QUANTIFYING DEGRADED SUBTROPICAL THICKET STRUCTURE AND COMPOSITION: A MULTI-SCALE APPROACH IN THE EASTERN CAPE, SOUTH AFRICA

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QUANTIFYING DEGRADED SUBTROPICAL THICKET STRUCTURE AND COMPOSITION: A MULTI-SCALE APPROACH IN THE EASTERN CAPE, SOUTH AFRICA

MSC THESIS BY KYRA LUNDERSTEDT

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Abstract

The loss in canopy cover from over-browsing severely degrades the ecological integrity of spekboom-dominated thicket in the Eastern Cape. A homogenisation of species across the landscape and high heterogeneity at fine scales has been reported with little evidence of recovery. As an interlinked consequence, the loss in important biological structures and composition impacts greatly on soil resources and therefore function. This thesis provides a baseline of degraded thicket abiotic and biotic structure and composition over both spatial and temporal scales within the Greater Addo Elephant National Park (GAENP), including Darlington, Kabouga and Addo Main and within the Baviaanskloof. The study aimed to find correlates of species composition within sites and assess changes in composition with degradation and recovery times. Across the GAENP, landscape degradation was most evident in post-1960 aerial imagery. The duration since sampled sites have been incorporated into the GAENP did not influence species composition, however the period of degradation and severity, did.

Across the landscape, communities were strongly associated with each of the four sites and separated predominantly by rainfall, gravel and altitude. A total of 345 plant species were identified across the landscape and despite degradation, each site was characterised into three to five communities each, barring Baviaanskloof which had no significantly different communities. Across the landscape, matrix composition comprised predominantly of *Pentzia incana*, *Drosanthemum hispidum*, *Galenia pubescens* and *Cynodon* species. Woody cover within patches included smaller *Grewia robusta, Rhigozum obovatum* and *Vachellia karroo* and the larger *Pappea capensis* and *Euclea undulata.* The succulent shrub *Euphorbia caerulescens* in Darlington and succulent tree *Aloe ferox* in Baviaanskloof occurred abundantly as a consequence of degradation. Species richness was significantly correlated to patch size in all sites, but Kabouga had the greatest richness and probability of a suite of species occurring within a patch. Higher woody and succulent cover in Kabouga was therefore associated with higher soil C, root percentage and bulk density. Other sites were higher in Ca, Na, K and P.

The method of degradation scoring was not sufficiently accurate and it is recommended that indicator species within the matrix should be used instead of growth forms. The findings of this thesis are conceptualised within a double-cusped catastrophe model and recommendations for restoration are provided.

Table of contents

List of figures

List of tables

List of appendices

List of abbreviations and symbols

%	Percentage
%gravel	Percent gravel
%roots	Percent roots
%soil	Percent soil
<	Less than
>	Greater than
ABFRP	Addo Baviaanskloof Fish River Restoration Project
ANOSIM	Analysis of Similarities
ARC	Agricultural Research Council
ATB	Albany Thicket Biome
BG	Bare ground cover
BMR	Baviaanskloof Mega-Reserve
BNR	Baviaanskloof Nature Reserve
C	Carbon
C%	Carbon percentage
Ca	Calcium
Ca%	Calcium percentage
CAM	Crassulacean Acid Metabolism
CCBA	Climate, Community and Biodiversity Alliance
CDM	Clean Development Mechanism
CEC	Cation Exchange Capacity
CERs	Certified Emission Reductions
CFR	Cape Floristic Region
cmol	Centimole
cmol/kg	Centimole/kilogram
CO_2e	Carbon dioxide equivalent
COP	Conference of the Parties
DEA	Department of Environmental Affairs
DEM	Digital Elevation Model
DWAF	Department of Water Affairs
ECPTA	Eastern Cape Parks and Tourism Agency
g	Grams
g/cm^3	Grams per cubic centimetre
g/kg	Grams per kilogram
g/m^2	Grams per square metre
GAENP	Greater Addo Elephant National Park
GHG	Greenhouse gas
GIS	Geographical Information System
ha	Hectare
ha^{-1}	Per hectare
ha^{-1} $year^{-1}$	Per hectare per year
K	Potassium

Kg	Kilogram
kg ha^{-1} yr^{-1}	Kilogram per hectare per year
km^2	Square kilometres
M	Parameters
M	Metre
m^2	Square metres
Ma	Million years ago
MAP	Mean annual precipitation
Masl	Meters above sea level
MDS	Multi-dimensional scaling
MEA	Millennium Ecosystem Assessment
Mg	Magnesium
Mg	Milligram
Mg%	Magnesium percentage
mg/kg	Milligrams per kilogram
Mm	Millimetre
MMP	Mean monthly precipitation
MSP	Mean summer precipitation
MWP	Mean winter precipitation
My	Million years
N	Number of samples
Na	Sodium
Na%	Sodium percentage
NRM	Natural Resource Management
°C	Degrees Celsius
P	Phosphorous
p or *P*	P-value
Pa	Per annum
pH	Potential of hydrogen
R or *R*	Correlation coefficient
r^2	R-squared: Coefficient of determination
REDD+	Reduced Emissions from Deforestation and Degradation
S	State variables
SANParks	South African National Parks Board
SAWS	South African Weather Services
SE	Standard error
STEP	Subtropical Thicket Ecosystem Planning Project
STRP	Subtropical Thicket Restoration Programme
T	Ton
t C ha^{-1}	Tons of carbon per hectare
t C ha^{-1} yr^{-1}	Tons of carbon per hectare per year
UNCCD	United Nations Convention for Combatting Desertification
UNFCCC	United Nations Framework Convention for Combating Climate Change
VCS	Verified Carbon Standard

Ω	Ohms
x̄	Mean

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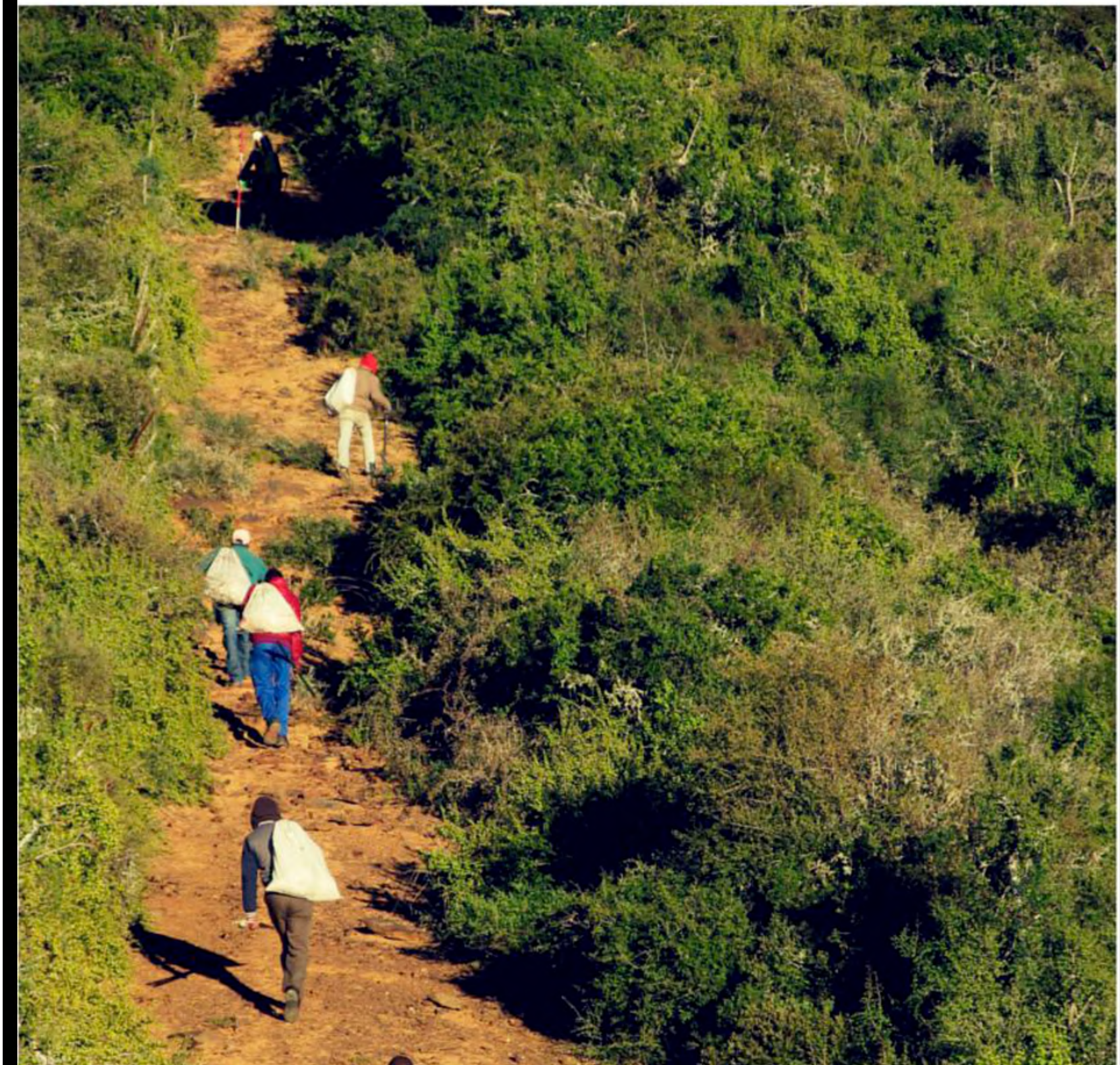
Thanks again,

Kyra

1 CHAPTER

GENERAL INTRODUCTION



CHAPTER 1: GENERAL INTRODUCTION

1.1. Drylands and degradation

Dryland systems as defined by the Millennium Ecosystem Assessment (MEA) are areas characterised by a limitation of water supply with major implications and strain placed on the dominant ecosystem services of primary production and nutrient cycling (Safriel *et al.*, 2005). The degree of water scarcity varies between the subtypes of drylands which cover roughly 41% of Earth's terrestrial area (Safriel *et al.*, 2005). Owing to the lack of a consistent water supply and the dependence of billions of people on dryland ecosystems, these areas are particularly vulnerable to degradation (Safriel *et al.*, 2005). Land degradation and the restoration of these lands in particular have become a major priority since the United Nations Convention to Combat Degradation and Desertification (UNCCD) was initiated in 1994 (UNCCD, 2012).

Land degradation in dryland ecosystems, commonly referred to as desertification, is defined as the continuous decline in the cumulative goods and services supplied by an ecosystem (Safriel *et al.*, 2005). The benefit of such a definition according to Scholes (2009) is three-fold: it is measurable based on ecosystem services, does not assume that a decline in land cover automatically results in degradation and excludes short-term fluctuations of the system. Similarly, the UN (1994) define land degradation as the biological or economic productivity of croplands, pastures, forests and woodlands that result in soil erosion, a loss in soil properties and a loss in vegetation cover and biodiversity with long-term effects. The exploitation of natural resources through agriculture and other farming practices are exacerbated by over-population and other socio-economic and political circumstances, especially when the system is inherently delicate (Kassas, 1995).

1.2. Concepts and models in understanding degradation processes in semi-arid ecosystems

Semi-arid systems are one of five sub-types of drylands as defined by Safriel *et al.* (2005). In describing semi-arid systems, Peters & Havstad (2006) design a conceptual framework (adapted in Figure 1) that incorporates multiple interconnected scales and non-linear dynamics. Five interacting elements affect connectivity within space and time (influenced by climate and disturbance) and include: historical influences, the site characteristics, wind, water and animal transport, resource distribution and lastly feedbacks (Peters & Havstad, 2006).

The framework highlights that the history of a landscape, be it geomorphological or land use related, is important in determining a baseline, which in turn impacts on the study area characteristics. At varying scales from landscape to plant or patch interspaces there is transport of resources and materials such as water, nutrients, litter and seeds by wind, water or animals (Peters *et al.*, 2006). This results in the distribution of resources, which in turn have feedbacks between the plants, animals and the soil. Natural or anthropogenic disturbances and changes in climate over time and space can affect resource distributions and feedbacks that put pressure on the thresholds of the system.

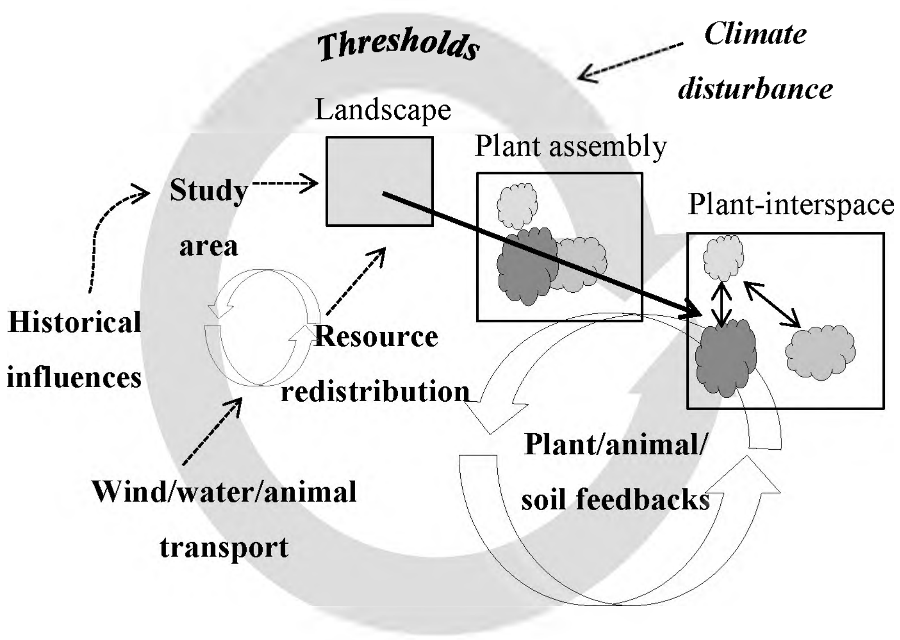


Figure 1: Conceptual framework of the dynamics of semi-arid systems. (Redrawn from: Peters & Havstad, 2006).

Proposed models of semi-arid degradation help in understanding the processes and interactions involved in degradation, resilience, thresholds and restoration success (Cortina *et al.*, 2006; King & Hobbs, 2006; Turnbull *et al.*, 2008). While some early research modelled degradation along linear models of change in ecosystem structure and function, such as that by Bradshaw (1984, in Cortina *et al.*, 2006), other models recognise the diversity of degradation on multiple scales and abiotic/biotic gradients, hence acknowledging the non-linearity in conceptualising degradation (Lockwood & Lockwood, 1993; Cortina *et al.*, 2006; King & Hobbs, 2006; Peters & Havstad, 2006; Turnbull *et al.*, 2008). Scholes (2009) alternatively describes degradation of drylands as a syndrome of multiple contributing symptoms, which directly relate to ecological structure and function. While detecting drivers or symptoms of degradation are important, the resilience of semi-arid areas are varied, making the identification of thresholds an important and difficult task in the conservation and restoration of reference vegetative states (Suding *et al.*, 2004; Cortina *et al.*, 2006).

1.2.1. Ecological thresholds, resilience and resistance

According to Peterson *et al.* (1998), the resilience of an ecological system is the amount of disturbance or change one ecological state, maintained by a suite of structural and functional processes, can withstand before it is transformed into another state, controlled by a different suite of functional and structural processes. However, Suding *et al.* (2004) refer to this as ecological resistance and rather resilience as the rate at which a system is able to return to its original state following major disturbance. Therefore, the point at which a system is no longer resistant and switches from one state to another, is known as the threshold. Large or small disturbances can result in large changes to a system and its structural and functional states, however the amount of change a system can take before changing to a different state is known as the threshold (Suding & Hobbs, 2009). When the system becomes persistent within an alternate state, having crossed a threshold, degradation occurs (Scholes, 2009).

1.2.2. Linear structure-function model

Ecosystem structure refers to the biotic (vegetation types and species) and abiotic (soil resources and nutrients) components of a system, while ecosystem function is the processes which retain ecosystem structure, such as abiotic nutrient and water cycling and biotic growth, establishment and mortality of species (Turnbull *et al.*, 2008). The model (Figure 2) illustrates degradation as occurring along an ecosystem structure and function gradient, where a loss in structure results in a loss in function and *vice versa* (Bradshaw, 1984, in Cortina *et al.*, 2006). The paths of degradation and recovery in this model are assumed to follow the same trajectory; however, this is often seen to not be the case in field studies (Maestre & Cortina, 2004). Therefore, Cortina *et al.* (2006) recommend that the linear structure function model (LSF model) by Bradshaw (1984) cited in Cortina *et al.* (2006), needs to integrate non-linear and even negative relationships in ecosystem structure and function and recognise alternate stable states.

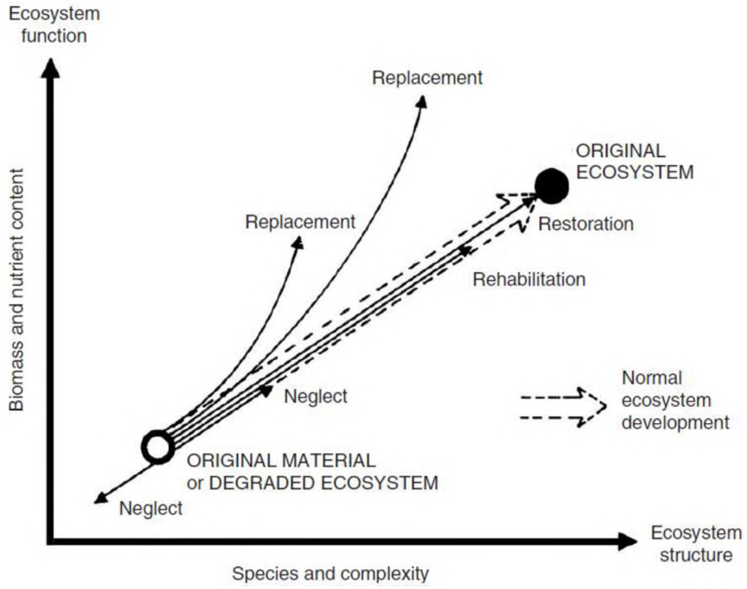


Figure 2: Linear Structure-Function Model (LSF) of changes in ecosystem structure and function in response to degradation (Source: Cortina *et al*., 2006).

Furthermore, by merging such a model with state-and-transition models, Cortina *et al*. (2006) suggest that possible restorative states can be recognised to achieve a desired state of ecosystem structure and function.

1.2.3. State-and-transition models and alternate stable states

The state of an ecosystem is the “climate/soil/vegetation domains that encompass a large amount of variation in species composition” (Stringham *et al*., 2003:7). A change from one state to another requires crossing a threshold due to a loss in ecosystem integrity and therefore a change in the plant communities (Stringham *et al*., 2003). The application of state-and-transition models is intended for the management of semi-arid rangelands. Multiple vegetation states can exist within a single rangeland, therefore the model is designed to monitor shifts from grassland to shrubland or changes in plant communities that can arise from changes in management or environmental factors (Ash *et al*., 1994; Rietkerk & Koppel, 1997; Stringham *et al*., 2003; Suding *et al*., 2004; Quétier *et al*., 2007).

Bestelmeyer (2015) illustrates two state-and-transition models, the first (A) being a typical model between two states separated by an ecological threshold, while the other (B) represents multiple states in response to management of reversing or preventing a transition from one state to another in relation to multiple thresholds (Figure 3).

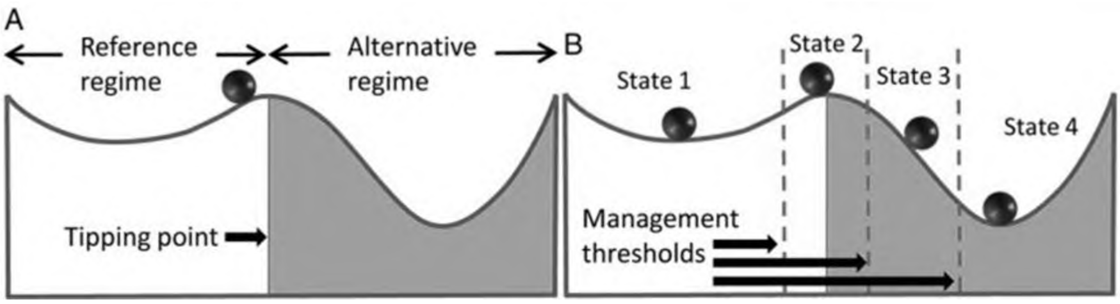


Figure 3: State-and-transition models of ecosystem thresholds, with and without management (Source: Bestelmeyer, 2015).

The ball represents the ecosystem and its movement. At state 2 for instance, the system can still be reversed and roll back to state 1. However, once state 4 is reached, the intervention to return the system back to its previous ecological integrity is much more difficult.

Stringham *et al.* (2003) found that using state-and-transition models was valuable in not only conceptualising vegetation change, but also in improving communication between managers of Australian rangelands and identifying knowledge gaps. The problem is that many state-and-transition model applications fail to fully acknowledge the relationship between ecosystem patterns and processes and therefore assume that the characteristics determining state thresholds are the same as the functional thresholds (Bestelmeyer, 2006).

Alternative states are the persistence of ecosystem states and environmental characteristics at varying spatial and temporal scales (Suding *et al.*, 2004). Beisner *et al.* (2003) describe the transition from one state to another as either occurring due to perturbations in variables defining the state or a change in the parameters controlling the state variables. These state variables include species diversity and composition, while the parameters refer to birth and death rates and carrying capacity (Beisner *et al.*, 2003; Suding *et al.*, 2006).

Alternative states can be viewed within a community and within an ecosystem. Where landscape is constant in a community, it changes within the ecosystem (Beisner *et al.*, 2003). A typical ball and cup analogy of changes from one state to another is conceptualised in Figure 4. Here Beisner *et al.* (2003) show that within an ecosystem, the parameters indicated by the letter 'M' change as a result of an external influence, which causes the ball to shift along a gradient of state variables indicated by the letter 'S'.

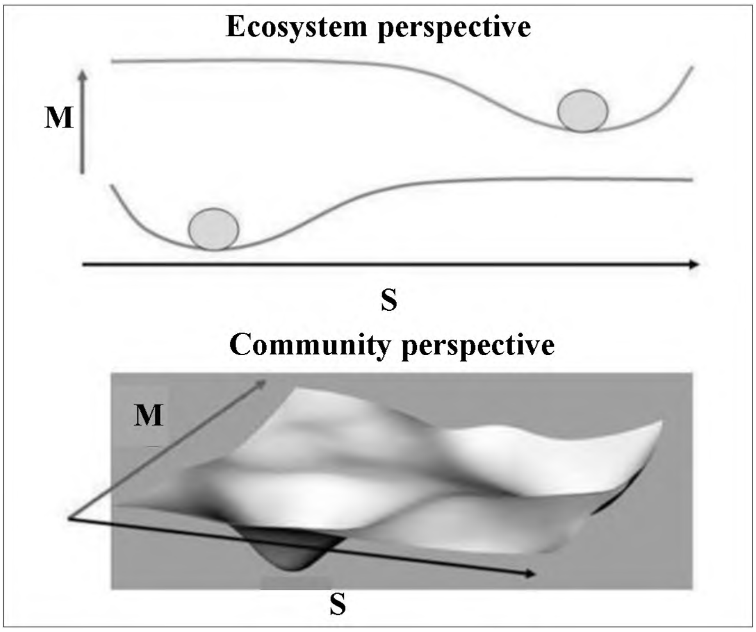


Figure 4: Alternate states in response to parameters (M) and state variables (S), within ecosystems and communities (Adjusted from: Beisner *et al.*, 2003:379).

In the community perspective however, the parameters are considered to be a state variable due to the feedbacks between it and the other state variables. Therefore, the ball is moved around the landscape because of the connectivity between the parameters and the state variables, which are separate within the ecosystem model (Beisner *et al.*, 2003).

Recognising degraded areas as alternative states is important in realising that trajectories of recovery differ from trajectories of degradation, otherwise known as hysteresis (Suding *et al.*, 2006). However, as highlighted by Beisner *et al.* (2003) the interactions between state variables and the parameters vary between community and ecosystem scales, which need to be incorporated into the management and restoration of degraded landscapes.

1.2.4. Cusp-catastrophe model

Lockwood & Lockwood (1993) describe the cusp-catastrophe model as incorporating both linear and state-and-transition models. Turnbull *et al.* (2008:31) hypothesise for the case of ecohydrological interactions, that "dynamics of land degradation are conceptualised by a cusp-catastrophe model in which the two controlling variables are abiotic structural connectivity and abiotic functional connectivity, which implicitly account for ecosystem resilience and biotic structural and functional connectivity." Five concepts underpin catastrophe theory as illustrated in Figure 5a (Lockwood & Lockwood, 1993; Turnbull *et al.*, 2008) and include: *bimodality* where two different states of vegetation exist within the same ecosystem, represented by the shift from grassland to shrubland in Figure 5b, a *region of inaccessibility*, defined as an unstable and non-persistent vegetative state between the two bimodal states, a *sudden jump* to an alternate state, which occurs when a system is forced to the edge of the cusp, *divergence* where slight changes in the state variables incur major changes to ecosystem function during a transition and lastly, *hysteresis*, which occurs when the trajectories of recovery and degradation or transition differ from each other; a shift from grassland to shrubland will therefore be different to the shrubland-grassland transition or jump.

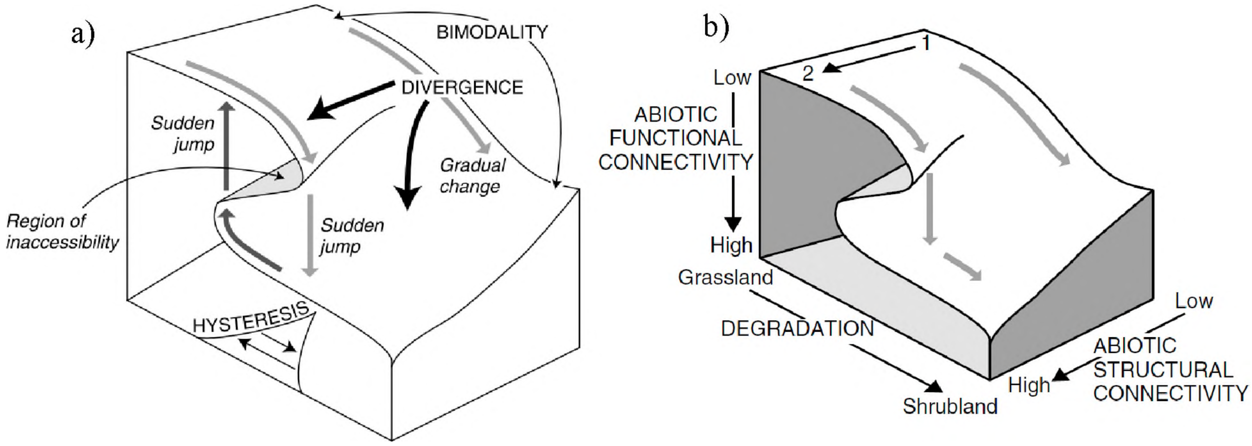


Figure 5: a) Diagram of cusp-catastrophe model theory and b) the shift from grassland to shrubland as a result of impacts on abiotic structural and functional connectivity (Source: Turnbull *et al.*, 2008).

The cusp-catastrophe model is beneficial in that it conceptualises the connections between processes at varying levels and feedbacks, while incorporating resilience (King *et al.*, 2012). The model was successfully used to hypothesise ecohydrological interactions in Kenyan rangelands in evaluating the various management techniques on *Sanseviera volkensii* invasion in grasslands (King *et al.*, 2012). Furthermore, cusp and state-and-transition theory have been used to model the relationships between abiotic and biotic variables. The critical transition as a system approaches a threshold is defined by the increase in abiotic stress and a decline in facilitation, which impacts on plant density (Verwijmeren *et al.*, 2013).

Plant density and resource availability are linked to water infiltration, where a decline in plant density is associated with limited infiltration and plant nutrient uptake (Rietkerk & Koppel, 1997). Similarly, fine textured soils characteristic of increased water-holding capacity and plant productivity occur where rainfall is higher, while lower rainfall areas have coarse soils, lacking moisture retention (Gosz & Sharpe, 1989).

It is evident that all of the above-mentioned models share many of the same basic elements determining the transition or degradation of a system from one vegetation state to another, be it ecosystem structure or function, pattern or process, or state variables and parameters; all these models illustrate the process of vegetation change. These interactions occur along different and often interlinking scales which many models fail to incorporate (Bestelmeyer *et al.*, 2006). Therefore, the role of scale should not be overlooked in assessing ecological systems and their degradation and restoration potential.

1.3. Scale, hierarchy theory and spatial organisation in ecology

The concept of scale in ecology is a difficult concept to define (Sayre, 2005). According to Turner *et al.* (1989), the scale of an object or process has both spatial and temporal dimensions. Temporally, the relationship among components of a system and between ecosystem states can be stable over certain periods of time, along hourly, yearly and even centennial scales (Sayre, 2005). Practically, spatial scales are useful in defining boundaries of measurement. However, in reality, nature has few definitive boundaries in space and time (Sayre, 2005). Furthermore, deductions at one scale of research may differ from those at another scale, therefore scaling down or up is not an applicable method of extrapolating local system characteristics, for example to the landscape (Wiens, 1989; Marriot & Carrère, 1998; Sayre, 2005). Nevertheless, scale is characterised by the grain and extent of the research area. The grain is the finest level within a data set, while the extent is the size of the study area (Turner *et al.*, 1989). The fine-grained studies generally occur within an area of small extent due to the complexity and size of the data set that would be required for fine-grained studies at large extents (Sayre, 2005).

The concept of hierarchy theory incorporates multiple temporal and spatial scales into the assessment or monitoring of biodiversity at multiple levels of organisation (Franklin *et al.*, 1981, in Noss, 1990). Lower levels within the hierarchy are generally nested within higher levels (Wu & David, 2002) and the scales of pattern exist due to the presence of process and *vice versa* (Turnbull *et al.*, 2008). Levels of organisation include three interlinking attributes of ecosystems, namely structure, function and composition (Noss, 1990). Among these attributes exist indicators of environmental condition at varying levels of spatial organisation. Noss (1990) lists four levels of spatial organisation, which include the regional landscape, the community-ecosystem, the population-species and genetic levels. These refer specifically to the biodiversity (i.e. only biotic components). Similarly, the levels of spatial organisation align with Forman (1995) and ecological principles of land mosaics. However, these mosaics include the human-ecological interface and not explicitly the ecological hierarchies as monitored by ecologists at varying organisational levels.

The regional landscape level refers to the combination of both the landscape and region in simplifying the complexity of the two often interchangeable scales (Noss, 1990). The landscape is a series of local ecosystem types or land uses that are contiguous over a landform and exist within a region of any chosen or previously defined scale (Noss, 1990; Forman, 1995). The community-ecosystem level includes the "populations of species which co-exist within a site", while the ecosystem refers to the abiotic and biotic interdependent components of the community (Noss, 1990:360). In the population-species level, focus is on individual species and the distribution of these species within populations (Noss, 1990). The genetic level of organisation is not relevant to the scope of this study.

1.4. Using ecological indicators to monitor degradation and vegetation change

Monitoring of ecosystem change requires much dedication from multidisciplinary networks to establish a good monitoring programme. Lindenmayer & Likens (2010:1318) define long-term monitoring as "repeated field-based measurements that are collected continuously and then analysed for at least 10 years." They suggest that adaptive monitoring be applied to improve long-term monitoring projects as new questions arise over time (Lindenmayer & Likens, 2009). While monitoring ecosystems is an admirable task, many monitoring projects fail because they try to monitor too much, are not driven by good, scientifically based questions, haven't incorporated a good statistical design and are generally just managed poorly (Lindenmayer & Likens, 2010). While these can be managed and controlled, there are some extra-ordinary circumstances that can occur during the monitoring project, such as loss of key staff, loss in funding or even natural disasters that affect the integrity of the data collected (Lindenmayer & Likens, 2010).

Using species abundance and distributions and their connections to the physical environment, biodiversity monitoring aims to look at the status and changes in biodiversity over spatial and temporal scales (Niemelä, 2000). Furthermore, biodiversity monitoring can include many levels and entities for assessment (Niemelä, 2000) and can be monitored using a range of biological indicators specific to ecosystem structure, function and composition (Noss, 1990).

Biological *function* is not an objective of this thesis. However, monitoring indicators of functional integrity at the regional and landscape scale include processes of disturbance, rates of nutrient cycling, energy flows, turnover rates and hydrological processes (Noss, 1990). At the community-ecosystem level, these include measuring herbivory, colonisation, patch dynamics and biomass rates, while at the population and species level, functioning can include species recruitment and mortality rates, life history strategies and adaptation (Noss, 1990).

Biodiversity *structure* can be measured using indicators of heterogeneity and connectivity, patchiness, fragmentation and habitat pattern at the regional landscape level. Within the domain of communities and ecosystems, structure can be measured using the indicators of slope and aspect, soil variables, vegetation biomass and canopy cover, while at the population and species level, structure is indicated by dispersal mechanisms and population structure, such as the age and sex of individuals (Noss,1990).

Biodiversity *composition* can be indicated by distribution, richness and joint patterns of species distributions and richness at the regional landscape; by species and growth form, threatened and endangered species proportions and dominance-diversity curves within the community-ecosystem; as well as by abundance of species, cover values and densities at the population-species levels (Noss, 1990).

At the regional-landscape scale, measurement often uses Geographical Information Systems (GIS) for analysis of aerial imagery, remote sensing, time series analysis and various statistical and mathematical indices (Noss, 1990). The same can be said for the community-ecosystem and population-species level but includes more ground-truthing and rigorous sampling methods and modelling (Noss, 1990). Monitoring of some of these indicators, especially after establishing a baseline of the current state of a system at varying scales, is vital in identifying areas of importance where ecological function, structure and composition is being influenced by external disturbances.

1.5. Land degradation and implications to ecological integrity

The integrity of an ecosystem or landscape can be defined as the intactness of the indigenous vegetation and soil structure and the maintenance of these by functional processes (Ludwig *et al.*, 2004). Degradation has different significant impacts depending on the level at which disturbance or degradation occurs, as well as the type and severity of disturbance over space and time scales. Disturbance can be defined as “a change in the minimal structure caused by a factor external to the level of interest” (Pickett *et al.*, 1989:132). Some systems, however, experience degradation from disturbance factors specific to non-external pastoral and agro-pastoral interests. Much of the semi-arid degradation literature focuses on grassland degradation through over-grazing (Milchunas *et al.*, 1989; Marriot & Carrère, 1998; Ludwig *et al.*, 2004; Snyman & Du Preez, 2005), but other disturbances and factors increasing degradation include: over-browsing (Lechmere-Oertel *et al.*, 2005a; Hester *et al.*, 2006; Sigwela *et al.*, 2009); drought (Vetter, 2009) and long-term climate change (Scheiter & Higgins, 2009); as well as a total transformation of land for agriculture (Rouget *et al.*, 2003; Lunt & Spooner, 2005).

In both moderately over-grazed and over-browsed ecosystems, species heterogeneity may be high at local levels, however across the entire degraded landscape, grazing and browsing cause a homogenisation of species composition (Asner *et al.*, 2003; Lechmere-Oertel *et al,* 2005b; Rutherford *et al.*, 2012). Homogenisation occurs when plant species assemblages become dominated by a few widespread species (Mace *et al.*, 2005). Furthermore, studies of highly utilised and lightly utilised sites (grazed or browsed) show that areas that are more severely degraded have lower species diversity, increased bare ground and reduced soil quality (Tessema *et al.*, 2011; Rutherford *et al.*, 2012), as well as a higher incidence of alien and annual species and increased soil bulk density (Yates *et al.*, 2000). Increased aliens and annuals in response to disturbance in degraded systems not only change the species composition but also the guild or growth form structure (Holmes & Cowling, 1997; Lechmere-Oertel *et al.*, 2005b). In grasslands, over-grazing allows for the colonisation of shrubby species, which over time and with consistent grazing causes the grasslands to become shrublands (Peters *et al.*, 2006). In over-browsed areas, woody species decline in cover and abundance and reveal bare areas colonised by annual grasses, dwarf shrubs and herbaceous weeds (Anderson & Hoffman, 2006; Rutherford *et al.*, 2012). At fine scales or at the species-population level, degradation changes the structure of vegetation where plants exhibit architectural shifts in leaf, stem and root structures that are adapted to harsher conditions and increased exposure to herbivory (Anderson & Hoffman, 2006; Quétier *et al.*, 2007).

Geomorphic processes such as runoff and erosion that are exacerbated by wind and water and the loss in vegetation biomass, fall under a modern research interest of ecohydrology. Ecohydrology has become a necessary transdisciplinary research paradigm in the understanding of plant, water and nutrient feedbacks between degraded semi-arid patches and inter-patches (Ludwig *et al.*, 2004). Understanding these feedbacks assists in understanding the connectivity between ecosystem structure and function and therefore ecological integrity.

The feedbacks between vegetation and soil become most apparent with degradation, as impacts are more visible through erosion features. Soil erosion occurs when there is a loss in vegetation cover and root biomass to hold and shelter the soil from raindrops, runoff and wind (Safriel *et al.*, 2005). These sediment and sand transport processes leave degraded areas often riddled with deep gullies, rills and tussocks (King & Hobbs, 2006; Kakembo, 2009; Dickie & Parsons, 2012), reducing soil fertility and nutrients, often causing a loss in both biological and chemical soil properties (Lavelle *et al.*, 2005). Furthermore, over-grazing often causes compaction of the soil, which constrains the growth of roots and hence the nutrients they provide to the plants (Yates *et al.*, 2000). Degraded soils are often characterised as having a high pH, high electrical conductivity, reduced soil carbon and nitrogen as well as a risk of salinisation (Oldeman, 1992; Tongway *et al.*, 2003; Snyman & Du Preez, 2005; Traoré *et al.*, 2015).

1.6. Natural vegetation recovery and restoration

Following cessation of or a decline in degradation and disturbance, ecosystems may undergo a series of changes in vegetation composition in which the ecosystem starts to recover. Depending on the type and severity of the disturbance and the resilience of the system, the natural recovery, as explained before, may not follow a linear path, but rather recovers through multiple states (Cortina *et al.*, 2006). Multiple stable states according to Young *et al.* (2001) occur during species assembly, as species colonise, establish and interact to form a community. This differs from community succession, which assumes a single climax state. However, multiple states are identified in succession as those which have not achieved the climax reference condition (Young *et al.*, 2001).

Plants interact within an intricate system of abiotic and biotic stresses that allow for competition and facilitation between species (Callaway & Walker, 1997). Under extreme conditions, such as that following disturbance or degradation, plants compete for available nutrients and water, with the first colonising species showing better adaptation to harsher environmental stress-gradients (Odum, 1985). The study of primary succession aims to understand the change of species on surfaces which have been severely disturbed and are infertile and unstable (Walker & Del Moral, 2008). Furthermore, primary succession is valuable for temporal studies, such as chronosequences and can provide insight into soil development over the long term (Walker & Del Moral, 2008). In secondary succession, the vegetation establishes on a much less severe surface than in primary succession and occurs in disturbed areas, such as old agricultural lands (Finegan, 1984). In succession, environmental changes occur that are either autogenic or allogenic. Autogenic changes occur due to the presence of plants, while allogenic changes are external, such as variations in climate (Finegan, 1984). Theories of such changes include facilitation, tolerance and inhibition. Facilitation theory, which is autogenic, occurs when early successional species change the environment, improving the conditions and allowing later successional species to establish (Connell & Slatyer, 1977). Tolerance alternatively occurs when later successional species persist in low resource environments, simultaneously with early successional species (Connell & Slatyer, 1977). Lastly, inhibition occurs when initial vegetation creates long term stability, preventing the establishment of other species (Connell & Slatyer, 1977). By understanding and combining knowledge of the recovery, succession and community assembly of multiple stable states and their structure and function in degraded and transformed lands, better recommendations for the restoration of these lands can be made (Prach & Hobbs, 2008; Walker & Del Moral, 2008; Prach & Walker, 2011).

Restoration provides assistance to the natural recovery process following the degradation or transformation of an ecosystem and has the potential of improving resilience (Bullock *et al.*, 2011; Wortley *et al.*, 2013). Restoration aims to improve biological diversity and in so doing improve ecosystem function and the services that they provide (Prach & Hobbs, 2008; Bullock *et al.*, 2011). Methods of restoration can include improving the soil conditions and reducing the erosion potential, revegetating areas through direct planting or re-seeding the landscape (Snyman, 2003; Baasch *et al.*, 2012). Wortley *et al.* (2013) found that 63% of reviewed literature used planting as the dominant method for ecological restoration. Simply planting for example, can be tricky since focusing on a particular service or variable of ecosystem recovery could have negative consequences to other ecosystem services or the recovery of other species (Bullock *et al.*, 2011). While restoration is focused on returning a system back to its reference condition, it should rather be recognised that such goals are not always adequate and rehabilitation to different multiple stable states is often greatly more reachable (Aronson *et al.*, 1993).

1.6.1. Old lands: recovery and restoration

Old lands are the result of a complete transformation of a system and provide important opportunities to study secondary succession and recovery (Cramer *et al.*, 2008). The recovery and restoration of abandoned agricultural lands becomes more difficult when abiotic and biotic thresholds such as soil composition, nutrient cycling and seed dispersal are crossed as a function of increased extent, duration and intensity of agricultural activity (Cramer *et al.*, 2008). Differences in land use history and cropping have been shown to influence community ordination and succession, respectively in semi-arid Spanish old fields (Bonet, 2004). High turnover of species was found in mesic old fields, but colonisation declined after five years and successional transitions were associated with drought events (Bartha *et al.*, 2003). Lack of vegetation structure was observed in initial successional old field communities, however, an increase in woody species in the second successional phase 10 years later, found that patch size had a positive effect on community composition (Schweiger *et al.*, 2000). Furthermore, the establishment of woody species in old fields declines with latitude (Wright & Fridley, 2010). Reisman-Berman *et al.* (2006) suggest that dispersal and establishment in old fields are limited and interact to determine processes of recolonisation.

1.7. Desertification in semi-arid South Africa

Livestock farming has contributed significantly to changes in species composition and soil quality across South Africa (Milton & Dean, 1995; Rutherford & Powrie, 2013), with impacts on plant cover and soil fertility being recognised as early as the 1930s (Potgieter, 1970). The observed hydrological impact on soil and rivers over the years was directly attributed to over-grazing in many South African rangelands and not to any decline in rainfall (Milton & Dean, 1995). Changes in plant structure and composition in response to degradation vary between South African biomes and under different land uses (Rutherford & Powrie, 2013). Historically, land under private commercial tenure were better resourced compared to communal areas, indicating an expected difference in the degradation processes (Meadows & Hoffman, 2002). For instance, cattle grazing in savannas results in bush encroachment due to reduced competition from grasses for emergent trees, while continual defoliation from browsers substantially decreases the cover and the diversity of plant functional types (Scholes, 2009). Alternatively, desertification processes in the eastern Karoo are thought to cause a shift from grassland to shrubland, however, whether this is due to climate or over-stocking by domestic livestock, is fiercely debated (Hoffman *et al.*, 1995).

Angora goats were introduced to South Africa in 1838 and were farmed almost exclusively in the Eastern Cape where they browsed on all plant types not commonly eaten by other livestock (Hugo, 1972: in Potgieter, 1972). Between 1956 and 1960 there were 863 000 Angora goats and 1 567 000 Boer goats farmed commercially (Potgieter, 1976). Total goat numbers in South Africa decreased from 2 770 000 in 1961-1965 to 2 211 000 in 1971-1975 (Potgieter, 1976). In semi-arid and arid areas of the Eastern Cape, goats have had the greatest contribution to degradation of the Subtropical Thicket Biome (Lechmere-Oertel, 2003) and have become the focus of research into the impacts of over-browsing on thicket structure, composition and function.

1.8. The case of the Subtropical Thicket Biome

Subtropical Thicket is a highly diverse biome with at least 20% endemic species (Vlok & Euston-Brown, 2002) and linkages to Cape, Karoo-Namib and Tongaland-Pondoland phytochorological regions (Cowling, 1983). The Subtropical Thicket Biome (See Chapter 2 for full description) includes 112 divisions of thicket (Vlok & Euston-Brown, 2002) and historically covered an area of 47 442 km^2, including both solid and mosaic thicket types (Lloyd *et al.*, 2002; Vlok & Euston-Brown, 2002). Thicket is characterised by a dense canopy of small woody trees and large woody shrubs of between 0.5 and 3.0 m tall (Vlok *et al.*, 2003). Furthermore, the canopy is intertwined with lianas and below the canopy a combination of shade-tolerant herbs, succulents and grasses can be found (Vlok *et al.*, 2003). Of greatest importance to this study, as well as for the purpose of reducing greenhouse gas emissions, are the spekboom-dominated thickets that occur in the semi-arid to arid regions of its spatial extent. Spekboom (*Portulacaria afra*) is a keystone species within semi-arid areas of the Subtropical Thicket Biome (Lechmere-Oertel, 2003). It is a succulent shrub and tree that can switch from C3 photosynthesis to Crassulacean Acid Metabolism, otherwise known as CAM photosynthetic pathway (Ting & Hanscom, 1977). It is a specialised plant capable of sequestering large amounts of carbon into the soil from its roots and leaf litter (Mills & Cowling, 2006) and has become an important plant for the restoration of degraded thicket through potential funding from carbon credit incentives (Marais *et al.*, 2009). Its photosynthetic method allows it to endure periods of drought of up to 130-140 days (Guralnick & Ting, 1987) by closing its stomata and preventing water loss (Ting & Hanscom, 1977). It thus provides valuable fodder to livestock and game in these drought periods but over-stocking has major implications to spekboom abundance and the degradation of spekboom-dominated thickets (Kerley *et al.*, 1995).

1.8.1. Degradation and recovery of the Subtropical Thicket Biome

The semi-arid, spekboom-dominated thickets have been moderately to severely degraded from over-browsing by goats, dating back to the late 1800s (Lechmere-Oertel, 2003). However, with a sharp rise in Boer and Angora goat pastoralism since the 1960s, the degradation of these thickets has become much more prevalent (Lloyd *et al.*, 2002; Lechmere-Oertel *et al.*, 2005b) and was predicted to have major links to desertification in the future (Acocks, 1988). At least

42% of the solid thicket types have been severely degraded by domestic livestock or have been transformed for agriculture and settlement (Lloyd *et al.*, 2002). The arid thicket types, containing the highest abundance of spekboom, showed the most degradation, with 60% of the solid thicket types and 88% of the mosaic thicket types, showing severe degradation (Lloyd *et al.*, 2002).

Severely degraded thickets have a substantially reduced woody biomass and complete loss in functionality, while moderately degraded thickets show structural changes in vegetation and a decline in standing biomass, yet retain their functionality (Lloyd *et al.*, 2002). The structural and functional implications from over-browsing by goats are especially evident through the study of fence-line contrasts of vegetation and soil composition with intact reference conditions (Kerley *et al.*, 1995; Lechmere-Oertel, 2003; Sigwela *et al.*, 2009; van Luijk *et al.*, 2013), as well as more fine-grained studies of individual species and processes (Stuart-Hill, 1992; Moolman & Cowling, 1994).

The Subtropical Thicket Biome has vegetation characteristics that are not typical of semi-arid environments and its dynamics are less understood compared to studies of rangelands and savanna (Kerley *et al.*, 1995; Lechmere-Oertel *et al.*, 2008; Sigwela *et al.*, 2009). Despite this, it does show some similar responses to degradation of other semi-arid regions, such as declines in overall species richness and diversity, with particular declines in woody shrubs, succulent shrubs and woody trees (Kerley *et al.*, 1995; Lechmere-Oertel *et al.*, 2005b; Rutherford *et al.*, 2012). Loss in above and below ground biomass increases bare ground patches and decreases soil moisture and retention (Lechmere-Oertel *et al.*, 2005a; van Luijk *et al.*, 2013). This increases the runoff potential where sediment loads are recorded as being six-fold more in transformed thicket compared to intact thicket in the Baviaanskloof (van Luijk *et al.*, 2013). The loss in top soil has severe implications to the loss of nutrients in the soil, which coupled with reduced plant biomass and litter, reveals substantial losses in total carbon, soil carbon and nitrogen content and reductions in soil organic matter (Mills & Fey, 2004; Lechmere-Oertel *et al.*, 2005a; Lechmere-Oertel *et al.*, 2008; Powell, 2009).

Thicket does not recover following degradation, due to a lack of regeneration of woody thicket seedlings (Stuart-Hill & Danckwerts, 1988). Seedlings in the Sundays River Valley were barely found in spekboomveld, however in spekboom thicket 94% of seedlings were found beneath thicket clump canopies (Sigwela *et al.*, 2009), indicating the importance of nurse plants in the establishment and regeneration of thicket species. Furthermore, germination of many species depends on long periods of increased soil moisture (Wilman *et al.*, 2014), which is higher in canopy micro-sites (van Luijk *et al.*, 2013). For the establishment of *P. afra*, the woody shrub *R. obovatum* was found to be an important nurse plant in arid regions, while woody tree seedlings also depend on remnant *P. afra* clumps (Adie & Yeaton, 2013). However, although woody plant regeneration does occur, recovery to an intact thicket state is much more difficult. In its degraded state, thicket is said to persist within an alternate stable state which would require restoration to return the system back to its reference condition (Van der Vyver *et al.*, 2013).

