# Herbaceous species diversity, redundancy and resilience of Mopaneveld across different land-uses

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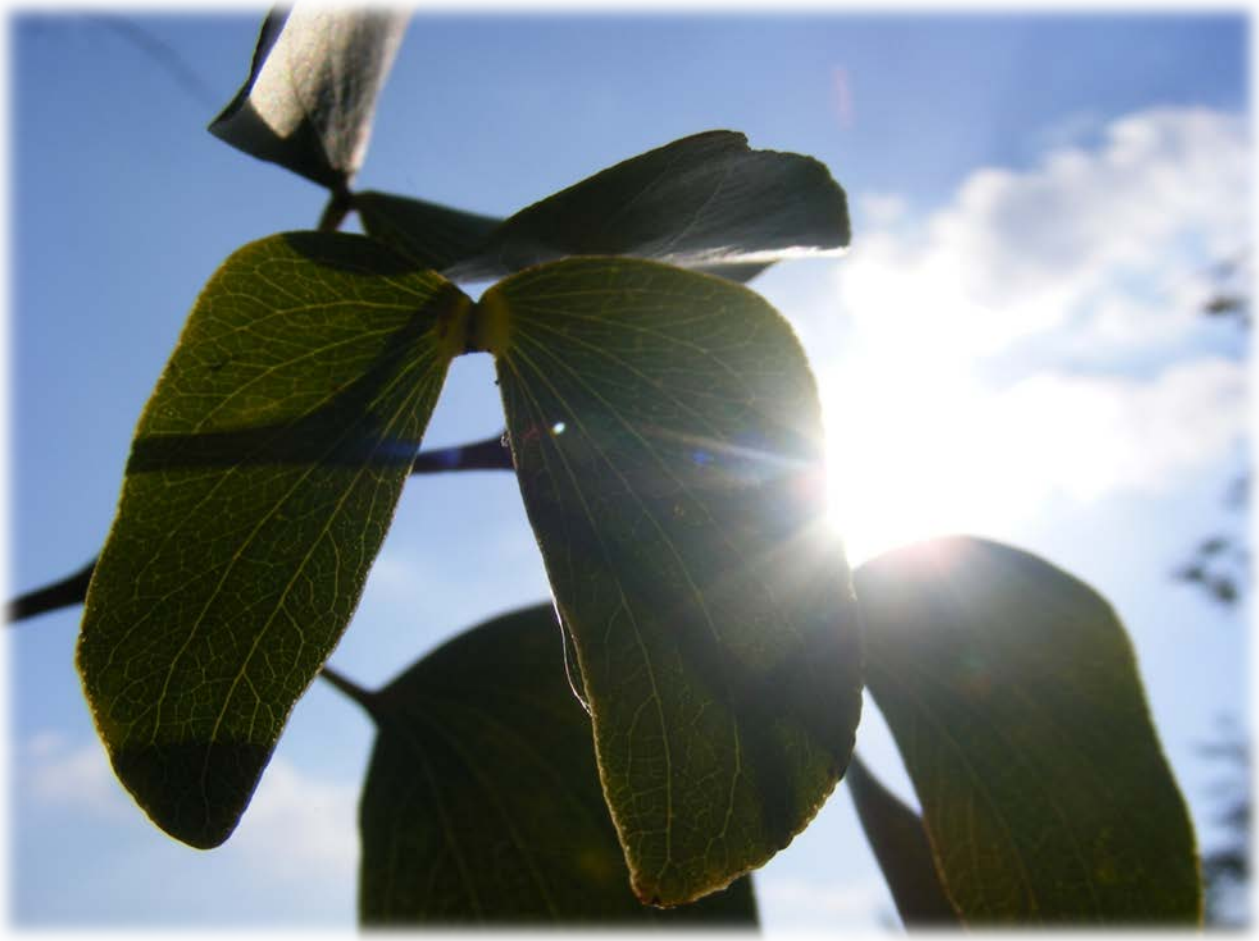

***By space the universe encompasses me and swallows me up like an atom; by thought I comprehend the world.***

**-Blaise Pascal**

**Abstract**

Savanna ecosystems are under increasing arthropogenic pressure. In semi-arid Mopaneveld, few studies have aimed to quantify and evaluate the extent to which anthropogenic disturbances affect plant diversity and function of the herbaceous layer. This study aimed to quantify the effect of various land-use practices on herbaceous plant community structure, which included productivity (biomass) as well as richness, evenness and diversity at species- and functional level. The objectives of this study were to i) determine to what extent land-uses affect species composition of herbaceous plant communities, ii) assess and compare land-use effects on species richness, evenness and diversity, iii) determine if land-uses adversely affects native species diversity, iv) quantify and compare response diversity of transformed and protected Mopaneveld, v) identify and describe plant functional groups of the herbaceous layer in Mopaneveld, vi) compare functional richness, evenness and diversity of traits and groups of each land-use and vii) relate observed species diversity and functional diversity patterns to habitat changes to facilitate comments regarding the level of resilience of anthropogenically disturbed Mopaneveld.

The herbaceous layer of five land-uses was sampled using the fixed quadrat method. Eight plant traits were selected. PRIMER 6 software, Paleontological Statistics (PAST), STATISTICA version 11 and Canoco for Windows version 4.5 were used for data analyses, which included Non-metric Multidimensional Scaling (NMDS) ordinations, One-way Analysis of Similarities (ANOSIM), Similarity Percentage Analysis (SIMPER), non-parametric Analysis of Variance (Kruskal-Wallis ANOVA), One-way Analysis of Variance (ANOVA), Tukey's post-hoc HSD (honestly significant difference) for unequal N, hierarchical cluster analyses, Principal Co-ordinate Analysis (PCoA) and several multivariate analyses.

This study revealed that communal lands, strip mines and mine dumps have a filtering effect on species- and functional assemblages. Six unique plant functional groups, associated with life form, life history and weediness, were identified for anthropogenically disturbed Mopaneveld. Each land-use were characterised by distinctive trait sets and functional groups. Certain species with unique traits in a certain functional group fulfil important ecological roles in land-use plant communities. Species evenness was found to be sensitive to marginal disturbances and total transformation. Trait evenness was found to be sensitive to marginal disturbances. Low levels of species diversity were displayed by strip mined and mine dump plant communities. Dominant plant traits were considered to provide high trait-based redundancy and hence contributed to resilience of land-use plant communities. Response patterns of species diversity corresponds to response patterns of functional diversity for Mopaneveld, communal lands, strip mines as well as for Simpson diversity (on species-, trait- and group level) of koppies and mine dumps. Different response patterns were observed for Shannon-Wiener diversity on species-, trait- and group level of koppies and mine dumps. It is expecited that resilience can be considered high in Mopaneveld if species– and functional diversity is high.

This study can be used as a framework for conservation actions and rehabilitation programmes in anthropogenically disturbed Mopaneveld. Inclusion of species and functional diversity provided valuable

baseline information regarding redundancy and resilience. More studies are required to unravel long-term land-use effects in Mopaneveld to ensure the safeguarding of ecosystem resilience.

**Key words:** communal; forb; herbaceous layer; koppies; land-use; mining; plant functional groups; plant functional traits; response diversity; savanna; semi-arid.

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# Chapter 1

# Introduction

## 1.1. Background

The Savanna Biome is one of the most widely globally distributed terrestrial biomes and covers approximately 50% of the African continent (Huntley & Walker, 1982). In South Africa 33% of the land surface comprises of savanna (Mucina & Rutherford, 2006). Van As *et al.* (2012) emphasized the importance of savannas as it provides grazing for domestic livestock, timber and firewood, resources for informal and subsistence farmers, plays an important function in the carbon cycle and as a source of biological diversity. A savanna can be defined as a tropical or sub-tropical seasonal system, consisting of a continuous herbaceous layer (mostly C4-grass species and forbs) with a discontinuous woody component (trees and shrubs) (Skarpe, 1992; Venter *et al.*, 2003; Van As *et al.*, 2012). Semi-arid savanna ecosystems, such as Mopaneveld, are highly dynamic, heterogeneous landscapes driven by complex relationships and combinations of environmental factors such as climate, fire, soil nutrients and herbivory (Westoby *et al.*, 1980; Walker, 1987; Skarpe, 1992; Siebert *et al.*, 2003; Venter *et al.*, 2003; Jacobs & Naiman, 2008; Furley, 2010; Siebert *et al.*, 2010).

Savanna landscapes are not only exposed to natural disturbance factors but also to anthropogenic land-uses. On a global scale, approximately 13% of savannas are protected (Chape *et al.*, 2005; Newmark, 2008). However, these protected areas are usually surrounded by some form of anthropogenic land-use (Buitenwerf *et al.*, 2011). According to Mucina and Rutherford (2006) there is a substantial loss of savanna outside protected areas, which can be ascribed to land-uses such as cultivation, harvesting of natural sources and invasion by alien species. Certain anthropogenic land-use practices, such as overgrazing and overharvesting in communal lands, are considered as disturbance factors that are responsible for biodiversity loss and degradation of savannas (Rutherford *et al.*, 2012). In Mopaneveld savanna ecosystems, few studies have focused exclusively on the effect of anthropogenic disturbances on plant diversity and function of the herbaceous layer (Shackleton, 1993; Shackleton *et al.*, 1994; Shackleton, 2000; Rutherford & Powrie, 2013).

## 1.2. The herbaceous layer of Mopaneveld savannas

Mopaneveld is a semi-arid, dystrophic (nutrient-poor) savanna type dominated by a broad-leaved deciduous legume tree, *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Leonard (Scholes & Walker, 1993; Scholes *et al.*, 2003; Siebert *et al.*, 2003; Venter *et al.*, 2003; Davis *et al.*, 2013). Despite its homogeneous woody component (Mapaure, 1994; Kennedy & Potgieter, 2003) the herbaceous layer of Mopaneveld savannas are temporaly and spatially variable (Skarpe, 1992; Siebert

*et al.*, 2003; Siebert *et al.*, 2010). In this study, the term 'herbaceous layer' refers to graminoids and forbs, which includes non-graminoid monocotyledonous and dicotyledonous species (Siebert & Scogings, 2015). Few studies have included the forb component (as part of the herbaceous layer) since identification of forb species is often complicated and requires good knowledge of closely related species (Trollope *et al.*, 2014). Furthermore, forbs are generally treated as an unimportant herbaceous component with low grazing value and are usually neglected (Ngwenya, 2012; Hempson *et al.*, 2014; Scott-Shaw & Morris, 2014). In grasslands (Van Oudtshoorn *et al.*, 2011; Scott-Shaw & Morris, 2014) and Mopaneveld savanna (Rutherford *et al.*, 2012) the forb layer is considered as an important herbaceous component since forbs make out the largest proportion of herbaceous species richness and diversity (Trollope *et al.*, 2014; Siebert & Scogings, 2015), and form an important part of the diet of grazers and browsers (Abusuwar & Ahmed, 2010; Koerner *et al.*, 2014; Siebert & Scogings, 2015). Leguminous forb species contribute to soil nitrogen content and are often used in mine rehabilitation practices (Bradshaw, 1997).

### 1.3. Disturbance theories

The herbaceous layer in semi-arid and arid ecosystems is driven by disturbance events, which leads to dynamic responses between species. Some species will tolerate or even thrive when exposed to disturbances whereas others will be negatively affected (Skarpe, 1992; Yachi & Loreau, 1999; Díaz & Cabido, 2001; Elmqvist *et al.*, 2003; Hanke *et al.*, 2014). For species to survive in their environment, certain responses and alterations are induced on plant communities (Díaz & Cabido, 2001), which can be associated with modifications in plant morphology and physiology (Box, 1996; Díaz & Cabido, 2001; Pausas *et al.*, 2003; Moretti & Legg, 2009; Wesuls *et al.*, 2012; Pérez-Harguindeguy *et al.*, 2013). Anthropogenic disturbances are known to alter abiotic and biotic conditions of ecosystems, causing vegetation change over time due to its filtering effect (Shackleton *et al.*, 1994; Bradshaw, 1997; Vitousek *et al.*, 1997; Chapin *et al.*, 2000; Hillebrand *et al.*, 2008). This filtering effect, which infers that species without the ability to adapt to disturbances will be lost, has a direct effect on plant community structure, i.e. productivity, richness, diversity and evenness at both the species and functional level (Chapin *et al.*, 2000; Loreau *et al.*, 2001; Hillebrand *et al.*, 2008; Flynn *et al.*, 2009; Crowder *et al.*, 2010; Ellis *et al.*, 2012; Rutherford & Powrie, 2013). Therefore from a species-based approach, species richness, evenness and diversity may be used as measures of ecosystem stability (McCann, 2000; Purvis & Hector, 2000; Wittebolle *et al.*, 2009) when considering the following four hypotheses/theories. Firstly, the rivet hypothesis suggests that each species fulfils an important ecological role and hence contributes significantly to ecosystem function (Zhang *et al.*, 2012). Changes in species composition (whether there is a gain or loss of certain species) will affect ecosystem function (Clements & Rohr, 2009; Wickson, 2014). Secondly, anthropogenic land-uses, as a major disturbance, are responsible for species diversity loss (Vitousek *et al.*, 1997; Flynn *et al.*,

2009; Bullock *et al.*, 2011; Mouillot *et al.*, 2013). Darwin and Wallace (1858) were the first to propose that more diverse communities are more productive due to the co-existence of species, each with its own set of ecological adaptations which suggests that species loss would negatively affect ecosystem processes. Therefore in accordance with the diversity-stability hypothesis, loss of diversity will result in loss of ecosystem function and hence unstable ecosystems (MacArthur, 1955; Gardner & Ashby, 1970; McNaughton, 1977; Chapin *et al.*, 2000; McCann, 2000; Allan *et al.*, 2011; Hautier *et al.*, 2015). Thirdly, the insurance hypothesis suggests that high diversity provides a buffering effect or insurance against environmental fluctuations (Yachi & Loreau, 1999; Chapin *et al.*, 2000; McCann, 2000; Loreau *et al.*, 2001; Kotschy, 2013). Ecosystems with lower diversity may then be less resilient to disturbances since less diverse communities may be more subjected to degradation and consequently the provision of ecosystem services will deteriorate (Vitousek *et al.*, 1997; Bullock *et al.*, 2011; Mori *et al.*, 2013). Lastly, the model of Grime (1973) may also be applicable. This model suggests that communities with minimum disturbances will display low diversity levels due to competitive exclusion, while exposure to high disturbance levels will also lead to low diversity and will promote the dominance of fast colonizing species (Grime, 1973; Hoopes & Harrison, 1998; Wilkinson, 1999; Shea *et al.*, 2004). Between these extremes lies an optimum, known as the level of intermediate disturbance, where species richness and/or diversity is optimal, following the hump-back relationship (Grime, 1973). This relationship is referred to as the intermediate disturbance hypothesis. This unimodal response of species richness to disturbance levels has been tested in various ecosystems, including a semi-arid savanna ecosystem in South Africa. Van Coller and Siebert (2015) used biomass as a proxy for disturbance and found that herbaceous species richness and diversity levels peaked at intermediate levels of biomass, which confirmed that intermediate disturbance is necessary for optimal plant diversity. Further studies revealed that anthropogenic land-uses, such as communal land that express an intermediate disturbance, have a positive effect on species diversity (Shackleton, 2000; Rutherford *et al.*, 2012).

Considering these four disturbance theories and different land-use practices as disturbance events of varying intensities, studying the effect of different land-uses on plant community structure should therefore improve our understanding of the ability of semi-arid savanna ecosystem to withstand changes (Diaz *et al.*, 1998; Laliberté & Legendre, 2010; Lebrija-Trejos *et al.*, 2010; Lavorel *et al.*, 2011; Carreño-Rocabado *et al.*, 2015; Mandle & Ticktin, 2015).

### 1.4. Modern views of disturbance ecology

Plant species diversity is usually considered a proxy for conservation efforts and management practices (Fraser *et al.*, 2014). However, it fails to quantify disturbance effects with reference to ecosystem functioning (Lacroix & Abbadie, 1998; Mouillot *et al.*, 2013) and stability (Mori *et al.*, 2013) as processes of how community assembly - not species diversity *per se* - is affected by land-use change (Mayfield *et al.*, 2010). Recent studies have indicated that vegetation change related to disturbances are better detected at the level of functional groups than at species level (Laliberté & Legendre, 2010; Mayfield *et al.*, 2010; Mori *et al.*, 2013; Mouillot *et al.*, 2013; Pillar *et al.*, 2013; Fry *et al.*, 2014; Hanke *et al.*, 2014; Lewis *et al.*, 2014; Moreno García *et al.*, 2014). Therefore plant traits can be studied to explore prevailing relationships between species and their environment (Wesuls *et al.*, 2012). Species functional diversity is more sensitive to a fluctuating environment and therefore can be seen as a useful tool to determine ecosystem function (Díaz & Cabido, 2001; Mayfield *et al.*, 2005; McIntyre & Lavorel, 2007; Zhang *et al.*, 2012; Kotschy, 2013; Mori *et al.*, 2013) since functional traits are reliable indicators of adaptation (Díaz & Cabido, 2001; Moretti & Legg, 2009; Pérez-Harguindeguy *et al.*, 2013), the driving force (Díaz & Cabido, 2001; McIntyre & Lavorel, 2007; Mokany *et al.*, 2008; Schumacher & Roscher, 2009; Mouillot *et al.*, 2011; Moretti *et al.*, 2013) and better predictors of ecosystem processes (Díaz *et al.*, 1999; Mouillot *et al.*, 2013; Pérez-Harguindeguy *et al.*, 2013), and are described as the centre of community assembly (Mayfield *et al.*, 2010).

Species may display a high diversity of responses (i.e. traits) across disturbance gradients which contribute similarly to a specific ecosystem function (Elmqvist *et al.*, 2003; Chillo *et al.*, 2011; Mori *et al.*, 2013) and hence, to ecosystem redundancy (Yachi & Loreau, 1999). Redundancy and response diversity foster resilience (Folke *et al.*, 2004; Laliberté & Legendre, 2010; Chillo *et al.*, 2011; Mori *et al.*, 2013) and therefore safeguards ecosystems against deterioration of ecosystem processes which is in accordance with the insurance hypothesis (Naeem, 1998; Yachi & Loreau, 1999; Díaz & Cabido, 2001; Elmqvist *et al.*, 2003; Folke *et al.*, 2004; Zhang *et al.*, 2012; Mori *et al.*, 2013; Baskett *et al.*, 2014). Ecosystem resilience can be defined as the ability and/or capacity of an ecosystem to absorb changes and still be able to return to a former self-organising, optimal functioning state after the occurrence of a disturbance (Holling, 1973; Díaz & Cabido, 2001; Elmqvist et al., 2003; Folke et al., 2004; Kotschy, 2013; Mori et al., 2013). Focusing on the insurance hypothesis, high species richness does not necessarily imply greater resilience (Elmqvist *et al.*, 2003), since high levels of response diversity can be maintained at lower levels of species richness (Laliberté & Legendre, 2010). However, the relationship between species richness, response diversity, redundancy and resilience may be more complex in its responses to land-use change (Petchey & Gaston, 2002; Flynn *et al.*, 2009; Laliberté & Legendre, 2010; Mayfield *et al.*, 2010). The combination of species and functional diversity should provide a better understanding of Mopaneveld ecosystem functionality, which will

ultimately lead to improved management and conservation practices (Díaz & Cabido, 2001; Zhang *et al.*, 2012; Moretti *et al.*, 2013). If the response patterns of species diversity and functional diversity (at the functional group and -trait level) follow similar trends (i.e. species diversity and functional diversity is high), despite the potential loss of species, it can be assumed that redundancy is high (Flynn *et al.*, 2009; Mayfield *et al.*, 2010). The level of redundancy can then be used as an indication of resilience of Mopaneveld, i.e. determine whether plant diversity has the ability to buffer Mopaneveld against the degrading effects of land-uses.

Therefore, to assess the conservation value of a human-managed landscape, the combination of multifaceted framework, including functional traits, species richness and diversity, is required (Villéger *et al.*, 2010; Mandle & Ticktin, 2013; Mandle & Ticktin, 2015). Lavorel *et al.* (1998) described the combination of species diversity and functional diversity as the key to resilience in disturbed environments. If the relationship between species diversity and functional diversity is understood, it may assist decision-making to safeguard ecosystem services (Moretti *et al.*, 2013) and improve conservation management plans (Díaz & Cabido, 2001; McIntyre & Lavorel, 2007; Zhang *et al.*, 2012) in the face of global change

### 1.5. Rationale

Most ecological studies in semi-arid savannas have focused on the effects caused by disturbances such as herbivory, fire, rainfall and other management variables (e.g. tree thinning, communal land tenure or conservation management) on species richness, composition and vegetation structure of the herbaceous layer (Thrash *et al.*, 1993; Shackleton, 2000; McIntyre & Lavorel, 2007; Buitenwerf *et al.*, 2011; Rutherford *et al.*, 2012; Rutherford & Powrie, 2013; O'Connor, 2015). However, Mopaneveld is also transformed by a variety of other land-uses such as mining, agriculture and human settlements (Mucina & Rutherford, 2006; Rutherford *et al.*, 2012; Davis *et al.*, 2013). According the Endangered Wildlife Trust (2011), Mopaneveld does not recover to its former state after intensive land-use practices. This perceived inability to recover might negatively impact ecosystem services provided by Mopaneveld, such as soil nutrient enrichment for crop cultivation, livestock forage, firewood and mopane worms, an important source of protein for local communities (Shackleton, 2000; Musvoto *et al.*, 2007; Rutherford *et al.*, 2012).

Disturbance theories are best studied in ecosystems exposed to disturbances of various magnitudes. At the intermediate disturbance level (e.g. communal land-use), previous studies suggested that some savanna species are tolerant of disturbance, which are expressed through higher species richness (Shackleton, 2000; Rutherford *et al.*, 2012). In Mopaneveld savannas, little is known about the vegetation responses to disturbances of higher magnitude. The main aim of this study is therefore to quantify the effect of disturbances of various magnitudes on herbaceous plant community structure

(i.e. productivity (biomass), richness, diversity and evenness at both the species and the functional level). Anthropogenic land-uses are used as proxies for disturbance, which vary from protected areas managed for biodiversity conservation (low disturbance), to highly disturbed mining areas, which are managed for land remediation.

### 1.6. Objectives

- Determine to what extent land-use affects distribution and abundance (species composition) of herbaceous plant communities;
- Assess and compare the effect of various land-use practices on species richness, evenness and diversity;
- Determine if land-use adversely affects native species diversity;
- Compare the response diversity of transformed (i.e. marginally disturbed communal lands, totally transformed strip mines and totally transformed mine dumps; See Chapter 3 section 3.5) and protected Mopaneveld (i.e. untransformed Mopaneveld and koppies; See Chapter 3 section 3.5.3);
- Describe plant functional groups of the herbaceous layer in Mopaneveld;
- Determine if land-uses in Mopaneveld are characterised by distinctive sets of functional groups;
- Compare functional richness, evenness and diversity of traits and functional groups across land-uses;
- Translate observed species diversity and functional diversity patterns into a measure of resilience of anthropogenically disturbed Mopaneveld.

### 1.7. Hypotheses

(Note that all increases or decreases mentioned in hypotheses are relative to an undisturbed control, namely protected Mopaneveld.)

i. If land-use disturbance entails total transformation (i.e strip mines and mine dumps; See Table 4.1 p.50), then the richness and diversity of the herbaceous layer of Mopaneveld will decrease and evenness will increase as species are lost;

ii. If land-use disturbance entails marginally disturbances (i.e. intermediate disturbance levels; communal lands; See Table 4.1 p.50), which creates open niche spaces and favours rapid colonization by r-strategists, then the richness and diversity of the herbaceous layer of Mopaneveld will increase and evenness will decrease;

iii. If land-use disturbance entails total transformation, then trait richness and trait diversity of the herbaceous layer of Mopaneveld will decrease and the trait evenness will increase;

iv. If land-use disturbance entails marginally disturbances (i.e. intermediate disturbance levels), then trait richness and trait diversity of the herbaceous layer of Mopaneveld will increase and trait evenness will decrease;

v. If land-use disturbance entails total transformation then plant functional group richness, plant functional group diversity and plant functional group evenness will increase;

vi. If land-use disturbance entails marginally disturbances (i.e. intermediate disturbance levels), then the plant functional group richness, plant functional group diversity and plant functional group evenness will increase.

### 1.8. Study layout

This dissertation follows the guidelines as described by the North-West University and it consists of seven chapters. Literature applicable to this study is presented in Chapter 2, followed by the study area (Chapter 3) and the methodology (Chapter 4). The results and discussions are collated in two chapters (i.e. Chapters 5 and 6) and the format followed is in accordance with the preparation of manuscripts for submission to scientific journals. Chapter 7 provides the main conclusions of this study as well as future recommendations regarding conservation and management of the herbaceous layer of anthropogenically altered Mopaneveld. Each chapter contains its own reference list. Contents of each chapter are briefly summarized below:

**Chapter 2**

An overview is presented on relevant literature and important terms are introduced. Impacts of land-uses on species diversity measures, functional traits and response diversity are addressed. Possible relationships between species richness, response diversity, redundancy and resilience are described. The chapter is concluded with a brief summary regarding the necessity of combining species- and functional diversity in studies aimed to determine vegetation shifts caused by disturbances.

**Chapter 3**

Locality, climate, vegetation and soil characteristics of the study area are described. Each land-use class with its associated land-use is characterized and discussed in detail.

**Chapter 4**

The methodology, including field data collection, trait selection and data analysis used during this study are described. To accommodate the format of the results and discussion chapters, methodology that addresses specific research questions will be described in more detail in chapters 5 and 6 and are not repeated here.

**Chapter 5**

This chapter considers the effects of land-uses on herbaceous species assemblages and species diversity. This chapter is prepared as a manuscript for submission to a scientific journal.

**Chapter 6**

This chapter focuses on identifying unique plant functional assemblages of different land-uses. Diversity components are explored at the level of functional traits and functional groups. This chapter is prepared as a manuscript for submission to a scientific journal.

**Chapter 7**

Main conclusions of the dissertation are presented. Recommendations for future land-use management and conservation actions of the herbaceous layer in Mopaneveld are provided.

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# Chapter 2

# Literature review

## 2.1. Land-use as a disturbance

Anthropogenic land-use practices have one primary goal on global and local scales being to utilize natural resources (Foley *et al.*, 2005). Consequently natural terrestrial habitats are transformed to anthropogenic biomes (anthromes) through the replacement of native ecosystems with agricultural lands or settlements (Ellis & Ramankutty, 2008; Ellis *et al.*, 2012). Furthermore environmental conditions are also altered which contribute to land-use changes (Bradshaw, 1997; Lavorel *et al.*, 1997; Chapin *et al.*, 2000; Mackey & Currie, 2001; Pausas *et al.*, 2003; Fraterrigo *et al.*, 2006; Hobbs *et al.*, 2009; Biswas & Mallik, 2010; MacDougall *et al.*, 2013; Lewis *et al.*, 2014; Jauni *et al.*, 2015). Such land-use changes may lead to long-lasting environmental changes, which are best observed in changing vegetation patterns (Fraterrigo *et al.*, 2006). When natural areas are transformed to alternative land-uses for direct human and economic benefits, the natural vegetation is usually displaced, loss of vegetation biomass occurs and open patches are created for potential colonization opportunities for stress-tolerant plant species (Lavorel *et al.*, 1997; Ellis *et al.*, 2012). Therefore, some land-use practices may be considered as successive filters for plant communities (Fortuny *et al.*, 2014). In a world where the pressure on natural resources increases due to a growing human population, it is important to understand the interactions between land-use change, species diversity, functional diversity and ecosystem functioning to facilitate predictions and conservation approaches to safeguard the provisioning of ecosystem services (Foley *et al.*, 2005; Gross *et al.*, 2009; Mayfield *et al.*, 2010; Cadotte *et al.*, 2011; Mori *et al.*, 2013; Carreño-Rocabado *et al.*, 2015; Mandle & Ticktin, 2015).

## 2.2. Land-use and species diversity

Certain anthropogenic land-use practices affect composition, species richness, evenness and diversity in plant communities (Chapin *et al.*, 2000; Mayfield *et al.*, 2005; Fraterrigo *et al.*, 2006; Hillebrand *et al.*, 2008; Crowder *et al.*, 2010). Generally, land-uses (excluding protected areas where natural disturbance factors are considered drivers of vegetation change) are considered responsible for loss in diversity (Foley *et al.*, 2005; Mayfield *et al.*, 2005; Cardinale *et al.*, 2012; Allan *et al.*, 2015) and thus homogenization of plant communities (McKinney & Lockwood, 1999; MacDougall *et al.*, 2013; Amici *et al.*, 2015). Diversity measures can be used to quantify and evaluate changes in diversity patterns associated with changing land-use practices (Kent, 2012) and include species richness (the total number of species sampled in a quadrat, community or geographical unit), evenness (the relative abundance of species sampled) and diversity indices (a combined index of species richness and

evenness) including Shannon-Wiener and Simpson diversity (Purvis & Hector, 2000; Begon *et al.*, 2006; Kent, 2012).

### 2.2.1. Impacts of anthropogenic disturbances on measures of species diversity

Species richness is positively linked to the maintenance of some ecosystem processes (Bullock *et al.*, 2007; Bullock *et al.*, 2011; Balvanera *et al.*, 2014). According Yachi and Loreau (1999) species richness provides insurance to an ecosystem. Therefore plant communities with high species richness may be more resilient to disturbance events. Various responses of species richness to disturbance are found in the literature (Armesto & Pickett, 1985; Hobbs & Huenneke, 1996; Shackleton, 2000; Fulbright, 2004; McKinney, 2008; Flynn *et al.*, 2009; Biswas & Mallik, 2010; Mayfield *et al.*, 2010; Rutherford & Powrie, 2011; Anawar *et al.*, 2013; Rutherford & Powrie, 2013; Schnoor *et al.*, 2015). The most predictable relationship is that species richness peaks at intermediate levels of disturbances (Figure 2.1), following the hump-back, or unimodal relationship (Grime, 1973; Connell, 1978; Wilkinson, 1999; Mackey & Currie, 2001; McKinney, 2008; Svensson *et al.*, 2012; Kershaw & Mallik, 2013; Huston, 2014). Five studies have provided further support for the intermediate disturbance hypothesis (Shackleton, 2000; Fulbright, 2004; Svensson *et al.*, 2007; Biswas & Mallik, 2010; Rutherford *et al.*, 2012). In accordance with the intermediate disturbance hypothesis, studies focusing on the effect of communal grazing or land abandonment found that these plant communities are species rich and therefore considered resilient (Armesto & Pickett, 1985; Shackleton, 1993; Shackleton *et al.*, 1994; Lavorel *et al.*, 1998; Harrison & Shackleton, 1999; Todd & Hoffman, 1999; Shackleton, 2000; Otto *et al.*, 2006; Cramer *et al.*, 2008; Rutherford & Powrie, 2011; Rutherford & Powrie, 2013). Yet anthropogenic disturbances may be responsible for declining species richness of native species which are then replaced by exotic species that contribute positively to species richness (Ellis *et al.*, 2012). In accordance with the hump-back curve (Figure 2.1), McKinney (2008) and Flynn *et al.* (2009) suggested that plant species richness declined with land-use intensification due to competitive exclusion (Grime, 1973), since stress-tolerant r-selected annual species dominated disturbed plant communities (McIntyre *et al.*, 1999; Mackey & Currie, 2001; Van Noordwijk *et al.*, 2004; Mayfield *et al.*, 2005; Begon *et al.*, 2006; Martínez-Ruiz *et al.*, 2007; Mandle & Ticktin, 2013; Olsson & Ödman, 2014). Communities dominated by stress-tolerant species may therefore display low evenness and be more subjected to invasion of alien or exotic species (Chapin *et al.*, 2000; Wilsey & Potvin, 2000; Foster *et al.*, 2002; Smith & Knapp, 2003; Smith *et al.*, 2004; Zavaleta & Hulvey, 2007; Hillebrand *et al.*, 2008), hence lower resilience is expected (Wittebolle *et al.*, 2009; Crowder *et al.*, 2010).


**Figure 2.1. Graphical hump-back relationship as suggested by the intermediate disturbance hypothesis. Figure adapted from Wilkinson (1999).**

Although species richness displays divers responses to disturbance levels, using species richness alone is not sufficient for the detection of the effects of anthropogenic disturbances (Purvis & Hector, 2000; Wilsey *et al.*, 2005; Crowder *et al.*, 2010; Hanke *et al.*, 2014). Compared to one another, results of evenness and species richness indicated different responses to disturbance (Svensson *et al.*, 2012); especially for plant communities the relationship between species richness and evenness is often negatively correlated (Stirling & Wilsey, 2001; Wilsey *et al.*, 2005). Several studies suggested that evenness tends to be more sensitive to disturbance than species richness (Chapin *et al.*, 2000; Hillebrand *et al.*, 2008; Wittebolle *et al.*, 2009; Crowder *et al.*, 2010). Studies conducted by Rutherford *et al.* (2012) and Rutherford and Powrie (2013) revealed that evenness expressed the observed changes better than species richness under heavy grazing practices. Therefore evenness may outweigh the richness component of diversity (Stirling & Wilsey, 2001; Rutherford & Powrie, 2013). For diversity studies, specifically when diversity is being measured as a response variable, both species richness and evenness should be taken into consideration (Hurlbert, 1971; Hanke *et al.*, 2014). Even though species richness and evenness vary independently from one another (Mason *et al.*, 2005), by considering species richness as well as evenness, the full complexity of diversity is emphasised and insight regarding community function is provided (Wilsey & Potvin, 2000; Wilsey *et al.*, 2005). Therefore diversity indices such as Shannon-Wiener (H') and/or Simpson diversity (1- λ') can be used to determine the combined effects of species richness and evenness as a single value (Pielou, 1966; DeBenedictis, 1973; Mackey & Currie, 2001; Stirling & Wilsey, 2001; Kent, 2012). Species diversity is often viewed to regulate resilience of ecosystems under environmental changes (Chapin *et al.*,

2000; McCann, 2000). The diversity stability hypothesis suggests that communities with high diversity will be the most likely to be the most stable when environmental fluctuations occur (MacArthur, 1955; Gardner & Ashby, 1970; McNaughton, 1977; Chapin *et al.*, 2000; McCann, 2000; Allan *et al.*, 2011; Hautier *et al.*, 2015) due to the contribution and buffering effect of each species to ecosystem function (Yachi & Loreau, 1999; Clements & Rohr, 2009; Wickson, 2014).

### 2.3. Land-use as a filter of traits

Environmental filters select species with similar ecological tolerances or strategies (Kotschy, 2013; Pérez-Harguindeguy *et al.*, 2013) with either divergent or similar response traits (Moretti & Legg, 2009) under different environmental conditions (Lebrija-Trejos *et al.*, 2010). Anthropogenic land-uses also act as an environmental filter (Diaz *et al.*, 1998; Mayfield *et al.*, 2005; Mandle & Ticktin, 2013; Batriu *et al.*, 2015) due to alterations in abiotic conditions of plant communities (Shackleton *et al.*, 1994; Bradshaw, 1997; Chapin *et al.*, 2000; Fraterrigo *et al.*, 2006; Gross *et al.*, 2009; Mouillot *et al.*, 2013; Lewis *et al.*, 2014). Not only are certain species filtered out by land-use practices, but the traits of plant species as well (Box, 1996; Lavorel *et al.*, 1997; Díaz & Cabido, 2001; Lavorel & Garnier, 2002; Kotschy, 2013; Mori *et al.*, 2013; Mouillot *et al.*, 2013; Carreño-Rocabado *et al.*, 2015; Mandle & Ticktin, 2015). Consequently certain response traits are favoured which enable plant species to adapt and/or tolerate environmental stress (Keddy, 1992; Pausas *et al.*, 2003; Mayfield *et al.*, 2005; Violle *et al.*, 2007; Lebrija-Trejos *et al.*, 2010). Response traits are thus considered as good indicators of adaptation to indicate the relationship between plants and their environment (Pérez-Harguindeguy *et al.*, 2013).

Diverse responses of plant communities under land-use regimes have been reported in the literature (Lavorel *et al.*, 2011; Carreño-Rocabado *et al.*, 2015). However, all these studies indicated that certain traits are favoured under different land-use intensities. For instance, under light or moderate grazing practices, as well as abandoned farmlands (including rangelands and old fields), plants with tall erect, flat and/or erect rosette growth forms with wind dispersed (characteristic of soil disturbed areas) or exozoochorous dispersal modes were more abundant, since these species have more time to recover between grazing events and can be easily dispersed by wind and passing animals (McIntyre *et al.*, 1995; Lavorel *et al.*, 2011). Furthermore McIntyre *et al.* (1995) pointed out that plant life form, dispersal morphology and reproductive modes were traits which were evenly distributed in lightly grazed communities. In contrast, under intensive grazing, certain traits can be expected to dominate in plant communities. According to Moreno García *et al.* (2014), plant species subjected to frequent and intense grazing must be adapted to defoliation, trampling, as well as increased nutrient input by herbivores. Therefore it can be expected that species with fast growth rates and ability for rapid recovery (Moreno García *et al.*, 2014), and species displaying certain grazing avoidance strategies (Hempson *et al.*, 2014) will dominate.

Numerous studies found that under intensive land-use practices, including soil disturbance (by vehicles or machinery), livestock grazing and agricultural disturbances, annual plants (therophytes) of short stature were favoured (McIntyre *et al.*, 1995; Lavorel *et al.*, 1998; Sternberg *et al.*, 2003; Flynn *et al.*, 2009; Lavorel *et al.*, 2011; Rutherford *et al.*, 2012; Rutherford & Powrie, 2013; Hempson *et al.*, 2014; Moreno García *et al.*, 2014; Carreño-Rocabado *et al.*, 2015; Mandle & Ticktin, 2015) and hence vegetation shifts may be caused (Todd & Hoffman, 1999). This phenomenon is ascribed to the stress-tolerant nature of therophytes (Kelly & Walker, 1976; Olsson & Ödman, 2014). Further, wind-dispersal contributes to the success of these species in disturbed habitats (McIntyre *et al.*, 1995). In grasslands, composition of plant species was altered due to high grazing pressure with grazing-tolerant species dominating in the herbaceous layer (O'Connor, 2005). Mandle and Ticktin (2015) found that plant species subjected to grazing displayed anti-grazing defence mechanisms and internal animal transport was the favoured mode of dispersal. Grazing overall favoured annual over perennial plants, short plants over tall plants, prostrate over erects plants and stoloniferous and rosette over tussock growth forms (Todd & Hoffman, 1999; Shackleton, 2000; Diaz *et al.*, 2007; Rutherford & Powrie, 2011; Rutherford *et al.*, 2012; Hempson *et al.*, 2014; Moreno García *et al.*, 2014). Thus life history, plant height, life form and growth form responds to grazing. Life form was recognised by McIntyre *et al.* (1995) as the most useful trait for the characterization of plant species' responses across a grazing gradient since phanerophytes, chamaephytes and geophytes were stress-sensitive while therophytes were more stress-tolerant.

Mined landscapes are characterised by early successional stages, low native species diversity and harsh abiotic conditions (Lemke *et al.*, 2013). Traits of invasive plant species correspond to required traits of plants, such as fast colonisation abilities, persistence under harsh biotic conditions and adaptation to nutrient poor habitats, selected for restoration goals (e.g. land stabilisation and nitrogen fixing ability) (Lemke *et al.*, 2013). Annual exotic species were found to be dominant on stockpiled soil after the occurrence of mineral sand mining in western Australia (Bellairs & Bell, 1993). On reclaimed coal mines in Spain, Alday *et al.* (2011) found that fast-growing annual species with wind or animal dispersal were the most important traits in early successional stages of primary succession. Annual and/or biennial species were favoured on rehabilitated bauxite mines in Australia (Norman *et al.*, 2006) as well as on tailings facilities of an iron ore mining site in China (Yan *et al.*, 2013). A recent study conducted by Ilunga wa Ilunga *et al.* (2015) in Katanga, D.R. Congo, found that plant species selected to re-vegetate metal-rich bare soil should consist of annual species (therophytes) with a wet season growth phenology. Root systems growing to a depth 0-10 cm were ideal. Seeders with a small dispersule size (<2 mm x 2 mm) and species dispersed by adhesion were also favoured. Drought resistant species with nitrogen fixing abilities and persistence traits (e.g. annual life history, wind

dispersal, animal dispersal) were found to be important for rehabilitating mining landscapes (Holecheck *et al.*, 1982; Ward *et al.*, 1996; Norman *et al.*, 2006; Suding & Hobbs, 2008; Alday *et al.*, 2011; Yan *et al.*, 2013).

### 2.4. The relationship between species richness and functional diversity

Species richness governs ecosystem functioning through trait diversity (Flynn *et al.*, 2009). Therefore a relationship prevails between species richness and functional diversity. Diverse responses of species richness and functional diversity have been observed (Petchey & Gaston, 2002; Gross *et al.*, 2009; Biswas & Mallik, 2010; Laliberté & Legendre, 2010; Mayfield *et al.*, 2010; Carreño-Rocabado *et al.*, 2015). Generally studies indicated that land-use intensification reduced species richness and functional diversity (Naeem, 2002; Srivastava & Vellend, 2005; Garnier *et al.*, 2007; Flynn *et al.*, 2009; Gross *et al.*, 2009; Laliberté & Legendre, 2010; Mayfield *et al.*, 2010; Pakeman *et al.*, 2011; Mouillot *et al.*, 2013; Lewis *et al.*, 2014; Van Meerbeek *et al.*, 2014). Loss of species under land-use intensification may be ascribed to competitive exclusion (Grime, 1973; Gross *et al.*, 2007; Gross *et al.*, 2009). A study conducted by Biswas and Mallik (2010) indicated that functional richness and functional diversity decreased while species richness and species diversity increased in highly disturbed riparian plant communities. This finding was considered as an indication that most species were associated with similar functional groups which contributed to functional evenness (Biswas & Mallik, 2010).

In semi-natural grasslands increased fertilization and land abandonment were responsible for declines in species richness, which affected ecosystem function (Gross *et al.*, 2009). However studies conducted by Carreño-Rocabado *et al.* (2015) and Mandle and Ticktin (2015) observed that high land-use intensification is not responsible for declines in functional diversity and found that there are various responses of functional diversity which may have consequences for provisioning of ecosystem services. Carreño-Rocabado *et al.* (2015) concluded that along a land-use gradient of intensity, community assembly is mainly driven by two factors, namely biophysical filters and management strategies. Under moderate land-use disturbance, Mandle and Ticktin (2015) observed shifts in functional composition while species diversity and functional diversity increased and thus diversity was maintained and promoted by livestock grazing. In accordance with the intermediate disturbance hypothesis, Biswas and Mallik (2010) also found that functional richness and functional diversity peaked at intermediate disturbance levels.

Despite the various responses of species richness and functional diversity, four different hypotheses (Table 2.1) were suggested by Flynn *et al.* (2009) to predict possible relationships, driven by

redundancy, between species richness and functional diversity under land-use intensification. Little change was revealed for diversity measures across the intensity gradient while functional diversity values corresponded well with species richness, which suggested that hypothesis A (Table 2.1) would be applicable to plant communities under land-use intensification (Flynn *et al*. 2009).

