

**THE ANALYSIS OF THE NATIONAL WETLANDS VEGETATION DATABASE:
FRESHWATER LOWLAND PALUSTRINE WETLANDS**

By

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DECLARATION

I, declare that the thesis hereby submitted by me for the Masters degree at the University of the Free State is my own independent work and has not previously been submitted by me at another university/faculty. I furthermore, cede copyright of the thesis in favour of the University of the Free State.

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TABLE OF CONTENTS

TITLE	i
DECLARATION	ii
ACKNOWLEDGEMENTS	iii
TABLE OF CONTENTS	
LIST OF FIGURES	vii
LIST OF TABLES	ix
LIST OF ABBREVIATIONS	x
RESEARCH OUTPUTS	xi
ABSTRACT	xii
CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW	
1.1 Background	14
1.2 Wetlands and their importance in the environment	14
1.3 Classification of wetlands	17
1.4 Plants as indicators for wetland condition	22
1.5 National Wetland Vegetation Database	23
1.6 Structure of the database	75
1.7 Aims of the study	30
CHAPTER 2: METHODOLOGY	
2.1 Introduction	32
2.2 Software methods and tools	33
2.3 Classification: Cluster analysis	34

2.4 Indicator species analysis (ISA)	36
2.5 Ordination (Nonmetric Multidimensional Scaling (NMS) and Canonical Correspondence Analysis (CCA)	38
2.6 Group testing: Multi-response permutation procedure (MRPP)	41
2.7 Species response curves: Nonparametric Multiplicative Regression (NPMR)	43
2.8 Research procedure	46

CHAPTER 3: Sclerophyllous Wetlands Vegetation: patterns and ecological drivers

3.1 Sclerophyllous Wetlands Vegetation	50
3.2 Classification and Indicator Species Analysis	51
3.3 Ordination and group testing	56
3.3.1 Patterns of plant community distribution excluding soil data	65
3.3.2 Patterns of plant community distribution including soil data.....	58
3.3.3 Group testing (MRPP)	61
3.4 Species response curves	64
3.5 Description of communities	69
3.6 Discussion	81

CHAPTER 4: Temperate Grassy Wetland Vegetation: patterns and ecological drivers

4.1 Temperate Grassy Wetland Vegetation	84
4.2 Classification and Indicator Species Analysis	85
4.3 Ordination (NMS, CCA) and group testing (MRPP) results	91
4.3.1. Patterns of plant community distribution excluding soil data	91
4.3.2 Patterns of plant community distribution including soil data.....	94

4.3.3 Group testing (MRPP)	97
4.4 Species response curves	100
4.5 Description of communities	104
4.6 Discussion	119
CHAPTER 5: GENERAL DISCUSSION, CONCLUSION AND RECOMMENDATIONS	
5.1 Analysis and comparison	122
5.2 Species diversity and threats to wetlands	123
5.3 Species composition of wetland communities	125
5.4 Conclusions	127
5.5 Recommendations	128
REFERENCES	130
APPENDIX A: Vegetation sampling data form	138

LIST OF FIGURES

Figure 1.1 Map of South Africa showing positions of data captured by NWVD, including historic data as well as newly collected data entered in the database from 2010 to 2013.

Figure 1.2 Subdivision of available data of national wetlands on database system.

Figure 2.1 Example of scree plot showing stress as function of dimensionality.

Figure 2.2 Schematic flowchart displaying the decisions made for systematic analysis of the vegetation data in the South African Wetlands Vegetation Database, showing data subdivision, decision criteria and methods used for analysis.

Figure 3.1 The map shows the distribution of Sclerophyllous wetlands throughout the country, and one of the wetlands in the Western Cape.

Figure 3.2 Cluster dendrogram of Sclerophyllous wetland types based on species cover abundance.

Figure 3.3 NMS ordination biplot of dataset exclusive of soil variables. The symbols in the ordination indicate group identities the arrows and vectors indicate environmental variables that show trends along the axes.

Figure 3.4 NMS and CCA ordination biplot of dataset inclusive of soil data, showing group identities and the driving environmental variables.

Figure 3.5 NMS ordination of clusters B from first ordination, showing the differentiating environmental variables of communities.

Figure 3.6 NMS ordination of cluster D with plant communities that were inseparable in the first ordination analysis and their influential environmental variables.

Figure 3.7 Species response curves of two herbaceous wetland species in Sclerophyllous Wetlands Vegetation found in Western Cape and Eastern Cape.

Figure 3.8 Species response for five species occurring in Communities 16, 17, 18, and 19.

Figure 3.9 Species response curves of three species endemic to the Cape Floristic Region in Sclerophyllous Wetlands Vegetation.

Figure 3.10 Species response curves for four typical freshwater species in Sclerophyllous Wetlands Vegetation.

Figure 4.1 Map showing areas where temperate grassy wetlands are found, and a picture illustrating one of these wetlands in KwaZulu-Natal.

Figure 4.2 A cluster dendrogram of wetland vegetation types of Temperate Grassy Wetlands Vegetation.

Figure 4.3 NMS ordination for Communities 1 to 27 of Temperate Grassy wetlands Vegetation with all plots excluding extensive soil data.

Figure 4.4 NMS ordination diagram with Communities 27 to 34 of Temperate Grassy wetlands excluding soil data.

Figure 4.5 NMS and CCA biplot of Temperate Grassy Wetlands communities with plots that included extensive soil data.

Figure 4.6 NMS ordination diagram for the Communities 11 to 17 of Temperate Grassy wetlands with extensive soil data.

Figure 4.7 NMS ordination of Temperate Grassy wetlands showing driving factors of Communities 22 to 34.

Figure 4.8 Species response curves for two commonly found reeds throughout South Africa.

Figure 4.9 Species response curves for three species that are dominant in Communities 6, 7 and 8.

Figure 4.10 Species response curves for *Imperata cylindrica* and *Carex acutiformis* commonly associated with river banks and streams, particularly in the east and north-east of provinces of South Africa.

LIST OF TABLES

Table 1.1 Data requirements for building the NVWD as decided upon at the 2008 workshop (Sieben, 2011).

Table 1.2 Soil variables as measured by the Agricultural Research Council Institute for Soil, Water and Climate (ARC-ISWC). The abbreviations in the third column refer to the abbreviations used in ordination diagram and species response curves in the results section of Chapter 3. All of these variables have been transformed during analysis using the transformation $\log(X+1)$.

Table 3.1 Communities of Sclerophyllous Wetlands Vegetation (Main Cluster 1) with their indicator species. Monte Carlo test of significance of the observed maximum indicator value (IV) for each species based on 1000 randomizations. Only species that were statistically significant ($p < 0.05$) with maximum indicator value of 20% or higher are shown in this table.

Table 3.2 Inseparable group of Sclerophyllous wetlands communities in ordination space (see figure 3.3 above). Letters refers to the clusters in the ordination diagram.

Table 3.4 Test 2 results for group B: 8. *Carpha glomerata* Community/9. *Cliffortia graminea* Community/10. *Wachendorfia thyrsiflora* Community. The p-value suggests that these communities are similar in terms of environmental condition they occur in, but the agreement within groups expected by chance $A > 0.3$ which is fairly high.

Table 3.5 Test 3 results for 16. *Senecio umbellatus* Community and 17. *Elegia neesii* comm. Both these communities may occur in similar environments.

Table 3.6 Test 4 results for Communities 18 to 32

Table 3.7 Plant communities that are similar for historical and current findings

Table 4.1 Plant communities and associated indicator species for Temperate Grassy Wetland Vegetation (Main Cluster 6).

Table 4.2 The most ubiquitous species in Temperate Grassy wetland, appearing in five communities or more

Table 4.3 MRPP results for Community 11. *Cyperus marginatus* comm., Community 12. *Cynodon dactylon* comm. Community 13. *Trifolium repens*-*Paspalum dilatatum* comm., Community 14. *Cyperus denudatus* comm. and Community 17. *Hemarthia altissima* comm. of Temperate Grassy wetlands. MRPP recognised these communities as similar and NMS was used to visualise relationships among the communities.

Table 4.4 Test 2, for communities 22 to 34 of Temperate Grassy wetlands. MRPP identified these communities difference between these communities is very small and NMS verified that these communities are found in soils with same nutrient concentration.

Table 4.5 Plant communities that are similar for historical and current findings.

LIST OF ABBREVIATIONS

ARC- ISCW	Agricultural Research Council – Institute for Soil, Climate and Water
CCA	Canonical Correspondence Analysis
EC	Electrical Conductivity
GAM	Generalized Additive Modelling
GLM	Generalized Linear Modelling
HGM	Hydro-geomorphic
ISA	Indicator Species Analysis
IV	Indicator Value
MRPP	Multi-response Permutation Procedure
NWVD	National Wetland Vegetation Database
NMS	Non-Metric Multidimensional Scaling
NPMR	Non-Parametric Multiplicative Regression
PCA	Principal Components Analysis
SWV	Sclerophyllous Wetlands Vegetation
TGWV	Temperate Grassy Wetlands Vegetation
WRC	Water Research Commission

RESEARCH OUTPUTS

Publication of results in conference proceedings

1. Mtshali H., Sieben E.J.J. Analysis of South African wetlands vegetation database. Poster presented at National Wetlands Indaba, Limpopo, 23-26 October 2012.
2. Mtshali H., Sieben E.J.J. Analysis of South African wetlands vegetation database. 56th annual symposium of international association for vegetation science. Poster presented at Vegetation patterns and their underlying processes, Tartu, Estonia, 26-30 June 2013.
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ABSTRACT

The South African wetlands vegetation is not well known. Number studies were conducted to classify vegetation focusing mostly in small areas throughout the country. Data from all studies were collated and used to build the National Wetlands Vegetation database. This study was aimed at grouping the similar vegetation plots in the NWVD into plant communities, to find what extent environmental factors can explain patterns in plant species composition, to find which species can be used as environmental indicators in wetlands and to determine how the species respond to the environmental variables that drive the ecosystem. The database contains eight Main Clusters that are further subdivided into communities. Each of these Main Clusters is used as a starting point for further, more detailed analysis. Two of the Main Clusters, Sclerophyllous Wetlands Vegetation and Temperate Grassy Wetland vegetation were used for the purpose of the study. In order to understand the various types of wetlands and their environmental drivers, data analytical data analytical techniques were used to reveal patterns in species composition and their correlation with environmental factors. The multivariate methods used for the analysis of the database were cluster analysis, indicator species analysis, ordination, group testing, and species response curves. All of the above-mentioned methods make use of similarity measures among sample units. Sørensen similarity measure was the measure of choice. Analysis was performed using the two data analytical I packages PC-Ord 6 and HyperNiche 2. The most contrasting influential environmental variables for South African wetlands are Soil texture, Hydrogeomorphic type and the Wetness index. This study also contributes to the management and conservation of water resources. Recommendations are made as to how the vegetation can be used in the assessment of wetlands health/quality and monitoring of wetlands, as well as management.

Keywords: Classification, environmental conditions, group testing, indicator species, ordination, species response.

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

1.1 Background

This thesis is based upon work completed for a Water Research Commission (WRC) project in developing a database with wetland vegetation data. The intent of the project was to classify wetland vegetation communities and to understand their link with the physical environment of the wetlands. Wetland vegetation of almost all biomes of South Africa was used as an attempt of classification and analysis of data. This process highlighted the lack of wetland vegetation classification at national scale. Chapter 1 aims to introduce the context for this research, by providing an overview of existing knowledge and gaps. It starts by describing the background of wetlands in South Africa, particularly their importance. Section 1.2 provides brief overview of wetlands and their importance in the environment. Section 1.3 describes the classification of wetlands using hydrogeomorphic (HGM) units. Section 1.4 provides an overview of plants as indicators for wetland conditions, while Section 1.5 and 1.6 discusses how National Wetland Vegetation Database (NWVD) was built and its structure, respectively.

Based on the above overview, Section 1.7 highlights the aims and key questions are addressed as part of this study in classification of wetlands vegetation. Therefore, objective of this Masters thesis is to address that lack by classifying two of eight clusters in the National Wetland Vegetation Database (NWVD).

1.2 Wetlands and their importance in the environment

National Water Act of the Republic of South Africa defines wetland as:

"land which is transitional between terrestrial and aquatic ecosystems, where the water table is usually at or near the surface, or the land is periodically covered with shallow water, and which land in normal circumstances supports or would support vegetation typically adapted to life in saturated soil".

South Africa is regarded as an arid country, with an overall average rainfall of 452 mm per year and very few areas where annual rainfall exceeds evaporation. More than 50% of the wetlands in South Africa have been degraded and the remaining wetlands are

under pressure of human population growth and utilization (Kotze *et al.* 1995). Many of the remaining wetlands are in poor condition and are continuing to decline. The problem of supplying enough clean water to the rapidly rising population is exacerbated by the fact that the greatest concentration of people are in some of the drier areas (Davies and Day, 1998). Davies and Day (1998) stated that in a few decades to come, even the lowest estimates of water demand would exceed the total of surface water resources. This situation can be characterized as a water crisis and therefore, the country is in need of proper water management. There is also a need to conserve water for natural aquatic habitats and associated biota. If natural systems that store and regulate the flow of water are not managed carefully, the crisis of water shortage will worsen. Protection of wetlands is suggested as one factor that has the potential to contribute to water resource management (Sieben, 2010), even though wetlands account for only a small portion of the Earth's surface (Daily, 1997). The South African Water Act of 1998 aims at protecting, using, developing, conserving, managing and controlling water resources in a holistic way, and promoting the integrated management of water resources with the participation of various stakeholders.

Wetlands belong to the world's most productive habitats (Ramsar Convention, 1971). They are important because they do not only provide valuable resources directly used by humans, but also ecosystem services essential for maintaining biodiversity and the hydrological cycle (DWAF, 2005). Water for irrigation, food, areas for grazing, and cultivation, and varieties of plant species used as building materials and for craftwork are the valuable resources directly utilised by humans (Mitsch and Gosselink, 2000b). Wetlands maintain biodiversity and hydrological cycles by protecting and regulating water resources, water retention, reducing flood damage, soil erosion control, and removing pollutants from the water (USEPA, 2002). Destruction or degradation of headwater wetlands can have detrimental effects on the health and productivity of all the streams, lakes, and rivers downstream (Meyer *et al.*, 2003).

Identification and classification of vegetation types found in wetlands is regarded as one of the main activities that will be useful in strategically protecting and conserving these systems. In order to classify wetland vegetation collating and analysing data from previous vegetation studies has a role to play in the protection of wetlands. Classification therefore assists in extracting information on the occurrence of species and establishing plant community types for descriptive analysis (Jongman *et al.*, 1995). The vegetation

classification then serves as a starting point for strategic conservation for wetland biodiversity. It will be useful in providing an organized way of studying the plant species composition of wetlands and in knowing how plant species play a role in these aquatic ecosystems.

Wetlands help in controlling floods by means of storage and retention of large amounts of water in upstream areas (Keddy *et al.*, 2009). In most river basins peatlands and grasslands in the upper reaches act like sponges that absorb rainfall and allow it to seep slowly through the soil, thereby reducing the speed and volume of the runoff entering into streams and rivers (Ramsar Convention, 1971). Vegetation slows the speed of floodwaters and disperses the excess water over floodplains. The storage and breaking of the high speed of water flow reduces flood heights and erosive effects (USEPA, 1995). Additionally, wetlands act as natural filters that can improve water quality by purifying and trapping pollutants (Cronk and Fennessy, 2001), heavy metals and disease causing organisms (Daily, 1997) and thereby they reduce the threat of eutrophication (Mitsch and Gosselink, 2000a). Within the landscape, they are the main sinks of sediments (Davies and Day, 1998) and they help prevent soil erosion (DWAF, 2005).

Wetlands form an environment in which there is an abundant supply of water and thereby there are less constraints on primary productivity upon which a number of species of plants, animals, and humans depend for survival (Halls, 1997). According to the Ramsar Convention (1971), wetlands are important storehouses of genetic pool, for example food crops. Rice, a food crop that is the staple diet for more than half of humanity, is a wetland plant that is grown in artificial wetlands, rice paddies. Other types of wetlands, such as estuaries, serve as important breeding grounds for oceanic fish (Cronk and Fennessy, 2001)

Some wetlands are carbon sinks, with important implications for global climate change (Keddy *et al.*, 2009). Carbon can be stored under specific conditions in wetland sediments over a long period of time (Wylynko, 1999). The amount of carbon that a wetland stores and releases every year depends greatly on the hydrogeochemical characteristics of the ecosystem, which also determine the wetland plant communities (Bernal and Mitsch, 2012). Permanently inundated wetlands tend to accumulate organic litter for a number of years, and the decomposition rate is very slow, and as a result, carbon builds up in the soil for the long term (Bernal and Mitsch, 2012). When wetlands

dry out, parts of the carbon that the wetland produces can be released to the atmosphere as methane, a powerful greenhouse gas (USEPA, 2002).

Even while performing such important ecosystem services such as carbon storage and maintaining biodiversity, wetlands are among the most threatened ecosystems in the world (Ramsar Convention, 1971). More than half of the wetlands in South Africa have been destroyed and the remaining wetlands are under pressure of a growing human population and the associated utilization of natural resources (Kotze *et al.*, 1995). Degradation of wetlands affects water flow and quality in river catchments and can therefore have major impacts on land use downstream due to increased flooding, extinction of species, and decline in water quality (USEPA, 2002).

1.3 Classification of wetlands

Following the definition given by the Water Act 36 of 1998, wetlands are characterized by wet soils resulting from prolonged saturation, by the presence of water loving plants and by a high water table that results in the saturation of soils at or near the land surface (DWAF, 2005). All wetlands share some common hydrological, soil and vegetative characteristics (Smith *et al.*, 1995) but they vary in terms of size and complexity, as well as in terms of the details of physical, chemical, and biological processes (Mitsch and Gosselink, 2000b; Cowardin *et al.*, 1979). The hydrological conditions and their effects on soil chemistry are known to exert the greatest influence on the ecological functioning of a wetland (Mitsch and Gosselink, 2000b). The species tolerance ranges of wetland plants with respect to the frequency, depth, and duration of inundation exert strong controls on the distribution of plants and animals in wetlands (Ellery *et al.*, 2003).

One of the most important causes of variation in wetland habitat is derived from their water source (hydrology) and their position in the landscape (Van der Valk, 2006). Wetland ecosystems all share a common primary driving force water. Wetlands may receive water from several sources such as surface water flow, precipitation, groundwater discharge (e.g. springs and seeps). The water source and the nature of its movement through and out of the wetland are considered important in distinguishing different inland wetland types (Ellery *et al.*, 2005).

Ollis *et al.* (2013) proposed levels for classification of South African wetlands using hydrogeomorphic units. A Hydrogeomorphic (HGM) unit is defined as a functional unit of

an aquatic ecosystem differentiated from the surrounding landscape on the basis of a uniform landform and hydrology. They proposed a hierarchical classification of wetlands based on six levels of habitat descriptors, of which the HGM type is the most important. The proposed levels of classification are Connection to the sea (Level 1), Regional setting (Level 2), Landscape setting (Level 3), Hydrogeomorphic (HGM) unit (Level 4), Hydrological regime (Level 5) and various other more detailed Descriptors (Level 6). For the purpose of the current study the levels 3, 4 and 5 will be discussed in detail. The Landscape units (Level 3) distinguish wetlands on the basis of landscape setting (which is the topographical position) within which an aquatic ecosystem is situated. The hydrogeomorphic (Level 4) units distinguish wetlands on the basis of three factors. Firstly, there is landform, which determines the shape and localised setting of the aquatic ecosystem. Secondly, there are hydrological characteristics, which describe the nature of water movement into, through and out of the aquatic ecosystem. Thirdly, there is hydrodynamics, which describe the direction and strength of the flow through the aquatic ecosystem. Levels 3 and 4 are closely associated with each other, which will be seen at a later stage when looking at the data requirements for building the wetland vegetation database (see Table 1.1). There are HGM units that are typically associated with particular landscape settings, and thus identifying the landscape setting of an inland system may assist in the identification of the HGM Unit. The categories of landscape setting for the inland wetland ecosystems are: (1) valley floor, (2) slope, (3) plain and (4) bench.

(1) The valley floor is the base of the valley, situated between two distinct valley side slopes, where alluvial or fluvial processes typically dominate. A river or longitudinal wetland runs along a valley floor.

(2) The slope is an inclined stretch of the ground typically located on the side of the mountain, hill or valley, not forming part of the valley floor. It includes the scarp slopes, mid-slopes and foot slopes. The slopes range from vertical cliffs to gently sloping areas. Typical wetlands occurring on valley slopes are seepages and springs.

(3) The plain is an extensive area of low relief and is characterised by relatively level, gently undulating or uniformly sloping land with a gentle gradient (typically less than 0.01) that is not located within a valley. This unit includes coastal plains bordering the coastline, interior plains and plateaus. Plains are differentiated from valley floors by the absence of surrounding valley slopes.

(4) The bench is a relatively distinct area of mostly level or nearly level high ground, including hilltops (flat area at the top of a mountain or hill flanked down-slopes in all directions), saddles (relatively flat, high-lying areas flanked by down slopes on two opposite sides in one direction and up-slopes on two opposite sides in an approximately perpendicular direction) and shelves (relatively high-lying, localised flat areas along a slope, representing a break in slope with an up-slope on one side and a down-slope on the other side in the same direction). The benches occupy only a small portion of the landscape (Ollis *et al.*, 2013).

There are seven hydrogeomorphic (HGM) types defined by Level 4a of National freshwater Ecosystem Priority Areas (NFEPA) in South Africa defined by Ollis *et al.* (2013), and these are used to classify wetland ecosystem types on the basis of hydrology and geomorphology viz.: river, valley-head (or slope) seepage, valley bottom wetland, channelled valley bottom wetland, floodplain, flat and depression.

1. **River:** This is a linear landform with a clearly discernible bed and banks, which carries a concentrated flow of water either permanently or periodically. A river unit includes both the active channel as well as the riparian zone. The source of water is mostly concentrated surface flow from upstream channels and tributaries. Other water inputs are surface or subsurface flow from valley-side slopes, and/or groundwater inflow through springs.
2. **Floodplain wetlands:** This is a mostly flat wetland or gently sloping area adjacent to a river channel in its lower reaches that is subject to periodic inundation due to flood events. When there are floods, water and sediment enter into these areas. Floodplains generally occur on a plain and are typically characterised by a suite of geomorphological features associated with river-derived depositional processes, including point bars, oxbow lakes and levees.
3. **Channelled valley bottom wetland:** This is a valley bottom wetland with a river channel running through it. Water inputs into these areas are from adjacent valley side slopes and from the overtopping of the channel during floods. They are higher up in the catchment than floodplain wetlands and lack the geomorphological features associated with floodplains, such as oxbow lakes and levees.
4. **Unchannelled valley bottom wetland:** This is a flat bottom wetland area without a major channel running through it. It is characterized by the prevalence of diffuse flow, even during and after high rainfall events. Water mainly enters the wetland

through an upstream channel that loses confinement, but also from adjacent slopes.

5. **Depression:** This is a wetland or aquatic ecosystem in a closed (or nearly closed) basin with contours that increase in depth from the perimeter to the central area, and within which water usually accumulates. Occasionally there may be a drainage channel flowing into or out of the wetland. Depressions may have a flat bottom (in which case they are generally referred to as pans) or a concave bottom (in which case they are referred to as pools or lakes).
6. **Seepage:** This is a wetland area located on gentle to steep slopes, driven by water percolating through upper soil layer and movement of materials down-slope or groundwater discharge (in which case they are also referred to as springs). They are often located on the side-slopes of a valley but they do not extend onto a valley floor. Water input is from the subsurface flow that enters the wetland from the up-slope direction or deep groundwater
7. **Wetland flats:** This term refers to wetlands where the groundwater level is near the surface in a flat area, for example on the coastal plains. They receive water from precipitation, but this water does not drain away quickly and remains in the soil as groundwater. Wetlands flats are often found along the coast, where they get inundated when the water table rises to the land surface.

The Hydrological regime (Level 5) describes the behaviour of water in systems and for underlying soils in wetlands. The HGM unit combined with the hydrological regime of the wetland determines the way in which water behaves in a wetland. The hydroperiod refers to the length of time and portion of the year that an area holds water, the period and depth of inundation and saturation and it varies a lot, even within a single wetland. Some wetlands hold water for a very short time while others for a very long or permanent period. The behaviour of water and soil in wetlands system directly affects the physical, chemical and biological characteristics of and functioning of the ecosystem (Ollis *et al.*, 2013). The soil morphology and chemistry is affected by the frequency and duration of inundation and saturation of a wetland. Anaerobic conditions and saturated soils result in hydromorphic features that come into existence mainly because of the oxidation states of iron (Fe) and that are used as diagnostic features to delineate wetlands. The features include layers of soil material; odour produced by hydrogen sulphide gas and redoximorphic features (Fe/Mn based). In general, hydromorphic features are formed in

a soil when organic matter is present, when microorganisms are actively respiring and oxidizing organic matter, or, if the soil is saturated and when dissolved oxygen is removed from the soil. Hydromorphic soils are soils with prolonged water saturation within the upper 50 cm of the soil surface. The inundation depth-class categorises the maximum depth of inundation in permanently inundated systems i.e. open water bodies. The exact period of inundation and saturation is often not known but can be assessed in coarse terms by looking at the hydromorphic features in the soil (Ollis *et al.*, 2013).

Wetlands are generally found in areas where water does not drain fast, where the flow is impeded or where there is a net influx of water (Van der Valk, 2006). The hydrological condition in soils varies from temporary to permanent flooding, from flowing to standing water, from channelized to diffuse flow, and from saturated to inundated soils. The hydroperiod conditions in wetlands and open water bodies are classified according to the period of inundation (Level 5A), saturation (Level 5B) and inundation depth-class (Level 5C) in the case of permanently inundated open water bodies. The period of inundation has four categories relating to the frequency and duration of inundation, namely: permanently inundated (surface water throughout the year, in most years), seasonally inundated (surface water present during wet seasons, but drying up annually, either to complete dryness or saturation), intermittently inundated (hold surface water for irregular periods of less than one season), never /rarely inundated (covered by water for less than few days at time) (Ollis *et al.*, 2013).

Hydrology and geomorphology are characteristics that are useful in the characterization of wetlands and the classification into different types and they represent important factors in understanding their ecology. The hydrogeomorphic classification of wetlands serves as an important tool for researchers and resource managers (Hoagland, 2002). Hence, a classification system has become an integral component of a national wetland inventory and the associated conservation efforts. The HGM classification is necessary for the comparison of functions and values of different kinds of wetlands, the selection of appropriate sites representative of different wetland types for conservation and water management, and for developing scientifically sound management strategies (Cowardin and Golet, 1995).

1.4 Plants as indicators for wetland conditions

The most visible aspect of the wetland environment is represented by the vegetation (Sieben, 2010). Wetland plants are commonly defined as those “*growing in water or on a substrate that is at least periodically deficient in oxygen as a result of excessive water content*” (Cowardin *et al.*, 1979). Wetland plants are represented by both herbaceous and woody species that grow in still or flowing water, rooted in periodically or permanently flooded hydromorphic soils (Cronk and Fennessy, 2001). Some wetlands plants are floating or submerged (e.g. water lilies, pondweeds and algae), but most are emergent and referred to as helophytes (e.g. sedges, grasses).

The ecological functioning of wetlands is enhanced by the presence of vegetation (Corry *et al.*, 2011). Primarily, plants form the base of the food chain and as primary producers they are a major conduit for the energy flow in the ecosystem (Cronk and Fennessy, 2001). Wetland vegetation slows the water flow and influences water quality in downstream ecosystems by trapping nutrients, pollutants, and sediments. Some wetland plants remove nutrients and other chemical constituents from the substrate and the water column by sequestering them in their tissues and thereby improve water and soil quality (Cronk and Fennessy, 2001).

Plants can be regarded as excellent indicators of wetland condition for the following reasons: there is a large number of different species occurring in wetlands; they have rapid growth rates, and display a more or less direct response to environmental change (USEPA, 2002). There are certain plants and plant communities that have been described as characteristic of specific wetland environments (Tiner, 1993) and the presence of these communities can be associated with specific environmental conditions. The composition of the plant community is determined by abiotic factors such as climate, soil type, position in the landscape, as well as by biotic factors such as interaction and competition between plant species. Anthropogenic influences can result in the degradation of wetland ecosystems and this will cause shifts in plant community composition (USEPA, 2002). Thus, individual species may be used as indicators because they show a differential tolerance of environmental conditions and this result in the shifting of community composition in response to environmental changes (Tilman, 1988; USEPA, 2002). In the wetland environment water quality and quantity also affects the plant community by killing those plants that are intolerant of those conditions (Brinson, 1993).

The plants found in wetlands are not only plants native or indigenous to that particular area or region but also include weeds or alien invasive plants. An alien invasive plant is a non-indigenous species that has been introduced either accidentally or intentionally by man into places outside of their natural range of distribution and they become established and disperse, generating a negative impact on the local ecosystem and species (IUCN, 2014). Wetlands seem to be vulnerable to alien invasions (Zedler and Kercher, 2004). Such invasive plant species do not only affect biodiversity and ecosystem functioning but also the potential for human uses and the recreational value of wetlands (Zedler and Kercher, 2004).

Studying wetland vegetation patterns will assist in detecting changes in the environment, the hydrology and the management of wetlands because plant growth and productivity responds relatively quickly to such changes. Therefore, it is useful to make a wetland habitat classification based on plant community data. This is an example of a bottom-up classification system as opposed to a top-down classification system of the HGM classification (Sieben, 2010). A national wetland database was compiled with vegetation data and environmental data using historical data found in literature, such as student theses, journal articles, research reports, and newly collected data in order to classify South African wetlands at a larger scale.

1.5 National Wetlands Vegetation Database (NWVD)

The NWVD was built to store all existing vegetation data from previous studies on a wetland. The first step in building a national wetland vegetation database was compiling existing data from literature, environmental reports, and dissertations. This was then used to determine where there are still gaps in terms of regions investigated, wetland types and in terms of features recorded per site. Then in 2010 the Database was expanded by fieldwork to fill in the gaps in places that had been neglected. Figure 1.1 shows the areas where the data has been collected across the country up to 2012.

In 2008, a workshop convening several wetland and vegetation experts was organized to decide upon a list of minimum data requirements per vegetation plot for the data that was yet to be collected. The criteria decided upon after conclusion of this workshop are listed in Table 1.1. The Table contains 14 main variables that should be known for every

wetland site for it to be included in the database and four additional variables that are not always collected but would be desirable to be included as well (Sieben, 2011).

The database consists of vegetation-plot data collected by various vegetation scientists throughout the country. A standardized field data form with all the minimum data requirements was designed and used as a sampling protocol (Appendix A). This field data collection form serves to remind wetland vegetation ecologists what types of data are necessary to collect in any particular wetland (Sieben, 2011). Currently, the existing database consists of 5583 vegetation plots that were captured using the programme Turboveg (Hennekens and Schamineé, 2001), that provides a for storage and retrieval of plant community data.

The analysis of the national wetlands vegetation database will serve as reference data so that it becomes clear what wetlands look like under natural conditions and this will assist in identifying which plant species become abundant under certain environmental conditions. This data would also be useful in conservation planning, wetland monitoring using indicator species and rehabilitation purposes.

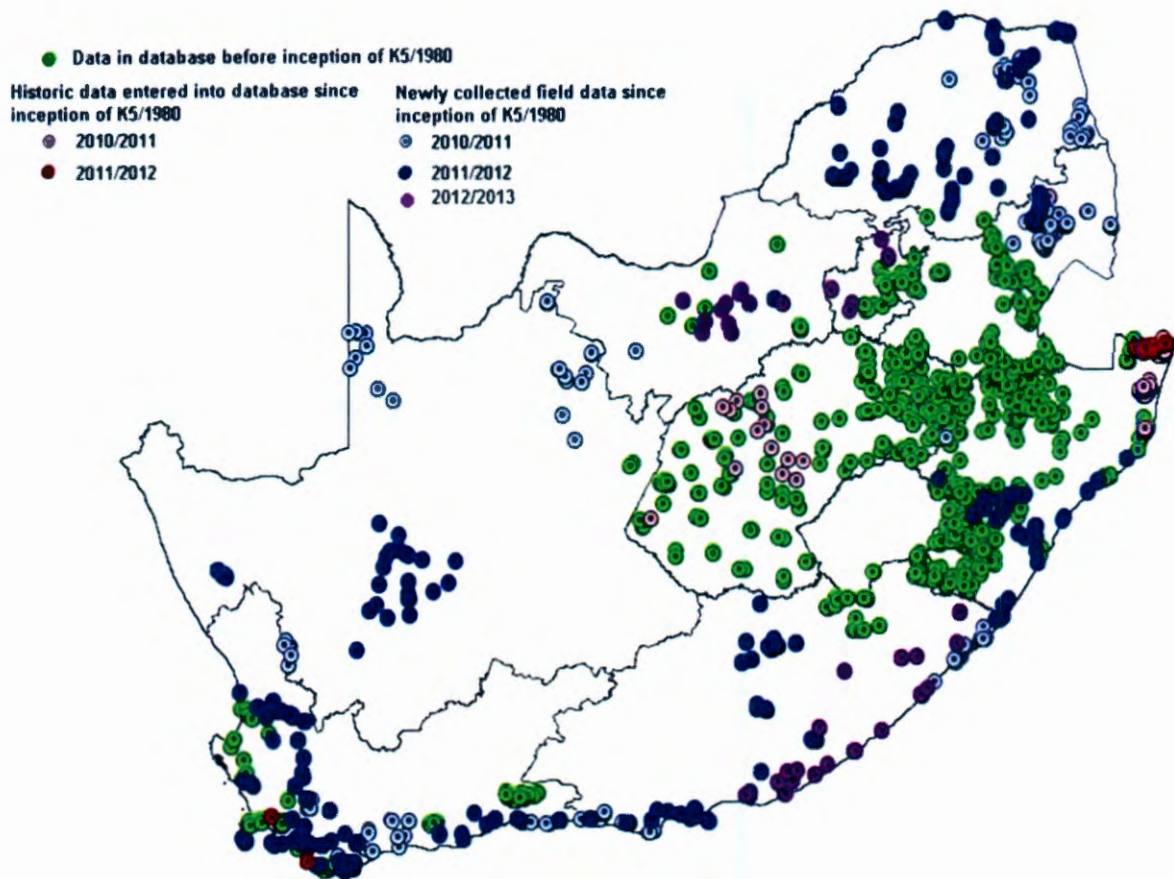


Figure 1.1 Map of South Africa showing positions of data captured by NWVD, including historic data as well as newly collected data entered in the database from 2010 to 2013.