Old lands occupy a small percentage of degraded thicket (Powell, 2009) yet the risk for future clearing of thicket by both communal and commercial farmers, especially in mesic thicket, is high (Lloyd *et al.*, 2002). Old lands typically occur in bottomland regions adjacent to drainage lines, where it is expected that both root and soil carbon is higher as a function of the deeper soils (Powell, 2009). In Baviaans Spekboom Thicket, old lands had 3.43±0.78 and 24.06±2.34 t C ha^{-1} of root and soil carbon, respectively (Powell, 2009). Furthermore, old lands in Baviaanskloof are associated with *V. karroo* and *Searsia* species (Powell, 2009). Old lands on a commonage in Bathurst, surrounded by mesic valley thicket, showed recovery of open woodland into grassland, where the trees were on average <2 m in height and dominated by *V. karroo* (Puttick *et al.*, 2011).

1.8.2. Global incentives to and restoration of Subtropical Thicket

The commissioning of the Baviaanskloof Subtropical Thicket Research Pilot Project by the Department of Water Affairs and Forestry (DWAF) in 2003, had success in testing the viability of restoring degraded thicket landscapes and establishing a restoration programme for the entire biome (Powell *et al.*, 2006). This led to the development of the Subtropical Thicket Restoration Programme (STRP), under the Working for Woodlands Programme. The STRP currently operates under the Working for Ecosystems Programme of the Natural Resource Management Programme (NRMP), headed by the Department of Environmental Affairs (DEA). The STRP focuses on the benefits of adopting restoration of degraded lands to improve biodiversity and sequester carbon as a way to promote investment into the Eastern Cape through the carbon economy (Marais *et al.*, 2009; Mills *et al.*, 2015). The Subtropical Thicket Ecosystem Planning (STEP) Project was initiated in 2000 to raise awareness of thicket degradation and transformation and promote conservation strategies (Knight *et al.*, 2011). The STEP classification of vegetation type and condition have become a vital and compulsory resource in the restoration of degraded lands and the conservation of pristine vegetation with the onset of socio-economic pressures (Knight *et al.*, 2011).

Restoring thicket is not a simple or quick rewarding task (Marais *et al.*, 2009; Powell, 2009; Van der Vyver *et al.*, 2012). It is unlikely that the leading option for restoration through planting *P. afra* truncheons will return the thicket back to its pristine state, but rather a different more functional alternate system state that is better in providing ecosystem services and improving ecosystem integrity than a degraded state (Marais *et al.*, 2009). As a keystone species of thicket, *P. afra* truncheons are used in the restoration of thicket due to its capability of establishing roots from cut stems (Powell, 2009; Van der Vyver *et al.*, 2012). Planting truncheons are more effective than planting seeds of varying thicket species that aren't guaranteed to germinate (Wilman *et al.*, 2014), or planting nursery propagated woody species (Van der Vyver *et al.*, 2012). Furthermore, *P. afra* is able to sequester large amounts of carbon in excess of 100 t C ha^{-1} at rates between 1.2 and 4.2 t C ha^{-1} per year, adding monetary incentive for restoration of these lands through carbon credits (Marais *et al.*, 2009).

The system of carbon credits stems from the Clean Development Mechanism (CDM), one of the Kyoto Protocols' three methods of reducing emissions in a clean and cost effective manner (UNFCCC, 2014). The CDM allows countries to earn and trade certified emission reductions (CERs) equivalent to one ton of carbon-dioxide or carbon-dioxide equivalent (CO_2e). The CDM is designed for more developed countries with assumed higher GHG emissions to invest in sustainable and registered projects within developing countries. Furthermore, REDD+ (Reduced Emissions from Deforestation and Degradation), founded in December 2010 following the 16th COP (Conference of the Parties) UNFCCC Conference, aims to mitigate the impacts that deforestation and degradation has on climate change (UN-REDD, 2011). The plus refers to the conservation of these forests whilst enhancing their carbon stocks and managing them sustainably (UN-REDD, 2011). According to UN-REDD (2011), the adoption of REDD+ is as a result of the 15-17% contribution of deforestation and degradation to global greenhouse gas emissions. In aiming to protect forests and reduce carbon emissions via deforestation and land degradation, REDD+ can also act as a co-benefit to the conservation of both floral and faunal biodiversity (Harrison *et al.*, 2012) and acts as an incentive to restore degraded landscapes.

The STRP and its various restoration projects within protected thicket areas as well as private lands, are registered projects with the Verified Carbon Standard (VCS), who monitor GHG programmes and strive for global best practice among its carbon projects (VCS, 2016). Furthermore, the Addo Elephant National Park, Baviaanskloof Nature Reserve and Fish River Nature Reserve Restoration Project (ABFRP) is a registered project with the Climate, Community and Biodiversity Alliance (CCBA) (SGS, 2011). The CCBA is an international NGO whose mission is "to stimulate and promote land management activities that credibly mitigate global climate change, improve well-being and reduce the poverty of local communities, and conserve biodiversity" (CCBA, 2016). Following the baseline research of the ABFRP, the planting of *P. afra* is intended to improve carbon pools, including litter, soil, deadwood and biomass (SGS, 2011). So far the STRP has planted over 10 000 ha of spekboom truncheons at a density of 2 500 stems per hectare and has the world's largest on-going restoration experiment (Mills *et al.*, 2015). The baseline data collected from the ABFRP, one of the STRP projects, has provided the opportunity to carry out the following research.

1.9. Purpose of the research

The majority of thicket degradation research has focused on the contrasts of intact versus degraded states and the impacts that over-browsing has had on abiotic and biotic structure and function (Lechmere-Oertel *et al.*, 2005a; Lechmere-Oertel *et al.*, 2005b; Lechmere-Oertel *et al.*, 2008; Sigwela *et al.*, 2009; Rutherford *et al.*, 2012) or contrasts in thicket degradation between different land tenures (Evans *et al.*, 1997; Fabricius *et al.*, 2002). With few exceptions, many studies have been localised to tractable research areas of small spatial extent. Extrapolating such findings at fine scales is not necessarily applicable to the ecosystem or regional-landscape, especially in the diverse thicket biome. This study recognises degraded thicket as possibly having multiple distinct vegetation states on a large scale and assumes that there is diversity and heterogeneity in species composition, regardless of the degraded nature of the study area.

The study therefore aims to use baseline data from STRP projects, collected for long-term monitoring of spekbooom restoration projects, to quantify both abiotic and biotic structure and composition at varying spatial extents, levels of organisation and temporal scales. The study further aims to distinguish scales of degradation within areas defined as being severely degraded and compare species composition, soil composition and patch attributes among scales. It is hoped that insights into degraded thickets of the Greater Addo Elephant National Park and the Baviaanskloof will be used in applying restoration techniques that follow models of system states and recognise the connectivity of such structural components with functional components that are beyond the scope of this thesis.

Chapter 2 is a comprehensive description of the study sites with particular comparison made between climate, geomorphology and topography, as they are important in interpreting the results in Chapter 3.

Chapter 3 seeks to find A relationship between species composition and the environmental characteristics within the landscape and within sites. It further looks at growth form structure, species richness and soil composition within each site. Using growth form as an indicator of intactness, degradation scores were developed to distinguish gradients of degradation, which were then tested for differences in species and soil composition.

Chapter 4 further uses these degradation scores to assess how patch attributes differ between scores and within and between sites. An analysis of vegetation cover change over time using GIS on aerial and satellite imagery from 1939 to 2009, aimed to see if the duration of degradation influenced current species composition. Furthermore, dates of proclamation into a protected area were used to look at recovery times.

Chapter 5 synthesises the results into a model of thicket degradation, with reference to abiotic and biotic structure and composition and resilience and provides recommendations for restoration.

2 CHAPTER

STUDY AREAS

CHAPTER 2: STUDY AREAS

2.1. The regional landscape: the Subtropical Thicket Biome

Originally classified under Karoo or Karroid veld types and known as Valley Bushveld (Acocks, 1953: in Evans *et al.*, 1997), the Subtropical Thicket Biome has had a long history of classification and description. Acocks (1988) describes Valley Bushveld as occurring within the river valleys that drain into the Indian Ocean and highlights six divisions. These include a Southern and a Northern Variation, Fish River Scrub, Addo Bush, Sundays River Scrub and Gouritz River Scrub. While the Northern Variation is more open, with fewer succulents and *Euphorbias* and more grasses, the Southern Variation is denser and dominated by tree *Euphorbias* within a scrub forest (Acocks, 1988).

Fish River Scrub has adapted from Valley Bushveld to the higher temperatures, lower rainfall and wider, flatter valleys of the region (Acocks, 1988). Intact Fish River scrub is an "extremely dense, semi-succulent, thorny scrub, about two metres high" (Acocks, 1988: 61), where thorny and succulent plants are considered to be characteristic. Sundays River Scrub is similar to the Fish River Scrub, however is taller with fewer succulents (Acocks, 1988). Addo Bush, is a "short, dense and dry forest" (Acocks, 1988:63). Both Addo Bush and Sundays River Scrub appear to have lineages with Alexandria forest due to a lack of obstruction between it and the Indian Ocean (Acocks, 1988). Gouritz River Scrub is very similar to Sundays River Scrub, however Aloe species replace the tree *Euphorbia* species (Acocks, 1988). Of equal importance is the noorsveld, which occupies an area central to the Sundays River Valley. In its intact state, it resembles degraded Fish River Scrub and is dominated by *Euphorbia caerulescens* (noors) in amongst small tree species (Acocks, 1988). Spekboomveld is found on the northern slopes of the mountains adjacent to noorsveld (Acocks, 1988).

Following Acocks' classification, Cowling (1983a) described the Valley Bushveld as 'Subtropical Transitional Thicket' containing two communities; Kaffrarian thicket and Kaffrarian Succulent Thicket. Kaffrarian Succulent Thicket differs from Kaffrarian Thicket by its' Karoo-Namib phytochorological links (Cowling, 1983a). Everard (1987; in Lechmere-Oertel, 2003) later expanded the Succulent Transitional Thicket to include both a mesic and xeric form of Kaffrarian Thicket and Kaffrarian Succulent Thicket. It was only almost 10 years later that Low & Rebelo (1996) defined thicket as being its own biome. Their classification consisted of five vegetation units: dune thicket, valley thicket, xeric succulent thicket, mesic succulent thicket and spekboom succulent thicket.

The most substantial and detailed classification of the vegetation types within the Thicket Biome came following a large-scale project known as STEP (Figure 6). Vlok & Euston-Brown (2002) defined and mapped 112 different thicket types whilst Lloyd *et al.* (2002) quantified the extent of their degradation, for use in conservation planning within the Subtropical Thicket Biome.

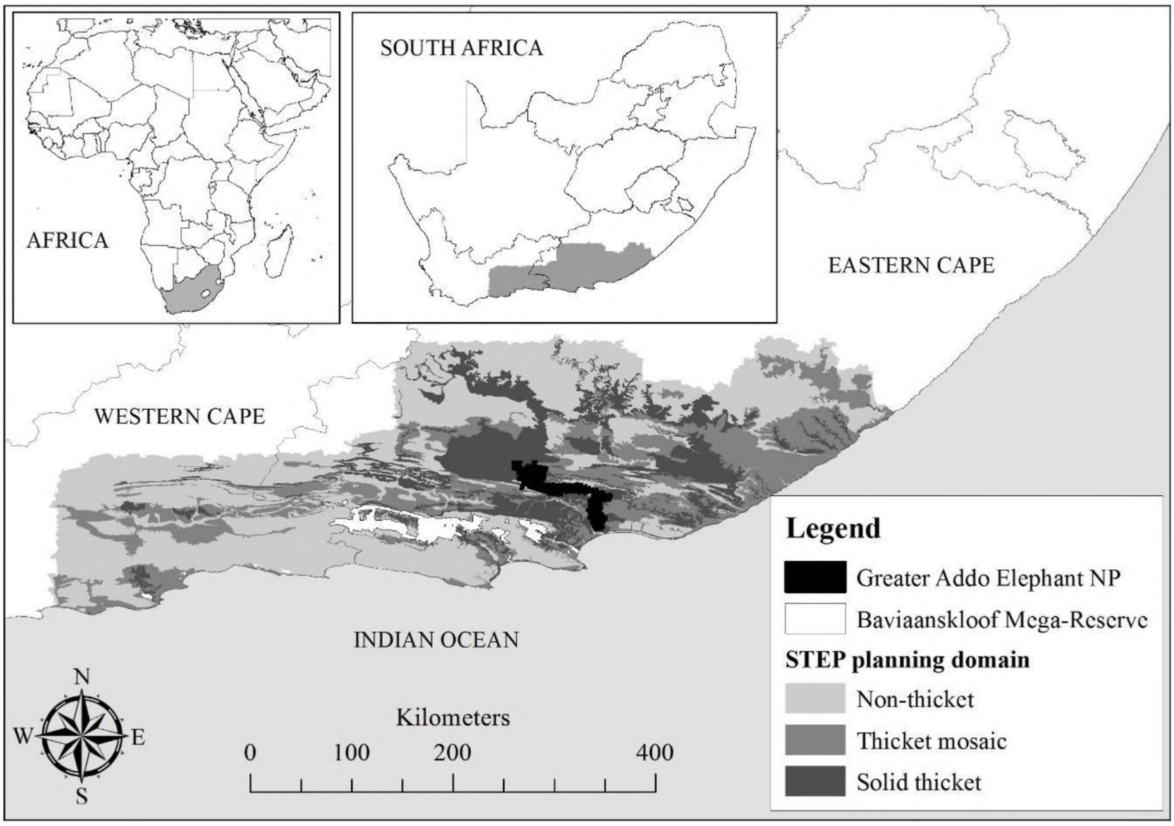


Figure 6: The spatial extent of the STEP planning domain in South Africa (Adapted from STEP, Vlok & Euston-Brown, 2002).

Two categories of thicket are identified, namely mainland and dune thicket. Mainland thicket consists of three main vegetation units: valley thicket, arid thicket and thicket (Vlok & Euston-Brown, 2002). Thicket sub-types were classified along the drainage basins and took into account the vegetation grain (solid or mosaic), the climate and the floristics (Vlok & Euston-Brown, 2002). Hoare *et al.* (2006) refer to the Subtropical Thicket Biome as the Albany Thicket Biome, consisting of 14 vegetation units. However, the classification by Vlok & Euston-Brown (2002) is the preferred classification used in this study, due to the fine-grain mapping of thicket types and units with description of species composition. Furthermore, Lloyd *et al.* (2002) defined the degradation of the thicket types.

2.1.1. Defining thicket

Four factors determine the occurrence of thicket within a region, namely rainfall, temperature, soil quality and fire (Vlok & Euston-Brown, 2002). These factors allow for either the expansion or reduction of small woody bush clumps, which either join to make larger bush clumps of consolidated thicket or remain as isolated thicket bush clumps within a matrix of another vegetation type (Vlok & Euston-Brown, 2002). Additionally, thicket occurs where the summer and winter rainfall regime is at approximately 50-50% and becomes fragmented at the eastern and western extremities of the planning domain, where there is a 40-60% or 60-40% winter, summer rainfall regime (Vlok & Euston-Brown, 2002).

The Subtropical Thicket Biome acts as an ecotonal vegetation type adjacent to many of South Africa's other biomes, but also contains its own ecotonal species, particularly spekboom, *Portulacaria afra* (Vlok & Euston-Brown, 2002). Acocks (1988) recognised spekboomveld as occurring adjacent to noorsveld on northern-slopes around Jansenville. According to Vlok & Euston-Brown (2002), spekboomveld occurs alongside a fire-driven vegetation type and defines this subunit as spekboom occurring in abundance among more arid thicket types, while spekboom thicket is alternatively an abundance of spekboom within more mesic thicket types (Vlok & Euston-Brown, 2002).

The Subtropical Thicket Biome is large in its extent and covers an area of 105 454 km^2. Within the biome, many national parks, nature reserves and private game reserves take up a substantial area ensuring both the preservation and conservation of the thicket (Lloyd *et al.*, 2002). Two such protected areas are the Greater Addo Elephant National Park (GAENP) and the western section (Westernkloof) of the Baviaanskloof Mega-Conservancy, both of which are the focus areas for this study. The GAENP occurs within the Sundays River Valley and falls within the greater thicket type called Sundays River Thicket. The Baviaanskloof occurs within the Groot River Valley and the vegetation types fall under Groot River Thicket.

2.2. Location and history of sites within the Subtropical Thicket Biome

Four sites were selected for this study. Three of the sites are within the GAENP along an altitudinal gradient and the fourth in the Westernkloof section of the Baviaanskloof. Collectively, the sites cover approximately 18 000 km^2 of the Subtropical Thicket Biome and exist within two of the drainage basins that define thicket vegetation compositional distributions, namely the Groot and Sundays River basins.

2.2.1. The Greater Addo Elephant National Park

The GAENP is managed for the state by South African National Parks (SANParks) and over the years has seen vast expansions in area (Figure 7). Before the area was conserved, the vegetation type Addo Bush (Acocks, 1988) extended over an area of 17 087 ha into the Zuurberg and was the home to populations of elephant (*Loxodonta africana*), Cape buffalo (*Syncerus caffra*) and black rhinoceros (*Diceros bicornis*) (Potgieter, 1970). The destruction of Addo Bush for agriculture and development reduced the area for the elephants to inhabit, increasing the threat to croplands and farmers' livelihoods, therefore 150 or 130 elephants were culled to just 15 or 16 individuals (Potgieter, 1970; Hoffman, 1993). In 1922 following the construction of the Lake Mentz dam wall, 4 272 ha of land unsuitable for citrus farming, was demarcated for conserving the remaining elephant population (Potgieter, 1970).

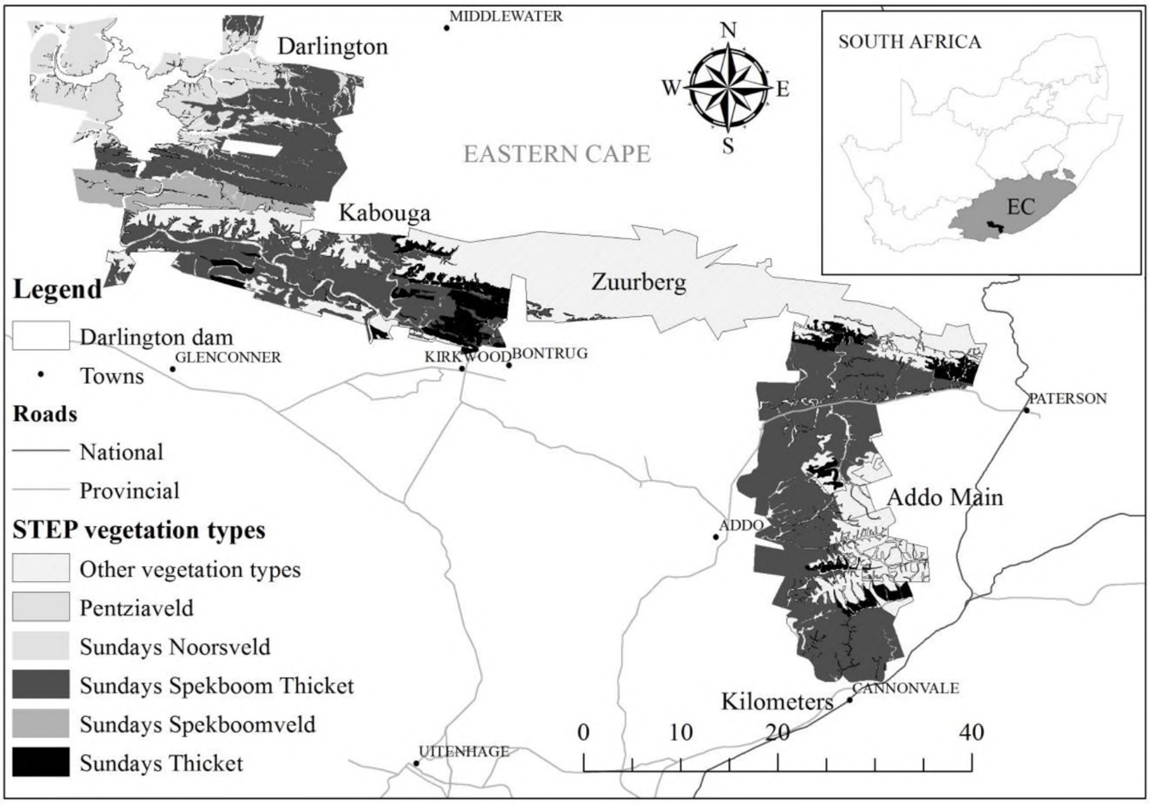


Figure 7: The location and vegetation of the Greater Addo Elephant National Park (Adapted from STEP vegetation spatial data, Vlok & Euston-Brown, 2002).

In 1931, 6 880 ha of Addo Bush was proclaimed as the Addo Elephant National Park. SANParks (2008) state however that this proclamation occurred in 1939 at just 2 230 ha as a means to protect the last 11 remaining elephants in the area. The demarcated area was only successfully fenced in the 1950s, protecting by then 22 elephants (Potgieter, 1970; SANParks, 2008). By 1966 the elephant numbers increased to 43 (Potgieter, 1970).

The AENP later joined with the fynbos and afromontane forest rich Zuurberg National Park (33°20’ S 25°44’ E) in 1995 and the Woody Cape Nature Reserve (33°43’ S 26°23’ E) on the coast in 2001 (SANParks, 2008). In 2006, the park expanded to an area of 164 000 ha, which incorporates the Darlington section in the north, Kabouga section in the central west, Zuurberg section in the central east and the Addo Main section and Woody Cape coastal sections in the south. The planning domain for future expansion of the Greater Addo Elephant National Park includes a terrestrial area of 686 000 ha (SANParks, 2008).

The Darlington section surrounds the Darlington Dam (33°10’ S 25°8’ E), previously known as Lake Mentz (SANParks, 2008). The dam water surface area is 4 350 ha (SANParks, 2008) and the Darlington section of the GAENP is about 38 237 ha (Powell *et al.*, 2010). The dam has a large catchment area and receives water from the smaller Voël and Volker rivers in the east and the Klein Reit, which joins with the Sundays River from the west. The Sundays River flows from the dam, through the Kabouga section, directly south of Darlington. The dam additionally receives water from an inter-basin transfer scheme from the Orange River (SANParks, 2008) and is the first dam owned by SANParks (Timmermans and Sisitka, nd). The section is south of the R400 provincial road which runs east to west, between the towns Riebeeck East and Jansenville. Nearby farming communities are in the small towns of Waterford, Middelwater and Klipfontein, all adjacent to the R400. This area of land has gradually been purchased from land owners (who previously used the land for small livestock farming) by SANParks between 2002 and 2005 (McManus, 2009; Reeler *et al.*, 2011).

Extending roughly 30 km north from Cannonvale, straddling the town of Addo to the West and Paterson to the East is the Addo Main Camp section. The privately run Riverbend section is separated to the north of Addo Main Camp by the R342 provincial road between Paterson and Addo at 33°42′S and 25°76′E. The Krom River runs through the Riverbend section and joins with the Sundays River Valley, which runs west of Addo Main. The two sections are about 42 000 ha in extent.

The Kabouga section is situated north-west of the citrus-farming town of Kirkwood and about 9 km north of Glenconnor. It runs from west to east for about 25 km along the Sundays River Valley from the Klein Winterhoek mountains to the Zuurberg (33°17’ S 25°14’ E). The section is therefore west of the Zuurberg and south of Darlington. The stretch from the Kabouga section to the Zuurberg section is roughly 52 100 ha.

2.2.2. The Baviaanskloof Mega-Reserve

In 1923 the Baviaans Forest Reserve, managed by the Department of Forestry, initiated interest in conserving the catchments and promoting a sustainable water supply surrounding the Baviaanskloof and Kouga mountains (Boshoff, 2005). From 2004 it has been managed by the Eastern Cape Parks and Tourism Board and is known as the Baviaanskloof Nature Reserve (BNR) (Boshoff, 2005). The main conservation area of the BNR comprises an area of 184 385 ha with an additional 15 332 ha of privately owned and 4 338 ha of state owned land, which has been incorporated into the Baviaanskloof Mega-Reserve (BMR) (Boshoff, 2005). The creation of the BMR (Figure 8a) was the main priority of the Baviaanskloof Mega-Reserve Project, which commenced in 2002 and aimed to form the collaboration of multiple stakeholders in conserving and managing the vast biodiversity of the area (Boshoff, 2005).

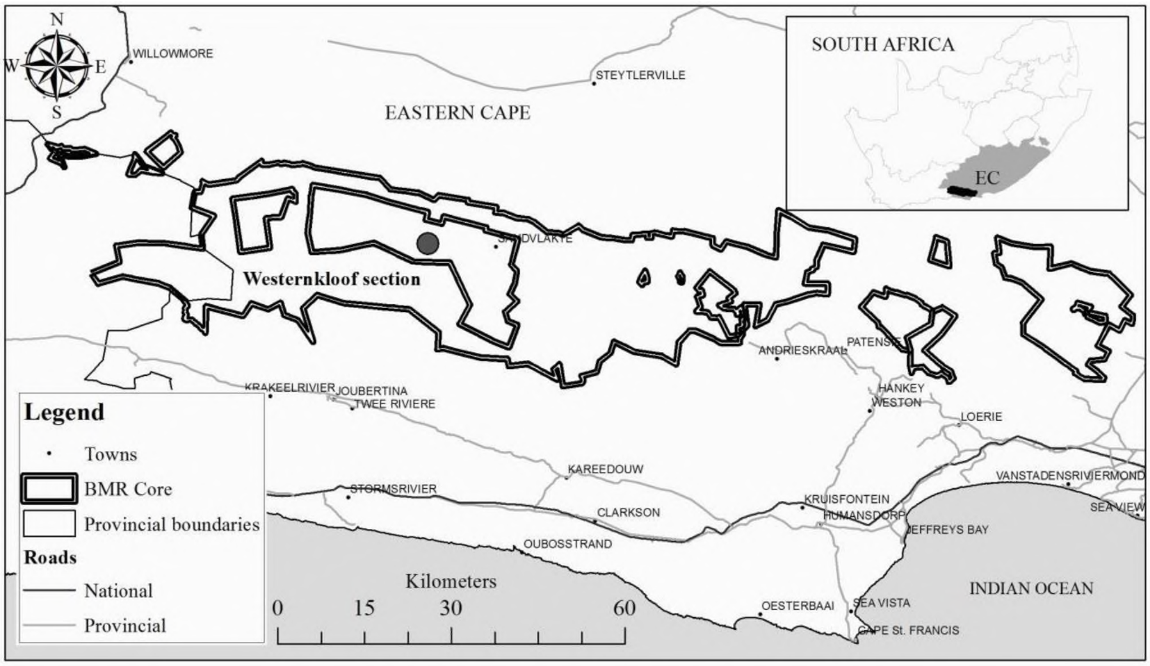


Figure 8a: Location of the Baviaanskloof Mega-Reserve (Adapted from STEP vegetation spatial data: Vlok & Euston-Brown, 2002).

Seven nature reserves exist adjacent to the BNR known as the Baviaanskloof Reserve Cluster and 56 000 ha of farming area exist within the BNR known as the western sector (Boshoff, 2005). The fact that there are multiple land-users and land-use types compromising a large area of environmental and climatic gradients, with high biodiversity conservation potential, qualifies the BMR for mega-conservancy status (Boshoff, 2005). In 2004 the BMR was proclaimed as a World Heritage Site, owing to its beauty, biodiversity and threatened species (Boshoff, 2005).

The greater area of the BMR stretches from Patensie in the east to Willowmore in the west and lies between the Baviaanskloof and Kouga mountain ranges. Central to the core of the BNR is the western sector (Westernkloof) where the study was located (Figure 8b). It lies between the small farming towns of Studtis and Sandvlakte at 33°31’59” S, 23°58’59” E and 33°35’03” S, 24°09’52” E, respectively.

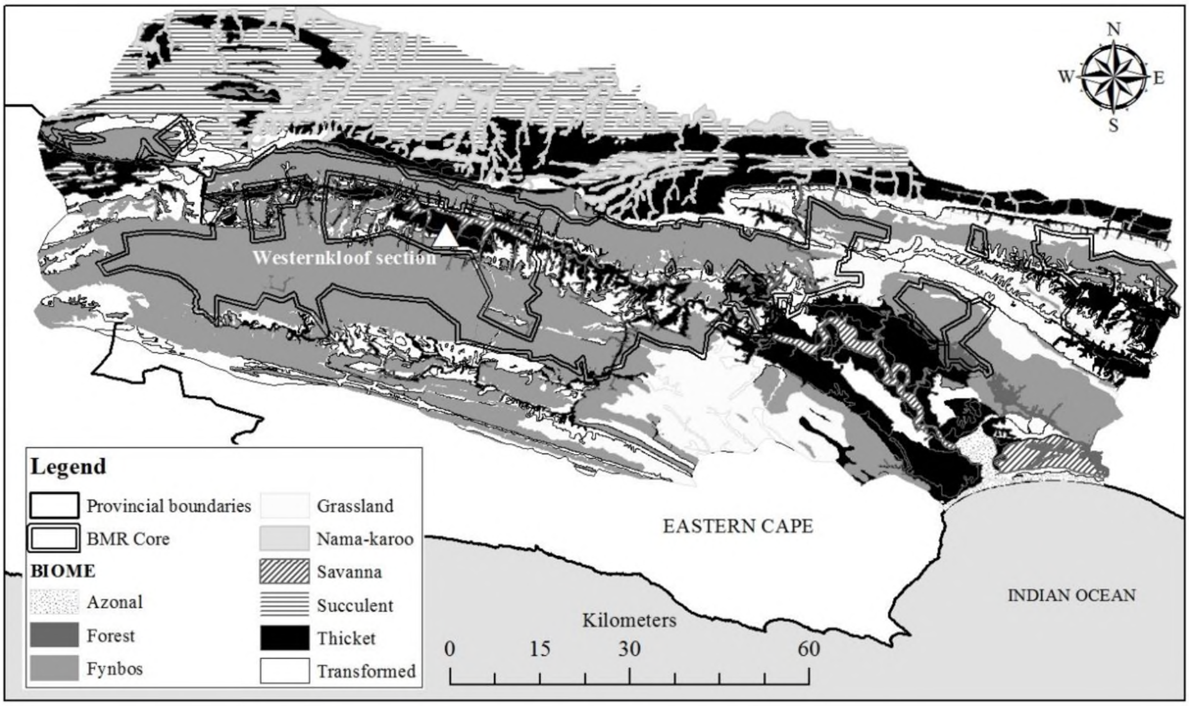


Figure 8b: Vegetation map of the Baviaanskloof Mega-Reserve (Adapted from STEP, Vlok & Euston-Brown, 2002).

2.3. Climate

Both study areas are within a semi-arid to arid zone. Within the GAENP, the Darlington section is impacted by a rain-shadow from the mountains above Kabouga to the south. It therefore has relatively low annual rainfall of between 250 mm in the south and 280 mm in the north (Table 1). Mean summer and winter temperatures are 26 °C and 11 °C, respectively (South African Weather Services, 2014). Kabouga and Addo Main Camp experience similar mean summer rainfall, however Addo Main, which is closer to the coast has much higher winter rainfall of between 29 and 31 mm per month. Mean annual rainfall for Addo Main is between 430 and 530 mm and the mean summer temperature is 27 °C, dropping to an average of 11 °C in winter (SAWS, 2014).

Table 1: Mean rainfall across study sites.

		Rainfall (mm)			
Site	*Rainfall stations*	*Annual*	*Monthly*	*Summer*	*Winter*
Darlington	Darlington Dam	250	21.3	25.5	14.9
	Middelwater	280	23.7	29.2	16.9
Addo Main	Addo	530	33.0	37.2	28.5
	AENP	430	37.0	43.1	30.8
Kabouga	Kirkwood	280	30.4	39.9	20.9
Baviaanskloof	Sandvlakte	298	28.5	34.0	22.8
	Studtis	278	28.7	33.4	25.0

The town of Kirkwood is the only reference point for the Kabouga section and receives 280 mm per annum and the most rainfall in summer at 39.9 mm (SAWS, 2014). The Westernkloof area of the Baviaanskloof receives between 278 and 290 mm per annum, with the majority of rainfall falling during the summer months. Temperatures in the Baviaanskloof can surpass 35 °C in the summer and drop below 5 °C in the night during winter months (McManus, 2009).

2.4. Geology and soil

The area covered by the GAENP and the Baviaanskloof constitutes two main geological Supergroups: the Cape and Karoo; tertiary formations from the Uitenhage and Algoa Groups as well as quatenary formations.

2.4.1. Geological types

The Cape Supergoup occurred between 500 and 330 Ma during the early Ordovician and early Carboniferous periods (Thamm & Johnson, 2006). It has three main geological groups, namely the Table Mountain Group, Bokkeveld Group and Witteberg Group (Thamm & Johnson, 2006). The GAENP consists only of the Witteberg Group, while the Baviaanskloof consists of all three. The Table Mountain Group is dominated by sandstones deposited by both shallow-marine and fluvial environments (Thamm & Johnson, 2006). The Bokkeveld Group consists of fossil-rich shale and sandstones deposited in a deltaic environment and the Witteberg Group consists of both sandstone and mudstone, deposited in shallow-marine and deltaic environments (Thamm & Johnson, 2006).

The Cape Supergroup was subsequently overlain by the Karoo Supergroup, which is defined as a retro-arc foreland basin (Johnson *et al*., 2006). The Groups of importance to this study include the Dwyka, Ecca and Beaufort Groups. The Dwyka Group consists of diamictite, mudstone and drop stones released as debris from ice sheets (Johnson *et al*., 2006).

The Fort Brown formation of the Ecca Group consist of mudstone, sandstone and rhythmite. The rhythmite is indicative of deltaic environments with a regular supply of sediment, while the sandstones and mudstones are indicative of flood conditions (Johnson *et al*., 2006). The Waterford formation of the Ecca Group also consists of sandstones and mudstones, however ripples within the formation suggest that the depositional environment was more shallow. The Fort Brown formation is overlain by the Waterford formation and occurred during the Permian period, 300 Ma. The Fort Brown and Waterford formations occur in the Darlington section.

Following the deposition of the Karoo sediments, the lithologies of the Uitenhage Group were formed during the Jurassic period about 150 Ma. The Uitenhage Group occurs within the Algoa Basin, which represents a series of faults that formed horst and graben structures to form the basin (Shone, 2006). Three formations, including the Enon, Kirkwood and Sundays River Formations comprise the Uitenhage Group. The Enon group occurs in Baviaanskloof, while the Kirkwood and Sundays River formations are found in Addo Main.

The Enon formation conglomerates are derived from Cape Supergroup quartzites and shales that formed pebbles and cobbles in alluvial fans (Shone, 2006). Succeeding the Enon formation is the Kirkwood formation, which consists predominantly of sandstone, interbedded with mudstone and siltstones, deposited during a fluvial period into the basin. This formation is also rich in both faunal and floral fossil diversity (Shone, 2006). The Sundays River Formation was deposited in a shallow marine environment, which could have included estuaries and lagoons (McLachlan & McMillian, 1976: in Shone, 2006). Evidence of such an environment stems from the abundance of shell portions and carbonate within the sandstone (Shone, 2006). Lastly, the Algoa Group formation overlies the Uitenhage Group. The Nanaga formation within the Algoa group exists in the south of Addo and consists of conglomerates and calcareous sandstones deposited in a marine environment (Roberts *et al*., 2006).

2.4.2. Geology of sites

Distribution of geological types relative to sites was obtained from GIS spatial data of the Geology of South Africa. The Darlington section occurs above lithologies from both the Karoo and Cape Supergoups (Figure 9a). The majority of the area consists of Ecca group lithologies, including Waterford and Fort Brown formations that straddle the Beaufort group lithologies. To the south, adjacent to the Witteberg, are Dwyka group lithologies and on the plateau of the Witteberg group in the south of Darlington exists the Lake Mentz subgroup. The plots occur mostly in the Ecca and Witteberg groups in the central and southern portions of Darlington.

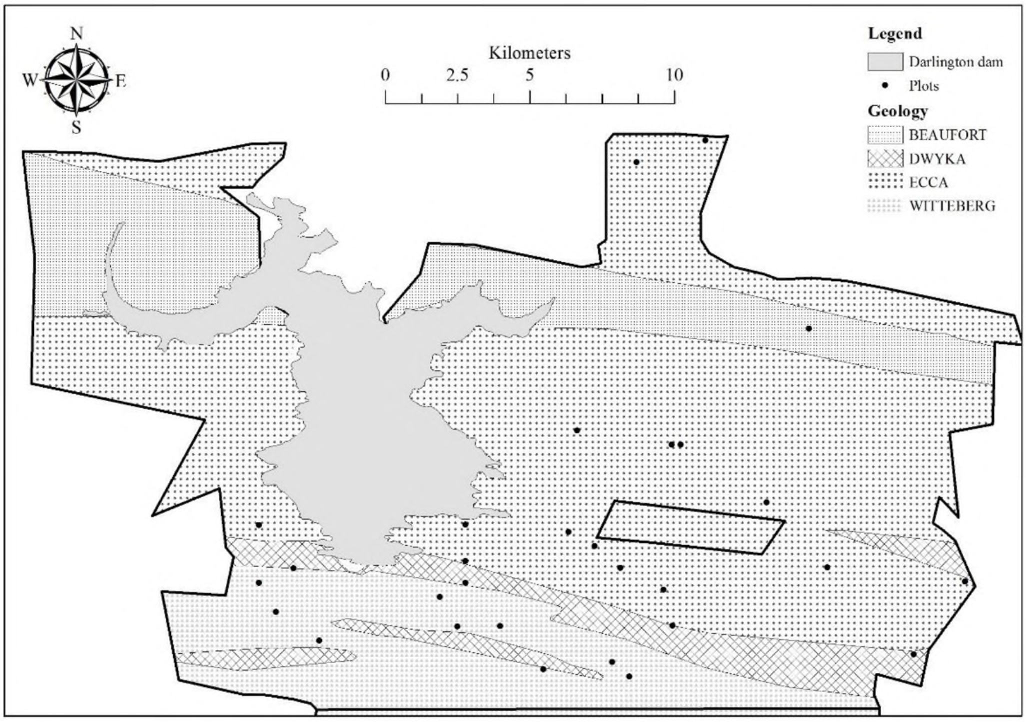


Figure 9a: Geology of the Darlington section in GAENP.

The plots in the Riverbend section of Addo occur on quatenary formations that would have formed after the Algoa Group in the last 1.8 My (Johnson *et al.*, 2006). Plots to the north of Addo Main occur in the Kirkwood formation, while central plots occur in the Sundays River formation of the Uitenhage Group (Figure 9b). The southernmost plots are situated on Algoa Group lithologies of the Nanaga formation.

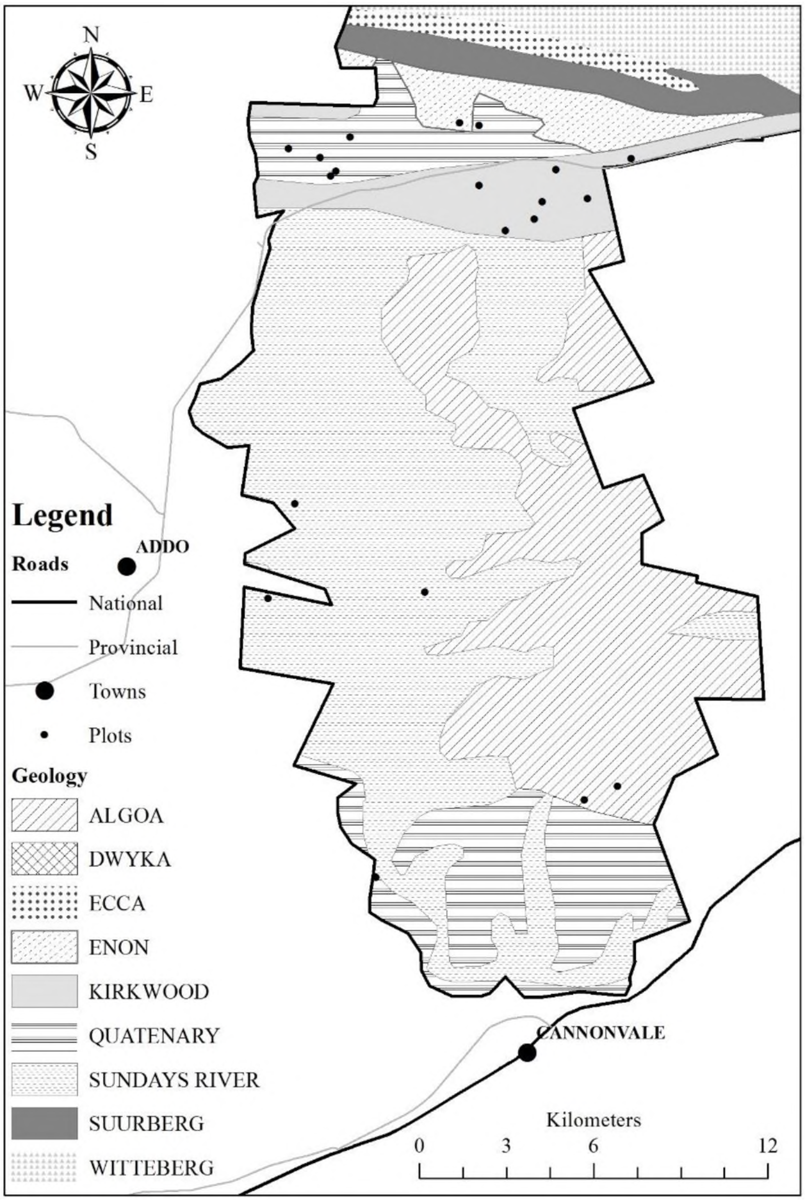


Figure 9b: Geology of Addo Main Camp and the Riverbend section in GAENP.

The Kabouga section is dominated by the Witteberg group, which surrounds the Sundays River Valley in this region (Figure 9c). A band of Dwyka stretches through the central valley, with a portion of Ecca in the southeast. The majority of plots are located on the Witteberg Group.

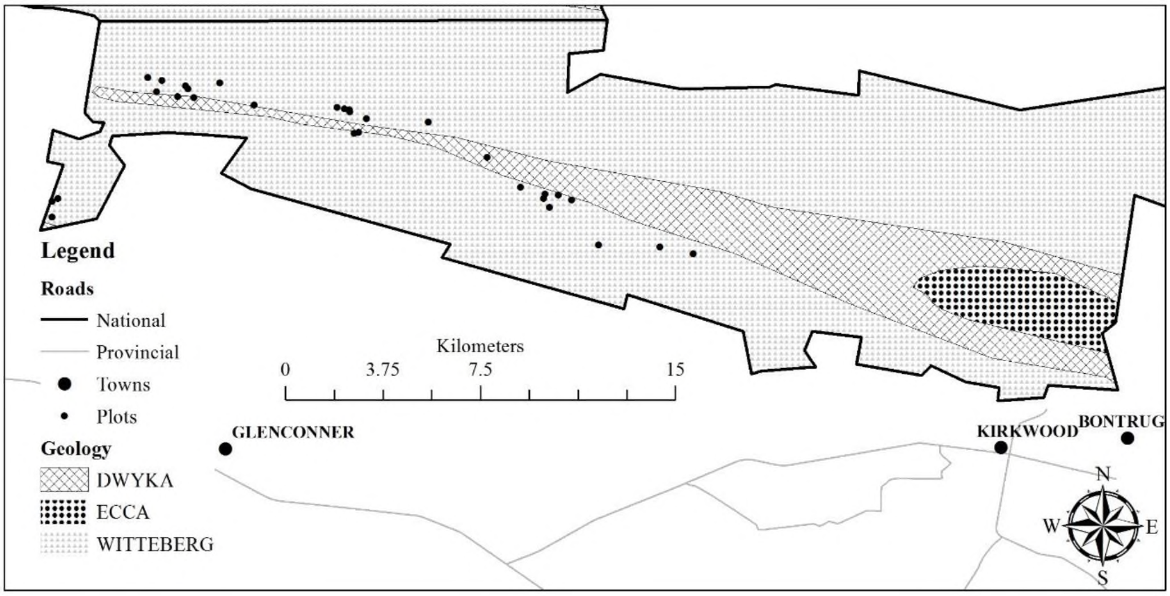


Figure 9c: Geology of the Kabouga section in GAENP.

The Westernkloof section of the Baviaanskloof, where the study plots are situated, are predominantly on Table Mountain formation sandstone of the Cape Supergroup. Within the central valley is exposed Bokkeveld (Cape) and Enon (Uitenhage) formation lithologies. There is a portion of quatenary geology; however, no plots occur on this geology type (Figure 9d).

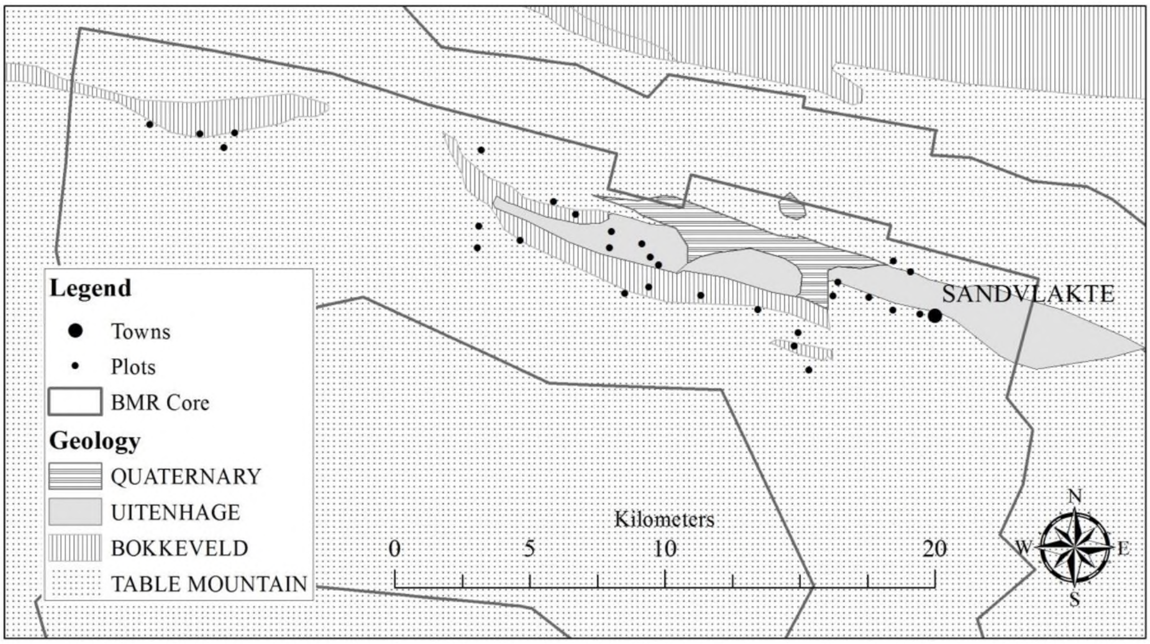


Figure 9d: Geology of the Westernkloof section of the Baviaanskloof.

2.4.3. Soils

Much of the Eastern Cape region surrounding the GAENP and Baviaanskloof are dominated by lithic soils, between 30-60% and >60% cover (Fey, 2010). Lithic soils have a close relationship with underlying parent material and are common in arid areas and on convex slopes (Fey, 2010). Cowling (1983b) however, describes much of the 'Subtropical Transitional Thicket' as occurring on deep, well-drained and fertile soils in the south-eastern Cape. Additionally, in a site near Kirkwood, Mills & Cowling (2006) indicate that soils from Ecca Group shale are highly erodible, while Beaufort Group shale soils have more stable soils. The FAO (1998: in Mills & Cowling, 2006) list other soils around Kirkwood namely, Calcaric Cambisols, Calcic Luvisols, Rhodic Luvisols and Calcaric Regosols, while in Addo Main the soils are derived from the Uitenhage Group sandstones and mudstones and are characterised as deep, red sandy loams (Moolman & Cowling, 1994). In the Baviaanskloof, soils are derived from a highly variable geology and terrain and include Ferralsols, Cambisols and Leptisols (Mills & Cowling, 2010).

2.5. Topography

An elevation gradient is observed in the GAENP from Addo Main in the south to Darlington in the north. The Darlington section rests on a relatively flat plateau of 140 masl, particularly in the north and west, surrounding the Darlington Dam. The south-eastern topographies include small, yet mostly steep E-W trending ridges between 400 and 600 m high. The ridges become less defined in the central east and gradually decrease in abundance to the north.

Highly heterogeneous topographies and elevations exist within the Kabouga section. The northern section boundary separates Kabouga from Darlington with deeply incised Witteberg quartzites of the Klein Winterhoek and extend into the Zuurberg mountain range at elevations in excess of 850 masl. The Sundays River cuts through the quartzite from the Darlington Dam and through the central area of Kabouga. In some areas, the river flows through low-lying flood plains (175 masl) adjacent to large hills (approximately 250 masl) and in other areas it passes through a network of undulating hills ranging from 200 to 450 masl, but it also cuts against steep cliffs within the valley.

The majority of Addo Main Camp, as well as the Riverbend section, consists of flat and gently sloping hills riddled with old agricultural lands. The Riverbend section extends further north into a series of larger undulating and well-vegetated hills at over 250 masl. The elevation in Addo Main Camp increases abruptly to over 200 masl, from its lowest point in the southern-most extremity of the park at 80 masl. Here, especially in the eastern portions of the park, the landscape becomes more mountainous.

