Current status and impact (2004-2015) of indigenous ungulate herbivory on the vegetation of Sanbona Wildlife Reserve in the Little Karoo

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Dissertation presented for the degree of Master of Science
In the Department of Biological Sciences
University of Cape Town
March 2017

DECLARATION

I know the meaning of plagiarism and declare that all of the work in the dissertation, save for that which is properly acknowledged, is my own.

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Date: 10th March 2017

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ACKNOWLEDGEMENTS

My appreciation and gratitude goes to:

My supervisors, Simon Todd and Timm Hoffman for their guidance, advice and patience.

Nelmarie Saayman, Hannes Botha, Christie Rheeder and Rudi Swart from the Department of Agriculture, for their invaluable assistance in the annual surveys, and for those that assisted before I started.

Andrew Slater who assisted with reorganising 12 years’ worth of field survey data.

Sanbona and the Caleo Foundation in allowing me the opportunity to improve my knowledge for conservation sake.

And to Layla, Mia and Paul in my absence in our family life while I was trying to achieve this.

ABBREVIATIONS

AS	Aeolian Sands
BC	Bray-Curtis
GPS	Global Positioning System
LAU	Large Animal Unit
LKQV	Little Karoo Quartz Vygieveld
MQF	Matjiesfontein Quartzite Fynbos
MSF	Montagu Shale Fynbos
MSR	Montagu Shale Renosterveld
NLSF	Northern Langeberg Sandstone Fynbos
NMS	Non-metric multidimensional scaling ordination
OL	Old Lands
PD	Percentage Dissimilarity
SLSF	South Langeberg Sandstone Fynbos
SR	Species Richness
UCT	University of Cape Town
WLK	Western Little Karoo

ABSTRACT

Game farming is becoming more popular in southern Africa and the introduction of large indigenous ungulates into confined enclosed areas could alter plant communities and ecosystem processes. This is of particular concern in semi-arid rangelands of the Succulent Karoo where the evolutionary history of grazing is not clear and the compatibility of large herbivores in confined areas remains to be demonstrated. The establishment of Sanbona Wildlife Reserve, a 54 000 hectare private game reserve in the Little Karoo, which converted from livestock farming to game farming, allows an opportunity to study the vegetation dynamics in a confined plant-herbivore system. This study investigates the current community structure and the changes in the floral composition and vegetation structure of enclosed and comparable sites subjected to grazing by large herbivores after twelve years (2004-2015). It also determines the relative effect of grazing and rainfall on the observed patterns. Finally, the implications of these findings for management are discussed.

Data from drop-point surveys in fenced (exclosure) and unfenced (grazed) plots in the dominant vegetation types as well as annual and seasonal rainfall totals, stocking rates of herbivores and annual game census information, were analysed. These were used in multivariate ordination techniques, regressions and linear mixed-effects models to determine the communities and their relationship with herbivory and rainfall over time and identify a set of indicator species. The annual game census information was used to determine areas of herbivore preference or ‘hotspots’ and for the identification of highly-utilised areas.

Cluster analysis, using the flexible beta method in PC-Ord, was used to determine the current plant communities. Non-metric multidimensional scaling ordination (NMS) was used to determine the relationship of these communities with the environmental variables and illustrate the trajectories in floristic data. Species were also assigned to plant growth forms and examined as communities and growth form types. The Bray-Curtis distance measures were used to investigate the difference between each treatment over time, within each vegetation community and between treatments. Finally, the effects of rainfall and herbivory were examined using linear mixed-effects models of change over time vs the various potential determinants of change using lmer functions in R.

Four communities were identified. These communities corresponded well with to the vegetation type descriptions for Western Little Karoo, Little Karoo Quartz Vygieveld and Renosterveld as described in the National Vegetation Map of Mucina and Rutherford (2006). However, the Western Little Karoo was too broad and two communities were recognised within this vegetation type. The finer scale mapping by Vlok et al. (2005) corresponded relatively well to these communities.

Results showed an increase in species richness, abundance and cover over time, with the ungrazed plots experiencing more change than the plots exposed to grazing. Most growth forms exhibited an increase in cover, although low leaf succulents declined in both grazed and ungrazed plots. Medium evergreen shrubs declined in the exclosures and stem succulents declined in the grazed plots. The effects were found in both grazed and ungrazed treatments. In addition, many species which declined in abundance were unpalatable or toxic to herbivores. Because of this, the decline in cover of such species was not attributed to grazing, but was instead interpreted as being a response to other disturbance mechanisms, to competitive displacement and to rainfall events. The low stocking rates in the first five years of the study resulted in there being very little difference evident between the treatments. However, once stocking rates increased from 2008, both species richness and cover increased more rapidly in the ungrazed plots, compared to the grazed plots. An increase in palatable and unpalatable species was observed within both ungrazed and grazed plots indicating that grazing did not change the proportion of palatability classes. However, specific plots in the areas of high animal utilisation were more affected as indicated by the response of cover, species richness and palatable species in these specific plots. This suggests that the grazing pressure may be too high within those areas. The linear mixed-effect model supports the argument that grazing pressure is the dominant driver of the community change within grazed plots. Similarly, the results show that rainfall is the primary driver of the vegetation community in the absence of grazing. Timing, amount and intensity of rainfall can mask these impacts. Thus, the contribution of grazing to vegetation change can probably only be detected by tracking the trends over decades or longer.

The use of indicators as a management tool is well documented. In order to identify indicators, a theoretical framework for determining indicators species in the different vegetation communities was created. This was based on the correlation between species abundance and sampling period in the different treatments, which identified species that have significantly increased or decreased over time as a result of the change in land use. Species identified as potential indicators were selected on the basis based on their abundance and ranged in lifespans and palatability. The indicators chosen need to be monitored into the future to confirm their utility as indicators.

A small but significant difference between grazed and ungrazed plots suggest that herbivore impact is apparent. Identifying this trend indicates that the monitoring programme is providing a useful tool for assessing the impact of herbivores on an ongoing basis. The recovery process following the withdrawal of domestic livestock from Sanbona was much slower in the grazed plots than in the protected plots. Therefore, for the continued recovery of the vegetation to occur and for there to be a sustained increase in cover, active management of animal numbers needs to take place. The results from this study can contribute to future management decisions on the reserve and form a basis for future analyses.

1. *INTRODUCTION*

South African ecosystems have a long evolutionary history of grazing by indigenous herbivores (Rutherford & Powrie, 2013) and many of these ecosystems are considered to be resilient to grazing pressure. Herbivores have influenced the species composition and distribution of the plants on which they feed (McNaughton, 1979; Cumming, 1982; Milchunas, et al., 1988; Stuart-Hill, 1992; Augustine & McNaughton, 1998; Augustine & McNaughton, 2006). In response, plants have developed a number of mechanisms to deter feeding. These can be either physical such as thorns, spines or hairs or chemical by means of producing secondary compounds or toxic substances in order to reduce digestibility (Milton, 1991; Wolfson & Tainton, 1999; Cingolani, et al., 2005; Rutherford, et al., 2006). When plants do get browsed, they can recover lost biomass rapidly by either coppicing or increasing their vegetative reproduction. This relationship between plants and herbivores has evolved to the point where some plants benefit from herbivory through increased reproductive output or seed dispersal (Milton & Dean, 2001; Rutherford, et al., 2006).

The Succulent Karoo biome is a semi-arid mediterranean-type climatic area which in the southern part of its distribution separates the relatively more mesic Fynbos biome from the more arid, summer-rainfall interior (Mucina, et al., 2006). The evolutionary grazing history of the Succulent Karoo is poorly known, although evidence suggests that the occurrence of large herbivores was intermittent (Dean & Milton, 2003) and probably more concentrated in the riverine areas than on the plains (Milton, et al., 1990). Todd and Hoffman (2009) suggest that the biome has a relatively short history of intensive grazing and that vegetation types with a short evolutionary history are more sensitive to grazing pressures than those ecosystems with a long history of exposure (Cingolani, et al., 2005).

In the past, wild ungulates generally moved unrestricted across the landscape in search of forage and water (Esler, et al., 2006; Skead, 2011). Variation in seasonal rainfall patterns across a region would have influenced forage availability, leading to fluctuations in grazing pressure across space and time. This unrestricted movement of herbivores would have been important in moderating their impact as the extended absence of herbivores would allow for the recovery of the vegetation in an area. Over the past 300 years, however, domestic livestock have replaced these wild animals and livestock farming currently prevails in most areas, particularly in the semi-arid rangelands where extensive livestock grazing is the predominant form of land use. Livestock farming practices often result in overstocking while continuous grazing is also relatively common. Such practices often do not allow for grazing deferment, which may result in land degradation. Such land degradation has been suggested as one of the main causes of biodiversity loss in rangelands (Scholes & Biggs, 2005).

As a result of changed socio-economic circumstances in South Africa many farms are now converting back from stock farming to game farming. Under these circumstances, however, larger indigenous ungulates are generally confined to relatively small enclosed areas and the characteristic migrations that once took place are no longer possible (Dean & Milton, 2003). Such restrictions on animal movement has the potential to alter the effects of ungulates on plant communities and ecosystem processes (Augustine & McNaughton, 1998). The grazing pressure within these enclosed areas is potentially much higher than in the past, pre-stock farming era. Indigenous herbivores are also difficult to manage because they are not herded and the variety of species present often have different grazing habits (Du Toit, 1995; Fritz, et al., 2002). In addition, many species are independent of water (Du Toit, 2016), making it difficult to control their movements. Even though ungulates may historically have occurred in an area, changes to the habitat may make it no longer suitable (Novellie & Knight, 1994; Castley, et al., 2001). Therefore, the degree of restriction of animals to specific areas as well as the condition of the vegetation in an area needs to be considered when deciding on the number and breed of animals to be introduced.

The impacts of indigenous herbivores have been studied, across a variety of different South African ecosystems but particularly in the grassland and savanna ecosystems (Owen-Smith & Cooper, 1987; Stuart-Hill, 1992; Kerley, et al., 1995; Waldram, et al., 2008; Asner, et al., 2009; Novellie & Gaylard, 2013; Wigley, et al., 2014). These impacts are less well known in the Karoo of the central and south-western Cape. To date, most herbivore studies within the semi-arid rangelands of South Africa have focused on the impact of grazing by domestic livestock (Milton, 1995a; Anderson & Hoffman, 2007; Todd & Hoffman, 2009; Haarmeyer, et al., 2010; Rutherford & Powrie, 2013). Only a few studies have focussed on the impact of indigenous herbivores on the vegetation of the semi-arid Karoo (Novellie & Bezuidenhut, 1994; Kraaij & Milton, 2006; Hoffman, et al., 2009), and those that have been undertaken have been of relatively short duration.

Arid and semi-arid ecosystems, like the Karoo, have a high variation in the timing, amount and intensity of rainfall events (Hoffman & Cowling, 1987), coupled with large annual and daily ranges in temperature (Desmet & Cowling, 1999). This unpredictable climate, together with the unusual vegetation of the region makes the Karoo more challenging to understand and manage than in other parts of South Africa (Esler, et al., 2006). Vegetation changes are also notoriously slow in semi-arid regions (Noy-Meir, 1973; O'Connor & Roux, 1995; Rahlao, et al., 2008), and the effects of grazing or sparing management on natural communities of long-lived plants generally take decades to become evident (Wiegand & Milton, 1996). In order to understand the dynamics of these systems, studies need to be over long periods of time to observe the response to a range of influences. Kraaij and Milton (2006) concluded that to differentiate rainfall-induced fluctuations from directional changes in vegetation dynamics caused by herbivory, monitoring needs to be conducted for extended periods that include several rainfall cycles. Studies of long duration in these semi-arid rangelands are important since they have not had the same history of grazing pressure like the savanna and grassland ecosystems and hence may not be as resilient to grazing impact (Todd & Hoffman, 2009).

What is of concern within arid and semi-arid rangelands, is that there is insufficient understanding of land degradation and biodiversity loss and as a result the resilience of these areas to herbivory (Rutherford & Powrie, 2013). According to the National Protected Area Expansion Strategy for South Africa (DEAT, 2008) the least protected biomes are Grassland, Nama-Karoo and Succulent Karoo. The protected area network is also biased towards particular ecosystems, and it does not conserve a representative sample of biodiversity for all biomes. It also excludes several key ecological processes (DEAT, 2009). Protected areas in the Western Cape have formerly been limited to large tracts of mountainous terrain, with water catchment areas in mind. Unfortunately, very few lower-lying areas have received conservation attention primarily because these are the more productive areas in the landscape and therefore are usually highly sort after for agricultural purposes (DEAT, 2009; Begon, et al., 2015). Private conservation areas are especially important in conserving lower elevation habitats, and by association, significant tracts of endangered vegetation (Gallo, et al., 2009).

Sanbona Wildlife Reserve, hereafter referred to as Sanbona, is a 54 000 hectare reserve located in the Little Karoo region of the Western Cape, South Africa. It was established in 2002, with the intention of sustainably conserving the biodiversity of the area and reintroducing indigenous ungulates into the Little Karoo, Western Cape. The reserve straddles two biomes, the Succulent Karoo and Renosterveld vegetation types of the Cape Fynbos Biome, both of which are recognised as global biodiversity hotspots (Myers, et al., 2000). Sanbona will be receiving protected area status under the CapeNature Stewardship Programme in 2017. This biodiversity Stewardship Programme was established to secure protected area expansion on private land, in order to contribute to national protected area targets (SANBI, 2014). However, in order to contribute to these targets, the management of these areas needs to be compatible with the persistence of the unique and regionally endemic plant communities that characterise the Succulent Karoo biome (Hoffman, et al., 2009). Because the impact of large indigenous herbivores on the vegetation of the Succulent Karoo Biome has not been demonstrated there is concern that the presence of such animals in confined areas may compromise the conservation value of protected areas.

The establishment of Sanbona has created an opportunity to investigate vegetation dynamics following the withdrawal of livestock and the subsequent introduction of indigenous herbivores to the Little Karoo. To these ends, permanent plots were established on Sanbona in 2004 and have been surveyed annually as the basis for a sustained monitoring programme, aimed at quantifying the extent and nature of vegetation change in response to climate and indigenous herbivore stocking rates (Hoffman, et al., 2009). In order to differentiate climate-induced impacts from herbivore effects, fenced plots have been paired with an adjacent unfenced plot, which has been subject to grazing and browsing by indigenous ungulates. An analysis of this data set forms the basis for this thesis, with the intention of addressing the questions as detailed below.

The objectives of the study are to:

- Review the literature on the impact of indigenous herbivores on arid and semi-arid rangelands, globally, within South African and in the Little Karoo, to identify gaps, uncertainties and implications relevant for the current study;
- Characterise the current vegetation communities and their properties, including the cover, species richness and unique species as a baseline for future comparisons;
- Use the time series of vegetation data to determine whether any directional changes in cover, species composition, growth form, and community-level have occurred after the twelve-year period of monitoring in both the fenced and unfenced plots and assess the relative influence of grazing and rainfall on the vegetation over this period;
- Identify indicator species that could be used to determine thresholds of concern and discuss the management implications of the findings in terms of game stocking rates, long-term vegetation dynamics and management-orientated monitoring programmes.

2. *LITERATURE REVIEW*

2.1. Indigenous animals and their impact on arid and semi-arid rangelands

Plants have to deal with a complex of environmental factors, of which herbivore impact is only one (McNaughton, 1979). Coevolution of plants and herbivores has influenced ecosystems to what they are presently. Plants have developed compensatory mechanisms, that are activated by grazing. For instance, plants may increase photosynthetic rates, have stimulated vegetative growth, change their growth forms (McNaughton, 1984) or increase seed set (McNaughton, 1983). McNaughton (1979), for example, reported that the saliva from ruminants can stimulate plant growth separately from the act of grazing. Milchunas and Lauenroth (1993) collated a number of studies and found that grazing had a small, but positive influence on plant production globally when consumed at low levels for a moderate time period. Under such conditions there was usually also a change in species composition. This is particularly well noted for graminoids. Similarly, browsing can produce a dense, highly branched canopy that protects the interior foliage by making it physically less accessible (McNaughton, 1984). Diaz et al. (2007) found that heavy grazing and browsing pressure favoured annuals over perennial plants, short plants over tall plants and prostrate over erect plants. Plants growing in arid areas have additional adaptations for conserving water as well as reducing herbivory either by being small, fibrous and tough, having waxy or hairy cuticles, high salt concentrations, tannins, alkaloids and phenolic compounds (Dean & Milton, 1999; Cingolani, et al., 2005). Consequently, herbivores need to be tolerant of these defences or highly selective for undefended plant parts (Dean & Milton, 1999).

Even though the plants have adaptations, heavy grazing can still have a detrimental impact. This has been shown to be one of the main causes of degradation and loss of biodiversity in arid and semi-arid environments (Westoby, et al., 1989; Milchunas, et al., 1988; Noy-Meir, et al., 1989; Cowling & Hilton-Taylor, 1999; Haarmeyer, et al., 2010). Grazing impacts include: 1) an alteration of species composition, including decreases in density and biomass of individual species, reduction of species richness and changing community organization; 2) a disruption of ecosystem functioning, including interference in nutrient cycling and ecological succession; 3) an alteration of ecosystem structure including changing vegetation stratification, which contributes to soil erosion and a decrease in the availability of water for biotic communities (Fleischner, 1994).

Herbivores are known to be selective feeders, choosing plants to satisfy their nutritional requirements as effectively as possible (Farmer & Milton, 2006). Selective grazing in heavily stocked areas leads to an increase in densities of unpalatable species (Seymour, et al., 2010). It can also lead to the reduction or even elimination of palatable species thus increasing the competitive advantage of less preferred plant species (Milton, 1994; Burke, 1997). Because of this, palatable species are often slow to recover due to the continued pressure from grazing. The reduction in seed availability due to lower densities and possible increased competition from unpalatable species further affects the ability of palatable species to survive in heavily grazed rangelands. The low density of palatable species also implies a lower seed production and seed bank, and a lower possibility of recruitment of these species (Milton, 1992a). Milton (1995b) found that competition by established plants had greater influence on seedling survival than herbivory, which reduced the size of *Osteospermum sinuatum* seedlings but did not influence their survival. Midoko-Iponga et al. (2005) found that both plant competition and herbivore densities had a synergistic or substitutive effect on plant performance while Gurevitch et al. (2000) found that herbivory had a greater effect on an organism’s growth and subsequent phytomass than competition. Eldridge et al. (1990) showed that grazing had no effect on population dynamics but that shrub size was affected. Milton et al. (1992) found that repeated utilisation of new shoots of thorny species such as *Lycium* and *Ruschia spinosa* reduced their defence and thus increased their accessibility for further herbivory. Continuous heavy grazing in the past has led to a lower diversity of palatable species (Seymour, et al., 2010). This loss may not affect grazing potential in times of low stress, but if external perturbations (e.g. climate change) cause a shift in plant species composition, the palatable species that could respond by becoming more abundant may not be present to do so (Seymour, et al., 2010).

Local differences in soil-moisture and nutrient status can also lead to uneven use of sites and habitats by animals. Milton (1990), found that the influence of animals on plants increased from the plains through washes to drainage lines. Plant species which occurred in these mesic sites in drainage lines and rocky ridges defended themselves against damage by mammals by possessing fine short spines or long hard thorns and were zoochorically dispersed. This was evident by the presence of small soft burrs, or larger diaspores on plants from medic sites (Milton, 1990; Milton, et al., 1990; Milton, 1991). In contrast, plants which occurred on the plains had no spines although they did possess finely divided branches and tough aromatic or deciduous leaves. Such traits suggest that these plants are probably better defended against excessive damage by birds and insects than by mammals (Milton, et al., 1990).

Evergreen plants have long-lived leaves that are exposed to herbivory throughout the year. By comparison with deciduous and fugitive plant species, evergreen plants are chemically well defended against generalist herbivores (Milton, 1993). This led to Milton et al. (1990) suggesting that large, herbivorous mammals which were resident in the Little Karoo during the past 10 000 years tended to be solitary rather than herding species. In more productive habitats that support a large diversity and biomass of herbivorous mammals, epizoochoric dispersal and thorniness have evolved in plants. In the semi-arid Karoo, however, a large proportion of endemic plants lack epizoochoric diaspores and thorns. There is also a low abundance and diversity of plants with adhesive fruits. This suggests that the Karoo flora has evolved with little impact from large, herbivorous mammals. It also suggests that the vegetation of the semi-arid Karoo has a relatively low carrying capacity and is likely going to be sensitive to heavy grazing pressure (Milton, et al., 1990).

Long-term grazing and trampling can compact the soil through the hoof action of animals. This increases the risk of flooding and erosion and can lead to a decrease in water infiltration (Snyman, 1998). Lower infiltration in turn will alter the species and structural composition of the vegetation and often results in the loss of grass cover. This further reduces water infiltration rates, as grasses are better able to retard the movement of water over a landscape than shrubs (Snyman, 1998). The hoof action of animals can also damage important microbiotic soil crusts. These soil crusts are common in semi-arid environments (Belnap, 2006; Jimenez Aguilar, et al., 2009) and increase the organic matter, available phosphorus, carbon and nitrogen of soils, help to stabilize soils and enhance water infiltration as well as influence soil biodiversity (Bowker, et al., 2005; Belnap, et al., 2008; Johnson, et al., 2012). Crusts also play an important role in providing favourable sites for the germination of vascular plants (Fleischner, 1994) and influence the plant communities (Belnap, 2006).

Within the Succulent Karoo, most studies have focused on the effects of grazing pressure by livestock on species richness and diversity. These studies have shown variable responses. Hendricks et al. (2005) reported a decline in species richness along a grazing intensity gradient, as did Haarmeyer et al. (2010), but specific to quartz plots, while Rutherford & Powrie (2013) reported an increase in species richness at higher grazing pressure. Other studies found that species richness and diversity increased with increased grazing pressure at a fine scale and this was attributed to compositional shifts to smaller, ephemeral species such as geophytes and annuals or alien plant species (Anderson & Hoffman, 2007; Todd, 2006). Todd and Hoffman (2009), found that local species richness is not necessarily affected. Instead, the effect is on a landscape level because the area under constant livestock pressure is transformed and recovery to its former state is not possible in a short time frame. What was more evident was the change in composition and cover.

Todd and Hoffman (1999) found that grazing tolerant species increased while palatable species and leaf succulents decreased in grazed areas and that these palatable species reduced in volume, reduced flower production and seedling recruitment. Anderson and Hoffman (2007) found a loss in plant cover in the highly-grazed areas and a composition shift, with a reduction in large succulent and woody shrubs but an increase in smaller dwarf shrubs. Hanke et al. (2014) reported that heavier grazing reduced total plant cover and altered the species and functional composition. Hanke et al. (2014) found that a decline in grazing-sensitive species may be replaced by grazing-tolerant species. However, if grazing regimes go beyond the historical range experienced by a system it can induce a decline in species diversity.

Todd and Hoffman (1999) also found that palatable species were reduced in volume, had fewer flowers and lower levels of seedling recruitment. Dreber and Esler (2011) found that in heavily-grazed areas, soil seed banks were persistent and accumulated seeds over time. However, the species composition of the seed bank may be affected and usually increases in annuals. Medinski et al. (2010) stated that soil properties like infiltration, clay or silt content, pH and electrical conductivity can affect plant species distribution. Water infiltration into the soil after rain is important. It increases where soil is coarser and vegetation cover improves infiltration, while protecting the soil from the sun. In other words, shading and manuring can even improve the moisture status of soils (Hanke, et al., 2011; Hanke, et al., 2015). Hanke et al. (2011) stated that low-intensity rainfall may not filter through and reduce the amount of soil-wetting. Microcatchments would not be of any use because heavier rainfall events usually fall outside the growing season. But microcatchments could promote seedling germination and enhance the survival and growth of established plant individuals (Hanke, et al., 2011).

Large-bodied herbivores have a dramatic effect on the species composition of plant communities in arid and semi-arid regions (Fleischner, 1994). Both feeding strategies and physical disturbance by the large herbivores can alter ecosystem properties resulting in long-term changes in communities (Mucina & Rutherford, 2006). Even though more than 13% of the land in South Africa is used for game ranching (Cloete, et al., 2007) very few studies, especially in semi-arid southern Africa, have examined the effects of indigenous herbivores on rangelands. Hoffman et al. (2009), however, found no impact of grazing after five years at Sanbona Wildlife Reserve while Novellie and Bezuidenhout (1994) found that the effect of grazing on plant species composition in Mountain Zebra National Park was slight compared with that of rainfall. A study by Kraaij and Milton (2006) on the effects of indigenous ungulate grazing on the vegetation of the Karoo National Park, after the replacement of domestic stock by wild herbivores, found a decrease in annual grass cover and an increase in perennial grass cover as well as an increase in species richness. Changes were also more rapid in permanently fenced exclosures than in areas exposed to herbivory (Kraaij & Milton, 2006).

Even though their preferences are similar, indigenous herbivores are generally considered less detrimental to rangelands than domestic livestock because of the wider range of plant species that they consume. Indigenous herbivores also eat plants that are considered less palatable or even toxic to domestic animals (Farmer & Milton, 2006). Fenwick (2008) investigated the diet selection of indigenous herbivores on Sanbona and found that, while they fed on similar species to domestic livestock, indigenous herbivores had different preferences and were not dependent on the availability of the preferred plant. An important conclusion from this study was that vegetation that has little potential to support domestic small stock would also be unsuitable for indigenous herbivores. Similarly, overstocking with indigenous herbivores will also influence the vegetation composition in the same way as overstocking with domestic small stock (Farmer & Milton, 2006).

Vegetation could also be utilised and affected by a number of other animals which are endemic to the area such as tortoises, lagomorphs, porcupines, rock hyrax and rodents as well as ostrich. In a study by Milton (1992b), leopard tortoises (*Geochelone pardalis*) switched to succulents when green grass was unavailable. The succulent species selected by tortoises included plants that had spines such as *Euphorbia stellispina* and *Ruschia spinosa* and chemically defended species including *Tylecodon spp.* and other *Crassulaceae* that contain cardiac glycosides. Tortoises also selected plants within the *Mesembryanthemoideae* (hereafter referred to as mesembs), which have high concentrations of oxalic acid, sodium or the alkaloid, mesembrine. Indigenous antelope generally avoid these species. Cape hare (*Lepus capensis*) were observed eating foliage and flowers of forbs and shrubs (Kerley, 1990) while seed capsules of mesembs were eaten by Smith's red rock rabbit (*Pronolagus rupestris*) (Dean & Milton, 1999). Rock hyraxes (*Procavia capensis*) feed selectively on the new growth of forbs and shrubs, including *Pteronia pallens,* which is toxic to other herbivores (Dean & Milton, 1999). Whistling rats (*Parotomys brantsii*) and Karoo bush rat (*Otomys unisulcatus*) have a great deal of dietary overlap (Dean & Milton, 1999). Their diet is high in succulents (Kerley, 1989) including toxic succulent and woody plants (Vernon, 1999). Both feed opportunistically on annual plants. Ostriches (*Struthio camelus*) are selective herbivores that feed on new growth, short-lived forbs and grasses and so they prefer open habitats with short forb and grass cover (Milton, et al., 1994) and therefore most likely compete with springbuck. They avoid woody or dead material and plant species that are known to chemically deter mammalian herbivores (Milton, et al., 1994). Little is known about how these animals in addition to ungulate herbivores could be impacting rangelands.

A potential positive influence of indigenous herbivores on natural vegetation is their role in endozoochory. Endozoochory is frequent in natural ecosystems with high diversities or densities of herbivorous mammals (Janzen, 1984). Milton and Dean (2001) found that dung from indigenous animals had twice the intact seed density than that of livestock. Although the floras of the Karoo are considered to be largely wind and water-dispersed, endozoochory is a primary or secondary dispersal mechanism in many plant families and within many plant life-forms (Milton & Dean, 2001). For ecosystem management and rehabilitation, herbivorous mammals provide an effective service in that they disperse large quantities of viable seeds to predictable microsites. Certain insectivorous mammals such as the aardvark, have also been found to disperse seed. The aardvark ingested the seed while feeding on their preferred diet of ants, which they lick from excavated nest-mounds (Milton & Dean, 2001). Similarly, the bat-eared fox can also be a secondary disperser of seed. Many herbivores also create high densities of plants in their dung middens and assist in the dispersal of leaf succulent species within the *Aizoaceae* that have short distance primary dispersal mechanisms. The consumption of their seed capsules by herbivores provides an opportunity to occasionally be dispersed over longer distances. Shiponeni and Milton (2006) suggested that populations of indigenous antelope could also play a role in the restoration of vegetation via the dispersal of seed from natural vegetation to abandoned fields. Eland dispersed seeds of indigenous species with small hard seeds (Shiponeni & Milton, 2006).

Lastly, indigenous ungulates can influence nutrient enrichment of the soil and contribute to the transformation of vegetation (Milton, et al., 1992; Palmer, et al., 1999). Dung and urine inputs, for example, result in high concentrations of phosphorous, potassium, nitrogen, salts and organic matter in habitat patches intensively utilised by herbivorous mammals (Barker, et al., 1990), particularly in middens, leks or zoogenic mounds, locally known as heuweltjies. Heuweltjies means ‘little hills’ in Afrikaans and are small earth mounds that can reach up to 32 m in diameter and 2.4 m in height and can be found throughout the Succulent Karoo Biome (Lovegrove & Siegfried, 1989; Potts, et al., 2009; Kunz, et al., 2012; Midgley, et al., 2012). Schmiedel et al. (2016) found that there were visually distinct zones on heuweltjies. Towards the centre of the heuweltjie there was an increase in annual plants and soil pH. However, the vegetation cover, species richness and perennial plant cover decreased. These findings support the statement that herbivores can influence nutrient enrichment of soil since overgrazing has resulted in high utilisation and nutrient accumulation in the centres of heuweltjies.

2.2. The influence of climate on semi-arid rangelands

Arid and semi-arid ecosystems are characterized by a stochastic and low annual rainfall (Noy-Meir, 1973). The timing, amount and intensity of rainfall has been shown to have a marked influence on the dynamics of plant populations as well as on the composition of these arid communities, more so than herbivory or fire (Westoby, et al., 1989; Hoffman & Cowling, 1990; Milchunas & Lauenroth, 1993; Burke, 1997; Desmet & Cowling, 1999; Illius & O'Connor, 1999; Reynolds, et al., 2007). Milchunas and Lauenroth (1993) state that annual weather fluctuations and long-term climatic cycles may often override or mask grazing effects. Therefore, in order to differentiate between the effects of grazing and rainfall it is imperative to track trends of vegetation change over very long periods of a decade or longer (Novellie & Strydom, 1987).

In these arid and semi-arid regions, the variability of the precipitation increases with decreasing annual total (Hoffman & Cowling, 1987; Tainton & Hardy, 1999). However, within the semi-arid areas in South Africa, the Succulent Karoo generally has more reliable rainfall than other biomes for a given rainfall total. In the Succulent Karoo biome, rain falls predominantly within the late autumn and winter months (April-August) (Hoffman & Cowling, 1987; Cowling, et al., 1998) and growth, flowering, germination and recruitment of plants is closely tied to this relatively predictable input of moisture (Hoffman & Cowling, 1987). The Little Karoo falls in the transition zone between the winter and summer rainfall areas where rain may fall at any season. Rainfall seasonality influences the relative abundance of summer- and winter-growing plants (Hoffman & Cowling, 1990; Milton & Dean, 1995). Summer rainfall has a greater effect on grass abundance than does grazing (Hoffman, et al., 1990) while shrub canopy cover in the Succulent Karoo was correlated with rainfall of the previous winter's growing season (Stokes, 1994). Fossil records exist indicating that this grass:shrub ratio has occurred in response to natural fluctuations in rainfall over a long time (Dean, et al., 1995). Bond et al. (1994) used carbon isotopes from soils to confirm that in the Karoo, summer rainfall was important in determining variations in grass cover. However, they found that the impact of grazing was starting to change this relationship and had driven the decline in grasses.

Gunster (1993) felt that the timing of the rainy season was more important than the total amount of rainfall. For the Succulent Karoo biome, small rainfall events are common while significant rainfall events (greater than 10 mm) usually occur in the winter months only (Hoffman & Cowling, 1987). It is the larger events that probably have the greatest influence on biological processes like reproduction and biomass production (Noy-Meir, 1973). Plants have a very short growth period before water becomes limiting and growth slows. The timing between events and the intensity of each event will also determine the amplitude of the biological processes. There is also a high spatial variation in rainfall in arid and semi-arid areas at scales of 0.1-10 km (Noy-Meir, 1973). This can be attributed to orographic increase in rainfall with altitude as well as the effect of the direction and speed of wind, degree of slope and rain angle on different slopes in hilly regions (Noy-Meir, 1973). This interacts with exposure, soils, aspect etc to create a diversity of different vegetation communities.

Vegetation composition can also be altered by droughts in arid environments depending on their severity (Milton, et al., 1995). Droughts act like herbivory, by reducing plant size. Therefore, adaptations for capturing below-ground resource are important (Milchunas & Lauenroth, 1993). In severe droughts, with high mortality of plants, gaps are created (Milton, et al., 1995) and they may offer a window of reduced competition allowing other species opportunities to germinate (Milton & Hoffman, 1994). Thus, like rainfall, droughts also play an important role in recruitment events. Likewise, selective grazing following a drought will also influence the vegetation composition and cover and this needs to be kept in mind. The variety of survival and regeneration responses in vegetation, developed under highly variable rainfall, ensures that natural rangeland can recover from droughts and remain productive during both summer and winter rainfall cycles (Milton, et al., 1995).

In the Karoo, the long-term variation in rainfall and ‘back-to-back’ years of both drought and high rainfall all influence shifts in plant biomass and species composition. Karoo vegetation must be interpreted in terms of how climatic variability influences biomass, productivity and species assemblages as well as in terms of the longer-term environmental history of the Karoo (Dean, et al., 1995).

2.3. Current concepts of rangeland dynamics

The dynamics of arid and semi-arid systems are currently understood in terms of non-equilibrium dynamics. Heshmati & Squires (2009) describe the non-equilibrium model as natural ecosystems shifting between different ecological states through ecological transition zones in response to natural or human-induced factors, rather than following a prescribed successional path. In other words, species densities do not remain constant over time at each spatial location (Chesson & Case, 1986; Gillson & Hoffman, 2007). In contrast, the equilibrium model does not take into account the spatial heterogeneity and climatic variability of semi-arid rangelands (Vetter, 2005). Although the quality of the Karoo shrub forage is high, the composition and quantity supplied at any given movement varies significantly because it is influenced by the total amount of rainfall, the temperature prevailing (Esler, et al., 2006), the timing of the rainfall (Du Toit, 2003), as well as the soil and topography. Under the non-equilibrium view of rangeland dynamics, climatic variability prevents plant and herbivore populations from being at equilibrium.

The intermediate disturbance hypothesis was created to account for patterns of diversity. All communities are subject to disturbances that exhibit different frequencies and intensities (Townsend, et al., 1997). Such disturbances have important implications for the maintenance of biodiversity and species richness. The intermediate disturbance hypothesis is based on that concept that ecological communities seldom reach an equilibrium state, in which the competitively superior species exclude others.

Therefore, disturbances that kill or damage individuals will continually set back the process of competitive elimination by opening space for colonization by less competitive individuals. The highest diversity is maintained at intermediate levels of disturbance (Begon, et al., 2015).

Sullivan and Rohde (2002) maintain that non-equilibrium and equilibrium dynamics are not mutually exclusive. They argue that ecosystems exist across a gradient between these extremes, and that this all depends on the scale of observation. Even though the dynamics of arid and semi-arid rangelands are generally considered to be non-equilibrial, Benjaminsen et al. (2006) suggest that the Succulent Karoo Biome tends towards the equilibrium spectrum of the gradient. They argue that the regular and reliable winter rain of the Succulent Karoo biome which falls in the cool period of the year, together with the particular ecology of the succulent vegetation of the region leads to a stable and predictable environment more in keeping with the equilibrium than non-equilibrium view of rangeland dynamics. Vetter (2005), Gillson and Hoffman (2007) and Todd and Hoffman (2009) recognised that most arid rangelands show elements of both equilibrium and non-equilibrium dynamics. It was recommended by Todd and Hoffman (2009) that the diversity in structure, function and response to grazing pressure of different African ecosystems needs to be appreciated, and they cannot all be grouped within a single model.

A suggestion by Illuis and O’Connor (1999) and Vetter (2005) was that key resources regulate populations in semi-arid areas by influencing the amount of forage available in the dry season. In consequence, animal numbers are regulated in a density-dependent manner by the amount of forage available in key resource areas, especially during droughts. Hempson et al. (2015) found that with reduced forage availability during droughts, there was a loss in body condition in the domestic livestock measured in the study. This led to lower pregnancy rates and fewer lambs and kids with a reduced survival of juveniles.

While the calculation of a carrying capacity is possible in relatively unchanging environments, it may be difficult to apply to non-equilibrium environments because the number of animals an area can support varies on several timescales. Carrying capacities also vary spatially within and between landscapes and temporally under different climate patterns (Vetter, 2005). With the conversion from livestock farming to wild herbivores, a reserve requires a baseline to determine an appropriate stocking rate for the area. However, if the area is considered as functioning according to non-equilibrium dynamics with fluctuating carrying capacity, how is this possible to manage? It would not be viable to manipulate animal numbers annually, since it is difficult to remove or cull wild animals one year then purchase the following year. The handling of wild ungulates as opposed to livestock is far more challenging both financially and physically. There are also seasonal constraints which limits the timing of certain management interventions. For example, the capture and movement of wild ungulates is a specialised field that is usually permitted only in the autumn and winter season. This is to reduce the risk of target animals overheating during the capture and translocation process (La Grange, et al., 2016). The handling of wild animals can also be dangerous and requires considerable logistical planning. Permits are also required from local conservation authorities which take time to secure (La Grange, et al., 2016). In addition, the impact of predators on herbivores and the need to maintain sufficient available prey for them is also an imperative.

Herbivore numbers also fluctuate depending on the dynamics of predators both within and between years. The non-equilibrium concept also implies that vegetation shifts should be relatively rapid and driven largely by rainfall and not by herbivores (Sullivan & Rohde, 2002). If this is indeed the case, then is there even a need for herbivore management? Key resource areas are possibly a better technique in deciding on the number of animals (Illius & O'Connor, 1999) since there are certain vegetation communities that may be smaller but are preferred such as riparian vegetation. Such habitats are a main focus for elephant, rhino, hippo, zebra and giraffe and the lack of vegetation in a drought would severely impact their survival. These key resource areas may be species-specific and therefore each species and its key resource area would need to be investigated as well as the interaction of other species that utilise the same area.

Conservation managers require guidance in the determining the number of animals that can be sustainably supported on their reserves. The problem is that the methods for arriving at the correct number are in dispute. Until this matter has been resolved, the long-term average annual rainfall for a district can provide a reasonable guide to the expected grazing capacity of the veld (Esler, et al., 2006). However, the high variability of climate in arid and semi-arid regions must be taken into account when the carrying capacity of a conservation area is determined, to avoid overstocking and subsequent degradation, especially during drought periods (Burke, 1997).

2.4. Vegetation monitoring

Vegetation change in arid ecosystems is often slow to become apparent. This is because the dominant species can have life-spans of decades, the unpredictable and low rainfall slows plant growth and there are also a limited number of recruitment events (Wiegand, et al., 1995; Wiegand & Milton, 1996; Lawley, et al., 2013). Data must be collected over decades to gain an understanding of how vegetation responds to short-term, inter-annual variation in rainfall as well as long-term cyclic rainfall patterns, episodic rainfall events and grazing pressure (Kraaij & Milton, 2006; Lindenmayer & Likens, 2010).

Van Rooyen et al. (2015) noted that there is a lack of long-term data on vegetation dynamics in the Succulent Karoo. Jurgens et al. (1999) conducted a 15-year study in the Richtersveld and reported that patterns of mortality and recruitment showed substantial differences among species which were not all due to rainfall patterns. Rahlao et al. (2008) reported on a 67-year study in the Worcester area, and found a significant and directional response to rest on both termitaria and off termitaria sites. Schmiedel et al. (2012) monitored vegetation change in the Knersvlakte over a 12-year period and found inter-annual changes in population size, species richness and species composition. Van Rooyen et al. (2015) looked at vegetation dynamics in Namaqualand over 40 years, and found that the effects of heavy-grazing by livestock was reversible although the number of indigenous animals must be actively managed to avoid vegetation degradation.

Long-term research and monitoring can provide important ecological insights and is crucial for the improved management of ecosystems and natural resources, particularly if it is linked to the objectives (Lindenmayer & Likens, 2009; Wiegand & Jeltsch, 2000; Brown & Havstad, 2004). It is important for managers to acquire and use information and knowledge to promote sound management of natural resources (Williams & Brown, 2014). For long-term monitoring, the use of permanent sample sites is excellent for detecting temporal change (Elzinga, et al., 1998) because they allow for the separation of spatial variation from temporal change. Paired designs are very powerful ways to isolate single factors in the field setting. For the monitoring of rangelands, pairs of plots are selected such that the plots are 'identical' except that one plot is grazed while the other is not grazed. The most serious problem with this design in practice is that it is usually very difficult to find two adjacent spots that are identical (McCune & Grace, 2002) in, for example, rockiness and soil depth, therefore, in species composition and cover. Even though exclosures are very useful tools for examining the effects of grazing on plant composition, in semi-arid areas they need to be used as medium to long-term indicators of range condition (Mbatha & Ward, 2010).

Most permanent plot studies are subject to some degree of error from changes in observers and inexact relocation of sampling sites (McCune & Menges, 1986). It is best to conduct surveys more frequently as large intervals would more than likely introduce new observers and therefore increase observer bias (Novellie & Strydom, 1987). Point surveys recording the nearest plant to each point (Mentis, 1984) are potentially less susceptible to operator bias, but this method has the limitation of yielding only proportional species composition, and not the absolute abundance of individual species. Changes in species composition could thus be difficult to interpret, since a decline in relative abundance of one species could be due either to a die-off of that species or to an increase in the abundance of any of the other species. This limitation would be particularly important in semi-arid regions where there may be a marked difference between species in seedling establishment following good rains (Novellie & Strydom, 1987).

Another important source of variation, particularly in semi-arid areas, is between-year differences in rainfall (Novellie & Strydom, 1987). This can make it difficult to distinguish the effects of climate on the vegetation from the effects of grazing. The fact that rainfall fluctuations can have so marked an effect on the vegetation argues in favour of a high frequency of repeat surveys. In order to compare results obtained during each of the annual surveys it is important to conduct repeat surveys at the same site and at the same time of the year. The best time in the semi-arid Karoo is at the end of the growing season (Du Toit, 2003).

The number of plots used in the monitoring design can also have an effect on the results. A design that uses ‘many-but-small’ sample plots will yield relatively accurate abundance estimates for the most common species but will yield a very incomplete species list. The ‘large-but-few’ design on the other hand will yield a relatively complete species list but will tend to overestimate the cover of rarer species. It will also likely yield imprecise estimates of the more common species (McCune & Grace, 2002).