Table 1.1 Data requirements for building the NVWD as decided upon at the 2008 workshop (Sieben, 2011).

Minimum data Requirements for Wetland vegetation		
1	Vegetation description	Complete Braun-Blanquet data with cover-abundance classes in 9 categories
2	Vegetation structure	Assessment of height and cover of different vegetation strata
3	Locality description	GPS coordinates (WGS datum) and altitude
4	Date of recording	Important for assessing seasonal aspects
5	Slope and aspect	Slope in categories Flat (0-0.5%), Slight (0.5-1%), Very Gentle (1-2 %), Gentle (2-3%), Moderate (3-10%), Steep (> 10%), Aspect in categories N, NE, E, SE, S, SW, W, NW
6	Hydrogeomorphic unit (wetland type)	Level 3 of the wetland classification system (Ollis <i>et al.</i> , 2013)
7	Topography	Position in the landscape (floor, foot, slope, top, plain)
8	Hydroperiod	Three classes assessed on Hydromorphic features in soil (see Kotze <i>et al.</i> , 1996)
9	Inundation depth	Assessed at time of recording
10	Soil type	Texture of topsoil, assessed in seven categories: Bedrock, Sand, Clay, Loam, Peat, Silt/Mud, Saltcrust. Includes soil depth, up to 50 cm, the presence of impermeable layers below like a clay lens and the amount of organic material in three categories: Mineral, Humic/Dark and Peaty
11	Water velocity	Three classes (stagnant, slow-flowing, fast-flowing), recorded at time of survey
12	Salinity of water	Yes/No
13	Disturbance	If applicable, notes about disturbance, grazing, fire, etc.
14	Reference	Field number and reference to original study
	Additional data	
15	Soil Form	Soil Form according to the Soil Classification Working Group (1991)
16	Nutrient status	If chemical analysis of soils has been carried out, supply a reference to that study
17	Hydrology	Source of water and assessments of the contribution to water in the wetland
18	Landscape	Natural landscape, Agricultural landscape or Urban landscape

1.6 Structure of the database

Most of the historical wetland data were not collected using standardized protocols and therefore in many cases not all the desired data were available and no detailed header data were provided. For the latest data that were yet to be collected, a need for standardized protocols were now accepted as a priority and the need for more detailed data has been clearly recognised.

Each plot available in the database contains vegetation data (species composition including cover-abundance scales according to Braun-Blanquet) and to various extents environmental data. The environmental data can either be complete with respect to the minimum data requirements in Table 1, or incomplete (only in the case of historical data). Soil samples have been collected for a limited number of plots (and never for more than one plot per wetland in case there is more than one vegetation sample in a single wetland) due to the costs involved in soil analyses. This has been done in newly collected plots and in two of the recent dissertations by Collins (2011) and Corry (2011). The soil samples were dried and brought to Agricultural Research Council - Institute for Soil, Water, and Climate (ARC-ISWC) in Pretoria for analysis. The soil samples were analysed for the concentration of important soil nutrients. The standardized list of variables measured for each soil sample is presented in Table 2.

For every wetland plot sampled in the wetland, vegetation data (species composition) and environmental conditions were recorded. The environmental data include locality (coordinates and altitude), slope, aspect, wetland type (hydrogeomorphic unit), topography, hydroperiod, inundation depth, soil type (soil texture), salinity, and soil form according to the Soil Classification Working Group (1991). The soil samples that were analysed by the ARC-ISWC: organic content, electrical conductivity, soil particle size composition, pH, and soil mineral nutrients [nitrogen (N), potassium (K), phosphorus (P), calcium (Ca), sodium (Na), and magnesium (Mg)]. The environmental data was used in different types of analysis (see Chapter 2) in order to find how the environmental data can help to explain patterns in the vegetation

Table 1.2 Soil variables as measured by the Agricultural Research Council Institute for Soil, Water and Climate (ARC-ISWC). The abbreviations in the third column refer to the abbreviations used in ordination diagram and species response curves in the results section of Chapter 3. All of these variables have been transformed during analysis using the transformation $\log(X+1)$.

Variable	Measurement	Abbreviation
pH	Water extraction	pH
Electrical Conductivity	Measured in mS/m	EC
Nitrogen	Summed up concentration of Nitrate, Nitrite and Ammonium, each of which measured in mg/kg	Nitrogen
Phosphorus	P-Bray I method, in mg/kg	Phosphorus
Sodium, Potassium, Magnesium, Calcium	1:10 water extraction measured in mg/kg	Na, K, Mg, Ca
Soil particle distribution	In mass percentages for three fractions Clay (<0.002 mm), Silt (0.05 – 0.002mm), Sand (2 – 0.05 mm)	%Clay, %Sand, %Silt
Organic matter	Using the Walkley-Black method, expressed in mass %	%Carbon

The amount of information that is available per plot determines what kind of analysis can be carried out with the data. For this reason, the data in the database is subdivided into three tiers in terms of the amount of information available per plot. Some vegetation plots in historical records fell short of the minimum requirements. An additional field in the database informs the user about the suggested ‘completeness’ of the data. This field has the value 1 if the data fits in with the minimum data requirements, value 2 if one or two fields are missing, and value 3 if the data is considered incomplete. The presence of soil data for some plots adds another layer of data resolution so that the most detailed analysis can be carried out only on a subsection of the overall dataset.

The absence or presence of certain types of information available for each plot will determine the type of analysis that can be carried out with those plots. Therefore, the database has been subdivided into three levels of data resolution, namely (i) vegetation plots with only vegetation data available, environmental data not complete; (ii) vegetation plots with complete environmental data available; and (iii) vegetation plots with environmental data as well as detailed soil data available. These three categories, together with the number of plots and the selection criteria within the database are illustrated in Figure 1.2. The data with the above mentioned values of ‘completeness’ were integrated within the three tiers, so level 1 represents all data with completeness of

1, 2 and 3, level 2 represents the data with completeness 1 only, and level 3 the subsection of the data with completeness level 1 that also has soil data available.

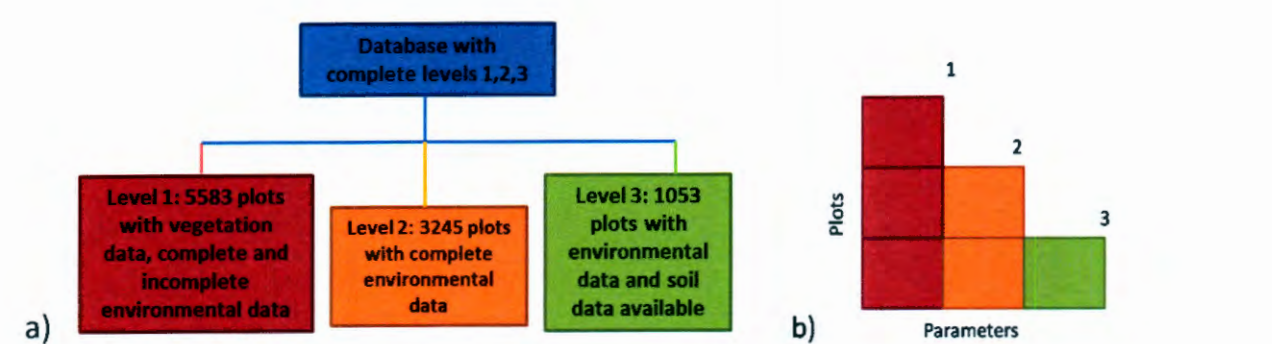


Figure 1.2 Subdivision of available data of national wetlands on database system a) represent subdivision of the dataset in database, b) shows how the three matrices fit together based on data resolution, which is the amount of data available per plot. Matrix 1 represent all the plots but with limited data available per plot. Matrix 2 represents a subsection of those plots but with more environmental data. Matrix 3 represents the small subsection of the plot with all possible environmental data available.

The database has been subdivided into Main Clusters, because it is not practical to the deal with data-analytical procedure of the whole database at once. Provisional classifications have been reported upon in previous progress reports (Sieben, 2012) for the Water Research Commission and in the final version the database was subdivided into eight Main clusters. This subdivision has been achieved with the help of the programme JUICE (Tichý, 2002) using subsequent classifications built on previous classifications that were based on a smaller number of plots. Initially, the TWINSpan procedure (Hill, 1979) was used, but this was improved upon by manual tabulation using JUICE (Tichý, 2002). These Main Clusters were then used as a starting point for subsequent analyses that used data-analytical methods

The Main Clusters are (in bold the two clusters that are subject of the current study):

Main Cluster 1: Sclerophyllous Wetlands Vegetation

Main Cluster 2: Swamp Forest

Main Cluster 3: Subtropical Wetland Vegetation

Main Cluster 4: Estuarine, Brackish, and Saline Wetland Vegetation

Main Cluster 5: Montane Grassy Wetland Vegetation

Main Cluster 6: Temperate Grassy Wetland Vegetation

Main Cluster 7: Short Lawn Grassy Wetland Vegetation

Main Cluster 8: Hydrophytic Vegetation

Only Sclerophyllous Wetlands Vegetation (Main Cluster 1) and Temperate grassy Wetland Vegetation (Main cluster 6) were used for the purpose of this study. Both clusters have detailed data available and contain the largest number of plots. These clusters are highlighted in this thesis to illustrate some methods of analysis that were not always comparable between the various other Main Clusters (Sieben *et al*, 2014).

1.7 Aims of the study

Wetlands of South Africa have been receiving a lot of attention since the inception of the Working for Wetlands Programme, but until recently not much attention was paid to the vegetation types found within these systems. The focus was mainly on the wetland types based on hydrogeomorphic setting.

Since wetlands have been recognised as playing a vital role in the ecosystem it is crucial that attention is focused on the vegetation that is found in these systems. In order to appropriately conserve and manage wetlands it is necessary to have a clear understanding of how they function in their natural condition, and what such a natural condition looks like. In order to have a clear picture it is important to know the vegetation composition and the environmental factors controlling the distribution of plant species in a wetland. The latest vegetation map of South Africa included wetlands but acknowledged that much more work needs to be carried out on them (Mucina and Rutherford, 2006). A larger number of studies in wetlands have been carried out since then. Nel *et al*. (2011) suggested that available data should be analysed using more appropriate scientific methods e.g. group wetland vegetation with the help of cluster analyses. Information from this study will act as a baseline for future planning and management to prevent unnecessary damage to wetlands.

This study therefore builds upon previous wetland vegetation research conducted in different areas across the country. It is important in providing a synthesis of two main groups of wetland types in South Africa, thus the main aims are:

- To group similar vegetation plots in the database into plant communities using data analytical procedure,
- to find the way in which environmental factors can explain patterns in plant species composition,
- to find which species can be used as environmental indicators for specific conditions in wetlands, and
- to determine how the species respond to a range of important environmental variables.

Since many of South Africa's wetlands are susceptible to alien invasion (Le Maitre *et al.*, 2000) and many have been altered and damaged, it has become increasingly important to know which plants are suitable environmental indicators for wetlands. That is why the classification of vegetation into community types, and identification of indicator/diagnostic species representing these communities can be useful in the assessment of the wetland ecosystem condition, and in the monitoring of changes occurring there.

CHAPTER 2

METHODOLOGY

2.1 Introduction

Vegetation data analysis uses data analytical techniques. Multivariate analyses comprise a set of techniques meant for the analysis of datasets with more than one response variable. Multivariate analysis in ecology provides an easy summarization of the data, which facilitates the understanding, and provides a means for effective communication of results (Gauch, 1982). These analytical techniques are mostly used for exploratory data analysis in order to generate hypotheses and it helps ecologists to discover the structure in the dataset and to analyse the effects of the environmental factors on groups of species (Bergmeier, 2002; Anderson *et al.*, 2006).

Classification involves extracting similar entries from a set of raw data and placing them into groups (Kent and Coker, 1992). Classification can be subjective or objective and in that last case it can be computer assisted. The classification of communities helps to detect structure in complex multivariate data sets, which in vegetation ecology are represented by matrices of samples by species. There are two general kinds of hierarchical classification: divisive and agglomerative. A divisive method starts with the entire set of samples, and progressively divides it into smaller and smaller groups. An agglomerative method starts with individual samples, and progressively joins them into larger and larger clusters, until the entire data set is joined in a single cluster (Pielou, 1984). Classification therefore assists in extracting information on the occurrence of species and determining clusters for descriptive analysis (Jongman *et al.*, 1995).

Ordination has been widely used in plant ecology as the tool for examining relationships between environment and vegetation. Ordination refers to the multivariate techniques that arrange sites along axes based on species composition (Jongman *et al.*, 1995) or arranges species along axes based on their presence in plots (Kent and Coker, 1992). It serves to summarize community data (species abundance data) by producing a low-dimensional projection of ordination space in which similar species and samples are placed close together, and dissimilar species and samples are placed far apart (Peet, 1980). This technique can be enhanced to describe the relationships between species composition patterns and the underlying environmental factors that influence these patterns, if values for environmental variables are supplied. The increased computational

power and modern data analysis methods together make it possible to do the analysis of larger data sets. It also creates the potential to make all these tools available to non-statisticians.

2.2 Software packages and tools for exploratory data analysis

In this study, data analytical techniques were used to analyse wetland vegetation data available in the database. These techniques are available in the package PC-Ord (McCune and Grace, 2002) and HyperNiche (McCune and Mefford, 2009).

The data of the South African Wetlands Vegetation Database used for analysis were stored with the help of TURBOVEG (Hennekens and Schaminée, 2001). TURBOVEG is a database management system designed for storage, selection, import and export of vegetation data (relevés) in large quantities (Hennekens and Schaminée, 2001). The Main cCusters presented in Chapter 1 were used as a starting point for further classification. Various types of analyses were carried for the two Main Clusters in PC-Ord version 6 (McCune and Mefford, 2011) and HyperNiche version 2 (McCune and Mefford, 2009). The five main methods from PC-Ord that were used for data analysis are classification using hierarchical clustering methods, ordination using both Nonmetric Multidimensional Scaling (**NMS**) and Canonical Correspondence Analysis (**CCA**), group testing using the Multi-Response Permutation Procedure (**MRPP**), and lastly, Indicator Species Analysis (**ISA**). The programme HyperNiche was used for determining species response curves using Non-Parametric Multiplicative Regression (**NPMR**) for habitat modelling.

All data analytical methods are based on resemblance measures that express the similarity or dissimilarity among sample units. Bray-Curtis similarity index measure that was used for analysis except in CCA (CCA always use the chi-square distance) to compare groups of communities because it calculates the shared abundance between sample units. The Bray-Curtis similarity index is well known for quantifying the difference between samples and it is compatible with binary (0/1) data (McCune and Grace, 2002).

The distance measure equations use the following conventions: data matrix **A** has q rows which are sample units and p columns, which are species. Each cell in the

matrix a_{ij} , represents the abundance of species j in sample unit i . The distance between two sample units i and h is calculated in the following manner: the shared abundance among sample units is divided by the total abundance of all species in both sample units. In a formula:

$$\text{Bray-Curtis similarity measure: } D_{i,h} = \frac{\sum_{j=1}^p |a_{ij} - a_{hj}|}{\sum_{j=1}^p a_{ij} + \sum_{j=1}^p a_{hj}}$$

2.3 Classification: Cluster analysis

Classification methods assist in identifying and grouping plots/samples that share common properties (in our case species occurrence and abundance). It involves tools that use a hierarchical agglomerative process (Peck, 2010). This is a bottom-up classification where the algorithm finds the most similar pairs of plots and then joins them using a specific linkage method (Kent and Coker, 1992; McCune and Grace, 2002). The combination of these two plots is then reused in the same data set and the procedure is repeated until all plots are connected.

In order to join the sample units or plots a linkage method is required. The linkage method is a criterion used to link groups and clusters. The linkage methods calculate which pairs of observation should be joined when used with a suitable distance measure. One effect of classification structure that requires attention is the fact of chaining. Chaining in a dendrogram is where each sample is linked to the next by a slightly higher tie bar, gradually stepping up evenly from the left to the right, suggesting there are no clusters in the dataset. Some linkage methods can result in straggly (long and thin) and too many clusters due to the chaining effect. In the current study Ward's Method (= minimum variance method) was the linkage method of choice used to construct the cluster dendrogram because it tends to result in a limited amount of chaining (McCune and Grace, 2002). The linkage method should be used in combination with an appropriate distance measure (dissimilarity measure). In this case the Sørensen similarity measure was used in combination with Ward's method and both were compatible. However, McCune and Grace (2002) recommend that flexible beta linkage $\beta = -0.25$ and Sørensen works well together in classification.

The Ward's method is distinct from other methods because it uses an analysis of variance approach to evaluate the distance between clusters. Cluster membership is assessed by calculating the total sum of squared deviations from the cluster centroid. The criterion for fusion is that it should produce the smallest possible increase in the error sum of squares. The error sum of squares is defined as the sum of squares of distances from each individual member to the centroid of its group. The fusion of two groups S_p and S_q occurs when it yields the least increase in the error sum of squares of the two groups. The classification procedure is complete after all the items in the dataset are joined together.

The basis of hierarchical cluster analysis (HCA) in PC-Ord is as follows: A $n \times n$ (n = number of plots) dissimilarity matrix is calculated and each of the elements is squared.

The algorithm then performs $n - 1$ loops (clustering cycles) in which the following steps are taken:

- The smallest element(d_{pq}^2) in the dissimilarity matrix is sought (the groups associated with this element are S_p and S_q).
- The objective function E_n (the amount of information lost by linking up to the cycle n) is incremented according to the rule $E_n = E_{n-1} + \frac{1}{2d_{pq}^2}$ [$E_0 = 0$]

Group S_p is replaced by $S_p \cup S_q$ while group S_q is rendered inactive. All elements of the dissimilarity matrix of the new group S_p are recalculated.

The dendrograms or cluster trees are used to show the structure of 'relatedness' between plots because similar plots end up on the same branch of the dendrogram. Clustering helps to determine the relevance of the difference between vegetation plots, group plots into communities and identify sample units or plots that are outliers. An outlier is a sample unit, plot or species which is very different from the other plots in a data set in terms of species composition (Barnett *et al.*, 1979). A common situation where we find outliers is when there is a high abundance of a rare species in a sample plot. Outliers may affect the conclusions of the study and in most cases they are better left out in subsequent analyses as they do not add much value to the analysis (McCune and Grace, 2002).

2.4 Indicator species analysis (ISA)

The indicator species analysis is used for community data, to describe the indicator value of individual species in groups. It combines information on the concentration of species abundance in a particular group and the faithfulness of occurrence of a species in a particular group (McCune and Grace, 2002). Fidelity is defined as the degree of preference of species for a given association (Barkman, 1989).

A perfect indicator species for a particular group should always be present in that group, and never be present in any of the other groups. Dufrêne and Legendre's (1997) indicator species analysis calculates indicator values for every species in each group, based on the standards of a perfect indicator. These values are then tested for statistical significance using a randomization technique (Monte Carlo test). The indicator species can be used to contrast the performance of individual species among groups of sample units. The method is only applicable to species and not to other kinds of variables because it is based on the abundance (concentration of species within particular groups) and frequency (the percentage of sample units in each group that contain that species) (McCune and Grace, 2002). In order to test for the significance of an indicator value, the dataset is subjected to a permutation procedure and the indicator values are calculated for each permutation. The null hypothesis is that the maximum indicator value (IV max) is not larger than would be expected by chance (i.e. that the species has no indicator value). Only those species where this null hypothesis is rejected are true indicator species.

The steps involved in calculating the indicator value for a species in a cluster are as follows (McCune and Grace, 2002):

- The Proportional abundance of a particular species in a particular group relative to the abundance of the species in all groups is calculated

A = sample unit x species matrix

a_{ijk} = abundance of species j in sample unit i of group k

n_k = number of sample units in group k

g = total number of groups

RA_{jk} = Relative abundance

RF_{kj} = Relative frequency

B = matrix of presence-absence is derived from the sample x species matrix **A**

The mean abundance of x_{kj} of species j in group k is calculated first

$$x_{kj} = \frac{\sum_{i=1}^{n_k} a_{ijk}}{n_k}$$

Then the relative abundance RA_{kj} of species j in group k is calculated as

$$RA_{jk} = \frac{x_{kj}}{\sum_{k=1}^g x_{kj}}$$

- The proportional frequency of species j in each group is calculated. **A** is first transformed to a matrix of presence-absence, **B**: $b_{ij} = a_{ij}^0$

Then the relative frequency RF_{kj} of species j in group k is calculated

$$RF_{kj} = \frac{\sum_{i=1}^{n_k} b_{ijk}}{n_k}$$

- The two proportions calculated above are combined by multiplying them. The results are presented as a percentage, yielding an indicator value (IV_{kj}) for each species j in each group k .

$$IV_{kj} = 100 (RA_{kj} \times RF_{kj})$$

- The highest indicator value (IV_{\max}) for a given species across groups is stored as a summary of the overall indicator value of that species.
- The statistical significance of IV_{\max} is evaluated by means of a Monte Carlo permutation method. Sample units are randomly assigned to groups repeated for 1000 times. For each randomization IV_{\max} is calculated. The probability of type I error is the proportion of times that the IV_{\max} from the randomized data set equals or exceeds the IV_{\max} from the actual data set. The null hypothesis is that IV_{\max} is not larger than would be expected by chance. Only species for which the null hypothesis is rejected are true indicator species and are reported as such.

An additional use of ISA is a criterion for the optimal number of clusters to be used in cluster analysis. Different classifications can be made with a different number of clusters. Using the same clustering method it is possible to attain a different number of clusters depending on what is defined as a cluster. Then, the indicator value for each species at each level of grouping is calculated and their significance tested with a Monte Carlo permutation procedure. The average p-value for this test is an indicator of how well these groups are defined given the overall dataset. The steps are repeated with a different

number of groups until the averaged p -value is at minimum. The species that are characterized as indicator species are ecologically the most important species in terms of recognizing wetland communities and understanding the wetland environment. They also play a role in the classification of plant communities as they are diagnostic (they help to recognize the communities). For this reason, these are species that are selected at a later stage for further detailed analysis including species response curves. Most of the plant communities can be defined with the help of a high indicator value for at least one such indicator species. In this way ISA also assisted with the classification.

2.5 Ordination: Nonmetric Multidimensional Scaling and Canonical Correspondence Analysis

An ordination method summarizes the patterns of variation in the data set. It is used as an exploratory analysis to identify the relationships between many variables simultaneously (e.g. species composition and environmental variables). It attempts to organize the plots (or the species) along axes of maximal variation and plot them in a reduced (two dimensional) space that similar plots end up close to one another and dissimilar plots end up far removed from one another. The environmental gradients that explain the environmental patterns are then interpreted by the user. Several ordination methods exist, but in this study, NMS was the method of choice and was compared with results from CCA.

NMS is used to reduce the dimensionality of a database and explore patterns and it can be used for highly heterogeneous datasets where there are no assumptions about response curves of species along gradients. Dimensionality refers to various phenomena that arise when analysing and organizing data in high-dimensional spaces that occur in low dimensional settings such as the three-dimensional physical space. It seeks an ordination in which the distances between all pairs of sample units are as much as possible in rank-order agreement with their similarities in species composition in order to find the most suitable number of dimensions to plot the ordination (Peck, 2010). Unlike other ordination methods, NMS makes few assumptions about the nature of the data. For example, Correspondence Analysis (CA) and Canonical Correspondence Analysis (CCA) assume unimodal relationships of species responses versus environmental variables whereas NMS makes no such assumptions (Holland, 2008). NMS is suited for a wide variety of data types and allows the use of any measure whether Euclidean

distance, Bray-Curtis resemblance, city block distance or chi-squared resemblance, unlike methods like CA and CCA which depend on a specific measure, in this case Chi-square.

Canonical Correspondence Analysis is based on Chi-square statistics and thereby assumes a unimodal response curve in the dataset. CCA is constrained by multiple regressions of species on environmental variables that are included in a matrix. This means that the ordination of samples and species is constrained by their relationships to environmental variables included in second matrix. CCA is most likely to be useful when species responses are unimodal (hump-shaped), and all the important underlying environmental variables have been measured. CCA is called a method for "direct gradient analysis" (ter Braak, 1986) because the environmental matrix shapes the ordination results, unlike in most other ordination techniques. However, McCune and Grace (2002) argue that this technique has dangers because it includes the multiple regressions of community gradients on environmental variables, and is subject to all of the hazards of multiple regressions.

The dangers as stated by McCune and Grace (2002) are as follows: *"Multicollinearity is a particular problem and it may be believed that a relatively high coefficient of multiple correlations implies a highly significant result which it may not. As the number of environmental variables increases relative to the number of observations, the results become increasingly dubious as the appearance of very strong relationships becomes inevitable."*

The steps involved in the calculation of dissimilarities in NMS are listed below (McCune and Grace, 2002):

(\mathbf{X} = coordinates of n sample units in a k -dimensional space, k = number of preferred dimensions, x_{il} is the coordinate of sample unit i in dimension l , Δ = matrix of dissimilarity coefficients from the original data, δ_{ij} = elements of Δ , \mathbf{D} = matrix of interpoint distances in the k -space, d_{ij} = elements of \mathbf{D}).

- The dissimilarity matrix Δ is calculated
- The sample units are assigned to a random starting configuration in the k -space with a random number generator
- The matrix \mathbf{X} is normalized by subtracting the axis means for each axis l and dividing by the overall standard deviation of scores

$$\text{normalised } x_{il} = \frac{x_{il} - \bar{x}_l}{\sqrt{\sum_{l=1}^k \sum_{i=1}^n (x_{il} - \bar{x}_l)^2 / (n \cdot k)}}$$

- **D** containing Euclidean distances between sample units in k -space is calculated
- Elements of Δ are then ranked in an ascending order
- The elements of **D** are put in the same order as they appear in Δ
- The matrix \hat{D} is calculated containing elements of \hat{d}_{ij} (these being the results of replacing elements of **D** which do not satisfy the monotonicity constraint)
- Then the stress is evaluated using the sum of squared differences between **D** and \hat{D} measured by Kruskal's stress computed as :

$$S = \sqrt{\frac{\sum_{i=2}^n \sum_{j=1}^{i-1} (\delta_{ij} - \hat{\delta}_{ij})^2}{\sum_{i=2}^n \sum_{j=1}^{i-1} \delta_{ij}^2}}$$

The stress decreases as the rank-order agreement between distances and dissimilarities improves and therefore aims to find the ordination with the lowest possible stress. The best ordination is sought by an iterative search or trial-and-error optimization process, also by trying different values of k (the number of dimensions in which the solution is projected, which can be chosen as an integer between 1 and 6). The lowest possible stress is sought by using a suitable choice of data standardization and dissimilarity measure, plus the choice for the number of dimensions to be used. Then a randomization using a Monte Carlo test with for example 500 runs, is conducted to evaluate whether the NMS ordination is extracting stronger axes than would be expected by chance. A scree plot (An example of which is shown in **Figure 2**) is drawn to seek the values of k (number of dimensions) that result in minimum stress but that are also significant compared with the results of the Monte Carlo test. It is used as guide in deciding on the number of dimensions (k) required (McCune and Grace, 2002). A sharp break in the slope of the curve, beyond which further reductions in stress are small, suggests a dimensionality suitable for the final analysis.

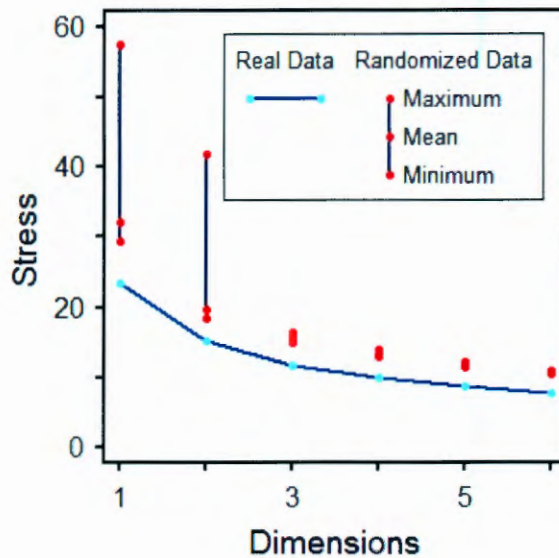


Figure 2.1 Example of a scree plot which shows stress as a function of the dimensionality (k) of the scaling. The first two axes provide far greater reductions in stress than in later axes. In this particular case a two dimensional solution would be the most optimal choice (McCune and Grace, 2002).

2.6 Group testing: Multi-response permutation procedure (MRPP)

MRPP is a non-parametric multivariate procedure for testing the hypothesis of no difference between any groups of variables of two or more groups that have been defined a priori. In the case of vegetation data, they can be used to find out whether there are differences in the combined environmental variables between clusters that have been defined a priori based on species composition (McCune and Grace 2002). It is a non-parametric version of Multivariate Analysis of Variance (MANOVA). It strives to calculate a value T as the ratio of difference between the observed and expected mean distance and the standard deviation of the expected difference. It further calculates a value p that describes the chance of obtaining this value by chance, and a value A describing within-group homogeneity that can be regarded as the 'effect size' that is independent of sample size (McCune and Grace, 2002). The environmental variable that lies at the base of this contrast is not found using the MRPP procedure and needs to be sought by means of other methods, such as an NMS ordination specific for those clusters where a contrast was found.

The steps involved in calculating the significance of group differences are as follows:

- The distance matrix **D** is calculated using a distance measure of choice (Sørensen measure as it was applied in this study)
- The average distance in each group $i = x_1$ is calculated. In each case, n_1 is the number of items in group i , g is the number of groups, and C_i weight applied in each item in group i .
- Calculate delta (weighted mean within-group distance). A weighted mean within-group distance is calculated using the Sørensen distance measure.

$$\text{delta} = \delta = \sum_{i=1}^g C_i x_i$$

For g groups, where C_i is a weight that depends on the number of items in group i

- Determine the probability of obtaining a specific value for δ by calculating the number of possible permutations (M) for two groups:

$$M = N! * n_2!$$

- The p value is calculated for obtaining that value of δ or smaller is determined:

$$p = \frac{1 + \text{no. small delta}}{\text{total no. possible partions}}$$

A p value is approximated by using a Pearson type III distribution that has three parameters, namely the mean (m_δ), the standard deviation (s_δ), and gamma g (the skewness for delta (δ) under the null hypothesis). The standardized test statistic under the null hypothesis is calculated as:

$$T = \frac{\delta - m_\delta}{s_\delta}$$

- Then the T statistic is calculated as the ratio of the difference between the observed and expected mean distance and the standard deviation of the expected difference.

$$T = \frac{\text{observed } \delta - \text{expected } \delta}{\text{s.dev. of expected } \delta}$$

This statistic describes the separation between groups. The more negative T is, the stronger the separation between groups.

- The probability value expresses the likelihood of getting a delta as extreme as or more extreme than the observed delta, given the distribution of possible deltas. A p value associated with T is determined by the numerical integration of the Pearson type III distribution. This p value is used to evaluate the likelihood of achieving the observed difference (T) by chance.

- The procedure then calculates an *A* statistic that is an estimate of the within-group homogeneity, compared to the expectation under a random allocation of members to groups. This statistic provides an estimate of the 'effect size' that is independent of the sample size (McCune and Grace, 2002). The chance-corrected within-group agreement (*A*) is calculated as follows

$$A = 1 - \frac{\delta}{m_{\delta}} = 1 - \frac{\text{observed } \delta}{\text{expected } \delta}$$

A measures the 'effect size'-magnitude of difference between two groups. When all plots are identical within groups it will result in *A* = 1, if heterogeneity within groups equals expectation by chance, then *A* = 0. If there is less agreement within the groups than expected by chance then *A* < 0. In community ecology, values for *A* are mostly less than 0.1 (McCune and Grace, 2002).

To determine whether groups represent the same environmental condition, the distances are measured or calculated between all pairs of members of each group and the average distance is calculated for each group. If group members are clustered together, then the intragroup distance will be small compared to the cases where the group members are spread out and overlap with other groups. The strategy of MRPP is to compare the observed intragroup average distances with the average distances that would have resulted from all the other possible group allocations of the data under the null hypothesis. The test statistic, symbolized with delta, δ , is the average of the observed intragroup distances weighted by relative group size. The observed delta (δ) is compared to the possible deltas resulting from every permutation of plots in groups (McCune and Grace, 2002).

2.7 Species response curves: Nonparametric Multiplicative Regression (NPMR)

Traditionally, species response curves have been assumed to be approximate normal (Gaussian) curves, i.e. the curves are symmetric and bell-shaped in relation to an environmental gradient (Austin, 1987). But this assumption does not always hold and it is useful to look into methods that can determine the species response curve that fits the observed data more precisely. In order to find the function best describing the response of species to an environmental variable Generalized Linear Models (GLM), General Additive Models (GAM) and NPMR for habitat modelling are used (McCune and Grace, 2002).

