The Ecology, Plant Functional Composition and Ecosystem Services Across a Range of the Afromontane and Afroalpine Palustrine Wetlands in Lesotho

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GENERAL ABSTRACT

Although wetlands are among the most socio-economically and ecologically valuable ecosystems worldwide, global coverage and condition of wetlands is declining, both to the detriment of ecosystem service delivery. Classification and description of wetland vegetation provide an understanding of how wetland vegetation is related to its environment, as well as the associated spatial variation and information for biodiversity conservation and water resource management. Furthermore, understanding the distribution of wetland ecosystem services across landscapes is essential for planning the conservation of the wetlands for a sustainable provision of the services. This study aimed to achieve four main objectives: (1) to classify and describe the Afromontane wetland vegetation in Lesotho, (2) to classify and describe the montane palustrine wetland vegetation of the Maloti-Drakensberg and the surrounding areas, (3) to assess the plant functional composition of the Afromontane palustrine wetlands of Lesotho and link this to environmental variables, and (4) to assess the Afromontane palustrine wetland ecosystem services in Lesotho and link them to environmental factors and functional traits, as well as to assess the level of threat to the delivery of the services.

For the first objective, data on vegetation and different environmental variables were collected from the Afromontane wetland vegetation in Lesotho using the Braun-Blanquet method and a recommended protocol developed for environmental information of wetlands in South Africa, respectively. Regarding the second objective, the montane subset of the National Wetland Vegetation Database of South Africa (also collected using the same methods) was selected and coupled with the new data collected from the Lesotho part of the Maloti-Drakensberg. To achieve the third objective, in addition to the data collected for the first objective, plant functional trait data were also collected from the Afromontane wetlands of Lesotho using methods recommended in literature. For the purposes of the fourth objective, the WET-EcoServices tool was used to collect data on wetland ecosystem services and this was coupled with the data collected for the first and third objectives. For all the objectives, the data were analysed mainly by means of clustering, indicator species analysis and ordination techniques.

The study distinguished 22 Afromontane wetland plant communities in Lesotho and these displayed a high level of diversity in terms of species richness. With respect to species composition and diversity, the communities at higher altitudes were more diverse and were quite different from those at lower altitudes. While the higher-altitude communities mainly exhibited the dominance of C_3 plants, those at lower altitudes were mainly dominated by C_4 species. As revealed by the ordination, variation in the wetland vegetation in the country was mainly related to altitude, longitude (directly correlated with rainfall in the context of Lesotho), slope, inundation, soil parent material, landscape, potassium content, total organic carbon, soil texture, nitrogen, electrical conductivity and latitude. In terms of distribution, the occurrence of some plant communities was limited to either the Lowlands or Highlands, while others were widely distributed along the altitudinal gradient, occurring in both regions. For the Maloti-Drakensberg montane palustrine wetlands, the classification produced 42 wetland plant communities, which were summarised into 16 major vegetation types. These major vegetation types were rich in species and also displayed remarkable variation along the altitudinal gradient. This variation was mainly attributed to changes in the conditions of the environment that include the amount of precipitation, temperature and the underlying parent material. The ordination indicated that the variation in the vegetation types could more specifically and mainly be ascribed to variation in altitude, longitude, latitude, nitrogen content, soil depth, inundation depth and electrical conductivity. However, slope, pH, total organic carbon, sodium content, soil texture and degree of wetness were also important factors. Furthermore, with respect to species composition, significant variation was also observed between higher-altitude and lower-altitude plant communities. In terms of distribution, the montane wetland vegetation was more concentrated in the Maloti-Drakensberg than the other parts of the region, although some vegetation types also occurred in the lower altitudes of Lesotho and in all of the South Africa provinces.

In terms of plant functional composition, eight plant functional types were obtained from the functional classification of the plant species in the Afromontane wetlands in Lesotho. The functional types were dominated by plants with C_3 photosynthetic pathway, particularly in the high-altitude wetlands. Plant communities in the Lesotho exhibit the coexistence of species from different plant functional types, which highlights functional differentiation to exploit microhabitat heterogeneity. Both functional traits and functional composition of the communities were mainly and broadly influenced by altitude, longitude and slope, and more finely by edaphic factors that include electrical conductivity, total organic carbon, nitrogen, clay percentage, potassium, magnesium and calcium. Thus, functional differentiation of wetland vegetation along environmental gradients was demonstrated in this study. Furthermore, the study highlights the possibility of alterations in plant functional traits, types and functional composition in the face of environmental alterations, including climate change.

Although the wetlands were all important for ecosystem service delivery, higher-altitude wetlands differed distinctively from the lower-altitude wetlands in the services they deliver most. The highest scoring ecosystem services for the higher-altitude wetlands were carbon storage, provision of natural resources, streamflow regulation, maintenance of biodiversity and erosion control, while natural resources, cultivated foods, nitrate removal, phosphate trapping and streamflow regulation scored highest for the lower-altitude wetlands. The most important environmental factors influencing the delivery of wetland ecosystem services in this study were altitude, longitude, landscape, soil parent material, slope and soil depth. The delivery of ecosystem services was also correlated with the functional traits of the dominant plant species in each wetland type where specific leaf area, total dry mass, shoot mass, root mass, rooting depth and plant height were the most important traits influencing ecosystem service delivery. For example, carbon storage and maintenance of biodiversity were positively correlated with plant shoot mass, total plant biomass and rooting depth, while specific leaf area and root/shoot mass ratio had a positive and strong correlation with supply of natural resources, cultivated foods and cultural significance. The ecosystem services provided by a given wetland are thus dependent on the location and environmental characteristics of the wetland within a catchment and the functional characteristics of the dominant wetland plant species. However, the supply of ecosystem services in Lesotho is threatened, with the level of threat higher in the lower-altitude than in higher-altitude wetlands. The threats, which are largely anthropogenic, are mainly associated with crop cultivation, overgrazing and trampling by livestock and economic development.

The diversity exhibited by the wetlands in Lesotho and the Maloti-Drakensberg, coupled with their restricted habitat and distribution at high altitudes, capacity to support endemic species, their role in water resources and supply of other ecosystem services, points to the high conservation value of these ecosystems, particularly in the face of biodiversity loss and climate change. Thus, given the reported threats, the conservation of these montane palustrine wetlands is indispensable and should be set as a priority. Based on these findings that can contribute the information needed for biodiversity conservation planning and sustainable provision of wetland ecosystem services in Lesotho and beyond, the study recommends urgent attention and up-scaling of the conservation efforts to protect these Afromontane palustrine wetlands and the services they provide.

Keywords
Afromontane
Biodiversity
Carbon storage
Climate change
Community-weighted mean
Conservation
Ecosystem function
Ecosystem service
Functional composition
Maloti-Drakensberg
Mountain
Ordination
Palustrine wetland
Phytosociology
Plant community
Photosynthetic pathway
Plant functional trait
Plant functional type
Threat
Vegetation classification
WET-EcoServices

DECLARATION

I, Peter Chatanga (Student number: 217079718), declare that the work presented in this thesis is my own original work and has not been presented in whole or in part for the award of a degree at any other university. This thesis is being submitted for the degree of Doctor of Philosophy in Environmental Science in the School of Agricultural, Earth and Environmental Sciences at the University of KwaZulu-Natal, Westville, South Africa. Any assistance received is fully acknowledged. However, some of the results chapters have been published in different journals with my supervisors and other people who contributed in various ways, as co-authors.

[redacted] ________________________ Date: 10 December 2019

Peter Chatanga (PhD Candidate)

____ Date: ______________________

Dr. Erwin J.J. Sieben (Supervisor)

____ Date: ______________________

Dr. Tom W. Okello (Co-supervisor)

DEDICATION

I dedicate this doctoral thesis to my son (Matinzwaishe Hallowed Chatanga) who was born during the course of this study and could not get enough fatherly attention because of the commitments related to the PhD studies. I also dedicate this work to all people who love and care about nature and the natural environment, including palustrine wetland ecosystems. Above all, this thesis is also dedicated to the Almighty God, the creator of nature, biomes, ecosystems (including montane palustrine wetlands) and ecological communities.

Frontispiece

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LIST OF ACRONYMS AND ABBREVIATIONS

a.s.l.	Above sea level
CCA	Canonical Correspondence Analysis
CWM	Community-weighted mean
DWAF	Department of Water Affairs and Forestry
ES	Ecosystem services
HCA	Hierarchical cluster analysis
HGM	Hydrogeomorphic
IPBES	Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
ISA	Indicator species analysis
LHWP	Lesotho Highlands Water Project
MDTP	Maloti Drakensberg Transfrontier Park
MEA	Millennium Ecosystem Assessment
ORASECOM	Orange-Senqu River Commission
PFTs	Plant functional types
RDA	Canonical Redundancy Analysis
SADC	Southern African Development Community
SANBI	South African National Biodiversity Institute
SAWCS	South African wetland classification system
SLA	Specific leaf area
TEEB	The Economics of Ecosystems and Biodiversity
UNWWAP	United Nations World Water Assessment Programme
WC	Wetland cluster

CHAPTER 1: GENERAL INTRODUCTION

1.1 Background to the Study

Wetlands and biodiversity degradation and loss form two of the ten most pressing global environmental issues (McNeely et al., 2005). More than 50% of the world's wetlands have already been lost since 1900, largely due to anthropogenic factors (UNWWAP, 2003; Rolon & Maltchik, 2006; Moreno-Mateos et al., 2012; Russi et al., 2013; Daryadel & Talaei, 2014; Davidson, 2014; Mitsch & Gosselink, 2015). A global review on wetland loss (Davidson, 2014) reports a 57–61% loss for natural inland wetlands alone. The Global Wetland Outlook, published recently by the Ramsar Convention on Wetlands (2018), presents a gloomy picture about the status and trends of wetlands across the globe. It reports that between 1970 and 2015, wetland decline has been estimated at 35%, which is three times the rate of forest loss. Southern Africa is no exception to the global trend of continued degradation and loss of wetlands (Taylor et al., 1995; Breen et al., 1997). For example, in excess of 50% of the wetlands in South Africa have been destroyed (Day & Malan, 2010; Van Ginkel et al., 2011). Many wetlands have reportedly been lost in Lesotho as well and the majority of the remaining ones have numerous signs of degradation (Meakins & Duckett, 1993; Turpie et al., 2014a, b).

Concomitantly, populations of wetland dependent species follow the same trend of overall wetland loss (Millennium Ecosystem Assessment, 2005b; Russi et al., 2013). With this loss of wetlands, human welfare is also being threatened at a time of increasing water scarcity and demand (Daryadel & Talaei, 2014) and decreasing sources of livelihoods. Constraints to wetland conservation and management are, inter alia, the lack of understanding of the factors influencing the processes and functioning of wetlands (Rolon & Maltchik, 2006; Daryadel & Talaei, 2014; Sieben et al., 2014a; Mitsch & Gosselink, 2015; Irvine et al., 2016), the importance and value of wetlands (Turner et al., 2000; Rolon & Maltchik, 2006; Mitsch & Gosselink, 2015; Irvine et al., 2016), and the link of wetland ecosystem processes and functioning to the socio-economic services they deliver (Day & Malan, 2010; Maltby & Acreman, 2011; Gopal, 2015).

Wetlands are "land areas where surface water collects or underground water discharges to the surface, making the area wet for extended periods of time" (Cowardin et al., 1979; Collins, 2005; Ewart-Smith et al., 2006; Reddy & DeLaune, 2008). The presence of water, whether permanent or seasonal, is the primary determinant for wetland habitats and the associated vegetation (Mucina & Rutherford, 2006). Freshwater palustrine wetlands are distinctive ecosystems in many landscapes across the globe and can be regarded as isolated “islands” within terrestrial environments. Palustrine freshwater wetlands are non-tidal wetlands characterised by plant communities and all such wetlands that are found within tidal areas where salinity derived from ocean salts is below 0.5 parts per thousand and can exist within or directly adjacent to the riverine, lacustrine or estuarine ecosystems (Mitra et al., 2003; Mitsch & Gosselink, 2015). They also include wetlands without vegetation but characterised by the following: (1) area not exceeding 8 ha; (2) lack of active shoreline features formed by bedrock or waves; (3) depth of water at the deepest part of the basin of not more than two metres at low water level; and (4) salinity resulting from ocean salts of not more than 0.5 parts per thousand (Mitsch & Gosselink, 2015). Palustrine wetlands, perhaps the most diverse of all wetland types, make up approximately 95% of the world’s wetlands (Mitsch & Gosselink, 2015).

Covering about 6% of the earth’s land surface, palustrine wetlands are among the most ecologically sensitive, while at the same time are very important ecosystems globally, in part because of their distinct role in biogeochemical cycles (Williams, 1990; Mitsch & Gosselink, 2000; Adedipe et al., 2005; Erwin, 2008; Maltby & Acreman, 2011; Junk et al., 2013; Mitsch & Gosselink, 2015). These ecosystems are unique habitats within terrestrial environments that harbour a lot of biodiversity and are among the most productive and socio-economically valuable ecosystems globally (Millennium Ecosystem Assessment, 2005b; Brander et al., 2006; Niu et al., 2012; Mitsch & Gosselink, 2015).

Traditionally, wetlands were viewed as wastelands and concomitantly, large areas of wetlands have been mined, drained or modified for other land uses that include agriculture, water abstraction, infrastructure development and other developmental activities (Kennedy & Mayer, 2002; Brand et al., 2013; Brander et al., 2013). However, because of their critical role in providing a range of ecosystem services for human sustenance and for the ecosystem as a whole (Millennium Ecosystem Assessment, 2005b; Macfarlane et al., 2007; SADC, 2008; Russi et al., 2013), the value of wetlands is now well recognised globally. The interest in the conservation of wetlands worldwide bloomed in the 1970s following a concern about the rate at which wetlands were being lost or degraded (Daryadel & Talaei, 2014). This paradigm shift has been ascribed to the adoption of the Ramsar Convention in the 1970s, as well as to more research conducted on the wetlands, which have unveiled the significance of these sensitive and fragile ecosystems (Brand et al., 2013).

Subsequently, palustrine wetlands are now viewed as irreplaceable environmental components, which are highly threatened globally due to a myriad of anthropogenic activities (Millennium

Ecosystem Assessment, 2005b; Ewart-Smith et al., 2006; Brown & Cook, 2014; Mitsch & Gosselink, 2015). Wetlands in general are central to the delivery of ecosystem services because of their key role in the hydrological cycle and many other biogeochemical cycles (Mitsch & Gosselink, 2015), and they are often linked to an alternative metabolism under anaerobic conditions (Cronk & Fennessy, 2001; Mitsch & Gosselink, 2015). Wetlands come second after rain forests in the diversity of plants and animals that rely on them for feeding, breeding and habitat (Munishi et al., 2011). Wetlands harbour more than 40% of the species of all life forms globally (Mitra et al., 2003; Hu et al., 2017). They also make a significant contribution to the overall vascular plant diversity, particularly for angiosperms (Sieben et al., 2017b). Their ecosystem services per unit area are typically higher than those of other types of ecosystems (CBD Secretariat, 2015).

Particularly because of their capacity to provide a range of ecosystem services and to reduce the risk of disasters such as droughts and floods, the conservation of wetlands becomes indispensable in the face of climate change and its impacts that include increased water scarcity. Moreover, given their role in harbouring high biodiversity and forming the basis of extensive food chains that also extend beyond their boundaries, wetland ecosystems are important conservation sites (Howard-Williams & Thompson, 1985; Rolon & Maltchik, 2006). Wetlands provide up to 40% of the world's renewable ecosystem services (Zedler & Kercher, 2005). Montane wetlands, in particular, are important in the ecology and hydrology of the local environment and downstream systems of rivers whose catchments are in those montane areas. Montane wetlands occur within the headwaters of the major river basins and provide water for many transboundary rivers (Chatterjee et al., 2010). Because they represent the headwaters of those rivers, their importance actually extends to the entire river system. Thus, these wetlands are considered to be of international importance, even though they are generally absent from the Ramsar designated wetland lists, which are focused more on extensive flat marshy areas that form the main habitat for water birds. Furthermore, hundreds of rivers in southern Africa often originate in wetlands (Taylor et al., 1995).

While freshwater palustrine wetlands are a common feature in many regions across the globe, they vary to a large extent and there are distinct differences among them in terms of hydrology, soil types, ecosystem functioning, plant communities and species richness (Reddy & DeLaune, 2008; Brand et al., 2013; Tiner, 2017). Thus, different classification systems are used to categorise wetlands. Cowardin et al. (1979) define a useful classification system that is based on ecological systems, which broadly recognises five major types of wetlands, namely, Marine, Estuarine, Riverine, Lacustrine and Palustrine wetlands. A top-down and more focused wetland classification system (Kotze et al., 2007; Macfarlane et al., 2007; Ollis et al., 2013; Ollis et al., 2015), which is based on the hydrogeomorphic (HGM) characteristics of the wetlands, was developed and is now widely used in South Africa. The HGM system is based on the wetland geomorphic setting, the source of water and the way in which the water flows into, through and out of the wetland (Ollis et al., 2013; Ollis et al., 2015).

Because of the many types of environmental changes such as climate change and degradation that are expected to have a negative impact on wetlands, Sieben et al. (2014a) emphasise the need for an understanding of the link between plant community composition and the physical environment in wetlands. Environmental factors such as geological substrate, altitude, edaphic characteristics, land use, water chemistry and hydrological fluctuations are regarded as predictors for richness, composition and structure of plant communities in wetland ecosystems (Rolon & Maltchik, 2006). Vegetation is the most conspicuous feature of wetlands, which also plays a fundamental role in their functioning (Cronk & Fennessy, 2001; Sieben et al., 2010a). As primary producers, plants are the most important component of wetland systems because they provide habitat for other organisms (Howard-Williams & Thompson, 1985; Rolon & Maltchik, 2006). Primary producers influence ecosystem functioning not only by forming the primary pathway for energy flow through the ecosystem, but also by providing a link between the abiotic and biotic components of the ecosystems through processes such photosynthesis, absorption and assimilation, and decomposition (Mitsch & Gosselink, 2015). Furthermore, the vegetation of a wetland gives a characterisation of the habitat types within the wetland system (Sieben, 2011).

While three important factors (geomorphology, hydrology and vegetation), which are closely interlinked, underpin the general functioning of a wetland system (Turner et al., 2000; Collins, 2005; Macfarlane et al., 2007; Maltby & Acreman, 2011; Kotze et al., 2012; Mitsch & Gosselink, 2015), local climate and hydrological regime are the two important determinants of the composition and structure of wetland vegetation (Kotze & O'Connor, 2000). Kotze and O'Connor (2000) and Sieben et al. (2010b) observe that the structural and functional features of a wetland are strongly related to the degree of soil wetness. This is also confirmed by Brand et al. (2013), who state that hydrogeological conditions and substrates (soil or bedrock) also have more influence on the floristic structure, composition and dynamics in high-altitude montane wetlands than microclimate.

Given that altitudinal gradients are associated with considerable spatial variation in physical features, such as topography, soils and geology (Kotze & O'Connor, 2000; Sharma et al., 2010), a wide variation in wetland plant composition and diversity can be anticipated in Lesotho where the highest point differs altitudinally from the lowest by more than 2000 m. In fact, Sieben et al. (2010a) acknowledge the existence of a substantial number of vegetation types in the montane wetlands of Lesotho. Owing to their high sensitivity to variations in rainfall and temperature, montane regions are more susceptible to climate change (Chatterjee et al., 2010; Lee et al., 2015). Mountain regions are also characterised by sensitive and fragile ecosystems, localised climate in terms of rainfall and temperature, enhanced occurrences of extreme weather events, and natural catastrophes (Sukumar et al., 1995).

Montane wetlands in particular are often rich in endemics as many species remain isolated at these high altitudes (Sharma et al., 2010; Junk et al., 2013). The rates of speciation are often quite high in mountainous regions. By providing isolated habitats with limited possibilities of dispersal between them following colonisation, mountains promote diversification and concomitant speciation (Crochet et al., 2004). Moreover, the diversity of habitats along environmental gradients, which is associated with mountain areas, is thought to provide an opportunity for sympatric (in-situ) speciation to occur (Drovetski et al., 2013). Montane wetlands thus serve as refugia for the biodiversity of high-altitude habitats, which includes many rare and threatened montane species (Jayachandran, 2013).

Wetland vegetation is not only influenced by, but also influences, the hydrology and edaphic factors in the ecosystems (Cronk & Fennessy, 2001; Mitsch & Gosselink, 2015). Because wetland vegetation is azonal (Sieben, 2011; Brand et al., 2013) and responds quickly to changes in local environmental conditions (Cronk & Fennessy, 2001; Sieben et al., 2014a), plant species inhabiting wetlands can be used as indicators of the conditions in the environment and ecological changes occurring in these ecosystems (Schulze et al., 2002; Sieben et al., 2014a; Mitsch & Gosselink, 2015). Additionally, plants also provide important information about the factors that influence wetland structure because they are fixed, having to cope with year-round stresses and variability in the hydrological regime and climate (Sieben et al., 2010a). Hence, wetland vegetation can also be used in wetland classification (Sieben et al., 2014a).

Following the paradigm shift from emphasising the conservation of specific species and their habitats towards conserving the complex networks of species and large-scale ecosystems, understanding the factors that determine the structure and functioning of wetlands is imperative (Ostfeld et al., 1997). Therefore, the concept of functional diversity (Smith et al., 1997) was developed where plant species are grouped into functional groups, on the basis of similarities in their functional roles within an ecosystem. Plant functional types are groups of plant species that, because they tend to share certain important functional traits, have similar functioning at the organismal level, have similar responses to conditions of the environment and/or similar roles in (or have similar effects on) ecosystems (Cornelissen et al., 2003). Sieben (2012) observes that plant functional types provide an understanding of the adaptations acquired by plants to survive in particular environments. The same author also highlights that plant functional traits can be used to describe the attributes of plant communities in which they occur and communities that are similar in functional composition are likely to exhibit some similarity in ecosystem functioning.

Plant functional traits have been defined as morphological, physiological and phenological attributes, which impact individual fitness through their effects on the survival, growth and reproduction of a plant (McGill et al., 2006; Violle et al., 2007). Plant functional traits do not only give insights into the opportunities and challenges faced by plants in different habitat types, but also provide an understanding of the influence of functional diversity on ecosystem processes and the subsequent ecosystem services (Pérez-Harguindeguy et al., 2013). There is a growing body of literature supporting that ecosystem functions and processes are not only influenced by species richness, but also by their functional characteristics (Grime et al., 1997; Díaz & Cabido, 2001; Lavorel & Garnier, 2002; Garnier & Navas, 2012; Díaz et al., 2013; Zhang et al., 2015). Wetlands are regarded as an important platform for studying plant functional traits (Sieben, 2012) and the study of plant functional traits in wetlands is gaining popularity (Sieben, 2012; Sieben et al., 2014a; Zhang et al., 2015; Lhotsky et al., 2016; Moor et al., 2017; Sieben & le Roux, 2017). However, detailed measurements of functional traits of wetland vegetation are still limited (Sieben, 2012; Moor et al., 2015; Zhang et al., 2015; Lhotsky et al., 2016; Sieben & le Roux, 2017). Moor et al. (2017) further observe that trait-based approaches to the effects of plants on wetland functioning is still lagging behind in comparison to the knowledge base for other types of habitats.

The montane wetlands of Lesotho are critical in supplying ecosystem services, including biodiversity conservation, ecosystem products and water resources. The wetlands constitute an important source and form of freshwater in southern Africa (SADC, 2008). Lesotho is an important watershed and hydrological reservoir for a number of countries in southern Africa (Makhoalibe, 1999; Nüsser & Grab, 2002). For example, the montane wetlands of Lesotho form the headwaters of one of the most well-known and important international watercourses of southern Africa (the Senqu-Orange River) (Olaleye et al., 2012; ORASECOM, 2015), which is important for Lesotho, South Africa and Namibia. Directly and indirectly, wetlands in Lesotho have been estimated to contribute about 30% of the total employment in the country and 22% of the country's gross domestic product (GDP) (Department of Environment, 2014).

Hydrologically, the wetlands in Lesotho are important for, inter alia, water storage, water discharge and recharge, flow attenuation, sediment retention and organic material production and export (Grobbelaar & Stegmann, 1987). The Lesotho highlands represent a key water resource for both Lesotho and South Africa, and wetlands play a critical role in the supply of water and hydroelectric power generation. The watersheds of the highlands of Lesotho are considered an essential catchment for the Lesotho Highlands Water Project (LHWP), whose responsibility is to transfer water to South Africa (Grab & Deschamps, 2004). A study by the Maloti Drakensberg Transfrontier Park (MDTP) (2007) highlights that the montane wetlands of Lesotho, though rapidly degrading, are unique and play a pivotal role in providing a sustainable supply of high quality water throughout the year. Thus, Lesotho is considered the "water factory" of southern Africa because it is one of the few places where annual precipitation exceeds evaporation, giving rise to a net run-off (MDTP, 2007; Ellery et al., 2009).

1.2 Rationale of the Study

Notwithstanding their widespread distribution across the continent, knowledge of the African wetlands is still incomplete and inadequate to support the needs for effective management of the ecosystems (Rebelo et al., 2010). Montane wetlands in general, because they are not fully understood, are degraded for short-term gains, despite being central to water, food and environmental security (Singha, 2011). Additionally, despite their uniqueness and importance, detailed vegetation surveys on the Lesotho wetlands have been scarce and scattered (Sieben, 2011). Limited understanding of the link of wetland ecosystem processes and functioning to socio-economic services inevitably leads to unsustainable utilisation and poor policy decisions. The need for more information on wetland vegetation to enhance the conservation, monitoring, restoration and management of wetlands in southern Africa has been emphasised (Mucina & Rutherford, 2006; Sieben, 2011).

Although many studies have been conducted in the wetlands of the surrounding South Africa where a central National Wetland Vegetation Database has been established from data collected from all over the country (Sieben et al., 2014a), no detailed countrywide study has been carried out on the wetlands of Lesotho. Furthermore, Sieben et al. (2014a) highlight that there are neither current nor recent studies on the Lesotho wetlands and Sieben et al. (2016c) emphasise the need for more information on wetland species composition, ecology and distribution. A recent study (Wondie, 2018) also reports that wetland ecosystem services remain poorly documented and under-researched, especially in the African nations. Considering that environmental factors driving wetland community composition differ spatially among geographical locations and among various types of the wetlands (Sieben et al., 2014a) and that wetlands exhibit high geographical variation (Macfarlane et al., 2007), area-specific studies of wetlands are needed. Moreover, the Ramsar Convention does not only emphasise the conservation and wise use of wetlands, but also encourages research and exchange of information regarding wetlands and their biodiversity (Ramsar Convention Secretariat, 1971). In addition, recent studies (Irvine et al., 2016; Sieben et al., 2016c) emphasise that the ecology, hydrology and social-ecology of montane palustrine wetlands is generally poorly understood. Lesotho's national strategy on biological diversity also explicitly calls for research on the importance and ecology of wetlands in the country (National Environment Secretariat, 2000).

Most of the wetland vegetation surveys conducted in Lesotho were descriptive studies based on expert opinion, rather than on formal assessment methods. Only one study (van Zinderen Bakker & Werger, 1974), which was conducted more than four decades ago, made an attempt to assess in detail the wetland vegetation of Lesotho. However, the study concentrated on only three wetlands at an altitude of 3200 m and did not consider detailed environmental information except for pH. A few other studies concentrated on a few wetlands in localised areas of the country and are either outdated (Guillarmod, 1962, 1963) or are limited in detail on some important information (Grobbelaar & Stegmann, 1987; Du Preez & Brown, 2011; Brand et al., 2015). In addition, only a couple of studies (Sullivan et al., 2008; Lannas & Turpie, 2009), which also concentrated on few wetlands, attempted to assess the ecosystem services provided by the wetlands. It is also noteworthy that no study has been conducted on the functional traits of wetland plants in the country. Moreover, knowledge on how wetland properties and vegetation vary along major environmental gradients in Lesotho is lacking. Therefore, the current study attempts to address these gaps. The study also provides vital baseline information against which the success of management interventions and future environmental changes can be assessed.

1.3 Aim, Objectives and Key Research Questions

1.3.1 Aim

Because of their remarkable diversity, uniqueness, and ecological and socio-economic importance, the Afromontane palustrine wetlands of Lesotho require ecological studies to inform their conservation planning and management for sustainable provision of ecosystem services. This study is the first to make a detailed countrywide ecological survey of the palustrine wetlands. Hence, to improve the knowledge on wetland ecology and ecosystem service provision, and to better inform wetland policy and decision-making in Lesotho, the study developed the following aim:

- To classify the vegetation and assess the vegetation-environment relationships, plant functional composition and ecosystem services of the Afromontane palustrine wetlands of Lesotho

1.3.2 Study Objectives

The study intends to achieve the above-stated aim by addressing the following objectives:

I. To classify and describe the Afromontane wetland vegetation of Lesotho
II. To classify and describe the montane wetland vegetation of the entire Maloti-Drakensberg region and the surrounding areas
III. To assess the plant functional composition of the Afromontane palustrine wetlands along an altitudinal gradient in Lesotho and link this to environmental variables
IV. To assess the Afromontane palustrine wetland ecosystem services in Lesotho and link them to environmental factors and functional traits

1.3.3 Key Research Questions

This study intends to achieve its objectives by addressing the following pertinent questions on the Afromontane palustrine wetlands of Lesotho:

1. Which plant communities are associated with the palustrine wetlands in the country?
2. What are the vegetation types of the montane wetlands of the Maloti-Drakensberg region and the surrounding areas?
3. What is the influence of major gradients (geological substrate, altitude and west-east/ dry-wet) on wetland environment and the vegetation in Lesotho and the Maloti-Drakensberg and the surrounding areas?
4. What is the influence of major environmental factors on the distribution and diversity of wetland plant communities and species?

5. Which wetland plant functional types occur in Lesotho and what are some of the major plant functional traits displayed by the wetland plants and how do they relate to environmental gradients and explanatory variables?
6. How does wetland plant functional composition vary with environmental gradients and explanatory variables?
7. What ecosystem services are provided by the wetlands in Lesotho and how do they relate to environmental factors?
8. How does wetland ecosystem service delivery compare between higher-altitude and lower-altitude wetlands?
9. What is the relationship of wetland ecosystem services to wetland plant functional traits?
10. What is the level of threat faced by wetland ecosystem services in Lesotho and how do the threat level compare between higher- and lower-altitude wetlands?

1.4 Structure and Outline of the Thesis

This thesis comprises eight chapters (Table 1.1). The thesis is structured in such a way that most of the chapters are stand-alone papers (particularly the results chapters), although the main themes under investigation are interlinked (Figure 1.1). Given such a format, some degree of overlap is unavoidable, especially in terms of some concepts, some aspects of the study area and the methods. Nevertheless, for consistency in the thesis, some formatting and editorial differences may be found between the published versions and the versions that appear in the chapters in this thesis.

Chapter 1 (General Introduction) sets the background and context, and outlines the problem statement, rationale, aim, objectives and research questions of the study. The review of literature on palustrine wetlands, including their global distribution and extent, environment factors, biodiversity, loss and threat factors, ecosystem services and conservation, is provided in Chapter 2. Chapter 3 describes the area in which the study was conducted (the country of Lesotho and the Maloti-Drakensberg). The results of the study are presented in Chapters 4 – 7 and two of the chapters have been published in different journals, while the third is still in review and the fourth is almost ready for submission (Table 1.1). One of these chapters has also been presented at a conference, while another has been accepted for presentation (Table 1.1). Chapters 4 and 5 present the classification, description and environmental factors of the Afromontane wetlands in Lesotho, and the entire Maloti-Drakensberg region, respectively. This is followed by the exploration of the plant functional composition of the Afromontane palustrine wetlands that exist along the altitudinal gradient in Lesotho and the linkage to environmental factors (Chapter 6). Chapter 7 focuses on the assessment of ecosystem services delivered by the Afromontane wetlands of Lesotho and the relationship of the services to environmental factors and plant functional traits. The level of threat faced by the wetlands in the provision of ecosystem services is also reported in the same chapter. The last chapter (Chapter 8) concludes the entire study by summarising the key findings, conclusions, recommendations and research needs identified from the study.

Table 1.1: Chapters making up the thesis

Chapter	Title/ Theme	Co-author(s)	Journal	Current status
Chapter 1	General introduction			
Chapter 2	Literature review			
Chapter 3	Study area			
Chapter 4	Ecology of palustrine wetlands in Lesotho: Vegetation classification, description and environmental factors	E.J.J. Sieben	Koedoe	Published
†Chapter 5	Classification, description and environmental factors of montane wetland vegetation of the Maloti-Drakensberg region and the surrounding areas	D.C. Kotze, M. Janks & E.J.J. Sieben	South African Journal of Botany	Published
§Chapter 6	Variation in plant functional composition of the Afromontane palustrine wetlands along an altitudinal gradient in Lesotho	E.J.J. Sieben	Plant Ecology	Almost ready for submission
Chapter 7	Ecosystem services of high-altitude wetlands: The case of Lesotho Afromontane palustrine wetlands	D.C. Kotze, T.M. Okello & E.J.J. Sieben	Ecosystem services	In review
Chapter 8	General conclusions and recommendations			

†Chapter also presented (as a poster) at the 2018 National Wetlands Indaba, 8-11 October 2018, at the Mittah Seperepere International Convention Centre in Kimberly, South Africa.
§Chapter has also been accepted for oral presentation at the SAAB2020 (46th Annual SAAB) Conference, 7-10 January 2020, at University of the Free State, QwaQwa Campus, Phuthaditjhaba, South Africa.

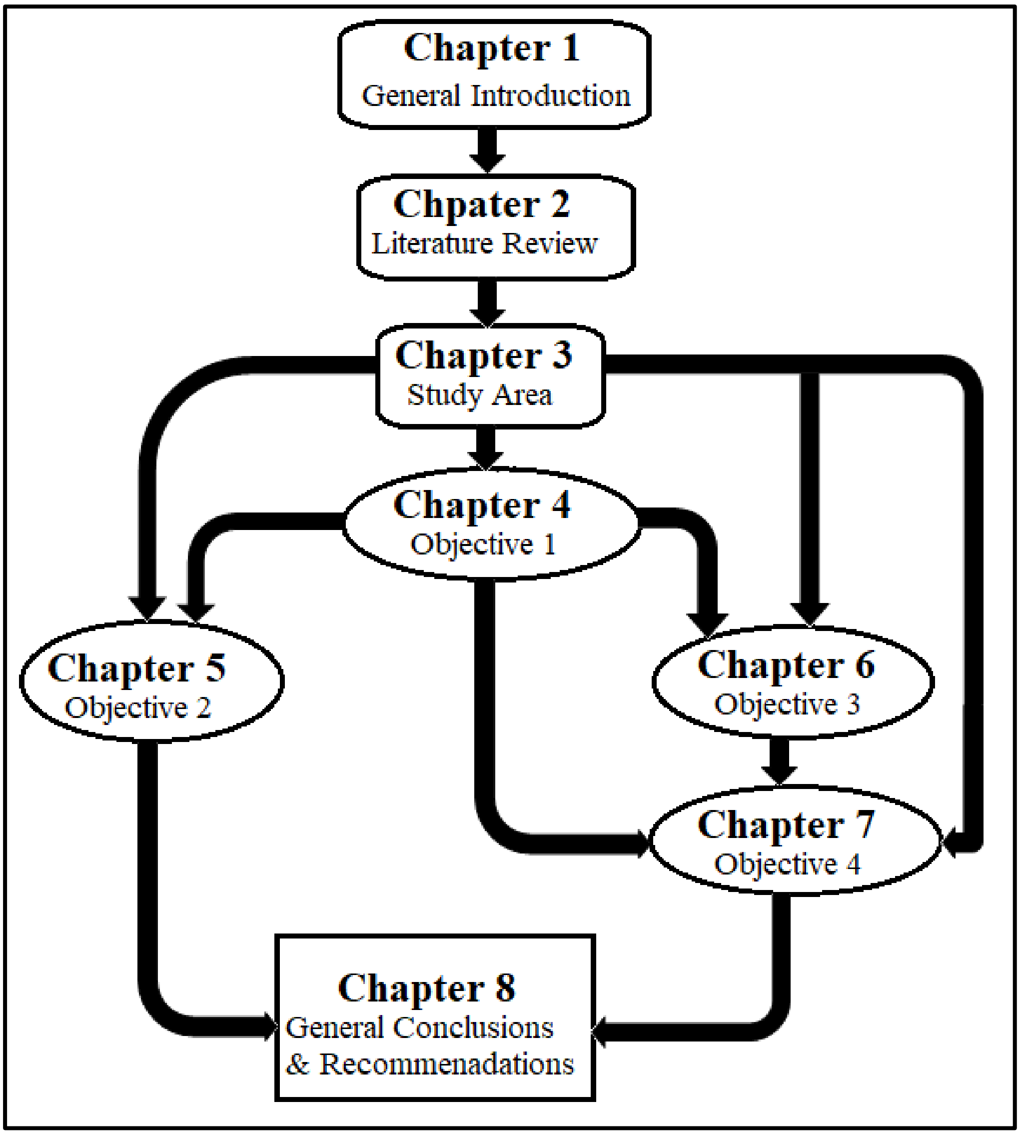


Figure 1.1: Linkages among the chapters making up the thesis

CHAPTER 2: LITERATURE REVIEW

2.1 Introduction

Wetlands are among the most productive and important ecosystems worldwide. There is a need to understand and enhance knowledge and sustainability in the functioning of these sensitive and fragile systems. Much research has been directed towards various aspects of these ecosystems. A considerable amount of interest has been building with regard to the understanding of wetlands, their ecosystem services and conservation (Zhang et al., 2010; Stelk & Christie, 2014). Global trends in wetland research highlight a continuous growth in the literature on wetlands, especially after 1990 (Figure 2.1 and Table 2.1) (Zhang et al., 2010). In their review, Zhang et al. (2010) report that global studies on wetlands mainly focus on the ecology, vegetation, biodiversity and conservation, water quality improvement, circulation of materials (biogeochemical cycling), wetland restoration, artificial wetlands, ecosystem services and the economic valuation of the services delivered by wetlands. The review also predicts that the number of scientific publications with a focus on wetlands will still grow in future, with artificial wetlands and wetland biodiversity being the main areas of interest.

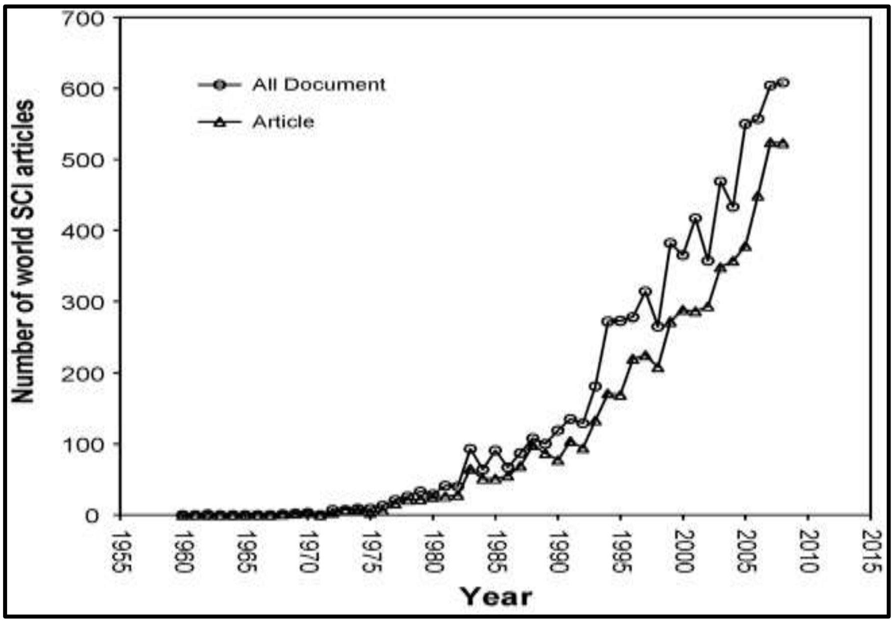


Figure 2.1: Number of Science Citation Index publications, which referred to "wetland" and "wetlands", over time. Reproduced from Zhang et al. (2010).

A summary of examples of studies carried out in different areas of the world, covering various aspects of wetland ecosystems is presented in Table 2.1. While Figure 2.1 indicates an incredible increase in wetland research globally, not much attention has been paid to the wetlands of Lesotho recently, particularly with regard to vegetation and ecosystem services.

Much of the wetland research conducted in Lesotho has emphasised wetland soils (Olaleye & Sekaleli, 2011; Olaleye et al., 2012; Mapeshoane, 2013; Olaleye, 2016). Furthermore, Table 2.1 highlights that, while some wetland aspects have been studied quite widely (e.g. wetland environments), others have received very little attention (e.g. plant functional traits and ecosystem services).

This chapter reviews related literature and provides an overview of wetland ecosystems, their ecology and socio-economic and ecological significance. The chapter begins by defining wetlands and presenting their global distribution and extent, typology and classification. The factors characterising wetland environments, wetland vegetation and wetland plant functional traits are also explored. Further, the importance of wetlands, particularly the socio-economic and ecological roles of these ecosystems is also reviewed. The question of how much wetland area has been lost and what are the main threats implicated in the loss and degradation is also addressed. The chapter also discusses the options currently employed in the management and conservation of wetlands. The last section concludes the chapter and provides the knowledge gaps identified during the review of literature.

Table 2.1: Examples of major studies conducted on various aspects of wetlands

Main aspect of wetlands	Country/ area of study	Publications
General description of wetland ecosystems (environment)	Global	Millennium Ecosystem Assessment (2005b); Moreno-Mateos et al. (2012); Junk et al. (2013); Gopal (2016)
	United States of America	Cowardin et al. (1979); Sather and Smith (1984); Snodgrass et al. (2000); Mitsch et al. (2014); Cohen et al. (2016); Tang et al. (2017)
	African continent	Hughes and Hughes (1992); van Dam et al. (2014)
	Southern Africa	Hughes and Hughes (1992); Taylor et al. (1995)
	South Africa	Collins (2005); Ewart-Smith et al. (2006); DWAF (2007); Macfarlane et al. (2007); Ellery et al. (2009); Day and Malan (2010); Riddell (2011); Sieben (2011); Sieben et al. (2011, 2014a, b, 2017b); Grundling (2014); Junk et al. (2014); Ollis et al. (2015)
	Lesotho	Guillarmod (1962, 1963, 1972); van Zinderen Bakker and Werger (1974); Meakins and Duckett (1993); Backéus and Grab (1995)
Environmental factors, including soils (edaphic factors)	Global	Gopal (2016)
	United States of America	Sather and Smith (1984); Snodgrass et al. (2000); Anderson and Mitsch (2006); Rolon and Maltchik (2006); Burris and Skagen (2013); Lee et al. (2015); Tang et al. (2017),
	African continent	Hughes and Hughes (1992); van Dam et al. (2014)
	Southern Africa	Hughes and Hughes (1992); Taylor et al. (1995)

	Zimbabwe	Mapaure and McCartney (2001)
	Switzerland	Wettstein and Schmid (1999)
	France	Grasset et al. (2017)
	Canada	Wilson and Bayley (2012)
	South Africa	Hughes and Hughes (1992); Kotze et al. (1996); Kotze and O'Connor (2000); Collins (2005); Garden (2008); Ellery et al. (2009); Riddell (2011); Sieben (2011); Sieben et al. (2010b, 2014a, b, 2016c, 2017b); Bird (2012); Pretorius (2016)
	Lesotho	Grobbelaar and Stegmann (1987); Grab and Deschamps (2004); Grab (2010); Olaleye et al. (2012); Mapeshoane (2013); Grundling et al. (2015); Mats'ela et al. (2015); Olaleye (2016)
Wetland biodiversity	Global	Moreno-Mateos et al. (2012); Gopal (2016); Ramsar Convention on Wetlands (2018)
	United States of America	Sather and Smith (1984); Rolon and Maltchik (2006); Rolon et al. (2010); Mitsch et al. (2014); Tang et al. (2017)
	Southern Africa	Hughes and Hughes (1992); Taylor et al. (1995); Mucina and Rutherford (2006)
	Ghana	Campion and Venzke (2011)
	Asia	Naqinezhad et al. (2009); Kamrani et al. (2011); Gopal (2015)
	Morocco	Green et al. (2002)
	Zimbabwe	Mapaure and McCartney (2001)
	Switzerland	Wettstein and Schmid (1999)
	Canada	Wilson and Bayley (2012); Wilson et al. (2013)
	South Africa	Hughes and Hughes (1992); Kotze and O'Connor (2000); Ellery (2004); Mucina and Rutherford (2006); Sieben et al. (2004, 2010b, 2014a, b, 2016a, b, c, 2017a, b); Sieben (2011); Van Ginkel et al. (2011); Bird (2012); Brand et al. (2013); Janks (2014); Khan et al. (2014); Pretorius (2016)
	Lesotho	Guillarmod (1962, 1963, 1972); van Zinderen Bakker and Werger (1974)
Plant functional traits	Global	de Bello et al. (2010)
	United States of America	Keddy (1983); Boutin and Keddy (1993); Snodgrass et al. (2000); Sutton-Grier et al. (2013)
	China	Zhang et al (2015)
	Sweden	Moor et al. (2015, 2017)
	Hungary	Lhotsky et al. (2016)
	South Africa	Sieben (2012); Sieben et al. (2014a); Sieben and le Roux (2017)
Provision of wetland ecosystem services	Global	Turner et al. (2000); Millennium Ecosystem Assessment (2005b); de Bello et al. (2010); Maltby and Acreman (2011); Junk et al. (2013); Russi et al. (2013); Ghermandi and Fichtman (2015); Mitsch et al. (2015); Gopal (2016)
	United States of America	Sather and Smith (1984); Mitsch and Gosselink (2000); Mitsch et al. (2014); Ricaurte et al. (2014); Stelk and Christie (2014)
	Asia	Gopal (2015)
	African continent	van Dam et al. (2014)
	Sub-Saharan Africa	Rebelo et al. (2010)
	Southern Africa	Taylor et al. (1995)
	Netherlands	Gandarillas et al. (2016)
	Mexico	Camacho-Valdez et al. (2013)
	Sri Lanka	McInnes and Everard (2017)
	Canada	Kennedy and Mayer (2002); Pattison-Williams et al. (2018)

	China	Yang et al. (2008)
	Bangladesh & China	Sun et al. (2017)
	Botswana	Setlhogile et al. (2011)
	South Africa and Lesotho	Kotze et al. (2007); Sullivan et al. (2008); Lannas and Turpie (2009)
Economic valuation of wetland ecosystem services	Global	Turner et al. (2000); Millennium Ecosystem Assessment (2005b); Brander et al. (2006); Russi et al. (2013)
	United states of America and Europe	Lannas and Turpie (2009); Brander et al. (2013); Stelk and Christie (2014)
	China	Yang et al. (2008)
	Mexico	Camacho-Valdez et al. (2013)
	Botswana	Setlhogile et al. (2011)
	South Africa and Lesotho	Sullivan et al. (2008)
Artificial wetlands	Global	Millennium Ecosystem Assessment (2005b); Zhang et al. (2010); Ghermandi and Fichtman (2015)
	United States of America	Mitsch et al. (2013, 2014); Mitsch and Gosselink (2015)
	Canada	Kennedy and Mayer (2002); Wilson and Bayley (2012)
	China	Yang et al. (2008); Niu et al. (2012)
	Finland	Wahlroos et al. (2015)
Threats to, loss and conservation of wetlands	Global	Turner et al. (2000); Millennium Ecosystem Assessment (2005b); Dudgeon et al. (2006); Finlayson (2012); Junk et al. (2013); Daryadel and Talaei (2014); Davidson (2014); Ramsar Convention on Wetlands (2018)
	United States of America	Keddy (1983); Ricaurte et al. (2014); Lee et al. (2015)
	Asia	Gopal (2015)
	Sub-Saharan Africa	Mitchell (2013)
	southern Africa	Taylor et al. (1995)
	Global, Bangladesh, Vietnam, India Canada	Erwin (2008)
	Morocco	Green et al. (2002)
	China	Niu et al. (2012)
	Canada	Kennedy and Mayer (2002)
	Nepal	Singha (2011)
	South Africa	Du Preez and Brown (2011)
	Lesotho	Grundling et al. (2015)

2.2 What are wetlands?

Given that the word wetland is generic, wetlands are diverse and that wetland characteristics are transitional between truly aquatic and purely terrestrial, there is no one, universally adopted definition of a wetland; the definition depends on the objectives and the interest of the user (Cowardin et al., 1979; Collins, 2005; Brander et al., 2006; Bhandari, 2009; Mitsch & Gosselink, 2015; Gopal, 2016). Therefore, many definitions have been put forward (Ramsar

Convention Secretariat, 1971; Cowardin et al., 1979; Kenna, 1990; Cronk & Fennessy, 2001; Collins, 2005; DWAF, 2008; Reddy & DeLaune, 2008). Cowardin et al. (1979), who provide one of the earliest and most widely adopted definitions, define wetlands as "lands transitional between terrestrial and aquatic systems where the water table is usually at or near the surface or the land is covered by shallow water". The same authors also view wetlands in general terms as lands where water saturation is the primary determining factor of the nature of the soil that develops and the types of communities of plants and animals living in the soil and on its surface. Collins (2005) regards wetlands as "areas where surface water collects or underground water discharges to the surface, making the area wet for extended periods of time". Internationally, wetlands are viewed by the Ramsar Convention as "areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish, or salt including areas of marine water, the depth of which at low tide does not exceed six meters" (Ramsar Convention Secretariat, 1971). While a fen is a peat-forming wetland receiving some water from the mineral soil in the surroundings and normally supporting marsh-like vegetation, a bog is a peat-forming wetland with no substantial inflows or outflows of water and harbours acidophilic mosses (Mitsch & Gosselink, 2000; Cronk & Fennessy, 2001).

