9	8	8	9	13	7	11	11	10	13	14	12
Calc. of infiltration	9	9	9	7	8	9	8	9	8	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
Infiltration/Runoff	28	28	28	23	22	21	26	22	26	31	34	32	31	28	30	29	27	28	30	34	28	31	32	30	34	34	33
Nutrient Cycling status	14	15	15	11	10	8	14	11	14	18	20	18	17	14	16	15	14	14	15	19	13	17	18	16	19	20	18

Soil Stability%	41	40	39	44	34	38	33	41	42	42	45	44	43	30	36	39	34	32	41	47	39	37	39	41	45	45	45
Infiltration/Runoff%	49	50	50	41	39	37	45	39	45	55	60	57	54	48	53	51	47	48	52	59	50	55	56	53	59	60	57
Nutrient Cycling status%	34	35	36	26	23	18	32	25	34	41	47	43	39	33	38	35	32	32	35	45	31	40	41	37	44	46	41



Appendix 4: Record of data captured over the study period including both individual captures (black) and recaptures (red).

Date	Label	Site	Rep Number	ID - Species	Gender	Reproductive Status	Breeding	Weight (g)	Body Length (mm)
21/8/2017	A1	D	2	<i>Gerbillurus paeba</i>	F	J	Y	25	185
21/8/2017	A2	D	1	<i>Gerbillurus paeba</i>	F	J	N	24,1	165
22/8/2017	B1	D	3	<i>Gerbillurus paeba</i>	M	A	N	31	130
22/8/2017	A1	D	2	<i>Gerbillurus paeba</i>	F	J	Y	25	185
22/8/2017	A2	D	1	<i>Gerbillurus paeba</i>	F	J	N	24,1	165
22/8/2017	B2	D	1	<i>Gerbillurus paeba</i>	M	A	Y	25,9	225
22/8/2017	B3	D	1	<i>Gerbillurus paeba</i>	M	J	Y	25,8	180
22/8/2017	B4	E	1	<i>Gerbillurus paeba</i>	M	J	N	16,7	185
23/8/2017	A1	D	2	<i>Gerbillurus paeba</i>	F	J	Y	25	185
23/8/2017	C1	D	2	<i>Gerbillurus paeba</i>	M	J	N	28,1	190
23/8/2017	C2	D	2	<i>Gerbillurus paeba</i>	F	J	N	27,5	195
23/8/2017	A2	D	1	<i>Gerbillurus paeba</i>	F	J	N	24,1	165
23/8/2017	B2	D	1	<i>Gerbillurus paeba</i>	M	A	Y	25,9	225
23/8/2017	B3	D	1	<i>Gerbillurus paeba</i>	M	J	Y	25,8	180
23/8/2017	C3	D	1	<i>Gerbillurus paeba</i>	M	A	Y	35	245
23/8/2017	C4	E	3	<i>Gerbillurus paeba</i>	M	A	Y	35	220
23/8/2017	C5	E	3	<i>Gerbillurus paeba</i>	M	A	Y	33,4	210
23/8/2017	C6	E	1	<i>Gerbillurus paeba</i>	F	J	N	30	220
23/8/2017	C7	E	1	<i>Gerbillurus paeba</i>	M	A	Y	36,7	250
23/8/2017	C8	E	1	<i>Gerbillurus paeba</i>	F	J	N	21,2	205
23/8/2017	C9	E	1	<i>Gerbillurus paeba</i>	M	J	N	31,1	210
24/8/2017	B3	D	1	<i>Gerbillurus paeba</i>	M	J	Y	25,8	180
24/8/2017	D1	E	3	<i>Elephantulus rupestris</i>	F	A	N	36,7	205
24/8/2017	C6	E	1	<i>Gerbillurus paeba</i>	F	J	N	30	220
25/8/2017	C1	D	2	<i>Gerbillurus paeba</i>	M	J	N	28,1	190
25/8/2017	E1	D	1	<i>Gerbillurus paeba</i>	F	J	N	31	225
25/8/2017	E2	E	2	<i>Gerbillurus paeba</i>	M	J	N	9,8	130
25/8/2017	E3	E	2	<i>Gerbillurus paeba</i>	M	A	Y	33	205
25/8/2017	C7	E	1	<i>Gerbillurus paeba</i>	M	A	Y	36,7	250
25/8/2017	E4	E	1	<i>Gerbillurus paeba</i>	M	A	Y	32,8	210