GLM's are an extension of linear models that allow for regression in more complex situations where the error terms are not normally distributed, but involve a link function. GLM have three components: a random component, which is the response variable and its probability distribution, the systemic component, which represents the predictors of the model, which might be continuous and/or categorical and the link function that links the random and the systemic component (Quinn and Keough, 2002). Generalized Additive Models (GAM) are modifications of GLM where explanatory variables are included in the model as non-parametric smoothing functions (Hastie and Tibshirani, 1990). This allows for a wider range of shapes of response curves than can be found by normal linear regression and therefore a more realistic model without too many assumptions. Like GLM, GAM uses a link function to establish the relationship between the mean of the response variable and a smoothed function of the explanatory variables (Guisan *et al.*, 2002). The GAMs have the ability to deal with non-linear and non-monotonic relationships between the response and explanatory variables.

The programme HyperNiche (McCune and Mefford, 2009) builds a habitat model based on the environmental variables in those plots where a certain species occurs. These habitat models are built using Non-Parametric Multiplicative Regression (NPMR) models (McCune, 2009). The use of NPMR for habitat modelling occurs with a number of variants. NPMR uses a method for evaluating the model quality that can be applied to any habitat model. The model quality is evaluated using a cross-validated R^2 value (xR^2). Habitat models identify the relationship between a species and the factors that control its occurrence.

The model used in the current study is a Local Linear (NPMR) weighting function with a Quantitative response. When comparing a Local Mean (Gaussian) estimator to a Local Linear (Quantitative) estimator, it should be noted that a local mean estimator is biased towards the extremes values on which the estimate is based. (Bowman and Azzalin, 1997). This bias is removed by using a local linear estimator rather than a local mean estimator. The local linear estimator is a weighted least squares problem, the weights provided by the kernel function so that points close to the central value receive more weight than points far from the target point. The bias is reduced near the edges of the data set, and as the kernel function becomes broad, the fitted curve will smoothly

approach a traditional least squares regression while the local mean smoothly approaches a horizontal line parallel to the predictor axis with an intercept equal to the global mean (McCune and Grace, 2009). The local linear model was proposed as early as Cleveland (1979) and it was developed further by Fan and Gijbels (1996) and Fan (1993).

HyperNiche has an option for data screening using a free search method. This method seeks for the best model from the predictor variables (environmental variables). The free search method chooses the best models (those with the highest xR^2) depending on the options set e.g. the model type and kind of data (binary or quantitative). The habitat model is then evaluated using a method known as a leave-one-out form of cross validation. For each regression the 'Sensitivity' and 'Tolerance' parameters are calculated. Tolerance corresponds to the smoothing parameter for each quantitative parameter. Sensitivity evaluates the importance of individual variables by evaluating the effects of changing the value of a variable in the final output of the model. A value of 1 implies that on average, nudging a predictor results in a change in response of equal magnitude, and 0.5 implies that the response is half the magnitude of the change in the predictor (McCune, 2009).

In this study, quantitative response data was used for species response analysis. The model evaluation is as follows:

- The model quality is evaluated in terms of the residual sum of squares (RSS) in relationship to the total sum of squares (TSS), when the response variable is quantitative
- This is called "cross R " (xR^2) because the calculation incorporates a cross validation procedure.
- When the model is weak, it is common for $RSS > TSS$ and xR^2 becomes negative.

$$xR^2 = cross R^2 = 1 - \frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{\sum_{i=1}^n (y_i - \bar{y})^2}$$

- For the quantitative data the model estimates the abundance of species at a certain point as the mean abundance of the species in the whole data set. The model quality is evaluated by the cross-validated R^2 value (xR^2). The maximum possible xR^2 is 1.0.

2.8 Research procedure

The data from the South African wetlands vegetation database have three 'levels' of resolution as was illustrated in Figure 1.2. These different levels appear again in Figure 2.2 but in this figure it is supplemented with the methods or procedures that were used for each data matrix at the different levels of data resolution. Not all analyses have been carried out on all data, as not all data plots have the same amount of data available, given that the vegetation plots come from a variety of sources.

A data matrix for environmental and species data was made. The dataset was improved to represent the three levels of data resolution by removing plots that do not have certain environmental data available and adding environmental data for those plots that have soil data available. The data for the major Cations (Ca, Mg, Na and K) coming from different studies were transformed into the same standard units (Table 1.2). The data for concentrations and fractions were first log transformed using the log-transformation $\log(x + 1)$ as is standard practice for such variables (Legendre and Legendre, 2012). Then it was standardized by subtracting the mean and dividing the standard deviation s_y of the variable $z_i = \frac{y_i - \bar{y}}{s_y}$, z_i (*Standardized variable*) is expressed as standard deviation unit (Legendre and Legendre, 2012). This was done for the major cations as there seemed to be an inconsistency in one of the studies.

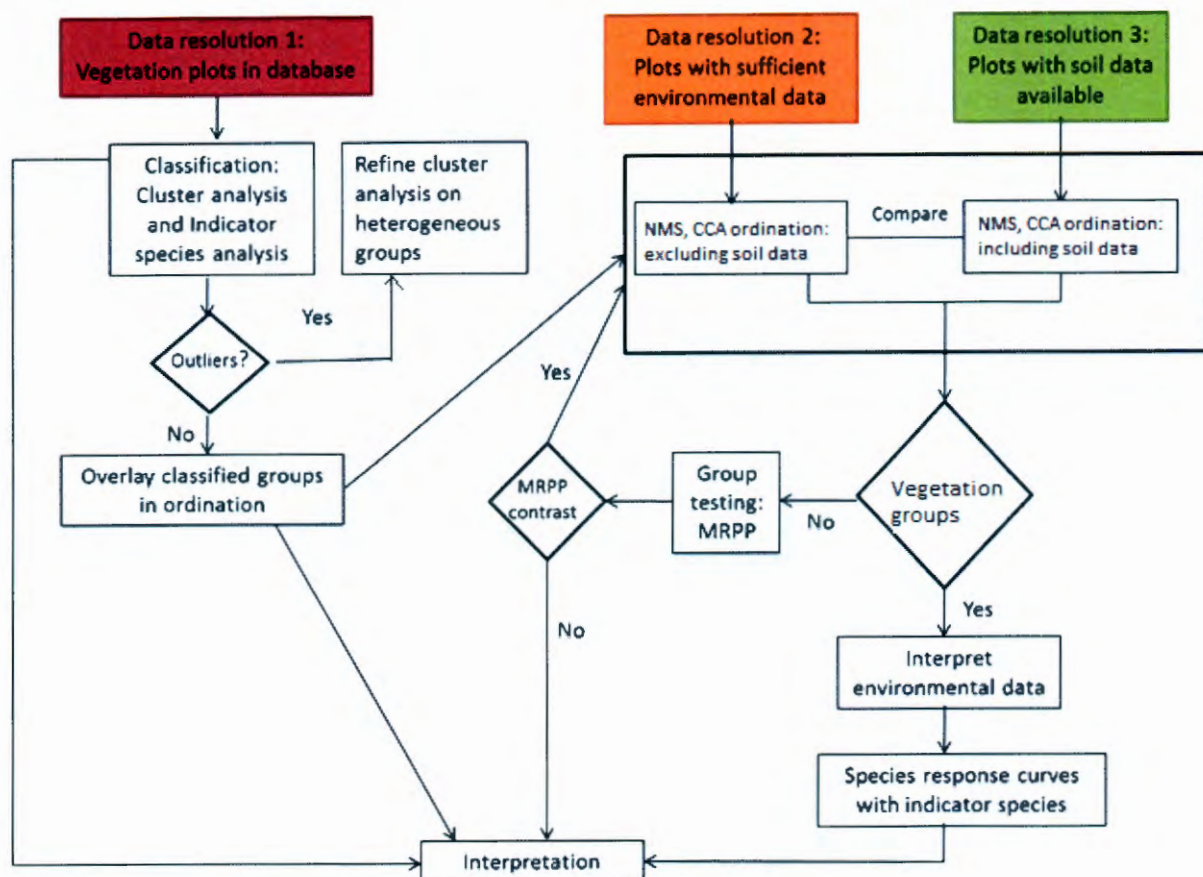


Figure 2.2 Schematic flowchart displaying the decisions made for systematic analysis of the vegetation data in the South African Wetlands Vegetation Database, showing data subdivision, decision criteria and methods used for analysis.

Classification was used to group vegetation plots that have similar patterns into plant communities using a hierarchical, agglomerative method, based on a similarity matrix of Bray-Curtis resemblance and Ward's method. The cluster analysis for both Main Clusters (SWV and TGW) was conducted using a hierarchical cluster analysis in combination with Indicator Species Analysis (ISA) to determine the optimal number of clusters. Indicator species analysis can provide a quantitative, objective criterion for picking the most ecologically meaningful level to prune a dendrogram resulting from cluster analysis (McCune and Grace, 2002). The p -value for all species was averaged, repeating this for each step of clustering. The number of clusters that yielded the lowest average p -value in ISA was chosen as the optimal number of clusters.

Then indicator species analysis constructed indicator values for each species in each group and tested for statistical significance using the Monte Carlo test with 1000 runs. A level of 20% (for the Indicator Value) with 95% significance (p value < 0.05) was chosen as a cut-off level for identifying indicator species for selecting them for presentation

(Dufrêne and Legendre, 1997). The species that were used to provide names for the plant communities were those that were either dominant in those communities or had the highest maximum indicator values.

The NMS ordination was run with vegetation data while the program was set on the autopilot mode with slow and thorough speed. Autopilot is the mode that is used to assist the user in making multiple runs, choosing the best solution at each dimensionality, and testing for significance. At autopilot mode all options are set automatically except for the distance measures. An overlay of an explanatory matrix (environmental data) to response data (vegetation data) was run to identify the environmental variables that influence the distribution of the vegetation types. The autopilot mode is a feature in PC-Ord with NMS that assists the user in making multiple runs, and choosing the best solution for each dimensionality while testing for significance. Fifty iterations with real data and 250 iterations with randomized data were compared to select a dimensionality and to find a stable solution with minimal stress (McCune and Grace, 2002). To verify the results of the autopilot mode, manual adjusting of the parameter setting and options was done, because when the autopilot mode is selected all options are set as default except for the distance measure. An NMS scree plot was drawn and used as a guide in deciding on the number of dimensions required. After the NMS autopilot mode has selected the suitable dimensionality (the number of dimensions resulting in minimum stress). NMS was re-run with the recommended number of the dimensionality after inspecting the NMS scree plot, using 250 runs with real data to verify the final 'stress test' solution. It was run at least 3–5 times using the same manual settings. Ordination diagrams were drawn using vegetation plots in each group with an overlay of the explanatory variables (environmental data) to explore which variables were most influential in defining the plant communities. CCA was carried out using Hill's (1979) method on PC-Ord and results were compared with that of NMS. The arrows in ordination diagrams indicate the patterns of environmental data.

In the case where there were two or more groups of communities that overlap in the ordination space, the differences between environmental variables of each vegetation cluster were evaluated using Multi-Response Permutation Procedure (MRPP) by making a pairwise comparison for each pair in the group of clusters that overlap. This analysis was conducted using the defined clusters by overlaying them on the explanatory variables (environmental variables). The dissimilarity or similarity between groups was

evaluated using a test statistic (p). Ordination analysis (NMS) was re-run for plant communities that were significantly distinct after comparison to identify the influential environmental variables.

MRPP only tested whether clusters were distinct in terms of environmental variables but it does not show the influential variables themselves. The distinctiveness was shown using an additional ordination with only the relevant clusters. The cut-off value for significant separation was $p < 0.001$. The communities that were subjected to MRPP are the ones that were clustered in the first ordination analysis for all plant communities and had no clear influential variable distinguishing them from the other communities.

Species response curves by means of a local linear model (LLR) were conducted using plots that contained specific indicator species (response) with the soil data belonging to those plots (explanatory). The best explanatory model was sought using the free search method in the programme HyperNiche using NMPR. The model selected was a Local Linear-Quantitative (LLR-NMPR) weighting function with a Gaussian response. The percentage improvement for including new predictors into the model was set at 5%. The best predictors were selected and were then used to plot species responses to environmental variables. The goodness of fit/model quality was expressed in terms of a cross validated $R^2(xR^2)$.

CHAPTER 3

Main Cluster 1: Sclerophyllous Wetlands Vegetation: Patterns and ecological drivers

3.1 Sclerophyllous Wetland Vegetation

Sclerophyllous Wetlands Vegetation (SWV) represents wetlands that are found on well-leached nutrient-poor sandstone soils (van Wilgen and le Maitre, 1981; Witkowski and Mitchell, 1989), mostly in the in the Western Cape (Table Mountain Sandstone) and in similar nutrient poor substrates in the Eastern Cape (Msikaba Formation) and Limpopo (various rock formations of the Waterberg, Wolkberg and Soutpansberg). This shows that wetlands plants are much more flexible in their dispersal than the plants from the surrounding uplands. These wetlands are unique and have high conservation value in South Africa.

Sclerophyllous Wetlands Vegetation is found embedded in Lowland Fynbos as well as around highest mountain peaks in the Fynbos Biome, and many of these wetlands are associated with rivers located in the foothills (Sieben *pers. comm.* 2013). These wetlands are associated with various types of wetland including depressions, channelled and unchannelled valley bottoms, valley head seepages, springs and floodplains wetlands. They are found on sandy soils derived from sandstone that are therefore deficient in nutrients (Cowling *et al.*, 1997) or on peat that is rich in organic matter but also very nutrient-poor (Sieben *et al.*, 2004). The wetlands are dominated mainly by restios, dwarf shrubs, large sedges and grasses. The proportion of woody plants is often higher than in any other wetland vegetation type.

Two types of Azonal vegetation are described by Mucina and Rutherford (2006) that fit in with this Main Cluster, namely Cape Lowland Freshwater Wetlands (AZf1) and Fynbos Riparian Vegetation (AZa1). Many wetlands in this cluster are however associated with rivers and riparian vegetation and wetlands often share many species (for example *Prionium serratum* (palmiet) and *Cliffortia strobilifera*), so a more detailed look at the actual plant communities may reveal that there would be actually quite some overlap between the two types described by Mucina and Rutherford (2006).

The map and photograph displayed in Figure 3.1 shows the distributions of Sclerophyllous Wetlands Vegetation in South Africa. The subset of the overall database that was used for data analysis of Sclerophyllous Wetlands Vegetation consists of 299

vegetation plots containing a total of 663 plant species. Seventy one percent of the species (species with fewer than three occurrences) were left out during the analysis.

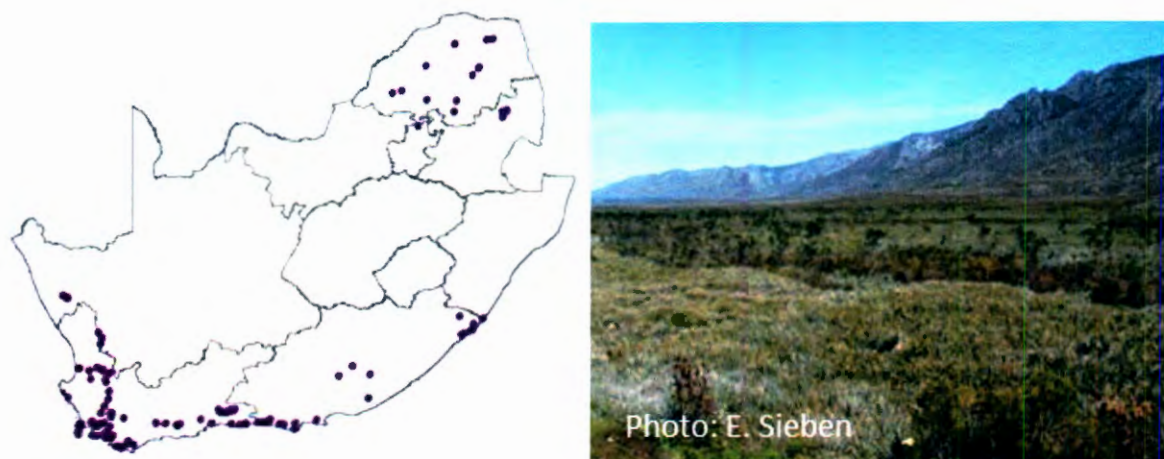


Figure 3.1 The map shows the distribution of Sclerophyllous wetlands throughout the country, and one of the wetlands in the Western Cape.

3.2. Classification and Indicator species analysis

Cluster analysis was carried out on the dataset of 299 vegetation plots and ISA was used to determine the optimal number of clusters in terms of being distinct from one another and capturing the variation. The use of Indicator Species Analysis as an objective criterion for picking ecologically meaningful clusters [following Dufrêne and Legendre (1997)] was invaluable. The cluster number that yielded the smallest average p -value was 34 plant communities, and the dendrogram with the number of clusters is displayed in Figure 3.2. Three of the classified communities (Communities 6, 11 and 14) were not represented well and were therefore regarded as under sampled, each represented by only two plots. It is important to consider collecting more samples in the mountain wetlands of the Fynbos Biome in the future, as there may still be a considerable range of wetland vegetation types that have been left under sampled.

ISA also yielded a list of indicator species. A Monte Carlo test of significance of observed maximum indicator values (IV) for each species was carried out, with 1000

randomizations and the p-values of this test are shown in Table 3.1. Only those species that were statistically significant ($p < 0.05$) and had a Maximum indicator value of 20% and upwards were listed as Indicator species. From the 190 species present in Sclerophyllous wetlands, 28 percent were identified as having a significant indicator value for any of the communities ($p \leq 0.05$) after randomization. Significant values suggest that those species are more likely to occur in particular vegetation type. Very few of the plots from the database have the significance of alien plants invasion, but there are occasional records of *Acacia mearnsii*, *Oenothera rosea*, *Salix babylonica*, and *Verbena bonariensis*,

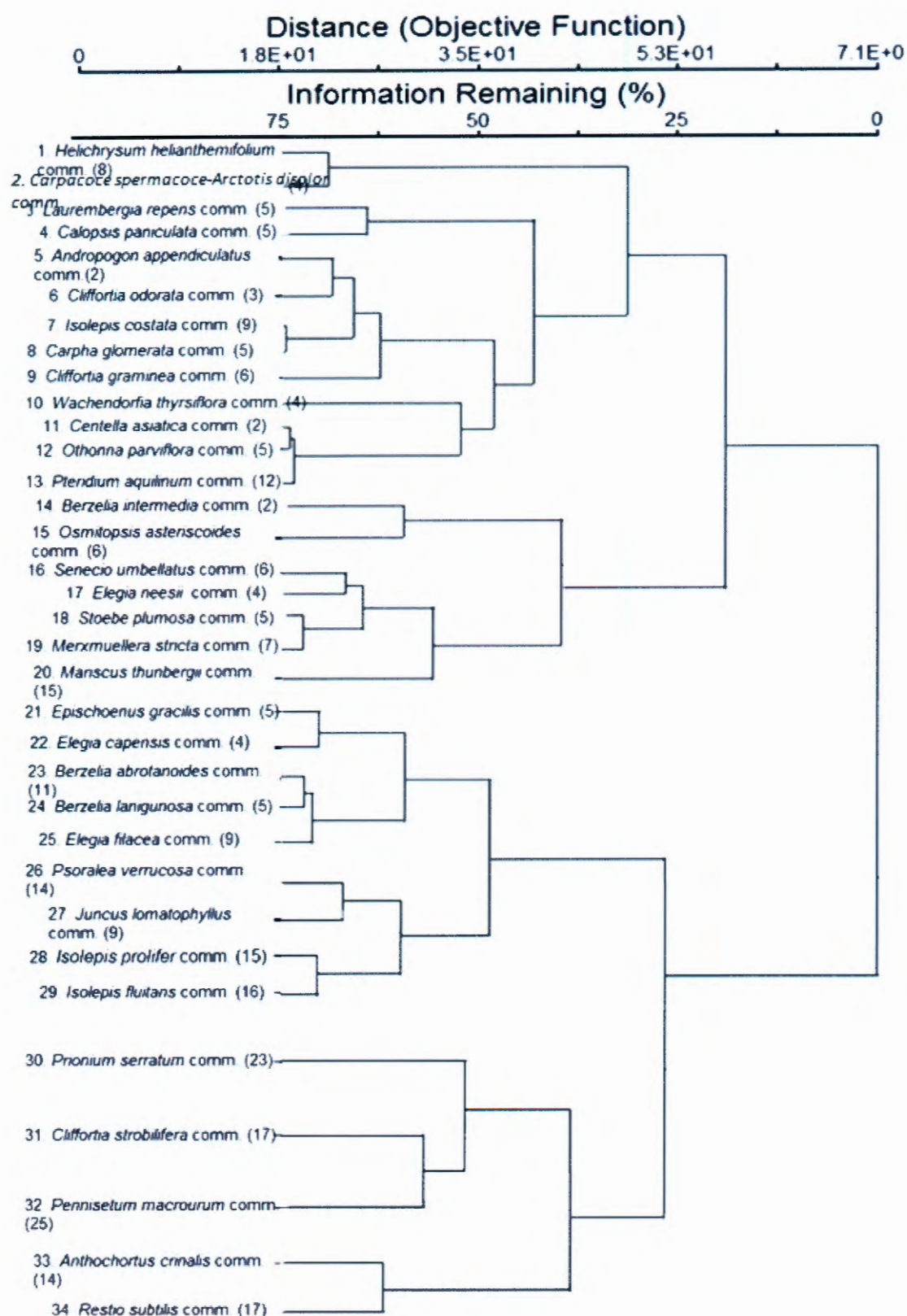


Figure 3.2 Cluster dendrogram of Sclerophyllous wetland types based on species cover abundance. The dendrogram is scaled by Wishart's (1969) objective function, expressed as the percentage of information remaining at each level of grouping (McCune & Grace, 2002). The vegetation clusters are named after either with species with the highest indicator value or with the abundant species in groups with plants that have minimum indicator value, the number in brackets is the number of plots within a cluster.

Table 3.1 Communities of Sclerophyllous Wetlands Vegetation (Main Cluster 1) with their indicator species. Monte Carlo test of significance of the observed maximum indicator value (IV) for each species based on 1000 randomizations. Only species that were statistically significant ($p < 0.05$) with maximum indicator value of 20% or higher are shown in this table.

Cluster	No. of plots	Dominants	Indicator Species	Indicator Value (IV)	p-value
1	8	<i>Helichrysum helianthemifolium</i>	<i>Helichrysum helianthemifolium</i>	26	0.0058
2	4	<i>Carpacoe spermacoea</i>	<i>Carpacoe spermacoea</i>	23.2	0.0102
3	5	<i>Laurembergia repens</i> subsp. <i>brachypoda</i>	<i>Laurembergia repens</i> subsp. <i>brachypoda</i>	38	0.0002
		<i>Senecio purpureus</i>		20	0.00764
4	5	<i>Calopsis paniculata</i>	<i>Calopsis paniculata</i>	25.9	0.0112
5	2	<i>Andropogon appendiculatus</i>	<i>Andropogon appendiculatus</i>	44	0.0002
6	3	<i>Cliffortia odorata</i>	<i>Cliffortia odorata</i>	70.8	0.0002
7	9	<i>Isolepis costata</i>	<i>Isolepis costata</i>	55.7	0.0006
8	5	<i>Carpha glomerata</i>	<i>Carpha glomerata</i>	34	0.0018
9	6	<i>Cliffortia graminea</i>	<i>Cliffortia graminea</i>	53	0.0004
10	4	<i>Wachendorfia thyrsiflora</i>	<i>Wachendorfia thyrsiflora</i>	43.2	0.0024
		<i>Watsonia angusta</i>		34	0.0352
11	2	<i>Centella asiatica</i>	<i>Centella asiatica</i>	62.7	0.001
		<i>Eragrostis curvula</i>		46.4	0.009
		<i>Persicaria decipiens</i>		47.9	0.0018
		<i>Arctotis discolor</i>		29	0.0292
		<i>Agrostis bergiana</i>		50	0.0214
12	5	<i>Othonna parviflora</i>	<i>Othonna parviflora</i>	20	0.002
13	12	<i>Pteridium aquilinum</i>	<i>Pteridium aquilinum</i>	40.4	0.002
14	2	<i>Berzelia intermedia</i>	<i>Berzelia intermedia</i>	84.2	0.0002
		<i>Chrysitrix junciformis</i>		30	0.0162
15	6	<i>Restio purpurascens</i>	<i>Restio purpurascens</i>	32.5	0.0044
		<i>Carpacoe spermacoea</i> subsp. <i>spermacoea</i>		37.3	0.005
		<i>Osmitopsis asteriscoides</i>		64.7	0.0002
		<i>Psoralea aphylla</i>		22	0.0438
16	6	<i>Elegia thyrsifera</i>	<i>Elegia thyrsifera</i>	43.5	0.002
		<i>Senecio umbellatus</i>		45.2	0.002
		<i>Ehrharta rehmannii</i> subsp. <i>rehmannii</i>		31.2	0.0038
		<i>Hippia pilosa</i>		41.7	0.003
		<i>Protea laticolor</i>		33	0.0384
17	4	<i>Elegia neesii</i>	<i>Elegia neesii</i>	76.8	0.0002
		<i>Restio bifidus</i>		30.6	0.0064
		<i>Erica maderi</i>		57.9	0.0014

Table 3.1 (Continued)

Cluster	No. of plots	Dominants	Indicator Species	Indicator Value (IV)	p-value
		<i>Staberoha distachyos</i>		25	0.0434
		<i>Staberoha multispicula</i>		34	0.0218
		<i>Ehrharta rehmannii</i> subsp. <i>rehmannii</i>		20	0.0954
		<i>Ursinia pinnata</i>		25	0.0954
18	5	<i>Stoebe plumosa</i>	<i>Stoebe plumosa</i>	25.6	0.0134
19	7	<i>Merxmuellera stricta</i>	<i>Merxmuellera stricta</i>	65.9	0.0006
20	15	<i>Mariscus thunbergii</i>	<i>Mariscus thunbergii</i>	58.2	0.0002
21	5	<i>Epischoenus gracilis</i>	<i>Epischoenus gracilis</i>	53	0.0008
		<i>Erica bergiana</i>		21	0.0838
22	4	<i>Elegia capensis</i>	<i>Elegia capensis</i>	60.9	0.0008
23	11	<i>Berzelia abrotanoides</i>	<i>Berzelia abrotanoides</i>	31.7	0.0068
		<i>Tetraria cuspidata</i> var. <i>cuspidata</i>		24	0.0102
24	5	<i>Berzelia lanuginosa</i>	<i>Berzelia lanuginosa</i>	71.2	0.0002
		<i>Leucadendron xanthoconus</i>		27	0.0384
		<i>Erica myriocodon</i>		20	0.1974
25	9	<i>Elegia filacea</i>	<i>Elegia filacea</i>	54.3	0.002
		<i>Elegia cuspidata</i>		31	0.0446
		<i>Erica cubica</i>		20	0.0846
26	14	<i>Psoralea verrucosa</i>	<i>Psoralea verrucosa</i>	55.6	0.0008
		<i>Watsonia fourcadei</i>		29.8	0.0088
		<i>Helichrysum cymosum</i> subsp. <i>cymosum</i>		26	0.0326
27	9	<i>Juncus lomatophyllus</i>	<i>Juncus lomatophyllus</i>	51.8	0.0002
28	15	<i>Juncus capensis</i>	<i>Juncus capensis</i>	24.7	0.0118
		<i>Isolepis prolifer</i>		45.2	0.0014
		<i>Isolepis rubicunda</i>		20	
29	16	<i>Isolepis fluitans</i>	<i>Isolepis fluitans</i>	38	0.0002
30	23	<i>Prionium serratum</i>	<i>Prionium serratum</i>	56.2	0.0002
31	17	<i>Cliffortia strobilifera</i>	<i>Cliffortia strobilifera</i>	36.7	0.0002
32	25	<i>Pennisetum macrourum</i>	<i>Pennisetum macrourum</i>	58.1	0.0002
33	14	<i>Anthochortus crinalis</i>	<i>Anthochortus crinalis</i>	70.2	0.0002
		<i>Epischoenus villosus</i>		43	0.0006
		<i>Ehrharta setacea</i> subsp. <i>setacea</i>		27.7	0.0114
		<i>Senecio crispus</i>		45.8	0.0016
		<i>Elegia intermedia</i>		48.2	0.0016
		<i>Cliffortia tricuspidata</i>		46.2	0.002
34	17	<i>Restio subtilis</i>	<i>Restio subtilis</i>	76.5	0.0002

Table 3.1 (Continued)

Cluster	No. of plots	Dominants	Indicator Species	Indicator Value (IV)	p-value
		<i>Tetraria cuspidata</i>		32.7	0.008
		<i>Grubbia rosmarinifolia</i> <i>subsp. rosmarinifolia</i>		42.5	0.005
		<i>Ursinia caledonica</i>		36.3	0.004
		<i>Restio corneolus</i>		34.9	0.0018
		<i>Chondropetalum deustum</i>		39.5	0.0026
		<i>Restio versatilis</i>		47.1	0.003
		<i>Elegia mucronata</i> (<i>Chondropetalum mucronatum</i>)		58.4	0.0006

3.3. Ordination and group testing

Nonmetric Multidimensional Scaling and Canonical Correspondence Analysis were used to reveal the variation on environmental gradients within the dataset and create ordination diagrams for plots, with inclusive and exclusive soil data. Cluster identity was used as an overlay in these ordination diagrams as well as environmental variables, so that it can be seen which vegetation types occur in which environments. The results of various types of ordination (CCA compared to NMS, inclusive and exclusive soil data) were compared afterwards. CCA was used only for the subset of the data that had extensive soil data available.

3.3.1. Patterns of plant community distribution excluding soil data

Nonmetric Multidimensional Scaling was run using environmental variables with various dimensionalities in an ‘autopilot’ mode using the slow and thorough options. The most optimal (low stress) solution was a solution with 2 dimensions. The low stress value of the NMS was 16.24 in two dimensions. The distribution of relevés along the axes is given in a scatter diagram (Figure 3.3) for dataset of that did not include soil variable. Distinct plant communities can be seen in the diagram. The HGM unit, wetness and soil texture distinguish these plant communities. Clusters including 1. *Helichrysum helianthemifolium*

Community, 2. *Carpacoe spermacoea* Community, 3. *Laurembergia repens* Community, 4. *Calopsis paniculata* Community, 5, *Cliffortia odorata* Community, and 6. *Isolepis costata* Community appear isolated from the rest of the groups (Figure 3.3). These groups are clearly different from each other in terms of the environmental conditions because they are separated in ordination space. For communities that were not clearly separated in the ordination space, a group testing method using MRPP (see section 3.4 for the results) was conducted to investigate why the clusters do not separate well in ordination space. The plant communities that were clustered in ordination space are listed in Table 3.2.

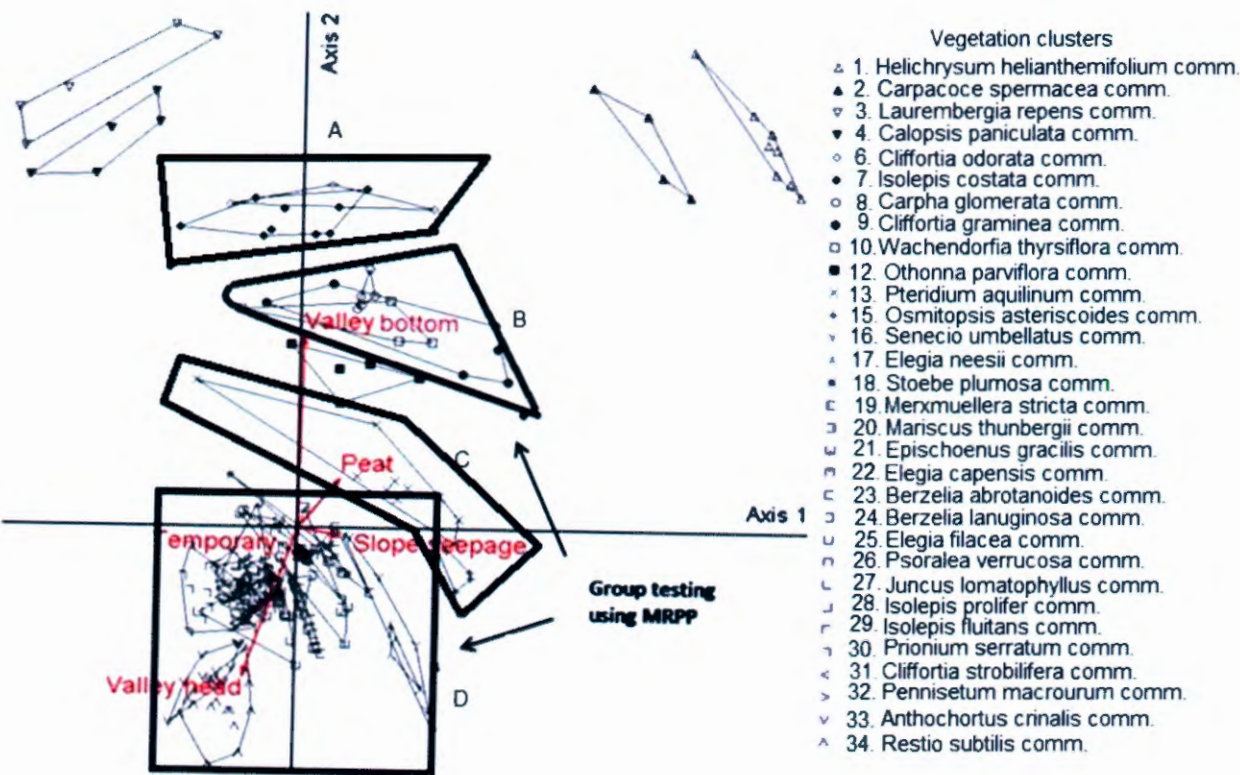


Figure 3.3 NMS ordination biplot of dataset exclusive of soil variables. The symbols in the ordination indicate group identities the arrows and vectors indicate environmental variables that show trends along the axes.