The different definitions for a wetland have made it difficult for wetland managers, scientists, policy makers and other stakeholders to develop a common understanding of what constitutes a wetland. However, the single feature that all wetland definitions have in common is the substrate or soil, which is at least covered by or intermittently saturated with water. Wetlands often have characteristics of both terrestrial and aquatic ecosystems (Reddy & DeLaune, 2008; Mitsch & Gosselink, 2015; Moor et al., 2017). Wetlands have three important aspects that should be captured in their definition, namely, hydrology, soil wetness and hydrophytic vegetation (Cowardin et al., 1979; Collins, 2005; Maltby & Acreman, 2011; Brand et al., 2013; Mitsch & Gosselink, 2015). By this, an area qualifies to be a wetland if at the minimum it meets one of the following criteria:

- ❖ at least intermittently, the land is predominantly characterised by hydrophytes (macrophytes);
- ❖ the substrate is mainly hydric soil. Hydric soils form under conditions of permanent or seasonal water saturation or inundation, which allow anaerobic conditions to develop in the upper part of the soil profile (Mapeshoane, 2013). Indicators of hydric soils include the presence of redoximorphic features;
- ❖ the substrate is covered by shallow water or saturated with water for a significant period of time during the growing season.

Although it is well known and recognised internationally, the Ramsar definition views wetlands in a very broad sense where dams, lakes, rivers and marine ecosystems are also included, in addition to palustrine ecosystems. According to Maltby and Acreman (2011), the ambiguity within the scientific community on what exactly constitutes a "wetland" is largely in relation to whether or not to include rivers, lakes and marine ecosystems. The broad scope in some of the definitions regards wetlands to be the same as pure aquatic systems and thus ignore the role of vegetation, which forms an important part of wetland environments and determines, to a large extent, its functions and ecosystem services. Despite many definitions having been developed over the years, the old local and common terms are still in use and this adds further to the confusion on what precisely constitutes a wetland (Gopal, 2015).

For purposes of the current study, which focuses on inland palustrine wetlands, I adopted the definition originally developed by Cowardin et al. (1979) in the United States of America and later modified in the South African legislation, as well as by Mitsch and Gosselink (2015). This definition, found in Mitsch and Gosselink (2015) and also in the South African National Water Act (No. 36 of 1998) (DWAF, 2004, 2008; Ollis & Malan, 2014) describes a wetland as "land which is transitional between terrestrial and aquatic systems where the water table is at or near the surface, or the land is periodically covered with shallow water, and which in normal circumstances supports or would support vegetation typically adapted to life in saturated soils". Legal definitions, such as the one found in the South African National Water Act, are necessary for wetland managers and for the conservation of wetlands at the national level because they remain the same. The above definition is consistent with the more precise working definition of wetlands and therefore caters only for a subset of the ecosystems covered in the Ramsar definition; the palustrine wetlands. Furthermore, some of the wetlands covered by the Ramsar definition, such as coral reefs and estuaries do not exist in Lesotho. While the Ramsar definition includes water depth, the South African legislative definition modifies this aspect. Furthermore, Gopal (2016) argues that wetlands are different from deep open-water systems such as lakes, reservoirs and rivers, and thus should be considered separately although fringes of such systems may be considered wetlands.

Unlike the Ramsar definition, the South African legislative definition excludes rivers, estuaries, dams and deep lakes, which is consistent with the current study. This definition can be a solution to the problem of the confusion that arises by the inclusion of systems such as lakes, dams and rivers under the broad wetland definition, as in the Ramsar definition, which takes wetlands to refer to all aquatic ecosystems except deep marine systems (Ollis et al., 2013). The definition is also consistent with Du Preez and Brown (2011) who view wetlands to comprise a wide variety of waterlogged habitats, which include bogs, peatlands, fens, marshes, floodplains, seeps, swamps, pans, estuaries and springs located on various topographical locations and elevations. Given that wetlands are such unique and distinct types of aquatic ecosystems, Ollis et al. (2013) recommend that they should specifically be called palustrine wetlands in order to make a clear distinction from other systems such as rivers, ponds, dams, lakes and other open waterbodies.

2.3 Global distribution and extent of wetlands

Wetlands are found in almost all parts of the globe (Daryadel & Talaei, 2014; Mitsch et al., 2015; Mitsch & Gosselink, 2015). Despite their wide occurrence across the globe, different views on what constitutes a wetland, as evidenced by the various definitions and classification systems, make it difficult to obtain an agreed estimate on the global coverage and distribution of wetlands. Additionally, different regions have different types of wetlands, such as the saline pans that make up the main parts of wetlands in semi-arid regions of South Africa (Sieben et al., 2016b). Lehner and Döll (2004) report that wetlands cover about 9.2 million km^2 of the global surface area and the African continent accounts for 14.33% of this. Initially, Sahagian et al. (1997) estimated wetland coverage to be 1% of the earth's land surface but more recently, Russi et al. (2013) place the estimate at 6.5%. However, it has generally and widely been accepted that wetlands account for about 6% of the global land surface (Adedipe et al., 2005; Erwin, 2008; Maltby & Acreman, 2011; Junk et al., 2013; Russi et al., 2013). This highlights that the global wetland coverage was initially underestimated but the estimate has gone up in recent literature. Regionally, wetlands are estimated to cover about 20% of South America, 10% of North America, 3% of Australia, 7% of China, 10% of Russia, 3% of the tropical and subtropical Asia, 7% of Africa and 5% of Europe (Junk et al., 2013). Inland freshwater or non-tidal wetlands, perhaps the most diverse of all wetland types, make up approximately 95% of the world's wetlands (Mitsch & Gosselink, 2015).

Wetlands also occur widely in southern Africa (UNWWAP, 2003; SADC, 2008; Ellery et al., 2009; Rebelo et al., 2010). Excluding smaller wetlands such as narrow riverine floodplains, smaller seasonal pans and high-altitude sponges, wetlands constitute approximately 7% of the whole African continent and about 9% the Sub-Saharan African landmass (Junk et al., 2013; Mitchell, 2013). However, excluding lakes, reservoirs and rivers, Rebelo et al. (2009, 2010) put the estimate of the extent of wetlands in Sub-Saharan Africa at 4.7%. Freshwater marshes and floodplains are the most extensive wetland types within the region (Rebelo et al., 2010).

While Africa as a whole hosts about 350 (16%) of the world’s 2178 designated Ramsar sites by number (Daryadel & Talaei, 2014), Sub-Saharan Africa hosts a total of 190 designated Ramsar sites, representing 41.4 % (78 962 080 ha) by area of all Ramsar sites globally (Mitchell, 2013). Thus, on average, African Ramsar sites tend to be quite large in surface area compared with the wetlands on other continents. The substantial variability in landscapes and climatic conditions in southern Africa is manifested in a great range of types of wetlands and associated biota (Mucina & Rutherford, 2006; Kotze et al., 2012). Table 2.2 presents the distribution, extent and wetland types occurring in the ten countries of southern Africa. Despite this widespread distribution and diversity across Africa, knowledge of the wetland ecosystems on the continent is still far from being adequate and to meet the needs for their management (Rebelo et al., 2010). Rebelo et al. (2010) further highlight that because of limited scientific investigation, coupled with inconsistent mapping policies and the lack of a universal classification system, the precise estimate of the total wetland extent in Africa remains unknown.

Table 2.2: Types and extent of non-lake wetlands in the ten southern African countries. Information sourced from Hughes and Hughes (1992), with modifications from Taylor et al. (1995) and Frenken and Mharapara (2001)

Country	Wetland types and distribution	Country Area (km^2)	Wetland area (km^2)	Wetland area (%)
Angola	Complex wetland systems Upland palustrine emergent types, riverine and lacustrine wetlands, with marine and estuarine intertidal mangroves and salt marshes. Upland sponges, dambos, swamps, floodplains and endorheic lakes occur	1 246700	4750	0.3 (sponges, most dambos, river floodplains and lakes were excluded)
Botswana	Most of the wetlands are associated with the Okavango and Zambezi rivers in the north. Okavango Delta, Inyanti/Chobe River and small pans; no systematic review	569582	28310	4.9
Lesotho	Primarily montane sponges and mires, with riverine sedge or reed swamps in the lower areas. Highest frequency of wetlands in the mountains (> 2,000 m a.s.l.) and a decline in frequency towards the southern and western lower areas.	30344	425	1.4
Malawi	Mainly dambos, swamps and marshes, floodplains and rivers	118484	2730	2.9 (excluding major lakes)
Mozambique	All wetland types exist and it is hypothesised that their biological and physical diversity is extensive	784755	18835	2.4 (palustrine wetlands)
Namibia	Predominantly extensive seasonal inland pans, floodplains, coastal wetlands and several artificial impoundments.	824295	11807	1.43

South Africa	All types of wetlands occur, including man-made dams, coastal wetlands, montane wetlands, swamps, marshes, floodplains and pans.	1184825	284358	2.4
Swaziland	Mostly upland peat bogs and sponges, forming stream headwaters, especially in the country's western parts and are the sources of water for the dams	17365	Probably >100; no reliable estimate	>0.58
Zambia	Diverse and widespread and includes permanent and seasonal marshes, swamps, riverine wetlands, pans, floodplains, shallow lakes, lake edges and artificial wetlands	752952	112946	15
Zimbabwe	Mainly lakes, rivers, widespread dambos, sponges, swamps, pans, floodplains and dams; no systematic review has yet been undertaken	390310	12800	3.3

More recent reports portray a different picture in some of the southern African countries. Approximately 300 000 wetlands, accounting for about 2.4% of the country's surface area occur in South Africa (SANBI, 2013), which is much higher than the 0.39% reported by Taylor et al. (1995). In Lesotho, although mainly concentrated in the highlands, the wetlands occur across the country and are estimated to cover 2.72% of the country's land surface area (Department of Environment, 2014), which is also higher than the proportion in Table 2.2. Nevertheless, the estimates of the wetland coverage at any spatial scale differ substantially across studies because of the variation in the definitions of a wetland and the methods used in wetland delineation (Rebelo et al., 2010). Therefore, it is noteworthy that the confusion caused by different definitions and classification of wetlands has also made it difficult to achieve precise estimates of the wetland extent on a regional and national level.

2.4 Wetland typology and classification

Wetland typology is important in providing useful information for biodiversity conservation and water resource management (Sieben et al., 2017c). Wetlands are classified in many ways. The differences and changes in hydrological behaviour, soils and vegetation form the most appropriate criteria to classify and distinguish different types of wetlands (Mitsch & Gosselink, 2000). A recent study (Sieben et al., 2017c) describes two main approaches to wetland classification: (1) top-down approaches, where wetland ecosystems are divided into a number of categories on the basis of a conceptual understanding of the functioning of the wetland (mostly regarding water flows), (2) bottom-up approaches, whereby wetlands are classified on the basis of the data collected from the wetland, which is then subjected to various techniques of clustering (mainly regarding biodiversity). Top-down approaches emphasise and considers the connection of a wetland to the drainage network, as well as water inflows, through-flows and outflows of the wetland but bottom-up approaches focus on wetland habitats. Thus, while the former approach to wetland classification is more suitable for water resource planning, the latter is more useful for biodiversity conservation. Table 2.3 presents the comparison of the top-down and the bottom-up approaches.

Table 2.3: Comparison of the top-down and bottom-up approaches in wetland classification. Source: Sieben et al. (2017c)

Top-down	**Bottom-up**
Based on a conceptual model	Based on the actual field data on aspects of the wetlands
Useful mostly in water resource planning	Useful mostly in conservation planning
Remains the same and is used in legislation	Dynamic and changes regularly as more data becomes available
Classifies the actual whole wetland unit	Classifies wetland habitats and vegetation types

In top-down classification, wetlands can be broadly classified into five major categories, namely, marine, estuarine, riverine, lacustrine and palustrine wetlands (Ramsar Convention Secretariat, 1971; Cowardin et al., 1979; Mitsch & Gosselink, 2015). In this classification, a set of mainly independent physical variables (mainly landform, hydrology, climate and vegetation structure) is used as initial characteristics to classify ecosystems in a conceptual model (Sieben et al., 2017c). Palustrine (vegetated inland) wetlands have a wide variety in terms of size, type, hydrology, soil types, vegetation types, species richness and ecosystem functioning (Reddy & DeLaune, 2008; Brand et al., 2013; Tiner, 2017). These ecosystems generally comprise a variety of waterlogged habitats, which mainly include marshes, mires (bogs and fens), swamps and similar ecosystems, located along a range of altitudes and topographical locations (Adedipe et al., 2005; Du Preez & Brown, 2011; Maltby & Acreman, 2011; Mitsch & Gosselink, 2015). Depending on topography, soils or sediment, climate, water quality and dominant vegetation, wetlands demonstrate substantial diversity within the main generic category (Maltby & Acreman, 2011). Wetlands are thus remarkably diverse and every wetland is unique (Macfarlane et al., 2007). It is this diversity that made it necessary for a classification system to be developed in order to categorise the different wetland ecosystems, which would enable the selection of wetlands to be conserved for the protection of multiple ecological values (Mitsch & Gosselink, 2015).

Wetland classification plays a critical role in conservation planning (Sieben et al., 2011). According to Cowardin et al. (1979), the primary goal of wetland classification is to delineate wetland systems for purposes of inventory, evaluation, conservation and management. Wetland classification also helps in providing information about the ecosystem services delivered by a given wetland (Sieben et al., 2017c). However, the same complexity that made it difficult for scientists to have a precise and universal definition of a wetland has also concomitantly resulted in the development of many different wetland classification systems internationally (Cowardin et al., 1979; Brinson, 1993; Dini et al., 1998; Ewart-Smith et al., 2006; Kotze et al., 2007; Macfarlane et al., 2007; DWAF, 2008; Ollis et al., 2009, 2013, 2015; Sieben et al., 2011; Mitsch & Gosselink, 2015). For example, while the Ramsar Convention (1971) recognises three major systems of wetlands (inland, marine/coastal and artificial wetlands), in the United States of America Cowardin et al. (1979) classify wetlands into five major ecological systems (marine, estuarine, lacustrine, riverine and palustrine wetlands) and in South Africa, wetlands are divided into six major systems (marine, estuarine, lacustrine, riverine, palustrine and endorheic systems) (De Klerk et al., 2016).

While some wetland classification systems attempt to capture the predominant hydrological characteristics (Collins, 2005) and some reflect the variation in vegetation or wetland structure and/ or function (Collins, 2005; Ellery et al., 2009), others emphasise and consider the water source, hydrodynamics and geomorphic setting of the wetlands (Brinson, 1993; Ewart-Smith et al., 2006; Ollis et al., 2009, 2013, 2015). Nevertheless, the major wetland attributes that are frequently and commonly used in most wetland classification systems are the hydrogeomorphic features (geomorphic and hydrological regime), vegetation physiognomic type, and plant and/or animal species (Mitsch & Gosselink, 2015). While hydrodynamics is the strength and direction of flow or movement of water within the wetland, geomorphic setting describes the location and shape of the wetland with respect to the terrain of the surroundings in terms of lithology and topography and these control the hydrology of the wetland (i.e., sources of water, including groundwater, precipitation and surface flow) (Brinson, 1993).

Cowardin et al. (1979) developed one of the most useful and comprehensive hierarchical classification systems that is based on hydrological, geomorphic, chemical and biological features, which broadly recognises five major wetland systems. This classification progresses from Systems (five) and Subsystems (ten) at the most general levels at the top of the hierarchy to Classes (11), Subclasses (28) and an unspecified number of Dominance Types at the bottom of the hierarchy (Cowardin et al., 1979). Because hydrology and geomorphology are now recognised as important features that determine the existence of wetland ecosystems and how they function, the hydrogeomorphic (HGM) approach is currently adopted as the most useful type of top-down wetland classification, both internationally (Brinson, 1993; Keddy, 2010; Mitsch & Gosselink, 2015; Tiner, 2017) and in South Africa (DWAF, 2004, 2008; Kotze et al., 2007; Macfarlane et al., 2007; Ollis et al., 2009, 2013, 2015; Sieben et al., 2011, 2017c). The HGM classification methods can be updated (Ollis et al., 2013, 2015; Sieben et al., 2017c).

Unlike the Cowardin classification system that has no provision for subsystems of palustrine wetlands, the HGM system provides for palustrine subsystems, known as HGM Units. The HGM classifications have been successful around the world (Sieben et al., 2014a). The HGM approach has become so widespread that many HGM-based classifications have been developed in South Africa to date (Table 2.4). Moreover, techniques that have been developed for the assessment of wetland ecological condition (WET-Health) (Macfarlane et al., 2007; Kotze et al., 2012) and the services delivered by wetlands (WET-EcoServices) (Kotze et al., 2007) are essentially based on the HGM system of wetland classification. Information on the HGM units helps to provide some indications of the ecological processes operating in a wetland, sources of water and the impacts that are likely to occur (Sieben et al., 2011). Given that Lesotho does not have a wetland classification system and also because of its geographical location in relation to South Africa (it is an enclave), the South African wetland classification system, which may be applicable to Lesotho, is briefly described here.

Based largely on the HGM units, a national system of classifying wetland ecosystems and other aquatic systems in South Africa was initially developed (Dini et al., 1998) and has been further developed and refined (Ewart-Smith et al., 2006; Ollis et al., 2009, 2013, 2015). This hydrogeomorphic classification system is top-down and based on the geomorphic setting (*geomorph*- characteristics) of the wetland, the source of water and the way in which the water flows in, through and out of the wetland (*hydro*- characteristics) (DWAF, 2004, 2008; Ollis et al., 2009, 2013, 2015; Brown & Cook, 2014). Being hierarchical in nature, the classification system categorises palustrine wetlands, primarily based on the abiotic features that determine their functionality and, at a finer scale, according to their biotic features (Figure 2.2) (Ollis et al., 2009). This classification system, mainly designed for palustrine (vegetated) inland wetlands, recognises seven HGM units (DWAF, 2004, 2008; 2013, 2015; Ollis et al., 2015). Underlain by the assumption that the functioning of aquatic ecosystems is dependent on landscape settings, the hydrogeomorphic classification approach attempts to classify aquatic systems in a way that explains how the ecosystems function (Ollis et al., 2013, 2015; Sieben et al., 2017c).

Table 2.4: Classification of HGM Units for wetland ecosystems and other inland aquatic ecosystems developed to date in South Africa. Modified from Ollis et al. (2015).

Study	Kotze et al. (1994)	Kotze (1999)	Collins (2005)	Ewart-Smith et al. (2006)	DWAF (2007)	Kotze et al. (2007); Macfarlane et al. (2007)	Ollis et al. (2009)	Sieben et al. (2011)	Brown and Cook (2014)	Ollis et al. (2013, 2015)
Classification	*Crest/Scarp/ Midslope/ Footslope/ Valley head/ Young valley bottom/ Mature valley bottom:* • Flat • Depression • Channel • Slope • Fringe • Channelled flat • Channel-disrupting flat	• Channel • Channelled valley bottom • Non-channelled valley bottom • Hill slope • Flow concentration area • Depression	*Slope wetlands:* • Surface water-fed • Surface and groundwater-fed • Groundwater-fed *Valley bottom wetlands:* • Surface water-fed • Surface and groundwater-fed • Groundwater-fed *Depression wetlands:* • Surface water-fed • Surface and groundwater-fed • Groundwater-fed	*Non-isolated:* • Channel (river) • Valley bottom • Floodplain • Depression linked to a channel • Seep with channelled outflow *Isolated:* • Isolated depression • Seep without channelled outflow	*Valley bottoms:* • River • Lake • Unchannelled valley bottom • Channelled valley bottom • Meandering floodplain *Slopes:* • Seepage (isolated) • Seepage (connected) *Crests:* • Seepage (connected) • Pans and depressions	• Floodplain • Valley bottom, channelled • Valley bottom, unchannelled • Hillslope seepage, linked to a stream • Isolated hillslope seepage • Depression (incl. pans)	*Valley floor/Slope/ Plain/Bench:* • Channel (river) • Channelled valley-bottom wetland • Unchannelled valley-bottom wetland • Floodplain wetland • Hillslope seep • Valleyhead seep • Depression • Flat	• Floodplain • Valley bottom with a channel • Valley bottom without a channel • Valleyhead seepage • Hillslope seepage feeding a stream • Hillslope seepage not feeding a stream • Depression/Pan • River margin and vegetated channel deposits • Flat/Groundwater rest-level wetland • Isolated spring • Dolomite cave • Raised bog • Geothermal spring	• Pans and depressions (including lakes); • Seepage wetlands; • Unchannelled valley bottoms; • Channelled valley bottoms; • Floodplains	• River • Floodplain wetland • Channelled valley-bottom wetland • Unchannelled valley-bottom wetland • Depression • Seep • Flat wetland

The South African wetland classification system (SAWCS) is six-tiered (Level 1 to level 6) in structure (Figure 2.2) (Ollis et al., 2013). The first four levels, forming the core units of the classification, differentiate between the different types of aquatic systems based on primary discriminators, which are criteria that can consistently distinguish categories at a given level (Ollis et al., 2009, 2015). The HGM-based classification system has been extensively used in South Africa, especially for wetland assessment, wetland inventories and conservation planning initiatives for freshwater systems (Sieben et al., 2011; Ollis et al., 2015).

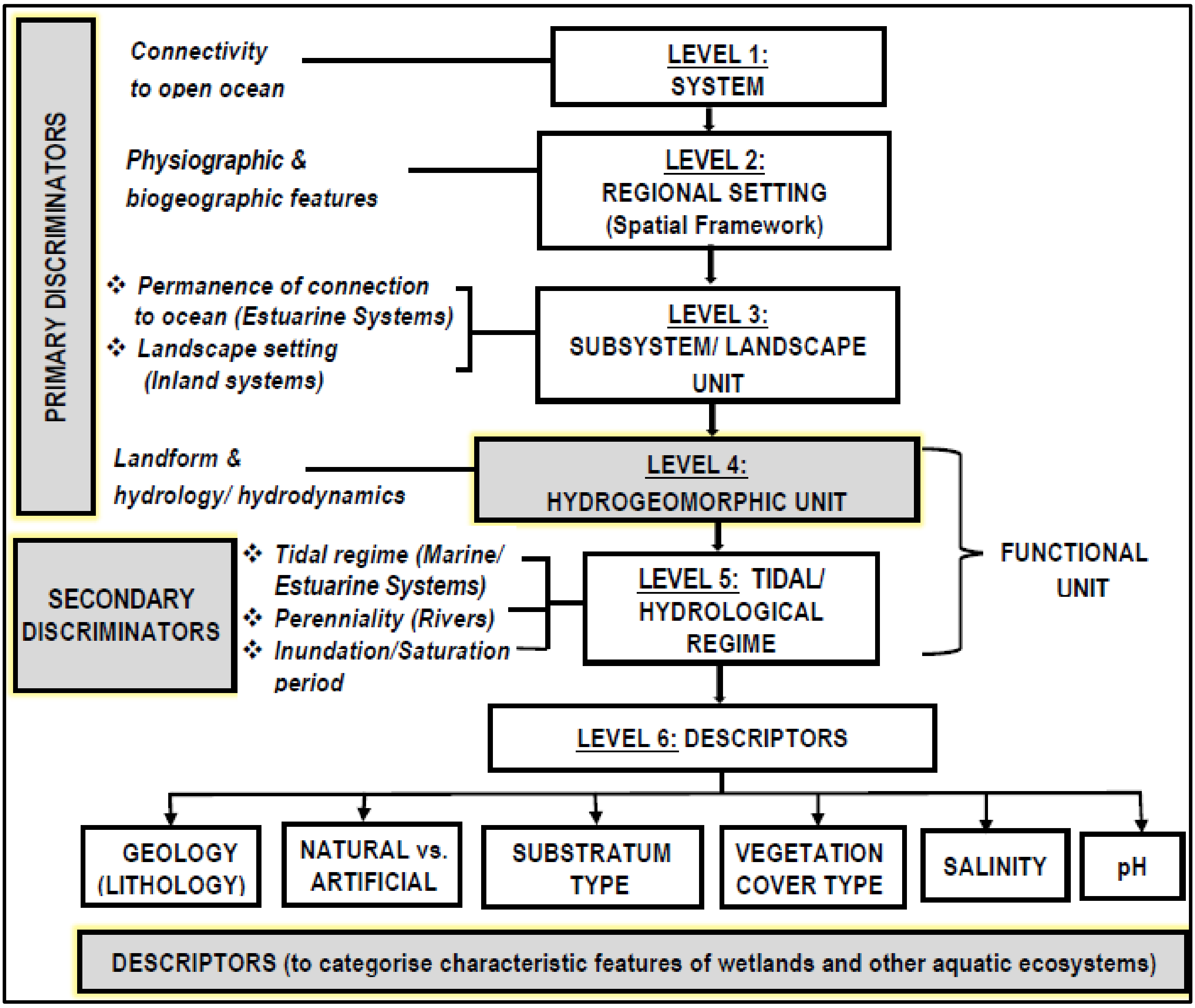


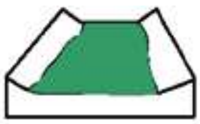
Figure 2.2: Conceptual overview of the system of classification for wetlands and other aquatic ecosystems, showing how 'primary discriminators' are applied up to Level 4 to classify Hydrogeomorphic (HGM) Units, with 'secondary discriminators' applied at Level 5 to classify the Tidal/ Hydrological Regime, and Descriptors applied at Level 6 to categorise the characteristics of aquatic ecosystems classified up to Level 5 (Ollis et al., 2009, 2015).

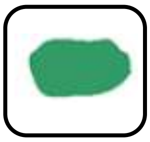
The way the classification works, as described by Ollis et al. (2015), is briefly highlighted here. The tiered structure progresses from systems (Marine, Estuarine and Inland) at the largest spatial scale (Level 1), through the setting at a regional scale (Level 2) and landscape units (Level 3), to the HGM Units at the individual wetland level or part of a wetland complex (Level 4). Levels 2 and 3 provide the broader biogeographical and landscape context for classifying HGM Units or Functional Units (Figure 2.2). Collins (2005) and Ollis et al. (2009, 2013, 2015) also highlight the main locations of wetlands on the landscape (level 3), which are further divided into HGM Units (Level 4) based on dominant mechanisms of water transfer to produce subtypes (on the basis, for example, of the dominant mechanism of water transfer, that is, ground water or surface water, or their combination).

Secondary discriminators are applied at Level 5 and 6. These two finer levels of the classification provide for the description of the habitat units occurring within a single wetland, and this is where most of the environmental changes in a wetland can be detected (Sieben et al., 2014a, 2017c). At Level 5, wetlands are differentiated from each other on the basis of hydrological regime (permanent, seasonal or temporary inundation) (Sieben et al., 2017c). Using six descriptors, Level 6 provides an in-depth description of the characteristics of a particular HGM Unit or Functional Unit (Figure 2.2) and this allows wetlands to be distinguished based on structural, chemical, and/or biological characteristics. While Levels 1 to 5 provide for wetland classification in terms of 'how they work' (i.e. the functional aspects relating to the processes occurring), Level 6 allows for the classification of wetlands in terms of 'what they look like' (i.e. the structural aspects relating to the observable pattern/s) (Ollis et al., 2009). The current study mainly focuses on the two finer levels of classification (Level 5 and 6) that emphasise wetland habitats more than whole wetlands.

With the HGM Unit (Level 4) being the focal point of the classification system, higher levels provide a broader biogeographical context for classifying functional units of a wetland at the HGM level and the lower levels provide an in-depth description of the characteristics of a given HGM Unit (Ollis et al., 2013). Level 4 uses seven HGM types (Table 2.5) to classify palustrine wetlands based on geomorphology and hydrology (Ollis et al., 2013, 2015). Figure 2.3 presents the conceptual relationship of HGM Units (Level 4) to the lower and higher levels of the SAWCS. According to Sieben et al. (2011), wetland classification at levels below the HGM unit, where habitats are described, is particularly important for biodiversity conservation, given that the different habitat types are indicative of where rare species occur or can be expected. The seven hydrogeomorphic types of palustrine wetlands recognised by the classification system are Depressions, Isolated hillslope seepage wetlands, Stream channel-linked hillslope seepage wetlands, Channelled valley bottoms, Unchannelled valley bottoms, Flat and Floodplains (Table 2.5). Some wetland systems may be divided into a number of HGM types (Functional Units) (Ollis et al., 2013) and such a system is referred to as a wetland complex.

Table 2.5: Wetland HGM types associated with inland wetland ecosystems in South Africa. Adapted from DWAF (2004); Kotze et al. (2007); Macfarlane et al. (2007); Ollis et al. (2013)

Hydrogeomorphic types		**Description**	**Source of water for the wetland**[a]	
Type	**Illustration**		**Surface**	**Sub-surface**
Floodplain		Valley bottom areas with a clearly defined river/ stream channel, flat to gently sloping and characterised by features of a floodplain that include natural levees and oxbow depressions and the alluvial (by water) transport and sediment deposition, usually giving rise to a net sediment accumulation. The adjacent slopes and the overspill from the main channel are the major water inputs for the wetland. It experiences periodic inundation as a result of flooding during the rainy season.	■■■	■
Channelled Valley bottom		Valley bottom areas with a clearly defined stream channel but features of a floodplain are absent. May have gentle slopes and exhibits a net alluvial deposit accumulation or may be steep sloping and be characterised by a net sediment loss. The wetland receives water inputs from adjacent slopes and from the main channel (when channel banks overspill) during floods or as lateral seepage from the channel.	■■■	■/ ■■■
Unchannelled Valley bottom		Valley bottom areas with a connection to a drainage network but without a clearly defined stream channel, usually gently sloping and exhibiting deposition of alluvial sediment, generally giving rise to a net sediment accumulation. It is usually dominated by water that flows diffusely at or near the surface, especially after rainfall events. Water inputs mainly come from an upstream channel that enters the wetland and also through seepage from adjacent slopes	■■■	■/ ■■■
Hillslope seepage linked to a Stream channel		Slopes on hillsides experience colluvial (gravity-driven) movement of materials. These are typical concave wetlands located on gently sloping areas at the head of a drainage line. Sub-surface flow is the primary source of water inputs and outflow is usually through a clearly defined stream channel, connecting the area directly to a stream channel.	■	■■■

Isolated Hillslope seepage		Hillside slopes characterised by the colluvial unidirectional movement of water and materials. Water inputs mostly from sub-surface flow and outflow is either very limited or through diffuse sub-surface and/or surface flow but there is no direct surface water connection to a stream channel. It is usually located on a gently to steeply sloping area.	■	■■■
Depression (includes Pans)		An area with a basin (concave) shape where elevation contour is closed or nearly-closed, allowing surface water to accumulate (i.e. water drains inward). The system may also receive sub-surface water. Usually, there is no outlet, and thus wetland is normally isolated from the network of the stream channel. Sometimes the system can be very flat and in this case it is known as a pan and can easily be confused for a flat wetland. Depressions have various potential water source inputs but hydrodynamics are normally dominated primarily by vertical fluctuations that are seasonal.	■/ ■■■	■/ ■■■
Wetland Flat		A wetland area that is level or near-level, normally situated on a Plain or a Bench, where the groundwater is usually near the surface, commonly on coastal plains, and precipitation is the primary water source except for Wetland Flats that occur on coastal plains where groundwater may be on the surface or near the ground surface. The flow is hardly noticeable and these wetlands are essentially a transition between a valley bottom wetland and a depression.	■/ ■■■	■

[a]Precipitation is an essential source of water and evapotranspiration an essential output in all of the above situations

Water source: ■ Contribution normally small  Wetland

■■■ Contribution normally large

■/ ■■■ Contribution may be small or important depending on the local circumstances.

NB. It is noteworthy that these are all types of PALUSTRINE wetlands

By including six additional HGM units, Sieben et al. (2011) have contributed to the expansion of the HGM-based system of classification of Kotze et al. (2007) and Macfarlane et al. (2007) (Table 2.4). Sieben et al. (2011) also provide a list of discriminators that can be used for differentiating the types of habitats in an HGM unit at a more detailed (lower) level of classification. An HGM Unit (Level 4) and its hydrological regime (Level 5) are together considered to form the Functional Unit of a wetland, indicating that the functioning of inland aquatic systems is greatly determined by the hydrological regime and hydrogeomorphic characteristics of the ecosystem. Therefore, Ollis et al. (2013) strongly recommend that, at the very least, an inland wetland system should be classified on the basis of its HGM Units (at Level 4). However, it is noteworthy that, while the importance of the different mechanisms of water transfer may change temporally, the contribution of the different mechanisms of water transfer may also differ spatially due to differences in climate (contribution of precipitation versus evaporation) (Collins, 2005).

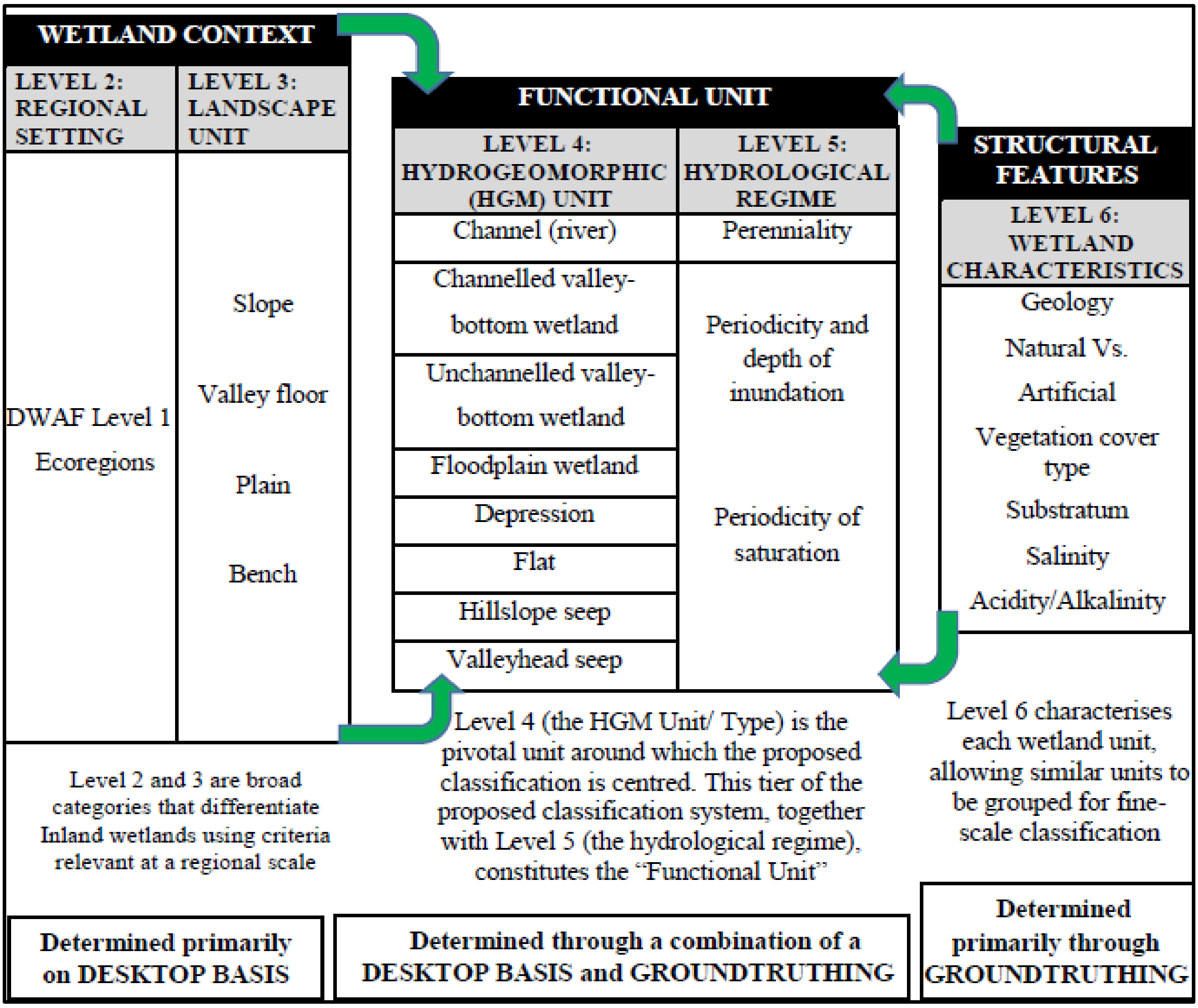


Figure 2.3: The conceptual relationship of HGM Units (at Level 4) to the higher and lower levels of the classification system for Inland Systems (Ollis et al., 2009).

An important aspect of the HGM classification system is the hydroperiod, a function of inundation and / or saturation period, which is defined as the average amount of time that a certain patch of a wetland is inundated annually. An inundated wetland is one whose underlying substratum (soil) is covered by water, while a saturated wetland has its substratum (soil) waterlogged (i.e. the air spaces of the substratum/soil are water-filled) but usually without surface water (Ollis et al., 2013, 2015). In the SAWCS, saturation is assessed within the upper 50 cm of the soil surface (the most accepted soil depth at which saturation is usually assessed for the purposes of wetland delineation) (DWAF, 2007).

These areas exhibiting varying duration of reduced soil (waterlogging) conditions are known as hydrological (wetness) zones (Collins, 2005; Brown & Cook, 2014). Depending on the hydrology, a given wetland can have all the three wetness zones (permanent/semi-permanent, seasonal and temporary/intermittent), any two, or only one of them (Collins, 2005). These can be identified based on hydromorphic features that include presence of mottles, which are explained in Section 2.5. Ollis et al. (2013) also use water depth to classify wetlands where systems that are less than 2 m deep are described as littoral and those deeper than 2 m as limnetic; 2 m is the maximum depth at which rooted emergent hydrophytes can be supported. Nevertheless, the authors caution that, due to uncertainty and lack of confidence, it can generally be challenging to sub-divide an HGM Unit based on differences in the hydrological regime.

The use of HGM units in wetland classification is very useful at landscape scale for strategic conservation planning (Macfarlane et al., 2007). Nonetheless, Sieben et al. (2014a) argue that the system is limited in scope, especially for management goals within the wetland where environmental variables can be modified by disturbances that affect ecosystem health. Wetland health is a measure of similarity in structure and function of a wetland to its natural or reference condition (Kotze et al., 2006; Macfarlane et al., 2007; Ellery et al., 2009). Sieben et al. (2014a) point out that the biodiversity of a locality is not exclusively determined by large-scale top-down processes, but depends mostly on specific local conditions as well. Thus, a more recent study (Sieben et al., 2017c) recommends that top-down approaches to wetland classification (such as the HGM described above) should be complemented with the bottom-up approach, especially if the objective is determine the functioning of the wetland and the ecosystem services it can provide. The same study emphasises that the top-down approach is more suitable for the management of water resources, while the bottom-up is more suitable for biodiversity conservation because it is based on the actual biodiversity of the wetland, especially the use of vascular plant community data.

The vegetation, consisting of vascular plants, is the most suitable feature to consider over a wide range of habitats because it is often present in all palustrine wetlands and is the most easily observed feature of the ecosystem (Sieben et al., 2014a). In addition, because it is very common for the entire wetland plant community to be dominated by just one or two species, wetland vegetation types can easily be distinguished and classified based on their dominant species (Boutin & Keddy, 1993; Sieben et al., 2010a). Therefore, wetland habitats can be classified according to the plant communities present in the ecosystem (Collins, 2005; Sieben et al., 2010a, 2011). Using this approach in the Maloti-Drakensberg Transfrontier Park, Sieben et al. (2010a) attempted to classify wetland habitats based on the dominant plant community types. Sieben et al. (2014a) also attempted to produce an overall structural classification of the South African wetland vegetation, based on the vegetation cover, the main functional groups, vegetation height and species diversity. Subsequently, the authors recognised and described about 275 plant communities occurring in the South African wetlands but highlighted that there could be more. However, the major limitation of using vegetation as an indicator is that it can only be applied successfully in the field during the growing season and requires expertise to identify the species.

Sieben et al. (2014a) also recommend long term monitoring of plants that are regarded as characteristic of given wetland environments in order to detect significant changes if they would occur in those wetlands. Usually, vegetation types coincide with the types of habitat within a wetland ecosystem, albeit, some types of habitat may support a variety of vegetation types (Sieben et al., 2011). Nonetheless, besides vegetation, other types of data, including water quality, soils or other biota, such as invertebrates, can also be used for a bottom-up classification (Sieben et al., 2017c). It is noteworthy that a closer look at Table 2.4 reveals that, despite advances towards a universal classification system (HGM approach), differences (including on types) still occur among the different classification systems developed to date. This implies that further refinement on the wetland classification systems is needed for a more common understanding among wetland scientists and managers.

2.5 Environmental factors influencing wetland ecosystems

Landform and hydrological characteristics are fundamental determinants for the existence of all wetland ecosystems (Sieben et al., 2011). Given that freshwater palustrine wetlands are ecotonal between terrestrial and aquatic systems, they often have characteristics of both ecosystems (Reddy & DeLaune, 2008; Mitsch & Gosselink, 2015). Wetlands are a product of the unique contributions of different abiotic and biotic processes that interact to produce unique habitats and plant assemblages observed across landscapes (Aylward et al., 2005; Brand et al., 2013; Mitsch & Gosselink, 2015). These ecosystems comprise the abiotic characteristics of an area (including climate, water, geology, soil and nutrient supply) and the biotic communities adapted to the prevailing conditions of the environment and regimes of natural disturbances (Collins, 2005; Macfarlane et al., 2007; Kotze et al., 2012). Wetlands occur where the landform (topography) or geology reduces or obstructs water movement through the catchment or drainage into the soil (e.g. on a flat area), or where groundwater causes the surface soil layers in the area to be permanently, seasonally or temporarily wet (Collins, 2005). These ecosystems vary widely hydrologically, in soil nutrients and in salinity regimes and further variation among wetlands occurs as a result of geology and climate (Gopal, 2015). Plants in wetlands in turn influence the hydrology and soil, e.g. by further reducing water movement and by producing organic matter that potentially accumulates in the soil (Collins, 2005).

Because it presents changes in climate and stresses, altitude represents an important gradient, which plays a large role in regulating species composition between wetlands through its great effects on habitat diversity (Shimono et al., 2010). In montane environments, rapid changes in climate with altitude over relatively short horizontal distances are associated with dramatic changes in vegetation and hydrology (Sharma et al., 2010). Many researchers have confirmed the role of altitude in regulating plant species richness patterns (Bruun et al., 2006; Körner, 2007; Maltby, 2009; Shimono et al., 2010; Sieben et al., 2010a, b). Sieben et al. (2010b) highlight that, in Lesotho and the Drakensberg area, altitude is a suitable proxy for climate and provides an indirect gradient, whose influence is mainly through rainfall and temperature. This is because changes in altitude are associated with tremendous spatial variation in physical features (Kotze & O'Connor, 2000). In fact, Velazquez (1994) emphasises that altitude is generally an indirect measurement of precipitation and temperature.

Although the decline in the number of species with altitude has been widely accepted as a general trend in ecology (Rosenzweig, 1995), the understanding of the relation between altitude and species richness still appears to be immature and inconclusive (Rahbek, 1995). In a critical analysis of the effect of altitude on species richness, Rahbek (1995) demonstrates that about half of the pattern distributions indicated that diversity was highest at intermediate altitudes, about 25% showed a monotonically decreasing pattern, and about 25% followed other distributions. Given the variation in the patterns documented, the author concludes that it is not known whether a universal relationship exists between species richness and altitude. Furthermore, assessments of the changes in species diversity and distribution with altitude and other environmental gradients in montane areas can be useful in assessing the effect of climate change on biodiversity because mountains are suitable areas for detecting climate change and assessing its impacts (Sharma et al., 2010). Because of the increasing importance of recognising and conserving the world’s biodiversity, it is crucial that patterns in species richness in wetlands be elucidated (Begon et al., 2006). Few studies have investigated plant diversity-altitude relationships in wetland ecosystems (Rolon & Maltchik, 2006), particularly in southern Africa (Sieben et al., 2010b; Brand et al., 2013).

Another important trend in wetland species diversity is associated with transitional zones where species diversity is highest in ecotonal habitats such as seasonal wetland habitats and habitats on sloping ground (Kark, 2013). Ecotones are transitional areas between ecological communities, ecosystems or ecological regions. Seasonal wetland habitats harbour more species than permanent and temporal wetlands, as well as terrestrial habitats (Sieben et al., 2016a). These trends can be attributable to the increased environmental heterogeneity associated with such habitats that provide a diversity of ecological niches for more species to occupy; wetland and terrestrial plant species coexist in such habitats.

In general, environmental factors such as climate, wetland size, geological substrate, altitude, land use, water chemistry and hydrological fluctuations determine plant community richness and composition in wetlands, as well as the general functioning of the system (Rolon & Maltchik, 2006). The differences in the richness of wetland plants may result from heterogeneity in the environment on the landscape scale (e.g. altitudinal variation, hydroperiod, ecosystem size and connectivity) or on micro-scales, e.g. physicochemical conditions of the sediment and water, and habitat diversity (Rolon et al., 2010). While hydrology, geomorphology and vegetation underpin the general functioning of a wetland (Turner et al., 2000; Collins, 2005; Macfarlane et al., 2007; Maltby & Acreman, 2011; Kotze et al., 2012; Mitsch & Gosselink, 2015), local climate and hydrological regime are the two key determinants of wetland plant community composition and structure (Kotze & O'Connor, 2000).