**Table 2.1 Four hypotheses suggested by Flynn *et al.* (2009) concerned with the relationship between species richness, functional diversity and redundancy in communities.**

| Hypotheses | |
|---|---|
| **A** | When functional redundancy levels are low, species richness and functional diversity will decline at the same rate. Functional diversity will decline with land-use intensification due to random species loss. |
| **B** | If functional redundancy levels are high, species richness will decline, however functional diversity levels will remain constant. Species loss is random and functional diversity is insensitive to land-use intensification. Ecosystem services are still provided at high levels. |
| **C** | Under land-use intensification, redundant species will be lost first. Functional diversity will decline with declining species richness, but at a slower rate. Species loss is non-random. Consequently a community with high species richness and redundancy in its trait diversity will be replaced by a community with unique species but with low species richness. |
| **D** | Species with unique functional traits are lost first. Functional diversity will decline more severely than species richness. Species loss is non-random since only species with a specific trait set will be able to persist under land-use intensification due to habitat filtering. Land-use intensification significantly affects functional diversity levels even though only a small number of species are filtered out from the system. |

## 2.5. Functional response diversity

A functional response trait is defined as the component of an individual's phenotype, ranging from physiological, morphological or phenological characteristics (Mori *et al.*, 2013; Pérez-Harguindeguy *et al.*, 2013), which responds consistently to the abiotic environment (Violle *et al.*, 2007; Mlambo, 2014) and reveals impacts of disturbances (Lewis *et al.*, 2014). Species contributing to a similar ecosystem function and thus share a particular response trait or trait combination can then be classified into a functional group (Peterson *et al.*, 1998; Kotschy, 2013). Diversity of responses of various species due to environmental change within a functional group is referred to as response diversity (Elmqvist *et al.*, 2003; Mori *et al.*, 2013). The number of species present in each functional group can be seen as a measurement of redundancy and is described as a useful method for measuring

functional resilience (Peterson *et al.*, 1998; Kotschy, 2013; Mori *et al.*, 2013). Response diversity (Elmqvist *et al.*, 2003; Chillo *et al.*, 2011; Baskett *et al.*, 2014) and redundancy (Naeem, 1998; Elmqvist *et al.*, 2003; Nyström, 2006; Laliberté & Legendre, 2010) are two critical components which determine the level of resilience in a plant community.

Resilience and resistance determine ecosystem stability (Díaz & Cabido, 2001) which is promoted by the diversity of functional groups and not by species richness (Peterson *et al.*, 1998). According to Elmqvist *et al.* (2003), functional groups with a high response diversity at a certain point in time, may even be more vulnerable to extinction. Therefore, preserving functional groups will contribute to optimal ecosystem function as response diversity safeguards (buffers) ecosystems against functional degradation (Lavorel *et al.*, 1998; Elmqvist *et al.*, 2003; Laliberté & Legendre, 2010; Mori *et al.*, 2013; Baskett *et al.*, 2014). Effects of land-use change on ecosystem functioning can be determined by measuring response diversity (Lavorel & Garnier, 2002; Elmqvist *et al.*, 2003; Folke *et al.*, 2004; Laliberté & Legendre, 2010; Mori *et al.*, 2013; Mouillot *et al.*, 2013) and resilience can be managed by the interpretation thereof (Kahiluoto *et al.*, 2014). Therefore, there is an existing relationship between response diversity, redundancy and resilience. High redundancy enhance resilience levels (Naeem, 1998; Pillar *et al.*, 2013), but this relationship is only valid if species richness values correlate with response diversity values (Laliberté & Legendre, 2010). Laliberté and Legendre (2010) observed that land-use intensification was responsible for declines in both functional redundancy and response diversity within functional groups and hence ecosystem resilience to future disturbances decreased. Consequently the vulnerability of species increased (Kahiluoto *et al.*, 2014). However, ecosystems dominated by well adapted species (displaying high response diversity due to their traits) to resist or recover quickly after a disturbance, may display a greater level of resilience than heterogenous ecosystems. Thus higher levels of resilience can be reached with less species diversity, but higher response diversity (Baskett *et al.*, 2014; Kahiluoto *et al.*, 2014).

Furthermore, response diversity also depends on the ecological state displayed by the ecosystem (Baskett *et al.*, 2014). An ecosystem exhibits alternative stable states, where a certain state prevails under certain environmental conditions. However, disturbance can cause the ecosystem to reach an unstable threshold in population densities that can cause a shift between states (Ellis & Swift, 1988; Scheffer *et al.*, 2001; Beisner *et al.*, 2003; Scheffer & Carpenter, 2003). If alternative stable states prevail, ecological resilience can be considered as a central component of the disturbance response or can also be described as the probability of an ecosystem maintaining a given state following a disturbance (Holling, 1973). However disturbance history, frequency and intensity are considered as important factors which will determine whether a community will undergo a shift in species and functional assemblages (Díaz *et al.*, 1999).

**Box 1. Glossary of important concepts regarding functional diversity**

**Ecosystem function:** The provision of materials and energy flow by means of interactions between biotic and abiotic components of ecosystems. Ecosystem processes (i.e. primary production, trophic interactions, nutrient cycling, biogeochemical cycles, water cycling etc.) are included which are responsible for the maintenance and provision of natural resources (ecosystem goods and services) utilized by humans. (Díaz & Cabido, 2001; Srivastava & Vellend, 2005; Fisher *et al.*, 2009; Mace *et al.*, 2012; Mori *et al.*, 2013).

**Ecosystem resilience:** The ability and/or capacity of an ecosystem to absorb changes and still be able to return to a former self-organising, optimal functioning state after the occurrence of a disturbance (Holling, 1973; Díaz & Cabido, 2001; Elmqvist *et al.*, 2003; Folke *et al.*, 2004; Kotschy, 2013; Mori *et al.*, 2013).

**Ecosystem resistance:** The ability of an ecosystem to persist in the same ecological state when exposed to disturbances (Díaz & Cabido, 2001).

**Ecosystem stability:** The ability and/or capacity of an ecosystem to persist in a steady ecological state after a disturbance. It encompasses two components i.e. resistance (persisting in the same state during a disturbance) and resilience (Holling, 1973; Díaz & Cabido, 2001; Ives & Carpenter, 2007).

**Functional compensation:** If species loss due to disturbance occurs, the remaining functionally similar species are able to compensate for lost species and thus maintain a particular ecosystem process (Díaz & Cabido, 2001; Kotschy, 2013; Mori *et al.*, 2013).

**Functional diversity:** A component of biodiversity which reflects ecosystem function. It is defined as the value (presence and relative abundance of unique values or various trait characteristics) and range (differences between trait values) of species and traits which significantly influence ecosystem functioning (Díaz & Cabido, 2001; Tilman, 2001; Zhang *et al.*, 2012). Thus functional traits can be considered as a component of a plant's phenotype which influences ecosystem processes (Petchey & Gaston, 2006). Functional diversity can be measured on the level of functional traits (Zhang *et al.*, 2012) or functional groups (Hanke *et al.*, 2014). Functional richness and functional evenness are components of functional diversity (Mason *et al.*, 2005; Mouchet *et al.*, 2010; Mouillot *et al.*, 2013).

**Functional evenness:** The regularity of distribution of functional trait or functional group abundances which fill a niche space for a certain plant community (Mason *et al.*, 2005; Villéger *et al.*, 2008; Mouchet *et al.*, 2010; Pakeman *et al.*, 2011; Mouillot *et al.*, 2013).

**Functional richness:** The amount of niche space occupied by functional traits or groups which is independent of abundance (Mason *et al.*, 2005; Villéger *et al.*, 2008; Mouillot *et al.*, 2013). Can also be defined as the difference between one or more functionally relevant traits or groups and can be measured as the number of functional types/groups (Díaz & Cabido, 2001).

**Plant functional group:** Groups of species displaying similar trait-collections or trait-combinations due to a certain disturbance or environmental factor. Effect traits and response traits are classified into effect groups/types or response groups/types respectively (Lavorel *et al.*, 1997; Lavorel *et al.*, 1998;

Díaz & Cabido, 2001; Lavorel & Garnier, 2002; Kooyman & Rossetto, 2008; Morais & Cianciaruso, 2014).

**Plant functional trait:** Physiological, morphological and phenological characteristics of plants, representing ecological strategies, in response to environmental conditions, which influence the fitness or performance of the plant and effects ecosystem properties (Pérez-Harguindeguy *et al.*, 2013). Two types of functional traits can be distinguished: 1) traits determining the species' effect on ecosystem processes are referred to as functional effect traits and 2) traits responding to its biotic and abiotic environment (i.e. disturbance regime, resource availability and climate) are identified as functional response traits (Díaz & Cabido, 2001; Mori *et al.*, 2013).

**Redundancy:** The number of different species which contribute similarly to a specific ecosystem function. If some species are lost from a community, then these functionally similar species can compensate and thus provide 'back-up' to the plant community (Walker, 1992; Chapin *et al.*, 1997; Nyström, 2006; Laliberte *et al.*, 2010; Mayfield *et al.*, 2010; Mori *et al.*, 2013).

**Response diversity:** Refers to the variety or diversity of different species' responses to environmental change, which each contribute to a specific ecosystem function within a functional response group (Chapin *et al.*, 1997; Elmqvist *et al.*, 2003; Laliberté & Legendre, 2010; Baskett *et al.*, 2014; Kahiluoto *et al.*, 2014).

### 2.6. Linking species diversity and functional response diversity

From a conservation perspective, since species richness, evenness and diversity respond differently to habitat fragmentation or habitat loss (Wilsey *et al.*, 2005), the more diversity measures included, the better the information available with respect to ecological processes, resilience and ecosystem stability for ecosystems under continuous pressure (McNaughton, 1977; Díaz & Cabido, 2001; Stirling & Wilsey, 2001; Wilsey *et al.*, 2005; Hillebrand *et al.*, 2008). Various studies have successfully incorporated taxonomic diversity and functional diversity measures (Lavorel *et al.*, 1998; Mayfield *et al.*, 2005; Biswas & Mallik, 2010; Mayfield *et al.*, 2010; Villéger *et al.*, 2010; Pakeman *et al.*, 2011; Hanke *et al.*, 2014).

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# Chapter 3

# Study area

## 3.1. Locality description

The study was conducted near the town of Phalaborwa (23°56'45.47"S 31°08'46.23"E) in the Limpopo Province of South Africa (Figure 3.1). The study area consisted of four sites: i) Pompeye (strip mine and protected Mopaneveld) and the informal settlement, ii) Lulekani (communal land), occur north of Phalaborwa, iii) Palabora Copper (PC; mining area), previously Palabora Mining Company (PMC) and iv) Cleveland Nature Reserve (CNR; protected koppies and Mopaneveld) are situated south west of Phalaborwa (Figure 3.1).

The dominant vegetation type of the region, the Phalaborwa-Timbavati Mopaneveld (Mucina & Rutherford, 2006), is characterised by an undulating open tree savanna landscape (Figure 3.2) with a distinctive, dynamic and event-driven herbaceous layer (Westoby *et al.*, 1980; Skarpe, 1992; Du Plessis, 2001; Siebert *et al.*, 2003; Siebert *et al.*, 2010). Quarts-feldspar rocks of the Makhutswi Gneiss are the main constituent of the geology except in the northwest regions where Lekkersmaak Granite intrudes. The dominant land type in the Phalaborwa region is the Fb-land type (Mucina & Rutherford, 2006). The Fb land type refers to Glenrosa and/or Mispah soil forms where lime is present in low-lying soils but rare or absent in the upland soils. Shallow soils are characterized by topsoil underlain by weathered rock (Glenrosa) or hard rock (Mispah) giving rise to lithocutanic horizons, which is associated with lithic soils (AGIS, 2007; Bezuidenhout, 2009; Fey, 2010). Furthermore, clayey soils characterise bottomlands while sandy soils can be expected on uplands (Venter *et al.*, 2003).

The Selati River, a tributary of the Olifants River, (Seymore, 1994) flows through the Phalaborwa region It passes PC and runs through CNR where it flows into the Olifants River. The western boundary of the Kruger National Park (KNP) is situated approximately 6 km from the Selati-Olifants confluence (Seymore, 1994) to the east of PC.

The study area is exposed to various land-uses, varying from subsistence and commercial farming, mining practices and land managed for conservation (nature reserves and KNP). The Phalaborwa-Timbavati Mopaneveld is classified as ‘Least Threatened’ and is well conserved in KNP and other nature reserves (Mucina & Rutherford, 2006). Human settlements and mining practices are mainly responsible for the 5% transformation of natural vegetation in the Phalaborwa region (Mucina & Rutherford, 2006).

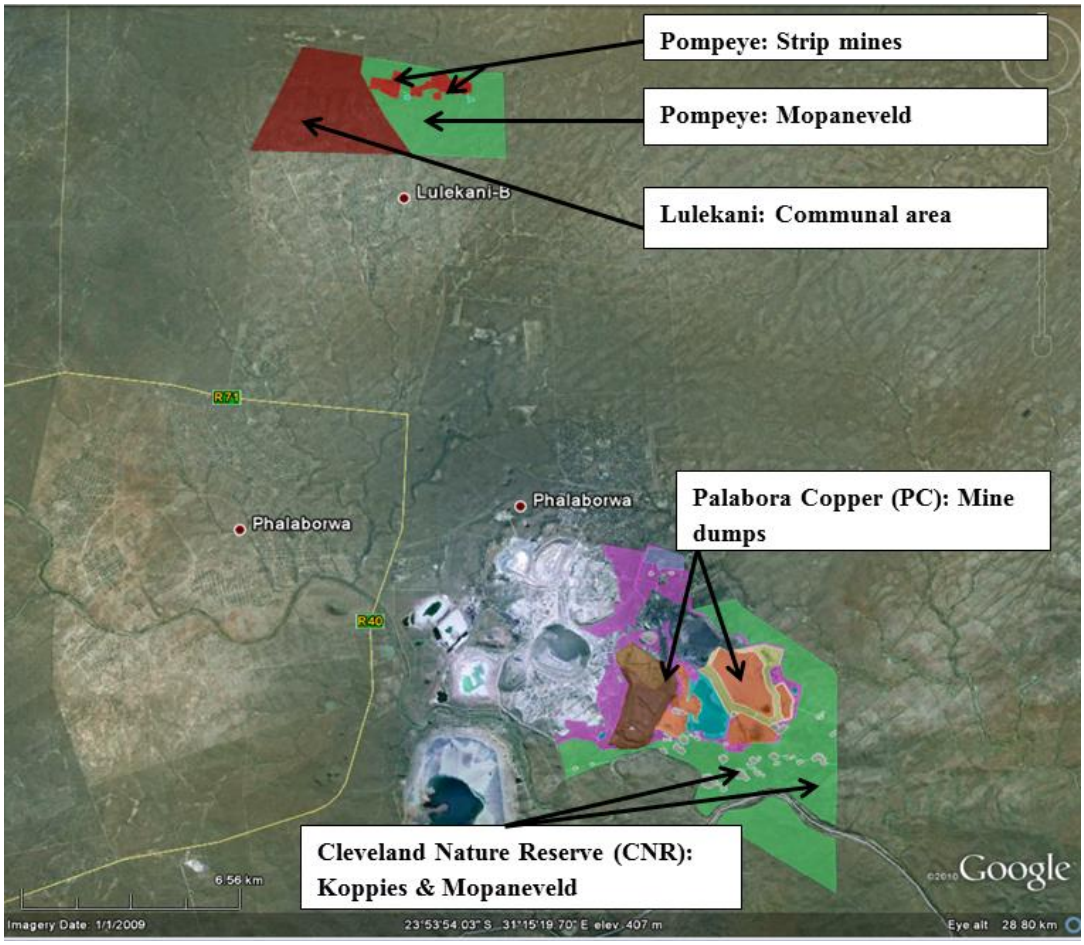


**Figure 3.1. The four study sites of the borader study area in the Phalaborwa region.**

**Figure 3.2. Undulating landscape of Phalaborwa-Timbavati Mopaneveld. (Photo taken by N. van Staden)**

### 3.2. Climate

The Phalaborwa region receives summer rainfall, with a mean annual precipitation (MAP) of 514 mm (Mucina & Rutherford, 2006). Very warm and humid conditions prevail with a mean monthly maximum temperature of 38.4°C in January. Winters are dry and frost free with a mean monthly minimum temperature of 5.7°C in July (Mucina & Rutherford, 2006).

Soil moisture availability is described as a limiting factor in savanna ecosystems (Skarpe, 1992; Scholes & Archer, 1997). Inter-annual rainfall variability is high in Mopaneveld (Buitenwerf *et al.*, 2011) and is considered a primary driver of annual changes in herbaceous species composition (O'Connor, 1985; Siebert *et al.*, 2003; Jordaan *et al.*, 2004; Buitenwerf *et al.*, 2011; O'Connor, 2015). Rainfall during the sampling period was erratic. The year 2012 was characterised by normal to high rainfall (annual precipitation=614 mm), while annual precipitation for 2013 was higher than expected for the Phalaborwa region (725.5 mm). However, 2014 (annual precipitation=254.5mm) can be considered as a dry year compared to the long-term MAP for the area (Figure 3.3).

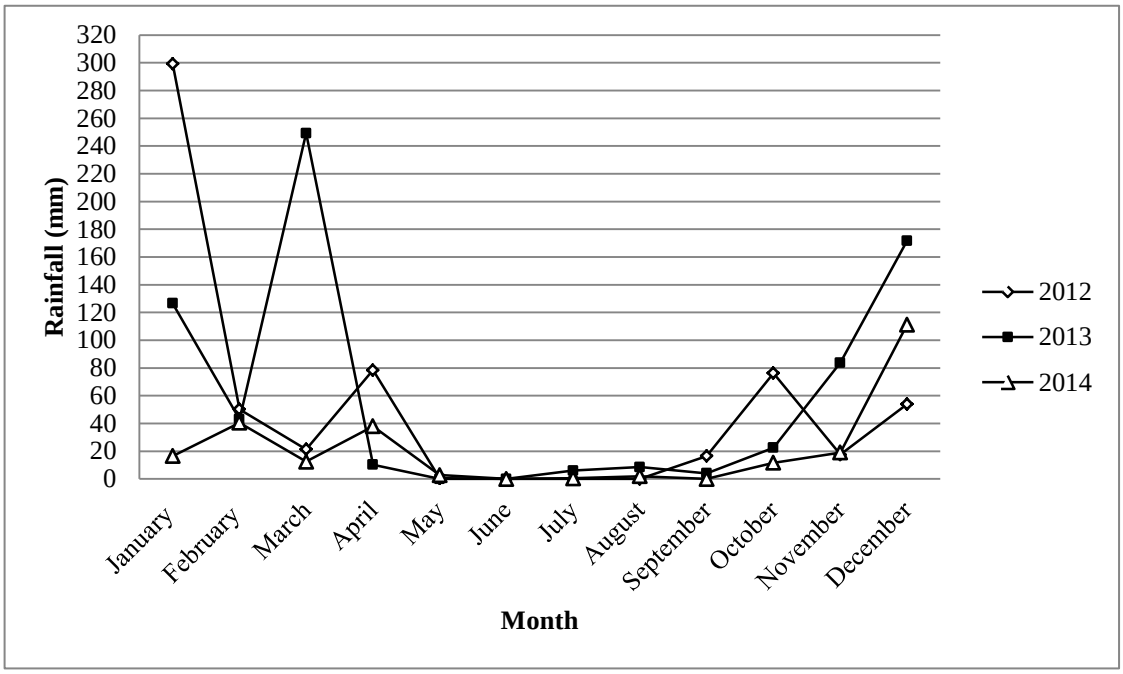


**Figure 3.3. Monthly rainfall for the years 2012, 2013 and 2014 as measured by using the manual rain gauge at SAEON Ndlovu Node, Phalaborwa. MAP for each year: 2012 = 614mm; 2013 = 725.5 mm and 2014 = 254.5 mm.**

### 3.3. Vegetation

Savanna landscapes are characterised by a herbaceous layer which is dominated by various grass and forb species (Skarpe, 1992; Venter *et al.*, 2003; Van As *et al.*, 2012), while *Colophospermum mopane* is distinct within the woody component in Phalaborwa-Timbavati Mopaneveld (Rutherford *et al.*, 2012). Some of the important herbaceous species listed by Mucina and Rutherford (2006) are the grass species *Digitaria eriantha, Schmidtia pappophoroides, Themeda triandra* and the forb species *Evolvulus alsinoides, Kohautia virgata* and *Ipomoea magnusiana*. Forbs are a valuable diversity asset (Rutherford *et al.*, 2012; Eby *et al.*, 2014; Trollope *et al.*, 2014; Siebert & Scogings, 2015) and also

contribute to the diet of ungulates (Codron *et al.*, 2007; Abusuwar & Ahmed, 2010; Van der Merwe & Marshal, 2012; Koerner *et al.*, 2014; Siebert & Scogings, 2015). The landscape is also rich in termite mounds (Mucina & Rutherford, 2006), which contribute to forb richness and landscape heterogeneity (Moe *et al.*, 2009).

### 3.4. Soil

Soil moisture availability and soil nutrients are described as the key determinants of savanna vegetation (Skarpe, 1992). Generally savannas have well-drained soils (Scholes & Archer, 1997) and can be classified into dystrophic (nutrient-poor) or eutrophic (nutrient-rich) based on their edaphic characteristics (Huntley, 1982; Scholes, 1990; Scholes *et al.*, 2003). Soils of dystrophic semi-arid savannas are derived from granite or sandstone and are dominated by broad-leaved woody species in the Combretaceae and Caesalpinaceae (Scholes *et al.*, 2003; Venter *et al.*, 2003). Mopane (*C. mopane*) trees occur mainly on relatively fertile loam and clay soils (clay content more than 15%) (Venter *et al.*, 2003) with water and nutrients primarily located in the topsoil (Scholes & Archer, 1997). Mopane trees (Skarpe, 1992; Belsky, 1994; Scholes & Archer, 1997; Hagos & Smit, 2005; Mlambo *et al.*, 2005; Smit, 2014) and termite mounds (Schuurman, 2006; Rutherford *et al.*, 2012), two of the most characteristic components of Mopaneveld, contribute to soil fertility by the deposition and regulation of soil organic matter.

### 3.5. Land-use classes

The three main land-use classes (Scholes & Biggs, 2005) of this study were urban (mine dumps and strip mining), degraded (old fields and rangelands) and protected (koppies and Mopaneveld in reserves).

#### 3.5.1 Urban land-use class

##### 3.5.1.1. Mine dumps

Mine dump facilities were located at PC and included a rock dump and a tailings dam. The mine dumps have all been rehabilitated and capped. The capping, consisting of a soil and vermiculite mixture, was seeded with a mixture of indigenous grass species. Trees were planted where it was possible. For the purpose of this study, mine dumps are considered as an urban, totally transformed land-use class, despite its rehabilitated state since the vegetation introduced on these sites is different from the surrounding natural vegetation.

a. Rock dump

Rock dumps were distinct from tailings dams. Waste rock and overburden (soil and organic matter) were usually disposed on the rock dumps (Coil *et al.*, 2012). According to Van Dyk (2012), PC dispose of waste rock from the open cast copper mine as well as rubber (old tyres) on the rock dumps (Figure 3.4 a, b). The rock dump was covered by a dense grass sward and scattered bush clumps. Furthermore the rock dump had three (3) levels, each with their own age, i.e. level 1=42 years; level 2=32 years and level 3=28 years.

b. Tailings dam

After extraction of valuable minerals from ore, the waste material is deposited in the form of 'slurry', a combination of solid waste and water on a tailings dam (Coil *et al*, 2012; Gavett, 2012). However, the contents of tailings dams depend on the mineral that is mined (Gavett, 2012). According to Van Dyk (2012), the composition of tailings at PC vary in waste material derived from copper, vermiculite and magnetite processing (Figure 3.4 c, d). The tailings dam surveyed was derived from tailings from the copper extraction plant. The copper tailings dam was covered by a sparse grass and forb layer. Four levels was associated with the rock dumps which also varied in age, i.e. levels 1-2=32 years; level 2=30 years; level 3=24 years and level 4=20 years.

#### 3.5.1.2 Strip mining

Strip mining is described as surface mining where vegetation, top soil and rock material located above a seam layer (e.g. quartz-feldspar), is removed with the goal to reach the layer of minerals (Hustrulid, 2013). Deep trenches (furrows) or large bare strips are the end result of the process. The strip mine facilities were located at Pompeye quarts mine and consisted of older trench and recent strip mines. No rehabilitation practices have been implemented on strip mines and human intervention is limited to the placing of topsoil and shaping of the landscape (Figure 3.4e).

a. Strip mines

Heavy equipment first removed the overburden (i.e. vegetation, top soil and rock material) and excavators extracted the mineral resource. Thereafter, the overburden was pushed back across the landscape and shaped. Vegetation was left to regenerate naturally, with the mined area supporting a dense grass sward and bush clumps along drainage lines.

b. Trench mines

Trench mines were implemented before 1980. Quartz-feldspar was mined with a back-actor which formed trenches 10-50 m in size and 50-100 m apart. Unlike the strip mines, overburden was not placed back in the trenches. These trenches were abandoned after mining and is now characterised by natural vegetation regeneration of tree cover and a ground layer dominated by forbs. Pebbles and stones cover the soil surface in thick layers in and around the trenches.

### 3.5.2 Degraded land-use class

#### 3.5.2.1 Communal lands

Communal areas were situated in and around Lulekani, the informal settlement of Phalaborwa (Figure 3.4 f, g). These areas were mainly utilized for subsistence farming and consists of old fields and rangelands. Extensive wood harvesting, ploughing and overgrazing have degraded this semi-arid Mopaneveld. Furthermore, communal areas were considered to be marginally disturbed.

a. Old fields

Old fields were described as abandoned agricultural crop lands (Cramer & Hobbs, 2007). The top soil was mainly disturbed by ploughing. In Lulekani, fields are not cultivated annually. Fields that have been unplanted and bare for one or more seasons are characterised by a dense herbaceous layer of forbs and grasses. Shallow erosion gulleys were a common feature.

b. Rangelands

Communal rangelands were used as grazing areas for livestock (Figure 3.4f). Households also used these areas for the harvesting of natural resources, such as fire wood, fruit, thatch grass and construction wood (Shackleton, 2000). Cattle, donkeys, sheep and goats were frequently encountered during this study. Foot paths and erosion gullies were also characteristic of the landscape (Figure 3.4g). The vegetation was typical Mopaneveld with stunted, small trees as a result of extensive wood harvesting.

### 3.5.3 Protected land-use class

Protected areas, with their comparatively limited anthropogenic disturbance, consisted of koppies and natural Mopaneveld (Figure 3.4h). The protected area at Pompeye is bordered by Groot Letaba Wildlife Resort and the Lulekani informal settlement. CNR is bordered by Hans Merensky Golf Estate, KNP and PC. Animals move freely between CNR and KNP. Elephant, buffalo, impala, koedoe and lion have regularly been observed at CNR.

3.5.3.1 Koppies (Inselbergs)

The term inselberg is derived from German, ‘insel’ meaning island and ‘berg’ meaning mountain (Porembski & Barthlott, 2000). Inselberg or koppies are isolated rock outcrops with large areas of bare rocky slopes (Porembski *et al.*, 1997) or can be defined as ‘remnants of erosion processes, forming isolated mountains which can range in elevation’ (Burke, 2003). The southern slopes are densely vegetated in contrast to the northern slopes. Koppies which were included in this study were situated in CNR (Figure 3.1).

3.5.3.2 Mopaneveld

Mopaneveld is characterised by a homogenous plant structure (Mapaure, 1994). However, the herbaceous layer is very dynamic since vegetation changes in plant communities are driven by stochastic events (Siebert *et al.*, 2003). Disturbances were limited to herbivory within protected and managed reserves. Therefore the only two major disturbances, in protected Mopaneveld, are rainfall events and herbivory. Animals that were observed included buffalo, koedoes, impala, elephant and water buck.

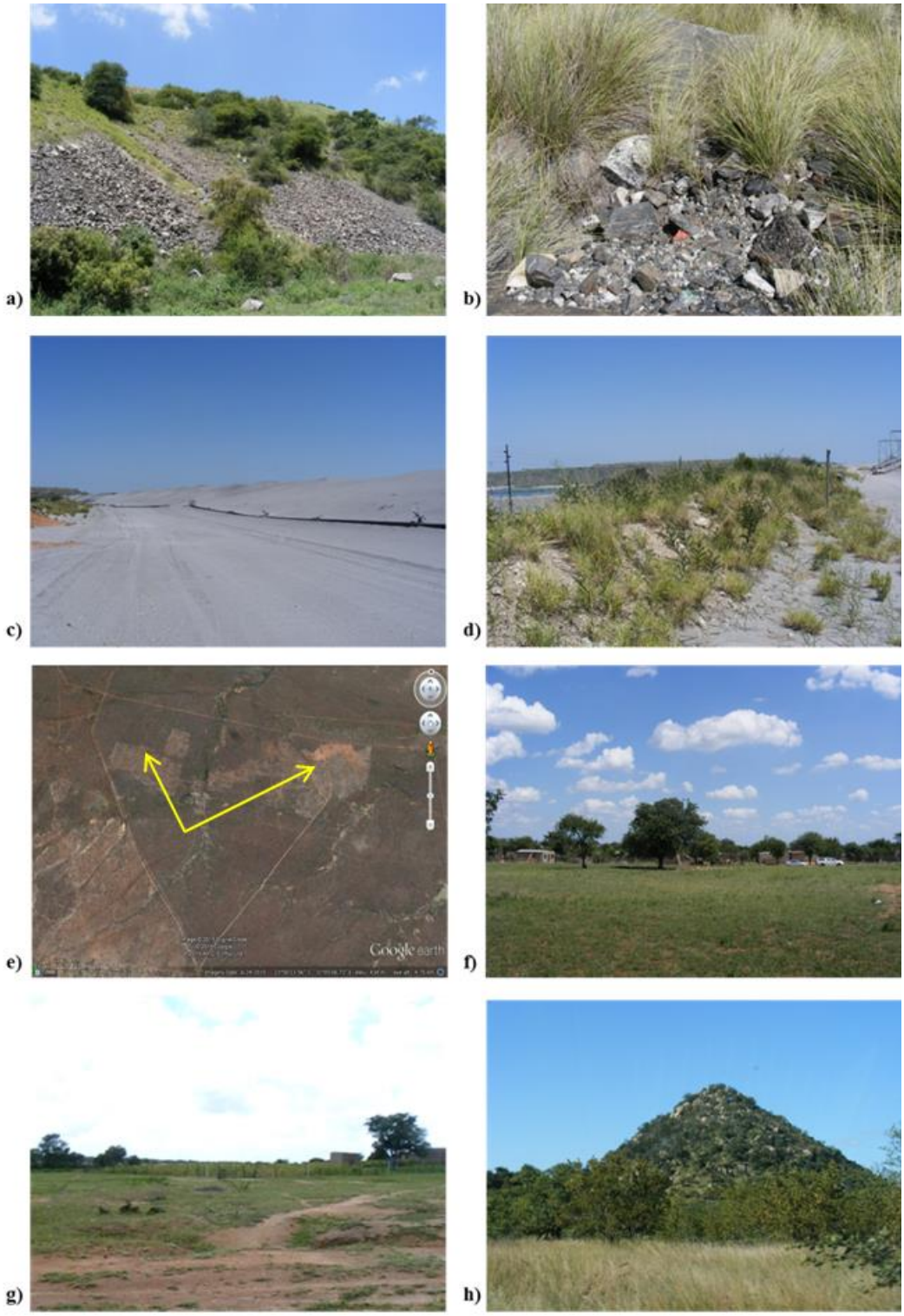


**Figure 3.4. a) Rock dumps were characterized by steep slopes with trees and b) high rock cover. c) Sandy slopes of the tailings dam covered by d) grass and forb species. e) Google Earth image of the strip mines indicated by yellow arrows. f) Communal lands were characterized by grazing lawns as well as g) footpaths and deep trenches. h) Koppies in a matrix of Mopaneveld in a protected area. (Photos taken by N. van Staden).**

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# Chapter 4

# Methodology

## 4.1 Field data collection

The following three land-use classes were identified within the study area based on the classification of Scholes and Biggs (2005): 1) protected areas (untransformed: Mopaneveld and koppies), 2) degraded (marginal disturbance such as top soil alteration through overgrazing and cultivation: communal land) and 3) urban (total land transformation through complete removal of topsoil: strip mines and mine dumps) (Table 4.1). Within each land-use class one or more sites of various use were identified. A minimum of 20 plots were sampled randomly within each of these sites.

The herbaceous layer of each land-use was sampled by means of the fixed quadrat method during February 2013. Quadrats were randomly placed and the position recorded with a GPS (Figure 4.1a, b). In the southern hemisphere, northern slopes of koppies are characterised by a warmer and drier habitat, while southern slopes are cooler and moister. Therefore the northern and southern slopes of three (3) different koppies were sampled in CNR. For all three (3) koppies, a total of twenty two (22) plots were sampled both on the northern and southern slopes respectively, i.e. a total of forty four (44) plots on koppies (Table 4.1). Where the topography allowed, koppies were stratified in lower-, mid- and upper elevation zones. The lower slopes were considered as transition zones between natural Mopaneveld and inselberg vegetation, and therefore were omitted. Additional field data for natural Mopaneveld was collected during the end of April 2014. A total of 210 1m² quadrats were sampled (Table 4.1). All grass and forb species were identified to species level and individuals per species were counted (Figure 4.1c, d). Percentage cover for grass, forbs, bare soil, rock and debris was visually estimated with a frame consisting of 16 divisions of 25 x 25 cm each. The tallest grass species in each quadrat was identified and measured. Standing herbaceous biomass was collected from 400 cm² in all quadrats (Figure 4.1e, f) and dried at 30 ºC for 24 hours. The dry material was weighed with a scale and converted to kilograms per hectare (kg/ha) by multiplying the dry mass (g) with 500. Unknown specimens were identified by the Pretoria National Herbarium (PRE) and voucher specimens of all taxa were deposited in the A.P. Goossens Herbarium (PUC) and Skukuza Herbarium (KNP).

**Table 4.1. Number of quadrats sampled per site per land-use class.**

*one quadrat of Mopaneveld was considered as an outlier and omitted, thus 209 quadrats were used for species and functional diversity analyses.

| Land-use classes | Level of degradation | Site description, including nature of use | Number of quadrats |
|---|---|---|---|
| Protected | None | Koppies: northern slope | 22 |
| Protected | None | Koppies: southern slope | 22 |
| Protected | None | Mopaneveld: Cleveland | 20* |
| Protected | None | Mopaneveld: Pompeye | 23 |
| Degraded | Marginal disturbance | Communal: rangelands | 20 |
| Degraded | Marginal disturbance | Communal: old fields | 20 |
| Urban | Total transformation | Strip mining: trenches | 20 |
| Urban | Total transformation | Strip mining: strips | 21 |
| Urban | Total transformation | Mine dumps: rock dump | 21 |
| Urban | Total transformation | Mine dumps: tailings dam | 21 |
| | | 10 | 210 |


**Figure 4.1. a) GPS coordinates of quadrats were taken, b) grid frames were used to sample 1m² plots, c) grass and forb species were identified and counted, d) data was recorded on field forms, and e, f) standing biomass was collected. Photos taken by N. van Staden.**

## 4.2. Trait selection

Plant functional traits are defined as any physiological, morphological and/or phenological characteristics of plants induced by environmental factors or effects on ecosystem functioning (Díaz & Cabido, 2001; Pérez-Harguindeguy *et al.*, 2013). This study exclusively focused on response traits (see Box 1, Glossary, Chapter 2) since land-use disturbances were considered as the most important determinant factor (Díaz & Cabido, 2001; Mori *et al.*, 2013). Various studies have investigated which traits respond significantly to land-use disturbances (McIntyre *et al.*, 1995; Lavorel *et al.*, 1997; Lavorel *et al.*, 1998; McIntyre *et al.*, 1999; Todd & Hoffman, 1999; Shackleton, 2000; Burke, 2002; Cornelissen *et al.*, 2003; Garnier *et al.*, 2007; Biswas & Mallik, 2010; Laliberte *et al.*, 2010; Geldenhuys, 2011; Lavorel *et al.*, 2011; Rutherford *et al.*, 2012; Kotschy, 2013; Pérez-Harguindeguy *et al.*, 2013; Van der Walt, 2013; Lewis *et al.*, 2014; Pakeman & Stockan, 2014; Batriu *et al.*, 2015; Mandle & Ticktin, 2015). In Table 4.2 the relevance of traits selected for this study are indicated with supporting literature. Field guides (Germishuizen, 1997; Van Wyk & Malan, 1998; Van Wyk, 2000; Smith & Crouch, 2009; Van Oudtshoorn, 2009; Bromilow, 2010; Crouch *et al.*, 2011; Kirby, 2013), various Floras (Germishuizen & Meyer, 2003; Huntley *et al.*, 2007; Hyde *et al.*, 2015; JSTOR, 2015; KEW Royal Botanical Gardens, 2015) and insightful websites (Kyffhäuser, 2014; Biodiversity Explorer, 2015; South African National Biodiversity Institiute (SANBI), 2015) were used to assign traits to species. The following response traits were selected as these were considered important for adaptation in environments prone to disturbance, and were easy to determine:

### 4.2.1 Weediness

A weed is defined as ‘a wild plant growing where it is not wanted, especially among crops or garden plants’ by the Oxford Advanced Learner's Dictionary (2010). Weeds have the tendency to invade disturbed areas where they establish successfully and may be native or exotic species (Nabors, 2004; Bromilow, 2010). Exotic plant species, as indicated by Germishuizen and Meyer (2003) and native species described as a weed in the literature were assigned to the category ‘weedy’ (Table 4.2).

### 4.2.2 Growth form

Each species was assigned to one of six growth form categories (Table 4.2). Plant species which root in the soil but use other species or substrates (trees or rocks) for external structural support to grow upward (Cornelissen *et al.*, 2003; Pérez-Harguindeguy *et al.*, 2013) were assigned to the category ‘climbers’. Species with circularly organized leaves, usually carried on a condensed stem or rhizome near the soil surface, were placed in the ‘rosette’ category (Cornelissen *et al.*, 2003; Kirby, 2013; Pérez-Harguindeguy *et al.*, 2013). If plant species were described as prostrate (also procumbent; plants rooted at one place in soil, with stems lying flat on the soil surface without root forming at nodes) or decumbent (plants are rooted at one place in the soil with stems lying flat on the soil surface without root forming at nodes, but with stem ends growing upwards) in the literature, these species

were assigned to the category ‘prostrate’ (Van Wyk & Malan, 1998; Kirby, 2013; Kotschy, 2013). However, if root forming tended to occur at the nodes of trailing stems (thus forming stolons or runners), these species were classified as ‘creepers’ (Van Wyk & Malan, 1998; Kotschy, 2013; Pérez-Harguindeguy *et al.*, 2013). Species growing upright, with the leaves concentrated in the middle or top parts of the stem, were classified as ‘erect’ (Cornelissen *et al.*, 2003). Many perennial grasses, and some sedges, with leaves concentrated and sprouting from a basal meristem to form prominent tufts were assigned to the ‘tussock’ category (Cornelissen *et al.*, 2003; Pérez-Harguindeguy *et al.*, 2013).

### 4.2.3 Life history

Species were assigned to one of two categories, namely annual or perennial (Table 4.2). Annual species produce seeds in mass, which remain dormant in the soil during unfavourable seasons, and complete their life cycle in one year (Pérez-Harguindeguy *et al.*, 2013). Perennial species have the ability to persist for a minimum of approximately three growing seasons (Pérez-Harguindeguy *et al.*, 2013). Species were categorised according to Plants of southern Africa (Germishuizen & Meyer, 2003), with biennial species included under annuals. It was reasoned that due to the semi-arid climate of the study area, biennials will respond similarly to annuals.

### 4.2.4 Raunkiaer’s life form

The categories of life forms were initially developed and described by Raunkiaer (1934). Based on the position of perennating buds which will determine if a plant species will be able to survive unfavourable conditions, Raunkiaer (1934) assigned plant species to one of five categories, namely phanerophytes, chamaephytes, hemicryptophytes, cryptophytes and therophytes (Table 4.2). In this study the definitive features of these five categories, together with descriptions by Cornelissen *et al.* (2003), were used to assign a species to a life form. Phanerophytes were defined as plants which have the habit to grow taller than 0.5m (Cornelissen *et al.*, 2003) and have perennating tissue which is carried on air projecting shoots (Raunkiaer, 1934). For this study climbers were classified as phanerophytes. All dwarf shrubs and plants which do not grow taller than 0.5m (Cornelissen *et al.*, 2003; Kotschy, 2013) were classified as chamaephytes. Perennial grass species, sedges, prostrate and rosette growth forms with remnant root systems near the soil, were grouped as hemicryptophytes (Cornelissen *et al.*, 2003; Kotschy, 2013). Plant species with underground storage (bulbs, tubers) or reproductive (rhizomes) organs such as geophytes and ferns were classified as cryptophytes (Raunkiaer, 1934; Cornelissen *et al.*, 2003; Kotschy, 2013). All annual plant species were classified as therophytes, i.e. plants with root systems dying off after seed production and complete their life cycle within one year (Raunkiaer, 1934; Cornelissen *et al.*, 2003).

### 4.2.5 Clonality

Herbaceous species were assigned to four categories (Table 4.2) as proposed by Cornelissen *et al.* (2003) and Pérez-Harguindeguy *et al.* (2013). Plant species with no specialized clonal organs, dependent on sexual reproduction only, were classified as 'non-clonal'. Clonal species were divided into three different categories i.e. i) clonal above ground (stolons are formed), ii) clonal below ground (rhizomes, tubers, bulbs, corms and tuberous roots present), and iii) clonal above and below ground.

### 4.2.6 Dispersal mode

Classification of dispersal modes were based on descriptions provided by Cornelissen *et al.* (2003) and Pérez-Harguindeguy *et al.* (2013). Five categories were used to group plant species (Table 4.2). Unassisted dispersal grouped species which have no long-distance dispersal aids. Species whose seeds fall passively from the plant and species which disperse by launching (ballistichory) were included in this category. Wind dispersal included species with small dust-like seeds, seed with long hairs, pappus, trichomes or wing-like structures as well as species tumbled by the wind. Animal transported seeds were divided into two categories. Species with colourful fleshy fruits eaten by vertebrates where the seeds pass through the gut of the animal were grouped in the 'internal animal transport' category. Seeds with adhesive structures such as sticky substances, hooks, barbs, awns or burs which become attach to animals (fur, feathers, hoofs, legs etc.) or humans (clothing) were assigned to the category 'external animal transport'. Ant dispersal was also included under this category. Lastly, if species made use of various modes of dispersal it was classified under the category 'unspecified'.

### 4.2.7 Nitrogen fixing ability

Cornelissen *et al.* (2003) described various nutrient uptake strategies used by plants. In this study it was decided to only focus on the nitrogen-fixing ability of species. Plant families and species, known from literature to live in symbiosis with $N_2$-fixing bacteria and have nodules were assigned to the category 'present' (Table 4.2). Information was primarily obtained from field guides, Floras and especially the article by Sprent *et al.* (2013).

### 4.2.8 Shade tolerance

According to Valladares and Niinemets (2008), shade tolerance is obtained through complex mechanisms dependent on carbon gain efficiency under low light conditions as well as resistance to biotic and abiotic stresses prevailing in the understory environment. Disturbed areas are primarily subjected to high sun exposure (Baker, 1967). Therefore plant species which can tolerate high sunlight exposure (i.e. shade intolerant) will have a selective advantage over shade tolerant species (Baker, 1967; Pons & Poorter, 2014) in disturbed areas. Plant species were assigned to one of three categories, namely shade (shade tolerant), sun (shade intolerant) and unspecified tolerance which included plant species which can grow successfully in shade and sunlight (Table 4.2).

## 4.3. Data analysis

### 4.3.1 Species diversity (Chapter 5)

A species abundance-plot matrix was constructed whereafter a two-phase approach was adopted. The first was to characterise species composition of different land-use plant communities and the second was to compare the diversity between different land-uses.