Table 3.2 Inseparable group of Sclerophyllous wetlands communities in ordination space (see figure 3.3 above). Letters refers to the clusters in the ordination diagram.

Vegetation clusters
A. 6. <i>Cliffortia odorata</i> comm., 7. <i>Isolepis costata</i> comm.
B. 8. <i>Carpha glomerata</i> comm., 9. <i>Cliffortia graminea</i> comm., 10. <i>Wachendorfia thyrsiflora</i> comm.
C. 16. <i>Senecio umbellatus</i> comm., 17. <i>Elegia neesii</i> comm.
D. 18. <i>Stoebe plumosa</i> comm., 19. <i>Merxmuellera stricta</i> comm., 20 <i>Mariscus thunbergii</i> comm., 21. <i>Epischoenus gracilis</i> comm., 22. <i>Elegia capensis</i> comm., 23. <i>Berzelia abrotanoides</i> comm., 24. <i>Berzelia lanuginosa</i> comm., 25. <i>Elegia filacea</i> comm., 26. <i>Psoralea verrucosa</i> comm., 27. <i>Juncus lomatophyllus</i> comm., 28. <i>Isolepis prolifer</i> comm., 29. <i>Isolepis fluitans</i> comm., 30. <i>Prionium serratum</i> comm., 31. <i>Cliffortia strobilifer</i> comm., 32. <i>Pennisetum macrourum</i> comm, 33. <i>Anthochortus crinalis</i> comm., 34. <i>Restio subtilis</i> comm.

3.3.2. Patterns of plant community distribution including soil data

The ordination diagram of NMS of plots with extensive soil data (Figure 3.4) indicates that the first axis is mainly correlated to organic matter content. The two communities associated with high organic matter content are 1. *Helichrysum helianthemifolium* Community and 12. *Othonna parviflora* Community. Other communities like 9. *Cliffortia graminea* Community and 22. *Elegia capensis* Community are found in places with very low organic matter content. Two other variables that are strongly correlated to the first axis are the electrical conductivity and Mg contents. This is suggesting that an increase in organic content is accompanied by an increase in electrical conductivity and magnesium. As reported by Iranpour et al., 2014 organic matter can influence soil electrical conductivity through changing the pH level in the soil. This is caused by cation exchange in soil. Studies have shown that the decomposition of organic matter in soil produces organic acids causing the soil pH to drop and thereby increase the availability of nutrients. The same applies to the second axis which is negatively correlated with phosphorus and nitrogen contents. Community 2 (*Carpacoce spermacoce*a Community), Community 3 (*Laurembergia repens* Community), Community 4 (*Calopsis paniculata* Community) and Community 19 (*Merxmuellera stricta* Community.) are found in soils which are relatively high in sodium.

The most important driving factors based on mineral concentrations within SWV displayed by ordination are Sodium, Phosphorus and organic matter.

The results of CCA and NMS do not contradict each other, with the difference that some communities in CCA are not clearly separated. The results of the CCA of plots including extensive soil data are shown in Figure 3.5. The variation on the first axis in NMS and CCA (Figure 3.4 and 3.5) is mainly explained by organic content, electrical conductivity and magnesium. The community that stands out mostly in Figure 3.4 is Community 1 (*Helichrysum helianthemifolium* Community) which is found in highly organic soils. Similarities or distinction among groups is explained by overlaying exploratory variables on an ordination space.

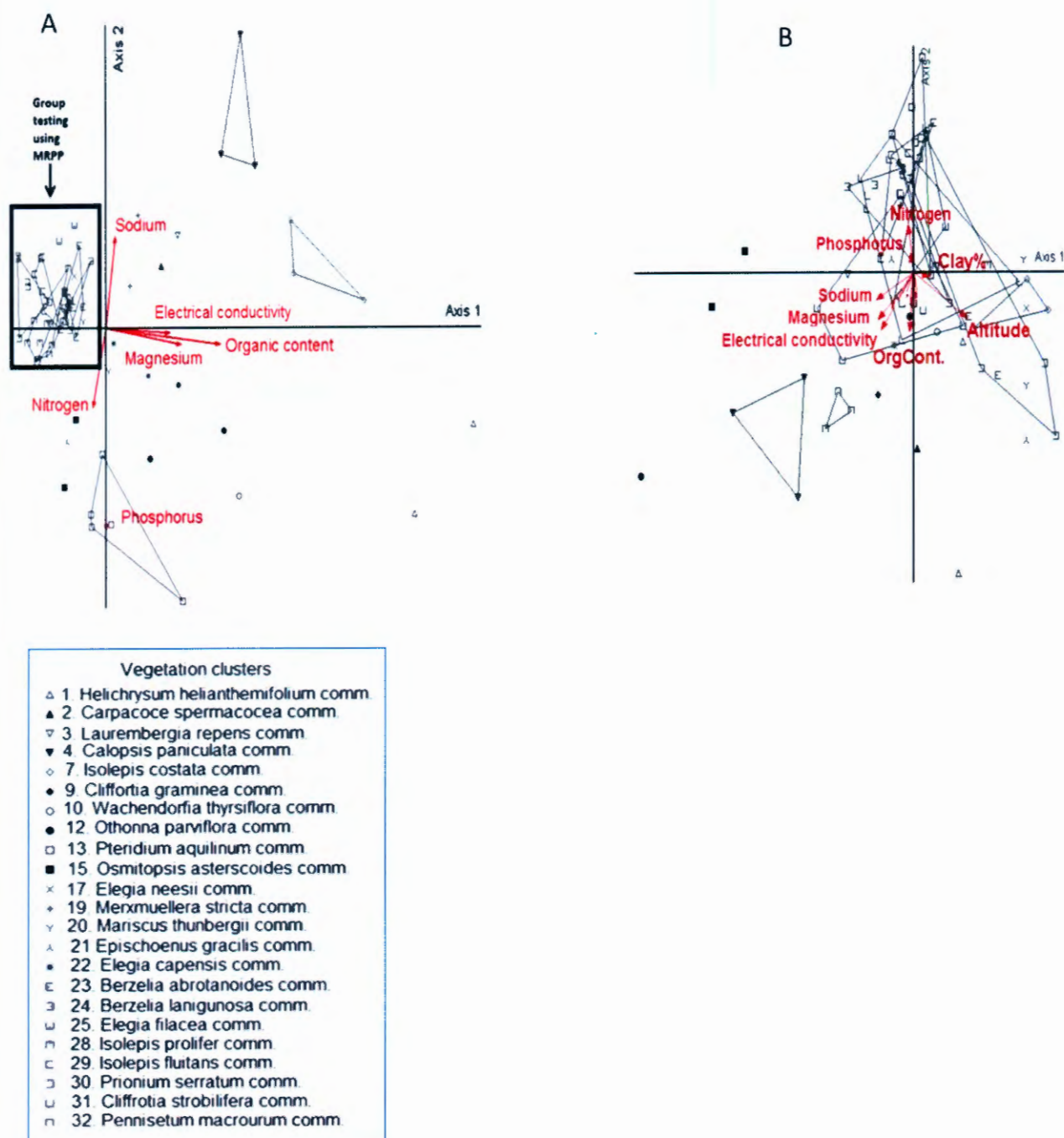


Figure 3.4 NMS and CCA ordination biplot of dataset inclusive of soil data, showing group identities and the driving environmental variables. The symbols in the ordination indicate group identities the arrows and vectors indicate environmental variables that show trends along the axes. Both methods produced more or less similar results when compared. In the CCA ordination clusters are not as clearly distinguished as in the NMS ordination which means that environmental variables do not.

3.3.3 Group testing (MRPP)

Multi-response Permutation Procedure was applied in those cases when different clusters were overlapping in ordination space.

The hypothesis for this analysis was that the clustered plant communities in ordination space are not different from each other in terms of their environment. The test was carried out on the basis of the environmental data of those plant communities that were overlapping in ordination space (Figure 3.3 and 3.4). MRPP was applied to the matrix of plots to establish whether plant communities that were overlapping in space are similar in terms of the environment they were found in. The cut off value for determining significance is $p < 0.001$. If the calculated probability is zero, this means that the chance for the environmental variables characterizing these plant communities to be similar is zero. As outlined in the methodology section, a small probability value (p -value) would indicate that these communities are different in terms of the environmental factors that determine their occurrence.

All the tests (groups A-D) conducted proved that the communities of all these groups could occur in similar environments. After group testing the communities were overlaid in an ordination diagram to further investigate the influential environmental factors. Communities 6 and 7 are found in depression and valley bottom wetlands. The test results (Tables 3.3 to 3.6 and ordination diagrams Figure 3.5 to 3.6) showed that there is no detectable difference between the two communities. The T statistic for 6. *Cliffortia odorata* Community versus 7. *Isolepis costata* Community, and for 16. *Senecio umbellatus* Community versus 17. *Elegia neesii* Community representing the aggregation between these vegetation communities were negative (range -0.90 to 0.5) and not significant ($p > 0.05$). The A statistic indicating the within-group homogeneity ranged between 0.05 and 0.07 . If the results indicate that the null hypothesis of no difference should be accepted against a threshold value of $p < 0.001$, this means that these communities could occur in similar environments. It can be seen from Figures 3.7 and 3.8 that not all communities that were overlapping in the first ordination diagram are influenced by the same environmental conditions. An example is made by group B, consisting of 8 *Carpha glomerata* Community, 9. *Cliffortia graminea* Community and 10 *Wachendorfia thyrsiflora* Community. These communities were originally overlapping in ordination space, but subsequently an MRPP similarity test found them to be slightly different ($p = 0.065$) but another NMS ordination (Figure 3.4) shows that their distribution is mostly influenced by different environmental conditions (soil type,

wetness and type of wetland). The same procedure was followed for all clusters that were overlapping. Several wetland communities are restricted to valley bottom wetlands, namely 9. *Cliffortia graminea* Community, 31. *Cliffortia strobilifera* Community, 32. *Pennisetum macrourum* Community, 33. *Anthochortus crinalis* Community, 13. *Pteridium aquilinum* Community, 1. *Helichrysum helianthemifolium* Community and 2. *Carpacoe spermacoea* Community.

Table 3.3 Test 1 results for Group A: 6. *Cliffortia odorata* Community versus 7. *Isolepis costata* Community. These are likely to occur under similar environmental conditions, as the p-value is much more than the statistical significance of $p < 0.001$.

Groups were defined by values of: Valley bottom	
Test statistic: T =	-0.97235393
Observed delta =	0.51098641
Expected delta =	0.54040715
Variance of delta =	0.91550032E-03
Skewness of delta =	-0.55762065
A =	0.05444181
p =	0.1617241

Table 3.4 Test 2 results for group B: 8. *Carpha glomerata* Community/9. *Cliffortia graminea* Community/10. *Wachendorfia thyrsiflora* Community. The p-value suggests that these communities are similar in terms of environmental condition they occur in, but the agreement within groups expected by chance $A > 0.3$ which is fairly high.

Groups were defined by values of: Slope seepage	
Test statistic: T =	-1.6388214
Observed delta =	0.49025582
Expected delta =	0.52255578
Variance of delta =	0.38845490E-03
Skewness of delta =	-0.69108289
A =	0.38720634
p =	0.06498014

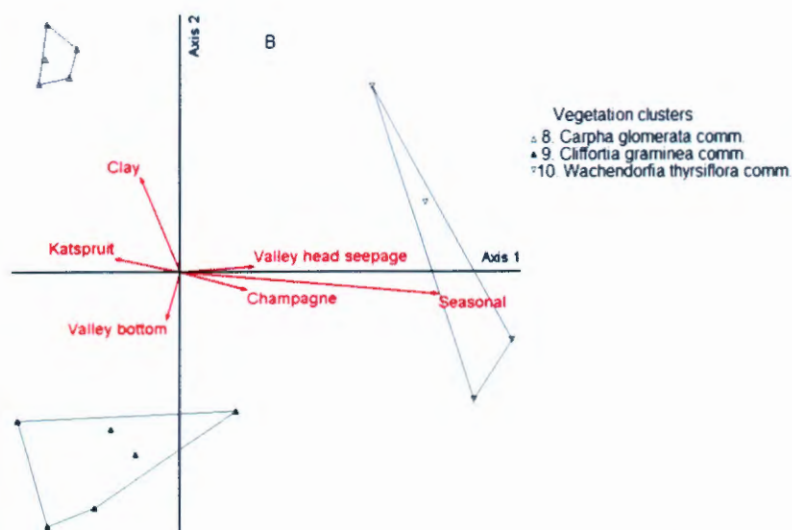


Figure 3.5 NMS ordination of cluster B from first ordination, showing the differentiating environmental variables among the three plant communities. In this ordination diagrams groups appear to be influenced by different environmental variables. The symbols in the ordination indicate group identities the arrows and vectors indicate environmental variables that show trends along the axes.

Table 3.5 Test 3 results for 16. *Senecio umbellatus* Community and 17. *Elegia neesii* comm. Both these communities may occur in similar environments.

Groups were defined by values of: Slope seepage

Test statistic: T = -1.6388214

Observed delta = 0.49025582

Expected delta = 0.52255578

Variance of delta = 0.38845490E-03

Skewness of delta = -0.69108289

A = 0.06181150

p = 0.06498014

Table 3.6 Test 4 results for Communities 18 to 32.

Groups were defined by values of: Temporary

Test statistic: T = -1.5047115

Observed delta = 0.49289903

Expected delta = 0.52255578

Variance of delta = 0.38845490E-03

Skewness of delta = -0.69108289

A = 0.05675327

p = 0.07873442

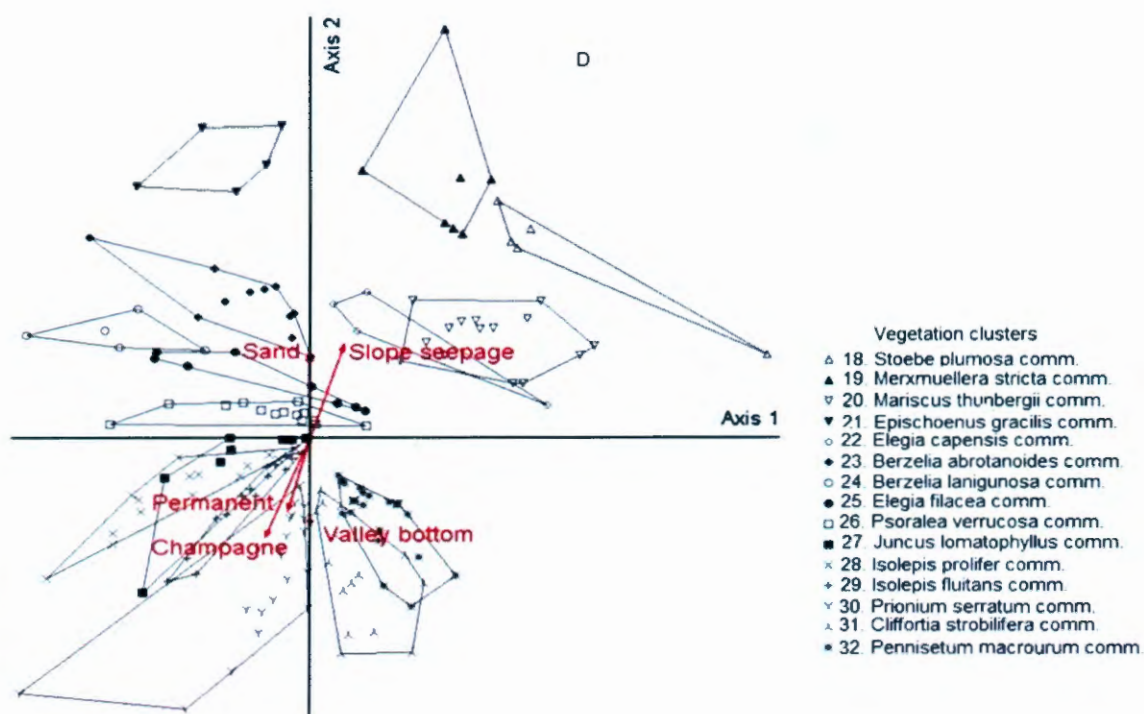


Figure 3.6 NMS ordination of cluster D showing plant communities that were inseparable in the first ordination (Figure 3.3) analysis and their influential environmental variables. The symbols in the ordination indicate group identities the arrows and vectors indicate environmental variables that show trends along the axes.

3.4 Species response curves

The species response curves assist in interpreting how species respond to environmental changes and how individual species are distributed along the gradient. Species do not respond to a single environmental factor in isolation but to a composite of several environmental variables in interaction (Whittaker, 1956). This indicates differences of tolerance and the form of the species response curve is rarely a perfect bell shape (Austin, 1987). The response curves of indicator plant species to environmental gradients were based on measured field data and vegetation relevés. The measured data were available for pH, soil particle size, electrical conductivity, nitrogen, phosphate, sodium, potassium, magnesium, calcium, sulphur, and organic matter (see Table 1.2). The response curves were modelled using the HyperNiche program of McCune and Mefford (2009).

The free search method in HyperNiche was used to seek the best response variables (environmental variables), using a local linear model. Thereafter, the species data were

plotted against a small selection of quantitative environmental variables, namely those that gave the strongest responses for that group of species. The results were presented for the best evaluated models that were found by the free search method. The three best predictor models that were identified during the free search method include the linear model, the hump shaped model and the bimodal model. Sixty four percent of the indicator species fit in with these predictor models.

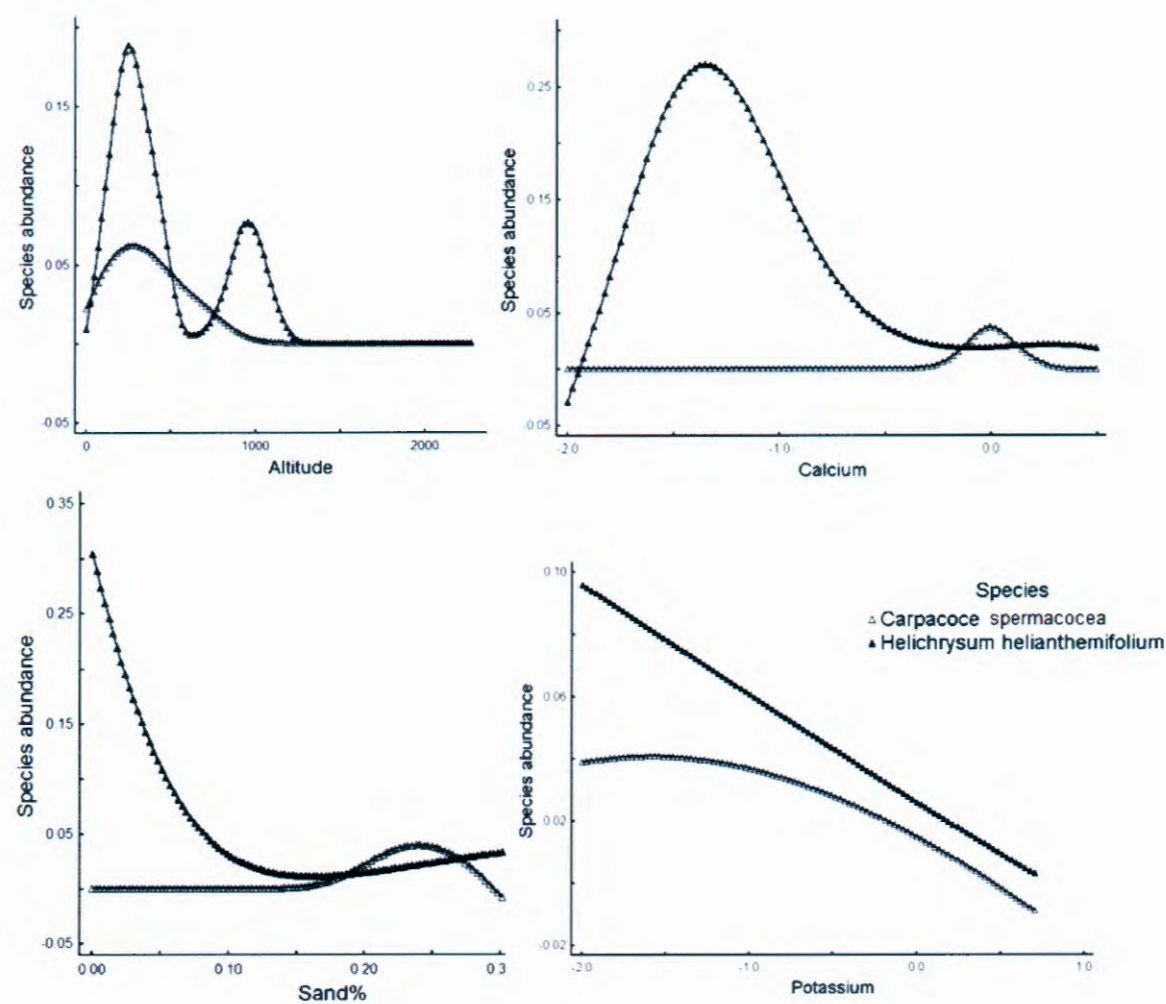


Figure 3.7 Species response curves of two herbaceous wetland species in Sclerophyllous Wetlands Vegetation found in Western Cape and Eastern Cape.

The species in Figure 3.7 are less common in wetlands of Main Cluster 1. *Helichrysum helianthemifolium* and *Carpacoce spermacoce* are associated with damp slopes in low altitudes. It is clear that both species responds negatively to Calcium and Potassium. In terms of sand fraction, *H. helianthemifolium* decreases with higher sand percentage in soil.

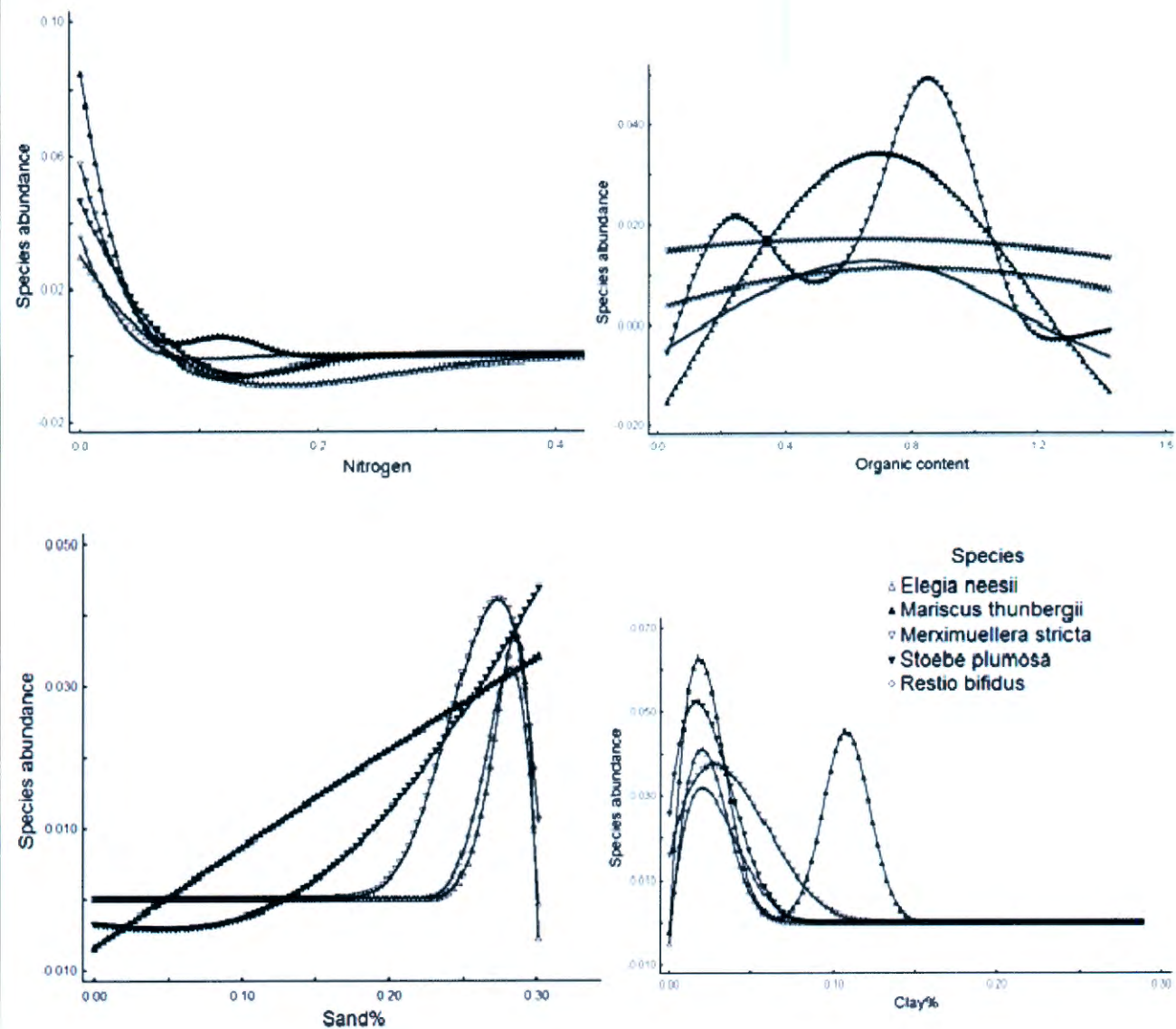


Figure 3.8 Species response for five species occurring in Communities 16, 17, 18, and 19.

The response curves indicated in Figure 3.8 are of species dominant in Communities 16, 17, 18, and 19 and all of them are under sampled. All species become less dominant when Nitrogen increases, and have distinct response to organic content. The species become dominant in high sand content than clay.

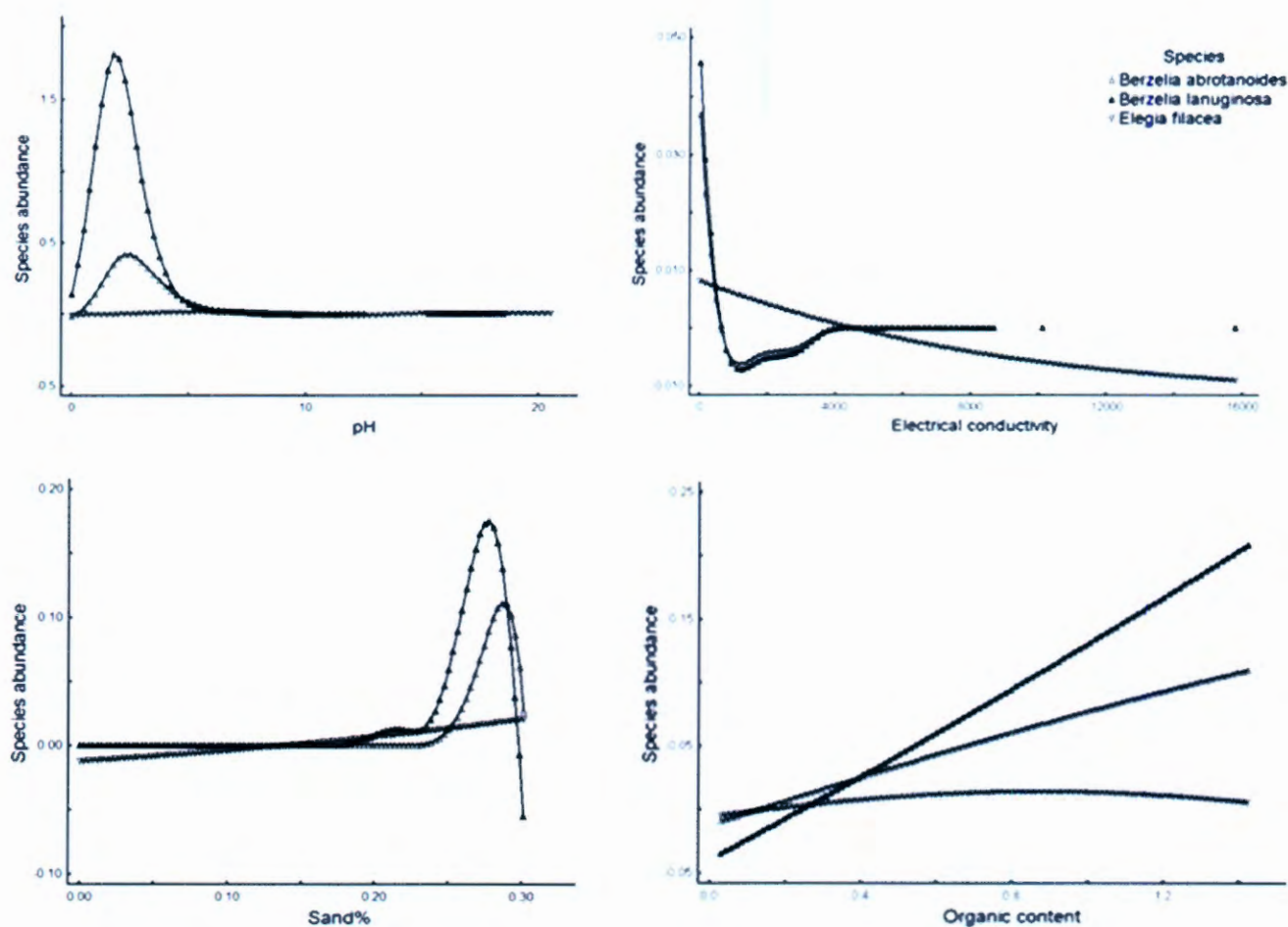


Figure 3.9 Species response curves of three species endemic to the Cape Floristic Region in Sclerophyllous Wetland Vegetation.

The response curves indicated in Figure 3.9 are of three species endemic to the Cape Floristic region. *Berzelia abrotanoides* and *B. lanuginosa* have a unimodal distribution for lower pH, higher sand percentage, and the two species declines when Electrical Conductivity is high. All the species show a positive incline under situations where there is high organic content, but *B. lanuginosa* is most competitive.

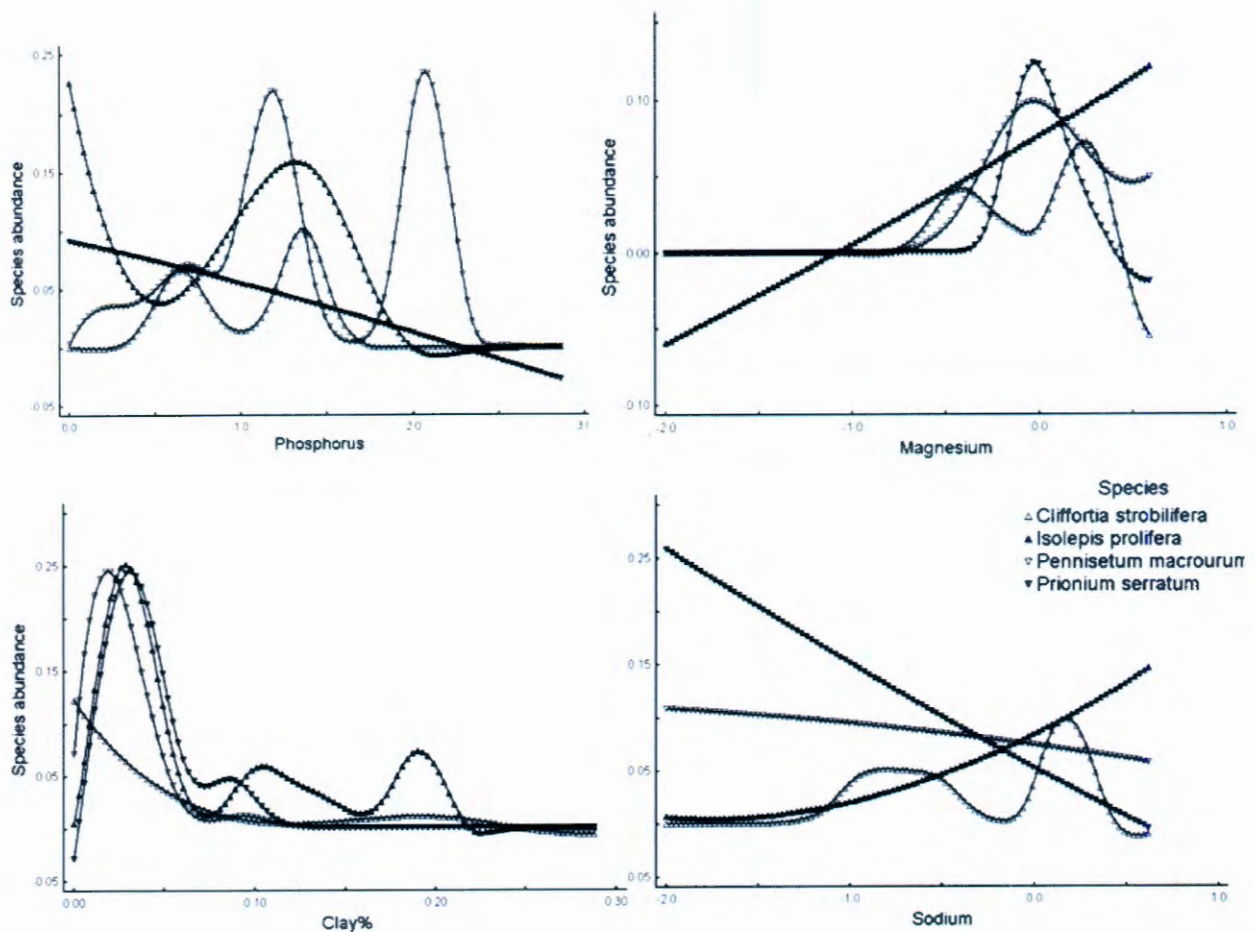


Figure 3.10 Species response curves for four typical freshwater species in Sclerophyllous Wetlands Vegetation.