In terms of climate, wetlands can occur in areas where water supply is greater than evaporation for at least part of the year (Scholes & Biggs, 2004), across a broad range of latitudes, and from sea level up to higher than 5500 m above sea level (Gopal, 2015). The wide variety of wetland types in southern Africa is primarily attributable to the remarkable variability in landscape, geology, drainage and climatic conditions (Mucina & Rutherford, 2006; Ellery et al., 2009; Kotze et al., 2012). Wetlands in southern Africa are among the most diverse in the world, both biologically and physically (Taylor et al., 1995). The dominant geology in the catchment of a wetland, and within the wetland itself, is important because of its deterministic role on the formation and functions of different wetland systems (Ollis et al., 2013). The wetlands that rely primarily on rainfall are likely to occur in areas of exceptionally high rainfall and low rates of potential evaporation and in southern Africa, such conditions are only found in areas such as the Lesotho Highlands and along the southern and eastern coastal regions of South Africa (Ellery et al., 2009). Nonetheless, Brand et al. (2013) indicate that special hydrogeological conditions (waterlogging) and substrates (soil or bedrock) have more influence on floristic composition, structure and dynamics than microclimates in wetlands.

Three factors (hydrology, geomorphology and vegetation), that are closely interlinked (Figure 2.4) underpin the functioning and thereby the health of a wetland (Turner et al., 2000; Collins, 2005; Macfarlane et al., 2007; Maltby & Acreman, 2011; Kotze et al., 2012; Mitsch & Gosselink, 2015). Hydrology is affected by geomorphology and the two influence vegetation, which in turn may have feedback effects on geomorphology and hydrology (Kotze et al., 2012) (Figure 2.4). Vegetation does not only play a significant role in wetland formation, but also in defining wetland types (Tiner, 2017). The interactions among these three factors have a deterministic effect on the significance and the general characteristics of the processes that occur in a particular wetland (Turner et al., 2000; Macfarlane et al., 2007; Mitsch & Gosselink, 2015). A combination of climate, basin geomorphology and hydrology is referred to as wetland hydrogeomorphology (Mitsch & Gosselink, 2015). Therefore, as alluded to in Section 2.4, the floristic composition, structure and functioning of wetlands are fundamentally influenced by the hydrogeomorphology of the wetland (Brinson, 1993; Kotze & O'Connor, 2000). The three important indicators, namely, hydrology (shallow water or saturated conditions), soils (hydric soils) and vegetation (hydrophytes i.e. typically adapted to wet conditions) characterise wetland ecosystems (Cowardin et al., 1979; Collins, 2005; Maltby & Acreman, 2011; Mitsch & Gosselink, 2015; Tang et al., 2017).

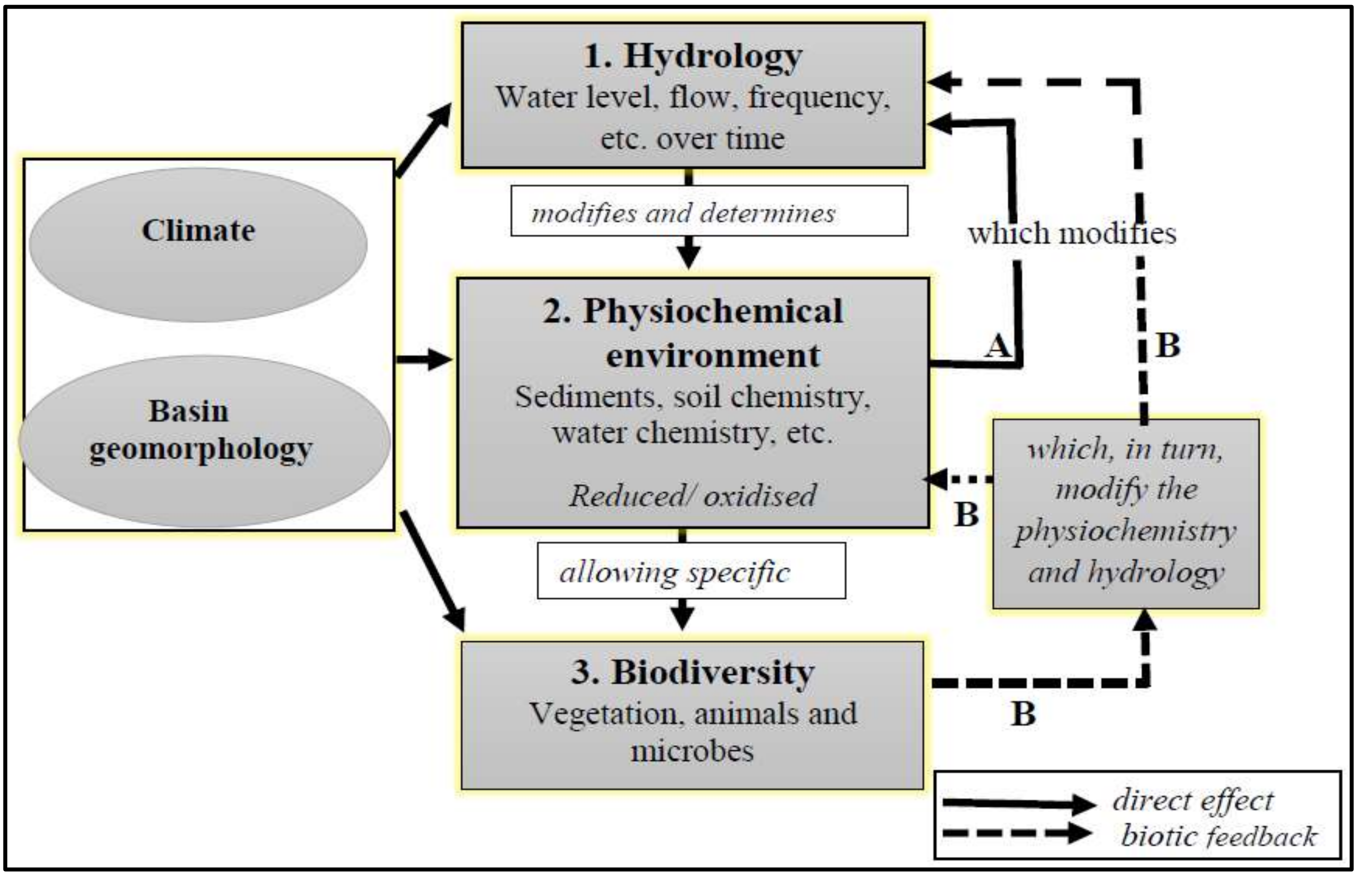


Figure 2.4: Conceptual diagram showing the interrelationships of hydrology, geomorphology and biota (especially vegetation) and their effects on wetland function. Pathways A and B are feedbacks to the hydrology and physicochemistry of the wetland (Mitsch & Gosselink, 2015).

It is the balance between water inputs and outputs in a wetland that determines the wetland hydrological functioning, including control of floods and recharge of ground water (Collins, 2005). The water balance determines the hydroperiod of a wetland, which strongly influences the establishment and maintenance of the processes and plant communities in the wetland (Collins, 2005; Tiner, 2017). Topography and hydrological regime generally play the most important deterministic role for the establishment and maintenance of specific wetland types and processes, creating the unique physical and chemical conditions that distinguish wetlands from both well-drained terrestrial ecosystems and deepwater aquatic systems (Millennium Ecosystem Assessment, 2005b; Mitsch & Gosselink, 2015). Water enters wetlands from a variety of sources: precipitation, groundwater, tides, runoff from melting snow, ice frozen soil and overflow from waterbodies (Collins, 2005; Tiner, 2017).

Hydrology is a function of three major aspects, namely, hydroperiod, waterflow through the system and the quality of the water. The conditions of hydrology in a wetland tremendously affect many important processes and characteristics, including the development of anoxic conditions in the soil (waterlogging), accumulation of organic matter, availability of nutrients and other solutes, nutrient cycling, nutrient inflows, sediment fluxes, plant species composition and diversity, and primary productivity (Collins, 2005; Macfarlane et al., 2007; Mitsch & Gosselink, 2015). Hydrological conditions at a given site determine whether it is temporary or permanently flooded, the water is flowing or standing still, the flow is diffuse or channellised, the soils are saturated or inundated, and where the various types of sediments are deposited in the wetland (Sieben et al., 2014a). Kotze and O'Connor (2000) and Sieben et al. (2010b) report that the degree of soil wetness is strongly related to the structural and functional features of a wetland. Wetland vegetation is azonal to a large extent, which means that plant communities respond more readily to local edaphic conditions, including the amount and periodicity of water and salts, than to geological and macroclimatic patterns across the landscape (Sieben, 2011). However, wetland vegetation can also be considered to be "intrazonal" which means that the vegetation does not only respond to local factors but can also be influenced by factors operating at a landscape scale. Thus, to account for both categories of factors, top-down classification should be complemented with bottom-up classification approaches.

Wetland hydrology has a tremendous influence on biogeochemistry and, coupled with a diverse geomorphology, can provide considerable spatial heterogeneity within a given wetland (Mitsch & Gosselink, 2015). Hydrological processes and functioning play a deterministic role on many physical and biochemical interactions within wetland ecosystems, which in turn influence wetland functioning and the provision of ecosystem services (Maltby & Acreman, 2011).

Hydrology is so critical that, in many countries in southern Africa, ephemeral (temporal) wetlands may remain for a number of years or even decades without water, but when water comes, the biotic characteristics (both vegetation and fauna) of the wetlands reappear, e.g. the Makgadikgadi Pans of Botswana (Taylor et al., 1995).

The presence of water, whether permanent or seasonal, is the primary determinant for suitable wetland habitats as it induces anaerobic conditions (Mucina & Rutherford, 2006). Slight changes in wetland hydrological conditions can result in massive biotic changes, particularly in species composition and richness and in ecosystem productivity (Mitsch & Gosselink, 2015). The behaviour of water within a wetland and the soils directly influences the physicochemical and biological characteristics, as well as the overall functioning of the wetland system (Ollis et al., 2013). Water regime components such as water depth, water chemistry and flow rate are the major drivers of the structure (e.g. species richness) and functioning (e.g. primary production) of the vegetation in wetlands (DWAF, 2004).

Hydroperiod, an aspect of hydrology, is the most fundamental habitat descriptor in wetland systems that directly influences the growth of plants and it is the average amount of time in a year that a given area experiences inundation or saturation, with subsequent development of anoxic conditions (Kotze et al., 1996; Maltby & Acreman, 2011; Sieben et al., 2011, 2014a, 2016a; Junk et al., 2014; Gopal, 2015; Mitsch & Gosselink, 2015). In simple terms, hydroperiod is the duration, depth and frequency of flooding in a wetland system (Moor et al., 2017). Wetland hydroperiod characterises each wetland habitat type and thus is the wetland's hydrological signature (Kotze et al., 1996; Sieben et al., 2014a; Mitsch & Gosselink, 2015), which can influence the vegetation types. The hydroperiod can have profound seasonal and inter-annual variations and still remains the major determinant of the processes in a wetland (Sieben et al., 2011; Mitsch & Gosselink, 2015). Hydrological pathways that include groundwater, tides, precipitation, surface runoff and flooding rivers are responsible for transporting energy and nutrients to and from wetlands (Mitsch & Gosselink, 2015). Mitsch and Gosselink (2015) observe that water flow patterns and depth, and frequency and duration of flooding, resulting from the inputs and outputs of hydrology, influence the soil biochemistry and are important factors in the ultimate community assembly of wetland organisms.

The conditions of hydrology can enhance or constrain the occurrence of organisms (microorganisms, vegetation and animals), including their composition and diversity (Collins, 2005; Mitsch & Gosselink, 2015). While flood intensity increases available moisture and nutrients, longer periods of flooding increase stresses and problems caused by anoxic conditions in the rooting zone and can actually decrease the length of the growing season (Mitsch & Gosselink, 2015). Anaerobic conditions promote the development of hydromorphic features in wetland soils. Because the influence of hydrological processes and the subsequent functioning extend far beyond the wetland boundaries, there are also substantial interactions with, and influences on, the broader landscapes within which they occur (Maltby & Acreman, 2011). According to Mitsch and Gosselink (2015), four principles underscore the importance of hydrology:

1. Hydroperiod gives rise to distinct plant community composition but can enhance or constrain species richness.
2. Primary productivity and other ecosystem functions in wetlands are often enhanced by pulsing hydroperiod and flowing water but are often depressed by stagnant conditions.
3. By determining decomposition, primary productivity and export of particulate organic matter, hydrology controls the accumulation of organic material in wetlands.
4. Hydrological conditions (mostly flow of water) strongly influence both nutrient cycling and availability.

Depending on the conditions of hydrology, a wetland can have all three hydrological zones (temporary, seasonal and permanent), any two, or only one of them (Kotze et al., 1996; Collins, 2005; Brown & Cook, 2014). The presence of all the three hydrological zones within a wetland creates a hydrological gradient that ranges from permanent saturation (at its deepest end) to intermittent saturation (at the shallowest end) (Figure 2.5) (Kotze et al., 1996; Collins, 2005; Ollis et al., 2013; Brown & Cook, 2014). At a certain point within the hydrological gradient the average amount of time in which the soil is saturated becomes inadequate for reduced soil conditions to develop, and for the area to thus be regarded as a wetland (Collins, 2005; Brown & Cook, 2014). While soil organic matter increases, mottle abundance increases and then decreases along the continuum from temporary to permanently wet areas (Kotze et al., 1996).

The second important factor is the geomorphology of the landscape and basin (Mitsch & Gosselink, 2015). The shape of the basin where water accumulation occurs also has a great influence on the balance of water in a wetland (Kjellin et al., 2007). This is because, to a great extent, the shape of the body where water accumulates determines how the water enters and exits the wetland, as well as how it flows through the system (Sieben et al., 2017c). The same authors observe that, by preventing excess flow and promoting flooding, these properties then influence the amount of water that can be stored in the basin, which in turn affects the functioning and ecosystem services delivered by the wetland.

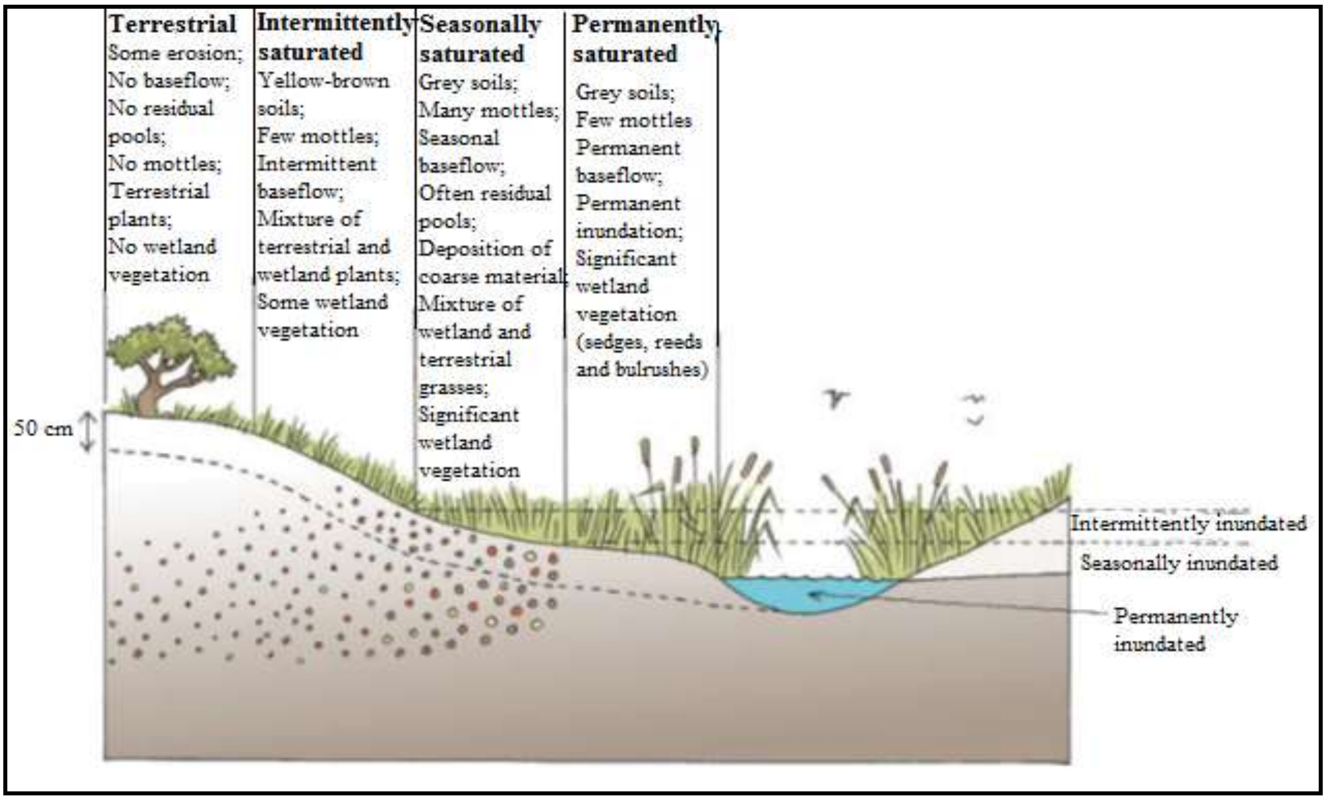


Figure 2.5: Cross-section through a hypothetical wetland system, highlighting the different hydrological zones that can occur and illustrating the typical response of the vegetation and the soil to the hydroperiod in the upper 50 cm of the ground surface. Adapted from Ollis et al. (2013) with modifications from Collins (2005).

The substrate underlying the soils in wetlands also plays a critical role in the type of wetland formed and the distribution and composition of the associated species (Kotze & O'Connor, 2000; Sieben et al., 2004). The hydromorphic features in a soil, which develop in response to water level fluctuations in the soil and in turn affect the redox potential and soil chemistry, result in patterns in soil form and colour that can be directly observed (Kotze et al., 1996). The duration and frequency of inundation and saturation in a wetland, for example, will determine the wetland's soil chemistry and morphology, and thus, is one of the primary determinants for the types of vegetation occurring in the wetland (Ollis et al., 2013). Prolonged waterlogging of the substrate causes hypoxia (deficiency of oxygen) or anoxia (its total absence) in the wetland soil and concomitantly, changes in the chemical characteristics of the soil (Gopal, 2015; Mitsch & Gosselink, 2015). This makes the habitat unsuitable for terrestrial plants, although a wide variety of woody and herbaceous plants are highly adapted to wetland habitats (Gopal, 2015).

Where soil saturation is not permanent, habitat conditions alternate between reduced (anaerobic) and oxidised states, giving rise to the development of bright spots of colour known as mottles (Ollis et al., 2013). Mottles (the black, yellow and red spots) are usually close to the surface of the soil in the temporary and seasonally wet zones of the wetland system, whereas they occur much deeper in the soil in non-wetland areas but are often much fewer or absent in permanently wet areas because they are usually devoid of oxygen (Brown & Cook, 2014). Mottles are conspicuous because of their chroma (the intensity of red or orange colour) that contrasts to the low chroma grey matrix. Mottles, as one of the major indicators of wetland habitats that are intermittently or seasonally saturated, are used to identify hydroperiod. Another characteristic that emerges in permanently wet conditions is gleying, which is the development of a uniform black, grey, or sometimes blue-grey or greenish colour (Mitsch & Gosselink, 2015).

Some wetlands have peat development (bogs and fens), which means they allow accumulation of peat due to slow decomposition of dead plant matter (Cronk & Fennessy, 2001; Ollis et al., 2013). Peat refers to soil with a substantially high amount of organic matter, normally up to 30% organic carbon by weight (Chatterjee et al., 2010; Du Preez & Brown, 2011; Ollis et al., 2013). However, Mitsch and Gosselink (2015) indicate that peat accumulates to some degree in all permanently wet wetlands as a result of either increased primary productivity or decreased decomposition and export, coupled with anaerobic conditions created by standing water or poorly drained conditions. It is both the diverse hydrological conditions and soil types in wetland ecosystems that tremendously influence biogeochemical processes, which in turn determine the overall wetland productivity (Mitsch & Gosselink, 2015). Peatlands can be categorised into fens and bogs.

It is noteworthy that it is not necessarily wetness that primarily determines the morphology and geochemistry of the soil in a wetland but rather, the anoxic conditions that develop as a result of prolonged saturation/ flooding in the soil (Kotze et al., 1996; Collins, 2005). Water quality and variables of hydrology directly or indirectly control a range of biological processes, which in turn determine the biodiversity (Sieben et al., 2014a; Gopal, 2015). Peat formation, gleying and mottling are all phenomena that are observed when the substrate is at least temporarily wet, and based on these characteristics, a habitat can be regarded as permanently wet, seasonal, temporary or non-wetland, or a transition between these zones (Kotze et al., 1996; Sieben et al., 2010b). The anaerobic conditions reduce the rate of organic matter decomposition and thus enhance the formation of peat in wetland systems. Furthermore, unlike the vegetation that changes with alterations in the hydrological regime, the morphological indicators of hydric soils are usually permanent (Collins, 2005). The degree to which wetlands assimilate pollutants and water does not only depend on the hydrology, but is also influenced by the size, soil type, location and vegetation of the wetland (Maltby & Acreman, 2011).

Sediment flux, an important aspect of geomorphology, is instrumental in shaping edaphic conditions and sediment accumulation and can be greatly influenced by hydrology, nutrient load and vegetation cover (Anderson & Mitsch, 2006). Sedimentation can influence the soil profile of a wetland. Despite being a water quality benefit and an important process, sedimentation in wetlands can also be one of the major pollution problems in these ecosystems (Gleason & Euliss, 1998) as pollutants in the water are allowed to settle. Through the dilution of ecosystem carbon by import of low carbon upland sediments into wetlands, sedimentation enhances carbon sequestration in wetlands by pulling soil carbon content below some pedogenic equilibrium value for the wetland ecosystem (McCarty et al., 2009).

Thirdly, wetland habitats are not only characterised by the stresses and conditions that constrain plant growth, but also by the conditions created by the dominant plants, which also affect the ecosystem processes such as stream flow, shading and evapotranspiration (Sieben, 2011). The vegetation in wetlands both controls and is controlled by its physical and chemical environment (Mitsch & Gosselink, 2015). Processes that include denitrification, sediment retention, absorption and uptake enable the storage or removal of nutrients, sediment, biocides and heavy metals by plants (Maltby & Acreman, 2011). Wetland plants are susceptible to the physicochemical and biological changes that occur in their habitat and the surrounding environment because they are immobile (Miller et al., 2006). Because plants are fixed and should cope with year-round challenges, as well as seasonal fluctuations of rainfall and hydrological regime, they are important indicators of the factors that influence significantly the structuring of wetlands (Sieben et al., 2010a). Furthermore, many attributes of plant communities and individual species are not only sensitive to disturbances (particularly human-induced), but can also be easily measured and quantified (Miller et al., 2006). A study on the East African wetlands report that, of the four wetland components (hydrology, geomorphology, vegetation and water quality), vegetation was the most sensitive to anthropogenic disturbances (Beuel et al., 2016).

Wetland vegetation can also be considered useful indicators of their soil substrate. In a review covering 90 wetlands along the U.S. Great Lakes, Johnston et al. (2007) concluded that plant forms are often indicators of wetland soil types. They found that submerged aquatic vegetation was indicative of silty soils, free-floating plants indicated clay soils, and sandy soil indicators tended to have graminoid forms, although graminoid plants could occur on multiple soil types. Wetlands contain a broad variety of plant communities that are linked to particular conditions of the environment that include wetness, soil type and nutrient content (Sieben et al., 2016c). A recent study (Sieben et al., 2017d) found that nutrient status greatly influences wetland vegetation. Directly or indirectly, hydrological variables and water quality regulate various biological processes, which in turn influence biodiversity and this also has feedback effects (Figure 2.6) (Gopal, 2015).

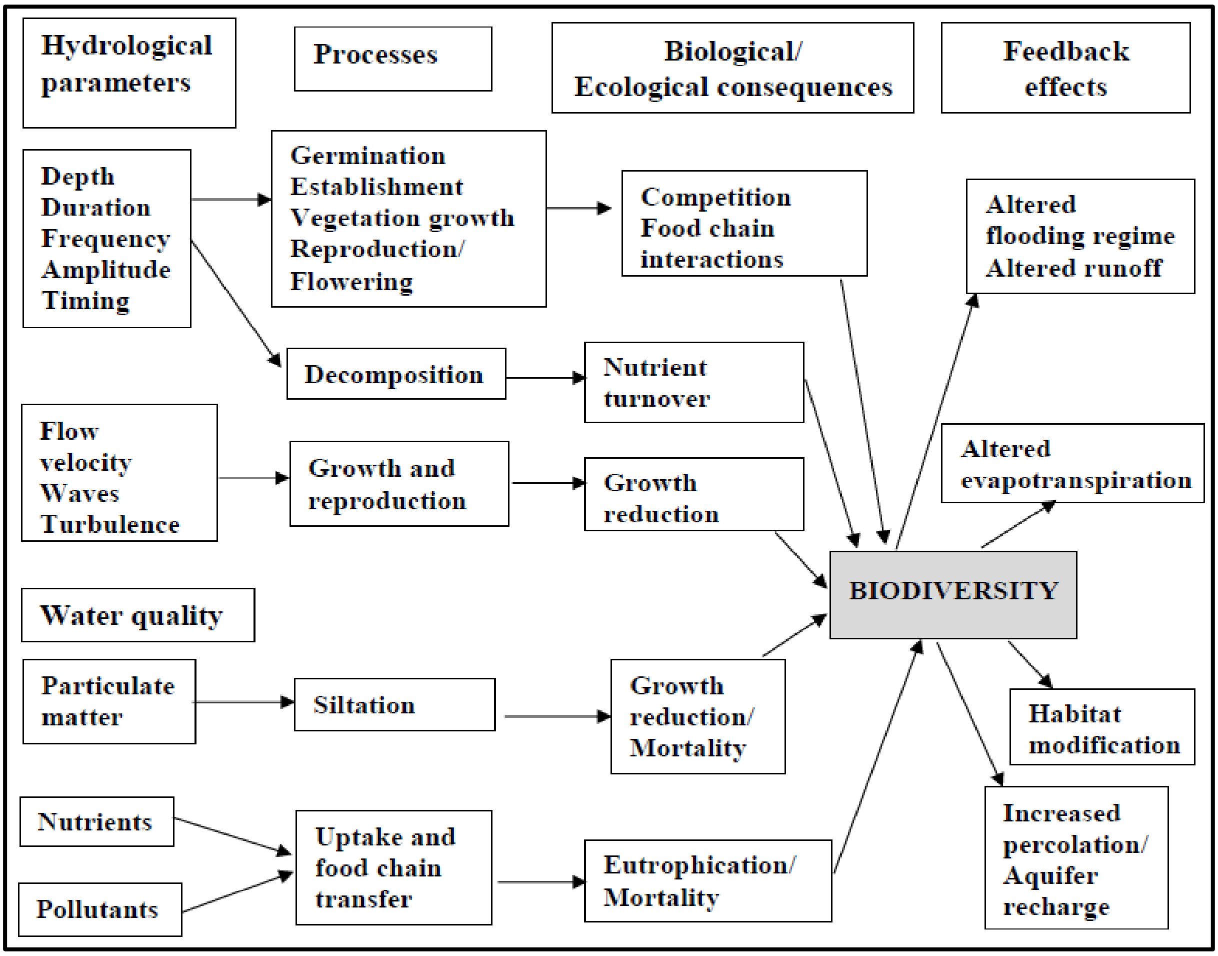


Figure 2.6: Variables of hydrology influencing biological processes and in turn the biodiversity of a habitat in a wetland (Gopal, 2015).

The stresses and problems encountered by plants in wetlands are so unique and, in some situations, so extreme that only well adapted species can occur, forming their own characteristic species composition (Sieben, 2011). Zonation patterns of herbaceous plant species along an inundation/wetness gradient are a conspicuous feature of many wetlands (Gopal, 2016). Mostly, typical wetland plants (reeds, rushes and sedges) occur in the permanently wet zone, where the soil is usually grey in colour with no or only a few mottles, and commonly experiences seasonal to permanent inundation (Ollis et al., 2013). Nevertheless, the occurrence of basically all herbaceous emergent hydrophytes is generally limited to depths not exceeding 2 m (Gopal, 2016). Because wetland soils are highly dependent on hydrology and in turn determine the vegetation that develops, soils and vegetation can be used as indicators of wetland conditions (Table 2.6). Hence, in the absence of long-term records of hydrology (which is normally the case), hydric soils and/or hydrophytic vegetation can be used as indicators of wetland hydrology, indicating that at some point the area is adequately wet for redoximorphic features to develop (Collins, 2005; Ollis et al., 2013). Unlike soil morphological characteristics which result from long-term conditions of hydrology, wetland vegetation is an indicator of recent conditions (Ollis et al., 2013).

Table 2.6: Soil wetness zones (degree of wetness) in wetland environments and the associated vegetation. Adapted from Ellery et al. (2009) with modifications from Collins (2005) and Ollis et al. (2013, 2015).

Indicator		Degree of soil wetness (soil wetness zones)			
		Non-wetland	**Temporary**	**Seasonal**	**Permanent/ semi-permanent**
Hydrological characteristics		No significantly prolonged saturation; Purely terrestrial	Intermittently/temporarily saturated – with all air spaces in the soil filled with water for irregular periods of less than one season (i.e. less than about 3 months). This corresponds to the temporary zone of a wetland	Seasonally saturated – with all the spaces between the soil particles filled with water for extended periods (generally from 3 to 9 months duration), usually during the wet season/s, but dry for the remaining part of the year. This corresponds to the seasonal zone of a wetland	Permanently/semi-permanently saturated – where all the air spaces in the soil are filled with water for the entire year, in most years. This equates to the permanent (inner) zone of a wetland
Soil characteristics	**0-10 cm depth**	Matrix usually brown/red (chroma >1)[a]; No/very few mottles; Low OM[b]; Non sulphidic[c]	Matrix is brown to greyish brown (chroma 0-3, usually 1-2)[a]; Few/no mottles; Low/ intermediate OM[b]; Non sulphidic[c]	Matrix is brownish grey to grey (chroma 0-2)[a]; Many mottles; Intermediate OM[b]; Sometimes sulphidic[c]	Matrix is grey (chroma 0-1)[a]; Few/no mottles; High OM[b]; Often sulphidic[c]
	30-40 cm depth	Matrix usually brown (chroma >2); No/few mottles	Matrix greyish brown (chroma 0-2, usually 1); Few/many mottles	Matrix brownish grey to grey (chroma 0-1); Many mottles	Matrix grey (chroma 0-1); No/few mottles;
Vegetation	**Description**	Dominated by species that usually occur extensively in non-wetland areas; hydrophytic species may occur in very low abundance	Predominantly grass species; a mixture of species that occur extensively in non-wetland areas, and hydrophytic plant species which are restricted largely to wetland areas	Predominantly hydrophytic grass and sedge species which are restricted to wetland areas, usually <1 m tall	Dominated by: (1) emergent plant species, including reeds (*Phragmites australis*), sedges and bulrushes (*Typha capensis*), usually >1 m tall (marsh); or (2) submerged or floating or aquatic plants
	Indicator status	Predominantly obligate upland (terrestrial) plants	Coexistence of mainly facultative upland and facultative wetland plants	Mainly facultative wetland plants; Obligate wetland plants and terrestrial wetland grasses also occur	Predominantly obligate wetland plants (sedges, reeds and bulrushes)

Key to Table 2.6:
[a]Chroma is the relative purity of the spectral colour, which declines with increasing greyness. A Munsell colour chart is often used to determine chroma. However, in its absence the colour of the soil matrix is characterised using the following colour descriptions (given in order of increasing greyness): brown/red, greyish brown, brownish grey, grey.
[b]High OM: soil organic carbon is more than 5%, often exceeding 10%.
Low OM: soil organic carbon is less than 2%
Intermediate OM: soil organic carbon is between 2% and 5%
[c]Sulphidic soil material has sulphides, giving it a characteristic "rotten egg" smell, and non sulphidic material lacks sulphides.

2.6 Wetland vegetation and its diversity

The most conspicuous and ubiquitous feature of palustrine wetlands, which also plays a fundamental role in the functioning of wetland ecosystems, is the vegetation (Cronk & Fennessy, 2001; Sieben et al., 2010a; Sieben, 2011; Gopal, 2016). Wetland vegetation consists mainly of vascular plants that are typically adapted to inundated or saturated conditions, termed macrophytes or hydrophytes (Mitsch & Gosselink, 2015). A hydrophyte can be considered as a plant that is adapted to life in water or intermittently flooded and/or saturated soils (hydric soils) and occurs in wetlands and deepwater habitats (Collins, 2005; Tiner, 2017). Collins (2005) highlights that the definition of a hydrophyte implies that not all individuals of a species should necessarily occur in wetlands for the species to be regarded a hydrophyte. This also means that not all individuals of a given species should necessarily occur in terrestrial environments for the species to be regarded as non-wetland. Given that wetlands are transitional ecosystems, the same author highlights that species typically considered to be adapted to well-drained conditions can also be found within transitional zones (seasonal and temporary hydrological zones). Thus, all species occurring in the transitional zones are considered wetland plants.

Generally, the type of vegetation contributes to a wide variety of ecosystem services of a wetland (Gopal, 2016). These are further discussed in sections 2.8–2.10. Because wetland vegetation composition and structure are essential features that form animal habitats, a description of plant communities is often used as a surrogate for biodiversity in general for a given wetland (Sieben et al., 2016a). Moreover, plants are so critical in wetlands that they are the most widely adopted biotic indicator for wetland condition (DWAF, 2004).

Within a given wetland, a huge diversity of habitats may occur, in terms of substrate type, sediment deposition or erosion and hydroperiod and subsequently, large differences in vegetation types may be observed (Sieben, 2011). All plant taxonomic groups are represented in wetlands, including algae, bryophytes, ferns, and herbaceous and woody angiosperms

(Gopal, 2015). However, Sieben et al. (2017b) report that, in the South African context, most of the plant families that commonly occur in wetlands belong to the Subclass Monocotyledons, especially the Poales. Grasses account for the five most common plant species in the South African wetlands (Sieben et al., 2014a). Furthermore, of the 15 most dominant wetland plant species representing five families in South Africa, ten are grasses (family Poaceae), while the other four families are Typhaceae, Cyperaceae, Araliaceae and Ranunculaceae (Sieben et al., 2014a). In decreasing order, the top five plant families in terms of number of species in the South African wetlands are Poaceae, Asteraceae, Cyperaceae, Iridaceae and Fabaceae (Sieben et al., 2017b). Despite the different climatic conditions, freshwater wetlands across the globe are more or less functionally similar as they exhibit similar functional types of plants (e.g. rhizomatous graminoids) and many common genera (Mitsch & Gosselink, 2015). Plants make a fundamental contribution in wetland ecosystems as follows (Mitsch & Gosselink, 2000, 2015; Cronk & Fennessy, 2001; Millennium Ecosystem Assessment, 2005b):

- ❖ Wetland vegetation forms the base of food chains and, thus, is the primary pathway for energy flow in the ecosystem. Plants link the abiotic and biotic environments through photosynthesis.
- ❖ Wetland vegetation provides habitat for other taxonomic groups, including fish, amphibians, macroinvertebrates, phytoplankton and epiphytic bacteria. The diversity in these other groups depends on the composition and diversity of the vegetation.
- ❖ Wetland vegetation is strongly linked to the water chemistry. Plants remove nutrients and other pollutants from the water and soil, through uptake and assimilation, yet they also move nutrients from the sediment into the water column.
- ❖ Through processes such as shoreline and sediment stabilisation, or by modifying currents and desynchronising flood peaks, wetland vegetation influences the sediment regime and hydrology.

Plants in wetlands exhibit various adaptations that allow their establishment, growth, persistence and reproduction in anaerobic soil conditions (Cronk & Fennessy, 2001). These plants are adapted to the temporary and permanent flooding conditions found in wetlands (Mitsch & Gosselink, 2015). Wetland plants without real adaptations to permanent saturation but can occur in temporarily wet habitats are described as flood-tolerant or amphibious (Sieben et al., 2017b). Nonetheless, the vegetation in wetlands is generally viewed as consisting of vascular plants adapted to flooding (Mitsch & Gosselink, 2015).

A typical pattern of wetland vegetation composition and structure on the soil wetness gradient is the dominance of grasses in temporarily wet wetland habitats, while the seasonal and permanent wetland habitats are dominated by sedges and other monocots (Sieben et al., 2010a). Plants that have been adapted to a wetland habitat to such an extent that they cannot occur in non-wetland habitats are described as obligate wetland plants and all submerged aquatic plants are included (Sieben et al., 2017b). Thus, obligate wetland plant species (e.g. bulrush *Typha capensis* and the common reed *Phragmites australis*), mostly occur in the permanently inundated or saturated zones of a wetland, while facultative wetland plant species (e.g. the red grass *Themeda triandra*) are usually found only in seasonally saturated habitats or on the edges of the wettest zone (Collins, 2005; Ollis et al., 2013). It is noteworthy that, although some wetland plant species are obligate and others facultative, many wetland species are also very widespread (Cronk & Fennessy, 2001), especially the deep-water specialists.

Prolonged waterlogging in the wetland substrate causes hypoxia or anoxia, giving rise to several changes in the soil chemical characteristics (Gopal, 2015). This results in serious physiological problems in all plants and even animals except those that are well adapted to life in water or saturated soil (Cowardin et al., 1979). While true aquatic plants are not equipped to cope with the periodic drainage that occurs in many wetlands, terrestrial plant species are stressed by long periods of flooding (Mitsch & Gosselink, 2015). This renders wetland environments unsuitable for many plants except for those that are particularly adapted to such conditions. In their study of the South African wetlands, Sieben et al. (2017b) found that species from 15 relatively small plant families that belong to diverse lineages of angiosperms and cryptogams were exclusively obligate wetland species. The DWAF (2008) provides a list of known obligate wetland plants in South Africa. Based on their expected frequency of occurrence in wetland systems, five categories of wetland plants (also called wetland indicator status) are recognised (Table 2.7).

Table 2.7: Wetland vegetation (plant indicator status) categories, on the basis of their frequency of occurrence in wetlands (Collins, 2005; DWAF, 2008; Mitsch & Gosselink, 2015).

Category	Symbol	Definition and description
***Obligate Wetland**	OBL	Plants that are almost always found in wetlands (estimated probability > 99%) under natural conditions, but may also occur rarely (estimated probability <1%) in non-wetlands.
***Facultative Wetland**	FACW	Plants that usually occur in wetlands (estimated probability of 67–99%), but occasionally (estimated probability 1–33%) found in uplands (non-wetlands)
Facultative	FAC	Plants that are equally likely to be found in wetlands or in uplands (estimated probability of 34– 66%).

Facultative Upland	FACU	Plants that occasionally occur in wetlands (estimated probability of 1–33%), but more often in non-wetlands (estimated probability of 67–99%).
Obligate Upland	UPL	Plants that occur rarely (estimated probability <1%) in wetlands but almost always (estimated probability >99%) in non-wetlands under natural conditions.

*Only Obligate Wetland and Facultative Wetland species are considered to be wetland indicator species.

Adaptations of wetland plants can be classified into three main categories (structural or morphological, physiological and whole plant strategies), and allow plants to tolerate anoxia in wetland soils (Table 2.8) (Mitsch & Gosselink, 2015). Because the absence of oxygen in the rooting zone defines a wetland ecosystem, the ways in which plant species are adapted to hypoxia or anoxia determine their success but may also confine some of the species to such habitats (Sieben et al., 2017b). One important structural adaptation in wetland vascular plants is the presence of pore space in the cortical tissues (aerenchyma), thus allowing oxygen to diffuse from the aerial parts to the roots of the plant to meet respiratory demands (Mitsch & Gosselink, 2015; Moor et al., 2017). This allows for root oxygenation and respiration. It is also generally accepted that clonality is an adaptation to waterlogging-derived stress (Song & Dong, 2002; Sieben et al., 2004; Sieben & le Roux, 2017). Clonal growth allows the development of monospecific stands of certain plant species, which reduces competition in these stressful environments and results in the dominance of such plants (Sieben et al., 2017b).

Table 2.8: Plant adaptations and responses to flooding and waterlogging conditions (Mitsch & Gosselink, 2015)

Structural/morphological	Physiological	Whole-plant strategies
❖ Aerenchyma tissue in roots and stem ❖ Adventitious roots ❖ Stem hypertrophy (e.g., buttress trunks) ❖ Fluted trunks ❖ Rapid vertical growth/ growth dormancy ❖ Shallow root systems/prop roots ❖ Lenticels ❖ Pneumatophores and cypress knees	❖ Pressurised gas flow ❖ Rhizospheric oxygenation ❖ Decreased water uptake ❖ Altered nutrient absorption ❖ Sulfide avoidance ❖ Anaerobic respiration	❖ Timing of seed production ❖ Buoyant seeds and buoyant seedlings (viviparous seedlings) ❖ Roots, tubers and seeds resistant to long periods of submergence

In response to the diversity of wetland habitat types, wetland plants have developed into various life forms (Collins, 2005). Given that duration and depth of flooding are two hydroperiod characteristics that are most critical in determining plant species distribution within wetlands, Cronk and Fennessy (2001) and Collins (2005) classify wetland plants into four categories:

- Emergent plants – these plants are rooted in the soil and their basal portions normally grow beneath the water surface, but their photosynthetic parts (stems and leaves) and reproductive organs are aerial, e.g. *Phragmites*, *Typha* and *Cyperus* species.
- Submerged plants – except for the flowering parts, these plants normally spend their whole life cycle below the water surface, e.g. *Paspalidium* and some *Potamogeton* spp.
- Floating-leaved plants – plant species with their roots anchored in the substrate but leaves float on the surface of the water, e.g. *Nymphaea* species.
- Floating plants – plants with leaves and stems floating on the surface of the water e.g. *Lemna* and *Pistia* species.

Wetland vegetation is usually organised into distinct plant communities, which are usually dominated by a single or a few species (DWAF, 2008; Sieben et al., 2014a; Gopal, 2015; Mitsch & Gosselink, 2015). The most common wetland plants are grasses (Poaceae), but sedges (Cyperaceae) tend to be dominant in the wettest parts of the wetlands (Kotze & O'Connor, 2000; Sieben et al., 2014a). While sedges generally tend to be associated with the wetter parts of the wetland system, grasses often dominate towards the drier end of the gradient (Sieben et al., 2010b). With a few exceptions (e.g. Polygonaceae and Lythraceae), most dicot families are poorly represented in wetland ecosystems (Sieben et al., 2017b). Notwithstanding that C_4 metabolism is generally thought to be an adaptation to hot, dry and high-light environments, many C_4 plants also occur in wetlands in warm regions (Kotze & O'Connor, 2000; Sieben et al., 2010a).

Given that only a single or two plant species (such as *Phragmites*, *Typha* and *Cyperus* species) may be dominant in the entire wetland system or a major part of it, a cursory look at the system is often misleading (Gopal, 2015; Mitsch & Gosselink, 2015; Sieben et al., 2017b) because it will appear like only one species is present, yet there may be more species than observed. Thus, to reveal the overall diversity of plant life in a wetland, a closer examination is essential. Most typical wetland plants have a clonal growth form, making them very efficient competitors for habitat space (Cronk & Fennessy, 2001). Hence, wetland vegetation is characterised by the uneven distribution of species. Sieben et al. (2017b) attribute this to the paradoxical situation that exists in wetlands where a strong environmental filter (mostly anoxia) excludes most species but those that get through the filter tend to flourish with limited competition. Additionally, species richness is a characteristic of different vegetation types and wetland vegetation dynamics is driven by the fact that the plants are clonal species that can effectively colonise an area and exclude other species (Sieben et al., 2014a).

A recent study by Sieben et al. (2017b) reports that, of all plant species occurring in South Africa, about 18.8% occur in wetlands and 4.5% of all the species are obligate wetland plants. These proportions underscore the profound contribution that wetlands make to the overall diversity of plants, especially angiosperms (Sieben et al., 2017b). Sieben et al. (2016b) emphasise that, notwithstanding that wetlands often occupy small proportions of the landscape, their vegetation, which is distinct from the surrounding landscape, requires assessment and description in its own right. Mitsch and Gosselink (2015) highlight that non-native plant species often also form a part of the vegetation in freshwater wetlands, particularly in disturbed ecosystems. Vegetation is such an important feature in a wetland that it can be used successfully in identifying wetland areas, because the presence of obligate wetland plant species is often considered to be diagnostic of wetland conditions (Collins, 2005; DWAF, 2008; Sieben et al., 2010a, 2011, 2014a). The DWAF (2008) document points out that, in the absence of readily identifiable obligate wetland plants, the zones can be assessed for the dominance of facultative wetland plants as follows:

- ❖ Where more than 50% of the zone is covered by facultative wetland plants (in either the woody or herbaceous layers), clear indications of wetland conditions can be assumed.
- ❖ Where facultative plants are present, but covering less than 50% of the zone, possible wetland conditions can be assumed. This can be confirmed with redoximorphic features in the soil.
- ❖ Where no facultative plants are present, absence of wetland conditions can be assumed, and the terrestrial status can be confirmed by determining soil redoximorphic features.

Wetland plants exhibit a remarkable diversity within and across wetlands. Within a single wetland, various communities from different vegetation types can occur together in the different habitats (Sieben et al., 2014b) because the wide variety of habitats in the wetland gives rise to many different vegetation types (Sieben, 2011). Thus, species composition differs from one wetland plant community type to the next (Sieben et al., 2014a). Ollis et al. (2013) recognise four primary categories of wetland vegetation (aquatic, herbaceous, shrubby/ thicket and forest). Most plants in wetlands are herbaceous but in some cases, woody species can also be prominent (Sieben et al., 2014a).

The establishment and thus distribution of plant species within a wetland is influenced by hydrological processes or characteristics that include underground water exchange, the timing and duration of flooding, and water depth, flow rates and patterns (Cronk & Fennessy, 2001; Collins, 2005). The duration and depth of flooding are the two most important of these characteristics (Collins, 2005). Consequently, on a wetness gradient, different wetland plant species occupy different wetness zones (Table 2.9) as indicated in Section 2.5. A decrease in the average number of plant species with increasing soil wetness has been reported (Sieben et al., 2014a). Because seasonal wetland habitats have oxygenated periods, they have the potential to support more species than the other wetland habitats (Sieben et al., 2016a). With wetlands being "transitional" ecosystems, it is expected that some of the species are adapted to grow on a wide range of hydroperiod (DWAF, 2008). Because of their specific environmental preferences, wetland indicator species can be useful as ecological indicators of habitat conditions, environmental changes or vegetation types (Collins, 2005; DWAF, 2008; Sieben et al., 2014a). Wetland plant forms can also be important indicators of their substrate. A study on the wetlands located along the Great Lakes coast of the United States of America concluded that plant forms are often indicators of wetland soil types (Johnston et al., 2007).