26/8/2017	C2	D	2	<i>Gerbillurus paeba</i>	F	J	N	27,5	195
26/8/2017	C5	E	3	<i>Gerbillurus paeba</i>	M	A	Y	33,4	210
26/8/2017	F1	E	3	<i>Gerbillurus paeba</i>	M	A	Y	34,7	225
26/8/2017	E3	E	2	<i>Gerbillurus paeba</i>	M	A	Y	33	205
26/8/2017	F2	E	2	<i>Gerbillurus paeba</i>	M	A	N	33,8	220
26/8/2017	B4	E	1	<i>Gerbillurus paeba</i>	M	J	N	16,7	185
27/8/2017	G1	D	1	<i>Gerbillurus paeba</i>	F	J	N	17	205
27/8/2017	C5	E	3	<i>Gerbillurus paeba</i>	M	A	Y	33,4	210
27/8/2017	C4	E	3	<i>Gerbillurus paeba</i>	M	A	Y	35	220
27/8/2017	E2	E	2	<i>Gerbillurus paeba</i>	M	J	N	9,8	130
28/8/2017	C5	E	3	<i>Gerbillurus paeba</i>	M	A	Y	33,4	210
28/8/2017	C4	E	3	<i>Gerbillurus paeba</i>	M	A	Y	35	220
28/8/2017	F2	E	2	<i>Gerbillurus paeba</i>	M	A	N	33,8	220
28/8/2017	E2	E	2	<i>Gerbillurus paeba</i>	M	J	N	9,8	130
28/8/2017	C7	E	1	<i>Gerbillurus paeba</i>	M	A	Y	36,7	250
28/8/2017	E4	E	1	<i>Gerbillurus paeba</i>	M	A	Y	32,8	210
28/8/2017	H1	SK	3	<i>Elephantulus rupestris</i>	M	A	Y	41,4	195
28/8/2017	H2	SK	3	<i>Elephantulus rupestris</i>	F	A	N	36,5	200
28/8/2017	H3	SK	3	<i>Elephantulus rupestris</i>	M	J	N	36	200
28/8/2017	H4	SK	3	<i>Gerbillurus paeba</i>	F	J	Y	27,3	215
28/8/2017	H2	SK	3	<i>Elephantulus rupestris</i>	F	A	N	36,5	200
28/8/2017	H4	SK	3	<i>Gerbillurus paeba</i>	F	J	Y	27,3	215
28/8/2017	H5	SK	2	<i>Gerbillurus paeba</i>	F	J	N	18,3	215
28/8/2017	H6	SK	2	<i>Elephantulus rupestris</i>	M	A	Y	42,5	230
28/8/2017	H7	SK	1	<i>Gerbillurus paeba</i>	M	J	N	31,4	225
28/8/2017	H8	SK	1	<i>Elephantulus rupestris</i>	M	A	N	43,3	220
28/8/2017	H9	SK	1	<i>Elephantulus rupestris</i>	F	A	N	42,4	230
29/8/2017	I3	SK	1	<i>Gerbillurus paeba</i>	F	J	Y	30,3	230
29/8/2017	I4	SK	1	<i>Gerbillurus paeba</i>	M	J	N	29,3	215
29/8/2017	H8	SK	1	<i>Elephantulus rupestris</i>	M	A	N	43,3	220
29/8/2017	I1	SK	3a	<i>Gerbillurus paeba</i>	F	J	N	28,3	210
29/8/2017	I2	SK	3a	<i>Elephantulus rupestris</i>	F	A	Y	33,3	205