The species in Figure 3.10 are often found together in freshwater wetlands except for *Isolepis prolifera*. In terms of Phosphorus the response curves are quite complex, but it is clear that *Prionium serratum* decreases with increasing Phosphorus content. All the species prefers soils with less content of Magnesium. *Prionium macrourum* gradually decreases as Sodium content becomes high and *Isolepis prolifera* peaks. *Cliffortia strobilifera* respond negatively to increase of clay percentage, whereas other species increase.

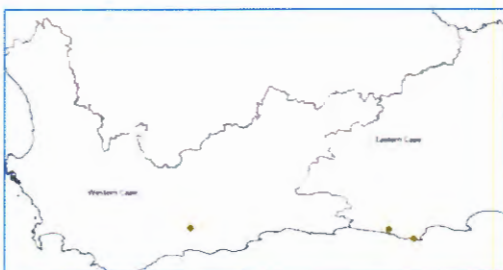
3.5 Description of communities



1. *Helichrysum*

helianthemifolium community

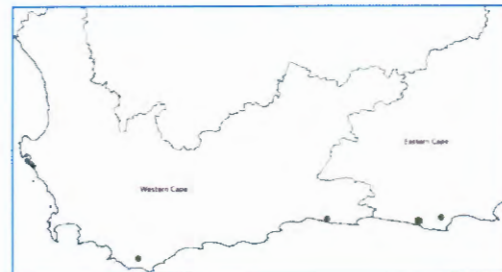
Stands of this community are found only in the Western Cape. This community is found in channelled and unchannelled valley bottoms, depressions, slope seepages and floodplain wetlands. The soils are sandy, peaty and loamy, mostly of the Champagne soil form. They are seasonally wet, high in magnesium and organic matter content. The average number of species is two per plot. *Helichrysum helianthemifolium* is the dominant species.



2. *Carpacoe* spermacoe.-

Arctotis discolor community

This community is found in valley bottom wetlands and slope seepages on loamy and peaty soils that are permanently flooded. The soils are relatively high in sodium concentration. The average number of species per plot is three. *Helichrysum helianthemifolium* and *Carpacoe spermacoea* are the dominant species.



3. *Laurembergia* *repens* community

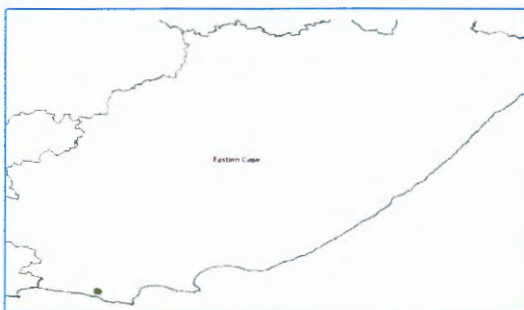
This community is associated with valley bottom and depression wetlands and is found in pioneer conditions on unconsolidated substrates. Soils are loamy, peaty or clayey belonging to the Katspruit soil form and they are seasonally to permanently wet. The sodium concentration of the soil is relatively high. The average number of species per sample plot is four. It is

dominated by the low creeping forb *Laurembergia repens* subsp. *brachypoda*.



4. *Calopsis paniculata* community

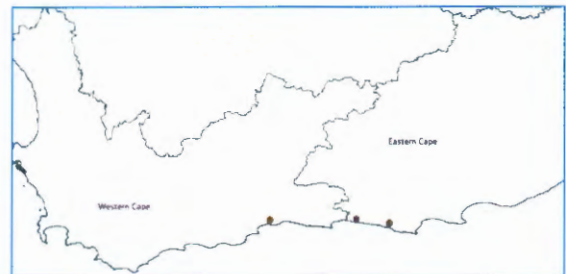
This community is found in a similar environment as *Laurembergia repens* comm. (community 3), but the soils are permanently wet. The average number of species per sample plot is three. *Calopsis paniculata* and *Cliffortia strobilifera* are the dominant species.



5. *Andropogon appendiculatus* community

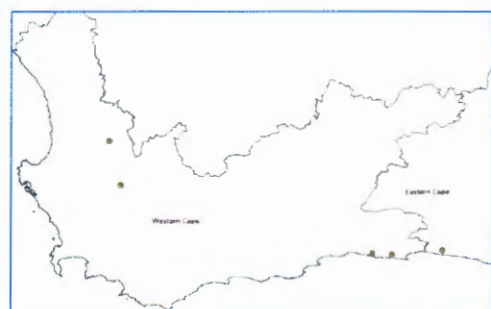
This community is restricted to the Eastern Cape around Port Elizabeth, occurring in valley bottom wetlands.

with loam soils that are semi-permanently wet. The average species richness per sample plot is six. *Andropogon appendiculatus* and *Carpha capitella* are the most abundant species.



6. *Cliffortia odorata* community

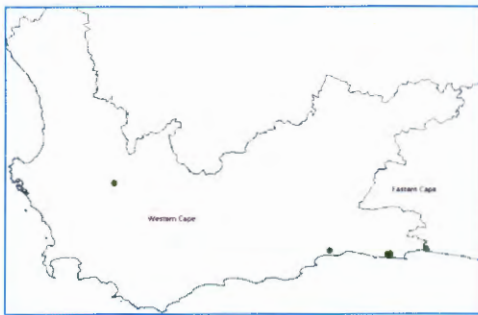
This community is found in valley bottom and depression wetlands with semi-permanently or permanently wet soils. The soils are peaty, loamy, or sandy. On average, four occur per sample plot and the dominant species is *Cliffortia odorata*.



7. *Isolepis costata* community

This community is found in similar habitats as community 7 (*Cliffortia*

odorata comm.) but in early successional conditions. The soils with which this community is associated are mostly are rich in organic matter. The average number of species per sample plot is 3 *Isolepis costata* and *Carpha glomerata* are the most abundant species.



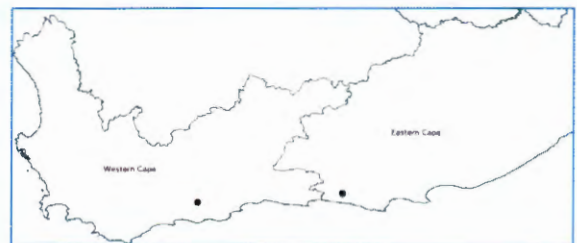
8. *Carpha glomerata* community

This community commonly occurs in the Southern Cape region but it is also found at the high altitudes of the Western Cape Province. The stands of this community are found in valley bottom wetlands that are semi-permanently to permanently wet clay soils of the Katspruit soil form. The average number of species per sample plot is one. *Carpha glomerata* is the dominant species.



9. *Cliffortia graminea* community

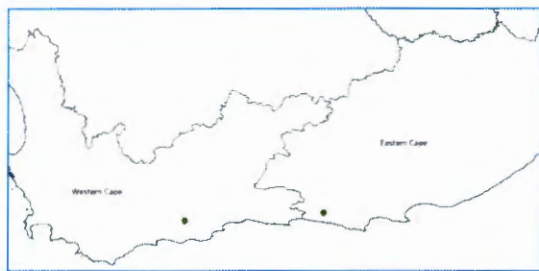
This community is commonly found in the Tsitsikamma region of the Southern Cape in valley bottom wetlands with soils that are high in organic matter and magnesium concentration. The soils are peaty or loamy, and permanently wet. This community is rich in species and dominated by various shrubs, restios, and sedges. The average number of species per sample plot is 3. *Cliffortia graminea* is the abundant species.



10. *Wachendorfia thyrsiflora* community

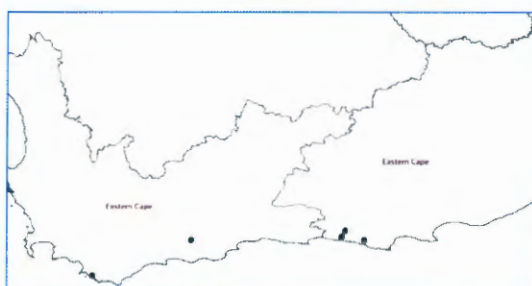
This community occurs in valley bottom wetlands. Peat, sand and loam soils that are permanently wet are associated with this community. They are high in magnesium and organic

matter content. On average, 4.8 are found per sample plot. *Wachendorfia thyrsiflora* is the most abundant species.



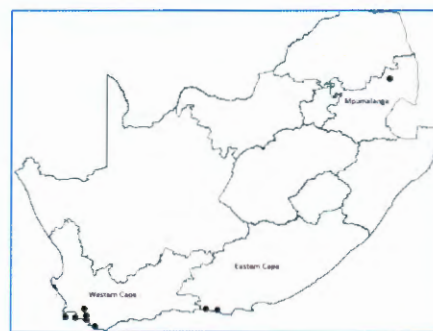
11. *Centella asiatica* community

This community occurs in valley bottom wetlands that are seasonally wet with loam soils. It is appearing as an outlier because it is undersampled (with only two plots in the cluster). There are on average eight species per plot. *Helichrysum helianthemifolium*, *Carpha glomerata*, and *Cliffortia graminea* are the most abundant species.



12. *Othonna parviflora* community

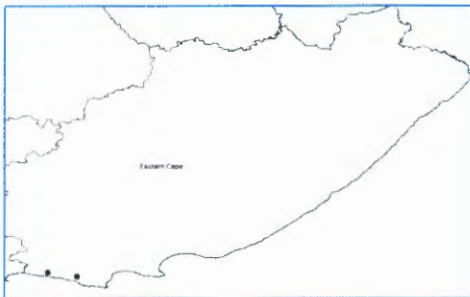
This community is found in channelled and unchannelled valley bottom wetlands which are seasonally to permanently wet. Peat soils or loam soils that are high in organic matter and magnesium are associated with this community. The average species number per sample plot is four. It is dominated by a mix of species found in the previous communities including *Calopsis paniculata*, *Helichrysum helianthemifolium*, *Carpha glomerata*, and *Wachendorfia thyrsiflora*.



13. *Pteridium aquilinum* community

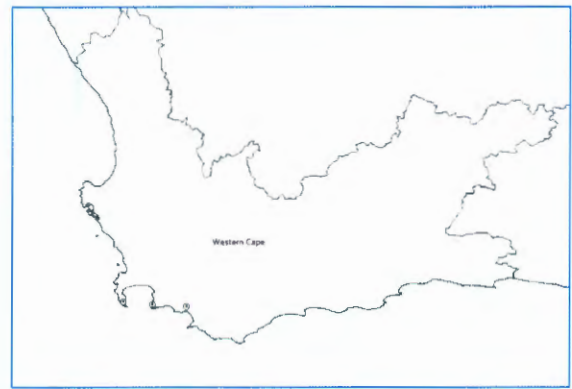
This community is distributed in low altitude areas in valley bottom wetlands and slope seepages. Soils associated with this community are seasonally to permanently wet, peaty, loamy, sandy or clayey with a high electrical conductivity, and a high nitrogen contents. On average threespecies occur per sample plot. *Pteridium aquilinum* is the most

dominant species. This species is found globally and has proven to be very resilient. It is commonly found in a wide variety of climates and soil types, and is most abundant in disturbed areas.



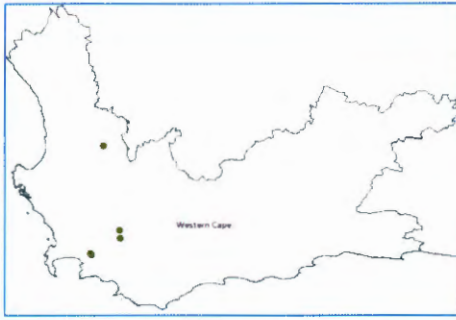
14. *Berzelia intermedia* community

This community appears as an outlier because it is under-sampled with only two plots. It is found in valley bottom wetlands with loam soils. These soils have a high electrical conductivity and pH as well as a high potassium concentration. On average, four species are found per sample plot. *Berzelia intermedia* and *Pteridium aquilinum* are the most abundant species.



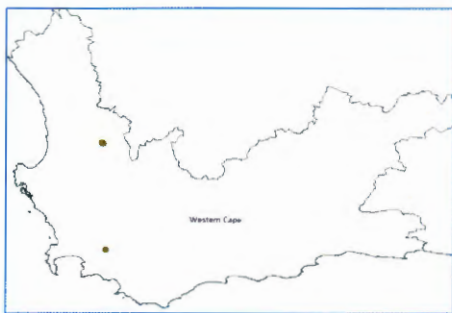
15. *Osmitopsis asteriscoides* community

This community is found in slope seepages and channelled valley bottom wetlands that are semi-permanently to permanently wet. The soils belong to the Champagne and Willowbrook soil forms, which are both rich in organic matter. The soils are also relatively high in nitrogen contents. There are on average four species found per sample plot. *Pteridium aquilinum*, *Restio purpurascens*, and *Osmitopsis asteriscoides* are the dominant species.



16. *Senecio umbellatus* community

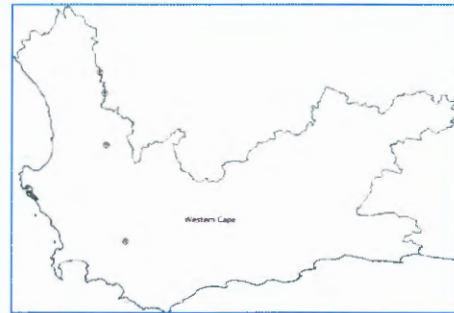
This community is found at high altitudes in slope seepages and channelled valley bottom wetlands. The soils are semi-permanently wet, and peaty, belonging to the Champagne soil form. Several species of shrubs and restios dominate this community. On average, there are three species per sample plot. The most abundant species are *Senecio umbellatus* and *Elegia thyrsifera*.



17. *Elegia neesii* community

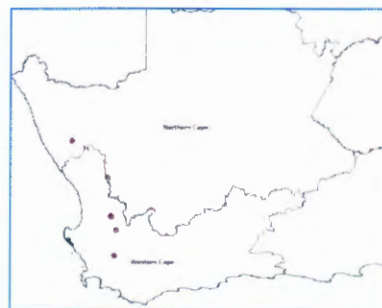
This community occurs together with community 16 (*Senecio umbellatus* comm.) at high altitudes in valley bottom wetlands and slope seepages. It is associated with sandy soils that

are very wet. An average four species occur per sample plot. The dominant species are *Elegia neesii*, *Erica maderi* and *Restio bifidus*.



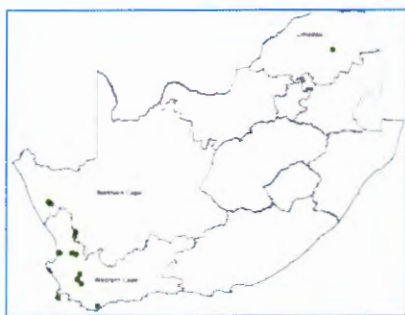
18. *Stoebe plumosa* community

This community is found in slope seepage and valley bottom wetlands on loamy or sandy soils high in organic matter contents. These soils are temporarily to permanently wet. This community becomes prominent when the wetness increases. On average, there are three species per sample plot. *Stoebe plumosa* is the dominant species.



19. *Merxmuellera stricta* community

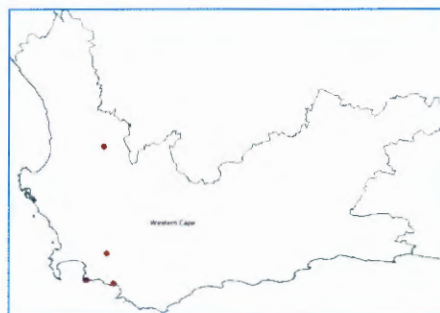
This community is found in slope seepage and channelled valley bottom wetlands that are seasonally wet with loamy or sandy soils. The soils are high in sodium contents. The average number of species per sample plot is 2.4. *Merxmuellera stricta* is the dominant species.



20. *Mariscus thunbergii* community

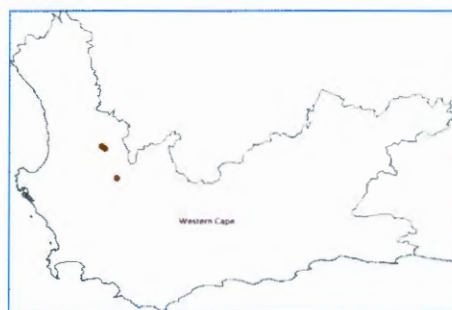
This is one of the most common communities in the Western Cape, and it also occurs in the Northern Cape and Limpopo. It is associated with various wetland types including floodplains, slope seepages, channelled and unchannelled valley bottom wetlands. The soils are temporarily or permanently wet, rich in phosphorus and iron, mostly loamy but sometimes also with sand or clay. On average, there are only two species per sample plot in this community so this represents one of the species-poor

communities. *Mariscus thunbergii* is the dominant species.



21. *Epischoenus gracilis* community

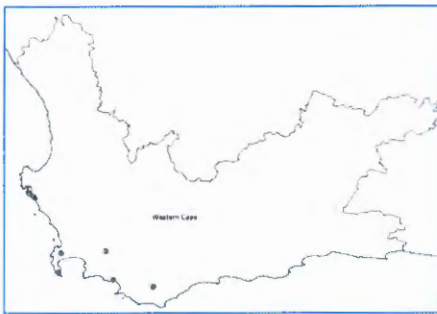
This community is found in slope seepages and valley bottom wetlands. Loamy and sandy soils that are temporarily or seasonally wet that are high in nitrogen are associated with this community. The average number of species found per sample plot is four and the most abundant species is *Epischoenus gracilis*.



22. *Elegia capensis* community

This community is restricted to the northern parts of the Western Cape (Cedarberg region). It is found in

seasonally wet slope seepages and channelled valley bottom wetlands with soils rich in organic matter, magnesium and sodium. It is associated with sand and loam soils. On average, three species occur per sample plot. *Elegia capensis* is the most abundant species.



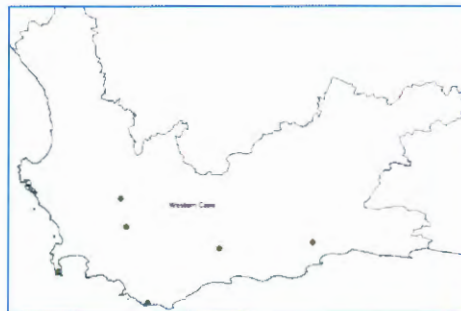
23. *Berzelia abrotanoides* community

This community is found in seasonally or semi-permanently wet valley-head seepages, slope seepages and depression wetlands. Sandy and loamy soils are associated with this plant community. There are on average three species found per sample plot. The most abundant species are *Berzelia lanuginosa*, *Berzelia abrotanoides*, *Tetralix cuspidata* and *Restio bifidus*.



24. *Berzelia lanuginosa* community

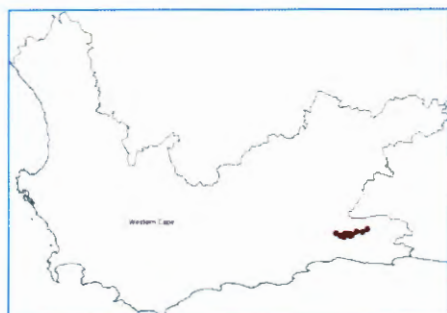
This is a community that is associated with semi-permanently wet flats and slope seepage wetlands. The soils are sandy and loamy belonging to the Fernwood and Willowbrook soil form. On average, three species are found per sample plot. *Berzelia lanuginosa* is the most abundant species.



25. *Elegia filacea* community

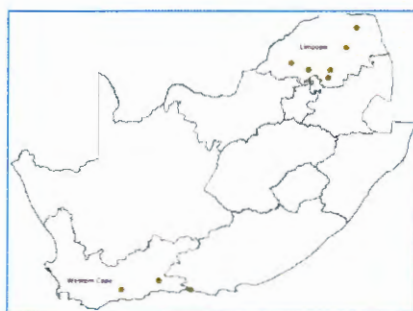
This community is associated with channelled or unchannelled valley bottom wetlands, and slope seepages that are temporarily or seasonally wet. The soils are sandy or loamy, and relatively rich in sodium. On average, there are three species found per sample plot. It is dominated by restios

(*Elegia filacea* and *Elegia mucronata*) and sedge (*Tetraria cuspidata*).



26. *Psoralea verrucosa* community

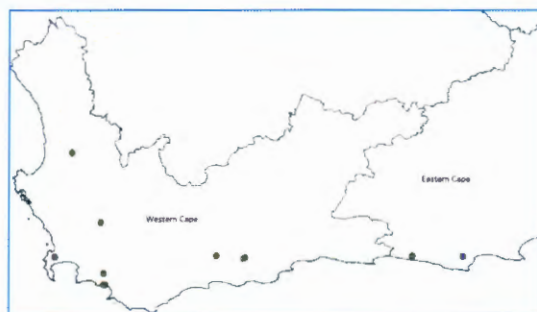
This community is found only in springs of the Kamanassie Mountains (Cleaver *et al.*, 2004). The soils are sandy, loamy or clayey in temporarily to permanently wet conditions. There is an average of one species found per sample plot. *Psoralea verrucosa*, *Helichrysum cymosum*, *Watsonia fourcadei* are the dominant species.



27. *Juncus lomatophyllus* community

This community is found in seasonally or permanently wet springs,

channelled and unchannelled valley bottom wetlands and seepage wetlands mostly under pioneer conditions in unconsolidated soils. It is found in clayey, loamy, and sandy areas where the water table is high. The most abundant species is *Juncus lomatophyllus* occurring with a mix of other species. This community is common in wetlands of the Southern Cape. It also occurs in Limpopo as a pioneer community on unconsolidated soils derived from sandstones and quartzites. There are on average two species found per sample plot.



28. *Isolepis prolifer* community

This community is found in valley bottom and depression wetlands that are permanently wet. Peaty and loamy soils are associated with these wetlands. The soils have a high pH and are rich in iron and sodium. There are on average two species per sample plot. The diagnostic species are *Juncus capensis*, *Isolepis prolifer*,

Laurembergia repens subsp. *brachypoda* and *Senecio rigidus*.



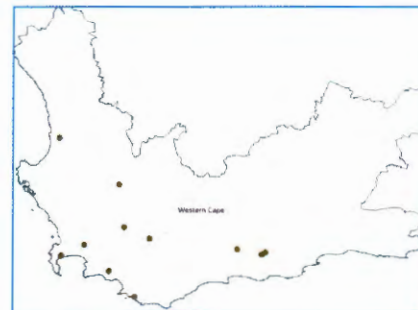
29. *Isolepis fluitans* community

This community is distributed in Limpopo, Mpumalanga, the Eastern Cape and the Western Cape in channelled and unchannelled valley bottom wetlands, lake shores and slope seepages. The soils are loamy, silty, peaty or sandy. On average, five species are found per sample plot. The diagnostic species are *Laurembergia repens* subsp. *brachypoda*, *Isolepis fluitans*, *Juncus lomatophyllus*, *Isolepis prolifer* and *Pycnus nitidus*.



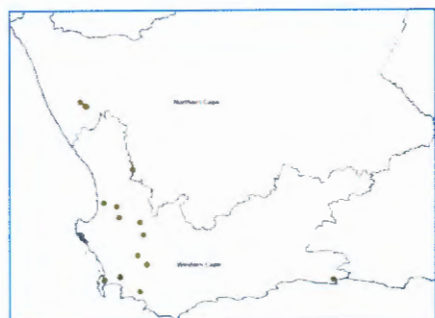
30. *Prionium serratum* community

Prionium serratum (Palmiet) occurs from the Western Cape to the northeast of the Eastern Cape. It is found on river banks found in clay and sandy loam soils, but mostly on, peat of the Champagne soil form. The soils are seasonally to permanently wet, alkaline, and high in iron. There is an average of five species found per sample plot. *Prionium serratum*, *Psoralea verrucosa*, *Cliffortia strobilifera*, *Calopsis paniculata*, and *Pteridium aquilinum* are the most abundant species.



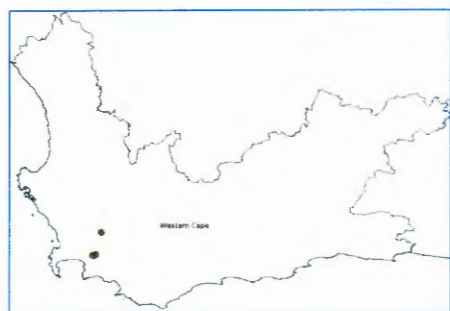
31. *Cliffortia strobilifera* community

This community is found in valley bottom wetlands in soils that are high in sodium contents. It is associated with sandy, loamy, and clayey soils that are seasonally to permanently wet. An average of one species found is found per sample plot. *Cliffortia strobilifera* is the dominant species.



32. *Pennisetum macrourum* community

This community is found in the Western Cape and Northern Cape region. It is associated with valley bottom wetlands, depression wetlands and slope seepages that are seasonally to permanently wet. The soils associated with this community are loamy, sandy or clayey, with a high pH and nitrogen contents. On average, 3.0 species are found per sample plot. *Pennisetum macrourum*, *Mariscus thunbergii*, and *Juncus lomatophyllus* are the most abundant species.



33. *Anthochortus crinalis* community

This community is associated with valley-head seepage wetlands. It has

peaty soils that are seasonally to permanently wet. The community has an average of two species per sample plot. The most abundant species are *Anthochortus crinalis*, *Senecio umbellatus*, *Merxmuellera stricta*, *Epischoenus villosus*, *Ehrharta setacea* subsp. *setacea*, *Senecio crispus*, *Elegia intermedia*, *Stoebe plumosa* and *Cliffortia tricuspidata*.



34. *Restio subtilis* community

This community commonly occurs on riverbanks that are seasonally inundated and where soils are sandy. The community is restricted to the Western Cape Mountains and is one of the communities that have the highest number of species per plot. The average species per sample plot is two. The community is dominated by grasses (*Merxmuellera stricta*), sedges (*Epischoenus villosus*, *Tetraria cuspidata*), shrubs (*Grubbia rosmarinifolia*) and restios (*Anthochortus crinalis*,

Chondropetalum mucronatum, *Restio versatilis*, *R. subtilis*, *R. corneolus* and *R. purpurascens*.

3.6 Discussion

Sclerophyllous Wetlands Vegetation are actually the clearly defined vegetation types as they grow exclusively on sandstone and other extremely nutrient-poor substrates. Wetlands in this cluster are unique and are of high conservation value in SA. The plant communities of SWV have low species richness as compared to the upland vegetation as they are found in nutrient-poor soils and where communities are dominated by 1 or 2 species. Some of these communities extend outside of the Western Cape towards the Subtropical Wetland Vegetation, where a certain subsection is also specialized in very nutrient-poor substrates and these communities can be mixed with species from Main Cluster 1. They consist of a range of species of restios, grasses, sedges and shrubs. The SWV shows a great functional diversity, with some plant communities dominated by graminoids like wetlands elsewhere in the country while other plant communities only comprise of woody and sclerophyllous species that are typical of Renosterveld and/or Fynbos, and some communities have a variable mix of herbaceous plants such as daisy (Asteraceae), pea (Fabaceae), gardenia (Rubiaceae) and grass (Poaceae) families. Even though some of the wetlands elsewhere in the country are threatened by alien plants invasion, not much of alien invasion is observed in these communities. However, these wetlands are vulnerable to invasion due the large number of endemic species present.

Very few of the identified communities are floristically associated with the plant assemblages described in historical studies. *Anthochortus crinalis* Community is similar to *Anthochortus crinalis-Elegia intermedia* Tall Closed Restioid community that was described in the previous study by Sieben *et al.* (2004), both these communities are species poor and this is also confirmed in this study. *Stoebe plumosa* Community is one of the under sampled communities and is similar to *Sporobolus africanus*–*Stoebe plumosa* community (Meek *et al.*, 2013) that is represented only by two relevés. Table 3.7 displays plant communities that are similar for historical and current findings with associated diagnostic species.

The vegetation is adapted to nutrient-poor soils, in particular phosphorus and nitrogen are very low and either of them may act as the limiting factor in the structure and function of the vegetation (Witkowski and Mitchell, 1987). Soils are poorly drained and the permanently inundated wetlands are poor in species number. Only four communities have a relatively high number of species rich viz. Community 10, *Wachendorfia thyrsiflora* comm., Community 15,

Osmitopsis asteriscoides comm., Community 34, *Restio subtilis* comm., and Community 33, *Anthochortus crinalis* comm.

The bracken fern (*Pteridium aquilinum*) community responded positively to a high concentration of phosphorus in soil. This is problematic for indigenous plants because this fern is considered to be the serious weedy plant in areas where intensive agriculture is not economically viable. It makes large colonies in a variety of habitats ranging from dry to wet areas and is very aggressive as it produces compounds that inhibit growth of other plant species (Yatskievych, 2014).

The findings have shown that the *Berzelia intermedia* is associated with moisture availability; *Cliffortia ferruginea*, *Epischoenus gracilis* with nitrogen and high altitudes; *Psoralea verrucosa* with sandy soils that are temporary wet, and *Wachendorfia thyrsiflora* with seasonal, valley head, champagne, organic content. This is evident in previous studies (Mergii and Privett, 2008; Schafer 2002; Werger et al., 1972). Whereas *Laurembergia repens*, *Carpha glomerata* and *Calopsis paniculata* are species that designate permanently wet soils (DWAF, 2005; Goldblatt and Manning, 2000; Kotze et al., 1994).

Table 3.7 Plant communities that are similar for historical and current findings

Publications	Identical community type from historical studies	Findings of current study	Diagnostic species for historical and current
Meek et al., 2013	<i>Sporobolus africanus</i> – <i>Stoebe plumosa</i> Community	<i>Stoebe plumosa</i> Community	<i>Juncus lomatophyllus</i> <i>Cliffortia strobilifera</i> <i>Stoebe plumosa</i>
Ramjukadh, 2014	<i>Calopsis paniculata</i> – <i>Carpha glomerata</i> – <i>Cliffortia strobilifera</i> Community <i>Prionum serratum</i> Community	<i>Carpha glomerata</i> community <i>Prionum serratum</i> Community	<i>Carpha glomerata</i> , <i>Cliffortia strobilifera</i> , <i>Wachendorfia thyrsiflora</i> <i>Prionum serratum</i>
Clever et al., 2005	<i>Berzelia intermedia</i> – <i>Psoralea verrucosa</i> shrubland		<i>Watsonia fourcadei</i> <i>Psoralea verrucosa</i> <i>Helichrysum cymosum</i> <i>Juncus lomatophyllus</i> <i>Stoebe plumosa</i> <i>Erica curviflora</i> <i>Platycaulos callistachyus</i> <i>Berzelia intermedia</i> <i>Clusia alaternoides</i>
Sieben et al., 2004	<i>Anthochortus crinalis</i> – <i>Elegia intermedia</i> Tall Closed Restioid	<i>Anthochortus crinalis</i> Community	<i>Anthochortus crinalis</i> <i>Epischoenus villosus</i> <i>Senecio crispus</i> <i>Elegia intermedia</i>
	<i>Tetraria capillacea</i> – <i>Restia subtilis</i> Short to Tall Restioid	<i>Restia subtilis</i>	<i>Restia subtilis</i> <i>Chondropetalum mucranatum</i> <i>Tetraria cuspidata</i> <i>Grubbia rasmanifolia</i>

CHAPTER 4

Main Cluster 6: Temperate Grassy Wetlands: Patterns and ecological drivers

4.1. Temperate Grassy Wetlands

The grassland biome of southern Africa covers the high elevated plateau of the interior of South Africa (Highveld), the mountainous areas of Lesotho, and the high-lying ground of the eastern seaboard (sub-escarpment areas of KwaZulu-Natal, Eastern Cape, and Mpumalanga). There are also azonal patches of grassland biome communities that occur outside the biome boundaries. This biome has two main subdivisions, subtropical grasslands, called (1) savannah, and (2) temperate grasslands. The landscape is mostly flat or undulating with hills and valleys to rocky mountain escarpments (Mucina and Rutherford, 2006). Grasslands occur where there is summer to strong summer rainfall and winter drought (Mucina and Rutherford, 2006). The rainfalls vary from 400 to 2 500 mm per year and this corresponds to the amount of rainfall found in other parts of the world where similar vegetation types are found (O'Connor and Bredenkamp, 1997). The winter season is generally cold and dry, with frequent frosts and snowfalls in the high lying areas (Mucina and Rutherford, 2006).

Wetlands occur abundantly in temperate grasslands, and are also found in savannah, Indian Ocean Coastal Belt where they form a conspicuous part of the landscape. The grassy wetlands are distributed throughout the country and have been studied most extensively in the KwaZulu-Natal, Free State and Mpumalanga provinces. These temperate grassy wetlands are found on sediments overlying fine-grained sedimentary rocks as well as on dolomites (Mucina and Rutherford, 2006). The vegetation is dominated by perennial grass and sedge species with occasional forbs and bulbous plants, which may become dominant in exceptional cases (Carbutt *et al.*, 2011). The vegetation cover is influenced by the intensity and type of grazing, fire as well as by the minimum temperature (Cowling, 1997). They include channelled and unchannelled valley bottom wetlands, depressions (pans), floodplains, slope seepages, riverbanks (edges of calmly flowing rivers) and springs.