Table 2.9: A summary of vegetation indicators to be expected in the different hydrological (wetness) zones of a wetland (DWAF, 2008)

Vegetation	Temporary zone	Seasonal zone	Permanent/semi-permanent zone
If herbaceous	Predominantly grass species; a mixture of species occurring extensively in non-wetland areas, and hydrophilic plants that are limited mainly to wetland areas	Hydrophilic sedge and grass species which are restricted to wetland areas; e.g. *Phragmites australis*	Dominated by: (1) emergent plants that include reeds (*Phragmites australis*), a mixture of bulrushes (*Typha capensis*) and sedges, usually > 1 m tall; or (2) submerged or floating or aquatic plants
If woody	Mixture of woody plants, occurring extensively in non-wetland areas, and hydrophilic plant species that are limited mainly to wetland areas	Hydrophilic woody species, which are limited to wetland areas	Hydrophilic woody species, which are limited to wetland areas. They are adapted morphologically to prolonged wetness (e.g. prop roots)

Given the threat of wetland degradation, it has become increasingly important to determine the wetland plants that can be used as biological indicators for use in the monitoring of the condition of particular wetlands (Sieben et al., 2014a). Nevertheless, there are arguments in support of emphasising groups of species that can be used as indicators, instead of individual indicator species (Day & Malan, 2010). The description of wetland habitats on the basis of the vegetation and the subsequent classifications can play a critical role in strategically planning the conservation of wetlands (Mitsch & Gosselink, 2015). Because the vegetation characterises an ecosystem and provide habitat for animals, a detailed wetland vegetation description can provide clues on the conservation value of the ecosystem (Sieben et al., 2010a, 2016b).

2.7 Functional characteristics of wetlands and constituent plants

2.7.1 Functional ecology

Quantifying biological diversity helps to understand how ecosystems function. Given the emphasis on conserving the complex networks of species and large-scale ecosystems (Ostfeld et al., 1997) that requires an understanding of the factors that determine the structure and function of these systems, the concept of functional diversity was developed (Smith et al., 1997). This concept entails grouping species into functional groups on the basis of similarities in their functional characteristics and their role within an ecosystem. One approach to describe plant communities is in terms of guilds or functional groups that can be defined by measurable plant traits (Keddy, 2010; Sieben, 2012; Moor et al., 2015).

The term guild, which defines species using the same class of resources, is used to describe groups of functionally similar species in a community (Boutin & Keddy, 1993). Within a community, a generalised guild groups species basing on association and disassociation patterns between species and reflects the combined result of interspecific interactions and dispersal (Sieben & le Roux, 2017). Plant functional types refer to groups of plant species that, because they tend to share certain key functional traits, have similar functioning at the level of the organism, respond in a similar way to environmental factors and/or have similar roles in (or effects on) ecosystems (Semenova & van der Maarel, 2000; Cornelissen et al., 2003; Mitsch & Gosselink, 2015). Plant functional types are defined based on, among other things, nutrient foraging strategies, morphology, physiology, location of perennation tissues and life span (Sieben et al., 2010b). The major distinction between generalised guilds and functional groups is that the former classify species based on how they respond to their biotic environment, while the latter classify the species on the basis of their characteristics that play a role in their interactions with their total environment (Sieben & le Roux, 2017).

The grouping of plant species into functional types has gained increased acceptance as a means of understanding ecosystem functioning (Ostfeld et al., 1997). The same authors also note the complexity of analysing ecosystems, which arises from the interaction of many species. Thus, functional grouping of wetland plants provides a way of reducing this complexity in plant-environment assessments (Boutin & Keddy, 1993; Sieben & le Roux, 2017). As a result, it is often recommended that species performing the same function in an ecosystem should be grouped together (Ostfeld et al., 1997; Sieben & le Roux, 2017). Plant functional types are important in ecological studies because they also provide clues to the adaptations that plants have developed for survival in particular environments (de Bello et al., 2010; Sieben, 2012; Moor et al., 2015).

The use of functional types to classify plants is also often applied as a means of elucidating vegetation patterns that result from environmental factors that structure communities (Sieben et al., 2010b). Plant functional types also allow vegetation types (from plant communities to formations) to be described in structural-functional terms even without the knowledge of regional details and thus, help in the understanding of ecological constraints of plants and their communities (Semenova & van der Maarel, 2000). Studies have demonstrated that, by taking into account the species that collectively account for 80% of the total biomass in a community, sufficient ecosystem properties can be captured (Garnier et al., 2004; Pakeman & Quested, 2007).

Plant functional types can also be important tools in predicting how changes in different sets of environmental factors would affect community composition and wetland dynamics (Boutin & Keddy, 1993; Sieben et al., 2014a). For example, they can be a useful tool for investigating the effect of climate change on communities and ecosystem functioning, and grouping of species into functional types is important to understand species responses to climatic variables (Kotze & O'Connor, 2000). Because wetland plants are sensitive to hydrology, functional groups can also be used in wetland delineation (DWAF, 2004). However, the application of functional ecology in wetland vegetation studies is a more recent development and has been used in only a few studies (Table 2.1). By classifying 43 wetland plant species in eastern North America based on 27 functional traits, Boutin and Keddy (1993) were among the first to employ functional traits in wetland vegetation studies. They grouped the species into three main functional groups (ruderal annuals, interstitial perennials and matrix perennials) and further subdivided them into seven guilds (obligate annual, facultative annual, interstitial reed, interstitial clonal, interstitial tussock, clonal stress tolerator and clonal dominant).

In classifying plant species according to their function in ecological communities, the functional approach emphasises the traits that influence processes such as nutrient uptake, competitive ability, stress tolerance and dispersal ability (Boutin & Keddy, 1993). Wetland plants can be classified into a number of functional types. Functional classifications of wetland plants can be based on a systematic measurement of many different functional traits of the plants (Boutin & Keddy, 1993; Sieben, 2012; Sieben et al., 2014a). In such classifications, the composition of wetland vegetation, in terms of the functional types, can be combined with the vegetation structure (cover and height of the various strata) and species diversity (Sieben et al., 2014a). The identification of groups of species that have similar functioning in communities is important in the identification of factors that determine the occurrence and performance of species within communities (Sieben & le Roux, 2017). Wetlands can also be characterised in terms of structure and their functional composition because the main functional types are influenced by specific ecological factors (Sieben et al., 2014a). The same authors indicate that, while indicator species are often used to recognise most plant communities, dominant species can also be useful in recognising plant communities.

Plant trait functional diversity has emerged as one that explains and can be explained by the most relevant components of biodiversity affecting ecosystem functioning (Semenova & van der Maarel, 2000; Díaz & Cabido, 2001; Mason et al., 2005; de Bello et al., 2009). Functional diversity of communities is defined as the extent of dissimilarity (variation) or diversity of plant traits among species coexisting within a given ecological community (Petchey & Gaston, 2002; de Bello et al., 2009; Garnier & Navas, 2012). Given the correlation between plant functional composition and ecosystem functioning (Díaz & Cabido, 2001; Lavorel & Garnier, 2002), it may be possible for ecosystems that have similar functioning to be also similar in functional composition because they present similar stresses to the plants (Sieben, 2012). There is both theoretical and empirical evidence for the effect of functional diversity on short-term ecosystem resource dynamics and long-term ecosystem stability (Díaz & Cabido, 2001). More recently, the concept has received considerable attention as it captures information on the role that species play in an ecosystem, which is not the case in traditional species diversity measures (Ricotta et al., 2014).

Functional diversity can be decomposed into three independent complementary components, namely, functional richness, functional evenness and functional dispersion (divergence) (Mason et al., 2005; Villeger et al., 2008). These help in examining the mechanisms linking biodiversity to ecosystem functioning and can be used as tools for quantifying community functional diversity. Functional richness is the amount of functional space occupied by the species in a community (Mouillot et al., 2005), while functional dispersion is the extent to which abundance distribution in the niche space maximises variation in functional characteristics in the community (Mason et al., 2005). Functional evenness refers to the extent of community biomass distribution in the niche space, allowing effective use of the whole range of available resources (Mason et al., 2005; Mouillot et al., 2005). Now, it is generally accepted that the link between species diversity and ecosystem functioning is via functional diversity but different types of traits, evenness, richness etc., play different roles (Grime et al., 1997; Mouillot et al., 2005; Roscher et al., 2012). Petchey and Gaston (2007) observe two main reasons for measuring functional diversity; (1) determining how functional trait composition varies between communities (assemblages), (2) to improve the understanding of the determinants of ecosystem functioning and how this functioning is influenced by the traits exhibited by the species.

2.7.2 Functional traits

Plant functional traits are morphological, physiological and phenological attributes, measurable on individual plants, which influence individual plant fitness through their effects on survival, growth and reproduction or can affect its environment (McGill et al., 2006; Violle et al., 2007; de Bello et al., 2010; Garnier & Navas, 2012; Pérez-Harguindeguy et al., 2013) and provide species adaptations to specific environments (Sieben et al., 2014a). Functional traits are important for community assembly and can be anatomical or morphological (such as specific leaf area, root depth, or seed size), or they can be ecophysiological measures that reflect the combined activities of several related processes of the plant (Kraft & Ackerly, 2014). Functional traits can be useful in describing plant community attributes (Sieben, 2012). These functional traits may vary within and across species (Kraft & Ackerly, 2014).

Plant functional traits do not only give insights into the opportunities and challenges faced by plants in various habitats (Grime et al., 1997; Westoby, 1998; Lavorel & Garnier, 2002; Reich et al., 2003; Grime, 2006), but also provide an understanding of how functional diversity influences ecosystem processes and the subsequent ecosystem services (Díaz & Cabido, 2001; Díaz et al., 2013; Pérez-Harguindeguy et al., 2013). There has been emphasis on the relationships among plant functional traits that affect attributes such as productivity, biomass and ability to withstand disturbances (Wang et al., 2012). Given that these traits can be measured on almost all plants within and across communities, they can provide a means for drawing generalisations across species and for explaining the mechanisms that shape community patterns (Kraft & Ackerly, 2014).

Because functional traits can be measured on individuals and are related to their functioning and modulate their fitness, the traits enable the determination of environment-organism interactions and provide a functional perspective in studying the factors that underpin biodiversity and ecosystem processes (McGill et al., 2006; Violle et al., 2007; Garnier & Navas, 2012). Plant functional traits show variation in relation to the major factors of the environment (Garnier & Navas, 2012). According to Weiher et al. (1999), these traits are critically important in, inter alia, trait-environment relationships, classification into functional groups of species with similar responses to the environment, assembly rules, comparative ecology, ecophysiology and the mechanistic understanding of plant responses to the environment.

The most important traits that address plant competitive ability are relative growth rate, plant height and seed mass (Westoby, 1998; Weiher et al., 1999). These three plant dimensions have been widely accepted as important in plant functioning and ecological strategies (Westoby, 1998). Some traits can highlight something quite fundamental about plant strategies, such as the examples that are given below. Specific leaf area, which is an important proxy of relative growth rate, can be an indicator of plant competitive ability (Weiher et al., 1999). Specific leaf area and leaf water content are strongly correlated with other morphological and operational traits that measure stress tolerance (Grime et al., 1997). Weiher et al. (1999) also highlight that competitive ability is strongly associated with plant height and above-ground biomass. The same authors further point to the dependence of fecundity on seed mass and aboveground vegetative biomass. Hence, specific leaf area, plant height and seed mass are fundamental plant functional traits (Westoby, 1998; Weiher et al., 1999).

2.7.3 Habitat filtering

In general terms, species that assemble to make up a community are filtered by dispersal constraints, environmental constraints and internal dynamics (Begon et al., 2006). Given that plants need to disperse to new sites, become established and subsequently, to persist, nearly all plant species face the primary challenges that include dispersal, establishment and continued existence (persistence) (Weiher et al., 1999). Persistence entails tolerating fluctuations in resource availability and the changes in the array of abiotic (e.g. pH and flooding) and biotic (e.g. competition and herbivory) conditions of a particular site (Weiher et al., 1999). Díaz and Cabido (2001) emphasise that, most often, species do not contribute equally to ecosystem processes, instead, dominant species are responsible for a large fraction of ecosystem functioning. This is because communities in nature are usually dominated by few species whereas the remainder is rare (Maire et al., 2012). Even in species-rich vegetation, most of the biomass is accounted for by only a small number of dominant species, whose functional characteristics have an overriding influence in the community and its functioning (Grime, 1998). This implies that the resilience and resistance of ecosystems are greatly determined by the traits of the most dominant plant species where communities characterised by the dominance of fast-growing plants tend to have low resistance and high resilience (Díaz & Cabido, 2001). Functional diversity is an important driver of ecosystem resilience to changes in the environment, ecosystem processes and delivery of ecosystem services (Laliberté & Legendre, 2010). Consequently, Díaz and Cabido (2001) observe that the loss of an entire functional type or addition of a new functional type (e.g. addition of invasive alien species) can have a significant impact on ecosystem functioning. Therefore, the fundamental traits that help plants to address the three important challenges (dispersal, establishment and persistence) should be investigated.

Two opposite niche-based deterministic processes were proposed to explain the relative abundances of species in communities: habitat filtering predicts that most co-existing species should display similar traits, whereas niche differentiation requires that co-existing species exhibit dissimilar traits for coexistence (Maire et al., 2012). These two processes are assumed to synergistically influence species abundance and distribution in highly competitive plant communities, although the two processes have different relative emphasis for rare and dominant species (Maire et al., 2012). Habitat filtering is a process that influences community assembly (Li et al., 2018). In a particular community, species are forced to converge towards an optimum value of a trait by habitat filtering and thus become functionally similar (Maire et al., 2012; Kraft & Ackerly, 2014). Within competitive mixtures, the role of functional similarity has been emphasised for dominance, while functional dissimilarity improves species coexistence by reducing interspecific competition (Maire et al., 2012).

Habitat filters refer to the factors (biotic and abiotic) that only permit species with particular traits or phenotypes to establish and persist in a particular location but prevent the establishment or persistence of other species (Geho et al., 2007; Maire et al., 2012; Kraft et al., 2014; Li et al., 2018). Thus, the absence of a species from a given locality, even if it has the potential to disperse to that site, can be explained by the fact that the conditions of that location are not suitable for the germination and growth of the species. For example, because they require special adaptations, wetland habitats support distinct plant trait complexes (Sieben, 2012). Prolonged waterlogging of the substrate, which causes hypoxia or anoxia in the wetland substrate and subsequently, chemical changes in the soil, excludes a large variety of plants (Gopal, 2015; Mitsch & Gosselink, 2015). Aerenchyma in the stem and floating leaves are specific examples of traits that vascular plants have acquired, which confer adaptations to wetland habitats (Cronk & Fennessy, 2001). Therefore, habitat filters are the mechanism through which habitat variation shapes community assembly and diversity patterns across landscapes. Because of the effect of habitat filtering, plant functional traits can be expected to be positively related to plant species abundance (Shipley et al., 2006).

Abiotic conditions and biotic interactions are responsible for shaping local community assemblages (Kraft et al., 2014). One important result of abiotic filtering is the typical change in species composition along environmental gradients and it has widely been accepted that plant communities change in predictable ways along environmental gradients of factors such light, water availability, soil fertility, elevation and latitude (Kraft & Ackerly, 2014). These changes in species identity are also often reflected in changes in their functional traits, such that average trait values across species in the community can shift along a gradient (Kraft & Ackerly, 2014). The dominant species in a community can also develop a huge competitive effect on the resources locally and thus become as a habitat filter as they exclude the less competitive species (Maire et al., 2012).

The need for studies on functional traits has resulted in the identification of structural traits that can easily be measured on plants, with subsequent shortlisting of important traits and standardised methods to assess them (Weiher et al., 1999; Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013). However, despite wetlands being considered an important case study for plant functional traits, detailed measurements of the traits of wetland vegetation are still limited (Sieben, 2012; Moor et al., 2015; Zhang et al., 2015; Lhotsky et al., 2016; Sieben & le Roux, 2017).

2.7.4 Ecosystem services–ecosystem functioning relationships

It has become necessary to determine the important mechanisms and characteristics through which plants influence ecosystem properties (Grime, 2006; de Bello et al., 2010). It has been established that ecosystem functioning and behaviour of plant functional types are related to environmental characteristics, and plant function is now described through plant traits (Semenova & van der Maarel, 2000; Gaucherand & Lavorel, 2007). Research on the relationships between biodiversity and ecosystem functioning has documented that functional composition is the main determinant of ecosystem processes (Gaucherand & Lavorel, 2007; Roscher et al., 2012; Zhang et al., 2015). Functional traits are considered the key mechanism by which species contribute in influencing ecosystem properties (Lavorel & Garnier, 2002; de Bello et al., 2010; Zhang et al., 2015). However, studies focusing on quantifying the relative effect of various plant traits on different ecosystem functions are few (de Bello et al., 2010; Moor et al., 2017; Schwarz et al., 2017). The identification of important plant functional traits may improve the understanding of the determinants of various ecosystem properties and processes (Roscher et al., 2012) and the subsequent ecosystem services (Sieben et al., 2017c).

Therefore, Sieben (2012) regards functional composition as a good indicator for the condition of the ecosystem or underlying ecosystem processes.

Plant functional traits influence ecosystem functions that include carbon storage, nutrient cycling and primary productivity in the ecosystem (Lavorel & Garnier, 2002; Garnier et al., 2004; Garnier & Navas, 2012). A recent study (Sieben et al., 2017c) further reports that plants, through their traits, are the primary determinant of the ecosystem services such as erosion control, enhancement of water quality, carbon sequestration, medicinal plants, livestock grazing, aesthetic beauty and crafts/construction material. Nonetheless, the relevant functional traits for different ecosystem processes and their effects are yet to be fully identified (Gaucherand & Lavorel, 2007; Roscher et al., 2012; Zhang et al., 2015). There is an increasing consensus that quantifying the diversity of functional traits in ecological communities can significantly play a role in ecosystem service assessment and management (de Bello et al., 2010; Zhang et al., 2015; Moor et al., 2017). With the increasing demand for ecosystem services, the identification of organisms or groups of organisms that are critical in controlling the ecosystem properties responsible for the provision of ecosystem services is needed for conservation and sustainable supply of those services (de Bello et al., 2010).

Given that they are the main ecological attributes through which various organisms and ecological communities affect ecosystem services, there is growing literature focusing on functional traits (de Bello et al., 2010; Sieben, 2012; Moor et al., 2015, 2017; Zhang et al., 2015; Lhotsky et al., 2016; Sieben & le Roux, 2017). Following a move to use ecosystem services as a way of valuing ecosystems and promoting their sustainable use (Millennium Ecosystem Assessment, 2005a), much attention has been paid to the contribution of various organisms to the provision of ecosystem services (Suding et al., 2008; de Bello et al., 2010).

The biomass ratio hypothesis indicates that the degree to which the traits of a species influence ecosystem properties is dependent on the abundance of the species in the ecological community (Grime et al., 1997; Gaucherand & Lavorel, 2007; Garnier & Navas, 2012; Sieben, 2012). For different organisms and ecosystems, the type, range and the relative abundance of functional traits in ecological communities have a great influence on various ecosystem services (de Bello et al., 2010). In a study to assess the relationship between plant diversity and ecosystem services, Zhang et al (2015) found a significant relationship between wetland ecosystem properties and some traits of the dominant species. The same study reports that ecosystem services are fundamentally products of ecosystem properties. Based on these results, the authors recommend that the dominant species in a community and their functional traits should be prioritised over the number of species in biodiversity management and in enhancing certain wetland ecosystem functions, particularly for the purpose of conservation and sustainable provision of ecosystem services. This also was the basis for Grime (1998) to suggest a need for a cautious interpretation of results where species richness (number of species) is found to be correlated with ecosystem properties and functioning, although the influence of species richness cannot be eliminated.

Measures of functional diversity (functional composition and functional richness) are correlated with ecosystem processes and functioning, more so than traditional measures of species diversity (Díaz & Cabido, 2001; Ricotta et al., 2014). Nonetheless, species richness in a community has a positive relationship with the chances of the presence of species with particular critical traits (sampling effect), which can drive the functioning of the ecosystem (Díaz & Cabido, 2001; Jaillard et al., 2014). This means that the chances that species with important traits are present in a community increase with increasing number of species in that community.

The relationship between species diversity and ecosystem functioning has become one global issue that has attracted considerable interest and attention, and measuring productivity is one important approach which can be used to evaluate ecosystem functions (Magurran, 2004b; Wang et al., 2007; Nogues-Bravo et al., 2008). Though species richness would be expected to increase with productivity (Schulze et al., 2002; Magurran, 2004b; Begon et al., 2006), different investigations on the species richness–productivity relationships failed to conclusively define a universal relationship between plant species diversity and productivity, mainly due to varying ecological contexts (Díaz & Cabido, 2001; Schulze et al., 2002; Begon et al., 2006; Wang et al., 2007; Adler et al., 2011). While a positive correlation between productivity and species richness has been demonstrated (Magurran, 2004a), the opposite has also been reported (Lavorel & Garnier, 2002).

In a comprehensive review covering eight different ecosystems, de Bello et al. (2010) assessed the connection of functional traits in various groups of organisms to a broad array of ecosystem processes and services. They found that wetlands had the lowest number of studies (less than 10 out of 548 entries) on the relationships between ecosystem services and functional traits, and this proportion highlights the need for more research linking traits to ecosystem services in wetland environments. The review also established a direct effect of functional traits on the provision of ecosystem services in the majority (69%) of the cases considered, while a complex relationship was reported in the other cases. The same study also highlights that the impact of biodiversity changes on the delivery of ecosystem services can be assessed by determining the vital characteristics of organisms that influence ecosystem processes and functions. A number of individual traits have a combined effect on the delivery of a range of services, and single services are often dependent on a variety of traits, giving rise to groups of associated traits and services (de Bello et al., 2010; Laureto et al., 2015).

In wetlands, plant functional types influence the emergent properties of the ecosystems (Sieben, 2012; Moor et al., 2015, 2017; Zhang et al., 2015). For instance, plant functional types also affect the type of peat formed in wetland ecosystems (Sieben, 2012). Given that plant traits are connected to ecosystem properties, both as response and effect traits (de Bello et al., 2010; Sieben, 2012; Moor et al., 2015, 2017; Zhang et al., 2015), a recommendation has been made for specific traits that help plants to survive in wetland environments to be investigated and linked to the indicator values of the plants (Sieben et al., 2014a). However, trait-based approaches to the effects of plants on wetland functioning and ecosystem services is still lagging behind in comparison to other habitat types (Moor et al., 2017).

2.8 Importance and ecosystem services of palustrine wetlands

Ecosystem services represent the benefits that people derive directly or indirectly from ecosystems (Costanza et al., 1997; Millennium Ecosystem Assessment, 2005b; Yang et al., 2008; Russi et al., 2013). Thus, ecosystem services are integral in the interactions between nature and society (Moor et al., 2015). In addition to their hydrological functions, wetlands are of socio-economic, ecological and cultural importance (Chatterjee et al., 2010). Because wetlands provide an anaerobic environment and they are linked to the hydrological cycle, they deliver various ecosystem services (Sieben et al., 2014a). Furthermore, as transitional ecosystems, wetlands play a key role in the environment, cushioning the interactions between aquatic and terrestrial systems (Kennedy & Mayer, 2002). They also enhance and maintain the functioning of other ecosystems and the services they provide, particularly water flows (Dixon et al., 2016). Because they provide a myriad of ecosystem services, wetlands have been cited as the most valued components of the landscape in the assessments of ecosystem services (Costanza et al., 2014; Mitsch & Gosselink, 2015). Moreover, they deliver a broad array of services that are underpinned by water, including tourism, agricultural production and fisheries (Russi et al., 2013).

The concept of ecosystem services received increased attention and became more popular by the publication of the United Nations Millennium Ecosystem Assessment (2005b). Ecosystem services have been defined differently (Costanza et al., 1997; Collins, 2005; Millennium

Ecosystem Assessment, 2005b; Niu et al., 2012; Russi et al., 2013; Hay et al., 2014). However, the Millennium Ecosystem Assessment (2005b) defines ecosystem services as the direct and indirect benefits that human beings obtain from ecosystem functions and processes. What is common among the different definitions is that ecosystem services are viewed as the direct and indirect benefits that society gets from ecosystem functions and processes, which contribute to human well-being (Collins, 2005; Millennium Ecosystem Assessment, 2005b; Russi et al., 2013; Hay et al., 2014).

The Millennium Ecosystem Assessment (2005b) and the Economics of Ecosystems and Biodiversity (TEEB) (Russi et al., 2013) reports provide a detailed analysis of human dependence on the services delivered by wetlands across the globe. Wetland ecosystems deliver numerous ecosystem services for human well-being and poverty alleviation (Millennium Ecosystem Assessment, 2005b). They have proven to be essential landscape elements in the provision of hydrological, biogeochemical and biological functions (Kotze et al., 2007; Cohen et al., 2016). The benefits provided by wetlands are important, disproportionately so for the area that they cover (Ricaurte et al., 2014). It has also been recognised that wetlands have a disproportionate deterministic role in large-scale ecosystem processes (Mitsch and Gosselink, 2000; Keddy, 2004; Schlesinger and Bernhardt, 2013) and they deliver a wide range of ecosystem services that are crucial for rural development (Kotze et al., 2008). Wetlands fall in the category of over-utilised components of the landscape, particularly in rural areas where people directly depend on the ecosystem services provided by nature (Sieben et al., 2016c). Brander et al. (2006) emphasise that the services provided by wetlands should not be confused with the wetland ecological and physical functions from which they are derived. Whereas wetland ecosystem functions are the natural ecological (habitat, biological or system) properties or processes occurring within wetlands, ecosystem services are the outputs of these functions that provide benefits for humans (Costanza et al., 1997; Stelk & Christie, 2014).

While the restoration, conservation and sustainable use of wetland ecosystems and their associated services feature prominently in two of the 17 Sustainable Development Goals (SDGs) of the United Nations (United Nations, 2015), wetlands are instrumental in meeting six of the 17 SDGs (CBD Secretariat, 2015). The goal on sustainable management and ensuring availability of water and sanitation (Goal 6), and the one on the conservation, management and sustainable use of terrestrial ecosystems and biodiversity (Goal 15) have objectives that explicitly make mention of wetlands (United Nations, 2015). Directly or indirectly, wetlands contribute to 75 SDG indicators (Ramsar Convention on Wetlands, 2018). Recently, wetlands have been reported to play a key role in meeting the Paris Agreement on

Climate Change and other related multilateral agreements (Ramsar Convention on Wetlands, 2018).

It is noteworthy that the Convention on Biological Diversity (CBD) (CBD Secretariat, 2015) also highlights the importance of wetlands in meeting all the 20 Aichi Biodiversity Targets (time-bound, measureable targets agreed by the Parties to the CBD in Nagoya, Japan, in October 2010 for the Strategic Plan for Biodiversity 2011-2020). The newly coined concept of nature-based solutions (Albert et al., 2017), which relates to the use of nature in addressing a variety of global environmental, economic and social challenges (Thorslund et al., 2017), is underpinned, in part, by healthy wetlands. These agreements and reports highlight the critical role that palustrine wetlands play in providing ecosystem services to society (Niu et al., 2012; Gopal, 2016). It is the high productivity of wetlands that enable them to support the livelihoods of substantial rural populations that are often dependent on their services (Chatterjee et al., 2010; Maltby & Acreman, 2011; Mitchell, 2013).

The values of palustrine wetland ecosystem services, per unit area, are considered to be typically higher than those of other types of ecosystems (CBD Secretariat, 2015). The total global economic flow (real supply) value of wetlands, excluding floodplains, per unit area has been estimated at US$14,785 ha^{-1} yr^{-1}, which is about 15% of the total global economic value of all ecosystem services (Costanza et al., 1997). The value would even be higher with the inclusion of floodplains. In estimating the value of the world's ecosystem services, Costanza et al. (1997) report that wetlands are 75% more valuable than lakes and rivers, 15 times more than forests, and 64 times more valuable than grasslands and rangelands. Notwithstanding the differences in the estimates of wetland values, there is no question on the socio-economic and ecological importance of intact wetlands (Millennium Ecosystem Assessment, 2005b). In a global review of the economic value of different types of wetlands, Brander et al. (2006) found freshwater palustrine wetlands to have the second highest among the wetland types, after unvegetated aquatic systems. Until recently, wetland benefits were often not recognised and concomitantly, many wetlands have been degraded or poorly managed (Collins, 2005; Millennium Ecosystem Assessment, 2005b; Sullivan et al., 2008; Mitsch & Gosselink, 2015).

Since the publication of the United Nations Millennium Ecosystem Assessment (2005b), the interest and attention in ecosystem services by both researchers and policy makers has grown quite substantially (Costanza et al., 2014; McDonough et al., 2017). For example, a review of the studies on ecosystem services in Africa found a general increase in the studies since 2005, although the studies were conducted mainly in few countries (Wangai et al., 2016). According to Costanza et al. (2014), the most important contribution that has been made by the widespread recognition of ecosystem services is that the relationship between human beings and ecosystems has been reframed. Ecosystems are now regarded as a critical component of human well-being and sustainable development. While decreasing direct dependence on wetland ecosystem services with wetland loss has been reported in developed countries, many people in the developing world remain directly dependent on wetland ecosystem services (Maltby & Acreman, 2011; Gopal, 2016). The Millennium Ecosystem Assessment (2005b) emphasises the importance of wetlands in delivering a broad variety of services for humanity.

Wetlands also play an essential role in the provision of habitats and breeding areas for wildlife (Macfarlane et al., 2007). They provide corridors for movement of organisms between natural terrestrial areas, or along river systems, as well as harbouring wetland-associated animals and plants, many of which rely exclusively on these systems for breeding, feeding or growing (Day & Malan, 2010). In terms of the number of animal and plant species that rely on ecosystems for feeding, breeding and habitation, wetlands are second only to the rain forests (Munishi et al., 2011).

For millennia, wetlands have been and continue to be part of many human cultures across the globe and communities benefit from the services supplied by these systems (Millennium Ecosystem Assessment, 2005b; Sullivan et al., 2008; Mitsch & Gosselink, 2015). Because human beings are connected to wetlands through the delivery of ecosystem services, they are considered an inextricable part of the wetland system. For this reason, Hay et al. (2014) argue that a wetland should be regarded as a social-ecological system instead of a purely ecological system. Communities whose livelihood strategies include utilising wetland resources account for a substantial proportion of the populations in developing countries (Silvius et al., 2000).

The livelihoods of many poor people in sub-Saharan Africa are dependent on wetlands through their delivery of many ecosystem services that include food (Rebelo et al., 2010). The southern African wetlands provide a multiplicity of services to the people living in and around them, as well as to communities living downstream (Scholes & Biggs, 2004). Wetland productivity, which provides a great variety of functions and benefits underpin these livelihoods. Because of their role in water filtration and high productivity, wetlands are described as “kidneys of the landscape” and “nature’s supermarkets”, respectively (Daryadel & Talaei, 2014; Mitsch et al., 2015; Mitsch & Gosselink, 2015).

Classification of wetland ecosystem services is difficult because of the diversity and interrelationships displayed by wetland functions (Kennedy & Mayer, 2002). While the values of wetlands were historically divided into three hierarchical ecologically familiar levels (population, ecosystem, and global) (Mitsch & Gosselink, 2015), a paradigm shift came with the Millennium Ecosystem Assessment (2005b), which also classified the ecosystem services into four categories according to how they benefit society. Overall, wetland ecosystem services are broadly categorised into direct and indirect services (Costanza et al., 1997; Collins, 2005; Brander et al., 2006; Kotze et al., 2007; Sullivan et al., 2008). However, the general classification of wetland ecosystem services into four categories, namely, provisioning, cultural, regulating and supporting services is the most widely followed (Turner et al., 2000; Millennium Ecosystem Assessment, 2005b; Kotze et al., 2007; Sullivan et al., 2008; Turpie & Kleynhans, 2010; de Groot et al., 2012; Hay et al., 2014; Stelk & Christie, 2014; Mitsch et al., 2015; Mitsch & Gosselink, 2015; Gopal, 2016). The four categories are briefly described here.

Provisioning services

Provisioning ecosystem services are the tangible products ("goods") that are delivered by wetlands. These are, inter alia, food, fibre, freshwater, genetic resources, peat, timber, natural medicines, biochemical products, fisheries, pharmaceuticals, valuable land for cultivation and grazing for livestock (Silvius et al., 2000; Collins, 2005; Millennium Ecosystem Assessment, 2005b; Kotze et al., 2007; Sullivan et al., 2008; Russi et al., 2013; Junk et al., 2014; Gopal, 2015; Mitsch et al., 2015; Mitsch & Gosselink, 2015). According to Sullivan et al. (2008), demand for direct provisioning services from wetlands is high, with great reliance on wetlands for a wide range of harvestable products. An important example of a wetland plant is rice, which feeds more than 50% of the world's human population (Gopal, 2016). As the most biologically productive ecosystems globally which are rich in species diversity (Gopal, 2016), wetlands are important repositories of plant genetic material, some of which are valued for human wellbeing (Munishi et al., 2011).

The importance of wetlands in supplying provisioning ecosystem services worldwide has been comprehensively documented in the Millennium Ecosystem Assessment (2005b) and the TEEB (Russi et al., 2013) reports. Wetlands contribute to water security, food security and human health (Government of South Africa, 2014; Dixon et al., 2016). They also recharge the underground aquifers that account for about 97% of the world's unfrozen freshwater (Mitra et al., 2003). This groundwater, mostly recharged through wetlands, plays a critical role in water supply and provides water for drinking to about 1.5–3 billion people, as well as serving 40% of industrial water use and 20% of irrigation globally (Millennium Ecosystem Assessment, 2005b). In the rural Amazonian Piedmont region in Colombia, Ricaurte et al. (2014) found that

77.7% of the livelihood strategies of the local people depended directly on the provisioning services provided by wetlands, with fishing and hunting being the most commonly valued.

It has been documented that, in countries in sub-Saharan Africa, wetlands are quite important in the supply of innumerable provisioning services like drinking water, livestock grazing, harvestable plants and animals (Munishi et al., 2011). In southern Africa, the relationships between wetland ecosystems and human well-being are more pronounced in poor rural communities because the lives of people there are directly dependent on the availability of ecosystem services (Scholes and Biggs, 2004). The demand for direct provisioning benefits from wetlands is high in the sub-region, with a high dependence on these ecosystems for food, grazing, medicinal plants, energy, water supply and crop production, among other things (Sullivan et al., 2008). Given that much of the southern African region experiences dry climatic conditions, the sub-region is regarded as susceptible to water scarcity (Taylor et al., 1995). Because of their fertile soils and ability to retain water throughout the year, wetlands are extremely important for sustainable water supply and agricultural production in this region. Furthermore, hundreds of rivers in southern Africa originate in wetlands (Taylor et al., 1995).

Wetlands are usually of high importance for agricultural production, particularly among rural subsistence and small-scale commercial farmers through crop cultivation and grazing of livestock in and immediately around wetlands and the drawing of water for irrigation or livestock watering outside the wetland (Hay et al., 2014). Because they continue to provide water even in dry periods, wetlands allow for year-round crop production (Lannas & Turpie, 2009). Wetland ecosystems, particularly those that are seasonally and temporarily waterlogged, provide important pasture for both wild and domestic grazers, especially during droughts and in the early growing season, when the amount of grazing material is low in the surrounding terrestrial areas (Collins, 2005). A study in Tanzania (Munishi et al., 2011) reports that the utilisation of wetlands alone contributed about 31% of the total economic benefits for each household, with the major wetland-based socio-economic activities being crop production, livestock production and fishing. The other economic benefits were from a variety of sources.

Cultural services

Cultural ecosystem services are direct non-material benefits, including aesthetic, heritage and cultural-safeguarding values that people derive from wetland functions (Silvius et al., 2000; Millennium Ecosystem Assessment, 2005b; Mitsch & Gosselink, 2015). These services include cognitive development, spiritual enrichment, recreation and ecotourism, education and research, inspiration, cultural heritage, reflection, indigenous knowledge systems and aesthetics (Kennedy & Mayer, 2002; Collins, 2005; Millennium Ecosystem Assessment, 2005b; Kotze et al., 2007; Du Preez & Brown, 2011; Russi et al., 2013; Junk et al., 2014; Gopal, 2015; Mitsch et al., 2015; Mitsch & Gosselink, 2015). According to Gopal (2015), wetland ecosystems enhance tourism and may be associated with important spiritual values in some cultures, thus contributing to cultural identity, human wellbeing and the economy. Ecotourism, a key ecosystem service provided by wetlands (Ricaurte et al., 2014), including bird-watching, is increasingly becoming of economic value with widespread benefits (Mitsch & Gosselink, 2015).

Regulating services

Regulating ecosystem services are indirect benefits derived through the role of wetlands in the regulating ecosystem processes, such as improving water quality, hydrology, air quality, climate, mitigating land degradation, natural hazard regulation, sediment trapping, global geochemical cycling, disease and pest regulation and erosion control (Millennium Ecosystem Assessment, 2005b; Kotze et al., 2007; DWAF, 2008; Sullivan et al., 2008; Chatterjee et al., 2010; de Groot et al., 2012; Russi et al., 2013; Junk et al., 2014; Stelk & Christie, 2014; Gopal, 2015; Mitsch et al., 2015; Mitsch & Gosselink, 2015). It is well documented that inland palustrine wetlands provide a broad spectrum of hydrological services, including the reduction of floods, promoting groundwater recharge, and regulating river flows, specifically augmenting low flows (Millennium Ecosystem Assessment, 2005b). By protecting and regulating water resources, holding water during floods and releasing it during dry periods, storm and flood mitigation, soil erosion control, and removing pollutants from the water, wetlands maintain hydrological cycles (Millennium Ecosystem Assessment, 2005b; Day & Malan, 2010; Sieben et al., 2014a). Wetlands help to maintain the flow of rivers throughout the year (Jayachandran, 2013) as they function as simple reservoirs or aquifers that store water during wet periods and release it during the drier periods, either through sub-surface drainage, runoff or evapotranspiration (Sharma et al., 2010; Jayachandran, 2013).

Wetland vegetation also plays a critical role in slowing down the flow of water and enhancing water quality by trapping pollutants, nutrients and sediments for downstream aquatic ecosystems (Sieben et al., 2014a). Wetlands contribute to the reduction in the risk of disasters that include droughts and floods (Government of South Africa, 2014). Sather and Smith (1984), who report a 60-80% reduction in flood peaks in watersheds with about 30% wetland area, regard the protection of wetlands in a watershed as the most economical way to control floods. The economic values for wetland regulating services that include water supply, flood control and nutrient recycling in agricultural landscapes of southern Africa have been estimated at US$1029 ha^{-1} yr^{-1} and a total of US$1512 million yr^{-1} (Junk et al., 2013).

The importance of wetlands in climate stabilisation has been well documented (Maltby & Acreman, 2011; Mitsch et al., 2013, 2015; Gopal, 2015; Joyce et al., 2016; Meng et al., 2017; Moomaw et al., 2018) as they are carbon sinks and climate stabilisers (CBD Secretariat, 2015; Mitsch & Gosselink, 2015). Through many functions and processes, wetlands have ameliorating effects on impacts of climate change through carbon sequestration and storage (Stelk & Christie, 2014; Joyce et al., 2016). Despite being responsible for the emission of about 20–25% of the current global methane emissions into the atmosphere (Mitsch et al., 2013; Mitsch & Gosselink, 2015), all wetlands have the highest capacity of any ecosystem to contribute to net carbon storage and sequestration (Mitsch et al., 2015; Joyce et al., 2016). The anoxic wet conditions that exist in wetlands make these ecosystems optimum natural environments for the sequestration and storage of carbon from the atmosphere (Mitsch et al., 2013, 2015; Mitsch & Gosselink, 2015).

Notwithstanding their limited coverage, wetlands account for about 35% of the global terrestrial ecosystem carbon storage (Meng et al., 2017). Furthermore, despite accounting for only about 3% of the world's land surface area, peatlands alone are significant carbon sinks that contain about 30% of the global soil carbon, which is equivalent to about 75% of all the carbon in the atmosphere and two times the carbon in the global forest biomass (Millennium Ecosystem Assessment, 2005b; Parish et al., 2008; Russi et al., 2013). This makes wetlands the most space efficient carbon sink in the world. In terms of carbon storage worldwide, peatlands are second only to oceans (Russi et al., 2013). This wetland service is gaining greater attention and recognition in the face of global climate change and a recent comprehensive review reports that wetlands are undervalued and irreplaceable tools against climate change (Moomaw et al., 2018)

Although mainly valued for being nutrient sinks, wetlands are valuable sinks, sources and transformers of a wide spectrum of chemical, biological and physical materials (Reddy & DeLaune, 2008; Mitsch & Gosselink, 2015). Within the wetland environments, particulate matter, including suspended soil particles, nutrients and other pollutants settle out (Adedipe et al., 2005). While dissolved nutrients (e.g. nitrogen and phosphorus) can be taken up by plants or lost to the atmosphere, other contaminants that include heavy metals can be retained in the sediment (Adedipe et al., 2005; Daryadel & Talaei, 2014). The storage or removal of heavy metals, biocides, nutrients and sediment is achieved through processes, such as denitrification, uptake, absorption and sediment retention (Maltby & Acreman, 2011). Wetlands reduce water nitrate concentration flowing from terrestrial systems by more than 80% (Millennium Ecosystem Assessment, 2005b). Thus, owing to their assimilative properties, natural wetlands are used for wastewater treatment (Kennedy & Mayer, 2002), for example, helophyte filters in the mining sector. The intrinsic water quality ameliorating function of wetlands has also been capitalised and applied in the environmentally friendly and cost-effective method of treating various forms of wastewater and agricultural run-off by artificial wetlands (Kennedy & Mayer, 2002; Millennium Ecosystem Assessment, 2005b; Rizzo et al., 2018). Subsequently, artificial wetlands, which are increasingly gaining popularity globally, are emerging as a low-cost treatment option to manage pollution from both point and non-point sources (Kennedy & Mayer, 2002; Palmer, 2009; Zhang et al., 2010; Rizzo et al., 2018).

Because they function as the downstream recipients of wastewater and water from both natural and anthropogenic sources, wetlands have been described as "kidneys" of the landscape and, by stabilising water supplies, they mitigate both floods and droughts (Daryadel & Talaei, 2014; Mitsch et al., 2015; Mitsch & Gosselink, 2015). As a result, by acting as sinks and regulating floods, wetlands have an essential cleansing function for the pollutants (Adedipe et al., 2005; Daryadel & Talaei, 2014; Mitsch & Gosselink, 2015). By affecting the abundance of human pathogens and disease vectors, wetland ecosystem processes also contribute to the regulation of diseases (Gopal, 2015). Table 2.10 presents the rating of some wetland regulating services potentially performed by a wetland based on its particular HGM type.

Table 2.10: Rating of the hydrological functions (services) potentially performed by a wetland, based on its specific hydrogeomorphic type (Kotze et al., 2007).

Wetland hydrogeomorphic type	**Regulating ecosystem services potentially provided by the wetland**							
	Flood attenuation		**Streamflow regulation**	**Enhancement of water quality**				
	Early wet season	Late wet season		Erosion control	Sediment trapping	Phosphate assimilation	Nitrate assimilation	Toxicant removal*
Floodplain	++	+	0	++	++	++	+	+
Valley-bottom (channelled)	+	0	0	++	+	+	+	+
Valley-botton (unchannelled)	+	+	+?	++	++	+	+	++
Hillslope seepage connected to a stream channel	+	0	+	++	0	0	++	++

Isolated hillslope seepage	+	0	0	++	0	0	++	+
Pan/Depression	+	+	0	0	0	0	+	+

Notes: *Toxicants are considered to include biocides and heavy metals.

Rating: 0 Service unlikely to be delivered to any significant degree;

\+ Service likely to be provided at least to some extent;

++ Service very much likely to be present (and often delivered to a high level)

Supporting services

The ability of wetland ecosystems to provide services is enhanced by some long-term processes and functions. The numerous physicochemical and biological processes over ecological time give rise to the formation of soil, which is essential for vegetation growth (Gopal, 2015). Thus, supporting wetland ecosystem services entail the basic ecosystem processes that are required to sustain the wetland functions that enable these ecosystems to deliver all the services in the other three categories (Kotze, 1999, 2010; Turner et al., 2000; Millennium Ecosystem Assessment, 2005b; Kotze et al., 2007; Sullivan et al., 2008; de Groot et al., 2012; Russi et al., 2013; Pinto et al., 2014; Gopal, 2015; Mitsch et al., 2015; Mitsch & Gosselink, 2015). While changes in provisioning, regulating, and cultural services have direct and short-term effects on people, the effects of changes in supporting services are usually indirect or occur gradually (Russi et al., 2013). Supporting ecosystem services include biodiversity maintenance, primary production, pollination, soil formation and biogeochemical (nutrient and water) cycles. The Millennium Ecosystem Assessment (2005b) considers both supporting and regulating services to be critical for the sustenance of the vital ecosystem functions that deliver the other services to humankind. Some services, such as pollination and erosion regulation, can be considered as both regulating and supporting.

Wetlands have also been called “nature’s supermarkets” because they support extensive food chains and rich biodiversity (Daryadel & Talaei, 2014; Mitsch et al., 2015; Mitsch & Gosselink, 2015). These ecosystems have played an important role in the evolution of numerous species, contributing tremendously to biodiversity (Kotze et al., 1996; Kennedy & Mayer, 2002; Gopal, 2015). Thus, they are valuable sources and sinks of genetic materials (Reddy & DeLaune, 2008; Mitsch & Gosselink, 2015). By providing unique habitats for a broad range of species in the landscape, wetlands harbour high biodiversity, highly disproportionate to their areal extent (Kotze et al., 1996; Kennedy & Mayer, 2002) and their total biodiversity often exceeds that of many other ecosystems, including rivers, reservoirs and lakes (Gopal, 2015, 2016). As reported by Junk et al. (2014), wetlands also influence, in many ways, the species diversity of nearby upland and deepwater habitats. Furthermore, as they have very complex hydrology, edaphic conditions and vegetation composition, wetlands provide important habitats and contribute to the biodiversity of landscapes and species richness (Jeglum et al., 2011; Sieben et al., 2014a). As primary producers, wetland vegetation performs a critical role in wetlands, providing habitat and food for both terrestrial and aquatic organisms (Rolon & Maltchik, 2006).

Wetlands and the associated vegetation provide a critical habitat and breeding ground for waterfowl and other wetland-dependent animals (including mammals, reptiles, amphibians, fish, and invertebrates), as well as supporting a high diversity of organisms that have particular adaptations to living in the ecotonal habitats that exist between terrestrial and aquatic systems (DWAF, 2004; Wilson & Bayley, 2012). In some instances, freshwater wetlands also provide a suitable habitat for rare and endangered species (Sather & Smith, 1984; Jayachandran, 2013; Stelk & Christie, 2014) and levels of endemism are particularly high in these ecosystems (Millennium Ecosystem Assessment, 2005b). Wetlands harbour more than 40% of the world's species (Mitra et al., 2003; Hu et al., 2017).

The high productivity in wetlands make them sought-out areas for food provision. Thus, while some animal species may inhabit wetlands, others migrate seasonally and periodically into these ecosystems from other environments (Sather & Smith, 1984; Gopal, 2015). Gopal (2015) describes six categories of wetland animals: "(a) residents in the wetland proper; (b) regular migrants from deepwater habitats; (c) regular migrants from terrestrial uplands; (d) regular migrants from other wetlands (e.g. waterfowl); (e) occasional visitors and (f) those indirectly dependent on wetland biota (e.g. canopy insects)." All these groups are dependent on the wetlands in one way or another.