The Westernkloof forms part of a small section straddled between the Baviaanskloof and Kouga mountain ranges. The Baviaanskloof mountain range consists of deeply folded and incised quartzites and sandstones. The deeply incised mountains form alluvial fans at the base of the mountains (Bobbins, 2011), with many undulating hills existing between the many tributaries of the main river system. The Baviaanskloof River which flows between the mountain ranges is a braided river system within a wide floodplain valley.

With regard to the plots sampled within each of the sites, descriptive statistics of the elevation and slope values were calculated (Table 2). The plots in Darlington are elevated the most above sea level and plots were sampled on steeper slopes in Kabouga.

Table 2: Elevation and slope statistics of sampled plots in the four sites.

	Elevation (masl)			**Slope (degrees)**		
	Mean (±SD)	*Max.*	*Min.*	*Mean (±SD)*	*Max.*	*Min.*
Darlington	336±86	604	239	2.8±1.7	6.9	0.1
Addo Main	140±42	192	41	1.6±1.1	4.0	0.1
Kabouga	257±72	443	144	5.3±2.9	11.2	1.1
Baviaanskloof	537±90	738	381	12.5±7.0	32.9	4.1

The highest elevations and slope values are however in the Westernkloof section of the Baviaanskloof, where slope values are more than double that of Kabouga. In Addo Main Camp, the maximum elevated plot was 192 masl, which is much less than the average elevations of the other sites. It also had the lowest slope values.

2.6. Vegetation types and condition

The Baviaanskloof Mega-Reserve is home to seven of South Africa's eight biomes and the GAENP is home to four (Boshoff, 2005; SANParks, 2008). Many vegetation types of both solid and mosaic grain exist within both the Baviaanskloof and GAENP, but the Baviaanskloof has the highest representation of vegetation mosaic diversity within thicket (Boshoff, 2005).

2.6.1. Thicket types and common species

The Darlington section consists of a combination of Sundays Spekboom Thicket and Sundays Spekboomveld, with Sundays Noorsveld and Pentziaveld occurring in the north-west. (Refer back to Figure 7). Addo Main and Kabouga consist of Sundays Spekboom Thicket, Sundays Thicket and Grassland Bontveld, while the Westernkloof section of the Baviaanskloof consists of a multitude of thicket vegetation types; however, those relevant to this study include Baviaans Spekboom Thicket and Groot Arid Spekboomveld (Vlok & Euston-Brown, 2002).

Within the GAENP, Sundays Thicket is situated in the valleys and moister regions of the park in the south of Addo Main. It consists of key tree *Euphorbia* species and abundant species such as *Cussonia spicata, Searsia chirendensis, Scutia myrtina, Schotia latifolia* and *Ptaeroxylon obliquum* (Vlok & Euston-Brown, 2002). Sundays Spekboom Thicket sees a replacement of tree *Euphorbias* by spekboom (*Portulacaria afra*). Spekboom is most abundant on north-facing slopes where irradiation is higher (Vlok *et al.*, 2003). In Addo Main, Sundays Spekboom Thicket has a definitive woody component that includes *Pappea capensis, Putterlickia verrucosa, Rhigozum obovatum, Searsia pterota, Searsia longispina* and *S. afra.* (Vlok & Euston-Brown, 2002). Sundays Spekboom Thicket north of Kirkwood, into Kabouga and Darlington, is less abundant in *P. capensis* and *Euclea undulata* (Vlok & Euston-Brown, 2002).

Sundays Spekboomveld in Darlington is characterised by an absence of the woody tree *Vachellia karroo* and an abundance of *P. capensis* and *S. afra* (Vlok & Euston-Brown, 2002). Perennial grasses in an intact state include *Cenchrus cilliaris, Digitaria argryograpta, Fingeruthia africana* and *Panicum maximum* (Vlok & Euston-Brown, 2002).

Within the greater vegetation type of the Groot River Thicket, both Baviaans Spekboom Thicket and Groot Arid Spekboomveld occur within the Westernkloof section of the reserve. Baviaans Spekboom Thicket is composed of drought resilient woody and succulent shrubs including *Cadaba aphylla, Carissa haematocarpa, Pegolettia baccharidifolia* and *R. obovatum* and woody trees *Boscia oleoides, E. undulata, P. capensis* and *S. afra* (Vlok & Euston-Brown, 2002). Here the abundance of *P. afra* occurs jointly with *Aloe speciosa*, an indicator species of where *P. afra* once occurred in the case of severe degradation (Vlok & Euston-Brown, 2002). Groot Arid Spekboomveld is more abundant in *Gymnosporia polyacantha* and *Gymnosporia szyszylowickzii* as the abundant shrubs and *E. undulata* instead of *P. capensis* (Vlok & Euston-Brown, 2002). *Euphorbia caerulescens* is present in intact Groot Arid Spekboomveld, along with a matrix of dwarf shrubs such as *Felicia muricata, Pentzia incana* and *Selago geniculata* (Vlok & Euston-Brown, 2002).

2.6.2. Degradation of thicket types

Owing to the abundance of small livestock farming throughout the Subtropical Thicket Biome, as well as clearing of land for agriculture, many of the thicket types have become severely degraded. The STEP project mapped the thicket types, providing an indication of condition.

Of the sites sampled, the area of degradation for each thicket type is shown in Table 3 and illustrated in Figure 10 for the GAENP and Figure 11a (thicket types) and 11b (degradation) for the Westernkloof.

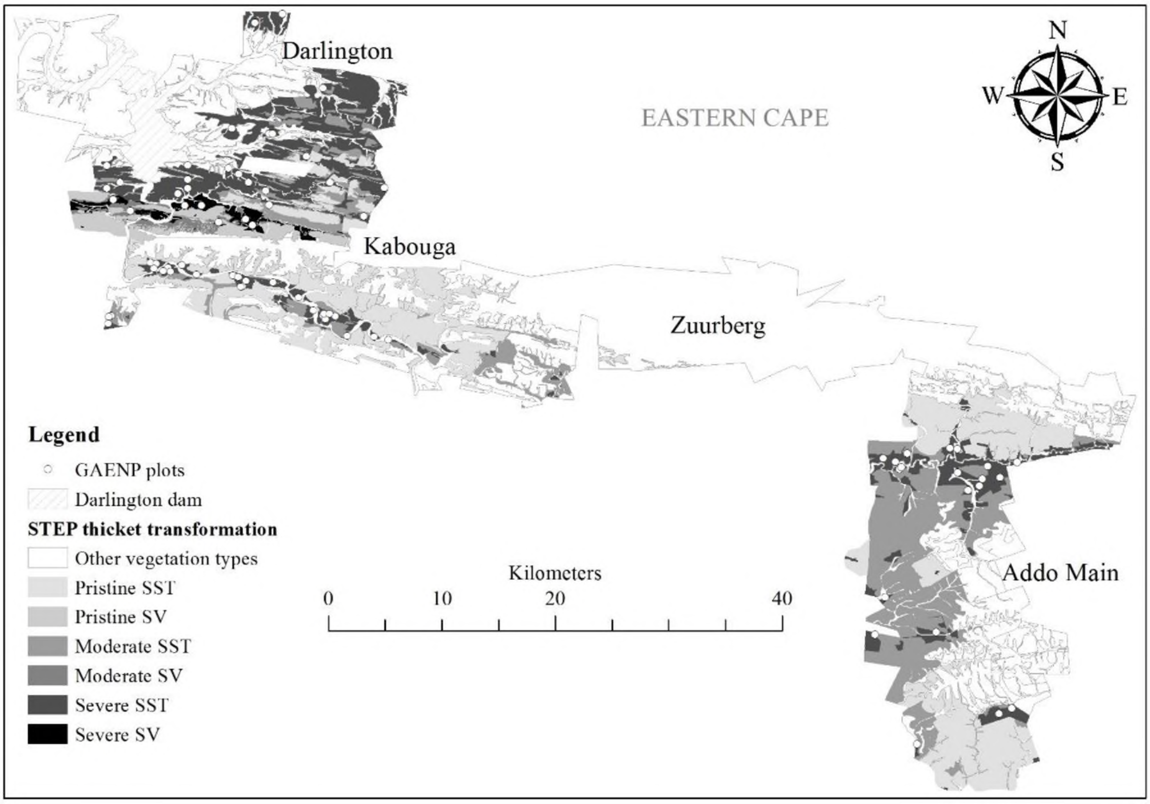


Figure 10: Vegetation condition in the Greater Addo Elephant National Park (Key: SST- Sundays Spekboom Thicket; SSV-Sundays Spekboomveld). (Adapted from STEP, Lloyd *et al.*, 2002; Vlok & Euston-Brown, 2002).

The Darlington section is severely degraded across almost the entire terrestrial area, with 28% and 20% of spekboomveld and 68% and 19% of spekboom thicket showing severe or moderate degradation, respectively; totalling an area of 12 636 ha. Figure 10 illustrates the condition of the GAENP and confirms the severe degradation of Darlington in comparison to the other sites within the GAENP. Severely degraded spekboomveld in Darlington is invaded, or rather expnaded by the indigenous succulent *E. caerulescens* which fast replaces *P. afra* following degradation (Vlok & Euston-Brown, 2002). Once the succulent layer has been lost, including *Crassula ovata*, a matrix of *P. incana* and *Atriplex lindleyi* dominates between the remnant woody trees (Vlok & Euston-Brown, 2002).

Within Addo Main, severe degradation is apparent on old agricultural lands where thicket has been transformed. Almost the entire midsection is moderately degraded. It is only in the south and northern Riverbend sections where there are intact areas, as well as the protected botanical reserve central to the park. A total of 15% and 44% of Addo Main and Riverbend are severely and moderately degraded. The old agricultural lands provide a unique opportunity to study succession in the park and host an array of grass and herbaceous species.

Table 3: Area of spekboom vegetation types per site and their condition.

Site	Vegetation type	Area within site (ha)	STEP degradation (ha)			
			Intact	*Moderate*		*Severe*
AD	Spekboomveld	4 417	2 322	880		1 216
	Spekboom Thicket	13 151	1 730	2 493		8 927
AM	Sundays Spekboom Thicket	25 037	10 233	11 034		3 769
AK	Sundays Spekboom Thicket	13 032	9 297	2 053		1 683
BK	Baviaans Spekboom Thicket	14 482	*P-M*	*M*	*M-S*	*S*
			6 626	349	1 719	5 789
	Groot Arid Spekboomveld	2 547	-	-	-	1 761

In Kabouga, the severe degradation is limited to the areas on either side of the Sundays River Valley, with only 13% showing severe degradation and 16% having moderate degradation. Much of this area is inaccessible, protecting it from over-browsing by domestic livestock in the past, which has ensured preservation of large areas of these mountains.

In the Westernkloof, two units are abundant in spekboom namely the Groot Arid Spekboomveld and Baviaans Spekboom Thicket. Almost 40% of Baviaans Spekboom Thicket is severely degraded at 5 789 ha. Groot Arid Spekboomveld is almost entirely severely degraded at 69%.

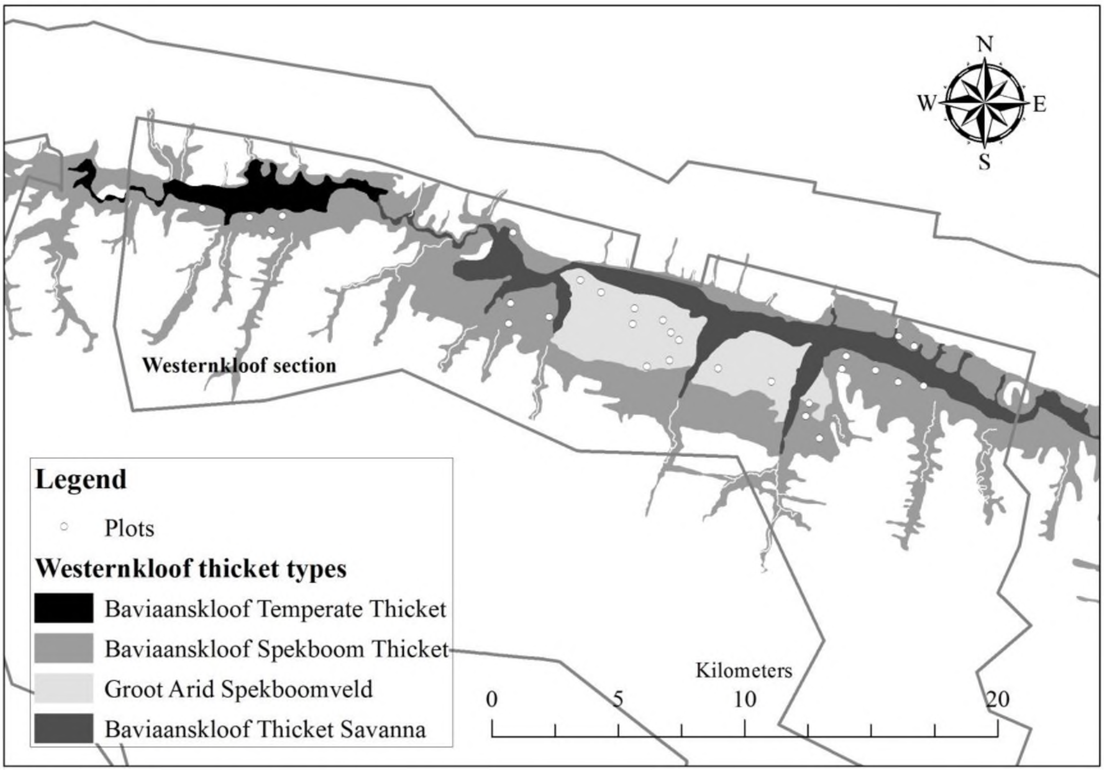


Figure 11a: Thicket vegetation map of the Westernkloof section of the Baviaanskloof (Adapted from STEP, Vlok & Euston-Brown, 2002).

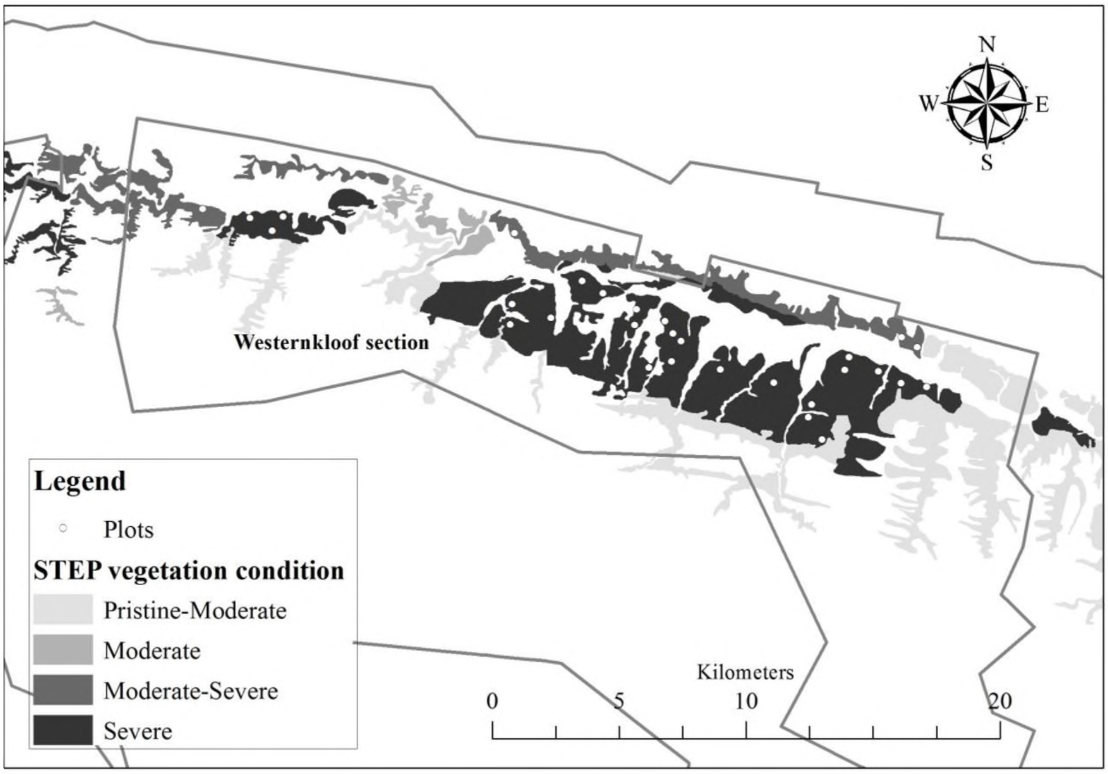


Figure 11b: Severity of thicket degradation in the Westernkloof section of the Baviaanskloof (Adapted from STEP, Lloyd *et al.*, 2002).

2.7. Fauna

Addo Main Camp is the only section of the GAENP which is home to all of the 'Big Five', including elephant, buffalo, black rhino, lion (*Panthera leo*) and leopard (*Panthera pardus*). As a mega-herbivore, the elephants have impacted much of the vegetation structure and density, especially surrounding water points (Landman *et al.*, 2012). As a long term research initiative, the park has fenced off a botanical reserve of thicket, which cannot be browsed by game and can be used as a reference site for the impact that elephants have on thicket vegetation (Johnson *et al.*, 1999). The recommended carrying capacity is two elephants per km^2 (Kerley & Boshoff, 1997: in SANParks, 2008). This was far exceeded with a population of 400 elephants in 2008, but the expansion of the park into the other sections is intended to remedy the over-population and improve biodiversity in the other sections (SANParks, 2008).

Carnivores, other than the six introduced lion (SANParks, 2016) and the two introduced leopard in Addo Main (Hayward *et al.*, 2006), include black-backed jackal (*Canis mesomelas*), the re-introduced spotted hyena (*Crocuta crocuta*) and caracal (*Caracal caracal*). Ungulate species include the common browsers kudu (*Tragelaphus strepciseros*) and bushbuck (*Tragelaphus scriptus*) and grazers such as Burchell's zebra (*Equus quagga burchelli*), eland (*Taurotragus oryx*) and the extra-limital warthog (*Phacochoerus africanus*).

The Darlington and Kabouga sections only have black rhino and leopard of the Big Five. Kudu, bushbuck and warthog are abundant due to the low abundance of predator species. Baboons (*Papio cynocephalus ursinus*) are common in the mountains of the Kabouga section, while vervet monkeys (*Cercopithecus pygerythus*) are more abundant in Addo Main. Avifaunal diversity across the planning domain of the STEP project is high with a species richness of 421 species, none of which are endemic to the subtropical thicket (Dean, 2002). According to SANParks (2008), the park is home to many suitable habitats for some Red Data list species, which include the Cuckoo Hawk (*Aviceda cuculoides*), Grass Owl (*Tyto capensis*), Kori and Stanley's Bustard (*Ardeotis kori* and *Neotis denhami*), Cape Vulture (*Gyps coprotheres*), Ground Hornbill (*Bucorvus leadbeateri*) and Martial Eagle (*Polemaetus beliicosus*). According to SANParks (2008), the park is home to 13 endemic reptile species and the endemic flightless dung beetle (*Circellium bacchus*).

The Baviaanskloof Mega-Reserve has seen a local extinction of all large carnivores except leopard (Boshoff, 2005). It supports a high diversity of reptiles (57 species), amphibians (17 species), fresh water fish (15 species) and birds (over 300 species) (Boshoff, 2005). Mammals comprising 58 species, include ungulates such as the Cape mountain zebra (*Equus zebra zebra*), klipspringer (*Oreotragus oreotragus*), bushbuck and kudu. The black rhino as well as the cape mountain zebra are on the Red Data List as highly threatened species (Boshoff, 2005).

2.8. Conclusion

The Baviaanskloof and GAENP are areas characterised by a high geological, topographical and climatic diversity, which relate greatly to the rich fauna and flora of the region. People have been living in the region for many decades, however the outcomes have not in many instances been sustainable and the threat to biodiversity has become increasingly apparent. The growing conservation expansions and initiatives within the STEP planning domain, encompassing the Baviaanskloof and GAENP, are vitally important if we are to sustain these landscapes and the ecosystem services they provide. The restoration of degraded thicket lands, in particular, will provide important socio-economic as well as ecological benefits to the region and therefore cannot be left unassisted.

3 CHAPTER

PLANT SPECIES COMPOSITION AND ABIOTIC CORRELATES IN DEGRADED SUBTROPICAL THICKET AT LOCAL AND LANDSCAPE SCALES

CHAPTER 3: PLANT SPECIES COMPOSITION AND ABIOTIC CORRELATES IN DEGRADED SUBTROPICAL THICKET AT LOCAL AND LANDSCAPE SCALES

3.1. Introduction

A vital element for ecologists, researchers and practitioners is disentangling the complexity behind the structure and dynamics of ecological systems at both fine and broad scales (Peters *et al.*, 2006). Understanding degraded subtropical thicket is no different, since the decline in ecological integrity doesn't conform to a linear change in response to a continuous and uniform degradation agent, such as climate change. Rather, the degradation of thicket by goats (and elephants) is varied across the landscape according to stocking density, duration of degradation, distance to water points and terrain (Stuart-Hill, 1989; Moolman & Cowling, 1994; Landman *et al.*, 2012). Furthermore, degradation is felt more severely in arid thicket types. Recovery through secondary succession, therefore relates to the abiotic correlates that interact with the landscape at varying spatial and temporal scales. Degradation through a transformation for agriculture represents a separate trajectory of regeneration as seen in old lands. Subtropical thicket occurs along-side other biomes where abiotic correlates determine the biome boundaries. Degraded thicket interacts with its environment differently to intact thicket and has characteristics of other neighbouring biomes and vegetation types. Therefore, disentangling the correlates of species composition and distribution in other vegetation types is important in understanding recovery processes and heterogeneity in degraded subtropical thicket.

3.2. Climatic and geomorphic determinants of vegetation and soil

Globally, ecological landscapes are controlled by primary and secondary determinants of species assembly, namely climate and geology, and fire and herbivory (Wiegand *et al.*, 2006). Climate interacts with the environment on both spatial and temporal scales. Seasonality of rainfall and the primary productivity of plants forms the biome boundaries in South Africa, where growing season is strongly related to precipitation (Wessels *et al.*, 2011). Bond *et al.* (2003) suggest that it is only the more arid areas of South Africa that are climate dependent and that mesic areas are controlled by fire. Such patterns are therefore the template upon which biotic communities are found (Monger & Bestelmeyer, 2006) and can further assist in predicting positive and negative feedbacks (Peters *et al.*, 2006).

The relationship between ecosystem structure and composition is dependent on the climatic and geomorphic templates that interact with the environment at varying spatial and temporal scales (Peters *et al.*, 2006). In southern African savannas, defined by the co-existence of grasses and trees (Scholes & Archer, 1997), woody plant density, canopy height and cover, as well as species richness and grass productivity are positively relation to increasing rainfall; while aridity increases the number of spinescent species (Scholes *et al.*, 2002; Shackleton & Scholes, 2011). In the Cape Floristic Region (CFR), rainfall is strongly correlated to species richness, with altitude also playing a strong role, but not substrate type (Linder, 1991). Water availability is in essence a function of rainfall, slope and soil type, which determines soil nutrient cycling within landscapes (Wang *et al.*, 2009) and is an important factor controlling soil fertility and plant production in southern African arid savannas (Scholes, 1990). Soil properties and nutrients in a natural landscape are a function of the geology (Wiegand *et al.*, 2006), however at fine scales, vegetation patches in savannas are vital for nutrient cycling especially in more arid gradients (Wang *et al.*, 2009).

Spatially, the geomorphic template including geology, aspect, altitude, slope and topography interact at varying scales, driving species composition and resource redistribution (Peters *et al.*, 2006). The soil-geomorphic template is important for biotic change since soil provides water and nutrients; topography affects the micro-climate and parent material influences water holding capacity and nutrient status (Monger & Bestelmeyer, 2006). In South African arid Karoo, quartz fields have specialist species with high endemism and shallow soils (Schmiedel & Jürgens, 1999). Furthermore, exposed surface rock shows increased species richness to perennial grasses and geophytes in a South African grassland. (Crous *et al.*, 2013). In arid environments of the northern hemisphere, aspects which have greater exposure to the sun often have increased vegetation cover, species richness, diversity and composition (Gallardo-Cruz *et al.*, 2009; Nadal-Romero *et al.*, 2014). However, seedling germination and sapling survival in thicket was better on south facing slopes (La Cock, 1992) where moisture availability is higher. In Canadian forests, slope position shows transitions in species distribution (Bridge & Johnson, 2000), while in arid to semi-arid African savannas, catenal contrasts show higher soil fertility on bottom slope positions than on ridgetops (Scholes, 1990) and increased herbaceous biomass with increased elevation (Augustine, 2003).

3.2.1. The role of drought and herbivory in accelerating degradation

In arid and semi-arid environments, where water availability is limiting, the distribution of soil nutrients is more heterogeneous, especially where there is evidence of land degradation (Wang *et al.*, 2009). Land degradation in semi-arid systems has ties to historical legacies of weather variability, such as drought, as well as livestock grazing (Peters *et al.*, 2006). Drought impacts more heavily when herbivory on vegetation and management practice is taken into account (Vetter, 2009). Drought can occur for a number of months to a few years. The loss in much needed water reduces water infiltration rates, plant uptake and growth, as well as a loss in non-resistant drought species (Holmes & Cowling, 1993; Hoffman *et al.*, 2009; Masubelele *et al.*, 2013). Reduced plant cover increases the cover of bare ground, exposing soil to the elements, increasing erosion rates, sediment losses and nutrient leaching (Snyman & Du Preez, 2005; Martin & Bolstad, 2009; van Luijk *et al.*, 2013). Coupled with grazing by livestock, fodder availability becomes insufficient to support the grazing pressures. Long periods of drought can therefore have major consequences to ecosystem thresholds and are often associated with transitions to other states (Vetter, 2009).

The risk of desertification in semi-arid and arid regions is increased under the impacts of drought and herbivory. A review of the literature on the impacts of drought on Karoo vegetation showed that certain species and leaf succulents showed extreme drought resistance and the impacts of drought were felt more severely when the pre-drought rainfall was low (Hoffman *et al.*, 2009). Drought in the Eastern Cape is relatively common, with periods of drought experienced between 1982 and 1984 as well as in the early 1990s, with dam levels dropping to 30% capacity (Jury & Levey, 1993a). Rainfall generally follows a 10-year cycle, however dry spells were found to recur between 1940 and 1970 at intervals of 3.5 and 18.2 years (Jury & Levey, 1993b; in Puttick *et al.*, 2011).

3.3. Abiotic correlates in the Subtropical Thicket Biome

The Subtropical Thicket Biome occurs on a wide range of geological types and lies within a summer-winter rainfall regime (Potts *et al.*, 2013). An aridity gradient exists from the coast, inland along the many watersheds of the Subtropical Thicket Biome, including the Sundays River Valley (Hoffman & Cowling, 1990) that encompasses the Greater Addo Elephant National Park in its southern extent. Compositional shifts in plant species and guilds are evident between mesic, semi-arid and arid thickets along the aridity gradients (Hoffman & Cowling, 1990; Vlok & Euston-Brown, 2002). Woody trees, tree Euphorbia*s* and large woody shrubs in the valleys and towards the coast dominate mesic thickets, while semi-arid and arid thickets see an increase in succulents, spinescent species and dwarf shrubs (Vlok & Euston-Brown, 2002).

The topography includes E-W trending mountain ranges across the spatial extent of the Thicket Biome, with large altitudinal gradients being evident (Boshoff, 2005). The succulent shrub *Portulacaria afra* typically dominates on north-facing aspects and is a keystone species in semi-arid to arid subtropical thicket (Lechmere-Oertel *et al.*, 2005b). Fire does not control species composition and structure in thicket, but rather determines the biome boundary with savanna and fynbos and their mosaics (Vlok & Euston-Brown, 2002). Frost is assumed a determinant of the biome boundary between thicket and nama-karoo vegetation, where the photosynthetic capacity of succulents relates to its freezing tolerance (Duker *et al.*, 2015). The lack of freezing tolerance of succulents in the thicket explains variability in thicket subtypes along the varying watersheds of the Eastern Cape coastline. During the glacial periods of the Pleistocene, thicket retracted into the protective valleys of the watersheds, preventing gene flow of species during this time (Potts *et al.*, 2013). Degradation of landscapes at varying scales makes understanding the climatic and geomorphic processes more important, especially for the identification of system thresholds, recovery trajectories and restoration targets. However, certain factors and secondary determinants have increased effects on species and soil composition, structure and function.

Drought during years of heavy livestock grazing would have exploited available natural resources and probably exceeded system thresholds. In semi-arid to arid subtropical thicket, herbivory by goats through a miscalculation of carrying capacity has severely to moderately degraded and even transformed the landscape. Remaining trees are particularly vulnerable to drought and show increased mortality (Lechmere-Oertel *et al.*, 2005b). The desertification of these thickets has therefore had major consequences to ecosystem structure and function of both abiotic and biotic components.

Both the Greater Addo Elephant National Park (AENP) and the Western Baviaanskloof have areas historically exploited by over-grazing and browsing by domestic livestock as well as a transformation of thicket for agriculture. The ‘pseudo-savanna’ of severely degraded thicket consists of isolated thicket trees in a matrix of annual grasses, herbs and dwarf shrubs (Lechmere-Oertel *et al.*, 2005b).

3.3.1. Degraded 'pseudo-savannas' in different thicket types

Here we define transformed thicket as land that has been cleared for agriculture, whilst severely degraded or moderately degraded thicket as land over-browsed and grazed by domestic livestock (Lloyd *et al.*, 2002). The severity and causes of degradation and the resulting impacts vary within the Thicket Biome as well as between thicket types (Lloyd *et al.*, 2002). Unfortunately, historical data on stocking density is difficult to come by, therefore the impacts to thicket are assumed through long-term visual interpretations and analyses of vegetation structure (Masubelele *et al.*, 2013), guild and species composition and diversity (Evans *et al.*, 1997; Fabricius *et al.*, 2002; Lechmere-Oertel *et al.*, 2005b), changes in litter mass (Lechmere-Oertel *et al.*, 2008) and soil fertility (Lechmere-Oertel *et al.*, 2005a; Mills & Fey, 2004).

3.3.1.1. Vegetation composition

Spekboomveld occurs in the more arid areas of the thicket biome and show compositional differences to degradation compared to the more mesic spekboom thicket types. *Pappea capensis, Euclea undulata* and *Boscia oleoides* are remaining dominant trees that characterise 'pseudo-savannas' in spekboomveld (Vlok & Euston-Brown, 2002). *B. oleoides* is more predominant surrounding the Baviaanskloof and together with *Rhigozum obovatum* and *Rhoicissus tridentata* becomes lost with increasing degradation in arid spekboomveld (Rutherford *et al.*, 2012). *P. afra* becomes completely absent within highly utilised sites. The woody shrub *Lycium ferocissimum* becomes significantly more abundant with increased browsing (Rutherford *et al.*, 2012). Within the matrix, grasses are particularly responsive to degradation and certain species show marked increases. These include *Chloris virgata, Aristida adscensonianis, Setaria verticillata, Tragus berteronianus* (Rutherford *et al.*, 2012), *Cynodon dactylon, Enneapogon desvauxii* and *Aristida congesta* (Vlok & Euston-Brown, 2002). The shrubs *Aizoon glinoides, Atriplex lindleyi subsp. inflata, Solanum tomentosum* (Rutherford *et al.*, 2012) and *Pentzia incana (*Vlok & Euston-Brown, 2002) show increases in cover and abundance with degradation. Furthermore, *P. incana* is a dominant shrub in the Karoo and noorsveld (Hoffman & Cowling, 1991). Degraded spekboom thicket, especially in the Sundays River Valley, contains *P. incana* owing to its capability of invading into other phytochorological areas (Gibbs-Russell & Robinson, 1981). *Pteronia incana* is more abundant in degraded Fish River thickets and abandoned lands (Evans *et al.*, 1997; Kakembo, 2009), while *Galenia africana* is increasingly present in degraded Groot Arid Spekboomveld in the Baviaanskloof (Vlok & Euston-Brown, 2002).

Spekboom thicket 'pseudo-savannas' are similarly defined by the remnant tree species *P. capensis* and *S. afra*. Both *Grewia robusta* and *E. undulata* are frequently found in degraded spekboom thicket, showing structural similarities to pristine thicket (Lloyd *et al.*, 2002). *E. undulata* is significantly lost through degradation, more so than *P. capensis* (Lechmere-Oertel *et al.*, 2005b) and the loss of it with *P. afra* results in a replacement by *Putterlickia pyracantha* and *Opuntia ficus-indica* in the Sundays River Valley (Hoffman & Cowling, 1990). In Baviaans Spekboom Thicket, *Aloe ferox* and *Aloe striata* become abundant when degraded (Vlok & Euston-Brown, 2002). The matrix vegetation typically comprises *Cenchrus cilliaris, C. dactylon, P. incana and Melinis repens* in the Baviaanskloof (Vlok & Euston-Brown, 2002). *P. incana* is therefore a common shrub found in almost all degraded lands.

3.3.1.2. Soil composition and litter

The loss in canopy cover and key species such as *P. afra* reveals feedbacks to reductions in the production and decomposition of plant litter and exposes soils to transport processes and harsh micro-climates. In degraded spekboom thicket of the Sundays River Valley, the 'pseudo-savanna' is associated with a decrease in soil nitrogen and carbon content, as well as Mg, with increases in Ca, P and silt content in the soil (Mills & Fey, 2004). In spekboomveld, P, K and Mg increase significantly with degradation as a function of increased stocking rates (Rutherford *et al.*, 2012). Under *P. capensis* canopies, soil conditions improve in the 'pseudo-savanna' with better infiltration and increased carbon, however infiltration is still less than in intact spekboom thicket (Mills & Fey, 2004). Soil infiltration is also higher in Baviaanskloof Spekboom Thicket below spekboom canopies and shows a 100-fold decline in infiltration rates in open degraded thicket (van Luijk *et al.*, 2013).

On average, the total loss of soil carbon to browsing-induced degradation is 57.23 t C ha^{-1} in the Baviaanskloof, where 21.56 and 24.06 t C ha^{-1} were measured in old and degraded lands, respectively (Powell, 2009). This differed substantially from results in the Sundays River Valley, where soil carbon in degraded thicket was measured at 95 t C ha^{-1} (Mills *et al.*, 2005). The study by Mills *et al.* (2005) did however have a much smaller sampling size (n=8) compared to Powell (2009), who further measured to a depth of 0-25 cm and not 0-10 cm (n=25 and n=44 for old lands and degraded thicket, respectively). The difference in soil depths and sampling number could explain the differences in soil carbon measured between the two sites, especially since nutrients accumulate most at the surface and in the topsoil (Thompson & Troeh, 1978). Fine scale differences in soil carbon, N, pH and P, moisture availability and infiltration can be observed even when the system is in a degraded state. Observed declines in C and N and an increase in pH within the matrix, rather than under the canopy in degraded thicket (Lechmere-Oertel *et al.*, 2005a), highlights the importance of tree and shrub cover in retaining a semblance of soil fertility and heterogeneity. The declines in soil carbon can be associated with declines in leaf litter, since the absence of a canopy to provide litter and protect the litter from transportation processes, results in a lack of litter decomposition into the soil.

The litter layer in subtropical thicket is well defined for a semi-arid system due to the high litter production from *P. afra* (Lechmere-Oertel *et al.*, 2008), as well as from the deciduous and dense tree layer. The loss of *P. afra*, in particular in degraded thicket, causes severe losses in litter biomass, where an increase in the degradation gradient from over-stocking is associated with an absence of leaf litter (Rutherford *et al.*, 2012). In spekboomveld surrounding the Sundays River Valley, production of litter in degraded thicket was 30% less at a landscape scale, reducing from 4 126 to 2 881 kg ha^{-1} yr^{-1} (Lechmere-Oertel *et al.*, 2008). The loss of litter has implications to the carbon cycle (Lechmere-Oertel *et al.*, 2008) with losses of 3.46 t C ha^{-1} experienced from intact to degraded Baviaans Spekboom Thicket (Powell, 2009) and 11 to 1.0 t C ha^{-1} in Sundays Spekboomveld (Mills *et al.*, 2005). Furthermore, losses in litter were higher under *P. capensis* and *E. undulata* than under *Searsia longispina* and *P. afra*, showing a growth form effect (Lechmere-Oertel *et al.*, 2008), where the single stemmed species would expose the litter layer to disturbance and transport processes.

Peters & Havstad (2006), highlight the components of a semi-arid system and the processes and feedbacks that determine species composition and structure. While studying the local and landscape processes and functional attributes of degraded thicket are too large for the scope of this thesis; assessing structure and composition is not. Therefore, the following chapter aims to assess plant and soil composition in relation to abiotic correlates. The study therefore assumes that heterogeneity exists in severely degraded thicket and seeks to find how this is related to the climate and geomorphic templates. It is hoped that recognising multiple states of degradation within the Thicket Biome and understanding structure and composition, relative to environmental characteristics and processes, can better inform restoration action.

Furthermore, finding scales of degradation through plant structure aimed to identify multiple states of vegetation and soil composition.

3.4. Objectives and key questions

Objective 1: To ascertain the correlations between abiotic factors and plant species richness and composition at local and landscape scale.

Key question 1.1: Is plant richness and community composition in degraded thicket correlated to abiotic attributes?

Objective 2: To assess the relative abundance of different plant growth forms and species richness at local and landscape scale.

Key question 2.1: How does growth composition and richness change between sites?

Objective 3: Identify degradation classes within each site and assess how plant species composition and abiotic variables change within these.

Key question 3.1: Is there a significant difference in the dominant plant species within each degradation class?

Objective 4: To quantify soil characteristics and quality among degradation classes.

Key question 4.1: Are there significant differences in soil characteristics between sites and degradation classes?

Key question 4.2: Which soil properties have the highest correlation with increasing degradation?

3.5. Methods

The data collection followed the Standard Operating Procedure (SOP) for carbon and biodiversity baselines of the Addo, Baviaanskloof and Fish River Restoration Project (ABFRP), developed from CDM methodology AR-AM0002 v3. Contractual areas for the restoration of spekboom within severely degraded thicket (Lloyd *et al*., 2002) were used to allocate random points for baseline monitoring within each site, using ArcGIS software. For the GAENP, a total of 30 plots were allocated for the Darlington and Kabouga sections, and 20 plots for the Addo Main section. The Baviaanskloof contained 29 plots. In total 109 plots were sampled across the four study sites. Each plot was 10 x 10 m and set up from the randomly allocated south-western point of the plot. The plot included four 2 x 2 m quadrats, two belt transects (50 m long and 1 m wide), four litter quadrats (50 x 50 cm), and six locations for soil sampling (Figure 12).

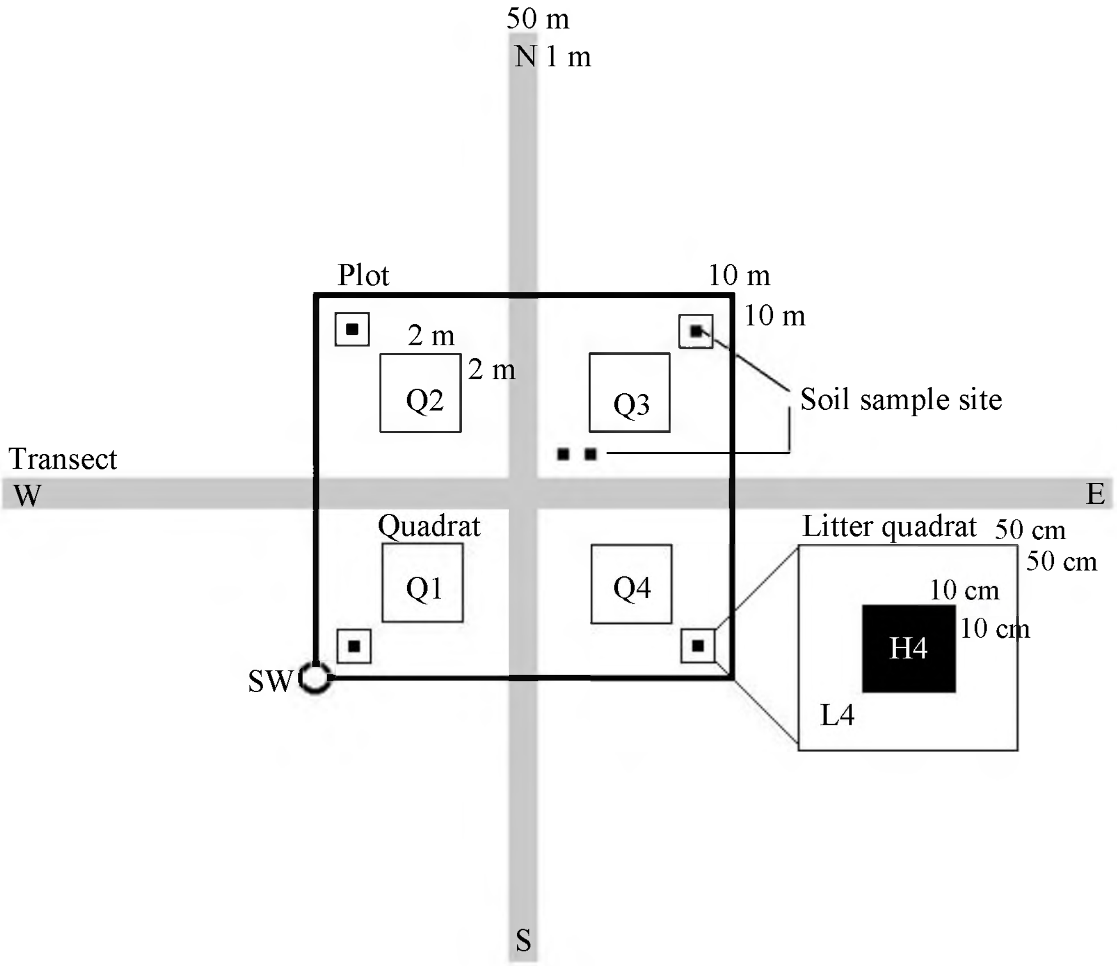


Figure 12: Sampling plot layout, including biodiversity, litter and soil carbon sampling positions, drawn to no particular scale. (Adapted from the ABFRP monitoring baselines SOP: DEA NRM, 2011).

The site codes are AD: Darlington, AM: Addo Main, AK: Kabouga and BV: Baviaanskloof. Sampling occurred in Darlington from November 2011 to March 2012; in Baviaanskloof from January 2012 to June 2012; Addo Main was collected in two periods, October 2011 and February and March 2013; lastly Kabouga was collected from April to June of 2013.

3.5.1. Botanical data

Each 2 x 2 m quadrat was situated 2.121 m from each corner of the 10 x 10 m plot towards the centre. The quadrats were sampled for percentage cover of all plant species, as well as bare ground percentage cover. Each additional unknown plant species was collected from outside of the sampling area (to avoid destruction within the monitoring plot), labelled with a temporary name matching the datasheet and pressed for later identification. The two 1 x 50 m belt transects bisected the plot from S-N and E-W. A compass was used for accuracy, but the transect line intersected the centre point between each corner of the 10 x 10 m plot. Within the belt, the length along a tape measure and width along a one metre rule of each woody and succulent tree and large woody shrub intersecting the belt were recorded.

3.5.2. Environmental data

Environmental variables for each plot included spatial variables such as topography and climate; soil variables and geology. A total of 38 variables were recorded (Appendix 1).

3.5.2.1. Spatial variables

ArcMap 10.1 was used to calculate slope, aspect and altitude of each plot. Digital Elevation Modelling (DEM) was used to perform slope and aspect analyses and obtain values for altitude. Monthly rainfall and temperature data were obtained from the South African Weather Services (SAWS) as well as Lynch (2004) patched rainfall data from the dates available for each area. Further calculations were performed to obtain the mean annual precipitation (MAP), the mean monthly precipitation (MMP), mean winter precipitation (MWP) and mean summer precipitation (MSP), as well as mean winter and summer temperatures.

3.5.2.2. Site record and geology

Litter

All plant litter (seeds, fruits, leaves, twigs and branches ≤5 cm in diameter) was collected in four 50 x 50 cm quadrats placed around a point located 1 m from each corner of the 10 x 10 m plot. Collected litter was sieved to remove sand, bagged and labelled.

Soil

Six holes (10 x 10 cm) were dug to a depth of 15 cm; these included the four within each litter quadrat (H1-H4) and H5 located 1.2 m from the centre towards H3. H6 is located one metre from H5, parallel to the biodiversity transect line (Figure 12). The dimensions, including lengths of each side, diagonals and depth of the holes, were recorded. The soil excavated from each hole was bagged and labelled, matching the hole number. Each hole was filled with sand from a bag weighing 2.5 kg. The left over sand was labelled to calculate the volume of the first hole. The second hole was further dug to 30 cm, and the soil added to the bag of soil from the first hole. The dimensions were again recorded and the hole filled with another 2.5 kg bag of sand. The left over sand was again labelled. The soils from five of the holes were used to calculate the average soil depth, root volume, gravel volume and soil carbon. The soil from H6 was used to calculate bulk density by dividing the dry weight of the soil by the volume of the soil.

Geology

Using ArcMap 10.1 and an available geology shapefile of South Africa, the geology underlying each plot was recorded. The geological group and stratigraphy were noted, as well as the dominant lithology, including sandstone, mudstone, calcrete, sand and conglomerate.

3.5.2.3. Soil analyses

From each of the six soil bags from each plot, a total of 50 g was removed, combined and thoroughly mixed. The 300 g soil sample for each plot was sent to BEMLab for soil analysis, including soil texture, resistance, stone volume and pH; exchangeable cations (Na, K, Ca, Mg); the base saturation of the exchangeable cations as well as the cation exchange capacity (CEC), P (Bray II), and percentage C. Soils had previously been sent to the Agricultural Research Council (ARC), therefore two carbon values for each plot are available; C(ARC) in mg/kg and C%.

3.5.3. Data analysis

3.5.3.1. Abiotic correlates

Species composition analyses were performed using PRIMER 6 +PERMANOVA (Plymouth Routines in Multivariate Ecological Research, Anderson *et al.*, 2008). The plant species percentage cover data was used as the biological abundance data and all non-botanical/abiotic variables were used as the environmental variables.

All species that occurred only once in a site or in the landscape were removed from the analysis. This was based on recommendations by Anderson *et al.* (2008) to remove all species that constitute <4% of the total number of species. The plant cover data was pre-treated to an overall

Log(x+1) transformation to reduce the influence of rarer species and a Bray-Curtis resemblance analysis for use in subsequent multivariate analyses. A draftmans plot was used to check for co-linearity in the environmental variables. Those which were co-linear were individually transformed to the function Log (v+1). The environmental variables were then normalised in PRIMER.

A BEST analysis was performed of regional and landscape data to find the combination of variables that best describe the resemblance among samples of the species data. This does not however describe the amount of variation that can be explained by the selected variables (Anderson *et al.*, 2008). Due to the large dataset at the landscape scale (all sites), a step-wise BEST (BVSTEP) was performed, but a BIOENV was used for the site level analyses. A LINKTREE analysis was used to visually represent the separation of plots according to species composition and environmental characteristics. The groupings were delineated into communities and used for further analysis.

To find a distinguishing axis of separation between two pre-defined groups (e.g. site), a CAP (Canonical analysis of principal co-ordinates) analysis was used (Anderson *et al.*, 2008). It works on the basis of validating a hypothesis through allocation into the pre-defined groups (Anderson *et al.*, 2008). A CAP in this instance was used to see if there is a clear separation between the communities as defined in the LINKTREE. The communities were added as a factor to the samples to test this. The same was done for the geological type and the site. Vectors of the environmental variables and the species which had between a >0.35 and >0.4 correlation to the communities, geologies and site were overlaid onto each graph. It must be noted however, that although these vectors provide insights to the relationship to the communities, they are in no way an absolute cause of the species compositions, but merely correlates (Anderson *et al.*, 2008). Furthermore, a one-way SIMPER test was used to tease out the most abundant species within each community and examine differences in species composition.

3.5.3.2. Growth form profile and species richness

Each species in the cover data was labelled to an assigned growth form (POSA, 2012). The eleven growth forms were woody tree, succulent tree, woody shrub, succulent shrub, shrub, dwarf shrub, herb, succulent herb, climber, geophyte and graminoid. The cover of each species per plot was summed according to growth form. The total cover of each growth form was averaged per site (regional) and across the landscape. The cumulative cover of these was represented in a stacked bar graph. The total number of species per growth form within each site was summed from the quadrat data to obtain a value of species richness. The total number of species per site was also recorded and pooled for the landscape.

3.5.3.3. Degradation scaling

Growth form composition and cumulative percentage cover of growth forms, species richness from both the quadrats and transects, as well as the area occupied by woody and succulent trees and large shrubs were used to derive a degradation score for each plot. Table 4 summarises the scoring system for each parameter. For this analysis, climbers were combined with shrubs, and succulent herbs were combined with herbs since both growth forms were low in species richness. *E. caerulescens* (noors) was removed from succulent shrubs and weighted separately as it is an indigenous invasive to the area, spurred by the loss in vegetation cover (Powell *et al.*, 2010).

By personal judgement, each growth form was weighted according to its importance to an intact thicket vegetation and its contribution to a less degraded state. Therefore, trees and shrubs were weighted greater than grasses. For example, if a woody tree with a score of 4 has a cover of 80% then the score given to that plot for trees is 4.8, but if the cover is 10% then the score is 4.1. Bare ground cover and the cover of noors were weighted as zero, however these were scored in reverse, where a higher cover of 90% was given a score of 0.1, while a lower cover of 10% was given a score of 0.9. Noors in Darlington is expanding into spekboomveld and thus its presence in a plot indicates degradation (Powell *et al.*, 2010). The same applies for bare ground cover, which is seen as an indicator of degradation. The species richness in the quadrats and transects was based on the number of species in a plot, while the woody area (m^2) was assigned a higher number for higher cover.