#### 4.3.1.1 Community composition

Plant community assemblages, based on species composition, were assessed independently of environmental data. Rare species with an abundance value of less than 11 individuals in the entire data set were omitted to prevent the overemphasis of these species (Lepš & Šmilauer, 2003) since it is assumed that rare species add noise to data analyses and provide restricted information regarding diversity patterns compared to common species (Gauch, 1982; McCune *et al.*, 2002; Pos *et al.*, 2014). To downweight the influence of more abundant species without losing the impact of relative abundance (Clarke, 1993) the data were fourth root transformed in PRIMER 6 software (2012). An indirect gradient analysis was performed with Non-metric Multidimensional Scaling (NMDS) using Bray-Curtis distance measure with one hundred restarts, in PRIMER 6 software (2012). The non-parametric One-way Analysis of Similarities (ANOSIM) of pair-wise comparisons, using the Bray-Curtis similarity index with 9999 permutations, was used to test for significant differences in species composition and community structure between land-uses (Clarke, 1993; Kent, 2012). An R-value approaching 1 indicated significant differences, while an R-value approaching 0 indicated no significant differences between land-uses (Venn *et al.*, 2014). Similarity Percentage Analysis (SIMPER) was conducted to identify key herbaceous species which contributed most to compositional differences between plant assemblages of land-uses (Clarke, 1993; Gooden & French, 2014). Paleontological Statistics (PAST) was used to perform ANOSIM and SIMPER (Hammer *et al.*, 2001).

#### 4.3.1.2 Diversity indices

Diversity data included species richness (S), total individuals, N (used in this study as a function of density), and the indices: Margalef's species richness (d), Pielou's evenness (J'), Shannon-Wiener Diversity (H') and Simpson Diversity (1-ʎ). Margalef species richness (Margalef, 1958) standardize species number in relation to the number of observations in a sample, is sensitive to sample size and compensates for sampling effects (Magurran, 2004; Gamito, 2010; Engemann *et al.*, 2015). Comparing Shannon-Wiener and Simpson diversity indices, the impact of evenness is clear as Simpson index combines evenness and richness while the Shannon-Wiener index is less sensitive to species evenness (Kent, 2011). Data were tested for normality in STATISTICA version 11 (2012) and fourth-root transformed where applicable. A One-way ANOVA was performed on data that met the assumptions of a parametric test, whereas a Kruskal-Wallis ANOVA was applied to non-normally

distributed data. One-way ANOVA results were accompanied by an unequal N Tukey's post-hoc HSD (honestly significant difference) to test for significant differences between land-uses, whereas two-tailed multiple comparison of p-values (independent grouping value) accompanied Kruskal-Wallis ANOVA results.

### 4.3.2 Functional diversity (Chapter 6)

#### 4.3.2.1 Identification of functional groups

A data matrix consisting of species (rows) and traits (columns) was constructed. Each trait was given a numerical score (binary or categorical) as listed in Table 4.2. Hierarchical cluster analysis using PRIMER 6 software (2012), was used to group plant species based on their trait values into plant functional groups (Laliberte *et al.*, 2010). The cluster analysis grouped species into homogeneous categories based on the similarity or dissimilarity of their traits (Scott & Knott, 1974; Statsoft, 2015a) in a hierarchical tree or dendrogram (Edwards & Cavalli-Sforza, 1965; Holland, 2006).

Since trait data consisted of binary and categorical data types, the modified Gower dissimilarity metric was selected (Gower, 1971; Podani, 1999; Botta-Dukát, 2005; Kotschy, 2013). From the dendrogram a horizontal cut-off point was selected to separate species into functional groups according to specific trait combinations. The cut-off limit was subjectively determined, and supported by botanical knowledge, at the height of 0.2 after visually inspecting the dendrogram. Each species was then assigned to a specific plant functional group (as indicated by the groupings below the 0.2 cut-off distance on the dendrogram). Multivariate analyses were performed on the new data matrix. Principal Co-ordinate Analysis (PCoA), an unconstraint type of ordination and an improved method of Principal Component Analysis (PCA) (Gower, 1966; Lepš & Šmilauer, 2003; Kent, 2012) which considers binary and categorical data types (Geldenhuys, 2011), was performed on trait data using PAST (Hammer *et al.*, 2001). Similarly to the cluster analysis, the Gower similarity index was selected.

#### 4.3.2.2 Diversity of functional traits and plant functional groups

Trait-species and functional group-species matrices were each multiplied with the species-abundance matrix using the MMult function in Microsoft Excel 2007 to produce trait-plot and functional group-plot matrices respectively. These trait-plot and functional group-plot matrices were used for the calculation of diversity indices and multivariate analysis.

Following the example of Hanke *et al.* (2014), PRIMER 6 software (2012) was used to calculate diversity indices for plant traits and functional groups. Diversity analysis was conducted to indicate richness, evenness and diversity for functional traits and plant functional groups. Richness of functional traits and plant functional groups were fourth root transformed. One-way Analysis of Variance (ANOVA) assumes that a dataset is normally distributed (The Pennsylvania State

University, 2015) and assess the equality of population means for a quantitative outcome and a single explanatory variable (Steltman, 2015). One-way ANOVA's and Tukey's HSD for unequal N post hoc tests were performed in STATISTICA version 11 (2012) to test for significant differences between land-use groups in terms of plant functional trait and functional group diversity and indices (Laerd Statistics, 2013; StatSoft, 2015b).

#### 4.3.2.3 Functional assemblages of land-uses

Patterns of functional assemblages of land-uses were analysed with Canoco for Windows version 4.5 (Ter Braak & Smilauer, 2002). Detrended Correspondence Analysis (DCA), with detrending by segments, was performed on the plant trait-plot and functional group-plot matrices to detect the length of the gradient (Lepš & Šmilauer, 2003). Gradient length is a measure of community heterogeneity (beta diversity; species turnover), hence homogenous data will have a short gradient length (Lepš & Šmilauer, 2003). A gradient length <4 indicated that the data was linearly distributed, while a longer gradient length (>4) indicated unimodal data distribution (Lepš & Šmilauer, 2003; Wehn *et al.*, 2014). In the case of linear data, Principal Component Analysis (PCA) and Redundancy Analysis (RDA) were performed on the data. If the data was unimodal, Correspondence Analysis (CA) and Canonical Correspondence Analysis (CCA) were conducted (Lepš & Šmilauer, 2003). A land-use-plot matrix was constructed in which land-uses were given binary scores and was then used as the environmental variable data. The 'down-weighting of rare species' and 'do not transform' options were selected for all ordination analyses. DCA indicated some samples as outliers and these were therefore omitted. In PCA and RDA 'inter-species correlations' and 'center by species' options were selected. In CA and CCA default options were selected (inter-sample distances, Hill's scaling). Significance of land-uses (as an environmental variable) was evaluated with RDA and CCA with the selection of the significance of the first ordinal axis option and with unrestricted Monte-Carlo permutation tests (499 permutations). Lastly, to visualize the frequency of each plant functional group per land-use, pie charts were constructed in Microsoft Excel 2007. Graphical plots of ordinations were constructed using CanoDraw 4.5 (Ter Braak & Smilauer, 2002).

**Table 4.2. Selected plant traits, categories and motivation for selection.**

| Plant trait | Unit | Category & code score | Motivation | References |
|---|---|---|---|---|
| Weediness | Binary | Yes-1<br>No-0 | Associated with anthropogenic disturbances | (Goodall & Naude, 1998; Nabors, 2004; Buckley *et al.*, 2007; Meek *et al.*, 2010; Schonbeck, 2013; Carreño-Rocabado *et al.*, 2015) |
| Growth form | Categorical | Climber-1<br>Rosette-2<br>Prostrate-3<br>Erect-4<br>Tussock-5<br>Creeper-6 | Plant strategy, response to soil disturbance, disturbance regime | (Lavorel *et al.*, 1997; Cornelissen *et al.*, 2003) |
| Life history | Categorical | Annual-1<br>Perennial-2 | Response to disturbance, persistence under disturbance | (Lavorel *et al.*, 1997; Lavorel *et al.*, 1998) |

| | | | | |
|---|---|---|---|---|
| Raunkiaer's life form | Categorical | Phanerophyte-1<br>Chamaephyte-2<br>Hemicryptophyte-3<br>Cryptophyte-4<br>Therophyte-5 | Indication of adaptations to survive unfavourable conditions, response to disturbance, regeneration | (Lavorel *et al.*, 1997; Cornelissen *et al.*, 2003; Pakeman *et al.*, 2011) |
| Clonality | Categorical | Non-clonal-1<br>Above ground-2<br>Below ground-3<br>Above and below ground-4 | Resource exploitation, response to disturbance, competitive ability, recovery, and persistence after disturbance | (Cornelissen *et al.*, 2003; Kahmen & Poschlod, 2004; Laliberte *et al.*, 2010; Pérez-Harguindeguy *et al.*, 2013) |
| Dispersal mode | Categorical | Unassisted-1<br>Wind-2<br>External animal-3<br>Internal animal-4<br>Unspecified-5 | Plant range size, colonization ability | (Cornelissen *et al.*, 2003; Pérez-Harguindeguy *et al.*, 2013) |

| | | | | |
|---|---|---|---|---|
| Nitrogen fixing ability | Binary | Present-1<br>Absent-0 | Adaptive strategy in habitats with deficient nutrient availability, promotes soil fertility | (Bradshaw, 1997; Cornelissen *et al.*, 2003; Sprent *et al.*, 2013; Domingo & David, 2014) |
| Shade tolerance | Categorical | Shade-1<br>Sun-2<br>Unspecified-3 | Influenced by various abiotic and biotic conditions, growth rate | (Valladares & Niinemets, 2008; Pons & Poorter, 2014) |

### 4.3.3. Environmental variables

The relationship between environmental variables, species abundance and functional groups were analysed using Canoco for Windows version 4.5 (Ter Braak & Smilauer, 2002) with similar steps as described for the multivariate analysis of functional assemblages.

### 4.3.4. Linking species- and functional diversity

No specific statistical analyses were conducted to test the correlation between species- and functional diversity. However to present preliminary observations, Box-and Whisker plots, generated with the analysis of diversity indices (on species-, trait- and functional group level) in STATISTICA version 11 (2012), were used to present and compare response patterns. These observations guided preliminary remarks concerned with redundancy and resilience.

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# Chapter 5

## Plant species composition and diversity of land-uses along a land-use gradient

### 5.1 Introduction

Biodiversity in all its components, stands central to ecosystem functioning as it provides and maintains a variety of ecosystem services (Díaz & Cabido, 2001; Wessels *et al.*, 2003; Van As *et al.*, 2012). Complex interactions between abiotic and biotic components in ecosystems determines the quantity, quality and reliability of these services (Mace *et al.*, 2012). In savanna landscapes, trees and shrubs provide various ecosystem functions through structural heterogeneity, whereas the herbaceous layer plays a major role in water infiltration and providing large quantities and greater quality of forage to livestock and game (Thrash *et al.*, 1993; Rutherford & Powrie, 2013). Not only are the survival of species dependent on these ecosystem functions, but the well-being of humanity is affected as well (Alcamo & Bennett, 2003; Mori *et al.*, 2013). However, humans have the ability to manipulate services to achieve desired results by means of land-use change and intensification.

Biodiversity loss due to land-use intensification is becoming an issue of great concern (Bullock *et al.*, 2011), since major threats are posed to ecosystem intactness world-wide (Yachi & Loreau, 1999; Wessels *et al.*, 2003; Wilson *et al.*, 2004; Scholes & Biggs, 2005). Transformation of natural vegetation by different land-uses is one such threat to biodiversity (Lavorel *et al.*, 1997), reducing species richness and altering evenness across various communities (Crowder *et al.*, 2010). More than three quarters of all terrestrial biomes have already been transformed to anthropogenic biomes (anthromes) through a variety of land-use practices (Wilson *et al.*, 2004). Environmental change is increasing due to climate change (Millennium Ecosystem Assessment, 2005), an escalating human population, habitat fragmentation, cultivation, invasive aliens, harvesting of natural resources and mining activities (Davis *et al.*, 2013).

Species react differently to environmental change (Yachi & Loreau, 1999) and responses are induced on plant community composition and diversity (Díaz & Cabido, 2001). Thus, the abundance of some species will increase whereas other will decrease based on their abilities to adapt to environmental stress. Severity, frequency and nature of the disturbance, resource requirements of individual species and the vegetation type play a significant role in the responses of individual species and communities (Grime, 1977; Armesto & Pickett, 1985; Pandey & Singh, 1985; Shackleton *et al.*, 1994). The status and dynamics of individual species is altered by different land-use management practices with the possibility that key species might be lost and ecosystems will become more susceptible to degradation (Shackleton, 2000). According to Shackleton *et al.* (1994) disturbance factors can override dominant abiotic variables that usually drives species composition and community structure. Disturbance can, however, result in favourable conditions with reference to specific aspects of community dynamics such as increased nutrient cycling, establishment of seedlings and increased diversity, whereas

unfavourable impacts include increased soil erosion and reduced canopy cover (Shackleton *et al.*, 1994). The disturbance theory is not well explored in savanna ecosystems and it may become essential to understand what the long-term effects will be in a modern and ever developing African landscape.

Generally land-uses are seen as a form of land degradation (Rutherford *et al.*, 2012) and are regarded as the main cause of biodiversity loss in semi-arid savannas (Scholes & Biggs, 2005; Rutherford *et al.*, 2012; Rutherford & Powrie, 2013). However some studies revealed that land-use change may have little or positive effects on species richness (Shackleton, 2000; McKinney, 2008; Flynn *et al.*, 2009; Biswas & Mallik, 2010; Rutherford *et al.*, 2012; Rutherford & Powrie, 2013) while the intermediate disturbance hypothesis predicts that some disturbance levels can govern high species diversity (Grime, 1973; Connell, 1978; Begon *et al.*, 2006; Biswas & Mallik, 2010). Therefore land-use change resulting in moderate levels of disturbance, relative to protected areas, may have comparatively high diversity. Studies of communal lands in Mopaneveld suggest that the dynamic character of the vegetation can compensate for species losses due to the tolerance of savanna species to disturbance (Rutherford *et al.*, 2012), with intermediate disturbance levels leading to increased levels of species richness. Furthermore, this increased species richness in Mopaneveld, according to the diversity-stability hypothesis, will provide insurance and minimize the deterioration of the ecosystem (Chapin *et al.*, 2000; McCann, 2000). Since high species diversity promotes ecosystem resilience and resistance (Chapin *et al.*, 2000), diverse ecosystems will be more stable during environmental disturbances.

Shackleton (2000) identified a need for studies on the effect of land-use disturbance intensities on savanna species richness. The heavily utilized and transformed mining landscape of Phalaborwa-Timbavati Mopaneveld (Mucina & Rutherford, 2006) provided an opportunity to test the effect of various land-uses on plant community composition and diversity. Five land-uses with varying intensities of disturbance, namely protected areas, communal land and land requiring remediation were compared to contribute to an understanding of the effects of anthropogenic disturbances at species and community level in semi-arid Mopaneveld. Linking the relationship between species diversity and composition with land-uses will allow decision makers to make predictions regarding future provisioning of ecosystem services (Moretti *et al.*, 2013) and improving management plans in the face of global change (Díaz & Cabido, 2001).

The objectives of this chapter were to examine if: i) land-use affects the distribution and abundance (species composition) of herbaceous plant communities; ii) land-use affect herbaceous species richness, evenness and diversity and iii) land-use adversely affect the native species diversity. The hypotheses relevant to this chapter are 1) if land-use disturbance entails complete land transformation

(i.e. strip mines and mine dumps), then the richness and diversity of the herbaceous layer of Mopaneveld will decrease and evenness increase and 2) if land-use disturbance entails marginally disturbed (i.e. intermediate levels of disturbance; communal lands), then the richness and diversity of the herbaceous layer of Mopaneveld will increase and evenness will decrease.

## 5.2 Data analysis

Methods for data collection and general data analyses are given in Chapter 4. Analyses specific to this chapter are dealt with here.

Plant community assemblages, based on species composition, were assessed with NMDS ordination using PRIMER 6 software (2012). Accordingly results were presented as two-dimensional plots. NMDS stress values are considered measures of good fit of data points. Stress values > 0.05 can be considered excellent representation, > 0.1 is great, >0.2 is good and stress values >0.3 poor and difficult to interpret.(Clarke & Warwick, 2001; Kent, 2012). The software program PAST (Hammer *et al.*, 2001) was used to conduct ANOSIM and SIMPER analyses on fourth root transformed abundance data. Bray-Curtis similarity measure was selected when ANOSIM and SIMPER analyses were conducted. To assess differences in species composition and community structure of land-use plant communities, a one way ANOSIM was performed. Key herbaceous species which contributed strongly to these compositional differences among land-uses were identified using SIMPER analyses.

Data were tested for normality in Statistica (2012), which lead to fourth root transformation of species richness and density data variables. Data used in the calculation of indices (i.e. Margalef species richness, Pielou's evenness, Simpson diversity and Shannon-Wiener diversity) were not transformed since application of indices to numeric data can be regarded as a type of data transformation in itself. However, when these untransformed data variables remained non-normally distributed, a non-parametric Kruskal-Wallis ANOVA was applied. A One-way ANOVA was applied to data variables that met the assumptions of normality, with or without transformation.

To determine whether land-uses were characterized by certain environmental variables, multivariate analyses were conducted on species abundance- and environmental variable data in Canoco (Ter Braak & Smilauer, 2002). In this study DCA analysis indicated that the data was unimodal distributed and therefore Canonical Correspondence Analyses (CCA) were conducted.

## 5.3. Results

### 5.3.1. Species composition

NMDS analyses revealed unique herbaceous species composition for each land-use type (NMDS stress value = 0.2) that differentiates them from one another (Figure 5.1). Distinct assemblages were evident for mine dumps, protected koppies and communal lands (Figure 5.1). ANOSIM analysis of pairwise comparisons (Table A1; Appendix A) indicated that koppies differ from communal lands

(R=0.707) and mine dumps (R=0.774), while mine dumps differed from strip mines (R=0.664) and communal lands (R=0.798). SIMPER analysis indicated that the average dissimilarity between any form of land-use and protected vegetation was very high (greater than 90%, Table 5.1). Across all land-uses seven grass and four forb species contributed to >20% of compositional differences with *Urochloa mosambicensis, Enneapogon cenchroides* and *Aristida adscensionis* as the most important grass species driving these differences (Table A2; Appendix A). When land-uses were individually compared to Mopaneveld, NMDS analyses indicated that species composition of communal rangelands (Figure 5.2a; NMDS stress value = 0.25) was more similar to protected Mopaneveld than to communal old fields. A low R-value (R=0.286) was obtained from ANOSIM analyses, emphasizing the lack of distinctive clustering observed for communal land and Mopaneveld. However *Portulaca hereroensis, Urochloa mosambicensis, Blepharis integrifolia, Ocimum americanum, Tragus berteronianus, Zornia glochidiata, Schmidtia pappophoroides, Enneapogon cenchroides, Aristida adscensionis, Corchorus confusus* and *Digitaria eriantha* contributed to >20% of compositional differences between protected Mopaneveld and communal land (Table A2; Appendix A). Composition of strip mines were similar compared to protected Mopaneveld (R=0.165) and thus overlapped (Figure 5.2b; NMDS stress value = 0.26). However assemblages of strip mine cuts and trench mines clustered apart from one another (Figure 5.2b). The grasses *Urochloa mosambicensis, Aristida adscensionis, Schmidtia pappophoroides, Enneapogon cenchroides,* and *Digitaria eriantha*, and forbs *Ocimum americanum, Phyllanthus incurvus, Tephrosia purpurea* and *Kyphocarpa angustifolia*, were responsible for >20% of compositional differences between strip mines and protected Mopaneveld (Table A2; Appendix A). Mine dumps displayed distinctive assemblages, with rock and tailings dumps showing an affinity to protected Mopaneveld (R=0.572), but less so with koppies (R=0.774) (Figure 5.2c; NMDS stress value = 0.17). Compared to protected Mopaneveld, the grasses *Enneapogon cenchroides, Cenchrus ciliaris, Stipagrostis hirtigluma* and *Urochloa mosambicensis* and forbs *Tephrosia purpurea* and *Sesbania bispinosa*, were responsible for >20% of compositional differences on mine dumps (Table A2; Appendix A). The grasses *Cenchrus ciliaris, Enneapogon cenchroides, Panicum maximum,* and *Stipagrostis hirtigluma* and forbs *Commelina benghalensis* and *Tephrosia purpurea* contributed >20% of compositional differences between mine dumps and koppies (Table A2; Appendix A).

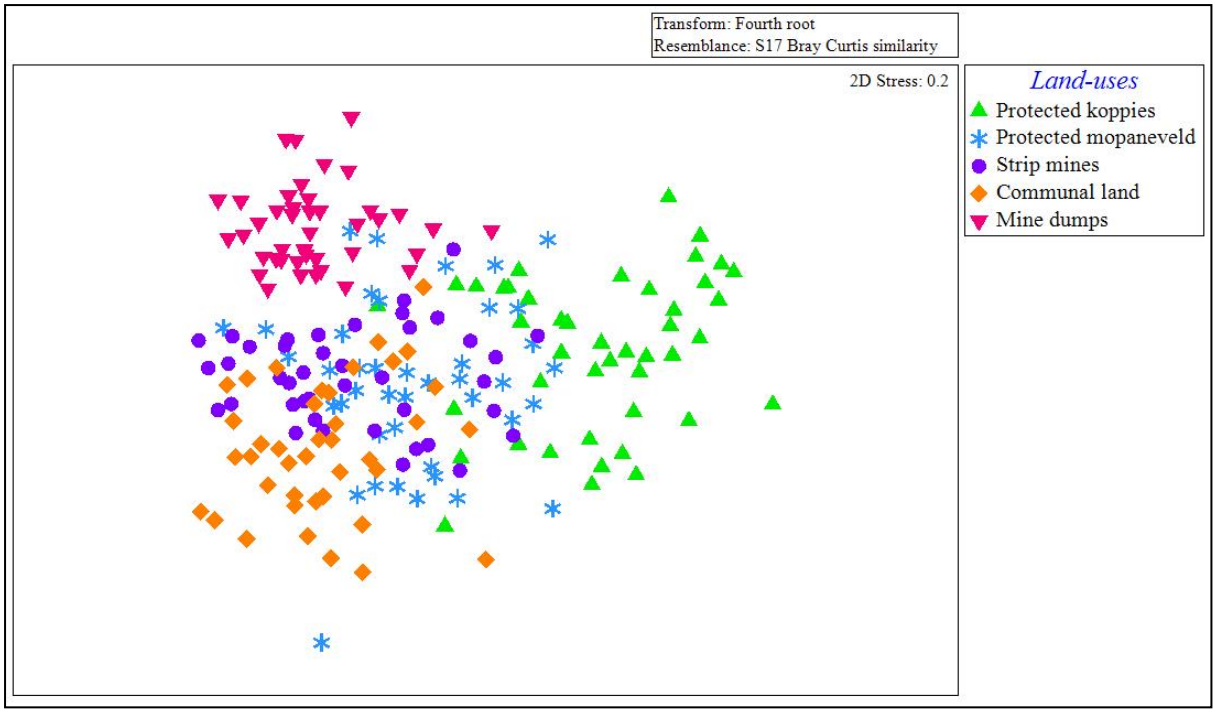


**Figure 5.1. Non-metric Multi-dimensional Scaling (NMDS) scatter plot of quadrats of the five land-uses.**

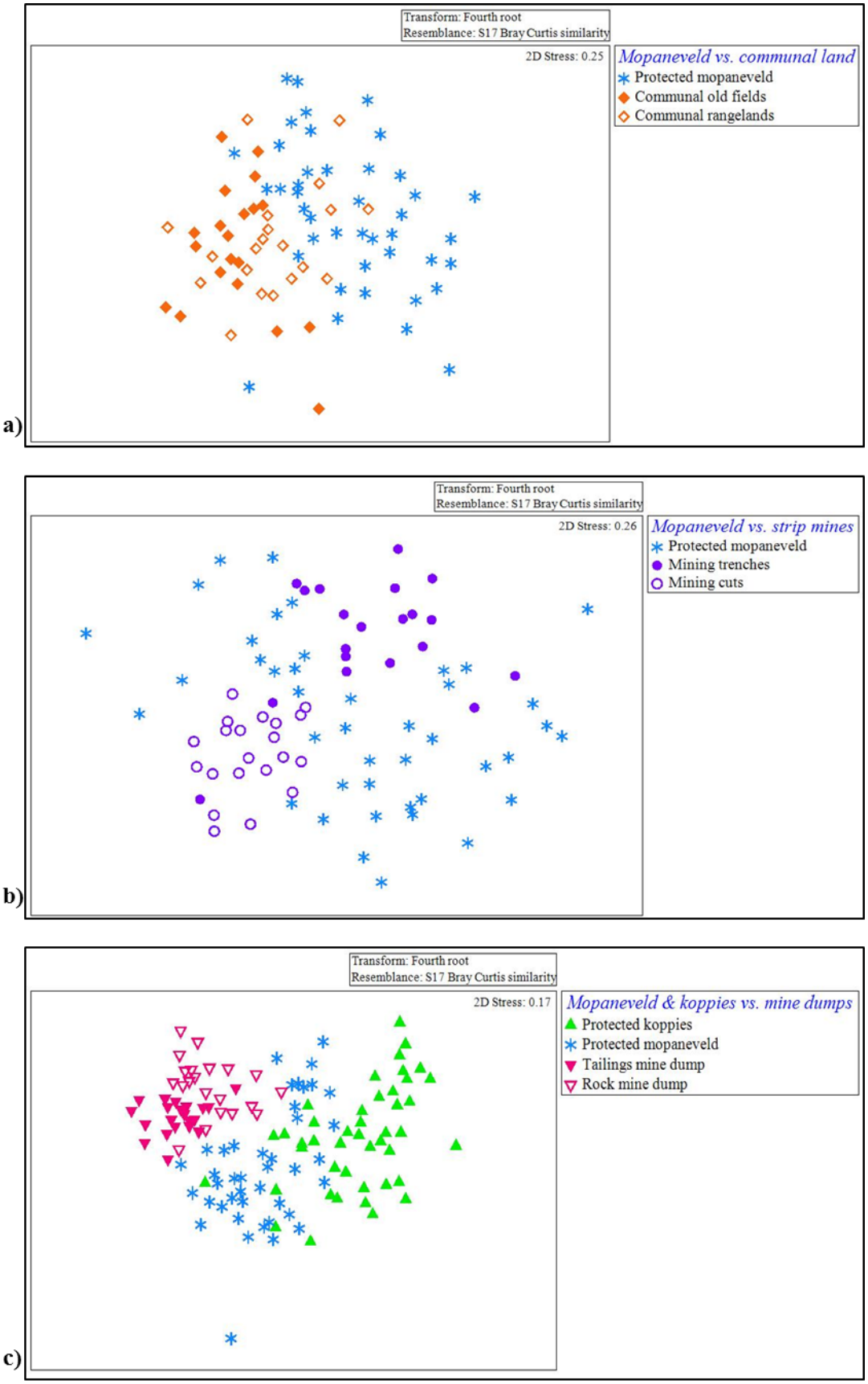


**Figure 5.2. Multi-dimensional Scaling (NMDS) scatter plots of species assemblages of various land-uses benchmarked against natural Mopaneveld (a, b). Note that mine dump vegetation was benchmarked against both protected Mopaneveld and koppies (c) due to the elevation of mine dumps.**

### 5.3.2. Species composition and environmental variables

CCA analyses identified bare soil, biomass, debris and vegetation height as the most important explanatory variables driving differences in community structure (Figure 5.3). Bare soil, vegetation height and debris were aligned along the first axis indicating a gradient of ground cover along this axis. Therefore the negative limit of the first axis was characterized by habitats with high bare soil, low debris and low vegetation height (i.e mine dumps and communal lands) while the positive limit was characterised by habitats with high debris and vegetation height (i.e. Mopaneveld and koppies) (Figure 5.3 and see Appendix A; Tables for weighted correlation matrix and additional statistical information). Biomass, grass and forb cover were aligned along the second axis indicating a gradient of herbaceous cover along this axis. The positive extremity of the second axis was characterized by samples with high biomass and herbaceous (grass and forbs) cover and vice versa for the negative extremity. No clear clustering of land-use samples were observed along the second axis (Figure 5.3).

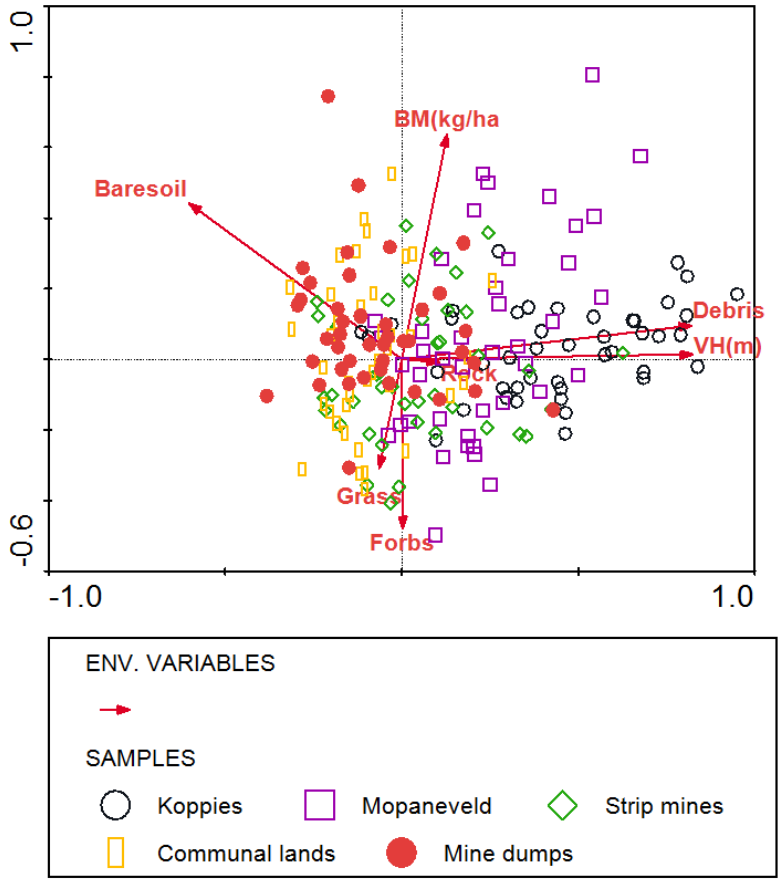


**Figure 5.3. CCA biplot comparing variables and land-uses based on species composition. Percentage cover of grass, forbs, rock, debris and bare soil; BM, biomass; VH, vegetation height.**

**Table 5.1. Summary of similarity percentage analyses (SIMPER) indicating cumulative contributions of species across land-uses. Species contributing ≥ 2% to compositional differences are presented in bold. Av. dis., Average dissimilarity; Cont.(%), Contribution (%).**

| Species | Across all land-uses | | Koppies *vs.* Mine dumps | | Mopaneveld *vs.* Mine dumps | | Mopaneveld *vs.* Koppies | | Mopaneveld *vs.* Strip mines | | Mopaneveld *vs.* Communal land | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Av. dis.** | **Cont. (%)** | **Av. dis.** | **Cont. (%)** | **Av. dis.** | **Cont. (%)** | **Av. dis.** | **Cont. (%)** | **Av. dis.** | **Cont. (%)** | **Av. dis.** | **Cont. (%)** |
| Overall | 91.37 | - | 96.63 | - | 91.11 | - | 92.33 | - | 85.51 | - | 87.78 | - |
| *Acalypha indica* | 1.16 | 1.269 | **2.075** | **2.148** | 1.305 | 1.432 | 1.772 | 1.919 | 0.955 | 1.117 | - | - |
| *Aristida adscensionis* | **2.56** | **2.802** | **2.388** | **2.471** | **2.301** | **2.526** | **2.43** | **2.632** | **3.133** | **3.664** | 1.821 | **2.075** |
| *Aristida congesta* | 1.349 | 1.477 | **2.03** | **2.101** | **2.046** | **2.246** | 0.967 | 1.047 | 1.016 | 1.189 | 1.256 | 1.431 |
| *Aristida scabrivalvis* | 1.355 | 1.483 | **2.429** | **2.514** | **2.338** | **2.566** | 1.295 | 1.403 | 1.054 | 1.232 | 1.217 | 1.386 |
| *Blepharis integrifolia* | 1.347 | 1.475 | - | - | - | - | - | - | 0.966 | 1.129 | **2.299** | **2.619** |
| *Cenchrus ciliaris* | 1.833 | **2.006** | **5.347** | **5.533** | **4.078** | **4.476** | - | - | - | - | - | - |
| *Commelina benghalensis* | 1.752 | 1.918 | **3.86** | **3.995** | - | - | **3.467** | **3.755** | 0.864 | 1.01 | - | - |
| *Digitaria eriantha* | 1.377 | 1.507 | - | - | 1.465 | 1.608 | **2.196** | **2.378** | 1.69 | 1.976 | 1.593 | 1.815 |
| *Enneapogon cenchroides* | **2.848** | **3.117** | **5.182** | **5.363** | **4.18** | **4.588** | **2.743** | **2.97** | **2.212** | **2.586** | **1.951** | **2.223** |
| *Hibiscus micranthus* | 1.198 | 1.311 | 1.427 | 1.477 | 1.744 | 1.914 | **2.147** | **2.326** | 1.57 | 1.836 | 1.382 | 1.574 |
| *Indigastrum costatum* | 0.976 | 1.068 | **2.762** | **2.859** | **2.229** | **2.446** | - | - | - | - | - | - |
| *Kyphocarpa angustifolia* | 1.569 | 1.717 | - | - | 1.528 | 1.678 | 1.77 | 1.917 | **2.128** | **2.489** | 1.438 | 1.638 |
| *Ocimum americanum* | **2.214** | **2.422** | - | - | **2.093** | **2.297** | **2.439** | **2.642** | **2.714** | **3.174** | **2.234** | **2.545** |
| *Panicum maximum* | **2.078** | **2.275** | **3.866** | **4.001** | 1.555 | 1.707 | **3.446** | **3.732** | 1.613 | 1.886 | 1.314 | 1.497 |
| *Phyllanthus incurvus* | 1.293 | 1.415 | - | - | - | - | - | - | **2.304** | **2.695** | 0.815 | 0.928 |
| *Portulaca hereroensis* | 1.191 | 1.303 | - | - | - | - | - | - | - | - | **2.751** | **3.134** |
| *Schmidtia pappophoroides* | 1.797 | 1.967 | - | - | **1.841** | **2.021** | **2.118** | **2.294** | **2.289** | **2.677** | **2.029** | **2.311** |
| *Sesbania bispinosa* | 1.019 | 1.115 | **3.15** | **3.26** | **2.461** | **2.701** | - | - | - | - | - | - |
| *Stipagrostis hirtigluma* | 1.183 | 1.295 | **3.651** | **3.778** | **2.859** | **3.138** | - | - | - | - | - | - |
| *Tephrosia purpurea* | **2.251** | **2.463** | **3.457** | **3.577** | **2.758** | **3.027** | 1.759 | 1.905 | **2.162** | **2.528** | 1.528 | 1.74 |
| *Tephrosia rhodesica* | 0.794 | 0.869 | **2.351** | **2.433** | **1.857** | **2.039** | - | - | - | - | - | - |
| *Tragus berteronianus* | 1.588 | 1.738 | - | - | - | - | - | - | 1.564 | 1.829 | **2.227** | **2.537** |
| *Urochloa mosambicensis* | **3.262** | **3.57** | **2.484** | **2.571** | **2.559** | **2.809** | **2.224** | **2.409** | **3.925** | **4.591** | **2.597** | **2.959** |
| *Zornia glochidiata* | 1.299 | 1.422 | - | - | 0.873 | 0.958 | 0.979 | 1.06 | 1.049 | 1.226 | **2.206** | **2.513** |

**Table 5.2. One-way ANOVA and Kruskal-Wallis ANOVA results of the mean values for herbaceous species richness, density and diversity measures across land-use types.**

| Statistical approach | Response | Data transformation | Source | *df* | SS | MS | F | p |
|---|---|---|---|---|---|---|---|---|
| **One-Way ANOVA** | Species richness | $4^{th}$ root | Land-use | 4 | 2.92 | 0.73 | 23.25 | <0.001* |
| | | | s.e. | 204 | 6.41 | 0.03 | | |
| | Simpson | – | Land-use | 4 | 0.20 | 0.05 | 1.69 | 0.15 |
| | | | s.e. | 204 | 6.16 | 0.03 | | |
| **Kruskal-Wallis ANOVA** | Density | $4^{th}$ root | Land-use | 4 | – | – | – | <0.001* |
| | Margalef species richness | – | Land-use | 4 | – | – | – | <0.001* |
| | Pielou's evenness | – | Land-use | 4 | – | – | – | <0.001* |
| | Shannon-Wiener diversity index | – | Land-use | 4 | – | – | – | 0.13 |

s.e., standard error; *df*, degrees of freedom; SS, sum of squared differences; MS, mean square; *F*, whether variability within and between treatments is significantly different; *p*, *p*-values marked with an * indicate significant differences between groups.

### 5.3.3. Species richness

One-way ANOVA revealed significant differences ($p<0.001$; $F=23.25$, Table 5.2) across land-use treatments for species richness. A total of 282 herbaceous plant species were recorded across all land-uses. In the communal lands a total of 141 species were recorded (Table 5.3). Communal farmlands had highest mean species richness (Figure 5.4a, c) which was significantly higher compared to koppies (Unequal N Tukey HSD test, $p<0.001$), protected Mopaneveld ($p=0.032$), strip mines ($p=0.005$) and mine dumps ($p<0.001$) (Figure 5.4a). In protected Mopaneveld 138 species were recorded (Table 5.3). The second largest mean species richness was displayed by protected Mopaneveld followed by strip mines (Figure 5.4a, c). Protected Mopaneveld had significantly higher species richness than koppies ($p<0.001$) and mine dumps ($p=0.005$) (Figure 5.4a). A total of 107 species was recorded on koppies (Table 5.3) and had lowest mean species richness (Figure 5.4a); i.e. significantly ($p<0.05$) lower compared to other land-uses. Mine dumps had the lowest mean Margalef species richness (Figure 5.4c) which was significantly lower compared to protected Mopaneveld ($p=0.002$) and communal land ($p<0.001$).

### 5.3.4. Number of individuals per plot (used as a measure of density)

Kruskal-Wallis ANOVA by ranks revealed significant differences ($p<0.001$, Table 5.2) across land-use treatments for density. In communal land, 7 825 individuals were recorded from 40 quadrats, whereas protected Mopaneveld had only 2 910 individuals from 42 quadrats (Table 5.4). Strip mines

had the second highest mean density, followed by mine dumps. Based on the 2-tailed multiple comparison, communal lands had significantly higher mean density per plot compared to koppies ($p<0.001$), protected Mopaneveld ($p<0.001$) and mine dumps ($p=0.010$) (Figure 5.4b). Mean density of strip mines was significantly higher compared to koppies ($p<0.001$) and protected Mopaneveld ($p=0.006$). A total of 1 503 individuals was recorded on koppies from 44 quadrats (Table 5.4) which had the lowest mean density and differed significantly from all other land-uses ($p<0.05$) (Figure 5.4b).

### 5.3.5. Evenness

Kruskal-Wallis ANOVA by ranks revealed significant differences ($p<0.001$, Table 5.2) across land-use treatments for evenness. Koppies had significantly higher mean evenness per plot compared to all land-uses ($p<0.05$) (Figure 5.4d). Natural, protected areas had the second highest mean evenness followed by mine dumps. Communal land and strip mines had the lowest mean evenness. Communal lands were primarily dominated by *Portulaca hereroensis, Bulbostylis burchellii, Bulbostylis humilis, Hypertelis bowkeriana* and *Urochloa mosambicensis.* Strip mines were dominated by *Urochloa mosambicensis, Portulaca hereroensis, Ocimum americanum, Aristida adscensionis* and *Bulbostylis burchellii.*

### 5.3.6. Diversity

No significant differences were detected for Shannon-Wiener (Kruskal-Wallis ANOVA; $p>0.05$, Table 5.2) and Simpson (One way ANOVA; $p>0.05$; $F=1.69$, Table 5.2) diversity indices across land-uses (Figure 5.4e, f). None-the-less, some patterns were discernable between land-uses. Since communal land displayed highest mean species richness and density but low evenness, diversity of communal land was not the highest. Protected Mopaneveld had the highest mean Shannon-Wiener diversity index followed by communal land (Figure, 5.4e). Koppies and protected Mopaneveld displayed the highest mean Simpson diversity index (Figure 5.4f). Strip mines had average species richness and density, but low evenness and thus the lowest mean Simpson diversity (Figure 5.4e, f).

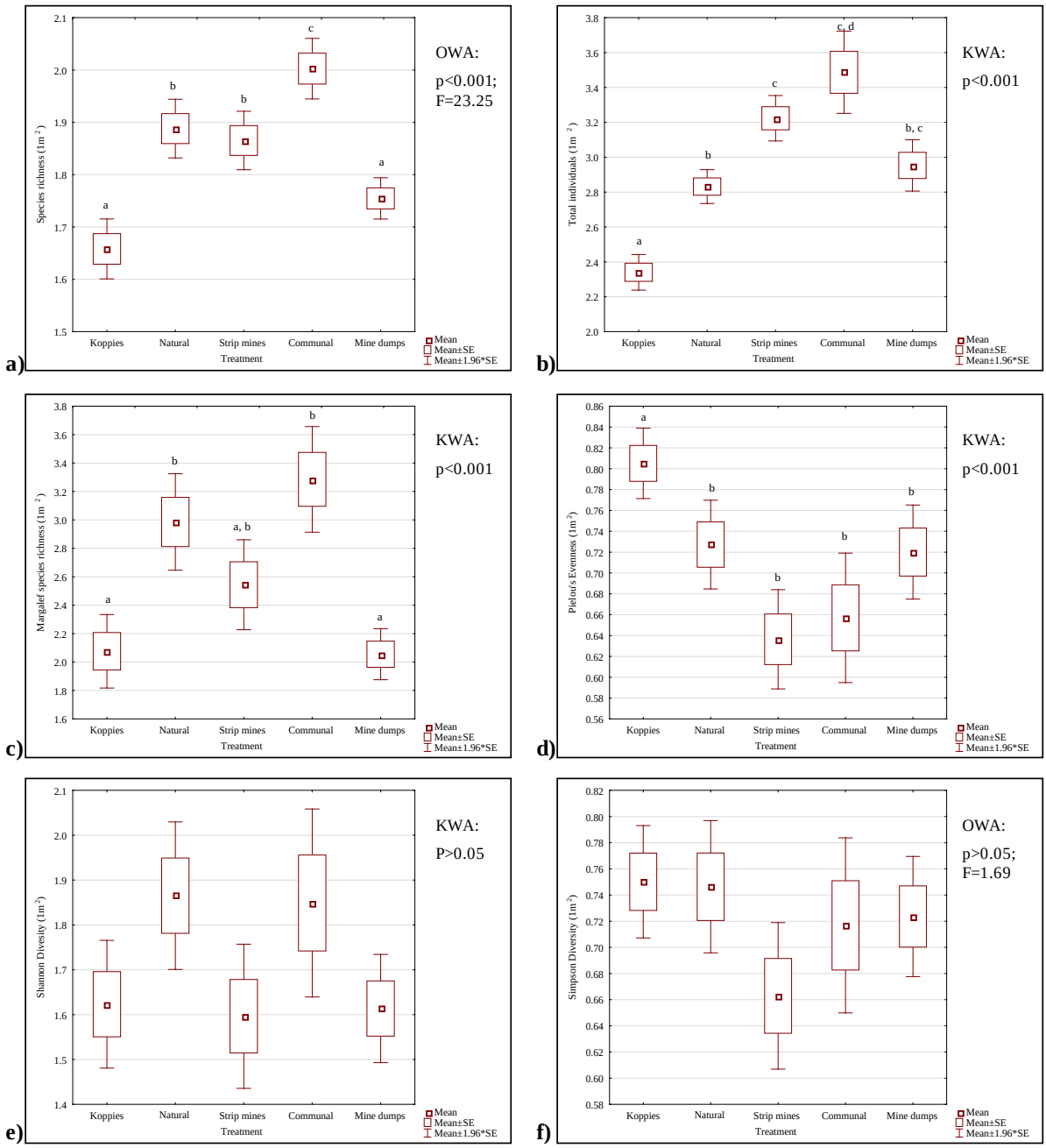


**Figure 5.4. Diversity indices of various land-uses, a) species richness, b) total individuals, c) Margalef's species richness, d) Pielou's evenness, e) Shannon-Wiener diversity and f) Simpson diversity. OWA: One-Way ANOVA; KWA: Kruskal-Wallis ANOVA. Similar letters denote no significant differences. (Natural denotes protected Mopaneveld).**

**Table 5.3. Summary of species richness across various land-uses as well as mean species richness per plot. The land-use with highest species richness is presented in bold. Note that untransformed species richness is displayed.**

| Land-uses | **Recorded species** | **Mean species richness per 1m² plot** |
|---|---|---|
| Koppies | 107 | 8.15909 |
| Mopaneveld | 138 | 13.42857 |
| Strip mines | 124 | 12.78049 |
| **Communal land** | **141** | **16.87500** |
| Mine dumps | 69 | 9.78571 |
| Overall | 282 | 12.11962 |

**Table 5.4. Summary of recorded individuals (as a function of density) across various land-uses as well as mean density per plot. The land-use with the highest density is presented in bold. Note that untransformed density is displayed.**

| Land-uses | **Recorded individuals** | **Mean density per 1m² plot** |
|---|---|---|
| Koppies | 1 503 | 34.1591 |
| Mopaneveld | 2 910 | 69.2857 |
| Strip mines | 4 899 | 119.4878 |
| **Communal land** | **7 825** | **195.6250** |
| Mine dumps | 3 727 | 88.7381 |
| Overall | 20 864 | 99.8278 |

### 5.3.7. Native and exotic diversity

Exotic species were present in all land-use plant communities (Figure 5.5 and Figure 5.6). Comparing the total number (Figure 5.5 a, c, e) and abundance of exotic species, koppies, Mopaneveld and strip mines had similar percentages. *Achyranthes aspera*, *Bidens bipinnata* and *Mollugo nudicaulis* were recorded on koppies. In Mopaneveld *Achyranthes aspera*, *Bidens bipinnata*, *Mollugo nudicaulis* and *Gomphrena celosioides* were recorded, whereas *Achyranthes aspera*, *Hybanthus enneaspermus*, *Mollugo nudicaulis* and *Portulaca oleracea* were present on strip mines. Compared to Mopaneveld and koppies, communal lands and mine dumps had higher percentages (Figure 5.6 a, c) of exotic species, which were also high in abundance (Figure 5.6 b, d). Communal lands had the highest number of exotic species, which consisted of *Gomphrena celosioides*, *Schkuria pinnata*, *Mollugo nudicaulis*, *Bidens bipinnata*, *Boerhavia erecta*, *Digitaria didactyla*, *Boerhavia cordobensis*, *Tridax procumbens*, *Acanthospermum hispidula*, *Alternanthera pungens*, *Achyranthes aspera*, *Boerhavia diffusa* and *Guilleminea densa*. The mine dumps had the highest abundance of exotic species. *Tridax*

*procumbens*, *Sesbania bispinosa*, *Pennisetum setaceum*, *Euphorbia hirta* and *Boerhavia erecta* were recorded on the mine dumps.