Accounting for more than 24% of the overall global primary productivity from only about 6% of the global land surface, wetlands contribute disproportionately to the world's primary productivity (Williams, 1990; Gonenc & Wolflin, 2004). Nevertheless, it is mainly their distinctiveness from the surrounding habitats that influence the contribution of wetlands to species diversity at a landscape scale (Kotze & O'Connor, 2000). In a study to assess the role of different ecosystems in supporting biodiversity in Tanzania, Munishi et al. (2011) found that wetlands were the highest in terms of biodiversity when compared to natural grasslands, wooded grasslands and miombo woodlands.

Directly and indirectly, biodiversity controls all ecosystem services (Pinto et al., 2014; Gopal, 2016). Wetland ecosystem services are a result of the interactions among the various components of biodiversity and their explanatory variables (Gopal, 2015). The importance of biodiversity in influencing the delivery of both ecosystem processes and the subsequent ecosystem services is well recognised (Millennium Ecosystem Assessment, 2005b; Pinto et al., 2014; Gopal, 2016). The delivery of ecosystem services, and thereby human well-being, is strongly influenced by biodiversity (Gopal, 2015). Thus, wetland biodiversity has a strong and direct relationship with ecosystem functioning and stability, which in turn is positively related to ecosystem service delivery (Pinto et al., 2014). Plants are the primary determinant of most of the regulatory and provisioning services delivered by wetlands (Sieben et al., 2017c).

By providing habitats for various organisms, supporting food chains and influencing ecosystem functioning, biodiversity itself is a supporting service that benefits humankind (Gopal, 2015). The knowledge of the nature of the biodiversity–ecosystem service relationship and the possible impact of the loss of biodiversity on the supply of ecosystem services is improving globally (Millennium Ecosystem Assessment, 2005b; Cardinale et al., 2012; Gopal, 2015). Threats to biodiversity also indirectly threaten biodiversity-dependent ecosystem processes and subsequent services. A recent review (Harrison et al., 2014) analysed in excess of 500 published articles with the aim of assessing the links between the attributes of biodiversity and the resulting ecosystem services. The review found that species richness and diversity had a positive correlation with ecosystem services that include pollination, pest regulation and atmospheric regulation. The study also reports that ecosystem services that include water flow regulation, water quality regulation and landscape aesthetics are enhanced as community and habitat area increases. Therefore, wetland functions and processes are critical for the supply of all wetland ecosystem services.

A summary of the four major categories of wetland ecosystem services is provided in Table 2.11. Notwithstanding the categorisation of wetland services, many ecosystem services are interrelated and they can rarely be considered in isolation (Gopal, 2015, 2016). Additionally, some of the services can fall into more than one category, e.g. water supply (provisioning and regulating), food (provisioning and cultural) and, nutrient cycling, pollination and primary production (regulating and supporting). Although the categorisation of ecosystem services is not fundamentally important, it makes it convenient for users, researchers and managers. It is also noteworthy that a wetland system may not provide the whole range of possible ecosystem services. Because the type, location and condition of a wetland determine to a large degree the capacity of ecosystem service delivery by the ecosystem, each wetland has different functions and uses, and delivers a different set of ecosystem services (Sullivan et al., 2008; Gopal, 2015). This is mainly because it is the characteristics of a wetland that determine the services that it provides (Brander et al., 2006; Gopal, 2015; Zhang et al., 2015).

Table 2.11: Categories of wetland ecosystem services and their description. Source of information (Collins, 2005; Millennium Ecosystem Assessment, 2005b; Kotze et al., 2007; Sullivan et al., 2008; Turpie & Kleynhans, 2010; de Groot et al., 2012; Russi et al., 2013; Hay et al., 2014; Gopal, 2015, 2016; Mitsch et al., 2015; Mitsch & Gosselink, 2015).

Classification			Ecosystem services	Description and examples	Significance
Direct	Provisioning	Natural tangible products obtained from wetland ecosystems	Fresh water supply	Retention and storage of water; supply of water for domestic, industrial, and agricultural (livestock and irrigation) use	High
			Food	Production of fish, fruits, wild game, grains, and so on	Medium
			Valuable land for crop cultivation	The provision of fertile areas in the wetland, which are conducive for food cultivation (e.g. rice), thereby contributing to food security and livelihoods	High
			Fibre, fuel and other raw materials	Production of craftwork material, construction material, timber, aggregates, ornamental resources, fuel e.g. from peat, fuelwood etc.	High
			Livestock fodder and grazing	Provision of palatable grazing material for livestock	High
			Biochemical products	Extraction of materials from biological resources	Medium
			Genetic resources	Medicines, genes for plant pathogen and crop pests resistance, ornamental species, products for material science, etc	Low
	Cultural	Non-material benefits people obtain from ecosystems through spiritual enrichment, cognitive development, reflection, recreation and aesthetic experiences	Spiritual and inspirational	Source of inspiration, personal feelings and well-being. Religious significance: aspects of wetlands are often associated with spiritual and religious values	High
			Landscape aesthetics (beauty)	Many people appreciate the aesthetic value or beauty in aspects of natural wetlands	High
			Educational and research	Opportunities for informal and formal education and training. Valuable sites within the wetland for education and research. Wetlands are unique ecosystems, which contain both aquatic and terrestrial elements, making them of high educational and research value, particularly if they are accessible.	High
			Cultural heritage	Areas in the wetland that have cultural significance, e.g., for baptism or harvesting culturally significant plants. Religious, historical, traditional knowledge system and/or archaeological values may be important for local communities and contribute to their national heritage.	High
			Tourism and recreation	Opportunities for tourism and recreation in wetland areas, often linked with scenic beauty and abundant birds. Wetlands provide opportunities for a range of activities for recreation that include hunting, fishing and boating, and may support tourism initiatives	High
Indirect	Regulating	Benefits obtained from the regulatio	Climate regulation e.g. through carbon storage	Regulation of greenhouse gases, temperature, precipitation, and other processes related to climate; atmospheric chemical composition. Wetlands typically contain higher organic matter content than terrestrial	Low

		and sequestration	habitats, acting as carbon sinks. By this, they play a critical role with respect to global climate change.	
		Hydrological regimes	Regulation of hydrological flows (e.g. sustaining streamflow during lowflow periods) through storing water for agricultural or industrial use; groundwater recharge and discharge	Low to high
		Natural hazard regulation	Flood control; storm protection. Wetlands play a role in flood attenuation as they reduce the amplitude and speed of flood waters and reduce downstream damage	Low to high
		Regulating diseases, pests and pathogens	Changes in the condition of ecosystems affect the abundance and prevalence of malaria, bilharzia, river fluke and other parasites, as well as invasive alien plants	?
		Pollution control (nutrient assimilation), and detoxification	Retaining, recovering, and removing and detoxifying excess nutrients and other pollutants. Wetland plants play a tremendous role in reducing the levels of nutrients from the system, thereby improving water quality for the downstream areas. Also, by playing a role in the assimilation of toxicants (e.g. metals, biocides and salts) contained in runoff waters, wetlands improve the quality of water.	High
		Erosion control and sediment trapping	Retaining soils and preventing changes in structure (e.g. coastal erosion, bank slumping, etc.); controlling erosion at the wetland site, mainly through the protection offered by vegetation. Wetland vegetation helps to hold sediment in place and trapping and retaining sediment carried in runoff waters, thereby controlling erosion and helping to maintain the functionality of the system.	High
		Refugia	Critical breeding, watering habitat or feeding for populations that are utilised elsewhere	Medium
Supporting	Basic ecosystem processes necessary for the production of all other ecosystem services	Primary production	Wetland vegetation and animals support food chains within and outside of the wetland ecosystems	High
		Soil formation	Retention of sediment and organic matter accumulation	High
		Nutrient and water cycling	Recycling, storage, processing and acquisition of nutrients and water	High
		Biodiversity maintenance	Through the provision of habitat, breeding place and food for resident and transient species and maintenance of natural processes and support of food chains, wetlands contribute to the maintenance of biodiversity	High
		Pollination	Habitat and support for pollinators	Low to high

The drivers and processes vary substantially in different wetlands and thus, in their ecosystem services (Gopal, 2015). Mitsch and Gosselink (2000) observe that the ecosystem services delivered by a particular wetland depend on the hydrogeomorphic location in which it is found. For example, a wetland located at the headwaters of a stream or river functions differently from the one located near the estuary (Mitsch & Gosselink, 2015). Table 2.12 provides some of the wetland ecosystem services that are delivered by wetlands and their associated main ecological/physical functions.

Table 2.12: Wetland ecosystem services and the associated ecological functions and processes (Costanza et al., 1997; Brander et al., 2006; Maltby & Acreman, 2011)

Wetland ecosystem services	Wetland functions and/or processes
Improvement in water quality and waste disposal through reduced nutrient	Nutrient retention and uptake and denitrification and other transformations of nutrients
Gas regulation	Regulating the chemical composition of the atmosphere
Disturbance regulation e.g. flood control, storm protection, drought recovery, etc.	Capacitance, damping and integrity of ecosystem response to fluctuations in the environment; storm buffering, sediment retention etc.
Augmentation of groundwater resources available for use by human beings	Recharging aquifers through water moving downward by gravitational force from the wetland system into underlying layers
Provisioning of water for industrial or agricultural processes or transportation.	Regulation of hydrological flows through groundwater recharge/discharge and storage and retention of water
Flood protection and reduction in downstream flood risk	Flood water storage /flood and flow control and water moving from rivers during high flows, leading to inundation of floodplain surfaces, filling of depressions and saturation of the soil
Control of erosion and retention of sediment	Retention of soil in an ecosystem through sedimentation
Soil formation	Processes leading to soil formation e.g. rock breakdown and organic material accumulation
Treatment of waste, pollution control, detoxification	Recovering moving nutrients and breaking down or removing excess nutrients and compounds
Pollination	Provisioning of pollinators
Biological control	Regulating populations through trophic-dynamics
Refugia	Inhabiting both resident and passing species
Provision of food and natural raw materials	Gross primary production
Genetic resources e.g. products for medicine, ornamental species and genes for improving plant resistance to pathogens and pests	Sources of unique biological products and materials
Recreation e.g. ecotourism, sport fishing, appreciation of species existence and other outdoor recreational activities	Natural environment and biodiversity
Cultural e.g. values of ecosystems for education, aesthetics, arts, religion, research and/or science	Natural environment and biodiversity
Climate stabilisation	Carbon storage and sequestration through the formation of peat from dead plant material during anoxic conditions and photosynthesis
Harvestable natural resources	Nursery and habitat and for plants and animals

Kotze et al. (2007) point out that the provision of ecosystem services by a wetland has a direct positive relationship with its surface area. However, the authors caution that this importance of wetland size varies substantially depending on the particular ecosystem service and the local circumstances around the wetland, such as catchment size. Even small wetlands are have a spatially interlinked network of habitats and are associated with numerous ecosystem services (Mitsch & Gosselink, 2000; Irvine et al., 2016). In a given catchment, the range of wetland ecosystem services delivered to society is directly related to the diversity of wetlands (Sullivan et al., 2008). The same set of abiotic and biotic processes results in many functions that are valued differently by different communities (Gopal, 2016). Gopal (2015) highlights important relationships that exist between various attributes (including biodiversity), ecosystem processes and functions of wetlands that supply various ecosystem services.

Because of the overlap that often exists between ecosystem service categories, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) (IPBES, 2018), has recently recommended some adjustments to the categorisation given by the Millennium Ecosystem Assessment (2005b), to recognise a system with three main groups: regulating, material and non-material. Furthermore, arguing that there is limited reflection of the full range of values of nature by the "ecosystem services concept", the IPBES has also recommended a shift from this concept to the notion of "nature's contributions to people (NCP)" (IPBES, 2018). "Nature's contributions to people" refer to "all the contributions, both positive and negative, of living nature (diversity of organisms, ecosystems and their associated ecological and evolutionary processes) to the quality of life for people" (Díaz et al., 2018).

2.9 Importance and ecosystem services of montane palustrine wetlands

Mountains form important water catchment areas. Montane ecosystems are regarded as ecologically sensitive and fragile systems that offer unique and critical habitat conditions for a great variety of plant and animal species (Du Preez & Brown, 2011). Montane wetlands are a special sub-division of freshwater palustrine wetlands that form an archipelago of isolated ecosystems embedded within terrestrial ecosystems in rugged mountain areas (Mucina & Rutherford, 2006). The wetlands are of high environmental, ecological and socio-economic importance as they provide a wide spectrum of crucial ecosystem services (Chatterjee et al., 2010). High-altitude wetlands supply essential ecosystem services that help to sustain human life, maintain the hydrological regime, conserve biodiversity and combat the impacts of climate change and thus contribute to water, food and environmental security (Singha, 2011).

Many montane wetlands are located in headwaters and are thus important in the ecology and hydrology of many streams and rivers that arise in the mountains. These wetlands are also regarded to be of international importance as they provide water for many transboundary rivers (Chatterjee et al., 2010), such as the Senqu-Orange River in southern Africa. Because transboundary rivers are often big, they are considered valuable for water resources. Thus, montane wetlands play a key role in the hydrology and ecology of major rivers. They function as simple reservoirs or aquifers that store water in the rainy season and release it in the dry season, either through runoff, subsurface drainage or evapotranspiration (Chatterjee et al., 2010).

Montane wetlands are often rich in endemics as many species remain isolated at these high altitudes (Sharma et al., 2010; Junk et al., 2013). The rate of speciation is often quite high in mountainous regions. By providing isolated habitats with limited possibilities of dispersal between them following colonisation, mountains promote diversification and concomitant speciation (Crochet et al., 2004). Moreover, the diversity of habitats along environmental gradients, that comes with sharp increases in altitude, is thought to provide an opportunity for sympatric (in-situ) speciation to occur (Drovetski et al., 2013). Montane wetlands also serve as repositories for the biodiversity of high-altitude habitats, and this includes many rare and threatened montane species (Jayachandran, 2013).

Montane wetlands generally remain far less impacted compared to those in the lowlands where water withdrawal, land-use change and direct destruction have led to substantial losses of wetland ecosystems over the past two centuries (Lee et al., 2015). Not only is this attributed to the natural environmental influences, but also to the low human population densities that are usually associated with montane areas which subject them to limited anthropogenic interference. For instance, the mountain regions of Lesotho, which account for about 60% of the country's surface area, harbour only about 19% of the country's population (Bureau of Statistics, 2009). For this reason, montane wetlands are important refugia for many plant and animal species. The importance of these montane wetlands as refugia is also enhanced by the fact that they are located in isolated cold-climate areas within a matrix of warm subtropical areas. However, it is noteworthy that even changes in the ecological processes of montane wetlands have potentially significant adverse consequences for downstream ecosystems and water resources (Chatterjee et al., 2010; Sharma et al., 2010).

The montane wetlands of Lesotho are essential for maintaining the regular flow of clean water and for livestock grazing (van Zinderen Bakker & Werger, 1974; Du Preez & Brown, 2011). Wetlands in the Highlands of Lesotho play a pivotal role in water resources for both Lesotho and South Africa. The montane seepage wetlands in the Maloti-Drakensberg area produce unique habitat types as the wetlands are located on a slope, which is why they are distinct from most wetlands in the lowlands and other areas (Mucina & Rutherford, 2006). For Lesotho, these wetlands are not only important for biodiversity and water supply, but also for the provision of a source of hydroelectric power and revenue, as well as acting as an incentive for accelerated development in the mountains and the associated employment creation. Given their significance for water resources, biodiversity and other services, wetlands in the Maloti-Drakensberg have been singled out as a landscape feature that conservation planning should focus on (Sieben et al., 2010a).

Commonly occurring in high-altitude montane wetlands, peat accumulation is important for energy provision and climate regulation. The main component of peat is plant-derived organic matter, which constitutes about 30% of the total content of peat in general, with the rest being inorganic material (Chatterjee et al., 2010). Chatterjee et al. (2010) emphasise that, while climate is considered to be the most important factor influencing the accumulation and distribution of peat, other factors such as landform, geography, hydrology and vegetation also play an important role. At high altitudes, anoxia as well as low temperatures and pH reduce the rate of decomposition, conditions which favour the accumulation of organic matter and peat formation (Chatterjee et al., 2010; Gopal, 2016). This makes montane wetlands critical in climate regulation because of their capacity for carbon sequestration and storage. In addition to peat formation, montane wetlands are biodiversity hotspots (Chatterjee et al., 2010). In South Africa, montane wetlands are considered to be among the most species-rich wetlands in the country (Sieben et al., 2014a). Montane wetlands do not only accumulate peat, but also act as sponges in accumulating run-off from the surrounding mountain slopes (Meakins & Duckett, 1993). Additionally, it is noteworthy that these wetlands, like other wetlands, also supply the other ecosystem services discussed in Section 2.8. In fact, they provide most of the upstream ecosystem services to a higher extent than the other wetlands.

2.10 Wetlands and water resource planning

Palustrine wetlands also play a critical role in the overall regional and global water cycles (Millennium Ecosystem Assessment, 2005b; Russi et al., 2013; Sieben et al., 2014a). The ecological integrity of the wetlands in the catchment areas underpins the quality and quantity of water in the downstream watercourses by supporting perennial runoff with low sediment loads (Nüsser & Grab, 2002). Through the release of stored water into streams and rivers as part of base flow, wetlands maintain dry season water supplies (SADC, 2008). Thus, wetlands ameliorate the effects of drought on both people and wildlife. With the eminent prospect of global climate change and the associated water shortages, the conservation of wetlands becomes a key factor for a sustainable supply of water. For example, dam water levels in southern Africa have dropped since the 2015 drought (Siderius et al., 2018). A large number of well-functioning wetlands would ameliorate such risks of drought, both for the dam operators and for local livelihoods. Wetlands have an essential link to water supplies (Acreman and Miller 2006, McCartney and Acreman 2009). This places them at the centre in some of the most contentious and urgent issues related to the management of water, a resource that is associated with strong competition and increasing uncertainty because of climate change (Maltby & Acreman, 2011).

Freshwater is an essential factor of production in the economies of all countries in southern Africa and wetlands constitute an important source of freshwater in the region (SADC, 2008). Hence, as the region strives to achieve socio-economic development, demand for freshwater is growing. There is a severe water stress in this region and the situation is expected to worsen because of population growth, changes in consumption patterns (Scholes & Biggs, 2004) and climate change (Grundling, 2014). Given that much of the region generally experiences semi-arid to arid climatic conditions, it is therefore regarded as susceptible to a water crisis (Taylor et al., 1995). Climate change predictions indicate that much of southern Africa will become drier (Mitchell, 2013). The SADC (2008) has projected that by 2025, South Africa and Malawi will be facing total water scarcity, Lesotho and Zimbabwe will be water stressed, while Botswana and Namibia are likely to experience water availability and quality problems, particularly in the dry season. Thus, the conservation of wetlands is critical for climate change mitigation and adaptation in terms of sustainable water provision and other services in the region.

With the loss and degradation of more than half of the world’s wetlands, human welfare is being threatened at a time of increasing and unprecedented water scarcity and demand (Daryadel & Talaei, 2014). Wetland drainage from anthropogenic factors can also adversely affect water flow and supply in the dry season (Daryadel & Talaei, 2014). An integrated approach to the management of water resources, including wetlands, that play an important role in water supply, is needed.

Lesotho entirely falls within the catchment of the Senqu-Orange River, which makes wetland conservation in the area important for sustainable water resources in the region. The Lesotho Highlands is an important catchment for both Lesotho and South Africa and wetlands in this area underpin the water supply and hydroelectric power generation. In fact, Lesotho is considered the “water factory” of southern Africa because it is the major catchment of one of the biggest rivers in the sub-region and it is one of the few places where annual precipitation exceeds evaporation, giving rise to a net run-off (MDTP, 2007; Ellery et al., 2009). The water, tapped through the largest international water transfer scheme in the world, the Lesotho Highlands Water Project (LHWP) (Meakins & Duckett, 1993; Earle & Bazilli, 2013), is also an essential source of revenue for Lesotho. The MDTP (2007) highlights that the montane wetlands of Lesotho, though rapidly degrading, are unique and play an important hydrological role in providing a sustainable supply of high quality water throughout the year. Naturally, the geographical location and agro-ecology of Lesotho makes the country, and therefore its wetlands, vulnerable to the effects of climate change. Therefore, faced with the threat of global climate change and associated water shortages, the conservation of these wetlands becomes a key factor for a sustainable supply of water.

The condition of a wetland determines its capacity to deliver ecosystem services such as water supply but this capacity can potentially diminish due to degradation. To society, the value of water provision and water quality management achieved by healthy wetlands becomes one of the most important financial values associated with these ecosystems (Sullivan et al., 2008). In Lesotho, this is important, particularly for the large dams: Katse, Mohale, Metolong and the one currently under construction (Polihali) that supply water for Lesotho and South Africa. Thus, the Lesotho Department of Environment (2014) emphasises the need for urgent action to protect the wetlands in the country because of their role in the water resources. Therefore, it is fundamental that any planning for water resources should incorporate, as an integral part, the wetlands found in the catchments. This ensures sustainability in the provision of water resources.

2.11 Wetland loss and major threats to wetland ecosystems

Despite the increasing recognition of their importance to humankind and the concerted efforts towards their inventory and conservation, wetlands remain among the most threatened ecosystems globally, mainly because of anthropogenic factors (Millennium Ecosystem Assessment, 2005b; Rai & Raleng, 2011; Russi et al., 2013; Junk et al., 2014). In spite of being the most globally diverse per unit area, freshwater palustrine wetlands are the most threatened and degraded type of ecosystems (Irvine et al., 2016). Degradation of the environment is more conspicuous in wetlands than in other ecosystem in all regions of the world, particularly in developing countries (Millennium Ecosystem Assessment, 2005b; Russi et al., 2013; Mitsch & Gosselink, 2015). Given that 17% of the Contracting Parties of the Ramsar Convention have reported deteriorating conditions in their Ramsar designated sites (Russi et al., 2013), the situation is expected to be worse for the other wetlands that are not necessarily listed because they tend to receive less attention.

Despite different estimates of wetland loss, there is a consensus among various authors that more than half of the world's natural wetlands have already been lost since 1900, mainly due to anthropogenic factors, with developing countries experiencing the greatest loss (Finlayson et al., 1999; UNWWAP, 2003; Rolon & Maltchik, 2006; Maltby & Acreman, 2011; Russi et al., 2013; Daryadel & Talaei, 2014; Davidson, 2014). A global review reports that as much as 87% of the natural wetlands may have been lost globally since 1700 (Davidson, 2014). In the recent decades, between 1970 and 2008, an estimated 30% decline in the global coverage of wetlands was experienced (Dixon et al., 2016). A recent publication, the Global Wetland Outlook (Ramsar Convention on Wetlands, 2018), reports that between 1970 and 2015, wetland decline has been estimated at 35%, which is three times the rate of loss of forests.

Wetlands, all over the world, remain vulnerable despite the various international agreements and national policies (Turner et al., 2000). The degradation and loss of wetlands, according to the Millennium Ecosystem Assessment (2005b), is more rapid than that of other ecosystems, and global climate change is likely to exacerbate the problem and the associated loss and decline in species diversity. A wetland is considered 'lost' if it gets degraded to an extent of losing most of its properties and ecosystem services (Rivers-Moore & Cowden, 2012). A comprehensive global assessment was conducted by the Millennium Ecosystem Assessment (2005b) to evaluate the changes in wetland ecosystems and their services over a period of 50 years, their causes and implications for human wellbeing, and the future trends of change. This and other global assessments (Meakins & Duckett, 1993; Finlayson et al., 1999; Zedler & Kercher, 2005; Junk et al., 2013; Russi et al., 2013; Daryadel & Talaei, 2014; Davidson, 2014) report that the majority of the remaining wetlands are showing signs of degradation or under threat. In presenting global changes in natural wetland area coverage between 1700 and 2000 and taking the year 1700 as a reference point, Davidson (2014) estimates that only 13% of the original wetland coverage had remained by the year 2000.

Because wetlands are dynamic and have a life cycle, they can also be lost in the long term due to natural factors. However, declines in the extent of wetlands due to anthropogenic factors have been estimated to be about 64-71% in the 20th century alone (Davidson, 2014; Gardner et al., 2015). The study by the TEEB (Russi et al., 2013) reports that the rate of wetland loss from the twentieth to early twenty-first centuries was 3.7 times higher than the average long-term rate of wetland loss. Wetlands have been degraded or destroyed over the last decades so much that their ecosystem services have substantially declined (Ricaurte et al., 2014). In a global review of wetland loss, Davidson (2014) observes that the highest average rate of loss occurred in the third quarter of the 20th century. The review also reports that since 1900, the average losses have consistently been higher and faster for inland than for coastal wetlands; natural inland wetlands alone experienced a loss of 57–61%. The same review further highlights that, though degraded and deteriorating, the health of most of the remaining wetlands is not documented. Notwithstanding the lack of sufficient information to substantiate the commonly reported "more than 50% loss in wetland area globally" (Finlayson, 2012; Davidson, 2014), there is a general consensus among many authors that wetland conversion and loss has been, and continues to be tremendous and widespread (Table 2.13). Concomitantly, trends in the status of species that depend on wetlands also follow the overall pattern of continuing wetland loss (Russi et al., 2013). However, published evidence for changes in wetland area over time is patchy and limited, particularly for Africa (Davidson, 2014), a continent where most of the areas are characterised by semi-arid to arid climatic conditions (Taylor et al., 1995). Hence, the inventory and conservation of all wetlands should be promoted, regardless of their areal extent (Taylor et al., 1995; Oertli et al., 2002).

Table 2.13: Estimated loss in wetland area coverage by location across the globe

Location	Period	Wetland loss (%)	Publications
Global	1900-2000	>50	Finlayson et al. (1999); UNWWAP (2003); Rolon and Maltchik (2006); Maltby and Acreman (2011); Russi et al. (2013); Daryadel and Talaei (2014); Davidson (2014)
	Since 1900	64	CBD Secretariat (2015)
	1997-2011	43	Costanza et al. (2014)
	1900-2000	30-90	Junk et al. (2013)
	Before 1900- early 21st century	54-57	Davidson (2014)
	1900-early 21st century	64-71	
	1900-1999	50	Finlayson et al. (1999)
	Until 2009	33	Hu et al. (2017)
	1970-2008	30	Dixon et al. (2016)
Europe	1900-2000	60-90	Barbier et al. (1997); Junk et al. (2013)
	1990-2006	2.7	Russi et al. (2013)
	Since 1900	60	
	1900-early 21st century	56.3	Davidson (2014)
United States of America	1500-2000	> 50	Stelk and Christie (2014)
	1700-2000	54	Russi et al. (2013)
North America	Since 1900	56.0	Davidson (2014)
Oceania	Since 1900	44.3	
Asia	Since 1900	45.1	

Southeast Asia	Since 1900	50	Junk et al. (2013)
China	1978-2008	33	Niu et al. (2012)
	Since 1960	36.5	Junk et al. (2013)
Africa	Since 1900	43.0	Davidson (2014)
Morocco	1978-1999	25	Green et al. (2002)
Southern Africa	1600-2000	9	Scholes and Biggs (2004)
South Africa	Since 1900	>50	Van Ginkel et al. (2011); Junk et al. (2013); SANBI (2013); Government of South Africa (2014)
Lesotho	Since 1900	>50	Mokuku et al. (2004)

Southern Africa is not exempted from the global trend of continued degradation and loss of wetlands (Taylor et al., 1995; Breen et al., 1997). However, data on wetland conversion rates and losses for the region are scarce and difficult to compare because of lack of historical wetland inventory studies and varying estimates of wetland coverage from different sources (Taylor et al., 1995). The few available studies for the region indicate that the rate of wetland degradation and loss is significantly high (Taylor et al., 1995; Scholes & Biggs, 2004). Estimated changes in the coverage of various wetland types in southern Africa between 1600 and 2000 are presented in Table 2.14. Some estimates of wetland loss are quite low; others are much higher and probably more reliable. While the estimates for other areas could reflect the true wetland loss, the 9% loss for southern Africa (Taylor et al., 1995) is very much likely to be an underestimate. For example, in South Africa alone, it has been estimated that in excess of 50% of the wetland area has been lost countrywide (Van Ginkel et al., 2011; Junk et al., 2013; Sieben et al., 2014a). Many wetlands have reportedly been lost in Lesotho as well and the majority of those remaining are showing numerous signs of degradation (Mokuku et al., 2004; Turpie et al., 2014a, b).

Table 2.14: Changes in the coverage of various types of wetlands in southern Africa between 1600 and 2000. Modified from Scholes and Biggs (2004).

Wetland type	**Soil/ geology**	**Climate**	**Area not transformed by agriculture or urbanisation ($\times 10^3$ km^2)**		
			1600	**2000**	**% in 2000**
Permanent wetland	Organic (peaty)	Any climate as long as water supply is greater than evaporation	172	153	89
Seasonal (dambo/vlei)			990	885	89
Estuaries & mangroves	Often racking clays (turf)		23	22	95
Salt pans			40	38	95
Inland water & coastal waterways	Saline, organic		197	197	100
Region			1422	1295	91

The degradation and loss of these ecosystems and the associated species and services continues in the twenty-first century, and exceeds that of other ecosystems (Millennium Ecosystem Assessment, 2005b; Finlayson, 2012). Wetlands listed as Ramsar sites are not spared from the degradation and loss as evidenced by the 48 sites on the Montreux Record, despite their special status (Ramsar Convention Secretariat, 2011). Maintained as a component of the Ramsar List, the Montreux Record documents wetland sites, listed as Wetlands of International Importance but undergoing negative changes resulting from developments, pollution or other anthropogenic interference. Furthermore, about 17% of the Ramsar Parties still report that the condition of their Ramsar sites is deteriorating (Russi et al., 2013). Moreover, in 2012, 28% of the national governments that reported to the Ramsar Convention highlighted a deteriorating overall status of their wetlands (Davidson, 2014).

While some countries supply information on changes in wetland ecological character, others may lack the capacity to assess and report such changes. Ecological character refers to the sum of the biological and physicochemical characteristics of the wetlands, and their interactions, which sustain the wetland and its functions, attributes and products that characterise the wetland in the natural state at any point in time (Millennium Ecosystem Assessment, 2005b; Russi et al., 2013). After nearly five decades of the existence of the Ramsar Convention, different parts of the world still experience significant wetland loss and degradation.

Despite increased efforts for raising awareness, there is still a limited understanding of the level of sensitivity of these essential ecosystems, their functioning and their benefits to society, by both policy makers and the general public (Turner et al., 2000; Maltby & Acreman, 2011; Daryadel & Talaei, 2014). The indirect impacts of various land-use practices, water management and other human activities on wetlands are also poorly understood (Turner et al., 2000). In addition, the public-good characteristics and the open-access nature of wetland ecosystem services often contribute to their being underrated in decisions relating to their management, conservation and use (Turner et al., 2000; Mitsch & Gosselink, 2015). Thus, either for short-term economic benefits or from limited understanding, there is continued wetland loss and irreversible degradation of wetlands worldwide (Mitchell, 2013). Once wetlands are lost, the concomitant loss of their functions and values is often irreversible (Mitsch & Gosselink, 2000). Effects of human activities on wetlands curtail their resilience and ecosystem functioning (Ricaurte et al., 2014) and also reduce their ability to support biodiversity and provide ecosystem services. The global trend of reduced ecosystem service provision as a result of the decline in extent and conditions of the ecosystems providing such services has been confirmed extensively (Millennium Ecosystem Assessment, 2005b; Cardinale et al., 2012; Russi et al., 2013; CBD Secretariat, 2015).

Historically, wetlands have been viewed as wastelands and concomitantly, were subjected to widespread loss and degradation (Kennedy & Mayer, 2002). Prior to 1975, the widely accepted and encouraged practices of draining and destroying wetlands resulted in the replacement of many wetlands by commercial and residential development and agricultural fields worldwide (Mitsch & Gosselink, 2015). This has resulted in significant changes in the coverage and ecological condition of many wetland ecosystems (Junk et al., 2013). Wetlands are the most threatened ecosystems in South Africa and a substantial 65% of the nearly 800 types of wetlands in the country are threatened, with 48% critically endangered, 12% endangered and 5% vulnerable (Day & Malan, 2010; SANBI, 2013; Government of South Africa, 2014, 2015). Montane wetlands in particular, and the catchments draining into them are increasingly threatened by land-use, upstream flow modification, unsustainable exploitation and climate change (Chatterjee et al., 2010).

Being naturally dynamic systems, wetlands respond to external events that happen at different spatial and temporal scales (Macfarlane et al., 2007; Kotze et al., 2012). Anthropogenic activities have adverse impacts on wetlands through the alteration of the critical wetland ecosystem determinants (Macfarlane et al., 2007). The effects result from activities both within the wetland (on-site e.g. cultivation, infilling, drainage and flooding by dams) and outside the wetland (off-site e.g. afforestation, crop production, mining and infrastructure development) (Collins, 2005; Macfarlane et al., 2007; Rebelo et al., 2009; Sieben et al., 2011). The response of a wetland to changes in the hydrology may be expressed in substantial habitat changes, as well as alteration in water quality and flood storage capacity (Collins, 2005). Collins also highlights that a change in land cover in the catchment from natural grassland to a *Eucalyptus* plantation, for example, would reduce the quantity of water flowing into the wetland. The author further observes that, in many cases, as people benefit from wetland ecosystems, their interaction with the ecological systems lead to adverse effects on the capacity of the wetlands to provide the services (Collins, 2005).

The major drivers of wetland loss and degradation can be classified into direct (directly impact wetland ecosystem processes and functioning) and indirect (underlying factors that prompt one or more direct factors and are often related to socio-economic, demographic, cultural and institutional processes) factors (Kennedy & Mayer, 2002; Millennium Ecosystem Assessment, 2005b). Examples of indirect drivers are briefly described below. The historical misconception that wetlands are wastelands that should be avoided or, as far as possible, be drained and filled has played a tremendous role in the degradation and loss of these ecosystems through hydrological alteration (Mitsch & Gosselink, 2015). The political and socio-economic factors are the primary indirect drivers of wetland loss and these are, among others, population increase, economic development, poor catchment management, high poverty levels, food insecurity, poor agricultural practices, frequent droughts, poor land management and institutional and policy intervention failures (Millennium Ecosystem Assessment, 2005b; Davidson, 2014).

Major direct drivers that have been, and continue to be implicated in the loss and degradation of wetlands and the associated species and services include agriculture, urban and infrastructure development, invasion by alien species, water abstraction, over-utilisation of wetland resources, mining, forestry, water pollution, wetland drainage and filling, tourism and global climate change (Keddy, 1983; Millennium Ecosystem Assessment, 2005b; Bhandari, 2009; Brander et al., 2013; Mitchell, 2013; Russi et al., 2013; Davidson, 2014; Mitsch & Gosselink, 2015). Bhandari (2009) summarises the direct threats to wetlands using the acronym, "COPIES (C – Conversion of wetlands for other purposes, O – Over-exploitation of resources, P – Pollution of water, I – Invasion by alien species, E – Encroachment to the area and S – Sedimentation of in the system)." These factors have been, and continue to be, implicated in the degradation of wetlands and their reduced functioning. It is noteworthy that most of these threats interact with each other and often cannot easily be considered in isolation. The impacts of the various direct drivers are discussed below.

2.11.1 Agriculture

The leading cause of wetland loss worldwide continues to be agriculture (Keddy, 1983; Millennium Ecosystem Assessment, 2005b; Bhandari, 2009; Brander et al., 2013; Mitchell, 2013; Russi et al., 2013; Davidson, 2014; Mitsch & Gosselink, 2015). Because of their high productivity and capacity to retain water for the entire year, many wetlands have a good potential for agricultural use (UNWWAP, 2003; Government of South Africa, 2014, 2015; Irvine et al., 2016). Particularly because of their values for agricultural and potential to be turned into an irrigation dam, floodplain wetlands have the highest fraction of critically endangered wetland types in South Africa (Government of South Africa, 2014, 2015). Increase in the global human population and the associated high demand for food and the quest for more arable land in recent years have promoted the drainage and subsequent conversion of wetlands for such uses, with subsequent loss and degradation of the ecosystems (Junk et al., 2013;

Daryadel & Talaei, 2014). As of 1985, an estimated 26% of the world's wetland area had been converted to intensive agriculture (Zedler & Kercher, 2005). The Millennium Ecosystem Assessment (2005b) report that, by 1985, an estimated 56−65% of coastal and inland marshes had been converted to intensive agriculture in Europe and North America, 6% in South America, 27% in Asia and 2% in Africa. About 60% of China's natural wetland loss has also been attributed to agricultural encroachment (Mao et al., 2018). Subsistence agriculture in wetlands is a major factor in many densely populated areas in South Africa (Sieben et al., 2016c).

In many parts of sub-Saharan Africa, wetlands provide an attractive opportunity for agricultural development and crop production, and thus many wetlands have been lost to crop production, a trend that is likely to continue (UNWWAP, 2003). Poor agricultural practices are thought to have played a major role in the estimated 50% loss of South Africa's wetland area (DWAF, 2008; Government of South Africa, 2014). Many crop fields have been established on wetlands and this has displaced the natural vegetation and animal species dependent on these systems (Du Preez & Brown, 2011). When a wetland is cultivated for crop production, the wetland's function of sediment trapping and holding the soil declines, which consequently undermines the wetland's capacity to purify water and control soil erosion (Collins, 2005).

Given the abundance and palatability of the vegetation they support, wetlands are often subject to overgrazing by livestock (Chatterjee et al., 2010). Overgrazing and trampling by livestock (e.g. cattle, horses, sheep and goats) has been implicated in wetland deterioration in many parts of the world (Meakins & Duckett, 1993; Backéus & Grab, 1995; Du Preez & Brown, 2011; Mitchell, 2013; Ricaurte et al., 2014; Government of South Africa, 2015; Grundling et al., 2015). While the South African wetlands are threatened by a number of anthropogenic activities, the degradation and destruction of wetlands in Lesotho due to agricultural activities such as grazing has been reported quite extensively (Guillarmod, 1962, 1963; van Zinderen Bakker & Werger, 1974; Backéus, 1989; Backéus & Grab, 1995; Du Preez & Brown, 2011). Wetland disturbance through agriculture increases the susceptibility of the ecosystem to alien species invasion. While wetland alteration through cultivation can adversely impact on wetlands, as well as downstream areas, protection of wetlands from degradation by agriculture will be difficult because of limited opportunities for livelihoods (Rebelo et al., 2010).

2.11.2 Infrastructure and urban development

Infrastructure development, including dam construction, transfer schemes between catchments, urban development and road construction put pressures on wetland ecosystems (Backéus &

Grab, 1995; Collins, 2005; Du Preez & Brown, 2011; Government of South Africa, 2014, 2015; Gopal, 2015; Mitsch & Gosselink, 2015). It is common for urban expansion to take place over ecologically important areas, including wetlands (UNWWAP, 2003). Some of the major cities of the world that include Christchurch in New Zealand, Chicago and Washington DC in the United States and Paris in France are located on sites that were once wetlands (Mitsch & Gosselink, 2015). Furthermore, the same authors provide examples of large airports (New Orleans in Boston and J. F. Kennedy in New York) that are situated on former locations of wetlands. Because of urbanisation and the expansion of urban populations, existing urban areas also extend into surrounding areas, which may also include wetlands.

Because of their ability to store water throughout the year, wetlands are often dammed and this poses a threat to the functioning of the wetland ecosystem (Backéus & Grab, 1995; Collins, 2005). Dam construction contributes either directly (flooding if the dam is built in the wetland) or indirectly (reduced water supply if the dam is located upstream) onto downstream wetlands that will experience a new flow regime. Either way, damming significantly alters the hydrology of the wetland to the detriment of ecosystem functioning and ecosystem service delivery (Gopal, 2015; Mitsch & Gosselink, 2015). Collins (2005) reports the flooding by dams of many wetlands that has occurred in South Africa. While dams perform certain functions similar to those performed by wetlands (e.g. water storage and sediment trapping), they cannot accomplish other functions well (e.g. providing habitat for specialised wetland-dependent species (Collins, 2005).

Both directly and indirectly, road construction also puts pressure on wetlands. In general, wetlands are more sensitive than uplands to road construction and the major effects, if the road passes through the wetland, are alteration of the hydrological regime, sediment loading and direct wetland removal (Mitsch & Gosselink, 2015). Besides altering the hydrological regime, road construction can also impact directly on wetlands either as the road passes through a wetland or through filling by gravel or other solid material dumped on the wetland or adjacent to it (Backéus & Grab, 1995; Government of South Africa, 2014). Other developments that can affect wetlands and impact on their ecological functioning are, inter alia, embankments and diversion structures (Gopal, 2015), transfer schemes between catchments (Government of South Africa, 2015), dykes and canals (Millennium Ecosystem Assessment, 2005b; Junk et al., 2013), housing, retail parks and industrial areas (Du Preez & Brown, 2011).

2.11.3 Terrestrial encroachment/ invasion by alien species

Invasive alien species are considered as the most detrimental factor in pristine and protected ecosystems and their associated biodiversity (Daryadel & Talaei, 2014; Ricaurte et al., 2014). Wetlands are quite susceptible to alien invasion when damaged or desiccated (Grab & Deschamps, 2004; Sieben, 2011). While habitat loss is the leading cause of freshwater species extinctions, introduced invasive non-native species are the second most important cause of the decline (Millennium Ecosystem Assessment, 2005b). Invasive alien plants are among the major drivers of wetland degradation and loss globally (Millennium Ecosystem Assessment, 2005b), in Colombia (Ricaurte et al., 2014), sub-Saharan Africa (Mitchell, 2013) and South Africa (Sieben et al., 2014a; Government of South Africa, 2015), among other areas. One major concern from the findings by Sieben et al. (2014a) is that, despite the study being biased towards natural and pristine wetlands, the fourth most dominant species in the South African wetlands was an alien species (*Paspalum dilatatum*), which occurs in 9.1% of all the wetland sample plots in the country's database (Sieben et al., 2014a).

2.11.4 Water abstraction

Abstraction or withdrawal of water from a wetland or its catchment (surface water and groundwater) for purposes of draining the wetland, irrigation or other purposes directly alters the hydrology of the wetland (Maltby & Acreman, 2011; Junk et al., 2013; Daryadel & Talaei, 2014). Drainage of wetlands or water-level drawdown can result in significant changes in soil biological and physicochemical properties (Daryadel & Talaei, 2014). Wetland habitat alteration through drainage also enhances invasion by terrestrial and alien species (and displacement of the native vegetation) (Du Preez & Brown, 2011). Alteration in the hydrology of wetlands through drainage can also adversely affect water flow and supply in the dry season, with subsequent negative impacts on downstream organisms, and on the quality of water through the increased pollutant concentration (Daryadel & Talaei, 2014). Furthermore, the capacity of the wetland to reduce and purify storm flow is significantly reduced to the detriment of downstream aquatic systems and water users.

2.11.5 Over-exploitation of wetland resources and mining

Excessive exploitation of resources (e.g. fish, wildlife, wild plants and peat) within wetlands and in their catchments are contributing to the degradation and loss of these ecosystems (Rebelo et al., 2009; SANBI, 2013). Exploitation of biological resources at a rate higher than the rate of regeneration is described as unsustainable use of resources. The over-exploitation of plant and animal resources, as well as peat extraction from wetlands have negative effects on wetland characteristics and functioning (Du Preez & Brown, 2011; Brander et al., 2013; Junk et al., 2013; Mitsch & Gosselink, 2015). Given that the wetland biota can also influence the soil and hydrology of the wetland (Mitsch & Gosselink, 2015), over-exploitation of the plants will alter the characteristics and functioning of the ecological system. Mining for minerals in the catchment of a wetland also contributes to the degradation of the wetland through changes in catchment hydrology, geomorphology (new drainage patterns, erosion and sedimentation) and pollution from mine drainage or chemicals from the mine itself (Mitchell, 2013). For example, in South Africa, many slime dams from mines are located in wetlands or directly next to them, leading to the destruction of natural vegetation and its dependent animals, as well as the total functioning of the ecosystem (Du Preez & Brown, 2011).

2.11.6 Forest plantations

Changes in land-use, either within the wetland itself or in its catchment, can adversely affect dry season water flow and supply (Daryadel & Talaei, 2014). Changes in water inputs from the catchment and changes in the retention and distribution patterns in the wetland can alter the hydrology of the system (Macfarlane et al., 2007). Commercial forestry within the wetland or in its catchment can have detrimental effects on the hydrology and ecological functioning of the wetland. Commercial forestry, which is encouraged by many governments, potentially exacerbates wetland loss and degradation because trees require large amounts of water per day. According to Collins (2005), changes in land cover from natural grassland to tree plantation would reduce the quantity of water getting into the wetland as a lot of water would be lost as the trees transpire. The establishment of *Eucalyptus* plantations, for example, can exceptionally deplete the local groundwater reserves, resulting in the drying up of the wetlands (Gabriel et al., 2018). Furthermore, many forest plantations were established in wetlands at the expense of the natural vegetation and the animals (Du Preez & Brown, 2011). This can have adverse effects on the habitat value of the wetlands (Collins, 2005) and downstream ecosystems, and water supply and quality.

2.11.7 Water pollution, including nutrient loading

Despite being regarded as natural sinks for waste, wetland ecosystems have been and continue to be subjected degradation as a result of pollution (including nutrient loading e.g. from fertilisers, sediments and urban wastewater) (Turner et al., 2000; Collins, 2005; Millennium Ecosystem Assessment, 2005b). Since 1950, increases in nutrients, such as nitrogen and phosphorus, have been of concern in wetland ecosystems (Millennium Ecosystem Assessment, 2005b). Wetlands are altered by excessive pollution from local or upstream runoff, thereby changing the quality of the water flowing out of them (Mitsch & Gosselink, 2015). They are also impacted when untreated industrial and domestic wastewater is discharged into them (Kennedy & Mayer, 2002; Millennium Ecosystem Assessment, 2005b; Gopal, 2015). Globally, inland wetland pollution from inorganic nitrogen has doubled since 1960, with the situation worse in many industrialised parts of the globe (Millennium Ecosystem Assessment, 2005b). Nutrient loading, which has emerged to become one of the major drivers of wetland ecosystem change, is projected with high certainty to significantly increase in the future (Millennium Ecosystem Assessment, 2005b). Pollution is among the major factors that have been implicated in the degradation or destruction of many wetlands in Europe (Adedipe et al., 2005). Pollutants and sediments from the surrounding landscapes form another serious and growing threat to wetland ecosystems in South Africa (Government of South Africa, 2015). Nutrient loading can adversely affect the ecological balance of a wetland system. Under nutrient-rich conditions, superior competitors may out-compete and eliminate the less competitive wetland plant species (Collins, 2005).

2.11.8 Tourism

Tourism is a human intensive activity that can affect and disturb the wetland ecological balance (Backéus & Grab, 1995; Du Preez & Brown, 2011; Daryadel & Talaei, 2014). The effect of tourism on wetland ecological functions results from the development of tourism-related infrastructure and tourist trampling on vegetation and soil (Mitsch & Gosselink, 2015). The landscape and the very ecosystem drawing the tourism can deteriorate because of human pressure (Mitsch & Gosselink, 2015). Footpaths, which can develop into large erosion gullies, contribute to wetland degradation as lateral drainage from the wetlands takes place, eventually leading to desiccation (Du Preez & Brown, 2011). Soil erosion, which results in sedimentation in wetlands and the subsequent death of the vegetation covered in sediment, has also been implicated in wetland degradation and, often, gullies cut through the wetland (Grobbelaar & Stegmann, 1987; Backéus & Grab, 1995; Grab & Deschamps, 2004; Du Preez & Brown, 2011).