For managers to confidently be making a conclusion from the data, they need to be familiar with the concept of statistical error. When testing for trends or differences in monitoring data, two types of errors can be made. Type I error or α, can conclude falsely that a difference or trend occurred when it in fact it did not. Type II or β, is when one may falsely conclude that a difference or trend did not occur when in fact it did (Gibbs, et al., 1999).

Finally, there are also practical constraint on human resources and capacity. To have an effective monitoring programme it needs to be statistically powerful yet labour efficient (Gibbs, et al., 1999). It also needs to provide useful information at a minimal cost and have few logistical problems. For example, time is generally at a premium within any commercial operation and should not be wasted trying to relocate the plots. It may also be necessary to minimize unproductive travelling time by clustering plots or having them in more easily accessible areas, particularly on a large reserve.

2.5. Management implications

In order to manage a system to its best potential, reserve managers need to understand the system they are managing, set objectives and choose indicators that could assist them in deciding on thresholds of potential concern (Rogers & Biggs, 1999; Biggs, et al., 2011). These thresholds are limits set in order to initiate a management change prior to undesirable ecosystem change.

Monitoring for management focuses on making continual adjustments to management inputs in response to assumed effects of changes in driving variables. Monitoring is an essential step to evaluate progress in meeting management objectives or in avoiding undesirable change (Brown & Havstad, 2004; Smit, et al., 2016). This forms an important part of adaptive management, which refers to a structured process of learning by doing, and adapting based on what is learned (Williams, 2011; Williams & Brown, 2014). The feedback between learning and decision making is a defining feature of adaptive management (Williams, 2011). However, in the same way that management objectives can be altered, an adaptive monitoring framework enables monitoring programmes to evolve and develop as new information emerges and research questions change (Lindenmayer & Likens, 2009). For example, it might be appropriate to alter the frequency of monitoring because there are changes that differ from those initially anticipated. In addition, if there are changes in the options available to management, then new ways to monitor might be needed to accommodate these changes, thus making the adoption of adaptive monitoring an important link to adaptive management (Lindenmayer, et al., 2011).

In summary, the gain in understanding from monitoring and assessment is used to inform the selection of management actions (Williams, 2011). As understanding evolves, so too does the decision making that is influenced by improved understanding. In this way, the cycle of decision making, monitoring and assessment leads gradually to improved management as a consequence of improved understanding.

Monitoring is meant to inform conservation managers. However, managers often do not know when to respond to monitoring results (Brown & Havstad, 2004; Smit, et al., 2016). It is, therefore, important to have monitoring thresholds so that monitoring does not become aimless. If monitoring indicates a trajectory towards an unacceptable state it requires intervention (Biggs, et al., 2011; Smit, et al., 2016). Identifying ecological thresholds and associated monitoring thresholds is difficult, especially when they are not known, which is usually the case (Smit, et al., 2016).

Gibbs et al. (1999) indicated that monitoring information is wasted if it is not analysed correctly, archived well, reported timely, or communicated appropriately with decision makers. Properly organized and archived data provides managers with opportunities to adapt to changing circumstances and new information (Gibbs, et al., 1999). Gibbs et al. (1999) also stressed the need for explicit documentation of sampling protocols so that new personnel can repeat monitoring measurements as closely as possible.

This study forms the first step towards adaptive monitoring for Sanbona by supplying managers with information obtained from the long-term monitoring plots. An important step would be in the identification of indicator species as it is easier to monitor trends in a few species than in many plots. These indicator species would then assist in deciding on the thresholds of potential concern. Once these thresholds have been set, then the monitoring programme needs to continuously give feedback so that sound management decisions can be made. To date, managers have relied on observations over time and on their experience to make certain decisions. Having the evidence from a well-designed scientific experiment is invaluable.

3. *STUDY AREA*

Sanbona Wildlife Reserve is a 54 000 hectare privately owned game reserve, situated in the Little Karoo between Montagu and Barrydale in the Western Cape Province (33°43’24’’ S; 20°36’55’’ E). It measures roughly 25 kilometres from north to south, and 30 kilometres from east to west (Figure 3.1).

Figure 3.1. The location of Sanbona Wildlife Reserve (green polygon) in the Little Karoo, South Africa.

3.1. Climate

Sanbona lies within a transition zone between summer and winter rainfall regions. Rainfall can occur throughout the year. Winter rainfall is typically frontal (cyclonic), with summer rainfall predominantly in the form of convectional thunderstorms that develop in the interior (Vorster, et al., 2016). Sporadic droughts are common in the area, but prolonged droughts are rare (Desmet & Cowling, 1999).

Annual rainfall (calculated from Oct-Sep to correspond with the growing season and with the timing of the annual vegetation surveys, from 2003 until 2015) is low with the mean annual rainfall of 248 mm, varying from 159 mm in the driest year to 400 mm in the wettest year, with a coefficient of variation of 29%. Rainfall varies across the reserve and is strongly influenced by the centrally positioned, east-west orientated, Warmwaterberg mountain which effectively divides the reserve into a northern section (Sanbona North) and a southern section (Sanbona South). Rainfall in the northern section peaks in the spring and summer months. The southern section of Sanbona receives a higher annual rainfall primarily in winter.

Two in situ weather stations are located on the reserve. One is located in Sanbona North at Brakriver, and one in Sanbona South at Kalkoenshoek. Temperature ranges from -2°C to 41.8 °C with a mean maximum temperature of 30.6°C for January, the hottest month. The mean minimum temperature for July, the coldest month is 4.9°C (Vorster, et al., 2016).

3.2. Physical Environment

The Warmwaterberg comprises the oldest geological formations on Sanbona. It is dominated by sandstones and quartzite and falls within the Rietvlei Formation and Skurweberg Formation (Almond, 2009), which forms part of the Table Mountain Group. The mountain range is characterised by steep to very steep slopes and consists predominantly of exposed rock with little soil. The low hills and valleys which surround the Warmwaterberg are comprised of sandstones and mud-rocks of the Bokkeveld Group, while the Witteberg Group forms the mountains in the west of the reserve (Almond, 2009). The dominant soil formations for the reserve are the Mispah and Glenrosa formations, with some Oakleaf, Hutton and Swartland.

The Mispah and Glenrosa formations are characterized by shallow and rocky soils that are slightly leached, with lime common. Mispah soil is horizontally orientated hard rock with a thin A horizon overlying it, without the vertical channels containing soil material (Kruger & Hex, 2009). Shale is typical of Mispah (Fey, 2010). Glenrosa soil form has an Orthic A horizon which merges into the underlying weathering rock (Kruger & Hex, 2009). The Oakleaf form is usually deep, alluvial and freely drained while the Hutton form is normally comprised of deep, poorly drained soils derived from mixed sources. The Hutton form is usually found on floodplains, stream terraces, and depressions (United States Department of Agriculture, n.d.) and is typically red in colour (Fey, 2010). The Swartland soil form is a blocky, structured horizon with variable depth and enriched with clay. Swartland soils can be susceptible to erosion (Fey, 2010).

3.3. Biological Environment

The reserve supports two internationally recognized vegetation biodiversity hotspots. These are the Fynbos Biome and the Succulent Karoo Biome (Mucina & Rutherford, 2006). The Fynbos Biome comprises the greatest concentration of higher plant species in the world, outside of the tropics, with only nine percent of the biome formally protected, while less than five percent of Renosterveld, an associated vegetation type, falls within protected areas (Rouget, et al., 2014). The Succulent Karoo Biome boasts the richest succulent flora on Earth, with high levels of endemism (Rutherford, et al., 2006). Only 7.8% of the Succulent Karoo is formally protected (Myers, et al., 2000).

The vegetation types as described by Mucina and Rutherford (2006) on Sanbona are Western Little Karoo (WLK), Little Karoo Quartz Vygieveld (LKQV), Montagu Shale Renosterveld (MSR), Matjiesfontein Quartzite Fynbos (MQF), Montagu Shale Fynbos (MSF), Northern Langeberg Sandstone Fynbos (NLSF) and South Langeberg Sandstone Fynbos (SLSF) and are illustrated in Figure 3.2.

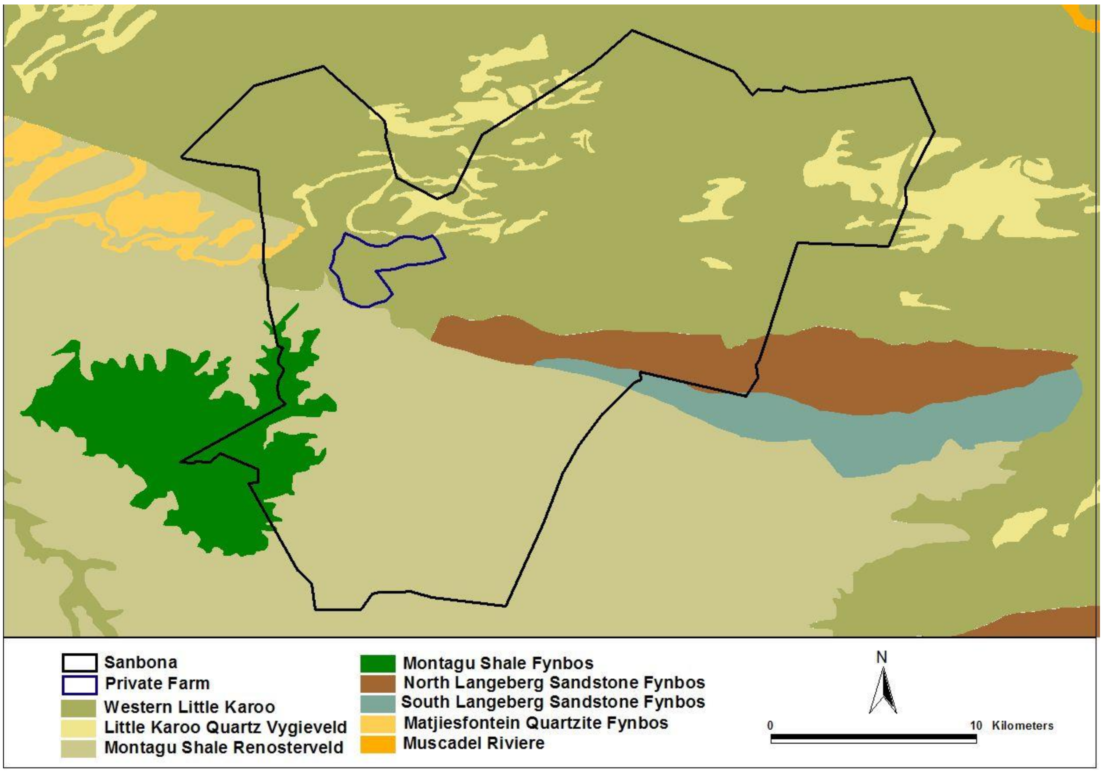


Figure 3.2. Vegetation types as described by Mucina and Rutherford (SANBI, 2012).

The Western Little Karoo (WLK) is the most extensive vegetation type on Sanbona and covers about 30 000 ha. According to Vlok and Vlok (2015), the lowland hills and ridges are dominated by small shrubs and leaf succulents such as *Berkheya cuneata*, *Hermannia filifolia* and *Cylindrophyllum comptonii* and by taller succulent shrubs within the genera *Ruschia*, *Crassula* and *Tylecodon*, and non-succulent, evergreen shrubs such as *Chrysocoma*, *Pentzia* and *Pteronia*. These slopes, where the shale-derived soils are very shallow are usually referred to as Randteveld (Vlok, et al., 2005). The gentle lower slopes where the soils are loamy or clayey are referred to as Apronveld (Vlok, et al., 2005). A selection of small shrubs within the genera *Eriocephalus*, *Hirpicium* and *Pteronia*, are common within this habitat type together with larger shrubs such as *Rhigozum obovatum* and *Carissa haematocarpa*. Grasses such as *Aristida*, *Digitaria* and *Ehrharta spp*. are abundant after good rains (Vlok & Vlok, 2015). Both the Randteveld and Apronveld habitat types are known to support high densities of grazing ungulates (Novellie, 1991) and are usually the first to show signs of over-utilisation by herbivores (Kraaij & Milton, 2006). The valley bottoms within WLK are referred to as Gannaveld, and are large open plains just above the River and floodplain habitats (Vlok & Vlok, 2015). Gannaveld is dominated by Gannabos, *Salsola spp.*, and *Lycium spp*. with many other shrub genera such as *Eriocephalus*, *Pentzia incana*, *Pteronia* and *Tripteris*. Succulents are usually uncommon (Vlok & Vlok, 2015). The soils are deeper, loamy and saline and often prone to soil erosion (Vlok, et al., 2005). Most of the species present in Gannaveld are very palatable and it is a favoured habitat of most of the small game species typical of the Little Karoo (Vlok, et al., 2005). Grass and trees are uncommon in Gannaveld except in certain areas that contain aeolitic red sands where grasses such as *Stipagrostis* are locally abundant. *Schotia afra, Euclea undulata* and *Nymania capensis* also occur together with shrubs such as *Zygophyllum foetidum* and *Melolobium candicans* (Vlok, et al., 2005). Some biologically important taxa, endemic to the WLK are *Drosanthemum delicatulum, Glottiphyllum depressum, Berkheya cuneata* and *Polygala uncinata* (SANBI, 2006-).

In the northern part of Sanbona there is about 2 600 ha of Little Karoo Quartz Vygieveld (LKQV). It is similar in climate and geology to the WLK but is characterised by localised quartz gravel plains. Gravel plains are a common physical feature of desert environments. However, in the Succulent Karoo these habitats support a high diversity of locally-adapted species restricted specifically to these habitats (Schmiedel & Jurgens, 1999). Gravel plains have been created by the erosion of surface material and the removal of the silty, acid or saline-sodic soil matrix. Such processes have left behind quartz pebbles on the surface, to create a landscape patchwork of edaphically diverse quartz patches at different stages of development (Desmet, 2007). These conditions create a unique habitat with a distinct flora dominated by succulent, compact, dwarf chamaephytes, mainly within the *Aizoaceae* (Haarmeyer, et al., 2010). Compared to other quartz-fields, the LKQV flora only contains 11 species however 10 of these species are endemic (Schmiedel & Jurgens, 1999). This small flora is highly distinctive and is almost certainly a consequence of this region's remoteness from the other quartz-field areas (Schmiedel & Jurgens, 1999). The dominant growth forms in the LKQV are dwarf leaf succulents, such as *Gibbaeum* spp. and members within the family *Crassulaceae*. Evergreen shrub genera such as *Pteronia* and *Salsola* are also common in this vegetation type. *Gibbaeum nuciforme* is a Little Karoo endemic and thus a biologically important taxon (Mucina, et al., 2006). *Pteronia pallens* and the alien halophyte, *Atriplex lindleyi* subsp. *inflata* are indicators of disturbance by overgrazing or trampling (Milton, et al., 1995).

The Montagu Shale Renosterveld (MSR) is the second most extensive vegetation type in Sanbona and occupies about 17 000 ha of the reserve. It consists of an undulating hilly landscape with broad valleys dominated by renosterbos (*Elytropappus rhinocerotis*) (Rebelo, et al., 2006). Renosterveld grows in nutrient-rich, fine-grained shale-derived soils (Shiponeni & Milton 2005), and has a large geophyte, forb and grass component. It is the Renosterveld that is thought to have supported the herds of large game that lived in the Fynbos Biome until they were hunted almost to extinction during the 19th century (Skead, 2011).

The soils and rolling topography of Renosterveld make it suitable for crop production, which is why it has been so extensively transformed (Shiponeni & Milton, 2006). The previously transformed areas cover about 2 000 ha within the MSR on Sanbona. They have a relatively low diversity primarily because they were cleared for cultivation up until 1997. Following complete rest from cultivation the old lands have since recovered some degree of indigenous vegetation cover. Weedy species such as *Atriplex semibaccata, Galenia africana* and *Delosperma spp*. are common within these transformed areas.

On the western side of the reserve is about 80 ha of Matjiesfontein Quartzite Fynbos (MQF). MQF occurs as a series of narrow bands in low flat mountains and parallel ridges surrounded by Succulent Karoo vegetation. This vegetation type supports mainly asteraceous and proteoid fynbos. Common genera and species include *Protea, Leucadendron, Euryops, Erica* and *Nylandtia spinosa.*

Montagu Shale Fynbos (MSF), covers about 1 900 ha of the reserve. This is an almost unknown vegetation unit (Rebelo, et al., 2006). The topography varies from undulating hills and valleys to steep mountains supporting moderately tall and dense shrublands with proteoid fynbos and asteraceous fynbos (Rebelo, et al., 2006). Trees such as *Protea laurifolia* and *Dodonaea viscosa var. angustifolia* are present as well as shrubs such as *Cliffortia ramosissima* and *Elytropappus rhinocerotis.* Common grasses include *Ehrharta calycina, Ehrharta capensis, Karroochloa purpurea* and *Tribolium hispidum*.

The Warmwaterberg is comprised of Northern Langeberg Sandstone Fynbos (NLSF) and South Langeberg Sandstone Fynbos (SLSF). NLSF covers about 3000 ha of gentle to steep, north-facing slopes. The vegetation is mainly proteoid and restioid fynbos with ericas present on the higher altitudes. More asteraceous fynbos occurs on the lower slopes where *Dodonaea viscosa var. angustifolia* is dominant (Rebelo, et al., 2006). The SLSF covers about 300 ha of gentle to steep south-facing slopes. A few trees are present such as *Euclea undulata, Maytenus oleoides* and *Rhus undulata* but they are stunted (Vlok, et al., 2005). Restios are not uncommon although there is a higher shrub component comprised of species such as *Chrysanthemoides monilifera, Cullumia bisulca, Erica speciosa* and *Euryops erectus*. On both NLSF and SLSF grasses such as *Cymbopogon marginatus, Cymbopogon plurinodis, Ehrharta capensis, Ehrharta ramose, Merxmuellera arundinacea, Merxmuellera stricta, Pentameris distichophylla* and *Pentaschistis pallida* are found. They are not particularly suitable for grazing purposes, except perhaps for bulk-grazers like Mountain Zebra (Vlok, et al., 2005).

Sanbona was previously used for wheat and livestock farming but was established as a conservation area in 2002. The reserve currently contains the following large to medium-sized herbivore species: Hippopotamus (*Hippopotamus amphibious*), elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis)*, white rhino (*Ceratotherium simum*), buffalo (*Syncerus caffer*), plains zebra (*Equus burchelli*), eland (*Tragelaphus oryx)*, oryx (*Oryx gazella*), red hartebeest (*Alcelaphus buselaphus)*, black wildebeest (*Connochaetes gnou*), springbuck (*Antidorcas marsupialis)*, grey rhebuck (*Pelea capreolu*s), kudu (*Tragelaphus strepsiceros)*, klipspringer (*Oreotragus oreotragus*), steenbok (*Raphicerus campestris*), grey duiker (*Sylvicapra grimmia*) and ostrich (*Struthio camelus*).

4. METHODS

4.1. Monitoring

Vegetation monitoring

Because Sanbona was the first reserve to introduce a range of indigenous herbivores (including mega-herbivores) to the Little Karoo, the conservation authority for the area, CapeNature was concerned about the impact of these animals on the vegetation of the reserve. CapeNature therefore insisted that the introduction of indigenous herbivores be conditional on the development of a suitable monitoring programme for the reserve. A recommendation by CapeNature, the Department of Agriculture and the Plant Conservation Unit, UCT was that 4-6 paired exclosure plots per vegetation type needed to be erected. The main vegetation types and habitat units of concern were the Western Little Karoo (WLK), Little Karoo Quartz Vygieveld (LKQV), Montagu Shale Renosterveld (MSR), transformed lands within the MSR (described from now on as Old Lands (OL)), Riverine habitat and *Schotia* woodland. The remaining vegetation types are found in mountainous terrain, far from access roads and would therefore be difficult to monitor. They are also less likely to be impacted by herbivores due to their inaccessibility and steepness of slope.

The WLK is a large diverse landscape that includes a number of habitat types. The areas of interest within this large area were the slopes, referred to by Vlok et al. (2005) as Randteveld and Apronveld, the flat areas or ‘vlaktes’ adjacent to floodplains, classified as Gannaveld by Vlok et al. (2005), as well as quartz areas within Apronveld and Gannaveld. The LKQV mapped by Mucina and Rutherford (2006) did not originally include all quartz patches but the adjusted vector geospatial dataset (NVM2012beta2 data, (SANBI, 2012)) incorporates most patches. Because of this diversity in the WLK, additional plots were added to this vegetation type during the course of the monitoring period.

In 2004, twenty plots of 20 m x 25 m each were laid out and fenced with a 1.2 m – 1.8 m high fencing wire which prevented any medium and large ungulates from feeding on the vegetation. Each fenced plot was paired with an adjacent unfenced plot, which was subject to grazing and browsing by indigenous ungulates. Four paired plots were located in five different areas of concern: Randteveld/Apronveld (Figure 4.1a), Gannaveld (Figure 4.1b), Quartz-gravels (Figure 4.1c), Renosterveld (Figure 4.1d); Old Lands (Figure 4.1e) and the Aeolian Sands (Figure 4.1f).

In 2005, an additional 14 plots were added to WLK and LKQV, giving a total of 34 pairs of plots. In 2010, five plots were added in the Riverine area that had never previously been monitored, making it 39 plots in total. In 2011 an additional habitat unit within the WLK was identified for monitoring. This habitat unit is called the Aeolian soils (AS), and is a unit within Gannaveld (Figure 4.1f). Personal observations indicated the herbivore impact on the grasses growing in these areas was noticeable. This area also included the *Schotia* woodland which was previously identified as an area of concern. Five paired plots were included, increasing the number of plots to 44 in total. In 2014 the monitoring plots in the Riverine areas were terminated. This was done because observations suggested that these areas, which had originally been used for cultivation, had recovered sufficiently from the impacts of previous farming and had also changed significantly as a result of flood events in the region. Table 4.1 below summarizes the number of plots monitored over time and Figure 4.2 shows their location within Sanbona. It is evident from Figure 4.2 that the quartz plots are not all within the Little Karoo Quartz Vygieveld and that some of the WLK plots are in the LKQV. This lack of congruency exists largely because the Mucina and Rutherford (2006) vegetation types in the area have not been mapped at a fine enough scale.

a) Randteveld within Western Little Karoo

b) Gannaveld within Western Little Karoo

c) Quartz gravels within Little Karoo Quartz Vygieveld

d) Renosterveld within Montagu Shale Renosterveld

e) Old Lands within Montagu Shale Renosterveld

f) Aeolian Sands within Western Little Karoo

Figure 4.1. Photographs showing the different habitat units monitored within the main vegetation types on Sanbona Wildlife Reserve, a) Randteveld, b) Gannaveld, c) Quartz gravels, d) Renosterveld, e) Old Lands and f) Aeolian Sands.

Table 4.1. Summary of the number of monitoring plots on Sanbona Wildlife Reserve and the year in which sampling of the plots was initiated. The -5 value for Riverine & Floodplain sites indicates that monitoring of these plots was terminated in 2014.

Vegetation type/habitat type	**2004**	**2005**	**2010**	**2011**	**2014**	**2015**
Randteveld/Apronveld	4	5				9
Gannaveld	4	5				9
Quartz patches	4	4				8
Renosterveld	4					4
Old Lands	4					4
Riverine & Floodplain			5		-5	0
Aeolian Sands				5		5
Total No. Plots	**20**	**34**	**39**	**44**	**39**	**39**

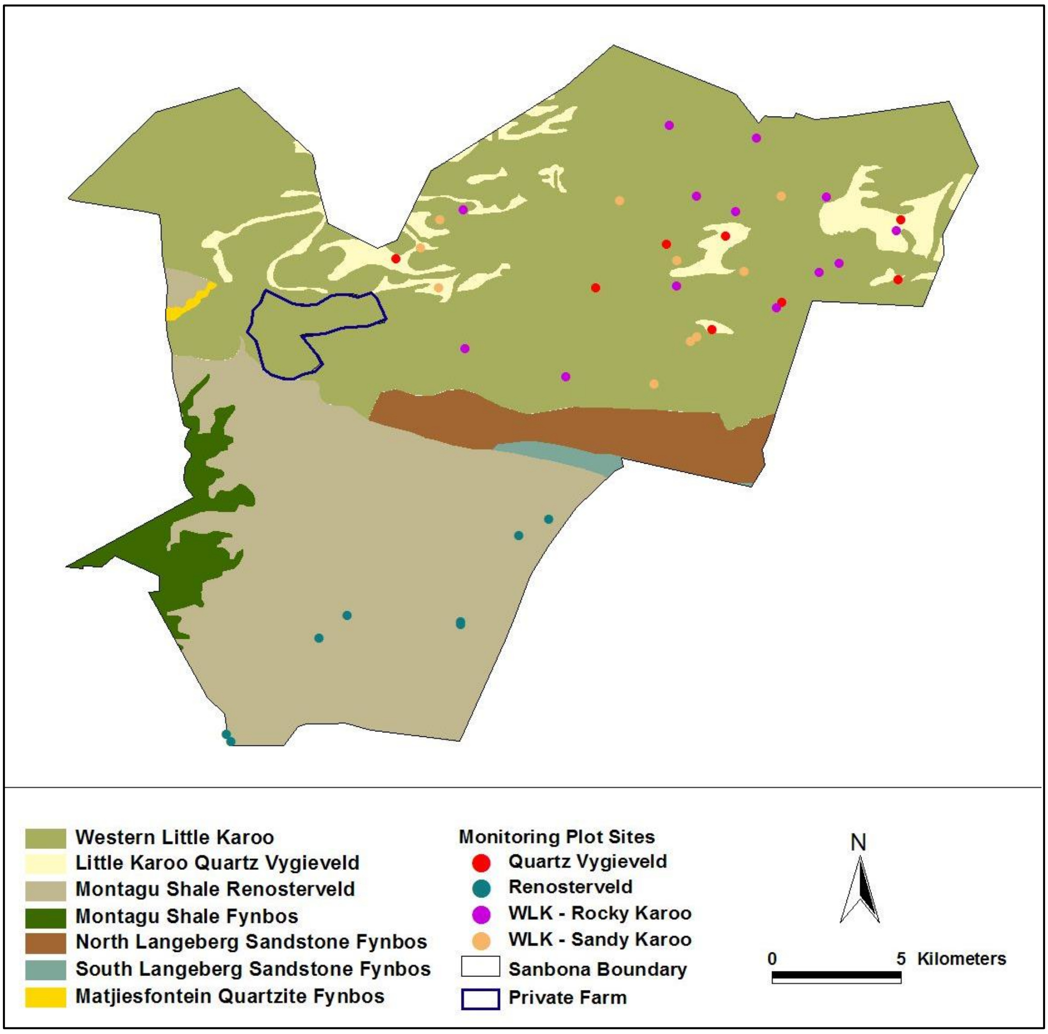


Figure 4.2. Monitoring plots distribution across the vegetation types described by Mucina and Rutherford (SANBI, 2012).

Although plots were selected for homogeneity in topography, Karoo vegetation typically displays a high degree of spatial variability at scales of 0.01-0.1 ha. Such variability is usually attributed to heterogeneity in the distributions of soil moisture, soil depth (Cowling & Hilton-Taylor, 1999) and plant–available nutrients (Palmer, et al., 1999).

Vegetation monitoring was initiated in 2004, two years after Sanbona was established as a game reserve. Monitoring has occurred every year since this date at the beginning of spring (September). This monitoring time was selected because more plants are usually in flower at this time and species identifications are more accurate. Observer bias and therefore between-observer variation in the accuracy of long-term monitoring assessments has been well documented (Novellie & Strydom, 1987). However, two of the observers have been part of the surveys since the inception of the monitoring programme and since 2010 the same observers have undertaken the surveys each year. Data from 2004 to 2015 was utilised for the study.

Field surveys

Drop point surveys were conducted in the plots using the method of Roux's (1963) point survey for canopy spread cover (Roux, 1963; Vorster, 1982; Novellie & Strydom, 1987), to determine vegetation composition and canopy cover. For this method, a metal rod is dropped at a set distance along a line and all plant species contacted by the rod are recorded. The descending-point method is sufficiently robust and accurate to record different veld-composition scores by measuring the canopy-spread cover (Du Toit, 2003). This method is well suited for the determination of changes in vegetation brought about by grazing practices and temporal changes in vegetation and the structure of plant communities (Roux, 1963).

In each plot, the points were arranged in 20 parallel rows of 25 points each with 1 m spacing between points and 1 m spacing between rows (totalling 500 points per plot). Five hundred point observations are the recommended number that was shown to minimize the degree of error versus sampling time (Du Toit, 1997). A sharp pointer descended vertically at each point on the grid and the identification of each plant touched was recorded. If the pointer hit more than one species, information was recorded for all species. At the soil surface the presence of litter and rock was also recorded, although this was not used in further analyses. Vegetation canopy cover was estimated as the percentage of points that contacted a living plant.

Rainfall

Rainfall data was collected from on-site weather stations (from 2006 to 2015). Annual rainfall data was calculated in 12 month periods ending at the time of vegetation monitoring, i.e. October – September, while seasonal rainfall totals were calculated for the periods April - September (Winter) and October - March (Summer) respectively. No on-site rainfall data was available for 2004 and 2005. In order to obtain an estimate other than the long-term average for these missing values, a regression was performed between data from on site (total, North and South) and the closest weather station (Die Vlakte) for 2006-2015. Using the equation from these regressions, values for the missing 2004 and 2005 data were obtained. Rainfall was broken down into different components to investigate the relationship between rainfall and certain vegetation parameters.

- Annual rainfall (Annual) – was taken as the 12 months preceding the survey (October to September).
- Summer rainfall (Summer) – represented the rainfall from October to December for the previous year plus January to March of the current year.
- Winter rainfall (Winter) – was the rainfall from April to September of the current year.

Stocking rates

Herbivore numbers were collated from annual census records undertaken on Sanbona for the period 2004 - 2015. From 2004 until 2013 these censuses were conducted by foot counts, with a line of counters walking about 100 metres apart, along contours of ridges to improve visibility. This counting method had to be completed in sections over a four-day period. Since 2014, Sanbona has conducted annual aerial game census with a helicopter within the month of October (Vorster, et al., 2016). Due to the size of the reserve, the area is divided into northern and southern sections along the Warmwaterberg Mountain and the central fence line. Each section requires an entire day (06:00 to 18:00) to survey. Pre-defined flight paths were created and uploaded to a GPS allowing the pilot to follow transects 400 (North) or 500 (South) metres apart. The helicopter maintains an air speed of 30 knots at an average height of 30 metres above ground level. The crew includes the pilot, two observers and a data capturer. The data is recorded using a GeoXM Trimble GPS with Cybertracker software. In an attempt to promote continuity, where possible, the same crew will fly annually.

Herbivore areas of preference

Since 2008 Sanbona has collected data for the movement of most animals, either by daily observations of the conservation staff or guides, as well as from the annual census information that is recorded by means of the Trimble GPS. From this information preferences in land use can be derived. However, because the daily observations are biased to siting's close to the roads, only the three years of aerial census data was utilised. The type of animal, location and number were recorded per GPS logged point. ArcView GIS 3.2a was used to create a map of areas of preference by animal distribution. The three years of data was then aggregated and the observations interpolated to create an estimated intensity of use map. This was created to determine whether any changes in vegetation could be explained by animal utilisation. The areas were coloured coded based on the combined population density using the spatial analyst tool for Arcview and converted to Large Animal Units (LAU). This method is not considered highly reliable at this point since it is based on 3 days' observations but never the less represents the distribution of animals across the whole reserve at three different points in time. As this will be done repeatedly in the future it will become increasingly reliable. A further limitation of this method is that seasonal variation in movement patterns are not included.

Soil sampling

Soil samples were collected in September 2016. Samples were taken from 1 to 11 cm soil depth on each plot. The soil was analysed for the following parameters: sand, clay, silt, stone, carbon, calcium, magnesium, potassium, sodium, boron, copper, manganese, sulphur, zinc, nitrogen, total cations, citric acid, pH (KCl) and resistance. The soil analyses were carried out by the Department of Agriculture, Elsenburg.

4.2. Data analysis

Identification of current plant communities

The number of plots have not stayed consistent since the start of the monitoring programme largely because additional plots have been created when areas of concern have been identified. Therefore, in order to determine the status, composition and richness of current plant communities, a cluster analysis was performed in PC-ORD (2010), using the Bray-Curtis flexible Beta method, where $\beta = -0.4$. The 78 plots (39 exclosures and 39 open) of the 2015 data set only was used.

The data was analysed using the non-metric multidimensional scaling (NMS) ordination technique. NMS is described as most appropriate for biotic community data in that it can accommodate large numbers of zero values, carries no assumption of multivariate normality and has been shown to produce the most accurate representation of underlying data structure (Clarke, 1993). It was used to determine current plant community patterns and their relationship with the environmental variables such as texture of the soil, the presence of stone and minerals as well the salinity and the pH of the soil. The ordinations were conducted using multiple runs and according to the stress and stability criteria recommended by McCune and Grace (2002).

Community change over time

NMS ordination was also used to assess the direction and consistency of changes in the plant community composition, using multiple runs. Each species identified in the study was assigned to one of 15 growth forms based on their structure, size and life history characteristics (Cornelissen, et al., 2003; Todd & Hoffman, 2009). The plant growth form concept has proved useful as it provides a means of classifying plants into groups of like structure and assumed similar function (Midgley & Van der Heyden, 1999). However, traditional growth form classification schemes are not well suited to the vegetation of the Succulent Karoo due to the unusual and specialised nature of the flora (Todd & Hoffman, 2009). Consequently, the modified classification scheme, developed by Todd and Hoffman (2009) which is better able to distinguish among succulent plant types, was used. This approach included the following categories: perennial grasses, perennial forbs, geophytes, dwarf succulents, leaf succulent shrubs, stem succulent shrubs, evergreen shrubs and deciduous shrubs. No annual grasses were recorded and there is therefore no need for this category. The definition, as well as the height range and some representative species of each growth form are shown in Table 4.2.

Changes in the abundance, cover and species richness of each different growth form was also analysed for each sampling period as well as each treatment (Exclosure and Open/Grazed), where:

- Abundance per species = sum of first and second strikes;
- Vegetation cover = number of strikes expressed as a percentage of the total number of possible strikes (500);
- Species richness = total number of species recorded per transect.

A Kruskal-Wallis one-way ANOVA and Dunn's multiple comparison test was performed using R, to identify significant differences in abundance and species richness of plots from the different plant communities.

In order to assess the change in community over time, the method used by Todd and Hoffman (2009) for the percentage dissimilarity (PD) in community composition was used. The percentage of dissimilarity between two items is equivalent to the Bray-Curtis distance measure, expressed as a percentage, which is used to quantify the compositional dissimilarity between two different sites (McCune & Grace, 2002). High values indicate a large degree of dissimilarity while low values indicate that samples are relatively similar in composition, and zero indicates identical composition. The PD was assessed for each treatment over time, for each vegetation community, as well as between treatments for each year.

Changes in the abundance of palatable and unpalatable species were assessed over time within each community. Species were assigned a palatability score based on grazing index values (Esler, et al., 2006; Du Toit, 2000; Du Toit, 1995) and grouped into broad palatable and unpalatable classes. The abundance of each group was plotted over time and differences between exclosures and grazed plots assessed by comparing the slopes of the regressions of their abundances over time.

Table 4.2. Classification of growth forms used in data analysis, with a height class, definition and representative species at the study sites on Sanbona.

Growth form	Sub division	Height range	Definition	Representative species
Annual Forb			Plants that produce seed and die within one year (Todd & Hoffman 2009) with shallow root systems (Hoffman & Cowling, 1987).	*Medicago spp.;* *Oncosiphon piluliferum;*
Perennial Forb			Plants that do not have aboveground woody tissue but that survive for more than one year (Todd & Hoffman 2009)	*Aptosimum indivisum,* *Bulbine succulenta,* *Crassula muscosa,* *Gazania spp.,* *Lotononis spp.,* *Viscum rotundifolium*
Perennial Grass			Graminoids that survive for more than one year (Todd & Hoffman 2009), with shallow, fibrous root systems (Hoffman & Cowling, 1987)	*Aristida congesta,* *Digitaria argyrograpta,* *Ehrharta spp.,* *Enneapogon spp.,* *Fingerhuthia africana,* *Plagiochloa unicolor,* *Stipagrostis spp.*
Geophyte			Plants with below-ground storage organs and part of the annual life cycle without living aboveground parts (Todd & Hoffman 2009)	*Bulbine frutescens,* *Bulbine mesembryanthemoides,* *Massonia depressa,* *Ornithoglossum undulatum*
Dwarf Succulent			Globbose, mat- and tuft- forming succulents without conspicuous aerial branched stems (Todd & Hoffman 2009) with shallow lateral root system (Hoffman & Cowling, 1987)	*Adromischus triflorus,* *Avonia papyracea,* *Gibbaeum spp.,* *Hereroa sp,* *Rhinephyllum muirii,* *Sceletium sp,*
Leaf Succulent Shrub	Low	<0.5m	Shrubs with woody stem and succulent leaves (Riginos & Hoffman, 2003) with a shallow lateral root system (Hoffman & Cowling, 1987)	*Crassula spp.,* *Drosanthemum delicatulum,* *Leipoldtia schultzei,* *Ruschia spp.,* *Trichodiadema spp.*
	Medium	0.5m-1m		*Cotyledon orbiculata,* *Drosanthemum bicolor,* *Ruschia multiflora,* *Ruschia pungens,* *Ruschia robusta,* *Tetragonia spp.*
Stem Succulent			Leafless photosynthetic stem with extensive, soft, water-storage tissue and only limited secondary growth (Perez-Harguindeguy et al. 2013)	*Euphorbia spp.,* *Monsonia spp.,* *Pachypodium succulentum,* *Psilocaulon spp.,* *Tylecodon spp.*

Evergreen Shrub	Low	<0.5m		*Berkheya cuneata,* *Felicia muricata,* *Hirpicium alienatum,* *Pentzia incana,* *Pteronia sordida,* *Pteronia viscosa,* *Rosenia spp.*
	Medium	0.5m-1m	Woody plant between 0.5m and 5m with canopy typically carried by several trunks that are usually thinner and younger than typical mature tree trunks (Perez-Harguindeguy et al. 2013). They usually have a thick, fibrous, undivided tap root extending some way into the soil before dividing into an extensive lateral root system (Hoffman & Cowling, 1987) .	*Berkheya spinosa,* *Blepharis capensis,* *Dicoma spinosa,* *Eriocephalus spp.,* *Euryops spp.,* *Felicia filifolia,* *Hermannia spp.,* *Monechma spp.,* *Psilocaulon simile,* *Pteronia spp.,* *Thesium lineatum,* *Zygophyllum microphyllum*
	Tall	>1m		*Cadaba aphylla,* *Carissa haematocarpa,* *Elytropappus rhinocerotis,* *Freylinia undulata*
	Tree	>2m		*Euclea undulata,* *Gloveria integrifolia,* *Maytenus heterophylla,* *Rhus longispina,* *Schotia afra*
Deciduous Shrub	Low	<0.25m	Leaf shedders usually with tap root that splits at the soil surface giving rise to many axes extending into the soil and branching in all directions (Hoffman & Cowling, 1987)	*Pelargonium karooicum*
	Medium	0.5m-1m		*Asparagus spp.,* *Crotalaria lebeckioides,* *Garuleum bipinnatum,* *Lycium spp.,* *Tripteris sinuata,* *Zygophyllum pygmaeum*
	Tall	>1m		*Calobota elongata,* *Lycium ferocissimum,* *Lycium oxycarpum,* *Rhigozum obovatum,* *Zygophyllum foetidum*

Role of herbivory versus rainfall in community change

In order to investigate and differentiate the relative effects of rainfall and grazing on plant community change over time, linear mixed-effects models were fitted to the data using the lmer function (Bates, et al., 2014) in R (R Core Team, 2012). However, the exclosure plots and open plots could not be included in the same model as the treatment effect of grazing is present only in the open plots and remains at zero for the duration of the trial within the exclosure plots. In order to avoid this confounding issue, two models were produced, with the only difference being that grazing pressure is included as a variable in the open plots but not in the exclosure plots. The expectation is that rainfall should emerge as a driver of vegetation change in the exclosures, whereas in the open plots, both grazing and rainfall are included in the model. If grazing is important, it should emerge as an important predictor variable. As the effect of rainfall and grazing may not be same in all areas of the study site, the plots were included in the model as a random-effects term, while community type, stocking rate and rainfall are included as fixed effects.

The models took the following form:

```
Fit.Open = lmer(Delta ~ Grp+Rainfall+(1|Plot), data=OpData)
Fit.Excl = lmer(Delta ~ Grp+Rainfall+LAU+(1|Plot), data=ExData)
```

Where:

- `Delta` is the inter-annual community change and the variable that the model is trying to explain. (Continuous)
- `Grp` is the community identity (Categorical).
- `Rainfall` is the annual rainfall preceding the sample period (Continuous)
- `LAU` is the stocking rate preceding the sample period (Continuous).
- `Plot` is a random effects term to account for the fact that the response may not take the same form across plots from different communities.
- `OpData` is the dataset of Open plots.
- `ExData` is the dataset of Exclosure plots.

Indicators for management

A useful indicator species should demonstrate change over time, either within one or both treatments. Therefore, a correlation between species abundances and sample period in the different treatments was used to identify species that significantly increased or decreased over the sample period across the vegetation communities. The correlation coefficient for the treatments were used to create a scatter plot. The correlation coefficient for each species from the exclosure was plotted against the y axis while the correlation coefficient for the open plot was plotted against the x axis, resulting in various potential combinations of response along each axis. This framework was developed on the principles of Dyksterhuis (1949) and the Key Species Method (Hardy et al. (1999) where species which respond sensitively to grazing are used as indicators. If the species in the exclosure was increasing and the open plot decreasing then the species was classified as being sensitive to grazing, and requiring protection. Species that increased in both treatments either reflect a recovery or that the veld is being managed well. If a species decreased in both treatments this indicated a factor probably not related to grazing. Species that declined in the exclosure but increased in the open do not need protection because they respond to grazing and are therefore known as grazing increasers (Figure 4.3). Species that did not change much, and would fall within the unshaded central area depicted in Figure 4.3, are considered to be poor indicators because they were either too variable to pick up a consistent pattern or because they are robust species that did not respond to the changes in land use over the sample period. Using this framework, a suite of known palatable and unpalatable species were selected as potential indicators. The final selection was also dependent on how abundant the species was within a community or whether the chosen species could be used in more than one vegetation community.