The scores for each of the parameters were then summed. Values for these ranged from 6.2 to 41.1. These were further simplified by giving each plot a degradation score from 1-4 at intervals of 10, starting at 15 (<15 = 1; ≥15 <25 = 2; ≥25 <35 = 3; ≥35 =4). Additionally, plots pre-defined as old agricultural lands and not degraded thicket lands were separated from the scoring. Therefore, plots had a score ranging from 1-4 and those which were old lands were labelled as OL. These old land plots only occurred in Addo Main. Although scores 1-4 are used in all the analyses, these can be extrapolated to severely degraded (score 1), severely to badly degraded (score 2), badly degraded (score 3) and badly to moderately degraded (score 4).

Table 4: Degradation scoring system for growth forms, species richness and woody and succulent area.

Parameter	Score
Noors and bare ground	0.9-0.1 (Reverse scale)
Graminoid and geophyte	1.1-1.9
Herb	2.1-2.9
Shrub	3.1-3.9
Woody shrub, succulent tree and woody tree	4.1-4.9
Succulent shrub	5.1-5.9
Species richness quadrats	>15 = 4; ≤15 >10 = 3; ≤10 >5 = 2; ≤5 >0 = 1
Species richness transects	>12 =5; ≤ 12 >8 =4; ≤8 >5 = 3; ≤5 >3 = 2; ≤ 2 >0 = 1
Woody and succulent area	>400 = 9, ≤400 >300 = 8, ≤300 >200 = 7, ≤200 >100 =6, ≤100 >50 = 5, ≤50 >30 = 4, ≤30 >10 = 3, ≤10 >5 = 2, ≤2 >0 = 1

According to Anderson *et al.* (2008:15) a "PERMANOVA is a routine for testing the simultaneous response of one or more variables to one or more factors in an analysis of variance experimental design on the basis of any resemblance measure, using permutation methods." A PERMANOVA was therefore used to assess significant differences between degradation scores within sites and degradation scores between sites, based on plant species compositional data. A one-way SIMPER was used to tease out the abundant species per degradation score.

3.5.3.4. Soil quality and composition

Twenty-two variables were used to characterise the soil properties and quality. Each of the variables were sorted according to site, as well as by degradation score, to calculate mean and SE values. The site and the degradation scores were used as factors in PRIMER to calculate significant differences between degradation scores and sites. This had to be done for each variable individually using the ANOSIM analysis tool. An ANOSIM according to Clarke & Warwick (2001) is a non-parametric permutation procedure that is based on a ranked similarity matrix underlying the classification of samples. It therefore tests for differences between pre-defined groups.

3.6. Results

The results section is broken down into a number of interleading subsections that are in accordance with the objectives. Firstly, abiotic correlates are tabulated to understand the most important environmental templates governing species composition per site and within the landscape in section 3.6.1. The landscape is the term given to all sites combined. Secondly, a landscape view of community composition in relation to a suite of environmental variables is presented in the form of a LINKTREE (section 3.6.2.1). Since the landscape scale analysis extracted community separation among site specific gradients, local scale assessments were based on site (section 3.6.2.2). For each landscape scale and local scale analysis, the communities from a LINKTREE were used as a factor in a CAP analysis. Each CAP is displayed as two graphs, one with vectors of environmental correlates and the other of plant species correlates. Additionally, the landscape scale includes a CAP where geology was used as a factor. Subsequent to each CAP at both landscape and local scales, a table of the dominant species for each community is presented.

Growth form cover is presented per site in section 3.6.3 and links to the subsequent section on degradation scaling. The section, which aims to delineate different degradation scales based solely on scores obtained from growth form cover, shows differences in species composition for each degradation score, compared between and within sites. A SIMPER highlights the dominant species per degradation score. The degradation scores were additionally used in section 3.6.5 to look at soil composition under varying degradation scales and per site. It was later found however, that the method of degradation scoring using growth forms was insufficient. Nevertheless, it provides some interesting insights into soil composition in relation to plant cover.

3.6.1. Abiotic correlates

The combination of abiotic variables that had the highest correlation to species composition assemblages per site and within the landscape are shown in Table 5.

Table 5: The results of a BEST analysis per site and within the landscape, showing the species correlation to a combination of abiotic variables.

Site	Correlation	Abiotic correlates
Darlington	0.54	Litter mass, stone volume, C%, Na% and Mg%. Others: %soil, resistance, slope, Ca% and bare ground.
Addo Main	0.40	Bare ground, shale and sand, K and Na. Others: Mudstone, Ca, C%, K% and CEC.
Kabouga	0.48	Altitude, %gravel, Mg, Ca% and CEC. Others: Mg%, Ca, C(ARC) and K.
Baviaanskloof	0.35	Altitude, bare ground, resistance, Mg and Ca%. Others: Tillite, K, Mg%, K%, aspect and stone volume.
Landscape	0.56	Altitude, MWP, MSP, bare ground, %roots, %gravel, sand, Na and Mg.

Additional variables that have been included in the table (Others) are those that were highlighted as being important variables in other combinations of variables, whose correlations were slightly less than those already stipulated. At a landscape level, 56% of the plots had species assemblages that were related to the altitude, rainfall, bare ground cover (suggestive of the vegetation cover), the percentage of both roots and gravel, sand as a lithological unit and Na and Mg. In Darlington, interesting correlates included litter mass, stone volume, resistance and slope. In Addo Main, correlates included different lithology. Since altitude appeared as an important correlative variable in relating to species composition in Kabouga and Baviaanskloof, an MDS (Multi-dimensional scaling) was used to represent altitude with scaled bubbles for all plots labelled by site (Figure 13).

It is evident that there is an obvious difference in altitude between sites, with plots in Addo Main (Site 2) which are closer to the coast, having the lowest altitude and Baviaanskloof (Site 4) having the highest. Darlington (Site 1) exists on the plateau above the mountains visible from Kabouga, and thus has a higher altitude than Kabouga (Site 3). Interestingly, Kabouga and Baviaanskloof, which are very mountainous sites, appear to separate the species compositions to the north and to the south.

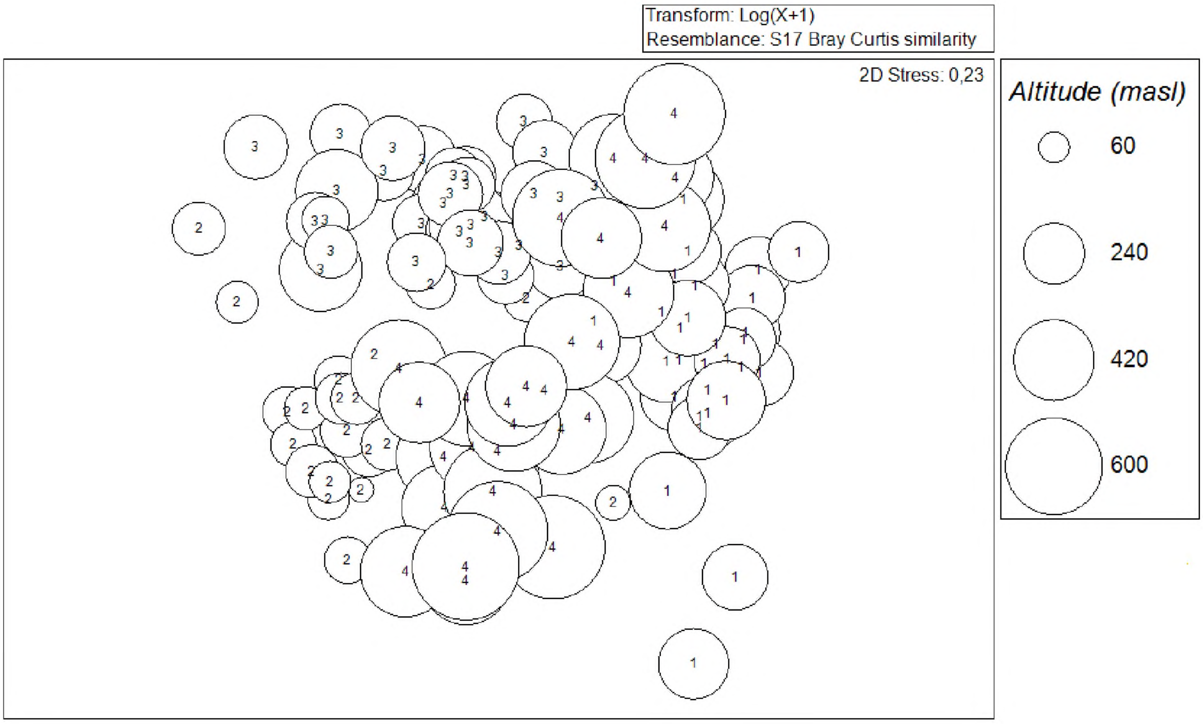


Figure 13: MDS representing altitudinal gradients (masl) across all four sites (1-Darlington; 2-Addo Main; 3- Kabouga; 4-Baviaanskloof).

3.6.2. Plant species composition

3.6.2.1. Landscape scale

Community delineation

The LINKTREE in Figure 14 shows the significant grouping (A-K) of all 109 plots according to species composition and the abiotic variables. Five main communities (1-5) were identified in the LINKTREE, split at A, B, C and I. Community 1 at ‘A’ consists of outlying plots from multiple sites and is separated by the high sodium content in the soil at >1.49 cmol/kg. Community 2 has a low soil carbon content of <3.73 g/kg, while community 3 has a carbon content of >5.6 g/kg. Community 4 has a low soil percentage in the holes of <0.34% while community 5 soil percentage is at least >0.45%. Except communities 1 and 4, further significant differences (5%) between plots are shown below the dominant split at ‘C’ and ‘I’.

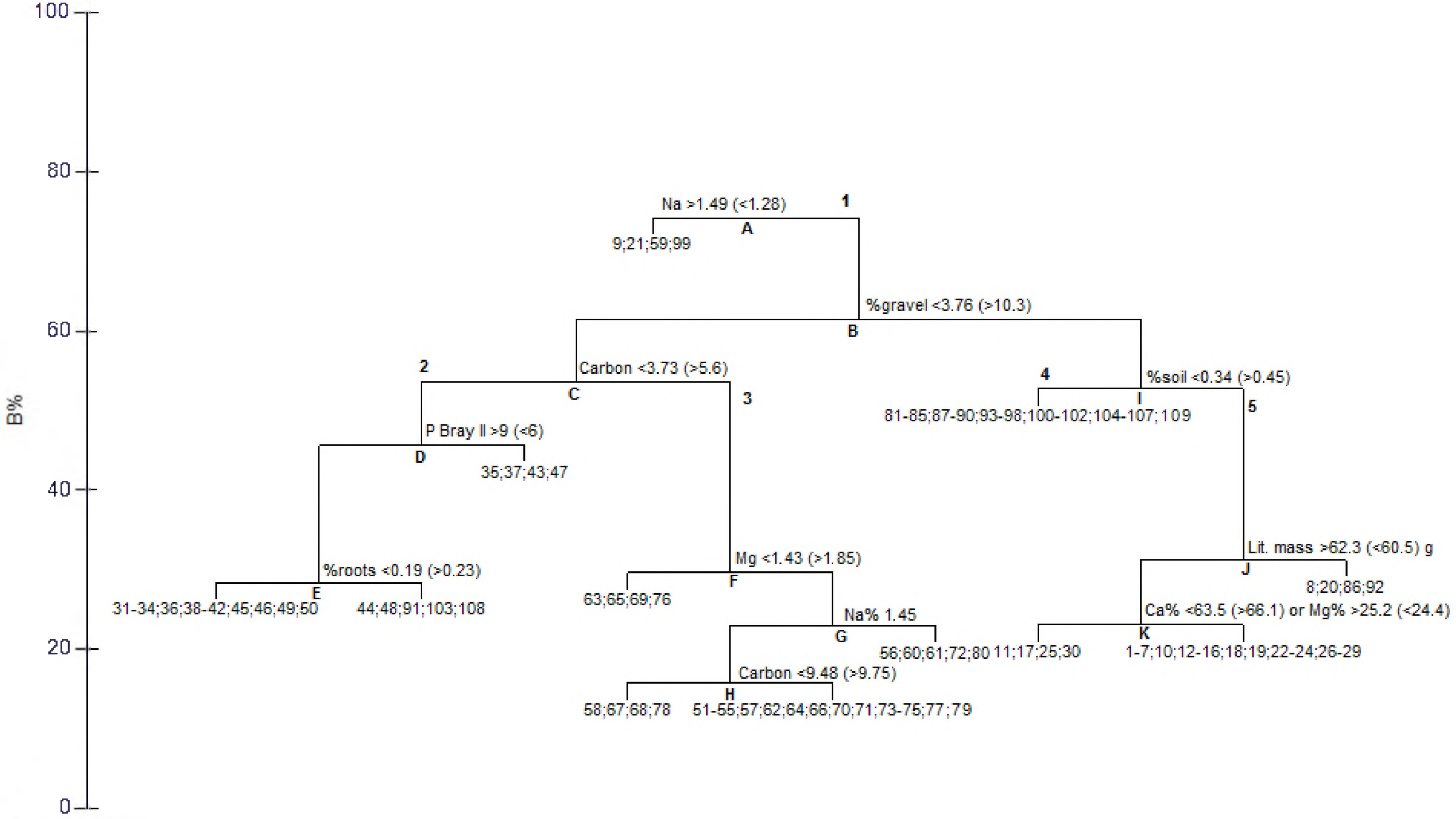


Figure 14: LINKTREE of all 109 plots in the landscape, with abiotic correlates separating each branch at A-K and communities at 1-5.

CAP analyses further illustrate the communities with vectors of environmental and species correlates. The CAP had an 88% allocation success to the communities in the LINKTREE. Plots in community 2 have a strong correlation to the rainfall, lithology, potassium and resistance of the soil (Figure 15a). The dominant species occurring in this community are *Cynodon incompletus, Hermannia althaeoides, Lepidium africanum* and *Conyza bonariensis* (Figure 15b).

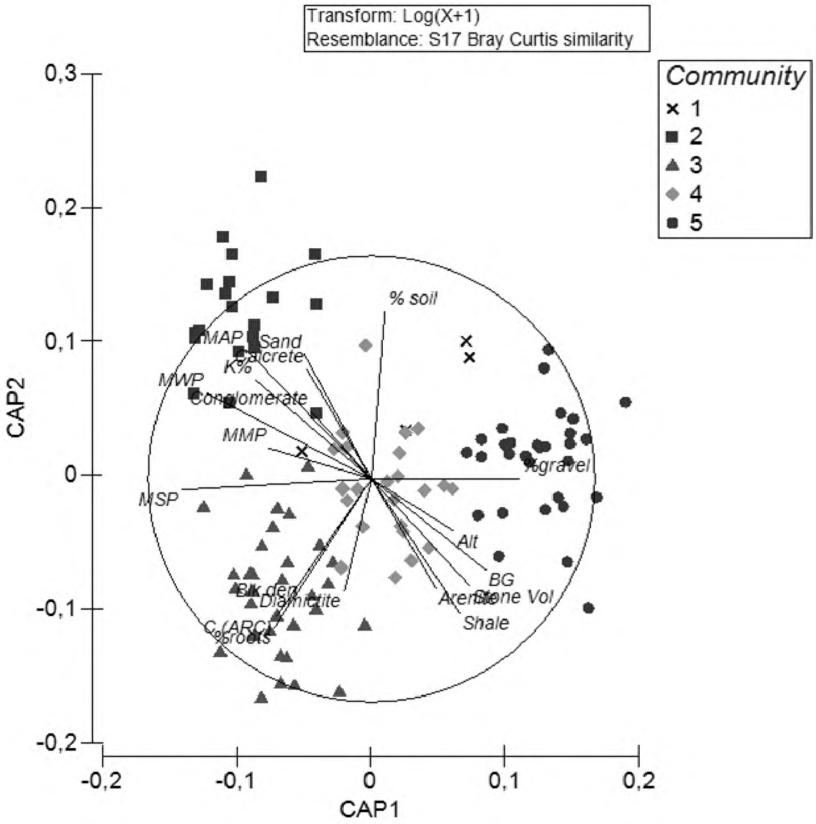


Figure 15a: CAP analysis of all sites factored by community with abiotic vectors at >0.4 correlation (n=109).

Community 3 has a higher bulk density, %roots and carbon. The species dominant in this community are *Panicum maximum, Jatropha capensis, G. robusta, P. pyracantha* and the invasive cactus, *Opuntia aurantiaca.* Common between these two communities are *Drosanthemum hispidum* and *Galenia pubescens.* Community 4 was not strongly correlated to any abiotic variables, however, Figure 15a suggests that altitude, lithology and bare ground cover have some relationship with this community. Community 5 shows a strong correlation with the percentage gravel and the species *E. caerulescens* and *Aizoon rigidum.*

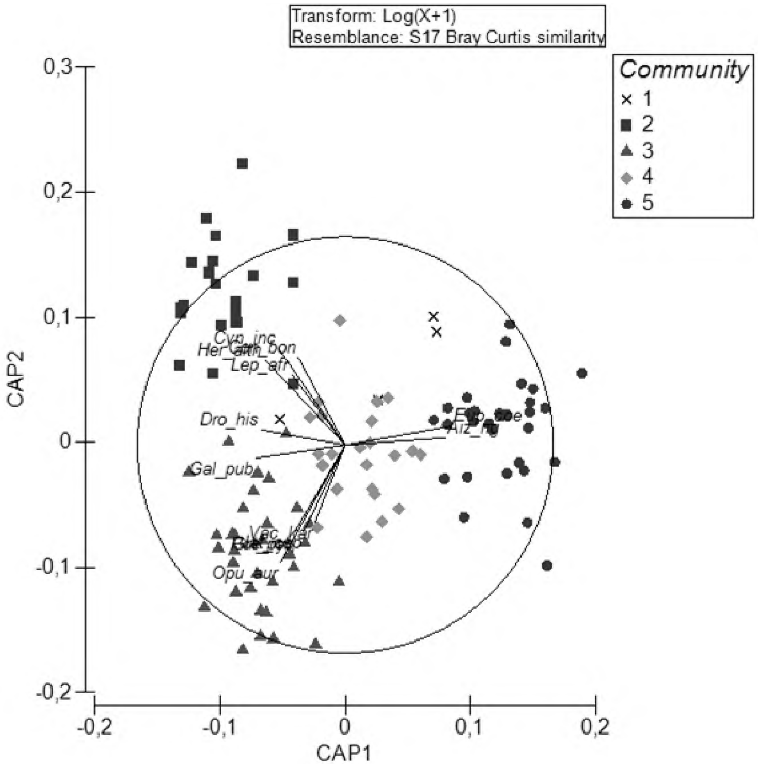


Figure 15b: CAP analysis of all sites factored by community with plant species vectors at >0.4 correlation (n=109).

Interestingly, apart from outliers in community 1, these communities are separated by site. Community 2, 3, 4, and 5 are dominated by plots from Addo Main, Kabouga, Baviaanskloof and Darlington, respectively. Six plots from Baviaanskloof do not fall within community 4 and are scattered between communities 1, 2 and 5.

A one-way SIMPER in Table 6 lists the dominant species within each community and the similarity of the plots to each other in terms of species composition. Community 4 with five dominant grasses, has the most grass species compared to the other communities and is the only community with the succulent tree *A. ferox* and tree species *E. undulata* and *P. capensis.* This does not however mean that these trees do not occur in other communities, just that they are not dominant. *E. caerulescens* is dominant in community 5, along with many dwarf and succulent shrubs. Community 5 has the highest similarity in plant composition and cover than any of the other communities at just over 29%.

Table 6: SIMPER of the plant species that contribute the highest to species composition within communities 1-5. Underlined species are unique in dominance to that community.

Community	Similarity (%)	Common plant species
1	7.7	*A. lindleyi* subsp. *inflata*, *Mesembryanthemum aitonis*, *Chenopodium mucronatum* and *Mesembryanthemum junceum.*
2	27.2	*C. incompletus*, *G. pubescens*, *D. hispidum*, *H. althaeoides*, *L. africanum*, *Selago geniculata*, *Atriplex semibaccata*, *Crassula expansa*, *C. bonariensis*, *C. dactylon*, *M. aitonis* and *Eragrostis curvula.*
3	27.9	*G. pubescens*, *P. incana*, *G. robusta*, *C. dactylon*, *D. hispidum*, *P. maximum*, *S. geniculata*, *O. aurantiaca*, *P. pyracantha*, *Vachellia karroo*, *J. capensis*, *A. semibaccata*, *R. obovatum*, *Asparagus capensis*, *Asparagus striatus* and *Isoglossa origanoides*.
4	23.4	*C. incompletus*, *P. incana*, *G. robusta*, *Lycium oxycarpum*, *R. obovatum*, *P. maximum*, *Justicia orchioides*, *P. capensis*, *G. pubescens*, *A. congesta*, *Eragrostis lehmanniana*, *C. cilliaris*, *P. pyracantha*, *Chrysocoma cilliata*, *E. undulata*, *C. mucronatum*, *A. ferox* and *L. africanum*.
5	29.2	*P. incana*, *E. caerulescens*, *R. obovatum*, *A. congesta*, *M. aitonis*, *A. rigidum*, *G. robusta*, *Galenia secunda*, *Eragrostis obtusa*, *Cuspidia cernua*, *Limeum aethiopicum*, *Panicum deustum*, *Mesembryanthemum guerichianum*, *C. mucronatum*, *Felicia filifolia*, *L. africanum*, *Barleria irritans* and *A. striatus*.

The BEST analysis in Table 5 and the CAP analysis in Figure 15a both highlight the importance of the soil properties in determining species composition. Therefore, another CAP was performed using geology as a factor (Figure 16a and b).

Geology

The CAP analysis revealed a 78% allocation success to the geological groups. Plots within the Cape Supergroup have a significant positive correlation with the altitude and percentage of roots and of carbon. The mean summer and winter rainfall is negatively correlated to the plots in the Karoo Supergroup, however these plots are in the Darlington section where a rain-shadow effect reduces rainfall in those areas (Cowling, 1983a).

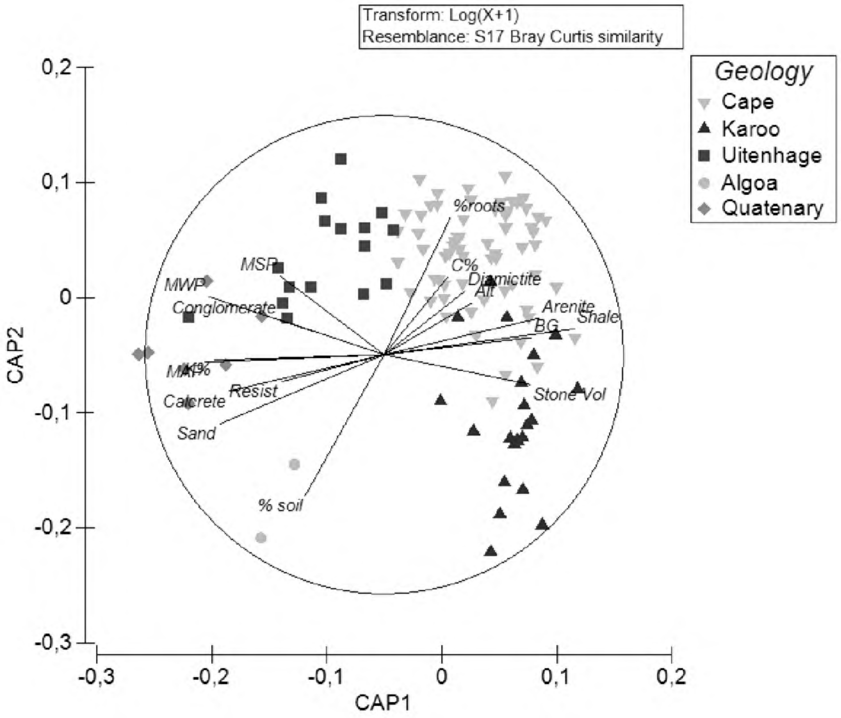


Figure 16a: CAP analysis factored by geology with abiotic vectors at >0.4 correlation (n=109).

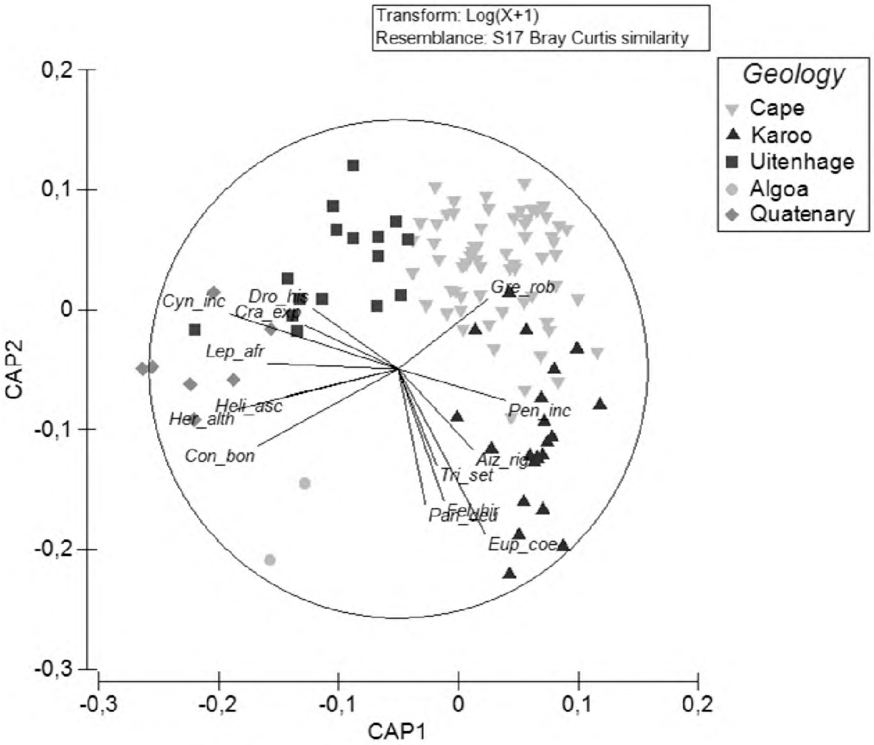


Figure 16b: CAP analysis factored by geology with plant species vectors at >0.4 correlation (n=109).

The Karoo Supergroup was dominated by *E. caerulescens, Felicia hirsuta, P. deustum, Trichodiadema setuliferum* and *A. rigidum* in 40% or more of the plots. The Quatenary formations are dominated by *C. incompletus*, *Helichrysum rosum* var. *aschersoniana*, *H. althaeoides* and *C. bonariensis* on sand and calcrete lithologies, high in resistance. The Algoa group is strongly related to an increase in the %soil. Only *G. robusta* has a >0.4% correlation to the plots in the Cape Supergroup.

A SIMPER analysis of the geology further confirmed the assumptions made from the vectors in Figure 16b. Table 7 summarises the most abundant species on each of the geologies. These are the top ten, or those which contribute at least 90% of the abundance in all of the plots, if ten are not listed. A one-way ANOSIM analysis found that species composition was significantly different when factored by geology (Global R= 0.39; p= 0.001), however the degree of variation, represented by the R value, is weak.

Table 7: SIMPER of the top ten dominant species on each geology. Underlined species are unique in dominance to that geology.

Geology group	Similarity (%)	Common plant species
Karoo	27.6	*P. incana, E. caerulescens, R. obovatum, M. aitonis, A. congesta, G. robusta, A. rigidum, C. dactylon, G. secunda* and *C. cernua.*
Cape	17.6	*P. incana, G. robusta, G. pubescens, P. maximum, R. obovatum, C. incompletus, C. datylon, P. pyracantha, S. geniculata* and *D. hispidum.*
Uitenhage	27.1	*C. incompletus, D. hispidum, G. pubescens, P. incana, L. africanum, S. geniculata, A. semibaccata, E. obtusa, H. althaeoides, M. aitonis.*
Quatenary	35.2	*C. incompletus, H. althaeoides, L. africanum, D. hispidum, G. pubescens, C. expansa, C. bonariensis, E. curvula* and *H. rosum* var. *aschersoniana.*
Algoa	20.1	*Lactuca capensis, C. dactylon, Plantago lanceolata, C. bonariensis* and *H. althaeoides.*

C. dactylon and or *C. incompletus* are common grass species throughout the landscape regardless of geology. *P. incana* however, becomes limited in the Quatenary and Algoa strata where the land use history is different and the rainfall is higher. The Karoo Supergroup lithology, where the Darlington site is located, is abundant in *E. caerulescens* and small shrubs including *A. rigidum, G. secunda* and *C. cernua,* which are more adapted to arid environments (Vlok & Euston-Brown, 2002). The dominant grasses, other than the common *Cynodon* species, change with geology. In the Karoo there is *A. congesta,* in the Cape *P. maximum* is most dominant, Uitenhage is *E. obtusa* and on the Quatenary formations *E. curvula* is abundant. Common woody shrubs include *R. obovatum* and *G. robusta,* but *P. pyracantha* is dominant only in the Cape geological groups.

3.6.2.2. Local scale

Climate variables were removed from the data for the community analyses since they are coarse attributes, with little to no variation in rainfall found within the sites. It was assumed that there would be site scale variations in climate, however available data to test this within the site were limited or unavailable. The landscape scale LINKTREE analysis of all plots revealed that despite all the areas sampled being degraded, there was still a split in plant species composition at a local level and more specifically per site. Therefore, site specific analyses are further used as the rationale for the study, instead of communities as defined by the LINKTREE in Figure 14. It was expected that the LINKTREE might reveal differences according to a degradation continuum, however this will need to be investigated on a site specific level as the plant species compositions are different among the sites. This was confirmed by a one-way ANOSIM analysis of species composition, factored by site (Global R= 0.671; p= 0.001).

LINKTREE analyses were performed for each site and the communities identified from these were used as a factor in a CAP analysis per site. Figures 17-19 show the separation in communities with plant species and abiotic vectors overlaid. Baviaanskloof, together with a SIMPROF test in the LINKTREE, as well as a CLUSTER analysis showed that all plots were significantly similar to each other and therefore did not split the site into communities. This confirms the results of the BEST analysis where only 35% of the data could be explained by a combination of variables. It is likely that the sampled area of the Baviaanskloof, unlike that of GAENP, has had a consistent land use history throughout the extent of the study area, thus no significant differentiation into communities can be found. A CAP and other community analyses could therefore not be performed for the Baviaanskloof.

Darlington

Three communities were identified from the LINKTREE analysis in Darlington with three outlying plots. The CAP in Figure 17a and 17b show that the majority of plots (73%) fall within community 3.

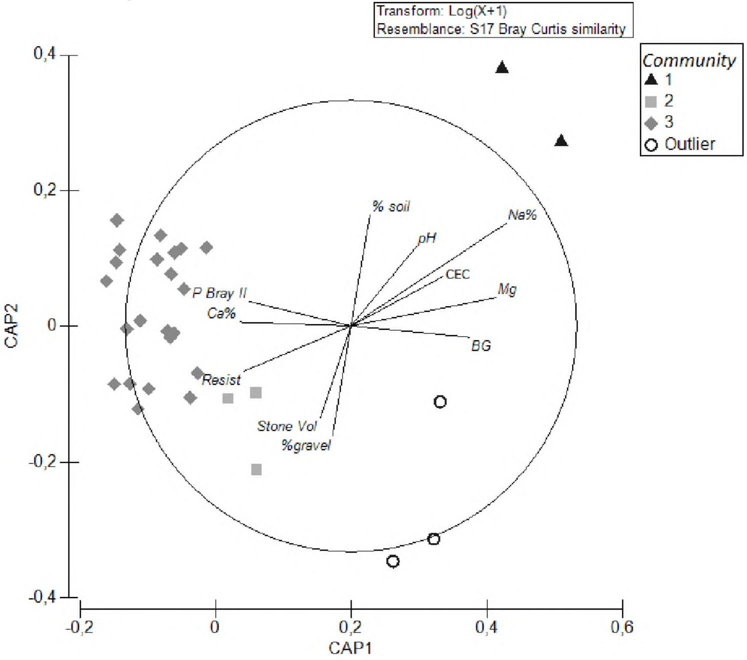


Figure 17a: Darlington CAP analysis with abiotic vectors at >0.4 correlation (n=30).

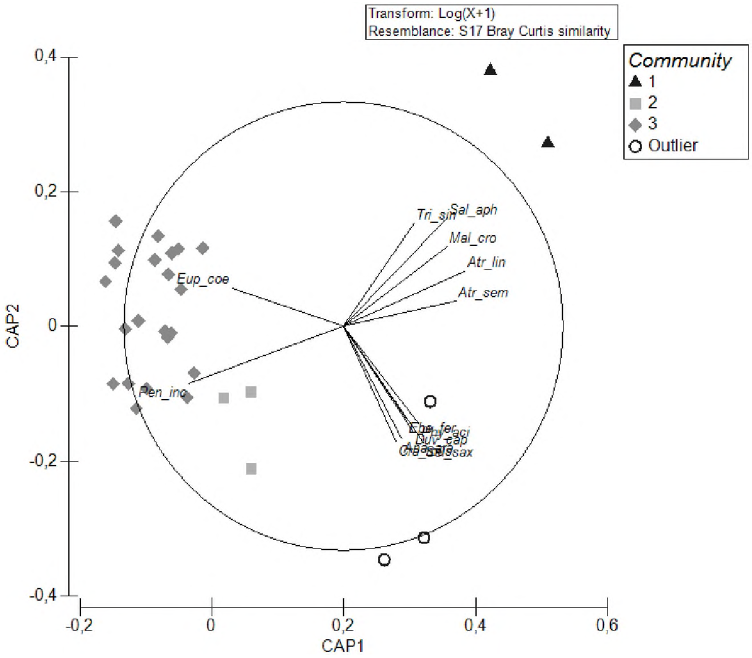


Figure 17b: Darlington CAP analysis with plant species vectors at >0.5 correlation (n=30).

The community host plots with higher soil resistance associated with a dominance of *P. incana* as well as plots of higher Ca% and P, dominated by *E. caerulescens*. Plots in community 2 are associated with high gravel and stones within the soil, while community 1 has high Na and pH.

The top dominant species contributing to a cumulative percentage of 90% from the three communities and outliers are listed in Table 8.

Table 8: SIMPER of the dominant plant species found in the Darlington communities.

Community	n	Similarity (%)	Common species
1	2	19.2	*M. aitonis, C. mucronatum, M. junceum* and *Salsola aphylla.*
2	3	27.9	*P. incana, E. obtusa, Rosenia humilis, R. obovatum, Drosanthemum lique, C. cernua, G. robusta, L. aethiopicum, A. striatus, Mestoklema tuberosum, Hermannia desertorum* and *G. secunda.*
3	22	35.3	*P. incana, E. caerulescens, M. aitonis, R. obovatum, A. rigidum, A. congesta, G. robusta, C. cernua, P. deustum, M. guerichianum, E. obtusa, F. hirsuta, L. africanum* and *C. mucronatum.*
Outliers	3	12.0	*P. incana* and *Selago saxatillis.*

P. incana is a common species throughout the Darlington region, except in community 1 which hosts a dominance of succulent shrub species. Community 3, which has the highest similarity of 35%, has a major dominance in the species *E. caerulescens*, while the other communities do not have this species.

Addo Main

Similar to Darlington, Addo Main separates into three communities with four outlying plots as distinguished from the LINKTREE analysis. Forty-five percent of the plots are within community 3 which, barring two plots, do not appear to have any correlation with any abiotic variables at 0.4 in the CAP (Figure 18a). Two of the plots do however seem to be associated with low carbon content in the soil. At a 0.45 correlation, community 3 includes the species *L. africanum*, *D. hispidum*, *C. dactylon* and *A. semibaccata* (Figure 18b).

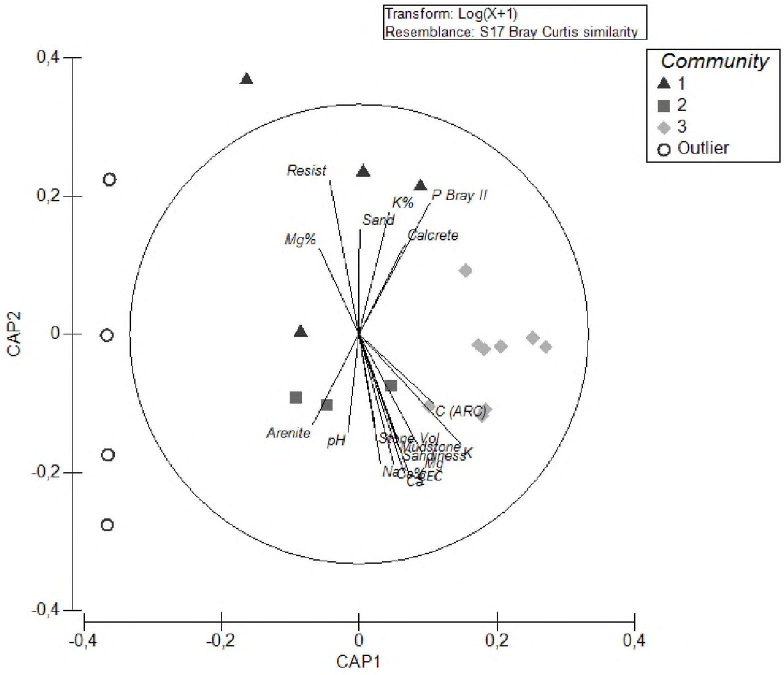


Figure 18a: Addo Main CAP analysis factored by community with abiotic vectors at >0.45 correlation (n=20).

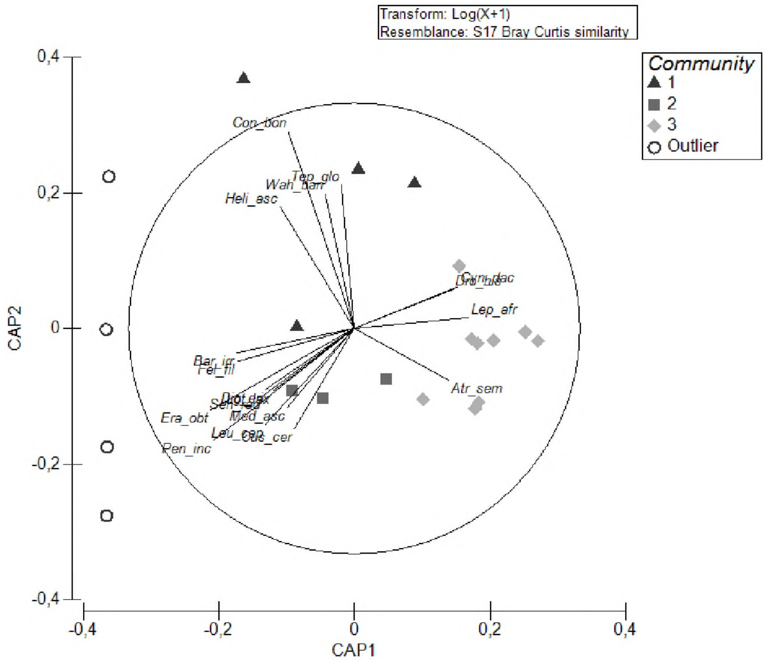


Figure 18b: Addo Main CAP analysis factored by community with plant species vectors at >0.45 correlation (n=20).

The LINKTREE alternatively showed that community 3 separates from the other communities by low Na (>0.13 cmol/kg) and low P (<11.9 mg/kg) in the soil. Community 1 is associated with *C. bonariensis, Wahlenbergia banksiana, Tephrosia glomeratus* and *H. rosum* var. *aschersoniana.* This is further confirmed in Table 9.

Table 9: SIMPER of the dominant plant species found in the Addo Main communities.

Community	n	Similarity (%)	Common species
1	4	38.6	*C. incompletus, D. hispidum, L. africanum, H. althaeoides, C. bonariensis, E. curvula, H. rosum* var. *aschersoniana, W. banksiana, G. pubescens* and *Sutera campanulata.*
2	3	30.4	*C. incompletus, G. pubescens, H. althaeoides, S. geniculata, C. bonariensis* and *A. semibaccata.*
3	9	35.3	*C. incompletus, D. hispidum, G. pubescens, L. africanum, H. althaeoides, A. semibaccata* and *M. aitonis.*
Outliers	4	12.0	*P. incana, E. obtusa, C. dactylon, G. pubescens, H. althaeoides, S. geniculata, Asparagus suaveolens, B. irritans,* and *C. expansa.*

The abundant species in each community are very similar, with few uniquely dominant species. Community 1 and the outlying plots have the highest number of unique species. The first listed dominant species in the outliers are different to those in the other communities. On further inspection, three of the four outlying plots were found to be in degraded land and not old agricultural fields.

Kabouga

Five communities, two being dominant, exist within the Kabouga section. The CAP in Figure 19a shows that community 3 has higher soil C and %gravel while community 5 has higher resistance, %soil and bulk density. It would appear from the CAP that community 1 and 2 have a relationship with altitude. Plant species associated with community 3 include *G. robusta, P. maximum, J. capensis* and *P. pyracantha.* Community 5 is defined by *L. africanum, J. orchioides, Trichogyne verticillata, C. expansa, D. hispidum* and *V. karroo* (Figure 19b).

Increased variance in plant species compositions occurred in Kabouga compared to Darlington and Addo Main. Additionally, the similarity between plots within each community in the SIMPER analysis is higher (Table 10).

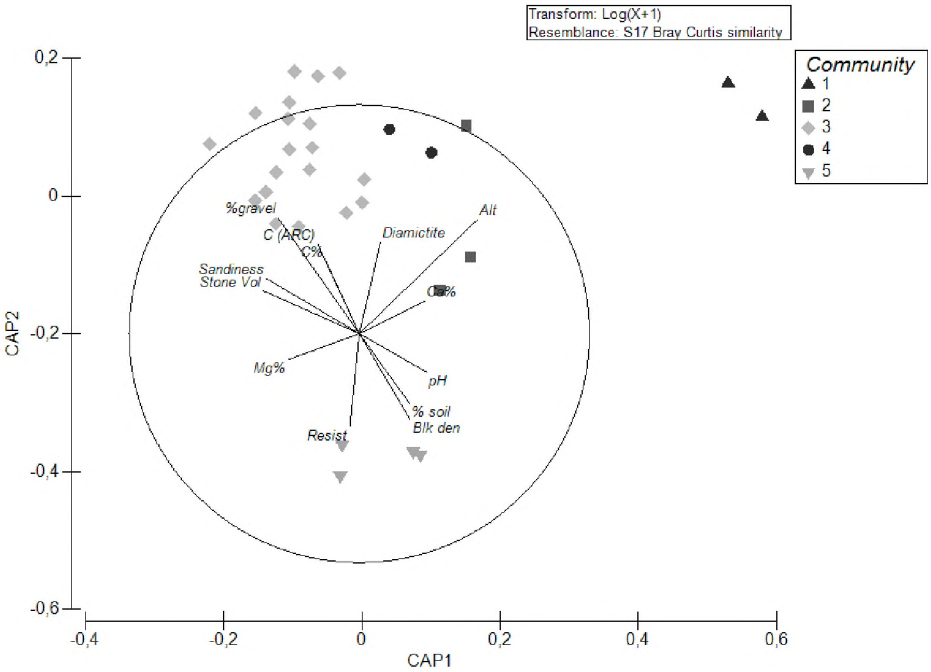


Figure 19a: Kabouga CAP analysis factored by community with abiotic vectors at >0.3 correlation (n=30).

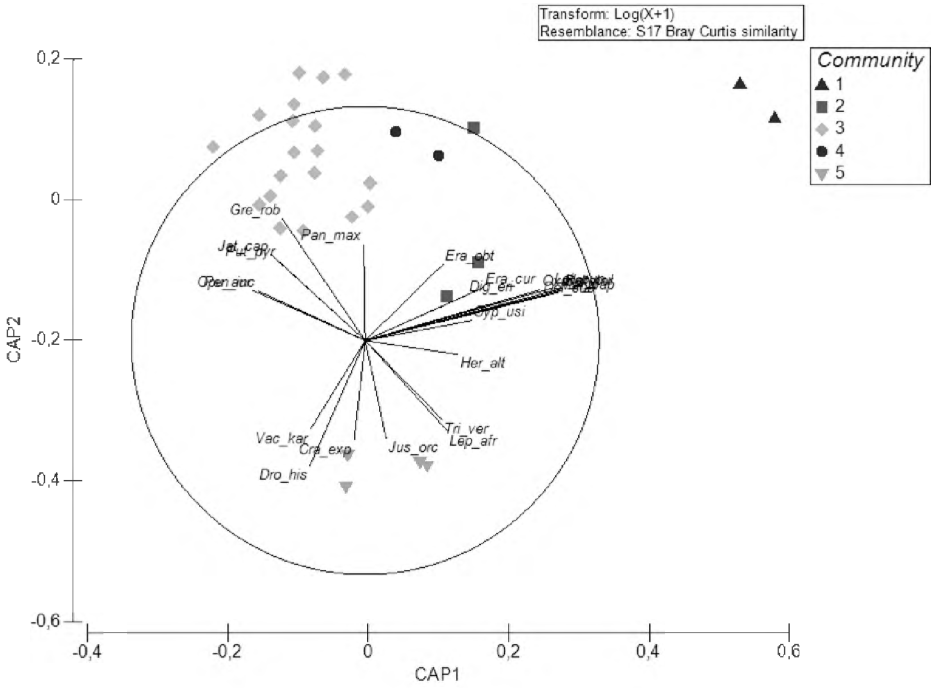


Figure 19b: Kabouga CAP analysis factored by community with plant species vectors at >0.4 correlation (n=30).

Table 10: SIMPER of the dominant plant species found in the Kabouga communities.

Community	n	Similarity (%)	Common species
1	2	40.6	*Delosperma subulata, S. geniculata, G. pubescens, P. maximum, Bulbine narcissifolia, A. semibaccata, E. obtusa, Lotononis pungens* and *Hermannia pulverata.*
2	3	27.4	*G. pubescens, P. maximum* and *C. dactylon.*
3	19	38.0	*G. pubescens, G. robusta, P. incana, C. dactylon, P. maximum, S. geniculata, O. aurantiaca, P. pyracantha, D. hispidum* and *J. capensis*.
4	2	45.4	*G. robusta, P. incana, L. capensis, A. capensis* and *A. suaveolens*.
5	4	48.7	*D. hispidum, G. pubescens, S. geniculata, C. dactylon, V. karroo* and *L. africanum*.

The majority of the plots in community 3 host a combination of grasses, dwarf shrubs, woody shrubs and succulent shrubs, but most uniquely *J. capensis* and *P. pyracantha. O. aurantiaca* is abundant in community 3. The increased vegetation provides protection and shelter to wildlife, who transport the cactus through the thicket, allowing it to invade quickly.

Baviaanskloof

As stipulated before, no communities were delineated in the LINKTREE analysis for the Baviaanskloof. A CLUSTER analysis with a SIMPROF test further revealed that all plots were significantly similar to each other at 5%. An ANOSIM analysis was not performed to test if communities per site were significantly different to each other. Clarke & Warwick (2001) stress that such would be erroneous and circular and ANOSIM should only be used for testing differences in pre-defined groups.

3.6.3. Growth form profile and species richness

The lowest average vegetative cover occurred in Darlington at <60% (Figure 20). The succulent shrub component contributes the most to vegetative cover in this site of about 15%, while bare ground cover was on average 54%. Kabouga has much higher cover values than the other sites, with the largest woody tree (26%) and woody shrub (32%) component.

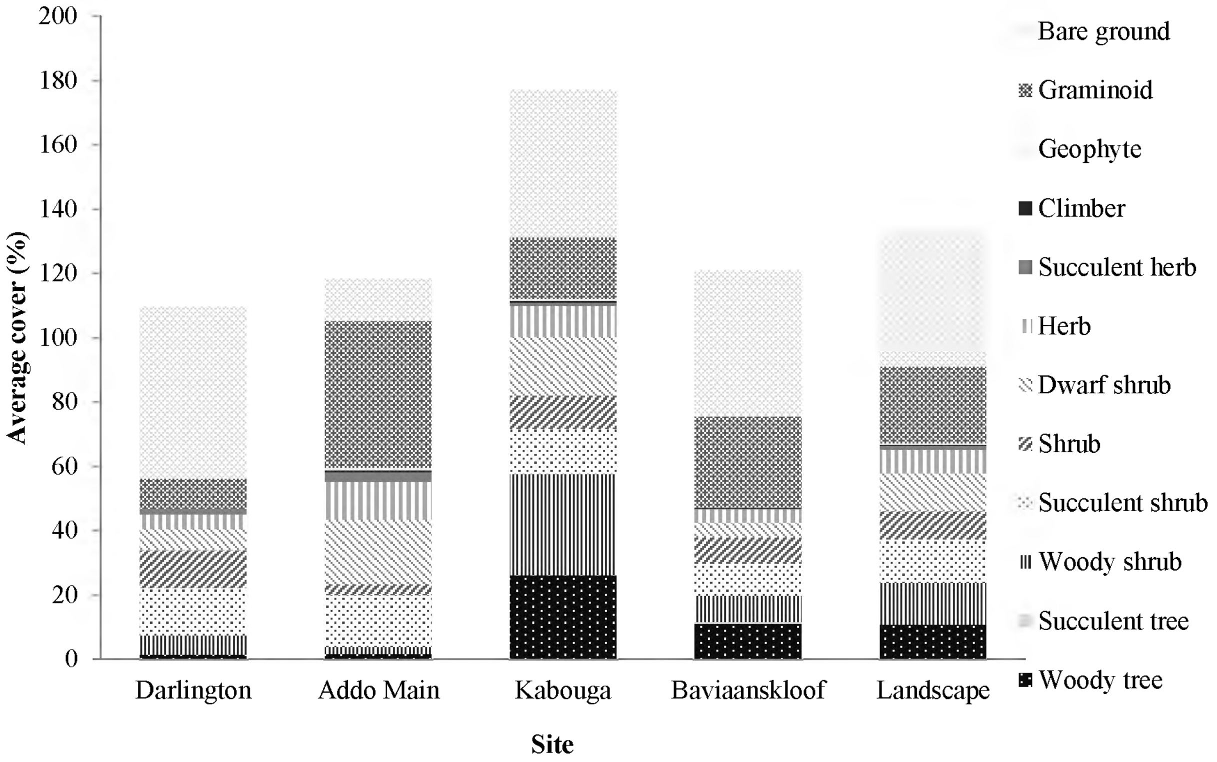


Figure 20: The average percentage cover of plant growth forms for each site and within the landscape.