2.11.9 Global climate change

Global climate change has also been implicated in the degradation and loss of inland wetlands (Niu et al., 2012; Davidson, 2014). Wetlands are among the ecosystems most susceptible to climate change, especially in mountain areas that are already experiencing pronounced climate change impacts (Jeglum et al., 2011; Lee et al., 2015). Research has shown that headwater areas, where many wetlands are found, are more vulnerable to climate change than other areas because of the conditions associated with high altitudes (Chatterjee et al., 2010) and localised climate (Sukumar et al., 1995). Given that wetlands, peatlands in particular, are the largest terrestrial storage of carbon on the planet (20-30%) (Junk et al., 2013), degraded wetlands are viewed as potential sources of carbon to the atmosphere (Daryadel & Talaei, 2014; Mitsch & Gosselink, 2015). Thus, degradation can change wetlands from being carbon sinks to carbon sources. Higher temperatures in summer will result in higher evapotranspiration, resulting in deeper water tables in the wetlands (Jeglum et al., 2011). Climate change will alter the hydrology of wetlands and specifically, the nature and variability of the hydroperiod and the frequency and severity of extreme events (Daryadel & Talaei, 2014). The change in wetland hydroperiod will concomitantly result in alterations in the spatial distribution of suitable wetland habitats (Lee et al., 2015). Furthermore, it is likely that the function and distribution of inland wetlands will also be affected negatively (Brander et al., 2006).

By modifying dominant plant functional traits, competition, distribution and diversity, climate change is expected to change plant community composition in wetland ecosystems (Joyce et al., 2016). The increase in temperature at higher altitudes will be greater and have a more adverse impact on the biological communities (Junk et al., 2013). Climate change is expected to cause hydrological alterations and potential changes in the distribution of wetlands in mountain landscapes and this could have detrimental effects on wetland functioning, as well as dependent species and extended biological networks (Lee et al., 2015). These authors also highlight that many species in montane wetland ecosystems are adapted to special hydrological regimes, which are projected to change with climate change (Lee et al., 2015). In China, the changing climate is the main background factor affecting wetlands (Niu et al., 2012). Global climate change effects will often worsen the impacts of other causes of degradation and loss of wetlands (Millennium Ecosystem Assessment, 2005b), and we are therefore likely to witness an increased pressure on the remaining wetlands (Sullivan et al., 2008). The effects of climate change on wetlands will lead to a reduction in the services delivered by these systems (Millennium Ecosystem Assessment, 2005b).

2.11.10 Implications of wetland loss and degradation

Wetlands are a valuable resource whose destruction has tremendous economic, as well as ecological and aesthetic repercussions for the nations and communities across the globe (Mitsch & Gosselink, 2015). Given that nearly two billion people in the world live in areas of high flood risk, the degradation and loss of wetlands will put many livelihoods at risk (Millennium Ecosystem Assessment, 2005b). The economic value of wetlands is very high, much higher than that of all activities taking place in the converted wetlands (Millennium

Ecosystem Assessment, 2005b; Mitchell, 2013). In addition, the total economic value of marshes per hectare was more than two and a half times the value of converted wetlands (Millennium Ecosystem Assessment, 2005b).

Notwithstanding the need to assess the loss in wetland ecological functioning in full, key services such as water storage, filtering, carbon storage, erosion control and baseflow maintenance can be severely compromised following wetland conversion (Grundling et al., 2015). Wetland-dependent biodiversity, including native plant and animal species, faces dramatic reduction following wetland degradation (Millennium Ecosystem Assessment, 2005b; Rolon et al., 2010; Moreno-Mateos et al., 2012; Russi et al., 2013; Ricaurte et al., 2014). For example, about 21% of the predominantly wetland-dependent bird species are going extinct or becoming threatened, and their status continues to decline faster than that of the birds in other habitat types (Millennium Ecosystem Assessment, 2005b). The Ramsar Convention on Wetlands (2018) reports that in excess of 10% of all inland and coastal wetland-dependent species are globally threatened and, since 1970, 81% of inland wetland species has declined. It is noteworthy that a 2014 global analysis on the loss of ecosystem services between 1997 and 2011 revealed that the reduction in the coverage of swamps and floodplains was responsible for about US$ 2.7 trillion losses of ecosystem services per annum (Costanza et al., 2014). Moreover, about 60% of the global ecosystem services are showing signs of degradation, and anthropogenic factors, such as intensive agriculture, are the main causes of this adverse change (Millennium Ecosystem Assessment, 2005b).

Streams associated with intact high-altitude wetlands tend to be perennial, while those associated with degraded wetlands dry up during the dry periods (Meakins & Duckett, 1993). With the current rate of wetlands loss, human welfare is being threatened at a time of increasing water scarcity and demand (Millennium Ecosystem Assessment, 2005b; Daryadel & Talaei, 2014; Ricaurte et al., 2014). In fact, the gap between availability and demand for water is increasing globally (Millennium Ecosystem Assessment, 2005b). Continued wetland destruction will curtail agricultural productivity, lead to less potable water, less reliable water supplies, increased erosion and downstream flooding and more threatened species of plants and animals, particularly in water-poor countries (Collins, 2005; DWAF, 2008).

Moisture regime changes will lead to alterations in the processes of decomposition and peat accumulation, the release of nutrients and dissolved organic matter and biodiversity (Keddy, 1983; Jeglum et al., 2011; Mitsch & Gosselink, 2015). Keddy (1983) developed a model that explains wetland alteration (direct or indirect) through the influence of water level, nutrient status and natural disturbance, which in turn affects wetland ecosystem health. Through human activity, the modification of any one of these factors can lead to changes in the ecological functioning of the wetland, either directly or indirectly. The degradation and loss of inland wetlands has impaired their natural capacity to ameliorate the effects of floods (Millennium Ecosystem Assessment, 2005b).

The fewer the remaining wetlands in a catchment, the more limited the range and magnitude of services delivered by the wetlands (Sullivan et al., 2008), yet the more dependent the catchment as a whole is on those wetlands. In response to changes that occur in wetland habitats across landscapes, plants may tolerate the change, change growth form or life cycle stage, move location or disappear altogether (DWAF, 2004). However, it is notable that some uses, such as sustainable harvesting of wetland plants, are much less harmful than others (e.g. cultivating crops and draining (Collins, 2005).

2.12 Conservation and management of wetlands

Until recently, the significance of wetlands was not recognised and wetlands were subjected to modification or degradation by anthropogenic activities (Brand et al., 2013). Because they support high biodiversity and form the basis of far-reaching food chains that also extend beyond their boundaries, as well as providing other ecosystem services, wetlands are critical sites for conservation (Howard-Williams & Thompson, 1985; Rolon & Maltchik, 2006). The recognition of the interdependence between people and wetland ecosystems and the need for a healthy wetland ecological character has elevated the call for their conservation (Millennium Ecosystem Assessment, 2005b). An increased interest in better understanding of wetlands and their conservation worldwide has been reported and an increasing effort is directed towards documenting and valuing the ecosystem services they deliver (Millennium Ecosystem Assessment, 2005b; Russi et al., 2013).

The interest in the conservation of wetlands bloomed worldwide in the 1970s as a result of a concern about the speed with which wetland ecosystems were being lost or degraded (Daryadel & Talaei, 2014). In recognition of the importance of wetlands worldwide, the Convention on Wetlands of International Importance (commonly known as the Ramsar Convention) was adopted in the Iranian City of Ramsar, on the 2nd of February 1971 and came into force in 1975, initially with the main focus on protecting the habitats of water birds. This has also led to the promotion of wetland research. However, even to date, many countries around the world do not have a specific law or policy for wetlands; instead wetland management and protection benefit from the application of laws and policies developed for other purposes (Mitsch & Gosselink, 2015).

Considering the role of wetlands in the hydrological cycle and all water-related ecosystem services, their conservation is now a topical issue globally. During the past few decades, wetland research and management has become increasingly important around the world (Junk et al., 2013). Moreover, the scope of scientific interest has broadened from focusing narrowly on wetland description, formation and ecological relationships to include the concept of wise use (Maltby & Acreman, 2011). The Ramsar Convention defines wise use as the sustainable utilisation of wetland ecosystems for the benefit of human beings in a way that is compatible with maintaining the ecological character of the wetlands. Wang et al. (2008) highlight that the wise use of wetlands is the most effective way to protect and use wetland resources in developing countries where there is limited funding. The maintenance of the ecological character of wetlands and their wise use now form the central focus of wetland studies (Wang et al., 2008; Sieben et al., 2016c).

The conservation of wetlands and the associated biodiversity is complicated by their position on the landscape as they are "receivers" of land-use effluent (Dudgeon et al., 2006). Climate change is also expected to present serious challenges to wetland conservation and restoration. Wetland restoration describes the combination of efforts/activities aimed at returning a wetland from a disturbed or altered condition caused by anthropogenic activities to a previously existing or original condition (Mitsch & Gosselink, 2015). The maintenance of the hydrology, control of alien vegetation, reducing pollution, and protecting biological integrity and diversity can contribute tremendously in enhancing the resilience of wetlands (Ferrati et al., 2005; Erwin, 2008). This will enhance the sustainable provision of important services under changing climatic conditions. The conservation, maintenance and restoration of wetland ecosystems do not only play a significant role in the overall climate change mitigation strategy, but also in the adaptations that society needs to make to be able to cope with the effects of climate change (Millennium Ecosystem Assessment, 2005b; Stelk & Christie, 2014). A recent review identifies the protection of wetlands from direct anthropogenic disturbance as one of the invaluable strategies of mitigating future climate change (Moomaw et al., 2018). However, conserving wetlands and the associated biodiversity is dependent on how they are valued at both local and national levels (Irvine et al., 2016).

Biodiversity plays a key role in wetland preservation by enhancing ecosystem resilience to perturbations (Maltby & Acreman, 2011; Costanza et al., 2014). Given that vegetation represents a major component of the biodiversity in a wetland, vegetation is worthy of conservation (Sieben et al., 2010a). Knowledge of the variation in wetland vegetation and the understanding of the major determinants of this variability is one of the requirements for the successful management of these ecosystems (Sieben et al., 2014b). Maintaining and restoring the biotic health and integrity of a wetland determine the success of the conservation of wetlands and their resources (Wilson et al., 2013).

The significance of wetland conservation (including protection, restoration, management and sustainable use) as a fundamental aspect of sustainable development cannot be overemphasised. The values of wetlands are now recognised worldwide and since the 1970s, a lot of effort has been directed towards the conservation of these important but sensitive and fragile ecosystems. Much attention has been paid to the development and operation of sustainable management strategies for wetland systems (Turner et al., 2000). Since the adoption of the Ramsar Convention, the focus of wetland conservation has changed over the last decades from emphasising bird conservation to sustainable utilisation and this has attracted the broader international commitment (Maltby & Acreman, 2011). This shift aimed at abating wetland loss and enhancing the protection of these systems, as well as promoting their wise use across the globe. The commitment has been in the form of other multilateral conventions and initiatives, including national policies and strategies. These ecosystems are now protected by many laws, regulations, management plans, strategies and other interventions in different countries and states across the globe (Mitsch & Gosselink, 2015). Internationally, many multilateral environmental agreements contribute to wetland conservation, either directly (mainly the Ramsar Convention) or indirectly (e.g. the Convention on Biological Diversity and others). There are also a number of non-governmental organisations (such as the International Union on the Conservation of Nature) that indirectly contribute to wetland conservation.

The adoption of the Ramsar Convention and the development of other initiatives to conserve wetlands were prompted by the worldwide rate of and continued loss and degradation of wetlands (Daryadel & Talaei, 2014). The mission of the Convention is to provide a framework for the conservation and wise use of all wetlands by means of local, regional and national actions. It also aims to foster cooperation internationally, as a contribution to achieving sustainable development across the globe (Mitsch & Gosselink, 2015). The most important goals of the Ramsar Convention include preventing global loss of wetlands and conserving the remaining wetlands through their wise use (Daryadel & Talaei, 2014). The Ramsar Convention was a significant stride in wetland conservation worldwide. In 1997, the Convention also introduced the World Wetlands Day and this also promotes the lobbying for wetland conservation. The World Wetlands Day is celebrated internationally each year on the 2nd of February, which is the anniversary of the signing of the Ramsar Convention (Ramsar Convention Secretariat, 2014).

The Ramsar Convention is the only global international convention that is dedicated to the conservation and wise management of a specific ecosystem type (wetlands) (Ramsar Convention Secretariat, 2014) and wetlands are the only type of ecosystem to have a dedicated convention. This is, in part, attributed to the supreme importance of these ecosystems. Many countries have joined the Ramsar Convention and have listed a large number of wetlands in the Ramsar List of Wetlands of International Importance (Ramsar Convention Secretariat, 2014). The current number of Contracting Parties to the Convention is 170 (Ramsar Convention Secretariat, 2014) and this underscores the value of wetlands and the need to protect this essential natural resource base across the globe. The Ramsar Convention has formally registered more than 252 million hectares of wetlands in all the countries of contracting parties as Ramsar sites (wetlands of international importance). It has been estimated that, between 1975 and 2012, about 10% of the global inland wetland coverage (excluding coastal and marine wetlands) was designated as Ramsar sites (Verones et al., 2013). Africa hosts about 16% of the world's designated Ramsar sites by number (Daryadel & Talaei, 2014) and sub-Saharan Africa hosts a total of 190 designated Ramsar sites, representing 41.4% by area of all Ramsar sites globally (Mitchell, 2013). Lesotho became a Party to the Ramsar Convention in 2004 and has one Ramsar-listed wetland site (Ramsar site number 1388), known as Lets'eng-la-Letsie. It is noteworthy that the Ramsar Convention does not only mandate Parties to the Convention to conserve and use wetlands wisely, but also to encourage research and exchange of information regarding wetlands and their plants and animals (Ramsar Convention Secretariat, 1971).

In addition to these efforts, various interventions are also carried out in an attempt to improve the status of wetlands worldwide. While Red Lists of threatened species by governments and non-governmental organisations are contributing to the protection of wetland species from a changing environment (Turner et al., 2000), some countries are creating wetland reserves to achieve the same goal (Niu et al., 2012). South Africa, which completely surrounds Lesotho, has put a lot of effort into wetland conservation. For example, in 2003, the Water Research Commission, in collaboration with other major role players, launched a National Wetlands Research Programme, which aimed at optimising wetland conservation, in the context of their management, protection, restoration and sustainable use in the country (Day & Malan, 2010).

On a global scale, the Strategic Plan for Biodiversity (2011–2020) and Aichi Targets by the Convention on Biological Diversity can be an opportunity for the development of a concerted worldwide approach to curb and reverse the decline of wetlands (Finlayson, 2012).

Information on the functioning of wetlands and the associated vegetation is crucial in the formulation of any sound management and conservation plans for wetland ecosystems. Given that effective conservation and management of wetlands is often hampered greatly by a serious lack of and/or limited information and awareness (Irvine et al., 2016), concerted efforts across the globe are directed towards the sharing and dissemination of wetland information. For example, some scientific journals such as Wetlands, Journal of Wetlands Ecology, and Wetlands Ecology and Management are dedicated to deal particularly with wetlands, although many other journals also publish articles on wetland ecosystems. Additionally, professional bodies, such as the Society of Wetland Scientists in the United States of America and the South African Wetland Society, bring together wetland experts, managers and other interested people, with the primary goal of advancing the science, protection, conservation, management, restoration and sustainable utilisation of wetlands. International organisations, including Wetlands International, are also dedicated to the conservation and restoration of wetlands.

The understanding of the links of socio-economic values to wetland ecosystem processes and functioning underlie the success of organising for wetland conservation. The knowledge of the health and condition of wetlands at any point in time underpins the success of wetland conservation and management. For sustainable provision of ecosystem services, wetland conservation should aim at maintaining the health and integrity of the wetlands. The health of a wetland determines the capacity of a wetland to provide habitats for organisms and to provide services to society. Macfarlane et al. (2007) highlight a direct positive relationship between wetland health and its capacity to deliver ecosystem services.

In determining the health of a wetland, the extent of deviation from the reference condition for the three important components of wetland ecological health (geomorphology, hydrology and vegetation) is assessed (Macfarlane et al., 2007). Tools for a rapid assessment of wetland ecological health/condition have been developed in South Africa (Macfarlane et al., 2007; Kotze et al., 2012). These tools enable the establishment of baseline information and subsequent monitoring of wetlands, which will allow the detection of any significant changes that occur in the ecosystems. The ecological properties of a wetland and its ability to deliver ecosystems services can be sustained by maintaining its hydrological regime and natural variability (Millennium Ecosystem Assessment, 2005b). While there is significant progress in wetland conservation globally, more still needs to be done to ensure the abatement of wetland loss and degradation. This is evidenced by the fact that, while 30% of the Ramsar Parties indicate an improving status in their Ramsar sites, 17% still report a declining status (Russi et al., 2013). Furthermore, while 28% of the Parties to the Ramsar Convention in 2012 reported an overall declining status of their wetlands, only 19% reported an improvement (Davidson, 2014). Moreover, the strong bias in the distribution of Ramsar sites by number (almost 50% in Europe) (Verones et al., 2013) further points to the need for more effort to conserve wetlands outside of Europe. However, in terms of area, it seems that Africa is well represented.

The improvement of wetland resilience and removal of existing pressures on these ecosystems form the most effective method of conserving and coping with the adverse effects of climate change (Millennium Ecosystem Assessment, 2005b). Wetlands are multi-functional systems, which can only be effectively conserved as integrated ecosystems (within a catchment). Integrity in the process and functioning of the entire wetland ecosystem underpins the sustainable provision of ecosystem services by the wetland. To optimise the landscape for wetland ecosystem values, about 5% of a watershed should be made up of wetlands (Mitsch & Gosselink, 2000).

A balanced (even) and stable community is critical for the natural functioning of wetland systems, and is therefore regarded as an indicator of good ecosystem health (Adedipe et al., 2005). Given that many different types of changes are expected to occur in wetland environments, the understanding of the link between plant community composition and the physical environment of the wetlands is crucial for conservation planning (Sieben et al., 2014a). Wetland vegetation and soil, as indicators of wetland hydrology, can be used to assess wetland health and integrity, as well as assessing the success of conservation projects (Vepraskas & Caldwell, 2008; Moreno-Mateos et al., 2012; Wilson & Bayley, 2012; Wilson et al., 2013). Plant species occurring in wetland environments are useful indicators of the conditions of the environment and ecological changes in the wetlands (Schulze et al., 2002; Sieben et al., 2014a).

Vegetation patterns can be useful in assessing the integrity and conservation status of a wetland once the links of vegetation patterns to edaphic factors and ecosystem functioning are established (Sieben et al., 2010a). Therefore, in order to detect any significant changes which could occur in wetlands, long term monitoring of the plants that are regarded as characteristic of specific wetland environments is important (Sieben et al., 2014a). Because the knowledge of the indicators of a healthy wetland is important for managing wetlands in the long term

(Sieben et al., 2016c), monitoring of the integrity of specific wetlands can be facilitated by the identification of indicator species for certain wetland habitat conditions (Sieben, 2011; Sieben et al., 2014a).

Because the wetlands in sub-Saharan Africa play a key role in the livelihoods of rural populations, the sustainable management of these ecosystems is necessary for the continued provision of ecosystem services (Rebelo et al., 2009). Wetlands are among the most intensively managed elements of the South African rural landscape, featuring prominently in water resource management strategic plans (Sieben et al., 2016c). The documentation of wetland biodiversity helps to inform the development of conservation management plans, as well as to monitor biodiversity changes with time (Chatterjee et al., 2010). The rapid degradation and loss of these wetlands raises an urgent need for sound ecological studies aimed at understanding the patterns of biodiversity in them to provide scientific basis for biodiversity conservation programs (Rolon and Maltchik, 2006).

Despite the various international agreements and national policies and initiatives, local economic development at the expense of wetland conservation is still widespread across the globe (Turner et al., 2000). Furthermore, many countries lack a distinct wetland policy (Maltby & Acreman, 2011). In South Africa, wetlands are the second most poorly protected ecosystem type, with about 71% of all wetland ecosystems not under any form of protection (Government of South Africa, 2014, 2015). Davidson (2014) recommends an urgent need for wetland inventories and analyses of change in wetlands, especially in Africa.

It is noteworthy that the recognition of the critical value of wetlands has made their conservation, restoration and creation to be considered worthy undertakings (Mitsch et al., 2013). These actions have increased over the past 40 years, especially in developed countries (Mitsch & Gosselink, 2015). Mitsch and Gosselink (2015) use the term “mitigating the loss of a wetlands” to refer to the process of wetland restoration and creation. Hence, mitigation of wetland losses through restored and artificial (man-made) wetlands is increasingly becoming important (Junk et al., 2013; Mitsch et al., 2015). Over the last 100 years, the restoration of degraded natural wetlands and creation of new ones have been practised, in an effort to restore wetland properties and functions lost because of destruction or degradation (Palmer, 2009).

After perturbation, natural wetland ecosystem structure and functioning usually recovers towards reference levels (Moreno-Mateos et al., 2012). This resilience is often compromised by continued exposure to anthropogenic factors. Given the effects of anthropogenic activities on wetland structure and functioning, and thus on human well-being, the conservation and restoration of wetlands is imperative (Sieben et al., 2011). In an attempt to recover the benefits from wetlands, ecological restoration of wetlands is on the rise globally (Maltby & Acreman, 2011). Wetland restoration efforts targeting specific ecological services also contribute to an improved condition of the ecosystem and to the well-being of the communities around the wetlands (Sieben et al., 2011).

Sieben et al. (2011) consider the Hydrogeomorphic (HGM) unit as the most suitable functional unit to work with for restoration. The aims of restoration often focus on particular ecosystem services, including flood amelioration, enhancing water retention or biodiversity conservation (Sieben et al., 2011). However, wetland restoration without addressing the factors responsible for the degradation in the entire landscape cannot be sustainable (Palmer, 2009). Accordingly, Sieben et al. (2011) strongly recommend that a detailed assessment of wetland functioning and the causes of the degradation should be conducted before planning restoration measures. The success of wetland restoration is strongly determined by the extent of degradation and some wetlands can take decades to centuries for significant recovery to occur (Aylward et al., 2005). The same authors further highlight that, in some cases, degraded wetlands cannot be restored at all because some edaphic factors would have been subjected to irreversible alteration. Nevertheless, despite the fact that restoration can be quite expensive, evidence from around the world suggests that restoration of degraded systems can bring significant benefits to society and often supply ecosystem services at a much lower cost than alternative artificial infrastructure (Russi et al., 2013). Before restoration attempts, it is important to conduct a cost-benefit analysis to determine whether the restoration is worth it.

Although it remains debatable, there is a notion that restored wetlands are functionally similar to natural wetlands, as they deliver the same goods and services to humankind (Yang et al., 2008). Often, restoration of wetlands does not restore ecosystem structure and functioning to pre-impact levels (Palmer, 2009). Although restored wetlands may recover biologically, their functioning may not be fully restored (Mitsch & Gosselink, 2015). In fact, in many wetlands, the delivery of ecosystem services may not fully recover even when the ecosystem appears to be biologically restored (Palmer, 2009; Moreno-Mateos et al., 2012). Hence, it remains debatable by both scientists and policymakers whether it is generally possible to restore wetlands with ecological and other functions that are comparable to, or better than, those of the degraded or lost natural wetlands (Palmer, 2009), although it depends largely on the ecosystem service.

A meta-analysis of 621 wetlands from around the world reveals that even 100 years after restoration efforts, the biological structure (mainly vegetation) and biogeochemical functioning, averaged 26% and 23% lower, respectively, than in the reference sites (Moreno-Mateos et al., 2012). The same study also found that the diversity of plant assemblages, which are the primary producers, exhibits the lowest recovery rates of all biotic groups and also remain significantly lower than the reference levels even after a century. The study further reports a significant reduction in the sequestration and cycling of nitrogen and carbon from pre-impact levels following degradation. Therefore, Moreno-Mateos et al. (2012) warn that the world cannot entirely depend on restoration of degraded habitats but has to put resources in the protection of pristine habitats. More recently, there have been reports that conserving functionally intact natural wetlands is economically more advantageous than restoring degraded ones or creating new ones (Costanza et al., 2014; Irvine et al., 2016).

In an attempt to further mitigate the loss of wetlands and the services they deliver, there has also been an increasing trend to develop artificial wetlands worldwide (Aylward et al., 2005; Palmer, 2009; Niu et al., 2012; Junk et al., 2013; Mitsch et al., 2013, 2014; Mitsch & Gosselink, 2015). Wetland creation entails the use of human activity to convert a persistent upland or shallow open water system into a vegetated wetland (Mitsch & Gosselink, 2015). The main objective for creating wetlands is to replace or mitigate for the lost ecosystem services (Palmer, 2009). The creation of wetlands is on the rise globally, especially in Europe and the United States of America (Aylward et al., 2005; Palmer, 2009; Niu et al., 2012; Junk et al., 2013; Mitsch et al., 2013, 2014; Mitsch & Gosselink, 2015). The Ramsar Convention on Wetlands (2018) estimates that artificial wetlands have doubled between 1970 and 2015. For example, between 1978 and 2008, China recorded an increase of 122% in artificial wetland area (Niu et al., 2012).

Despite wetland creation gaining popularity to compensate lost wetlands, one study (Daryadel & Talaei, 2014) found that artificial wetlands, like restored wetlands, rarely perform the same functions or harbour the same biodiversity as natural wetlands. Although artificial wetlands sequester more carbon and emit less methane than natural wetlands, as well as delivering a number of ecosystem services (Mitsch et al., 2013, 2014), it is unlikely that these systems can structurally and functionally completely replace natural wetlands (Aylward et al., 2005). In their study in Canada, Wilson and Bayley (2012) report that artificial marshes were actually in a poorer biotic condition compared to natural marshes. Additionally, the findings from the same study suggest that wetland ecosystem health generally deteriorates as artificial wetlands replace natural ones on the landscape scale.

Notwithstanding the wide use of wetland compensation (restoration and creation) to offset the loss and degradation of wetland ecosystems, the situation above highlights the importance of prioritising conservation over compensation (mitigation). This therefore points to the need to protect the health and condition of natural wetlands through the management of the factors that are often implicated in the degradation of these ecosystems. Therefore, it can justifiably be argued that wetland restoration and creation are not appropriate alternatives to the protection of mature, rare and sensitive natural wetlands that have evolved over millennia (Costanza et al., 2014) and should thus be the last option to be considered. The conservation of natural wetlands and the associated vegetation indirectly protects animal species and the sustainable provision of ecosystem services.

Because using natural wetlands for wastewater treatment, a common practice, can severely interfere with the natural wetland's functioning, Kennedy and Mayer (2002) recommend that natural wetlands should be spared from wastewater treatment and other degrading uses; instead they should be reserved for less damaging uses, such as sustainable harvesting of biological resources. Furthermore, Collins (2005) highlights that those uses of wetlands which do not alter wetland hydrology and which do not have adverse effects on the functioning of the system need to be promoted as this will help justify their conservation. Such uses include sustainable exploitation of tangible resources from the wetlands.

2.13 Conclusions and knowledge gaps

Covering an estimated 6.5% of the global area, wetlands are widely distributed across the globe. The current review established that palustrine wetlands are characterised by three important factors (hydrology, geomorphology and vegetation). Thus, a wetland is "land which is transitional between terrestrial and aquatic systems where the water table is at or near the surface, or the land is periodically covered with shallow water, and which in normal circumstances supports or would support vegetation typically adapted to life in saturated soils" (DWAF, 2004, 2008; Ollis & Malan, 2014; Mitsch & Gosselink, 2015). Given their diversity and existence on a continuum, it is important to complement top-down wetland classification with bottom-up approaches as this will cater for both biodiversity conservation and water resource management.

By harbouring a high biological diversity, which is disproportionate to their areal extent, and delivering a broad array of ecosystem services to humankind, palustrine wetlands, including those in montane areas, are of great ecological and socio-economic importance worldwide. Furthermore, wetlands in montane areas in particular, provide unique habitats and concomitantly support unique biodiversity, including rare and threatened species. Wetlands harbour more than 40% of the world's plant and animal species (Mitra et al., 2003; Hu et al., 2017). These ecosystems, which supply more ecosystem services than other freshwater ecosystems, contribute about 15% of the total global economic value of all ecosystem services (Costanza et al., 1997) and provide up to 40% of the world's annually renewable ecosystem services (Zedler & Kercher, 2005). Biodiversity, particularly vegetation, is central and most critical to wetland ecosystem functioning and, concomitantly, the ecosystem services supplied by the wetlands. The economic value of wetlands is much greater than that of all activities for which they can arguably be converted, degraded or lost. Thus, because human well-being depends heavily on the services delivered by healthy ecosystems (Pinto et al., 2014), alterations in wetland functioning can have direct and indirect impacts on humankind.

The utilisation of wetland ecosystem services by human beings has an effect on ecosystem functioning, which in turn affects wetland biodiversity (Pinto et al., 2014). Since 1900, more than 50% of all wetlands have been lost globally (Russi et al., 2013; Daryadel & Talaei, 2014; Davidson, 2014), mainly due to agriculture and socio-economic development. These negative trends will likely be exacerbated by global climate change. These reports indicate that, despite significant progress in wetland conservation globally, more still needs to be done to ensure the abatement of wetland loss and degradation.

In the last two decades, interest in understanding wetland ecosystems and their conservation has improved, as evidenced by the substantial increase in studies on wetland ecosystems (Figure 2.1). Much of the effort directed towards wetland conservation is often curtailed by the lack of information and awareness on the ecological functioning and value of these important ecosystems. Furthermore, there is apparent scarcity of data on most wetlands, particularly those not designated as Ramsar sites. Notwithstanding the increasing popularity of restored and artificial wetlands globally, these systems cannot achieve the ecosystem structure and functioning that is comparable to natural wetlands that developed over a very long ecological period. Thus, conserving functionally intact natural wetlands is ecologically and economically more advantageous than restoring degraded wetlands or creating new ones.

Because wetlands are complex multi-functional systems, their conservation can be more effective if it is integrated in the management of broader catchments. The conservation and wise-use of natural wetlands should be encouraged, particularly for those uses that do not alter the health and integrity of the ecosystem functionality. The conservation of these wetlands should aim at maintaining the three major components of wetland health (hydrology, geomorphology and vegetation), which are the determinants of wetland ecosystems. Though still at a stage of infancy, functional characterisation of wetland vegetation is featuring more prominently in current research. However, few studies have focused on wetland plant functional traits during wetland characterisation (Table 2.1).

Because of the diversity of wetlands and their vegetation being azonal, site specific ecological studies aimed at the characterisation of these systems are imperative to inform their conservation. Knowledge about the status and trends of the world's remaining natural wetlands is very patchy and limited. Thus, Gardner et al. (2015) strongly recommend country-specific information to be generated for effective national and sub-national responses to wetland loss and degradation. Given the supreme value of wetlands, recent studies (Irvine et al., 2016; Sieben et al., 2016c; Moor et al., 2017) emphasise this lack and need for more information on their species composition, distribution and ecology. The assessment of the physical functions that a given wetland performs is a prerequisite to the evaluation of a wetland's value to society (Brander et al., 2013). Subsequently, Irvine et al. (2016) recommend that the ecosystem functions and services of inland wetlands require considerable further research. Furthermore, studies in montane wetlands are needed as they can be useful in assessing the effect of climate change on biodiversity because mountains can represent unique areas for the detection of such changes (Sharma et al., 2010).

Three major constraints to the conservation and sustainable management of wetland ecosystems, especially in Africa, have been identified by the review of literature. Firstly, the limited understanding of the factors that underpin and influence the properties and functioning of specific wetlands often results in actions that are detrimental to wetland ecosystem functioning by, for example, altering their hydrology (Rolon & Maltchik, 2006; Rai & Raleng, 2011; Mitchell, 2013; Daryadel & Talaei, 2014; Sieben et al., 2014a; Mitsch & Gosselink, 2015; Irvine et al., 2016). This has led to the loss of wetlands and the concomitant decline in their capacity to supply ecosystem services. Thus, the understanding of the three determinants of wetland ecosystems (hydrology, geomorphology and vegetation) is key to the conservation and management of these systems.

Secondly, there is limited information on the importance and value of specific wetlands, and the effects of alternative management options, and this promotes conversion of wetland ecosystems for short-term gains (Rolon & Maltchik, 2006; Mitsch & Gosselink, 2015; Irvine et al., 2016). Environmental factors driving wetland community composition differ from one geographical location to another and among different wetland types (Sieben et al., 2014a).

Wetlands further exhibit high geographical variation (Macfarlane et al., 2007). Moreover, a review of the studies on ecosystem services on the African continent, which revealed that most of the studies were carried out in South Africa, Tanzania and Kenya and mainly covered provisioning services, emphasise the urgent need to extend the studies to the rest of the continent, as well as for the studies to focus more on local-scale assessments of numerous ecosystem services (Wangai et al., 2016). This makes area-specific studies of wetlands critical for their effective conservation. The assessment of the ecosystem services provided by a wetland is an important starting point for understanding the value of a wetland to society and the success of any efforts directed towards the conservation and management of the ecosystem. The IPBES (2018) has recently reported that, owing to the few studies assessing the value of "nature's contributions to human well-being," Africa's richness in biodiversity and ecosystem services is under-estimated. Furthermore, wetland ecosystem service assessment is considered the primary step toward promoting the protection of these ecosystems (Wondie, 2018).

Thirdly, the lack of understanding of the link of wetland ecosystem processes and functioning to socio-economic services delivered by the ecosystems often inevitably leads to unsustainable utilisation of these ecosystems and poor policy decisions (Day & Malan, 2010; Maltby & Acreman, 2011; Gopal, 2015). Although ecosystem services are fundamentally products of wetland ecosystem properties, which in turn are influenced by traits of the dominant species (Sieben, 2012; Moor et al., 2015; Zhang et al., 2015), trait-based approaches to the effects of plants on wetland functioning and ecosystem services still lag behind, compared to other habitat types (Lhotsky et al., 2016; Moor et al., 2017; Schwarz et al., 2017; Sieben & le Roux, 2017). The understanding of the links of socio-economic values to wetland ecosystem processes and functioning underpins the success of any lobbying for wetland conservation and management.

For the wetlands in Lesotho, very little has been done with respect to the above factors, despite their importance. In general, very little attention has been paid to these wetlands. Of the few studies that are available, most are outdated, are mainly descriptive and largely based on either expert opinion or review of literature, rather than on formal assessment methods. In addition, the surveys of the wetlands in Lesotho, in most cases, focused on the hydrological and sedimentological properties (Olaleye & Sekaleli, 2011; Olaleye et al., 2012; Mapeshoane, 2013; Olaleye, 2016), with only a superficial description of the vegetation. Given that the studies that attempted to assess the ecosystem services of the wetland ecosystems in the country are not only few but also localised, changes in the provision of ecosystem services delivered by wetlands along important gradients in the country remain unknown. Furthermore, the functional traits of wetland plants in the country have not been explored, as well as their links to environmental conditions and ecosystem service delivery.

The wetlands in Lesotho play an important role in sustaining perennial water flow and regulating the quality of water of the major rivers in the country, in addition to the delivery of other ecosystem services. Most of the areas in the country, particularly in the mountains are drained by the Senqu-Orange River and its tributaries. Thus, falling entirely in the catchment of the Senqu-Orange River, the wetlands in Lesotho are not only important for the country but also for countries located downstream along this river, namely South Africa and Namibia. These wetlands are also important in maintaining the levels of water in the Lesotho Highlands Water Project (LHWP) dams and those supplying the local population. Hence, the conservation of wetlands in Lesotho is key to the sustainable supply of water resources.

CHAPTER 3: STUDY AREA

3.1 Location

This study was carried out in Lesotho (officially known as the Kingdom of Lesotho), a country found in southern Africa. The country is a small mountainous enclave of its only neighbour, South Africa (Figure 3.1). Lesotho has a surface area of 30 355 km^2 and lies between 28^{o}S and 31^{o}S, and 27^{o}E and 30^{o}E (Pomela et al., 2000). It is bounded by three of South Africa's provinces: KwaZulu-Natal to the east, the Eastern Cape to the south, and the Free State to the north and west (Figure 3.1). The eastern and south-eastern boundaries of Lesotho, shared with KwaZulu-Natal and the Eastern Cape also represent the watershed between the Atlantic and Indian oceans (Pomela et al., 2000).

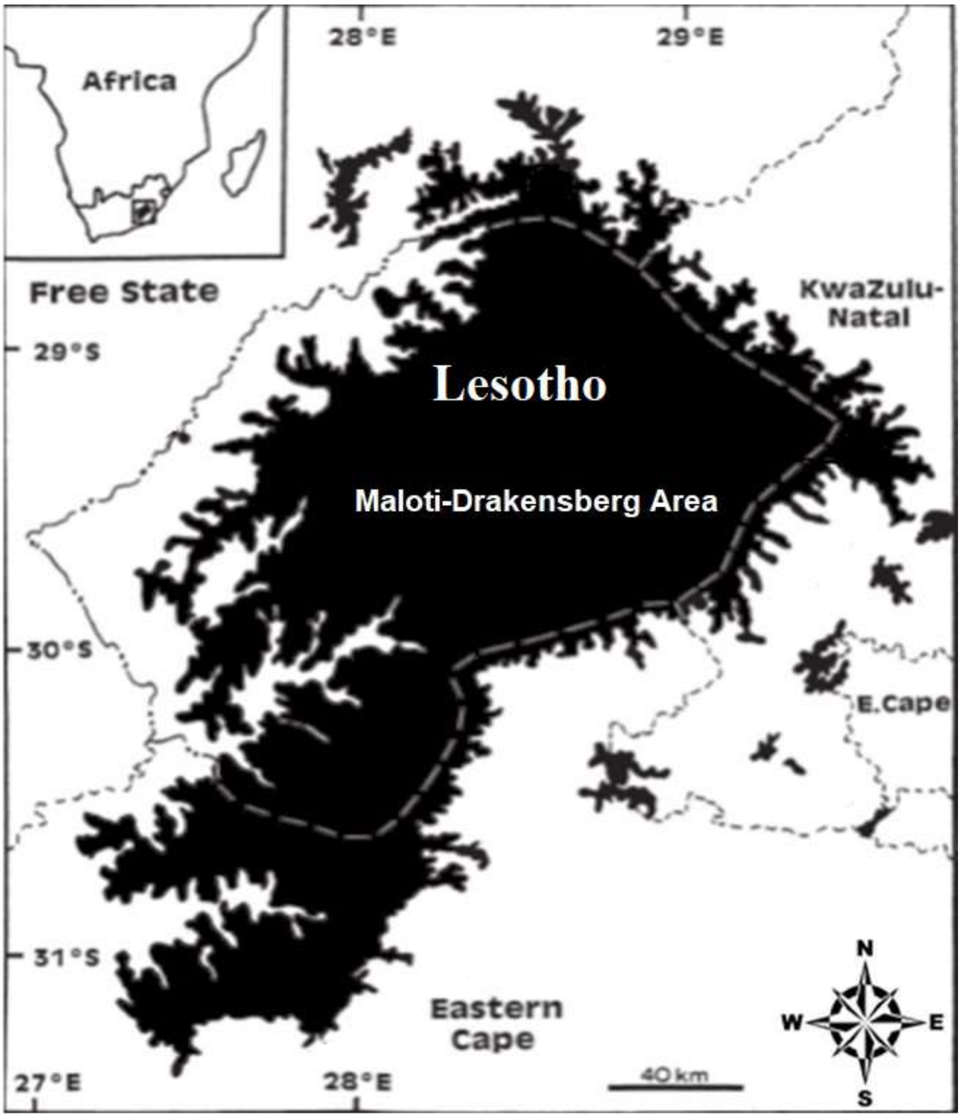


Figure 3.1: The location of Lesotho and the Maloti-Drakensberg area relative to the three bordering provinces of South Africa (Carbutt & Edwards, 2004).

Although the current study mainly focuses on Lesotho, the description of the study area also covers the Maloti-Drakensberg biodiversity hotspot area because one of the objectives of the study covers the entire Maloti-Drakensberg area. Furthermore, the greater proportion of Lesotho (about 70%) falls within this globally recognised Maloti-Drakensberg biodiversity hotspot, which covers about 40, 000 km^2 and is the centre of the Eastern Escarpment (Cowling & Hilton-Taylor, 1994; Carbutt & Edwards, 2006; Kopij, 2006) and known for high species endemism (Adams et al., 1999; Pomela et al., 2000). Lesotho also accounts for about 60% of the Maloti-Drakensberg hotspot area, which also extends into South Africa (Figure 3.1) (Pomela et al., 2000; Mokuku et al., 2004). Falling entirely in the Grassland Biome of southern Africa, the Maloti-Drakensberg hotspot forms the highest mountain region in southern Africa and is one of the sub-continent’s eight hotspots of botanical diversity in terms of species richness and endemism (Mucina & Rutherford, 2006). The hotspot is characterised by high biodiversity and many montane grassland endemics.

The Lesotho part of the Maloti-Drakensberg biodiversity area is called the Maloti Mountains and forms the highlands of the country. While the hotspot covers the districts of Mokhotlong, Thaba-Tseka, Qacha’s Nek, and Quthing almost completely, it also stretches into the eastern parts of the districts of Berea, Butha-Buthe, Leribe, Mafeteng, Maseru and Mohale’s Hoek (Mucina & Rutherford, 2006). The highest mountain peak in Africa, south of Kilimanjaro is found in Lesotho, with a summit at an altitude of 3482 m above sea level (a.s.l.) at Thabana-Ntlenyana (Backéus & Grab, 1995; Mucina & Rutherford, 2006). Lesotho is the only country in the world that lies entirely above 1,000 m a.s.l. (Ministry of Natural Resources, 2000). The country entirely falls within the catchment of the well-known Senqu-Orange River, contributing about 40% of the total runoff (ORASECOM, 2015). The Senqu-Orange River is the most developed shared river system in southern Africa.

3.2 Geology and soils

The highlands region of the country, accounting for more than two thirds of the country’s surface area, was formed by massive volcanic activity in the Jurassic period that gave rise to basaltic lavas that cover most of the country and the upper face of the Maloti-Drakensberg Escarpment with dolerite intrusions (Hughes & Hughes, 1992). The basalt is underlain by the softer sandstone (Clarens Formation) which is exposed at cliffs and overhangs below the escarpment and in great wind-sculpted boulders in the south (Carbutt & Edwards, 2004). Thus, the horizontally laid basaltic bedrocks dominate in the mountain areas of the country (covering about 73% of the landscape), while the Lowlands and the Foothills are dominated by sedimentary sandstone (Schmitz & Rooyani, 1987; Hughes & Hughes, 1992; Grundling et al., 2015). However, mudstones of the Elliot Group and shale are also present in some parts of the lowland areas. In geological terms, the Maloti Mountains are relatively young as evidenced by the noticeable weathering and erosion processes, indicating that the landscape is constantly changing (Grundling et al., 2015).

The nature of the underlying parent material has a great effect on the resultant soil in an area. The major types of soil in Lesotho have their origin in the sediments and basaltic lavas associated with the Karoo Supergroup (Schmitz & Rooyani, 1987; Maro, 2011). The soils in the mountains are commonly dark brown to black and fine textured, reflecting the influence of the basaltic parent material. Mucina and Rutherford (2006) indicate that these soils of the mountains are generally nutrient-rich and, by and large, reflect a strong influence of grassland vegetation. Soils derived from basalt are characterised by nearly equal proportions of coarse sand, silt, fine sand, clay and organic matter (Mucina & Rutherford, 2006). The high organic matter content (ranging from about 20% on the slopes up to about 26% in the valleys) account for the high water-retention capacity of the soil and water redistribution through seeps is frequent (Mucina & Rutherford, 2006). Because of the wide variations in altitude and slope, topography played an critical role in the formation of the soils of Lesotho by its direct controlling influence on the erosion and deposition processes (Schmitz & Rooyani, 1987). Mixing, remixing, sorting, soil creep, erosion, deposition and weathering processes have caused a great variety in soils of the Foothills and Lowlands (Schmitz & Rooyani, 1987).

The soils in the Lowlands and Foothills of the country are acidic and generally nutrient-poor, while those in the Highlands are neutral and nutrient-rich (Maro, 2011). The soils are black, very rich and thin on the Maloti Mountain summit but deeper in the Foothills (Schmitz & Rooyani, 1987). The same author highlights that the soils on the summit are often waterlogged in summer, while they freeze every night in winter. Two types of clayey soils are common throughout the country: young and shallow soils, and young and deep vertisols (Maro, 2011).

The Maloti Mountain summit is turned into unstable habitat for plants because of the freeze and thaw processes that heave the soil and rocks, an activity which is also responsible for the crescent-shaped scars on mountain slopes lower down (Mucina & Rutherford, 2006). The soil is normally less than 400 mm deep, is susceptible to erosion and is highly fragile (Meakins & Duckett, 1993). Hence, natural sheet and gully erosion are a common feature in the country, and therefore the landforms are susceptible to man-made erosion resulting from overgrazing and poor management of the grasslands.

3.3 Climate

The climate of Lesotho is characterised by stark contrasts between seasons as well as between day and night (Backéus & Grab, 1995). Entirely lying above 1,388 m a.s.l., Lesotho enjoys a temperate climate that is moderated by altitude (Kopij, 2006). In the high mountains of the country, the climate is alpine, continental and seasonal in nature (van Zinderen Bakker & Werger, 1974; Mokuku et al., 2004). Broadly, the country has two major seasons in a year, which are summer (October to April) and winter (May to September). Winters are generally dry and cold, while summers are wet and warm.

Precipitation is received mainly in the form of rainfall, snow and sleet. The country receives abundant orographic rainfall mainly in the form of warm moist air that comes from the Indian Ocean and cools down on rising up over the high eastern mountains (Sieben et al., 2010b). The rainfall, generally increasing eastwards due to rain-shadow effects, ranges from 500 mm to 2,000 mm annually, with the highlands receiving the highest amount and the Senqu-Orange River Valley the lowest (Pomela et al., 2000; Mokuku et al., 2004; Grundling et al., 2015). The high mountains of the Maloti Mountains receive an average annual rainfall above 2,000 mm (Taylor et al., 1995). However, the precipitation is quite variable both spatially and temporally, with totals showing considerable variation from year to year (Lesotho Meteorological Services, 2013).

About 85% of the total rainfall is received in summer, most frequently as heavy afternoon thunderstorms, usually accompanied by hail (Pomela et al., 2000; Kopij, 2006). However, extended periods of steady rainfall can occur as well. The Lesotho Department of Meteorological Services (2013) reports that the rainfall generally peaks from December to February and during this period, most areas in the country receive more than 100 mm monthly and an average of six days with rainfall of at least 5 mm. The Lesotho Department of Meteorological Services also highlights that the lowest rainfall is received in June where average monthly totals of less than 15 mm are recorded in most areas in the country. Lesotho has the greatest frequency of hail in southern Africa and, with about five to twelve strikes per km^2 per year, the country has one of the highest incidences of lightning in the world (Pomela et al., 2000). During winter, rainfall is rare, but heavy snowfalls frequently occur and the snow can persist on the ground for weeks or even months (van Zinderen Bakker & Werger, 1974; Backéus & Grab, 1995), especially on the south-facing slopes in the high mountains.

Generally, the climate in Lesotho is characterised by cold winters and hot summers, with mean temperatures of 15 ℃ and 25 ℃, respectively (Pomela et al., 2000). In the highlands, it is cool to warm in summer and cold to freezing in winter. The overall altitude of Lesotho partially accounts for the generally lower temperature in the country than that of other inland regions at similar latitudinal position in larger landmasses, both in southern and northern hemispheres (Lesotho Meteorological Services, 2013). The estimated drop of 1 ℃ for every 125 m gain in altitude in Lesotho (Pomela et al., 2000) implies a temperature difference of about 16.8 ℃ between the lowest and highest points in the country.