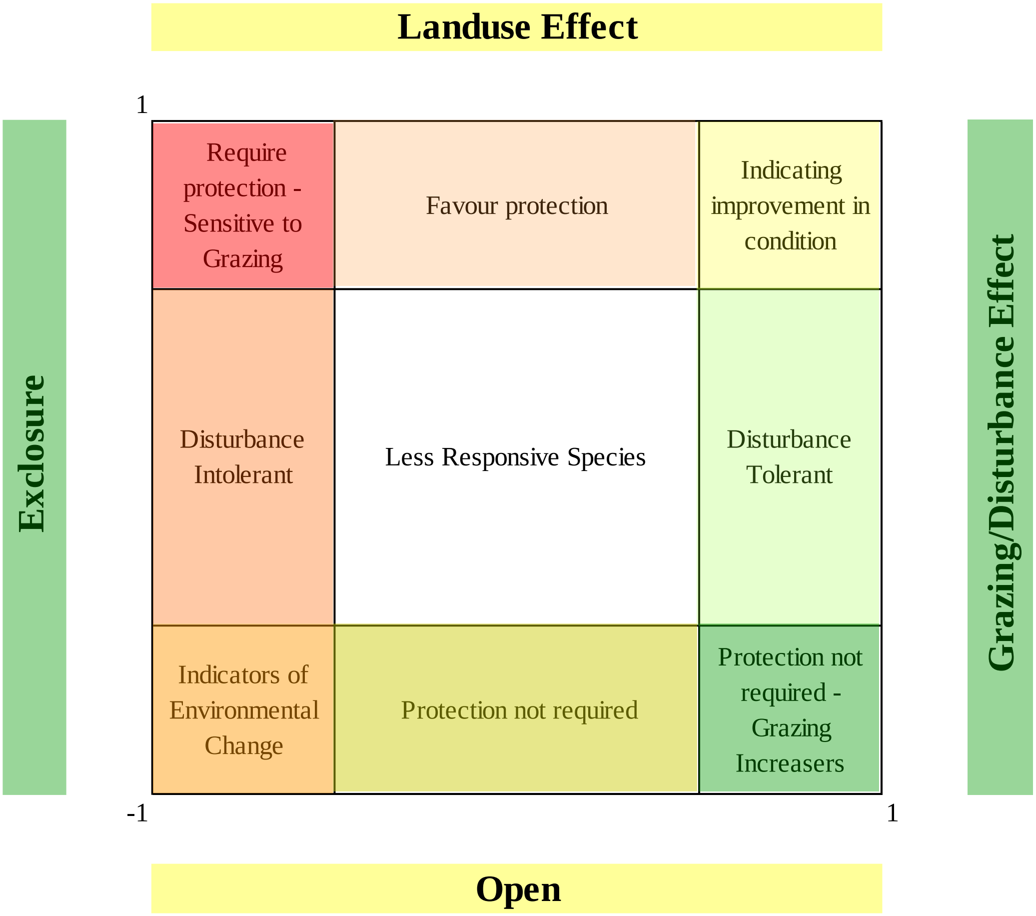


Figure 4.3. Framework to determine indicator species for each vegetation community, based on a scatterplot of the correlation coefficient of each species' abundance in exclosures plotted against the equivalent value from the open plots. As such, the potential values range from -1 to 1 along each axis. Species which plot into the central area have not responded significantly within exclosure or in the open plots, whereas those that have responded significantly along at least one axis result in various potential responses as indicated.

5. RESULTS

5.1. Vegetation communities

The cluster analysis resulted in four distinct groups from the 78 plots (39 exclosures and 39 open plots) as per the dendrogram (Figure 5.1). These four groups will be referred to as vegetation communities and reflected what was observed as communities on the ground. A finer division of plots would have created communities with too few plots in them and the levels used reflect well onto the field observations. These groups also broadly reflect the vegetation types defined by Mucina and Rutherford (2006). Their floristic affinities and composition are discussed later.

The red and blue groups in the dendrogram (Figure 5.1) correspond to the Western Little Karoo and are referred to here as the Rocky Karoo and Sandy Karoo communities. The green group is equivalent to Little Karoo Quartz Vygieveld and will be referred to as the Quartz Vygieveld community. Lastly, the purple group is equivalent to Montagu Shale Renosterveld and will be referred to as the Renosterveld community. The Rocky Karoo and Quartz Vygieveld are well defined and clearly different. The Sandy Karoo and Renosterveld are not as well defined and the Renosterveld community could possibly have been broken down further. However, this was not done as the groups would have been too small with too few plots in them.

The NMS ordination procedure for the 2015 data set produced a 3-d solution with a stress of 17.48 and instability of 0.0001. Presented here are all three axes, which produced a cumulative R^2 value between ordination distances and distances in the original n-dimensional space of 0.618. The first and third axes accounted for the greatest amount of variation and had an orthogonality of 99.3%. The first and third axes had an orthogonality of 99.5%, while the second and third axes had an orthogonality of 99.4%. These values are well within the range of values required to provide an acceptable ordination solution (McCune & Grace, 2002). Furthermore, by observing all three axes the four vegetation communities identified in the cluster dendrogram are distinctive (Figure 5.2).

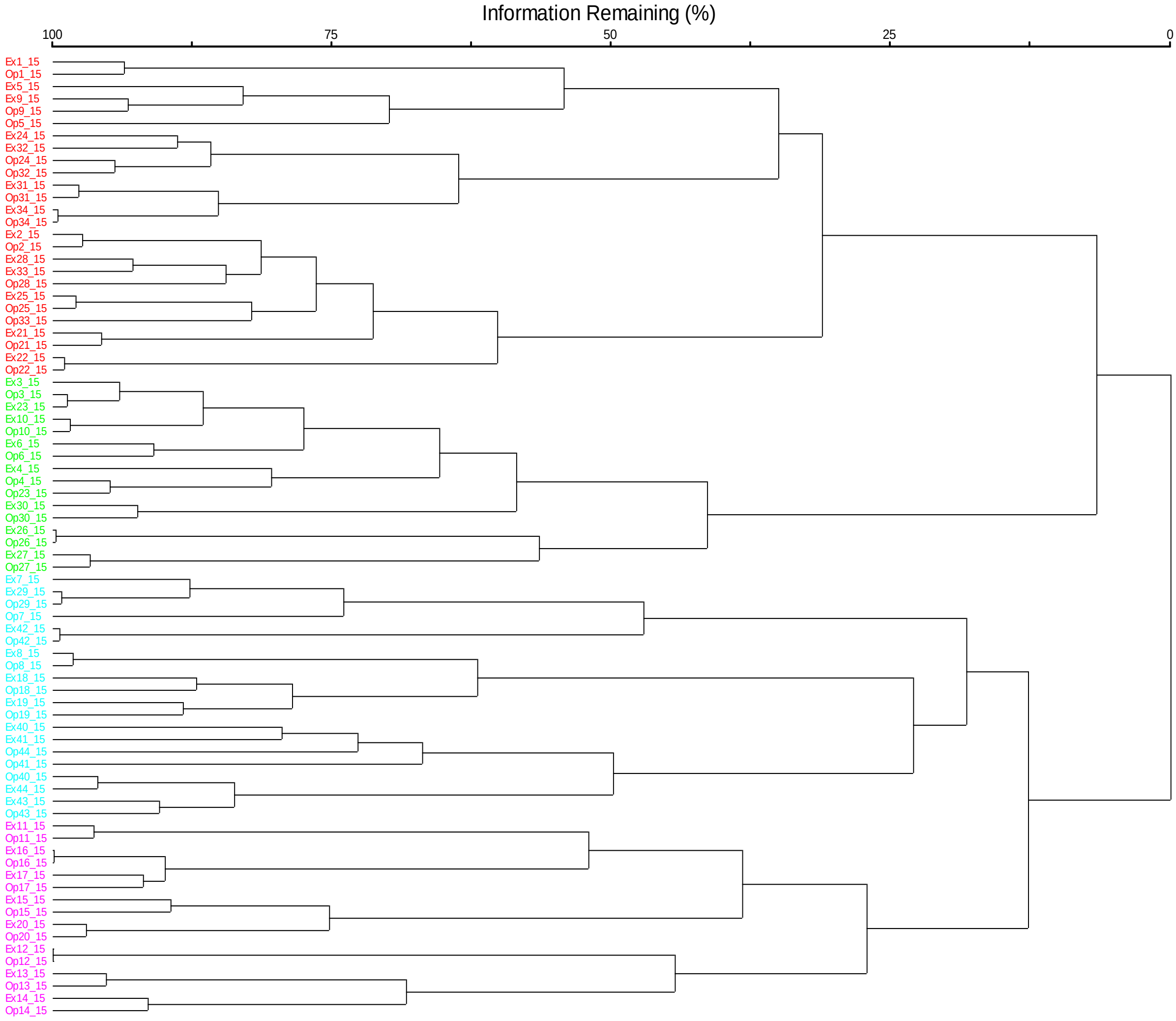


Figure 5.1. Cluster dendrogram of 2015 vegetation survey data, showing 4 vegetation communities; β = -0.4.

Soil characteristics are clearly an important driver of plant community composition as Axis 1, Axis 2 and Axis 3 were related to soil parameters (Figure 5.2). Axis 1 represented a gradient from stony soils, through to well drained more sandy soils, Axis 2 represents a gradient in sodium content while Axis 3 represents a gradient from silty, nutrient-rich soils through to sandy soils.

The Rocky Karoo is strongly associated with a higher stone content (13 pairs of plots indicated by the red triangles) and Sandy Karoo is associated with sandy soils over a range of salinity values (10 pairs of plots indicated by the blue circles) and both represent all the paired plots found in the WLK vegetation. It is difficult to differentiate between the plots on the Randteveld, Apronveld and Gannaveld habitat types described by Vlok et al. (2005). However, the Aeolian Sand plots (a habitat unit within the Gannaveld) are all in the Sandy Karoo, and are grouped together on the far right corresponding to less saline soils. These soils are very sandy and due to the high porosity are leached and consequently have lower sodium levels (higher resistance) than the remainder of the Sandy Karoo group. These plots are more closely correlated with axis 1 and are associated with the species *Stipagrostis ciliata*, *Stipagrostis obtusa, Ruschia pungens, Melolobium spp.* and *Gazania spp.* (Appendix A). The Rocky Karoo is associated with species like *Tripteris sinuata, Pteronia pallens* and *Hereroa odorata*.

The Quartz Vygieveld community, indicated by the green squares, contains all the quartz gravel plots associated with the LKQV vegetation type. All eight pairs fall within this group. The presence of stones is characteristic but they can vary in size. These gravel areas have a tendency to have higher salinities and therefore the resistance is lower. There is an overlap with plots in the Rocky Karoo community as the underlying geology, climate and other abiotic factors are similar. However, the species differ between these two communities. The Quartz Vygieveld is correlated with Axis 2 and associated with *Gibbaeum pubescens*, *Gibbaeum nuciforme, Salsola tuberculata, Psilocaulon simile, Pteronia succulenta* and *Pteronia viscosa* (Appendix A).

The Renosterveld community, indicated by the purple inverted triangles, is made up of eight plots located entirely within the MSR vegetation type and includes the Old Land (OL) plots. The Renosterveld areas are known to contain fine-grained, nutrient-rich soils. This is clearly shown in Figure 5.2, where axis 3 is associated with nitrogen and silt. One plot (plot 12), is on rockier terrain than the others, and is indicated by its outlier position on axis 1. Species like *Elyptropappus rhinocerotis, Euryops nodosus, Pteronia paniculata, Pteronia incana, Felicia muricata* and *Felicia filifolia* are highly correlated with Axis 3 (Appendix A).

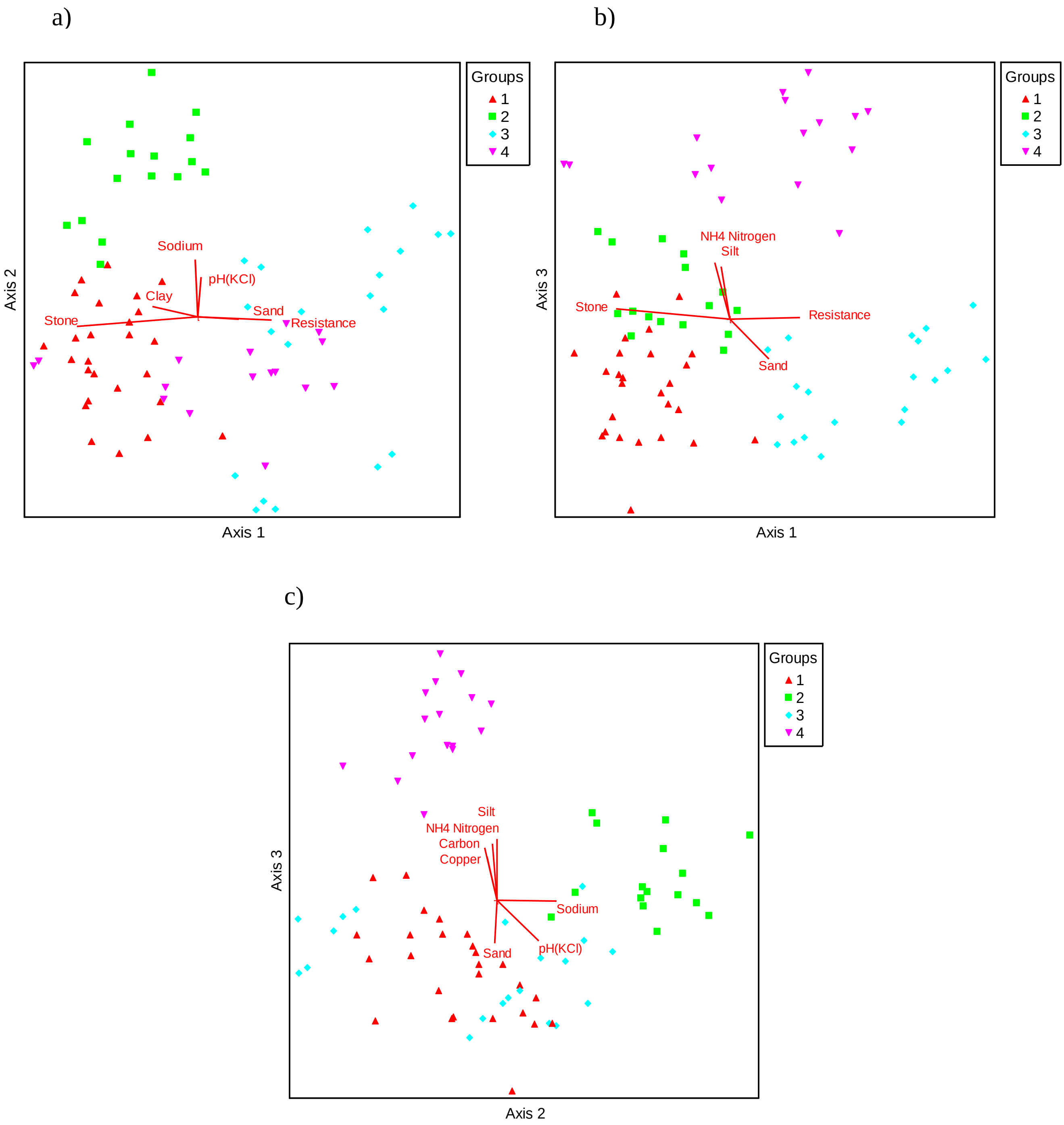


Figure 5.2. NMS ordination of 78 sampled plots from 2015 data, indicating the four vegetation communities, with the joint plot of the dominant soil parameters a) along axis 1 and 2, b) along axis 1 and 3 and c) along axis 2 and 3. Group 1 = Rocky Karoo, Group 2 = Quartz Vygieveld, Group 3 = Sandy Karoo and Group 4 = Renosterveld.

General description of the communities

Group 1 – Rocky Karoo

An NMS ordination of the Rocky Karoo sites (2015 data only) produced a 2-d solution with a stress of 14.91 and instability of 0.00001. The first and second axes accounted for the greatest amount of variation and produced a cumulative R^2 value between ordination distances and distances in the original n-dimensional space of 0.804 with an orthogonality of 94.4%. Within the Rocky Karoo community, all except two pairs of plots divide into two clusters representing the two habitat types (Randteveld and Gannaveld) as described by Vlok et al. (2005) (Figure 5.3). Axis 1 represents a gradient of clay and sodium. The plots falling within the less rocky areas and more sandy loam have a higher level of clay content. These soils do not drain as well and therefore, an accumulation of salts occurs. These plots (green squares) correspond with Gannaveld. Axis 2 corresponds to an increase in stone. The plots have a higher percentage of stone as well as loamy sand with less clay present in the soils. These plots (red triangles) correspond to Randteveld. Usually, due to the good drainage of the sandy soils as well as the slopes they are found on, the sodium levels tend to be lower. The fifteen most dominant species in the Rocky Karoo group are listed in Table 5.1, and represent 75% of the cover in these plots.

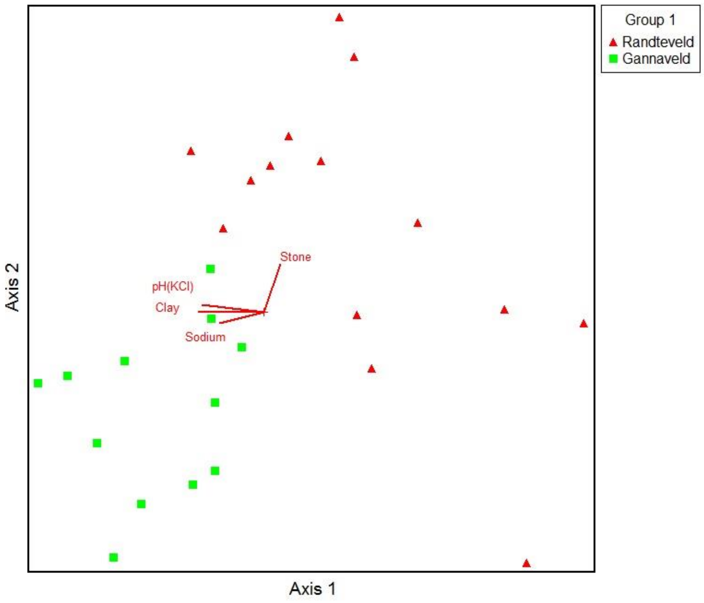


Figure 5.3. Group 1, Rocky Karoo ordination, using 2015 data, with soil parameters indicating the two further division in the vegetation community. These closely match the habitat type descriptions of Randteveld and Gannaveld as per Vlok et al. (2005).

Group 2 – Quartz Vygieveld

Quartz Vygieveld (2015 data only), produced an NMS ordination with a 2-d solution with a stress of 12.65 and instability of 0.00001 (Figure 5.4). The first and second axes accounted for the greatest amount of variation and produced a cumulative R^2 value between ordination distances and distances in the original n-dimensional space of 0.784 with an orthogonality of 95.3%. All the plots have quartz stone but they can vary from less than 1 cm diameter to about 3 cm diameter. Plot 27 has large block like quartz pebbles compared to plot 3 which is comprised of smaller quartz stones. The soils underlying the gravel also vary. Certain plots are in areas with finer, silty soils while other plots occur in areas where there is a higher resistance, indicating a lower sodium content. This would also be converse to the pH of the soil. The paired plots show similar underlying characteristics. The species that are most dominant in the Quartz Vygieveld group are listed in Table 5.1. These species represent 80% of the cover in these plots.

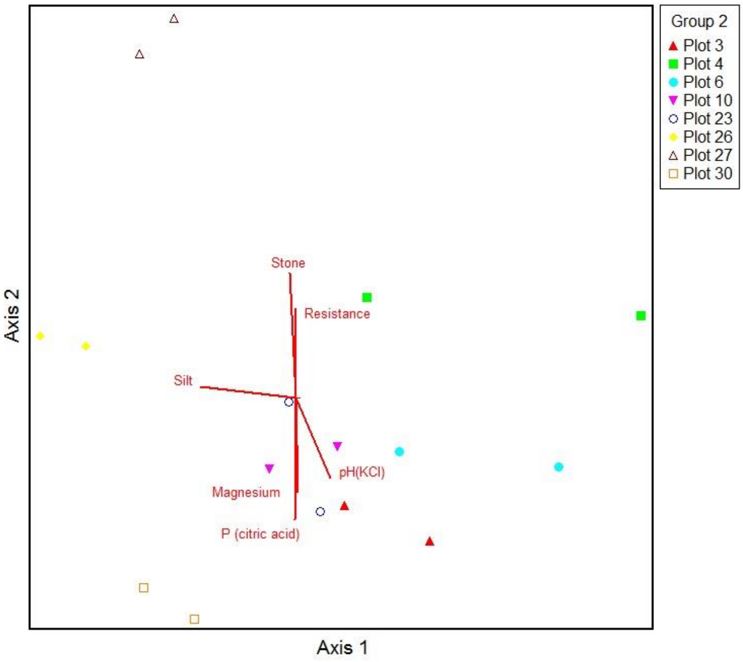


Figure 5.4. Group 2, Quartz Vygieveld ordination, using 2015 data, indicating the paired plots are closely related and they are all situated within different soil parameters.

Group 3 – Sandy Karoo

An NMS ordination on the Sandy Karoo (2015 data only) produced a 3-d solution with a stress of 7.73 and instability of 0.0000 (Figure 5.5). The first and second axes accounted for the greatest amount of variation and produced a cumulative R^2 value between ordination distances and distances in the original n-dimensional space of 0.657 with an orthogonality of 92.7%. The biplot for the Sandy Karoo group explained the habitat types as per Vlok et al. (2005). Axis 1 represents a gradient of stone, nitrogen and carbon, with the few rocky Randteveld plots strongly associated with this axis. Axis 2 corresponds with a gradient from sand to silt. The Aeolian Sand plots (described as a habitat unit within the Gannaveld) are well arranged on the lower part of the axis while the remainder of the Gannaveld plots are grouped where the silt values are higher. The outlying plot from the Aeolian Sands when viewed along the third axis is not separated from the remainder of the plots. The dominant species for the Sandy Karoo group are listed in Table 5.1 and represent 72% of the total cover for the plots.

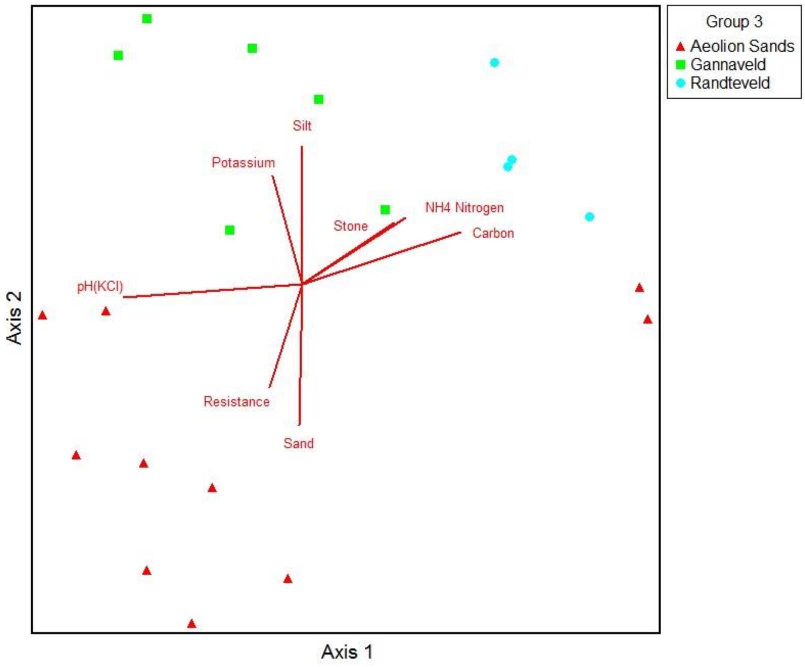


Figure 5.5. Group 3, Sandy Karoo ordination, using 2015 data, with soil parameters indicating the three further divisions in the vegetation community, which closely match the descriptions of the habitat units Randteveld, Gannaveld and Aeolian Sand deposits (within the Gannaveld habitat) as per Vlok et al. (2005).

Group 4 –Renosterveld

An NMS ordination on the Renosterveld group (2015 data only) produced a 3-d solution with a stress of 5.19 and instability of 0.0000 (Figure 5.6). The first and third axes accounted for the greatest amount of variation and produced a cumulative R^2 value between ordination distances and distances in the original n-dimensional space of 0.853 with an orthogonality of 99.9%. No further divisions where obvious and the Renosterveld and Old lands plots were indistinguishable. The biplot for the Renosterveld community explained the differences in the plots. Axis 1 represents a gradient of sand to silt, with calcium, magnesium and citric acid corresponding to several of the plots. Axis 3 corresponds with the presence of stone and manganese in certain plots. The most characteristic species for the Renosterveld group are listed in Table 5.1, and represent 74% cover for the plots.

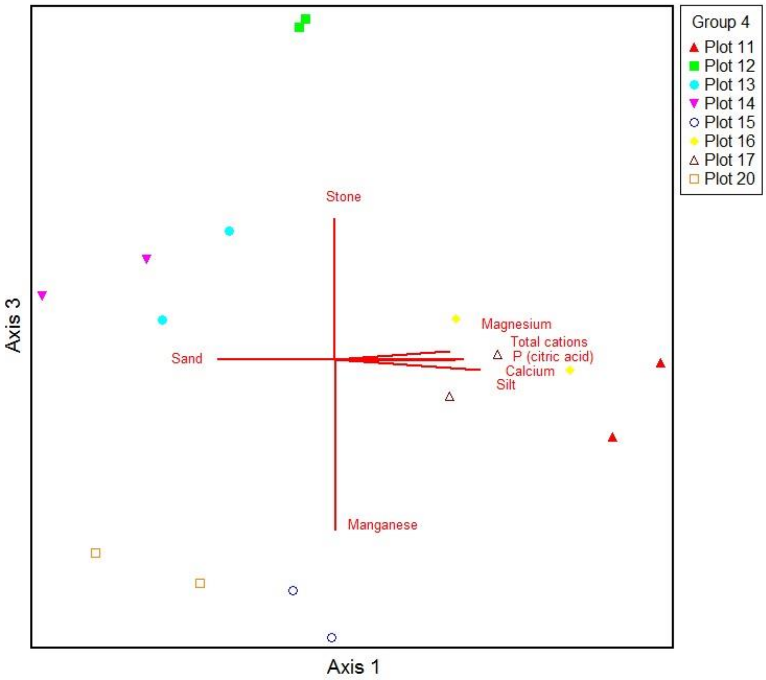


Figure 5.6. Group 4, Renosterveld ordination, using 2015 data, indicating the paired plots are closely related and dependent on different soil parameters.

Table 5.1. The most dominant species in each vegetation community, in descending order of dominance.

Rocky Karoo		**Quartz Vygieveld**		**Sandy Karoo**		**Renosterveld**	
Species	**% Cover**	**Species**	**% Cover**	**Species**	**% Cover**	**Species**	**% Cover**
Pteronia pallens	17.3	*Gibbaeum pubescens*	25.7	*Drosanthemum delicatulum*	9.6	*Pteronia incana*	9.9
Tripteris sinuata	10.3	*Pteronia succulenta*	11.2	*Leipoldtia schultzei*	8.4	*Pteronia paniculata*	8.2
Hereroa odorata	9.3	*Salsola tuberculata*	8.8	*Ruschia robusta*	6.6	*Drosanthemum delicatulum*	7.2
Ruschia spinosa	6.6	*Tripteris sinuata*	6.5	*Monechma incanum*	6.3	*Elytropappus rhinocerotis*	6.8
Eriocephalus ericoides	6.5	*Ruschia muricata*	4.8	*Crassula rupestris*	5.1	*Euryops nodosus*	6.5
Ruschia muricata	3.7	*Felicia sp 1*	4.5	*Psilocaulon junceum*	5.1	*Felicia muricata*	5.4
Rhigozum obovatum	3.6	*Berkheya cuneata*	4.4	*Euphorbia burmanii*	4.8	*Pteronia sordida*	4.8
Leipoldtia schultzei	3.4	*Pteronia viscosa*	2.2	*Chrysocoma ciliata*	4.5	*Pentzia incana*	4.7
Drosanthemum delicatulum	2.6	*Hereroa odorata*	2.1	*Salsola glabrescens*	4.3	*Galenia africana*	4.7
Zygophyllum microphyllum	2.4	*Salsola glabrescens*	1.9	*Stipagrostis obtusa*	4.3	*Selago geniculata*	3.9
Blepharis capensis	2.4	*Psilocaulon simile*	1.9	*Stipagrostis ciliata*	3.4	*Atriplex semibaccata*	2.8
Crassula rupestris	2.3	*Gnidia deserticola*	1.8	*Pentzia incana*	2.8	*Eriocephalus africanus*	2.5
Hirpicium integrifolium	1.8	*Gibbaeum nuciforme*	1.5	*Rhigozum obovatum*	2.3	*Felicia filifolia*	2.4
Galenia fruticosa	1.7	*Felicia filifolia*	1.5	*Ruschia muricata*	2.2	*Hereroa odorata*	2.3
Euphorbia burmanii	1.5	*Pteronia pallens*	1.5	*Ruschia pungens*	1.9	*Helichrysum ericaefolium*	2.3
Total cover	**75**		**80**		**72**		**74**

Cover

The percentage cover for the four vegetation communities, is shown in Figure 5.7. In all four communities, the exclosures had a higher percentage cover than the open plots. The difference between the exclosure plots to grazed plots in each of the four communities is 28%, 22%, 26% and 25% respectively.

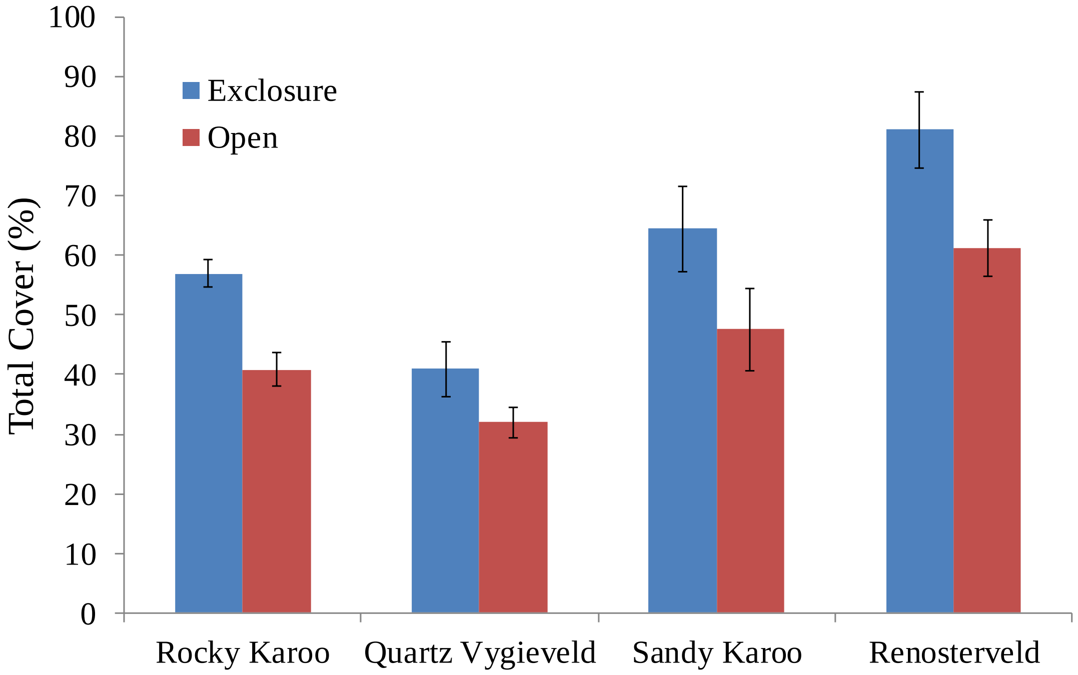


Figure 5.7. Mean % vegetation cover (±SE) in 2015 for open and exclosure plots within each of the vegetation communities investigated at Sanbona. Pairwise t-test comparisons showed significant differences between open and exclosure plots: Rocky Karoo (t = 2.179, df = 12, P = 0.0007), Quartz Vygieveld (t = 2.345, df = 7, P = 0.02), Sandy Karoo (t = 2.262, df = 9, P = 0.01) and Renosterveld (t = 2.364, df = 7, P = 0.0006).

Abundance

Of the 15 growth forms, low deciduous shrubs were so poorly represented that they were removed from any further analysis. Abundance was measured as the total number of first and second strikes (whereas cover is the percentage of the total possible strikes) (Table 5.2). Each vegetation type was represented by different growth forms (Figure 5.8) for 2015 data which included both treatments, since there was very little difference between the treatments. Medium (0.5-1 m) evergreen shrubs were the most prevalent growth form in all communities (Rocky Karoo and Quartz Vygieveld – 34%; Renosterveld - 54%) except the Sandy Karoo, where low leaf succulent shrubs were most common (22%). Quartz Vygieveld was distinguished by the high number of low dwarf succulents (31%) while the Renosterveld was the only community to have tall evergreen shrubs represented (9%) and a significant number of annuals and geophytes compared to the other vegetation communities.

Table 5.2. Mean abundance, with standard deviation of each growth form for 2015 data, within the four vegetation communities. The difference between the treatments was negligible so it was combined. The total is equivalent to the total number of hits in each community. Superscripts within each growth form indicate significant differences based on Kruskal-Wallis one-way ANOVA and Dunn’s multiple comparison test.

Plant Functional Type	**Rocky Karoo**	**Quartz Vygieveld**	**Sandy Karoo**	**Renosterveld**
Annual Forb	0 ± 0	2^{a} ± 0.3	3^{a} ± 0.7	11^{b} ± 1
Perennial Forb	89^{a} ± 5	45^{a} ± 7	235^{b} ± 12	49^{a} ± 6
Perennial Grass	198^{ab} ± 14	15^{a} ± 3	990^{b} ± 53	132^{a} ± 18
Geophyte	4^{a} ± 0.5	0 ± 0	1^{a} ± 0.2	75^{b} ± 10
Low Dwarf Succulent	586^{c} ± 19	888^{d} ± 20	11^{a} ± 2	156^{ab} ± 19
Low Leaf Succulent Shrub	1340^{b} ± 37	253^{a} ± 18	1241^{ab} ± 64	283^{a} ± 27
Medium Leaf Succulent Shrub	196^{ab} ± 8	41^{a} ± 3	675^{bc} ± 25	247^{b} ± 15
Stem Succulent	194^{b} ± 8	15^{a} ± 2	508^{b} ± 45	7^{a} ± 2
Medium Deciduous Shrub	784^{c} ± 28	220^{bc} ± 15	148^{b} ± 8	21^{a} ± 3
Tall Deciduous Shrub	234^{a} ± 16	0 ± 0	118^{a} ± 13	0 ± 0
Low Evergreen Shrub	579 ± 22	452 ± 21	564 ± 34	1129 ± 87
Medium Evergreen Shrub	2155^{a} ± 28	983^{a} ± 29	1047^{a} ± 38	3055^{b} ± 106
Tall Evergreen Shrub	3^{a} ± 0.6	0 ± 0	8^{a} ± 2	525^{b} ± 46
Evergreen Tree	1^{a} ± 0.2	1^{ab} ± 0.2	51^{b} ± 5	3^{ab} ± 0.7

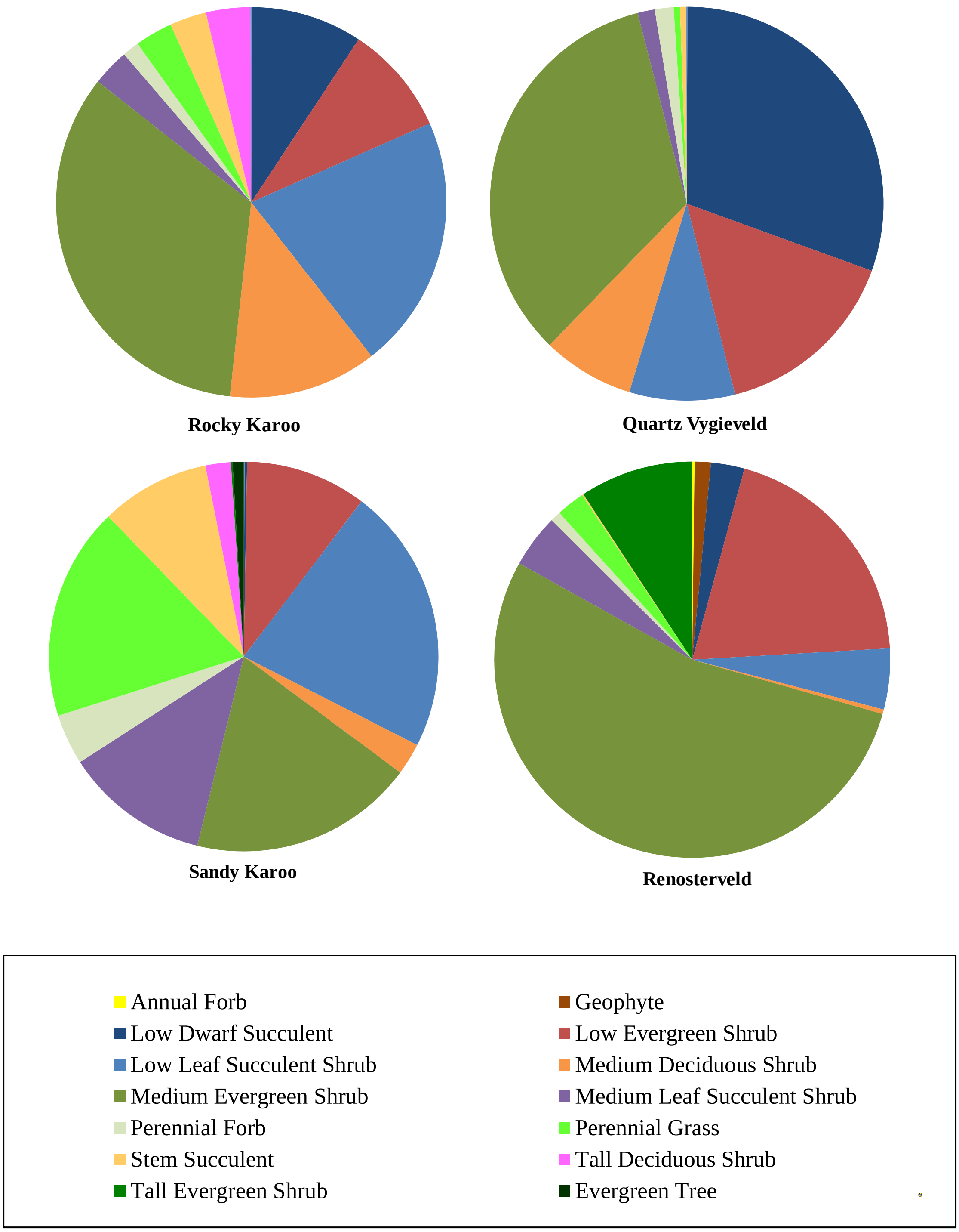


Figure 5.8. Relative abundance of different growth forms within each vegetation community.

Species Richness

Species Richness (SR) is a simple count of species per specified area (Rutherford & Powrie, 2013). Only 2015 data was utilised and this reflects the current species richness and will form a good foundation for future re-examination.

More than 70% of the species are comprised of medium and low evergreen shrubs, medium and low leaf succulent shrubs, low dwarf succulent, and medium deciduous shrubs. The other growth forms i.e. trees, tall evergreen shrubs, tall deciduous shrubs, grasses, forbs, geophytes and stem succulents form a small percentage of the total number of species (Figure 5.9).

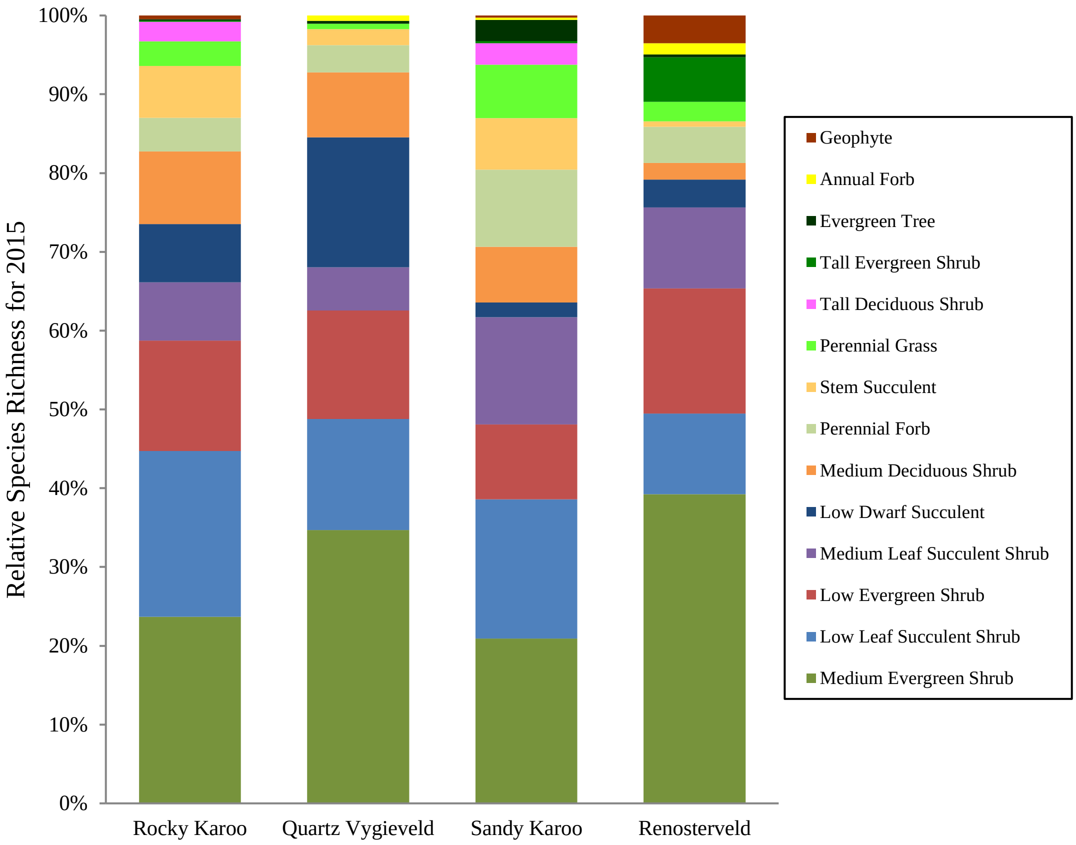


Figure 5.9. Relative species richness for 2015 data only, with each growth form expressed as a percentage of the total number of species within the vegetation type.

The total number of species in each growth form in each of the communities is shown in Figure 5.10. Medium, low and dwarf evergreen and succulent leaved shrubs dominate the vegetation of Sanbona. Some growth forms (e.g. geophytes, tall evergreen shrubs, trees) appear to more common in particular communities than others.