The soils are variable and include loam, sand, silt, clay and peat, of most commonly the Champagne, Katspruit, Dundee, and Rensburg soil forms. The soils are dark and rich in

nutrients. Figure 4.1 shows the distribution map of Temperate Grassy Wetlands Vegetation found in South Africa. The data of TGW (Main Cluster 6) comprises 1617 plots and 702 species. Forty eight percent of the species (species with fewer than three occurrences) were left out during the analysis, and only 52% were used.

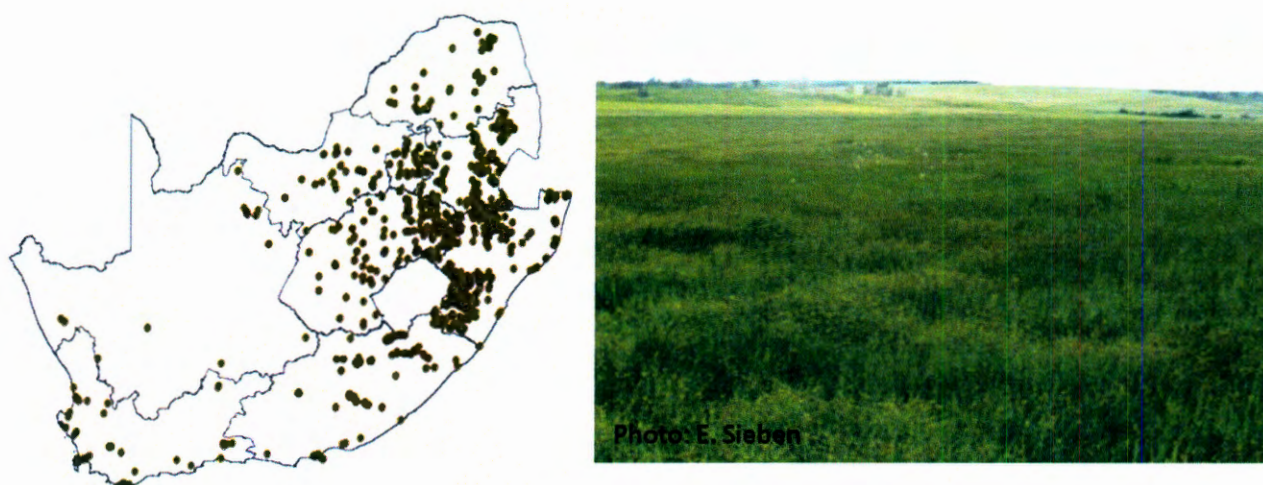


Figure 4.1 Map showing areas where Temperate Grassy Wetlands are found, and a picture illustrating one of these wetlands in KwaZulu-Natal.

4.2 Classification and Indicator species analysis

The classification analysis produced thirty four plant communities. A diagrammatic presentation of the hierarchical classification is given in Figure 4.2. In the figure Communities 27-34 have chaining spanning and this is an indication that they not fit with other clusters featured in the dendrogram due to their outlying character. The maximum indicator values that were calculated for each species were used to determine the indicator species for each of the clusters. Of all the species that were used in the analysis, there were only 48% that had significant indicator values ($p < 0.05$) in the permutation test for all plant communities.

Table 4.1 represents the indicator species with maximum indicator values of 20 or more ($IV \geq 20$) with a significant indicator value of $p < 0.05$. The communities identified after the classification of the TGW data occur in mountainous areas, hill-slopes, flat areas and along

the rivers of the grassland biome in South Africa. The most ubiquitous species (appearing in 5 clusters or more) are listed in Table 4.2.

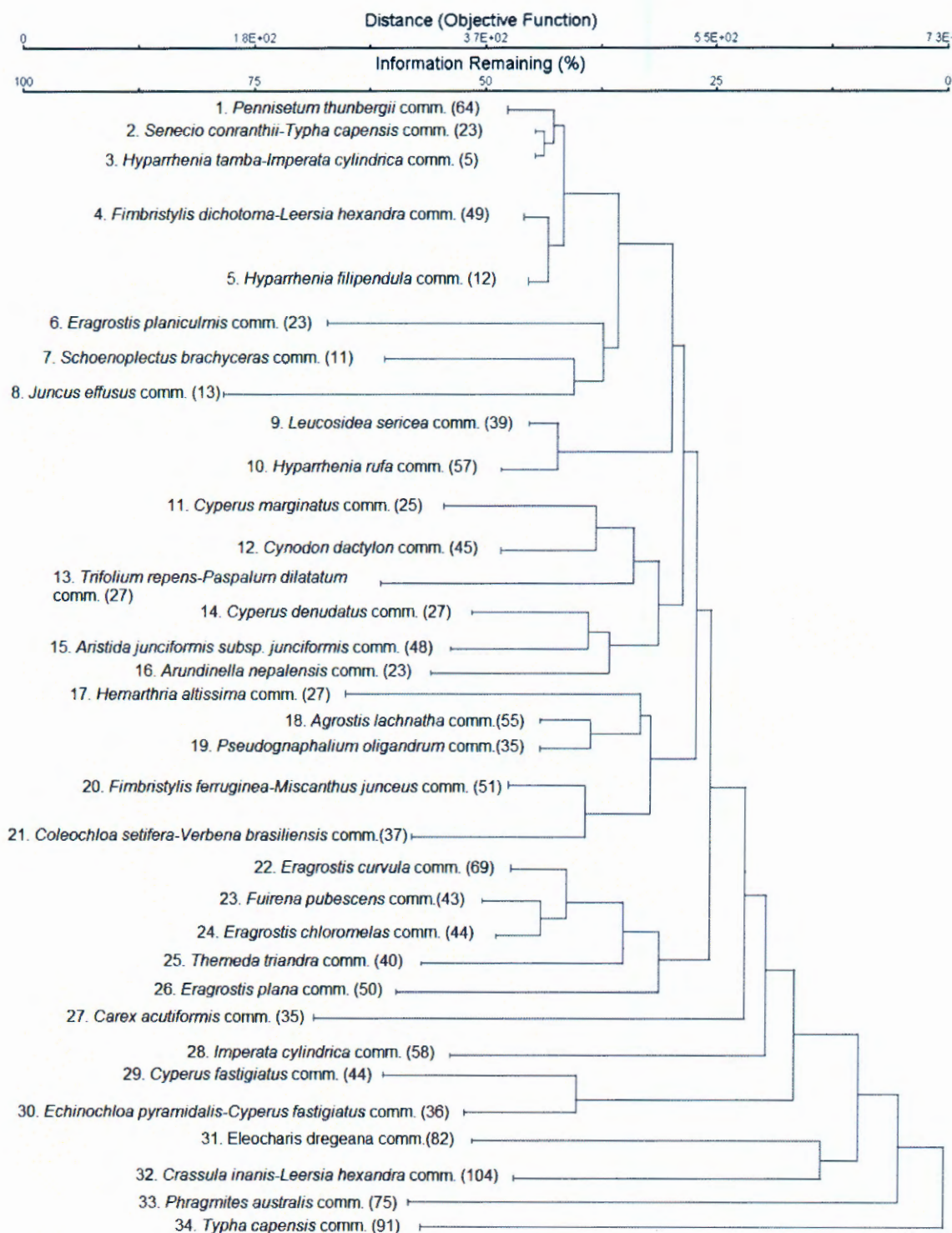


Figure 4.2 A cluster dendrogram of wetland vegetation types of Temperate Grassy Wetlands. The dendrogram is scaled by Wishart's (1969) objective function, expressed as the percentage of information remaining at each level of grouping (McCune & Grace, 2002).

Table 4.1 Plant communities and associated indicator species for Temperate Grassy Wetland Vegetation (Main Cluster 6).

Cluster	No. of plots	Dominants	Indicator species	Indicator value (IV)	p-value
1	64	<i>Pennisetum thunbergii</i>	<i>Pennisetum thunbergii</i>	20	0.0192
2	23	<i>Senecio conrathii</i>	<i>Senecio conrathii</i>	23.2	0.0002
		<i>Cyperus textilis</i>		20.3	0.0002
		<i>Salix babylonica</i>		20	0.0006
3	5	<i>Hyparrhenia tamba</i>	<i>Hyparrhenia tamba</i>	44.1	0.0002
		<i>Verbena bonariensis</i>		25.7	0.0002
		<i>Oenothera rosea</i>		21.6	0.0002
4	49	<i>Commelina diffusa</i> subsp. <i>Scandens</i>	<i>Commelina diffusa</i> subsp. <i>Scandens</i>	11.6	0.002
5	12	<i>Hyparrhenia filipendula</i>	<i>Hyparrhenia filipendula</i>	78.9	0.0002
		<i>Cymbopogon validus</i>		70.2	0.0002
		<i>Chironia purpurascens</i> subsp. <i>purpurascens</i>		66.7	0.0002
		<i>Rhus leptodictyla</i>		66.7	0.0002
		<i>Schoenus nigricans</i>		58.3	0.0002
		<i>Aristida bipartite</i>		53	0.0002
		<i>Senecio microglossus</i>		48.1	0.0002
		<i>Artemisia afra</i>		46.9	0.0002
		<i>Andropogon eucomis</i>		42.3	0.0002
		<i>Lippia rehmannii</i>		41.7	0.0002
		<i>Gomphostigma virgatum</i>		38.5	0.0002
		<i>Hypoxis argentea</i>		36.2	0.0002
		<i>Lippia javanica</i>		32.6	0.0002
		<i>Schoenoplectus corymbosus</i>		32.4	0.0002
		<i>Helichrysum cooperi</i>		29.7	0.0004
		<i>Eucomis autumnalis</i> subsp. <i>autumnalis</i>		28	0.0002
		<i>Scabiosa columbaria</i>		26.8	0.0008
		<i>Alepidea amatymbica</i>		25	0.0002
		<i>Bulbostylis hispidula</i>		25	0.0002
		<i>Mariscus rehmannianus</i>		25	0.0002
		<i>Dittrichia graveolens</i>		25	0.0002
		<i>Leonotis leonurus</i>		25	0.0002
		<i>Nuxia gracilis</i>		25	0.0002

Table 4.1 (Continued)

		<i>Kyllinga alba</i>		22.9	0.0002
		<i>Senecio gerrardii</i>		22.8	0.0002
		<i>Cliffortia nitidula</i> subsp. <i>nitidula</i>		22.3	0.0006
		<i>Cyperus sphaerospermus</i>		21.7	0.0014
6		<i>Eragrostis planiculmis</i>		51.3	0.0002
7		<i>Schoenoplectus brachyceras</i>		84.3	0.0002
8	13	<i>Juncus effusus</i>	<i>Juncus effusus</i>	61	0.0002
9	39	<i>Leucosidea sericea</i>	<i>Leucosidea sericea</i>	66.6	0.0002
10	57	<i>Hyparrhenia rufa</i>	<i>Hyparrhenia rufa</i>	32.1	0.0002
		<i>Acacia mearnsii</i>		20.9	0.0008
		<i>Polygonum hystriculum</i>		20.6	0.0004
11	25	<i>Cyperus marginatus</i>	<i>Cyperus marginatus</i>	59.4	0.0002
12	45	<i>Cynodon dactylon</i>	<i>Cynodon dactylon</i>	24.2	0.0002
13	27	<i>Trifolium repens</i>	<i>Trifolium repens</i>	38.1	0.0002
12	45	<i>Paspalum dilatatum</i>	<i>Cynodon dactylon</i>	26.9	0.0002
13	27	<i>Cyperus esculentus</i>	<i>Trifolium repens</i>	17.5	0.0002
14	27	<i>Cyperus denudatus</i>	<i>Cyperus denudatus</i>	43.9	0.0002
15	48	<i>Aristida junciformis</i> subsp. <i>junciformis</i>	<i>Aristida junciformis</i> subsp. <i>junciformis</i>	36.1	0.0002
14	27	<i>Pycnus unioides</i>	<i>Cyperus denudatus</i>	35.9	0.0002
15	48	<i>Ledebouria cooperi</i>	<i>Aristida junciformis</i> subsp. <i>junciformis</i>	34.6	0.0002
16	23	<i>Carex cognate</i>		31.5	0.0002
17	27	<i>Polygonum plebeium</i>	<i>Arundinella nepalensis</i>	29.8	0.0002
		<i>Isolepis fluitans</i>	<i>Hemarthria altissima</i>	24.7	0.0002
		<i>Rhynchospora brownii</i>		24.2	0.0002
		<i>Arundinella nepalensis</i>		43.2	0.0002
		<i>Hemarthria altissima</i>		41.9	0.0002
18	55	<i>Galium capense</i> subsp. <i>capense</i>	<i>Galium capense</i> subsp. <i>capense</i>	36.2	0.0002
17	27	<i>Aster squamatus</i>	<i>Hemarthria altissima</i>	28.1	0.0002
18	55	<i>Mentha longifolia</i> subsp. <i>capensis</i>	<i>Galium capense</i> subsp. <i>capense</i>	23.6	0.0004
19	35	<i>Cineraria lyratiformis</i>		22.9	0.0002
20	51	<i>Salix babylonica</i>	<i>Pseudognaphalium oligandrum</i>	22.4	0.0006
		<i>Ciclospermum leptophyllum</i>		21.1	0.0006
		<i>Pseudognaphalium oligandrum</i>	<i>Fimbristylis ferruginea</i>	37.9	0.0002
		<i>Fimbristylis ferruginea</i>		33.1	0.0002
19	35	<i>Miscanthus junceus</i>	<i>Pseudognaphalium oligandrum</i>	20	0.0004
21	37	<i>Coleochloa setifera</i>	<i>Coleochloa setifera</i>	41.3	0.0002

Table 4.1 (Continued)

		<i>Phymaspermum athanasioides</i>		33.5	0.0002
21	37	<i>Wahlenbergia undulata</i>	<i>Coleochloa setifera</i>	32.6	0.0002
22	69	<i>Oenothera tetraptera</i>	<i>Eragrostis curvula</i>	27.2	0.0002
		<i>Verbena brasiliensis</i>		26.2	0.0002
		<i>Senecio affinis</i>		20.4	0.0008
		<i>Eragrostis curvula</i>		13.4	0.0016
		<i>Eragrostis racemosa</i>		12.7	0.0034
23	43	<i>Fuirena pubescens</i>	<i>Fuirena pubescens</i>	22.5	0.0002
24	44	<i>Eragrostis chloromelas</i>	<i>Eragrostis chloromelas</i>	12.5	0.002
		<i>Setaria sphacelata</i>	<i>Setaria sphacelata</i>	11.3	0.0022
25	40	<i>Themeda triandra</i>	<i>Themeda triandra</i>	52.2	0.0002
26	50	<i>Eragrostis plana</i>	<i>Eragrostis plana</i>	27.2	0.0002
27	35	<i>Carex acutiformis</i>	<i>Carex acutiformis</i>	75.3	0.0002
28	58	<i>Imperata cylindrica</i>	<i>Imperata cylindrica</i>	41.3	0.0002
29	44	<i>Cyperus fastigiatus</i>	<i>Cyperus fastigiatus</i>	46.4	0.0002
30	36	<i>Echinochloa pyramidalis</i>	<i>Echinochloa pyramidalis</i>	59.4	0.0002
29	44	<i>Gamochaeta pennsylvanica</i>	<i>Cyperus fastigiatus</i>	44.2	0.0002
30	36	<i>Alternanthera sessilis</i>	<i>Echinochloa pyramidalis</i>	41.9	0.0002
31	82	<i>Persicaria senegalensis</i>	<i>Eleocharis dregeana</i>	35.4	0.0002
		<i>Persicaria attenuata subsp. africana</i>		29.7	0.0002
		<i>Grangea maderaspatana</i>		27.8	0.0004
		<i>Heliotropium indicum</i>		27.8	0.0004
		<i>Glinus lotoides</i>		23.7	0.0002
		<i>Rorippa madagascariensis</i>		22.2	0.0004
		<i>Ludwigia adscendens subsp. diffusa</i>		21.8	0.0002
		<i>Eleocharis dregeana</i>		41.8	0.0002
		<i>Schoenoplectus decipiens</i>		7.8	0.0104
32	104	<i>Crassula inanis</i>	<i>Crassula inanis</i>	3.8	0.0892
33	75	<i>Phragmites australis</i>	<i>Phragmites australis</i>	38.8	0.0002
34	91	<i>Typha capensis</i>	<i>Typha capensis</i>	44.6	0.0002

Table 4.2 The most ubiquitous species in Temperate Grassy Wetland Vegetation, appearing in five communities or more.

Species	No. of communities	Type
<i>Arundinella nepalensis</i>	6	
<i>Aristida junciformis</i> subsp. <i>Junciformis</i>	5	
<i>Cynodon dactylon</i>	6	Alien
<i>Cyperus fastigiatus</i>	5	
<i>Eleocharis dregeana</i>	10	
<i>Eragrostis plana</i>	12	
<i>Eragrostis planiculmis</i>	5	
<i>Fuirena pubescens</i>	5	
<i>Hemarthria altissima</i>	7	
<i>Imperata cylindrica</i>	6	
<i>Juncus effusus</i>	6	
<i>Oenothera tetraptera</i>	7	
<i>Paspalum dilatatum</i>	13	Alien
<i>Phragmites australis</i>	8	
<i>Schoenoplectus corymbosus</i>	5	
<i>Themeda triandra</i>	6	
<i>Typha capensis</i>	6	
<i>Verbena bonariensis</i>	8	alien

4.3. Ordination

The ordination analysis was split twice because some of the vegetation plots had detailed soil data available. One analysis involved all vegetation plots but with limited set of environmental variables, another one involved a subset with a broader range of environmental variables. The resulting dataset was then analysed with the help of Nonmetric Multidimensional Scaling and Canonical Correspondence Analysis.

4.3.1 Patterns of plant community distribution excluding soil data

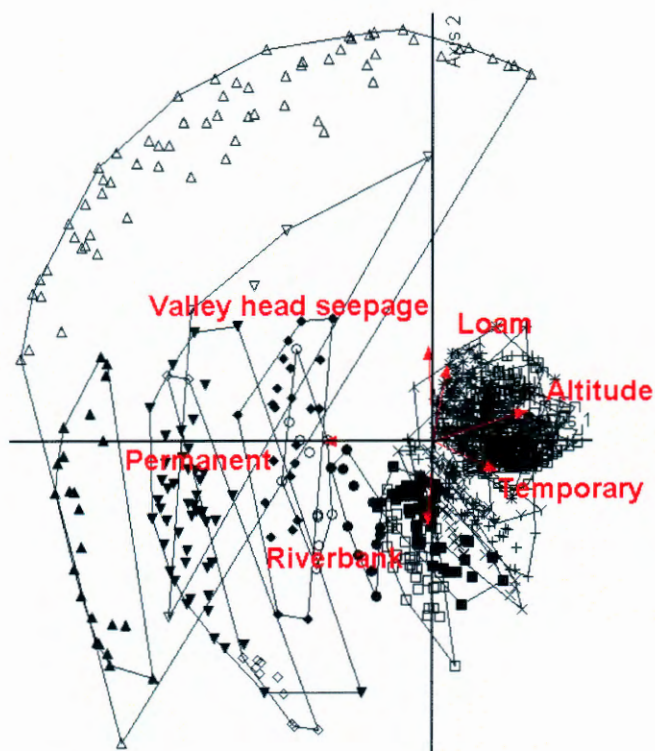
Ordination was used to determine the influential variables involved to the occurrence and distribution of plant communities. All communities are represented here. The dataset was split into two groups following the hierarchical clustering as the PC-Ord program has graphical limitation, for NMS only takes a maximum of 32 groups per analysis: these groups consisted of clusters 1 to 27 (first group) on the one hand and clusters 28 to 34 (second group) on the other. The minimum stress was found with a dimensionality of two axes for both groups. The final low instability for the first half (=communities 1 to 27) ordination

displayed in figure 4.3, reached $p < 0.00001$ at 128 of 250 iterations and 165 of 250 for the second half (=communities 28 to 34) in figure 4.4. The final stress of the model for both the first and the second half was near the upper limit 20 (stress value).

The results reveal patterns and relationships among communities when looking at vegetation groups in NMS ordination (Figure 4.3 shows the NMS ordination for plant communities 1 to 27 and figure 4.4 show communities 28 to 34).. NMS ordination indicates that a high proportion of the sites are very influenced by similar environmental variables with only the sites on the left of the ordination diagram (Figure 4.3) being substantially different. The variable that explains the difference between these communities are mainly soil wetness, hydrogeomorphic (HGM) setting, and soil texture.

In the ordination diagram displayed in figure 4.3, the first axis is mostly represented by wetness which is negatively associated with axis, and altitude is positively associated with axis. Communities that are found in permanently inundated wetlands include 2. *Senecio conraethii-Typha capensis* Community, 4. *Fimbristylis dichotoma-Leersia hexandra* Community, 6. *Eragrostis planiculmis* Community, 7. *Schoenoplectus brachyceras* Community. The communities found along the second axis are positively associated with valley head seepages and negatively with riverbanks.

Community 27 and 28 formed a distinct group in Figure 4.4 along the first and second axis respectively. Communities in the second axis are positively represented by floodplain and negatively by altitude. All the communities that are negatively associated with axis two are restricted to low altitudes. The descriptions for each community are discussed further in paragraph 4.4 (Descriptions of plant communities).



Vegetation clusters

- △ 1. *Pennisetum thunbergii* comm.
- ▲ 2. *Senecio conranthii*-*Typha capensis* comm.
- ▽ 3. *Hyparrhenia tamba*-*Imperata cylindrica* comm.
- ▼ 4. *Fimbristylis dichotoma* -*Leersia hexandra* comm.
- ◇ 5. *Hyparrhenia filipendula* comm.
- ◆ 6. *Eragrostis planiculmis* comm.
- 7. *Schoenoplectus brachyceras* comm.
- 8. *Juncus effusus* comm.
- 9. *Leucosidea sericea* comm.
- 10. *Hyparrhenia rufa* comm.
- × 11. *Cyperus marginatus* comm.
- + 12. *Cynodon dactylon* comm.
- Y 13. *Trifolium repens*-*Paspalum dilatatum* comm.
- λ 14. *Cyperus denudatus* comm.
- * 15. *Aristida junciformis* comm.
- E 16. *Arundinella nepalensis* comm.
- ⊙ 17. *Hemarthria altissima* comm.
- ⊞ 18. *Agrostis lachnantha* comm.
- ⊟ 19. *Pseudognaphalium oligandrum* comm.
- ⊠ 20. *Fimbristylis ferruginea*-*Miscanthus junceus* comm.
- ⊡ 21. *Coleochloa setifera*-*Verbena brasiliensis* comm.
- ⊢ 22. *Eragrostis curvula* comm.
- ⊣ 23. *Fuirena pubescens* comm.
- ⊤ 24. *Eragrostis chloromelas* comm.
- ⊥ 25. *Themeda triandra* comm.
- ⊦ 26. *Eragrostis plana* comm.

Figure 4.3 NMS ordination for Communities 1 to 27 of Temperate Grassy WetlandsVegetation excluding extensive soil data. This is first half of communities (Communities1 to 26). The symbols in the ordination indicate group identities the arrows and vectors indicate environmental variables that show trends along the axes.

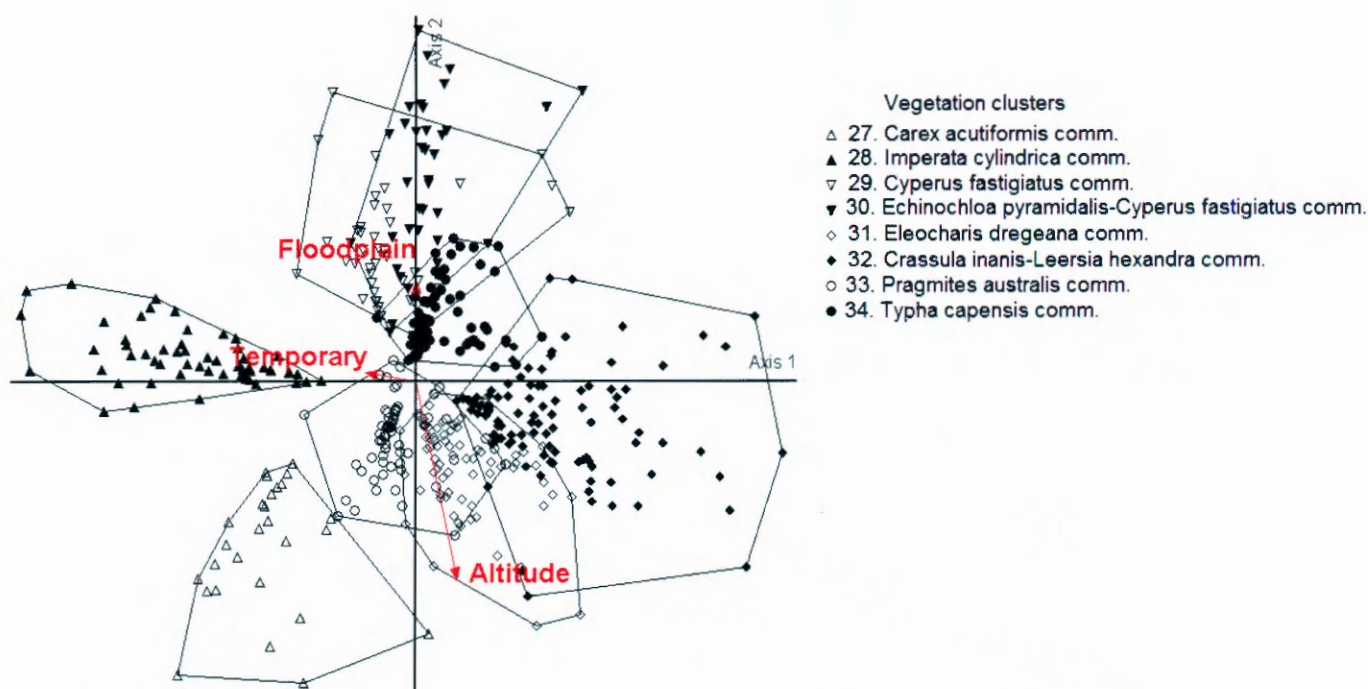


Figure 4.4 NMS ordination diagram with Communities 27 to 34 of Temperate Grassy Wetlands Vegetation excluding extensive soil data. This is the second half comprising of eight communities in the second half of Main Cluster 6. The symbols in the ordination indicate group identities the arrows and vectors indicate environmental variables that show trends along the axes.

4.3.2 Patterns of plant community distribution including soil data

The distribution of relevés along the first and second axis for NMS as well as CCA ordination is given in Figure 4.5 for those plots where soil data are available. A comparison of plots/communities showed a similar pattern among groups with only a few that are distinct.

The first axis of the NMS ordination (Figure 4.5 A) is positively represented by calcium and magnesium but it is not clear which communities stand out from the others along this axis. Communities 1, 2, 3, 4, 6, 7, 8, 9, 15 and 19 stood out from all the other communities. The second axis is positively represented with clay percentage. The CCA ordination diagram (Figure 4.5 B) shows that each axis is represented by more than one environmental variable with a mix of plots from different communities. The first axis is positively associated with electrical conductivity. The second axis is positively associated with phosphorus, sand percentage, magnesium and calcium; and negatively associated with nitrogen, organic

content, clay, and silt percentage. Sandy soils are indeed high in cation exchange capacity and tend to have high magnesium content.

This ordination diagram is crowded and messy with plots all over the ordination space and it does not give clear relations between plant communities and environmental variables. Therefore, a group test using the MRPP method was conducted to further investigate the group similarities.

4.3.3 Group testing

The results obtained from MRPP from the TGWV show that most plant communities are similar. Table 4.8 shows the results of test 1, group (i), communities 11, 12, 13, 14 and 17 that are clustered in ordination space in Figure 4.5 A. The p-value indicates that these communities are similar. Clear evidence of relationships among communities prevailed when the variables and communities were overlaid in on an ordination space. Figure 4.6 show the influential variables associated with these communities. Community 14 (*Cyperus denudatus* Community) is differentiated from all other communities by having a higher organic matter and nitrogen content, whereas Community 11 (*Cyperus marginatus* comm.) and Community 12. (*Cynodon dactylon* comm.) are both found in soils high in pH and electrical conductivity. Community 11 and 13 are low in all of the above variables.

Table 4.3 MRPP results for Community 11. *Cyperus marginatus* comm., Community 12. *Cynodon dactylon* comm. Community 13. *Trifolium repens-Paspalum dilatatum* comm., Community 14. *Cyperus denudatus* comm. and Community 17. *Hemarthia altissima* comm. of TGWV. MRPP recognised these communities as similar and NMS was used to see visualise relationships among the communities.

Groups were defined by values of: Organic content

Test statistic: T = -3.5310396

Observed delta = 0.56969579

Expected delta = 0.59136371

Variance of delta = 0.37655567E-04

Skewness of delta = -1.3444584

A = 0.03664059

p = 0.00689362

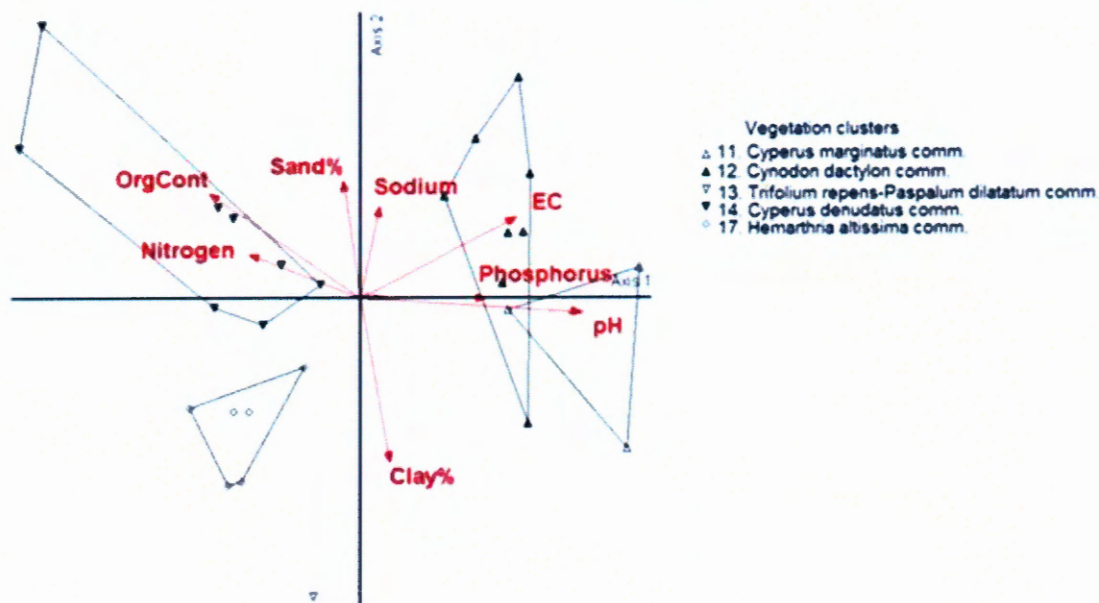


Figure 4.6 NMS ordination diagram for the Communities 11 to 17 of Temperate Grassy Wetlands Vegetation with extensive soil data. The symbols in the ordination indicate group identities the arrows and vectors indicate environmental variables that show trends along the axes.

The MRPP for the second group (Table 4.9) of communities 22 to 34 that were clustered in figure 4.5 A show that the differences between communities is very small. The variation along axis one is positively associated with high altitude, and low silt percentage and negatively associated with low calcium contents. The second axis is positively associated with high phosphorus and negatively associated with low clay percentage. Communities include Community 22. *Eragrostis curvula* comm., Community 23. *Eragrostis chloromelas* comm. and Community 25. *Themeda triandra* comm.

Table 4.4 Test 2, for communities 22 to 34 of TGWV. MRPP identified these communities difference between these communities is very small and NMS verified that these communities are found in soils with same nutrient concentration.

Groups were defined by values of: Sodium	
Test statistic: T =	-2.3356402
Observed delta =	0.40912366
Expected delta =	0.41143997
Variance of delta =	0.98351649E-06
Skewness of delta =	-0.88762123
A =	0.00562977
p =	0.02521625

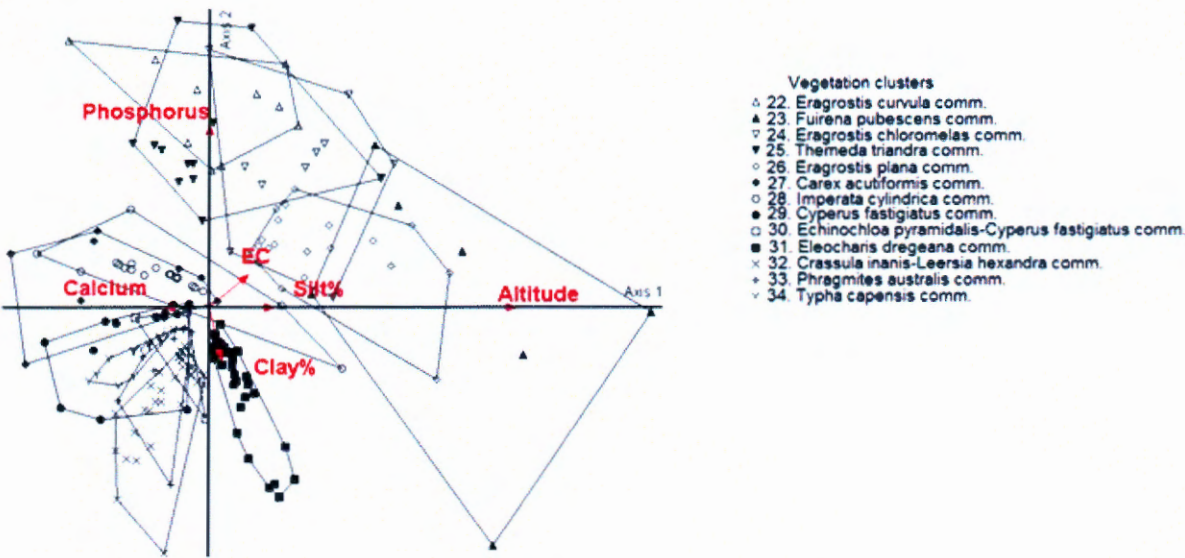


Figure 4.7 NMS ordination of TGWV showing variation between communities 22 to 34 that were clustered in ordination space. The symbols in the ordination indicate group identities the arrows and vectors indicate environmental variables that show trends along the axes.