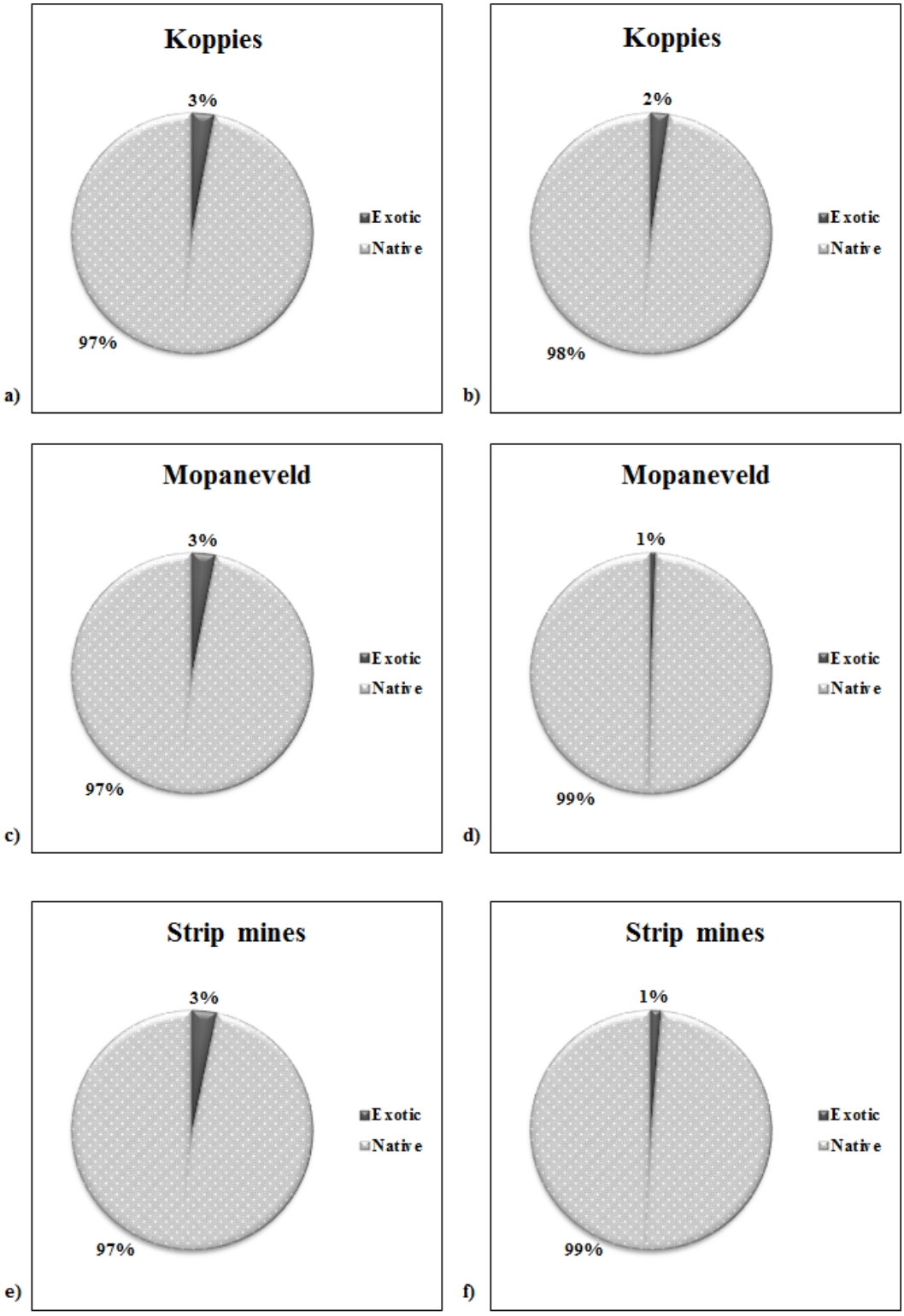


**Figure 5.5. Percentage exotic and native species recorded (a, c, e) and percentage abundance of these species (b, d, f) across land-uses.**

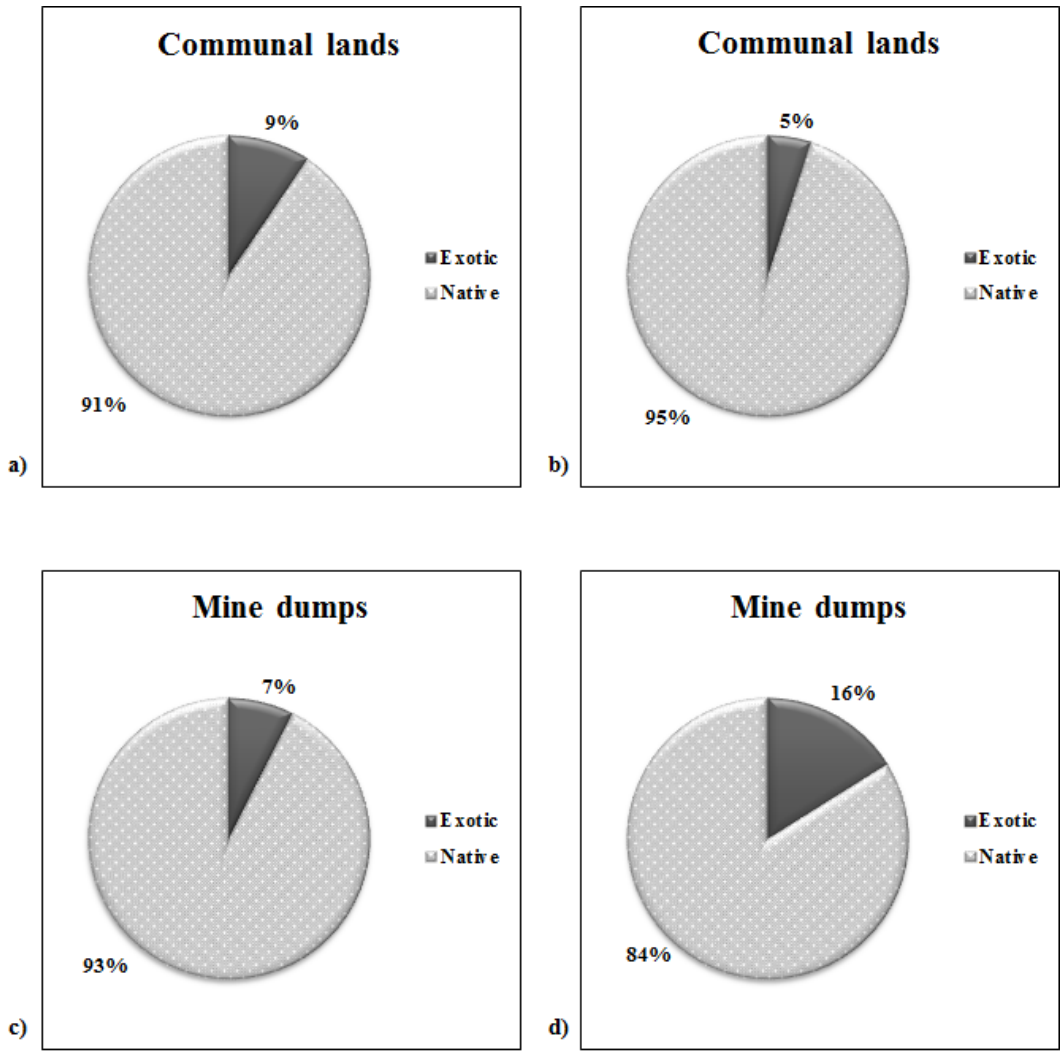


**Figure 5.6. Percentage exotic and native species recorded (a, c) and percentage abundance of these species (b, d) across land-uses.**

## 5.4. Discussion

This study revealed that drivers of plant community composition was associated either with natural environmental drivers (koppies and Mopanevelds) *vs.* anthropogenic disturbances (communal lands, strip mines and mine dumps) and natural succession (strip mines) *vs.* cultivation (communal lands) and remediation (mine dumps). Some environmental variables also contributed to observed compositional differences. Furthermore, each land-use was characterised by unique floristics.

### 5.4.1. Composition of different land-use plant communities

Land-uses are responsible for alterations in biotic (e.g. competition, species interactions, trophic structure) and abiotic (e.g. soil conditions, biogeochemical cycles, availability of resources) factors in human-dominated ecosystems (Shackleton *et al.*, 1994; Bradshaw, 1997; Vitousek *et al.*, 1997; Chapin *et al.*, 2000; Hillebrand *et al.*, 2008) and hence are considered as an environmental filter (Van

Noordwijk *et al.*, 2004; Mayfield *et al.*, 2005; Mandle & Ticktin, 2013). Different species in the species pool react differently to environmental stress (Yachi & Loreau, 1999), with some species not able to adapt to these conditions due to disturbance intolerance, stress-tolerant species will then establish successfully (Mackey & Currie, 2001). Communal land tenure, strip mining and mine dumps influenced herbaceous composition of Mopaneveld. Similar findings have been found where land-use practices influenced composition and species richness of various communities, including riparian, woody and herbaceous vegetation, across various biomes (Thrash *et al.*, 1993; Shackleton *et al.*, 1994; Parsons *et al.*, 1997; Todd & Hoffman, 1999; Hillebrand *et al.*, 2008; Meek *et al.*, 2010; Davis *et al.*, 2013; Rutherford & Powrie, 2013). The SIMPER analysis identified those key herbaceous species which were responsible for differences in the herbaceous plant composition found on the different land-uses. Grass species such as *Urochloa mosambicensis, Enneapogon cenchroides, Schmidtia pappophoriodes, Aristida adscensionis, Digitaria eriantha, Cenchrus ciliaris* and *Stipagrostis hirtigluma* and forbs *Ocimum americanum* and *Tephrosia purpurea* were responsible for driving differences between protected and anthropogenically disturbed plant communities and can be considered disturbance tolerant. Here, anthropogenic land-uses, excluding protected areas, can be considered as an environmental filter altering the species pool as stress sensitive species are replaced by stress-tolerant species (Van Noordwijk *et al.*, 2004; Mayfield *et al.*, 2005; Mandle & Ticktin, 2013). Therefore, species that are good colonisers under stressful environmental conditions will become dominant in the species pool of disturbed communities (Mackey & Currie, 2001; Begon *et al.*, 2006). As expected the key grass species that contributed the most to dissimilarities between land-use communities were mainly colonising pioneer, increaser II species and can be considered as good indicators of disturbed environments (Van Oudtshoorn, 2009). Secondary succession in these disturbed communities is promoted since key grass species can be facilitators (Begon *et al.*, 2006). It is expected that the two key forb species *Ocimum americanum* and *Tephrosia purpurea* have the ability to grow under stressful environmental conditions since it is known that some forbs are well adapted to be resistant against disturbance such as fire (Ngwenya, 2012), display certain defence mechanisms against herbivory (Abusuwar & Ahmed, 2010) and can successfully survive in harsh conditions like sodic zones (Van Coller *et al.*, 2013). Generally forbs are grouped as increaser II species; however some species tend to be decreasers (Ngwenya, 2012). Thus in a disturbed area, forbs can also fulfil a pioneer role similar to certain grass species.

Grazing and trampling affects the topsoil in communal lands. In semi-arid regions a shift from palatable to unpalatable vegetation is possible in communal land under heavy grazing Trampling caused by livestock alters soil conditions, such as reduced infiltration and water storage capacity (Harrison & Shackleton, 1999). Rutherford *et al.* (2012) reported reduced canopy cover and plant height in communal lands which is also applicable to communal lands of this study since percentage

bare soil increased and vegetation height decreased. With reference to strip mines, where the topsoil and savanna canopy is removed, the seed bank in the soil is disturbed (Blignaut & Milton, 2005), soil erosion is increased (Bradshaw, 1997; Yang *et al.*, 2014), soil organic matter and soil fertility is reduced (Bradshaw, 1997; Mills & Fey, 2003), the species composition and diversity of the herbaceous layer is altered (Yang *et al.*, 2014). In both communal lands and strip mines, fast colonising pioneer grass species, were evident. *Urochloa mosambicensis*, a weak perennial, palatable grass was especially prominent. Its stolons and dense growth form protect the soil against erosion and limit evaporation rates (Van Oudtshoorn, 2009). *Tragus berteronianus* and *Aristida adscensionis* are pioneer, annual, unpalatable grass species which colonise disturbed soil and eventually improve growing conditions for other herbaceous species (Van Oudtshoorn, 2009). *Enneapogon cenchroides*, an annual or weak perennial species, also protect disturbed veld (Van Oudtshoorn, 2009). However the drought resistant and grazing tolerant perennial grass species, *Schmidtia pappophoroides*, which is not characteristic of disturbed habitats (Van Oudtshoorn, 2009), was also found in the communal lands and strip mines, indicating that this grass may be resistant to disturbances. A shift in the grass layer is evident, to assemblages of unpalatable grass species. However, these grass species provide certain regulating ecosystem services in the communal lands. Furthermore, it is expected that the forb species *Ocimum americanum, Phyllanthus incurvus, Tephrosia purpurea* and *Kyphocarpa angustifolia* are adapted to prevail in marginal disturbances and totally transformed landscapes.

Mine dumps displayed a unique herbaceous composition in comparison with protected areas (koppies and Mopaneveld). This was not surprising as literature indicates that natural vegetation is completely altered by mining practices due altered abiotic conditions (Jonnalagadda & Nenzou, 1997; Sheoran *et al.*, 2010; Ashraf *et al.*, 2011; Anawar *et al.*, 2013; Domingo & David, 2014). It is well known that mining alters soil conditions and can be responsible for toxicity of certain accumulating metals in soil (Bradshaw, 1997; Martínez-Ruiz *et al.*, 2007). Species, characteristic to mine dump communities, display certain environmental preferences, enabling them to successfully establish in such a harsh environment. *Stipagrostis hirtigluma*, a perennial, unpalatable, increaser II pioneer grass species, prefers rocky and or sandy habitats (Van Oudtshoorn, 2009). *Cenchrus ciliaris*, a perennial, palatable decreaser species, prefers a variety of soil types (Van Oudtshoorn, 2009). *Aristida scabrivalvis*, an annual unpalatable pioneer and increaser II species, prefers disturbed sandy and shallow soils (Van Oudtshoorn, 2009). Forb species in the Fabaceae (legume family) were characteristic on mine dumps and included *Tephrosia purpurea, Tephrosia rhodesica, Sesbania bispinosa* and *Indigastrum costatum.* Species belonging to the Fabaceae are known to have nitrogen fixating abilities (Van Wyk & Malan, 1998). Nitrogen-fixating species have the ability to occur on a wide variety of substrates and in a variety of environmental conditions (Marrs & Bradshaw, 1993; Sprent, 1993; Bradshaw, 1997). According Pedrol *et al.* (2014) leguminous species is selected as pioneer species to improve

soil structure and soil fertility (Leisman, 1957; Domingo & David, 2014). Domingo and David (2014) found that leguminous species have the ability to significantly improve the concentration of phosphorous, increase organic matter and decrease concentrations of heavy metals on mine dumps. Therefore it is expected that these four forb species have a competitive advantage on mine dump facilities where it can contribute to soil nitrogen capital, deposition of organic matter (Bradshaw, 1997; Anawar *et al.*, 2013; Domingo & David, 2014) and also fulfil a facilitation role (Begon *et al.*, 2006). However since forbs are not included in seed mixes used on mine dumps, the selection of leguminous forb species may contribute to re-vegetation and fulfil important ecological roles (i.e. improve soil conditions, prevent soil erosion etc.) on mine dumps (Bradshaw, 1997; Domingo & David, 2014). This study therefore identifies the need for further investigations regarding the inclusion of forb species in rehabilitation practices.

Koppies displayed distinct assemblages which can be ascribed to the micro-climatic variability theory (Burke, 2002a; Burke, 2003) since aspect and altitude contributes to high species turnover (Burke, 2012). Generally it is hypothesized that koppies function as bioclimatic islands as stated by the island biogeography theory (Burke, 2003). Therefore the koppies in this study can be considered as scattered 'islands' in a matrix of Mopaneveld. It is also expected that species prevailing on the koppies are specialist species (Porembski *et al.*, 1996). Since rock-overhangs and trees over-shade the herbaceous layer on koppies, a suitable habitat is provided for species such as *Commelina benghalensis* and *Panicum maximum*, both shade-tolerant species.

### 5.4.2. Floristics of land-use communities

#### 5.4.2.1. Species richness

In this study communal land displayed highest species richness. This is in accordance with the intermediate disturbance hypothesis and compared favourably with studies of Shackleton (2000) and Rutherford *et al.* (2012) in savanna ecosystems. A study conducted in Namaqualand in the Succulent Karoo biome also found that communal rangelands are species rich (Todd & Hoffman, 1999). Todd and Hoffman (1999) reasoned that the fine-scale heterogeneity of Namaqualand contributed to observed species richness levels which also compared favourably with a study of Mediterranean rangelands of Israel (Naveh & Whittaker, 1980). However Naveh and Whittaker (1980) ascribed the high diversity of heavily grazed rangelands to the high evolutionary history of grazing under combinations of drought, fire and climate as well as the small-scale heterogeneous character of mountains. The studies of Naveh and Whittaker (1980) and Todd and Hoffman (1999) may be applicable to Mopaneveld. Since the protected Mopaneveld land-use type had the second highest species richness and diversity in this study it is expected that due to patch dynamics, undisturbed Mopaneveld surrounding communal areas may cause an influx of species into communal lands. Consequently, due to communal lands' high species richness, these plant communities can be buffered

against disturbances. Therefore this study compares favourably with other studies conducted in grassland and savanna areas which suggest that communal lands can be considered resilient. (Shackleton, 1993; Shackleton *et al.*, 1994; Harrison & Shackleton, 1999; Rutherford & Powrie, 2011). Low levels of species richness on the mine dumps can be ascribed to total land transformation of mining practices. Seed mixes introduced included grass species such as *Eragrostis tef, Anthephora pubescens*, *Cynodon dactylon,Cenchrus ciliaris*, *Panicum maximum*, *Digitaria eriantha* and *Chloris gayana* on mine dumps to promote succession (Surmon, 2010). Therefore the low species richness mine dumps may be ascribed to the possibility that not all seeds established successfully or that succession occurs slowly due to prevailing environmental stress (Bradshaw, 1997). Success of mine dump rehabilitation depends on selected plant species for re-vegetation which have the ability to overcome limiting factors on mine dumps (Domingo & David, 2014). The species richness of koppies is low, and also characterised by uniquely adapted species adapted to the prevailing environmental conditions that are much harsher than the surrounding matrix (Porembski *et al.*, 1996).

5.4.2.2. Density

According to Grace (1999) the level of density is determined by disturbance effects, biomass, colonization of species, species pool and spatial heterogeneity. Density levels seem to be associated with percentage of bare soil. Communal lands, strip mines and mine dumps were characterised by high bare soil percentages (i.e. loss in biomass) and high plant densities. With increasing land-use intensity (koppies=low, Mopaneveld=low; strip mines=higher, communal lands=intermediate; mine dumps=very high), the relationship between density and land-use intensity is considered to be unimodal,since density peaked at intermediate land-use intensity (communal lands). This finding is in accordance with the study of Grace (1999). High density of individuals on the communal land can be ascribed to intermediate levels of disturbance, fast colonising pioneer, stoloniferous or creeping species. Similarly strip mines were also dominated by fast colonising pioneer species, which contributed to the intermediate level of density. Marginal disturbances therefore enhance density. High density observed for the mine dumps is ascribed to rehabilitation practices which aim to prevent water and soil erosion. The koppies were characterised by low levels of density and can be ascribed to the unique micro-climatic conditions prevailing on koppies which are described as edaphically dry habitats, which lead to high levels of competition (Porembski, 2000; Brand *et al.*, 2010).

5.4.2.3. Evenness

The relationship between species richness and evenness is negatively correlated for plants (Stirling & Wilsey, 2001; Wilsey *et al.*, 2005; Hillebrand *et al.*, 2008). Evenness can thus be seen as an unique measure of diversity (Stirling & Wilsey, 2001; Wilsey *et al.*, 2005). Despite its low species richness, koppies displayed the highest evenness. Even though extreme harsh environmental conditions (i.e. low soil moisture availability, high exposure to sunlight, soil erosion) prevail on koppies, it seems that

these communities are the most stable. High evenness found on the koppies can be ascribed to the minimum level of anthropogenic disturbances on koppies, species exchange rates which are in equilibrium and specialist species persisting on koppies are evenly distributed (Porembski *et al.*, 1996; Burke, 2002b). The low levels of evenness on the mine dumps can be ascribed to the seed mixes used to re-establish vegetation on mine dumps which introduced a few species that has the ability to colonise rapidly. Strip mines were characterised by the most uneven plant communities, dominated by a few species. Uneven communities are less resilient to disturbance factors (Wittebolle *et al.*, 2009). Therefore these communities can be more easily invaded by alien species (Wilsey & Polley, 2002). Results from this study therefore supports previous findings that evenness i) responds more rapidly than species richness, ii) is sensitive to anthropogenic disturbances and iii) is an important component in measuring changing diversity in human-dominated environments (Chapin *et al.*, 2000; Wittebolle *et al.*, 2009; Crowder *et al.*, 2010).

#### 5.4.2.4. Diversity

Both Shannon-Wiener and Simpson diversity indices indicated that protected areas were the most diverse. Strip mines (no rehabilitation) were characterised by the lowest diversity (Shannon-Wiener and Simpson diversity). Simpson diversity can be considered as an indicator of heterogeneity, indicating that land-uses, excluding protected areas, may be responsible for the homogenization of plant communities (McKinney & Lockwood, 1999; Hobbs *et al.*, 2009; Ellis *et al.*, 2012; Püttker *et al.*, 2015).

However, plant species diversity fails to quantify disturbance effects regarding ecosystem functioning (Lacroix & Abbadie, 1998; Cadotte *et al.*, 2011; Mouillot *et al.*, 2013; Hanke *et al.*, 2014) and stability (Mori *et al.*, 2013). This is because processes of community assembly - not species diversity *per se* - is effected by land-use change (Mayfield *et al.*, 2010). According Díaz and Cabido (2001) functional diversity is strongly associated with ecosystem function. Therefore analyzing functional diversity at the level of functional traits and/or plant functional groups, may be of greater assistance to quantify land-use effects on ecosystem functionality (Lavorel *et al.*, 1998; Villéger *et al.*, 2010; Hanke *et al.*, 2014). Consequently an understanding of ecosystem stability will be promoted (Díaz & Cabido, 2001; Elmqvist *et al.*, 2003; Flynn *et al.*, 2009; Cadotte *et al.*, 2011).

#### 5.4.2.5. Native and exotic diversity

According to Ellis *et al.* (2012) few native plant communities are still undisturbed and without exotic plant species. In Mopaneveld all land-use plant communities had a number of exotic species. Exotic or alien species are usually associated with disturbed areas and are considered to increase in numbers under anthropogenic disturbances (Goodall & Naude, 1998; Buckley *et al.*, 2007; Meek *et al.*, 2010; Ellis *et al.*, 2012; Schonbeck, 2013; Carreño-Rocabado *et al.*, 2015). However, exotic species in

disturbed plant communities may fulfil similar ecological roles as native plant species do (Ellis *et al.*, 2012). Plant communities of communal lands and mine dumps are considered examples thereof. The high number of exotic species on communal lands may be ascribed to high niche availability, high levels of disturbance by humans and livestock as well as the possibility of the validation of the intermediate disturbance hypothesis in communal lands (Shackleton, 2000; Rutherford *et al.*, 2012; Rutherford & Powrie, 2013). Some of these exotic species also displayed adaptations for external animal transport such as seeds with adhesive structures (hooks, barbs, awns etc.) and therefore can be easily dispersed by animals and humans. A study conducted by Rutherford and Powrie (2013) found that lightly grazed and highly grazed sites displayed low levels of exotics, indicating the possibility that at intermediate grazed levels, levels of exotics may be higher. On mine dumps exotic species may have been included in seed mixes (Martínez-Ruiz *et al.*, 2007) since these species can assist ecological succession (Cramer *et al.*, 2008). *Pennisetum setaceum* is a perennial grass which prevents soil erosion, contributes to soil stabilization and soil organic matter on mine dumps (Rahlao *et al.*, 2014). *Sesbania bispinosa* is a nitrogen fixing forb which can withstand the nitrogen deficiency associated with soils on mine dumps and therefore contribute to soil nitrogen capital and soil fertility (Bradshaw, 1997; Rethman, 2000; Anawar *et al.*, 2013; Domingo & David, 2014; Pedrol *et al.*, 2014; Mensah, 2015). Furthermore leguminous species also have the ability to successfully colonize bare soil (Rodríguez-Echeverría & Pérez-Fernández, 2005). Overall native species diversity was only affected on communal lands and mine dumps.

### 5.5. Summary

The results of this chapter suggests that different land-uses are characterised by different herbaceous species composition and different levels of richness and diversity. Different land-uses were characterized by different herbaceous species assemblages. Communal, mining and strip mining land-use practices had a filtering effect on composition of plant communities. In accordance with the intermediate disturbance hypothesis, species richness and density were enhanced by marginal disturbances (e.g. communal land-use). Since communal lands were associated with high species richness, relatively high species diversity and low species evenness the relevant hypothesis stated in this study is supported. There is a relationship between density, percentage bare soil and disturbance in plant communities of communal land, strip mines and mine dumps. Evenness was not enhanced by marginal disturbances on strip mines and communal lands or by total transformation on mined lands, which displayed low evenness. Evenness is sensitive to land-use change and is a good indicator of ecosystem health of anthropogenically disturbed ecosystems; hence management for evenness is important. All land-use plant communities were characterized by different levels of diversity. Total land transformation were responsible for species loss, however species loss was more severe on strip mines where no rehabilitation occurred, indicating the significance of rehabilitation practices. The hypothesis concerned with total transformation is partially supported with reference to strip mines

since species richness levels was high while species diversity and evenness levels was low. However since mine dump plant communities were associated with low levels of species richness, low species diversity and high evenness patterns, the hypothesis is supported. According to the diversity stability theory, species loss can result in unstable ecosystems, emphasizing future implications for the provision of ecosystem services. Therefore strip mines and mine dumps may be in an unstable vegetation state. However, dominant species may be able to compensate for certain ecosystem functions due to their unique traits ascribed to exposure to distinctive prevailing environmental conditions. Native species diversity was not severely affected. However communal lands and mine dumps had a higher number of exotic species, which were also high in abundance.

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# Chapter 6

# Response diversity of herbaceous plant species across land-uses

## 6.1. Introduction

A community with high species diversity is buffered against environmental disturbances and if species loss occurs in a community, then the ecosystem processes and services may deteriorate (Yachi & Loreau, 1999; Mori *et al.*, 2013). According to the diversity-stability theory and insurance hypothesis, a less diverse community may be unstable in the face of disturbances and may be more vulnerable to degradation (Yachi & Loreau, 1999; Chapin *et al.*, 2000; McCann, 2000; Allan *et al.*, 2011; Mace *et al.*, 2012). However, from an ecosystem function perspective only a small number of key species perform major ecosystem functions (Purvis & Hector, 2000; Zhang *et al.*, 2012). Loss of some species may not necessarily have functional consequences since some species have similar effects on ecosystem function (Díaz & Cabido, 2001; Mori *et al.*, 2013) and thus provide redundancy to a community (Naeem, 1998). Dominant species (Díaz & Cabido, 2001; Hanke *et al.*, 2014), or species in the tail of the distribution (Walker *et al.*, 1999; Kotschy, 2013), are able to compensate for the loss of species (Mori *et al.*, 2013). However, according Díaz and Cabido (2001), the greater the variation between species' responses (response diversity) in a community, the lower the species richness required to buffer the community against environmental changes. Therefore species richness *per se* is described as an incomplete measurement for vegetation change across a disturbance gradient (Wilsey *et al.*, 2005; Hanke *et al.*, 2014).

Functional diversity assumes a mechanistic link between diversity and ecosystem functioning (Díaz & Cabido, 2001; Zhang *et al.*, 2012; Mori *et al.*, 2013). By incorporating functional response traits, drivers of vegetation change can be better identified across a disturbance gradient (Hanke *et al.*, 2014; Lewis *et al.*, 2014). Functional response traits are described as reliable indicators of adaptation (Moretti & Legg, 2009). Therefore disturbance effects on ecosystem function (Wesuls *et al.*, 2012) and ecosystem resilience can be measured (Elmqvist *et al.*, 2003). Response diversity and functional redundancy are essential measures which contribute to resilience levels under anthropogenic pressure (Elmqvist *et al.*, 2003; Laliberte *et al.*, 2010). When anthropogenic pressure increases, response diversity may decrease, which could lead to lower resilience and hence, degradation of an ecosystem (Mori *et al.*, 2013). Therefore high response diversity will safeguard ecosystems against degradation due to its buffering effect (Elmqvist *et al.*, 2003; Baskett *et al.*, 2014).

Several studies have revealed that anthropogenic disturbances may be responsible for severe and even in some cases irreversible degradation of natural ecosystems (Vitousek *et al.*, 1997; Folke *et al.*, 2004; Reyers, 2004; Duffy, 2009; Flynn *et al.*, 2009; Bullock *et al.*, 2011; Ellis *et al.*, 2012; Rutherford *et*

*al.*, 2012; Mouillot *et al.*, 2013; Nagendra *et al.*, 2013; Amici *et al.*, 2015; Corlett, 2015; Laurila-Pant *et al.*, 2015; McGill *et al.*, 2015). Therefore it is important to quantify and evaluate responses of plant communities exposed to various anthropogenic disturbances. This process requires the identification of certain ecosystem functions responsible for the maintenance of fundamental ecosystem services which should be subjected to prioritization for conservation actions (Reyers, 2004; Nagendra *et al.*, 2013; Corlett, 2015; Laurila-Pant *et al.*, 2015). Taxonomic diversity measures such as species richness may not adequately capture land-use disturbance effects on ecosystem function (Purvis & Hector, 2000; Wilsey *et al.*, 2005; Crowder *et al.*, 2010; Villéger *et al.*, 2010; Hanke *et al.*, 2014). However, response diversity may be of valuable assistance since it describes various responses of plant species in a specific community exposed to certain environmental disturbance factors (Lavorel & Garnier, 2002; Elmqvist *et al.*, 2003; Folke *et al.*, 2004; Laliberte *et al.*, 2010; Mori *et al.*, 2013; Mouillot *et al.*, 2013). Response diversity together with redundancy fosters ecosystem resilience during anthropogenic pressure (Naeem, 1998; Elmqvist *et al.*, 2003; Nyström, 2006; Laliberte *et al.*, 2010; Chillo *et al.*, 2011; Baskett *et al.*, 2014). Therefore, since present value and understanding of response diversity in semi-arid savannas are poorly understood, this study investigates the relationship between species diversity, response diversity, redundancy, resilience and ecosystem functioning of anthropogenically disturbed Mopaneveld. In this regard the main aim of this chapter is to compare the response diversity of transformed and protected Mopaneveld by i) describing the plant functional groups of the herbaceous layer in Mopaneveld, ii) determining if land-uses in Mopaneveld are characterised by distinctive sets of functional groups, iii) comparing functional richness, evenness and diversity of traits and functional groups across land-uses and iv) provide preliminary observations regarding herbaceous species diversity and functional diversity patterns to habitat changes, facilitating comments regarding the level of resilience of anthropogenically disturbed Mopaneveld. The stated hypotheses (Chapter 1) that will be tested in this chapter are i) if the land-use disturbance entails total transformation (i.e. strip mines and mine dumps) then trait richness and trait diversity will decrease and trait evenness will increase, ii) if the land-use disturbance entails marginally disturbed disturbances (i.e. intermediate disturbance levels; communal lands), then trait richness and trait diversity will increase and trait evenness will decrease, iii) if land-use disturbance entails total transformation, then plant functional group richness, plant functional group diversity and plant functional group evenness will increase, and iv) if the land-use disturbance entails marginally disturbances, then plant functional group richness, plant functional group diversity and plant functional group evenness will increase. Furthermore the applicability of the hypotheses of Flynn *et al.* (2009) on land-use plant communities will be examined to 1) assess prelimary response patterns of species richness, species diversity and functional diversity, and 2) contribute to conclusions regarding redundancy and resilience of anthropogenically disturbed Mopaneveld.

## 6.2. Data analysis

Methods for trait selection and general data analyses are given in Chapter 4. Analyses specific to this chapter are dealt with here.

A hierarchical cluster analysis in PRIMER 6 software (2012) was conducted to group species according the similarity of their traits into a dendrogram (see chapter 4 section 4.2. for a full description of the trait selection). Thereafter a Principal Co-ordinate Analysis (PCoA), using PAST (Hammer *et al.*, 2001) was conducted to describe functional groups based on their clustering due to characteristic plant traits. Some plant species were still unidentified at the time of data analysis. Such species were omitted from further analyses since species are trait specific. In Microsoft Excel 2007, trait-species and functional group-species matrices were each multiplied with a species-plot matrix using the MMult function to produce a trait-plot and functional group-plot matrix respectively. The trait-plot and functional group-plot matrices were used for further data analysis in PRIMER 6 software (2012), STATISTICA version 11 (2012) and Canoco for Windows version 4.5 (Ter Braak & Smilauer, 2002). Using PRIMER 6 software (2012), diversity analyses were conducted to indicate richness, evenness and diversity for functional traits and plant functional groups (Hanke *et al.*, 2014). In STATISTICA version 11 (2012), One-way ANOVA and Tukey's HSD for unequal N were performed on diversity indices to test for significant differences between land-uses. To determine whether land-uses were characterized by certain functional traits, functional groups and environmental variable data were further analysed in Canoco for Windows version 4.5 (Ter Braak & Smilauer, 2002). A DCA was conducted on traits, functional groups and environmental variables to determine if data had a unimodal or linear distribution by considering the gradient length. In this study, functional trait, functional group and environmental variable data were linear. Accordingly PCA and RDA analyses were performed since the variable data was linear (Ter Braak & Smilauer, 2002; Kent, 2012) (See Chapter 4 section 4.3.2.3). To emphasise the effects of certain land-uses on plant functional traits and plant functional groups of Mopaneveld, PCA was still included in the results as this indirect multivariate analysis is regarded as an effective analysis in plant ecology for analysing quadrats and abiotic variables (Kent, 2012). Note that environmental variable data was used to determine whether certain plant functional groups were associated with certain variables (See Chapter 4 section 4.3.3).

## 6.3. Results

### 6.3.1. Identification and description of plant functional groups

Eight plant traits across 272 herbaceous species in Mopaneveld were selected for analyses (see Chapter 4 section 4.1 and Table 4.2 for plant trait selection and categories). In the PCoA of plant functional traits, clusters of species were strongly associated with life history, weediness and Raunkiaer's life form (Figure 6.1). Each functional group was therefore labelled according to these

characteristic traits. From left to right across the ordination axis (Figure 6.1), groups were identifiable as weedy therophytes (Group 2), non-weedy therophytes (Group 6), weedy perennial hemicryptophytes and chamaephytes (Group 3), non-weedy perennial hemicryptophytes, chamaephytes and cryptophytes (Group 5), and leading into non-weedy perennial climbing phanerophytes (Group 1). The nitrogen fixers (Group 4) consisted of a combination of life forms, weedy, non-weedy, annual and perennial species (Table 6.1), which lead to clustering of these species in groups 2, 5 and 6 (Figure 6.1). Each plant functional group was described according to its associated plant traits (Table 6.1).

**Group 1 – Non-weedy perennial phanerophytes**

This group comprised of 18 species and was characterized by non-weedy perennial phanerophytes with a climbing habit (Table 6.1). Non-clonal species were most common (56%), as well as species with unassisted dispersal (44%). Shade tolerant species comprised 33% and shade intolerant species 28% of the group. Eleven of these species displayed a nitrogen fixing ability.

**Group 2 – Weedy therophytes**

This group consisted of 40 species of which all were weedy and annual (Table 6.1). Since all species were annual, the group was classified as therophytes. This group was characterized by erect (38%) and prostrate (30%) growth forms. Most species were non-clonal (84%). Species with unassisted dispersal comprised 40% of this group while species preferring external animal transport comprised 28%. Most of the weedy therophytes were sun tolerant (60%).

**Group 3 – Weedy perennial hemicryptophytes and chamaephytes**

This group consisted of 21 plant species of which all were perennial and weedy (Table 6.1). Species with an erect growth form were dominant (43%) followed by tussocked graminoids (29%). Only two life forms were present: hemicryptophytes (57%) and chamaephytes (43%). This group was characterized by non-clonal (67%) species. Unassisted dispersal comprised 43% of this group followed by species dispersed by means of internal animal transport (29%). More than half of the group's species were sun tolerant (52%).

**Group 4 – Nitrogen fixers**

This group consisted of 20 species and was distinguished as nitrogen fixing, non-clonal, unassisted dispersed, and sun tolerant species with predominantly erect (80%) growth forms (Table 6.1). Only 15% of species were weedy. Additionally 60% were annual therophytes, 25% were perennial chamaephytes and 15% perennial hemicryptophytes, explaining the separation of species in the PCoA (Figure 6.1).

**Group 5 – Non-weedy perennial hemicryptophytes, chamaephytes and cryptophytes**

This was the largest group, consisting of 128 plant species. All species were perennial and non-weedy (Table 6.1). A variety of growth forms were present in the group, however, erect (48%) and tussock (34%) growth forms were the most common. The characteristic life forms were identified as chamaephytes (47%) and hemicryptophytes (45%). Cryptophytes (9%) were only present in this group. More than two thirds of the species were non-clonal (69%). The mode of dispersal was diverse for this group and consisted mainly of unassisted dispersed (40%), wind dispersed (27%) and animal dispersed species (26%). Majority of species were sun tolerant (61%).

**Group 6 – Non-weedy therophytes**

Second largest group and consisted of 45 species of which all were non-weedy and annual (Table 6.1). The dominant life form was therophytes with an erect (49%) growth form. Species were mainly non-clonal (93%). Unassisted (44%) and wind (29%) dispersal was most common in this group. The group was characterized by shade intolerant species (67%).

### 6.3.2. Functional groups of land-uses

One-way ANOVA revealed significant differences across land-use treatments (Table 6.2) for functional group richness ($p<0.001$; $F=6.84$) and functional group evenness ($p<0.001$; $F=4.82$). No significant differences were detected for Shannon-Wiener ($p=0.54$; $F=0.78$) and Simpson ($p=0.11$; $F=1.94$) diversity of functional groups.

#### 6.3.2.1 Protected areas (koppies)

Plant functional groups that were strongly associated with the koppies included non-weedy perennial phanerophytes (PFG 1), weedy therophytes (PFG 2) and weedy perennial hemicryptophytes and chamaephytes (PFG 3) (Figure 6.2a), although all plant functional groups were present (Figure 6.4a). Groups with the highest frequency included non-weedy perennial hemicryptophytes, chamaephytes and cryptophytes (PFG 5 = 36%), PFG 2 (25%) and non-weedy therophytes (PFG 6 = 19%). Of all the land-uses, the koppies had the highest frequency of PFG 1 (4%) (Figure 6.4a), which was also positively correlated with koppies on the PCA and RDA axes respectively (Figure 6.2b, 6.3a). Nitrogen fixers (PFG 4 = 2%) was not common on the koppies and also negatively correlated with koppies (Figure 6.2b, 6.3a). Richness of functional groups of koppies was significantly lower ($p<0.05$) compared to all land-uses (Figure 6.5a). Highest evenness of functional groups was displayed by koppies, which was significantly higher than Mopaneveld ($p=0.002$) and strip mines

(p=0.002) (Figure 6.5b). No significant differences (p>0.05) could be detected in diversity of functional groups (Figure 6.5c, d). However koppies and mine dumps displayed similarly high Shannon-Wiener diversity of functional groups (Figure 6.5c). Koppies displayed the highest Simpson diversity of functional groups (Figure 6.5d) which can be ascribed to high level of functional group evenness.