Addo Main had the lowest bare ground cover of 13% but this is replaced by a much larger grass layer of 46%, a dwarf shrub layer of 20% and a succulent shrub layer of 16%. The Baviaanskloof has relatively low cover values for all growth forms, similar to that of Darlington, however the grass layer is much larger at 28% and also contains a succulent tree layer consisting entirely of *A. ferox*.

Total species richness was highest in Darlington with 163 species and lowest in the Baviaanskloof with 128 species (Table 11). Graminoids and herbs had the highest richness in Addo Main, where old lands prevail. Dwarf shrubs, succulent shrubs and woody shrubs were markedly higher in Darlington, likely due to the dual thicket types present in this area. In the sites that are predominantly degraded and not transformed, Kabouga has much higher herb richness and the lowest graminoid richness. A total of 345 species were identified across the degraded lands of the study extent.

Table 11: Species richness per growth form within each site, with ANOSIM analysis of significant differences.

	Global test				**Site**		
	R	*P*	*AD*	AM	AK	BK	**Landscape**
Graminoid	0.116	0.001	19^{a}	21^{b}	13^{c}	18^{bc}	**40**
Geophyte	0.01	0.228	8^{a}	12^{a}	10^{a}	7^{a}	**28**
Climber	-0.011	0.790	4^{a}	4^{a}	3^{a}	4^{a}	**10**
Succulent herb	0.175	0.001	5^{a}	4^{b}	3^{c}	3^{bc}	**8**
Herb	0.099	0.001	29^{a}	52^{b}	36^{b}	27^{a}	**91**
Dwarf shrub	0.122	0.001	36^{a}	29^{b}	24^{b}	24^{a}	**68**
Shrub	0.158	0.001	2^{a}	6^{b}	2^{c}	2^{cd}	7
Succulent shrub	0.089	0.001	29^{a}	16^{b}	18^{a}	22^{b}	**53**
Woody shrub	0.263	0.001	20^{a}	10^{b}	14^{c}	11^{d}	**25**
Succulent tree	0.167	0.001	0^{a}	0^{a}	0^{a}	1^{b}	**1**
Woody tree	0.144	0.001	7^{a}	4^{b}	8^{c}	9^{cd}	**14**
Total richness	**0.353**	**0.001**	**163^{a}**	**158^{b}**	**131^{c}**	**128^{d}**	**344**

Sites were significantly different to each other in richness among all growth forms, except in geophyte and climber richness. However, the Global R value was predominantly low and closer to a value of 0, indicating low separation between sites (Clarke & Warwick, 2001). Between site significant differences are indicated by letters.

3.6.4. Degradation scoring

Four degradation scores were defined across the landscape with the addition of old lands. Degradation score 4 only occurred in Baviaanskloof and old lands only occurred in Addo Main. The results of a PERMANOVA analysis in Table 12 showed that in terms of species composition, all sites were significantly different to each other at degradation scores of 2 and 3, some being more significant than others. However, degradation score 1 was homogenous between sites, showing no significant differences in species composition.

Table 12: Pair-wise PERMANOVA of within and between site differences in plant species composition among degradation scores.

			Within site						Between site		
Site	Degradation scores		t-value	p-value	Significance	Degradation scores	Site		t-value	p-value	Significance
Darlington	3	2	1.35	0.016	*	3	AD	AM	1.78	0.027	*
	3	1	1.61	0.112	NS		AD	AK	2.76	0.001	***
	2	1	1.40	0.047	*		AD	BV	1.96	0.001	***
							AM	AK	1.93	0.017	*
Addo Main	3	2	1.31	0.326	NS		AM	BV	1.34	0.013	*
	3	1	1.23	0.313	NS		AK	BV	2.43	0.001	***
	3	OL	1.68	0.018	*						
	2	1	1.43	0.335	NS	2	AD	AM	1.59	0.005	**
	2	OL	1.71	0.019	*		AD	AK	3.33	0.001	***
	1	OL	0.83	0.750	NS		AD	BV	2.77	0.001	***
							AM	AK	1.26	0.047	*
Kabouga	3	2	1.59	0.001	***		AM	BV	1.61	0.007	**
	3	1	1.69	0.002	**		AK	BV	2.60	0.001	***
	2	1	0.96	0.534	NS						
						1	AD	AM	-	-	-
Baviaanskloof	3	2	0.82	0.832	NS		AD	AK	1.35	0.242	NS
	3	1	1.15	0.176	NS		AD	BV	1.26	0.48	NS
	3	4	1.30	0.027	*		AM	AK	1.19	0.481	NS
	2	1	1.17	0.147	NS		AM	BV	1.06	0.476	NS
	2	4	1.43	0.011	*		AK	BV	1.51	0.109	NS
	1	4	1.60	0.184	NS						
						4 and OL	Sample size too small and does not cross over the sites				

*p< 0.05, ** p< 0.01, ***p< 0.001, NS Not significantly different

Old lands, as anticipated, showed significant differences to degradation scores 2 and 3, which are over-browsed rather than transformed. Interestingly, only Kabouga showed significant differences between scores 3 and 1. It would be expected that these should be different in other sites, but it is plausible then, that trees and woody shrubs were weighted too high and the matrix between trees is the same of that at a score of 1. The difference in composition between scores in Kabouga was much stronger than in the other sites. The Baviaanskloof showed significant differences between scores 2 and 3 and degradation score 4. However, score 4 has only two plots, which is insufficient to make accurate deductions with regard to differences in species composition. Tables 13 and 14 further highlight the top ten dominant species or the species that accumulate 90% of the average area per degradation score, within the landscape and between sites. Underlined species are those which are unique in dominance to that degradation score.

Table 13: SIMPER of the dominant plant species in each of the degradation scores within the landscape.

Degradation score	n	Similarity (%)	Common species
1	7	11.3	*C. incompletus, G. pubescens, A. congesta, C. datylon, A. lindleyi, D. hispidum, L. africanum* and *Chenopodium sp.1*.
2	52	17.9	*P. incana, G. pubescens, R. obovatum, G. robusta, P. maximum, C. dactylon, A. congesta, M. aitonis, E. obtusa* and *E. caerulescens*.
3	32	20.2	*P. incana, G. robusta, G. pubescens, C. incompletus, P. pyracantha, P. maximum, D. hispidum, R. obovatum, E. caerulescens* and *S. geniculata*.
4	2	32.2	*R. obovatum, P. pyracantha, A. capensis, G. robusta, E. lehmanniana, D. lique* and *A. ferox*.
OL	15	32.8	*C. incompletus, D. hispidum, G. pubescens, H. althaeoides, L. africanum, A. semibaccata, S. geniculata, C. bonariensis* and *C. expansa*.

Within the landscape, degradation score 1, which is homogenous across sites, is dominated by pioneer grasses, annual herbs and dwarf succulent shrubs, but only at an 11% similarity between all seven plots in this group (Table 13). The majority of the plots fall within degradation score 2 (48%) and degradation score 3 (29%). Both these degradation scores have similar dominant species, however the cover contributed by each species is different and degradation score 3 is dominated by *P. pyracantha* and *S. geniculata*. Old lands are most similar to each other in species composition at 32.8%. It cannot be expected that degradation scores have a high similarity to each other, due to differences in the original vegetation type.

Similarities within degradation scores for each site were much higher than for within the landscape (Table 14). In Darlington, degradation score 2 with 70% of the plots had a similarity of 30% and has a dominance of annual species, while degradation score 3 is replaced with *Felicia* species, which are small woody shrubs and *G. robusta*.

Plots in degradation score 2 and 3 in Addo Main only have two plots in each. Ninety percent of the area of the plots in degradation score 2 are dominated by just five species at a similarity of 30%. In Kabouga, 53% of plots occur in degradation score 2 with *S. geniculata* and *A. striatus* being unique in dominance. In degradation score 3 containing 37% of the plots, the unique species were *P. pyracantha, I. origanoides* and *J. capensis* at 39% similarity. Again, in Baviaanskloof, degradation score 2 was prevalent in 45% of the plots at 25% similarity. Unique species included *J. orchioides and C. cilliaris*. Degradation score 3, with 38% of the plots, saw the unique dominance of *P. capensis* and 24% similarity between plots of this score. *P. incana, G. pubescens* and either of the *Cynodon* species, feature as prevalent species in degraded areas within the inter-matrix of woody and succulent patches, regardless of score.

A one-way ANOSIM analysis of all plots, factored by degradation score, showed that degradation score 1 was significantly different to degradation score 3 and 2 (R= 0.433 and R= 0.301; p= 0.001, respectively) and OL (R= 0.37; p= 0.003). Old lands were significantly different to degradation score 3 and 2 (R= 0.539 and R= 0.412; p= 0.001, respectively) and 4 (R= 0.96; p= 0.007). Degradation scores 2 and 3, 3 and 4 and 1 and 4, were not different to each other in composition.

Table 14: SIMPER of the dominant plant species among degradation scores in all sites.

	Deg. score	n	Similarity (%)	Common species
Darlington	1	Sample size too small		
	2	21	29.8	*P. incana, M. aitonis, E. caerulescens, R. obovatum, A. congesta, A. rigidum, G. secunda, C. cernua, E. obtusa, M. guerichianum.*
	3	8	31.7	*P. incana, E. caerulescens, R. obovatum, P. deustum, G. robusta, Indigofera disticha, A. congesta, Ehrharta calycina, F. hirsuta, F. filifolia.*
Addo Main	1	Sample size is too small		
	2	2	37.3	*P. incana, G. pubescens, E. obtusa, A. suaveolens, C. dactylon.*
	3	2	29.0	*Helichrysum rosum* var. *arcuatum, Senecio radicans, C. dactylon, Mestoklema elatum, Digitaria eriantha, E. obtusa.*
	OL	15	32.8	*C. incompletus, D. hispidum, G. pubescens, H. althaeoides, L. africanum, A. semibaccata, S. geniculata, C. bonariensis, C. expansa.*
Kabouga	1	3	20.7	*G. pubescens, C. dactylon, Chenopodium sp. 1.*
	2	16	29.3	*G. pubescens, C. dactylon, S. geniculata, P. incana, P. maximum, G. robusta, D. hispidum, O. aurantiaca, R. obovatum, A. striatus.*
	3	11	38.8	*G. robusta, P. incana, P. pyracantha, G. pubescens, O. aurantiaca, I. origanoides, D. hispidum, C. dactylon, P. maximum, J. capensis.*
Baviaanskloof	1	3	25.6	*C. incompletus, A. congesta, P. incana.*
	2	13	25.1	*C. incompletus, P. incana, J. orchioides, G. pubescens, R. obovatum, L. oxycarpum, P. maximum, G. robusta, C. cilliaris, E. lehmanniana.*
	3	11	24.4	*C. incompletus, P. incana, G. robusta, L. oxycarpum, P. maximum, G. pubescens, A. congesta, P. capensis, D. hispidum, R. obovatum.*
	4	2	32.2	*R. obovatum, P. pyracantha, A. capensis, G. robusta, E. lehmanniana, D. lique, A. ferox.*

3.6.5. Soil quality and composition

Mean and SE values are tabulated per site and per degradation score in Tables 15 and 16. Significant differences between sites and degradation scores for each variable are indicated by letters. All sites showed significant differences in %gravel, %soil and bulk density. Barring Addo Main and Darlington, which were significantly different in litter mass, all sites showed significant differences in %roots and C(ARC).

3.6.5.1. Site level

Darlington soils were significantly lower in %soil and K and significantly higher in Mg compared to Addo Main soils and in Na compared to Addo Main and Baviaanskloof soils. Addo Main soils were significantly higher in %soil and resistance compared to all sites and had low Na, Ca, Mg, P and C. Bulk density of soils were significantly lower in Addo Main compared to soils in other sites. Soils from Kabouga were high in %roots, bulk density, C and P and low in Na. Baviaanskloof soils had a high CEC and are significantly different in P to Kabouga soils. Few variables were different across sites overall (Global test) and included litter mass, Mg, Ca and P. As a whole, a one-way ANOSIM analysis of all variables found that soils were significantly different to each other across sites (Global R= 0.452; p= 0.001).

3.6.5.2. Degradation scores

Among degradation scores, degradation score 1 was high in Na, K, Mg, P and CEC. Degradation score 3 was low in resistance while degradation score 4 was high in pH. Old lands were high in resistance and K and low in pH and P. Significant differences in carbon were only found between scores 1 and OL, 2 and 3 and 3 and OL, where carbon was significantly higher in score 1 and 3.

Few differences were found between degradation scores when comparing soil composition and quality within sites (Appendix 3). Within Darlington, degradation scores 3 and 2 show significant differences in dry litter mass and percentage K. Degradation scores 2 and 1 show significant differences in the exchangeable cations (mg/kg) Na, K and Mg, the percentage of Na and Ca, the T-value measuring CEC and resistance. In Addo Main, the percentage roots are significantly different in degradation scores 3 and OL. Degradation scores 2 and OL are significantly different in bare ground cover, percentage roots and the percentage of Ca.

Table 15: Soil attributes and composition per site and within the landscape (mean±SE, with ANOSIM analysis and significant differences represented by letters between sites).

	Global test		**Site**				
	R	*P*	*Darlington*	*Addo Main*	*Kabouga*	*Baviaanskloof*	*Landscape*
Site record variables							
Bare ground cover (%)	0.242	0.001	53.5±2.8^{a}	13.2±3.1^{b}	45.8±2.9^{c}	45.6±3.3^{cd}	41.9±2.0
%soil	0.823	0.001	59.5 ± 3.4^{a}	99.3 ± 0.2^{b}	1.1 ± 0.04^{c}	0.2 ± 0.04^{d}	33.9 ± 3.9
%roots	0.645	0.001	0.2 ± 0.04^{a}	0.1 ± 0.03^{a}	77.1 ± 3.5^{b}	50.4 ± 3.8^{c}	35.3 ± 3.5
%gravel	0.528	0.001	40.3 ± 3.4^{a}	0.6 ± 0.3^{b}	0.1 ± 0.04^{c}	49.5 ± 3.8^{d}	23.8 ± 2.6
Bulk density (g/cm^{3})	0.317	0.001	0.9 ± 0.05^{a}	1.4 ± 0.04^{b}	22.8 ± 3.5^{c}	0.7 ± 0.1^{d}	7.1 ± 1.4
Litter mass (g/m^{2})	0.008	0.284	236.4 ± 45.8^{a}	174.7 ± 21.4^{b}	178.0 ± 19.1^{ab}	282.5 ± 43.2^{ab}	214.8 ± 17.3
Exchangeable cations							
Na (cmol/kg)	0.069	0.002	0.7 ± 0.3^{a}	0.4 ± 0.1^{b}	0.4 ± 0.1^{ac}	0.4 ± 0.1^{bd}	0.5 ± 0.1
K (cmol/kg)	0.099	0.001	0.5 ± 0.04^{a}	0.9 ± 0.1^{b}	0.8 ± 0.1^{c}	0.7 ± 0.1^{cd}	0.7 ± 0.1
Ca (cmol/kg)	0.027	0.074	27.7 ± 8.2^{ac}	9.8 ± 1.5^{ab}	11.6 ± 1.1^{ab}	13.5 ± 0.9^{ac}	14.9 ± 2.3
Mg (cmol/kg)	0.028	0.063	2.8 ± 0.2^{a}	2.0 ± 0.2^{b}	2.8 ± 0.2^{ab}	2.4 ± 0.2^{ab}	2.5 ± 0.1
Na%	0.122	0.001	3.3 ± 0.7^{a}	3.1 ± 0.3^{a}	2.6 ± 0.2^{a}	2.0 ± 0.4^{b}	2.7 ± 0.2
K%	0.254	0.001	3.1 ± 0.2^{a}	8.5 ± 0.7^{b}	4.8 ± 0.4^{c}	4.2 ± 0.3^{cd}	4.8 ± 0.3
Ca%	0.061	0.004	74.7 ± 1.6^{ab}	71.2 ± 2.0^{a}	72.8 ± 1.2^{a}	78.2 ± 1.4^{b}	73.5 ± 1.0
Mg%	0.064	0.003	18.1 ± 1.2^{a}	15.9 ± 1.0^{ab}	19.0 ± 1.0^{a}	13.9 ± 0.6^{b}	16.9 ± 0.5
C%	0.17	0.001	0.9 ± 0.1^{a}	0.8 ± 0.1^{a}	1.3 ± 0.1^{b}	1.6 ± 0.1^{b}	1.2 ± 0.1
Other variables							
C(ARC) (g/kg)	0.414	0.001	0.9 ± 0.1^{a}	1.1 ± 0.2^{a}	14.2 ± 1.1^{b}	1.9 ± 0.2^{c}	4.9 ± 0.6
Stone volume (%)	0.306	0.001	4.1 ± 0.2^{a}	1.2 ± 0.1^{b}	3.6 ± 0.3^{c}	2.8 ± 0.2^{d}	3.0 ± 0.2
CEC (cmol/kg)	0.039	0.020	16.5 ± 1.2^{a}	13.2 ± 1.7^{b}	15.7 ± 1.3^{abc}	16.7 ± 1.0^{bc}	15.5 ± 0.7
P (mg/kg)	0.009	0.243	35.0 ± 5.0^{a}	20.1 ± 3.3^{a}	25.8 ± 4.9^{ab}	38.1 ± 5.2^{ac}	30.9 ± 2.5
K (mg/kg)	0.099	0.001	192.7 ± 14.7^{a}	378.4 ± 37.6^{b}	298.8 ± 44.2^{c}	284.0 ± 31.3^{cd}	277.7 ± 17.8
pH (KCl)	0.026	0.068	6.5 ± 0.1^{a}	6.2 ± 0.5^{bc}	6.6 ± 0.1^{abc}	6.7 ± 0.2^{c}	6.4 ± 0.1
Resistance (Ω)	0.056	0.003	27.7 ± 8.2^{acd}	1234.1 ± 173.4^{b}	784.7 ± 52.0^{cd}	818.3 ± 69.9^{d}	841.1 ± 45.9

Table 16: Soil attributes and composition per degradation score (mean±SE, with ANOSIM analysis and significant differences represented by letters between degradation scores).

	Global test		Degradation scores				
	R	*P*	*1*	*2*	*3*	*4*	*OL*
Site record							
Bare ground cover (%)	0.295	0.001	53.6±8.3^{a}	49.3±2.3^{b}	40.3±2.6^{b}	75.4±6.6^{a}	8.9±2.5^{c}
%soil	0.221	0.001	22.3 ± 14.4^{a}	28.0 ± 4.7^{a}	21.4 ± 6.0^{a}	0.3 ± 0.1^{a}	99.3 ± 0.3^{b}
%roots	0.020	0.211	47.6 ± 12.0^{a}	36.2 ± 5.2^{ab}	44.2 ± 6.4^{a}	51.1 ± 2.6^{a}	0.05 ± 0.01^{b}
%gravel	-0.013	0.657	20.8 ± 8.5^{a}	28.5 ± 3.8^{ab}	28.2 ± 5.0^{ab}	48.6 ± 2.5^{a}	0.7 ± 0.3^{b}
Bulk density (g/cm^{3})	0.025	0.247	10.2 ± 6.3^{a}	8.2 ± 2.2^{ab}	7.2 ± 2.3^{ab}	0.7 ± 0.04^{a}	1.4 ± 0.1^{b}
Litter mass (g/m^{2})	0.021	0.296	137.8 ± 26.9^{a}	185.5 ± 21.9^{ab}	315.5 ± 45.8^{abc}	374.8 ± 143.5^{ac}	167.8 ± 22.4^{bc}
Exchangeable cations							
Na (cmol/kg)	0.107	0.009	1.7 ± 1.0^{a}	0.4 ± 0.04^{b}	0.4 ± 0.04^{b}	0.1 ± 0.01^{ab}	0.34 ± 0.1^{b}
K (cmol/kg)	0.145	0.001	1.0 ± 0.2^{a}	0.6 ± 0.1^{b}	0.7 ± 0.1^{b}	0.6 ± 0.02^{abc}	1.0 ± 0.1^{bc}
Ca (cmol/kg)	0.003	0.424	13.2 ± 2.8^{a}	14.9 ± 3.0^{a}	22.5 ± 6.4^{a}	9.9 ± 1.4^{a}	9.8 ± 1.7^{a}
Mg (cmol/kg)	0.12	0.001	3.7 ± 0.8^{a}	2.5 ± 0.1^{b}	2.6 ± 0.1^{b}	1.5 ± 0.03^{ab}	2.0 ± 0.3^{b}
Na%	0.111	0.009	6.2 ± 2.2^{a}	2.5 ± 0.2^{b}	2.1 ± 0.2^{b}	0.9 ± 0.04^{ab}	2.8 ± 0.3^{b}
K%	0.235	0.001	6.2 ± 1.1^{a}	4.1 ± 0.3^{b}	3.8 ± 0.2^{b}	5.0 ± 0.7^{abc}	8.8 ± 0.7^{c}
Ca%	0.024	0.20	67.7 ± 2.8^{a}	75.0 ± 1.2^{ab}	76.4 ± 1.4^{b}	81.9 ± 2.3^{ab}	71.5 ± 1.8^{ab}
Mg%	-0.051	0.965	18.7 ± 1.6^{a}	17.1 ± 0.8^{a}	16.6 ± 1.0^{a}	12.2 ± 1.6^{a}	16.1 ± 1.1^{a}
C%	0.09	0.011	1.2 ± 0.2^{a}	1.1 ± 0.1^{ab}	1.4 ± 0.1^{a}	1.2 ± 0.5^{ab}	0.8 ± 0.1^{b}
Other variables							
C(ARC) (g/kg)	-0.004	0.493	5.7 ± 2.5^{a}	4.8 ± 0.9^{ab}	6.8 ± 1.4^{a}	1.3 ± 0.5^{ab}	1.1 ± 0.2^{b}
Stone volume (%)	0.132	0.001	2.9 ± 0.6^{a}	3.5 ± 0.2^{a}	3.4 ± 0.3^{a}	1.5 ± 0.5^{ab}	1.2 ± 0.1^{b}
CEC (cmol/kg)	0.074	0.023	19.7 ± 4.4^{ac}	15.6 ± 0.9^{bc}	16.4 ± 0.8^{b}	12.0 ± 1.3^{abc}	13.3 ± 2.0^{ac}
P (mg/kg)	-0.032	0.765	39.5 ± 10.4^{a}	33.2 ± 4.0^{a}	28.0 ± 4.3^{a}	26.0 ± 9.0^{a}	22.8 ± 4.2^{a}
K (mg/kg)	0.145	0.002	391.6 ± 78.2^{a}	245.6 ± 27.7^{b}	253.9 ± 22.0^{b}	229.0 ± 6.0^{abc}	403.9 ± 42.1^{c}
pH (KCl)	0.016	0.291	6.9 ± 0.26^{a}	6.5 ± 0.1^{a}	6.7 ± 0.1^{a}	7.2 ± 0.8^{a}	6.0 ± 0.6^{a}
Resistance (Ω)	0.142	0.004	873.8 ± 371.2^{acd}	799.0 ± 47.9^{b}	712.8 ± 39.2^{b}	1145.0 ± 215.0^{d}	1184.2 ± 173.9^{c}

In Kabouga degradation scores 3 and 2 are only different in dry litter mass. Degradation scores 3 and 1 are significantly different in bare ground cover and highly significantly different in Mg. Degradation scores 2 and 1 are also significantly different in bare ground cover and Mg. The Baviaanskloof is the only site that shows a significant difference in carbon between degradation score 3 and 2. Degradation scores 3 and 1 are significantly different in Na and percentage Ca, but highly significantly different to percentage K. Degradation scores 3 and 4 are significantly different in bare ground cover and percentage soil. Lastly, degradation scores 2 and 1 are significantly different in Na, K and Mg and percentage Na.

3.7. Discussion

3.7.1. Abiotic correlates with species composition

The findings show that there is marked species heterogeneity within degraded lands at the landscape level and within the GAENP, at local and community scale. Degraded lands in the Baviaanskloof were not found to be heterogeneous and confirm studies by Rutherford *et al.* (2012) who found a loss of plant heterogeneity at the landscape level within spekboomveld. Although no significant communities were delineated by the LINKTREE and CLUSTER analysis of the Baviaanskloof, similarity was still low between plots (23%), indicating that there are fine scale variations in species assemblages, but this would need to be further investigated. At the landscape level, variability in plant species composition was strongly associated with summer rainfall, percentage gravel and altitude, emphasising the importance of climate and geomorphic templates in determining species distributions. Rainfall is an important driver of species composition, especially in arid areas (Bond *et al.*, 2003) and has even been found to surpass the impacts of degradation in determining species composition within thicket (Rutherford *et al.*, 2012). Despite degradation and transformation, communities were still strongly associated with site, where climate, geomorphology and land use history are site specific, confirming then that community composition is correlated to abiotic attributes.

Rainfall and gravel were negatively correlated, where increased rainfall in Addo Main and Kabouga split from the high gravel and low rainfall areas of Baviaanskloof and Darlington. Gravel instead of soil is often more predominant in arid areas where low rainfall and high temperatures reduce the development of nutrient-rich soils and the decomposition of plant litter, increasing the gravel or alternatively the stone volume (Gosz & Sharpe, 1989). This was the case in Darlington where species composition was best correlated to increased stone volume, a low %soil and increased bare ground cover. However, the correlate of the relatively high litter mass (236±46 g/m^2) is interesting in this site, given the low vegetation cover that would otherwise contribute to litter. A multitude of factors could explain the higher litter mass; including a) the long-term mortality of trees and less resilient woody trees and shrubs in this site (Lechmere-Oertel *et al.*, 2005b), b) litter from abundant *E. caerulescens* expanding from adjacent noorsveld (Powell *et al.*, 2010), c) aridity in this area resulting in increased senescence of grass swards and other inter-matrix shrubs, or d) increased erosion linked to low soil resistance in this site, resulting in deposits of leaf litter in microsites (Peters & Havstad, 2006).

Altitudinal correlates in the landscape were evident in Baviaanskloof and Kabouga, both of which are mountainous areas where plots occurred at varying altitudes within a series of large undulating hills. Additionally, the characteristic mountainous areas of Baviaanskloof resulted in aspect also being an important correlate, but not enough to significantly separate communities within this site. South facing slopes show important relationships with seed germination and recruitment in xeric succulent thicket of the Fish River (La Cock, 1992), therefore aspect may be responsible for small changes in species composition in the Baviaanskloof.

The landscape grouped well within ordination space when factored by geology, at 78% allocation success. Addo Main was the only site, however where species assembly was best correlated to the parent material. Addo Main has the largest variety of geological types with species assembly being associated with sand, shale or mudstones. However, it could be argued that different geological types were preferred for certain land use functions and it has instead influenced species composition.

The soil nutrients, Na, Mg, K and Ca were important correlates across all of the sites. However, there was an alternation of correlative nutrients per site, where the following nutrients were not correlated to species composition; Na in Kabouga and Baviaanskloof, K in Darlington and Mg in Addo Main. Carbon was correlated to species assemblages in Addo Main and Kabouga for opposite reasons. In Addo Main, carbon content was low due to the transformation of land for agriculture in the past, resulting in a loss of succulent and woody above and below ground biomass, which contributes to soil carbon. Kabouga is high in both succulent and woody cover for a degraded landscape and still retains much of the root system, having the highest %roots of all sites (77±3.5%) and in turn the highest carbon content (14±1.1 g/kg). The high %roots explains the presence of %gravel as correlating to species composition in Kabouga, since %roots and %gravel (0.1±0.04%) are co-variates.

3.7.2. Community composition, growth form cover and richness

3.7.2.1. Darlington

Succulent shrubs had both the highest cover and richness compared to the other sites. In the community analyses, many succulent shrubs showed uniqueness to certain communities; however, *E. caerulescens* represented the highest contribution to cover. Species from the Mesembryanthemaceae family were common in abundance and included *M. aitonis* and *M. junceum* from community 1, *D. lique* and *M. tuberosum* from community 2 and *M. aitonis* and *M. guerichianum* from community 3. Succulent species are more adapted to arid environments and the Mesembryanthemaceae are common in arid areas and easily expand into transformed areas such as old lands in the Baviaanskloof (Powell, 2009) and showed no decline with grazing in Addo (Moolman & Cowling, 1994). Shrubs owed the second highest contribution to cover, but only had two shrub species namely *P. incana* which was found in all communities except community 1, where the second shrub *S. aphylla* occurred instead. *S. aphylla* is a common Karoo species associated with gannaveld and is typically found in bottomland areas, even adjacent to thicket (Bews, 1916; Becker *et al.*, 2015).

Graminoids represented the next tier of cover, where three species of grasses were found to be common alongside *E. caerulescens.* They included *A. congesta, E. obtusa* and *P. deustum*, with only *E. obtusa* contributing to large cover ratios in another community. *A. congesta* is found in poor condition rangelands in Bloemfontein (Snyman & Du Preez, 2005), while *E. obtusa* is common in intact mesic thickets (Puttick *et al.*, 2011) and intact grassland thicket mosaics (Evans, 1997). *P. deustum* is also indicative of intact states. Despite only three common grass species showing abundance within the SIMPER analysis, there were 19 graminoid species. Community 3, which was abundant in *E. caerulescens,* showed a possible relationship with P and Ca, which were both highest within the sites of the GAENP, while *P. incana* was associated with soil resistance, which was lowest among all sites.

3.7.2.2. Addo Main

Graminoids accounted for the greatest percentage of vegetation cover and had the highest richness of 21 species. The dominant grasses were *C. incompletus, C. dactylon, E. obtusa* and *E. curvula* across the site, however these vary in dominance and presence within each community. *E. curvula* occurs abundantly in moderate condition rangelands (Snyman, 2005). Dwarf shrubs accounted for 19% cover and included the species *H. althaeoides* and *G. pubescens*, common in all the communities and *S. geniculata.*

The interesting separation are the outliers, where at 12% similarity include *P. incana,* which does not occur in the other communities, but is abundant in other sites, as well as *A. suaveolens, B. irritans* and *C. expansa.* These outlying plots indicate the species composition of the Addo Main section when in a degraded and not a transformed state. Hoffman & Cowling (1990) found that *P. incana* was not common in Addo Bush when degraded, and Hall *et al.* (2003) did not find *P. incana* as a recovery species on revegetated mines in mesic thicket areas. This therefore confirms the lack of *P. incana* abundance in the majority of the communities in Addo Main, where rainfall is higher. Additionally, the more abundant ungulates in this section are likely to graze on the palatable *P. incana.* Grazing by sheep threatens the resilience of *P. incana,* since it reproduces vegetatively from branches that touch the ground and root (Milton & Dean, 1995).

Community 1 was more unique in species composition, containing *H. rosum* var. *aschersoniana, W. banksiana* and *S. campanulata.* It would appear that communities 2 and 3 are very similar, yet separated by the dominance of the succulent shrub *M. aitonis.* This species is also associated with areas that have been recovering for 1-2 years, indicating that it is a prevalent pioneer species (Hall *et al.*, 2003). It is possible that the community containing *M. aitonis* has therefore only recently been incorporated into the boundary of the AENP or its presence is a function of rainfall in correspondence to sampling time. There was an observed difference in biomass during sampling before and after rainfall and is recognised as a limitation of this study that cannot be ignored. The sampling period in October 2011, was preceded by 0.4 mm of rainfall in September, while October had 28.2 mm of rainfall (SAWS, 2014). February 2013 sampling period had 19.8 mm of rainfall, while March had 65 mm (SAWS, 2014). Therefore, the difference in species richness and cover, before and after rainfall, needs to be further explored.

Succulent shrubs accounted for 16% cover, most abundant in *D. hispidum,* but had the lowest richness of 16 species. The herbaceous weeds *C. bonariensis*, *A. semibaccata* and *L. africanum* along with other herbs accounted for 11% cover, the highest of all sites. Relatively high herbaceous cover is important in this site, since it improves water infiltration and therefore reduces run-off and erosion (Stuart-Hill, 1989). *L. africanum* was found on mine recovery areas of two and 10 years old, but was not found in thicket (Hall *et al*., 2003). Similarly, they found *A. semibaccata* to be a common species on all recovery chronosequences but did not identify *A. lindleyi* subsp. *inflata* as other studies of degraded thicket have (Vlok & Euston-Brown, 2002; Lechmere-Oertel *et al*., 2005b; Rutherford *et al*., 2012). *A. lindleyi* subsp. *inflata* was further only associated with a highly utilised degraded land in spekboomveld and not in the low utilised area (Rutherford *et al*., 2012). On closer inspection, this species was found in only four plots within each Baviaanskloof and Darlington; the only two sites to contain spekboomveld. Furthermore, the species is only found to be most abundant in degraded spekboomveld and not spekboom thicket (Vlok & Euston-Brown, 2002).

3.7.2.3. Kabouga

The five communities in this site were much more variable in terms of species composition per community, where similarity within each was much higher than in other sites. Again, *G. pubescens* and *D. hispidum* are common, however the site has an increased woody shrub and tree component as indicated by the high cover of these growth forms. The woody shrubs in the community analysis include *G. robusta*, *P. pyracantha* and *V. karroo*. Despite this, woody shrub richness is less than Darlington and woody tree richness is one species more. It can be assumed that this could be because Darlington consists of two reference states, namely spekboom thicket and spekboomveld, which each have a host of species that are specific to that vegetation type.

Kabouga has a higher average cover of succulent shrubs (14%), but only *D. subulata* was in the SIMPER analysis of communities, other than the commonly found *D. hispidum.* Herbaceous cover is 9.7% and richness is 36 species, however few herbs are evident from the SIMPER analysis, since their area relative to woody cover is much less. Regardless, *L. pungens* and *H. pulverata* were found in community 1 (n=2), *L. capensis* was found in community 4 and *L. africanum* in community 5. It would appear that the dwarf shrub *S. geniculata* competes with *P. incana* as the more dominant shrub in Kabouga and is seen as indicative of a more intact state within the matrix (Hoffman & Cowling, 1990). The dominant grass is *P. maximum* which is also associated with intact states (Vlok & Euston-Brown, 2002). *J. capensis*, which is abundant in community 3 germinates well in any environment (Wilman *et al.*, 2014) and becomes abundant in severely degraded Fish Valley Thicket (Vlok & Euston-Brown, 2002).

3.7.2.4. Baviaanskloof

Although no communities could be differentiated within the Baviaanskloof, community 4 from the landscape LINKTREE analysis consists entirely of plots from the Baviaanskloof. The succulent tree *A. ferox* was common in this site and is an indicator of degradation in Baviaans Spekboom Thicket (Vlok & Euston-Brown, 2002). Abundant species in this community, but not abundant in the other sites, included woody species such as *P. capensis, L. oxycarpum* and *E. undulata*, which are recorded as being common remnant species in degraded thicket (Vlok & Euston-Brown, 2002; Lechmere-Oertel *et al.*, 2005b). Furthermore, *L. oxycarpum* increases with browsing and is an unpalatable species (Stuart-Hill, 1992; Fabricius, 1997). Of the growth forms, the grasses *C. cilliaris* and *E. lehmanniana* and the dwarf shrubs *J. orchioides* and *C. cilliata* are most abundant. *C. cilliaris* is a problem grass in Australia where it reduces species richness and indigenous plant groups (Clarke *et al.*, 2005). Woody trees, graminoids and dwarf shrubs had cover values of 11%, 28% and 5%, with richness values of 9, 18 and 24 species, respectively.

3.7.2.5. Landscape

A total of 345 species were sampled in the quadrats across the GAENP and the Baviaanskloof. Arid areas including Darlington and Baviaanskloof are often dominated by succulence and had more succulent species (34 and 26, respectively) than Kabouga and Addo Main. The loss in spekboom is replaced by an invasion of *E. caerulescens* in Darlington and increased *A. ferox* in Baviaanskloof. The abundance of *P. capensis* and *E. undulata* in Baviaanskloof communities supports other studies showing the tree layer as consisting of these remnant species (Vlok & Euston-Brown, 2002; Lechmere-Oertel *et al.*, 2005b). Kabouga is the only site with an abundant alien invasive. *O. aurantiaca* is common throughout the site and a problem species in thicket (Wilson, 2004). Other studies in the same area found that *O. ficus-indica* was instead a more abundant invasive succulent shrub (Hoffman & Cowling, 1990; Vlok & Euston-Brown, 2002), however the introduction of a biological control agent for this species has declined its numbers substantially in the Eastern Cape (Vlok & Euston-Brown, 2002). Kabouga also had a higher cover of woody shrubs where Asparagaceae featured more dominantly. The presence of old lands in Addo Main has transformed the site into an area of thicket and 'grassland' mosaics. Degraded thicket in Addo Main experiences high browsing pressure from wildlife compared to the other sites, due to higher stocking of game as well as the presence of elephants (SANParks, 2008). The old land 'grasslands' show some shrub recovery with heterogeneity found in plant and growth form composition. The old lands are important sites for grazers such as zebra and wildebeest in Addo Main and are therefore important for ecotourism.

3.7.3. Soil quality and composition

Landscape soil pH in degraded thicket is on average 6.4±0.13 KCl. This is between the average pH of low and highly utilised degraded lands of spekboomveld (Rutherford *et al.*, 2012); less than the pH of intact thicket near Kirkwood (Mills & Fey, 2004) and more consistent with the average pH (6.4±1.13 KCl) beneath canopies of both intact and degraded sites in spekboomveld (Lechmere-Oertel *et al.*, 2005a). The pH is still less than 7.0, indicating that uptake of nutrients by plants in degraded thickets of this study is not limited (Thompson & Troeh, 1978).

The macro-nutrient Mg was lowest in Addo Main at 1.9±0.21 cmol/kg, where the transformation of thicket to grassland has resulted in a decline in Mg, consistent with that of a transformation to savanna (Mills & Fey, 2004). Magnesium is less resilient compared to other macro-nutrients, therefore its depletion can be expected with increased degradation or transformation (Thompson & Troeh, 1978). Calcium significantly increased in other studies within the 'pseudo-savanna' and with degradation (Mills & Fey, 2004; Rutherford *et al.*, 2012). Calcium was significantly higher in Darlington (27.7±8.23 cmol/kg), where the impact from goat-browsing and aridity is more severe. Furthermore, the Witteberg group sandstones are higher in Ca compared to mudstones and shales in the other sites, due to the marine depositional environment of the parent material (Thamm & Johnson, 2006). However, Ca is generally also higher in arid environments and linked to higher CEC (Thompson & Troeh, 1978), which is higher in Darlington at 16.5±1.17 cmol/kg. Sodium was also therefore highest in Darlington at 0.7±0.27 cmol/kg (equivalent to 261±105 mg/kg), but still exceptionally low since highly degraded sites in spekboomveld to 0-5 cm have 690.1 mg/kg of Na (Rutherford *et al.*, 2012).

Potassium was highest in Addo Main at 0.97±0.1 cmol/kg or alternatively 378.4±37.58 mg/kg (Bray II), where the majority of the land has been transformed. Potassium has been found to increase with degradation and a transformation to savanna (Mills & Fey, 2004; Rutherford *et al.*, 2012), confirming the results of this study. Phosphorous (Bray II) was very low in degraded thickets at 30.9±2.5 mg/kg within the landscape and differs substantially compared to other degradation studies in thicket. Phosphorous increased two-fold with degradation severity from 63.6 to 126.4 mg/kg in spekboomveld to a depth of 5 cm (Rutherford *et al.*, 2012) and increased from 68 mg/kg in intact thicket to 93 mg/kg to a depth of 10 cm in the 'pseudo-savanna' in spekboom thicket (Mills & Fey, 2004). Phosphorous was highest in Darlington where it is expected to coincide with increased Ca and pH (Thompson & Troeh, 1978). The disparities in soil depth between studies make it difficult for accurate comparison for all nutrients and it is possible that there is a dilution effect with increased soil depth. Ovington (1958) for example, found that Ca increased with depth, up to 15-20 cm and then steadily declined, while Mg declined with soil depth. This was however in a forest in England and not in a semi-arid environment.

Soil carbon decreases with degradation in spekboomveld from 3.5 to 1.44% (Rutherford *et al.*, 2012) and from 5.6% in thicket to 3.0% in the 'pseudo-savanna' (Mills & Fey, 2004). Furthermore, the carbon content was 3.1% in degraded spekboom thickets and 2.7% within matrix vegetation of degraded thicket to a depth of 10 cm (Lechmere-Oertel *et al.*, 2005a). Kabouga and Baviaanskloof have the highest soil carbon of 1.3 and 1.6%, which is more consistent with the highly utilised sites in spekboomveld, even though the soil depth is only 5 cm. The actual carbon content however, is highest in Kabouga at 14.2 g/kg, which is significantly more than any other site. The high soil carbon coincides with highest root biomass in this site of 77%, as well as significantly higher bulk density of 22.8±3.5 g/cm^3. Litter however is higher in the more arid sites and weighs on average 214.8±17.33 g/m^2 within the landscape. High litter mass could be due to an abundance of *E. caerulescens* and *A. ferox* in Darlington and Baviaanskloof, respectively. CEC is also higher in the arid sites.

3.7.4. Degradation gradients in species and soil composition

Old lands in Addo Main were associated with a combination of annual weeds and dwarf succulent and woody shrubs as well as the grass *C. incompletus*. Soil percentage was highest in old lands at 99.3% and was associated with the lowest Ca, Mg, P, pH and soil C and the highest resistance and K. Since degradation score 4 is not an accurate representation of a less degraded state, degradation score 3 is assumed to be the better score to use as a moderately degraded state. Moderately degraded thickets of degradation score 3 are therefore associated with higher litter, roots and carbon due to higher abundance of woody shrubs and trees. Calcium is highest in moderately degraded thicket, but was only significantly different to a degradation score of 1 and not old lands. Degradation score 1 and old lands were similar in many of the nutrients, except for Na, which was significantly higher in degradation score 1, compared to all degradation scores, except degradation score 4. Degradation score 1 is representative of a severely degraded, if not transformed thicket, with the same species commonly found in severely degraded thickets of other studies (Vlok & Euston-Brown, 2002; Lechmere-Oertel *et al.*, 2005b; Rutherford *et al.*, 2012). They include *Cynodon* species, *A. congesta, A. lindleyi.* subsp. *inflata, Chenopodium* spp. and *L. africanum.*

3.8. Conclusion

Degraded Subtropical Thicket studies across the GAENP and the Baviaanskloof have shown that species composition and the secondary successional species following degradation are still linked to the abiotic correlates of rainfall, altitude and gravel within the soil. Therefore, despite degradation processes and the landscape homogenisation that is expected from this (Rutherford *et al.*, 2012), there was still high heterogeneity within sites, which significantly split species composition into communities, both between and within sites. There were however a few species that were indicative of homogenisation (*P. incana, G. pubescens, D. hispidum, C. incompletus* and *C. dactylon*), but the significant split in community composition confirms a lack of homogenisation with degradation within the landscape. Furthermore, each site showed correlations with a suite of different abiotic variables, demonstrating the local-scale processes that determine species composition. For reasons yet unknown, the Baviaanskloof was the only site which did not have significantly different communities, however it needs to be further investigated if goats are still browsing some of the lands. If so, it would explain the lack of communities and confirm recovery processes in the other sites.

Degradation gradients between sites were all significantly different to each other in species composition, except when the landscape was severely degraded to a transformed state at a score of 1. However, the design of the degradation scores using growth form as a measure of intactness was not a suitable method and instead it is believed that indicator species and bare ground cover should have been used to determine the degree of degradation at site specific level and not as a whole within the landscape.

Regardless, increased degradation was associated with a reduction in Ca, Mg, P and soil C and an increase in Na. Old lands were specifically lower in pH and higher in K and soil resistance. The Kabouga site had a higher cover of the woody shrub growth form and therefore the highest root percentage within the soil, as well as soil carbon content. Moderately degraded thickets are therefore higher in woody shrubs, litter and roots at the landscape scale, however it was the arid sites containing *E. caerulescens* and *A. ferox* which had the highest litter mass at local scales. Furthermore, both Kabouga and Baviaanskloof had the lowest species richness, which is likely related to the mountainous surrounds, which would limit dispersal mechanisms. It could also be a consequence of less abundant zoochoria acting as dispersers in the area following degradation or increased seed predators preventing survival (Stuart-Hill, 1989).

4 CHAPTER

TEMPORAL DECLINE OF CANOPY COVER: PATCH ATTRIBUTES AND SPECIES COMPOSITION IN DEGRADED SUBTROPICAL THICKET

CHAPTER 4: TEMPORAL DECLINE OF CANOPY COVER: PATCH ATTRIBUTES AND SPECIES COMPOSITION IN DEGRADED SUBTROPICAL THICKET

4.1. Assessing vegetation cover change

Geographical Information Systems (GIS) are a valuable tool in combining multiple datasets (topographical, geological, vegetation cover, climate) for assessing and monitoring systems (Salem, 2003). GIS is used to describe landscape or ecosystem pattern by creating a visual interpretation of data, but it can also be used to explain processes through mathematical and geostatistical models (Swetnam & Reyers, 2011). GIS is used in landscape ecology to monitor landscape change and address research questions on landscape scales (Turner, 1989). Progressively however, it has been used to look at fine scale vegetation patches and even individual species (Malkinson *et al*., 2003). GIS is useful in evaluating vegetation cover change over time through comparing aerial imagery from multiple years, however this can often be tedious, time consuming and not always accurate due to the grain or resolution of the images (Hudak & Wessman, 1998). Remote sensing is better equipped to look at vegetation cover change from satellite imagery and predict changes in cover and vegetation distribution through models of climate change. Remote sensing is a much more reliable estimate of cover and has been successfully used in monitoring vegetation cover change at large scales (Nagendra, 2001).

The use of remote sensing is presently not applicable when trying to quantify the long-term impacts of past land use on vegetation cover, since satellite technologies were not available at the time when early aerial photography was conducted. Despite the time-consuming nature of GIS-based methods, studies have focused on textural analysis of aerial imagery (Hudak & Wessman, 1998), patch identification tools (Kakembo, 2009) and manual interpretation of cover types, based on the grey-scale of the images (Corrigan *et al*., 2010, Puttick *et al*., 2011). Analysing the grey-scale of the images in GIS allows the user to interpret the type of vegetation mosaic within the images and calculate cover values of different vegetation layers or land-use types within a given landscape (Turner, 1990).

4.2. Importance of patches within ecological landscapes

Landscapes and ecosystems are heterogeneous systems that exhibit complex interlinked interactions between abiotic and biotic structure, composition and function (Noss, 1990). Understanding the spatial structure of systems requires an incorporation of spatial and temporal scales and levels of organisation which can be indicated by patch dynamics (Noss, 1990; Gustafson, 1998). In high rainfall areas, the tree component controls the size and spacing of patches, while at low rainfall, run-off and deposition processes become more important in structuring the landscape (Ludwig *et al.*, 1999). Fire and herbivory further control the size and composition of patches, with fire being particularly important in savanna systems by inhibiting bush encroachment (Bond *et al.*, 2003; Wiegand *et al.*, 2006). However, the geomorphic template also plays an important role in patch structure. The terrain, such as slope angle will influence the rate at which material is transported, since steep slopes encourage water flow and smooth slopes foster increased wind velocity (Ludwig *et al.*, 2005).

Patches occur within a two-phase mosaic, as evident in semi-arid to arid environments, defined by the attributes of high plant cover patches within low plant cover patches, known as the matrix (Aguiar & Sala, 1999; King *et al.*, 2012). High plant cover patches in savanna systems occur in one of three spatial patterns that relate to topographical gradients, particularly slope and associated catenal soil fertility (Ludwig *et al.*, 1999). Strands and stripes have banded vegetation pattern and stipples are the same as spotted vegetation pattern. Strands of vegetation follow drainage lines at higher elevations; stripes of vegetation are perpendicular to ridges and areas of increased slope angle; and stipples occur on bottom-slope, gentle topographies (Ludwig *et al.*, 1999). Banded vegetation patches are much more efficient in harnessing available water and nutrients, compared to stippled vegetation and exhibit increased plant productivity (Ludwig *et al.*, 1999). The bands retain water, increase soil water infiltration and provide a depositional environment for water transported nutrients and leaf litter (Ludwig *et al.*, 2005; Saco *et al.*, 2007). Spotted vegetation is driven by wind, where wind dispersed seeds collect beneath isolated patches, but seeds can also be transported by biota such as ants and termites, which transport seeds to more fertile micro-sites (Adie & Yeaton, 2014).