4.4 Species response curves

The HyperNiche programme was used to determine the species responses to environmental variables for those plots that included soil data, using a local linear model. Eighty-four species out of a total of 702 species had been identified as indicator species and were used for the species response curves. Species indicating clusters on the same main branch of the dendrogram are displayed together in a single graph.

The wetlands of Main Cluster 6 are most likely to be found throughout the country and used for agricultural activities and are subject to monitoring programme. Therefore, it is important to look at how each indicator species respond to environmental conditions. One example on how environmental factors can influence occurrence of species in wetlands is of the two commonly found species throughout South Africa, *Phragmites australis* in Community 33 and *Typha capensis* in Community 34 (Figure 4.8). Both species are found in permanently wet soils, and are abundant in nitrogen and magnesium rich soils. The contrast between these species consists of that *Typha capensis* is more abundant in soils with low clay contents whereas *Phragmites australis* is more abundant in soils with high clay content. The species response curve shows that *Phragmites australis* does not deal well with high potassium concentrations, whereas *Typha capensis* performs very well under those conditions. The species become competitive when there is high nitrogen and sodium in soil. A different pattern is seen with soil particle size, where both species are not competitive. *Phragmites australis* increases when clay percentage is high, while when it low *Typha capensis* increases.

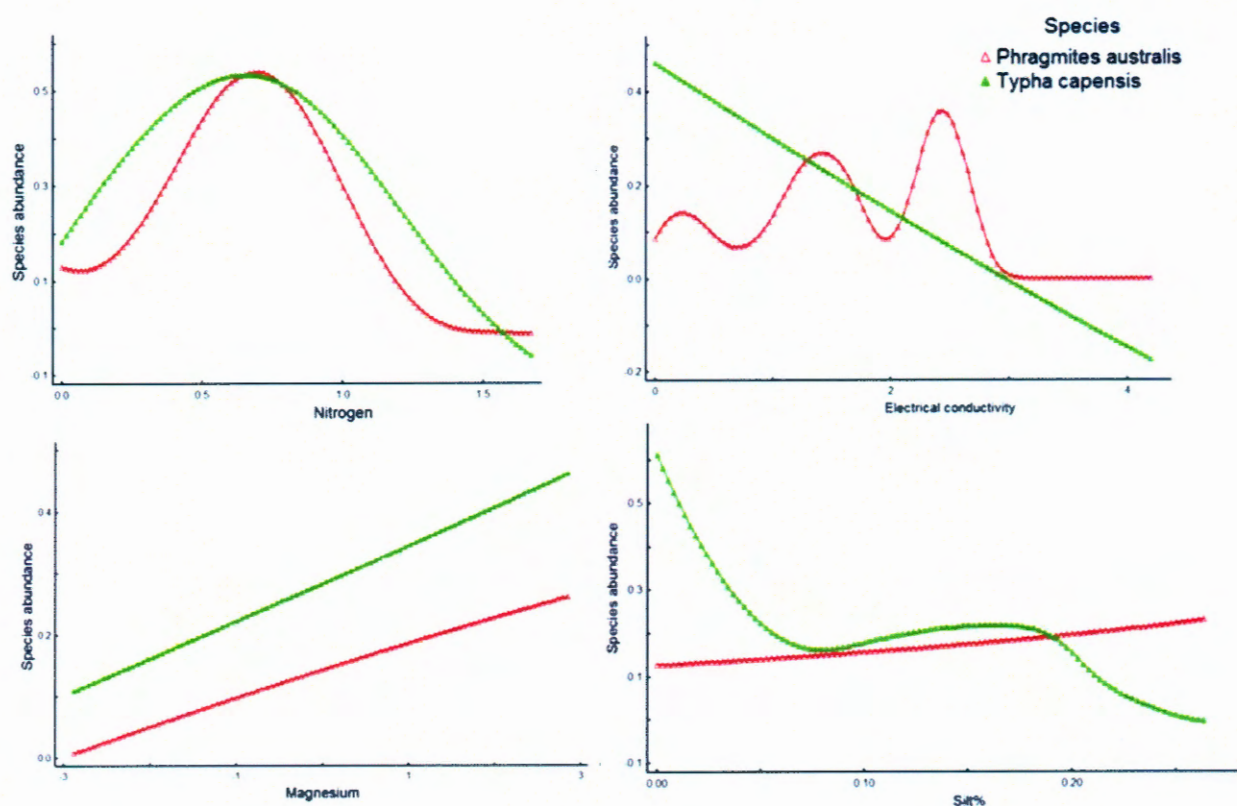


Figure 4.8 Species response curves for two commonly found reeds throughout South Africa.

The species represented in Figure 4.8 show those species that become dominant in Communities 33 and 34. The species response curves show that these two reeds increase in Nitrogen and Magnesium, but *Typha capensis* responds faster to such increase. From these graphs it becomes clear that *Phragmites australis* becomes dominant in conditions with high silt fraction and Electrical Conductivity. Emergent plants such as these can be used to identify permanently inundated wetlands, and also common in urban areas. These plants can withstand some degree of salinity, and both acidic and saline environments.

The species displayed in Figure 4.9 are dominant in Communities 6, 7, and 8. *Eragrostis planicumis* and *Schoenoplectus brachyceras* increase gradually with wetness. *Juncus effusus* is more adapted to a high silt fraction, and Electrical

Conductivity, while *Schoenoplectus brachyceras* declines in the similar conditions. Both species show weakest response to Sodium content in soil. *Eragrostis planiculmis* decreases with increasing Sodium

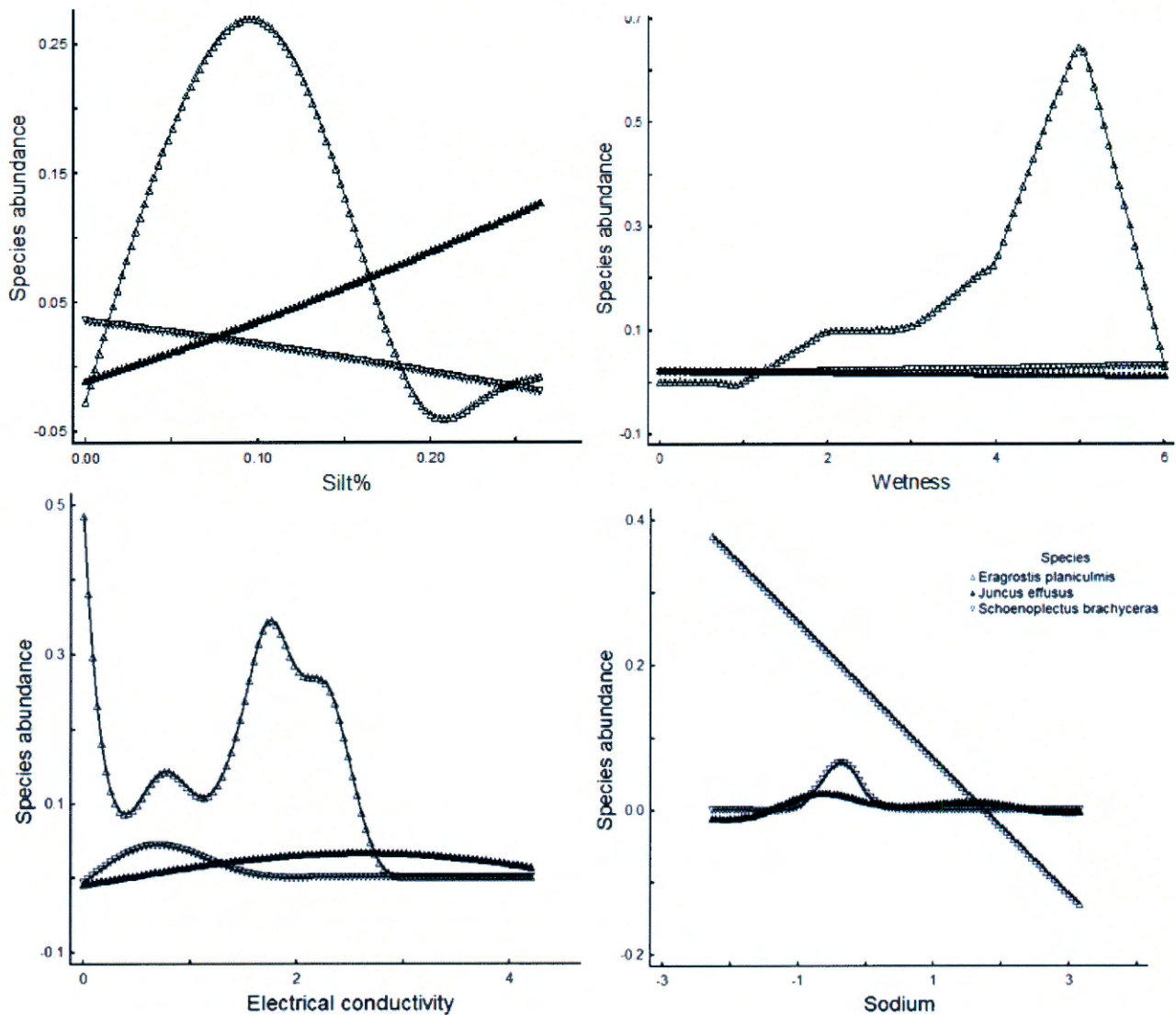


Figure 4.9 Species response curves for three species that are dominant in Communities 6, 7 and 8.

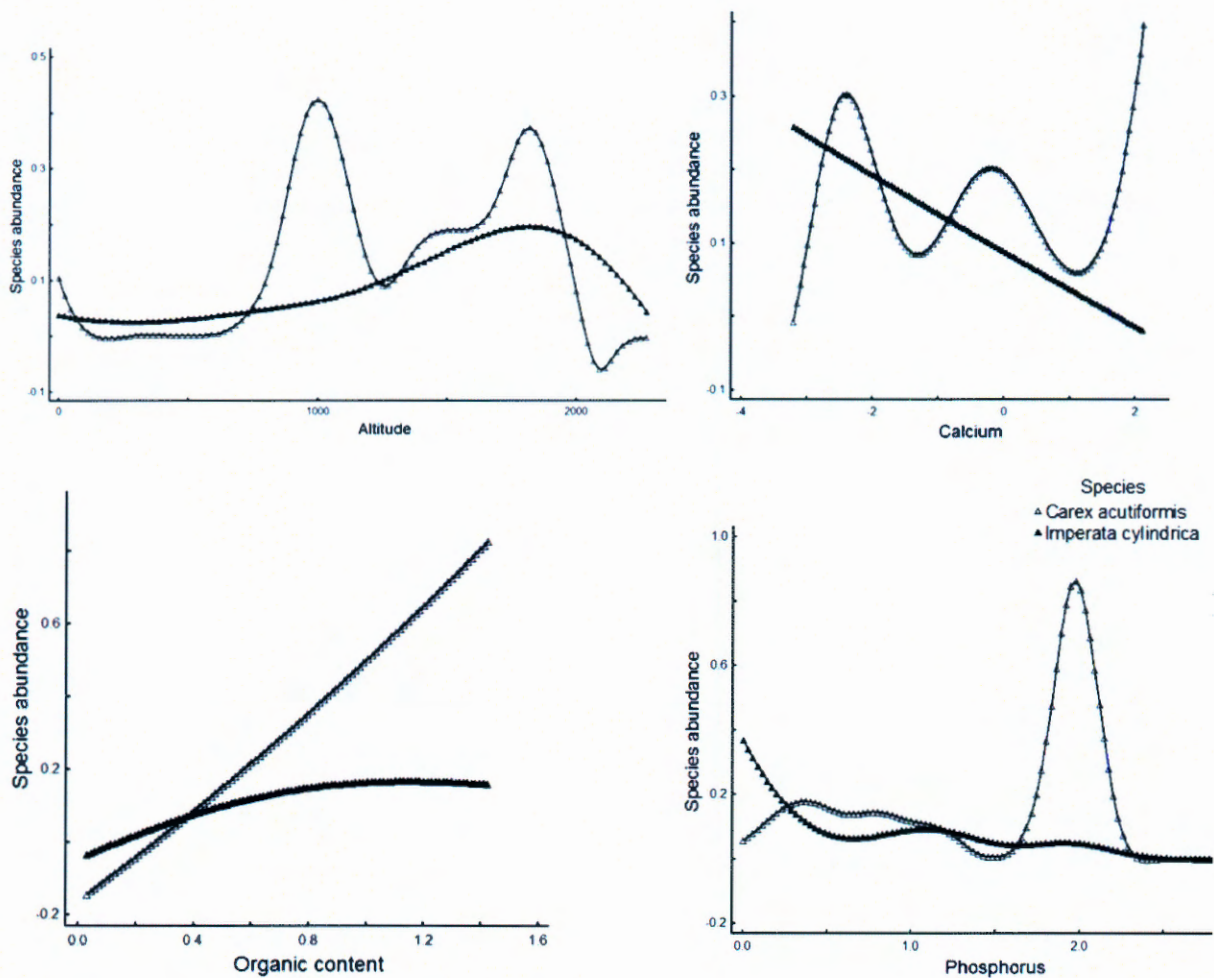
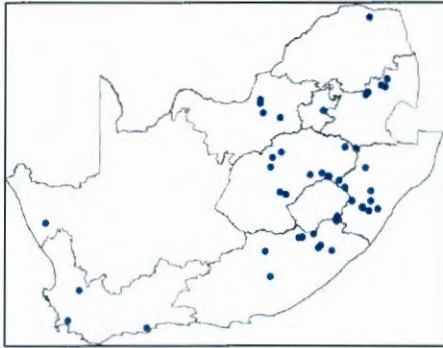


Figure 4.110 Species response curves for *Imperata cylindrica* and *Carex acutiformis* commonly associated with river banks and streams, particularly in the east and north-east of provinces of South Africa.

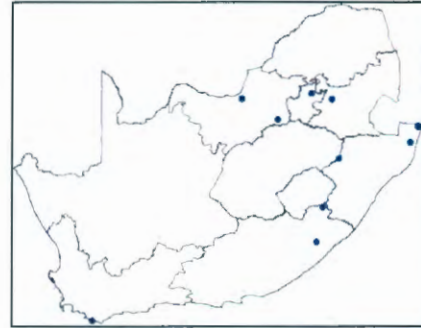
The two species in Figure 4.10 are associated with seasonal wetness as they commonly occur along streams banks. They become dominant in Communities 27 and 28. *Imperata cylindrica* prefers soils that have less Calcium and Phosphorus. Both *Carex acutiformis* and *Imperata cylindrica* are abundant in high organic content conditions.

4.5 Description of plant communities



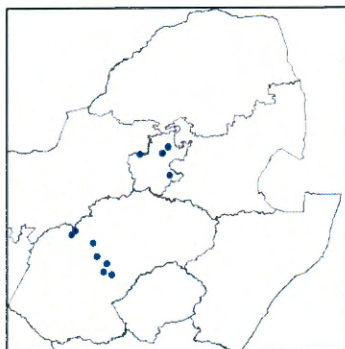
1. *Pennisetum thunbergii* comm.

This community is found mostly in the Highveld area and there's also an isolated population in the northern and western Cape. Wetlands associated with this community are valley-head seepages, valley bottom wetlands, floodplains and depressions. The species grow on clayey and loamy soils, of the Champagne and Katspruit soil form. The soil wetness ranges from temporary to permanent inundation. The average number of species per sample plot is 6. The diagnostic species are *Pennisetum thunbergii*, *Agrostis lachnantha*, and *Eleocharis dregeana*.



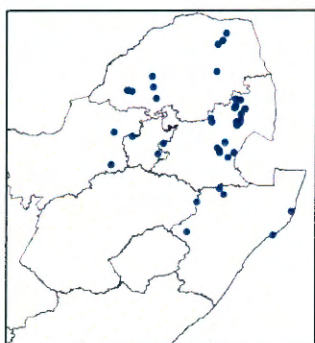
2. *Senecio conrathii-Typha capensis* comm.

This community is associated with a variety of wetland types, including valley-head seepages, slope seepage, channelled and unchannelled valley-bottom wetlands, floodplains and depressions. Silt, peat and clay soil of Katspruit, and Champagne form are found in these wetlands. The soils are temporary to permanently wet. The average number of species per sample plot is 9. The dominant species of this community are *Typha capensis* and *Phragmites australis*.



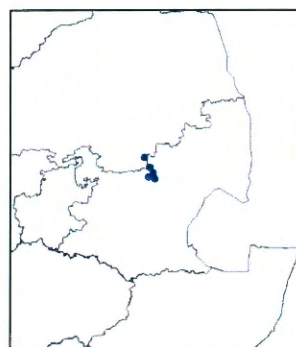
3. *Hyparrhenia tamba-Imperata cylindrica* comm.

This community is distributed only in Gauteng and Free State province. It is associated with valley bottom wetlands and slope seepages that have temporarily and seasonally wet sandy-loam soils. On average, 12 species are found per sample plot. The community is characterized by the presence of alien invasive species including *Verbena bonariensis*, *Paspalum dilatatum* and *Oenothera rosea*.



4. *Fimbristylis dichotoma-Leersia hexandra* comm.

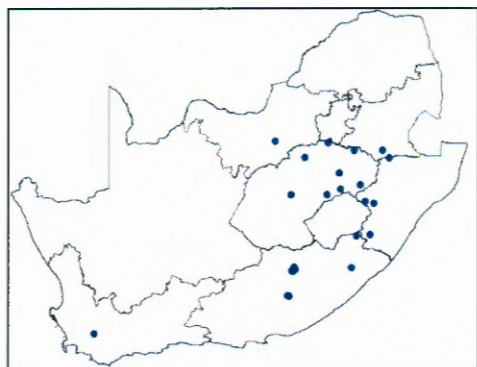
This community is found in channelled and unchannelled valley bottoms, slope seepages, floodplains, and depressions in the north of the country. It is found on a variety of soils including clay, loam, peat, and silt. These soils are temporary to permanently wet. On average, 9 species occur per sample plot. The most abundant species are *Leersia hexandra*, *Miscanthus junceus*, and *Typha capensis*.



5. *Hyparrhenia filipendula* comm.

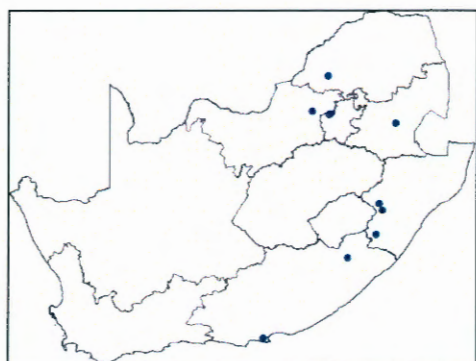
This community occurs on the border of Limpopo and Mpumalanga province. It occurs along riverbanks and slope seepages. The soils are sandy often with a small fraction of gravel, and temporarily or permanently inundated. On average, 4.3 species per sample plot

are found. *Hyparrhenia filipendula* is the most abundant species.



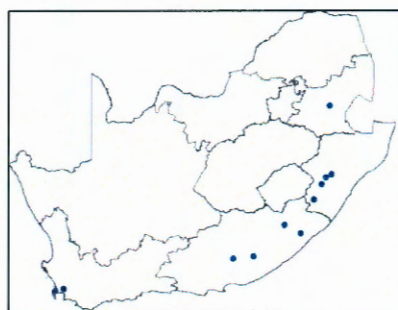
6. *Eragrostis planiculmis* comm.

This community is associated with channelled and unchannelled valley bottoms wetlands, floodplains and depressions on the Highveld. The species are found in loam and clay soils of the Katspruit form that are seasonally wet. On average, 4 species are found per sample plot. The most abundant species is *Eragrostis planiculmis*.



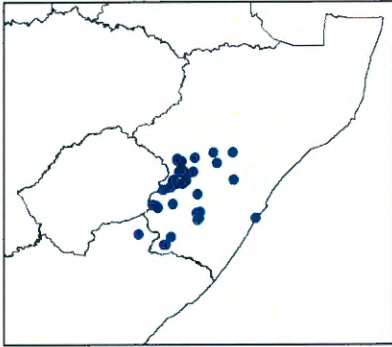
7. *Schoenoplectus brachyceras* comm.

This community is found on channelled and unchannelled valley bottom wetlands. The soils are loamy, temporarily to permanently wet. On average, 3 species are found per sample plot. The most dominant species are *Schoenoplectus brachyceras* and *Leersia hexandra*.



8. *Juncus effusus* comm.

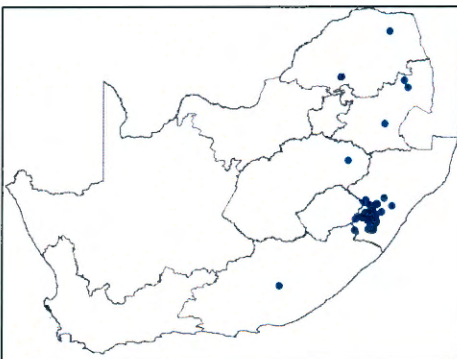
This community is found in similar habitat conditions as the previous community 7 (*Schoenoplectus brachyceras* community). On average, 5 species were found per sample plot. *Juncus effusus* is the dominant species.



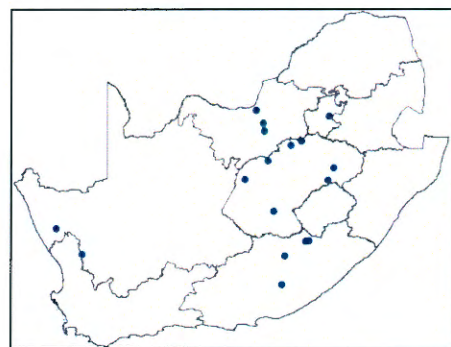
9. *Leucosidea sericea* comm.

This community is mostly associated with the Drakensberg foothills. It is found in floodplains and along riverbanks. It grows on deep, sandy or clayey soils and often in rocky soils that are temporarily wet. The average number of species per sample plot is 10. This community is dominated by *Arundinella nepalensis* and *Hyparrhenia hirta* and the shrubby *Leucosidea sericea*.

This community is associated with riverbanks, floodplains and valley bottom wetlands that are on temporarily wet soils. The soils are loamy and clayey of the Katspruit Form. The community has an average 5 species per sample plot. Alien invasive species are very prominent in this community as floodplains are prone to alien invasion as they are frequently disturbed by flood events (Richardson, 1997). The dominant species are *Acacia mearnsii*, *Cyperus congestus* (*Mariscus congestus*), *Hyparrhenia rufa*, *Paspalum urvillei*, *Polygonum hystriculum*, *Verbena bonariensis*, *Eragrostis plana*, *Sporobolus africana* and *Polygonum hystriculum*.



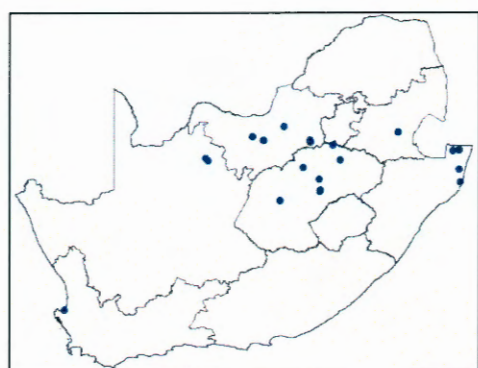
10. *Hyparrhenia rufa* comm.



11. *Cyperus marginatus* comm.

This community is found across the Highveld. It occurs in a variety of wetland types including slope seepages,

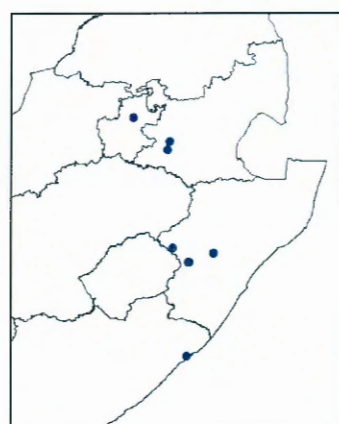
floodplains, depressions, channelled and unchannelled valley bottom wetlands. The soils are temporarily to permanently wet, clayey or loamy, of the Katspruit and Mayo forms. The species occurrence is influenced mostly by high pH and phosphorus concentration in the soil. On average, 10 species are found per sample plot. The most abundant species is *Cyperus marginatus*.



12. *Cynodon dactylon* comm.

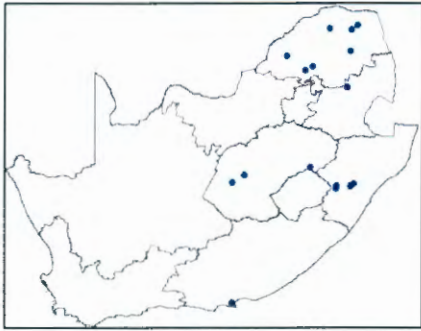
This community is located in valley bottom and depression wetlands on the Highveld. It is characterised by temporarily wet, loamy or clayey soils of Rensburg and Katspruit soil forms. The habitat is drier (temporarily to seasonally wet). The species are found where soils have high electrical conductivity and are rich in sodium. The average number of species found per sample plot is 9. *Cynodon dactylon* generally occurs in

disturbed areas (Van Oudtshoorn, 1999). Vegetation in this type of wetland emerges as a result of over-utilization by grazing livestock (Coetzee *et al.*, 1993). On average, 6 species are found per sample plot. The community is characterized by *Cyperus marginatus*, *Cynodon dactylon*, and *Tagetes minuta*.



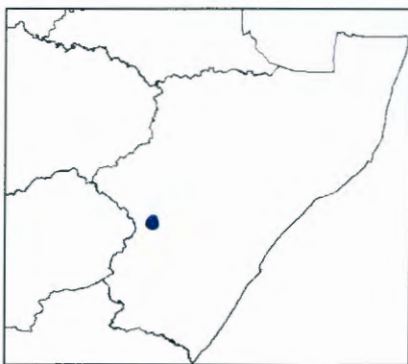
13. *Trifolium repens*-*Paspalum dilatatum* comm.

This community is found in channelled and unchannelled valley bottom wetlands, in temporarily to permanently wet soils. On average, 9 species are found per sample plot. It is largely dominated by alien species including *Paspalum dilatatum*, *Trifolium repens*, *Bidens pilosa*, *Cosmos bipinnata*, and *Cyperus esculentus*.



14. *Cyperus denudatus* comm.

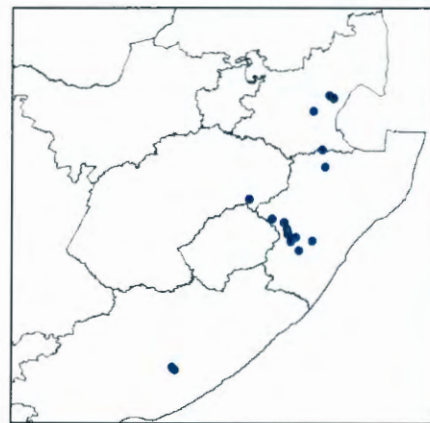
This community is associated with channelled and unchannelled valley bottom wetlands, as well as depressions and slope seepage wetlands. It is found in various soil types (peat, sand, silt and clay) of the Champagne, Dundee, Katspruit, and Longlands Soil Forms. On average, 7 species are found per sample plot. The most abundant species are *Cyperus denudatus* and *Andropogon appendiculatus*.



15. *Aristida junciformis* comm.

This community is restricted to the foothills of the Drakensberg in KwaZulu-

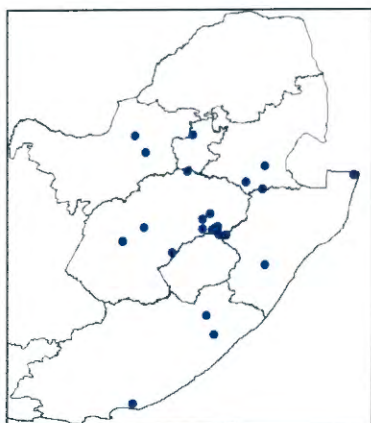
Natal. This community is associated with channelled and unchannelled valley bottom wetlands, slope seepages and floodplain wetlands. It occurs in loam, sand and peat soils of the Champagne, Katspruit and Dundee Soil Forms. The soil wetness varies from temporary to permanent. The average number of species per sample plot is 18. Soils associated with this community are low in salt content and high in organic content. It can be subjected to various degrees of grazing ranging from light grazing to heavy overgrazing (Walsh, 2004).



16. *Arundinella nepalensis* comm.

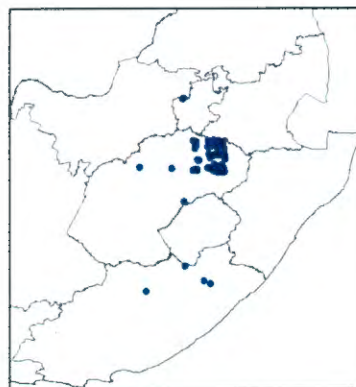
This community is found in the eastern provinces of the country. It occurs on peaty soils in channelled valley bottom wetlands associated with sandy, and peaty soils which are temporarily wet.

On average, 11 species occur per sample plot. *Arundinella nepalensis* is the dominant species because it grows so closely together and form a mat as it is associated with soils that are shallow (Burgoyne, 2000).



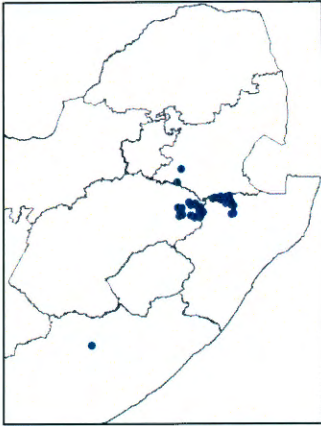
17. *Hemarthria altissima* comm.

This community is encountered in the eastern provinces of South Africa. It is found on channelled and unchannelled valley bottom wetlands, slope seepages, riverbanks and floodplain wetlands where soils are seasonally to permanently wet. The soils are sandy, clayey, loamy and peaty of the Champagne, Katspruit, and Dundee forms. On average, 8 species are found per sample plot. The most abundant species are *Hemarthria altissima* and *Paspalum dilatatum*.



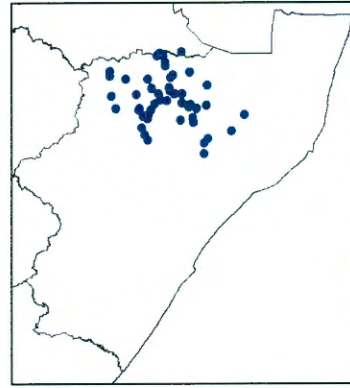
18. *Agrostis lachnantha* comm.

This community is mostly found in the in the Free State in floodplains, depressions and valley bottom wetlands. The soils are clayey and loamy of the Arcadia and Katspruit soil forms and are temporarily to seasonally inundated. The average number of species found per sample plot is 9. The most abundant species include *Agrostis lachnantha*, *Paspalum dilatatum*, *Hemarthria altissima*, *Pseudognaphalium ologandrum*, *Andropogon appendiculatus*, *Eragrostis plana*, *Oenothera rosea*, *Cyperus longus*, *Cynodon dactylon*.



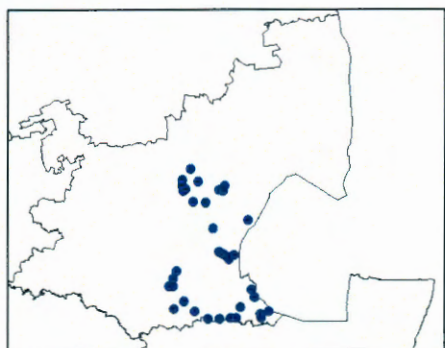
**19. *Pseudognaphalium*
oligandrum comm.**

This community occurs on the borders of the Free State, Mpumalanga and KwaZulu-Natal provinces as well as in the Eastern Cape. It is associated with floodplains, slope seepages, channelled and unchannelled valley bottom wetlands. It is found in loam and clay soils of the Katspruit or Dundee Soil forms that are temporarily to permanently wet. On average, 16 species are found per sample plot. The dominant species are *Paspalum dilatatum*, *Agrostis lachnantha*, *Eragrostis plana*, *Cyperus congestus* (*Mariscus congestus*), *Pennisetum sphacelatum*, *Juncus inflexus*, *Pennisetum sphacelatum*, and *Pseudognaphalium oligandrum*.