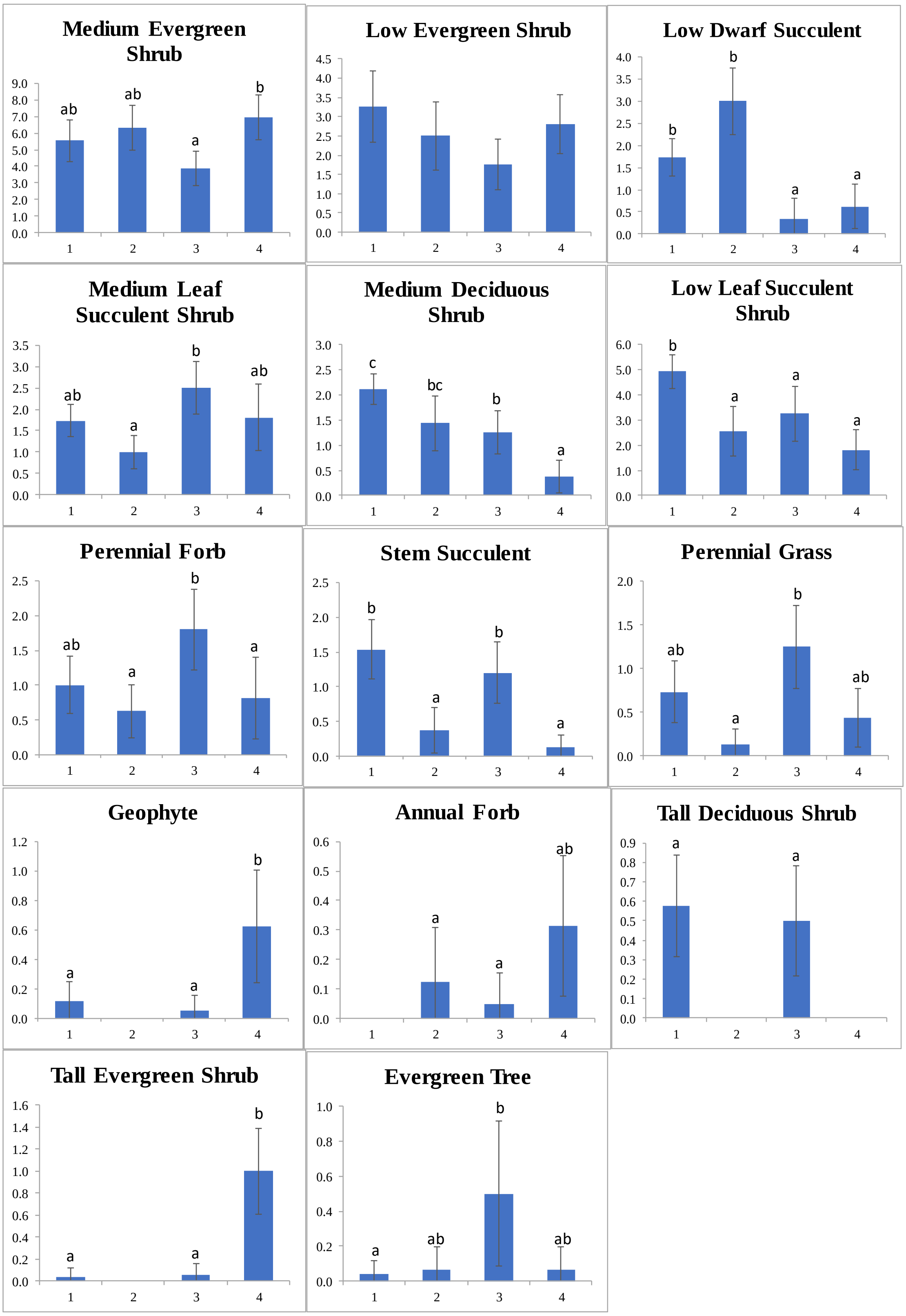


Figure 5.10. Mean species richness of each vegetation community within a specific plant growth form, where 1 = Rocky Karoo group, 2 = Quartz Vygieveld group, 3 = Sandy Karoo group and 4 = Renosterveld group. Error bars are 95% confidence limit. Note y axis is not equivalent. The letter indicates significant differences based on a Kruskal-Wallis one-way ANOVA and Dunn's multiple comparison test.

Unique species

Each vegetation community is differentiated not only by high values of certain dominant species but also by the presence of unique species that only occur in a particular community. The Renosterveld group had the highest number of unique species, while in Quartz Vygieveld, only 13% of its species can be considered unique to this community (Figure 5.11). A list of the unique species is recorded in Table B1 in Appendix B.

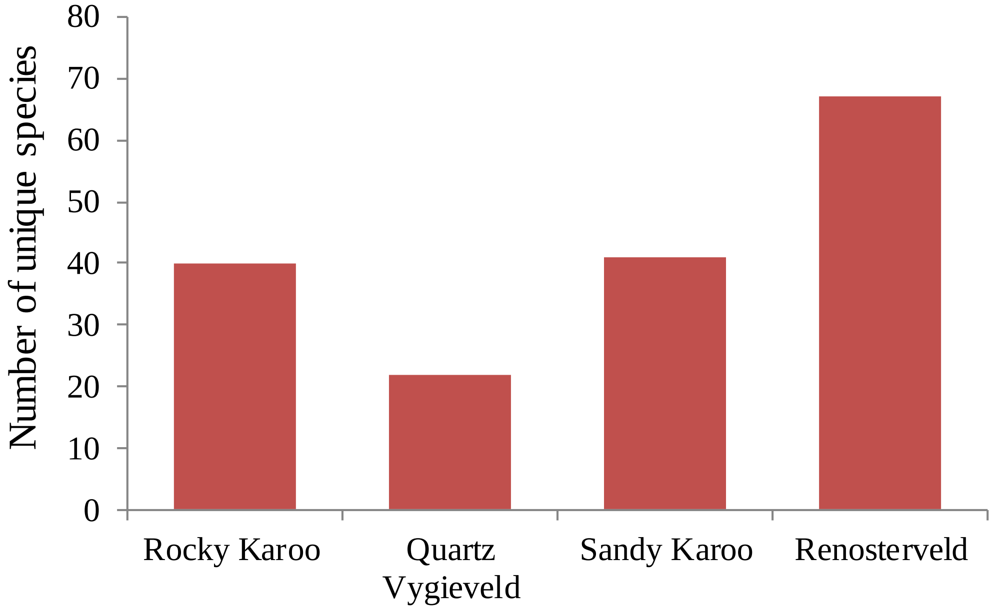


Figure 5.11. The number of unique species found in each vegetation community, Renosterveld has the highest number of unique species while Quartz Vygieveld has the least number of unique species.

5.2. Vegetation change from 2004 to 2015

Cover

There was an increase in cover on both treatments over time (Exclosures: $R^2 = 0.7972$, $p<0.01$; Open: $R^2 = 0.4034$) (Figure 5.12). The slope of the regression of the exclosure plots was significantly different from the slope of the regression for plots in the open. This suggests that herbivory had a significant impact in depressing the rate of recovery within plots that were open to herbivory compared to those that were protected from herbivory.

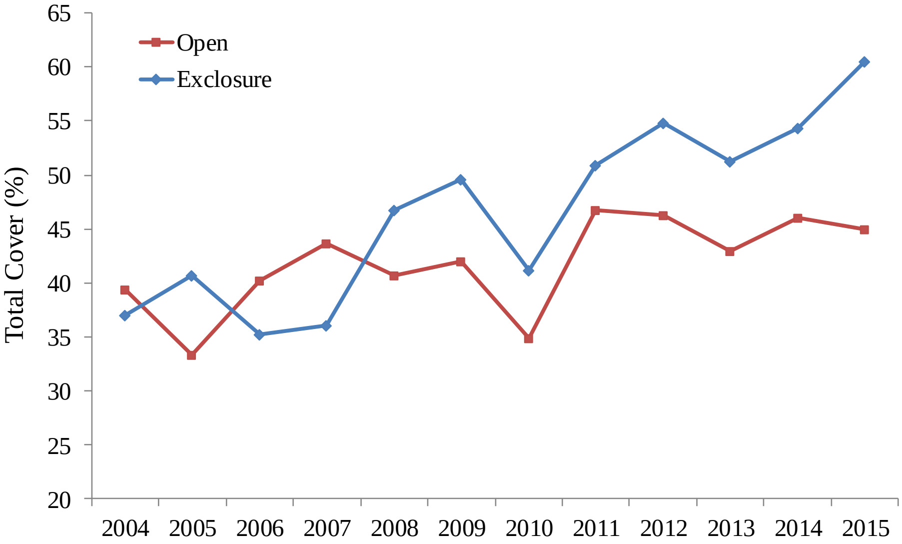


Figure 5.12. Total percentage cover for the combined exclosure plots and combined open plots, over the study period from 2003 – 2015. The slopes of the regression lines, which are not illustrated, are significantly different from one another ($t = 2.957$, $df = 20$, $P = 0.0078$).

Species Richness

Mean annual species richness increased significantly over time within the exclosures but not in the open plots (Exclosures: $R^2 = 0.8278$, $p<0.001$; Open: $R^2 = 0.0524$) (Figure 5.13). The graph clearly demonstrates that there was an initial recovery phase for the first four years where both treatments tracked each other closely. After 2008, however, the treatments diverged, probably in response to the introduction of a large number of game.

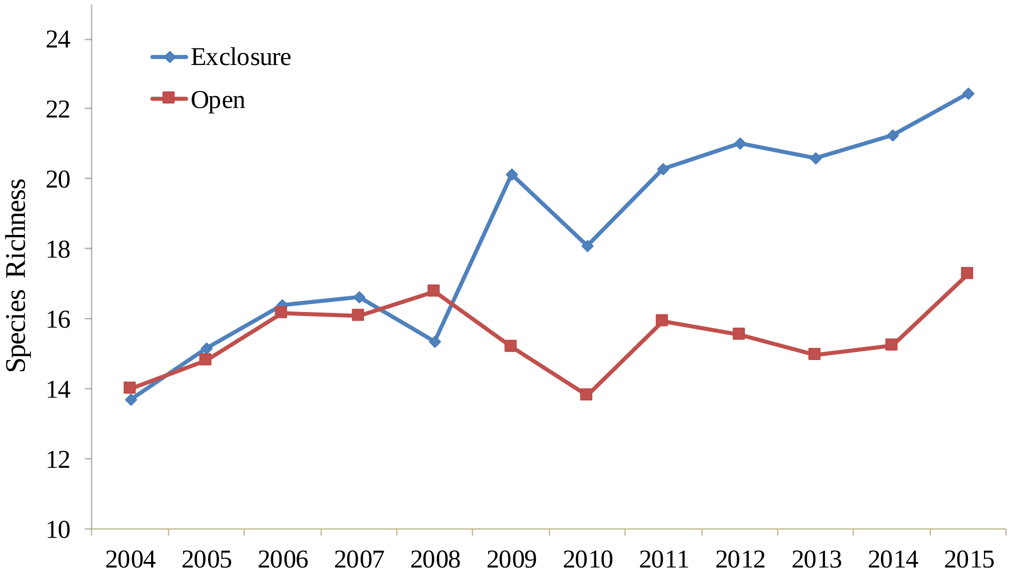


Figure 5.13. Species richness for the exclosure and open plots over the study period from 2004 – 2015. The slopes of the regression lines are significantly different from one another (t = 5.675, df = 20, P<0.0001).

Growth forms

The growth forms had different responses over time within the exclosure and open plots, as indicated in Figure 5.14 and Figure 5.15. The significance of the regression line for both treatments is portrayed in Figure 5.16. Of these changes, the most significant decrease in cover was for the low leaf succulent shrubs which occurred in both treatments. There was a moderately significant decrease in cover for medium evergreen shrubs in the exclosure plots while the cover of stem succulents decreased only in the open plots. The cover of perennial grasses, evergreen trees as well as low evergreen shrubs increased significantly in both treatments, although trends in the exclosure plots were only weakly significant. Geophytes increased in cover in the exclosure plots while medium evergreen shrubs increased in the open plots. Normally, a decrease within the open plot would indicate that grazing could be affecting the plots. However, stem succulents such as *Tylecodon*, *Cotyledon* and *Euphorbia* are usually unpalatable or toxic plants and they are the only growth form which exhibited a significant decrease in the open plots.

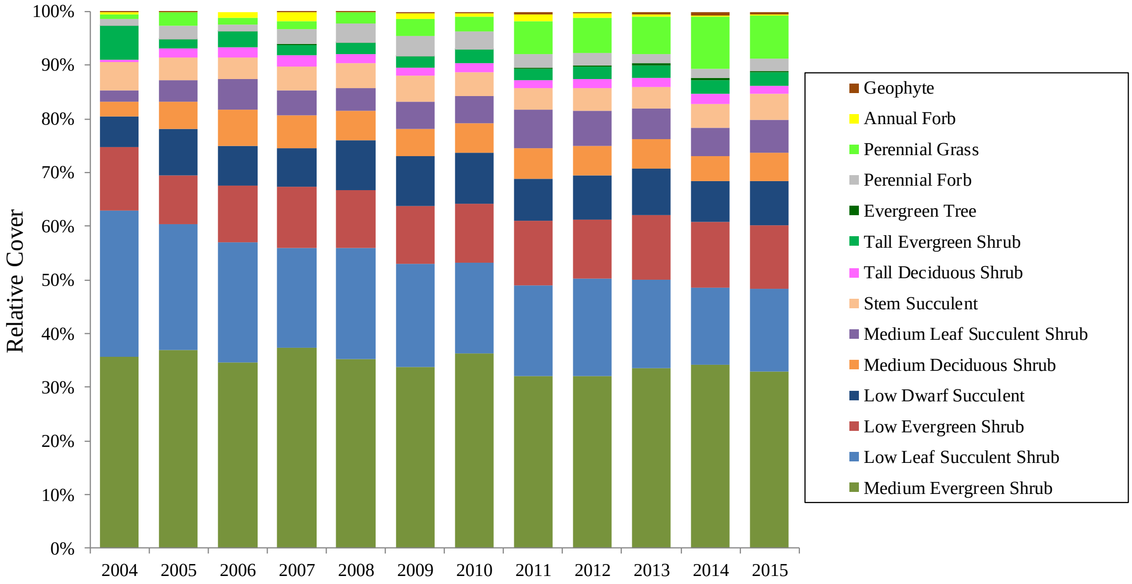


Figure 5.14. Relative cover (%) for the exclosure plots for each growth form for the period 2004 – 2015.

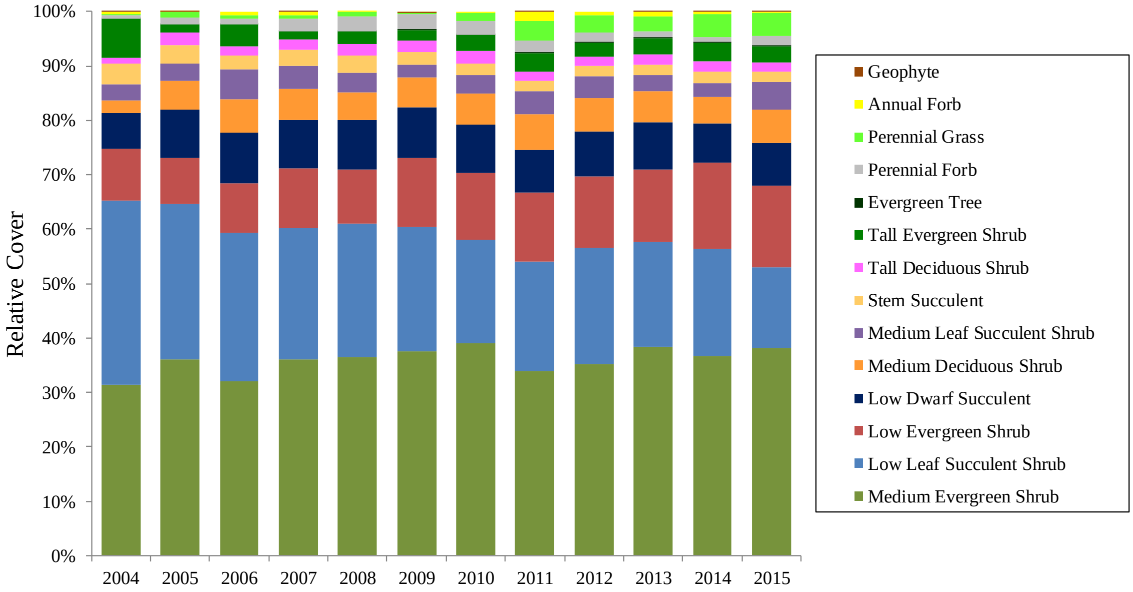
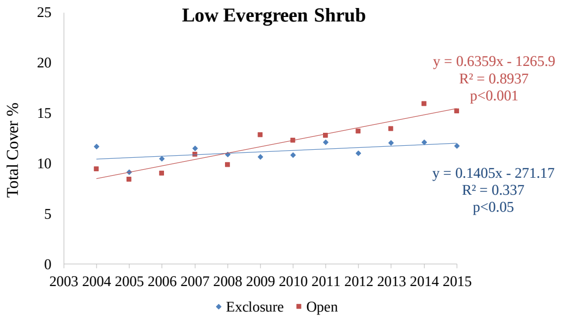
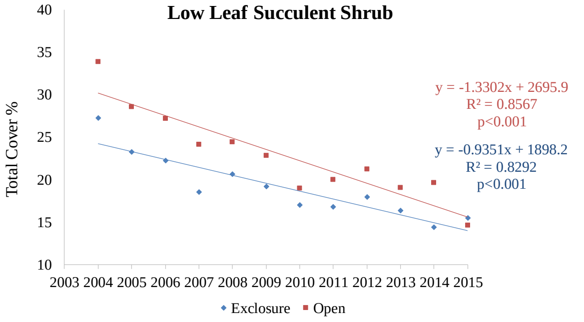
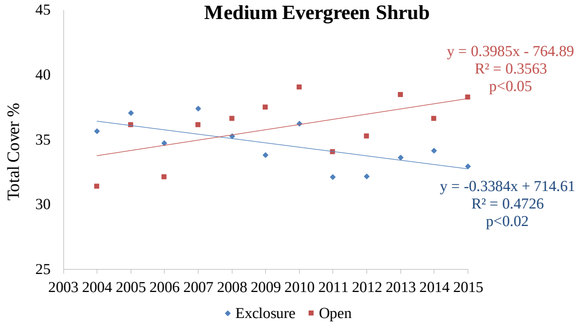
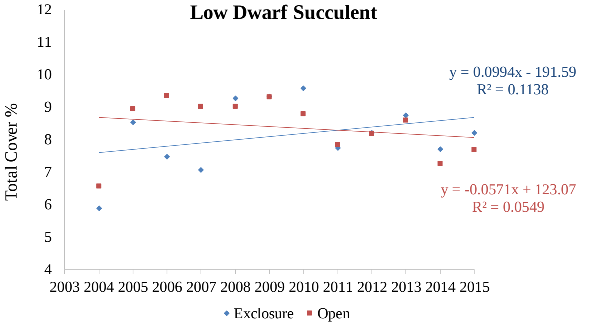


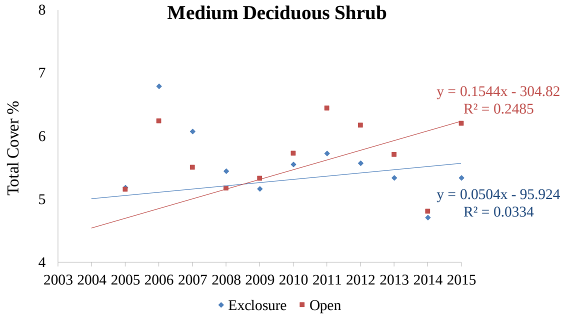
Figure 5.15. Relative cover (%) for the open plots for each growth form for the period 2004 – 2015.

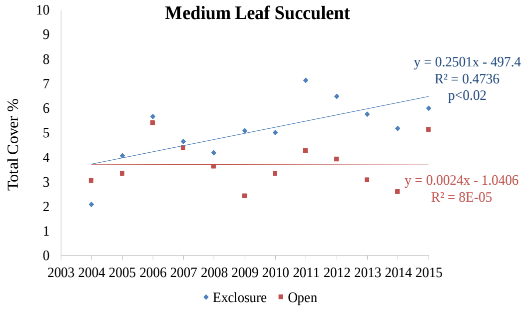

Low Evergreen Shrub
Total Cover %
0
5
10
15
20
25
2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015
y = 0.6359x - 1265.9
R² = 0.8937
p<0.001
y = 0.1405x - 271.17
R² = 0.337
p<0.05
◆ Exclosure ■ Open

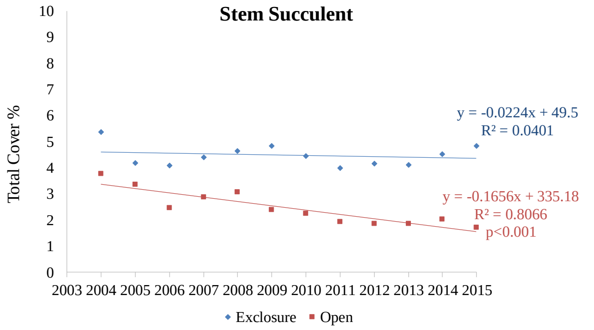

Low Leaf Succulent Shrub
Total Cover %
10
15
20
25
30
35
40
2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015
y = -1.3302x + 2695.9
R² = 0.8567
p<0.001
y = -0.9351x + 1898.2
R² = 0.8292
p<0.001
◆ Exclosure ■ Open

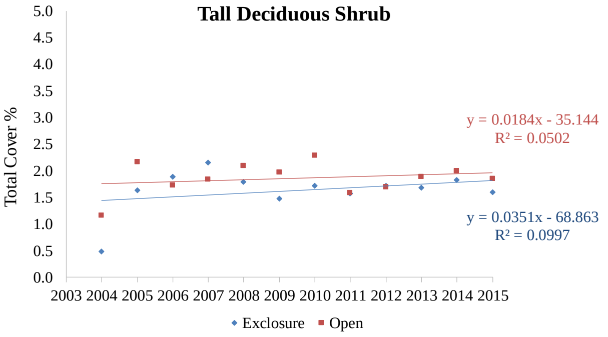

Medium Evergreen Shrub
Total Cover %
25
30
35
40
45
2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015
y = 0.3985x - 764.89
R² = 0.3563
p<0.05
y = -0.3384x + 714.61
R² = 0.4726
p<0.02
◆ Exclosure ■ Open

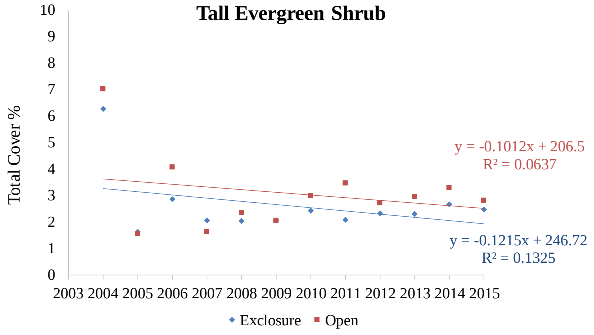

Low Dwarf Succulent
Total Cover %
4
5
6
7
8
9
10
11
12
2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015
y = 0.0994x - 191.59
R² = 0.1138
y = -0.0571x + 123.07
R² = 0.0549
◆ Exclosure ■ Open

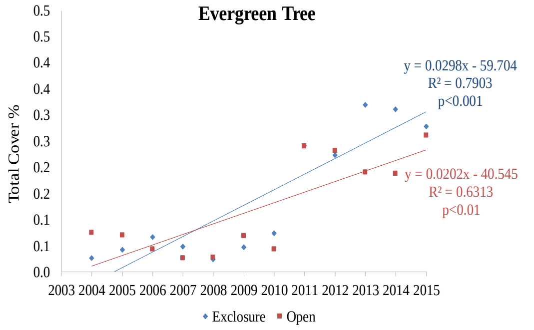

Medium Deciduous Shrub
Total Cover %
4
5
6
7
8
2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015
y = 0.1544x - 304.82
R² = 0.2485
y = 0.0504x - 95.924
R² = 0.0334
◆ Exclosure ■ Open


Medium Leaf Succulent
Total Cover %
0
1
2
3
4
5
6
7
8
9
10
2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015
y = 0.2501x - 497.4
R² = 0.4736
p<0.02
y = 0.0024x - 1.0406
R² = 8E-05
◆ Exclosure ■ Open


Stem Succulent
Total Cover %
0
1
2
3
4
5
6
7
8
9
10
2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015
y = -0.0224x + 49.5
R² = 0.0401
y = -0.1656x + 335.18
R² = 0.8066
p<0.001
◆ Exclosure ■ Open


Tall Deciduous Shrub
Total Cover %
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015
y = 0.0184x - 35.144
R² = 0.0502
y = 0.0351x - 68.863
R² = 0.0997
◆ Exclosure ■ Open


Tall Evergreen Shrub
Total Cover %
0
1
2
3
4
5
6
7
8
9
10
2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015
y = -0.1012x + 206.5
R² = 0.0637
y = -0.1215x + 246.72
R² = 0.1325
◆ Exclosure ■ Open


Evergreen Tree
Total Cover %
0.0
0.1
0.1
0.2
0.2
0.3
0.3
0.4
0.4
0.5
0.5
2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015
y = 0.0298x - 59.704
R² = 0.7903
p<0.001
y = 0.0202x - 40.545
R² = 0.6313
p<0.01
◆ Exclosure ■ Open

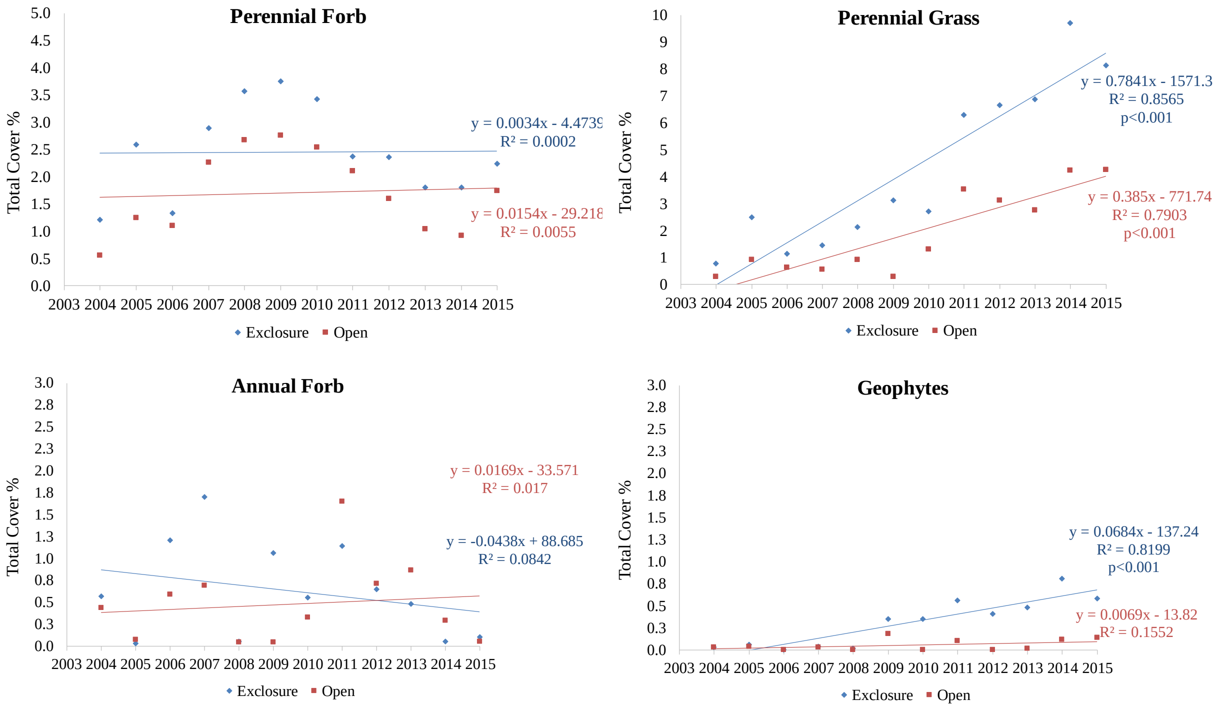


Figure 5.16. Regressions of the abundance of each growth form against time for exclosure and open plots. Note that because of the large variation in % cover values the y axis is not consistent across growth forms.

Community-level changes over time

The species richness of the exclosures was higher than the open plots from 2009 (Figure 5.17). Overall the species richness increased significantly in the ungrazed plots for each of the communities (Rocky Karoo: R^2 = 0.8009; p<0.001; Quartz Vygieveld: R^2 = 0.8569; p<0.001; Sandy Karoo: R^2 = 0.4188; p<0.05; Renosterveld: R^2 = 0.7519; p<0.001). However, in the grazed plots, there was only a slight but not significant increase in species richness in the Quartz Vygieveld (R^2 = 0.3071) and Renosterveld (R^2 = 0.2851). There was also a clear divergence in the species richness of exclosures and grazed plots over time, indicating that grazing pressure was the main driver of this change over time and that it appears that the increase in grazing pressure after 2009 had a particular impact.

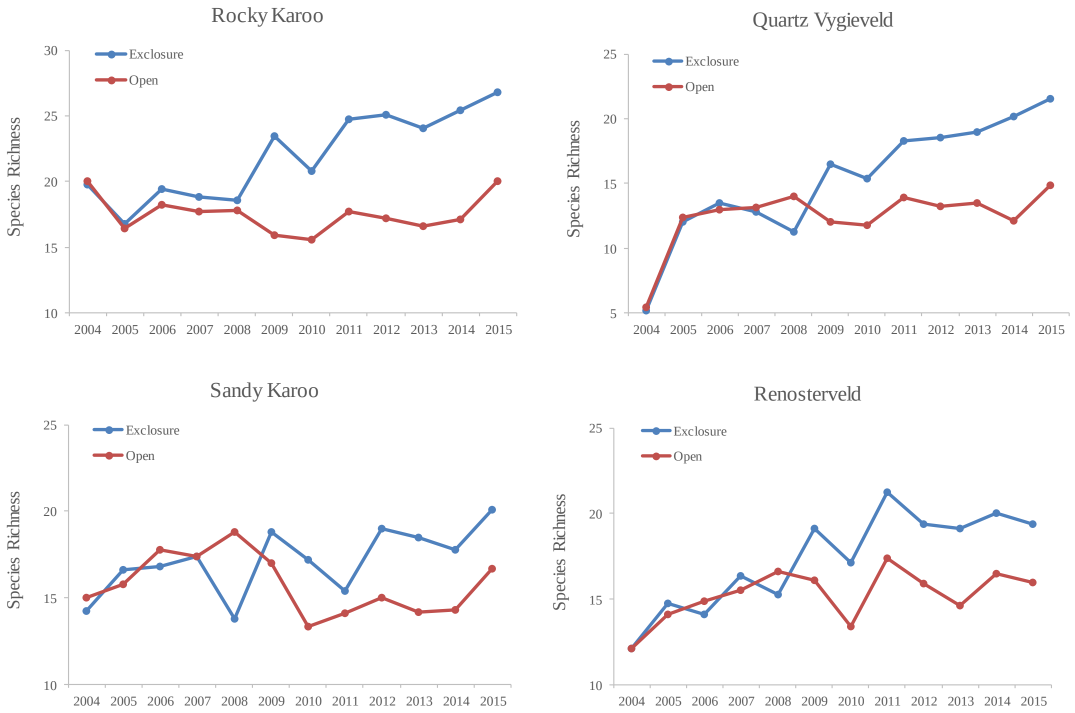


Figure 5.17. Species richness for each vegetation community for both treatments, exclosures and open plots over the period 2004 – 2015. The slopes of the regressions are significantly different from one another Rocky Karoo (t = 4.755, df = 20, P = 0.001), Quartz Vygieveld (t = 3.514, df = 20, P = 0.002), Sandy Karoo (t = 2.715, df = 20, P = 0.013) and Renosterveld (t = 2.731, df = 20, P = 0.013).

The NMS ordinations depict floristic compositional change over time within exclosure and open plots for each vegetation community (Figure 5.18 and Appendix C). This ordination represents the sum of each species for all the plots within a group for each year. The relatively low stress values and high proportion of variance accounted for by axes 1 and 2 in all vegetation types (Table D1 in Appendix D) suggests that there is little risk of drawing false inferences from the final two-dimensional solutions (McCune & Grace, 2002). The Rocky and Sandy Karoo groups had additional plots added in 2005. Therefore, analyses started with the 2005 data so that vectors could be illustrated, as this is not possible in PC-Ord when there are different sample sizes between years.

Over the period 2004-2015, exclosures and open plots in all of the vegetation communities exhibited similar trajectories. Plots subjected to the two treatments were similarly distant from each other in 2015 as they were initially in 2004/5. The major source of variation is the change from year to year. The degree of divergence between the exclosure and open plots was not significant, although there does seem to be some apparent divergence in the treatments in the Rocky Karoo (y = 0.477x-936; R^2 = 0.5104), Sandy Karoo (y = 0.2342x-434.3; R^2 = 0.0516) and Renosterveld communities (y = 0.7937x-566.3; R^2 = 0.4285). In contrast, plots in the Quartz Vygieveld which are open to herbivory and those which are fenced appear to be converging on each other (y = -0.8426x+1718.6; R^2 = 0.3684).

Group 1 – Rocky Karoo

In both treatments within the Rocky Karoo, there were significant increases in palatable species such as *Tripteris sinuata* and *Fingerhuthia africana* as well as unpalatable evergreen shrubs such as *Pteronia pallens* and succulents such as *Hereroa odorata* and *Leipoldtia schultzei* (Figure 5.19). (Palatable exclosure: R^2 = 0.8589; p<0.001; Palatable open: R^2 = 0.6094; p<0.01; Unpalatable exclosure: R^2 = 0.8176; p<0.001; Unpalatable open R^2 = 0.7039; p<0.001). The exclosure had more species that increased significantly over time than the open plots. Of particular significance are the evergreen shrubs, *Felicia muricata* and *Garuleum bipinnatum*. These two species are considered to be highly palatable and increased in the exclosure plots particularly from 2008. This explains, in part, the large movement in ordination space on the ungrazed plots (Figure 5.18). This response is confirmed in Figure 5.20. The increase in dissimilarity on the exclosure correlates with the increase in *F. muricata* and *G. bipinnatum*. The fact that the open plot did not respond similarly can be explained by the increase in herbivore numbers that year. Although it did not cause an obvious change in the open plot, it was very evident in the potential change that could have happened, as was experienced in the exclosure. Except for the differences observed in 2008 the plots generally track each other.

Floristic compositional changes are evident in both treatments from the change in trajectories. In 2006 in the exclosure plot an increase in species such as *Lotononis spp.*, and an unidentified *Pteronia spp.*, in response to the above average winter rainfall, resulted in a response that was opposite to the trajectories in the following years. Even though the average rainfall for this period was below the mean, the season that it occurred in was important. This floristic compositional change corresponds to the increase in cover for that year (Figure 5.21). 2009 and 2012 experienced above average rainfall but in a different season. In 2009 the majority of rain fell in the summer months prior to the surveys and influenced species in the exclosures within a variety of growth forms, such as the forb *Galenia secunda*, the evergreen shrub *Helichrysum ericaefolium*, the dwarf succulent *Crassula tecta* and even the succulent shrub *Cotyledon orbiculata.* In 2012, with above average rainfall in winter, the exclosure was influenced by species such as the evergreen shrub *Thesium lineatum* and leaf succulent shrub *Ruschia caroli*. In 2013 and 2014 the trajectories for the exclosure moved in the opposite direction to the general trend but stayed relatively close to the trajectory of the open plots largely because of an increase in *Pharnaceum spp*. In the open plots, 2007 and 2012 had the biggest impact on the observed trajectory. 2007 was influenced by *Crassula tecta*, and possibly several palatable species such as *Paspalum spp., Tripteris spp*., and *Pteronia membranacea.* This response cannot be explained by rainfall alone as 2007 was the lowest ever recorded rainfall for the study period. In 2012, with its above average annual rainfall which fell mostly in winter, the plots were influenced by species such as the deciduous *Lebeckia spp*., and the evergreen shrub, *Rosenia glandulosa.*

Group 2 –Quartz Vygieveld

In both open and exclosure plots within the Quartz Vygieveld there were increases in palatable deciduous species such as *Tripteris sinuata* and evergreen shrubs such as *Berkheya cuneata* and *Salsola tuberculata*. There were also increases in unpalatable species such as *Pteronia succulenta, Psilocaulon simile* and *Gibbaeum pubescens* (Figure 5.19) (Palatable exclosure: R^2 = 0.8459; p<0.001; Palatable open: R^2 = 0.7872; p<0.01; Unpalatable exclosure: R^2 = 0.8236; p<0.001; and Unpalatable open: R^2 = 0.7369; p<0.001). Similar results were found by Hoffman et al. (2009) but with fewer species. In their study, only *T. sinuata, B. cuneata* and *Pteronia adenocarpa* (misidentified in the earlier surveys and now called *P. succulenta)* increased. The only species that experienced a small decrease was the palatable deciduous shrub, *Rhigozum obovatum* which decreased in the grazed plots only.

The treatments in the Quartz Vygieveld are the only treatments within the four vegetation communities that show convergence towards each other. However, this response was not significant ($R^2 = 0.3684$), probably because of the small sample size. For 2004, the treatments are relatively distant in ordination space from one another. They are not only different to each other but also to subsequent years (Figure 5.18). This is possibly due to the low species abundance of all species for that year which probably resulted from the extremely low rainfall recorded during the 2003-2004 period. The high incidence of the unpalatable *Malephora lutea* and *Pteronia incana* in the open plots in 2004 probably also influenced the pattern of change. This can be seen in Figure 5.20, where the change from the first to the following year is great and thereafter the plots do not change much from year to year.

The floristic composition within the open plots in 2006 was strongly influenced by a high cover of *Delosperma spp*. and *Pelargonium spp*., which could have been as a result of high winter rain just prior to the survey. 2007 was influenced by the same *Pelargonium spp*. and *Pteronia sordida*. *Delosperma spp.* has subsequently not been recorded again.

2004, 2006 and 2007 also influenced the total cover for the open plots which had a higher percentage cover than the exclosure (Figure 5.21). In both treatments, however, vegetation cover has increased significantly over time (Exclosure: $y = 2.0902x - 4171$; $R^2 = 0.8965$; $p<0.001$; Open: $y = 1.2478x – 2482.8$; $R^2 = 0.7873$; $p<0.001$), with cover in the exclosure plots increasing more than in the open plots.

Group 3 – Sandy Karoo

In both treatments of the Sandy Karoo, there was a significant increase in the dominant species *Ruschia robusta, Salsola glabrescens* and *Stipagrostis obtusa*. As was the case in the Rocky Karoo, there was a greater number of species which increased in cover in the exclosure plots than in the open plots (Figure 5.21). This increase was mostly influenced by the significant increase in palatable species such as *Stipagrostis ciliata* and *Digitaria spp (*$R^2 = 0.8432$; $p<0.001$) (Figure 5.19) but several unpalatable species such as *Ruschia pungens, Helichrysum spp*., *Dicoma spinosa, Carissa haematocarpa,* and *Muraltia spinosa* also contributed. There was a decrease of dominant palatable species such as *Pentzia incana* and *Rhigozum obovatum*, in the open plots and the less abundant palatable *Ehrharta spp*., as well as a significant decrease in unpalatable species such as *Pteronia incana* and *Euphorbia mauritanica* (R^2 = 0.6440; $p<0.05$). This is reflected in the overall decrease in total cover for the open treatments, which was marginally not significant (Figure 5.21) (Open: $y = -0.5471x + 1147.9$; R^2 = 0.0627).

The change in ordination space in the exclosure plots between 2005 and 2007 could be a response to the abundance of *Crassula rupestris* which after an increase in 2005, decreased in 2006 and then increased again in 2008. The large change in ordination space between 2010 and 2011 (Figure 5.18) for both plots can be explained by the inclusion of the five additional Aeolian Sands plots. The most significant species, present in the new plots, and which influenced this change were *Stipagrostis obtusa, Salsola glabrescens*, *Ruschia pungens* and *Schotia afra*. This clarifies the spike in the graph of dissimilarity (Figure 5.20) as they were originally very dissimilar to previous years but thereafter the similarity increased and the peak flattened out.

Similarly, the trough in species cover (Figure 5.21) can be explained by the fact that the plots were overgrazed and had a very low cover in the initial year of survey (2010) which recovered with the above average rainfall received in 2011. The cover for the exclosure plot for the period 2012 – 2015 increased far more than values for the open plots because grazing took place and kept the cover from increasing.

The change in ordination score with time decreased which means that the floristic composition changed less with time. This is also observed in the percentage dissimilarities which stayed constant for the last few years.

Group 4 –Renosterveld

In the Renosterveld, the trajectories over time for both open and exclosure plots are relatively similar (Figure 5.18). The floristic composition within the open plots in 2006, was strongly influenced by an increase in annuals, and the short lived perennial herbs as well as the succulent shrub *Drosanthemum delicatulum.* After good winter rain, as was experienced in 2006, *D. delicatulum* germinated *en masse*. High winter rainfall also influenced the composition of species in the open plots in 2011 and 2012 with species such as *Malephora lutea, Euryops spp., Galenia africana* and *Oncosiphon piluliferum* abundant. The changes are also illustrated in Figure 5.20, where the open plots increase in dissimilarity in 2006 due to the increase in *D. delicatulum*. In 2011 with the increase in the aforementioned species dissimilarity between the open plots increased. However, in 2012 the open plots were relatively similar to each other and the dissimilarity measures, therefore, decreased.

The floristic composition of the exclosure plots was influenced by *Felicia filifolia* from 2004 to 2006 (Figure 5.18) when its abundance increased 120% in 2005 but then dropped again in 2006. This is also reflected in the spike in total percent cover for the exclosure plots in 2005 (Figure 5.21).

There is a marked difference in abundance of unpalatable and palatable plants in Renosterveld (Figure 5.19). The dominant species such as palatable *Felicia muricata* and *Pentzia incana* increased significantly in both open and exclosure plots over the period 2004-2015 (Palatable exclosure: $R^2 = 0.8694$; $p<0.001$; Palatable open: $R^2 = 0.6909$; $p<0.001$). Although unpalatable species such as *Elytropappus rhinocerotis, Pteronia incana* and *Euryops nodosus* increased in both treatments, it was only significant for the exclosures (Unpalatable exclosure: $R^2 = 0.4891$; $p<0.02$; Unpalatable open: $R^2 = 0.2346$). Some unpalatable species such *Pteronia paniculata* increased significantly, but only in the open plots. *P. paniculata* is known as a species which increases in response to overgrazing and because of this, could be an important indicator species. However, *Galenia africana*, another species that indicates overgrazing, decreased in abundance in both treatments.

The cover of the exclosure was marginally higher than the open plots, except in 2006 and 2007 (Figure 5.21). Overall, the cover increased in both treatments but for open plots this trend was only weakly significant (Exclosure: $y = 2.6642x - 5287.3$; $R^2 = 0.7305$; $p<0.001$; Open: $y = 1.48358x - 2918.3$; $R^2 = 0.4136$; $p<0.05$).