30/8/2017	H2	SK	3	<i>Elephantulus rupestris</i>	F	A	N	36,5	200
30/8/2017	H4	SK	3	<i>Gerbillurus pæba</i>	F	J	Y	27,3	215
30/8/2017	J2	SK	2	<i>Gerbillurus pæba</i>	M	J	Y	18	215
30/8/2017	H5	SK	2	<i>Gerbillurus pæba</i>	F	J	N	18,3	215
30/8/2017	H6	SK	2	<i>Elephantulus rupestris</i>	M	A	Y	42,5	230
30/8/2017	I3	SK	1	<i>Gerbillurus pæba</i>	F	J	Y	30,3	230
30/8/2017	I4	SK	1	<i>Gerbillurus pæba</i>	M	J	N	29,3	215
30/8/2017	H8	SK	1	<i>Elephantulus rupestris</i>	M	A	N	43,3	220
30/8/2017	H9	SK	1	<i>Elephantulus rupestris</i>	F	A	N	42,4	230
30/8/2017	I1	SK	3a	<i>Gerbillurus pæba</i>	F	J	N	28,3	210
30/8/2017	J1	SK	3a	<i>Gerbillurus pæba</i>	F	A	Y	33,2	250
31/8/2017	H3	SK	3	<i>Elephantulus rupestris</i>	M	J	N	36	200
31/8/2017	H4	SK	3	<i>Gerbillurus pæba</i>	F	J	Y	27,3	215
31/8/2017	K5	SK	3	<i>Gerbillurus pæba</i>	M	J	Y	17	160
31/8/2017	K6	SK	3	<i>Desmodillus auricularis</i>	M	A	Y	37,1	170
31/8/2017	K7	SK	3	<i>Elephantulus rupestris</i>	M	A	Y	41	225
31/8/2017	K3	SK	2	<i>Gerbillurus pæba</i>	F	J	Y	26,4	205
31/8/2017	K4	SK	2	<i>Elephantulus rupestris</i>	M	A	Y	41,3	230
31/8/2017	J2	SK	2	<i>Gerbillurus pæba</i>	M	J	Y	18	215
31/8/2017	I3	SK	1	<i>Gerbillurus pæba</i>	F	J	Y	30,3	230
31/8/2017	I4	SK	1	<i>Gerbillurus pæba</i>	M	J	N	29,3	215
31/8/2017	H8	SK	1	<i>Elephantulus rupestris</i>	M	A	N	43,3	220
31/8/2017	H9	SK	1	<i>Elephantulus rupestris</i>	F	A	N	42,4	230
31/8/2017	K1	SK	1	<i>Gerbillurus pæba</i>	M	J	Y	33,8	225
31/8/2017	K2	SK	1	<i>Elephantulus rupestris</i>	M	J	N	36	205
31/8/2017	I1	SK	3a	<i>Gerbillurus pæba</i>	F	J	N	28,3	210
04/05/2018	A1	E	2	<i>Desmodillus auricularis</i>	F	A	N	54	105
04/05/2018	A2	SK	3	<i>Elephantulus rupestris</i>	M	A	N	48	117
04/05/2018	A3	SK	3	<i>Gerbillurus pæba</i>	F	J	N	35	105
04/05/2018	A4	SK	2	<i>Gerbillurus pæba</i>	F	A	Y	42	90
04/05/2018	A5	SK	2	<i>Elephantulus rupestris</i>	F	A	Y	46	100

04/05/2018	A6	SK	2	<i>Elephantulus rupestris</i>	M	J	N	45	95
05/05/2018	B1	E	2	<i>Desmodillus auricularis</i>	M	A	Y	53	115
05/05/2018	A3	SK	3	<i>Gerbillurus paeba</i>	F	J	N	35	105
05/05/2018	A4	SK	2	<i>Gerbillurus paeba</i>	F	A	Y	42	90
05/05/2018	A6	SK	2	<i>Elephantulus rupestris</i>	M	J	N	45	95
06/05/2018	A4	SK	3	<i>Gerbillurus paeba</i>	F	A	Y	42	90
06/05/2018	A6	SK	2	<i>Elephantulus rupestris</i>	M	J	N	45	95
06/05/2018	C1	SK	2	<i>Gerbillurus paeba</i>	M	J	Y	35	85
07/05/2018	A3	SK	3	<i>Gerbillurus paeba</i>	F	J	N	35	105
07/05/2018	A4	SK	2	<i>Gerbillurus paeba</i>	F	A	Y	42	90
07/05/2018	A6	SK	2	<i>Elephantulus rupestris</i>	M	J	N	45	95
07/05/2018	D1	SK	2	<i>Gerbillurus paeba</i>	M	A	Y	37	100
07/05/2018	D2	SK	2	<i>Gerbillurus paeba</i>	M	A	Y	40	100
07/05/2018	D3	SK	1	<i>Elephantulus rupestris</i>	F	A	Y	63	110
08/05/2018	A5	SK	2	<i>Elephantulus rupestris</i>	F	A	Y	46	100
08/05/2018	E1	SK	2	<i>Gerbillurus paeba</i>	F	J	Y	35	93
08/05/2018	E2	SK	2	<i>Elephantulus rupestris</i>	M	A	N	43	100
08/05/2018	A6	SK	2	<i>Elephantulus rupestris</i>	M	J	N	45	95
08/05/2018	A3	SK	1	<i>Gerbillurus paeba</i>	F	J	N	35	105
09/05/2018	F1	SK	2	<i>Gerbillurus paeba</i>	F	A	Y	37	90
09/05/2018	A6	SK	2	<i>Elephantulus rupestris</i>	M	J	N	45	95
09/05/2018	A3	SK	3	<i>Gerbillurus paeba</i>	F	J	N	35	105
09/05/2018	F2	E	3	<i>Gerbillurus paeba</i>	M	J	Y	40	90
10/05/2018	A4	SK	2	<i>Gerbillurus paeba</i>	F	A	Y	42	90
10/05/2018	E2	SK	2	<i>Elephantulus rupestris</i>	M	A	N	43	100
10/05/2018	G1	SK	1	<i>Elephantulus rupestris</i>	M	A	N	58	95