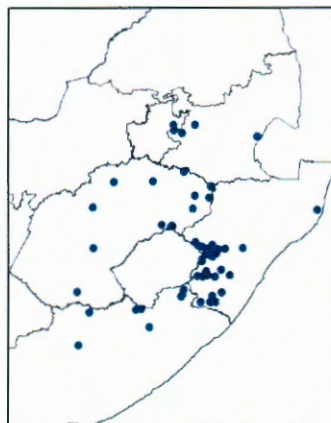
**20. *Fimbristylis* *ferruginea-*
Miscanthus junceus comm.**

This community is restricted to KwaZulu-Natal. It is associated with variable wetland types including channelled and unchannelled valley bottom wetlands, floodplains, and riverbank wetlands. It is found in clay, loam and sandy soils of the Rensburg, and Dundee soil forms that are temporarily to seasonally wet. The average number of species per sample plot is 13. The most abundant species are *Paspalum dilatatum*, *Eragrostis plana*, *Hemarthria altissima*, *Imperata cylindrica*, *Fimbristylis ferruginea*, *Leersia hexandra*, *Paspalum urvillei*, *Miscanthus junceus*, and *Phragmites australis*.



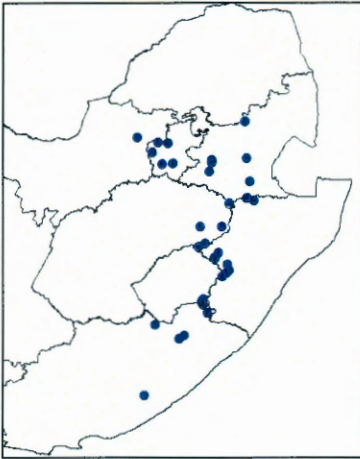
21. *Coleochloa setifera*-*Verbena brasiliensis* comm.

This community is restricted to the Mpumalanga province. It is associated with various types of wetland including channelled and unchannelled valley bottom, depression, slope seepages and valley head seepages. The soils are seasonally wet, high in clay percentage and belong to the Katspruit soil form. On average, 6 species are found per sample plot. *Verbena brasiliensis*, *Eragrostis plana*, *Imperata cylindrica* and *Arundinella nepalensis* are the dominant species.



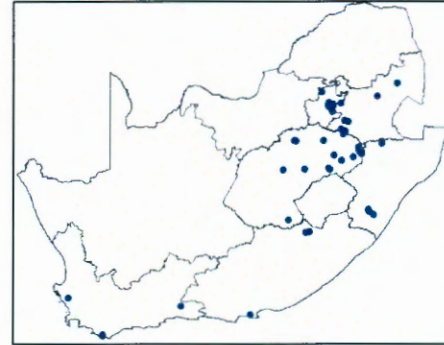
22. *Eragrostis curvula* comm.

This community is found in the eastern provinces of the country and is associated with various types of wetland, including floodplain, valley head seepage, slope seepage, channelled and unchannelled valley bottom and depression wetlands that have temporarily or seasonally wet soils. The soils of this community are sandy and loamy of Katspruit, and Pinepede soil form. The average number of species per sample plot is 11. The most abundant species are *Eragrostis curvula*, *Themeda triandra*, *Helichrysum aureonitens*, and *Eragrostis plana*.



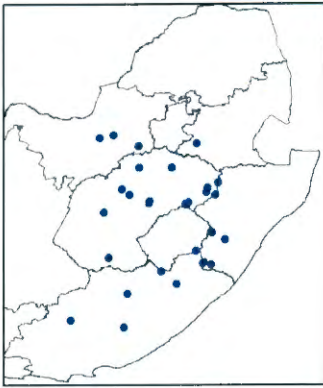
23. *Fuirena pubescens* comm.

This community is found on slope seepages, valley head seepages, floodplains, riverbank, channelled and unchannelled valley bottom wetlands that are seasonally to permanently wet. The soils are clayey, loamy and sandy belonging to the Katspruit, Longlands, Rensburg, and Champagne soil Forms. On average, 9 species are found per sample plot. The most abundant species are *Fuirena pubescens*, *Eragrostis plana*, *Paspalum dilatatum*, and *Helichrysum aureonitens*.



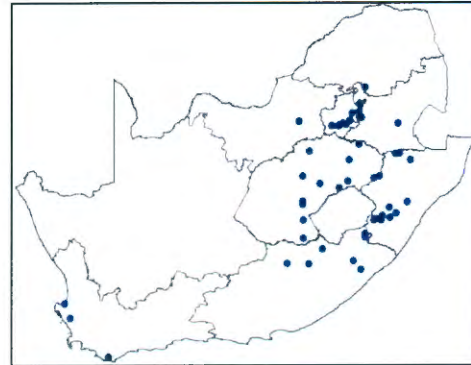
24. *Eragrostis chloromelas* comm.

This community is found in valley head seepages, slope seepages, channelled and unchannelled valley bottom wetlands, floodplains and depressions. Clayey, loamy and sandy soils that are temporarily or seasonally wet are associated with this community. The soils have a high electrical conductivity. On average, 9 species are found per sample plot. The most abundant species are *Eragrostis plana*, *Eragrostis chloromelas*, *Themeda triandra* and *Setaria sphacelata*.



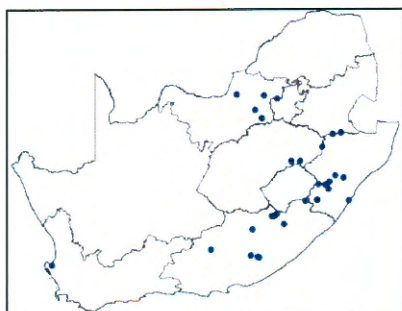
25. *Themeda triandra* comm.

This plant community is found in slope seepages, valley-head seepages, and valley-bottom wetlands. These are high altitude wetlands. The dominant grass species, *Themeda triandra*, grows in any type of soil but it prefers clay and soils with high in organic matter and phosphorus. The salt concentration is low to moderate. The soils are temporary or seasonally wet. On average, 11 species are found per sample plot. The most abundant species are *Themeda triandra*, and *Eragrostis curvula*.



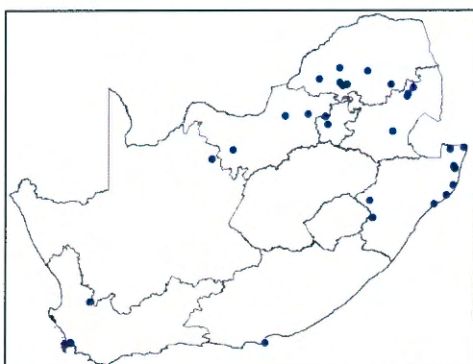
26. *Eragrostis plana* comm.

This grassy wetland community is found along riverbanks, depressions (pans), floodplain and valley bottom wetlands. The species and relevés making up this community occur mostly on the Highveld. The soils are clayey and loamy, of the Katspruit and Rensburg soil forms. On average, 9 species are found per sample plot. The dominant species *Eragrostis plana* is associated with temporarily and seasonally inundated soils. *Eragrostis plana* is considered to have a wide ecological range and is not considered to be diagnostic of any particular environment (Collins, 2011).



27. *Carex acutiformis* comm.

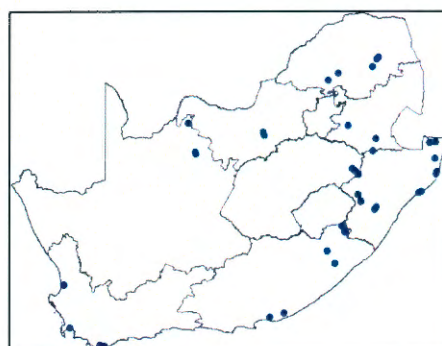
This community is found in channelled and unchannelled valley bottom, floodplain, and slope seepage wetlands. It is associated with peat, loam and clay soils that are seasonally to permanently wet. The soils associated with this community are high in calcium concentration. On average, 4 species are found per sample plot. *Carex acutiformis* is the diagnostic and most abundant species with few occurrences of *Leersia hexandra*.



28. *Imperata cylindrica* comm.

This community is found throughout the country except the Free State province. It occurs in valley bottom, floodplain,

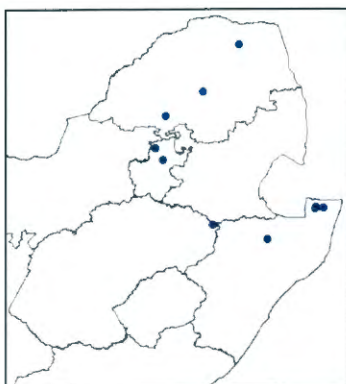
spring and depression wetlands. The soils are high in calcium and are temporarily to seasonally wet and consist of sand, loam, and clay. During wet periods much water is held in the soil and during dry seasons the soil may be cracked and dry (Burgoyne, 2000). On average, 6 species are found per sample plot. The most abundant species is *Imperata cylindrica*.



29. *Cyperus fastigiatus* comm.

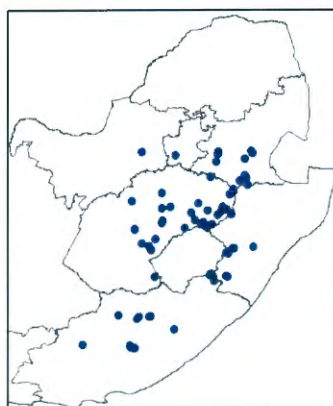
This community is also found throughout the country and is associated with channelled and unchannelled valley bottom, and floodplain wetland types. The soils are clayey, loamy, peaty or silty and are seasonal or permanent wet with relatively high pH and calcium concentration. The species abundance increases with increasing altitudes, sodium, and phosphorus concentration in soils. On average, 5 species are

found per sample plot. *Cyperus fastigiatus* is the most abundant species.



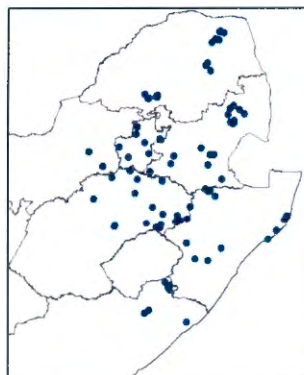
**30. *Echinochloa pyramidalis*-
Cyperus fastigiatus comm.**

This community is found in the north eastern parts on the country. It is associated with sand, clay, and loam soils which are temporarily to seasonally wet. On average, 9 species are found per sample plot. The community is dominated by *Cyperus fastigiatus*, *Echinochloa pyramidalis*, *Persicaria attenuata* subsp. *africana*, and *Alternanthera sessilis*.



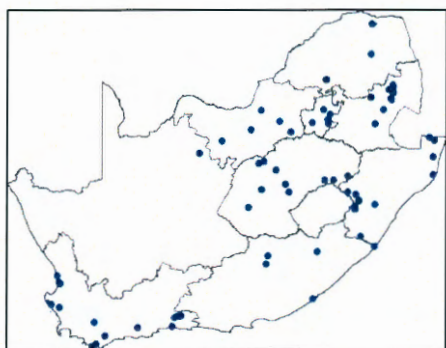
31. *Eleocharis dregeana* comm.

This community is associated with valley head seepages, depressions and channelled and unchannelled valley bottom wetlands. The soils are seasonally to permanently wet, belong to the Katspruit soil form and are subjected to moderate grazing pressure (Collins, 2011). On average, 6 species are found per sample plot. The most abundant species are *Eleocharis dregeana*, *Schoenoplectus decipiens*, *Leersia hexandra*.



32. *Crassula inanis*-*Leersia hexandra* comm.

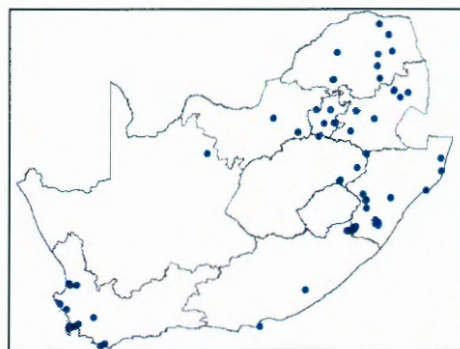
This community is found in the eastern provinces of the country. It is found in floodplains, channelled and unchannelled valley bottom wetlands, depressions, and spring wetlands. The soils are peaty, clay, loamy, and sandy and are temporarily to permanently wet. There are on average 6 species per sample plot. *Eleocharis dregeana* and *Leersia hexandra* are the dominant species.



33. *Phragmites australis* comm.

This is a widespread community found all over the country, but is most common on the Highveld. It grows in very wet soils but it is also found in temporary and seasonally wet soils. The soils where this community is found are clayey, loamy and peaty and are relatively high in sodium concentration.

On average, there are 4 species per sample plot. The most abundant species is *Phragmites australis*.



34. *Typha capensis* comm

This community occurs in the permanently wet areas. It is associated with various types of wetland including channelled and unchannelled valley bottom wetlands, floodplains, slope seepages, riverbanks, and depressions. The soils are sandy, loamy, peaty and clayey, and are high in pH. This community tends to occur mostly where there has been disturbance and can deal very well with water pollution. *Typha capensis* is most abundant in nutrient-rich soils with high concentrations of nitrogen, phosphorus and magnesium. There are on average 4 species per sample plot. *Typha capensis* is one of the most widespread of all reed species (Gibbs Russell *et al.*,

1990). *Typha capensis* and *Phragmites australis* species of Community 34 have similar growth habit. They both grow in muddy, standing waters where they colonise by means of creeping rhizomes.

4.6 Discussion

Temperate Grassy Wetlands Vegetation cluster represent the bulk of SA wetland vegetation where most wetlands are common, widespread and highly threatened. The TGWV has been studied extensively and more data are available for this cluster than for any of the other Main Clusters. The vegetation types belonging to this group are among the most common wetland vegetation types in South Africa. The highest species diversity within these communities is found in Community 22 *Eragrostis curvula*, which occurs in the temporarily wet zones of the wetland. Only a limited number of communities have a restricted distribution: Some of the communities are only restricted to one province, viz. Community 20 *Fimbristylis ferruginea-Miscanthus junceus* (KwaZulu-Natal), Community 21 *Coleochloa setifera-Verbena brasiliensis* (Mpumalanga), Community 15 *Aristida junciformis* (KwaZulu-Natal), Community 8 *Juncus effusus* (KwaZulu-Natal) and Community 5 *Hyparrhenia fillipendula* (Mpumalanga).

Many of the plant communities previously described in Free State province by Collins (2011) and Brand *et al.* (2009) also show floristic and habitat affinities with the plant communities described in the present study. The findings of the study that was conducted by Collins 2011 show that *Eleocharis dregeana* is absent from depression wetlands that are temporary wet, but well presented in those that are either permanently or seasonally wet. Community 25 and 26 are similar to *Themeda triandra-Eragrostis plana* dry/wet grassland described by Eckhardt *et al.* (1993) except that they are described as separate communities but dominated by similar species. Other plant communities similar to previously described vegetation types are shown in Table 4.5 together with the diagnostic species. Very few of the identified communities are floristically associated with the plant assemblages described in historical studies. According to Collins (2012) this can probably be ascribed to the high beta diversity that exists amongst individual wetlands. Dissimilar plant assemblages can establish in similar habitats. It is therefore likely that although plant communities identified in previous studies were sampled from similar habitats that the species assemblages do not correspond.

The most striking figure is of CCA ordination (Figure 4.5) is the unexplained variation between communities as plots are scattered over the axes. The amount of unexplained variation might be the result of aggregated distribution of species within plots. It is clear that the quantity of nitrogen in soil is well associated with organic matter content. Plants decompose in the soil to form organic matter which is the source of nitrogen in the soil. However, the vegetation patterns are not very well explained in NMS and CCA ordinations with the data that is available. More data, such as fire, grazing and climate conditions (minimum temperature, frost and amount of rainfall), that were not captured for the purpose of this study would have been useful in capturing more variation of grassy wetlands vegetation. Except for the widespread plant communities in this cluster, the communities are mainly centered in KwaZulu-Natal, Free State, Mpumalanga and Gauteng.

The Temperate Grassy Wetlands Vegetation are under severe threat due to alien plant invasion as they are heavily disturbed by overgrazing and frequent fires. A number of communities are still in good condition like Community 25, *Themeda triandra* which is known to be an indicator of veld that is in good condition and also known to be resistant to fire. Most of the communities have a small number of grass species and a large number of forbs, and these forbs contribute often more to species richness than grass or sedge species.

The grassland Biome where the temperate grassy wetlands supports high levels of agricultural utilization as well as a high human population, thereby placing it under severe threat and pressure (O'Connor and Kuyler, 2005). The wetlands are highly transformed and fragmented with much of its priority biodiversity located within production landscapes. As a result, the temperate grassy wetlands are considered the most altered terrestrial biome (Henwood, 2006). Hence, the wetlands found on this biome are under severe threat.

Table 4.5 Display plant communities that are similar for historical and current findings

Publications	Identical community from historical studies	Findings of current study	Diagnostic species for historical and current findings
Collins, 2011	<i>Eragrostis planiculmis</i> community	<i>Eragrostis planiculmis</i> Community	<i>Eragrostis planiculmis</i>
	<i>Schoenoplectus brachyceras</i> - <i>Juncus oxycarpus</i> sub-community	<i>Schoenoplectus brachyceras</i> Community	<i>Leersia hexandra</i> <i>Juncus oxycarpus</i> <i>Schoenoplectus brachyceras</i>
	<i>Eragrostis curvula</i> - <i>Heteropogon contortus</i> community	<i>Eragrostis curvula</i> Community	<i>Themeda triandra</i> <i>Eragrostis curvula</i>
	<i>Eragrostis chloromelas</i> - <i>Eragrostis plana</i> sub community	<i>Eragrostis chloromelas</i> Community	<i>Eragrostis chloromelas</i> <i>Eragrostis plana</i>
	<i>Themeda triandra</i> community	<i>Themeda triandra</i> community	<i>Themeda triandra</i> <i>Eragrostis chloromelas</i> <i>Digitaria eriantha</i>
	<i>Cyperus fastigiatus</i> sub-community	<i>Cyperus fastigiatus</i> Community	<i>Cyperus fastigiatus</i> <i>Leersia hexandra</i> <i>Typha capensis</i>
	<i>Eleocharis dregeana</i> community	<i>Eleocharis dregeana</i> Community	<i>Eleocharis dregeana</i> <i>Schoenoplectus decipiens</i>
	<i>Typha capensis</i> variant	<i>Typha capensis</i> Community	<i>Cyperus fastigiatus</i> <i>Typha capensis</i> <i>Persicaria lapathifolia</i>
	<i>Leucosidea sericea</i> - <i>Hyparrhenia hirta</i> community	<i>Leucosidea sericea</i> Community	<i>Leucosidea sericea</i> <i>Hyparrhenia hirta</i> <i>Rhus discolor</i> <i>Eragrostis curvula</i> <i>Eragrostis plana</i>
	<i>Themeda triandra</i> - <i>Eragrostis plana</i>	<i>Themeda triandra</i> Community	<i>Themeda triandra</i>
Eckhardt et al., 1998	dry/wet grassland	<i>Eragrostis plana</i> Community	<i>Eragrostis curvula</i>

CHAPTER 5

GENERAL DISCUSSION, CONCLUSION AND RECOMMENDATIONS

This chapter discusses the SWV and TGWV communities; the analysis and comparisons, species diversity and how wetlands are affected by threats such as grazing, fire and alien invasion.

5.1 Analysis and comparisons

The analysis that was carried out in Chapter 3 and 4 resulted in an overview of wetlands vegetation types within South Africa. The study has classified vegetation of Sclerophyllous and Temperate Grassy Wetlands to plant communities and linked vegetation patterns with environmental factors. This will aid in assessing wetlands condition and also assist in the application of the National water act No. 36 of 1998 and in conservation and management plans. Data analysis provided a number of insights into the distribution and environmental conditions where these plant communities occur. A number of findings have appeared from this research about the wetland vegetation of the two Main Clusters.

As a first step, sampled data were classified into plant communities for Main Cluster 1 (Sclerophyllous wetlands) and Main Cluster 6 (Temperate Grassy Wetlands Vegetation) using indicator species analysis. The vegetation units were based on the presence and abundance of the species that make them up and the environmental conditions observed where the vegetation units are located and were referred to. The species that make up the communities for both Main clusters can be separated into several functional categories, of which the graminoids are the most important: reeds, restios, sedges, grasses and rushes.

The multivariate techniques that were used here represent suitable methods to relate vegetation data to the environment (ter Braak, 1986). Cluster analysis and ISA identified 34 plant community groups. Of the 34 major communities identified for each Main clusters in this study, 10 were found to be similar to some that were described in previous wetland

vegetation studies (Eckhardt *et al.*, 1993; Venter *et al.*, 2003, Sieben *et al.* 2004 and Cleaver *et al.* 2005).

A review CCA and NMS are more or less comparable when looking at the ordination diagrams that were presented in previous chapters. The species showing peak abundances at certain values of the predictor variables can be used as indicators for such conditions and can be used in the management and monitoring. It is clear that the distribution of the plant communities is not determined by a single variable but by a composite gradient with various environmental variables interacting. Variation in species composition in wetland communities are mainly ascribed to differences in landscape type, wetness and soil type. An increase in the abundance of one species can cause a decrease of in growth an abundance of another (Levin, 2009). Species respond to more than one environmental factor and gradient, and also to interactions between species (Kent and Coker, 1992). Each species will have a different environmental response curve for every environmental factor and each will differ in form. Knowing the abundance of different species can provide an insight how communities function as a whole. MRPP confirmed that plant community groups identified by the cluster analysis to be significantly different from other ($p<0.05$). Multivariate techniques can be used to summarise the basic attributes of wetland vegetation in terms of plant communities (Little, 2013).

5.2 Species diversity and threats to wetlands

Sclerophyllous wetland communities have generally low species diversity in contrast to the surrounding Sclerophyllous vegetation. This low diversity is thought to be a consequence of numerous factors including physiological constraints such as flooding, associated with periodic inundation (Dwire *et al.*, 2006) and strong competition arising from relatively high productivity (Bartelheimer *et al.*, 2010; Kotowski *et al.*, 2006). Wetlands have a low diversity of species on in contrast to surrounding Sclerophyllous vegetation. The species richness at the regional scale is determined largely by environmental heterogeneity in terms of climate as there are sharp climatic gradients in the Western Cape (Cowling *et al.*, 1997).

In many cases, hydrogeomorphic setting plays a large role in determining the species composition in wetlands especially for temperate grassy wetlands. The influence of water

input into the wetland provides important clues of hydrogeomorphic forces at work in an ecosystem. The hydrological conditions in a wetland have an effect on the species composition, successional trends, primary productivity and the accumulation of organic matter (Cronk and Fennessy, 2001). The hydrology has an important influence on the composition of the plant community and the primary production by influencing the availability of nutrients, soil characteristics and the deposition of sediment (Cronk and Fennessy, 2001). The wetlands that permanently inundated are mostly inhabited by rhizomatous plants because the muddy substrate of these water bodies helps the plants to anchor its rhizomes firmly.

Even though there is more data available for TGWV than for any of the other Main Clusters, the results of the ordination in explaining vegetation differences within this cluster remains quite limited. This may reflect that in the grassland biome, there are several pressures playing an important role that has not been captured in the database very well, such as fire and grazing. It is well understood that grazing affects the species composition of grassland vegetation, with a distinction between decreaser species (species that are dominant only when grasslands are optimally grazed), increaser 1 species, (species that increase when a grassland is undergrazed), and increaser 2 species (species that increase when a grassland is overgrazed, so that unpalatable species become dominant) (Tainton 1999).

Overgrazing and fire in temperate grassy wetlands pose a threat when they are not managed well. Wetlands are fragile ecosystems and mismanaging them can result in the loss of area covered by the wetland or in some cases the total disappearance of some species in the wetland (Walmsley, 1988). For example, the vegetation of *Fimbristylis ferruginea-Miscanthus junceus* Community wetland community is intensively grazed by livestock, as they contain plant species that are highly desirable in the winter months when green plants are scarce for grazing animals. Burning takes place at intervals of between one and five years and this, accompanied by the grazing of the green shoots, trampling and increased evaporation, could lead to erosion and faster drainage of wetland systems and the surface area of the wetland shrinks until only moist grassland is left (Burgoyne *et al.*, 2000).

Grazing can alter the plant density/size, plant longevity, community composition and diversity. Heavy grazing in grassland areas appear to reduce the overall species richness and generally change the species composition as less palatable grasses become more

dominant, especially on nutrient-poor soils (Mucina and Rutherford, 2006). High concentration of livestock can alter plant species cover and composition and this can then subsequently lead to alien invasion.

The fire regime can also have a serious a serious effect on the condition of wetland vegetation: either too many fires or too few fires can have a detrimental effect on the vegetation (Trollope, 1989). Soil moisture and the type of grazing management applied in a certain area, plays an important role by determining the type of vegetation in an area (Eckhardt *et al.*, 1993). A field in a good condition is usually characterized by a high basal cover of ecological indicator species. The low cover of ecologically important grasses (mostly the palatable species) is indicative of veld in a poor condition (van Oudtshoorn, 1991). Conservation management for wetland communities, especially temperate grassy wetlands, should focus on regarding wetlands as distinct management units. It is of special importance to fence off wetlands from the rest of the grasslands when or if they are vulnerable, especially in a grazing programme, due to more palatable vegetation of wetlands (Tainton, 1981), as these areas are often more sensitive to degradation than the surrounding grasslands. The overgrazing will result in the deterioration of the wetland ecosystems, particularly the valley bottom grassland and sedge-meadow communities. It is of major concern at present, in South Africa and all over the world that man has succeeded in irreversibly degrading vast areas of wetland vegetation by development and poor land-use practices (Walmsley, 1998). Despite the relatively low plant species diversity encountered in wetlands, particular species are restricted to these habitats, and for this reason, wetlands play an important role in species conservation. Overgrazing and mismanagement are the main cause of this invasion.

5.3 Species composition of wetland communities

South Africa has wide range of plants and rich in plant species and lot of the species are under threat. One of the biggest threats is alien plant invasions and genetic contamination. The alien invaders have the ability to suppress the growth of indigenous plants (Bromilow, 2010). About half of the 34 plant communities identified have a high proportion of alien plant species as they are vulnerable to degradation and subsequent alien invasion. Temperate

Grassy Wetlands Vegetation are among the most vulnerable plant communities in the country when it comes to alien invasion. Table 4.2 summarises the most abundant species in wetlands. From this table it becomes clear that alien species are also prominent in wetland vegetation. These species may/or pose a threat to the health and normal functioning of wetlands system. The communities of Sclerophyllous wetlands are somewhat undisturbed in terms of alien invasion as few alien species (*Acacia* species) were noted in the communities. On the other hand, temperate grassy wetlands are quite often dominated by alien invasive species as they are susceptible to alien invasion. The invaders have the ability to suppress the indigenous species (Bromilow, 2010). Such invasion not only affects biodiversity and ecosystem functioning but also human use and enjoyment of wetlands. The communities that occur in the grassland biome are disturbed. The possible reason for this is the fact that grassland wetlands are part of grazing land. In my opinion, if wetlands are used for grazing, the number of livestock (especially large livestock) that will have access to wetlands should be limited. Sufficient resting would improve the state of degradation of many of these systems.

For example, the grass *Paspalum dilatatum* is a common invader (Gibbs Russell *et al.*, 1991) which has become naturalised in South Africa as it is palatable and often planted as a pasture grass on damp soils. The species is highly invasive in temperate grassy wetland communities. This indicates that these wetlands have been mismanaged or are currently mismanaged. Future management practices should thus strive to prevent further increases in the abundance of this species within wetlands and should aim to limit and reduce the presence of alien invasive species.

Weiher and Keddy (1999) state that there is a growing consensus that many communities are structured by rules, which can be understood by looking at patterns among community assemblages. Certain species choose to grow together in a particular environment because they have similar requirements for existence in terms of environmental factors. They may also share the ability to tolerate the activities of living animals and humans, such as grazing, burning, cutting or trampling (Kent, 2012). Some species like *Juncus lomatophyllus*, *Juncus capensis*, *Laurembergia repens* and *Isolepis prolifer* are the first to establish in wetlands and that could explain their dominance amongst other species in pioneer communities. In some

cases the late settlers are prevented from establishment even though they could have survived if they had got there first (Chase and Leibold, 2003).

5.4 Conclusions

This has been an attempt to use multivariate techniques at analysing vegetation data from the South African National Wetland Vegetation Database. The aims were to group the vegetation plots into plant communities and finding environmental factors that best explain patterns in species composition, finding species that can be used as environmental indicators and to determining how the species respond to the environmental variables that drive the ecosystem. Exploring different techniques to use for analysis proved to be very time-consuming and less time was available for the analysis of this data.

The aims of this study as set in Chapter 1 were attained. The wetland vegetation data of Sclerophyllous wetlands and Temperate Grassy wetlands were classified, the indicator species were identified, and the environmental conditions influencing vegetation were described. Classification of dataset of both Main clusters yielded 34 plant communities for each Main Cluster.

No similar analysis of wetland vegetation data has been carried out in South Africa previously. This research therefore provides valuable information about plants that are indicators of certain wetland types. The plant species identified from this study can now be included in wetland management plans and will result in a more comprehensive plant species list for the country. Therefore, this study should serve as a starting point for wetlands vegetation future classification studies that will be conducted, as exploratory data analysis leads to more detailed questions.

Classification together with indicator species was considered to have been suitable tools to finding the most ecologically meaningful plant communities from cluster analysis. Indicator species added an ecological meaning to groups discovered by identifying where to stop dividing clusters into subsets, and to point out the main levels in hierarchical classification of sites (Legendre and Legendre, 2013). The methodology (Ward's method using Sørensen index) used for classification proved to be useful and the cluster dendrogram was subjective to less chaining (few number of clusters). Despite the fact that McCune and Grace (2002)

warn against the combined use of Ward's method and Sørensen's index, they seem to lead to credible results.

The most important environmental factors that come out of ordination when extensive soil data was excluded from the ordination are wetness, hydrogeomorphic setting and soil texture, in all the wetland clusters. In the presence of soil data, variables that account for the further variation of plant communities include organic matter, nitrogen and electrical conductivity. Although the variation was encountered in the measured soil variables, including organic matter content, nitrogen, and electrical conductivity, the differences between communities was more evident in nominal variables. It is therefore concluded that nominal variables played a major role in influencing the variation of plant communities. Both methods of ordination reached more or less the same conclusions when compared. In my personal opinion both methods have advantages and disadvantages. NMS is better at ranking order of distances and it allows using any distance measure unlike CCA which only uses Chi-square distance for every cell calculated. With every run in NMS the graph come out differently but with the same stress level. When running an analysis with CCA each time it gives inexplicable error messages. The arguments presented by McCune and Grace (2002) in favour of NMS are valid in my opinion. One of the important questions that is raised from the results of this study is how similar are these plant communities from one another. Although MRPP analysis found them to be similar, some of them are clearly different from each other in terms of environmental factors.

The response curves depict that species can coexist but still respond differently to soil conditions whereas some may compete for the same nutrients. Thus, soil characteristics together with vegetation characteristics may be useful indication of a wetland. From the average amount of species within each plant community, the conclusion can be drawn that the number of different species represented in a community is indirectly proportional to the extent that one or more environmental factors are dominating the habitat.

5.5 Recommendations

Lessons learnt from this study for future projects involve recommendations on how, and what should be sampled in field for wetland vegetation studies. The classification of vegetation proved to be valuable but not enough samples plots were available especially for the Sclerophyllous wetland communities. Using NMS ordination analysis revealed some important useful information, but the same data could be analysed in different ways and compared with the current results.

The study would have benefited from more intensive sampling especially for SWV. Additional data such as climatic condition, grazing and fire could also be valuable in finding patterns that best explain variation of plant communities. Kent & Coker (1996) suggested that factors such as grazing, burning and human impact were often important, but it might be difficult to obtain reliable and consistent data on these variables. The following should be considered for similar future studies:

- Further research should be carried out to refine the data, more especially for the SWV since the dataset was small, leading to less information that can be used to define communities.
- Climate data should be collected for all the plots in order to identify the ecological response of species to climatic change and to define the most important climatic driver as the one that explains the distribution of species along a gradient. Hydrological conditions should also be considered when doing a study of this type.
- The classified wetland vegetation communities can be used to track wetlands with similar vegetation that have been visited. The information can also be used to better understand the distribution of wetlands throughout the country.
- The susceptibility of wetlands plant communities to alien invasion needs more attention. Conservators and managers should look into environmental factors that lead to alien invasion like overgrazing and nutrient availability that allows invasive species to take over.
- Field guides should be updated with wetlands plants to aid the wetland practitioners in identification of wetlands common species.
- Finally, when lists of indicator species are available for every region in the country, field guides can be developed that can help conservationists to identify indicator species for wetland health and assess the ecological conditions (Sieben, 2011).

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This form provides a standardized format for the collection of wetlands vegetation data.

South African Wetland Vegetation Survey - Field Dataform							
Releve number:		Date:		Area / Study			
Surveyor(s):		Latitude:		Wetland name:			
		Longitude:		Slope			
Plot size:		Altitude:		Aspect			
Vegetation structure:							
Layer:		Cover:		Av. Height		Dominants	
						Growth form	
Total cover:							
Wetland and habitat description:							
HGM Unit:		Hydroperiod:		Water velocity:			
Landscape setting:		Inundation depth:		Salinity:			
Urban/Rural/Pristine		Groundwater table:		Water source:			
Disturbance				Geology:			
Soil description:							
Texture of top soil		Mottling present:		Soil sample taken:			
Colour of top soil:		Soil depth:		yes/no			
Soil form:		Deep layer:					
Braun-Blanquet cover-abundance scale							
r = 1-2 ex, + = 3-10 ex, 1 = 11-100 ex, 2m = > 100 ex, <5%, 2a = 5 - 12.5%, 2b = 12.5 - 25%, 3 = 25 - 50%, 4 = 50 - 75%, 5 = 75 - 100%							
Vegetation sample:							
Species	Layer	Cover	Coll. Number	Species	Layer	Cover	Coll. Number
				Total number of species:			
Notes:							