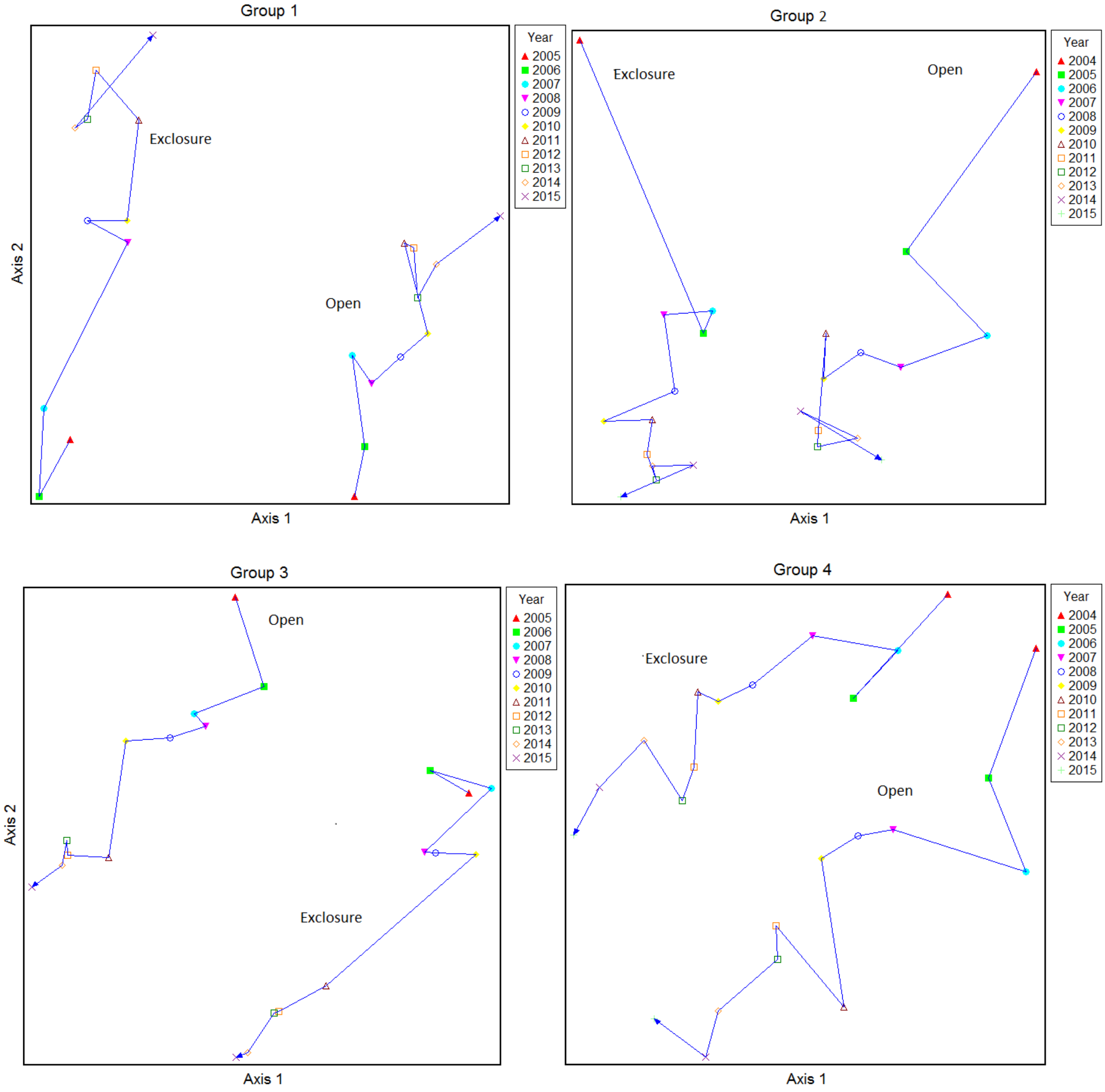


Figure 5.18. Nonmetric multidimensional scaling ordinations of the compositional change, where change represents the sum of species for all the plots within the four vegetation communities at Sanbona over time (2004 - 2015). Group 1 = Rocky Karoo, group 2 = Quartz Vygieveld, group 3 = Sandy Karoo and group 4 = Renosterveld.

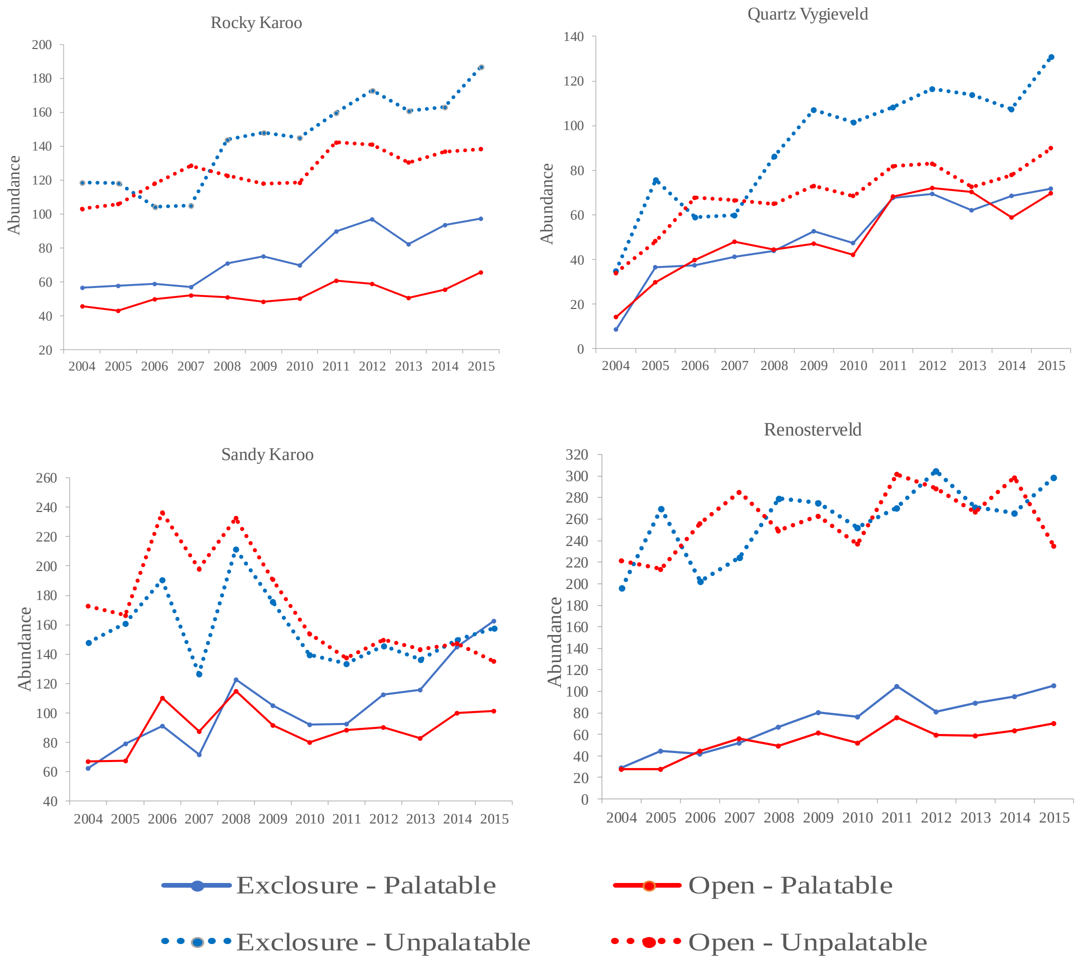


Figure 5.19. Comparison of the abundance of palatable and unpalatable species for each vegetation community for both treatments, exclosures and open plots over the period 2004 – 2015. The slopes of the regressions are significantly different from one another for Rocky Karoo palatable species (t = 4.278, df = 20, P<0.001), Rocky Karoo unpalatable species (t = 3.113, df = 20, P = 0.005), Quartz Vygieveld unpalatable species (t = 2.842, df = 20, P = 0.010), Sandy Karoo palatable species (t = 1.859, df = 20, P = 0.008), Renosterveld palatable (t = 2.908, df = 20, P = 0.009) but are not significant for the Quartz Vygieveld palatable species (t = 0.334, df = 20, P = 0.742), Sandy Karoo unpalatable species (t = 1.388, df = 20, P = 0.180), Renosterveld unpalatable species (t = 0.869, df = 20, P = 0.395).

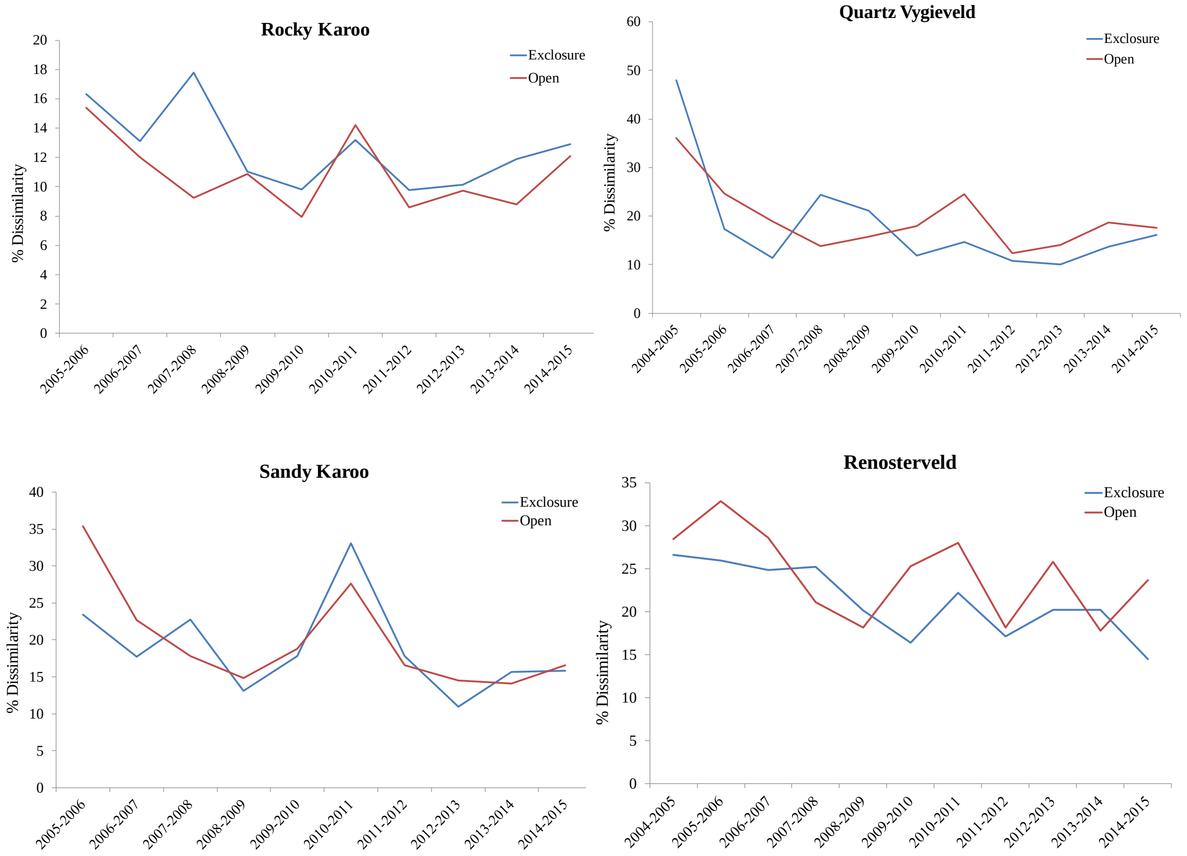


Figure 5.20. % Dissimilarity values showing that the different treatments in the different vegetation communities are following similar patterns. The slopes of the treatment regression lines for all communities are not significantly different from each another. Note that values for the y axis differ between communities.

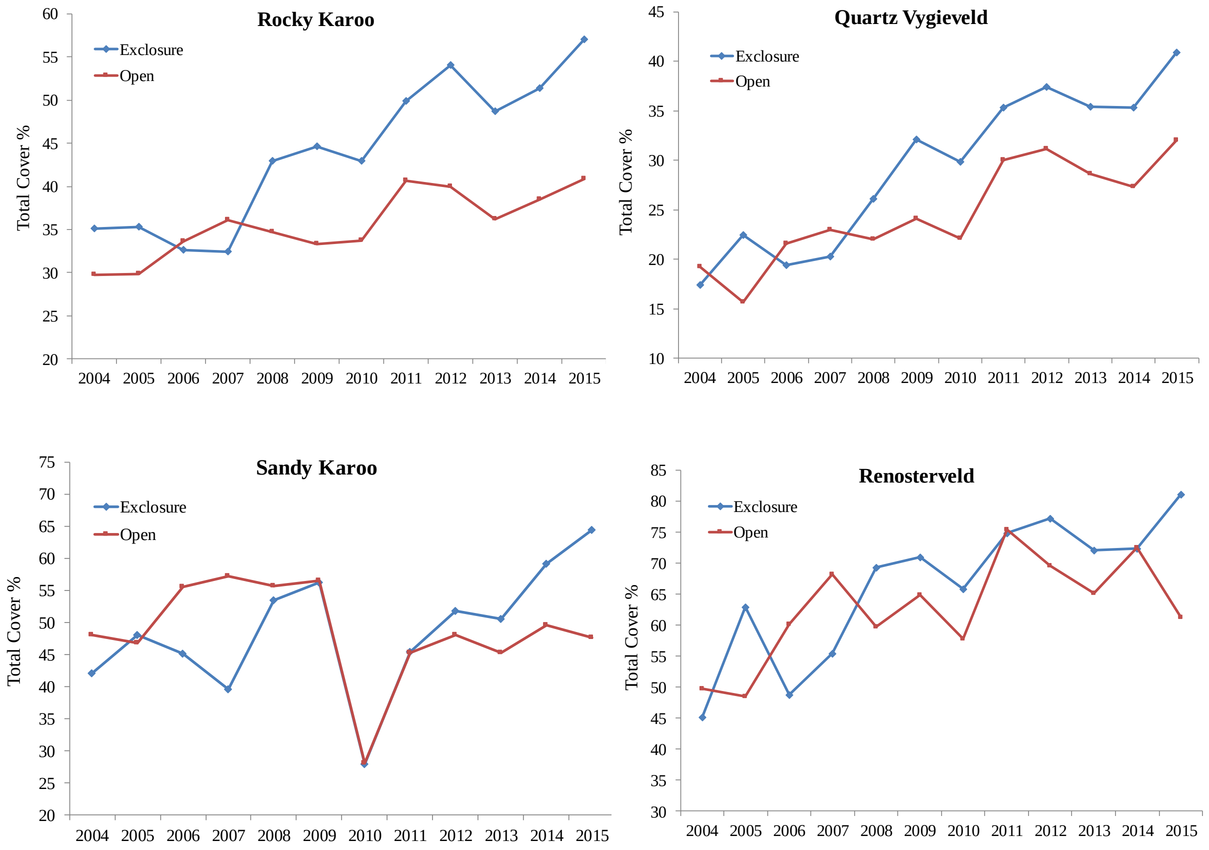


Figure 5.21. Total percent cover for each vegetation community for both treatments, exclosures and open plots over the period 2004 – 2015. The slopes of the regressions are significantly different from one another for Rocky Karoo (t = 3.781, df = 20, P = 0.001), Quartz Vygieveld (t = 2.770, df = 20, P = 0.012) but are not significant for the Sandy Karoo (t = 1.940, df = 20, P = 0.067) or Renosterveld (t = 1.559, df = 20, P = 0.135).

5.3. Rainfall

On site rainfall for 2006 - 2015 was compared to the Die Vlakte weather station. From the regression equations obtained, the missing data for 2004 and 2005 was determined for the entire reserve ($y = 0.3794x + 65.923$; $R^2 = 0.661$), Sanbona North ($y = 0.4124x - 10.287$; $R^2 = 0.6139$), Sanbona South ($y = 0.3464x + 142.13$; $R^2 = 0.5547$) and for summer ($y = 0.51x + 6.2405$; $R^2 = 0.7731$) and winter totals ($y = 0.1891x + 31.105$; $R^2 = 0.3135$) for Sanbona North, as well as summer ($y = 0.4452x + 38.558$; $R^2 = 0.8882$) and winter ($y = 0.4306x + 57.892$; $R^2 = 0.4714$) totals for Sanbona South (Appendix

E). This annual rainfall data is from October to the following year September to coordinate with the time of the surveys. The winter regression equations were not significant and were not used. Instead, the winter rainfall was calculated by subtracting the summer rainfall from the reserve total for each area.

Seasonal and annual totals were highly variable. The long-term average rainfall from October 2003 to September 2015 was 248 mm for the reserve (Figure 5.22). Sanbona South receives primarily winter rainfall and exhibits a higher annual rainfall of 308 mm (Figure 5.23), while the mean annual rainfall in Sanbona North is 191 mm, and rainfall peaks in the spring and summer months (Figure 5.24). The annual rainfall varied approximately two-fold from 221 to 431 mm rain in Sanbona South and approximately five-fold from 72 to 368 mm rain in Sanbona North. The highest recorded annual total was 400 mm for the period October 2013 to September 2014, while Sanbona South registering 431 mm and Sanbona North 368 mm.

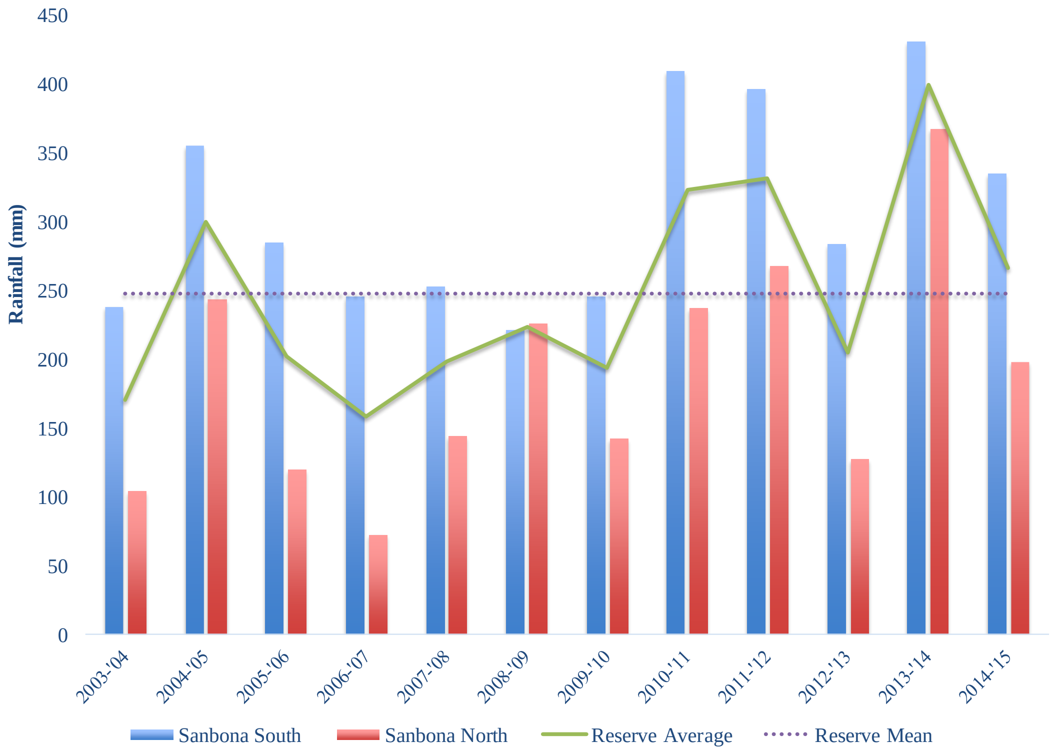


Figure 5.22. Average and mean annual rainfall data for the reserve as well as annual rainfall for Sanbona South and Sanbona North from October 2003 to September 2015.

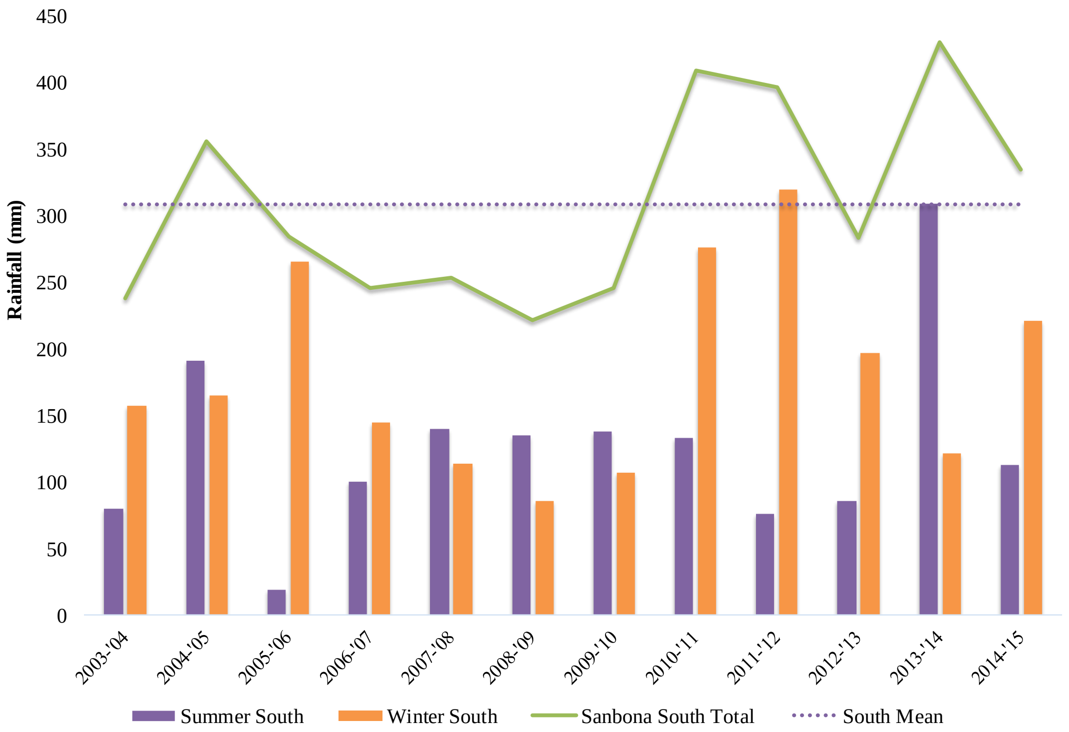


Figure 5.23. Annual rainfall data for Sanbona South, from October 2003 to September 2015, indicating that rainfall is prevalent in winter.

Figure 5.24. Annual rainfall data for Sanbona North, from October 2003 to September 2015.

5.4. Stocking rates

Following the removal of domestic livestock from Sanbona, indigenous herbivores and predators were introduced to the reserve in 2002 and kept low to allow for the vegetation to recover. In 2008 additional animals were introduced to enhance the tourism activities that sustain the reserve, creating a rapid increase in stocking rates (Figure 5.25). Since 2008, the number of Large Animal Units (LAU) has been influenced by the natural fluctuations in births and deaths and by purchases of additional game such as springbuck and red hartebeest. This practice of re-stocking is required from time to time as the predation rates on these species are particularly high.

Certain animal species present on Sanbona such as duiker, steenbok, klipspringer and giraffe either have such a small mean body mass or their numbers are so low that they have a negligible impact on the LAU. These species are therefore not illustrated as individual species on the graph, but are considered in the total LAU. At the outset of the monitoring programme the LAU was still low at 472 LAU, but in 2009 it had increased almost 170 %. Since the large number of introductions in 2008 and 2009, the average LAU value recorded by the game censuses has remained fairly constant. The mean for the period from 2008 to 2015 is 1124 LAU which reflects an average stocking rate of 48 ha/LAU for the 54 000 hectare reserve. This is over the recommended agricultural rate for Renosterveld (72 ha/LAU) but slightly under the recommended rate for Succulent Karoo vegetation on Sanbona (40 ha/LAU).

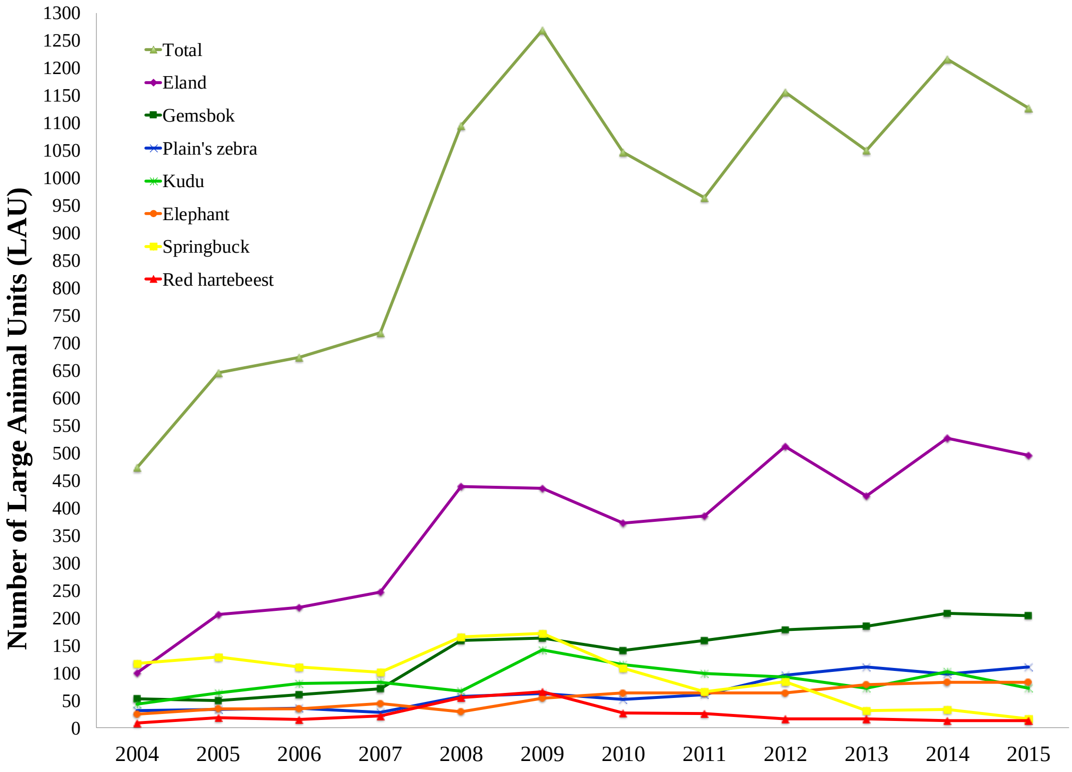


Figure 5.25. Stocking rates, expressed in Large Animal Units (LAU) on Sanbona from 2004 – 2015, showing the increase after large amounts of introductions in 2008/9, where LAU is calculated by multiplying a LAU equivalent for each species by the total number of animals for that species per year.

5.5. Areas of preference

Using three consecutive years of aerial game census information the type of animal, location and number are plotted where they were seen and this produced a map of area preference (Figure 5.26). It is clear that the springbuck prefer the open terrain typical of the WLK and LKQV, while klipspringer are found on the mountainous areas and not often near the plots. Zebras and kudu tend to spend more time in the riverine areas, for the availability of their preferred grass and cover respectively and zebra were not seen near Aeolian Sand plots or plots in the LKQV. Gemsbok and eland are not confined to specific areas and show a versatile usage of all habitat types and could have an impact on most vegetation communities.

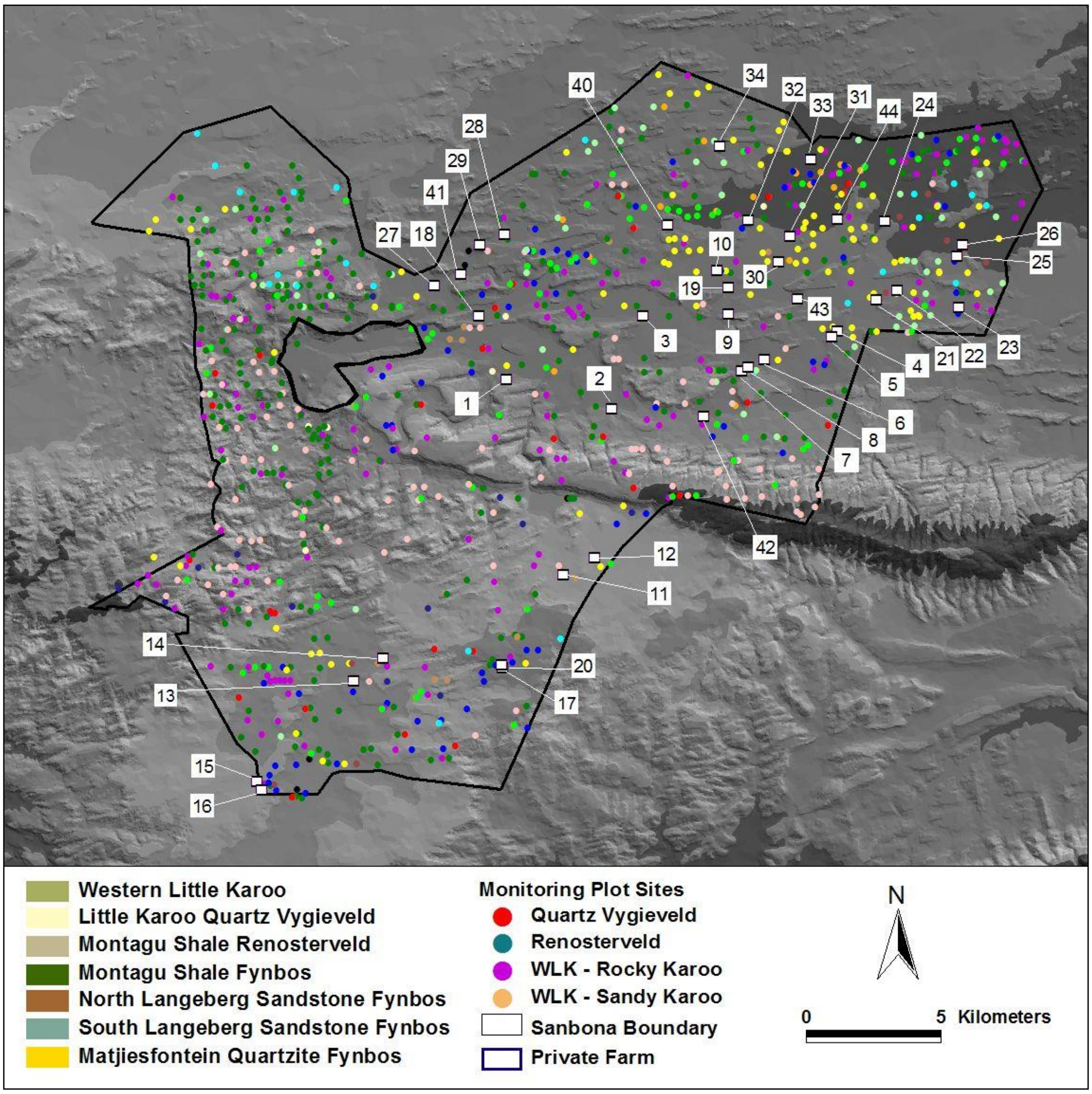


Figure 5.26. Map of animal census records for 2014-2016 on Sanbona indicating preferred areas of different species, with plots indicated that are discussed in text.

Figure 5.27 shows the density of animals in their preferred areas. It is clear from this figure that there is a higher density of animals along the river lines and large bodies of water and the density decreases away from permanent water and towards mountainous regions. The plots appear to be distributed evenly between areas of high density and low density areas. From these figures, it is evident that certain plots may be affected more by a particular herbivore species than others due to the animals' preferred area of utilisation. These maps can be used to assist with the interpretation of possible impact on specific plots. Currently it is just a small glimpse in time but as additional years of data are added this information will become critical for further interpretation.

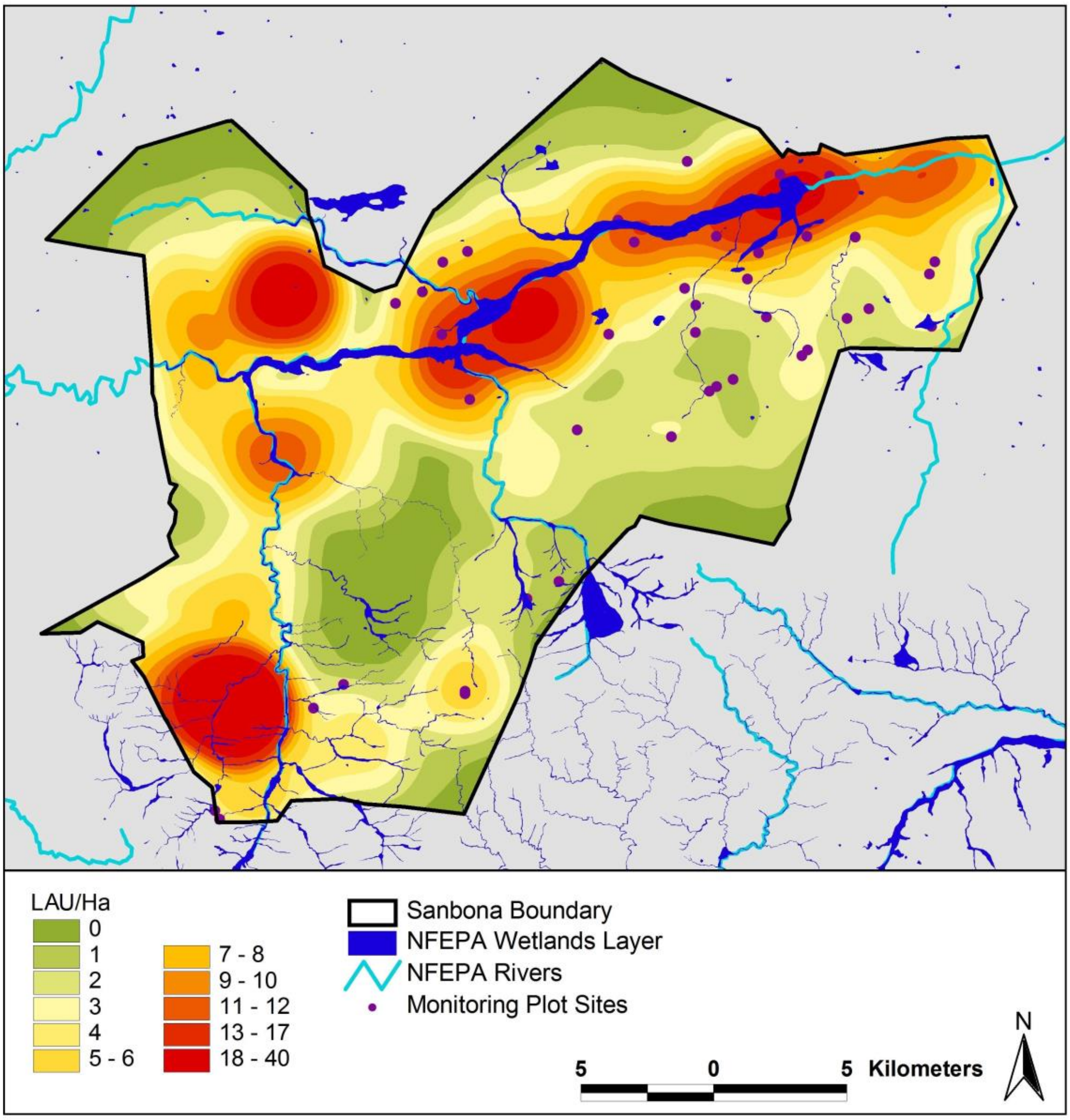


Figure 5.27. Map of animal census records of Sanbona for the period 2014-2016 showing the combined density of animals, indicating areas of potential higher impact.

5.6. Changes to the individual plots

For simplicity, characterising change according to different communities is sufficient to understand general trends however with the purpose of gaining the most insight so as to identifying particular thresholds of potential concern, it is vital to be able to identify specific areas within the vegetation communities that may indicate a pattern not following the general trend for the community. This would go unnoticed if individual plots were not examined as well.

There was no definite pattern among the Rocky and Sandy Karoo plots of the WLK, with some moving in the same direction while others oscillated around a similar position (Figure 5.28; Appendix C). Only one plot, plot 33, had treatments that were definitely experiencing different trajectories causing them to diverge over time (Figure 5.28b). When the percentage cover for these individual plots was examined, of the 23 plots in the WLK, more than 55% showed a significant increase in cover for both treatments (Appendix F). The grazed plot of eight of the pairs (Open plot: 1, 5, 18, 29, 31, 40, 43, 44) did not increase significantly while only two of these plots showed a decline in cover (plot 33 and 41). These plots are all within high animal density areas. It is apparent that the open plot 33 had a significant decrease ($R^2 = 0.6116$, $p<0.01$) while the exclosure significantly increased ($R^2 = 0.8241$, $p<0.0001$) (Figure 5.29a). This plot is in the Gannaveld and the most common species is the unpalatable *Pteronia pallens* which stayed constant while *Hereroa odorata*, *Salsola glabrescens* and *Ruschia muricata* decreased in cover. Although there are very few palatable plants species available, eland, zebra and springbuck prefer this area. Plot 33 is situated in a high-density area (Figure 5.26 and Figure 5.27). This open area is most probably preferred because of predator avoidance as the predators need cover and utilise the river line to hunt in and so these exposed areas offer a form of protection to the prey species. This results in trampling rather than overgrazing causing the divergence. Plot 41, is situated in the Aeolian Sands on the edge of a high-density area (Figure 5.26 and Figure 5.27) and is a preferred area of eland and gemsbok. The decrease in cover is not significant ($R^2 = 0.1683$, $p>0.1$) but attributed to the decrease in palatable *Stipagrostis obtusa* indicating possible overutilisation of this area (Figure 5.29b).

The treatments within the plots of the LKQV as well as between the plots has no specific pattern. In a few plots the treatments are following similar patterns indicating that there is very little difference in the vegetation composition to start and both treatments are changing over time but not converging, subsequently the floristic composition remains different (Figure 5.28d & e). Other plots jump all over the ordination space but stay together (Figure 5.28f) which indicates a comparable floristic composition that is responding similarly to influences over time. When cover was examined, the majority of the plots (seven of eight) increased significantly in cover in both treatments (Appendix F). Whereas in plot 30, there was almost no change in cover in the grazed plot (Figure 5.30). This plot is situated in an area with a high density of springbuck (Figure 5.26). *Gibbaeum heathii, Psilocaulon simile* and *Hypertelis salsaloides* increased in the exclosure. *H. salsaloides* can often be heavily browsed by game (Vlok & Vlok, 2015), while *P. simile* and *G. heathii* may not be palatable but their flowers may be eaten (florivory) in the grazed plot and so the plant seed bank is not replaced. The plants seem to be persistent in numbers in the open plot with a small increase in unpalatable *Pteronia pallens* and *Malephora lutea. Pteronia pallens* is an indicator of disturbance by overgrazing or trampling (Vlok & Vlok, 2015) and thus the slight increase of *P. pallens* but lack of increase of other species on the grazed plot, indicates overutilisation of the area around plot 30.

The plots in the MSR (including the OL) were more similar to each other as is reflected in the location of exclosure and open plots closer together in ordination space compared to LKQV and WLK (Figure 5.28g & h). Of the eight plots, half increased significantly in cover for both treatments (Appendix F). Plot 20, the open plot did not increase significantly (R^2 = 0.1801, p>0.1) (Figure 5.31a). The difference in the response between the treatments is the increase in the most dominant plants for the area in the exclosure plot such as *Elytropappus rhinocerotis, Felicia filifolia, Selago geniculata, Helichrysum ericaefolium* and *Pteronia membranacea*. Plot 20 is located in a transformed land, in an area that is highly utilised by eland, gemsbok, zebra and springbuck (Figure 5.26 and Figure 5.27). It provides a relatively open area, which has different plant types that are often preferred by animals. Additionally, it is in the proximity of the only water point in the area. This may influence the recovery period. The MSR plot in close proximity (less than 200m) to plot 20 is not affected in the same way.

The exclosure of plot 16 did not increase in cover significantly (R^2 = 0.3141, p<0.1), while the open plot did increase (R^2 = 0.7733, p<0.001) (Figure 5.31b). The open plot occurs in an area with a high density of utilisation mostly by eland, gemsbok and zebra (Figure 5.26 and Figure 5.27). Although there was an increase in palatable *Felicia filifolia* in the grazed plot it was not at the same rate as the unpalatable dominant species *Pteronia paniculata*, *Elytropappus rhinocerotis* and *Eriocephalus africanus*. This indicates that a grazing effect is causing the palatable species to be outcompeted in the open plot by unpalatable species.

Plot 15 is situated near plot 16 and therefore has the same herbivore impact. However, it is transformed land and has a different floristic composition. Neither treatment increased in cover significantly (Figure 5.31c), but the exclosure (R^2 = 0.3058, $p<0.1$) increased more than the open plot (R^2 = 0.0383, $p>0.1$). This difference can be attributed to the higher presence of palatable forbs in the exclosure such as *Atriplex semibaccata, Gazania spp., Lotononis spp*., as well as *Medicago spp*., and a low evergreen shrub *Indigofera sessilifolia* which would be grazed in the open plot.

Plot 11 was the only grazed plot which experienced a decrease in cover within the MSR vegetation community. The increase in the exclosure is attributed to significant increases in species such as the palatable *Pentzia incana, Crassula subaphylla, Eriocephalus ericoides* and unpalatable *Pteronia incana*, while the open plot had a small increase in unpalatable *Eriocephalus africana,* and *Elytropappus rhinocerotis*. Both plots have had a decrease in *Drosanthemum delicatulum* and *Galenia africana.* This pattern suggests that the there is an increase in palatable species in the exclosure while the open plot they had no opportunity to establish. Therefore, unpalatable species are being replaced by different unpalatable plants. Although it was not indicated to be in an area of high density of utilisation nor for which species utilise this area (Figure 5.26 and Figure 5.27), this plot is adjacent to a dam which, when it contains water is well utilised by springbuck, eland, zebra, gemsbok and even hippo. The impact was obvious in the difference in cover between treatments (Figure 5.31d) but was also noticeable in the field. Unlike the previous examples, the map has not been informative in this instance as it is just one point in time and the dam possibly did not have water in when the aerial surveys were conducted.