#### 6.3.2.2 Protected areas (Mopaneveld)

Protected Mopaneveld was associated with non-weedy perennial phanerophytes (PFG 1), weedy perennial hemicryptophytes and chamaephytes (PFG 3), non-weedy perennial hemicryptophytes, chamaephytes and cryptophytes (PFG 5) and non-weedy therophytes (PFG 6) (Figure 6.2a). Frequency of functional groups indicated a balance between annual (PFG 6 = 37%) and perennial non-weedy (PFG 5 = 39%) plants as well as equal frequencies of annual (PFG 2 = 8%) and perennial (PFG 3 = 8%) weedy plants (Figure 6.4b). Life history as a trait was important as suggested by long arrow lengths of PFG 5 and PFG 6 (Figure 6.2b). The direction of arrows are an indication of the direction in which abundance of plant functional groups increases rapidly, while arrow lengths are considered to have a stronger association with changes in plant functional group abundances. Therefore shorter arrow lengths indicate rapid change of functional groups in land-uses, while longer arrows indicate more gradual changes of functional groups. PFG 5 was positively correlated with the first axis suggesting higher abundance of non-weedy perennial plants with decreasing land-use intensity. PFG 6 was positively correlated along the first axis but negatively correlated along the second axis which implies that abundance of non-weedy therophytes was higher with increasing land-use intensity. Furthermore non-weedy perennial phanerophytes (PFG 1 = 1%) and nitrogen fixers (PFG 4 = 7%) had low frequencies (Figure 6.4b), but was positively correlated with Mopaneveld (Figure 6.2b, 6.3a). Protected Mopaneveld is negatively correlated with weedy perennial hemicryptophytes and chamaephytes (PFG 3) and non-weedy therophytes (PFG 6), suggesting that these groups are not favoured in this Mopaneveld ecosystem type (Figure 6.2b, 6.3a). Mopaneveld displayed relatively high functional group richness which was significantly higher than koppies (p=0.013) (Figure 6.5a). Mopaneveld (p=0.002) and strip mines (p=0.002) both displayed low functional group evenness, which was significantly lower than koppies (Figure 6.5b). With reference to group diversity, no significant differences (p>0.05) were detected (Figure 6.5c, d).

#### 6.3.2.3 Strip mines

Functional groups that were associated with strip mines included weedy perennial hemicryptophytes and chamaephytes (PFG 3), non-weedy perennial hemicryptophytes, chamaephytes and cryptophytes (PFG 5) and non-weedy therophytes (PFG 6) (Figure 6.2a; Figure 6.3a), which were also the groups

with highest frequencies (Figure 6.4c) in this land-use with PFG 6 (43%), PFG 5 (22%) and PFG 3 (21%). PFG 3 is characterised by a short arrow length and thus indicate rapid change of abundance of this group in land-use samples along the second axis. PFG 6 is positively correlated along the first axis, which suggests that this group was favoured by this land-use type (Figure 6.2b). Highest richness of functional groups was displayed by the strip mines, which was significantly higher than koppies ($p<0.001$) (Figure 6.5a). Despite the high functional group richness, evenness was the lowest for the strip mines, which was significantly lower than koppies ($p=0.002$) (Figure 6.5b). Intermediate levels of functional group diversity were displayed by the strip mines (Figure 6.5c, d).

#### 6.3.2.4 Communal lands

Similarly to strip mines, weedy perennial hemicryptophytes and chamaephytes (PFG 3), non-weedy perennial hemicryptophytes, chamaephytes and cryptophytes (PFG 5) and non-weedy therophytes (PFG 6) were also associated with the communal lands (Figure 6.2a). The frequency of these groups was also similar to strip mines (Figure 6.4d) with non-weedy therophytes (PFG 6 = 37%), non-weedy perennial hemicryptophytes, chamaephytes and cryptophytes (PFG 5 = 25%) and weedy perennial hemicryptophytes and chamaephytes (PFG 3 = 31%). Abundance of PFG 3 and PFG 5 is positively correlated along the second axis, indicating that weedy perennials and non-weedy perennials are favoured on communal lands. PFG 6 is positively correlated with the first axis, indicating high abundance of therophytes (Figure 6.2b). In addition, RDA analysis indicated that weedy therophytes (PFG 2) and PFG 3 is strongly correlated with communal land (Figure 6.3a). Additionaly PFG 5 and PFG 6 were also positively correlated with communal land but to a lesser extent (Figure 6.3a). Strip mines and communal lands were similar in their functional group composition which differed significantly from Mopaneveld (Figure 6.3a). Communal lands displayed high richness of functional groups which was significantly higher than koppies ($p<0.001$) (Figure 6.5a). Functional group evenness was relatively high however no significant differences ($p>0.05$) could be detected (Figure 6.5b). Overall, communal lands displayed high functional group diversity (Figure 6.5c, d).

#### 6.3.2.5 Mine dumps

DCA analyses indicated that mine dumps were associated with nitrogen fixers (PFG 4), non-weedy perennial hemicryptophytes, chamaephytes and cryptophytes (PFG 5) and non-weedy therophytes (PFG 6) (Figure 6.2a), whilst PCA ordination revealed that PFG 4, PFG 5 and non-weedy perennial phanerophytes (PFG 1) were associated with mine dumps (Figure 6.2b). Arch and compression effects of axes associated with DCA analyses as well as distortion effects of PCA analyses may be responsible for returning different results. Non-weedy therophytes (PFG 6; 32%), non-weedy perennial hemicryptophytes, chamaephytes and cryptophytes (PFG 5; 25%) and nitrogen fixers (PFG

4; 21%) had high frequencies. Of all the land-uses, mine dumps displayed the highest frequency of nitrogen fixers (Figure 6.4e). PFG 6 was positively correlated with the first axis indicating high abundance of non-weedy therophytes on mined dumps (Figure 6.2b). According RDA analysis, PFG 4 was strongly and positively correlated with mine dumps. PFG 6 and PFG 1 was also positively correlated (Figure 6.3a). Functional group composition of mine dumps was dissimilar compared to koppies (Figure 6.3a). Mine dumps displayed high functional group richness which was significantly higher compared to koppies ($p=0.018$) (Figure 6.5a). Evenness of functional groups was the second highest; however no significant differences ($p>0.05$) were indicated (Figure 6.5b). Diversity of functional groups on mine dumps was overall above average (Figure 6.5c, d). Shannon-Wiener diversity of functional groups of mine dumps was similar to koppies (Figure 6.5c), while Simpson diversity was still high but lower than for koppies (Figure 6.5c, d).

#### 6.3.2.6 Plant functional groups and environmental variables

RDA analysis indicated that certain plant functional groups were associated with certain environmental variables (Figure 6.3c). Non-weedy perennial phanerophytes (PFG 1) correlated positively with rock cover, debris and vegetation height (VH), but negatively with bare soil. Weedy therophytes (PFG 2) were strongly correlated with forb- and rock cover. A positive correlation was detected between weedy perennial hemicryptophytes and chamaephytes (PFG 3), grass cover and bare soil, while nitrogen fixers (PFG 4) correlated with forb- and rock cover. PFG 5 correlated with grass cover and was highly correlated with bare soil. PFG 6 correlated with bare soil, forb and rock cover. Furthermore, the functional group composition of land-use plant communities was also found to be associated with environmental variables (Figure 6.3c). The first axis are characterised by a gradient of soil cover. The negative component is associated with high bare soil exposure while the positive component with vegetation height and debris. Bare soil was best correlated with mine dumps, communal lands and strip mines while rock cover were associated with koppies and mine dumps. Mopaneveld was strongly associated with high percentages of debris and vegetation height (VH). The second axis can be considered to be a gradient of grass cover. High biomass percentages were associated with Mopaneveld and koppies while all land-uses had a level of forb and grass cover.

**Table 6.1. Plant functional groups and associated plant traits. Numbers denotes number of species.**

| Plant traits | | Plant functional groups | | | | | |
|---|---|---|---|---|---|---|---|
| | | Group 1 | Group 2 | Group 3 | Group 4 | Group 5 | Group 6 |
| | | Non-weedy perennial phanerophytes | Weedy therophytes | Weedy perennials | Nitrogen fixers | Non-weedy perennials | Non-weedy therophytes |
| Weediness | Weedy | - | 40 | 21 | 3 | - | - |
| | Non weedy | 18 | - | - | 17 | 128 | 45 |
| Growth form | Climbers | 18 | 2 | - | - | - | 3 |
| | Rosette | - | 1 | - | - | 2 | - |
| | Prostrate | - | 12 | 3 | 4 | 18 | 6 |
| | Erect | - | 15 | 9 | 16 | 62 | 22 |
| | Tussock | - | 7 | 6 | - | 44 | 14 |
| | Creeper | - | 3 | 3 | - | 2 | - |
| Life history | Annual | - | 40 | - | 12 | - | 45 |
| | Perennial | 18 | - | 21 | 8 | 128 | - |
| Raunkiaer's life form | Phanerophytes | 18 | - | - | - | - | - |
| | Chamaephytes | - | - | 9 | 5 | 60 | - |
| | Hemicryptophytes | - | - | 12 | 3 | 57 | - |
| | Cryptophytes | - | - | - | - | 11 | - |
| | Therophytes | - | 40 | - | 12 | - | 45 |
| Clonality | Non-clonal | 10 | 33 | 14 | 20 | 88 | 42 |
| | Above ground | 1 | 5 | 1 | - | 11 | 2 |
| | Below ground | 7 | 1 | 3 | - | 27 | 1 |
| | Above & below ground | - | 1 | 3 | - | 2 | - |
| Mode of dispersal | Unassisted | 8 | 16 | 9 | 20 | 50 | 20 |
| | Wind | 4 | 5 | 3 | - | 35 | 13 |
| | Internal animal | 6 | 4 | 6 | - | 24 | 9 |
| | External animal | - | 11 | 2 | - | 10 | - |
| | Unspecified | - | 4 | 1 | - | 9 | 3 |
| Nitrogen fixing | Absent | 11 | 40 | 21 | - | 128 | 45 |
| | Present | 7 | - | - | 20 | - | - |
| Shade tolerance | Shade (shade tolerant) | 6 | 2 | 3 | - | 12 | 5 |
| | Sun (shade intolerant) | 5 | 24 | 11 | 20 | 78 | 30 |
| | Unspecified | 7 | 14 | 7 | - | 38 | 10 |

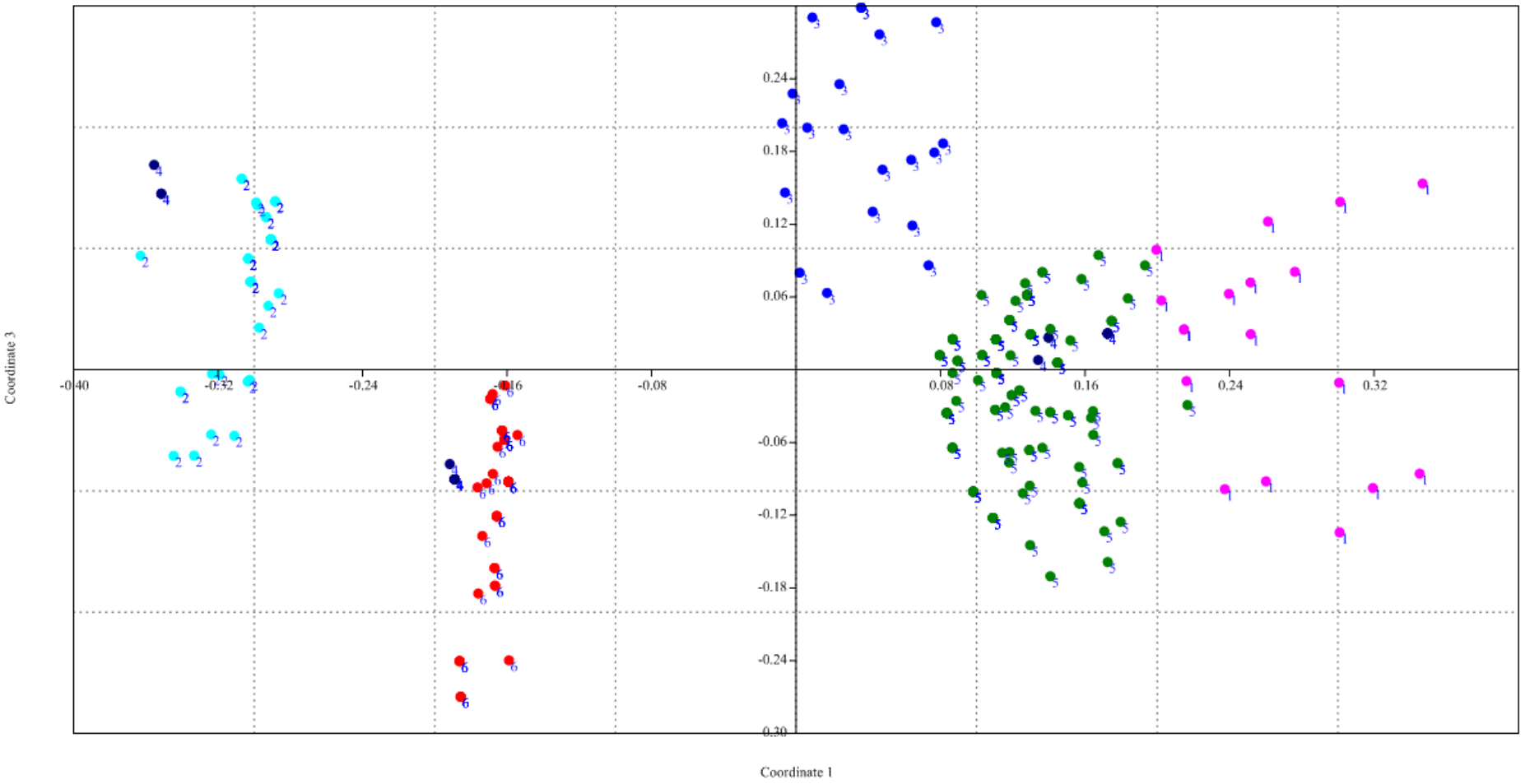


**Figure 6.1. Principal Coordinate Analysis (PCoA) of plant functional groups in protected and variously transformed Mopaneveld. Numbers denote specific functional group numbers.**

### 6.3.3. Functional traits of land-uses

One-way ANOVA revealed significant differences across land-use treatments (Table 6.2) for trait richness ($p<0.001$; $F=13.11$), trait evenness ($p<0.001$; $F=9.81$), Shannon-Wiener trait diversity ($p=0.02$; $F=4.98$) and Simpson trait diversity ($p<0.001$; $F=4.98$).

#### 6.3.3.1 Protected areas (koppies)

Plant functional traits associated with koppies included perennial life history, chamaephytes, clonal above ground, clonal below ground, non-weedy and external animal transport (Figure 6.2c). Koppies were strongly correlated with phanerophytes (climbers) and shade intolerant species (sun species) (Figure 6.2d, 6.3b). Cryptophytes and rosette growth forms were correlated with koppies (Figure 6.3b). Richness of functional traits was average on koppies, which was significantly lower than strip mines ($p=0.044$) and communal lands ($p=0.039$) but significantly higher than mine dumps ($p=0.008$) (Figure 6.6a). Highest trait evenness was displayed by the koppies, which was significantly higher compared to Mopaneveld ($p=0.009$), strip mines ($p<0.001$) and communal lands ($p<0.001$) (Figure 6.6b). Trait diversity was high on koppies (Figure 6.6c, d). Shannon-Wiener trait diversity was significantly higher compared to mine dumps ($p=0.014$) (Figure 6.6c) whereas Simpson trait diversity was significantly higher compared to all land-uses ($p<0.05$), which can be ascribed to high functional trait richness and evenness respectively (Figure 6.6d).

#### 6.3.3.2 Protected areas (Mopaneveld)

DCA analyses indicated that Mopaneveld was associated with weedy, non-clonal, clonal above ground, perennial life history and nitrogen fixers (Figure 6.2c), whilst PCA analyses revealed that shade intolerance, clonal above and below ground, hemicryptophytes, phanerophytes, internal animal transport, non-weedy species, perennial life history, tussock and prostrate growth forms were also associated with Mopaneveld (Figure 6.2d). Traits with low abundances were identified as non-clonal, therophytes, weedy, shade tolerant species, nitrogen fixing ability absent, wind dispersal and erect growth forms (Figure 6.2d). RDA analysis indicated that Mopaneveld is positively correlated with phanerophytes, cryptophytes and shade intolerance suggesting that these traits were favoured. Abundance of wind dispersed species and nitrogen fixing ability is positively correlated with the second axis and negatively correlated along the first axis, indicating that these traits are more associated with land-uses with high disturbance levels than with protected Mopaneveld (Figure 6.3b). Mopaneveld displayed high level of functional trait richness which was significantly higher than mine dumps ($p<0.001$) (Figure 6.6a). Trait evenness was average and no significant differences could be detected ($p>0.05$), although evenness was slightly higher in Mopaneveld compared to strip mines and communal lands (Figure 6.6b). Diversity of traits was relatively high (Figure 6.6c, d). Simpson diversity of traits was significantly lower than koppies ($p=0.010994$) (Figure 6.6d).

#### 6.3.3.3 Strip mines

Functional traits which were associated with strip mines were identified as hemicryptophytes, perennial life history, clonal above ground, external animal transport, shade tolerance, therophytes, and non-clonality (Figure 6.2c). Traits with high abundance in strip mines were clonal above ground, hemicryptophytes, perennial life history, external animal transport and prostrate growth forms (Figure 6.2d). Traits which decreased in abundance were unassisted dispersal, non-clonal, therophytes, erect growth forms, wind dispersal and nitrogen fixing absent (Figure 6.2d). Hemicryptophytes, chamaephytes and clonal above ground were strongly associated with strip mines (longest arrows) (Figure 6.3b). Strip mines displayed the second highest trait richness, which was significantly higher compared to koppies ($p=0.044$) and mine dumps ($p<0.001$) (Figure 6.6a). However lowest trait evenness was displayed by strip mines which was significantly lower than koppies ($p<0.001$) and mine dumps ($p<0.001$) (Figure 6.6b). With reference to trait diversity, strip mines displayed intermediate levels of diversity (Figure 6.6c, d). Shannon-Wiener trait diversity was slightly higher than trait diversity of mine dumps (Figure 6.6c) whereas Simpson trait diversity was the lowest, which can be ascribed to low trait evenness (Figure 6.6d).

#### 6.3.3.4 Communal lands

DCA analysis indicated that hemicryptophytes, clonal above ground, non-clonality, perennial life history, external animal transport, shade tolerance, therophytes and weediness were traits associated with communal lands (Figure 6.2c). Traits which increased in abundance in this land-use included above and below clonality, internal animal transport, hemicryptophytes, perennial life history, clonal above ground, tussock, prostrate and rosette growth forms. Shade tolerance, weediness, non-clonality, therophytes, nitrogen fixing ability absent and erect growth forms decreased (Figure 6.2d). RDA analyses indicated that internal animal transport, external animal transport, clonal above ground and clonal above and below ground were strongly and positively correlated with communal lands (Figure 6.3b). Communal lands displayed high trait richness which was significantly higher than koppies ($p=0.04$) and mine dumps ($p<0.001$) (Figure 6.6a). However, low trait evenness was displayed which was significantly lower than koppies ($p<0.001$) and mine dumps ($p=0.009$) (Figure 6.6b). Trait diversity was above average (Figure 6.6c, d) and similar to Mopaneveld. Simpson trait diversity was significantly lower than koppies ($p=0.016$) (Figure 6.6d).

#### 6.3.3.5 Mine dumps

Nitrogen-fixers, weedy plants, non-clonality, therophytes and shade tolerance were traits associated with mine dumps (Figure 6.2c). PCA analysis indicated that traits which increased in abundance were

nitrogen fixers, phanerophytes and shade intolerant species (Figure 6.2d). Non-clonal species, therophytes, unassisted dispersal, wind dispersal, nitrogen fixing ability absent and external animal transport decreased in abundance (Figure 6.2d). RDA analysis indicated that nitrogen fixing ability absent and wind dispersal were positively correlated along the second axis and negatively correlated along the first axis (Figure 6.3b). Therefore nitrogen fixing species and wind dispersed species are favoured. Mine dumps were characterized by low trait richness which was significantly lower ($p<0.05$) than all land-uses (Figure 6.6a). Trait evenness was second highest which was significantly higher than strip mines ($p<0.001$) and communal lands ($p=0.009$) (Figure 6.6b). Diversity of traits was low (Figure 6.6c, d). With reference to Shannon-Wiener ($p=0.014$) and Simpson ($p=0.011$) trait diversity, mine dumps had significantly lower trait diversity than koppies (Figure 6.6c, d).

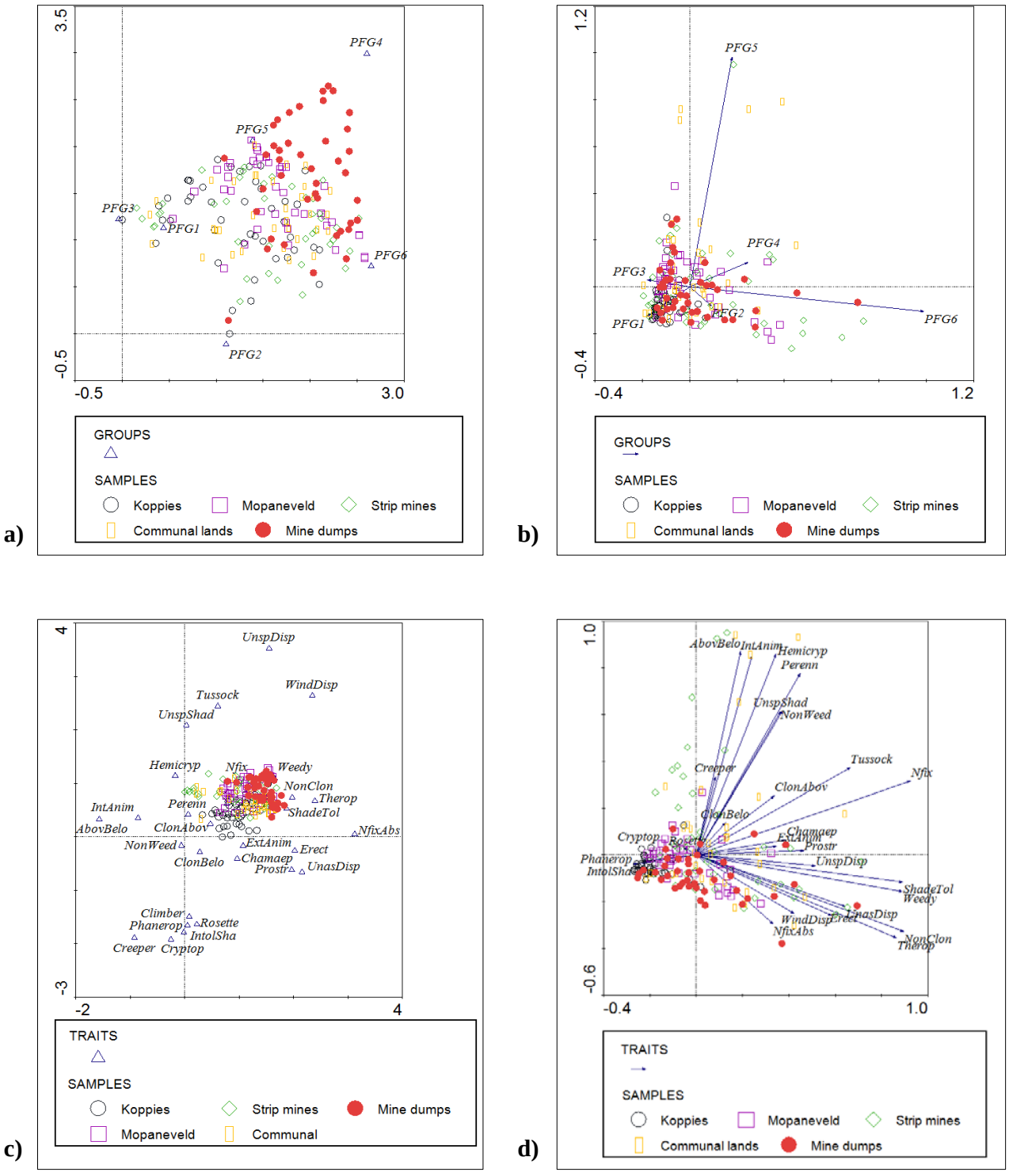


**Figure 6.2. DCA and PCA of plant functional groups (a, b) and functional traits (c, d) for land-uses. (See Appendix B for additional statistical information)**

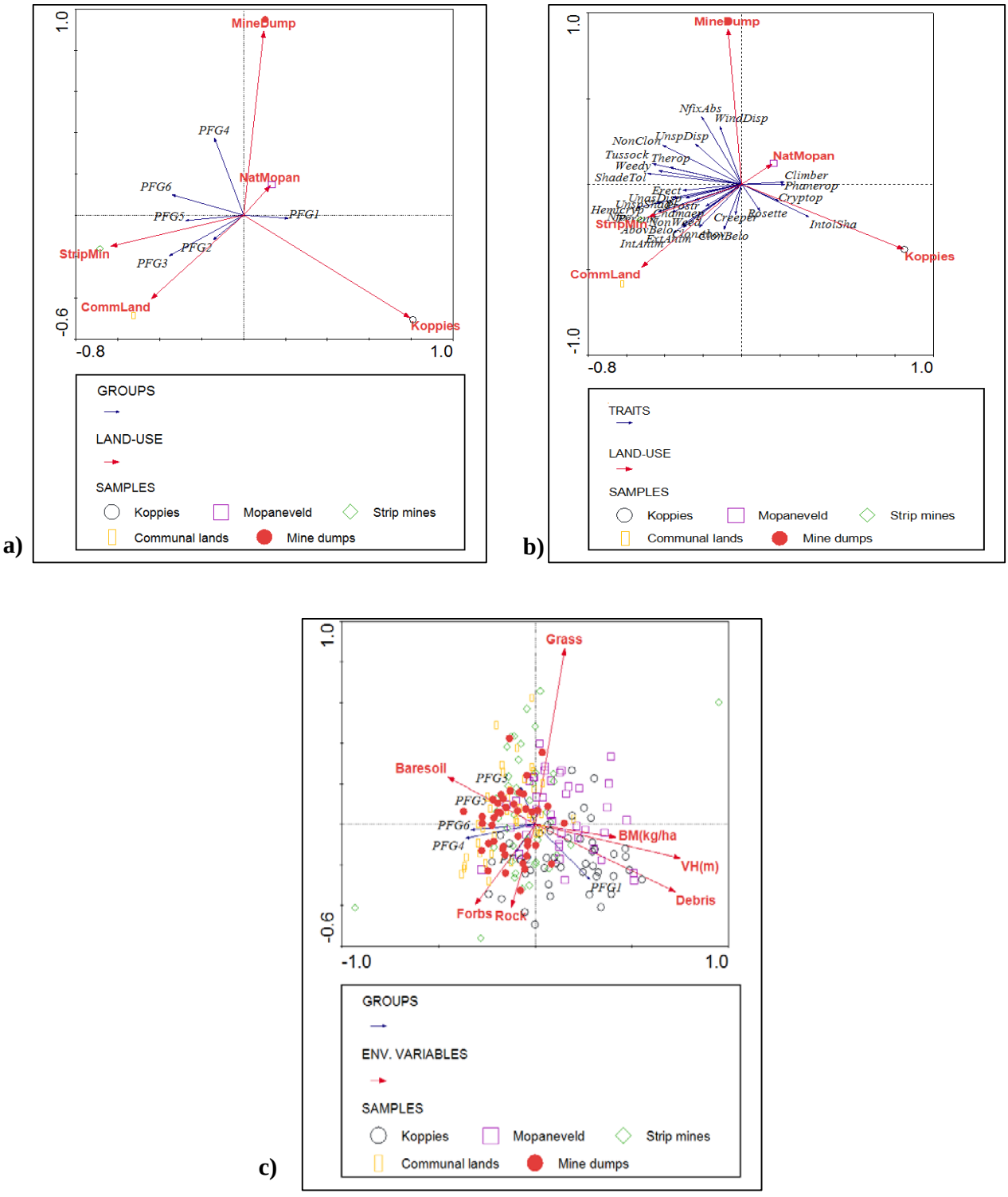


**Figure 6.3. RDA of plant functional groups (a), functional traits (b) and triplot comparing variables, land-uses and composition of functional groups (c). Percentage cover of grass, forbs, rock, debris and bare soil; BM, biomass; VH, vegetation height. (See Appendix B for additional statistical information).**

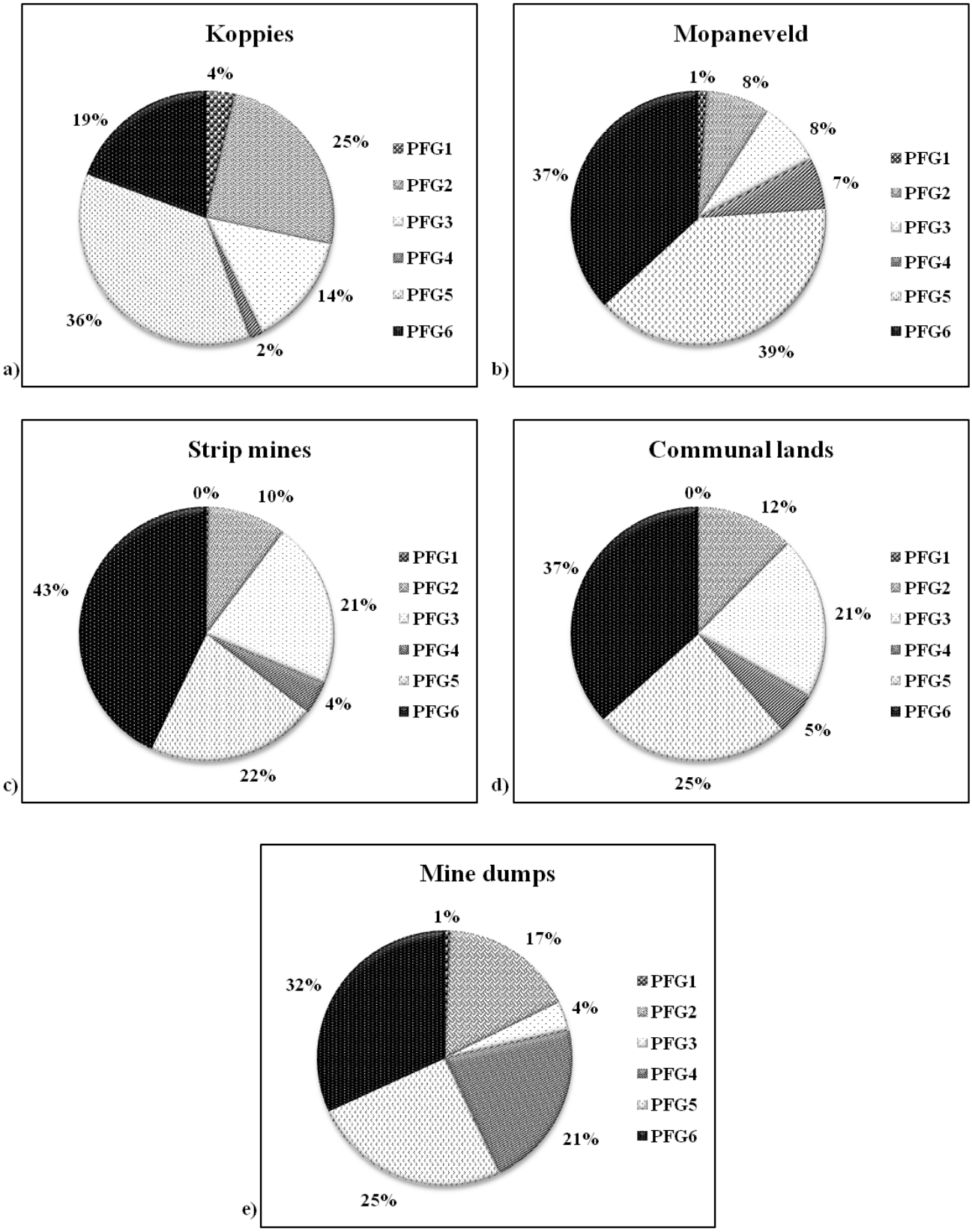


**Figure 6.4. Frequency of plant functional groups in each land-use.**

**Table 6.2. One-way ANOVA results of the mean values for plant functional group and functional trait richness, density and diversity measures across land-use types.**

| Statistical approach | Response | Data transfor-mation | Source | *df* | SS | MS | F | p |
|---|---|---|---|---|---|---|---|---|
| **Response on group level** | Richness | $4^{th}$ root | Land-use | 4 | 0.17 | 0.04 | 6.84 | <0.001* |
| | | | s.e | | 1.24 | 0.01 | | |
| | Evenness | – | Land-use | 4 | 0.60 | 0.15 | 4.82 | <0.001* |
| | | | s.e | | 0.03 | 0.03 | | |
| | Shannon-Wiener diversity index | – | Land-use | 4 | 0.28 | 0.07 | 0.78 | 0.54 |
| | | | s.e | | 18.29 | 0.09 | | |
| | Simpson diversity index | – | Land-use | 4 | 0.20 | 0.05 | 1.94 | 0.11 |
| | | | s.e | | 5.31 | 0.03 | | |
| **Response on trait level** | Richness | $4^{th}$ root | Land-use | 4 | 0.19 | 0.05 | 13.11 | <0.001* |
| | | | s.e | | 0.74 | 0.003 | | |
| | Evenness | – | Land-use | 4 | 0.07 | 0.02 | 9.81 | <0.001* |
| | | | s.e | | 0.35 | 0.001 | | |
| | Shannon-Wiener diversity index | – | Land-use | 4 | 0.28 | 0.07 | 2.95 | 0.02* |
| | | | s.e | | 4.82 | 0.02 | | |
| | Simpson diversity index | – | Land-use | 4 | 0.003 | 0.001 | 4.98 | <0.001* |
| | | | s.e | | 0.03 | 0.0002 | | |

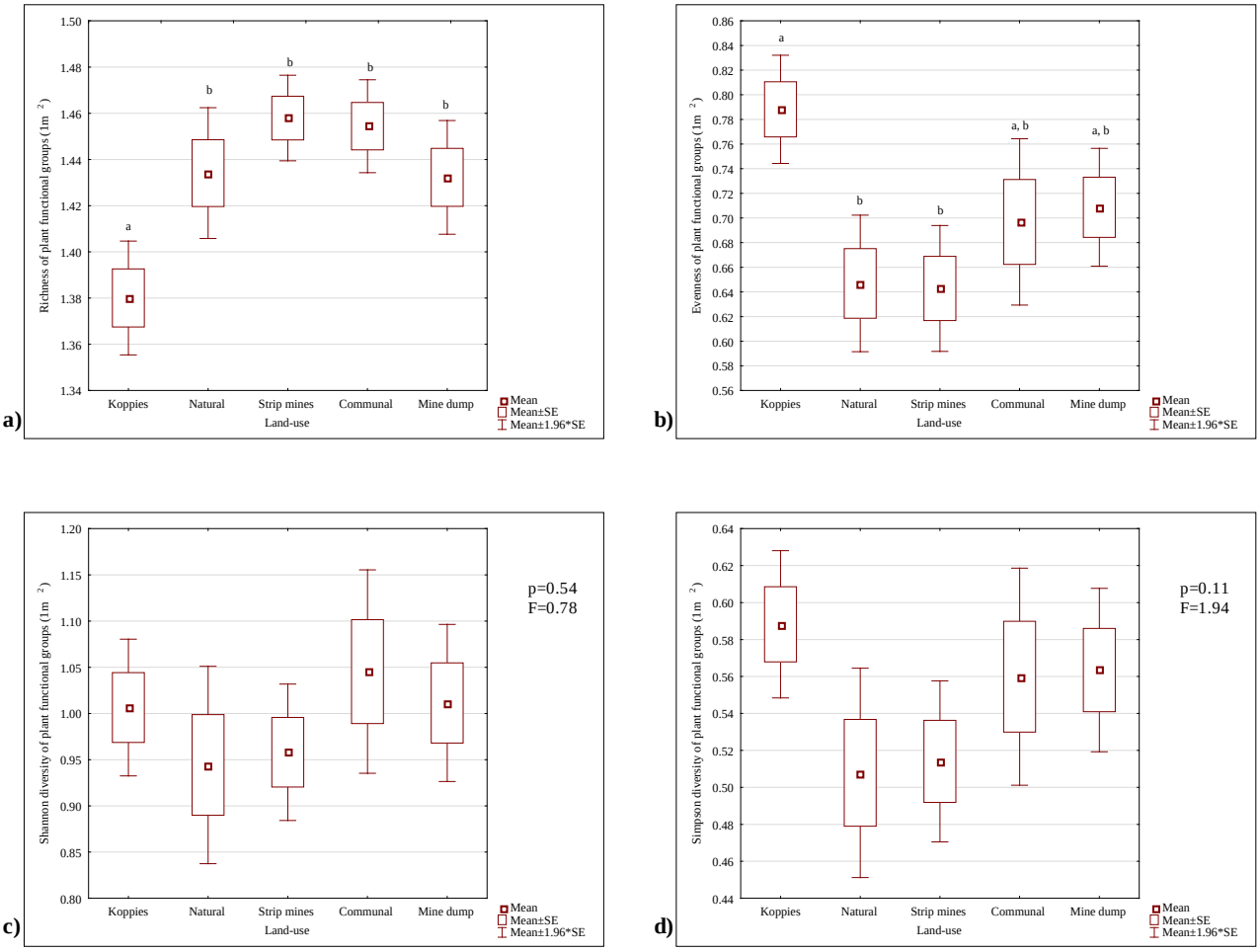


**Figure 6.5. Diversity indices for functional groups per plot across land-uses, a) group richness, b) group evenness, c) Shannon-Wiener group diversity and d) Simpson group diversity. Similar letters denote no significant differences. (Natural denotes protected Mopaneveld).**

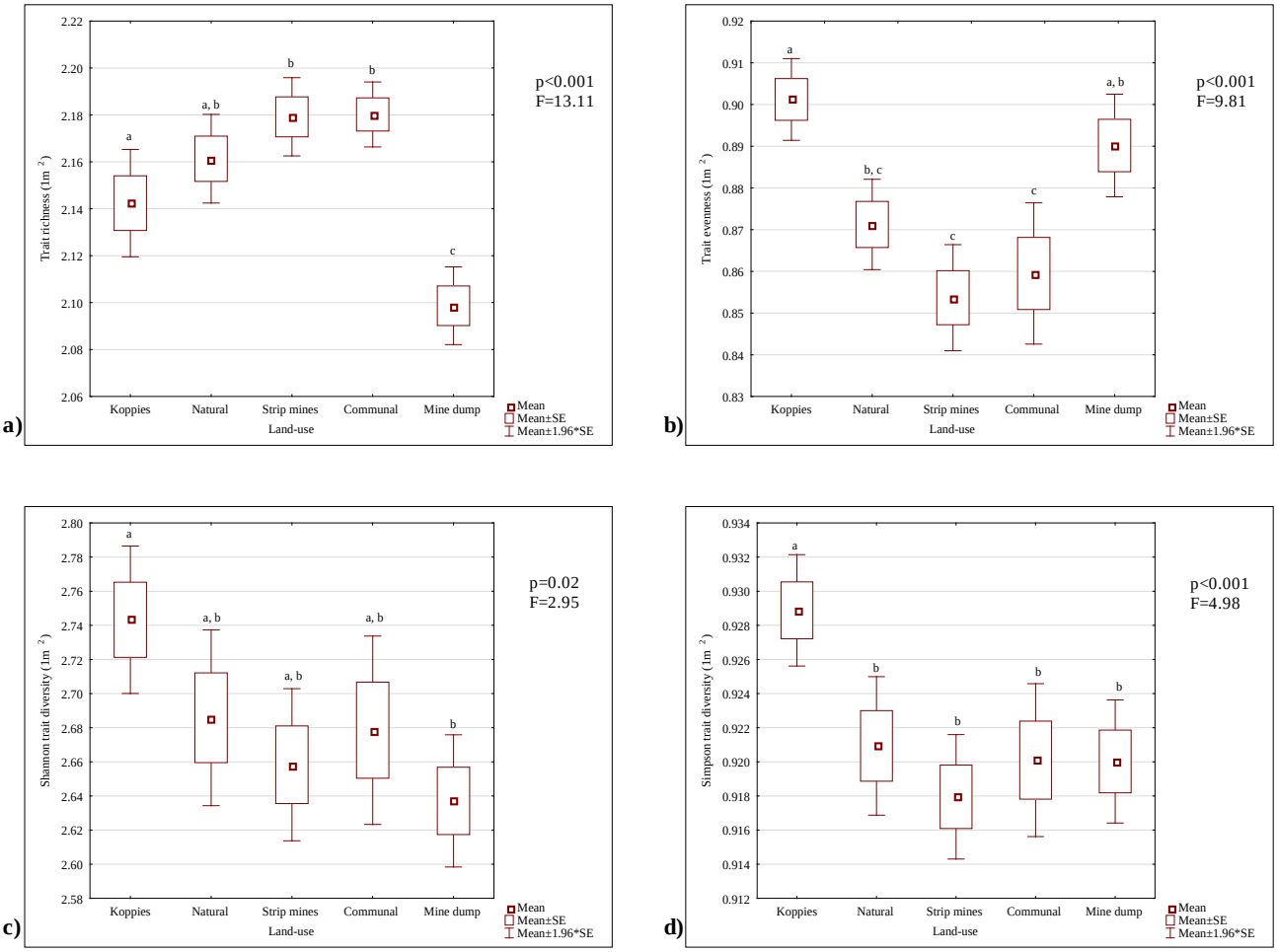


**Figure 6.6. Diversity indices for functional traits per plot across land-uses, a) trait richness, b) trait evenness, c) Shannon-Wiener trait diversity and d) Simpson trait diversity. Similar letters denote no significant differences. (Natural denotes protected Mopaneveld).**

## 6.4. Discussion

### 6.4.1 Plant functional groups of Mopaneveld land-uses

In this study, life history, weediness and Raunkiaer's life form were the three life form traits on which plant functional groups were defined. Life history is an indication of the persistence of species under disturbances and is therefore strongly related to land-use (Aronson *et al.*, 2007; Pérez-Harguindeguy *et al.*, 2013). Annual species are considered as r-strategists (Pianka, 1970) due to their high seed production rates and fast colonising abilities (Begon *et al.*, 2006). Furthermore annual plant species are stress-tolerant (Olsson & Ödman, 2014) and therefore characteristic of disturbed areas (McIntyre *et al.*, 1999). Disturbances reduce biomass and create open patches of bare soil in the field layer, favouring fast colonizing annual species that establish successfully due high resource availability and in the absence of competition (Pickett, 1980; McIntyre *et al.*, 1995; Hodgson *et al.*, 1999; Geldenhuys, 2011; Rutherford & Powrie, 2013; Graff & McIntyre, 2014). Therefore, pioneer annual species promote secondary succession (Connell & Slatyer, 1977; Jordaan *et al.*, 2004; Cramer *et al.*, 2008; Van As *et al.*, 2012). It was therefore expected that areas with lowest disturbance (e.g. koppies and Mopaneveld) would be associated with higher biomass and lower abundances of weedy, annual plants since anthropogenic disturbances were limited in these areas. Results

confirmed higher levels of biomass and taller herbaceous vegetation for koppies and Mopaneveld, as well as a larger portion of perennial non-weedy plants. According to Burke (2003), koppies serve as a source of perennial species which would normally be reduced by grazing practices in the surrounding lowland matrix. Furthermore weedy and alien species are mostly associated with areas subjected to anthropogenic disturbances (Goodall & Naude, 1998; Buckley *et al.*, 2007; Meek *et al.*, 2010; Schonbeck, 2013; Carreño-Rocabado *et al.*, 2015).

Even though weedy species are often perceived as problematic, they fulfil important ecological roles in plant communities. Some weedy plants are utilized as a food source by humans and livestock, while they also promote secondary succession and restoration of degraded soils by means of deposition of organic matter, soil stabilisation and protection against soil erosion (Coiffait-Gombault *et al.*, 2012; Schonbeck, 2013; Van Rensburg *et al.*, 2014; Ligenfelter, 2015; Nezomba *et al.*, 2015). Shackleton (2000) hypothesised that in communal areas, disturbances caused by humans and livestock create niches for weedy species to establish. Therefore it is expected that plant communities with a portion of generalist weedy species may be resilient, since these species are characterised by a certain trait set (i.e. fast colonizers, stress-tolerant). This weed trait set enables these species to provide certain functions and thus maintain temporary ecosystem functioning in disturbed areas (Côté & Darling, 2010). This hypothesis is supported in this study, as on mine dumps, annual weedy species fulfil the ecological role as pioneer species similar to the study conducted by Van Oudtshoorn *et al.* (2011). These annual weedy species will probably be outcompeted by later successional species as suggested by Meiners *et al.* (2002) and Van der Maarel (2005). Surprisingly weedy species had a high frequency on the koppies. A study conducted in North America by Wyatt and Allison (2000) suggested that koppies also serve as a source of weedy species, therefore it is expected that as for arid areas, in North America, semi-arid koppies serve as a source of perennial weedy species which have the ability to colonise disturbed areas.