Mean annual temperatures range from 7 ℃ in the highlands to 15.2 ℃ in the lowlands (Lesotho Meteorological Services, 2013). While temperatures can be higher than 30 ℃ in summer and as low as -7 ℃ during winter in the Lowlands, it is not unusual for the highlands to experience temperatures as low as -18 ℃ (Taylor et al., 1995; Bureau of Statistics, 2009). Above 2,500 m a.s.l., temperatures are typically cool (not exceeding 16 ℃) even during the summer months (van Zinderen Bakker & Werger, 1974; Grundling et al., 2015). Throughout the year, there is a wide range between the daily minimum and maximum temperatures and typical ranges are 18 ℃ difference in winter and 15 ℃ in summer (Pomela et al., 2000). The highest mean maximum temperatures throughout the country are recorded in January and they range between 20 ℃ in high altitude areas to 32 ℃ in the lowlands (Lesotho Meteorological Services, 2013). June is the coldest month with mean minimum temperatures of around 0 ℃ common. While mean monthly minimum temperatures ranging from -3 ℃ to -1 ℃ are recorded in the Lowlands, the highlands record between -8.5 ℃ and -6 ℃.

The Lesotho Department of Meteorological Services (2013) reports that the mean monthly totals of evaporation are in the range 60-70 mm in June and July, and 175-225 mm in December and January. Evaporation is generally higher in the Lowlands than in the highlands. For most of the days in summer, cloud cover is in the range of partly cloudy to overcast conditions, usually with widespread showers (Lesotho Meteorological Services, 2013). Daily frosts are experienced in winter, with mist occurring throughout the year, supplementing the rainfall (Mucina & Rutherford, 2006). In fact, frost can occur at any time in the Maloti Mountains while in the Lowlands, it is usually experienced for about 80 times per year (Pomela et al., 2000). The country receives 60-80% of the maximum possible sunshine throughout the year

(Lesotho Meteorological Services, 2013). The same department also reports that the annual total solar radiation over Lesotho is estimated to be in the range of 5,700 MJ/m² to 7,700 MJ/m².

Strong winds are common at high altitudes in summer, especially in the afternoons and evenings. Mean monthly wind speed ranges between 1.4 m/s in October to 8.0 m/s in August and the winds are generally westerly (Lesotho Meteorological Services, 2013). It is highlighted that wind speeds of up to 20 m/s can at times be experienced during summer thunderstorms. It is noteworthy that the weather in Lesotho is notoriously variable with snowfalls and cold spells possible at any time of the year. Occasionally, snowfalls have been observed even in the summer months, such as November.

3.4 Agro-Ecological zones

The geomorphological and topographical variations, including the influence of micro-climate have a substantial effect on the ecology of a region (Lesotho Meteorological Services, 2013). The mountains of the country are divided into three ranges from west to east, namely, Thaba-Putsoa, Central and the Quathlamba/ Drakensberg Range (the highest of the three ranges) (Grundling et al., 2015). The country has a wide altitudinal range, from about 1,388 to 3,482 m a.s.l. (Chakela, 1997; Pomela et al., 2000). Carbutt (2019) defines the Afromontane region as the area occurring between ±1,300 m and ±2,800 m a.s.l. and alpine as the region from ±2,800 to 3,482 m a.s.l. Thus, the entire Lesotho qualifies to be at least Afromontane.

While further north in Africa Afromontane vegetation occurs only above 2,000 m a.s.l., latitude compensates for altitude in Lesotho and the Maloti-Drakensberg mountains, allowing Afromontane communities to occur at much lower altitudes (Dowsett 1986; Cowling et al. 1997). Floristically, the Maloti-Drakensberg mountains are considered as the only truly alpine region in southern Africa (Carbutt & Edwards, 2006; Grab, 2010).

Based on climate and elevation, Lesotho has been divided into four major agro-ecological zones (AEZs): the Lowlands (1,388–1,800 m a.s.l. and accounts for 17% of the country's surface area), Foothills (between 1,800 and 2,000 m a.s.l. and occupying about 15%), Highlands, also known as the Maloti Mountains (2,000–3,482 m a.s.l. and covering about 59%) and Senqu River Valley, lying at 1400-2000 m a.s.l. (accounting for about 9%) (Figure 3.2) (Pomela et al., 2000; Bureau of Statistics, 2009). The mountain area of the country, which includes the Highlands (Mountains), Foothills and part of the Senqu River Valley lies above 1,800 m a.s.l. and cover more than 80% of the country's surface area, and is generally considered the highlands of the country (Hughes & Hughes, 1992; Kopij, 2006; Grundling et al., 2015).

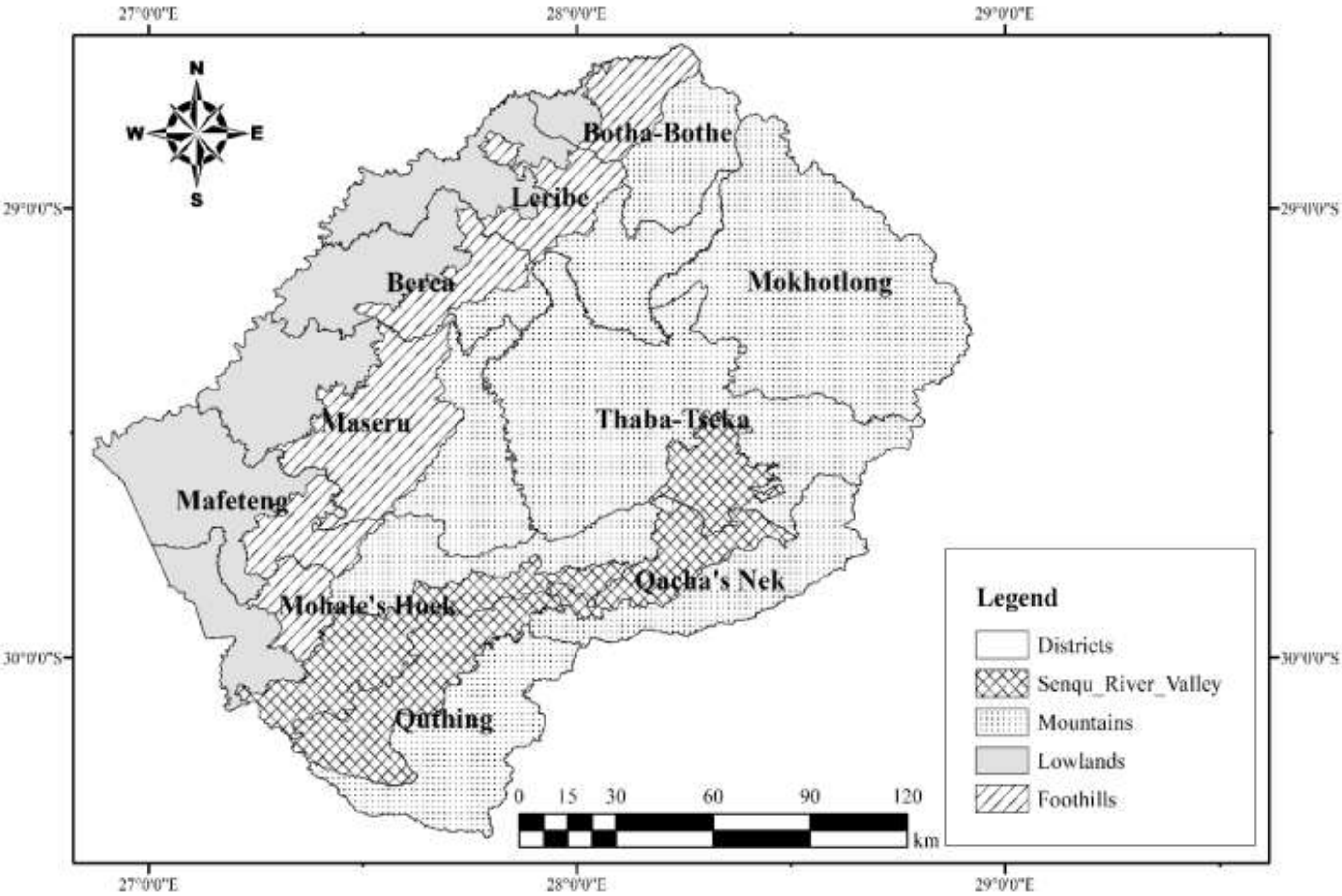


Figure 3.2: Distribution of the agro-ecological zones and administrative districts of Lesotho

The four categories in the AEZ classification are based on landforms rather than vegetation types. The Foothills are defined as the transitional area between the Highlands and the Lowlands. While the Lowlands zone forms a narrow strip along the country's western border, the Senqu River valley is found in the Lowlands and in the mountain region but at altitudes below 1,800 m. The Senqu River valley, which is an extension of the Lowlands, defines the narrow strip flanking the Senqu River and penetrating deeply into the Highlands, including the lower parts of the river's main tributaries (Lesotho Meteorological Services, 2013).

3.5 Vegetation and biodiversity

Based on the biomes of South Africa, Lesotho and Swaziland, Lesotho is characterised by high-altitude flora and is largely covered by the Grassland Biome of southern Africa (second largest biome in the region), dominated by grasses with few trees that are confined to river valleys

(Pomela et al., 2000; Kopij, 2006; Mucina & Rutherford, 2006). The extensive mountain area of Lesotho above 2200 m a.s.l. is largely treeless (van Zinderen Bakker & Werger, 1974). Mucina and Rutherford (2006) broadly divide the Grassland Biome of southern Africa into four bioregions (the Sub-Escarpment Grassland, Mesic Highveld Grassland, Dry Highveld Grassland and the Drakensberg Grassland). Lesotho is covered entirely by two of these bioregions: the Drakensberg Grassland Bioregion which covers the highlands (higher-altitude areas) of the country and the Mesic Highveld Grassland Bioregion, which occurs in the lower altitude areas of the country (Mucina & Rutherford, 2006). The former bioregion accounts for the greater proportion of Lesotho, although the latter is generally the largest of the four bioregions, being very extensive in South Africa. In South Africa, Lesotho and Swaziland, these two are the highest-lying bioregions in the sub-region, occurring at mean altitudes above 2,000 m and above 1,500 m, respectively (Mucina & Rutherford, 2006). The Drakensberg Grassland Bioregion is rich in endemic species (Du Preez & Brown, 2011). The grassland biome is among the most endangered habitats in southern Africa (Cowling et al. 1997), mainly because of extensive fragmentation attributed to agriculture. Thus, the montane grassland of Lesotho is under serious threat from human-induced pressures, especially economic development, cultivation and livestock grazing and trampling.

Pomela et al. (2000) recognise three major vegetation types that are related to altitude and fall within the two bioregions of the country: Highveld Grassland (from 1,388 to about 1,800 m a.s.l.); Afromontane Grassland (extending from about 1,800 to about 2,500 m a.s.l.) and Afroalpine Grassland (above 2,500 to 3,482 m a.s.l.) (Figure 3.3). While the Highveld grassland corresponds with the Mesic Highveld Grassland Bioregion, the Afromontane Grassland and Afroalpine Grassland correspond with the Drakensberg Grassland Bioregion of Mucina and Rutherford (2006). The Highveld grassland corresponds to the Lowlands of Lesotho and the lowest part of the Senqu River Valley (Kopij, 2006). The Afroalpine Grassland, which is characterised by severe climatic conditions, corresponds to the summit plateau over 2,500 m a.s.l., where rainfall is generally above 1,000 mm per annum. This Afroalpine Grassland is characterised by the dominance of *Festuca*, *Pentaschistis* and *Danthonia* grasses, which are interspersed by woody *Helichrysum* and *Erica* species (Grab, 2010). The Afromontane Grassland consists of the remainder of the Highlands, the upper Senqu valley and the Foothills (Pomela et al., 2000). Within the three vegetation zones (ecosystems) are wetlands that host a wide range of species.

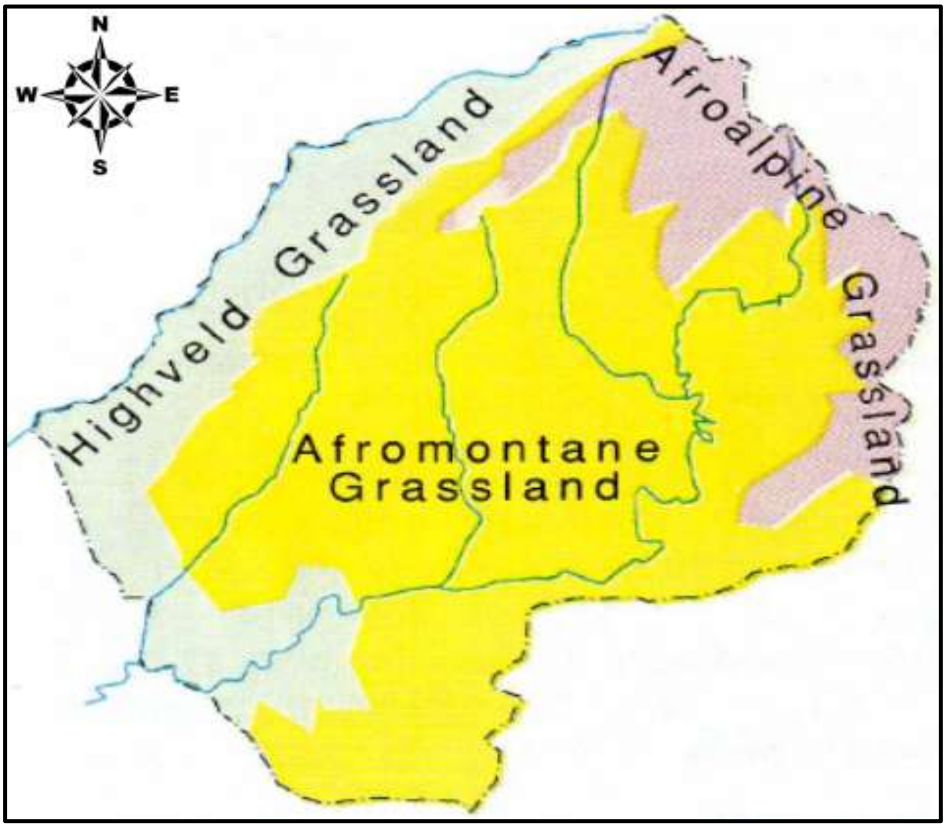


Figure 3.3: Map of Lesotho showing the distribution of the three major vegetation types (Pomela et al., 2000)

For its size, Lesotho has a remarkably high diversity of plants and animals (NES, 2000). The vegetation of the high mountain area of the country is in many ways unique in southern Africa and is of special economic interest (van Zinderen Bakker & Werger, 1974). The remarkable diversity of plant life (about 2,200 species and almost 400 endemics) in the highlands of Lesotho has been ascribed to the steep environmental gradients in the landscape and the harsh climatic conditions (Mucina & Rutherford, 2006). The mountains of Lesotho and the Maloti-Drakensberg area in general are a fragile ecosystem, while at the same time are globally important as a major centre of biodiversity and endemism, and a source of freshwater with unique wetland systems (Mokuku et al., 2004; Sieben et al., 2010a).

Various studies, which document the biodiversity of the Maloti-Drakensberg mountains, report varying levels of endemism that can be estimated at an average of 30% in the hotspot area (Pomela et al., 2000; Carbutt & Edwards, 2006; Kopij, 2006). The level of endemism in the Maloti-Drakensberg is ranked the third among the eight biodiversity hotspots in southern Africa (Pomela et al., 2000). This high level of endemism has been attributed to the unique habitats created by the high-altitude conditions found in the area (Carbutt & Edwards, 2006; Mucina & Rutherford, 2006). Because of its unique flora, the Maloti-Drakensberg has been widely recognised as a plant diversity centre of global importance. It is noteworthy that, given that the hotspot covers Lesotho and part of South Africa, most of the species in the mountains of the former also occur in the neighbouring mountains of the latter, especially on the edge of the escarpment.

While the extreme winds on the summit of the Maloti Mountains and on the face of the escarpment are responsible for the cushion forming dwarf shrubs that characterise the summit vegetation, larger woody plants are restricted to the sheltered places at lower altitudes (Mucina & Rutherford, 2006). Pomela et al. (2000) further divide the vegetation types and provide a finer and more detailed description of the vegetation. The *Themeda* Grassland zone (Seboku Grassland), locally known as "sweet veld" and dominated by *Themeda triandra*, occupies about 56% of the Highlands (including Senqu River Valley) and mainly occurs below 2700 m a.s.l., especially on the north-facing slopes (Pomela et al., 2000). The *Festuca-Merxmuewellera* Grassland zone (Letsiri Grassland), which is locally known as "sourveld", is dominated by *Festuca caprina* and occupies about 31% of the Highlands. Lastly, the Sehalahala Scrub, dominated by *Chrysocoma ciliata* and occurring mostly in degraded areas, occupies about 13% of the highlands (Pomela et al., 2000). The extent of Sehalahala Scrub has been observed to be on the increase because of overgrazing in the country.

Different species characterise and dominate different habitats in the country. Differences exist between slopes facing north and those facing south as a result of distinctive solar radiation patterns. The resultant ecological differences, including duration of snow cover and conditions of moisture between the warmer and drier north-facing slopes and the colder and moister south-facing slopes, contribute to the observed distribution of vegetation types (Nüsser, 2002). Thus, while *Themeda triandra* dominates at lower elevations and on slopes facing north in the Afromontane Grassland, *Festuca caprina* is dominant at higher altitudes and on south-facing slopes (Mucina & Rutherford, 2006). *Chrysocoma ciliata*, an invader of overgrazed and disturbed areas, especially on the warmer slopes, has been predicted to cover 90% of the country by 2050 (Pomela et al., 2000). Notwithstanding that *Kniphofia caulescens* has a wide distribution, it is more abundant in the upper half of the altitudinal range (2,500 to 2,900 m a.s.l.) (Mucina & Rutherford, 2006). Although limited in extent, shrublands, dominated by *Leucosidea sericea* (*cheche*) and *Rhus* species (*kolitšana*) alternate with patches of grassland in lower to medium basalt slopes in the southwestern parts of the country (Mucina & Rutherford, 2006). Except in the Afroalpine Grassland (at higher altitudes), small patches of indigenous forest also occur in a number of deep valleys, although its extent is limited. Of the

Lesotho endemic plants, the spiral aloe (*Aloe polyphylla*, *Kharatsa*) is the most spectacular and best known endemic of the country.

Lesotho animals consist of birds, mammals, herpetofauna (amphibians and reptiles), fish and invertebrates (Department of Environment, 2017). Herpetofauna (reptiles and amphibians) exhibits the highest endemism of all vertebrate groups, with a total of nine species being endemic to the Maloti Mountains (MDTP, 2007). *Otomys sloggetti* (ice rat), *Rhabdomys pumilio* (striped mouse) and *Eptesicus capensis* (cape serotine bat) remain the only abundant species out of the 82 mammal species recorded in Lesotho (Pomela et al., 2000). The limited number of mammals available suggests that mammals are the most threatened animals in the country (Department of Environment, 2017). Lesotho has a number of endemic mammal species, including *Otomys sloggetti* and *Mystromys albicaudatus* (white-tailed mouse) (Pomela et al., 2000; MDTP, 2007). However, monitoring reports in the Mohale and Katse dam catchments document significant declines in the number of groups and group sizes of species of carnivores, antelopes, hare/rock rabbits and small mammals (Turpie et al., 2014a; b).

Thirteen of the 340 recorded bird species occurring in Lesotho are Red Data listed (Department of Environment, 2014). The mountain region harbours a remarkably high proportion of endemic and near-endemic bird species (Turpie et al., 2014a; b). Examples of the endemic grassland bird species recorded include *Chaetops aurantius* (Drakensberg Rock-jumper), *Gypaetus barbartus* (Bearded vulture), *Gyps coprotheres* (Cape vulture), *Geronicus calvus* (Southern bald ibis), *Anthus chloris* (Yellow-breasted pipit) and *Anthus hoeschi* (Mountain pipit) (Turpie et al., 2014a; b). The Bearded vulture, whose numbers have been declining, is now only found in the Maloti Drakensberg Transfrontier Conservation Area and is highly threatened by hunting (MDTP, 2007).

3.6 Palustrine wetlands, rivers and dams

Lesotho supports a network of unique high-altitude palustrine wetlands, which are home to high biodiversity (Backéus & Grab, 1995; Department of Environment, 2017). The wetlands, locally known as *Mokhoabo* (singular, in Sesotho Language), are a common feature in Lesotho, especially in the mountains. The wetlands form conspicuous greener patches across the country's landscape due to their vegetation that is distinct from the surrounding grassland habitats. The major types of wetlands in the country are marshes (also called vleis or valley bottom wetlands) and mires (bogs and sponges) (Schwabe, 1995; Grundling et al., 2015; Department of Environment, 2017). Most of the high-altitude palustrine wetlands of Lesotho are seepages situated in the riverheads of river systems (van Zinderen Bakker & Werger, 1974). Mucina and Rutherford (2006) classify the Grassland Biome freshwater wetlands of the Maloti-Drakensberg, the entire Lesotho and the surrounding areas into Eastern Temperate Freshwater wetlands (AZf 3), Drakensberg wetlands (AZf 4) and Lesotho mires (AZf 5), which occur at altitudes 750-2,000, 1,800-2,500 and 2,500-3,400 m a.s.l., respectively.

The abundance of rainfall and the steep gradients in climate and geomorphological setting across the altitudinal and latitudinal gradients have led to a diverse array of wetland habitats in Lesotho and the Maloti-Drakensberg area (Sieben et al., 2010a). While both peat-forming mires and non-peat wetlands are found in the lower parts of the mountains, the wetlands at higher altitudes are largely peat-forming and form distinct ecosystems not found anywhere else in Africa (Backéus & Grab, 1995). Mucina and Rutherford (2006) observe that these high-altitude wetlands are influenced by both rain water and water seeping through the soil. The same authors also observe that the seepage water is eutrophic as the underlying basaltic parent material is rich in phosphorus, potassium, and calcium and has a pH of around 8. This makes the wetlands unique in southern Africa. A very common geomorphological and hydrological feature of these high-altitude wetlands is the formation of thufurs or hummocks (van Zinderen Bakker & Werger, 1974; Mucina & Rutherford, 2006).

Figure 3.4 presents the wetland map of Lesotho. While the map suggests a total absence of wetlands in the lower parts of the Lowlands, wetlands are known to occur in all the four agro-ecological zones in the country. Nonetheless, the greatest density of wetlands occur in the mountains, above 2,000 m a.s.l., mainly owing to the impermeable basalt rock characterising these mountains (Hughes & Hughes, 1992). In these mountains, the wetlands are particularly found at valley heads (Backéus & Grab, 1995). It can be observed on the map (Figure 3.4) that the highest frequency and density of the wetlands is associated with the central and north-eastern parts of the country. While more than half of the wetlands occur in the Afroalpine Grassland, the other two ecosystem types contribute almost equally to the remaining proportion (Pomela et al., 2000). However, the frequency and extent of wetlands decline towards the south and west along the interior mountain ridges, as the rainfall decreases and the altitude in general becomes lower (Guillarmod, 1962; Hughes & Hughes, 1992). In general, peat-forming mires occur more commonly above 2,750 m a.s.l. (in the alpine belt), while marshes and floodplains are more often found below this level (Hughes & Hughes, 1992; Schwabe, 1995; Grab, 2010; Grundling et al., 2015).

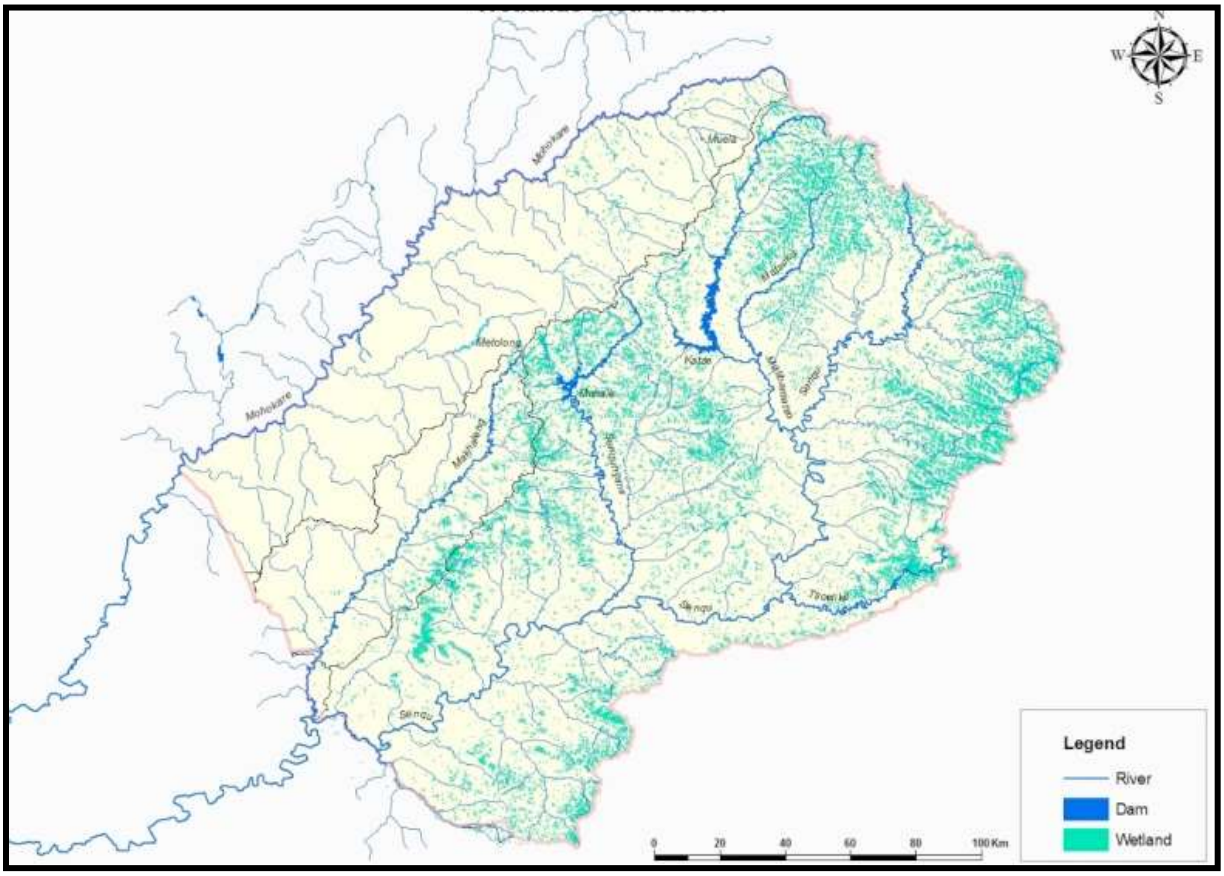


Figure 3.4: Distribution of wetlands in Lesotho (Department of Environment, 2014)

Various authors have acknowledged that the high-altitude peat forming wetlands of Lesotho are unique ecosystems that are not found elsewhere in the world and their flora and vegetation are distinctive (van Zinderen Bakker & Werger, 1974; Backéus & Grab, 1995; Sieben et al., 2010a). Although mainly concentrated in the highlands, the wetlands are known to occur throughout the country and are estimated to account for about 2.72% of the total land surface area of the country (Department of Environment, 2014). According to Mucina and Rutherford (2006), these mountain wetland ecosystems form an archipelago of patches that are isolated within the grassland biome. Individual montane wetlands are often small in size yet collectively, they cover many thousand hectares (Hughes & Hughes, 1992). The sources of most rivers and streams in Lesotho are associated with the high density of wetlands (Figure 3.4). However, while few wetlands in the country are still in their near-pristine condition, many of them are either showing severe levels of degradation or have been lost.

The mountains of Lesotho, with their unique wetland systems, are important as a major source of freshwater (Mokuku et al., 2004). The high-altitude montane catchments of the country form the greater part of the southern Africa's largest watershed, well-known for its large storage of water from their wetlands, vast rangelands that are rich and unique biodiversity (Mapeshoane, 2013). Lesotho's mires, marshes and sponges are the watershed of southern Africa that give rise to rivers flowing to two oceans, the Atlantic and Indian. Given that Lesotho catchments receive some of the highest yearly precipitation amounts in southern Africa, the country is a critically important hydrological reservoir and watershed for the downstream countries (Makhoalibe, 1999; Nüsser & Grab, 2002; Grundling et al., 2015). In fact, more than 43% of the total mean annual rainfall of southern Africa occurs within the borders of Lesotho (Grobbelaar & Stegmann, 1987).

These wetlands play an important role in maintaining the perennial water flow and regulating the quality of water in the rivers that flow to the Atlantic Ocean (Pooley, 2003). The wetlands also form the headwaters of the five major rivers of economic importance in the country, namely, the Senqu-Orange, Maliba-matšo, Mohokare (Caledon), Senqunyane and Makhaleng (Figure 3.5), which also feed the dams of the Lesotho Highlands Water Project (LHWP) (Department of Environment, 2014). However, the mountain area and the entire country is drained mainly through the Senqu-Orange River and its tributaries (Backéus & Grab, 1995). The Senqu-Orange River is the most important and developed shared river system in southern Africa. Lesotho entirely falls within the catchment of this river, with three sub-catchments, namely, the Senqu in the eastern part of the country (24,500 km^2), the Makhaleng in the centre of the country (3,000 km^2) and the Mohokare, which forms the western border with South Africa (6,850 km^2) (Ministry of Energy Meteorology and Water Affairs, 2016). The headwaters of the Senqu-Orange River and its tributaries drain southwards and, together with a vast network of montane wetlands, form a critical component of the water resources in southern African (Lesotho Meteorological Services, 2013). The LHWP dams include the Katse, Mohale, Muela and the one under construction (Polihali), and these underpin both the generation of hydroelectricity for Lesotho and the transfer of fresh water to the most densely populated area of South Africa's Gauteng Province. Dams that supply the local population with water, such as Metolong, also depend on the rivers and, in turn, on the wetlands. Directly and indirectly, wetland systems in Lesotho are estimated to contribute about 30% of the total employment in the country and about 22% of its GDP (Department of Environment, 2014).

3.7 Land use and conservation of wetlands and biodiversity

Lesotho is one of the least developed countries in the world that has high poverty levels and the majority of its people depend heavily on natural resources and subsistence agriculture for livelihoods. The country is mainly an agricultural economy, dominated by crop and livestock production, which provides the primary livelihoods for more than 80% of the population

(Government of Lesotho, 2014). Hence, land use in the country is mainly for agriculture and this has profoundly modified much of the three grassland types in the country. The livestock industry has long been an essential part of the social and economic structure in Lesotho (Government of Lesotho, 2014). Livestock production is largely supported by communal rangelands in the grassland. Wetlands in these rangelands are also considered a critical grazing resource for livestock, particularly in summer when thousands of sheep, goats, cattle and horses are observed grazing on these fragile ecosystems (Du Preez & Brown, 2011). In fact, much of the livestock grazing in the montane areas of Lesotho occurs in wetlands because they support the most palatable vegetation (Grab & Deschamps, 2004).

The mountain region, which accounts for more than 60% of the country's surface area, harbours only about 19% of the country's human population (Bureau of Statistics, 2009). However, the Basotho, who mostly inhabit the lowlands and traditionally took their herds of livestock to the mountain areas in summer and returned them to the lowlands in winter (Meakins & Duckett, 1993), now sometimes keep their livestock in the mountain areas throughout the year. This change could be attributed to climate change as it makes larger areas inhabitable. Thus, these mountains, are now heavily used for livestock grazing (Olaleye, 2016) and overstocking rates of between 50 and 300% are reported in the rangelands of the country (Marake et al., 1998). Overgrazing and trampling by livestock have been implicated in the degradation and loss of many wetlands in the mountain region (Backéus, 1989; Backéus & Grab, 1995). In fact, the widespread degradation and loss of wetlands in the country has been reported quite extensively, starting more than five decades ago (Guillarmod, 1962, 1963; van Zinderen Bakker & Werger, 1974; Backéus, 1989; Backéus & Grab, 1995; Olaleye, 2016). Many wetlands have been lost in the country and the majority of those remaining have numerous signs of degradation (Meakins & Duckett, 1993; Turpie et al., 2014a, b). Because of intense cultivation and human pressure, very few wetlands remain in the lowlands of the country (Backéus & Grab, 1995).

The Basotho way of life is based on the principle and understanding that all resources provided by nature are strictly communal and open-access (Mokuku et al., 2004). No land is privately owned in the country; land ownership is vested in paramount chiefs who grant the right to cultivate to individuals or groups, but all citizens can graze their livestock on all lands (Olaleye & Sekaleli, 2011). The resultant effect is over-utilisation of the land and most wetlands are over-grazed or over-utilised for cropping, leading to the loss of wetland biodiversity. Profound modifications have been witnessed in the three vegetation zones because of the present land use, especially developmental activities, cultivation and livestock grazing.

Because of the high density of people and livestock, the lowlands have been entirely transformed by human activity and settlement. Approximately, half of this zone has been cultivated and is now characterised by severe gully erosion because of poor agricultural practices (Pomela et al., 2000). Schmitz and Rooyani (1987) estimate that about 0.5% of the country's total land surface area has been damaged by erosion to levels beyond restoration. Covering more than half the country's surface area, the Afromontane Grassland is also characterised by settlements up to 2,500 m a.s.l. and heavy livestock grazing. The highest permanently inhabited place in the country is Letšeng-la-Terae, at 3,000 m a.s.l. where the mean temperature is frequently below freezing in June and July, with night temperatures commonly dropping below -10 ℃ (Pomela et al., 2000).

Several developmental activities carried out in the country also impact negatively on the wetlands, and these include diamond mining and damming, as well as the associated infrastructure development. These activities play a key role in the country's economy, even though this may come at the expense of the ecological systems that underpin the success of such activities, including maintaining the water levels in dams. The country benefits through the sale of water to South Africa, domestic water supply, hydroelectricity generation and development of the remote areas in the highlands of the country. Many areas that were historically terrestrial in the country are now dammed, making them aquatic. Carbutt and Edwards (2006) project that, upon completion of all the LHWP phases, a significant proportion of the country's total surface area will be inundated with water.

These activities have also involved construction of roads through mountain passes at altitudes above 3,000 m a.s.l. and this further threatens the unique montane ecosystems in the country, including wetlands (Meakins & Duckett, 1993). Furthermore, because roads have been constructed by mining companies and the LHWP, some areas in the highlands that were historically inaccessible are now accessible by road and some of these roads cut across wetlands. Subsequently, human population density has increased in these mountains that were historically characterised by low densities. While many areas in the mountains were historically inaccessible and thus considered "protected" by being remote, the development and the concomitant increased accessibility and increase in human population density have dramatically increased the threats to the ecosystems, including wetlands, in these once remote parts of the country. Afforestation and harvesting of native plants for subsistence and commercial purposes are also important forms of land use that can significantly affect wetlands and other ecosystems that exist in the country (Carbutt & Edwards, 2006).

The effect of land use on wetlands is compounded by the effect of the endemic ice rat (*Otomys sloggetti)* and by the occurrence of fire. The ice rat burrows and makes underground tunnels in non-waterlogged parts of the wetlands and drying of these ecosystems or parts thereof promotes ice rat invasion. The area above the underground tunnels can easily collapse and develop into gullies when water flows through them. The occurrence of fires in the Grassland Biome is natural and important for maintaining biodiversity. Nonetheless, Lesotho's rangelands are intentionally burnt annually in an attempt to enhance the grazing potential of the pasture. This deliberate burning increases fire frequency and changes the natural fire regime to the detriment of biodiversity. The wild fires are very frequent in the rangelands of the country during the dry season (May–September), especially in the highlands (Department of Environment, 2014).

Characterised by a severely eroded landscape (Grab & Deschamps, 2004), Lesotho has gullies as a common feature, which highlights the severity of soil erosion in the country. These erosion gullies have also been observed in some of the wetlands in the country (Turpie et al., 2014a, b). The country's high susceptibility to soil erosion, coupled with overgrazing, has contributed to the degradation of the wetlands (MDTP, 2007). The high level of soil erosion has been ascribed to factors that include steep slopes, a harsh climate, limited ground cover, thin regolith cover and intensive agriculture (Grab & Deschamps, 2004; MDTP, 2007). The problem of wetland degradation in the country is caused by the widespread grazing on these ecosystems and the current and most recent drought conditions are exacerbating the problem through increased desiccation (MDTP, 2007).

CHAPTER 4: ECOLOGY OF PALUSTRINE WETLANDS IN LESOTHO: VEGETATION CLASSIFICATION, DESCRIPTION AND ENVIRONMENTAL FACTORS

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Abstract

The description and classification of wetland vegetation is important for water resource management and biodiversity conservation as it provides an understanding of the wetland vegetation-environment relationships and information to interpret spatial variation in plant communities. This study discusses the vegetation of the palustrine wetlands of Lesotho based on a phytosociological approach. Data on vegetation and various environmental variables were collected using the Braun-Blanquet method and a standardized protocol developed for environmental information of wetlands in South Africa, respectively. The data were analysed mainly by clustering and ordination techniques. Twenty-two communities were found by the classification of the wetland vegetation. These communities were diverse in terms of species richness. The ordination revealed that the wetland vegetation is mainly influenced by altitude, longitude, slope, soil parent material, landscape, inundation, potassium content, soil texture, total organic carbon, nitrogen, electrical conductivity and latitude. Regarding species composition and diversity, plant communities in the Highlands were more diverse and were distinctively different from those in the Lowlands. High-altitude communities were also dominated mainly by C_3 plants, while those at low altitudes exhibited the dominance of C_4 species. Some communities were either restricted to the Highlands or Lowlands but others exhibited a wide ecological amplitude and occurred over an extensive altitudinal range. The diversity of most of the wetlands, coupled with their restricted habitat and distribution at high altitudes and their role in supplying ecosystem services that include water resources, highlights the high conservation value associated with these wetlands, particularly in the face of climate change and loss of biodiversity.

Conservation implications: The study can be invaluable to wetland scientists, managers, biodiversity conservationists, water resource managers and planners and vegetation ecologists in southern Africa. About 70% of Lesotho falls in the Maloti-Drakensberg, accounting for about 60% of the region and this makes the study important in biodiversity conservation planning, particularly in the Highlands. The wetlands in Lesotho face severe anthropogenic pressures that include overgrazing and economic development. Given that the Lesotho highlands as a water catchment is not only important for Lesotho, but also for South Africa and Namibia, the conservation of the associated wetlands and this critical water resource is indispensable.

Keywords: Anthropogenic; Biodiversity Conservation; Canonical Ordination; Climate Change; Maloti-Drakensberg; Plant Community; Plant photosynthetic pathway; Palustrine Wetlands; Phytosociology; Vegetation Classification.

4.1 Introduction

Palustrine wetlands, which cover about 6% of the earth's land surface, are among the most ecologically sensitive ecosystems and very important globally because of their unique role in biogeochemical cycles (Junk et al., 2013; Mitsch & Gosselink, 2015). Because they support azonal vegetation that is distinct from the surrounding vegetation (Mucina & Rutherford, 2006; Sieben et al., 2016c), wetlands are ecological 'islands' within terrestrial environments in different landscapes across the globe. The distinction results from the prolonged waterlogging that causes oxygen deficiency (hypoxia) or its total absence (anoxia) in the wetland soil, with subsequent chemical changes in soil characteristics (Gopal, 2015; Mitsch & Gosselink, 2015). The presence of water, whether seasonal or permanent, is the primary factor in creating wetland habitats and associated vegetation (Mucina & Rutherford, 2006). Nonetheless, it is not wetness per se that primarily influences the geochemistry and morphology of wetland soils but rather, the anaerobic conditions that result from the prolonged soil saturation or flooding (Kotze et al., 1996; Collins, 2005).

Montane palustrine wetlands are a special sub-division of freshwater palustrine wetlands that are embedded within terrestrial ecosystems in mountain areas (Mucina & Rutherford, 2006). These wetlands are often rich in endemics because many species remain isolated in high-altitude habitats (Junk et al., 2013). By providing a wide spectrum of ecosystem services, these ecosystems are of high ecological and socio-economic importance (Chatterjee et al., 2010). High-altitude wetlands provide essential ecosystem services which help to sustain human life, conserve biodiversity, preserve the hydrological regime and combat the impacts of climate change and are thereby key to water, food and ecological security (Singha, 2011). Montane wetlands are located in the headwaters of major river basins, providing water for many transboundary rivers and play an important role in the ecology and hydrology of the local environment and downstream systems. They also play a fundamental role in the overall global and regional water cycles (Russi et al., 2013; Sieben et al., 2014a).

The montane wetlands of Lesotho are important for the supply of ecosystem services, including biodiversity conservation, water resources, livestock grazing, harvestable plant products and environmental regulation. Lesotho forms an important hydrological reservoir and watershed for several countries in southern Africa (Nüsser & Grab, 2002). For example, the montane wetlands in the country form part of the headwaters of one of the most important international watercourses in southern Africa, the Senqu-Orange River (ORASECOM, 2015), which is not only important for Lesotho, but also for South Africa and Namibia. Lesotho entirely falls within the catchment of this river system (ORASECOM, 2015) and the country is drained by the river and its tributaries. Moreover, the high-altitude wetlands of Lesotho are critical in maintaining the water levels not only in dams supporting the Lesotho Highlands Water Project (LHWP) that transfers water to South Africa (Grab & Deschamps, 2004), but also in those supplying the local population. Directly and indirectly, wetlands in Lesotho are estimated to contribute about 22% of the country's gross domestic product (GDP) and 30% of the total employment in the country (Department of Environment, 2014). Furthermore, by providing fresh water that is transferred to the most densely populated and industrialised area of Gauteng, the wetlands in Lesotho also play a key role to the South African economy.

The most ubiquitous and conspicuous feature of the wetland environment, which also plays a critical role in wetland ecosystem functioning, is the vegetation (Cronk & Fennessy, 2001; Gopal, 2016). As a result, the description of wetland habitats based on vegetation and the associated classifications is useful in strategic planning for the conservation of wetlands (Mitsch & Gosselink, 2015). Plants are such a critical component of wetlands that they are the most widely supported biotic indicator for assessing wetland condition (Collins, 2005). Hence, vegetation is the most suitable feature to consider over a broad range of wetland habitats (Sieben et al., 2014a). Within a single wetland, a large diversity of habitats may occur and as a result, large differences in the types of vegetation may be observed in the same wetland (Mitsch & Gosselink, 2000). Therefore, wetland habitats can be classified based on the plant communities in the system (Collins, 2005; Sieben et al., 2010a).

Plant species occurring in a wetland can be used as indicators of environmental conditions and ecological changes taking place in the system (Mitsch & Gosselink, 2015) because wetland vegetation is azonal, responding quickly to local environmental changes (Cronk & Fennessy, 2001; Brand et al., 2013). Because the plant community gives a characterisation of habitat units within a wetland and also serves as habitat for associated animals, a detailed wetland vegetation description for a given wetland can be used as a proxy for the system's biodiversity in general, highlighting the conservation value of the wetland (Sieben et al., 2016c). Thus, the determination of wetland plants that are useful as biological indicators has become increasingly important for use in monitoring the integrity of specific wetlands (Sieben et al., 2014a). Wetland typology provides useful information for water resource management and biodiversity conservation (Sieben et al., 2014a).

Given the importance of wetlands, recent studies (Sieben et al., 2016c; Moor et al., 2017) have emphasised the need for more information about their species composition, ecology and distribution. Although many studies have been carried out in the wetlands of surrounding South Africa (e.g. Brand et al., 2013; Sieben et al., 2014a, 2016), no recent detailed countrywide survey has been conducted on the wetland vegetation of Lesotho. The current study is the first to provide a characterisation of the wetland vegetation in detail, covering many wetlands in the country.

The aims of this study for the palustrine wetlands of Lesotho are to:

1. produce a phytosociological classification and name the wetland plant communities.
2. map the distribution of the vegetation of the palustrine wetlands using the phytosociological method.
3. explore and describe the wetland vegetation-environment relationships.

4.2. Materials and Methods

4.2.1 Study design

The vegetation of the palustrine wetlands of Lesotho was characterised using a phytosociological approach. The selection of wetlands for sampling was performed in such a way that as much wetland variation as possible in the country was captured with the available time and resources. An attempt was also made to include wetlands in protected areas such as national parks and nature reserves. Fieldwork was carried out during the wet (summer) season, which commenced in February 2017 and ended in March 2018. The study focused on accessible wetlands. In general, the method followed Sieben et al. (2014a) to make the results compatible with the South African National Wetland Vegetation Database. Although many wetlands are showing signs of degradation, where wetland density was high and the systems showed little observable variation, large and/ or near pristine wetlands were selected for the assessment. Depending on the location, each wetland was classified as pristine, rural or urban (Table 4.1). A 3 m × 3 m representative sample plot (quadrat) was then located randomly in each visually distinct and homogenous vegetation type of each selected wetland where different attributes of the vegetation and environment were measured and recorded. This plot size has been recommended for grassy wetlands in southern Africa (Brown et al., 2013; Sieben et al., 2014a). The same plot size has also been recommended for overgrazed grasslands (Brown et al., 2013), a situation that is common in some parts of Lesotho where wetland disturbance by livestock grazing and trampling is widespread. The number of plots per wetland was dependent on the number of observable distinct and homogenous vegetation units within the wetland.

Table 4.1: Environmental variables that were measured or assessed and included in the analysis of the vegetation of the palustrine wetlands of Lesotho

Variable	Type of variable	Method of measurement or assessment	Units	Abbreviations or categories used in the ordination diagram
HGM type	Categorical	Level 4 of the South African Wetland classification system[1]	NA	Depression, VB, CVB, H, HW; Floodplain
Landscape	Index	Assessed in the field; increasing urbanisation: 1– pristine, 2 – rural, 3 – urban	NA	Urban
Wetness	Index	Assessment of soil hydromorphic features[2]; Index: 1–temporary, 2– seasonal, 3 – semi-permanent, 4 – permanent	NA	Wetness
Inundation depth or water table depth[a]	Ratio	Assessed in the field on standing water or water table depth	cm	Inundation
Parent material[b]	Categorical	Assessment based on a geological map[3]	NA	Basalt
Slope	Ratio	GPS	Degrees	Slope
Aspect[c]	Ratio	GPS	Degrees	Northness
Altitude	Ratio	GPS	Metres	Altitude
GPS coordinates	Ratio	GPS	Degrees	Longitude[d], latitude
Soil depth	Ratio	Soil augering	cm	Soil depth
Presence or absence of peat	Categorical	Checking for the presence of peat	NA	Peat
Total organic carbon†	Ratio	Walkley Black method	%mass	TOrg_C
Soil phosphorus†	Ratio	Bray 11 method	mg/kg	P
Soil nitrogen†	Ratio	Dumas method on the Leco Trumac CNS Analyzer	mg/kg	Nitrogen
Soil sulphur†	Ratio	Dumas method on the Leco Trumac CNS Analyzer	mg/kg	Sulphur
Major cations†	Ratio	Ammonium acetate extraction; measurement on plasma atomic absorption spectrometer	mg/kg	Ca, K, Mg, Na
Soil pH†	Ordinal	Water extraction	NA	pH
Exchangeable acidity†	Ratio	Titration method	mmol/100g	Exch_acidity
Electrical conductivity (EC)†	Ratio	Water extraction of soil; EC measured on filtrate using conductivity meter	uS/cm	Elec_cond
Soil texture†	Ratio	Gravimetric pipetting method	%mass	%Clay, %Silt, %Sand

Sources: [1]Ollis et al. (2013); [2]Kotze et al. (1996); [3]Leketa et al. (2018)

GPS – Geographic Positioning System (Garmin *eTrex* 30×); VB – unchannelled valleybottom; CVB – channelled valleybottom; H – hillslope seepage not feeding a watercourse; HW – hillslope seepage feeding a watercourse

†Variables were measured only on the plots where soil samples were collected.