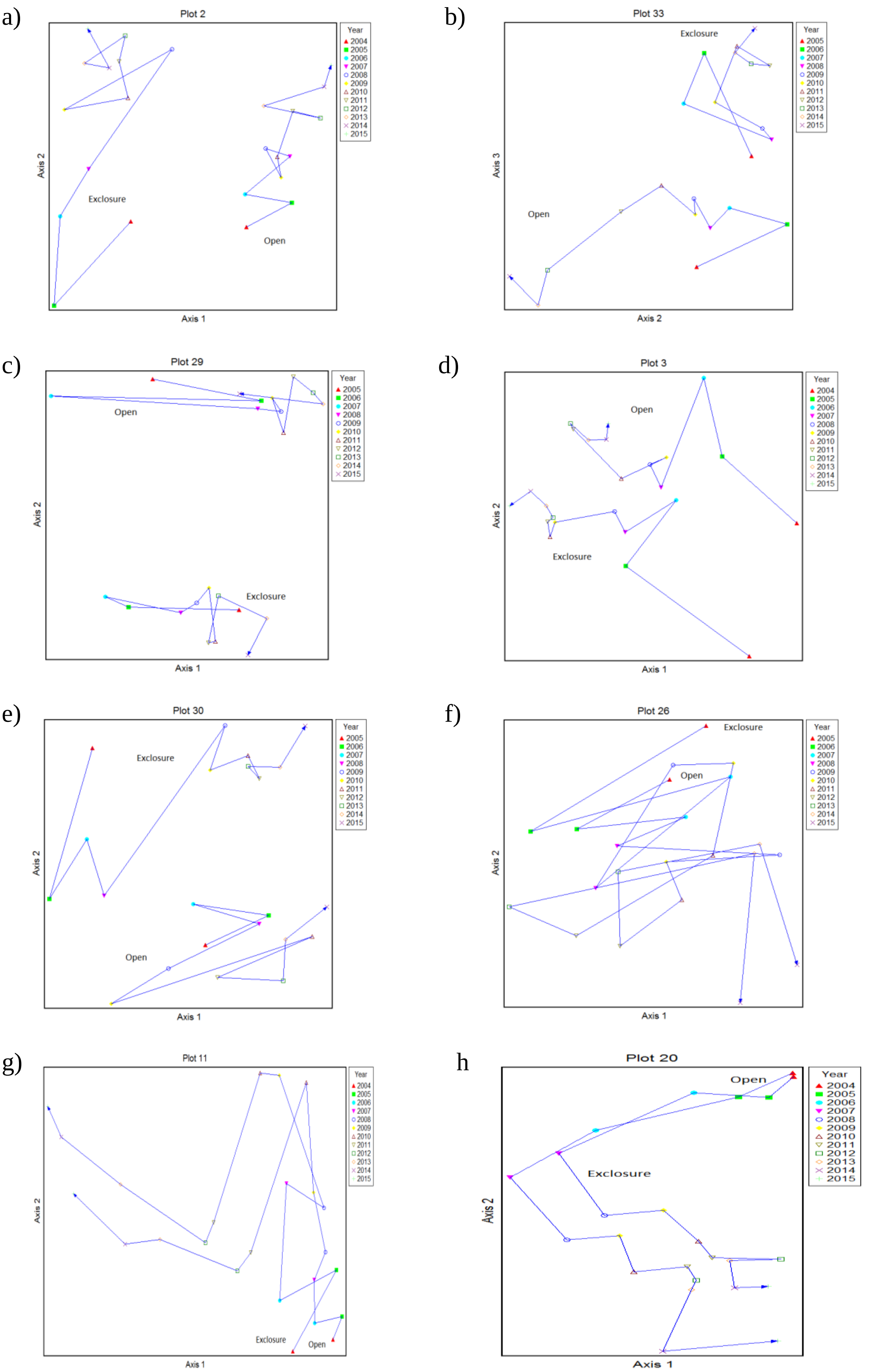


Figure 5.28. NMS ordinations of individual plots a) Plot 2, b) Plot 33, c) Plot 29 d) Plot 3, e) Plot 30 and f) Plot 26 g) Plot 11 h) Plot 20

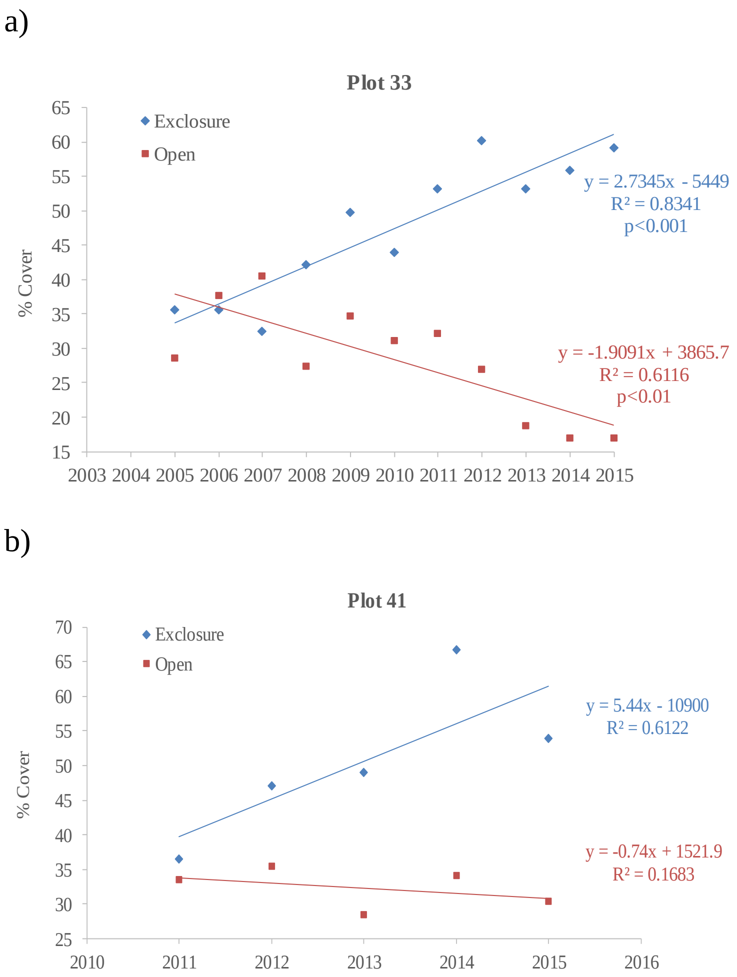


Figure 5.29. Regressions of percent cover vs time of a) plot 33 and b) plot 41 showing the decrease in cover in both open plots.

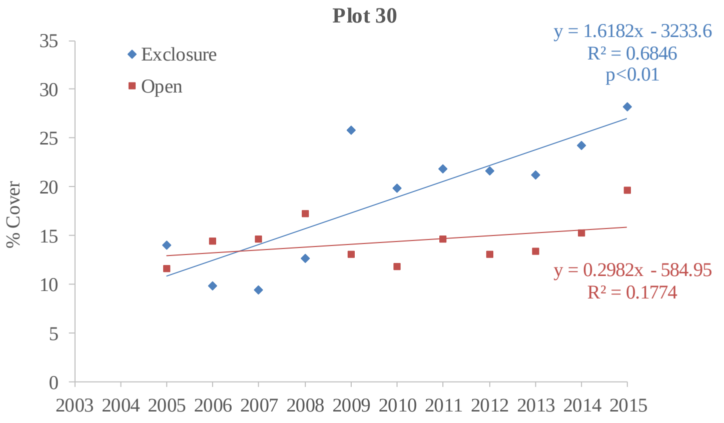


Figure 5.30. Regression of percent cover vs time of plot 30, the only plot in the Quartz Vygieveld that did not experience a significant increase in both treatments.

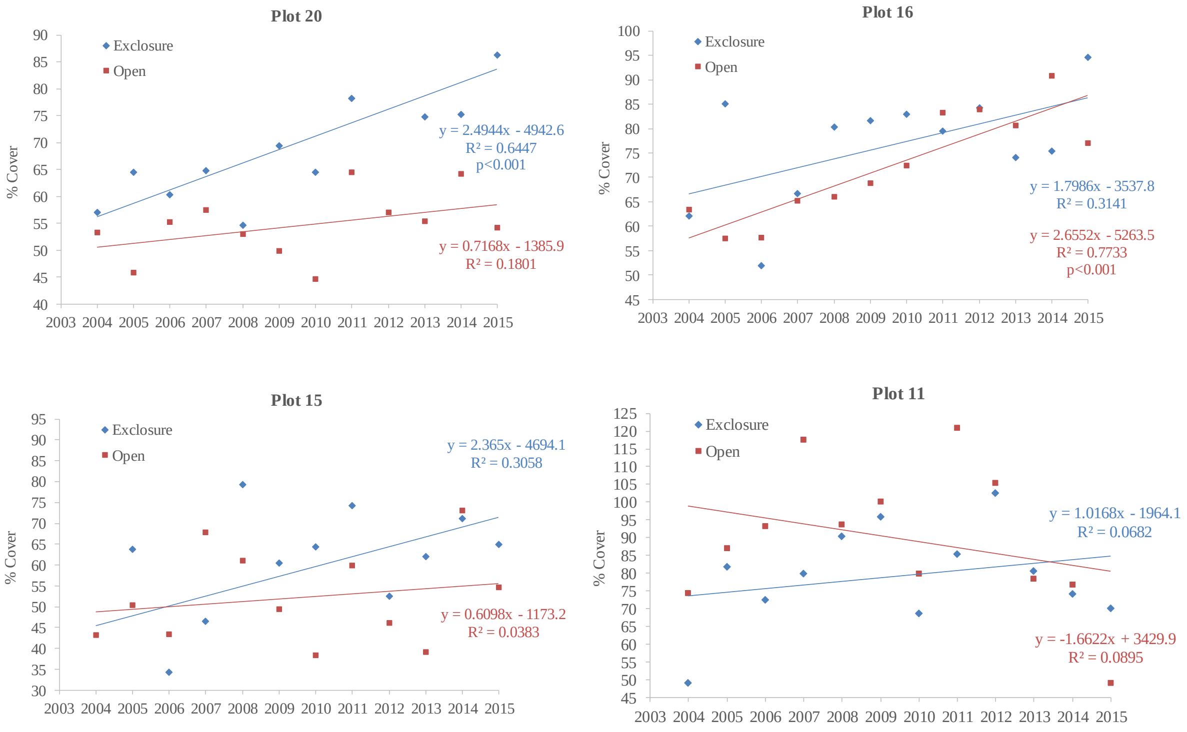


Figure 5.31. Regression of percentage cover versus time for individual plots in the Montagu Shale Renosterveld, a) Plot 20, b) plot 16, c) plot 15 and d) plot 11, showing different responses, with only one, plot 11 experiencing a decrease in cover in the grazed plot.

5.7. Rainfall and stocking rate as an influence on vegetation change

The mixed model for the open plots indicated that the primary driver of vegetation in these plots was grazing pressure and LAU was highly correlated with community change over time. Rainfall did not significantly contribute to the model, indicating that the effects of grazing pressure were dominant and masked any effects of rainfall (Table 5.3). For the exclosure plots, rainfall was observed to be significantly correlated with community change, indicating that rainfall was the primary driver of change when no grazing is present (Table 5.3). The overall performance of the model was however lower than the model for the open plots, indicating that the response in the exclosures was more variable and rainfall was able to account for less of the variation than grazing pressure.

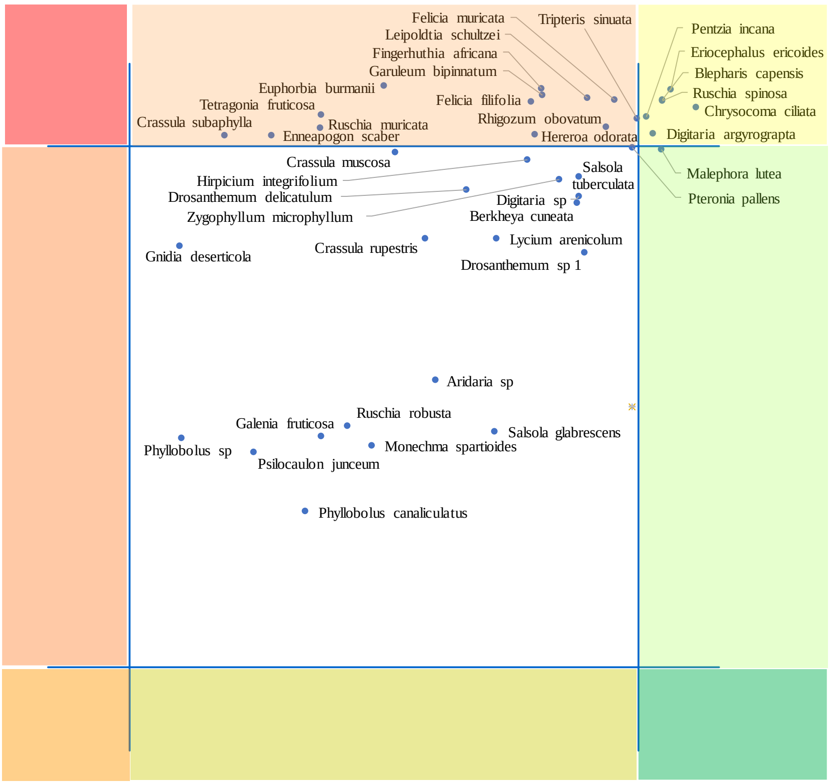
Table 5.3. Linear mixed-effects model for the difference in community composition over time, where rainfall (mm) and LAU (stocking rate) are compared to the BC dissimilarity measure. The two treatments were examined separately because the stocking rate effect is present only in the open treatment. Significance is indicated as P<0.000 = ***.

	Open (Grazed) Plot					**Exclosure (Ungrazed) Plot**				
	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**	**Sig**	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**	**Sig**
(Intercept)	37.510	3.578	10.48	< 2.0e-16	***	31.260	2.721	11.491	< 2.0e-16	***
GrpGrp2	1.43e-13	4.071	0.000	1		-5.31e-14	3.361	0.000	1	
GrpGrp3	-2.290	4.071	-0.562	0.57416		-2.697	3.361	-0.802	0.42284	
GrpGrp4	-0.276	4.071	-0.068	0.94592		-0.722	3.361	-0.215	0.83009	
Rainfall	0.009	0.007	1.31	0.19111		-0.021	0.005	-3.822	0.00016	***
LAU	-0.009	0.002	-4.173	3.81e-05	***					
Residual standard error:	9.548 on 344 degrees of freedom					7.883 on 345 degrees of freedom				
Multiple R-squared:	0.5127					0.389				
Adjusted R-squared:	0.4574					0.3217				
F-statistic:	9.28 on 39 and 344 DF					5.781 on 38 and 345 DF				
p value:	< 2.2e-16					< 2.2e-16				

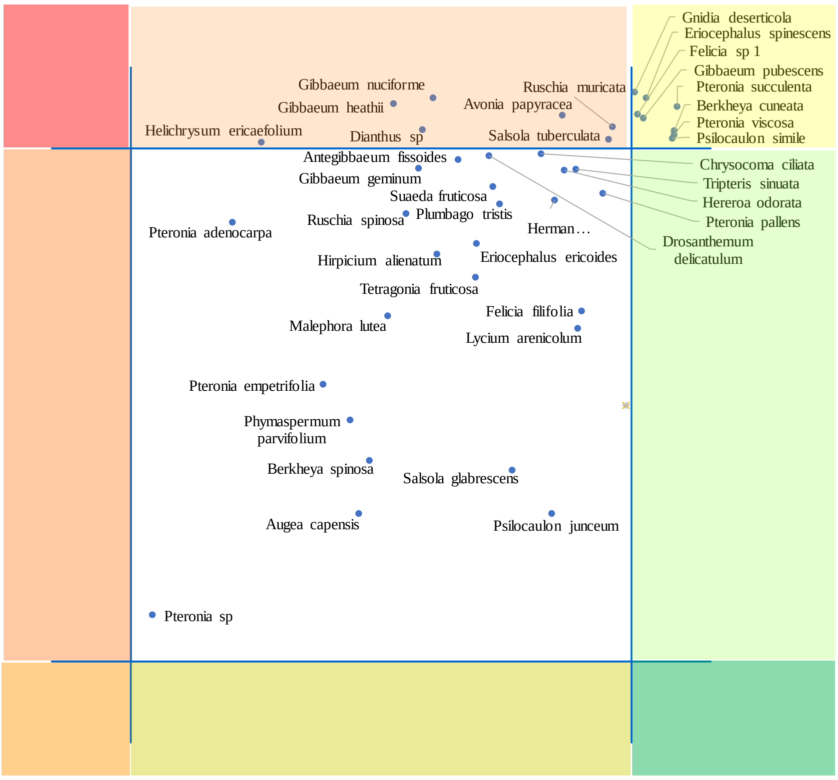
5.8. Indicator species

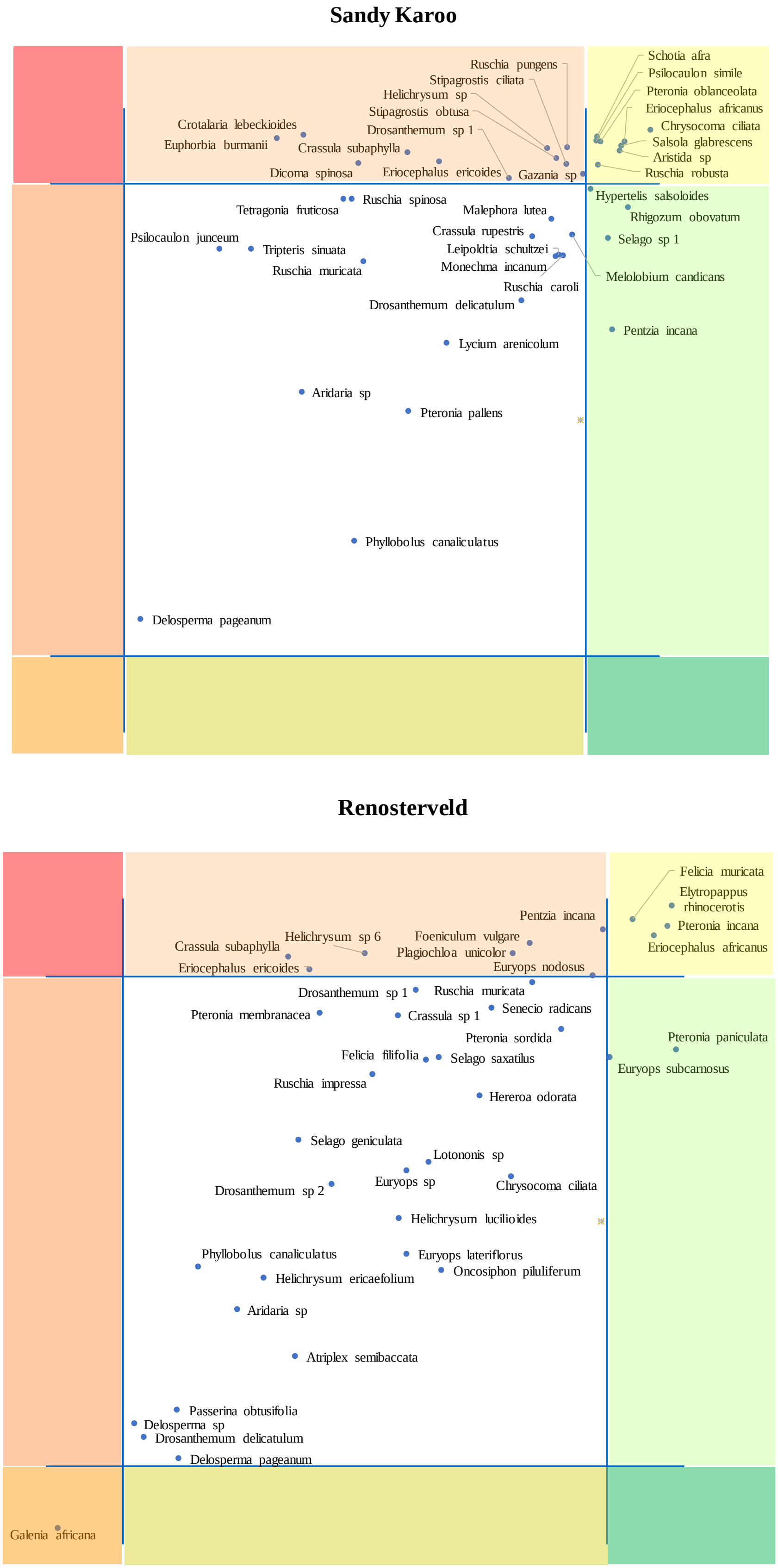
The indicators were chosen on the criteria that the species form a large proportion of the cover in each vegetation community, include a suite of unpalatable and palatable species, and are easy to recognise. The most dominant species in each vegetation community are listed in Table 5.1. This also demonstrates how diverse the communities are and supports the idea that each community requires its own indicator species. Using the framework that was developed, the 40 most dominant species for each vegetation community were graphed and indicators chosen according to where they were located on the scatter plot (Figure 5.32). Only the species that fall into the boundary areas are listed in Table 5.4 as these were the only species to show a significant response over time. From this list, the indicators chosen are indicated with an asterisk (*). The reason the specific indictors were chosen is described below.

Rocky Karoo



Quartz Vygieveld




Sandy Karoo

Renosterveld

Figure 5.32 Indicator species determination, where the most dominant species where graphed according to a correlation of species over time for each vegetation community.

Table 5.4. List of all the potential indicator species for the different vegetation communities, according to the position in the framework (🟧 = favours protection, 🟨 = improvement in condition, 🟩 = disturbance tolerant and 🟡 = indicator of change) and where green text indicates a palatable species, red text indicates an unpalatable species and orange text is less palatable with the chosen indicators per group indicated by a *.

Rocky Karoo	Quartz Vygieveld	Sandy Karoo	Renosterveld
Enneapogon scaber	*Salsola tuberculata**	*Stipagrostis obtusa**	*Plagiochloa unicolor*
*Tetragonia fruticosa**	*Dianthus sp*	*Stipagrostis ciliata*	*Pentzia incana*
Fingerhuthia africana	*Helichrysum ericaefolium*	*Gazania sp*	*Crassula subaphylla**
Garuleum bipinnatum	*Gibbaeum nuciforme**	*Crotalaria lebeckioides*	*Eriocephalus ericoides**
Felicia filifolia	*Gibbaeum heathii*	*Crassula subaphylla**	*Helichrysum sp 6*
Felicia muricata	*Avonia papyracea*	*Eriocephalus ericoides**	*Foeniculum vulgare*
Rhigozum obovatum	*Ruschia muricata*	*Euphorbia burmanii*	*Euryops nodosus**
*Tripteris sinuata**	*Gnidia deserticola*	*Helichrysum sp*	*Felicia muricata**
*Crassula subaphylla**	*Eriocephalus spinescens*	*Dicoma spinosa**	*Eriocephalus africanus*
*Hereroa spp.**	*Pteronia succulenta**	*Ruschia pungens*	*Elytropappus rhinocerotis**
Leipoldtia schultzei	*Berkheya cuneata**	*Drosanthemum sp 1*	*Pteronia incana*
Ruschia muricata	*Pteronia viscosa*	*Schotia afra*	*Pteronia paniculata**
Euphorbia burmanii	*Psilocaulon simile*	*Pteronia oblanceolata*	*Euryops subcarnosus*
Pentzia incana	*Gibbaeum pubescens**	*Eriocephalus africanus*	*Galenia africana**
Digitaria argyrograpta		*Aristida sp*	
*Eriocephalus ericoides**		*Salsola glabrescens**	
Blepharis capensis		*Chrysocoma ciliata*	
*Ruschia spinosa**		*Psilocaulon simile*	
Chrysocoma ciliata		*Ruschia robusta*	
Malephora lutea		*Hypertelis salsoloides*	
		Rhigozum obovatum	
		*Pentzia incana**	
		Selago sp 1	

According to Vlok and Vlok (2015), none of the species of Crassula are browsed by game. Fenwick (2008), however, found that *Crassula subaphylla* was favoured in the diet of eland, gemsbok and ostrich on Sanbona Wildlife Reserve. It is present in all four communities and can be a useful indicator across the reserve, although its abundance was very low in the Quartz Vygieveld. *C. subaphylla* significantly increased in the exclosure plots (Rocky Karoo: $R^2 = 0.6239$, p<0.01; Quartz Vygieveld: $R^2 = 0.6803$,

$p<0.001$; Sandy Karoo: $R^2 = 0.7361$, $p<0.001$; Renosterveld: $R^2 = 0.6732$, $p<0.01$). In the grazed plots, there was a decrease or only a slight increase which indicates that grazing effects are noticeable. *C. subaphylla* was present in the exclosure plots in the Quartz Vygieveld but has not had an opportunity to establish within the plots exposed to grazing. If it managed to establish, even though the numbers are low, it would indicate an improvement or low grazing pressure. It appears that *C. subaphylla* responds quickly to increases in grazing pressure and thus it is a good indicator of grazing or disturbance.

Similarly, the palatable *Tetragonia fruticosa*, had already shown a grazing effect in the Rocky Karoo where it stayed relatively constant in the open plots. In the exclosure plots on the other hand this species increased significantly over time ($R^2 = 0.7236$, $p<0.001$).

Tripteris sinuata is a highly palatable drought deciduous shrub and according to Vlok and Vlok (2015) an abundance of *T. sinuata* indicates healthy veld. It is a good indicator for the Rocky Karoo as it had a high and increasing abundance in both grazed and non-grazed plots (Exclosure: $R^2 = 0.7028$, $p<0.001$; Open: $R^2 = 0.5698$, $p<0.01$). It needs to be tested within the Quartz Vygieveld, which increased in both plots, although not significantly, as with the Sandy Karoo. If *T. sinuata* increases or stays constant it is an indicator of the good range conditions.

Eriocephalus ericoides is less palatable but has been recorded within the diet of eland (Watson & Owen-Smith, 2000). It is present in all the communities except the Quartz Vygieveld and therefore can also be used to test whether a broad indicator species could be viable. *E. ericoides* increased in the Rocky Karoo (Exclosure: $R^2 = 0.8527$, $p<0.001$; Open: $R^2 = 0.7315$, $p<0.001$), Sandy Karoo (only significant in exclosure ($R^2 = 0.6902$, $p<0.001$)) and in the Renosterveld exclosures ($R^2 = 0.6119$, $p<0.01$). It decreased in the open plots of the Renosterveld. This could indicate that there are less palatable species available in the Renosterveld and *E. ericoides* therefore forms part of a herbivore's diet because there is less choice. *E. ericoides* may have a slower response to grazing pressure but because it is a long-lived species could be a useful indicator of long-term changes rather than short-term change.

Hereroa is unpalatable. High densities of *Hereroa* are indicative of past disturbance or severe overgrazing (Vlok & Vlok, 2015). The numbers for *Hereroa* increased in the Rocky Karoo, Quartz Vygieveld and Renosterveld. However, it only increased significantly in the exclosure of the Rocky Karoo (Exclosure: $R^2 = 0.6283$, $p<0.01$). *Hereroa*, may have increased because of an increase in seed production. Animals may have eaten the flowers in the past, preventing the plant from being able to produce seed. Evidence from individual plots, however, shows that *Hereroa* decreased significantly in certain plots in response to trampling and disturbance. It could also be a result of an increase in florivory due to a lack of palatable species and thus a decrease in seed production. Because it is a short-lived plant, it would also recolonise bare ground after droughts if other shrubs die off.

Ruschia spinosa, is also unpalatable and increased significantly in both treatments (Exclosure: $R^2 = 0.7961$, $p<0.001$; Open: $R^2 = 0.691$, $p<0.001$). *Ruschia spinosa* may respond to change in management practise.

Within the Quartz Vygieveld the indicators chosen cannot be used in other vegetation communities. They are very specific to where they grow. *Salsola tuberculata*, and *Pteronia succulenta*, according to Vlok and Vlok (2015), are very palatable and their presence is indicative of well-managed veld. *Salsola tuberculata* experienced an increase in both treatments, although more slowly in the open plot (Exclosure: $R^2 = 0.6172$, $p<0.01$; Open: $R^2 = 0.4773$, $p<0.02$) whereas *Pteronia succulenta* strongly increased in both treatments (Exclosure: $R^2 = 0.7789$, $p<0.001$; Open: $R^2 = 0.8053$, $p<0.001$). *Berkheya cuneata* and *Gibbaeum nuciforme* are Little Karoo endemics and *G. nuciforme* is a biologically important taxon (Mucina, et al., 2006). *Berkheya cuneata* is also indicative of sound veld management (Mucina, et al., 2006). A more noticeable indicator would be *Gibbaeum pubescens*, as it is easy to recognise and is abundant. To date, *G. pubescens* increased significantly in both treatments (Exclosure: $R^2 = 0.7205$, $p<0.001$; Open: $R^2 = 0.6344$, $p<0.01$). The succulents may be more important in determining levels of disturbance rather than herbivory since most are unpalatable.

Within the Sandy Karoo, the palatable grass *Stipagrostis obtusa* increased in both treatments. This is a sign of recovery as the plots were overgrazed when they were established (Exclosure: $R^2 = 0.7051$, $p<0.001$; Open: $R^2 = 0.4394$, $p<0.02$). However, it has not increased as much in the open plots which suggests that grazing is still affecting it. *Stipagrostis obtusa* should be used as an indicator since it will show a decreasing trend as soon as there is evidence of overgrazing in those particular plots within the Sandy Karoo of the WLK. *Salsola glabrescens* is less palatable. However, it increased significantly in both treatments (Exclosure: $R^2 = 0.7768$, $p<0.001$; Open: $R^2 = 0.7666$, $p<0.001$). If *S. glabrescens* decreases, then it is a possible indicator of a lack of other palatable species being available.

The cover within Renosterveld plots increased. This is reflected in the increase in the abundance of both palatable species such as *Pentzia incana* (Exclosure: $R^2 = 0.823$, $p<0.001$; Open: $R^2 = 0.5685$, $p<0.01$), and unpalatable species such as *Elytropappus rhinocerotis* (Exclosure: $R^2 = 0.9601$, $p<0.001$; Open: $R^2 = 0.5428$, $p<0.01$) and *Euryops nodosus* (Exclosure: $R^2 = 0.5818$, $p<0.01$; Open: $R^2 = 0.4972$, $p<0.02$). *Pteronia paniculata* only increased in the open plots (Open: $R^2 = 0.9499$, $p<0.001$). This could be an indication that some of the Old Lands are still in recovery as grazing has not affected those species. It is important to have a variety of indicators. *Galenia africana* is a pioneer plant and its seedlings are weak competitors (Todd & Hoffman, 2009). This is visible as it significantly decreased in abundance in both treatments over time while most other species increased (Exclosure: $R^2 = 0.9265$, $p<0.001$; Open: $R^2 = 0.9036$, $p<0.001$). Because *Galenia africana* increases under highly disturbed conditions it is important to have as an indicator.

6. DISCUSSION

6.1. Plant communities

The classification and ordination of the floristic data resulted in four distinct vegetation communities, three of which correspond with vegetation types identified in the National Vegetation Map of Mucina and Rutherford (2006). However, the Western Little Karoo vegetation type, consisted of two well-supported communities with the Rocky Karoo community associated with the hills and the Sandy Karoo community associated with the adjacent plains. This differentiation has also been recognised elsewhere (Vlok et al. 2005) but is not captured in the National Vegetation Map on account of the coarse mapping scale of the Vegetation Map. However, the results of this study indicate that mapping these units separately may be warranted in the future. Regardless of how this is treated at the national scale, for the purposes of management at Sanbona, this differentiation is important especially as herbivore density as well as the impact of herbivores on these two communities is not likely to be the same.

The overall drivers of plant community differentiation at Sanbona are generally substrate conditions, with stone, salinity and soil-texture coming out as important drivers of community composition. Similar results were found by Schmiedel and Mucina (2006) as well as Schmiedel et al. (2015) where differences in soil properties changed vegetation patterns. There were also some significant differences in growth form composition between the plant communities identified. The Little Karoo Quartz Vygieveld (LKQV) in particular, having a high abundance of dwarf succulents compared to the other communities while the Sandy Karoo had a high abundance of grasses compared to the other communities which were all dominated by woody shrubs.

6.2. Vegetation change over time

The results of this study show that there was an increase in cover, abundance, and species richness indicating a gradual improvement in plots protected from herbivory as well as plots which had been grazed. As was found by Hoffman et al. (2009), the patterns in the grazed and ungrazed plots were similar and they were not able to detect a change at Sanbona for the first five years of the study. However, the treatments diverged thereafter, with an increase in grazing pressure, and changes in the vegetation in grazed and ungrazed plots were then detected. These findings are similar to the study in the Karoo National Park by Kraaij and Milton (2006), where fenced plots changed more rapidly than open plots over 10 years while the overall condition of the rangeland improved under both treatments. Our results differ in one important aspect from those obtained for the Karoo National Park in that Kraai and Milton (2006) report a reduction in vegetation cover over time while at Sanbona vegetation cover increased over the study period. Even though there was an indication that an impact of grazing exists on Sanbona, as there were differences between the treatments, across the board the reserve is in a better condition than before. The change from stock farming to game farming and subsequent reduced stocking rate had a positive impact on the recovery of the rangeland even with the variable rainfall experienced over the study period.

Yeaton and Esler (1990) noted that the detection of changes in karoo shrub assemblages is difficult due to the very slow rate of population turnover. This is due to the low and variable rainfall. The findings from this study support this view since trends are only starting to appear after 12 years of annual measurements undertaken at Sanbona. With more time, the directionality of the initial trends observed will be more clearly established. Schmiedel et al. (2012) found that the total annual rainfall only explained part of the dynamics in populations, indicating that the timing and amount of single rainfall events may be critical as well. Arid and semi-arid regions with a high inter-annual variability of rainfall require annual monitoring in order to understand the response of plant populations to various driving factors, particularly climate and land use (Jurgens, et al., 2012). Schmiedel et al. (2012) reiterated that long-term monitoring is important to fully understand the potential impacts of climatic change on the vegetation of the Succulent Karoo.

The only significant declines in growth forms were found in low and medium shrub assemblages. The most significant decline in both the grazed and ungrazed plots was that of low leaf succulent shrubs. Burke (1997) found that leaf succulents were more abundant when grazing was excluded. Similarly, Todd and Hoffman (1999) found leaf succulents to be grazing decreasers. Rahlao et al. (2008) support this by stating that leaf succulents are particularly susceptible to grazing impacts and trampling. However, both open and fenced treatments in Sanbona showed similar results, eliminating herbivory or trampling as likely drivers. Instead, it appears that changes in the cover of low leaf succulents appear to be influenced more by rainfall since their responses mimic the oscillations in the rainfall patterns, particularly in terms of the rainfall for Sanbona North.

Cowling et al. (1994) further noted that the Succulent Karoo experiences the occasional drought which can have catastrophic effects on the succulent flora, resulting in up to 90% mortalities in certain species. Similarly, Jurgens et al. (1999) found widespread mortality specifically in leaf succulents after a drought in the Richtersveld. Plants with short lifespans, like leaf succulents, need regular recruitment events. In an area which has relatively reliable winter rainfall, most years result in successful seeding establishment. However, occasional droughts do occur and can result in catastrophic mortality from which populations can take a long time to recover (Jurgens, et al., 1999). The reduction in these short-to medium-lived succulent shrubs seems to correspond to the incident of drought on Sanbona. The changes could also be due to the variations in abundance found in these leaf succulent species such as *Delosperma spp., Phyllobolus spp., Malephora lutea* and *Drosanthemum delicatulum*. Many plants within arid areas experience temporal variation in reproductive success that is largely caused by variability in precipitation (Esler, 1999; Clauss & Venable, 2000; Schmiedel, et al., 2012). Many plants respond by either reducing reproductive success through water limitation or signalling germination with increased water available (Levine, et al., 2008). Mass germination events followed by years of high die-off (Milton, et al., 1999), are common with these species, especially amongst plants that produce many small seeds that have a low probability of establishing (Esler, 1999; Moles & Westoby, 2006). Stem succulents, in particular *Psilocaulon junceum, Tylecodon spp.* and *Euphorbia* *burmanii,* declined in grazed plots, while medium evergreen shrubs such as *Berkheya spinosa, Eriocephalus spp., Euryops spp., Felicia filifolia* and *Pteronia spp.,* declined only in the exclosures. Many of the plants are known to have carbon-based metabolites such as oxalic acid (*Drosanthemum*), mesembrine (*Psilocaulon*) and other alkaloids (*Pteronia pallens*), which make them toxic or unpalatable to mammals (Milton, 1990), thus making grazing an unlikely cause for their decline. Stem succulents are very low in abundance and their decline is more than likely due to a small decrease in numbers resulting from disturbance, leading to a significant reduction overall. Even though there was a decrease in the cover of medium evergreen shrubs in the exclosures, there was an overall increase in cover which could indicate competitive displacement.

Besides the stem succulents, leaf succulents and medium evergreen shrub, there were general increases in cover for all other growth forms in both treatments with the most significant increases in grasses such as *Fingerhuthia africana* and *Stipagrostis obtusa*, low evergreen palatable shrubs such as *Pentzia incana, Felicia muricata* and *Berkheya cuneata* as well as less palatable low evergreen shrubs *Pteronia pallens* and *Pteronia paniculata*. In the ungrazed plots, however, the cover of palatable medium leaf succulents such as *Tetragonia spp*. as well as unpalatable shrubs such as *Drosanthemum bicolor, Ruschia multiflora, Ruschia pungens* and *Ruschia robusta* increased over time. The increase in grass cover could be the best indicator of a decrease in grazing pressure, as well as higher rainfall in the latter years of the study period. Stokes (1994) and Riginos and Hoffman (2003) found that heavy grazing suppressed the reproductive output of succulent shrubs, thereby reducing seed production and the seed bank and lowering the possibility of recruitment of these species (Milton, 1992a). Similarly, Milton (1994) and Todd (2000) found this to be the case for palatable perennial shrubs in the Succulent Karoo. With the change of management and reduction in grazing pressure, the plants were able to produce seed and recruit during the window of low grazing pressure. Novellie and Bezuidenhout (1994) suggested that stones help to preserve grass cover by reducing the accessibility of grass seedlings to large herbivores and by increasing moisture availability by concentrating rainfall run-off around their margins. Under these circumstances, moisture penetrates more deeply in stony soil than when the soil was stone free, which could explain why they are more prominent on the rocky slopes.

All vegetation communities experienced an increase in cover in both grazed and ungrazed plots except for the Sandy Karoo, which experienced a decrease in the plots exposed to grazing. Because of this increase in cover, it seems that, in general, herbivory has not had an adverse effect on vegetation cover of Sanbona. However, there are specific plots where the impacts have been more discernible and are cause for concern. The selective grazing and browsing by herbivores, which greatly reduces or even eliminates palatable species, can increase the competitive advantage of less preferred plant species (Burke, 1997). Such processes appear more noticeable in the plots situated in the areas of high animal density. The LKQV and MSR each had only one plot that decreased in cover, while in the WLK only two of the 23 plots showed a significant decline in the plots subject to herbivory. The majority of the plots increased in cover while about a third of all plots showed little change in cover. This suggests that any negative effects of grazing pressure on vegetation cover is highly localised and large areas are not currently negatively affected.

6.3. Vegetation change in response to rainfall and stocking rate

Patterns of change in cover, abundance, and species richness were similar in grazed and ungrazed plots for the first five years of the study, after which they diverged. The assumption is always that grazing is the cause for changes in population dynamics (Milchunas & Lauenroth, 1993; Todd & Hoffman, 1999; Diaz, et al., 2007), but the availability of water can be the greatest limitation to plant growth and distribution, particularly in semi-arid environments (Desmet & Cowling, 1999).

Large mammalian herbivores not only depend on plant communities for their existence but can cause major changes in plant community composition and structure (Augustine & McNaughton, 1998). Vegetation cover increased in both treatments, but the slope of the increase in the exclosure was significantly different from the grazed plots. This suggests that herbivores had a significant negative impact on the rate of recovery of the vegetation within the reserve. The same pattern was observed in the response of species richness, which for the first five years was similar in grazed and ungrazed treatments and then diverged, with the exclosure continuing to increase across the sample period while the grazed plots increased initially but fluctuated around a point thereafter. The relatively rapid response of the vegetation to the introduction of indigenous herbivores is, however, surprising. The rapid divergence in species richness in exclosures and open plots is best explained by the large number of animals that were introduced which resulted in a 170% increase in the stocking rate at this time. Studies have demonstrated that selective herbivory can either lead to the dominance of unpalatable, chemically defended plant species in communities, or it can even increase the dominance of highly palatable species in the plant communities (Augustine & McNaughton, 1998). An increase in both palatable and unpalatable species was observed which indicates that the grazing effect was not severe. The effect of trampling should also not be eliminated from this change (Snyman, 1998; Riginos & Hoffman, 2003), because of the herding nature of many herbivores or just because of their sheer size alone. The impacts of herbivores can be noted on particular plots, specifically in areas of high animal utilisation.

The total annual rainfall, the seasonal timing of rainfall as well as the efficiency of a single event can have an effect on population dynamics in arid biomes (Schmiedel, et al., 2012). Within-season precipitation patterns are at least as important as precipitation totals in determining seedling growth and survivorship as well as species diversity through their effects on germination and seedling establishment (Schwinning, et al., 2004). Milton (1995a), for example, found that the water availability during the growing season significantly limited growth, flowering and seed production in the Karoo shrubs *Pteronia pallens* and *P. empetrifolia*. Because rainfall has a significant effect on population dynamics, the effect of grazing may be mediated by rainfall. Increasing rainfall may reduce pressure by increasing vegetation biomass in relation to the number of herbivores, thus temporarily masking grazing effects (Milchunas & Lauenroth, 1993; Novellie & Bezuidenhut, 1994). In other words, when rainfall is high, so too is plant productivity. Even though grazing is having an effect it is not always noticeable because of this increased plant productivity. However, if there is a drought, the plant production decreases due to water stress and so grazing can mediate the effects of rainfall and drought. Stokes (1994) summarised this by suggesting that grazing increases the susceptibility of rangeland vegetation to the effects of drought while moisture stress increases the susceptibility of vegetation to the effects of grazing.

The results of the mixed model clearly support the contention that rainfall is the primary driver of the vegetation in the absence of grazing. However, within the open plots, grazing pressure is the dominant driver of community change. Although it is likely that rainfall also has some influence on the open plots, at high grazing pressures, this effect is not apparent and is obscured by the effects of grazing. This is of some concern and suggests that grazing pressures may be too high within many of the plots. However, this is not necessarily indicative of degradation because some recovery of the vegetation is still apparent. It is clear from the results that grazing pressure is retarding the recovery of the vegetation and if the current high stocking rates are maintained, then some degradation of preferred areas is likely to occur. As there is a high degree of spatial variability in animal distribution and associated grazing pressure, information regarding this should be collected on a regular basis to better characterise grazing pressure in the future and provide more detailed input for the model so that the actual stocking rates at which negative effects become apparent can be identified.

O’Connor and Roux (1995) found that the effects of rainfall can mask those of grazing over the short term and that individual species may wax and wane depending on year-to-year rainfall variability. However, over the long term, a small annual response to a particular grazing treatment will be consistent in direction and therefore accumulate to a considerable magnitude over time. This will occur when the effect of herbivory is no longer secondary to rainfall and provides the rationale for continued monitoring. Short-term trends may differ from long-term trajectories which will become increasingly apparent with time.