This study supports the idea that life form is a good predictor of the effects of land-use in a semi-arid Mopaneveld savanna. Land-use does not only affect the dominant life history and the portion of weedy species in plant communities, but also species' morphology due to changes in life form characteristics of the herbaceous layer (Lavorel *et al.*, 1998; Diaz *et al.*, 2007; Lavorel *et al.*, 2011). Life form as a morphological trait is an indication of species' ability to survive unfavourable environmental conditions (Raunkiaer, 1934; Cornelissen *et al.*, 2003). More specifically life form is positively associated with disturbance regime (Geldenhuys, 2011; José-María *et al.*, 2011; Lavorel *et al.*, 2011; Batriu *et al.*, 2015), soil disturbance (McIntyre *et al.*, 1995) and successional trends (McIntyre *et al.*, 1995; Raevel *et al.*, 2013). Therefore life form can be considered as an indicator of species' adaptation to environmental stress (Schnoor *et al.*, 2015). Therophytes are usually favoured by soil disturbances, whereas hemicryptophytes and chamaephytes are more sensitive to disturbance (McIntyre *et al.*, 1995), explaining the decreasing frequencies of these latter perennial life forms in plant communities of disturbed land-uses such as strip mines, communal land and mine dumps. Climbing phanerophytes are more sensitive to marginal disturbances and are more associated with habitat availability on koppies and Mopaneveld. Results of this study therefore emphasise the filtering effect of anthropogenic land-uses (excluding protected areas) on plant communities (Diaz *et al.*, 1998; Díaz

*et al.*, 1999; Lavorel & Garnier, 2002; Batriu *et al.*, 2015; Mandle & Ticktin, 2015) since traits of life history (annual *vs.* perennial), life forms (therophytes *vs.* chamaephytes, hemicryptophytes and phanerophytes) and weediness (weedy *vs*. non-weedy species) were favoured.

### 6.4.2 Functional group assemblages of land-uses and their ecological role

#### 6.4.2.1 Protected areas

Koppies displayed various functional groups (high Shannon-Wiener and Simpson functional group diversity) which supports the idea that koppies are heterogeneous entities (Burke, 2003). Evenness of traits and functional groups on koppies was high as no traits or groups dominated on these landscapes due to low disturbance levels and persisting environmental conditions, preventing the domination of certain traits and/or groups. Based on our preliminary results of various plant functional groups each with their unique traits and high evenness, it indicates that plant communities of koppies may have high redundancy, hence indicating high resilience. Heterogeneity on koppies can be ascribed to 1) various microclimatic conditions, 2) aspect specific vegetation, 3) effect of altitude and 4) harsh environmental conditions including high exposure to sunlight, high soil temperatures, soil erosion, shallow soils and limited soil moisture availability (Phillips, 1982; Porembski *et al.*, 1996; Porembski *et al.*, 1997; Barthlott & Porembski, 2000; Porembski, 2000; Szarzynski, 2000; Burke, 2003; Brand *et al.*, 2010; Burke, 2012; Speziale & Ezcurra, 2012; De Paula *et al.*, 2015). These unique and stressful environmental conditions select for certain plant functional traits to allow these species to persist (Barthlott & Porembski, 2000; Porembski, 2000). Shade intolerant species were favoured due to increased sun exposure (Baskin & Baskin, 1988), especially on the northern slopes of koppies. Species with clonal organs (above or below ground), with drought avoidance, storage or reproductive function, have the ability to survive harsh environmental conditions and have successful reproductive rates (Biedinger & Fleischmann, 2000; Gröger, 2000; Hopper, 2000; Porembski, 2000; Raghoenandan, 2000; Jacobi *et al.*, 2007; Migliore *et al.*, 2013; Brand *et al.*, 2015; Kleyer & Minden, 2015). Such species were associated with plant communities on the koppies.

According to Porembski *et al.* (1998) clonal species have a competitive benefit on inselbergs since these species 1) can increase to form large populations in their isolated micro-habitats, 2) have the ability to persist in the long term since they can successfully colonise an area due to older established populations, 3) reduces the risk of mortality under extreme environmental conditions and 4) spread horizontally to quickly occupy suitable habitats. With reference to life forms, most studies indicate that therophytes are the dominant life form on inselbergs since these species can persist under unfavourable conditions (Phillips, 1982; Porembski *et al.*, 1995; Porembski *et al.*, 1997; Biedinger & Fleischmann, 2000; Porembski, 2000; Seine & Becker, 2000). However, this study indicated that chamaephytes, hemicryptophytes and phanerophytes are more associated with Mopaneveld koppies than therophytes, a state similar to inselbergs in Brazil (Porembski *et al.*, 1998; Safford & Martinelli, 2000), Madagascar (Fischer & Theisen, 2000), Seychelles (Biedinger & Fleischmann, 2000) and Argentina (De Paula *et al.*, 2015). With uncertainty due to limited literature of Mopaneveld koppies, the lack of therophytes can be ascribed to four possible reasons. Firstly inselberg size

is a determinant factor of the proportion of perennial species. Large koppies tend to have a higher proportion of perennial species while annual species will increase on smaller sized koppies (Porembski, 2000). Secondly, due to presence of trees, Mopaneveld koppies presumably have deeper soils, limiting rainwater runoff to favour the establishment of perennial species (Belsky, 1990; Wyatt & Allison, 2000). Thirdly, seasonal rainfall could also have contributed to the occurrence of perennial species (Porembski, 2000) as it is known that stochastic events are an important driver of the dynamics of the herbaceous layer in semi-arid savannas (Skarpe, 1992; O'Connor, 1998; Buitenwerf *et al.*, 2011; Rutherford *et al.*, 2012). Lastly, due to limited anthropogenic disturbances on the koppies, the perennial species could be maintained even though koppies had high frequencies of weedy functional groups (Safford & Martinelli, 2000).

Koppies may serve as a source of weedy species and hence koppies may be susceptible to invasion. The persistence of these weedy species can be ascribed to harsh environmental conditions on koppies which may be similar to conditions in disturbed environments, hence colonization of surrounding disturbed habitats may be possible due to well-adapted modes of dispersal (Seine & Becker, 2000). However, weedy plants do not dominate on koppies of this particular study site, suggesting some level of resilience to invasion, possibly due to unique environmental conditions (Seine & Becker, 2000; Van der Plas, 2013).

Similarly to the koppies, Mopaneveld was also characterised by various plant functional groups. Considering the frequency of each functional group, equal frequencies of annual and perennial non-weedy as well as annual and perennial weedy species prevailed. This finding supports the idea that weedy species are not restricted to anthropogenically disturbed areas, but were also found in less disturbed natural plant communities (Goodall & Naude, 1998; Begon *et al.*, 2006; Davis *et al.*, 2011). In comparison with strip mines, communal lands and mine dumps, the frequency of annual weedy species was low in Mopaneveld due to less intensive anthropogenic disturbances. Since anthropogenic disturbances were minimal, rainfall and herbivory, the two characteristic driving forces of vegetation dynamics in savanna landscapes (Skarpe, 1991; Skarpe, 1992; O'Connor, 1998), were also considered as the key disturbances in this ecosystem. Rainfall and herbivory were therefore regarded as the primary drivers of functional assemblages in this plant community (Diaz *et al.*, 1998). In times of drought, a shift in the herbaceous layer is found since annual species are favoured above perennial species and *vice versa* after good rainfall occurred (Skarpe, 1992; Shackleton, 2000; Jordaan *et al.*, 2004; Buitenwerf *et al.*, 2011; Rutherford *et al.*, 2012). Therefore it is not surprising that hemicryptophytes and phanerophytes, which are also disturbance sensitive, displayed high abundances in protected Mopaneveld (McIntyre *et al.*, 1995). In this study the high abundance of hemicryptophytes can be ascribed to their tolerance to light grazing due to the position of the perennating buds (McIntyre *et al.*, 1995). Under heavy grazing, abundance of hemicryptophytes decline and therophytes are more dominant due to disturbance tolerance as found on communal areas of this study. Similarly to the study of Shackleton (2000) this study also found that tussock growth forms, associated with perennial grass and sedge species (hemicryptophytes), as well as prostrate growth forms, a grazing-avoidance strategy of herbaceous species, increased. Thus tussock and prostrate growth forms were favoured above erect growth forms in response to light grazing (Lavorel *et al.*, 1997; Lavorel & Cramer, 1999; Diaz *et al.*, 2007). Hemicryptophytes together with species with above and below ground clonality have competitive vigour

since they persist under frequently light grazing practices and resprout quickly after favourable rainfall due to stored nutrients and water in below-ground organs (Cornelissen *et al.*, 2003; Kahmen & Poschlod, 2004; Clarke *et al.*, 2013; Pérez-Harguindeguy *et al.*, 2013). It is not surprising that internal animal transport was associated with forb and grass species of Mopaneveld, since this savanna type has an evolutionary grazing history (Walker *et al.*, 1981; Skarpe, 1992; Cingolani *et al.*, 2005; Koerner *et al.*, 2014).

Considering functional diversity of Mopaneveld, this plant community is characterised by a high number of traits and functional groups but certain traits or functional groups dominated, hence the lower functional diversity of traits and functional groups observed for Mopaneveld. Lower diversity does not necessarily imply that Mopaneveld has less redundancy, but that it is a non-equilibrium system subjected to temporary shifts in the herbaceous layer, driven by grazing and erratic rainfall events (Walker, 1987; Ellis & Swift, 1988; Westoby *et al.*, 1989; Todd & Hoffman, 1999; Sullivan & Rohde, 2002; Siebert *et al.*, 2003; Jordaan *et al.*, 2004; Buitenwerf *et al.*, 2011; O'Connor, 2015). Therefore specific redundant species with specific traits providing a certain ecosystem function in the community that contributes to resilience in the temporary stable state (Mouillot *et al.*, 2013; Hanke *et al.*, 2014).

6.4.2.2 Marginal disturbances

Topsoil of communal lands is mainly altered by humans (foot paths, cultivation of crops), livestock (grazing and trampling), increased sun exposure (harvesting of trees for fire wood and timber) and soil erosion (wind and water) (Shackleton, 1993; Todd & Hoffman, 1999; Shackleton, 2000; Musvoto *et al.*, 2007; Makhado *et al.*, 2009; Van Oudtshoorn *et al.*, 2011; Makhado *et al.*, 2012; Rutherford *et al.*, 2012; Davis *et al.*, 2013; Rutherford & Powrie, 2013). Non-weedy therophytes, non-weedy perennials, weedy perennials as well as weedy therophytes were more frequent in disturbed communal land. Heavy grazing on the rangelands favoured annual species (Kelly & Walker, 1976; Skarpe, 1992; Todd & Hoffman, 1999; Shackleton, 2000; Diaz *et al.*, 2007; Rutherford & Powrie, 2013) and is considered to promote old field succession (Wilson *et al.*, 2004; Cramer *et al.*, 2008), especially annual weeds which fulfil the role of pioneer species (Van Oudtshoorn *et al.*, 2011; Kotschy, 2013). However, in this study established perennial species was thought to promote soil conditions on old fields (similar to strip mines), are grazing-resistant (Rutherford & Powrie, 2013) or have a grazing avoidance strategy. Grazing avoidance strategies which were favoured included prostrate and rosette growth forms with meristems below feeding ranges of grazers (Noy-Meir *et al.*, 1989; Lavorel *et al.*, 1999; Diaz *et al.*, 2007; Rutherford & Powrie, 2011; Rutherford *et al.*, 2012; Wesuls *et al.*, 2012; Hanke *et al.*, 2014; Hempson *et al.*, 2014). In addition, with similar functions as described for strip mines, prostrate and rosette growth forms also contributed to soil protection (Kramer & Weaver, 1936). Most studies found that tussock species were filtered out by grazing (Diaz *et al.*, 2007; Rutherford *et al.*, 2012). However, this study showed that short tussock grass and sedge species persisted in these communities, implying that these species were grazing-tolerant on communal grazing lawns (McIntyre *et al.*, 2003; Cingolani *et al.*, 2005; Hempson *et al.*, 2014) and protect the soil against erosion.

Low frequencies of erect growth forms and shade tolerant species on the communal lands can possibly be ascribed to the effect of herbivory (Diaz *et al.*, 2007; Rutherford & Powrie, 2011; Rutherford *et al.*, 2012)

and high sun exposure. In accordance with various studies, stoloniferous (clonal above ground) (Shackleton, 2000; McIntyre *et al.*, 2003; Diaz *et al.*, 2007; Rutherford & Powrie, 2011; Moreno García *et al.*, 2014) and species possessing underground rhizomes or storage organs (clonal above and below ground) (Lavorel *et al.*, 1998; Hempson *et al.*, 2014) were found to be abundant on grazed lands. These species have a competitive advantage on communal lands due to resource allocation. Therefore these species will be able to persist and resprout easily after drought or grazing (Walker *et al.*, 1981; Eriksson, 1989; Prach & Pyšek, 1994; Lavorel *et al.*, 1998; Lötscher, 2006) and contribute to soil protection and soil organic matter (Kramer & Weaver, 1936; Jankauskas & Jankauskiene, 2003). Similarly, as described for strip mines, weedy plants also contribute to soil quality on communal lands (Kort *et al.*, 1998; Jankauskas *et al.*, 2008; Zhou *et al.*, 2012; Veum *et al.*, 2014). The association of weedy functional groups can be ascribed to the fact that weeds are mainly associated with areas subjected to high human activities, which create niches under which these species thrive (Baker, 1972; Shackleton, 2000; Meek *et al.*, 2010). These niches included low inter-specific competition contributing to successful colonization and germinating opportunities, high sun exposure, low soil moisture availability and increased dispersal opportunities by humans or livestock (Baker, 1967; Brändle *et al.*, 2003; Sutherland, 2004; Thuiller *et al.*, 2012; Zimmermann *et al.*, 2014). Therefore, in this study external animal transport was the mode of dispersal preferred by some weedy species. However, since it is a grazing environment, internal animal transport was also associated with the communal rangelands (Auffret, 2011; Wesuls *et al.*, 2012; Anderson *et al.*, 2014; Hempson *et al.*, 2014; Albert *et al.*, 2015).

Semi-arid communal lands are not only species richness (Shackleton, 2000; Rutherford *et al.*, 2012) but this study also found that these communities are also rich in functional traits and functional groups. This finding suggests that the these functional traits and functional groups provide insurance and thus maintain ecosystem functioning. In this study the increase of functional traits and functional groups can be ascribed to intermediate disturbance levels (Grime, 1973; Armesto & Pickett, 1985; Shackleton, 2000; Biswas & Mallik, 2010), as well as increased patchiness which provided opportunities for various functional groups to establish (Shackleton, 2000). However evenness of traits was not enhanced since some traits dominated. Especially those traits known to improve soil conditions and species that are tolerant or tend to avoid defoliation by herbivores (Vetter, 2009). Thus various traits contributing to similar ecosystem functions provide redundancy (Díaz & Cabido, 2001; Laliberte *et al.*, 2010). High trait-based redundancy causes a decline in trait dominance since these specific traits dominated (Díaz & Cabido, 2001; Hanke *et al.*, 2014).

Functional groups were well distributed since group evenness was relatively high. Lavorel *et al.* (1998) found that old field plant diversity contributes to resilience and the existence of several functional groups under different environmental conditions is described as the key to persistence of these systems facing disturbances. Therefore this finding is applicable to communal lands since this plant community is considered as functionally diverse and various functional groups can buffer communal plant communities against environmental perturbations (Lavorel *et al.*, 1998; Mori *et al.*, 2013). Therefore these functional groups provide resilience to communal plant communities and thus the insurance hypothesis may also be applicable to functional group diversity (Díaz & Cabido, 2001; Lavorel & Garnier, 2002; Elmqvist *et al.*, 2003). Communal lands can be considered as resilient communities which are event-driven and can be in a

temporary stable state since communal lands are described as non-equilibrium systems (Ellis & Swift, 1988; Shackleton, 1993; Shackleton *et al.*, 1994; Harrison & Shackleton, 1999; Rutherford *et al.*, 2012; Rutherford & Powrie, 2013).

6.4.2.3 Total land transformation

Strip mining practices are mainly associated with disturbances of the topsoil, which include removal of the seed bank, soil compaction, decrease in soil fertility, exposure to soil erosion and increased soil temperature (Tacey & Glossop, 1980; Soane, 1990; Zhang *et al.*, 1997; Singh *et al.*, 2002; Carrick & Krüger, 2007; Shrestha & Lal, 2011; Macy, 2014; Mensah, 2015). Dominance of non-weedy therophytes, some non-weedy perennials and weedy perennials, were expected as these species are well adapted to such soil disturbances (Lavorel & Garnier, 2002). Therophytes can persist under harsh environmental conditions (Waaland & Allen, 1987; Jordaan *et al.*, 2004; Olsson & Ödman, 2014), their roots induce soil de-compaction (Glinski & Lipiec, 1990; Bengough *et al.*, 2006) and promotes favourable conditions for late successional (perennial) species to establish successfully (Prach, 1987; Wilcox, 1998). Similarly to the study Ecke and Rydin (2000) some perennial herbaceous species may be stress tolerant, including weedy and non-weedy perennial species. Perennial species contributes to soil organic matter (Zhou *et al.*, 2012; Veum *et al.*, 2014) and also limits water erosion (Kort *et al.*, 1998; Jankauskas *et al.*, 2008) and therefore promote soil quality and water holding capacity.

In this study species that spread by means of stolons (clonal above ground) and prostrate growth forms were the most important plant traits associated with strip mines. Roots of sod-forming (stolon forming) grass species prevent soil erosion, promote water holding capacity and when roots die, also contribute to soil organic matter (Kort *et al.*, 1998; Jankauskas & Jankauskiene, 2003; Jankauskas *et al.*, 2008; Kinderiene & Karcauskiene, 2012; Granger & O'Connor, 2015). A study conducted by Kim (1983) found that species with a prostrate growth form have lower evaporation rates since these plants are not exposed to turbulence of wind compared to erect species. Therefore these species can be considered as drought tolerant (Jauffret *et al.*, 2003; Reynolds, 2015) and it is expected that prostrate species will have a competitive advantage on strip mines where the water holding capacity of the soil is low. An increase in prostrate cover contributes to lower soil temperatures since these plants will increase radiation usage, hence higher soil moisture availability is promoted and wind erosion is limited (Leys, 1991; Richards, 1996; Webb *et al.*, 2009; Reynolds, 2015).

Despite the high richness of functional traits and functional groups on strip mines, it was expected that functionally unique species of Mopaneveld were lost on the strip mines due to habitat filtering. Certain species with specific trait sets dominated since trait evenness and trait diversity was low. Therefore habitat filtering was responsible for functional convergence (species with similar traits are favoured) (Flynn *et al.*, 2009; Mori *et al.*, 2013). Furthermore dominant species (with similar traits) have the ability to compensate for the loss of certain traits thus contributed to functional compensation (Grime, 2006; Lavorel *et al.*, 2011). Species within functional groups that responded similarly to disturbances may, for instance improve soil conditions, which provide trait-based redundancy to strip mine plant communities (Elmqvist *et al.*, 2003; Mayfield *et al.*, 2005; Laliberte *et al.*, 2010; Mori *et al.*, 2013). Therefore, high redundancy in this

community is responsible for low evenness levels of functional traits and functional groups (Díaz & Cabido, 2001; Hanke *et al.*, 2014). Dominant species influence resilience and since strip mines were dominated by therophytes, resilience will be high but resistance will be low (Díaz & Cabido, 2001), since biomass of fast-growing herbaceous species is sensitive to drought (MacGillivray *et al.*, 1995). Low resistance indicates that ecosystem stability is low, suggesting the possibility that strip mines can be more vulnerable to future disturbances (such as drought) causing degradation (Díaz & Cabido, 2001; Downing *et al.*, 2012; Pillar *et al.*, 2013). Since there is a lack of documentation regarding strip mines, it is assumed that strip mines are in a temporary successional state dominated by specific species maintaining ecosystem functions, which could be stable or at a threshold. More long-term studies are required to promote our understanding of the dynamics of this community to determine whether succession will continue to reach the climax community or whether the community will be driven past the threshold to a more degraded state.

Extreme environmental conditions prevail on mine dumps. Plant species selected for re-vegetation purposes must deal with altered soil conditions, low nutrient availability, steep slopes, high sun exposure (absence of trees), toxic heavy metals, wind and water erosion (Bradshaw, 1997; Rethman, 2000; Cooke & Johnson, 2002; Sheoran *et al.*, 2010; Pedrol *et al.*, 2014; Granger & O'Connor, 2015; Ilunga wa Ilunga *et al.*, 2015; Mensah, 2015; Shutcha *et al.*, 2015). Furthermore, this study shows that wind dispersed species were associated with the mine dump plant community. Wind dispersed plant species characterise dry (Howe & Smallwood, 1982) and soil disturbed habitats (Lavorel *et al.*, 1998). Therefore these species are able to easily colonize open dry soil patches on mine dumps (Walker & Shiels, 2013) to promote succession (Wang *et al.*, 2010; Chang *et al.*, 2014).

Fast growing annual grass species (i.e. therophytes), tolerant of acid soil conditions, rapidly provide surface cover and stabilize steep slopes (Macy, 2014; Granger & O'Connor, 2015; Mensah, 2015), while perennial grasses produce root biomass, enhancing soil organic carbon and microbial enzyme activity (Zhou *et al.*, 2012; Macy, 2014; Veum *et al.*, 2014). Since nitrogen is a limiting factor on mine dumps (Mensah, 2015), it was not surprising that nitrogen fixing species were characteristic on mine dumps. Leguminous plant species live in a mutualistic relationship with nitrogen-fixing soil bacteria living in root nodules (Bradshaw, 1997; Nabors, 2004; Santi *et al.*, 2013; Sprent *et al.*, 2013). Nitrogen-fixing plant species have competitive vigour over non-nitrogen-fixing plants especially in nitrogen deficient habitats (Santi *et al.*, 2013) since these plant species have the ability to rapidly fix and accumulate nitrogen, and thus contribute to nitrogen capital in nitrogen deficient soils (Bradshaw, 1997). Therefore leguminous plant species have the ability to improve soil fertility on rock dumps and tailings facilities through their contribution to soil organic matter, improve nitrogen and phosphorus levels and reduce levels of heavy metals (Bradshaw, 1997; Anawar *et al.*, 2013; Domingo & David, 2014; Pedrol *et al.*, 2014; Mensah, 2015). In combination with leguminous species, annual and perennial grass species is an appropriate method to re-vegetate mine dumps (Brofas *et al.*, 2007; Anawar *et al.*, 2013; Pedrol *et al.*, 2014) and to combat erosion and promote succession (Sheoran *et al.*, 2010; Pedrol *et al.*, 2014). Since weedy species can function as pioneers (Van Oudtshoorn *et al.*, 2011;

Kotschy, 2013; Shutcha *et al.*, 2015) and provide ecosystem functions similar to non-weedy species (Baker, 1967; Mensah, 2015), they are often selected to be included in seed mixes to promote succession on mine dumps. Weedy therophytes control soil erosion (Bellairs *et al.*, 2006), while perennial invasive grass species such as *Pennisetum setaceum* is selected for soil stabilization purposes (Rahlao *et al.*, 2014). On the long term, weedy therophytes can be outcompeted by non-weedy therophytes or perennial species as succession progresses (Baker, 1967; Meiners *et al.*, 2002).

Mine dumps are depauperate in plant functional traits since selected plant species must provide a specific ecosystem function, i.e. soil stabilization, promote soil properties and prevent water and wind erosion. These dominant plant traits contribute to the redundancy of these communities (Díaz & Cabido, 2001; Hanke *et al.*, 2014). Low trait diversity can be ascribed to the total land transformation that occurred, hence functional trait assemblages are homogeneous which is in accordance with the study conducted by Laliberte *et al.* (2010). Each functional group has an important ecosystem function to provide and it is expected that due to abiotic conditions, associated with mine dumps and rehabilitation management, the dominance of some functional groups were prevented. It is the diversity within functional groups which contribute to ecosystem maintenance and hence provide redundancy (Elmqvist *et al.*, 2003). However a functional group with high redundancy may be more vulnerable to future invasions of exotic herbaceous species due to low resistance (Díaz & Cabido, 2001). Mine dumps are therefore considered as functionally diverse since unique functional groups are equally represented.

### 6.5. Shortcomings and further analyses

After careful consideration it is recommended that certain aspects of this study should be revised to improve the current results:

- Weediness – a ‘fuzzy’ trait

Using the term ‘weed’ as a plant functional trait may be considered as a ‘fuzzy’ trait (Dreber, 2015) since these plants are characterised by certain specific features (i.e. short life cycle, rapid growth rates, rapid germination rates, high reproductive allocation, dormant soil seed banks) which contribute to competitive vigour of weeds in disturbed areas (Goodall & Naude, 1998; Nabors, 2004; Sutherland, 2004; Gunton *et al.*, 2011; Schonbeck, 2013; Zimmermann *et al.*, 2014). Therefore weedy plant species should rather be categorised as ruderal plants (adapted to survive persistent and severe disturbances under low stress, but high disturbance levels) following the CSR-classification scheme which refer to ecological strategies of plants with the C-dimension referring to competitive plants, S-dimension to stress tolerant plants and R-dimension to ruderal plants (Grime, 1974; Grime, 1977). Various studies found that the CSR classification system (as a categorical trait) is of great relevance to land-use studies and therefore can be considered of valuable assistance for identifying land-use impacts on vegetation as well as promote our understanding regarding ecosystem functioning (Lepš *et al.*, 1982; Hodgson, 1989; Hodgson, 1991; Hodgson *et al.*, 1999; Caccianiga *et al.*, 2006; Marini *et al.*, 2007; Catorci *et al.*, 2011; Gunton *et al.*, 2011; Schellberg & Pontes, 2012;

Negreiros *et al.*, 2014). Therefore the CSR classification system will be included as a categorical trait when further analyses will be conducted when this chapter is prepared as a manuscript. Weediness as a trait will be omitted.

- Nitrogen fixing ability as a trait

Further statistical analyses can be conducted on the nitrogen fixing functional group. The trait (nitrogen fixing ability) can be omitted to possibly observe better clustering on the dendrogram and PCoA (Dreber, 2015) since species in this functional group consisted of a combination of life forms, life histories and weediness. If it is decided to omit nitrogen fixing ability, it is expected that these species will cluster together with similar species based on their life form and life history traits. Consequently other valuable ecosystem functions associated with these species, which were initially masked by the inclusion of nitrogen fixing ability as a trait, can then be revealed.

- Species with rare traits

Species with rare traits may be omitted or should be included under other similar traits e.g. the trait clonal above and below ground may be included under either clonal above ground or clonal below ground (Dreber, 2015). Furthermore plant functional group 5 (non-weedy perennials) and 6 (non-weedy therophytes) can be inspected to determine which traits are responsible for clustering of certain species in smaller groups on the dendrogram and thus clustering on the PCoA can be refined. It can also be considered to examine and compare the major life form and/or major growth form per land-use (McIntyre *et al.*, 1995; Lavorel *et al.*, 1997; Landsberg *et al.*, 1999; McIntyre *et al.*, 1999; McIntyre & Lavorel, 2001; Clarke *et al.*, 2005; Burylo *et al.*, 2007; Dreber, 2015). Traits within major life form or growth form groups can then be analysed separately to identify trait responses which could have been obscured by patterns associated with the major groups (Landsberg *et al.*, 1999; McIntyre *et al.*, 1999). Therefore the relationship between the major groups and the environment can be examined (McIntyre & Lavorel, 2001; Clarke *et al.*, 2005; Burylo *et al.*, 2007). A PCA can then be conducted on a site-trait abundance matrix to determine whether land-uses display certain dominant life and growth forms (Dreber, 2015).

- Transformed versus untransformed data

With reference to the Box and Whisker plots, transformed data is displayed for trait and functional group richness. However, transformed data may be confusing for the reader and therefore untransformed data should also be displayed (Dreber, 2015). It may also be confusing when referring to Shannon-Wiener- and Simpson diversity of traits and functional groups, yet it is still considered as a measure of functional response diversity, but only on the level of traits and groups (Hanke *et al.*, 2014; Dreber, 2015). For future consideration it may be more appropriate to consider actual functional diversity indices to be able to make the study more conclusive and comparative (Petchey & Gaston, 2002; Mason *et al.*, 2005; Petchey & Gaston, 2006; Villéger *et al.*, 2008; Flynn *et al.*, 2009; Laliberté & Legendre, 2010; Schleuter *et al.*, 2010; Robin, 2011; Van der Walt, 2013).

- Redundancy and resilience of Mopaneveld: preliminary observations

Results of species diversity and functional diversity may indicate contradicting effects on ecosystem functioning. Species diversity studies, supporting the rivet hypothesis, insurance hypothesis and diversity-stability theory, suggest that if species loss occurs, ecosystem function will be subjected to degradation due to low levels of species diversity which are not able to buffer the system against disturbances (Yachi & Loreau, 1999; Chapin *et al.*, 2000; Clements & Rohr, 2009; Zhang *et al.*, 2012; Mori *et al.*, 2013; Wickson, 2014). Therefore, by focusing only on species diversity, results may be misleading regarding disturbance effects (Mouillot *et al.*, 2013). Results of Hanke *et al.* (2014) emphasised that species diversity *per se* is not sufficient for detecting vegetation shifts caused by disturbances and that functional trait-based diversity measures should rather be used. Early warning signs can then be better detected by analysing functional traits before species loss becomes evident in the community (Mouillot *et al.*, 2013). However, according to the hypotheses of Flynn *et al.* (2009), there is a relationship between species richness, functional diversity and redundancy (see Table 2.1, Chapter 2). Linking results of species diversity measures to those of functional diversity, provides i) a broad view regarding impacts of land-use disturbances on ecosystem resilience and ecosystem functioning and ii) provides valuable insight into management and conservation policies of ecosystems (Lavorel *et al.*, 1998; Díaz *et al.*, 1999; Díaz & Cabido, 2001; Mayfield *et al.*, 2010; Zhang *et al.*, 2012; Moretti *et al.*, 2013; Mori *et al.*, 2013; Mouillot *et al.*, 2013; Hanke *et al.*, 2014).

According to the hypothesis of Flynn *et al.* (2009), if functional redundancy is low, species richness and functional diversity will decline with random species loss in plant communities (hypothesis A). Therefore if species diversity and functional diversity respond similarly on group and trait level, despite the potential loss of species, then it is assumed that redundancy is high (Flynn *et al.*, 2009; Mayfield *et al.*, 2010). In this study results of species and functional diversity measures have not been linked statistically, although preliminary results (based on comparisons of means) suggest that hypotheses A, C and D of Flynn *et al.* (2009) may be applicable to land-use plant communities of Mopaneveld (See Chapter 2 section 2.4 and Table 2.1).

Hypothesis A may be applicable to protected Mopaneveld and communal land since high levels of species richness, Shannon-Wiener and Simpson diversity (on functional trait and group level) were displayed (Appendix B, Figures B1 and B2). Mine dumps with intermediate levels of species richness were characterised by relatively low trait diversity (Shannon-Wiener and Simpson) and high functional group diversity (Shannon-Wiener and Simpson) (Appendix B, Figures B1 and B2). Unique functional groups prevail on mine dumps. Some of species of these groups are selected for ecosystem services (rehabilitation) whereas others can be considered to have successful colonization rates and hence promote succession based on specific traits ensuring their survival. It is suggested that further investigations are needed to determine which of these functional groups are the result of rehabilitation and which the result of succession. Furthermore hypothesis A may be applicable with reference to functional groups of mine dump plant communities. However, with reference to trait diversity (Shannon-Wiener and Simpson), hypothesis C may also be applicable to mine dump plant communities since functional trait diversity was low with low species richness (Appendix B, Figures B1 and B2). This is an example of a plant community which was

characterised by high species richness and redundancy in its trait diversity (protected Mopaneveld) being replaced by a community with species with unique traits during re-vegetation practices, but with low species richness due to the selection of these plant species by managers. Strip mines may be considered vulnerable and hypothesis D (Flynn *et al.*, 2009) is applicable to this plant community since species richness was high, but with low levels of Shannon-Wiener diversity (traits and groups) and intermediate levels of Simpson diversity (traits and groups) (Appendix B, Figures B1 and B2). Only species with a certain trait set are able to persist on the strip mines due to habitat filtering while a small number of species with unique traits are lost. Therefore functional diversity will decline more severely than species richness. Evenness on species-, trait-, and group level were low (Appendix B, Figures B1 and B2) suggesting that the evenness component of diversity measures must be included. In accordance with Hanke *et al.* (2014) the evenness component of functional diversity is important to determine disturbance effects on the herbaceous layer of Mopaneveld. Since evenness declined for traits and functional groups, a certain level of trait-based redundancy may be provided by dominant species (Díaz & Cabido, 2001; Hanke *et al.*, 2014). However, the koppies responded differently. Species richness levels were exceptionally low while Shannon-Wiener and Simpson diversity on trait and functional group level were high (Appendix B, Figures B1 and B2). Therefore koppies are characterised by unique functional assemblages with high evenness on species-, trait- and functional group level which can be ascribed to the various environmental conditions prevailing on these habitats.

The following patterns were observed from preliminary results after analyses that attempted to compare species and functional diversity: it is suggested that response patterns of species diversity are similar to functional diversity with reference to Mopaneveld, communal lands, strip mines, as well as for Simpson diversity (on species-, trait- and group level) of koppies and mine dumps. Therefore it is assumed that redundancy and resilience are high in these communities if species diversity and functional diversity increases and low if species diversity and functional diversity decreases in response to disturbance (Appendix B, Figures B1 and B2). Response patterns varied for Shannon-Wiener diversity on species-, trait- and group level of koppies and mine dumps. Despite low Shannon-Wiener species diversity on the koppies, functional diversity of traits and plant functional groups provided redundancy and hence contributed to resilience of these landscapes. High Shannon-Wiener functional group diversity of mine dumps may provide redundancy which compensated for the loss of species and traits (Appendix B, Figures B1 and B2).

Strip mines and mine dumps may have a lower degree of redundancy since response patterns of species diversity may correspond to those of functional diversity. The redundancy that is being provided by dominant species can be considered as trait-based redundancy. With reference to communal land the studies of Mouillot et al. (2013) and Hanke et al. (2014) are supported by this study‘s preliminary observations that continuous disturbances in the communal land are responsible for the selection of certain functional traits such as tussock, prostrate and rosette growth forms; above and below clonality; therophytes; stoloniferous species; internal animal transport and weedy plants.Vulnerable species will decline while functionally redundant species will increase. However further statistical analyses are required to test these observations related to species richness, species diversity and functional diversity.

## 6.6. Summary

According to expectations, anthropogenic disturbances in Mopaneveld promote unique plant functional groups. Functional groups were mainly associated with dominant life form, life history and weediness. These three traits can be considered as suitable predictors of land-use effects on the herbaceous layer of Mopaneveld since anthropogenic land-uses (excluding protected areas) have a filtering effect on functional assemblages. Species with an annual life history, weeds and therophytes were favoured by disturbances. Protected areas successfully conserve unique plant functional traits. Koppies are heterogeneous entities in their functional assemblages since harsh environmental conditions favour specific traits, each with their specific ecosystem function. Mopaneveld koppies were associated with chamaephytes, hemicryptophytes and cryptophytes while tussock and prostrate growth forms were favoured in natural Mopaneveld. The strip mines displayed high trait richness and high trait diversity and low trait evenness. Therefore the hypothesis stated in this study regarding total transformation (for traits) is not supported for the strip mines. Considering functional groups, strip mines displayed high functional group richness and high functional group diversity but low functional group evenness and therefore the hypothesis (regarding functional groups and total transformation) is partially supported. Furthermore strip mines were characterised by therophytes, stress-tolerant perennial, prostrate growth forms and stoloniferous species which provided high redundancy. Hence, strip mines are resilient but may be subjected to degradation in the future. The hypothesis regarding marginal disturbance (for traits) is supported since communal lands displayed high trait richness and trait diversity while trait evenness was low. Since functional group richness, functional group diversity and functional group evenness were high for communal plant communities, the hypothesis (regarding functional groups and marginal disturbance) is supported. Communal lands favoured herbaceous species with grazing avoidance strategies i.e. prostrate and rosette growth forms as well as stoloniferous species. Functional assemblages were enhanced on communal lands due to intermediate disturbance and habitat variability. In accordance with the insurance hypothesis, diverse functional groups buffer communal land against environmental fluctuations, hence communal land was resilient in their functional assemblages. Mine dumps displayed low trait richness and trait diversity while trait richness was high. The hypothesis of total transformation is thus supported with reference to mine dump plant communities. Total transformation is responsible for homogenisation of plant traits, since certain trait sets are selected to provide certain ecosystem functions on mine dumps (nitrogen fixers and wind dispersed species). Considering functional groups of mine dumps, the hypothesis concerned with total transformation is supported since these plant communities displayed high functional group richness, functional group diversity and functional group evenness. Functional group and functional trait evenness respond differently compared to one another. Functional group evenness is linked to the homogeneous or heterogeneous character of land-use plant communities since functional group evenness increased on the koppies (heterogeneous environment), decreased on Mopaneveld (homogeneous nature) and strip mines (homogeneous due to disturbance) and increased on communal lands (heterogeneous due to patchiness and niche-availability). However compared to Mopaneveld, strip mines and communal lands, mine dumps (considered homogeneous due total transformation) had higher functional group evenness which is ascribed to effective rehabilitation strategies. Trait evenness is sensitive to marginal disturbances (i.e.

communal land) as well as strip mined land and was not enhanced. Dominant plant traits of marginal disturbances and total land transformation provide high trait-based redundancy and therefore provide high resilience. Functional group evenness is enhanced on the mine dumps due to effective management strategies and functionally diverse plant groups provide redundancy.

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# Chapter 7

# Conclusions

This study provided valuable knowledge regarding the effects of various land-uses on herbaceous plant species- and response diversity of Mopaneveld. Major findings of this study are listed, followed by recommendations regarding future management and conservation strategies.

## 7.1. Main findings

### Chapter 5

- Land-uses were characterised by different herbaceous species assemblages.
- Protected koppies, mine dumps and strip mines displayed distinctive species assemblages.
- Environmental conditions are considered a driver responsible for driving unique species assemblages of koppies. Anthropogenic disturbances filtered species composition of mine dumps and strip mines. Rehabilitation practices on mine dumps and natural succession on strip mines can also be considered important factors influencing compositional differences.
- The filtering effect of land-uses on species composition is evident since certain species were more associated with certain land-uses (i.e. communal lands, strip mines and mine dumps).
- Different herbaceous species responded differently to the disturbance levels associated with different land-uses.
- Key grass and forb species fulfil important pioneering roles and provide valuable ecosystem functions on communal lands, strip mines and mine dumps.
- Each land-use displayed different patterns of species richness, density, evenness and diversity.
- Species richness was enhanced on communal lands, suggesting that the intermediate disturbance hypothesis is applicable to these plant communities.
- Density was enhanced on communal lands and strip mines.
- A negative relationship was observed between biomass and land-use intensity as well as between biomass and density. However the relationship between density and land-use intensity was found to be unimodal.
- Evenness was sensitive to anthropogenic disturbances since strip mines, communal lands and mine dumps had low evenness whereas protected areas (koppies and Mopaneveld) had higher evenness.
- Benchmarked against Mopaneveld, mine dumps and strip mines displayed a lack of species, suggesting the occurrence of species loss due to absence of colonisation of species. However, diversity levels were more severely affected on strip mines, where no rehabilitation occurred, indicating the significance of rehabilitation on mine dumps.These two plant communities may be in a certain state which may be resilient to future disturbances due to the occurrence of dominant stress-tolerant species. These species may be able to maintain ecosystem functioning (by means of their traits) and thus provide valuable ecosystem services at the current disturbance state.

- Certain exotic species did occur in each land-use community. However native species diversity was not adversely affected by land-uses. However communal lands and mine dumps displayed higher numbers of exotic species, which were also high in abundance.

**Chapter 6**

- Anthropogenic disturbance in Mopaneveld govern unique plant functional groups.
- Six plant functional groups were identified and described based on unique trait sets.
- Plant functional groups were primarily associated with the traits life form, life history and weediness.
- Life form, life history and weediness may be considered as suitable predictors regarding land-use effects on the herbaceous layer of Mopaneveld.
- Land-uses were associated with different plant functional groups and hence different plant functional traits.
- Since certain traits were associated with different land-use plant communities, land-uses (excluding protected areas) have a filtering effect on functional assemblages.
- Protected areas (i.e. Mopaneveld and koppies) conserve unique plant functional traits, however environmental conditions are considered as the main drivers of these traits.
- Chamaephytes, hemicryptophytes and cryptophytes were associated with the koppies.
- Tussock and prostrate growth forms were associated with protected Mopaneveld.
- Therophytes, stress-tolerant perennial, prostrate growth forms and stoloniferous species were associated with strip mines. Plant species with these traits provided a level of redundancy in strip mine plant communities. Therefore strip mines may be considered resilient.
- Species with grazing avoidance strategies such as prostrate, rosette and stoloniferous growth forms were favoured in communal lands.
- Wind dispersed species, therophytes, certain perennial species, nitrogen fixing species and weedy species fulfil important ecosystem functions (i.e. soil stabilization, promote soil properties and prevent water and wind erosion) on mine dumps.
- Functional group richness was enhanced on strip mines and communal lands.
- Functional group evenness can be linked to heterogeneity or homogeneity of land-use plant communities since functional group evenness increased on koppies (heterogeneous), decreased on Mopaneveld (due to Mopaneveld's homogeneous character), strip mines (homogeneous due to disturbance and increased on communal lands (heterogeneous due to patchiness and niche-availability). However mine dumps (also be considered homogeneous) had higher functional group evenness (compared to Mopaneveld, strip mines and communal lands).
- Koppies, communal lands and mine dumps displayed high functional group diversity. Functionally diverse plant functional groups have the ability to buffer plant communities against disturbances and hence provide redundancy. Therefore these plant communities may be considered resilient.
- Trait richness was enhanced on protected areas, marginal disturbances and strip mines. Loss of traits was evident on mine dumps.

- Functional group and functional trait evenness responded differently to one another.
- Since trait evenness was lower on the strip mines and communal lands when compared to protected Mopaneveld, trait evenness is considered to be sensitive to these disturbances.
- Dominant traits, associated with marginal disturbances and total land transformation, provide high trait-based redundancy. Therefore these communities may also be resilient to further disturbance.
- To some extent, strip mines, communal lands and mine dumps were associated with loss in trait diversity compared to koppies and Mopaneveld.
- Flynn *et al.* (2009) suggested four different hypotheses signifying possible relationships between species richness, functional diversity and redundancy. In this study three of these hypotheses (hypotheses A, C and D) may be applicable to land-use plant communities of Mopaneveld.
- Hypothesis A (functional redundancy is low when species richness and functional diversity decline and species loss is random) may be applicable to protected Mopaneveld and communal lands. Mopaneveld and communal land had high levels of species richness, Shannon-Wiener- and Simpson diversity on functional trait- and functional group level, suggesting high redundancy.
- When considering species richness and functional diversity on group level of the mine dumps hypothesis A may be applicable. Mine dumps had intermediate levels of species richness and various functional groups suggesting a level of redundancy.
- However hypothesis C (redundant species are lost first under land-use intensification, functional diversity decline with declining species richness at a slow rate; a community with high species richness and redundancy in its trait diversity is replaced by a community with unique species but with low species richness) may be also applicable to mine dumps when considering functional trait diversity. Mine dumps displayed low trait diversity with low species richness. Therefore mine dumps display unique functional traits which was selected for re-vegetation purposes but with low species richness. These species with their unique traits may be providing trait-based redundancy.
- Hypothesis D (species with unique functional traits are lost first and functional diversity declines more severely than species richness. Species loss is non-random since only species with a certain trait-set can persist under land-use intensification due to habitat filtering) is applicable to strip mines. Species richness was high but Shannon-Wiener diversity on functional trait- and functional group level was low whereas Simpson diversity (on trait and functional group level) was intermediate. Only certain species were able to persist in this community while a number of species with unique traits were lost due to habitat filtering.
- Koppies were the exception since these plant communities displayed low species richness levels but with high Shannon-Wiener- and Simpson diversity (on trait- and functional group level). Therefore koppies are characterised by unique functional assemblages with high evenness (on species-, trait- and functional group level) suggesting that koppies may be redundant.
- Evenness on species-, trait- and functional group level is important to determine land-use effects on the herbaceous layer.