At local scales, patches are important in abiotic functioning through nutrient cycling and are vital catchment zones creating islands of fertility in arid or degraded landscapes (Schlesinger *et al.*, 1990; Peters *et al.*, 2006). A loss in landscape patchiness causes nutrient leaching from exposed soils and reduces functional processes. Ecohydrological interactions in dryland patches are particularly important to understand the function of patches and interpatches. Patches and interpatches are interlinked within a site where patches have positive feedbacks with resources, while interpatches are limited in resources (Tongway *et al.*, 2003; Ludwig *et al.*, 2005; King *et al.*, 2012). Interpatch areas which have low vegetation cover and very low germination rates, lose soil nutrients through run-off due to impacts to the exposed soil surface from raindrops and reduced infiltration (King *et al.*, 2012).

Patch shape, size and frequency are therefore essential to retain landscape and ecosystem function. Patch size shows significant positive correlations with species richness and diversity and are therefore vital to species heterogeneity. Degradation, especially through herbivory by livestock, reduces the cover and size of patches and sees a reduction of less resilient species.

4.2.1. Degradation of thicket canopy cover, bushclumps and patches

Intact Subtropical Thicket is formed through a series of fine scale woody patches, which over time, grow and join with other patches to form a bushclump. Gradually the bushclumps that exist within a mosaic of another vegetation type join to form a dense and closed canopy of thicket (Vlok & Euston-Brown, 2002). A dense layer of succulent *Portulacaria afra* patches join with trees and shrubs in a matrix of small succulent shrubs and few bare ground patches. Browsing by goats has severely reduced canopy cover of thicket, especially of succulent species like the abundant *P. afra*. When degraded, the system almost mimics its early successional state of isolated and largely dispersed bushclumps in a matrix of small patches of woody shrubs, dwarf karroid shrubs, grasses and bare ground (Lechmere-Oertel, 2003), therefore acting within a two-phase mosaic. The accompanying reduction in soil organic matter and soil fertility with the loss of above-ground biomass has resulted in a landscape that has passed system thresholds and is resistant to recovery processes.

At fine scales, isolated evidence of regeneration has been found in degraded spekboom thicket (La Cock, 1992), but not within degraded spekboomveld (Sigwela *et al.*, 2009). Seedlings are however present in intact arid thicket types (Adie & Yeaton, 2013). Diversity in degraded patches has been reduced to a few hardy woody trees with umbrella-like canopies from browsing below the canopy, as well as small bushes of sturdy palatable woody shrubs. The 'pseudo-savanna' of degraded thicket also therefore mimics savanna patterns and processes and patch dynamics. The spatial organisation however, is much more inconsistent with the types of vegetation pattern as found in savannas and is simply a combination of vegetation patterns depending on the mode of degradation.

The impact of degradation on species composition and structure varies between thicket types, severity and duration of degradation, cause of degradation and along topographical and climate gradients (Stuart-Hill, 1989). The severe loss in vegetation canopy cover in previously spekboom-dominated thickets provides an opportunity to study the attributes of patches within these degraded landscapes and within compositionally different sites. GIS allows for the assessment of vegetation, where large-scale projects such as STEP (Subtropical Thicket Ecosystem Planning Project) have been invaluable in providing the baselines of thicket vegetation distributions, conditions and associated maps, which are important for the start of understanding the state of biodiversity within a region (Vlok & Euston-Brown, 2002; Lloyd *et al.*, 2002; Lombard *et al.*, 2003; Swetnam & Reyers, 2011). STEP has provided a platform for research into the comparison and linkages of past land-use to current states and types of thicket vegetation, and opened the opportunities for future research into thicket dynamics at various scales and degradation.

The aim of this chapter was therefore to assess the change in thicket canopy cover over time through aerial and satellite imagery and quantify patch attributes over different spatial scales in severely degraded thicket. Furthermore, the study aimed to look at patch composition and richness and assess the loss in *P. afra* and invasion by *Euphorbia caerulescens* in spekboomveld, where *P. afra* has become absent.

4.3. Objectives and key questions

Objective 1: To quantify vegetation cover change through time from aerial imagery between 1939 and 2009 in the Greater Addo Elephant National Park (GAENP).

Key question 1.1: Is there a significant change in vegetation cover between time intervals within each site?

Key question 1.2: Is there a correlation between aerial canopy cover and sampled woody cover and area?

Key question 1.3: Does the duration of degradation and the time of recovery affect species composition?

Objective 2: To measure patch attributes and species composition in degraded subtropical thicket of the GAENP and the Baviaanskloof.

Key question 2.1: Where do the highest numbers of species occur within patches and can this be related to a nurse plant effect?

Key question 2.2: What is the proportion of woody trees, shrubs and succulents and how does this vary between sites?

Key question 2.3: Is there a difference in patch attributes between sites with different degradation scores?

Objective 3: Assess the relative abundance of established spekboom and invasion of noors into spekboom-dominated thicket.

Key question 3.1: What is the current distribution and abundance of spekboom and noors within degraded areas of the GAENP and the Baviaanskloof?

4.4. Methods

4.4.1. Data collection

4.4.1.1. Assessment of vegetation cover over time

Scanned historical aerial imagery for 1939, 1960, 1978 and 2000-2001 were obtained from National Geo-Spatial Information (NGI) and georeferenced using ArcMap 10.1 software. Images were projected to Transverse Mercator, WGS 1984 datum, central meridian 25 for the GAENP. Geographically accurate 1:10 000 ortho-photographs were used for 2009. A 200 x 200 m grid network of polygons known as a fishnet, was placed over the study areas. The grids that most contained or intersected with the coinciding sampled 50 x 50 m field plots (extrapolated from the extremities of the transects, see Figure 12, Chapter 3) were used to analyse vegetation cover. Within each 200 x 200 m grid, 100 random points were generated for each sampling period, separated by at least one meter. At a scale of 1:500 the points were labelled from 1-4 in the attribute table as intersecting with:

1. A woody tree/shrub (canopy)
2. On the edge of a tree/shrub and bordering the matrix (canopy edge)
3. Inter-canopy matrix vegetation or bare ground (matrix)
4. River or road (other)

Furthermore, dates at which farms were proclaimed and included within the borders of the GAENP were obtained from SANParks, as well as from government gazettes (Republic of South Africa, 2013; 2014). It is assumed that the date of proclamation is the date at which degradation from livestock ceased. With regard to the Baviaanskloof, a consistent photo record spanning the entire study area could not be completed, nor a land use history to test the objectives. It has thus been excluded from looking at vegetation cover change over time, as well as correlated with patch attributes.

4.4.1.2. Woody and succulent tree and shrub sampling

A total of 109 plots were sampled for plant diversity across the GAENP and the Baviaanskloof. Each 10 x 10 m plot contained four 2 x 2 m quadrats to measure the percentage cover of all plant species. Two 50 x 1 m transects bisected the plot from S-N and E-W. The transects, which are most relevant to this chapter, measured the length along a 50 m tape measure and the width along a one metre rule of every woody tree, large woody shrub, succulent tree and large succulent shrub. In the GAENP, 30 plots were sampled in Darlington (AD), 20 plots in Addo Main (AM), 30 plots in Kabouga (AK) and 29 plots in the Baviaanskloof (BK).

4.4.1.3. P. afra *and* E. caerulescens *sampling*

Within the entire 10 x 10 m plot, the number of living spekboom (*P. afra*) plants and noors plants (*E. caerulescens*) were sampled. Each spekboom plant was counted and their stem diameters measured at the base using digital callipers. Similarly, each noors plant was counted and the stem height from the ground was recorded using a one-meter rule and a measuring tape attached to a ranging rod, for taller stems.

4.4.3. Data analysis

4.4.3.1. Vegetation cover change

The number of points in each grid identified as either the canopy, edge of the canopy, matrix or other, per year from 1939-2009, was averaged per site and depicted in a stacked bar graph. A regression analysis was used to look at the relationship between trees and or shrubs over time, while a repeated measures ANOVA was used to look at the change in vegetation cover over time, using STATISTICA.

The dates at which there was a noticeable decline in vegetation cover per grid was used as the date at which degradation started. Furthermore, each grid was visually evaluated for cover and assigned either moderate or severe degradation status. If degradation was seen in the earliest imagery, then that was used as the date at for which degradation was present. However, the severity of degradation accounts for the amount of degradation at that time. The date at which the coinciding farm (to a sampled plot) was proclaimed into the GAENP, was used as the date at which degradation ceased for that grid and natural recovery is assumed to have started. The period of degradation and the period of recovery was used to look at differences in species composition, using the percentage cover data collected from four 2 x 2 m quadrats within each plot. An ANOSIM analysis was performed using PRIMER to test for significant differences in the period of rest or recovery and the year and severity of degradation.

4.4.3.2. Patch attributes and composition

A patch, for the purpose of this study, is defined as a contiguous segment of vegetation, separated from another by at least 2 m of non-woody or succulent cover. For each site and degradation score (Chapter 3, section 3.5.3.3.3) the number of patches, the mean patch size and the mean number of species and plants per patch were calculated from the transect data. A PERMANOVA analysis was used to test for significant differences (Clarke & Warwick, 2001) in these values, using site and degradation score as a factor. An ANOSIM looked at the differences in patch attributes for site alone. A regression of patch length and species richness was performed to see if species richness increases with patch size. This was performed for each site and per degradation score. Additionally, the frequency distribution of patch size was tabulated for each site.

Each woody and succulent species recorded in the two transects were categorised according to growth form, namely: woody tree, woody shrub, succulent tree and succulent shrub. The area of each species was calculated and aggregated according to each of the growth forms per transect. These values were used to find the average proportion of growth forms per site. Furthermore, the likelihood of finding a number of common established woody and succulent species within a patch, was calculated as the percentage probability for each site and degradation score.

4.4.3.3. P. afra *and* E. caerulescens *abundance*

The mean number of plants and stems and the mean stem diameter or height was calculated for spekboom and noors within the 10 x 10 m plots of each site. The mean cover of spekboom and noors in the 2 x 2 m biodiversity quadrats was calculated as well as the mean area in the transects. Spekboom and noors percentage cover data was summed to calculate the percentage of the total sampled area occupied by these two species.

4.5. Results

4.5.1. Vegetation cover change over time

Changes in vegetation cover from 1939 to 2009 showed a distinct decline in tree cover for all sites. From the 1960s, cameras were able to cover a much larger area in a single photograph compared to the 1939 imagery. Photographs for 1960, 1978 and 2000 are thus much more pixilated, which made it difficult to obtain accurate estimations of vegetation cover for these years. However, this could also be due to issues with scanning resolution. Aerial imagery from 1939 and 2009 were clearer and should be used as a main reference for vegetation cover decline over a 70-year period.

The Darlington section of the GAENP had an average of 34% canopy cover in 1939, which declined to 23% by 2009 (Figure 21a). Canopy edge cover declined into 2009 and matrix cover increased from 36% in 1939 to 60% in 2009. The results of a regression of tree cover by year revealed no significance, however matrix cover showed a weak but significant relationship with time ($p= 0.04$; $r^2= 0.037$).

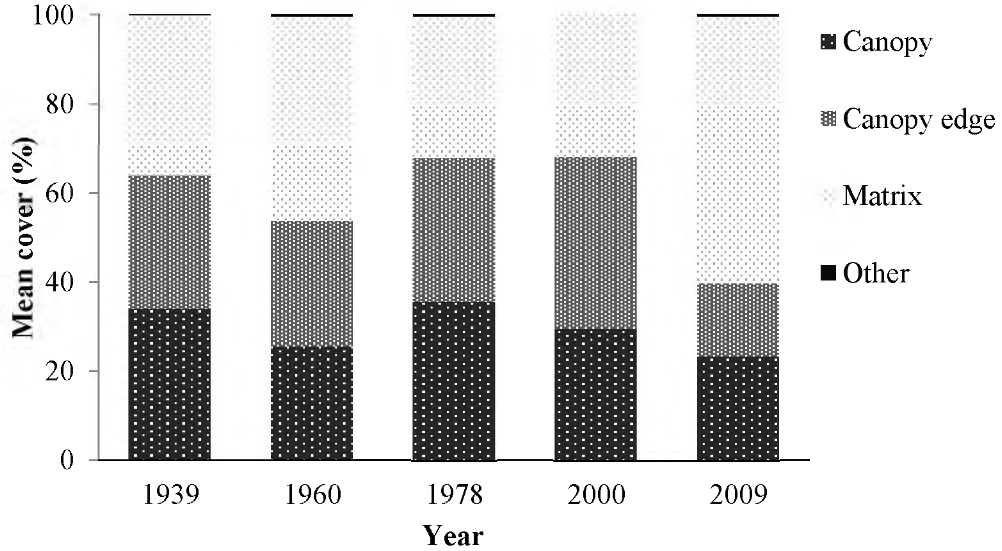


Figure 21a: Tree and shrub cover change over time in Darlington.

In Addo Main, canopy and edge of canopy cover started to show a decline in the 1970s (Figure 21b). Canopy cover declined from 37% in 1939 to 6% in 2009. The majority of plots show a substantial decline in canopy cover due to a transformation of intact thicket into agricultural land. Matrix cover increased from 43% in 1939 to 83% in 2009. A regression analysis showed a significant relationship in canopy decline and matrix cover increase over time ($p < 0.0001$; $r^2 = 0.2$).

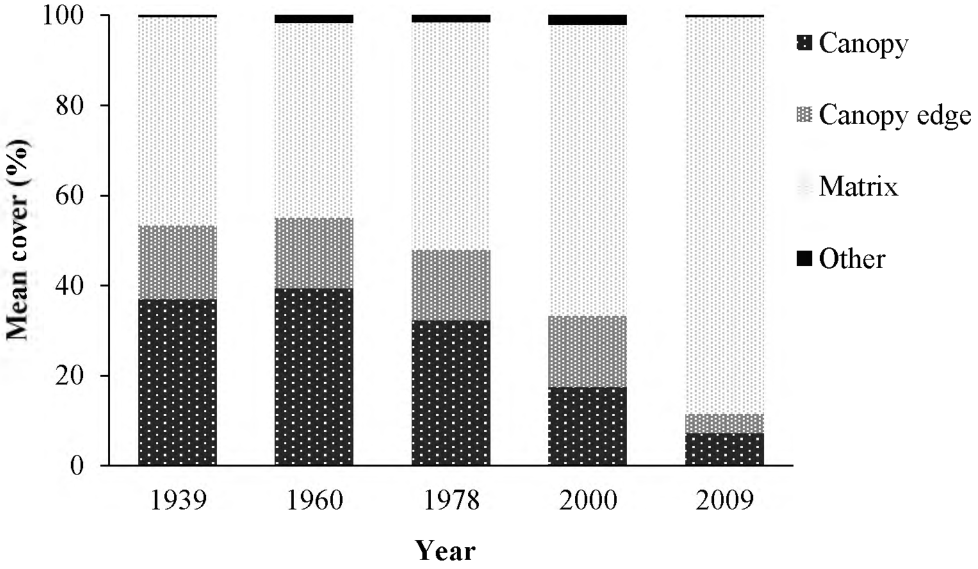


Figure 21b: Tree and shrub cover change over time in Addo Main.

In 1939, Kabouga showed the highest average canopy cover at 53% in comparison to plots from Addo Main and Darlington (Figure 21c). Canopy cover revealed a progressive decline from the 1960s ($p = 0.001$; $r^2 = 0.3$). Canopy cover in 2009 was at 26% and matrix cover at 60%.

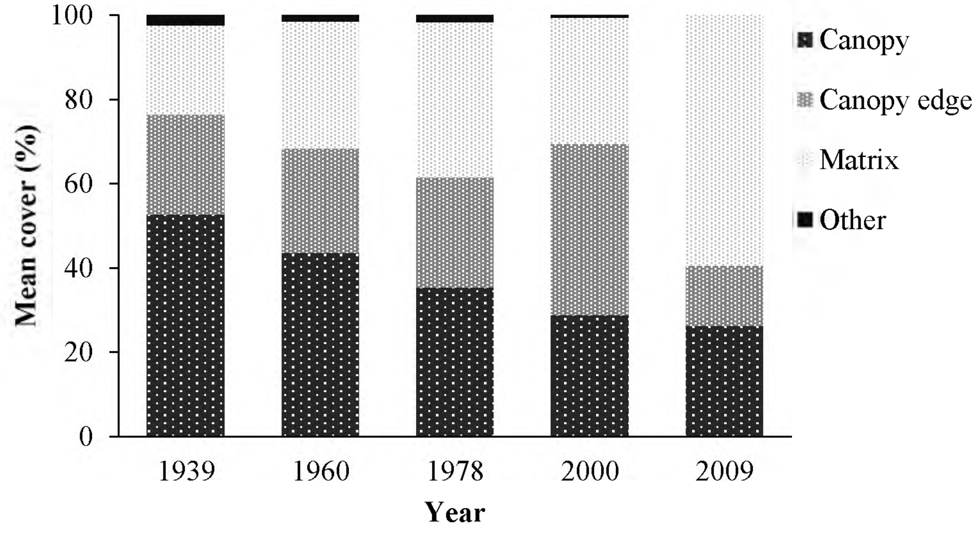


Figure 21c: Tree and shrub cover change over time in Kabouga.

A repeated measures ANOVA found that canopy and canopy edge cover significantly declined for all sites at $p < 0.05$, while matrix cover significantly increased from 1939 to 2009.

4.5.2. Temporal degradation in relation to present vegetation composition and structure

It was predicted that there would be a correlation between the number of patches measured in the transects and the estimated cover from 2009 aerial imagery. However, this was not the case. Darlington had a negative correlation of r^2= -0.47 between the 2009 canopy cover and the number of patches per plot. This could be attributed to the low height of noors plants which are not distinguished as canopy cover in aerial imagery, but are measured as patches on the ground. The correlation in Addo Main was r^2= 0.2, while Kabouga had a low correlation of just r^2= 0.04.

4.5.2.1. Duration of degradation

Using the dates at which degradation visibly occurred and the dates of proclamation into the GAENP, a CAP analysis using duration and severity of degradation as a factor was performed (Figure 22). The method acknowledges and assumes pre-1939 degradation by indicating the severity of degradation at the date of the earliest imagery.

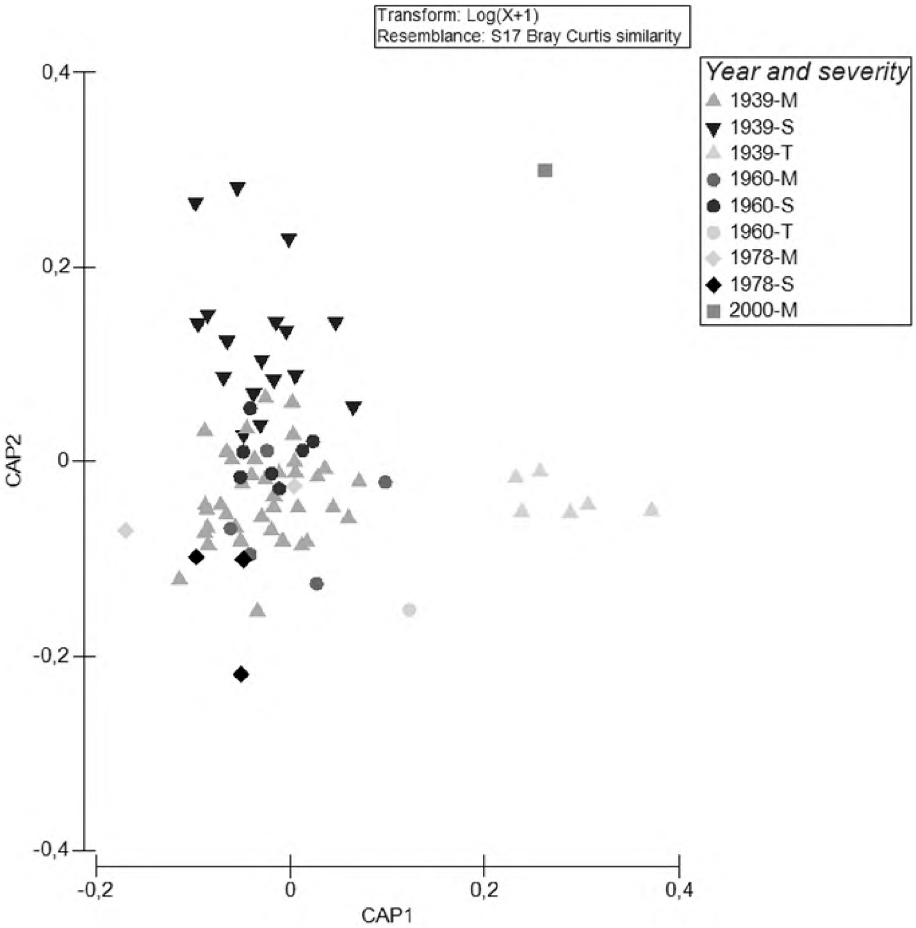


Figure 22: CAP analysis of all plots using the year at which degradation was visible and the severity of degradation as a factor (Key: M- Moderate, S- Severe and T- Transformed).

The CAP revealed that the dates at which degradation is clearly visible and the severity at that time, does not influence present day species composition. The allocation success was less than 50%. Plots which showed a transformed state in 1939, did however separate out from those plots which show degradation from browsing, as did the plot which only showed degradation post 2000.

In Addo Main, the plots that were severely degraded in 1939, compared to the plots that were transformed in 1939, showed significant differences in plant species composition (R= 0.453; p= 0.002) following a one-way ANOSIM analysis. Severely degraded plots in Kabouga that showed visible degradation in 1960 and 1978, were significantly different in species composition (R= 0.518; p= 0.036), while Darlington showed no significant differences in the year and severity of degradation.

4.5.2.2. Period of rest

The time from proclamation to the time of sampling was considered as the period of rest, where natural recovery, if any, could have taken place. Figure 23 depicts the distribution of plots, factored by the period of rest and labelled by site. All of the plots grouped according to site, however the grouping for Addo Main (Site 2) was much more dispersed, as its land use history is more diverse. While no differences were found in species composition between rest periods in Addo Main, the overall test showed that the plots were dissimilar (Global R: 0.31; p= 0.04). Furthermore, the plot in Addo Main which has been recovering for 39 years, showed consistencies with species composition of plots in Kabouga. Areas of Kabouga have either been recovering for 10 or 18 years. The CAP revealed a slight overlap between these two rest periods in species composition.

In Darlington however, the overlap between plots recovering for seven and nine years is much more prevalent, indicating that there is no difference in species composition with a two-year lead in recovery. This was further confirmed by a one-way ANOSIM analysis, which showed no significant difference in species composition between seven and nine years' recovery (R= -0.03; p= 0.77), nor three and seven years' recovery (R= 0.43; p= 0.06). It did however confirm a significant difference between three and nine years' recovery (R= 0.6; p= 0.029). No other significant differences were found in the other sites and the overall allocation success was only 55%.

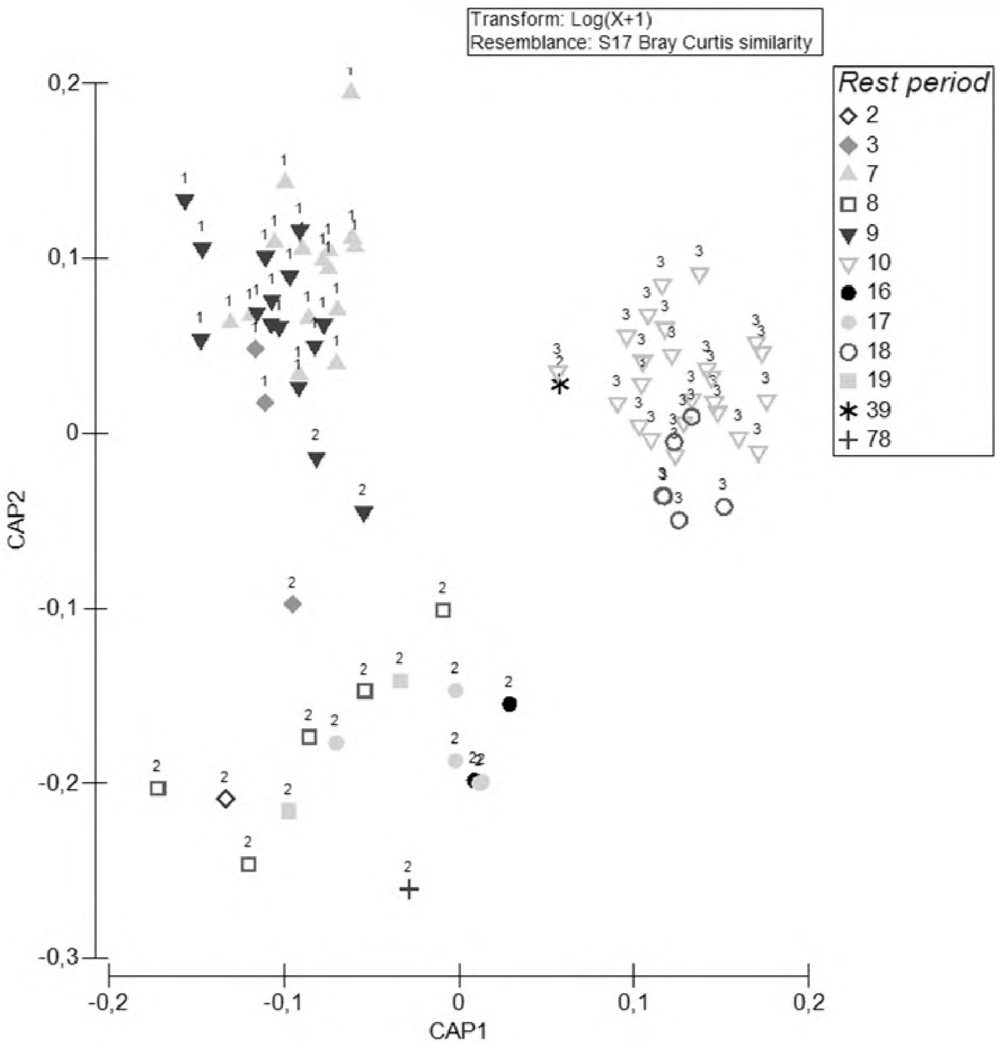


Figure 23: CAP analysis of species composition, factored by the period of rest (Key: 1- Darlington, 2- Addo Main, 3- Kabouga).

4.5.3. Degraded subtropical thicket patches

4.5.3.1. Patch attributes

The values in Table 17 present the patch attributes. They are categorised according to site and degradation score. Darlington had the highest mean number of patches (10.4±0.5) per transect and mean number of plants (4.0±0.2) per patch, however the species richness was slightly lower than the other sites, except for Addo Main. Darlington and Kabouga had a very similar number of patches for degradation scores 2 and 3, however the species per patch for these scores were higher for Kabouga.

Table 17: Patch characteristics for degradation scores per site (mean±SE).

Site	Deg. Score	Plots (n)	No. of patches/100m^2	Patch length (m)	No. of plants/patch	No. of spp./patch
Darlington	*1*	1	-	-	-	-
	2	21	10.7 ± 0.6	3.4 ± 0.2	3.6 ± 0.2	1.9 ± 0.1
	3	8	10.3 ± 1.1	5.8 ± 0.7	5.4 ± 0.6	2.6 ± 0.2
	Site	**30**	**10.4 ± 0.5**	**4.0 ± 0.3**	**4.0 ± 0.2**	**2.1 ± 0.1**
Addo Main	*1*	1	-	-	-	-
	2	2	4.5 ± 1.5	2.4 ± 1.1	1.8 ± 0.6	1.2 ± 0.2
	3	2	8.0 ± 0.0	5.8 ± 1.4	6.5 ± 1.8	3.4 ± 0.7
	OL	15	1.2 ± 0.7	1.4 ± 0.4	1.6 ± 0.4	1.0 ± 0.2
	Site	**20**	**2.8 ± 1.0**	**2.8 ± 0.6**	**3.0 ± 0.6**	**1.7 ± 0.3**
Kabouga	*1*	3	6.7 ± 2.8	2.7 ± 0.6	2.0 ± 0.4	1.6 ± 0.3
	2	16	10.3 ± 0.8	3.9 ± 0.3	1.3 ± 0.3	2.2 ± 0.1
	3	11	10.1 ± 0.6	5.9 ± 0.6	5.3 ± 0.5	3.5 ± 0.2
	Site	**30**	**9.9 ± 0.6**	**4.6 ± 0.3**	**4.0 ± 0.3**	**2.6 ± 0.1**
Baviaanskloof	*1*	3	8.0 ± 2.6	4.6 ± 1.0	3.9 ± 0.9	2.4 ± 0.3
	2	13	7.3 ± 0.6	4.0 ± 0.5	2.9 ± 0.3	1.8 ± 0.1
	3	10	8.6 ± 0.9	4.2 ± 0.5	3.8 ± 0.4	2.2 ± 0.1
	4	2	8.5 ± 0.5	6.7 ± 1.4	6.3 ± 1.4	3.3 ± 0.6
	Site	**29**	**7.9 ± 0.5**	**4.3 ± 0.3**	**3.6 ± 0.3**	**2.2 ± 0.1**
Landscape	*1*	8	6.4 ± 1.6	3.6 ± 0.6	2.8 ± 0.5	1.9 ± 0.2
	2	52	9.5 ± 0.4	3.7 ± 0.2	3.3 ± 0.2	2.0 ± 0.1
	3	32	9.5 ± 0.7	5.2 ± 0.3	4.8 ± 0.3	2.8 ± 0.1
	4	2	8.5 ± 0.5	6.7 ± 1.4	6.3 ± 1.4	3.3 ± 0.6
	OL	15	1.2 ± 0.7	1.4 ± 0.4	1.6 ± 0.4	1.0 ± 0.3
		109	**8.2 ± 0.4**	**4.2 ± 0.2**	**3.8 ± 0.1**	**2.3 ± 0.1**

Naturally, with an abundance of old lands with few species, Addo Main had low values for all patch attributes. Within the landscape, the average number of patches found within 100 m^2 was 8.2±0.4 with a length of 4.2±0.16 m and a species richness of 2.3±0.1. Generally, significant differences in one patch attribute reflect in the other attributes, indicating a relationship between the length of the patches, plant abundance and species richness. An ANOSIM analysis further showed differences in patch attributes between sites in Table 18.

Table 18: ANOSIM analysis of the difference in patch attributes between sites.

Site*		No. of patches/ 100 m^2		Patch length (m)		No. of plants/patch		No. of spp./patch	
		R	*P*	*R*	*P*	*R*	*P*	*R*	*P*
AD	AM	**0.629**	**0.001**	**0.258**	**0.001**	**0.277**	**0.001**	**0.421**	**0.001**
AD	AK	0.011	0.22	0.003	0.349	-0.012	0.707	0.022	0.120
AD	BK	**0.125**	**0.002**	-0.012	0.67	-0.008	0.545	-0.011	0.643
AM	AK	**0.573**	**0.001**	**0.341**	**0.001**	**0.259**	**0.001**	**0.374**	**0.001**
AM	BK	**0.476**	**0.001**	**0.282**	**0.001**	**0.271**	**0.001**	**0.395**	**0.001**
AK	BK	0.040	0.058	-0.020	0.864	-0.014	0.702	-0.009	0.578
Global test		**0.275**	**0.001**	**0.121**	**0.001**	**0.109**	**0.001**	**0.171**	**0.001**

*values in bold are significantly different at $p< 0.05$.

Addo Main was significantly different to all sites in all patch attributes due to the low number of measured patches. Addo Main is riddled with old lands, which are lacking in woody trees and shrubs. Darlington was significantly different to Baviaanskloof in the number of patches per 100 m^2 (R= 0.125; p= 0.002). The global test was significant for all sites; however, the degree of variation was very weak for all variables. The number of patches showed the greatest variability between sites, in terms of the global R value.

In the landscape analysis (Table 19), only degradation score 3 and 4 were not significantly different to one another in patch attributes, with the number of patches being less different for most comparisons. Addo Main was the only site which showed significant differences in the number of patches. Score 3 and old lands were significantly different in patch attributes (df=16; t=4.92; p= 0.004), where the average number of patches varied by at least seven patches (Table 19). Furthermore, all other attributes between score 3 and OL in Addo Main and patch length between score 2 and OL, were significantly different. Score 3 and 2 in Darlington and score 1 and 3 in Kabouga were significantly different in all attributes, barring the number of patches. Scores 2 and 3 and scores 1 and 3 in Kabouga were different in the number of species per patch and plants per patch, with the addition of patch length between scores 1 and 3. Baviaanskloof degradation scores were significantly different in none of the attributes, barring the number of species per patch between scores 2 and 4 (t=3.41; df=13; p= 0.02).

Table 19: Pair-wise PERMANOVA analysis of significant differences between the within site degradation scores, for a number of patch attributes.

Site*	Deg. Score		df	No. of patches/100 m^2		Patch length (m)		No. of plants/patch		No. of spp./patch	
				t	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Darlington	*1*	*2*	20	1.22	0.28	0.92	0.32	1.11	0.23	0.94	0.23
	1	*3*	7	1.02	0.57	1.28	0.34	1.09	0.34	1.15	0.32
	2	*3*	27	0.34	0.79	**3.01**	**0.01**	**2.26**	**0.04**	**2.56**	**0.01**
Addo Main	*1*	*2*	1	1.73	0.65	1.43	0.66	1.50	0.62	2.31	0.33
	1	*3*	2	3.50	0.26	2.45	0.24	1.78	0.45	5.03	0.27
	1	*OL*	14	0.43	0.87	0.53	0.94	0.53	1.00	0.62	1.00
	2	*3*	3	2.35	0.10	1.50	0.30	1.69	0.20	4.31	0.11
	2	*OL*	15	1.67	0.14	**3.49**	**0.02**	2.29	0.07	2.06	0.10
	3	*OL*	16	**4.92**	**0.004**	**7.48**	**0.002**	**6.39**	**0.002**	**8.21**	**0.001**
Kabouga	*1*	*2*	17	1.70	0.13	1.93	0.07	1.79	0.06	1.53	0.13
	1	*3*	12	1.75	0.11	**2.44**	**0.02**	**3.60**	**0.001**	**3.53**	**0.002**
	2	*3*	25	0.55	0.63	1.40	0.17	**4.17**	**0.001**	**2.96**	**0.01**
Baviaanskloof	*1*	*2*	14	0.40	0.74	1.20	0.28	1.20	0.28	1.10	0.28
	1	*3*	11	0.27	0.85	1.11	0.26	1.11	0.26	1.36	0.20
	1	*4*	3	0.15	0.89	2.30	0.11	2.30	0.11	6.19	0.11
	2	*3*	21	1.16	0.29	0.64	0.57	0.64	0.57	1.16	0.29
	2	*4*	13	0.72	0.50	1.57	0.16	1.57	0.16	**3.41**	**0.02**
	3	*4*	10	0.04	1.00	0.74	0.48	0.74	0.48	1.63	0.13
Landscape	*1*	*2*	52	**2.01**	**0.05**	**2.42**	**0.02**	**2.23**	**0.03**	**2.45**	**0.03**
	1	*3*	32	**2.97**	**0.00**	**3.06**	**0.01**	**3.12**	**0.01**	**4.38**	**0.00**
	1	*4*	5	0.89	0.41	**3.41**	**0.01**	**3.80**	**0.03**	**9.19**	**0.01**
	1	*OL*	18	**2.69**	**0.02**	**2.33**	**0.03**	1.68	0.12	**2.40**	**0.03**
	2	*3*	76	1.60	0.12	**2.67**	**0.01**	**3.19**	**0.002**	**4.60**	**0.001**
	2	*4*	49	0.15	0.88	**2.24**	**0.03**	**2.33**	**0.02**	**3.43**	**0.002**
	2	*OL*	62	**7.57**	**0.00**	**5.51**	**0.001**	**4.44**	**0.001**	**6.12**	**0.001**
	3	*4*	29	0.51	0.60	0.65	0.57	0.51	0.65	0.95	0.37
	3	*OL*	42	**9.50**	**0.00**	**6.20**	**0.001**	**5.68**	**0.001**	**8.62**	**0.001**

*values in bold are significantly different at $p < 0.05$.

The size of patches varied from <1 m to over 20 m in length and are divided into size classes in Table 20. A quarter of the patches in the landscape were less than a metre long. Eleven percent and 18% of patches were 2-3 m or 5-7 m and 1-2 m or 3-5 m in length, respectively. Twenty percent of patches in Kabouga and 19% in Baviaanskloof were between 3-5 m long.

Table 20: Percentage frequency distribution of patch sizes per site.

		Patch size (m)							
Site	**n**	**0-0.9**	**1-1.9**	**2-2.9**	**3-4.9**	**5-6.9**	**7-8.9**	**9-10.9**	**>11**
Darlington	316	27	19	8	16	11	9	3	6
Addo Main	55	51	18	2	7	7	4	5	5
Kabouga	287	19	17	13	20	13	3	6	9
Baviaanskloof	271	23	18	13	19	10	5	4	8
Landscape	930	25	18	11	18	11	6	4	8

Kabouga and Baviaanskloof also had the largest percentage of patches greater than 11 m long, with the largest patch in Baviaanskloof exceeding 35 m, likely classified more as a bushclump. Darlington had similar patterns to Kabouga and Baviaanskloof in the frequency distribution of patch length. A chi-square confirmed this, finding no significant differences in the frequency distribution of patches between Darlington and Baviaanskloof and Kabouga and Baviaanskloof. There was however a difference between Kabouga and Darlington (X^2=22.97; p= 0.002), while Addo Main was expectedly different to all sites at p< 0.001.

4.5.3.2. Relationship between patch length and species richness

The relationship between woody and succulent species richness and patch size is depicted in Figures 24 and 25. The correlation between patch size and tree and shrub species richness was best in Addo Main (p= 0.002; r^2= 0.65). In Darlington, the r^2 value was lower at 0.26 (p< 0.0001) due to patches mainly consisting of tightly growing *E. caerulescens* plants. The majority of patches had <5 tree and shrub species. Kabouga had many larger patches and higher tree and shrub species richness per patch. The highest number of species was 11 for a patch, one of 8 m and another of 19 m in Kabouga.

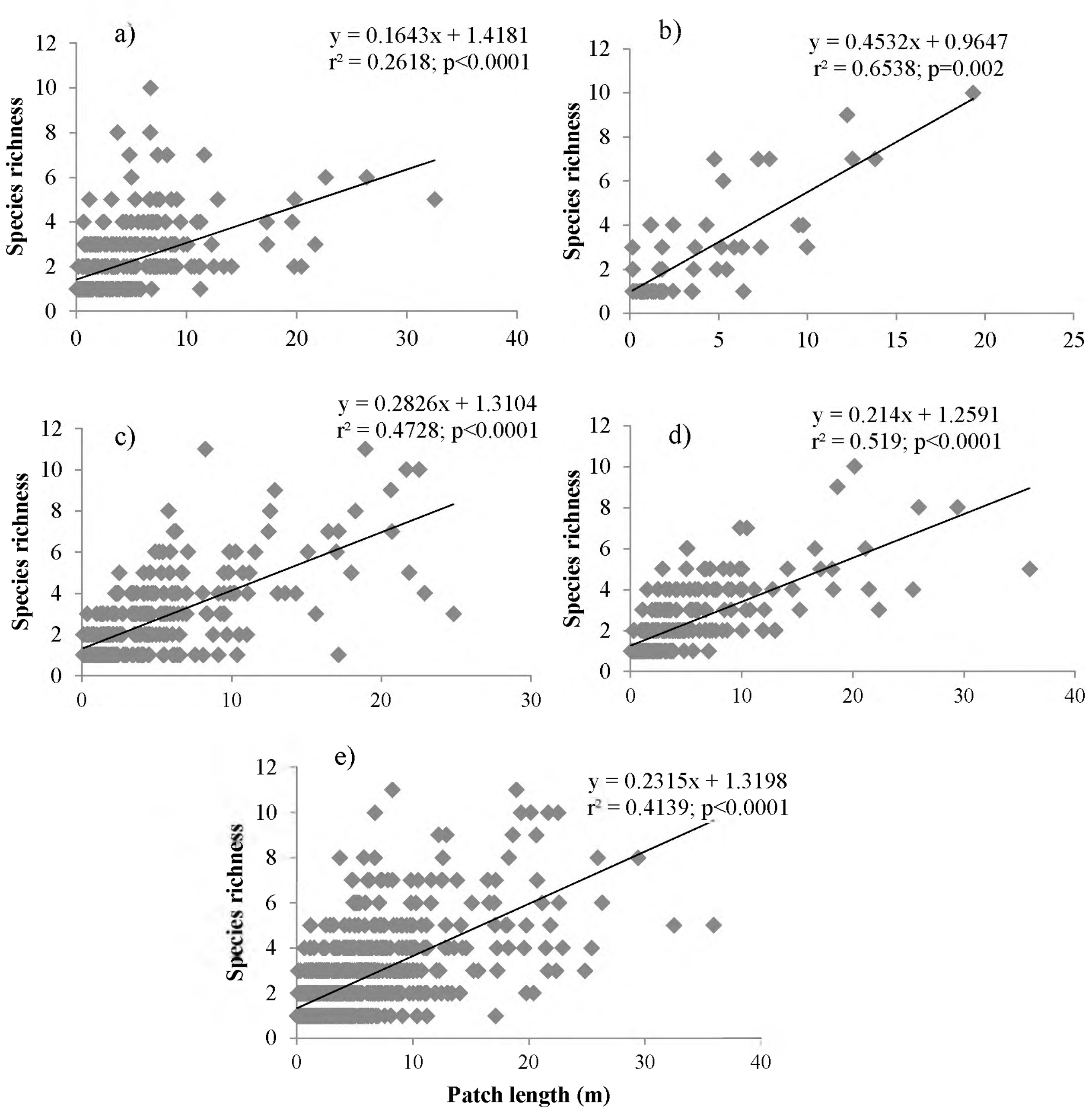


Figure 24: The relationship between species richness and patch length in a) Darlington, b) Addo Main, c) Kabouga, d) Baviaanskloof and e) Landscape.

Following a categorisation of patches into degradation scores (Figure 25), it was found that despite degradation, patch size still showed a significant relationship with species richness. Degradation scores 2 and 3 are more abundant in the number of patches (515 and 320 patches in each score) compared to degradation scores 1 and 4, but this can also be attributed to the higher number of plots per score.

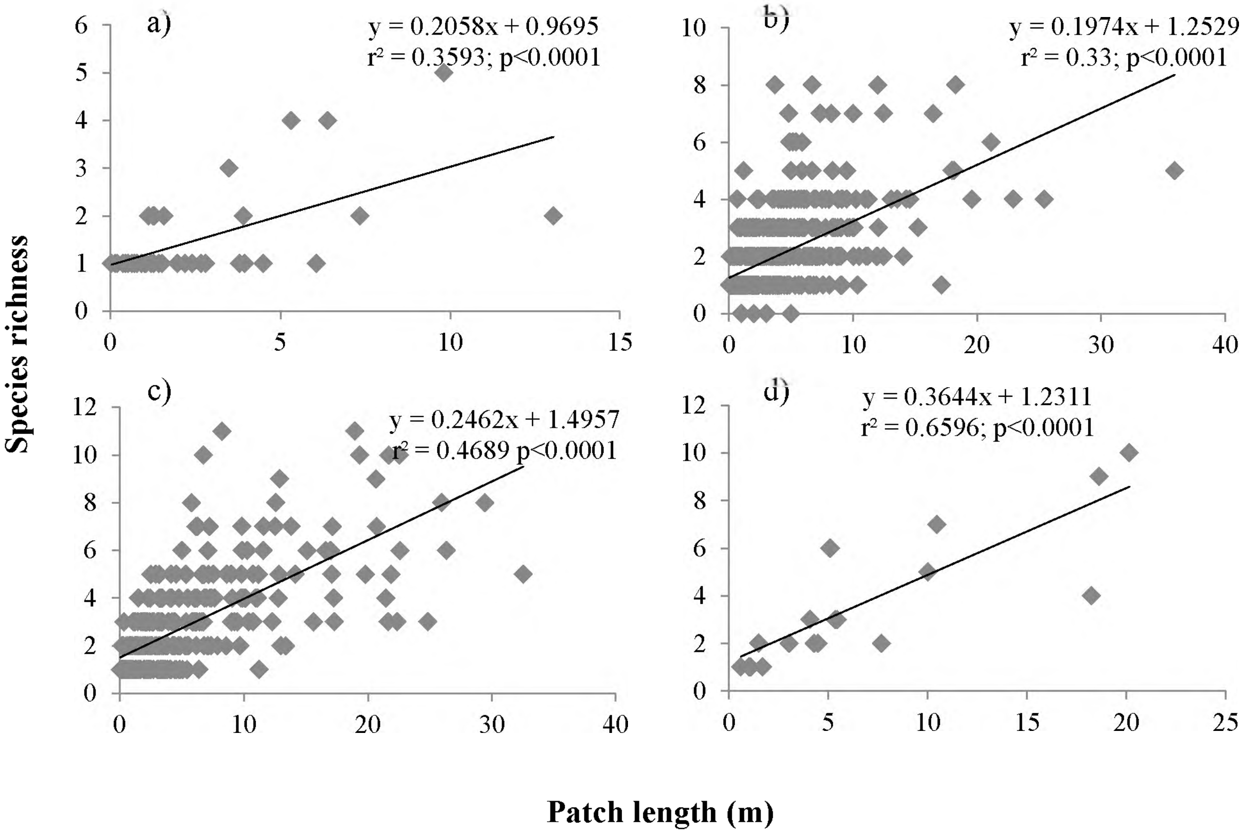


Figure 25: The relationship between species richness and patch length in degradation scores 1-4 represented by figures a) to d), respectively.

Degradation score 1 had lower richness and patch length, while degradation score 3 had a higher species richness and patch length. The majority of points in Figure 25b were below a species richness of 8, while they were below a species richness of 12 in Figure 25c.

4.5.3.3. Growth form area and species probability

The average canopy area of woody and succulent trees and shrubs in the four sites showed that Addo Main had a low cover of all growth forms, especially woody trees and shrubs (Figure 26). *Portulacaria afra* was considered as a succulent tree in this analysis so as to separate it from the succulent shrub *E. caerulescens*. Baviaanskloof and Addo Main had a similar area of succulent trees at 1.8 and 1.6 m^2, respectively.

Woody trees occupied the most canopy area per site, except for Darlington, which had a large succulent shrub canopy area of 13.7 m^2 and woody shrub canopy area of 11.5 m^2. Kabouga had the highest canopy area of woody trees and woody shrubs of 21.4 m^2 and 18.5 m^2, respectively.

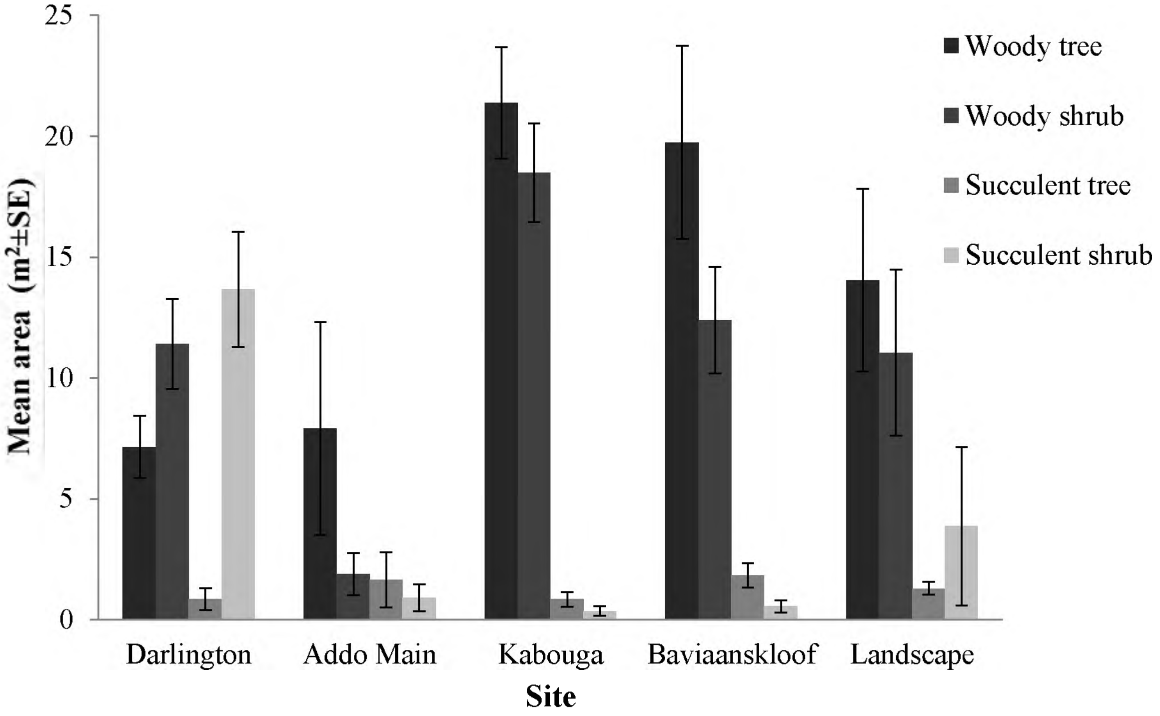


Figure 26: Average canopy area per 100 m^2 of woody and succulent trees and shrubs, per site.

Common species of woody and succulent trees and shrubs in Table 21 and 22 vary between sites and degradation scores according to both original vegetation type and land use history. The most abundant tree species within a patch was *V. karroo* in all sites, except for Baviaanskloof, which had a much higher abundance of *P. capensis,* found in 19.6% of patches (Table 21). Cumulatively, Kabouga had the greatest area of trees found within patches, including a relatively high abundance of *E. rigida* and *E. undulata* found in 4% and *S. afra* in 6% of patches.