6.4. Implications for management and conservation

Stocking rates

Animals express habitat preferences and use a landscape in a markedly non-random fashion (Kerley & Landman, 2010). This usually occurs as a result of variation in topography and vegetation structure as well as seasonal variations in forage preferences and water availability (Coughenour, 1991; Bailey, et al., 1996; Dekker, et al., 1996). Topography may also influence the microclimate of a site as a result of its influence on the orientation of the sun or prevailing winds. Different topographies can also be used by ungulates for predator avoidance. In addition, animals change their diet depending on the location and availability of preferred plants in the landscape. For example, because the grass component in the Karoo is dependent on rainfall events, it is unreliable over periods of years and decades. Grazing ungulates in the Karoo, therefore, deal with the variations in available grass by switching from a largely grass diet to a Karroid dwarf shrub diet (Esler, et al., 2006). These animals often need to range over different parts of the landscape in order to find suitable forage. Cape mountain zebra, black wildebeest and red hartebeest are particularly adept in this regard (Esler, et al., 2006). Understanding the spatial and temporal dynamics of landscape use by free-ranging herbivores is critical for ecosystem management (Coughenour, 1991; Bailey, et al., 1996).

Stocking rates should be determined using only areas that are preferred by animals together with the size of available preferred areas. Areas that are not used frequently or at all by herbivores should be excluded from the calculation since their inclusion would serve to increase the impact of animals on preferred areas. These would compare to the key resource areas. Although Sanbona is 54 000 hectares in extent, not all the area is accessible to the animals as the reserve is very mountainous. Physical constraints such as steep slopes may limit access to high resource areas (Adler, et al., 2001; Coughenour, 1991; Bailey, et al., 1996; Cingolani, et al., 2003). The areas or ‘hotspots’ where particular herbivores focus tend to be in the lower lying regions, in particular along the drainage lines and near water points.

Information from the annual census was used to map the animal preference areas and this clearly showed their use of the landscape on Sanbona. Certain species like klipspringer, eland and gemsbok make use of the mountainous terrain. However, the klipspringer are habitat-specific and show high selectivity for rocky habitats (Kerley & Landman, 2010), while eland and gemsbok are more catholic (Radloff, 2008; Van der Walt, et al., 1984) and utilise the entire reserve. Kudu, zebra and red hartebeest tend to prefer the riverine areas which provide cover as well as browsing and grazing material. Kudu preferred cover, while gregarious animals such as springbuck show a strong preference for open areas (Bigalke, 1972; Milton, et al., 1992; Burger, et al., 2000), in particular open areas in the Little Karoo Quartz Vygieveld.

The Western Little Karoo had the highest biomass and the greatest species density of animals. Fortunately, in the most densely populated parts of Sanbona the predator effect has prevented the number of ungulates from increasing exponentially. The difference is noticeable in that part of Sanbona where no large predators occur, and the numbers of eland and gemsbok have increased accordingly. This predator-free area is in the Montagu Shale Renosterveld. This predation factor must be considered carefully when determining the stocking rates, as one section of the reserve requires higher animal numbers to sustain the predators while the other section would need the active management of animal numbers to avoid vegetation degradation (Van Rooyen, et al., 2015). Active management of animals is not always easy as it is costly and the terrain can make the capture and removal of animals difficult.

There is an interaction between rainfall and drought that also affects the stocking rate used for a particular reserve, management unit or vegetation type. When rainfall is above average then the presence of large numbers of animals is not as noticeable. The plants are productive and sufficiently abundant to satiate the grazer’s requirement and thus able to persist under these stocking rates (Westoby, 1974; Noy-Meir, 1981). But once reduced to a low level, in times of drought, key forage species may not be able to persist or re-establish under the same stocking rate (Westoby, 1974; Noy-Meir, 1981). The very quick response of the vegetation to the introduction of the large number of game in 2008 and 2009, which resulted in a 170% increase in the stocking rate, was a clear indicator of a threshold of potential concern. The change in the responses of the exclosure and open plot was enough to raise concern. Although there was still a slow increase in cover and abundance, the vegetation probably does not have a large buffering capacity. A large portion of the vegetation in the Little Karoo is unpalatable and heavy grazing on palatable species very quickly becomes apparent.

Although the composition of the vegetation is currently still mostly dependent on the effect of rainfall, there is clear evidence that herbivory is also having a significant influence. The individual monitoring plots that are found in the areas with high animal densities suggest that the stocking rates should be reduced or at least monitored carefully to check for further negative effects. According to the density map of preferred areas, an area of approximately 40 000 ha should only be considered as potentially suitable habitat available, and stocking densities for the reserve adjusted accordingly.

Indicator species

There is a shortage of information available for the management of private protected areas in the Cape and in particular the Little Karoo. Because of this information deficit, it is difficult for managers to determine the condition of the land easily and decide on thresholds. Determining a number of indicator species would be valuable as they can potentially provide an early forewarning of impending change (Carignan & Villard, 2002). Early warnings provide important additional opportunities to avoid degradation through timely corrective management intervention (Stokes, et al., 2009). A suite of indicators that are spatially and temporally representative of different responses to grazing would be beneficial. Such indicators could be used to interpret short-term responses from short-lived species, moderate responses from plants with a moderate longevity and long-term responses from long-lived species. An indicator species should be an easily identifiable species that can preferably be used for the entire reserve. However, since Sanbona is a large area it has distinct vegetation types with different species and so using the same indicators for the entire reserve is not feasible.

With this in mind, a number of key species were identified within the different vegetation communities. These species were chosen, as they are easy to identify, were abundant within their vegetation communities, possessed a range of palatability, had different lifespans and could possibly be tested as indicators for all of the vegetation communities. Of the chosen indicators, some species, such as *Tetragonia fruticosa, Tripteris sinuata* and *Stipagrostis obtusa* are relatively palatable and would very easily show a response to grazing. Others, however, such as *Eriocephalus ericoides, Crassula* *subaphylla* and *Salsola glabrescens* are less palatable. Species such as *Pteronia paniculata, Galenia africana, Hereroa* and *Gibbaeum pubescens* are unpalatable and more community specific. *Pteronia. paniculata* is known as a species which increases in response to overgrazing (Saayman, et al., 2009), and *Galenia africana* also indicates overgrazing, but in this case decreased in abundance in both treatments. Therefore, changes within these species could indicate other thresholds of potential concern besides overgrazing. These indicator species are of particular importance in monitoring the stocking rate of Sanbona, as well as the impact of other disturbances.

When using indicators, it is important to be able to interpret the outcome with the purpose of making informed management decisions. For instance, if there is a reduction in *Tripteris sinuata,* when is the reduction large enough to affect the recruitment of palatable species? Also, it is important as to why vegetation condition is deteriorating. Several reasons could be advanced including:

1. There has been a reduction in the abundance and cover of nurse plants. Nurse plants are an important facilitator for the germination and seedling growth of *T. sinuata* (Riginos, et al., 2005);
2. Grazing at certain times will affect the future recruitment of plants. Milton (1992a) found that grazing during flowering and seed set, by sheep stocked at recommended rates, reduced potential seed set of *T. sinuata* by as much as 90%.
3. There is a depleted soil seedbank. As Todd and Hoffman (1999) pointed out, shrubs do not form large soil seedbanks and a short drought of only one or two years can deplete the seedbanks and result in irreversible changes in plant community composition.

Although the use of indicators is well known and been used for decades (Landres, et al., 1988; Rogers & Biggs, 1999; Carignan & Villard, 2002), it is surprising that few standardised and well-accepted methods to identify indicator species have been developed (Dufrene & Legendre, 1997). The use of indicator species within a conservation area in the Little Karoo and as outlined here, is relatively novel. It is important that these species are monitored and that adaptive monitoring be implemented to adjust the approach if the indicator species prove not to be sensitive enough to detect change within the system. It is expected that in time, because of the increased sampling size that the framework boundaries will shift as well as the movement of the species within the scatter plot.

Adaptive management

Monitoring programmes need to evolve and develop as new information emerges and research questions change (Lindenmayer & Likens, 2009). The results of this study show that the data supports the classification of the different vegetation communities. The length of the sampling also appeared to be able to identify trends in the floristic composition even though the monitoring programme has been running for a relatively short period of time, for a semi-arid system. An adaptive monitoring framework enables a monitoring programme to be reviewed and make changes if necessary which is an important link to adaptive management (Lindenmayer, et al., 2011).

Two questions arose regarding the current monitoring programme:

1. Is it necessary for the field surveys at Sanbona to continue on an annual basis?
2. Is the current distribution of plots across the reserve able to demonstrate trends?

It is possible to oversample such that a greater monitoring effort is expended than what is needed (Gibbs, et al., 1999). Semi-arid rangelands have multiple ecological states resulting from a complex interaction between slow (e.g. soil fertility) and fast (e.g. rainfall variation) variables operating at different temporal and spatial scales (Reynolds, et al., 2007). Infrequently occurring climatic conditions, such as exceptional rainfall, may bring about episodes of seedling establishment. These episodes could alter the subsequent structure of plant communities and may persist for many years. Factors such as grazing pressure, at the time of such an episode, may have a more critical influence than at any other time. Novellie and Strydom (1987) stated that if the frequency of repeat surveys is too low then uncommon events, such as high rainfall events and droughts, may go unrecorded and thus could seriously impair the interpretation of trends in the results. In order to continue improving on the management of the reserve, to determine whether the indicator species are performing and to establish the magnitude of change in the vegetation that is acceptable in terms of the conservation goals for the reserve (Novellie & Strydom, 1987) it is recommended that the sampling intensity stay at its current annual survey.

When a reserve is established, the animal preference areas and areas of high animal density, indicating high-utilisation, are unknown. Plots are placed over a variety of habitats to try monitor the impact. Only once animal patterns have been determined can high utilisation areas be identified and compared to the results of the monitored plots. This study indicates that the plots in areas of high animal density definitely are subject to grazing affects. The fact that a reaction was noted indicates that the plots are situated in the correct positions. Since there are plots beyond the areas of high utilisation we will be able to test the utilisation map going forward as grazing pressure in the mixed model can be adjusted to account for the spatial variation in animal density. There are however additional areas of high utilisation that are currently not being monitored and it would be advisable to add addition monitoring plots into these areas. The more we know about this ecosystem the better we can adapt our management to avoid veld degradation and maintain productivity without loss of species diversity and natural resources (Esler, et al., 2006).

Adaptations from recommendations

Hoffman et al. (2009) made a number of suggestions that have since been addressed by Sanbona:

1. A recommendation was that more detailed species-specific monitoring approaches were needed to detect the impact of indigenous herbivores on key indicator species.
2. Can management discern whether the surveys have indicated an impact by herbivores?

To date, most studies have focused on the mega-herbivores such as elephant and giraffe. These studies have proved that the areas the plots are situated in are not preferred areas for these animals, as it does not meet their requirements. Proposed research also aims to determine specific dietary preferences for ungulates on Sanbona as palatability varies widely between ungulate species (Farmer & Milton, 2006; Fenwick, 2008). A number of other monitoring projects have been initiated with fixed-point photography as a key driver.

It takes time to understand the balance between the number of herbivores required to sustain a small predator population in the Little Karoo as well as the impact of meso-carnivores (jackals, caracals, hyena) on prey. As stated by Hoffman et al. (2009), not enough time had elapsed for changes to become evident after 5 years. Kraaij and Milton (2006), Burke (1997), Rahlao et al. (2008) and Van Rooyen et al. (2015) stated that in order to detect any change in semi-arid rangelands, monitoring programmes need to be conducted over a lengthy period. For years, the impact caused by the increasing numbers of herbivores on Sanbona was not apparent. Above-average rainfall may have masked the effect of herbivory by increasing vegetation biomass in relation to the number of herbivores, thus reducing grazing pressure (Novellie & Bezuidenhut, 1994). Since the end of 2010, rainfall has been largely above-average and the veld seemed to be in a very good condition. However, with the lack of rain since mid-2015, it has become evident that management must take action. A decision was made prior to the completion of this study to remove a large number of herbivores, in particular eland and gemsbok. This study validates this decision since an effect of herbivory is noticeable and it was apparent that animal numbers need to be reduced.

7. CONCLUSION

Vegetation changes generally occur unpredictably in the short term (years) in response to rainfall, and episodically in the long term (several decades) in response to rare events, or due to grazing pressure, climatic change, altered disturbance regimes, or a combination of these factors (Wiegand & Jeltsch, 2000). The timing, amount and intensity of rainfall has been shown to have an influence on the dynamics of plant populations as well as the composition of these arid communities (Westoby, et al., 1989; Hoffman & Cowling, 1990; Milchunas & Lauenroth, 1993; Burke, 1997; Desmet & Cowling, 1999; Illius & O'Connor, 1999; Reynolds, et al., 2007). The great variability introduced by rainfall means that the contribution of grazing to vegetation change can probably only be detected by tracking vegetation trends over very long periods (Novellie & Strydom, 1987; Lawley, et al., 2013), or through experimental designs specifically aimed at differentiating the two. After twelve years of monitoring on Sanbona, the results indicate that there has been an initial recovery period during the initial five years of low stocking density, followed by a more stable period with less change thereafter, concomitant with a large increase in the stocking rate of herbivores. In this latter period, there is evidence that the herbivores are affecting the continued recovery of the vegetation and in some areas of high use are likely changing the vegetation at the study site.

In arid and semi-arid areas, rainfall usually drives changes in cover, species richness and recruitment while grazing usually influences species composition (Todd & Hoffman, 2009). In general, the results of this study show that there was an increase in species richness, abundance and cover. However, increases in the ungrazed plots were at a significantly faster rate than the plots exposed to grazing. This suggests that the rate of recovery is retarded for areas exposed to grazing. The low stocking rates in the first five years resulted in very little difference between the treatments. However, once stocking rates increased, both species richness and cover increased more rapidly in the ungrazed plots, compared to the grazed plots. The increase in species richness and cover is a result of an increase in an array of palatable and unpalatable plants in both treatments with species specific to each community. The Rocky Karoo and Quartz Vygieveld experienced an increase in cover in both grazed and ungrazed plots. The

Sandy Karoo is the only community where there was a decrease in cover which was attributed mostly to palatable species. The findings are consistent with Novellie (1991) indicating that this vegetation type, in low lying areas, is known to support high densities of grazing ungulates and therefore is the first to shows of over-utilisation by herbivores (Kraaij & Milton, 2006). In the Renosterveld, the plots exposed to grazing are less responsive compared to the ungrazed plots. The effect of grazing may be more noticeable because of the lack of palatable species found in Renosterveld. Because of the low density of palatable species, grazing can cause a rapid reduction in the palatable species which are present. A subsequent increase in unpalatable plant species may then result due to the reduced competition. This is very often enhanced by the increase in seed production, following a decrease in florivory on unpalatable species. Very little is known about the influence of large mammals on the vegetation in this biome (Rebelo, et al., 2006) and therefore studies like these are important.

Most growth forms experienced an increase in cover. The most significant increase was seen in the cover of perennial grasses and low evergreen shrubs. A concern would be the decline in cover for low leaf succulent shrubs. However, this decline was across both treatments, which eliminated grazing as a causative effect. The decline in low leaf succulents can be attributed to the oscillations in annual rainfall events. Leaf succulents may often experience substantial losses during droughts, and populations can take decades to recover. They may also experience typical mass germination events after rain, with a subsequent high die-off with a lack of follow up rain. Stem succulents also decreased in the plots exposed to grazing. This decrease could also not be a direct result of herbivory since most of the stem succulents are toxic, or unpalatable. It is rather a result of trampling or stochastic effects associated with their low numbers. Medium evergreen shrubs experienced a decline in the ungrazed plots, but since there was an overall increase in cover the decline was attributed to competitive displacement.

Although, grazing is having an effect on the reserve, it is not necessarily indicative of degradation at this point because some continued recovery of the vegetation is still apparent. The annual rainfall fluctuations also have some influence on the ungrazed plots and can override or mask the grazing effects. However, at high grazing pressures this effect is not apparent and is swamped by the effects of grazing. It is clear from the results that grazing pressure is retarding the recovery of the vegetation and if the current high stocking rates are maintained, then some degradation of preferred areas is likely to occur.

Herbivory may not be the only reason for negative trends. Trampling can be just as deleterious in certain areas. There is a high degree of spatial variability in animal distribution and associated grazing pressure and disturbance. Areas of high utilisation or preference exist for specific species of herbivores. This was confirmed by the census data. This data is important, and should continue to be collected on a regular basis to better characterise the effects of rainfall and grazing pressure in the future. This could also be verified using camera traps or similar ground-based approach.

A sound, long-term management policy is based primarily on an understanding of the seasonal usage by animals of the available habitat diversity. For this reason, indicator species have been selected for each vegetation community to investigate grazing impacts. The use of indicators as a management tool is well documented. In order to identify indicators, a theoretical framework for determining indicators species in the different vegetation communities was created. This was based on the correlation between species abundance and sampling period in the different treatments. These species were abundant and ranged in lifespans and palatability. The indicators are representative of palatable and unpalatable species, with different life time spans that can indicate short- or long-term responses. The consistent changes in these species should indicate grazing impacts separately from rainfall effects. The indicators are a new monitoring method that also needs to be tested carefully to prove the validity of this method.

To be able to marry science and conservation management is not an easy task. There is usually a big gap between the two. An adaptive monitoring system must promote monitoring and adaptive management tools. The method for monitoring and analysis needs to be simple enough for the land owner to perform, without a rigorous statistical method. Statistical programmes, academic institutions and consultants are not available to all land owners. The current monitoring programme seems to be capable of detecting change and therefore does not need to be altered. To better monitor the high utilisation areas, a few more plots could be established within these potential areas of concern.

The recovery process was much slower in the grazed plots than in the protected plots. Therefore, for the continued recovery of the vegetation to take place and for there to be a sustained increase in cover, active management of animal numbers would need to occur. High rainfall, as has been experienced for the latter part of the study, can reduce the impact of herbivory on the veld and since there is evidence that grazing is having an effect while rainfall is above average, numbers need to be reduced to prevent detrimental effects during dry periods. Grazing pressure prevailing during and after a drought may be a critical factor in determining vegetation change (Palmer, et al., 1999). Certain areas, within the high animal density regions are clearly demonstrating a negative impact. Areas of preferred use should determine and influence stocking rates rather than total reserve size.

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9. *APPENDICES*

Appendix A Most significant species corresponding to the axes.

Table A1. Species corresponding to the three NMS Axis scores, from an NMS calculated on the 2015 data for all plots, indicating the top 20 most significant, where green presents ($p<0.005$), purple ($p<0.025$).

Species	Ax1	Species	Ax2	Species	Ax3
Stipagrostis ciliata	0.378	*Gibbaeum pubescens*	0.55	*Elytropappus rhinocerotis*	0.492
Ruschia pungens	0.376	*Salsola tuberculata*	0.482	*Euryops nodosus*	0.492
Stipagrostis obtusa	0.359	*Pteronia succulenta*	0.395	*Pteronia paniculata*	0.47
Gazania sp	0.303	*Psilocaulon simile*	0.383	*Pteronia incana*	0.403
Zygophyllum microphyllum	-0.313	*Pteronia viscosa*	0.356	*Felicia muricata*	0.334
Ruschia spinosa	-0.325	*Gibbaeum nuciforme*	0.338	*Felicia filifolia*	0.325
Eriocephalus ericoides	-0.368	*Salsola glabrescens*	0.314	*Pteronia sordida*	0.315
Tripteris sinuata	-0.406	*Thesium lineatum*	-0.324	*Galenia africana*	0.297
Pteronia pallens	-0.418	*Pteronia incana*	-0.336	*Drosanthemum delicatulum*	-0.302
Hereroa odorata	-0.578	*Monechma incanum*	-0.336	*Hypertelis salsoloides*	-0.349
Schotia afra	0.292	*Felicia muricata*	-0.346	*Leipoldtia schultzei*	-0.357
Chrysocoma ciliata	0.288	*Rhigozum obovatum*	-0.395	*Euphorbia burmanii*	-0.363
Lycium ferocissimum	0.281	*Pentzia incana*	-0.401	*Psilocaulon junceum (utile)*	-0.373
Melolobium sp	0.279	*Ruschia robusta*	-0.414	*Salsola glabrescens*	-0.378
Hypertelis salsoloides	0.278	*Crassula rupestris*	-0.477	*Ruschia spinosa*	-0.386
Salsola glabrescens	0.273	*Gibbaeum heathii*	0.288	*Aridaria sp*	-0.39
Helichrysum sp	0.272	*Psilocaulon junceum (utile)*	0.28	*Pteronia pallens*	-0.398
Elytropappus rhinocerotis	0.27	*Crassula subaphylla*	-0.28	*Plagiochloa unicolor*	0.294
Blepharis capensis	-0.267	*Microloma sagittatum*	-0.284	*Selago geniculata*	0.279
Monsonia salmoniflorum	-0.272	*Hirpicium integrifolium*	-0.284	*Phyllobolus canaliculatus*	-0.296

Appendix B Species unique to each vegetation communities

Table B1. List of the unique species for each group, representing the four vegetation communities.

Rocky Karoo (Group 1)

Aloe variegata
Anacampseros filamentosa
Aptosimum spinescens
Aristida congesta
Bulbine abyssinica
Bulbine frutescens
Cadaba aphylla
Crassula congesta
Drosanthemum sp 6
Euphorbia multiceps
Euphorbia pillansii
Fingerhuthia africana
Gibbaeum shandii
Helichrysum sp 1
Hereroa sp
Hermannia cuneifolia
Justicia cuneata
Lachenalia karooica
Lampranthus sp
Lessertia inflata
Limeum aethiopicum
Lotononis rigida
Lotononis sp
Mesembryanthemum crystallinum
Monechma spartioides
Nenax microphylla
Pelargonium alternans
Pelargonium karooicum
Peliostomum leucorrhizum
Pentzia spinescens
Pteronia sp
Selago sp
Sericocoma avolans
Sphalmanthus sp
Thesium sp
Thesium sp 2
Trichodiadema attonsum
Trichodiadema setuliferum
Wiborgia sp
Zygophyllum incrustatum

Quartz Vygieveld (Group 2)

Antegibbaeum fissoides
Atriplex lindleyi
Augea capensis
Bulbine mesembryanthemoides
Crassula columnaris
Crassula nudicaulis var platyphylla
Dianthus sp
Felicia sp 1
Gibbaeum nuciforme
Gibbaeum geminum
Gibbaeum pilosulum
Hermannia sp
Hermannia filifolia
Kochia pubescens
Kochia salsoloides
Lithops sp
Mesembryanthemum
Mesembryanthemum subtruncatum
Phymaspermum parvifolium
Rhinephyllum muirii

Sandy Karoo (Group 3)

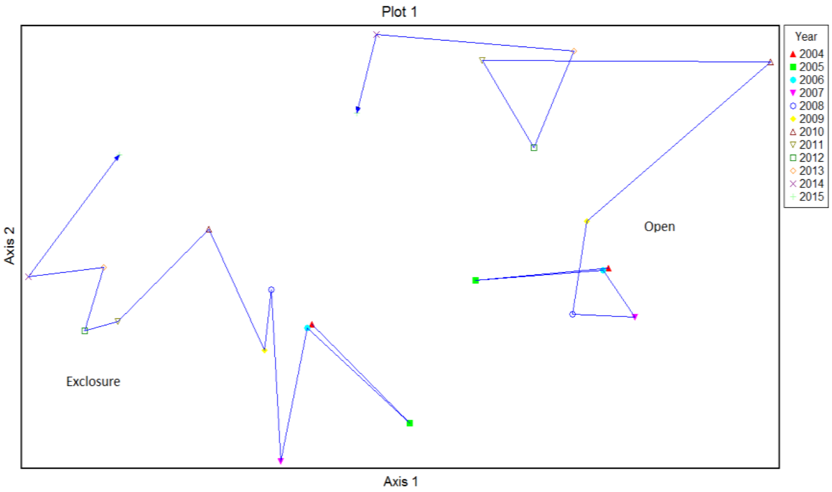
Amphiglossa tomentosa
Arctotis sp
Atriplex vestita
Calobota elongata
Cissampelos capensis
Cotyledon sp
Crassula nudicaulis
Crotalaria lebeckioides
Diospyros lycioides
Drosanthemum creeper
Drosanthemum sp 5
Ehrharta capensis
Ehrharta sp
Enneapogon sp
Eragrostis curvula
Felicia sp 2
Gloveria integrifolia
Grass sp
Helichrysum sp 2
Helichrysum sp 5
Heliophila suavissima
Ifloga glomerata
Lycium ferocissimum
Lycium oxycarpum
Lyperia tristis
Muraltia spinosa
Othonna cylindrica
Oxalis sp
Pharnaceum sp 3
Psilocaulon sp
Pteronia fasciculata
Schotia afra
Helichrysum lucilioides
Species 1 (looks like Walafrida)
Species 2 (looks like Struthiola)
Stapelia hirsuta
Stipagrostis ciliata
Struthiola eckloniana
Viscum rotundifolium
Zygophyllum foetidum

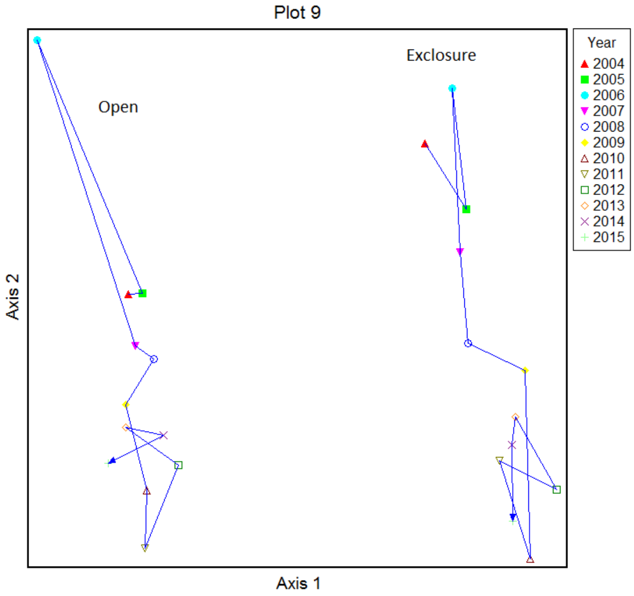
Renosterveld (Group 4)

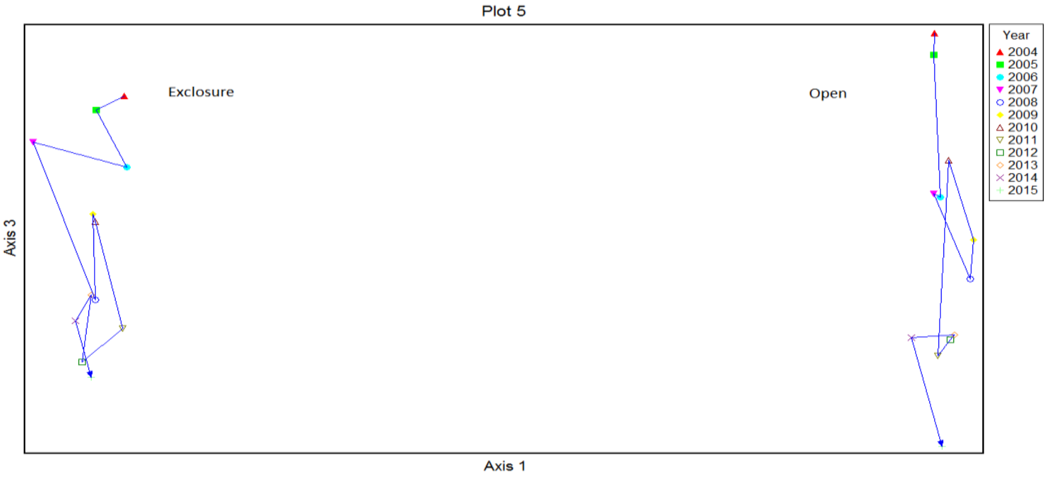
Albuca concordiana or spiralis
Anthospermum aethiopicum
Asclepias fruticosa
Asclepias sp
Asparagus capensis
Bulb
Bulb (3 leaves)
Cephalophyllum purpureo-album
Conyza canadensis
Crassula pubescens
Crassula sericea
Delosperma speciosum
Dimorphotheca cuneata
Drosanthemum bicolor
Drosanthemum sp 2
Drosanthemum sp 3
Elytropappus rhinocerotis
Erigeron sp
Euryops lateriflorus
Euryops nodosus
Euryops rehmannii
Euryops subcarnosus
Exomis microphylla
Felicia ovata
Felicia sp
Felicia sp 3
Freylinia undulata
Gasteria brachyphylla
Gladiolus venustus
Grass sp
Grass sp (Bristle grass)
Grass sp (similar to Tragus)
Helichrysum pumilio
Helichrysum sp 10
Helichrysum sp 3
Helichrysum sp 4
Helichrysum sp 6
Helichrysum sp 7
Helichrysum sp 9
Hordeum sp
Lightfootia nodosa
Massonia depressa
Medicago sp
Metalasia muricata
Oncosiphon piluliferum
Osteospermum clandestinum
Osteospermum sp
Passerina obtusifolia
Pelargonium abrotanifolium
Plumbago sp
Rhus longispina
Ruschia impressa
Ruschia sp (tall)
Ruschia sp
Schismus sp
Selago geniculata
Selago ramosissimum
Selago saxatilis
Senecio paniculatus
Stapelia sp
Sutera uncinatum
Sutherlandia frutescens
Tetragonia sarcophylla
Tritonia securigera
Veltheimia capensis
Wahlenbergia thunbergiana

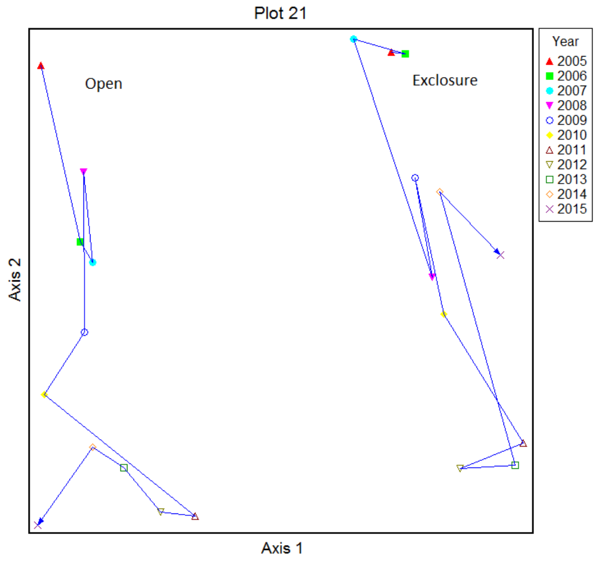
Appendix C Ordination for the individual plots

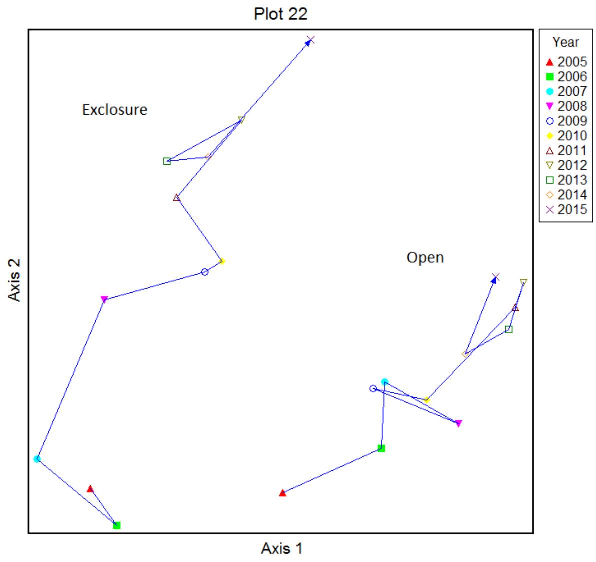
Group 1 - Western Little Karoo (Rocky Karoo)

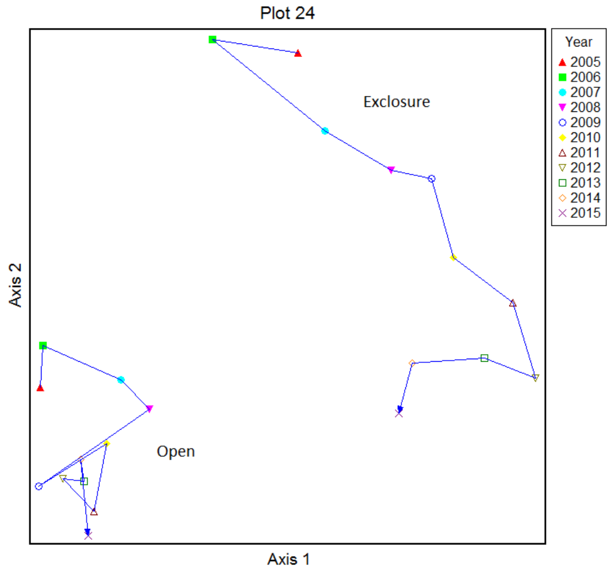


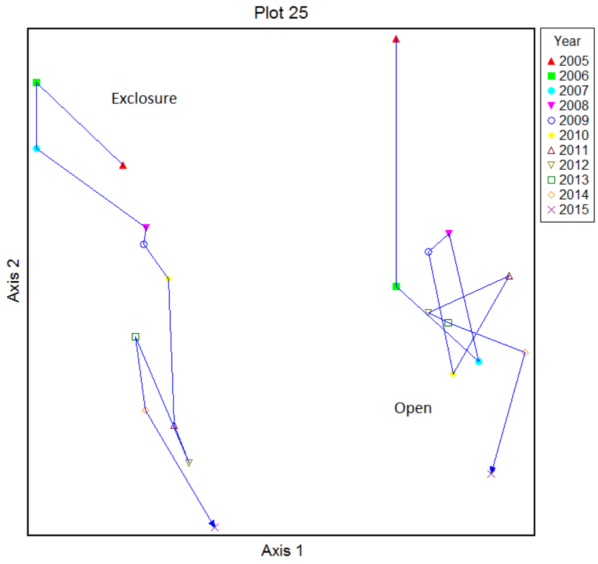





Plot 21


Plot 22


Plot 24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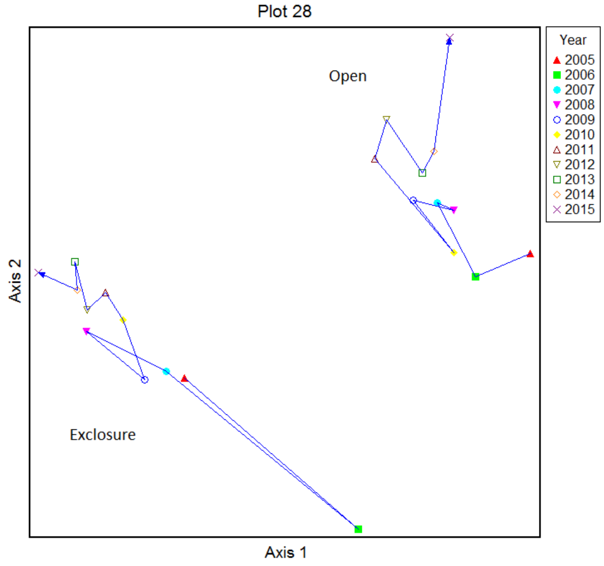
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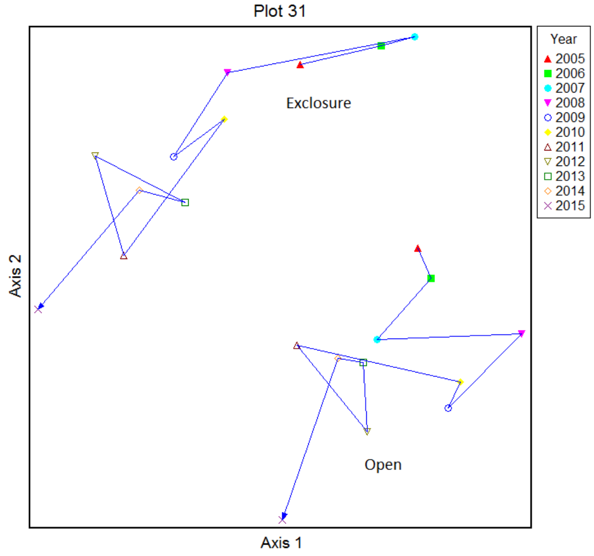
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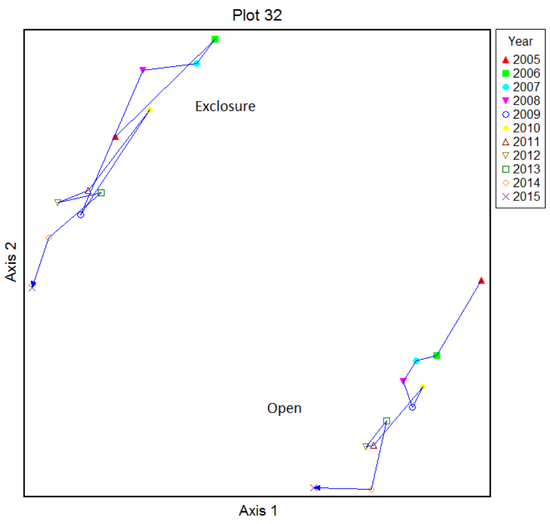
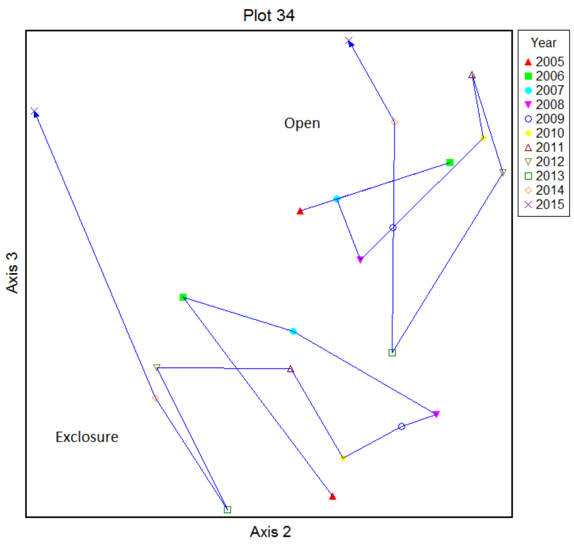
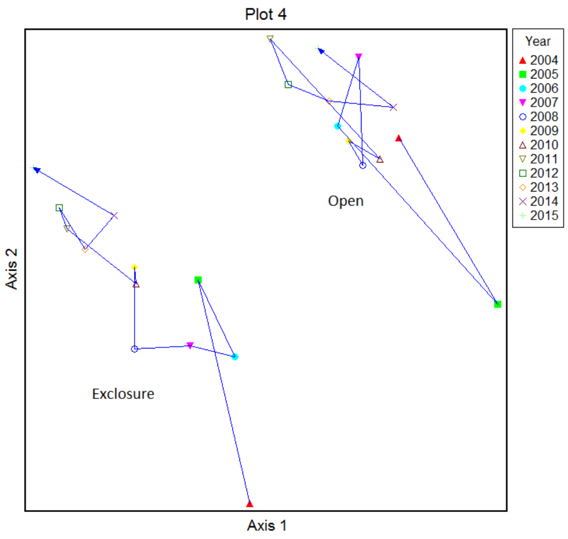
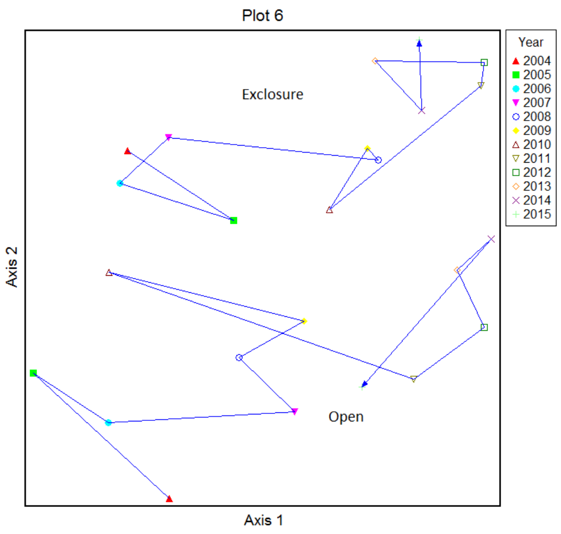
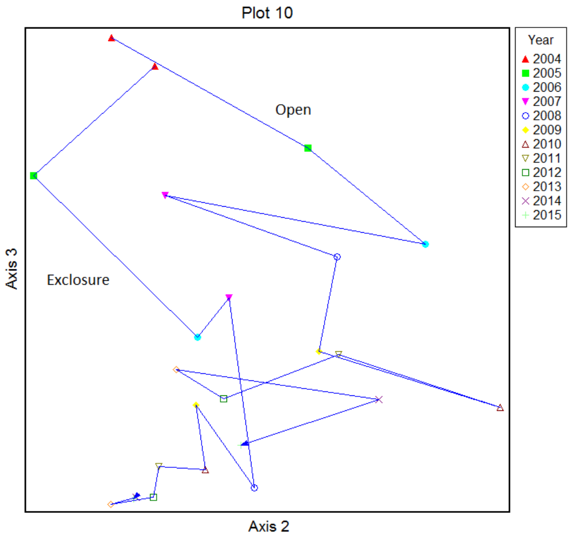


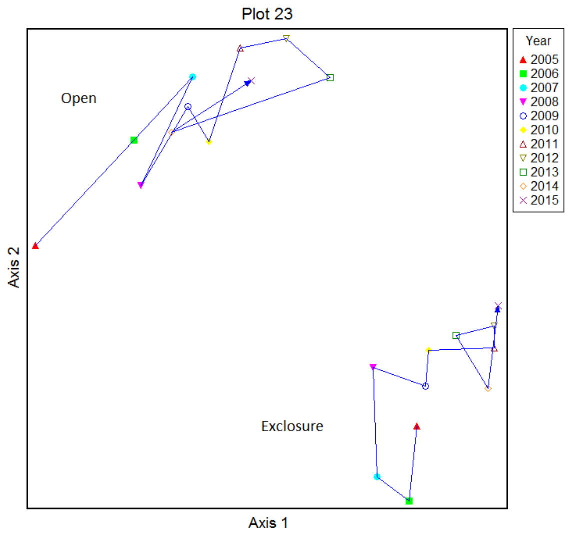


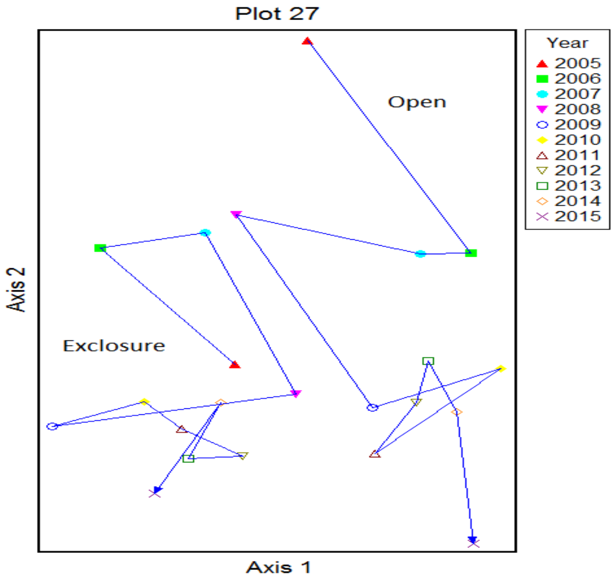
Group 2 – Little Karoo Quartz Vygieveld (Quartz Vygieveld)