- Preliminary results suggest that response patterns of species diversity are similar to functional diversity with reference to Mopaneveld, communal lands, strip mines as well as for Simpson diversity (on species-, trait- and group level) of koppies and mine dumps. It is assumed that redundancy and resilience are high in these communities if species diversity and functional diversity increases and low if species diversity and functional diversity decreases.
- Similar response patterns of species diversity and functional diversity were observed for Mopaneveld, communal lands and strip mines.
- Response patterns varied for Shannon-Wiener diversity on species-, trait- and group level of koppies and mine dumps. Despite low Shannon-Wiener species diversity on the koppies, functional diversity of traits and plant functional groups provided redundancy and hence contributed to resilience of these landscapes. High Shannon-Wiener functional group diversity of mine dumps may provide redundancy which compensated for the loss of species and traits.
- Different response patterns were observed for Shannon-Wiener diversity on species-, trait- and group level of koppies and mine dumps. Despite low Shannon-Wiener species diversity on the koppies, functional diversity of traits and plant functional groups provided redundancy and hence contributed to resilience of these landscapes. High Shannon-Wiener functional group diversity of mine dumps may provide redundancy which compensated for the loss of species and traits.
- Mine dumps and strip mines may be more vulnerable to future disturbances especially if redundant plant functional groups and traits are lost.

### 7.2. The way forward

Anthropogenic land-use practices influence herbaceous species diversity and response diversity of Mopaneveld. Plant diversity patterns found in this study have the potential to contribute to the understanding of land-use effects on the herbaceous layer of Mopaneveld along with insight regarding management and conservation approaches.

Rehabilitation of Mopaneveld is important as Mopaneveld cannot be restored to its initial form. This was evident when the mine dumps and strip mines were compared to one another. From a conservation perspective biodiversity and conservation studies should incorporate richness and evenness measures to attain insight regarding species diversity patterns exposed to land-use change since these measures do not react similarly to anthropogenic disturbances. Yet species richness, evenness as well as diversity measures can be seen as good indicators of ecosystem health. Evenness is more sensitive to land-use change than species richness and is a good indicator of ecosystem health of anthropogenically disturbed ecosystems. Therefore management for evenness is important in Mopaneveld to improve diversity levels. Consequently plant communities with high evenness may be more stable since uneven communities may be less resistant to future environmental stress or become subjected to invasion of exotic species. Since strip mines had the lowest species richness and low trait and group evenness, future rehabilitation studies may be initiated to improve evenness and diversity levels by means of different treatments (e.g. organic soil enrichment, re-

seeding of native grass and forb species). In the long term, more studies are required to unravel the effects of community evenness and ecosystem processes. Even though communal lands are resilient in its species and functional assemblages, community based resource management may be required to educate local people in managing available land to maintain valuable provisioning ecosystem services and hence ensure their livelihood on the long-term. Furthermore koppies must be included under conservation policies as these landscapes have unique species and functional assemblages. Therefore koppies may be able to contribute to resilience of surrounding landscapes and can serve as stepping stones for the distribution of some matrix and non-matrix species with short dispersal ranges. Re-vegetation on the mine dumps should still be monitored to ensure that rehabilitation practices are sustainable in the long term.

Understanding different disturbance effects on species and functional diversity is of great importance for conservation planning. Conservationists should not only focus on the results produced by species diversity measures but must also include results of functional diversity measures. Functional diversity may detect vegetation change faster than species diversity. The loss of an entire functional group may have greater implications on ecosystem function than the same number of species from different plant functional groups. Future studies in Mopaneveld can focus on direct measurements of plant traits in plant communities subjected to various land-use practices. Consequently measured traits can be linked to ecosystem processes and as a result provide accurate information regarding ecosystem functioning in land-use plant communities. Therefore conservation of various species providing vital ecosystem functions, by means of their traits, must be incorporated to ensure that redundancy is provided. If redundancy is high, resilience will be high. Conservation management should consider the safeguarding of resilience by identifying the primary diversity responsible for the fostering of high resilience levels. Resilience may then also be achieved with less species diversity and ecosystems will then be able to absorb and recover from anthropogenically driven disturbances.

## Appendices

Appendix A: Additional statistical information of species diversity analyses with regards to applications in ANOSIM, SIMPER and multivariate analysis (Chapter 5).

### Table A1. Pairwise comparisons of ANOSIM R-values.

Permutation N:9999

Mean rank within:6154

Mean rank between:1.202E04

R:0.5398

p:0.0001

| | Koppies | Mopaneveld | Strip mines | Communal | Mine dumps |
|---|---|---|---|---|---|
| Koppies | | | | | |
| Mopaneveld | 0.4257 | | | | |
| Strip mines | 0.5913 | 0.1652 | | | |
| Communal | 0.7074 | 0.2864 | 0.3125 | | |
| Mine dumps | 0.7735 | 0.5719 | 0.6639 | 0.7976 | |

### Table A2. Summary of similarity percentage analyses (SIMPER) indicating cumulative contributions of species across land-uses.(†Cumulative contribution: up to 60%).

| Species | Av. dis. | Cont. (%) | Cum. (%)† |
|---|---|---|---|
| a) Across all land-uses (average dissimarity:91.37) | | | |
| *Urochloa mosambicensis* | **3.262** | **3.57** | **3.57** |
| *Enneapogon cenchroides* | **2.848** | **3.117** | **6.687** |
| *Aristida adscensionis* | **2.56** | **2.802** | **9.489** |
| *Tephrosia purpurea* | **2.251** | **2.463** | **11.95** |
| *Ocimum americanum* | **2.214** | **2.422** | **14.37** |
| *Panicum maximum* | **2.078** | **2.275** | **16.65** |
| *Cenchrus ciliaris* | **1.833** | **2.006** | **18.66** |
| *Schmidtia pappophoroides* | 1.797 | 1.967 | 20.62 |
| *Commelina benghalensis* | 1.752 | 1.918 | 22.54 |
| *Tragus berteronianus* | 1.588 | 1.738 | 24.28 |
| *Kyphocarpa angustifolia* | 1.569 | 1.717 | 25.99 |
| *Digitaria eriantha* | 1.377 | 1.507 | 27.5 |
| *Aristida scabrivalvis* | 1.355 | 1.483 | 28.99 |

| | | | |
|---|---|---|---|
| *Aristida congesta* | 1.349 | 1.477 | 30.46 |
| *Blepharis integrifolia* | 1.347 | 1.475 | 31.94 |
| *Zornia glochidiata* | 1.299 | 1.422 | 33.36 |
| *Phyllanthus incurvus* | 1.293 | 1.415 | 34.77 |
| *Corchorus confusa* | 1.236 | 1.353 | 36.13 |
| *Hibiscus micranthus* | 1.198 | 1.311 | 37.44 |
| *Portulaca hereroensis* | 1.191 | 1.303 | 38.74 |
| *Stipagrostis hirtigluma* | 1.183 | 1.295 | 40.04 |
| *Acalypha indica* | 1.16 | 1.269 | 41.3 |
| *Phyllanthus parvulus* | 1.115 | 1.221 | 42.53 |
| *Heteropogon contortus* | 1.052 | 1.152 | 43.68 |
| *Sesbania bispinosa* | 1.019 | 1.115 | 44.79 |
| *Chloris virgata* | 0.9998 | 1.094 | 45.89 |
| *Melinis repens* | 0.9757 | 1.068 | 46.95 |
| *Indigastrum costatum* | 0.9756 | 1.068 | 48.02 |
| *Brachiaria deflexa* | 0.9356 | 1.024 | 49.05 |
| *Indigofera vicioides* | 0.9304 | 1.018 | 50.06 |
| *Pupalia lappacea* | 0.8878 | 0.9716 | 51.04 |
| *Polygala serpentaria* | 0.8712 | 0.9535 | 51.99 |
| *Talinum arnotii* | 0.8566 | 0.9375 | 52.93 |
| *Tephrosia rhodesica* | 0.7942 | 0.8692 | 53.8 |
| *Achyranthes aspera* | 0.7513 | 0.8223 | 54.62 |
| *Enteropogon macrostachyus* | 0.7362 | 0.8057 | 55.42 |
| *Leucas glabrata* | 0.7226 | 0.7909 | 56.21 |
| *Aristida bipartida* | 0.6573 | 0.7194 | 56.93 |
| *Dicoma tomentosa* | 0.6304 | 0.6899 | 57.62 |
| *Bulbostylis hispidula* | 0.6273 | 0.6865 | 58.31 |
| *Kyllinga alba* | 0.6228 | 0.6816 | 58.99 |
| *Eragrostis trichophora* | 0.6227 | 0.6815 | 59.67 |
| *Rhynchosia minima* | 0.6196 | 0.6781 | 60.35 |
| b) Koppies *vs.* Mine dumps (average dissimilarity:96.63) | | | |
| *Cenchrus ciliaris* | **5.347** | **5.533** | **5.533** |
| *Enneapogon cenchroides* | **5.182** | **5.363** | **10.9** |
| *Panicum maximum* | **3.866** | **4.001** | **14.9** |
| *Commelina benghalensis* | **3.86** | **3.995** | **18.89** |
| *Stipagrostis hirtigluma* | **3.651** | **3.778** | **22.67** |
| *Tephrosia purpurea* | **3.457** | **3.577** | **26.25** |
| *Sesbania bispinosa* | **3.15** | **3.26** | **29.51** |
| *Indigastrum costatum* | **2.762** | **2.859** | **32.37** |
| *Urochloa mosambicensis* | **2.484** | **2.571** | **34.94** |
| *Aristida scabrivalvis* | **2.429** | **2.514** | **37.45** |
| *Aristida adscensionis* | **2.388** | **2.471** | **39.92** |
| *Tephrosia rhodesica* | **2.351** | **2.433** | **42.35** |
| *Acalypha indica* | **2.075** | **2.148** | **44.5** |
| *Aristida congesta* | **2.03** | **2.101** | **46.6** |

| | | | |
|---|---|---|---|
| *Eragrostis trichophora* | 1.845 | 1.91 | 48.51 |
| *Polygala serpentaria* | 1.833 | 1.897 | 50.41 |
| *Tridax procumbens* | 1.455 | 1.505 | 51.92 |
| *Achyranthes aspera* | 1.446 | 1.497 | 53.41 |
| *Hibiscus micranthus* | 1.427 | 1.477 | 54.89 |
| *Pupalia lappacea* | 1.287 | 1.332 | 56.22 |
| *Melinis repens* | 1.263 | 1.307 | 57.53 |
| *Heteropogon contortus* | 1.26 | 1.304 | 58.83 |
| *Pennisetum setaceum* | 1.241 | 1.284 | 60.12 |
| c) Mopaneveld *vs.* Mine dumps (average dissimilarity:91.11) | | | |
| *Enneapogon cenchroides* | **4.18** | **4.588** | **4.588** |
| *Cenchrus ciliaris* | **4.078** | **4.476** | **9.064** |
| *Stipagrostis hirtigluma* | **2.859** | **3.138** | **12.2** |
| *Tephrosia purpurea* | **2.758** | **3.027** | **15.23** |
| *Urochloa mosambicensis* | **2.559** | **2.809** | **18.04** |
| *Sesbania bispinosa* | **2.461** | **2.701** | **20.74** |
| *Aristida scabrivalvis* | **2.338** | **2.566** | **23.31** |
| *Aristida adscensionis* | **2.301** | **2.526** | **25.83** |
| *Indigastrum costatum* | **2.229** | **2.446** | **28.28** |
| *Ocimum americanum* | **2.093** | **2.297** | **30.57** |
| *Aristida congesta* | **2.046** | **2.246** | **32.82** |
| *Tephrosia rhodesica* | **1.857** | **2.039** | **34.86** |
| *Schmidtia pappophoroides* | **1.841** | **2.021** | **36.88** |
| *Hibiscus micranthus* | 1.744 | 1.914 | 38.79 |
| *Heteropogon contortus* | 1.6 | 1.756 | 40.55 |
| *Panicum maximum* | 1.555 | 1.707 | 42.26 |
| *Polygala serpentaria* | 1.533 | 1.682 | 43.94 |
| *Kyphocarpa angustifolia* | 1.528 | 1.678 | 45.62 |
| *Digitaria eriantha* | 1.465 | 1.608 | 47.22 |
| *Eragrostis trichophora* | 1.461 | 1.604 | 48.83 |
| *Rhynchosia minima* | 1.319 | 1.448 | 50.28 |
| *Acalypha indica* | 1.305 | 1.432 | 51.71 |
| *Corchorus confusus* | 1.219 | 1.338 | 53.05 |
| *Tridax procumbens* | 1.163 | 1.276 | 54.32 |
| *Ruellia cordata* | 1.099 | 1.206 | 55.53 |
| *Phyllanthus parvulus* | 1.023 | 1.123 | 56.65 |
| *Melinis repens* | 0.9599 | 1.054 | 57.7 |
| *Pennisetum setaceum* | 0.9432 | 1.035 | 58.74 |
| *Brachiaria deflexa* | 0.9412 | 1.033 | 59.77 |
| *Zornia glochidiata* | 0.8728 | 0.958 | 60.73 |
| d) Mopaneveld *vs.* Koppies (average dissimilarity: 92.33) | | | |
| *Commelina benghalensis* | **3.467** | **3.755** | **3.755** |
| *Panicum maximum* | **3.446** | **3.732** | **7.487** |

| | | | |
|---|---|---|---|
| *Enneapogon cenchroides* | **2.743** | **2.97** | **10.46** |
| *Ocimum americanum* | **2.439** | **2.642** | **13.1** |
| *Aristida adscensionis* | **2.43** | **2.632** | **15.73** |
| *Urochloa mosambicensis* | **2.224** | **2.409** | **18.14** |
| *Digitaria eriantha* | **2.196** | **2.378** | **20.52** |
| *Hibiscus micranthus* | **2.147** | **2.326** | **22.84** |
| *Schmidtia pappophoroides* | **2.118** | **2.294** | **25.14** |
| *Acalypha indica* | 1.772 | 1.919 | 27.06 |
| *Kyphocarpa angustifolia* | 1.77 | 1.917 | 28.97 |
| *Tephrosia purpurea* | 1.759 | 1.905 | 30.88 |
| *Pupalia lappacea* | 1.63 | 1.766 | 32.64 |
| *Enteropogon macrostachyus* | 1.6 | 1.733 | 34.38 |
| *Corchorus confusus* | 1.541 | 1.669 | 36.05 |
| *Phyllanthus parvulus* | 1.403 | 1.52 | 37.57 |
| *Achyranthes aspera* | 1.379 | 1.494 | 39.06 |
| *Aristida scabrivalvis* | 1.295 | 1.403 | 40.46 |
| *Ruellia cordata* | 1.262 | 1.367 | 41.83 |
| *Heteropogon contortus* | 1.219 | 1.32 | 43.15 |
| *Justicia flava* | 1.206 | 1.306 | 44.46 |
| *Kyllinga alba* | 1.119 | 1.212 | 45.67 |
| *Brachiaria deflexa* | 1.06 | 1.148 | 46.82 |
| *Hibiscus calyphyllus* | 1.03 | 1.115 | 47.93 |
| *Eragrostis superba* | 0.9858 | 1.068 | 49 |
| *Zornia glochidiata* | 0.9789 | 1.06 | 50.06 |
| *Indigofera vicioides* | 0.9759 | 1.057 | 51.12 |
| *Talinum arnotii* | 0.9738 | 1.055 | 52.17 |
| *Aristida congesta* | 0.9671 | 1.047 | 53.22 |
| *Waltheria indica* | 0.9423 | 1.021 | 54.24 |
| *Bothriochloa radicans* | 0.8537 | 0.9245 | 55.16 |
| *Rhynchosia minima* | 0.8093 | 0.8765 | 56.04 |
| *Hibiscus sidiformis* | 0.7901 | 0.8557 | 56.9 |
| *Ocimum filamentosum* | 0.7313 | 0.792 | 57.69 |
| *Commelina eckloniana* | 0.7139 | 0.7731 | 58.46 |
| *Melhania forbesii* | 0.708 | 0.7668 | 59.23 |
| *Ipomoea magnusiana* | 0.7067 | 0.7653 | 59.99 |
| *Lantana rugosa* | 0.6981 | 0.756 | 60.75 |
| e) Mopaneveld *vs.* Strip mines (average dissimilarity: 85.51) | | | |
| *Urochloa mosambicensis* | **3.925** | **4.591** | **4.591** |
| *Aristida adscensionis* | **3.133** | **3.664** | **8.254** |
| *Ocimum americanum* | **2.714** | **3.174** | **11.43** |
| *Phyllanthus incurvus* | **2.304** | **2.695** | **14.12** |
| *Schmidtia pappophoroides* | **2.289** | **2.677** | **16.8** |
| *Enneapogon cenchroides* | **2.212** | **2.586** | **19.39** |
| *Tephrosia purpurea* | **2.162** | **2.528** | **21.91** |
| *Kyphocarpa angustifolia* | **2.128** | **2.489** | **24.4** |

| | | | |
|---|---|---|---|
| *Digitaria eriantha* | 1.69 | 1.976 | 26.38 |
| *Panicum maximum* | 1.613 | 1.886 | 28.27 |
| *Hibiscus micranthus* | 1.57 | 1.836 | 30.1 |
| *Tragus berteronianus* | 1.564 | 1.829 | 31.93 |
| *Chloris virgata* | 1.478 | 1.729 | 33.66 |
| *Aristida bipartida* | 1.427 | 1.669 | 35.33 |
| *Phyllanthus parvulus* | 1.38 | 1.614 | 36.94 |
| *Indigofera vicioides* | 1.348 | 1.577 | 38.52 |
| *Talinum arnotii* | 1.337 | 1.564 | 40.08 |
| *Heteropogon contortus* | 1.33 | 1.555 | 41.64 |
| *Corchorus confusus* | 1.256 | 1.468 | 43.11 |
| *Ruellia cordata* | 1.161 | 1.357 | 44.46 |
| *Brachiaria deflexa* | 1.142 | 1.335 | 45.8 |
| *Dicoma tomentosa* | 1.11 | 1.298 | 47.1 |
| *Aristida scabrivalvis* | 1.054 | 1.232 | 48.33 |
| *Zornia glochidiata* | 1.049 | 1.226 | 49.55 |
| *Aristida congesta* | 1.016 | 1.189 | 50.74 |
| *Ocimum filamentosum* | 1.012 | 1.184 | 51.93 |
| *Leucas glabrata* | 0.9918 | 1.16 | 53.09 |
| *Blepharis integrifolia* | 0.9655 | 1.129 | 54.22 |
| *Acalypha indica* | 0.9548 | 1.117 | 55.33 |
| *Melinis repens* | 0.947 | 1.108 | 56.44 |
| *Waltheria indica* | 0.923 | 1.079 | 57.52 |
| *Pupalia lappacea* | 0.9162 | 1.072 | 58.59 |
| *Kyllinga alba* | 0.8639 | 1.01 | 59.6 |
| *Commelina benghalensis* | 0.8634 | 1.01 | 60.61 |
| f) Mopaneveld *vs.* Communal land (average dissimilarity: 87.78) | | | |
| *Portulaca hereroensis* | **2.751** | **3.134** | **3.134** |
| *Urochloa mosambicensis* | **2.597** | **2.959** | **6.093** |
| *Blepharis integrifolia* | **2.299** | **2.619** | **8.712** |
| *Ocimum americanum* | **2.234** | **2.545** | **11.26** |
| *Tragus berteronianus* | **2.227** | **2.537** | **13.79** |
| *Zornia glochidiata* | **2.206** | **2.513** | **16.31** |
| *Schmidtia pappophoroides* | **2.029** | **2.311** | **18.62** |
| *Enneapogon cenchroides* | **1.951** | **2.223** | **20.84** |
| *Aristida adscensionis* | **1.821** | **2.075** | **22.92** |
| *Corchorus confusus* | 1.75 | 1.994 | 24.91 |
| *Digitaria eriantha* | 1.593 | 1.815 | 26.72 |
| *Tephrosia purpurea* | 1.528 | 1.74 | 28.47 |
| *Kyphocarpa angustifolia* | 1.438 | 1.638 | 30.1 |
| *Hibiscus micranthus* | 1.382 | 1.574 | 31.68 |
| *Brachiaria deflexa* | 1.367 | 1.558 | 33.23 |
| *Panicum maximum* | 1.314 | 1.497 | 34.73 |
| *Aristida congesta* | 1.256 | 1.431 | 36.16 |

| | | | |
|---|---|---|---|
| *Aristida scabrivalvis* | 1.217 | 1.386 | 37.55 |
| *Hypertelis bowkeriana* | 1.208 | 1.377 | 38.93 |
| *Gomphrena celosioides* | 1.163 | 1.325 | 40.25 |
| *Bulbostylis hispidula* | 1.118 | 1.274 | 41.52 |
| *Mollugo nudicaulis* | 1.013 | 1.154 | 42.68 |
| *Leucas glabrata* | 0.9367 | 1.067 | 43.74 |
| *Ruellia cordata* | 0.9165 | 1.044 | 44.79 |
| *Talinum arnotii* | 0.9005 | 1.026 | 45.81 |
| *Kyllinga alba* | 0.8916 | 1.016 | 46.83 |
| *Heteropogon contortus* | 0.8582 | 0.9777 | 47.81 |
| *Chloris virgata* | 0.8581 | 0.9775 | 48.79 |
| *Phyllanthus parvulus* | 0.8475 | 0.9655 | 49.75 |
| *Oxygonum sinuatum* | 0.8214 | 0.9357 | 50.69 |
| *Sporobolus nitens* | 0.8187 | 0.9327 | 51.62 |
| *Phyllanthus incurvus* | 0.8149 | 0.9283 | 52.55 |
| *Portulaca trianthemoides* | 0.814 | 0.9273 | 53.48 |
| *Eragrostis superba* | 0.7824 | 0.8913 | 54.37 |
| *Bothriochloa radicans* | 0.7759 | 0.8839 | 55.25 |
| *Indigofera vicioides* | 0.7592 | 0.8649 | 56.12 |
| *Limeum dinteri* | 0.7552 | 0.8603 | 56.98 |
| *Ipomoea magnusiana* | 0.7465 | 0.8505 | 57.83 |
| *Portulaca quadrifida* | 0.7412 | 0.8444 | 58.67 |
| *Pogonarthria squarrosa* | 0.7251 | 0.8261 | 59.5 |
| *Sporobolus ioclados* | 0.7136 | 0.8129 | 60.31 |

**Table A3. DCA eigenvalues and gradient lengths of species abundance data an environmental variables.**

| Axes | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| Eigenvalues* | 0.783 | 0.671 | 0.586 | 0.526 |
| Lengths of gradient | 6.709 | 8.401 | 4.520 | 4.029 |
| Cumulative percentage variance of species data | 3.2 | 5.9 | 8.3 | 10.5 |
| *sum of all eigenvalues = 24.504 | | | | |

**Table A4. CCA eigenvalues, species-environment correlations and cumulative variance.**

| Axes | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| Eigenvalues | 0.475 | 0.309 | 0.236 | 0.215 |
| Species-environment correlations | 0.843 | 0.778 | 0.75 | 0.677 |
| Cumulative percentage variance of species data | 1.9 | 3.2 | 4.2 | 5 |
| Cumulative percentage variance of species-environment relation | 28.8 | 47.6 | 61.9 | 74.9 |
| Sum of all eigenvalues=24.504; sum of all canonical eigenvalues=1.648 | | | | |

**Table A5. Weighted correlation matrix for CCA.**

| | SPEC AX1 | SPEC AX2 | SPEC AX3 | SPEC AX4 | ENVI AX1 | ENVI AX2 | ENVI AX3 | ENVI AX4 |
|---|---|---|---|---|---|---|---|---|
| SPEC AX1 | 1 | | | | | | | |
| SPEC AX2 | 0.0313 | 1 | | | | | | |
| SPEC AX3 | 0.0206 | -0.0348 | 1 | | | | | |
| SPEC AX4 | -0.0083 | -0.0918 | -0.0191 | 1 | | | | |
| ENVI AX1 | 0.8426 | 0 | 0 | 0 | 1 | | | |
| ENVI AX2 | 0 | 0.7778 | 0 | 0 | 0 | 1 | | |
| ENVI AX3 | 0 | 0 | 0.7501 | 0 | 0 | 0 | 1 | |
| ENVI AX4 | 0 | 0 | 0 | 0.6775 | 0 | 0 | 0 | 1 |
| Forbs | -0.0691 | -0.291 | 0.217 | -0.3698 | -0.082 | -0.3741 | 0.2892 | -0.5458 |
| Grass | -0.1138 | 0.6808 | 0.1901 | -0.0604 | -0.1351 | 0.8753 | 0.2534 | -0.0892 |
| Bare soil | -0.4515 | -0.0369 | -0.1315 | 0.259 | -0.5358 | -0.0475 | -0.1754 | 0.3822 |
| Rock | 0.1166 | -0.3745 | -0.2311 | -0.0278 | 0.1383 | -0.4815 | -0.3081 | -0.0411 |
| Debris | 0.6887 | 0.0113 | 0.189 | 0.0277 | 0.8173 | 0.0145 | 0.252 | 0.0409 |
| Biomass (kg/ha) | 0.1841 | 0.1033 | 0.0485 | 0.4211 | 0.2184 | 0.1328 | 0.0647 | 0.6216 |
| Vegetation height(m) | 0.6732 | 0.3239 | -0.0143 | -0.0592 | 0.7989 | 0.4165 | -0.019 | -0.0874 |

**Table A6. Weighted correlation matrix of environmental variables for CCA.**

| | Forbs | Grass | Bare soil | Rock | Debris | Biomass (kg/ha) | Vegetation height (m) |
|---|---|---|---|---|---|---|---|
| Forbs | 1 | | | | | | |
| Grass | -0.2729 | 1 | | | | | |
| Bare soil | -0.065 | -0.3213 | 1 | | | | |
| Rock | -0.1928 | -0.3106 | -0.4517 | 1 | | | |
| Debris | -0.1482 | 0.0105 | -0.5034 | -0.1166 | 1 | | |
| Biomass (kg/ha) | 0.0032 | 0.1515 | -0.1153 | -0.1109 | 0.1413 | 1 | |
| Vegetation height (m) | -0.0407 | 0.1595 | -0.3234 | -0.0948 | 0.4513 | 0.1964 | 1 |

**Table A7. Weighted correlation matrix and inflation factor.**

| | Name | (Weighted) mean | Stand. dev. | Inflation factor |
|---|---|---|---|---|
| 1 | SPEC AX1 | 0 | 1.1292 | |
| 2 | SPEC AX2 | 0 | 0.8598 | |
| 3 | SPEC AX3 | 0 | 0.7406 | |
| 4 | SPEC AX4 | 0 | 0.7727 | |
| 5 | ENVI AX1 | 0 | 0.9515 | |
| 6 | ENVI AX2 | 0 | 0.6688 | |
| 7 | ENVI AX3 | 0 | 0.5556 | |
| 8 | ENVI AX4 | 0 | 0.5235 | |
| 1 | Forbs | 12.0818 | 10.0828 | 43.5457 |
| 2 | Grass | 21.6875 | 13.7813 | 80.8752 |
| 3 | Bare soil | 40.485 | 18.4732 | 152.3409 |
| 4 | Rock | 12.4185 | 16.0659 | 113.1025 |
| 5 | Debris | 13.1347 | 12.7142 | 69.6673 |
| 6 | Biomass (kg/ha) | 1065.0361 | 874.6599 | 1.0681 |
| 7 | Vegetation height (m) | 0.7073 | 0.2972 | 1.3351 |

**Table A8. Summary of Monte-Carlo test. (Test of significance of first canonical axis).**

| | |
|---|---|
| Eigenvalue | 0.475 |
| F-ratio | 3.975 |
| p-value | 0.0340 |

Appendix B: Additional statistical information with regards to regarding multivariate analysis of plant functional assemblages and response patterns of species- and functional diversity (Chapter 6).

## B1. Plant functional groups

### Table B1. DCA eigenvalues and gradient lengths.

| Axes | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| Eigenvalues* | 0.401 | 0.268 | 0.130 | 0.080 |
| Lengths of gradient | 2.577 | 2.647 | 2.055 | 2.130 |
| Cumulative percentage variance of functional group data | 31.0 | 51.8 | 61.8 | 68.0 |
| *sum of all eigenvalues = 1.291 | | | | |

### Table B2. PCA eigenvalues and gradient lengths.

| Axes | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| Eigenvalues* | 0.406 | 0.234 | 0.187 | 0.113 |
| Cumulative percentage variance of functional group data | 40.6 | 64.0 | 82.7 | 94.0 |
| *sum of all eigenvalues =1.000 | | | | |

### Table B3. RDA eigenvalues, plant functional group-environment correlations and cumulative variance.

| Axes | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| Eigenvalues* | 0.092 | 0.022 | 0.018 | 0.005 |
| Functional group-environment correlations | 0.552 | 0.328 | 0.296 | 0.191 |
| Cumulative percentage variance of functional group data | 9.2 | 11.4 | 13.2 | 13.7 |
| Cumulative percentage variance of functional group-environmental relation | 67.1 | 83.1 | 96.3 | 100.0 |
| *sum of all eigenvalues=1.000; sum of all canonical eigenvalues=0.137 | | | | |

**Table B4. Weighted correlation matrix for RDA.**

| | PFG AX1 | PFG AX2 | PFG AX3 | PFG AX4 | ENVI AX1 | ENVI AX2 | ENVI AX3 | ENVI AX4 |
|---|---|---|---|---|---|---|---|---|
| PFG AX1 | 1 | | | | | | | |
| PFG AX2 | -0.3069 | 1 | | | | | | |
| PFG AX3 | 0.1716 | -0.3158 | 1 | | | | | |
| PFG AX4 | -0.2261 | 0.3582 | 0.2928 | 1 | | | | |
| ENVI AX1 | 0.5518 | 0 | 0 | 0 | 1 | | | |
| ENVI AX2 | 0 | 0.3283 | 0 | 0 | 0 | 1 | | |
| ENVI AX3 | 0 | 0 | 0.2957 | 0 | 0 | 0 | 1 | |
| ENVI AX4 | 0 | 0 | 0 | 0.1912 | 0 | 0 | 0 | 1 |
| Koppies | 0.4388 | -0.1634 | -0.0466 | -0.059 | 0.7951 | -0.4977 | -0.1576 | -0.3086 |
| Mopaneveld | 0.0702 | 0.0471 | -0.002 | 0.1876 | 0.1271 | 0.1435 | -0.0069 | 0.9814 |
| Strip mines | -0.3507 | -0.0494 | -0.2187 | -0.031 | -0.6356 | -0.1506 | -0.7397 | -0.1619 |
| Communal | -0.2439 | -0.1334 | 0.234 | -0.0218 | -0.442 | -0.4063 | 0.7915 | -0.1141 |
| Mine dump | 0.0534 | 0.2932 | 0.0489 | -0.0778 | 0.0968 | 0.8931 | 0.1652 | -0.4071 |

**Table B5. Weighted correlation matrix of land-uses for RDA.**

| | Koppies | Mopaneveld | Strip mines | Communal | Mine dump |
|---|---|---|---|---|---|
| Koppies | 1 | | | | |
| Mopaneveld | -0.2721 | 1 | | | |
| Strip mines | -0.2639 | -0.2562 | 1 | | |
| Communal | -0.2389 | -0.2319 | -0.2249 | 1 | |
| Mine dump | -0.268 | -0.2602 | -0.2523 | -0.2284 | 1 |

**Table B6. Weighted correlation matrix and inflation factor.**

| | Name | (Weighted) mean | Stand. dev. | Inflation factor |
|---|---|---|---|---|
| 1 | PFG AX1 | 0 | 1.8121 | |
| 2 | PFG AX2 | 0 | 3.046 | |
| 3 | PFG AX3 | 0 | 3.3823 | |
| 4 | PFG AX4 | 0 | 5.2302 | |
| 5 | ENVI AX1 | 0 | 1 | |
| 6 | ENVI AX2 | 0 | 1 | |
| 7 | ENVI AX3 | 0 | 1 | |
| 8 | ENVI AX4 | 0 | 1 | |
| 1 | Koppies | 0.2189 | 0.4135 | 1.6193 |
| 2 | Mopaneveld | 0.209 | 0.4066 | 1.6014 |
| 3 | Strip mines | 0.199 | 0.3993 | 1.5825 |
| 4 | Communal | 0.1692 | 0.3749 | 1.5198 |
| 5 | Mine dump | 0.204 | 0.403 | 0 |

**Table B7. Summary of Monte-Carlo test. (Test of significance of first canonical axis).**

| | |
|---|---|
| Eigenvalue | 0.092 |
| F-ratio | 19.848 |
| p-value | 0.0020 |

## B2: Plant functional traits

**Table B8. DCA eigenvalues and gradient lengths.**

| Axes | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| Eigenvalues* | 0.171 | 0.078 | 0.064 | 0.037 |
| Lengths of gradient | 1.826 | 1.304 | 1.274 | 1.398 |
| Cumulative percentage variance of functional trait data | 26.4 | 38.5 | 48.4 | 54.1 |
| *sum of all eigenvalues = 0.650 | | | | |

**Table B9. PCA eigenvalues and gradient lengths.**

| Axes | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| Eigenvalues* | 0.521 | 0.192 | 0.091 | 0.056 |
| Cumulative percentage variance of functional trait data | 52.1 | 71.3 | 80.4 | 86.0 |
| *sum of all eigenvalues =1.000 | | | | |

**Table B10. RDA eigenvalues, plant functional group-environment correlations and cumulative variance.**

| Axes | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| Eigenvalues* | 0.168 | 0.024 | 0.012 | 0.002 |
| Functional trait-environment correlations | 0.583 | 0.413 | 0.387 | 0.218 |
| Cumulative percentage variance of functional trait data | 16.8 | 19.2 | 20.3 | 20.5 |
| Cumulative percentage variance of functional trait-environmental relation | 81.7 | 93.3 | 99.0 | 100.0 |
| *sum of all eigenvalues=1.000; sum of all canonical eigenvalues=0.205 | | | | |

**Table B11. Weighted correlation matrix for RDA.**

| | PFT AX1 | PFT AX2 | PFT AX3 | PFT AX4 | ENVI AX1 | ENVI AX2 | ENVI AX3 | ENVI AX4 |
|---|---|---|---|---|---|---|---|---|
| PFT AX1 | 1 | | | | | | | |
| PFT AX2 | -0.2171 | 1 | | | | | | |
| PFT AX3 | -0.07 | 0.1444 | 1 | | | | | |
| PFT AX4 | 0.0184 | 0.025 | 0.0314 | 1 | | | | |
| ENVI AX1 | 0.5829 | 0 | 0 | 0 | 1 | | | |
| ENVI AX2 | 0 | 0.4133 | 0 | 0 | 0 | 1 | | |
| ENVI AX3 | 0 | 0 | 0.3868 | 0 | 0 | 0 | 1 | |
| ENVI AX4 | 0 | 0 | 0 | 0.2184 | 0 | 0 | 0 | 1 |
| Koppies | 0.4931 | -0.1571 | 0.0317 | -0.0796 | 0.846 | -0.3802 | 0.082 | -0.3646 |
| Mopaneveld | 0.0932 | 0.0491 | -0.1034 | 0.2059 | 0.1599 | 0.1188 | -0.2672 | 0.9428 |
| Strip mines | -0.2841 | -0.0796 | -0.2948 | -0.083 | -0.4874 | -0.1927 | -0.7622 | -0.38 |
| Communal | -0.3043 | -0.2003 | 0.2686 | 0.0222 | -0.522 | -0.4847 | 0.6944 | 0.1018 |
| Mine dump | -0.0414 | 0.3741 | 0.1141 | -0.065 | -0.071 | 0.9051 | 0.295 | -0.2978 |

**Table B12. Weighted correlation matrix of land-uses for RDA.**

| | Koppies | Mopaneveld | Strip mine | Communal | Mine dump |
|---|---|---|---|---|---|
| Koppies | 1 | | | | |
| Mopaneveld | -0.2756 | 1 | | | |
| Strip mine | -0.263 | -0.2554 | 1 | | |
| Communal | -0.2376 | -0.2306 | -0.2201 | 1 | |
| Mine dump | -0.2714 | -0.2635 | -0.2515 | -0.2271 | 1 |

**Table B13. Weighted correlation matrix and inflation factor.**

| | Name | (Weighted) mean | Stand. dev. | Inflation factor |
|---|---|---|---|---|
| 1 | PFT AX1 | 0 | 1.7156 | |
| 2 | PFT AX2 | 0 | 2.4195 | |
| 3 | PFT AX3 | 0 | 2.5852 | |
| 4 | PFT AX4 | 0 | 4.5796 | |
| 5 | ENVI AX1 | 0 | 1 | |
| 6 | ENVI AX2 | 0 | 1 | |
| 7 | ENVI AX3 | 0 | 1 | |
| 8 | ENVI AX4 | 0 | 1 | |
| 1 | Koppies | 0.2211 | 0.415 | 1.6148 |
| 2 | Mopaneveld | 0.2111 | 0.4081 | 1.5971 |
| 3 | Strip mine | 0.196 | 0.397 | 1.5688 |
| 4 | Communal | 0.1658 | 0.3719 | 1.5056 |
| 5 | Mine dump | 0.206 | 0.4045 | 0 |

**Table B14. Summary of Monte-Carlo test. (Test of significance of first canonical axis).**

| | |
|---|---|
| Eigenvalue | 0.168 |
| F-ratio | 39.132 |
| p-value | 0.0020 |

## B3: Plant functional groups and environmental variables

**Table B15. DCA eigenvalues and gradient lengths of plant functional group abundance data and environmental variables.**

| Axes | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| Eigenvalues* | 0.474 | 0.301 | 0.170 | 0.136 |
| Lengths of gradient | 2.635 | 2.274 | 1.556 | 2.065 |
| Cumulative percentage variance of functional group data | 30.9 | 50.5 | 61.6 | 70.5 |
| *sum of all eigenvalues = 1.534 | | | | |

**Table B16. RDA eigenvalues, plant functional group-environment correlations and cumulative variance.**

| **RDA functional groups** | | | | |
|---|---|---|---|---|
| Axes | 1 | 2 | 3 | 4 |
| Eigenvalues* | 0.065 | 0.013 | 0.007 | 0.005 |
| Functional group-environment correlations | 0.369 | 0.234 | 0.244 | 0.175 |
| Cumulative percentage variance of functional group data | 6.5 | 7.7 | 8.4 | 8.8 |
| Cumulative percentage variance of functional group-environment relation | 73.0 | 87.3 | 94.8 | 99.9 |
| *sum of all eigenvalues=1.000; sum of all canonical eigenvalues=0.088 | | | | |

**Table B17. Weighted correlation matrix for RDA (plant functional groups and environmental variables).**

| Correlation matrix 5 of RDA (plant functional groups and environmental variables) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | PFG AX1 | PFG AX2 | PFG AX3 | PFG AX4 | ENVI AX1 | ENVI AX2 | ENVI AX3 | ENVI AX4 |
| PFG AX1 | 1 | | | | | | | |
| PFG AX2 | 0.0888 | 1 | | | | | | |
| PFG AX3 | 0.4674 | 0.2216 | 1 | | | | | |
| PFG AX4 | -0.0327 | 0.4104 | 0.0688 | 1 | | | | |
| ENVI AX1 | 0.3691 | 0 | 0 | 0 | 1 | | | |
| ENVI AX2 | 0 | 0.2343 | 0 | 0 | 0 | 1 | | |
| ENVI AX3 | 0 | 0 | 0.244 | 0 | 0 | 0 | 1 | |
| ENVI AX4 | 0 | 0 | 0 | 0.1755 | 0 | 0 | 0 | 1 |
| Forbs | -0.1145 | -0.0928 | 0.1072 | -0.0663 | -0.3102 | -0.3962 | 0.4394 | -0.3778 |
| Grass | 0.0567 | 0.2035 | -0.0305 | -0.03 | 0.1536 | 0.8683 | -0.1252 | -0.1712 |
| Bare soil | -0.1671 | 0.0546 | 0.0788 | 0.1215 | -0.4527 | 0.2329 | 0.3227 | 0.6924 |
| Rock | -0.046 | -0.0959 | -0.0992 | -0.0783 | -0.1245 | -0.4091 | -0.4064 | -0.4461 |
| Debris | 0.2675 | -0.0779 | -0.0168 | -0.0097 | 0.7247 | -0.3323 | -0.0689 | -0.0554 |
| Biomass (kg/ha) | 0.154 | -0.015 | 0.054 | 0.0587 | 0.4172 | -0.0642 | 0.2213 | 0.3347 |
| Vegetation height (m) | 0.2774 | -0.0391 | -0.0887 | 0.0052 | 0.7516 | -0.167 | -0.3635 | 0.0298 |

**Table B18. Weighted correlation matrix of environmental variables for RDA.**

| Correlation matrix 6 of RDA (plant functional groups and environmental variables) | | | | | | | |
|---|---|---|---|---|---|---|---|
| | Forbs | Grass | Bare soil | Rock | Debris | Biomass (kg/ha) | Vegetation height (m) |
| Forbs | 1 | | | | | | |
| Grass | -0.2919 | 1 | | | | | |
| Bare soil | -0.0394 | -0.1751 | 1 | | | | |
| Rock | -0.0733 | -0.3513 | -0.4398 | 1 | | | |
| Debris | -0.18 | -0.0818 | -0.5796 | -0.1573 | 1 | | |
| Biomass (kg/ha) | -0.0474 | 0.2008 | -0.1367 | -0.1527 | 0.178 | 1 | |
| Vegetation height (m) | -0.0323 | 0.0007 | -0.3731 | -0.0141 | 0.4681 | 0.2367 | 1 |

**Table B19. Weighted correlation matrix and inflation factor.**

| | Name | (Weighted) mean | Stand. dev. | Inflation factor |
|---|---|---|---|---|
| 1 | PFG AX1 | 0 | 2.7091 | |
| 2 | PFG AX2 | 0 | 4.2675 | |
| 3 | PFG AX3 | 0 | 4.0975 | |
| 4 | PFG AX4 | 0 | 5.6986 | |
| 5 | ENVI AX1 | 0 | 1 | |
| 6 | ENVI AX2 | 0 | 1 | |
| 7 | ENVI AX3 | 0 | 1 | |
| 8 | ENVI AX4 | 0 | 1 | |
| 1 | Forbs | 10.5885 | 8.9786 | 69.4793 |
| 2 | Grass | 21.1244 | 13.4504 | 153.5647 |
| 3 | Bare soil | 36.0574 | 19.6984 | 337.8833 |
| 4 | Rock | 13.4019 | 16.6762 | 240.6344 |
| 5 | Debris | 18.7943 | 16.7912 | 243.5745 |
| 6 | Biomass (kg/ha) | 1209.1053 | 964.3029 | 1.124 |
| 7 | Vegetation height (m) | 0.8309 | 0.3531 | 1.3508 |

**Table B20. Summary of Monte-Carlo test. (Test of significance of first canonical axis).**

| **Monte-Carlo test**<br>**Test of significance of first canonical axis** | |
|---|---|
| Eigenvalue | 0.065 |
| F-ratio | 13.860 |
| p-value | 0.03 |