The most common shrub species found within patches across all sites was *R. obovatum* and *G. robusta. G. robusta* was most abundant in patches of Kabouga (40%) and Baviaanskloof (41%), while *R. obovatum* was most abundant in patches of Darlington (43%) and Baviaanskloof (33%). Dominant shrub species that occurred in patches of Kabouga included *J. capensis* (21%), *L. ferocissimum* (24%) and *P. pyracantha* (24%), while the most abundant in Baviaanskloof was *A. ferox* (30%) and *S. longispina* (12%).

Table 21: Probability (%) of common tree and shrub species occurring in a patch, as measured in the four sites.

		Site			
		AD	**AM**	**AK**	**BK**
Trees	*Ehretia rigida*	2.4	0.6	4.1	0.0
	Euclea undulata	2.3	1.9	4.5	6.1
	Olea europaea subsp. *africana*	0.0	0.0	0.7	0.0
	Pappea capensis	3.0	0.6	9.4	19.6
	Ptaeroxylon obliquum	0.7	0.0	0.6	0.0
	Schotia afra	2.5	2.8	6.1	0.0
	Vachellia karroo	5.9	10.0	14.4	2.0
Shrubs	*Aloe ferox*	0.0	0.0	0.0	30.0
	Azima tetracantha	2.1	5.8	7.3	3.3
	Carissa haematocarpa	4.3	1.9	0.8	7.5
	Euphorbia caerulescens	48.9	1.3	0.0	2.5
	Grewia robusta	26.0	6.0	40.2	41.3
	Gymnosporia capitata	0.5	0.0	4.5	1.4
	Gymnosporia polyacantha	0.0	7.7	0.0	0.0
	Gymnosporia szyszylowickzii	9.4	0.0	0.0	0.0
	Jatropha capensis	2.3	0.0	20.5	2.5
	Lycium ferocissimum	4.6	9.2	24.3	0.9
	Lycium horridum	0.0	0.0	5.4	0.0
	Lycium oxycarpum	0.0	6.3	5.4	10.1
	Portulacaria afra	3.1	2.5	8.2	4.2
	Putterlickia pyracantha	6.9	0.6	23.6	15.2
	Rhigozum obovatum	43.1	0.6	16.5	33.2
	Searsia longispina	1.1	4.4	9.8	11.5
	Searsia lucida	0.0	1.7	0.0	4.1
	Searsia pallens	2.6	3.5	0.6	0.9
	Searsia refracta	3.4	0.0	3.8	0.0

The high abundance of multiple species in a single patch in Kabouga and Baviaanskloof could be indicative of nurse plant relationships or remnant patches still prevalent in the region. Addo Main, despite the few patches that were found in non-agricultural lands, was most abundant in *V. karroo* and *G. polyacantha*, with a probability of occurring in a patch at 10% and 9.2%, respectively.

Close to half (49%) of the patches within Darlington contained the succulent shrub *E. caerulescens*, compared to just 2.5% and 1.3% in Baviaanskloof and Addo Main. Climax thicket species such as *P. obliquum* and *O. europaea* subsp. *africana* are not very abundant tree species found within degraded lands, but are found most in Kabouga. In old lands, *L. ferocissimum* and *V. karroo* can be expected to occur in 12% and 7% of patches, respectively (Table 22).

Table 22: Probability (%) of common tree and shrub species occurring in a patch under varying degradation scores.

		Degradation scores				
	Species	**1**	**2**	**3**	**4**	**OL**
Trees	*Ehretia rigida*	1.4	0.9	4.7	0.0	0.0
	Euclea undulata	6.3	1.8	7.5	18.2	0.0
	Olea europaea subsp. *africana*	0.0	0.2	0.3	0.0	0.0
	Pappea capensis	8.0	6.4	15.9	24.4	0.0
	Ptaeroxylon obliquum	0.0	0.8	0.0	0.0	0.0
	Schotia afra	5.4	2.7	3.7	0.0	0.7
	Vachellia karroo	1.8	9.6	8.0	0.0	6.7
Shrubs	*Aloe ferox*	9.4	7.1	10.2	49.4	0.0
	Azima tetracantha	4.2	3.9	6.2	9.1	2.7
	Carissa haematocarpa	2.1	2.9	5.9	26.1	0.0
	Euphorbia caerulescens	0.0	20.3	15.9	0.0	0.0
	Grewia robusta	13.2	34.2	43.1	21.6	0.0
	Gymnosporia capitata	0.0	1.7	3.3	0.0	0.0
	Gymnosporia polyacantha	0.0	0.6	1.6	0.0	4.7
	Gymnosporia szyszylowickzii	0.0	2.7	4.5	0.0	0.0
	Jatropha capensis	0.0	5.1	15.3	0.0	0.0
	Lycium ferocissimum	9.7	8.3	12.1	0.0	12.2
	Lycium horridum	0.0	1.2	3.0	0.0	0.0
	Lycium oxycarpum	5.6	2.6	8.9	9.1	6.7
	Portulacaria afra	2.1	3.7	9.5	0.0	0.0
	Putterlickia pyracantha	1.4	12.5	21.0	17.0	0.0
	Rhigozum obovatum	16.5	33.0	24.6	61.9	0.0
	Searsia longispina	2.6	6.9	10.4	17.0	0.0
	Searsia lucida	0.0	0.6	1.6	18.8	2.2
	Searsia pallens	1.4	1.6	2.3	13.6	0.0
	Searsia refracta	0.0	1.6	4.2	0.0	0.0

In a degradation score of 1, these are replaced in dominance by the woody shrubs *G. robusta* and *R. obovatum* at 13% and 17% probability of occurring. The most abundant trees in degradation score 1 were *P. capensis* and *E. undulata* found in 8% and 6% of patches.

Degradation score 2 and 3 showed similar patterns in probabilities, however values in degradation score 3 were higher for all species except for *P. obliquum, V. karroo* and *E. caerulescens.* Degradation score 3 had the highest probability of finding *P. afra* at 10%.

4.5.4. Abundance of noors and spekboom

Spekboom was distributed the most in Kabouga, being found in six of the 30 plots with an average of 0.97±3.02 plants per plot (Table 23). Furthermore, Kabouga has the highest average percentage cover in the quadrats of 1.0±3.8%. Of the total area sampled in the transects, only 0.39% was occupied by spekboom in Baviaanskloof, compared to 1.7% in Addo Main. Addo Main however, only had one plot containing spekboom, equating to an average of only 0.05±0.22 plants sampled. The Baviaanskloof had the most stems per spekboom plant.

Noors was not found in Kabouga and was only found in one plot in Addo Main and two plots in Baviaanskloof. Noors is most prevalent in Darlington, where it was sampled in 23 of the 30 plots (Table 23). The Darlington section was occupied by 13.6% noors compared to a mere 0.2% in Baviaanskloof. The mean number of plants sampled in the plots was 654±674, each with an average of 14.2±14.7 stems. The average cover of noors in the quadrats was 7.6±9.6%.

Table 23: Spekboom and noors statistics as gathered from entire plots, quadrats and transects.

		Plot			Quadrats	Transects		
Spekboom	n plots	x̄ stems per plot	x̄ plants per plot	x̄ stem diameter (cm) per plot	x̄ cover (%)	x̄ area m²/100m²	Sum of area (m²)	% of sampled region
Darlington	1	2.55 ± 13.51	0.14 ± 0.73	0.71 ± 3.74	0.03 ± 0.15	1.51 ± 0.45	22.6	0.75
Addo Main	1	1.65 ± 7.38	0.05 ± 0.22	0.37 ± 1.65	0.00 ± 0.00	1.37 ± 0.45	34.31	1.72
Kabouga	6	4.82 ± 13.23	0.97 ± 3.02	2.34 ± 6.93	1.03 ± 3.75	0.72 ± 0.26	23.81	0.79
Baviaanskloof	2	9.62 ± 51.43	0.38 ± 1.70	1.80 ± 7.03	0.63 ± 3.04	0.81 ± 0.25	11.31	0.39
Landscape	10	4.86 ± 27.53	0.45 ± 1.97	1.44 ± 5.64	0.45 ± 2.52	1.06 ± 0.19	92.03	0.92
Noors				x̄ stem height (cm) per plot				
Darlington	23	14.20 ± 14.70	653.97 ± 674.34	32.27 ± 20.97	7.59 ± 9.58	0.69 ± 0.04	406.5	13.55
Addo Main	1	- -	- -	- -	- -	2.04 ± 0.47	4.08	0.2
Baviaanskloof	2	0.38 ± 1.70	9.62 ± 51.43	1.80 ± 7.03	0.27 ± 1.44	0.32 ± 0.08	4.45	0.15

4.6. Discussion

4.6.1. Temporal changes in vegetation cover and species composition

4.6.1.1. Vegetation cover change

Degradation was most commonly observed post 1960, as also observed by Rutherford *et al.* (2012) in spekboomveld between Jansenville and Kirkwood. Domestic livestock farming and stocking rates drastically increased post 1960, due to a boom in the Mohair trade (Hugo, 1972: in Potgieter, 1972). Angora and Boer goats were suited to farming within the semi-arid Eastern Cape as they had little browse-preference and as a result caused major losses in vegetation cover in a short period (Hugo, 1972: in Potgieter, 1972; Stuart-Hill, 1989). Boer goats have been found, however to feed initially on *V. karroo*, thereafter they browse on *P. afra*, but this observation was not significant and *P. afra* was generally avoided (Haschick & Kerley, 1997). The change in vegetation cover was significant for all sites from 1939 to 2009, signifying that over-browsing and the transformation of thicket has had significant impacts on canopy, canopy edge and matrix cover over time. Using satellite imagery between the years 1973 to 2010, Kakembo *et al.* (2015) also found a significant increase in non-canopy cover in the GAENP, including an area east of the Zuurberg, with specific increases in transformed and degraded thicket, as well as bare ground cover, typically associated with severe degradation (Stuart-Hill, 1989). However, the rate of degradation is more severe in the Addo Main Camp section due to the number of elephants, which are not present in the other sections. Impacts from elephants have been recorded for many decades, but their impact to vegetation structure and composition has been less severe than that by goats (Stuart-Hill, 1992; Moolman & Cowling, 1994). Landman *et al.* (2014) however, suggest that the accumulated browsing by elephants could have landscape scale consequences to degradation in Addo, changing the structure of tree and shrub communities. Furthermore, the impacts by elephants are more severe surrounding water points (Landman *et al.*, 2012) and increased fragmentation of thicket canopy is evident between 1973 and 2010, in areas of elephant expansion (Kakembo *et al.*, 2015).

No correlation was found between aerial estimations of canopy cover and measured woody cover in any of the sites. Li & Wu (2004) highlight that often correlation is misused in the analysis of landscape pattern due to the complexities of landscape scale. Therefore, the transect scale assessment of woody cover cannot be and was incorrectly correlated to the 200 x 200 m grids used in the aerial analysis.

4.6.1.2. *Duration and severity of degradation*

Plots which showed a transformation in vegetation to agriculture in 1939, showed significant differences in composition to those plots which were severely degraded from over-browsing in 1939. Therefore, old lands represent very different trajectories of both degradation and recovery compared to lands which have been severely degraded through livestock farming. Crop agriculture changes the soil profile through tillage and increases the likelihood of nutrient leaching from the soil (Lavelle *et al.*, 2005). Pioneer species and weeds are better adapted to poor soil conditions and are generally the species found on old lands (Cramer *et al.*, 2008). Further research would need to be undertaken to look at the proportion of annuals and perennials in old and degraded lands, where the benefit of early colonising species promotes the facilitation of other species, by improving soil resources (Finegan, 1984).

The separation of species composition in ordination space for plots showing degradation in the aerial imagery in 1978 and 2000, compared to the other years, suggests that prolonged degradation has had greater impacts on species composition in the plots which were degraded in 1939 and 1960. For Kabouga, degraded plots from 1978 and 2000 showed significant differences in species composition, indicating that the duration of degradation was less from 2000 and a threshold was unlikely to have been crossed. The duration and intensity of degradation can affect species composition (Cramer *et al.*, 2008), however, only a few plots showed significant differences and the dynamics of past land use on local study area characteristics are likely much more complex.

4.6.1.3. *Period of rest*

Species composition was strongly linked to site scales. The period of rest showed no significant differences in composition per site. Addo Main is not grouped as clearly as Kabouga and Darlington, however this was not a function of the rest period, but is likely attributed to a combination of rainfall, geology, past land use and an increase of elephants at different times. Stuart-Hill (1989) highlights that recovery of succulent thicket following defoliation depends variably on the intensity and season of browsing and the environmental conditions during the recovery process. Lack of species compositional differences in periods of rest confirm many statements that thicket does not, or is slow to recover following degradation (Stuart-Hill & Danckwerts, 1988; Stuart-Hill, 1992; Kerley *et al.*, 1995). From in-field observations, it is recommended that fine scale analyses of species recruitment need to be undertaken on a large scale, especially in relation to bushclumps and smaller patches.

4.6.2. Degraded patch characteristics and composition

Few significant differences were found in patch attributes between sites. The contribution of proportional changes in patch length was different between all sites, when compared to Addo Main as well as between Darlington and Kabouga. Darlington had significantly more patches, 27% of which were <1 m in length, whereas Kabouga had more patches of 2-3 m and 3-5 m in length. Hester *et al.* (2006) found no difference in the number of patches between browsed and unbrowsed plots in subtropical savanna, with an average of 14 patches per 40 m transect, which is more than the average number of patches found in degraded thicket of this study. The most species found in a patch was 11, however species richness was highest in Kabouga patches, although this was not significant at site level. In subtropical savanna, unbrowsed plots mostly consisted of <5 species (Hester *et al.*, 2006). Of the few patches measured in Addo Main, more than half were <1 m in length, with an average species richness of 1.7±0.3.

Although few differences were found between sites, many differences were found when comparing degradation scores within sites. Significant differences found in patch lengths reflected the same differences to one or both of the number of plants and species per patch. Baviaanskloof did not reflect the same patterns as the other sites. No significant differences were found between degradation score 1 and the other scores. On closer inspection, the degradation scores all had very similar mean patch lengths and number of plants and species per patch. It is possible that for Baviaanskloof, the weighting of various growth forms proved incorrect for degraded lands. For instance, *A. ferox* was weighted highly, but its presence should have been weighted down, since it is an indication of degraded Baviaans Spekboom Thicket (Vlok & Euston-Brown, 2002).

Among the patch attributes, there was a strong positive relationship between species richness and patches among degradation scores and per site. Fabricius (1997) also observed a highly significant relationship between bushclump area and species richness, however above an area of 10 m^2, the rate of species richness increase began to decline. Species belonging to the woody tree growth form occupied the largest area within the transects, especially within Kabouga and Baviaanskloof. Darlington, however, had a high succulent shrub and woody shrub area. From the list of species that predominate within patches, *E. caerulescens* was the most abundant succulent shrub and represented on average 13 m^2 of the transect area and occurred in 49% of patches. Adjacent and transitional vegetation types, such as noorsveld, expand into severely degraded succulent thicket (Hoffman & Cowling, 1991), therefore the abundance of *E. caerulescens* in this site is unsurprising. A concern is that a persistence of this species in Darlington could result in successional inhibition, whereby it prevents the establishment of other species (Finegan, 1984; Teague, 1989).

Kabouga had the highest percentage occurrence of almost all listed tree species, the most abundant being *V. karroo, P. capensis* and *S. afra*. In subtropical savanna, which is transitional with thicket, *V. karroo* is common on bushclump edges and is therefore an important species in facilitating growth of bushclumps (Hester *et al*., 2006). P. *capensis* was 10% more abundant in Baviaanskloof than in Kabouga and occurred in 19.6% of patches. *P. obliquum* was only found in patches of Kabouga (0.6%) and Darlington (0.7%), while *O. europaea* subsp. *africana* was only found in Kabouga (0.7%). *P. obliquum* is a vital species in the regeneration of thicket and has the highest germination of seedlings in xeric thicket in Fish River Reserve (La Cock, 1992).

Of the woody shrubs, *R. obovatum* was more abundant in the arid sites including Baviaanskloof and Darlington, while *G. robusta* was abundant in Kabouga, but not Darlington. *G. robusta* is an important indicator species in the management of goat farming, where 50% leaf defoliation is equivalent to a 30-40% defoliation in *P. afra* (Stuart-Hill, 1989). Furthermore, it is a sensitive species to environmental changes (Stuart-Hill, 1989) and its decreased abundance in Darlington could be as a result of severe degradation (Stuart-Hill, 1992), where noorsveld has expanded, or it's abundance is simply less in spekboomveld. Kabouga was also abundant in *J. capensis*, *P. pyracantha* and *L. ferocissimum*. *L. oxycarpum* is found to increase with goat browsing (Stuart-Hill, 1992), therefore increased abundance of *L. ferocissimum* could be attributed to the same. Furthermore, *J. capensis* is abundant in poorly vegetated, south facing slopes on the edge of bushclumps and is an important species for seed germination of *P. afra* (La Cock, 1992).

4.6.3. Abundance of spekboom and noors

Spekboom was most abundant in Kabouga, where browsing by goats has affected easily accessible areas the most, leaving the mountain areas slightly more vegetated. The multiple farms in Kabouga are assumed to have had different stocking rates in the past, which has likely also created some diversity within the browsing-induced degradation dynamics by domestic livestock and the impacts on vegetation. Noors (*E. caerulescens*) has prevailed through spekboomveld, expanding from the adjacent noorsveld (Hoffman & Cowling, 1991) due to a lack of competition from *P. afra* and increased open spaces for it to establish.

4.7. Conclusion

The prolonged exploitation of subtropical spekboom-dominated thickets through over-browsing by domestic livestock has substantially reduced vegetation canopy cover. The period of rest that the degraded lands have had since last utilised (assuming that the date of degradation cessation is the same as that of the proclamation into SANParks), does not seem to have a great influence on the species composition within the landscape and species are associated according to site. However, the duration of degradation does appear to have some influence on species composition. Transformation of thicket by clearing for agriculture in Addo Main has resulted in a complete loss of canopy cover, with only *L. ferocissimum* and *V. karroo* showing establishment within the old lands. There is a definite difference in the number and size of patches between sites, with certain species being more abundant in patches than others. Regardless of the proportion of patches and number of patches present, all sites and all degradation scores had a significantly positive correlation between patch length and species richness. The patches confirmed findings by other studies and were dominated by the trees *P. capensis* and *E. undulata* (Vlok & Euston-Brown, 2002; Lechmere-Oertel *et al.*, 2005b). *G. robusta* and *R. obovatum* were also abundant woody shrubs across all sites. The invasion of *E. caerulescens* in Darlington is evident by high cover values and abundance as found in both plots and transects, as well as a high percentage of patches containing noors. *P. afra* is particularly low in all sites, but remnants are most common in the Kabouga section, where other woody canopy dominants are more abundant than in other sites.

The study concurs that recovery is not occurring within these degraded lands, however this is only on a landscape and site level scale. To fully quantify this, further research needs to look at the presence of seedling establishment of multiple species across a range of thicket vegetation types. Furthermore, recovery needs to incorporate duration and severity of degradation to make accurate deductions of where restoration priorities need to be focused. Degradation and recovery processes are interlinked and are a secondary factor driving species composition, soil quality and associated feedbacks. Remnant bushclumps and patches are vitally important in the conservation and management of degraded thicket. Complex relationships exist between individual species in recruitment dynamics with patches (La Cock, 1992). Management therefore requires a complex understanding of possible multiple states in both space and time and along a trajectory of degradation that varies between and within sites. Doing so can further aid in restoring ecological integrity and resilience of subtropical thicket.

5 CHAPTER

CONCEPTUALISING SUBTROPICAL THICKET DEGRADATION: A SYNTHESIS OF RESEARCH FINDINGS

CHAPTER 5: CONCEPTUALISING SUBTROPICAL THICKET DEGRADATION: A SYNTHESIS OF RESEARCH FINDINGS

5.1. Adapting semi-arid frameworks and models of degradation to thicket landscapes

Understanding semi-arid to arid landscape dynamics requires determining a baseline of the system centred on its history, characteristics and abiotic and biotic structural and functional processes (Peters & Havstad, 2006). The program behind the work of this thesis aimed to determine a baseline of degraded thicket biodiversity as well as carbon with the intention of quantifying the benefits of restoration through future long-term monitoring. The baseline data allowed for more in-depth landscape and site scale analyses of plant community composition, soil characteristics and degraded woody and succulent patch attributes. An additional analysis of aerial imagery helped to quantify the loss in canopy cover over time. Synthesising the findings of this thesis entails conceptualising the system using Peters & Havstad's (2006) model of semi-arid landscape dynamics (Chapter 1, section 1.2). Understanding the degradation of thicket has been incorporated into a double cusp-catastrophe model adapted from Lockwood & Lockwood (1993) and Turnbull *et al.* (2008) and includes the theory of multiple stable states.

Both abiotic and biotic structure and composition were quantified and assessed for the purpose of this thesis. Four severely degraded spekboom-dominated sites were sampled, one in the Westernkloof section of the Baviaanskloof and three along an altitudinal gradient in the Greater Addo Elephant National Park (GAENP); Darlington, Kabouga and Addo Main. *Biotic* structure and composition was assessed through the measurement of vascular plant species cover within quadrats, which were extrapolated to include species and growth form composition and richness. Furthermore, the incidence and attributes of patches along a transect were calculated and the species composition was recorded. *Abiotic* structure included climate-soil-geomorphic templates within each of the sites. Abiotic composition was indicated by an analysis of soil composition and quality. By quantifying the biotic and abiotic structure and composition of degraded thicket, one can assume the implications and feedbacks these will have on function, since they are inherently linked (Turnbull *et al.*, 2008).

5.1.1. Conceptualising thicket degradation through semi-arid landscape dynamics

5.1.1.1. Historical legacy

Semi-arid to arid subtropical thicket has been degraded through a loss of canopy cover, as a consequence from the farming of Angora and Boer goats, which boomed during the 1960s (Hugo, 1972; in Potgieter, 1972). The expansion of human settlement into the Eastern Cape also increased arable farming, especially of citrus in the Sundays River Valley (Potgieter, 1970), which confined the range for elephants in the area to co-exist with humans. Transformed thickets and degraded thickets from both goats and elephants (in Addo) are abundant across the thicket biome and have changed landscape pattern and process (Stuart-Hill, 1992; Lechmere-Oertel *et al.*, 2005b). A loss of canopy cover is associated with a loss in biotic structure and function, including a loss in above ground biomass, a change in guild diversity and composition, increased weedy or annual species and a reduction or loss in biotic functions such as dispersal, germination and recruitment (Lechmere-Oertel *et al.*, 2005b; Sigwela *et al.*, 2009; Rutherford *et al.*, 2012). Biotic structure, composition and function are strongly related to abiotic structure and function with feedbacks existing between the two. The loss in canopy cover increases the incidence of bare ground, reducing water infiltration and increasing the rate of nutrient leaching through erosion (Gosz & Sharpe, 1989; van Luijk *et al.*, 2013). Remnant woody patches are important for the functioning of the system and aid in retaining isolated nodes of soil fertility, which facilitate the retention of other species.

Temporal evaluations of canopy cover change from aerial imagery, found that on average, canopy cover had already declined prior to 1939 for Darlington and Addo Main, but less so for Kabouga. The significant decline in woody canopy and edge of canopy cover between 1939 and 2009, supports other studies of thicket degradation over time (Rutherford *et al.*, 2012; Kakembo *et al.*, 2015), where the associated increase in bare ground cover is indicative of severe degradation (Stuart-Hill, 1989). The duration and the severity of degradation before proclamation into the GAENP, showed significant differences in species composition within sites. Therefore, browsing dynamics in land-use histories are important in determining degraded thicket resilience, where further research is required into the management of different farms and how this relates to thicket degradation and recovery.

5.1.1.2. Study area characteristics and abiotic correlates

Species composition was strongly related to site, each representing its own climate and geomorphic templates. Geological type was consistent with significant differences in species composition, however, within the landscape, rainfall, gravel, bare ground and altitude were the dominant correlates which differentiated communities. Mountainous sites, such as Kabouga and Baviaanskloof, were foremost correlated to altitude, with Baviaanskloof communities also showing a correlation to aspect. Species composition in Addo Main was related to lithology, such as mudstone, shale and sand. However, while it is easy to deduce that species composition is related to the lithology, it could be a function of preference for certain land-use types. In Darlington, litter mass was an interesting correlate, together with slope angle and stone volume. Percentage gravel and rainfall were negatively correlated in the landscape, where higher rainfall areas, such as Kabouga and Addo Main, often increase the development of nutrient-rich soils (Gosz & Sharpe, 1989).

5.1.2. Double cusp-catastrophe model of GAENP and Baviaanskloof degraded thicket: abiotic and biotic structure and composition

Once degraded, thicket is perceived to not recover and is not resilient (Stuart-Hill & Danckwerts, 1988; Stuart-Hill, 1992; Kerley *et al.*, 1995). However, isolated evidence has been found of regeneration of canopy seeds (La Cock, 1992; Sigwela *et al.*, 2009). Cusp-catastrophe models highlight how a system, through the loss of biotic structure and function, can be pushed to the edge of one state and transition into another state when disturbed, either over the short-term (drought) or long-term (over-utilisation). Cusp-catastrophe models have been used among other things to illustrate the conversion of grassland of low structure and function to shrubland of higher structure and function (Turnbull *et al.*, 2008). In thicket however, degradation causes a shift from a high to a low structure and function.

The adapted cusp-catastrophe model in Figure 27 depicts the degradation of thicket in two distinct cusps to represent the multiple or alternate stable states that can be defined within degraded thicket. The diagram assumes that with high biotic structural connectivity, the system has a high biotic functional connectivity. Furthermore, biotic structure and function is inherently linked to abiotic structure and function and can be used in the same respect. Over time, increased degradation from over-browsing reduces biotic structure and therefore function and pushes thicket into different states of degradation.

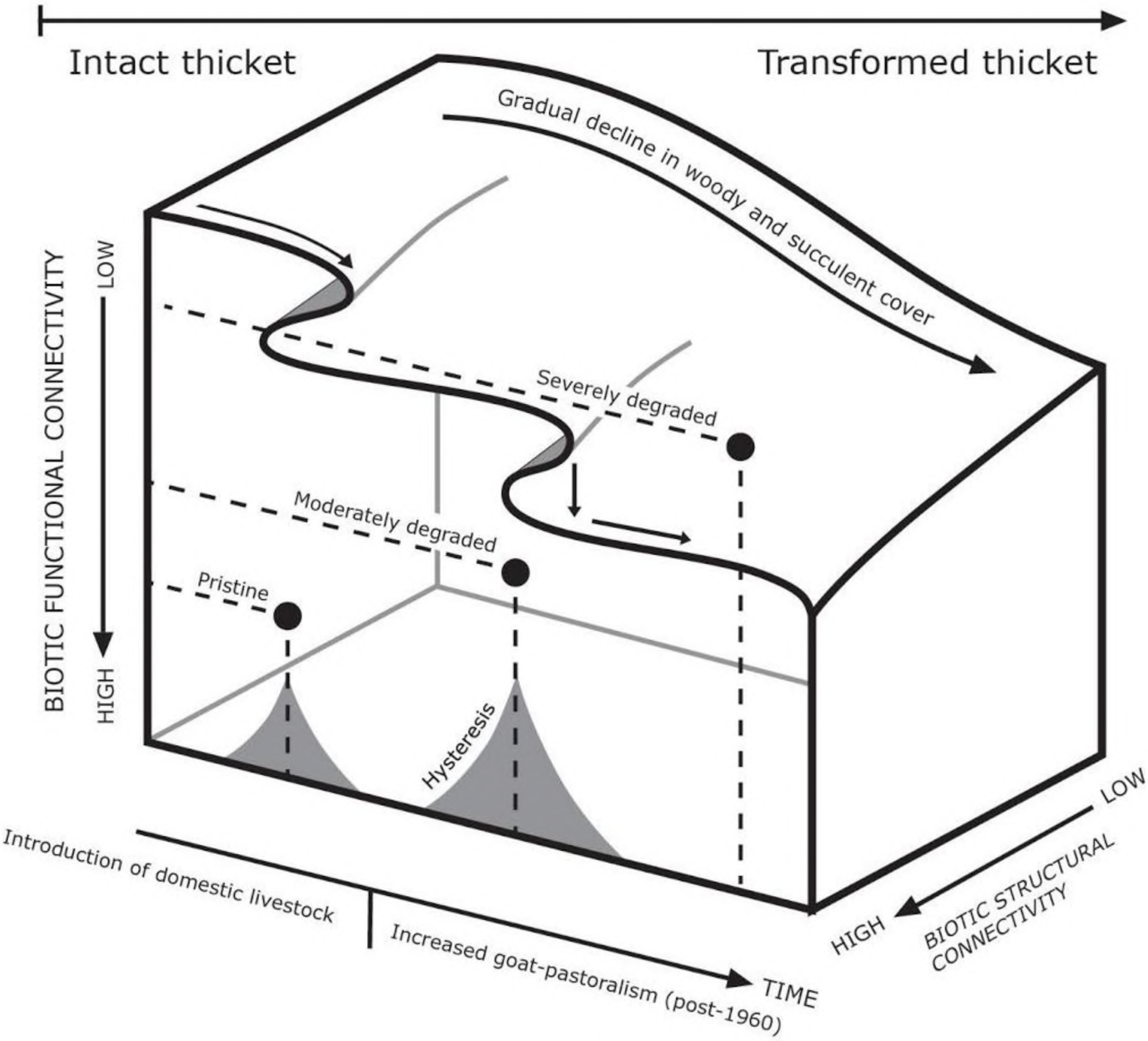


Figure 27: Double cusped-catastrophe model of Subtropical Thicket degradation with estimation of site position (Adapted from Lockwood & Lockwood (1993); Turnbull *et al.* (2008)).

In the GAENP and the Baviaanskloof, the decline of thicket canopy cover from over-browsing, results in a reduced function and the system falls into a moderately degraded state at the first cusp. Severely degraded thicket occurs when structure and function are very low and the system falls over the second cascading cusp. Transformed thicket skips all cusps and exists at the lowest point of structure and function, much like grassland. Such transitions are said to exist at the critical point of vegetation density and facilitation, resource availability, water infiltration and soil texture (Gosz & Sharpe, 1989; Verwijmeren *et al.*, 2013).

5.1.2.1. Moderately degraded thicket

Kabouga

In its entirety, the Kabouga section of the GAENP (AK) is predominantly only moderately degraded, since structure and composition are better established than the other sites. However, as can be seen in Figure 28, stark changes exist in vegetation cover between plots and within a small locality. Image A shows gully erosion and little tree canopy cover, while image B and C show increased plant density on southern facing slopes. Furthermore, image C illustrates how the landscape can change within a small area of only ±60 ha., highlighting the lack of uniformity in degradation through over-browsing. Biotic composition was well developed in comparison to other sites, with heterogeneity evident by the delineation of five significantly different communities. Matrix composition mostly consisted of a few homogenous species such as *Galenia pubescens*, *Pentzia incana* and *Selago geniculata*, however the dominant community consisted uniquely of *Putterlickia pyracantha*, *Jatropha capensis* and the invasive cacti *Opuntia aurantiaca*.

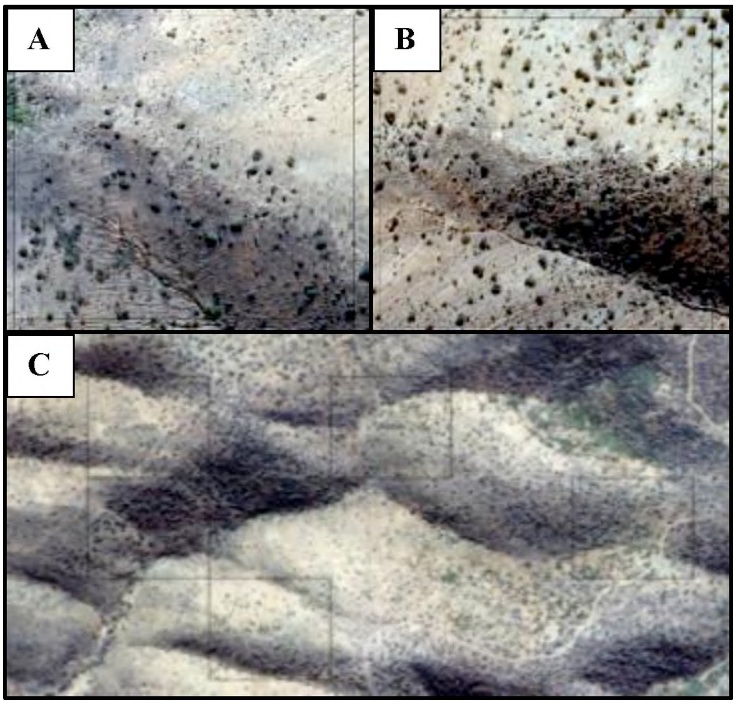


Figure 28: Degraded lands of Kabouga. Image 'A' and 'B' are of an area of 200 x 200 m. Image 'C' shows how much the landscape can change within a small area of approximately 60 ha.

The cover of plant species was much higher, especially of the woody tree and shrub growth form. Biotic structure was also, therefore, well developed, where the probability of a suite of species occurring within a patch was rich. The dominant species occurring within a patch were the woody trees, namely *Vachellia karroo*, *Pappea capensis*, *Schotia afra*, *Euclea undulata* and *Ehretia rigida* and the woody and succulent shrubs *Grewia robusta*, *P. pyracantha*, *Lycium ferocissimum* and *J. capensis*. Patches in Kabouga were frequent within the transects and had a longer average length and highest species richness per patch. Due to the increased cover and area of woody trees and shrubs, the abiotic composition and structure differed significantly to the other sites. Highest percentage of roots occurred in Kabouga, consistent with the highest soil carbon content and bulk density.

5.1.2.2. Severely degraded thicket

Severely degraded thickets fall over the second cascading cusp as a result of major losses to abiotic and biotic structure and composition. Darlington (AD) and Baviaanskloof (BK) exist within different vegetation reference conditions, therefore the state of degradation will be different between the two in terms of biotic structure and composition.

Darlington

Although Darlington had a relatively high biotic structure of patches and richness of species, it has been expanded and homogenised by the indigenous succulent shrub *Euphorbia caerulescens*, from adjacent noorsveld. Such invasion is a major concern and the influence of this species in inhibiting succession, requires further investigation. In terms of biotic composition, only three communities could be found and were rich in species from the Mesembryanthemaceae family. As evident in Figure 29, biotic structure varies within the landscape. Darlington had the highest number of patches per transect but more than a quarter of these were <1 m in length. The probability of *E. caerulescens* occurring in a patch was 49%, with *Rhigozum obovatum* representing the next most dominant species.

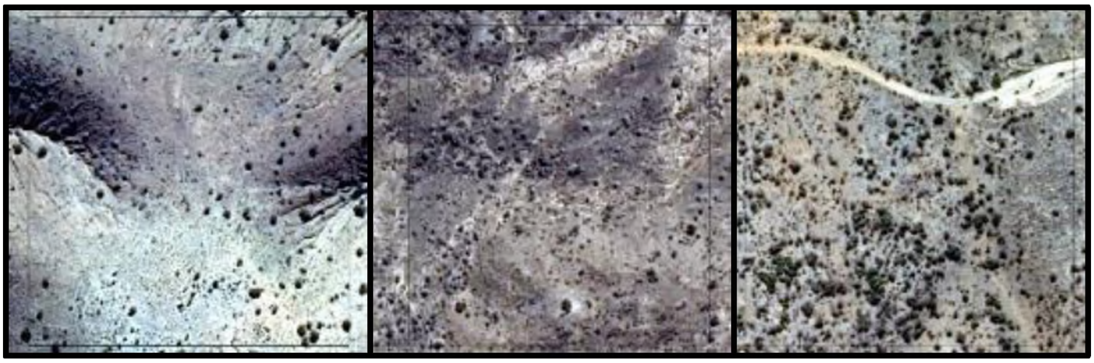


Figure 29: Images of 2009 satellite imagery in Darlington over a 200x200 m area.

It is assumed that the high litter mass of abiotic structure is a function of *E. caerulescens* in this site, as well as the correlate of slope which could transport such resources. Abiotic composition was weak, with high calcium and phosphorus content associated with high stone volume and a low resistance.

Addo Main

Degraded lands of Addo Main (AM-D) are exposed to increased herbivory by indigenous ungulates, as well as mega-herbivores, such as elephants and black rhino (Figure 30 'A'). Increased herbivory would prevent the recovery of thicket in this region or grazing would allow for selective recovery of disturbance adapted or less palatable species.

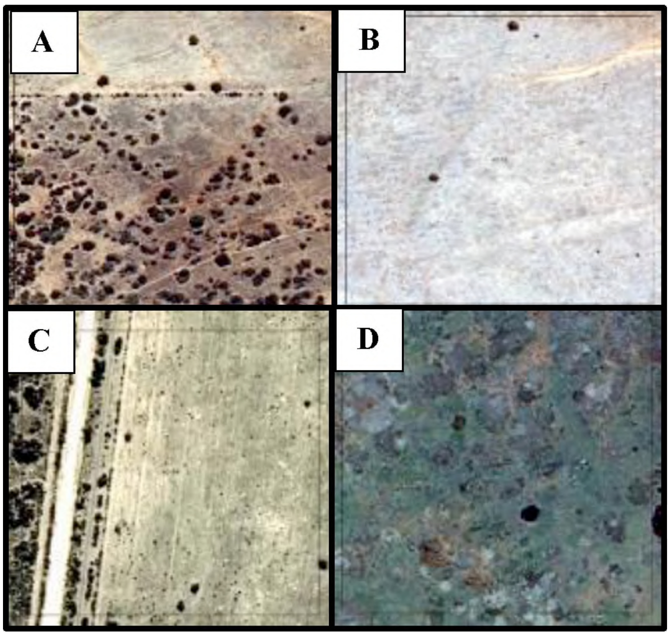


Figure 30: Images from 2009 Satellite imagery over Addo Main in 200 x 200 m grids. Image 'A' is degraded over-browsed plots, note the many footpaths surrounding the bushclumps which are not evident in other sites, 'B' are old lands in the Riverbend section, 'C' are old ploughed lands in the south of Addo Main and 'D' are old lands in the south of Addo Main that have been recovering for some time.

Herbaceous species have the highest richness and cover in this site, which is important in improving water infiltration and preventing erosion (Stuart-Hill, 1989). Despite three communities delineated, abiotic composition consisted of a mostly homogenised matrix of *Cynodon incompletus*, *Drosanthemum hispidum*, *Lepidium africanum*, *G. pubescens* and *Hermannia althaeoides*. However, most plots occurred in old lands (AM-OL- Figure 27), where visual differences in old lands alone are evident in Figure 30: B, C and D. Biotic structure in degraded lands of Addo are more variable than old lands, due to increased growth form composition and richness, as well as a woody tree and shrub layer. Of the few patches found in old lands, these mainly consisted of *V. karroo* and *L. ferocissimum*. Patches in degraded lands of Addo included *Azima tetracantha*, *Gymnosporia polyacantha* and *Searsia longispina*. Only 55 patches were measured in Addo Main, more than half of which were <1 m in length, with the lowest number of species per patch. Abiotic structure and composition consisted of the lowest magnesium and highest potassium concentration, associated with high soil percentage and resistance.

Baviaanskloof

Only one community occurred within Baviaanskloof and it is assumed that the site has undergone severe homogenisation. Dominant biotic composition which differed to the other sites consisted of the species *Lycium oxycarpum*, *Justicia orchioides*, *P. capensis*, *Eragrostis lehmanniana*, *Cenchrus cilliaris* and *Chrysocoma cilliata*. The succulent tree *Aloe ferox* occurred substantially within patches, indicative of a degraded state where lack of competition allows for the recruitment of Aloes from seed. Furthermore, trees indicative of severely degraded thickets in a 'pseudo-savanna' were abundantly in patches. Matrix vegetation was the same throughout the site, indicated by the lack of distinct communities. A lack of regional diversity in biotic composition makes Baviaanskloof degraded thickets less resilient to disturbance. Abiotic composition was characteristic of a high CEC, low soil percentage and low Mg.

5.2. Defining scales of degradation in the landscape: are they consistent?

The study, in addition to quantifying severely degraded abiotic structure and composition, aimed to find scales of degradation, by using growth form as indicators of degradation. While the method of using growth forms and the scoring system was not found to be accurate, it still provides some interesting insights into possible relationships between cover and other characteristics. Four scales were defined, given by scores from 1-4. Additionally, old lands were defined from observation and aerial imagery and used as an additional degradation type.

5.2.1. Degradation scores

In terms of species composition, the plots which were scored as severely degraded (Score 1), were not significantly different to each other across sites, indicating homogenisation of the species within the landscape at this level of degradation. Species composition included *A. lindleyi* subsp. *inflata* as well as pioneer and resilient grass species. Throughout the landscape, most patch attributes were lower for all sites at degradation score 1 and contained a large richness in the probability of species occurring in a patch, most abundant being *A. ferox*. Sodium and CEC was significantly higher in this score and calcium was lower.

Degradation score 2 contained the most plots (n= 52), where *M. aitonis* and *E. obtusa* were unique in dominance within the quadrats. In terms of abiotic composition, no values stand out as being higher or lower than another degradation score and therefore I assume that soil composition is relatively average. Patches were the same and had similar attributes to degradation score 3. Plots did however have a high probability of *R. obovatum* occurring in a patch.

Score 3 had no uniquely dominant species compared to the other sites, however *S. geniculata* does occur in this score, which does not occur in any of the other scores, except in old lands. Abiotic composition and structure included higher roots, litter mass, and carbon, due to increased woody cover, due to the nature of the scoring system. Furthermore, calcium was also highest in this score. Patch attributes were improved at a score of 3, with increased patch length and richness. Multiple tree and shrub species are present in patches of this score, however, again this is due to the nature of the scoring system which favours trees and shrubs as indicative of less degraded.

The high number of trees and the succulent tree *A. ferox* did not aid in accurately representing this score as being more moderately degraded. It is representative of a typical 'pseudo-savanna' of isolated trees in a matrix of grasses and bare ground and is instead, more severely degraded.

5.2.2. Old lands

Old lands occurred in Addo Main (n=15) with the highest similarity in species composition of 32%. Uniquely dominant species include *H. althaeoides*, *Conyza bonariensis* and *Crassula expansa.* Abiotic structure and composition included a high percentage of soil and low CA, Mg, P, pH and soil C. Of the few patches measures, the dominant species included *V. karroo* and *L. ferocissimum.*

The method of degradation scoring was found to not be accurate, especially for the Baviaanskloof. Woody trees and succulent trees were weighted too highly as a measure of intactness and the matrix cover should have been used in more detail. Species-specific relationships to degradation, as well as bare ground cover, should be used in the future to establish gradients of degradation within spekboom-dominated thickets. It is within the matrix where, over time, competition, facilitation and replacement occur in the recovery process. Species identified as increasing with degradation in the literature at local scales should therefore be used as indicators to establish a gradient of degradation.

5.3. Recommendations for the restoration of degraded thicket

Degraded thickets consist of a number of small and isolated thicket patches in a karroid-like grass and shrub matrix. Additionally, the appearance of degraded thicket is that of a 'pseudo-savanna' (Lechmere-Oertel *et al.*, 2005b) and occurs within a two-phase mosaic. Since the formation of subtropical thicket is believed to occur through the joining of a number of patches and bushclumps in a matrix of another vegetation type over time (Vlok & Euston-Brown, 2002), it is recommended that focus for restoration of these degraded lands should be on the remnant patches. Vegetation patches retain soil nutrients and create micro-climates for natural recovery processes. Figure 31 is a photograph of possible spekboom regeneration in a bushclump of the Kabouga section, one of two spekboom clumps seen on this slope. Smaller green patches are visible on the slope too.

Figure 31: Possible evidence of spekboom regeneration in Kabouga.

The planting of woody canopy dominants to restore thicket was not found to be economically feasible in restoration studies near Kirkwood (Van der Vyver *et al.*, 2012). However, the planting of *P. afra* truncheons has been a widely used technique of restoring degraded thicket, with great success in survival following planting as well as improvements in soil carbon content and biodiversity regeneration (Van der Vyver *et al.*, 2013). Simply planting for restoration is not seen as a holistic method for improving ecological integrity. Furthermore, focusing on a single variable of an ecosystem could have dire consequences for other components (Bullock *et al.*, 2011). Additionally, brush piles and dung have been successfully used to improve soil fertility in degraded thicket restoration treatments (Todkill *et al.*, 2006), with rhino dung also rapidly increasing seed germination of *P. capensis* (La Cock, 1992).

Figure 32 is a simplified illustration of a typical degraded thicket with soil restoration treatments and already planted spekboom truncheons. While this thesis highlights that severely degraded lands of the Eastern Cape are heterogeneous, the restoration plan requires modification to different states.

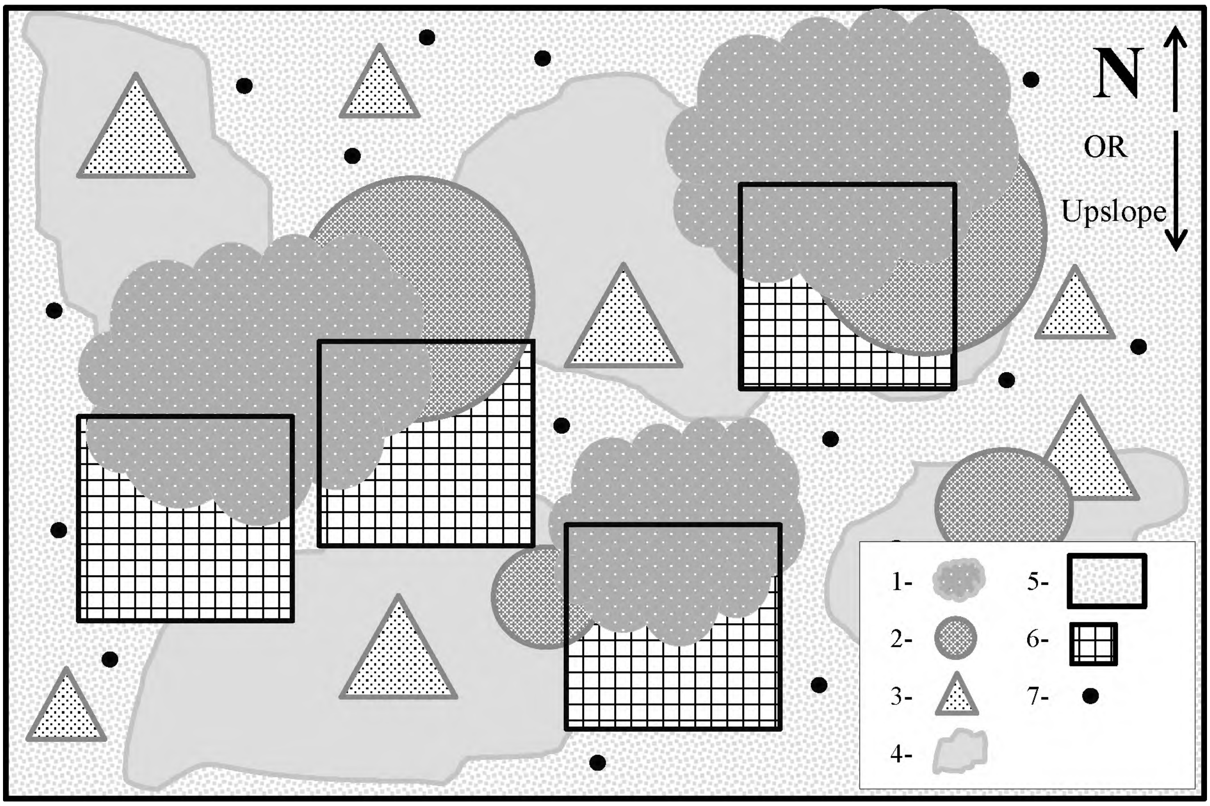


Figure 32: Illustration of a typical degraded thicket area with restoration grids, drawn to no particular scale (Key: 1- large woody tree; 2- large woody shrub; 3- small woody shrubs; 4- bare ground patches; 5- matrix vegetation; 6- soil restoration grid; 7- *P. afra* truncheons).

Degraded thicket consisted of large woody trees such as *P. capensis* and *E. undulata* adjacent to large woody shrubs, such as *Searsia* species and smaller woody shrubs, including *V. karroo, G. robusta* and *R. obovatum*. The matrix vegetation consisted predominantly of *P. incana, G. pubescens, D. hispidum* and *Cynodon* species. For the assisted recovery, it is suggested that larger bushclumps or diverse patches be identified within the landscape.

Yates *et al.* (2005) suggest that in order to restore areas which have crossed a threshold, a method of capturing resources and retention, as well as improving remnant micro-climates, needs to be found. Therefore, once a remnant patch has been found, roughly 5 x 5 m soil restoration quadrats need to be established. If the bushclump is on a slope, then the quadrat should be placed above the patch, since nutrients accumulate above patches where they are better protected from erosion and leaching (Ludwig *et al.*, 1999). If the patch is on a flat to gentle slope, the quadrat should be placed on the southern-side of the patch, where it will receive more shade, improving decomposition rates, organic matter content and therefore infiltration, soil resource retention, as well as increased soil micro-fauna (Adie & Yeaton, 2014).

For each soil restoration quadrat, spekboom litter from intact reference sites (taken in moderation) should be collected, together with dung and *V. karroo* and spekboom branches to make brush piles. The branches placed on top of dung and litter should protect the quadrats from run-off, wind and to a degree, trampling by wildlife. Furthermore, the quadrat should be placed beneath single-stemmed trees such as *P. capensis*, if the below-canopy microsite is bare, since the canopy will soften the rain-drop impact. Furthermore, placing restoration quadrats beneath single stemmed trees will improve the litter mass, since litter was found to be less beneath single stemmed species (It might be difficult to place quadrat beneath *Searsia* species, since it is often dense and impenetrable from browsing. In which case the quadrat can be placed adjacent to the patch on the southern side or upslope).