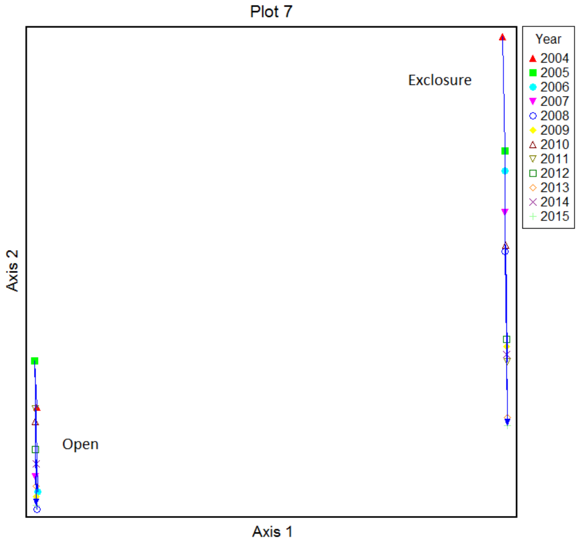


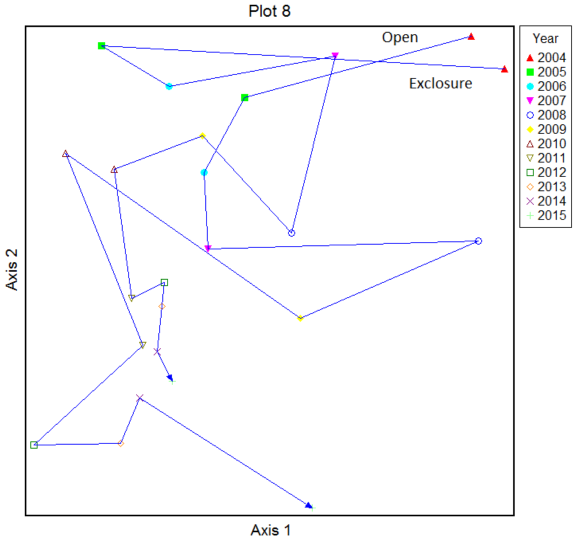


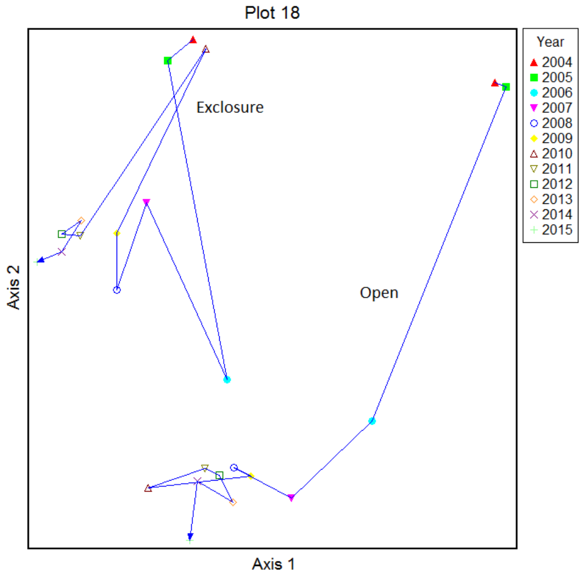


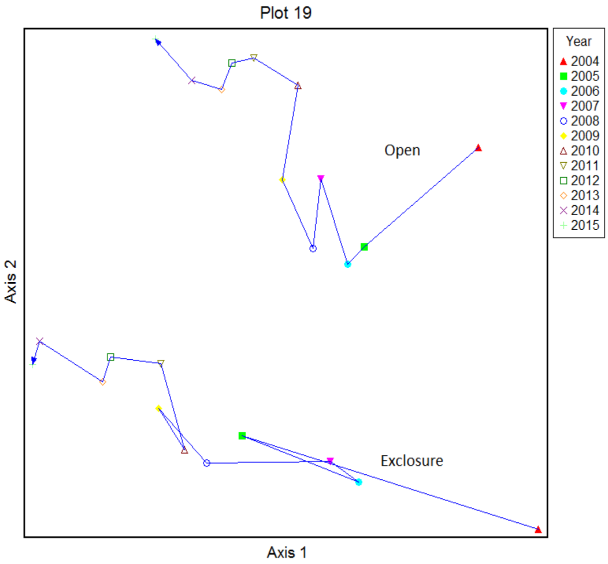


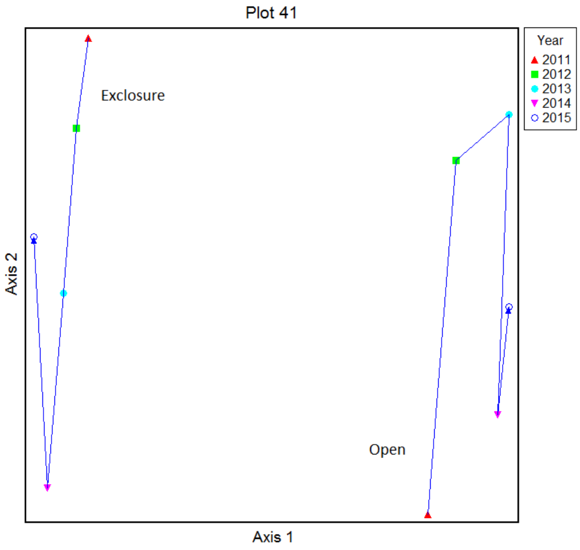
Group 3 - Western Little Karoo (Sandy Karoo)

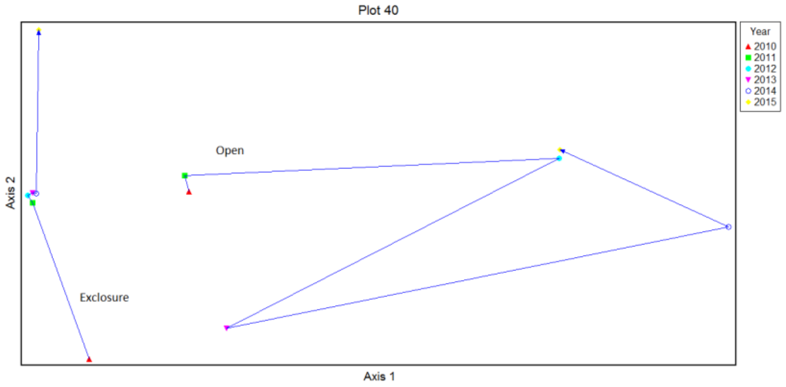









Plot 41
Exclosure
Open
Axis 1
Axis 2
Year
▲ 2011
■ 2012
● 2013
▼ 2014
○ 2015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Open
Exclosure
Axis 1
Axis 2
Year
▲ 2010
■ 2011
● 2012
▼ 2013
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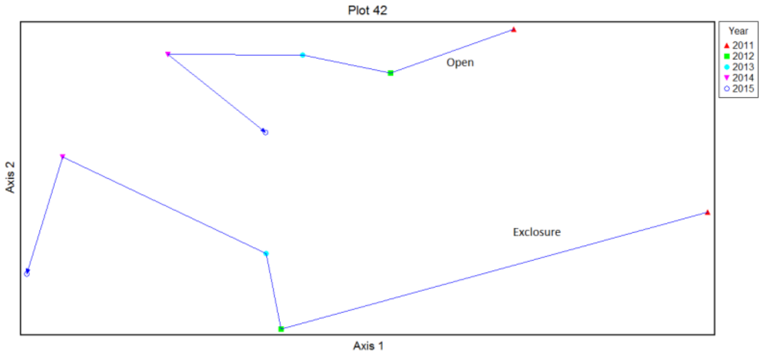
● 2015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Open
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Axis 1
Axis 2
Year
▲ 2011
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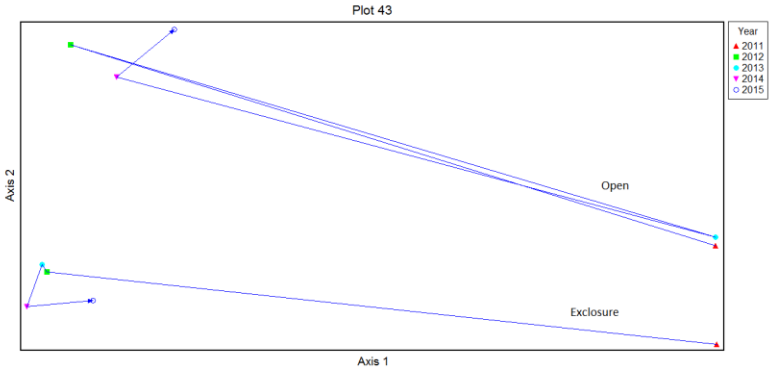
● 2013
▼ 2014
○ 2015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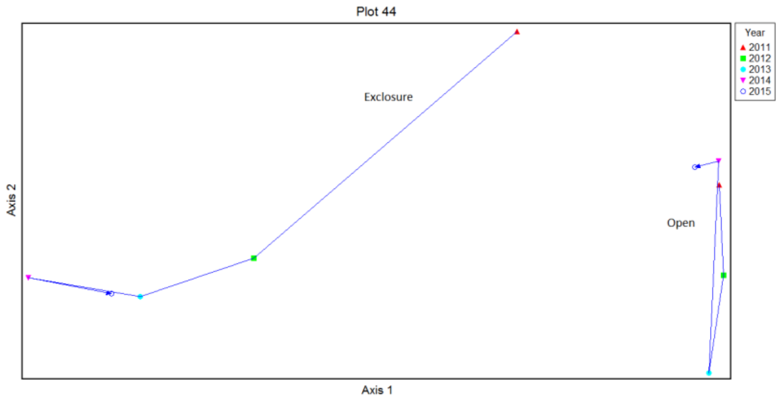
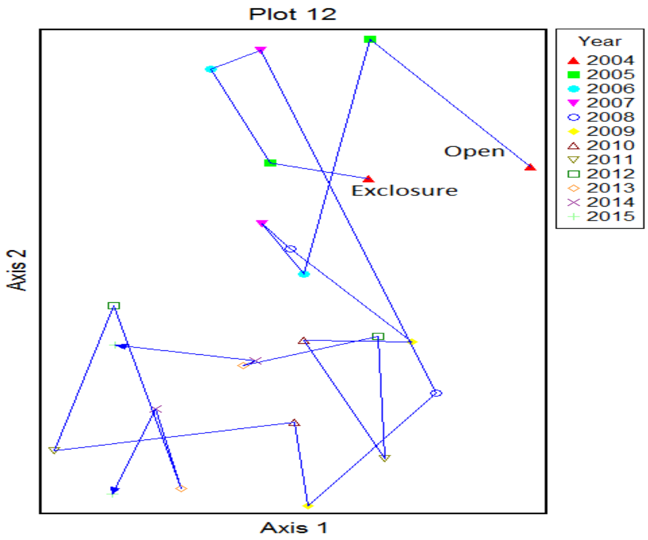
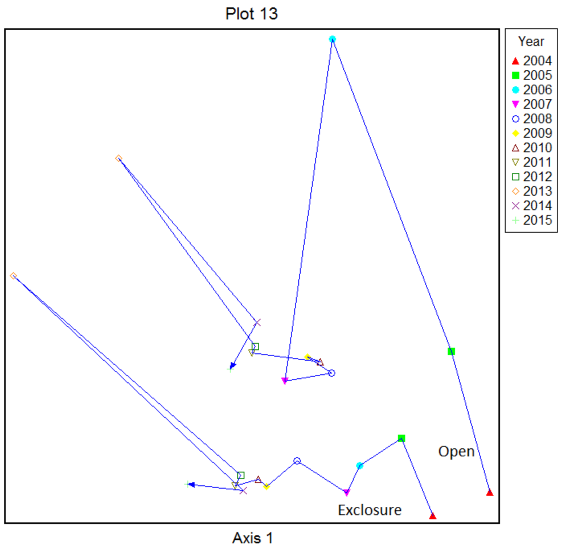
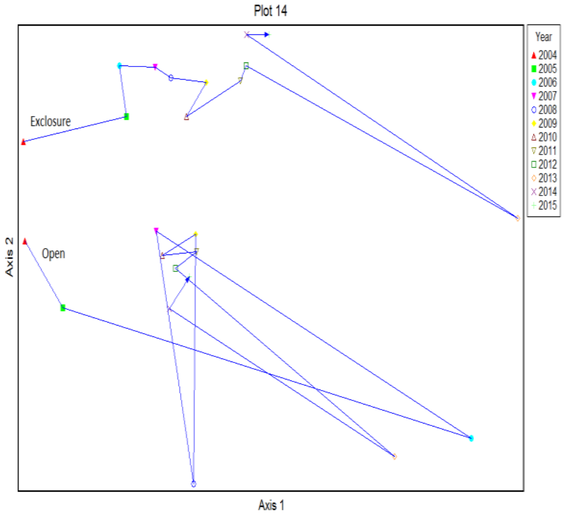
Axis 1
Axis 2
Year
▲ 2011
■ 2012
● 2013
▼ 2014
○ 2015

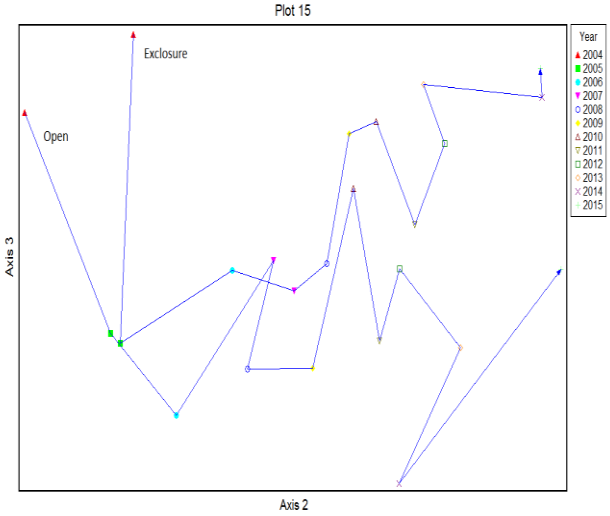

Plot 44
Exclosure
Open
Axis 1
Axis 2
Year
▲ 2011
■ 2012
● 2013
▼ 2014
○ 2015

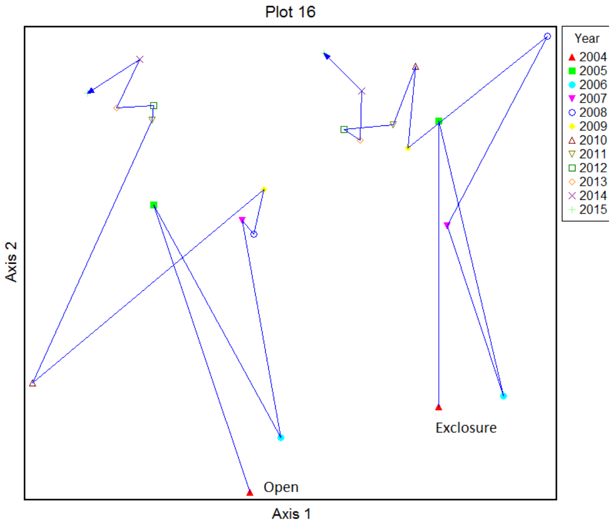
Group 4 – Montagu Shale Renosterveld

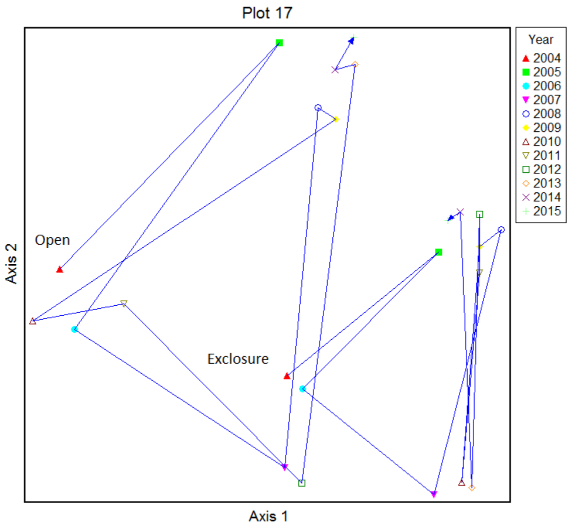












Appendix D Stress and variance for different communities

Table D1. Stress and proportion of variance values for the NMS ordination of the different communities.

Group	Vegetation Type	Stress	% Variance	Orthogonality (%)	Exclosure		Open	
					Axis 1	**Axis 2**	**Axis 1**	**Axis 2**
1	Rocky Karoo	6.296	0.923	95	NS	$p<0.001$	$p<0.001$	$p<0.001$
2	Quartz Vygieveld	5.193	0.843	93.5	NS	$p<0.01$	$p<0.001$	$p<0.001$
3	Sandy Karoo	6.167	0.890	100	$p<0.001$	$p<0.001$	$p<0.001$	$p<0.001$
4	Renosterveld	11.6	0.766	92.9	$p<0.001$	$p<0.001$	$p<0.001$	$p<0.001$

Appendix E Comparison of Die Vlakte weather station information with Sanbona Reserve, Sanbona North, Sanbona South, summer and winter rainfall

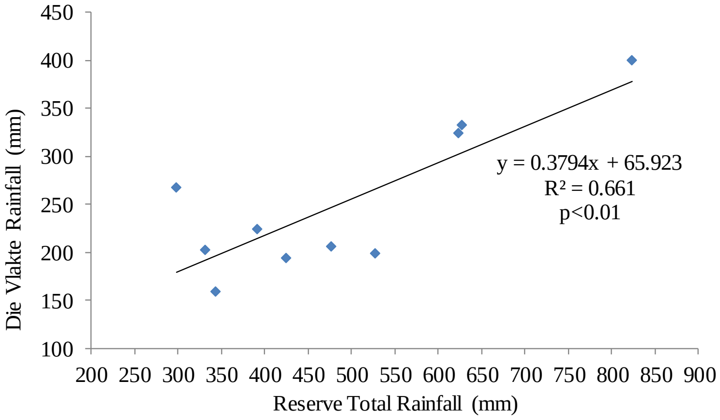


Figure E1 Comparison of Die Vlakte and Sanbona Reserve rainfall

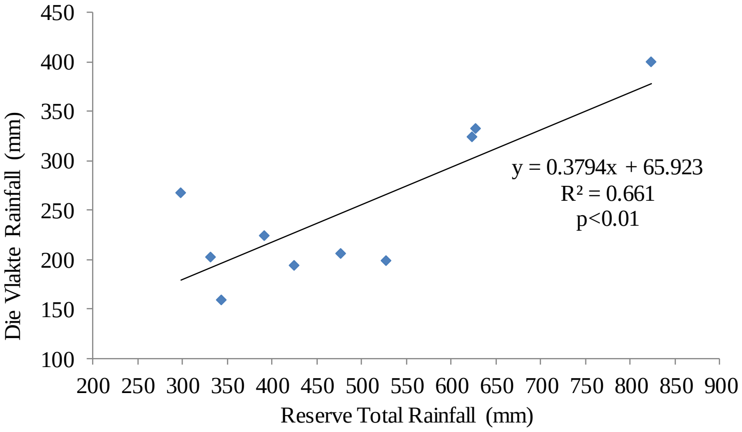


Figure E2 Comparison of Die Vlakte and Sanbona North rainfall

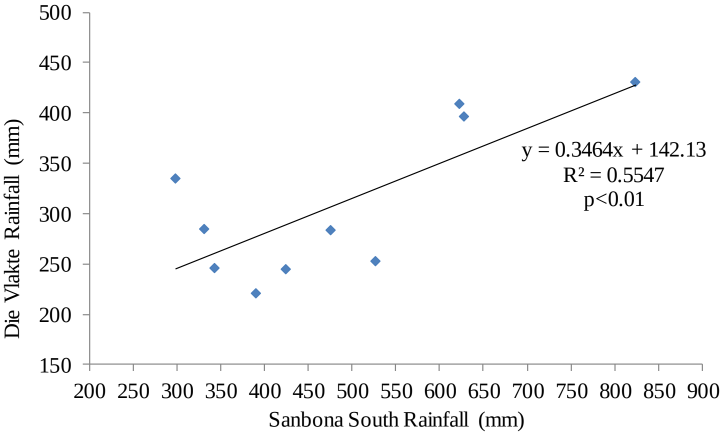


Figure E3 Comparison of Die Vlakte and Sanbona south rainfall

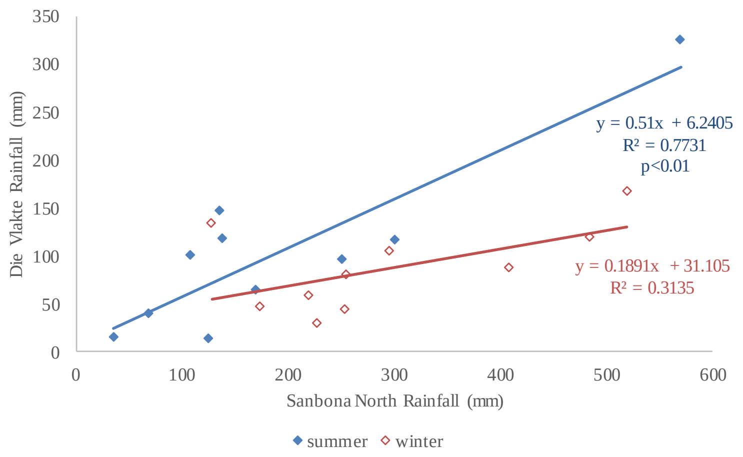


Figure E4 Comparison of Die Vlakte summer and winter rainfall to Sanbona North summer and winter rainfall, where the summer rainfall was significant and used to determine missing data.

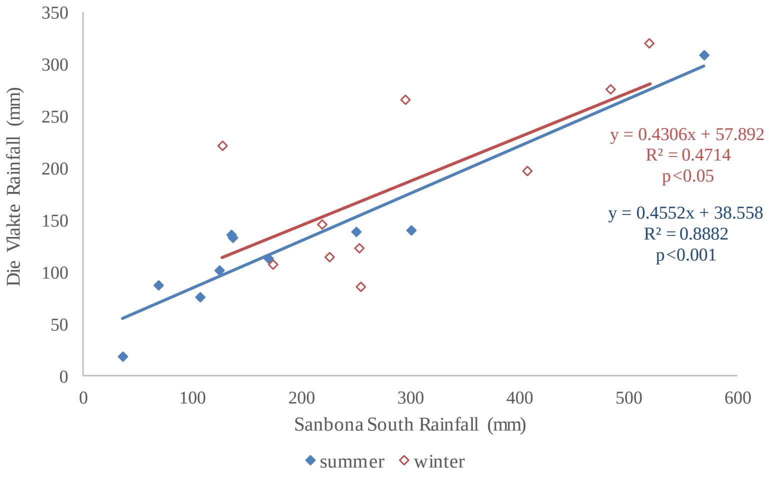
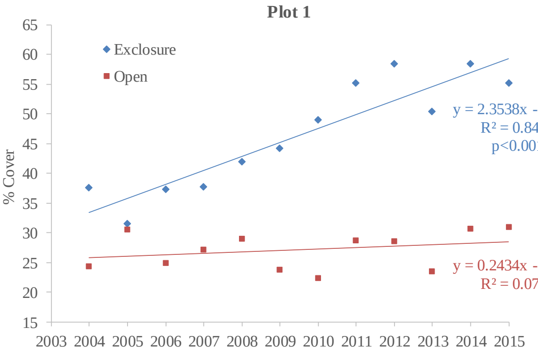


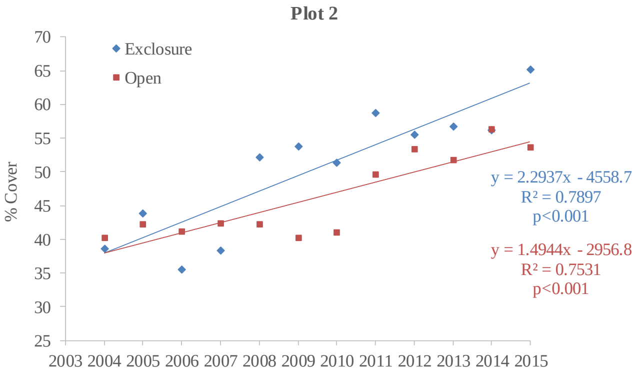
Figure E5 Comparison of Die Vlakte summer and winter rainfall to Sanbona South summer and winter r, where the summer rainfall was more significant than the winter rainfall and used to determine missing data.

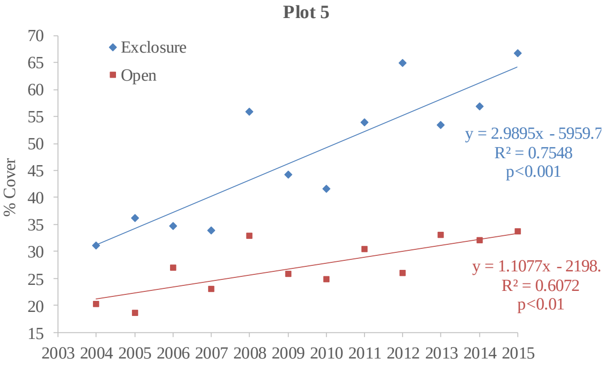
Appendix F Percentage cover of each treatment for each individual plot

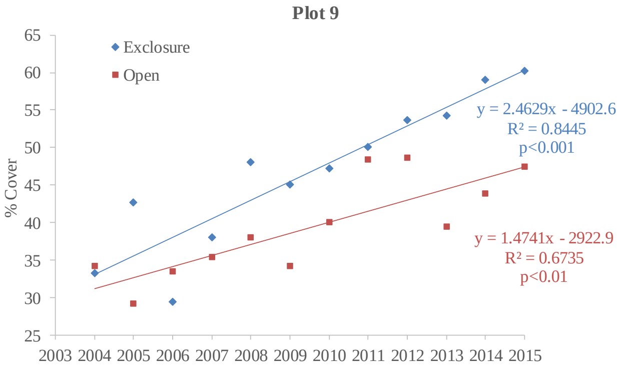
Western Little Karoo

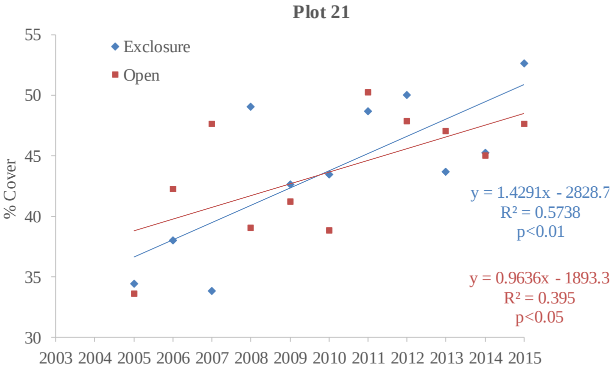
Group 1 (Rocky Karoo)

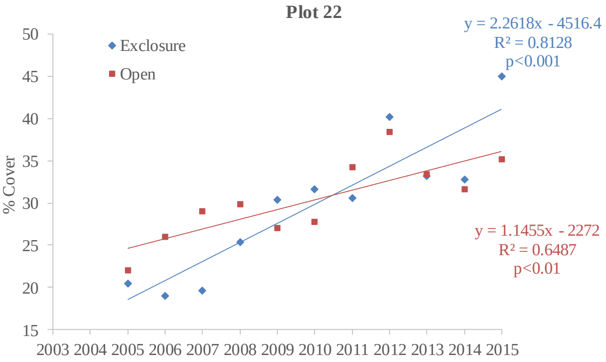


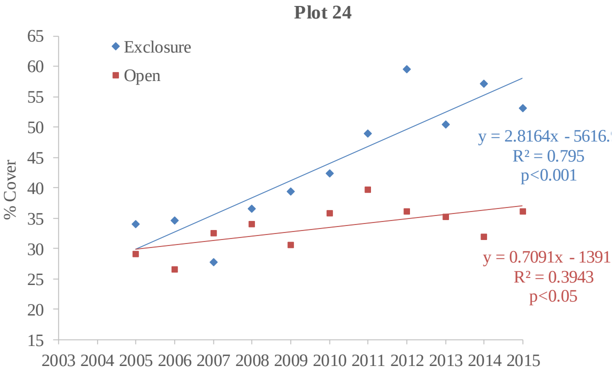


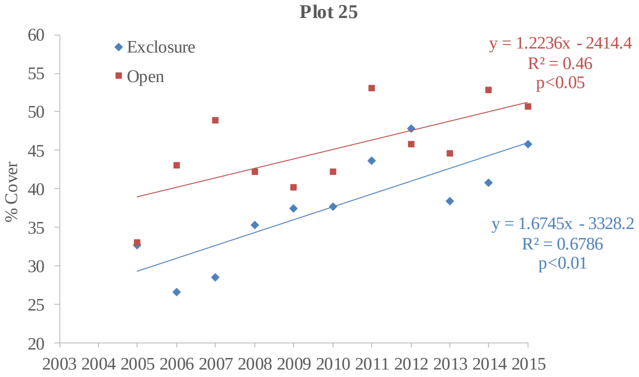


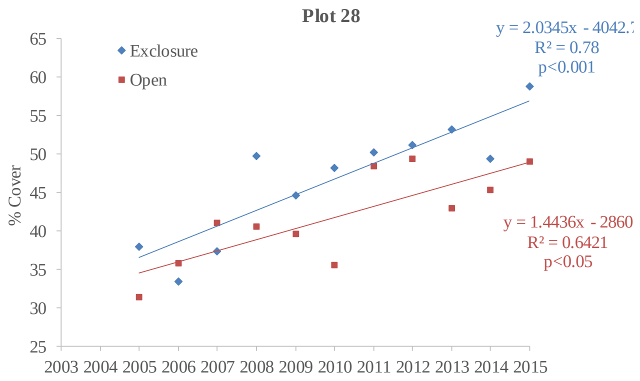


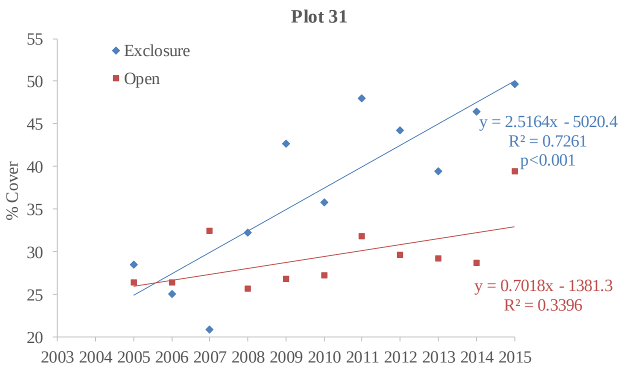


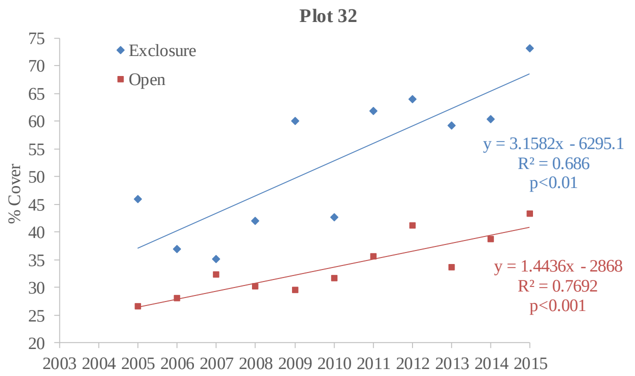


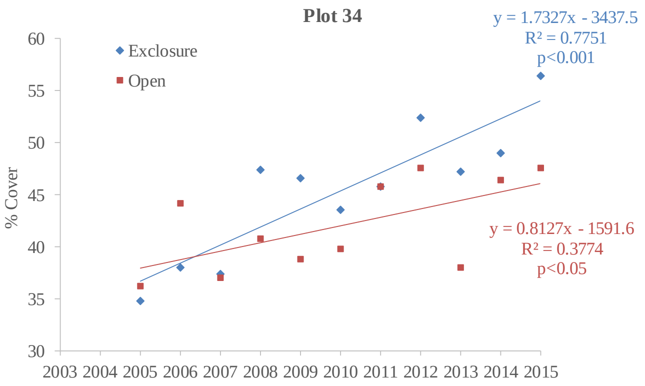












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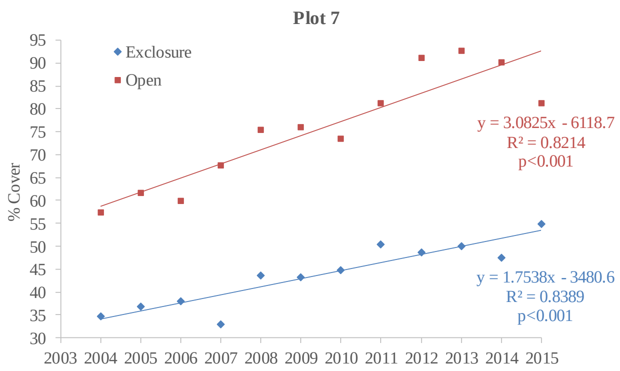
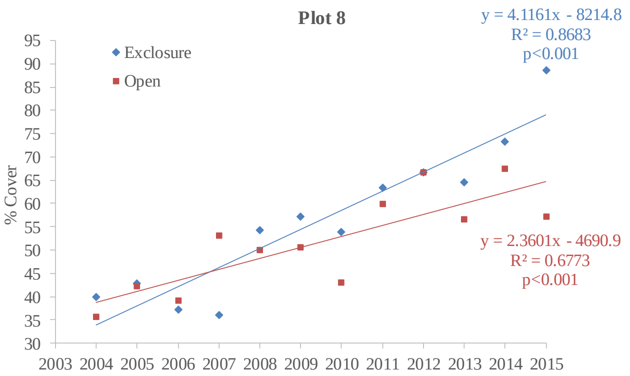
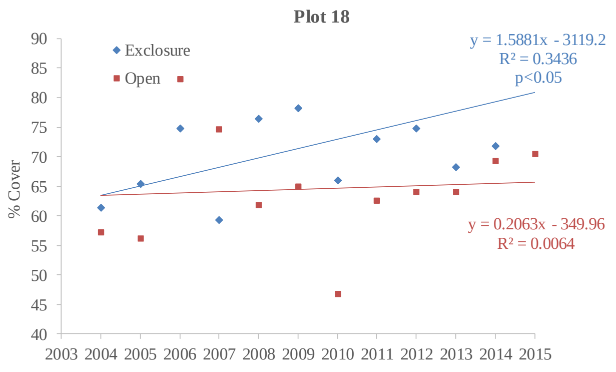
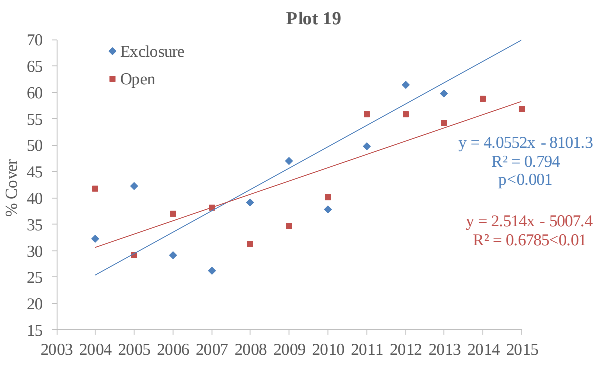
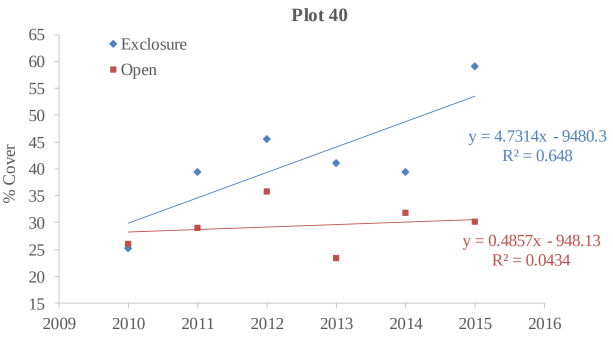
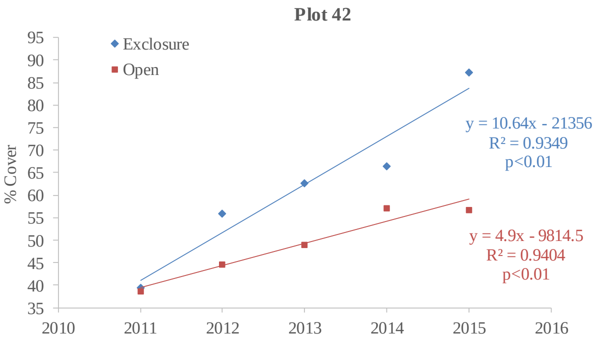


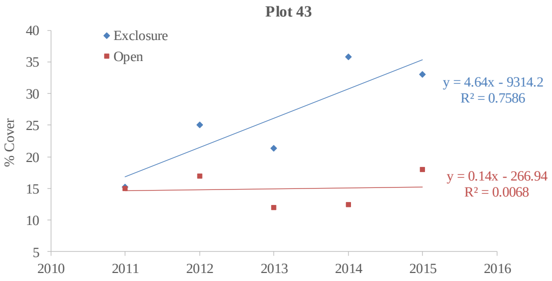


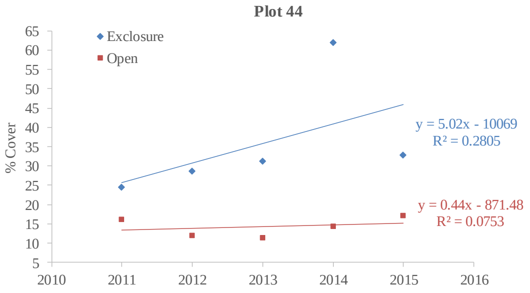




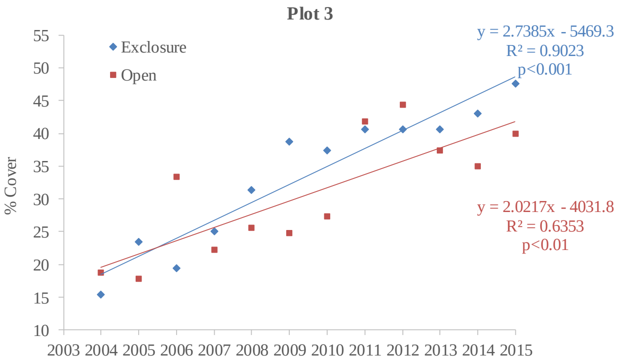


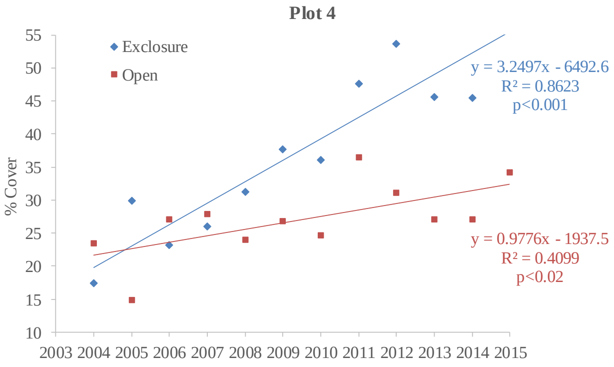


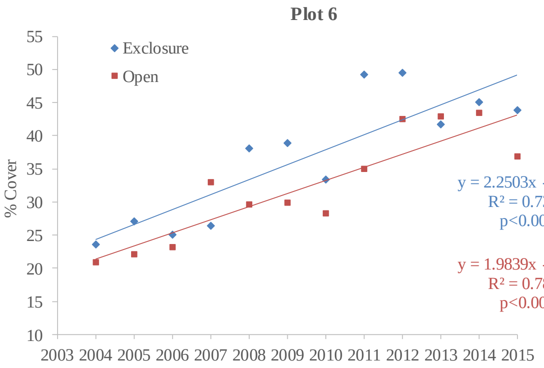


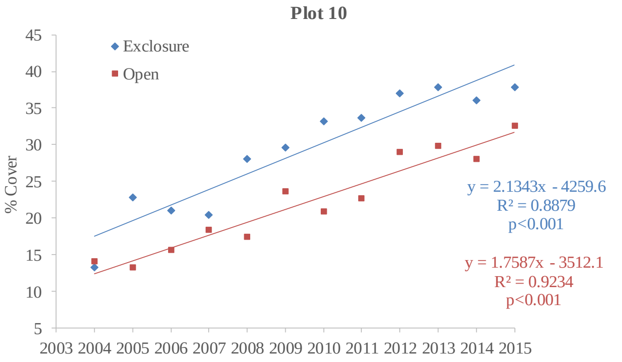


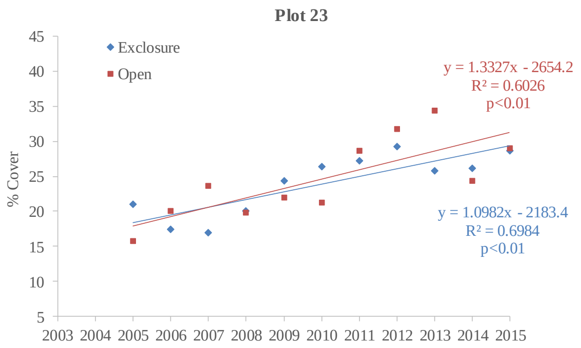
Little Karoo Quartz Vygieveld

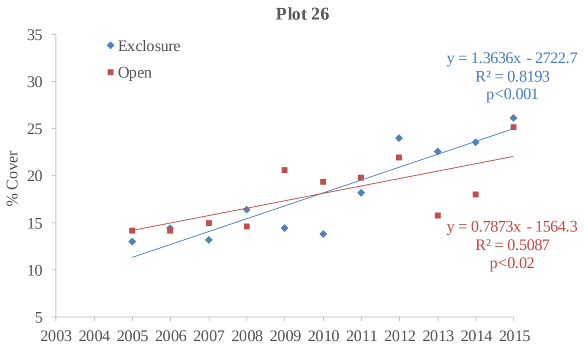


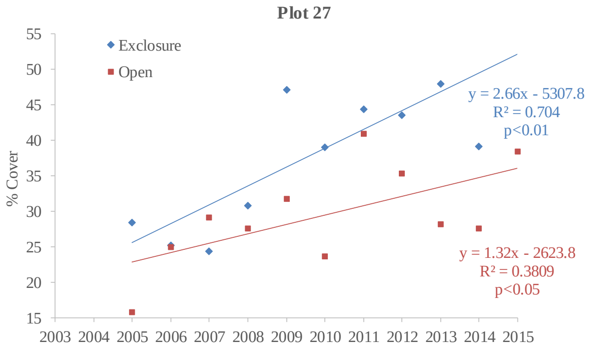












Montagu Shale Renosterveld