## B2: Box and Whisker graphs

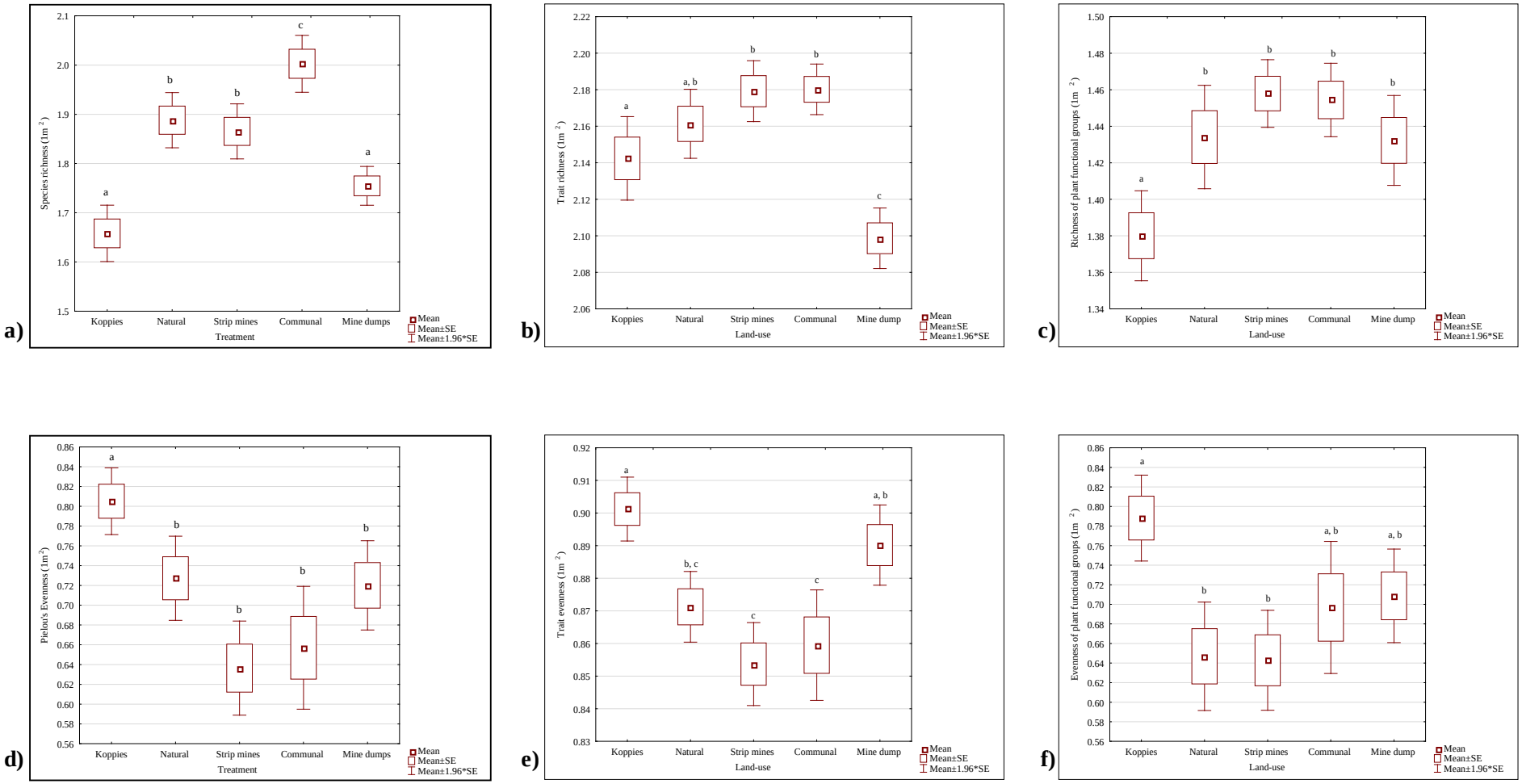


**Figure B1. Diversity indices for a) species richness, b) trait richness, c) functional group richness, d) species evenness, e) trait evenness and f) functional group evenness per plot across land-uses. Similar letters denote no significant differences.**

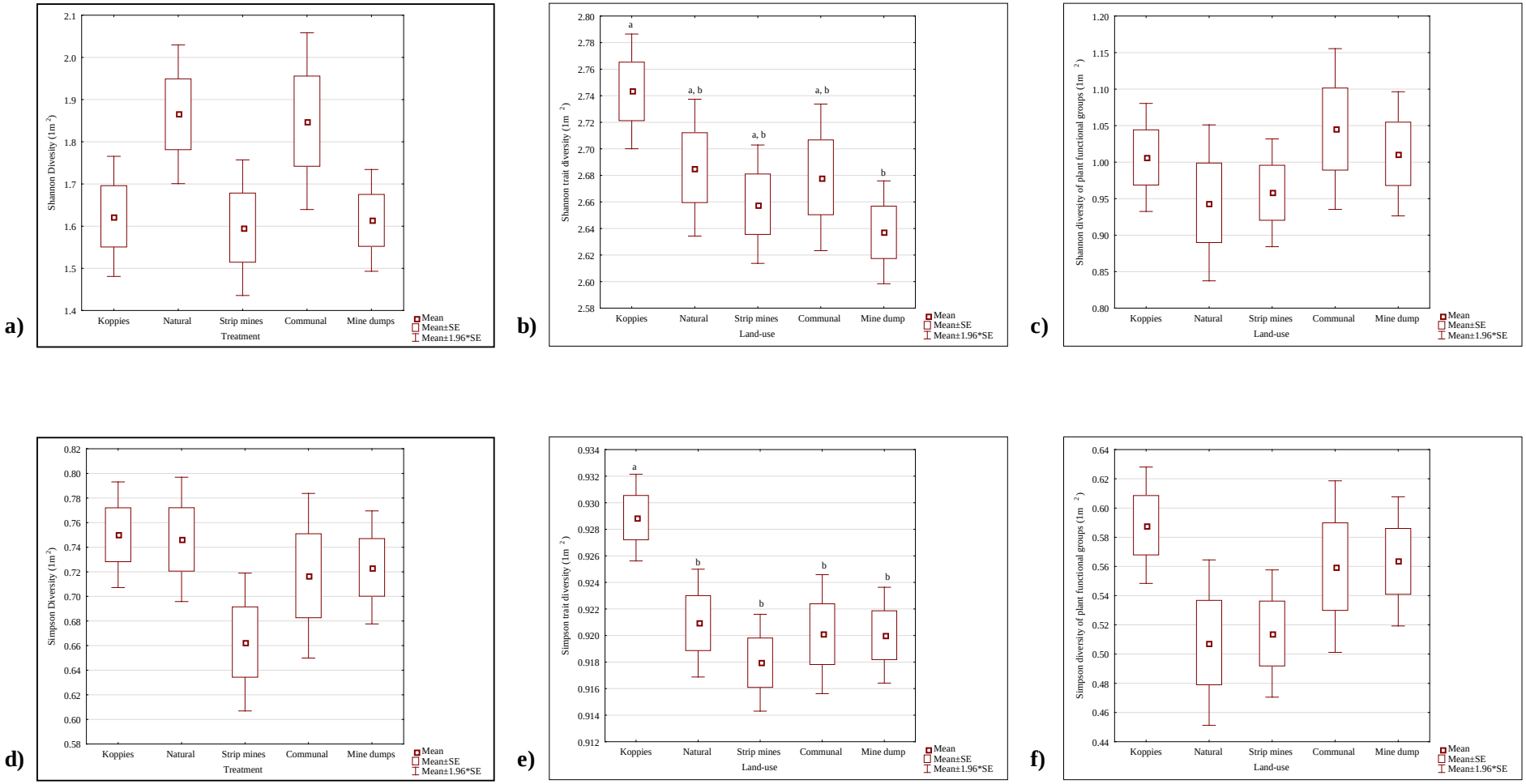


**Figure B2. Diversity indices for Shannon-Wiener diversity on a) species-, b) trait- and c) functional group level as well as Simpson Diversity on d) species-, e) trait- and f) functional group level. Similar letters denote no significant differences.**

Appendix C: Species and trait list

Key: Y=yes; N=no; A=annual; P=perennial; Ph=phanerophytes; Ch=chamaephyte; Hemicryp=hemicryptophyte; Cryptop=cryptophyte; Th=therophyte; N-Cl=non-clonal; Cl-abogr=clonal above ground; Cl-belgr=clonal below ground; Cl-abo&bel=clonal above and below ground; Int-anim=internal animal transport; Ext-anim=external animal transport; Ext & int-anim=external and internal animal transport; Unass=unassisted dispersal; Unspec=unspecified.

| Plant name | Family | Exotic | Weed | Growth form | Life history | Raunkiaer life form | Clonality | Dispersal mode | N- fixer | Shade tolerance |
|---|---|---|---|---|---|---|---|---|---|---|
| *Abrus precatorius* | Fabaceae | N | N | Climber | P | Ph | N-Cl | Int-anim | Y | Shade |
| *Abutilon austro-africanum* | Malvaceae | N | N | Erect | P | Ch | N-Cl | Wind | N | Unspec |
| *Abutilon fruticosum* | Malvaceae | N | N | Erect | P | Ch | N-Cl | Unspec | N | Unspec |
| *Abutilon grandiflorum* | Malvaceae | N | N | Erect | A | Th | N-Cl | Wind | N | Unspec |
| *Acalypha indica* | Euphorbiaceae | N | N | Erect | A | Th | N-Cl | Wind | N | Shade |
| *Acanthospermum hispidum* | Asteraceae | Y | Y | Erect | A | Th | N-Cl | Ext-anim | N | Unspec |
| *Achyranthes aspera* | Amaranthaceae | Y | Y | Erect | P | Ch | N-Cl | Ext-anim | N | Shade |
| *Acrachne racemosa* | Poaceae | N | N | Tussock | A | Th | N-Cl | Int-anim | N | Shade |
| *Acrotome hispida* | Lamiaceae | N | N | Erect | P | Ch | N-Cl | Ext-anim | N | Sun |
| *Agathisanthemum bojeri* | Rubiaceae | N | N | Erect | P | Ch | N-Cl | Unass | N | Sun |
| *Alternanthera pungens* | Amaranthaceae | Y | Y | Creeper | P | Ch | Cl-abogr | Ext-anim | N | Sun |
| *Andropogon chinensis* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Wind | N | Sun |
| *Andropogon gayanus* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Wind | N | Shade |
| *Aptosimum lineare* | Scrophulariaceae | N | N | Erect | P | Ch | N-Cl | Unass | N | Sun |
| *Aristida adscensionis* | Poaceae | N | N | Tussock | A | Th | N-Cl | Unspec | N | Sun |
| *Aristida bipartita* | Poaceae | N | N | Tussock | A | Th | N-Cl | Wind | N | Sun |
| *Aristida congesta* | Poaceae | N | N | Tussock | A | Th | N-Cl | Unspec | N | Sun |
| *Aristida scabrivalvis* | Poaceae | N | N | Tussock | A | Th | N-Cl | Unspec | N | Sun |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Barleria affinis* | Acanthaceae | N | N | Erect | P | Ch | N-Cl | Unass | N | Unspec |
| *Barleria elegans* | Acanthaceae | N | N | Erect | P | Ch | Cl-abogr | Unass | N | Unspec |
| *Barleria galpinii* | Acanthaceae | N | N | Prostrate | P | Ch | Cl-abogr | Unass | N | Unspec |
| *Barleria lancifolia* | Acanthaceae | N | N | Erect | P | Ch | Cl-abogr | Unass | N | Sun |
| *Barleria senensis* | Acanthaceae | N | N | Erect | P | Ch | N-Cl | Unass | N | Shade |
| *Berkheya bipinnatifida* | Asteraceae | N | N | Erect | P | Ch | N-Cl | Wind | N | Unspec |
| *Bidens bipinnata* | Asteraceae | Y | Y | Erect | A | Th | N-Cl | Ext-anim | N | Unspec |
| *Blepharis integrifolia* | Acanthaceae | N | N | Prostrate | P | Ch | N-Cl | Ext-anim | N | Sun |
| *Boerhavia coccinea* | Nyctaginaceae | N | Y | Prostrate | A | Th | N-Cl | Ext-anim | N | Unspec |
| *Boerhavia cordobensis* | Nyctaginaceae | Y | Y | Prostrate | A | Th | N-Cl | Ext-anim | N | Unspec |
| *Boerhavia diffusa* | Nyctaginaceae | Y | Y | Prostrate | A | Th | N-Cl | Ext-anim | N | Unspec |
| *Boerhavia erecta* | Nyctaginaceae | Y | Y | Prostrate | A | Th | N-Cl | Ext-anim | N | Unspec |
| *Bonatea speciosa* | Orchidacea | N | N | Erect | P | Cryptop | Cl-belgr | Unass | N | Shade |
| *Bothriochloa insculpta* | Poaceae | N | N | Tussock | P | Hemicryp | Cl-abogr | Wind | N | Sun |
| *Bothriochloa radicans* | Poaceae | N | N | Tussock | P | Hemicryp | Cl-abogr | Wind | N | Sun |
| *Brachiaria deflexa* | Poaceae | N | Y | Tussock | A | Th | N-Cl | Int-anim | N | Unspec |
| *Brachiaria xantholeuca* | Poaceae | N | N | Tussock | A | Th | N-Cl | Int-anim | N | Unspec |
| *Bulbostylis burchellii* | Cyperaceae | N | Y | Tussock | P | Hemicryp | N-Cl | Wind | N | Sun |
| *Bulbostylis hispidula* | Cyperaceae | N | N | Tussock | A | Th | N-Cl | Wind | N | Sun |
| *Bulbostylis humilis* | Cyperaceae | N | N | Tussock | A | Th | N-Cl | Wind | N | Sun |
| *Calostephane divaricata* | Asteraceae | N | N | Erect | A | Th | N-Cl | Wind | N | Sun |
| *Cardiospermum corindum* | Sapindaceae | N | N | Climber | P | Ph | N-Cl | Unass | N | Shade |
| *Cenchrus ciliaris* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Unspec | N | Sun |
| *Ceratotheca triloba* | Pedaliaceae | N | Y | Erect | A | Th | N-Cl | Unass | N | Sun |
| *Chamaecrista absus* | Fabaceae | N | N | Erect | A | Th | N-Cl | Unass | Y | Sun |
| *Chascanum pinnatifidum* | Verbenaceae | N | N | Prostrate | P | Ch | N-Cl | Unass | N | Sun |
| *Cheilanthes virides* | Pteridaceae | N | N | Erect | P | Cryptop | Cl-belgr | Wind | N | Unspec |
| *Chloris mossambicensis* | Poaceae | N | N | Tussock | P | Hemicryp | Cl-abo&bel | Wind | N | Sun |
| *Chloris roxburghiana* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Wind | N | Sun |
| *Chloris virgata* | Poaceae | N | Y | Tussock | A | Th | N-Cl | Unspec | N | Unspec |
| *Chlorophytum recurvifolium* | Anthericaceae | N | N | Erect | P | Cryptop | Cl-belgr | Unass | N | Sun |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Chlorpohytum galpinii* | Anthericaceae | N | N | Erect | P | Cryptop | Cl-belgr | Unass | N | Sun |
| *Cissus quadrangularis* | Vitaceae | N | N | Climber | P | Ph | N-Cl | Int-anim | N | Shade |
| *Cleome angustifolia* | Capparaceae | N | N | Erect | P | Ch | N-Cl | Unass | N | Sun |
| *Cleome monophylla* | Capparaceae | N | Y | Erect | A | Th | N-Cl | Unass | N | Sun |
| *Clerodendrum ternatum* | Lamiaceae | N | N | Erect | P | Ch | N-Cl | Unass | N | Sun |
| *Commelina africana* | Commelinaceae | N | Y | Erect | P | Ch | N-Cl | Unass | N | Unspec |
| *Commelina benghalensis* | Commelinaceae | N | Y | Creeper | A | Th | Cl-abo&bel | Unass | N | Shade |
| *Commelina eckloniana* | Commelinaceae | N | N | Prostrate | P | Ch | N-Cl | Unass | N | Shade |
| *Commelina erecta* | Commelinaceae | N | N | Prostrate | P | Ch | N-Cl | Unass | N | Unspec |
| *Commelina forskaolii* | Commelinaceae | N | N | Prostrate | A | Th | Cl-abogr | Unass | N | Unspec |
| *Commelina livingstonii* | Commelinaceae | N | N | Erect | P | Ch | N-Cl | Unass | N | Shade |
| *Convolvulus sagittatus* | Convolvulaceae | N | Y | Prostrate | P | Hemicryp | Cl-belgr | Unass | N | Sun |
| *Corbichonia decumbens* | Molluginaceae | N | N | Prostrate | A | Th | N-Cl | Unass | N | Sun |
| *Corchorus asplenifolius* | Tiliaceae | N | N | Prostrate | P | Hemicryp | N-Cl | Unass | N | Sun |
| *Corchorus confusus* | Tiliaceae | N | N | Prostrate | P | Hemicryp | N-Cl | Unass | N | Sun |
| *Corchorus longipedunculatus* | Tiliaceae | N | N | Erect | A | Th | N-Cl | Unass | N | Unspec |
| *Crabbea velutina* | Acanthaceae | N | N | Rosette | P | Hemicryp | N-Cl | Ext-anim | N | Shade |
| *Crassula expansa* | Crassulaceae | N | N | Prostrate | P | Ch | N-Cl | Unass | N | Sun |
| *Crotalaria damarensis* | Fabaceae | N | N | Erect | A | Th | N-Cl | Unass | Y | Sun |
| *Crotalaria sphaerocarpa* | Fabaceae | N | Y | Erect | A | Th | N-Cl | Unass | Y | Sun |
| *Crotalaria steudneri* | Fabaceae | N | N | Erect | A | Th | N-Cl | Unass | Y | Sun |
| *Cucumis africanus* | Cucurbirtaceae | N | Y | Prostrate | P | Hemicryp | N-Cl | Unass | N | Unspec |
| *Cucumis anguria* | Cucurbirtaceae | N | N | Climber | A | Th | N-Cl | Int-anim | N | Unspec |
| *Cucumis metuliferus* | Cucurbirtaceae | N | N | Climber | A | Th | N-Cl | Int-anim | N | Unspec |
| *Cucumis zeyheri* | Cucurbirtaceae | N | N | Prostrate | P | Hemicryp | N-Cl | Unass | N | Sun |
| *Cyathula lanceolata* | Amaranthaceae | N | N | Prostrate | P | Hemicryp | N-Cl | Unass | N | Unspec |
| *Cymbopogon caesius (Cymbopogon excavatus)* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Wind | N | Sun |
| *Cynodon dactylon* | Poaceae | N | Y | Creeper | P | Hemicryp | Cl-abo&bel | Int-anim | N | Sun |
| *Cyperus dubius* | Cyperaceae | N | N | Tussock | P | Hemicryp | Cl-belgr | Int-anim | N | Sun |
| *Cyperus indecorus* | Cyperaceae | N | N | Tussock | P | Hemicryp | Cl-belgr | Int-anim | N | Unspec |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Cyperus obtusiflorus* | Cyperaceae | N | N | Tussock | P | Hemicryp | Cl-belgr | Int-anim | N | Sun |
| *Cyperus rubicundus* | Cyperaceae | N | N | Tussock | P | Hemicryp | N-Cl | Int-anim | N | Sun |
| *Cyperus rupestris* | Cyperaceae | N | N | Tussock | P | Hemicryp | N-Cl | Int-anim | N | Sun |
| *Cyperus zollingeri* | Cyperaceae | N | N | Tussock | A | Th | Cl-belgr | Int-anim | N | Sun |
| *Dactyloctenium aegyptium* | Poaceae | N | Y | Creeper | A | Th | Cl-abogr | Int-anim | N | Sun |
| *Dactyloctenium australe* | Poaceae | N | N | Creeper | P | Hemicryp | Cl-abogr | Int-anim | N | Shade |
| *Dactyloctenium geminatum* | Poaceae | N | N | Creeper | P | Hemicryp | Cl-abogr | Int-anim | N | Unspec |
| *Dalechampia galpinii* | Euphorbiaceae | N | N | Climber | P | Ph | Cl-belgr | Unass | N | Sun |
| *Danthoniopsis dinteri* | Poaceae | N | N | Tussock | A | Th | N-Cl | Wind | N | Sun |
| *Dicoma tomentosa* | Asteraceae | N | N | Erect | A | Th | N-Cl | Wind | N | Sun |
| *Digitaria didactyla* | Poaceae | Y | Y | Creeper | P | Hemicryp | Cl-abo&bel | Int-anim | N | Unspec |
| *Digitaria eriantha* | Poaceae | N | N | Tussock | P | Hemicryp | Cl-abogr | Int-anim | N | Sun |
| *Dolichos trilobus* | Fabaceae | N | N | Climber | P | Ph | Cl-abogr | Unass | Y | Unspec |
| *Drimiopsis davidsoniae* | Hyacinthaceae | N | N | Rosette | P | Cryptop | Cl-belgr | Unass | N | Unspec |
| *Enneapogon cenchroides* | Poaceae | N | N | Tussock | A | Th | N-Cl | Wind | N | Unspec |
| *Enneapogon scoparius* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Wind | N | Unspec |
| *Enteropogon macrostachyus* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Unspec | N | Shade |
| *Eragrostis chloromelas* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Int-anim | N | Sun |
| *Eragrostis curvula* | Poaceae | N | Y | Tussock | P | Hemicryp | N-Cl | Int-anim | N | Sun |
| *Eragrostis gummiflua* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Ext-anim | N | Sun |
| *Eragrostis heteromera* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Ext-anim | N | Sun |
| *Eragrostis lehmanniana* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Int-anim | N | Sun |
| *Eragrostis nindensis* | Poaceae | N | N | Tussock | P | Hemicryp | Cl-belgr | Ext-anim | N | Unspec |
| *Eragrostis rigidior* | Poaceae | N | N | Tussock | P | Hemicryp | Cl-abogr | Ext-anim | N | Unspec |
| *Eragrostis rotifer* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Int-anim | N | Sun |
| *Eragrostis superba* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Unspec | N | Sun |
| *Eragrostis trichophora* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Ext-anim | N | Sun |
| *Eriospermum porphyrovalve* | Eriospermaceae | N | N | Erect | P | Cryptop | Cl-belgr | Wind | N | Sun |
| *Euphorbia hirta* | Euphorbiaceae | Y | Y | Prostrate | A | Th | Cl-abogr | Unass | N | Sun |
| *Euphorbia neopolycnemoides (Phyllanthus* | Euphorbiaceae | N | N | Erect | A | Th | N-Cl | Unass | N | Unspec |

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|---|---|---|---|---|---|---|---|---|---|---|
| *neopolycnemoides)* | | | | | | | | | | |
| *Evolvulus alsinoides* | Convolvulaceae | N | N | Prostrate | A | Th | N-Cl | Unass | N | Sun |
| *Fimbristylis ferruginea* | Cyperaceae | N | N | Tussock | P | Hemicryp | Cl-belgr | Int-anim | N | Sun |
| *Fingerhuthia africana* | Poaceae | N | N | Tussock | A | Th | N-Cl | Unass | N | Sun |
| *Fockea angustifolia* | Apocynaceae | N | N | Climber | P | Ph | Cl-belgr | Wind | N | Unspec |
| *Geigeria burkei* | Asteraceae | N | Y | Erect | P | Ch | N-Cl | Unspec | N | Sun |
| *Gisekia africana* | Gisekiaceae | N | Y | Prostrate | A | Th | N-Cl | Unass | N | Sun |
| *Gnidia rubescens* | Thymelaeaceae | N | N | Erect | P | Ch | N-Cl | Wind | N | Unspec |
| *Gomphocarpus tomentosus* | Apocynaceae | N | N | Erect | P | Ch | N-Cl | Wind | N | Sun |
| *Gomphrena celocioides* | Amaranthaceae | Y | Y | Prostrate | P | Hemicryp | N-Cl | Unass | N | Sun |
| *Gossypium herbaceum* | Malvaceae | N | N | Erect | P | Ch | N-Cl | Wind | N | Sun |
| *Guilleminea densa* | Amaranthaceae | Y | Y | Prostrate | A | Th | Cl-belgr | Ext-anim | N | Sun |
| *Helichrysum candolleanum* | Asteraceae | N | N | Prostrate | P | Hemicryp | N-Cl | Wind | N | Sun |
| *Heliotropium ciliatum* | Boraginaceae | N | Y | Erect | P | Ch | Cl-belgr | Unass | N | Sun |
| *Heliotropium lineare* | Boraginaceae | N | Y | Erect | P | Ch | N-Cl | Unass | N | Sun |
| *Heliotropium steudneri (Heliotropium ovalifolium)* | Boraginaceae | N | Y | Erect | A | Th | N-Cl | Unass | N | Sun |
| *Heliotropium strigosum* | Boraginaceae | N | Y | Erect | A | Th | N-Cl | Unass | N | Sun |
| *Hermannia boraginiflora* | Sterculiaceae | N | N | Erect | P | Ch | N-Cl | Unass | N | Sun |
| *Hermannia glanduligera* | Sterculiaceae | N | Y | Erect | P | Ch | N-Cl | Unass | N | Unspec |
| *Hermbstaedtia odorata* | Amaranthaceae | N | N | Erect | P | Ch | Cl-belgr | Unass | N | Sun |
| *Heteropogon contortus* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Unspec | N | Sun |
| *Hibiscus calyphyllus* | Malvaceae | N | N | Erect | P | Ch | N-Cl | Wind | N | Unspec |
| *Hibiscus coddii* | Malvaceae | N | N | Erect | P | Ch | N-Cl | Wind | N | Sun |
| *Hibiscus engleri* | Malvaceae | N | N | Erect | P | Ch | N-Cl | Wind | N | Unspec |
| *Hibiscus micranthus* | Malvaceae | N | N | Erect | P | Ch | N-Cl | Wind | N | Unspec |
| *Hibiscus praeteritus* | Malvaceae | N | N | Erect | A | Th | N-Cl | Wind | N | Sun |
| *Hibiscus sidiformis* | Malvaceae | N | N | Erect | A | Th | N-Cl | Unass | N | Sun |
| *Hibiscus vitifolius* | Malvaceae | N | N | Erect | P | Ch | N-Cl | Wind | N | Sun |
| *Hybanthus enneaspermus* | Violaceae | Y | Y | Erect | P | Hemicryp | N-Cl | Unass | N | Sun |
| *Hypertelis bowkeriana* | Molluginaceae | N | N | Prostrate | P | Ch | N-Cl | Unass | N | Sun |

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|---|---|---|---|---|---|---|---|---|---|---|
| *Hyperthelia dissoluta* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Wind | N | Sun |
| *Hypoestes forskaolii* | Acanthaceae | N | N | Erect | P | Hemicryp | Cl-abogr | Unass | N | Unspec |
| *Indigastrum costatum* | Fabaceae | N | N | Erect | A | Th | N-Cl | Unass | Y | Sun |
| *Indigofera confusa* | Fabaceae | N | N | Erect | P | Hemicryp | N-Cl | Unass | Y | Sun |
| *Indigofera daleoides* | Fabaceae | N | N | Prostrate | P | Hemicryp | N-Cl | Unass | Y | Sun |
| *Indigofera filipes* | Fabaceae | N | N | Erect | A | Th | N-Cl | Unass | Y | Sun |
| *Indigofera heterotricha* | Fabaceae | N | N | Erect | P | Ch | N-Cl | Unass | Y | Sun |
| *Indigofera nebrowniana* | Fabaceae | N | N | Erect | P | Ch | N-Cl | Unass | Y | Sun |
| *Indigofera rhytidocarpa* | Fabaceae | N | N | Erect | A | Th | N-Cl | Unass | Y | Sun |
| *Indigofera species* | Fabaceae | N | N | Erect | A | Th | N-Cl | Unass | Y | Sun |
| *Indigofera trita* | Fabaceae | N | N | Erect | P | Ch | N-Cl | Unass | Y | Sun |
| *Indigofera vicioides* | Fabaceae | N | N | Prostrate | P | Hemicryp | N-Cl | Unass | Y | Sun |
| *Ipomoea bolusiana* | Convolvulaceae | N | N | Erect | P | Ch | Cl-belgr | Unass | N | Sun |
| *Ipomoea cairica* | Convolvulaceae | N | Y | Climber | P | Ph | Cl-belgr | Wind | N | Sun |
| *Ipomoea dichroa* | Convolvulaceae | N | Y | Climber | A | Th | N-Cl | Wind | N | Unspec |
| *Ipomoea magnusiana* | Convolvulaceae | N | N | Prostrate | P | Ch | N-Cl | Wind | N | Sun |
| *Ipomoea obscura* | Convolvulaceae | N | N | Prostrate | P | Ch | Cl-belgr | Unass | N | Sun |
| *Ipomoea plebeia* | Convolvulaceae | N | Y | Climber | A | Th | N-Cl | Wind | N | Unspec |
| *Ipomoea sinensis* | Convolvulaceae | N | N | Climber | A | Th | N-Cl | Unass | N | Unspec |
| *Justicia flava* | Acanthaceae | N | N | Erect | P | Ch | N-Cl | Unass | N | Unspec |
| *Justicia matammensis* | Acanthaceae | N | N | Erect | A | Th | N-Cl | Unass | N | Shade |
| *Justicia protracta* | Acanthaceae | N | N | Erect | P | Ch | N-Cl | Unass | N | Shade |
| *Kedrostis africana* | Cucurbirtaceae | N | N | Climber | P | Ph | Cl-belgr | Int-anim | N | Shade |
| *Kedrostis leloja* | Cucurbirtaceae | N | N | Climber | P | Ph | Cl-belgr | Int-anim | N | Unspec |
| *Kohautia cynanchica* | Rubiaceae | N | N | Erect | A | Th | N-Cl | Unass | N | Sun |
| *Kohautia virgata* | Rubiaceae | N | N | Erect | A | Th | N-Cl | Unass | N | Sun |
| *Kyllinga alba* | Cyperaceae | N | N | Tussock | P | Hemicryp | Cl-belgr | Wind | N | Sun |
| *Kyllinga welwitschii* | Cyperaceae | N | N | Tussock | P | Hemicryp | Cl-belgr | Wind | N | Sun |
| *Kyphocarpa angustifolia* | Amaranthaceae | N | N | Erect | A | Th | N-Cl | Wind | N | Sun |
| *Lantana rugosa* | Verbenaceae | N | N | Erect | P | Ch | N-Cl | Int-anim | N | Unspec |
| *Ledebouria revoluta* | Hyacinthaceae | N | N | Erect | P | Cryptop | Cl-belgr | Unass | N | Sun |

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|---|---|---|---|---|---|---|---|---|---|---|
| *Leucas glabrata* | Lamiaceae | N | N | Erect | P | Ch | N-Cl | Unass | N | Sun |
| *Leucas sexdentata* | Lamiaceae | N | N | Erect | A | Th | N-Cl | Unass | N | Sun |
| *Limeum dinteri* | Molluginaceae | N | N | Prostrate | P | Hemicryp | N-Cl | Unass | N | Sun |
| *Limeum viscosum* | Molluginaceae | N | N | Prostrate | A | Th | N-Cl | Unass | N | Sun |
| *Litogyne gariepina (Epaltes gariepina)* | Asteraceae | N | N | Erect | P | Ch | N-Cl | Wind | N | Sun |
| *Marsdenia sylvestris* | Apocynaceae | N | N | Climber | P | Ph | N-Cl | Unass | N | Shade |
| *Megalochlamys revoluta* | Acanthaceae | N | N | Erect | P | Ch | N-Cl | Unass | N | Sun |
| *Melhania acuminata* | Sterculiaceae | N | N | Erect | P | Ch | N-Cl | Wind | N | Unspec |
| *Melhania forbesii* | Sterculiaceae | N | N | Erect | P | Ch | N-Cl | Unass | N | Sun |
| *Melhania prostrata* | Sterculiaceae | N | N | Erect | P | Ch | N-Cl | Unass | N | Unspec |
| *Melinis repens* | Poaceae | N | Y | Tussock | A | Th | N-Cl | Wind | N | Sun |
| *Merremia palmata* | Convolvulaceae | N | N | Prostrate | P | Ch | N-Cl | Unass | N | Unspec |
| *Microcharis galpinii* | Fabaceae | N | N | Prostrate | A | Th | N-Cl | Unass | Y | Sun |
| *Mollugo cerviana* | Molluginaceae | N | Y | Erect | A | Th | N-Cl | Unass | N | Sun |
| *Mollugo nudicaulis* | Molluginaceae | Y | Y | Rosette | A | Th | N-Cl | Unass | N | Sun |
| *Monadenium lugardiae* | Euphorbiaceae | N | N | Erect | P | Ch | Cl-belgr | Unass | N | Sun |
| *Monechma divaricatum* | Acanthaceae | N | Y | Erect | P | Ch | N-Cl | Unass | N | Unspec |
| *Monsonia glauca* | Geraniaceae | N | N | Erect | P | Ch | N-Cl | Wind | N | Sun |
| *Nidorella anomala* | Asteraceae | N | Y | Erect | P | Ch | N-Cl | Wind | N | Sun |
| *Ocimum americanum* | Lamiaceae | N | N | Erect | A | Th | N-Cl | Unass | N | Sun |
| *Ocimum filamentosum (Becium filamentosum)* | Lamiaceae | N | N | Erect | A | Th | N-Cl | Unass | N | Sun |
| *Ophioglossum polyphyllum* | Ophioglossaceae | N | N | Erect | P | Cryptop | Cl-belgr | Wind | N | Unspec |
| *Oropetium capense* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Int-anim | N | Sun |
| *Oxygonum delagoense* | Polygonaceae | N | Y | Erect | A | Th | N-Cl | Unass | N | Sun |
| *Oxygonum sinuatum* | Polygonaceae | N | Y | Erect | A | Th | N-Cl | Ext-anim | N | Unspec |
| *Panicum coloratum* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Int-anim | N | Unspec |
| *Panicum deustum* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Int-anim | N | Shade |
| *Panicum maximum* | Poaceae | N | Y | Tussock | P | Hemicryp | N-Cl | Int-anim | N | Shade |
| *Panicum schinzii* | Poaceae | N | Y | Tussock | A | Th | N-Cl | Int-anim | N | Sun |

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|---|---|---|---|---|---|---|---|---|---|---|
| *Pavonia burchellii* | Malvaceae | N | N | Erect | P | Ch | N-Cl | Unass | N | Shade |
| *Pavonia transvaalensis* | Malvaceae | N | N | Erect | P | Ch | N-Cl | Unass | N | Unspec |
| *Pegolettia senegalensis* | Asteraceae | N | N | Erect | A | Th | N-Cl | Wind | N | Sun |
| *Pellaea calomelanos* | Pteridaceae | N | N | Erect | P | Cryptop | Cl-belgr | Wind | N | Unspec |
| *Pennisetum setaceum* | Poaceae | Y | Y | Tussock | P | Hemicryp | N-Cl | Wind | N | Unspec |
| *Phyllanthus incurvus* | Euphorbiaceae | N | N | Erect | P | Ch | Cl-belgr | Int-anim | N | Unspec |
| *Phyllanthus maderaspatensis* | Euphorbiaceae | N | N | Erect | A | Th | N-Cl | Int-anim | N | Sun |
| *Phyllanthus parvulus* | Euphorbiaceae | N | N | Erect | P | Ch | N-Cl | Int-anim | N | Unspec |
| *Plectranthus fruticosus* | Lamiaceae | N | N | Erect | P | Ch | N-Cl | Unass | N | Unspec |
| *Pogonarthria squarrosa* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Ext-anim | N | Sun |
| *Polygala erioptera* | Polygalaceae | N | N | Erect | A | Th | N-Cl | Wind | N | Sun |
| *Polygala serpentaria* | Polygalaceae | N | N | Erect | P | Hemicryp | N-Cl | Unass | N | Sun |
| *Polygala sphenoptera* | Polygalaceae | N | N | Erect | P | Ch | N-Cl | Wind | N | Sun |
| *Portulaca hereroensis* | Portulacaceae | N | N | Prostrate | A | Th | Cl-abogr | Unass | N | Sun |
| *Portulaca oleracea* | Portulacaceae | Y | Y | Prostrate | A | Th | Cl-abogr | Unass | N | Sun |
| *Portulaca pilosa* | Portulacaceae | N | Y | Prostrate | A | Th | N-Cl | Unass | N | Sun |
| *Portulaca quadrifida* | Portulacaceae | N | Y | Prostrate | A | Th | Cl-abogr | Unass | N | Sun |
| *Portulaca trianthemoides* | Portulacaceae | N | N | Erect | A | Th | N-Cl | Unass | N | Sun |
| *Pupalia lappaceae* | Amaranthaceae | N | Y | Erect | A | Th | N-Cl | Ext-anim | N | Shade |
| *Rhinacanthus xerophilus* | Acanthaceae | N | N | Erect | P | Ch | N-Cl | Unass | N | Sun |
| *Rhynchosia confusa* | Fabaceae | N | N | Climber | P | Ph | N-Cl | Unass | Y | Sun |
| *Rhynchosia minima* | Fabaceae | N | N | Climber | P | Ph | N-Cl | Unass | Y | Unspec |
| *Rhynchosia totta* | Fabaceae | N | Y | Climber | P | Ph | Cl-belgr | Unass | Y | Unspec |
| *Ruellia cordata* | Acanthaceae | N | N | Erect | P | Ch | N-Cl | Unass | N | Unspec |
| *Sansevieria hyacinthoides* | Dracaenaceae | N | N | Erect | P | Cryptop | Cl-belgr | Int-anim | N | Unspec |
| *Schkuhria pinnata* | Asteraceae | Y | Y | Erect | A | Th | N-Cl | Wind | N | Sun |
| *Schmidtia pappophoroides* | Poaceae | N | N | Tussock | P | Hemicryp | Cl-abogr | Unspec | N | Unspec |
| *Secamone filiformis* | Apocynaceae | N | N | Climber | P | Ph | N-Cl | Wind | N | Unspec |
| *Secamone parvifolia* | Apocynaceae | N | N | Climber | P | Ph | N-Cl | Unass | N | Unspec |
| *Seddera suffruticosa* | Convolvulaceae | N | N | Erect | P | Ch | N-Cl | Unass | N | Sun |
| *Sericorema remotiflora* | Amaranthaceae | N | N | Erect | P | Ch | N-Cl | Wind | N | Sun |

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|---|---|---|---|---|---|---|---|---|---|---|
| *Sesbania bispinosa* | Fabaceae | Y | Y | Erect | A | Th | N-Cl | Unass | Y | Sun |
| *Setaria pumila* | Poaceae | N | Y | Tussock | A | Th | N-Cl | Unspec | N | Unspec |
| *Setaria sagittifolia* | Poaceae | N | N | Tussock | A | Th | N-Cl | Int-anim | N | Shade |
| *Setaria sphacelata* | Poaceae | N | N | Tussock | P | Hemicryp | Cl-belgr | Int-anim | N | Unspec |
| *Sida ovata* | Malvaceae | N | N | Erect | A | Th | N-Cl | Unass | N | Unspec |
| *Solanum delagoense* | Solanaceae | N | N | Erect | P | Ch | N-Cl | Int-anim | N | Sun |
| *Sorghum versicolor* | Poaceae | N | Y | Tussock | A | Th | N-Cl | Unspec | N | Sun |
| *Spermacoce senensis* | Rubiaceae | N | N | Erect | A | Th | N-Cl | Unass | N | Sun |
| *Sporobolus fimbriatus* | Poaceae | N | Y | Tussock | P | Hemicryp | Cl-belgr | Int-anim | N | Shade |
| *Sporobolus ioclados* | Poaceae | N | N | Tussock | P | Hemicryp | Cl-abo&bel | Int-anim | N | Sun |
| *Sporobolus nitens* | Poaceae | N | N | Tussock | P | Hemicryp | Cl-belgr | Int-anim | N | Sun |
| *Sporobolus panicoides* | Poaceae | N | N | Tussock | A | Th | N-Cl | Int-anim | N | Shade |
| *Stipagrostis ciliata* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Wind | N | Sun |
| *Stipagrostis hirtigluma* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Wind | N | Sun |
| *Stipagrostis obtusa* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Wind | N | Sun |
| *Streptopetalum serratum* | Turneraceae | N | Y | Erect | A | Th | N-Cl | Unass | N | Sun |
| *Striga asiatica* | Orobanchaceae | N | Y | Erect | A | Th | N-Cl | Unass | N | Sun |
| *Stylochaeton natalensis* | Araceae | N | N | Erect | P | Cryptop | Cl-belgr | Unass | N | Shade |
| *Syncolostemon canescens (Hemizygia canescens)* | Lamiaceae | N | N | Erect | P | Hemicryp | N-Cl | Unass | N | Sun |
| *Talinum arnotii* | Portulacaceae | N | N | Erect | P | Ch | Cl-belgr | Unass | N | Unspec |
| *Tephrosia purpurea* | Fabaceae | N | Y | Prostrate | A | Th | N-Cl | Unass | Y | Sun |
| *Tephrosia rhodesica* | Fabaceae | N | N | Erect | P | Ch | N-Cl | Unass | Y | Sun |
| *Tephrosia uniflora* | Fabaceae | N | N | Erect | P | Ch | N-Cl | Unass | Y | Sun |
| *Tetradenia brevispicata* | Lamiaceae | N | N | Erect | P | Ch | N-Cl | Int-anim | N | Sun |
| *Themeda triandra* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Unspec | N | Sun |
| *Tragia rupestris* | Euphorbiaceae | N | N | Climber | P | Ph | N-Cl | Wind | N | Shade |
| *Tragus berteronianus* | Poaceae | N | Y | Tussock | A | Th | N-Cl | Ext-anim | N | Sun |
| *Trianthema salsoloides* | Aizoaceae | N | N | Prostrate | A | Th | N-Cl | Unass | N | Sun |
| *Tribulus terrestris* | Zygophyllaceae | N | Y | Prostrate | A | Th | N-Cl | Ext & int-anim | N | Sun |

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| *Tribulus zeyheri* | Zygophyllaceae | N | N | Prostrate | P | Ch | N-Cl | Ext-anim | N | Sun |
| *Tricholaena monachne* | Poaceae | N | N | Tussock | P | Hemicryp | N-Cl | Unspec | N | Unspec |
| *Tricliceras glanduliferum* | Turneraceae | N | Y | Erect | A | Th | N-Cl | Unass | N | Sun |
| *Tricliceras longepedunculatum* | Turneraceae | N | N | Erect | P | Hemicryp | N-Cl | Unass | N | Sun |
| *Tridax procumbens* | Asteraceae | Y | Y | Prostrate | A | Th | N-Cl | Wind | N | Unspec |
| *Triumfetta rhomboidea* | Tiliaceae | N | Y | Erect | A | Th | N-Cl | Ext-anim | N | Unspec |
| *Urochloa mosambicensis* | Poaceae | N | Y | Tussock | P | Hemicryp | Cl-abo&bel | Int-anim | N | Unspec |
| *Urochloa oligotricha* | Poaceae | N | N | Tussock | P | Hemicryp | Cl-belgr | Unspec | N | Sun |
| *Urochloa panicoides* | Poaceae | N | Y | Creeper | A | Th | Cl-abogr | Unspec | N | Sun |
| *Vigna frutescens* | Fabaceae | N | N | Climber | P | Ph | N-Cl | Int-anim | Y | Sun |
| *Vigna unguilata* | Fabaceae | N | N | Climber | P | Ph | Cl-belgr | Int-anim | Y | Sun |
| *Waltheria indica* | Sterculiaceae | N | N | Erect | A | Th | N-Cl | Int-anim | N | Sun |
| *Xenostegia tridentata* | Convolvulaceae | N | N | Prostrate | P | Ch | N-Cl | Unass | N | Sun |
| *Zornia glochidiata* | Fabaceae | N | N | Erect | A | Th | N-Cl | Unass | Y | Sun |