5.4. Conclusion

Multiple stable states exist across degraded thickets, even within the relatively small spatial extent of the study area. The decline in canopy cover (biotic structure) is conceptualised within a double-cusped catastrophe model in which pristine thickets cascade into a moderately, followed by a severely degraded state of varying composition. Each site represents a suite of unique climate and geomorphic templates, which together with land-use pressures, have influenced species composition and structure as well as soil fertility. Restoration of these thickets needs to account for both abiotic and biotic structure, composition and function, to better achieve restoration targets. However, it should also be recognised that achieving the reference condition through restoration is likely not possible and instead realistic goals should be set which identify and adapt to different degraded states. The study can assist the STRP by providing an indication of restoration priority areas, where soil nutrients are most depleted and carbon content is low, owing to decreased organic matter content from a loss in above ground biomass and canopy cover. Furthermore, by acknowledging local-scale variations in soil quality and vegetation structure, the study can assist SANParks and the GAENP in identifying priority degraded areas for restoration. Acknowledging that multiple stable states exist among degraded lands of varying climate and geomorphic templates, can better assist SANParks in achieving the long-term goal of improving the ecological integrity and hence resilience of the park. However, multiple techniques should be undertaken which not only involve the planting of spekboom truncheons, but also methods of improving and preserving remnant bushclumps as well as soil fertility surrounding bushclumps. It is through a system and holistic approach that degraded thicket can be restored to a more stable state, however the cost of such would need to be further explored.

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Appendix 1: Abiotic variables: abbreviations and unit.

	Abbreviation	Description	Unit
Spatial	Alt	Altitude	masl
	Slope	Slope	degree
	Aspect	Aspect	bearing
	MAP	Mean annual precipitation	mm
	MMP	Mean monthly precipitation	mm
	MWP	Mean winter precipitation	mm
	MSP	Mean summer precipitation	mm
Site record	BG	Bare ground cover	%
	%soil	Percentage of soil	%
	%roots	Percentage of roots	%
	%gravel	Percentage of gravel	%
	Blk den.	Bulk density	g/cm^3
	Lit. mass	Dry litter mass	g/m^2
	C (ARC)	Soil carbon	g/kg
Lithology	Shale	Shale in the lithology	presence/absence
	Arenite	Arenite in the lithology	presence/absence
	Mudstone	Mudstone in the lithology	presence/absence
	Tillite	Tillite in the lithology	presence/absence
	Diamictite	Diamictite in the lithology	presence/absence
	Sand	Sand in the lithology	presence/absence
	Calcrete	Calcrete in the lithology	presence/absence
	Conglomerate	Conglomerate in the lithology	presence/absence
Soil attributes	Sandiness	Type of soil	1. Sand 2. Loam 3. Clay
	pH	pH of the soil	KCl
	Resist.	Resistance in the soil	Ohm
	Stone Vol.	Stone volume of the soil	%
	P Bray II	Phosphorous	mg/kg
	K	Potassium	mg/kg
	Na	Sodium	cmol/kg

	Abbreviation	***Description***	***Unit***
Soil attributes	K	Potassium	cmol/kg
	Ca	Calcium	cmol/kg
	Mg	Magnesium	cmol/kg
	C%	Carbon	%
	Na%	Sodium	%
	K%	Potassium	%
	Ca%	Calcium	%
	Mg%	Magnesium	%
	CEC	Cation exchange capacity	T-value (cmol/kg)

Appendix 2: Plant species abbreviations and occurrence.

List of all the species found within the quadrats, sorted by growth form (n=345). The number of plots a species occurred, within each site, is adjacent to each species abbreviation as used in the ordination graphs. If a species occurred only once amongst all 109 plots, then it is highlighted in bold text (n=131), as these were removed from the statistical analyses of community composition.

	Growth form	*Original name*	*Short name*	*AD*	*AM*	*AK*	*BK*
1	Climber	*Asparagus aethiopicus* L.	*Asp_aet*	1	1	2	2
2	Climber	*Cissampelos capensis* L.f.	*Cis_cap*	1	2		1
3	**Climber**	***Cynanchum capense* Thunb.**	***Cyn_cap***		**1**		
4	**Climber**	***Cyphia heterophylla* C. Presl ex Eckl. & Zeyh.**	***Cyp_het***	**1**			
5	Climber	*Kedrostis Africana* (L.) Cogn.	*Ked_afr*			2	
6	Climber	*Microloma massonii* (Schult.) Schltr.	*Mic_mas*	2			
7	Climber	*Myrsiphyllum asparagoides* (L.) Druce	*Myr_asp*			2	
8	Climber	*Rhoicissus tridentata* (L.f.) Wild & R.B. Drumm.	*Rho_tri*	1	1		1
9	Climber	*Rumex sagittatus* Thunb. (c.f)	*Rum_sag*	3			
10	Climber	*Sarcostemma viminale* (L.) R. Br.	*Sar_vim*	1			2
11	Dwarf shrub	*Adromischus cristatus* (Haw.) Lem.	*Ado_cri*	**1**			
12	**Dwarf shrub**	***Anthospermum spathulatum* Spreng.**	***Ant_spa***				**1**
13	Dwarf shrub	*Asparagus crassicladus* Jessop	*Asp_cra*	1		3	1
14	Dwarf shrub	*Asparagus striatus* (L.f.) Thunb.	*Asp_str*	10	1	9	4
15	Dwarf shrub	*Barleria irritans* Nees	*Bar_irr*	10	2		
16	**Dwarf shrub**	***Barleria obtusa* Nees**	***Bar_obt***				**1**
17	Dwarf shrub	*Blepharis capensis* (L.f.) Pers.	*Ble_cap*	7	1	1	
18	**Dwarf shrub**	***Chascanum cuneifolium* (L.f.) E. Mey.**	***Cha_cun***	**1**			
19	Dwarf shrub	*Chrysocoma ciliata* L.	*Chr_cil*			2	13
20	Dwarf shrub	*Exomis microphylla* (Thunb.) Aellen	*Exo_mic*		1	1	
21	**Dwarf shrub**	***Felicia aethiopica* (Burm.f.) Bolus & wolley-Dod ex Adamson & T.M. Salter (c.f)**	***Fel_aet***			**1**	
22	**Dwarf shrub**	***Felicia dubia* Cass.**	***Fel_dub***		**1**		
23	Dwarf shrub	*Felicia fascicularis* DC.	*Fel_fas*		2		
24	Dwarf shrub	*Felicia filifolia* (Vent,) Burtt Davy	*Fel_fil*	10	3	4	
25	Dwarf shrub	*Felicia hirsuta* DC.	*Fel_hir*	13			
26	Dwarf shrub	*Felicia muricata* (Thunb.) Nees	*Fel_mur*		1	6	5
27	**Dwarf shrub**	***Felicia ovata* (Thunb.) Compton**	***Fel_ova***	**1**			
28	**Dwarf shrub**	***Felicia* sp. 1 Cass.**	***Fel_sp1***			**1**	
29	Dwarf shrub	*Galenia pubescens* (Eckl. & Zeyh.) Druce	*Gal_pub*		15	29	18
30	Dwarf shrub	*Galenia secunda* (L.f.) Sond.	*Gal_sec*	19	1	5	
31	Dwarf shrub	*Garuleum bipinnatum* (Thunb.) Less.	*Gar_bip*	2			
32	Dwarf shrub	*Hebenstretia dura* Choisy	*Heb_dur*		2		
33	**Dwarf shrub**	***Helichrysum hirsuta* Mill.**	***Hel_hir***		**1**		
34	Dwarf shrub	*Helichrysum pentzioides* Less. (c.f)	*Hel_pen*	1			1
35	Dwarf shrub	*Helichrysum rosum* var. *arcuatum* (P.J. Bergius) Less.	*Heli_arc*		2	4	1

				Appendices			
	Growth form	*Original name*	*Short name*	*AD*	*AM*	*AK*	*BK*
37	Dwarf shrub	*Helichrysum rosum* var. *rosum* (P.J. Bergius) Less.	*Hel_ros*	2		3	
38	Dwarf shrub	*Helichrysum zeyheri* Less.	*Hel_zey*	3			
39	Dwarf shrub	*Hermannia althaeoides* Link	*Her_alth*	1	15	5	
40	Dwarf shrub	*Hermannia cuneifolia* Jacq.	*Her_cun*	1	1		
41	Dwarf shrub	*Hermannia desertorum* Eckl. & Zeyh.	*Her_des*	7			
42	Dwarf shrub	*Hermannia filifolia* L.f.	*Her_fil*	1			5
43	**Dwarf shrub**	***Hermannia fruticulosa* K. Schum**	***Her_fru***		**1**		
44	Dwarf shrub	*Hermannia pulverata* Andrews	*Her_pul*			2	9
45	Dwarf shrub	*Hermannia velutina* DC.	*Her_vel*			2	
46	**Dwarf shrub**	***Hermannia vestita* Thunb.**	***Her_ves***	**1**			
47	Dwarf shrub	*Hibiscus aridus* R.A. Dyer	*Hib_ari*	1		2	1
48	Dwarf shrub	*Hypertelis salsoloides* (Burch.) Adamson	*Hyp_sal*				4
49	**Dwarf shrub**	***Hypertelis trachysperma* Adamson**	***Hyp_tra***		**1**		
50	Dwarf shrub	*Indigofera pungens* E. Mey.	*Ind_pun*	4			
51	Dwarf shrub	*Jamesbrittenia aspalathoides* (Benth.) Hilliard	*Jam_asp*	4			
52	Dwarf shrub	*Jamesbrittenia atropurpurea* (Benth.) Hilliard	*Jam_atr*	1			1
53	**Dwarf shrub**	***Jamesbrittennia foliolosa*** (Benth.) Hilliard	***Jam_fol***		**1**		
54	**Dwarf shrub**	***Jamesbrittennia microphylla* (L.f.) Hilliard**	***Jam_mic***		**1**		
55	**Dwarf shrub**	***Jasmimum multipartitum* Hochst.**	***Jas_mul***			**1**	
56	Dwarf shrub	*Justicia orchioides* (L.f.)	*Jus_orc*	4		1	12
57	Dwarf shrub	*Leucas capensis* (Benth.) Engl.	*Leu_cap*	1	6	5	
58	Dwarf shrub	*Limeum aethiopicum* Burm.f.	*Lim_aet*	15		1	12
59	Dwarf shrub	*Lycium cinereum* Thunb	*Lyc_cin*	4	1		
60	**Dwarf shrub**	***Melolobium exudans* Harv.**	***Mel_exu***		**1**		
61	Dwarf shrub	*Monechma incanum* (Nees) C.B. Clarke	*Mon_inc*	1			1
62	**Dwarf shrub**	***Pegolettia baccaridifolia* Less.**	***Peg_bac***				**1**
63	Dwarf shrub	*Pelargonium alchemilloides* (L.) L'Hèr.	*Pel_alc*		8		
64	Dwarf shrub	*Phymaspermum aciculare* (E.Mey. Ex Harv.) Benth. & Hook. Ex B.D. Jacks	*Phy_aci*	2			
65	Dwarf shrub	*Polygala asbestina* Burch.	*Pol_asb*		1	1	
66	Dwarf shrub	*Polygala leptophylla* Burch.	*Pol_lep*	3			1
67	**Dwarf shrub**	***Polygala uncinata* E.Mey. Ex Meisn.**	***Pol_unc***				**1**
68	Dwarf shrub	*Rosenia humilis* (Less.) K.Bremer	*Ros_hum*	7			
69	**Dwarf shrub**	***Selago albida* Choisy**	***Sel_alb***		**1**		
70	Dwarf shrub	*Selago geniculata* L.f.	*Sel_gen*	5	13	21	5
71	Dwarf shrub	*Selago saxatilis* E.Mey.	*Sel_sax*	5			1
72	Dwarf shrub	*Selago* sp. 1 L.	*Sel_sp1*		3		
73	Dwarf shrub	*Thesium hystrix* A.W.Hill	*The_hys*	3			
74	Dwarf shrub	*Thesium lineatum* L.f.	*The_lin*	1			2
75	Dwarf shrub	*Tripteris sinuata* DC.	*Tri_sin*	2			1
76	**Dwarf shrub**	**Unidentified Asparagus sp. 1**	***Asp_unid***			**1**	
77	Dwarf shrub	*Verbena bonariensis* L.	*Ver_bon*		2		
78	**Geophyte**	***Albuca bakeri* Mart.- Azorin & M.B. Crespo (c.f)**	***Alb_bak***	**1**			
79	**Geophyte**	***Albuca* sp. 1 L.**	***Alb_sp1***				**1**
80	**Geophyte**	***Albuca* sp. 2 L.**	***Alb_sp1***		**1**		
81	Geophyte	*Ammocharis coranica* (Ker Gawl.) Herb.	*Amm_cor*		1		1

	Growth form	*Original name*	*Short name*	*AD*	*AM*	*AK*	*BK*
83	**Geophyte**	**_Bulbine frutescens_ (L.) Willd.**	***Bul_fru***		**1**		
84	Geophyte	*Bulbine narcissifolia* Salm-Dyck	*Bul_nar*		1	2	
85	Geophyte	*Cyanella lutea* (L.f)	*Cya_lut*	1	1		
86	**Geophyte**	**_Dipcadi viride_ (L.) Moench**	***Dip_vir***				**1**
87	Geophyte	*Drimia anomala* (Baker) Baker	*Dri_ano*	1	1		1
88	Geophyte	*Drimia elata* Jacq.	*Dri_ela*			1	3
89	Geophyte	*Drimia haworthioides* Baker	*Dri_haw*			2	
90	Geophyte	*Drimia intricata* (baker) J.C. Manning & Goldblatt	*Dri_int*				2
91	**Geophyte**	**_Empodium plicatum_ (Thunb.) Garside**	***Emp_pli***			**1**	
92	**Geophyte**	**_Empodium_ sp. 1 Salisb.**	***Emp_sp1***			**1**	
93	Geophyte	*Eriospermum brevipes* Baker	*Eri_bre*	2			
94	**Geophyte**	**_Eriospermum porphyrium_ Archibald (c.f)**	***Eri_por***			**1**	
95	Geophyte	*Lachenalia campanulata* Baker	*Lac_cam*			3	
96	Geophyte	*Ledebouria ensifolia* (Eckl.) S.Venter & T.J. Edwards	*Led_ens*	3			
97	Geophyte	*Ledebouria ovatifolia* (Baker) Jessop	*Led_ova*	4			
98	**Geophyte**	**_Ledebouria_ sp. 1 Roth**	***Led_sp1***		**1**		
99	**Geophyte**	**_Ledebouria_ sp. 2 Roth**	***Led_sp2***			**1**	
100	**Geophyte**	**_Moraea algoensis_ Goldblatt**	***Mor_alg***		**1**		
101	Geophyte	*Ornithogalum* sp. 1 L.	*Orn_sp1*	2			
102	Geophyte	*Sansevieria hyacinthoides* (L.) Druce	*San_hya*	1	2	1	1
103	**Geophyte**	**_Trachyandra affinis_ Kunth**	***Tra_aff***		**1**		
104	**Geophyte**	**_Trachyandra_ sp. 1 Kunth**	***Tra_sp1***		**1**		
105	**Geophyte**	**Unidentified Albuca sp. 1**	***Alb_unid***			**1**	
106	Graminoid	*Aristida congesta* Roem. & Schult.	*Ari_con*	21	1	4	16
107	Graminoid	*Aristida diffusa* Trin.	*Ari_dif*				5
108	**Graminoid**	**_Bothriochloa insculpta_ (Hochst. Ex A.Rich.) A. Camus**	***Bot_ins***			**1**	
109	**Graminoid**	**_Bromus catharticus_ Vahl**	***Bro_cat***		**1**		
110	Graminoid	*Cenchrus ciliaris* L.	*Cen_cil*	5			6
111	Graminoid	*Chloris virgata* Sw.	*Chl_vir*	1			1
112	**Graminoid**	**_Cymbopogon plurinodis_ (Stapf) Stapf ex Burtt Davy**	***Cym_plu***				**1**
113	Graminoid	*Cynodon dactylon* (L.) Pers.	*Cyn_dac*	5	6	23	
114	Graminoid	*Cynodon incompletus* Nees	*Cyn_inc*		16		24
115	Graminoid	*Digitaria argryograpta* (Nees) Stapf	*Dig_arg*	1			2
116	Graminoid	*Digitaria eriantha* Steud.	*Dig_eri*	5	2	3	2
117	Graminoid	*Ehrharta calycina* Sm.	*Ehr_cal*	5			2
118	Graminoid	*Enneapogon scaber* Lehm.	*Enn_sca*	7			6
119	Graminoid	*Enneapogon scoparius* Stapf	*Enn_sco*	3		2	
120	**Graminoid**	**_Eragrostis capensis_ (Thunb.) Trin.**	***Era_cap***		**1**		
121	Graminoid	*Eragrostis curvula* (schrad.) Nees	*Era_cur*	4	4	3	6
122	Graminoid	*Eragrostis lehmanniana* Nees	*Era_leh*				9
123	Graminoid	*Eragrostis obtusa* Munro ex Ficalho & Hiem	*Era_obt*	12	5	7	11
124	**Graminoid**	**_Eragrostis_ sp. 1 Wolf**	***Era_sp1***		**1**		
125	Graminoid	*Fingerhuthia africana* Lehm.	*Fin_afr*	2			4
126	Graminoid	*Melinis repens* (Willd.) Zizka	*Mel_rep*		1		2

	Growth form	*Original name*	*Short name*	*AD*	*AM*	*AK*	*BK*
128	Graminoid	*Panicum deustum* Thunb.	*Pan_deu*	8	1		
129	Graminoid	*Panicum maximum* Jacq.	*Pan_max*	6	6	17	12
130	**Graminoid**	***Pennisetum clandestinum* Hochst. Ex Chiov**	***Pen_cla***		**1**		
131	**Graminoid**	***Pentameris pallida* (Thunb.) Galley & H.P.Linder**	***Pen_pal***		**1**		
132	**Graminoid**	***Poaceae* sp. 1**	***Poa_sp1***		**1**		
133	**Graminoid**	***Poaceae* sp. 2**	***Poa_sp2***		**1**		
134	Graminoid	*Setaria flabellata* Stapf.	*Set_fla*				2
135	**Graminoid**	***Setaria* sp. 1 P.Beauv**	***Set_sp1***		**1**		
136	**Graminoid**	***Setaria sphacelata* (Schumach.) Stapf & C.E.Hubb. Ex M.B.Moss**	***Set_sph***		**1**		
137	**Graminoid**	***Setaria verticillata* (L.) P.Beauv.**	***Set_ver***	**1**			
138	**Graminoid**	***Sporobolus africanus* (Poir.) Robyns & Tournay**	***Spo_afr***		**1**		
139	Graminoid	*Sporobolus nitens* Stent	*Spo_nit*	6		3	
140	**Graminoid**	***Stenotaphrum secundatum* (Walter) Kuntze**	***Ste_sec***		**1**		
141	**Graminoid**	***Themeda triandra* Forssk.**	***The_tri***	**1**			
142	Graminoid	*Tragus berteronianus* Schult.	*Tra_ber*	4		2	10
143	**Graminoid**	**Unidentified Poaceae**	***Poa_unid1***			**1**	
144	**Graminoid**	**Unidentified Poaceae sp 2**	***Poa_unid2***			**1**	
145	**Graminoid**	**Unidentified Poaceae sp 3**	***Poa_unid3***			**1**	
146	**Herb**	**A2-15 Unknown 1**	***A215Unid1***		**1**		
147	**Herb**	**A2-15 Unknown 2**	***A215Unid2***		**1**		
148	Herb	*Abutilon sonneratianum* (Cav.) Sweet	*Abu_son*	1	2	5	3
149	**Herb**	***Anagallis arvensis* L.**	***Ana_arv***		1		
150	**Herb**	***Arctotheca calendula* (L.) Levyns**	***Arc_cal***		1		
151	**Herb**	***Arctotheca prostrata* (Salisb.) Britten**	***Arc_pro***		**1**		
152	Herb	*Arctotis arctotoides* (L.f.) O.Hoffm.	*Arc_arc*		6	2	
153	**Herb**	***Atriplex lindleyi* Moq.**	***Atr_inf***	**1**			
154	Herb	*Atriplex lindleyi* subsp.*inflata* Moq.	*Atr_lin*	4			4
155	Herb	*Atriplex semibaccata* R.Br.	*Atr_sem*	3	9	11	3
156	Herb	*Cheilanthes parviloba* (Sw.) Sw.	*Che_par*				3
157	Herb	Chenopodiaceae sp. 1	*Che_sp1*			11	
158	**Herb**	***Chenopodium album* L.**	***Che_alb***		**1**		
159	Herb	*Chenopodium mucronatum* Thunb.	*Che_muc*	15	1		12
160	Herb	*Cinerarea platycarpa* DC.	*Cin_pla*		3	2	
161	**Herb**	***Cinerarea saxifraga* DC.**	***Cin_sax***				**1**
162	**Herb**	***Cirsium vulgare* (Savi) Ten.**	***Cir_vul***		**1**		
163	Herb	*Commelina africana* L.	*Com_afr*		4		1
164	**Herb**	***Commelina benghalensis* L.**	***Com_ben***		**1**		
165	**Herb**	***Convolvulus sagitattus* Thunb.**	***Con_sag***		**1**		
166	Herb	*Conyza bonariensis* (L.) Cronquist	*Con_bon*	1	11	1	1
167	**Herb**	***Conyza obscura* DC.**	***Con_obs***		**1**		
168	Herb	*Cuspidia cernua* (L.f.) B.L. Burtt subsp. cernua	*Cus_cer*	16	3		
169	Herb	*Cyclospermum leptophyllum* (Pers.) Sprague ex Britton & P. Wilson	*Cic_lep*		2		
170	Herb	*Cyperus rubicundus* Vahl	*Cyp_rub*	1	2	1	1
171	Herb	*Cyperus usitatus* Burch.	*Cyp_usi*			2	1
172	Herb	*Dolichos falciformis* E. Mey	*Dol_fal*			2	

	Growth form	*Original name*	*Short name*	*AD*	*AM*	*AK*	*BK*
174	**Herb**	**Fabaceae sp. 1**	***Fab_unid***		**1**		
175	Herb	*Galenia africana* L.	*Gal_afr*	1			1
176	**Herb**	***Gazania linearis* (Thunb.) Druce**	***Gaz_lin***		**1**		
177	Herb	*Hermannia coccocarpa* (Eckl. & Zeyh.) Kuntze	*Her_coc*	3			
178	Herb	*Indigofera disticha* Eckl. & Zeyh.	*Ind_dis*	7		1	
179	**Herb**	***Indigofera procumbens* E. Mey.**	***Ind_pro***		**1**		
180	Herb	*Isoglossa origanoides* (Nees) Lindau	*Iso_ori*		1	8	
181	Herb	*Lactuca capensis* Thunb.	*Lac_cap*		4		
182	Herb	*Lasiopogon glomerulatus* (Harv.) Hilliard	*Las_glo*	9			3
183	**Herb**	***Leidesia obtusa* (Thunb.) Müll.Arg.**	***Lei_obt***		**1**		
184	Herb	*Lepidium africanum* (Thunb.)	*Lep_afr*	18	13		15
185	Herb	*Lepidium desertorum* (Eckl. & Zeyh.)	*Lep_des*	2			
186	Herb	*Lepidium ecklonii* Schrad.	*Lep_eck*			7	
187	Herb	*Lessertia pauciflora* Harv.	*Les_pau*	1	1		
188	Herb	*Lotononis laxa* Eckl. & Zeyh	*Lot_lax*	6	3		1
189	Herb	*Lotononis pungens* Eckl. & Zeyh	*Lot_pun*		1	2	
190	**Herb**	***Malva parviflora* L.**	***Mal_par***			**1**	
191	Herb	*Mariscus capensis* (Steud.) Schrad.	*Mar_cap*			2	
192	Herb	*Medicago aschersoniana* Urb.	*Med_asc*		7		
193	**Herb**	***Medicago laciniata* (L.) Mill.**	***Med_lac***	**1**			
194	**Herb**	***Mohria caffrorum* (L.) Desv.**	***Moh_caf***			**1**	
195	Herb	*Nemesia capensis* (Spreng.) Kuntze	*Nem_cap*	11	2		5
196	Herb	*Oenothera rosea* L'Hér. Ex Aiton	*Oen_ros*		2		
197	Herb	*Oligocarpus calendulaceus* (L.f.) Less.	*Oli_cal*	4	2	1	8
198	**Herb**	***Oncosiphon piluliferum* (L.f.) Källersjö**	***Onc_pil***	**1**			
199	**Herb**	***Otholobium* sp. 1 C.H. Stirt**	***Oth_sp1***				**1**
200	Herb	*Oxalis commutata* Sond.	*Oxa_com*	2			2
201	**Herb**	***Oxalis imbricata* Eckl. & Zeyh.**	***Oxa_imb***			**1**	
202	**Herb**	***Oxalis* sp. 1 L.**	***Oxa_sp1***		**1**		
203	Herb	*Oxalis stellata* Eckl. & Zeyh.	*Oxa_stel*	3		2	3
204	Herb	*Oxalis stenorryncha* T.M. Salter	*Oxa_sten*		1	3	
205	**Herb**	***Pellaea calomelanos* (Sw.) Link**	***Pel_cal***				**1**
206	**Herb**	***Pharnaceum salsoloides* Burch.**	***Pha_sal***			**1**	
207	Herb	*Plantago lanceolata* L.	*Pla_lan*		2		
208	Herb	*Pollichia campestris* Aiton (c.f)	*Pol_cam*	5		1	3
209	**Herb**	***Polygonum aviculare* L.**	***Pol_avi***		**1**		
210	Herb	*Portulaca oleracea* L.	*Por_ole*	2			3
211	**Herb**	***Pseudognapholium undulatum* (L.) Hilliard & B.L. Burtt**	***Pse_und***		**1**		
212	Herb	*Scirpus globiceps* C.B. Clarke	*Sci_glo*		2		
213	Herb	*Senecio inaequidens* DC.	*Sen_ina*		2		
214	Herb	*Sonchus oleraceus* L.	*Son_ole*		2		
215	Herb	*Stachys aethiopica* L.	*Sta_aet*	1	1	1	
216	**Herb**	***Stachys grandifolia* E.Mey. Ex Benth.**	***Sta_gra***			**1**	
217	Herb	*Sutera campanulata* (Benth.) Kuntze	*Sut_cam*		7	1	
218	Herb	*Sutera halmifolia* (Benth.) Kuntze	*Sut_hal*			4	

219	Herb	*Sutera polyantha* (Benth.) Kuntze	*Sut_pol*	1	3		2
220	Herb	*Sutera revoluta* (Thunb.)	*Sut_rev*				3
221	**Herb**	***Taraxacum officinale* Weber**	***Tar_off***		**1**		
222	Herb	*Tephrosia glomeratus*	*Tep_glo*		2		
223	Herb	*Teucrium africanum* Thunb.	*Teu_afr*	1	1		
224	**Herb**	***Tribulus terrestris* L.**	***Tri_ter***				**1**
225	Herb	*Trichogyne verticillata* (L.f.) Less.	*Tri_ver*	5	1	2	1
226	Herb	*Troglophyton capillaceum* (Thunb.) Hilliard & B.L. Burtt	*Tro_cap*	3			2
227	**Herb**	**Unidentified Arctotis sp. 1**	***Arc_unid***			**1**	
228	**Herb**	**Unidentified Leguamaceae sp. 1**	***Leg_unid***			**1**	
229	**Herb**	**Unidentified Oxalis sp. 1**	***Oxa_unid***			**1**	
230	**Herb**	**Unidentified Pelargonium sp. 1**	***Pel_unid***			**1**	
231	**Herb**	**Unidentified sp 4**	***Unid_sp4***			**1**	
232	**Herb**	**Unidentified sp. 1**	***Unid_sp1***			**1**	
233	**Herb**	**Unidentified sp. 2**	***Unid_sp2***			**1**	
234	**Herb**	**Unidentified sp. 3**	***Unid_sp3***			**1**	
235	**Herb**	**Unidentified sp. 6**	***Unid_sp6***		**1**		
236	Herb	*Wahlenbergia banksiana* A.DC.	*Wah_ban*		4	1	
237	Shrub	*Pentzia globifera* (Thunb.) Hutch.	*Pen_glo*		3		
238	Shrub	*Pentzia incana* (Thunb.) Kuntze	*Pen_inc*	28	5	19	21
239	**Shrub**	***Pentzia lanata* Hutch. (c.f)**	***Pen_lan***		**1**		
240	Shrub	*Plumbago auriculata* Lam.	*Plu_aur*		2	1	
241	Shrub	*Salsola aphylla* L.f.	*Sal_aph*	2			
242	**Shrub**	***Solanum linnaeanum* Hepper & Jaeger**	***Sol_lin***		**1**		
243	Shrub	*Solanum tomentosum* L.	*Sol_tom*		2		2
244	Succulent herb	*Aizoon rigidum* L.f.	*Aiz_rig*	21			
245	Succulent herb	*Anacampseros arachnoides* (Haw.) Sims	*Ana_ara*	4			1
246	Succulent herb	*Crassula corallina* Thunb.	*Cra_cor*	2			
247	Succulent herb	*Crassula expansa* Dryand.	*Cra_exp*		11	4	2
248	Succulent herb	*Crassula muscosa* L.	*Cra_mus*	6	2	5	7
249	**Succulent herb**	***Euphorbia inaequilatera* Sond.**	***Eup_ina***		**1**		
250	**Succulent herb**	***Galenia papulosa* (Eckl. & Zeyh.) Sond.**	***Gal_pap***			**1**	
251	Succulent herb	*Senecio radicans* (L.) Sch.Bip.	*Sen_rad*	1	2		
252	**Succulent shrub**	***Aloe striata*Haw.**	***Alo_str***			**1**	
253	**Succulent shrub**	***Bergeranthus vespertinus* (A. Berger) Schwantes**	***Ber_ves***			**1**	
254	**Succulent shrub**	***Cotyledon velutina* Hook.f.**	***Cot_vel***				**1**
255	**Succulent shrub**	***Crassula dependens* Bolus**	***Cra_dep***		**1**		
256	Succulent shrub	*Crassula mesembryanthoides* subsp. *mesembrryanthoides* (Haw.) D. Dietr.	*Cra_mes*		1	1	
257	**Succulent shrub**	***Crassula ovata* (Mill.) Druce**	***Cra_ova***				**1**
258	**Succulent shrub**	***Crassula rupestris* Thunb.**	***Cra_rup***				**1**
259	Succulent shrub	*Crassula subaphylla* var. *subaphylla* (Eckl. & Zeyh.) Harv.	*Cra_sub*		6		
260	Succulent shrub	*Crassula tetragona* L.	*Cra_tet*	1	1		
261	**Succulent shrub**	***Delosperma echinatum* (Aiton) Schwantes**	***Del_ech***			**1**	
262	Succulent shrub	*Delosperma frutescens* L. Bolus	*Del_fru*			2	5
263	Succulent shrub	*Delosperma* sp. 1 N.E.Br. Emend. Lavis	*Del_sp1*			5	

	Growth form	*Original name*	*Short name*	*AD*	*AM*	*AK*	*BK*
265	**Succulent shrub**	***Drosanthemum crassum* L. Bolus**	***Dro_cra***				**1**
266	Succulent shrub	*Drosanthemum hispidum* (L.) Schwantes	*Dro_his*	1	14	19	8
267	Succulent shrub	*Drosanthemum lique* (N.E.Br.) Schwantes	*Dro_liq*	7	1		9
268	Succulent shrub	*Duvalia caespitosa* (Masson) Haw.	*Duv_cae*	2			
269	Succulent shrub	*Eberlanzia ferox* (L. Bolus) L. Bolus	*Ebe_fer*	4			1
270	Succulent shrub	*Euphorbia caerulescens* Haw.	*Eup_coe*	2			1
271	Succulent shrub	*Euphorbia catervifolia* N.E.Br.	*Eup_cat*	1			1
272	**Succulent shrub**	***Euphorbia esculenta* Marloth**	***Eup_esc***	**1**			
273	Succulent shrub	*Euphorbia mauritanica* L.	*Eup_mau*	2	1		8
274	**Succulent shrub**	***Euphorbia rhombifolia* Boiss.**	***Eup_rho***		**1**		
275	**Succulent shrub**	***Huernia thuretii* F. Cels**	***Hue_thu***				**1**
276	Succulent shrub	*Jatropha capensis* (L.f.) Sond.	*Jat_cap*	3		11	1
277	Succulent shrub	*Kalanchoe rotundifolia* (Haw.) Haw.	*Kal_rot*			2	
278	**Succulent shrub**	***Lampranthus* sp. 1 N.E.Br.**	***Lam_sp1***	**1**			
279	**Succulent shrub**	***Lampranthus spectabilis* (Haw.) N.E.Br.**	***Lam_spe***	**1**			
280	Succulent shrub	*Malephora crocea* (Jacq.) Schwantes	*Mal_cro*	2			6
281	Succulent shrub	*Malephora* sp. 1 N.E.Br.	*Mal_sp1*	4			
282	Succulent shrub	*Mesembryanthemum aitonis* Jacq.	*Mes_ait*	24	6		4
283	Succulent shrub	*Mesembryanthemum guerichianum* Pax	*Mes_gue*	12			3
284	Succulent shrub	*Mesembryanthemum junceum* Haw.	*Mes_jun*	7			
285	Succulent shrub	*Mestoklema copiosum* N.E.Br. ex Glen	*Mes_cop*		1	2	
286	Succulent shrub	*Mestoklema elatum* N.E.Br. ex Glen	*Mes_ela*	3	3		
287	Succulent shrub	*Mestoklema tuberosum* N.E.Br. ex Glen	*Mes_tub*	5	1		
288	Succulent shrub	*Opuntia aurantica* Lindl.	*Opu_aur*	4		22	
289	Succulent shrub	*Opuntia ficus-indica* (L.) Mill.	*Opu_fic*			1	1
290	Succulent shrub	*Portulacaria afra* Jacq.	*Por_afr*	1	1	5	2
291	Succulent shrub	*Psilocaulon articulatum* (Thunb.) N.E.Br.	*Psi_art*				4
292	Succulent shrub	*Psilocaulon granulicaule* (Haw.) Schwantes	*Psi_gra*		1	1	
293	**Succulent shrub**	***Rhombophyllum rhomboideum* (Salm-Dyck) Schwantes**	***Rho_rho***	**1**			
294	**Succulent shrub**	***Ruschia* sp. 1 Schwantes**	***Rus_sp1***		**1**		
295	**Succulent shrub**	***Salsola kali* L.**	***Sal_kal***	**1**			
296	**Succulent shrub**	***Senecio articulatus* (L.) Sch.Bip.**	***Sen_art***	**1**			
297	**Succulent shrub**	***Stapelia* sp. 1 L.**	***Sta_sp1***				**1**
298	Succulent shrub	*Tetragonia fruticosa* L.	*Tet_fru*	2			1
299	Succulent shrub	*Trichodiadema bulbosum* (Haw.) Schwantes	*Tri_bul*	1	1		
300	Succulent shrub	*Trichodiadema setuliferum* (N.E.Br.) Schwantes	*Tri_set*	9			
301	**Succulent shrub**	**Unidentified Crassulaceae sp. 1**	***Cras_unid***			**1**	
302	Succulent shrub	Unidentified Delosperma sp.1	*Del_unid*			2	
303	**Succulent shrub**	**Unidentified sp. 5**	***Unid_sp5***			**1**	
304	Succulent shrub	*Zygophyllum retrofractum* Thunb.	*Zyg_ret*	2			3
305	Succulent tree	*Aloe ferox* Mill.	*Alo_fer*				9
306	Woody shrub	*Asparagus africanus* Lam.	*Asp_afr*			4	
307	Woody shrub	*Asparagus capensis* L.	*Asp_cap*	2		10	3
308	Woody shrub	*Asparagus retrofractus* L.	*Asp_ret*	2			
309	Woody shrub	*Asparagus suaveolens* Burch.	*Asp_sua*	3	4	4	3

310	Woody shrub	*Asparagus subulatus* Thunb.	*Asp_sub*	2	1	1	
311	**Woody shrub**	***Aspargus mucronatus* Jessop**	***Asp_muc***		**1**		
312	Woody shrub	*Azima tetracantha* Lam.	*Azi_tet*		2	2	
313	Woody shrub	*Capparis sepiaria* var. *citrifolia* (Lam.) Toelken	*Cap_sep*		1	1	
314	Woody shrub	*Carissa haematocarpa* (Eckl.) A.DC	*Car_hae*			2	1
315	Woody shrub	*Diospyros austro-africana* De Winter	*Dio_aus*	5			
316	**Woody shrub**	***Eriocephalus ericoides* (L.f.) Druce**	***Eri_eri***	**1**			
317	Woody shrub	*Grewia robusta* L.	*Gre_rob*	14	1	21	17
318	**Woody shrub**	***Gymnosporia capitata* (E. Mey. ex Sond.) Loes.**	***Gym_cap***			**1**	
319	**Woody shrub**	***Gymnosporia polyacanthus* (Sond.) Szyszyl.**	***Gym_pol***		**1**		
320	Woody shrub	*Gymnosporia szyszylowiczii*	*Gym_szy*	3			
321	Woody shrub	*Hypoestes aristata* (Vahl) Sol. Ex Roem & Schult.	*Hyp_ari*		1	5	
322	Woody shrub	*Lycium ferocissimum* Miers	*Lyc_fer*	6	3	8	
323	Woody shrub	*Lycium horridum* Thunb.	*Lyc_hor*	10		4	2
324	**Woody shrub**	***Nymania capensis* (Thunb.) Lindb.**	***Nym_cap***				**1**
325	**Woody shrub**	***Polygala myrtifolia* L.**	***Pol_myr***				**1**
326	Woody shrub	*Putterlickia pyracantha* (L.) Szyszyl.	*Put_pyr*	2		12	7
327	**Woody shrub**	***Putterlickia* sp. 1 Endl.**	***Put_sp1***		**1**		
328	Woody shrub	*Rhigozum obovatum* Burch.	*Rhi_obo*	2		7	12
329	Woody shrub	*Viscum obscurum* Thunb.	*Vis_obs*	1			1
330	Woody shrub	*Viscum rotundifolium* L.f.	*Vis_rot*	1			1
331	**Woody tree**	***Boscia oleoides* (Burch. Ex DC.) Toelken**	***Bos_ole***				**1**
332	**Woody tree**	***Brachylaena ilicifolia* (Lam.) E.Phillips & Schweick**	***Bra_ill***			**1**	
333	Woody tree	*Ehretia rigida* (Thunb.) Druce	*Ehr_rig*	1		1	
334	**Woody tree**	***Euclea schimperi var daphnoides* (Hiern) De Winter**	***Euc_sch***				**1**
335	Woody tree	*Euclea undulata* (Thunb.)	*Euc_und*	2	1	1	4
336	Woody tree	*Lycium oxycarpum* Dunal	*Lyc_oxy*		1	2	15
337	Woody tree	*Pappea capensis* Eckl. & Zeyh.	*Pap_cap*	1		3	7
338	Woody tree	*Schotia afra* (L.) Thunb.	*Sch_afr*	1		5	
339	Woody tree	*Schotia latifolia* Jacq.	*Sch_lat*				1
340	Woody tree	*Searsia longispina* (Eckl. & Zeyh.) Moffett	*Sea_lon*			4	2
341	Woody tree	*Searsia lucida* (L.) F.A. Barkley	*Sea_luc*				2
342	Woody tree	*Searsia pallens* (Eckl. & Zeyh.) Moffett	*Sea_pal*	2	2		
343	Woody tree	*Searsia refracta* (Eckl. & Zeyh.) Moffett	*Sea_ref*	3			4
344	Woody tree	*Vachellia karroo* Hayne	*Vac_kar*	3	1	9	

Appendix 3: Mean and SE of soil and site attributes per degradation score within each site.

			Site record variables					
Site	*Deg score*	*n*	*BG cover (%)*	*% soil*	*%roots*	*%gravel*	*Bulk density*	*Litter mass*
AD	1	*1	77.5	74.9	0	25.1	1.2	75.4
	2	21	54.9±3.2	59±4.1	0.2±0	40.8±4.1	0.8±0.1	160.5±27.4
	3	8	47.8±5.32	59±7.1	0.2±0.1	40.8±7.2	0.8±0.1	455.5±132.2
AM	1	*1	33.8	100	0	0	1.5	115.2
	2	2	37.5±8.75	98.9±0.3	0.1±0.1	0.9±0.4	1.3±0.1	166.2±47.6
	3	2	11.3±7.5	99.6±0.2	0.3±0.2	0.1±0	1.3±0.1	264.2±148.8
	OL	15	8.9±2.61	99.3±0.3	0.1±0	0.7±0.3	1.4±0	167.8±22.4
AK	1	3	59.6±17	1±0.2	74.3±13.2	0±0	25.7±13.2	177.6±60.7
	2	16	47.4±3.6	1±0.1	75.2±5.3	0.1±0	24.7±5.3	132.4±19.9
	3	11	39.7±3.9	1.1±0.1	80.5±5	0.2±0.1	19.3±5.1	244.4±32.7
BK	1	3	46.3±12.1	0.3±0.2	52.5±6	47.2±6.1	0.7±0.1	126.4±38.6
	2	13	46.3±5.4	0.2±0.1	52±7	47.8±7	0.7±0.1	294.4±64.5
	3	10	41.5±3.7	0.1±0	47.7±5.9	52.1±5.9	0.7±0.1	294.1±80.8
	4	2	75.4±6.6	0.3±0	51.1±2.6	48.6±2.5	0.7±0	374.8±143.5

*number of plots in the degradation score is the only plot, therefore no average or SE. Instead, the absolute value for that plot is shown.

			Exchangeable cations (cmol/kg)			
Site	*Deg score*	*n*	*Na*	*K*	*Ca*	*Mg*
AD	1	*1	8.3	1.0	24.0	7.0
	2	21	0.4±0.1	0.4±0	19.4±7.2	2.5±0.2
	3	8	0.4±0.1	0.6±0.1	50.1±23.9	3±0.3
AM	1	*1	0.1	0.3	1.5	0.5
	2	2	0.7±0.3	1.2±0.3	13±9.2	2.2±0.5
	3	2	0.3±0	0.6±0.2	11.1±0.3	1.8±0.3
	OL	15	0.4±0.1	1±0.1	9.8±1.6	2±0.3
AK	1	3	0.7±0.4	0.9±0.3	13.2±4.9	4.1±1.4
	2	16	0.3±0.1	0.8±0.2	10.9±1.6	2.6±0.3
	3	11	0.4±0.1	0.7±0.1	12.1±1.4	2.8±0.2
BK	1	3	1.2±0.6	1.3±0.4	13.5±2.1	3.3±0.9
	2	13	0.3±0.1	0.6±0.1	13±1.5	2.3±0.2
	3	10	0.3±0.1	0.7±0.1	14.9±1.3	2.4±0.3
	4	2	0.1±0	0.6±0	9.8±1.3	1.4±0

			Exchangeable cations (%)				
Site	*Deg score*	*n*	*Na*	*K*	*Ca*	*Mg*	*C*
AD	1	*1	20.7	2.5	59.5	17.4	0.5
	2	21	2.9±0.4	3±0.2	76.2±1.7	17.5±1.4	0.9±0.1
	3	8	2.2±0.3	3.4±0.4	72.7±3.7	19.9±2.9	1±0.1
AM	1	*1	5.0	11.7	56.6	17.5	0.2
	2	2	5.2±1.4	8.9±3.6	67.3±14.1	16.6±7	0.7±0.4
	3	2	1.8±0.1	4.3±1.3	80.8±2.5	13.1±1	1±0.1
	OL	15	2.8±0.3	8.8±0.7	71.5±1.8	16.1±1.1	0.8±0.1
AK	1	3	2.9±1	5±0.5	70.5±2.9	21.6±3.8	1.3±0.3
	2	16	2.4±0.3	5.1±0.6	72.6±1.9	18.9±1.5	1.2±0.1
	3	11	2.7±0.4	4.2±0.4	73.7±1.9	18.4±1.3	1.4±0.2
BK	1	3	5.2±2.1	6.8±1.5	71.4±4.4	16.6±1.6	1.5±0.3
	2	13	1.8±0.3	4±0.5	76.8±2.4	14.3±1	1.5±0.2
	3	10	1.6±0.5	3.6±0.3	81±1.3	13.1±0.8	1.7±0.2
	4	2	0.9±0	5±0.7	81.9±2.3	12.2±1.6	1.2±0.5

			Other variables						
Site	*Deg score*	*n*	*C (ARC)*	*Stone vol.*	*P (Bray II)*	*K (mg/kg)*	*(CEC)*	*pH*	*Resistance*
AD	1	*1	0.6	4.0	10.0	387.0	40.3	7.7	60.0
	2	21	0.8±0.1	3.9±1.0	38±5.6	172.2±48.3	15.5±1	6.5±0.2	664.8±62.2
	3	8	1.1±0.1	4.6±0.9	30.4±11.3	216.6±114.0	16.4±1.7	6.4±0.2	678.8±73.3
AM	1	*1	0.2	1.0	19.0	124.0	2.7	5.7	3310
	2	2	0.9±0.3	1.5±0.7	8±3	457±147.1	17.2±10	6.7±0.9	795±195
	3	2	1±0.2	1.0±0.0	12±6	235.5±122.3	13.8±0.8	7.5±0.1	1010±290
	OL	15	1.1±0.2	1.2±0.1	22.8±4.2	403.9±4.2	13.3±1.9	5.9±0.6	1184.2±173.9
AK	1	3	13.2±3.5	3.7±2.5	31.3±11.3	354.3±209.8	18.8±6.9	6.9±0.4	766.7±237.1
	2	16	12.7±1.6	3.5±2.0	26.8±8.5	311.3±310.9	14.7±1.9	6.6±0.2	868.8±71.4
	3	11	16.6±1.3	3.8±1.7	23±4.6	265.4±118.8	16.2±1.6	6.6±0.2	667.3±69.1
BK	1	3	1.8±0.3	2.3±0.6	64.3±18.2	519.7±254.2	19.3±3.8	6.9±0.4	440±173.5
	2	13	2±0.4	3.2±1.2	37.3±7.8	247.4±146.3	16.5±1.7	6.4±0.3	930.8±126.2
	3	10	2±0.2	2.6±0.8	34.1±8.4	272.9±146.8	17.2±1.3	6.8±0.2	729.1±53.7
	4	2	1.3±0.5	1.5±0.5	26±9	229.0±6.0	12±1.3	7.2±0.8	1145±215

Appendix 4: Large woody and succulent plant species per site.

	Species name	***AD***	***AM***	***AK***	***BK***
1	*Aloe ferox*				x
2	*Aloe striata*			x	
3	*Azima tetracantha*	x	x	x	x
4	*Boscia oleoides*			x	x
5	*Brachylaena ilicifolia*	x		x	
6	*Cadaba aphylla*	x	x		x
7	*Capparis sepiaria* var. *citrifolia*		x	x	
8	*Carissa haematocarpa*	x	x	x	x
9	*Crassula ovata*	x			x
10	*Diospyros austro-africana*	x			
11	*Diospyros lycioides*	x			
12	*Diospyros scabrida*	x		x	
13	*Dodonaea angustifolia*				x
14	*Ehretia rigida*	x	x	x	
15	*Euclea schimperi* var. *daphnoides*				x
16	*Euclea undulata*	x	x	x	x
17	*Euphorbia caerulescens*	x	x		x
18	*Euphorbia tetragona*	x			
19	*Flueggea verrucosa*			x	
20	*Grewia robusta*	x	x	x	x
21	*Gymnopsopria sp.*		x		
22	*Gymnosporia capitata*	x		x	x
23	*Gymnosporia polyacantha*		x		
24	*Gymnosporia szyszylowiczii*	x			
25	*Jatropha capensis*	x		x	x
26	*Lycium ferocissimum*	x	x	x	x
27	*Lycium oxycarpum*		x	x	x
28	*Nymania capensis*			x	x
29	*Olea europaea* subsp. *africana*			x	
30	*Opuntia aurantiaca*			x	
31	*Opuntia ficus-indica*	x	x	x	x
32	*Ozoroa mucronata*			x	
33	*Pappea capensis*	x	x	x	x
34	*Plumbago auriculata*			x	x
35	*Polygala myrtifolia*				x
36	*Portulacaria afra*	x	x	x	x
37	*Psilocaulon corianum*			x	
38	*Ptaeroxylon obliquum*			x	
39	*Putterlickia pyracantha*	x	x	x	x
40	*Rhigozum obovatum*	x	x	x	x
41	*Rhoicissus tridentata*	x	x	x	
42	*Schotia afra*	x	x	x	

	Species name	***AD***	***AM***	***AK***	***BK***
43	*Schotia latifolia*				x
44	*Searsia chirendensis*		x		
45	*Searsia glauca*			x	
46	*Searsia longispina*	x	x	x	x
47	*Searsia lucida*		x		x
48	*Searsia pallens*	x	x		x
49	*Searsia refracta*	x	x	x	
50	*Vachellia karroo*	x	x	x	x
51	*Viscum obscurum*			x	
52	*Viscum rotundifolia*			x	
53	*Zygophyllum foetidum*	x			x