[a]Inundation represents both inundation (positive) and water table depth (negative)

[b]The parent material in Lesotho is mainly basalt or sandstone.

[c]Aspect was assessed as northness during the analysis, with values ranging from 0^{o} to 180^{o}. For increasing northness, values in both the east and west of the compass were considered to increase towards the north, from 180^{o} to the 0^{o} point.

[d]Longitude is a proxy for the dry-to-wet gradient because rainfall generally increases from west to east in Lesotho.

4.2.2 Assessment of vegetation and environmental variables

In each plot, the Braun-Blanquet method, a protocol often used for collecting vegetation data in South Africa (Brown et al., 2013; Sieben et al., 2014a), was used for vegetation assessment. Because this method has been applied in South Africa for several decades, it is possible to make comparisons between current and historical data (Brown et al., 2013), which allows for effective plant community comparisons. The method involves assessing wetland vegetation in a stratified manner where plots are placed randomly in each distinct plant community and the species composition is recorded by determining the species present, as well as estimating the cover for each species using a cover-abundance scale. Placing vegetation plots in a stratified manner ensures that as much variation as possible in the wetland is captured, including the different categories of indicators species – obligate wetland (OBL), facultative wetland (FACW), facultative (FAC), facultative upland (FACU) and obligate upland (UPL) (Mitsch & Gosselink, 2015). Vegetation structure was described by making estimations of the proportion of the plot covered by vegetation and visually estimating the average height of the vegetation. In case of inundation, the average vegetation height was estimated from the soil surface (Sieben et al., 2014a). During the survey, the plant species were identified with the help of botanical field guides (Pooley, 2003; Van Oudtshoorn, 2014) and those that could not be identified in the field were collected and later taken to the Roma Herbarium (ROML) at the National University of Lesotho for identification.

For each plot, in addition to the vegetation attributes, a standardised protocol developed for environmental information of wetlands in South Africa was also used to systematically measure or assess a number of environmental variables that have been recommended for wetlands (Sieben et al., 2014a). In at least one plot per wetland, a soil sample was collected from the top 15 cm of the soil (vegetation rooting zone) using a soil auger. Both vegetation and environmental data were recorded in a wetland vegetation survey field dataform (Appendix 4.1). Because of the limited funding for the study, soil sampling was limited to one plot per wetland. The plot chosen for soil sampling would be the one representing the most widespread distinct community in the wetland. The samples were packaged in air-tight (zipped) plastic bags for further analysis as recommended by Stohlgren et al. (1998). The soil samples were air-dried for at least 48 h and later analysed for different variables (Table 4.1). The soil analyses were performed by the Analytical Laboratory Services of the Institute for Commercial Forestry Research in Pietermaritzburg, South Africa. The environmental and soil variables included in the study, as well as the methods used for their measurement or assessment, are briefly described (Table 4.1). While most variables were measured or assessed on site in all vegetation plots, additional soil variables (indicated with an asterisk in Table 4.1) were measured in the laboratory and only on those plots where soil samples were collected. After describing the plots in each wetland, as much of the wetland would be surveyed to record species occurring within the wetland system but were not encountered in the plots. This was in an attempt to ensure a species list that is as complete as possible for the wetland system, for additional floristic analysis.

4.2.3 Data Analysis

Both vegetation and environmental data were captured in Microsoft Excel spreadsheets from which they were imported into PC-Ord (Mjm Software Design, Gleneden Beach, OR, USA) and CANOCO (Microcomputer Power, Ithaca, NY, USA) programs for analysis. Prior to importing into these programmes for analysis, the Braun-Blanquet vegetation cover values were converted into percentage cover (Mueller-Dombois & Ellenberg, 1974; van der Maarel, 1979; Omar et al., 2016). ArcGIS, Version 10.2, was used to map the distribution range of the wetland vegetation plots in the study area and to determine the distribution range of the wetland plant communities in Lesotho.

Based on the recommendations by Brown et al. (2013), species richness, diversity and evenness were determined. For each plot, these were determined by calculating Shannon-Weiner index (H') and evenness index (E), as well as listing the species. The fraction of the plot that was occupied by species *i* was referred to as p_i, and this value is an indication of the relative abundance of species *i*. The p_i was used to calculate the *H’* and *E*, which are surrogates of species diversity, by the following formulae (Ludwig & Reynolds, 1988):

1. $H' = -\sum pi \ln pi$ where p_i is the proportion of species *i* and *ln* is the natural logarithm.

2. $E = \dfrac{H'}{\ln S}$ where *s* is the species richness (number of species).

To elucidate the ecological patterns in the vegetation of the palustrine wetlands of Lesotho, a number of multivariate statistical techniques were employed. For these multivariate ecological community data analyses, three main types of analyses were employed: (1) hierarchical cluster analysis (HCA), (2) indicator species analysis (ISA) and, (3) canonical correspondence analysis (CCA). These were performed mainly following Sieben et al. (2014a).

4.2.3.1 Classification and Indicator Species Analysis

Cluster analysis was used to classify sites with respect to similarity or dissimilarity (van Tongeren, 1995). Classification makes use of similarity between vegetation plots such that plots that are more similar in species composition are grouped together. Classification facilitates the description and ecological interpretation of plant communities from a large amount of vegetation data. Classification and description of vegetation do not only provide an understanding of the vegetation-environment relationships, but also provide information to interpret the spatial variation between plant communities (Clegg & O'Connor, 2012). Thus, to obtain vegetation typology of the palustrine wetlands of Lesotho, agglomerative HCA was performed on vegetation data to identify homogenous plant communities in the wetlands. This would enable vegetation plots that are similar in species composition to be grouped together, with emphasis on the relationships between them (van Tongeren, 1995; McCune & Mefford, 2011).

The classification was performed by grouping vegetation plots based on species composition and abundance data. PC-Ord, Version 6.0, was used for the classification (McCune & Mefford, 2011). Non-transformed percentage plant cover data were used for the clustering. The best interpretable classification was produced by the combination of the Sørenson's (Bray-Curtis) similarity index and Ward's linkage method. The Bray-Curtis similarity index does not only have an advantage of including species abundances in the analysis, but its scale is also easy to understand and interpret as 0% means the samples are very different and 100% implies that the samples are exactly the same. The Ward's method has an advantage of producing clearly defined clusters (Pla et al., 2012). The plant communities obtained were named following the guidelines by Brown et al. (2013). However, in cases where there was no clear dominant, the name was derived from the description (structure and distribution) of the community.

Indicator Species Analysis (ISA) was used as an objective criterion for determining the optimal number of clusters in the final dendrogram. This was achieved by repeating the clustering algorithm while varying the number of clusters (Dufrêne & Legendre, 1997) and the number that gave the lowest average p-value of the indicator species was used in the final dendrogram (Peck, 2010). The ISA was also used in characterising different wetland plant communities obtained from the final clusters. Indicator species with indicator values (IVs) greater than 20 and significant ($p \leq 0.05$) in the Monte Carlo permutation test were considered good indicators (Sieben et al., 2016c) and were thus listed for each cluster. The indicator value of a given species is the product of specificity (calculated from the relative abundance) and fidelity (relative frequency) of that species, expressed as a percentage. This means that the maximum possible indicator value for a species would be 100 (Dufrêne & Legendre, 1997). The ISA is often used to test the fidelity (faithfulness) of a species to a given community. Monte Carlo permutation test (also available in PC-Ord) was also used to test for the statistical significance of the fidelity of the indicator species to the communities (Dufrêne & Legendre, 1997). The ISA was also conducted in PC-Ord. For each community obtained from the classification, the median and range for species richness, diversity index and evenness, and means for vegetation height and cover were determined.

4.2.3.2 Ordination

Another important feature of the analysis was the relationship between wetland plant communities and explanatory variables. Thus, to examine the influence of environmental variables and gradients on wetland vegetation, the vegetation and environmental variable data, as well as the plant communities obtained from the classification were subjected to canonical ordination (Ter Braak & Šmilauer, 1998). This was performed twice: (1) constrained CCA on all vegetation plots using species abundance data and environmental variables and (2) constrained CCA only on those vegetation plots where soil samples had been taken, using species abundance data and more detailed explanatory data. Log-transformed percentage plant cover data were used for the ordination. The choice for CCA for the ordination was based on the fact that the response (species abundance) data were compositional and had a unimodal response curve (Lepš & Šmilauer, 2003). The canonical ordination was performed using CANOCO, Version 5.11 (Ter Braak & Šmilauer, 1998). The statistical significance of the constrained ordination (relationship of communities with environmental variables) was tested using the unrestricted Monte Carlo permutation test available in CANOCO (Ter Braak, 1995). The primary objective of canonical ordination is to detect the main pattern in the species-environment or community-environment relationships (Ter Braak, 1995).

The CCA helps to detect patterns of variation in the species data that can be explained best by the supplied environmental variables (McGarigal et al., 2000). In the ordination output, the total variation in the data set is the sum of all the eigenvalues of all axes. The proportion of this total variation that is explained by the supplied explanatory variables is described as the variation explained and is the sum of all canonical eigenvalues divided by the total variation (Ter Braak, 1995). The variation among the communities in terms of average vegetation height, species diversity and environmental variables was also assessed by plotting boxplots in the Program PAST 3.20 (Hammer et al., 2001).

4.3 Results

Overall, 150 vegetation plots from 30 palustrine wetlands in Lesotho were analysed in this study (Figure 4.1). A total of 312 plant species belonging to 51 families occurred in the wetlands (Appendix 4.2). Of the 312 species, 276 were encountered in the 150 plots and the remaining 36 species occurred within the wetlands but outside the plots (Appendix 4.2). Five most dominant families, accounting for most of the species occurring in the wetlands, were Poaceae (20.19%), Asteraceae (19.23%), Cyperaceae (14.10%), Scrophulariaceae (4.17%) and Polygonaceae (3.85%) (Appendix 4.3). From these results, it can be observed that 3 (Poaceae, Asteraceae and Cyperaceae) out of the 51 families account for 53.52% of all the species occurring in these wetlands. While the species richness of whole wetland units ranged between 10 and 53, the number of species per 3 × 3 m plot ranged from 1 (monospecific communities, e.g. community 19) to 27 (highly diverse communities, e.g. communities 3 and 4), with a median species richness of about 14. The highest median number of species for whole wetland units (41.5) was recorded in the Highlands and the lowest (26) in the Lowlands. The five most frequently occurring species in the wetlands all represent different families (Ranunculaceae, Leguminosae (Fabaceae), Asteraceae, Poaceae and Cyperaceae) (Appendix 4.2). The type of metabolism (C_3/ C_4) is also indicated in Appendix 4.2 for most of the species. The species that were collected during fieldwork were deposited in the ROML at the National University of Lesotho.

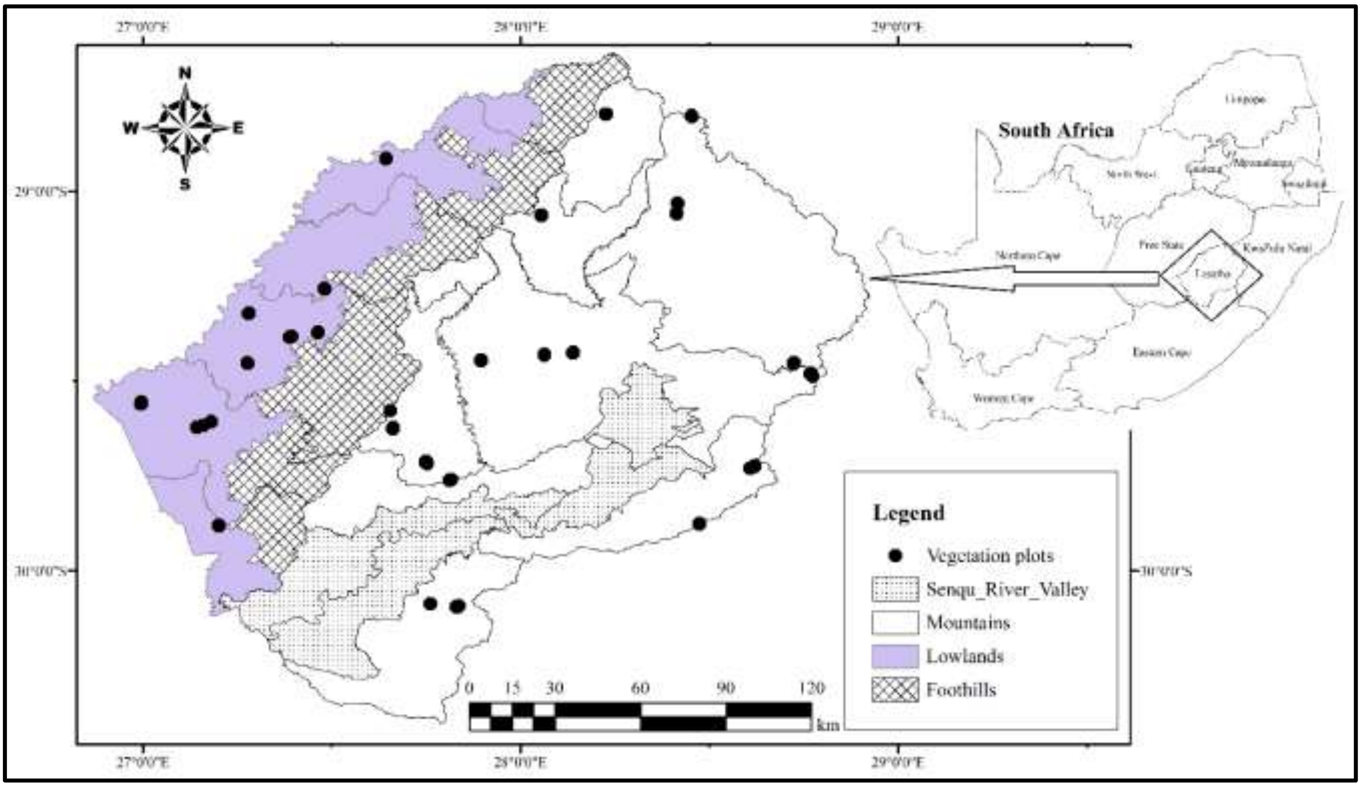

Figure 4.1: Distribution of the vegetation plots in the palustrine wetlands of Lesotho

4.3.1 Classification

Clustering of all the vegetation plots produced 22 different communities (Figure 4.2). Some of these communities are pictorially presented in Figure 4.3. The 22 communities are described in terms of their dominant species, indicator species and the associated IVs (Table 4.2). These communities were also grouped into five main clusters (wetland types), four highland wetland types (wetland types 1-4) and one lowland type (wetland type 5). While most of the high-altitude communities exhibited the dominance of C_3 plants, most of the dominants in the low-altitude communities were C_4 species. Exceptions are communities such as *Schoenoplectus paludicola*, *Potamogeton thunbergii* and *Typha domingensis–Phragmites australis*, which although dominated by C_3 pants, occurred at low altitudes. However, a mixture of C_3 and C_4 plants dominated the communities with a wide ecological amplitude (see Appendix 4.2 for the photosynthetic pathways of most of the species). The synoptic table for the classification of the wetland vegetation, prepared following Brown et al. (2013), is provided in Appendix 4.4.

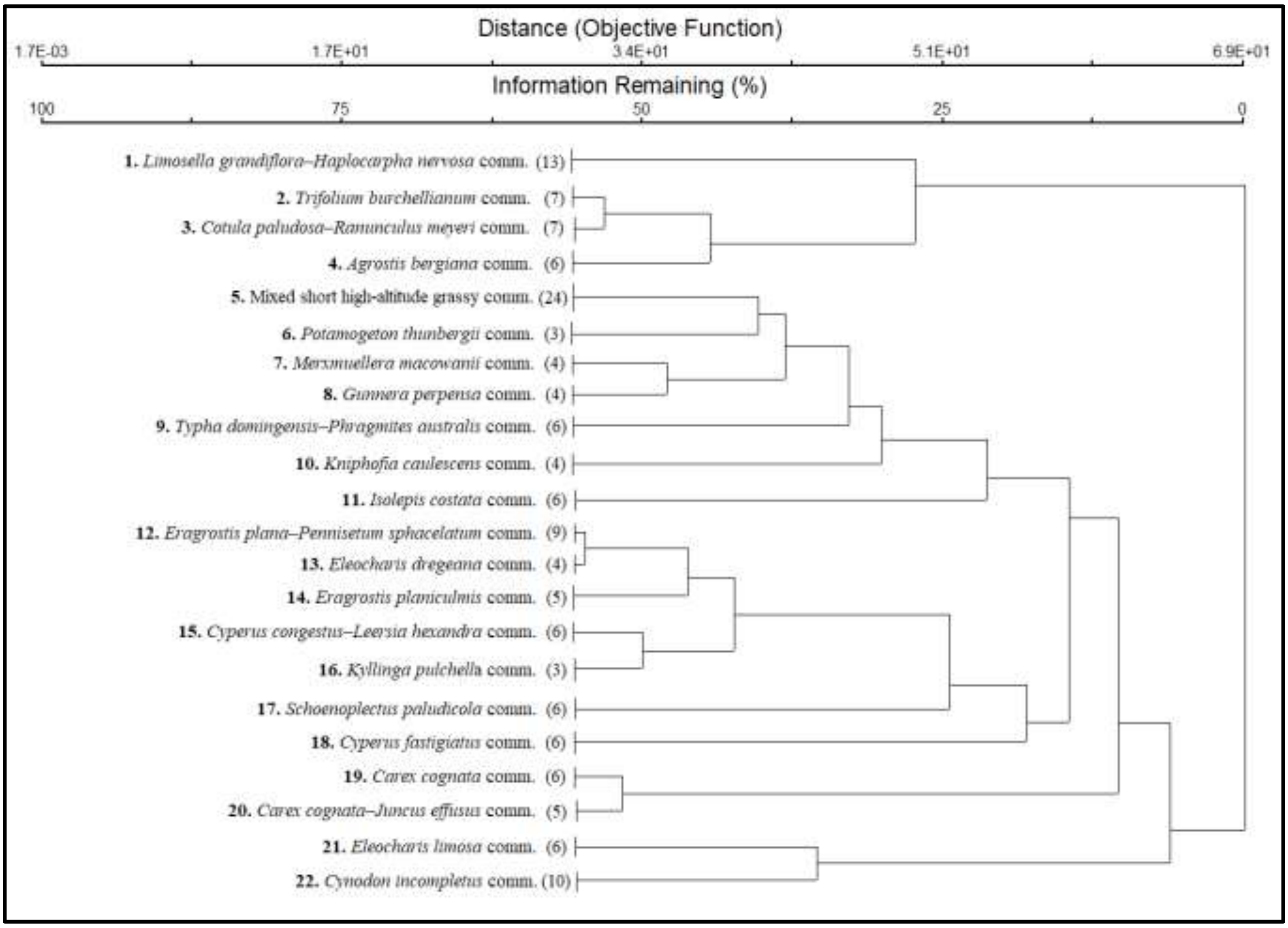

Figure 4.2: Dendrogram showing plant communities of the palustrine wetlands of Lesotho. Numbers in brackets are the numbers of plots in that community.

Figure 4.3: Some of the plant communities occurring in the Afromontane palustrine wetlands of Lesotho: *Limosella grandiflora–Haplocarpha nervosa* community (A), Mixed short high-altitude grassy community (B), *Potamogeton thunbergii* community (C), *Merxmuellera macowanii* community (D), *Gunnera perpensa* community (E), *Typha domingensis–Phragmites australis* community (F), *Kniphofia caulescens* community (G), *Carex cognata* community (H) and *Eleocharis limosa* community (I)

Table 4.2: Indicator species of the palustrine wetland communities of Lesotho. Only species with indicator values of more than 20 and p-values less than 0.05 are presented. All p-values less than 0.001 were given as < 0.001.

No.	**Name of plant community**	**Indicator species†**	**Indicator value**	**p-value**
1	*Limosella grandiflora–Haplocarpha nervosa* comm.	*Haplocarpha nervosa*	21.7	0.027
2	*Trifolium burchellianum* comm.	*Trifolium burchellianum*	31.2	0.038
		Isolepis angelica	32.4	0.012
3	*Cotula paludosa–Ranunculus meyeri* comm.	*Festuca caprina*	32.9	0.029
4	*Agrostis bergiana* comm.	*Catalepis gracilis*	32.3	0.019
		Cotula hispida	25.4	0.030
		Helichrysum subglomeratum	81.9	<0.001
		Poa binata	68.3	<0.001
		Agrostis bergiana	27.5	0.032
5	Mixed short high-altitude grassy comm.	No indicator species	–	–
6	*Potamogeton thunbergii* comm.	*Potamogeton thunbergii*	27.5	0.033
7	*Merxmuellera macowanii* comm.	*Oxalis obliquifolia*	25.7	0.026
		Senecio macrocephalus	29.5	0.016
8	*Gunnera perpensa* comm.	*Gunnera perpensa*	20.3	0.046
		Cineraria dieterlenii	47.7	0.003
		Nidorella undulata	41.4	0.004
		Peucedanum thodei	27.8	0.017
		Scirpus ficinioides	32.6	0.011
9	*Typha domingensis–Phragmites australis* comm.	*Schoenoplectus corymbosus*	33.3	0.020
		Typha domingensis	47.7	0.003
		Phragmites australis	41.4	0.004
10	*Kniphofia caulescens* comm.	*Kniphofia caulescens*	43.9	0.004
11	*Isolepis costata* comm.	*Juncus oxycarpus*	44.0	0.006
		Pentzia cooperi	33.3	0.017
		Isolepis costata	25.0	0.039
12	*Eragrostis plana–Pennisetum sphacelatum* comm.	No indicator species	–	–
13	*Eleocharis dregeana* comm.	*Brachiaria eruciformis*	26.5	0.025
		Digitaria eriantha	32.6	0.010
		Fingerhuthia sesleriiformis	27.5	0.021
		Fuirena ecklonii	50.0	0.004
		Panicum maximum	30.7	0.018
		Polygonum aviculare	50.0	0.004
14	*Eragrostis planiculmis* comm.	*Bromus catharticus*	20.5	0.042
		Hordeum capense	25.1	0.029
15	*Cyperus congestus–Leersia hexandra* comm.	*Cyperus congestus*	20.1	0.048
		Leersia hexandra	21.7	0.041
16	*Kyllinga pulchella* comm.	*Andropogon eucomus*	33.3	0.039

		Conyza albida	30.0	0.027
		Potamogeton pusillus	33.3	0.039
		Trifolium africanum	33.3	0.039
17	*Schoenoplectus paludicola* comm.	*Schoenoplectus paludicola*	30.7	0.016
18	*Cyperus fastigiatus* comm.	*Cyperus fastigiatus*	37.6	0.007
19	*Carex cognata* comm.	*Agrostis eriantha*	26.7	0.019
		Carex cognata	23.0	0.033
20	*Carex cognata–Juncus effusus* comm.	*Juncus effusus*	20.2	0.048
		Pennisetum thunbergii	22.8	0.039
21	*Eleocharis limosa* comm.	*Persicaria amphibia*	33.3	0.017
22	*Cynodon incompletus* comm.	*Cynodon incompletus*	20.1	0.048
		Lepidium schinzii	21.7	0.041

†Author names for the species are provided in Appendix 4.2

4.3.2 Ordination

The CCA ordination diagram for all vegetation plots is presented in Figure 4.4. In this ordination, the environmental variables supplied account for 18.18% of this. The Monte Carlo permutation test indicated that the model was significant (F = 2.1, p = 0.002). The first axis of the ordination is positively correlated with altitude, longitude, soil parent material and peat but negatively correlated with landscape, inundation and aspect. Communities located on the right side of the ordination diagram (e.g. communities 1, 3, 5, 7, 10 and 20) are associated with near-pristine and high-altitude areas that are underlain by basalt and located in the eastern part of the country. Communities on the left side of the diagram (e.g. communities 6, 15, 16, 17, 18, 21 and 22) are associated with more inundated wetlands in the western lowland and more urbanised areas of the country that are underlain by sandstone. These communities are also associated with a shallower water column. The second axis of the ordination is best explained by slope but wetness and soil depth are also important factors. However, some communities occur on a wide range of altitudinal gradient and these include communities 12, 13 and 14.

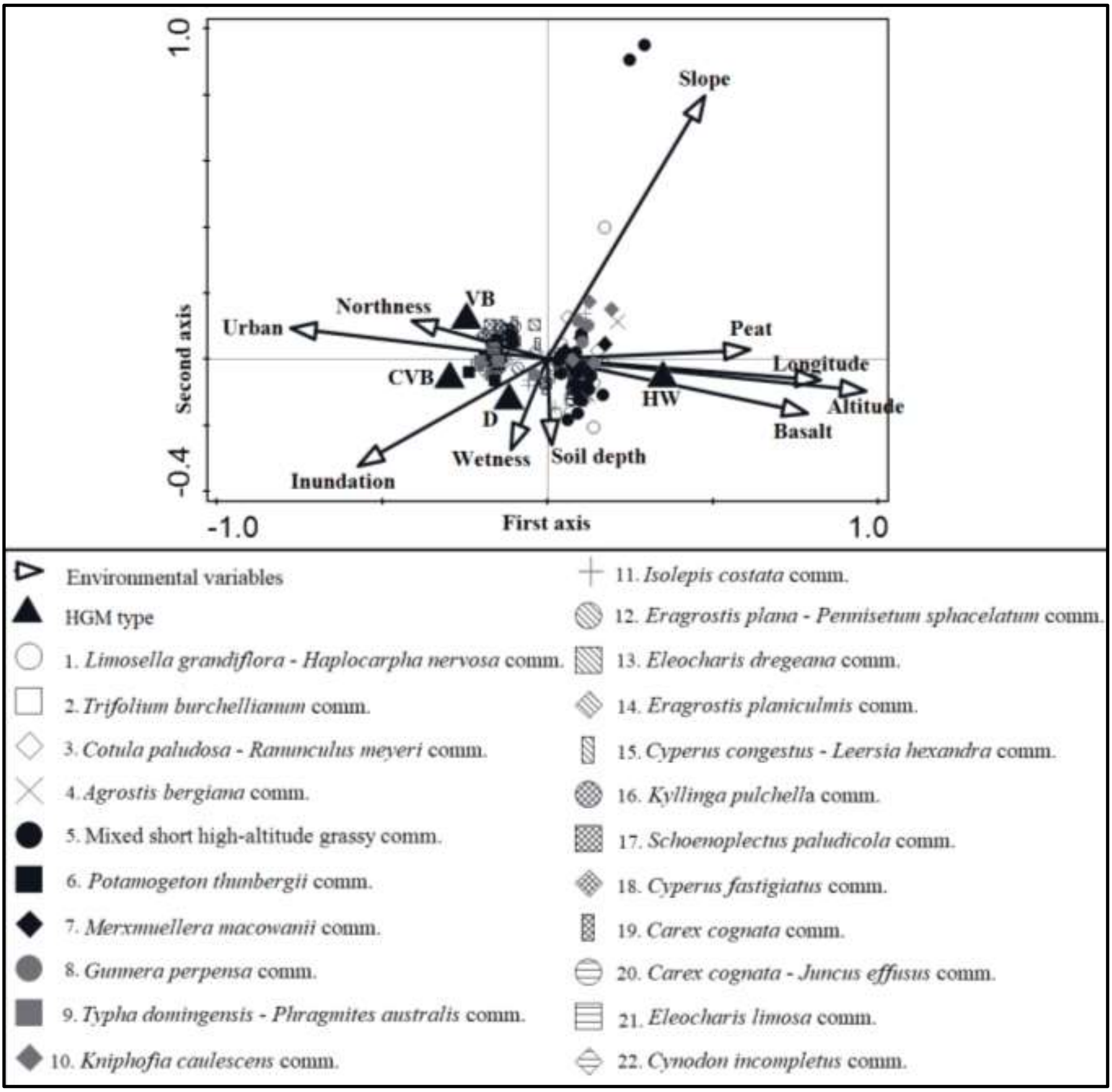

Figure 4.4: Canonical correspondence analysis ordination diagram showing plant communities in the palustrine wetlands of Lesotho, with all plots and using the same classification presented in Figure 4.2.

Thirty of the 150 vegetation plots had detailed soil data and this subset of the vegetation plots represents 15 of the 22 plant communities presented in Figure 4.2. The CCA ordination diagram for this subset of the vegetation plots is presented in Figure 4.5. The model was significant ($F = 1.3$, $P = 0.002$) in the Monte Carlo permutation test. The supplied explanatory variables explained 65.40% of the total variation. The first axis is positively correlated with potassium and percentage clay but is negatively correlated with altitude, longitude, total organic carbon, nitrogen, sulphur, percentage sand and sodium. While potassium and percentage clay have a strong positive correlation, total organic carbon, nitrogen, sulphur, percentage sand and longitude also have a strong positive correlation. The second axis is negatively correlated with latitude and positively associated with electrical conductivity, soil depth, magnesium and calcium content. Communities on the left side of the ordination diagram (e.g. communities 1, 3, 4, 8, 19 and 20) are in high-altitude areas and are associated with sand soils with high organic carbon, nitrogen, sulphur and sodium content and those on the right side (e.g. communities 9, 13, 17, 18, 21 and 22) are in the Lowlands and on soils with high potassium and clay levels. Those communities on the upper part of the ordination diagram, including communities 8, 9, 11, 12, 17, 19 and 20, are associated with high levels of electrical conductivity, calcium and magnesium, as well as deeper soils.

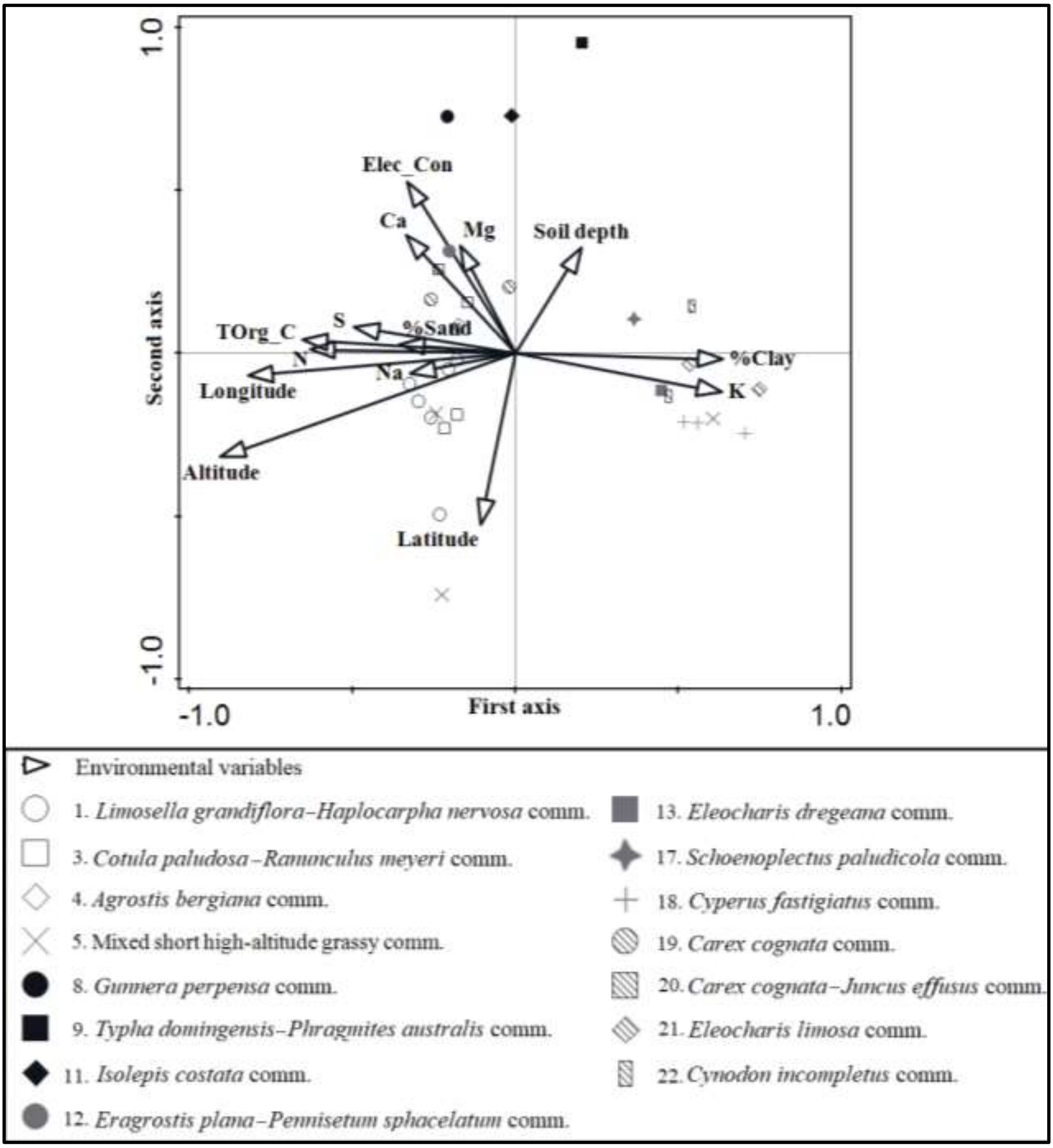

Figure 4.5: Canonical correspondence analysis ordination diagram showing plant communities in the palustrine wetlands of Lesotho, with only plots with soil data and using the same classification presented in Figure 4.2.

4.3.3 Description and distribution of wetland plant communities

The 22 plant communities were further described in terms of their most dominant species, structure, diversity and environmental conditions (Table 4.3, Figure 4.6 and Figure 4.7). Species that are protected by law in the country are also highlighted in Table 4.3. The distribution range of the wetland vegetation in Lesotho is also presented in Figure 4.1.

Table 4.3: Description and environmental conditions of plant communities in the palustrine wetlands of Lesotho

No.	Name of community	No. of plots	Dominants	Community structure	Species richness†	Shannon†	Evenness†	Environmental conditions and notes on important species in the community
1	*Limosella grandiflora–Haplocarpha nervosa* comm.	13	*Haplocarpha nervosa, Limosella grandiflora*	Dense, short (2-10 cm) forb-dominated grassland (Figure 4.3A)	10 (5-14)	1.71 (0.52-1.98)	0.66 (0.29-0.85)	▪ Altitude: > 2400 m ▪ Habitat: seepages or valleybottom wetlands ▪ Soil: ≥ 50 cm deep; permanently wet; peat or clay ▪ *H. nervosa*: low creeping and rosette-forming forb; endemic to the Grassland Biome of southern Africa[1]; dominant among other forbs and grasses
2	*Trifolium burchellianum* comm.	7	*Trifolium burchellianum, Cotula paludosa, Lobelia galpinii, Alepidea pusilla*	Open to dense, short (2-15 cm) forb-dominated grassland	12 (9-19)	1.68 (1.14-2.12)	0.68 (0.49-0.71)	▪ Altitude: > 2400 m ▪ Habitat: seepages or valleybottom wetlands ▪ Soil: ≥ 20 cm deep; seasonally to permanently wet; peat or clay loam ▪ *T. burchellianum*: low creeping and mat-forming but becomes dominant among other forbs and grasses
3	*Cotula paludosa–Ranunculus meyeri* comm.	7	*Cotula paludosa, Ranunculus meyeri*	Dense, short to medium tall (2-40 cm) forb-dominated grassland	14 (10-25)	1.88 (1.69-2.56)	0.74 (0.62-0.80)	▪ Altitude: > 2400 m; also occurs at lower altitudes ▪ Habitat: seepages ▪ Soil: ≥ 20 cm deep; seasonally to permanently wet; peat or clay loam ▪ *R. meyeri* and *C. paludosa*: low creeping and mat-forming but become dominant among grasses and other forbs. At lower altitudes, *R. meyeri* can be as much as four times its high altitude size.
4	*Agrostis bergiana* comm.	6	*Agrostis bergiana, Trifolium burchellianum, Helichrysum subglomeratum, Alchemilla colura*	Dense, short (2-20 cm) graminoid-dominated grassland	13.5 (9-27)	1.76 (1.26-2.43)	0.68 (0.55-0.75)	▪ Altitude: > 2400 m ▪ Habitat: seepages or depressions ▪ Soil: ≥ 40 cm deep; wide range of wetness degree; peat or clay loam

5	Mixed short high-altitude grassy comm.	24	No clear dominant	Open to dense, short to medium tall (2-80 cm) sedgeland or grassland, dominated by forbs or graminoids (Figure 4.3B)	9.5 (2-20)	1.20 (0.11-2.07)	0.58 (0.10-0.75)	▪ Altitude: 1400 to above 3000 m ▪ Habitat: seepages or valleybottom wetlands ▪ Soil: ≥ 10 cm deep; wide range of wetness degree and soil texture; peat ▪ Heterogeneous community and may contain *M. drakensbergensis*§, *M. macowanii*§ and *Mentha longifolia*§
6	*Potamogeton thunbergii* comm.	3	*Potamogeton thunbergii*	Short to medium tall (30-80 cm) community; low diversity (Figure 4.3C)	3 (2-4)	0.50 (0.44-0.65)	0.32 (0.31-0.59)	▪ Altitude: 1400–1800 m; also occurs at high altitudes ▪ Habitat: depressions or valleybottom wetlands ▪ Soil: 20–40 cm deep; permanently wet; clay or clay loam ▪ *P. thunbergii*: typical aquatic plant whose leaves float on the water surface
7	*Merxmuellera macowanii* comm.	4	*Merxmuellera macowanii*	Dense, medium tall (40-80 cm) tussock grassland; low evenness (Figure 4.3D)	13.5 (7-19)	1.41 (0.87-2.05)	0.53 (0.42-0.68)	▪ Altitude: > 2500 m ▪ Habitat: seepage or valleybottom wetlands ▪ Soil: ≥ 20 cm deep; temporarily or seasonally wet; peat or clay ▪ Found throughout the Maloti-Drakensberg ▪ Community can be monospecific and usually quite distinct within the surroundings ▪ *M. macowanii*§: economically important; used for making handcrafts and for thatching houses in Lesotho
8	*Gunnera perpensa* comm.	4	*Gunnera perpensa*	Dense, medium tall (30-60 cm) conspicuous forb-dominated community (Figure 4.3E)	11.5 (7-23)	1.72 (0.73-2.20)	0.64 (0.35-0.77)	▪ Altitude: > 2200 m; also occurs at lower altitudes ▪ Habitat: seepages or valleybottom wetlands ▪ Soil: ≥ 20 cm deep; seasonally to permanently wet; peaty, loam or clay; slightly acidic and high electrical conductivity ▪ Community may also contain *M. longifolia*§. ▪ This community was described as variant 3.2.4 of the *Helictotrichon longifolium–Pennisetum sphacelatum*

								sub-community of the *Fingerhuthia sesleriiformis–Andropogon appendiculatus* community[2]. ▪ *G. perpensa*§: conspicuous forb; economically important (used for medicinal purposes in Lesotho)[3]
9	*Typha domingensis–Phragmites australis* comm.	6	*Typha domingensis, Phragmites australis*	Dense, tall (150-300 cm) reedland; low evenness (Figure 4.3F)	8.5 (2-16)	0.92 (0.46-1.71)	0.47 (0.36-0.60)	▪ Altitude: 1400-1800 m ▪ Habitat: valleybottom wetlands ▪ Soil: ≥ 10 cm deep; seasonally or permanently wet; peat or clay soils; rich in nutrients and high in electrical conductivity ▪ Many bird species nest in this habitat ▪ *T. domingensis* and *P. australis*: economically important (used for handcrafts); very competitive and benefit from high nutrient levels[4] ▪ Vegetatively, *T. domingensis* resembles *T. capensis.*
10	*Kniphofia caulescens* comm.	4	*Kniphofia caulescens*	Conspicuous dense, medium tall (30-50 cm) grassland; low diversity (Figure 4.3G)	5.5 (3-12)	0.47 (0.12-1.32)	0.25 (0.09-0.52)	▪ Altitude: > 2500 m ▪ Habitat: seepage or valleybottom wetlands ▪ Soil: ≥ 50 cm deep; seasonally to permanently wet; peat or loam ▪ Restricted and endemic to the Maloti-Drakensberg and is quite common in Lesotho ▪ *K. caulescens*§ has cultural significance; its beauty makes the community attractive and distinct
11	*Isolepis costata* comm.	6	*Isolepis costata*	Dense, medium tall (30-60 cm) sedgeland	9.5 (5-13)	1.39 (0.79-1.57)	0.57 (0.44-0.65)	▪ Altitude: > 1700 m ▪ Habitat: seepages or valleybottom wetlands ▪ Soil: ≥ 30 cm deep; seasonally to permanently wet; peat or clay soils ▪ May be associated with *G. perpensa*§ and *K. caulescens*§
12	*Eragrostis plana–Pennisetum*	9	*Eragrostis plana, Pennisetum sphacelatum,*	Open to dense, short to medium tall (5-60 cm)	10 (4-15)	1.62 (1.17-1.88)	0.66 (0.56-0.76)	▪ Altitude: 1400–2600 m ▪ Habitat: seepages or valleybottom wetlands

	sphacelatum comm.		*Paspalum dilatatum, Eleocharis dregeana*	grassland, dominated by graminiods				▪ Soil: ≥ 15 cm deep; temporarily or seasonally wet; clay or clay loam; high electrical conductivity ▪ The community may include *Bulbine narcissifolia*§, *G. perpensa*§, *M. longifolia*§ and *M. aquatica*§
13	*Eleocharis dregeana* comm.	4	*Eleocharis dregeana*	Dense, medium tall (30-60 cm) sedgeland	20.5 (13-21)	1.80 (1.57-1.95)	0.60 (0.52-0.70)	▪ Altitude: 1600–2600 m ▪ Habitat: valleybottom wetlands ▪ Soil: ≥ 80 cm deep; temporarily or seasonally wet; clay or clay loam ▪ The community may also contain *M. aquatica*§
14	*Eragrostis planiculmis* comm.	5	*Eragrostis planiculmis, Schoenoplectus decipiens*	Dense, medium tall (50-80 cm) grassland dominated by graminoids	11 (6-16)	1.39 (1.00-1.92)	0.58 (0.51-0.68)	▪ Altitude: 1400–2600 m ▪ Habitat: valleybottom wetlands but can also occur in depressions ▪ Soil: ≥ 20 cm deep; temporarily or seasonally wet; clay or clay loam
15	*Cyperus congestus–Leersia hexandra* comm.	6	*Cyperus congestus, Leersia hexandra*	Open to dense, medium tall (30-60 cm) sedgeland	12 (4-18)	1.73 (0.78-2.03)	0.67 (0.48-0.71)	▪ Altitude: 1400–2400 m a.s.l. ▪ Habitat: valleybottom wetlands but can also occur in depressions ▪ Soil: ≥ 10 cm deep; seasonally or permanently wet; clay or clay loam ▪ This community may contain *M. aquatica*§ ▪ *L. hexandra* is a common wetland grass in the Lowlands
16	*Kyllinga pulchella* comm.	3	*Kyllinga pulchella*	Dense, short (20-40 cm) sedgeland that occurs in small patches	12 (11-16)	1.55 (1.41-1.81)	0.62 (0.55-0.64)	▪ Altitude: 1400–1800 m ▪ Habitat: valleybottom wetlands or depressions ▪ Soil: 5–60 cm deep; seasonally or permanently wet; sand or clay loam ▪ *K. pulchella* is a short attractive sedge ▪ The community also occurs as small patches in wet disturbed areas.

17	*Schoenoplectus paludicola* comm.	6	*Schoenoplectus paludicola*	Open to dense, short (25-50 cm) sedgeland	9.5 (7-11)	1.28 (0.98-1.50)	0.57 (0.41-0.67)	▪ Altitude: 1400–1800 m ▪ Habitat: valleybottom wetlands ▪ Soil: 30–70 cm deep; seasonally or permanently wet; clay or clay loam
18	*Cyperus fastigiatus* comm.	6	*Cyperus fastigiatus*	Open to dense, medium to tall (60-100 cm) sedgeland	5 (4-7)	0.88 (0.80-1.23)	0.53 (0.41-0.63)	▪ Altitude: 1400–1800 m ▪ Habitat: valleybottom wetlands or depressions ▪ Soil: ≥ 70 cm deep; seasonally or permanently wet; clay or clay loam; slightly acidic or neutral ▪ *C. fastigiatus* usually forms monocultures ▪ This community has been reported in South Africa[4]
19	*Carex cognata* comm.	6	*Carex cognata*	Dense, medium tall (30-70 cm) sedgeland; low evenness (Figure 4.3H)	7.5 (1-14)	1.14 (0-1.68)	0.49 (0-0.62)	▪ Altitude: > 2200 m but also occurs at lower altitudes ▪ Habitat: seepage or valleybottom wetlands ▪ Soil: ≥ 100 cm deep; seasonally to permanently wet; peat or clay; high in electrical conductivity ▪ A form of sedgeland that occurs at high altitudes but has a wide ecological amplitude ▪ *C. cognata* is similar to *C. acutiformis* ▪ The community may contain *M. longifolia*§ and *M. aquatica*§
20	*Carex cognata–Juncus effusus* comm.	5	*Juncus effusus*, *Carex cognata*	Dense, medium tall (30-70 cm) sedgeland	11 (7-16)	1.65 (0.92-2.22)	0.67 (0.44-0.80)	▪ Altitude: > 2400 m ▪ Habitat: seepage or valleybottom wetlands ▪ Soils: ≥ 50 cm deep; permanently wet; peat or clay ▪ A form of sedgeland that occurs at high altitudes
21	*Eleocharis limosa* comm.	6	*Eleocharis limosa*	Dense, medium tall (40-80 cm) sedgeland (Figure 4.3I)	5 (3-9)	1.12 (0.72-1.42)	0.60 (0.40-0.68)	▪ Altitude: 1400–1800 m ▪ Habitat: depressions or valleybottom wetlands ▪ Soil: ≥ 60 cm deep; seasonally or permanently wet; clay or clay loam ▪ The community is similar to *Eleocharis dregeana* community

22	*Cynodon incompletus* comm.	10	*Cynodon incompletus*, *Cyperus marginatus*, *Eleocharis limosa*, *Cyperus rotundus*	Dense, short to medium tall (20-70 cm) sedge grassland	9.5 (4-15)	1.37 (0.65-1.82)	0.60 (0.40-0.71)	▪ Altitude: 1400–1800 m ▪ Habitat: valleybottom wetlands ▪ Soils: ≥ 10 cm deep; seasonally or permanently wet; clay or clay loam ▪ May also contain *M. longifolia*§

Sources: [1]Mucina and Rutherford (2006), [2]Brand et al. (2013), [3]Mugomeri et al. (2016), [4]Sieben et al. (2017a)

Comm – community, Shannon – Shannon-Weiner index

Authors of the species are provided in Appendix 4.2.

§Species are protected by law in Lesotho (Lesotho Legal Notice No. 39 & 93 of 2004; No. 81 of 2006)

†Species richness, Shannon-Weiner and Evenness are given as median values, with their range in parenthesis

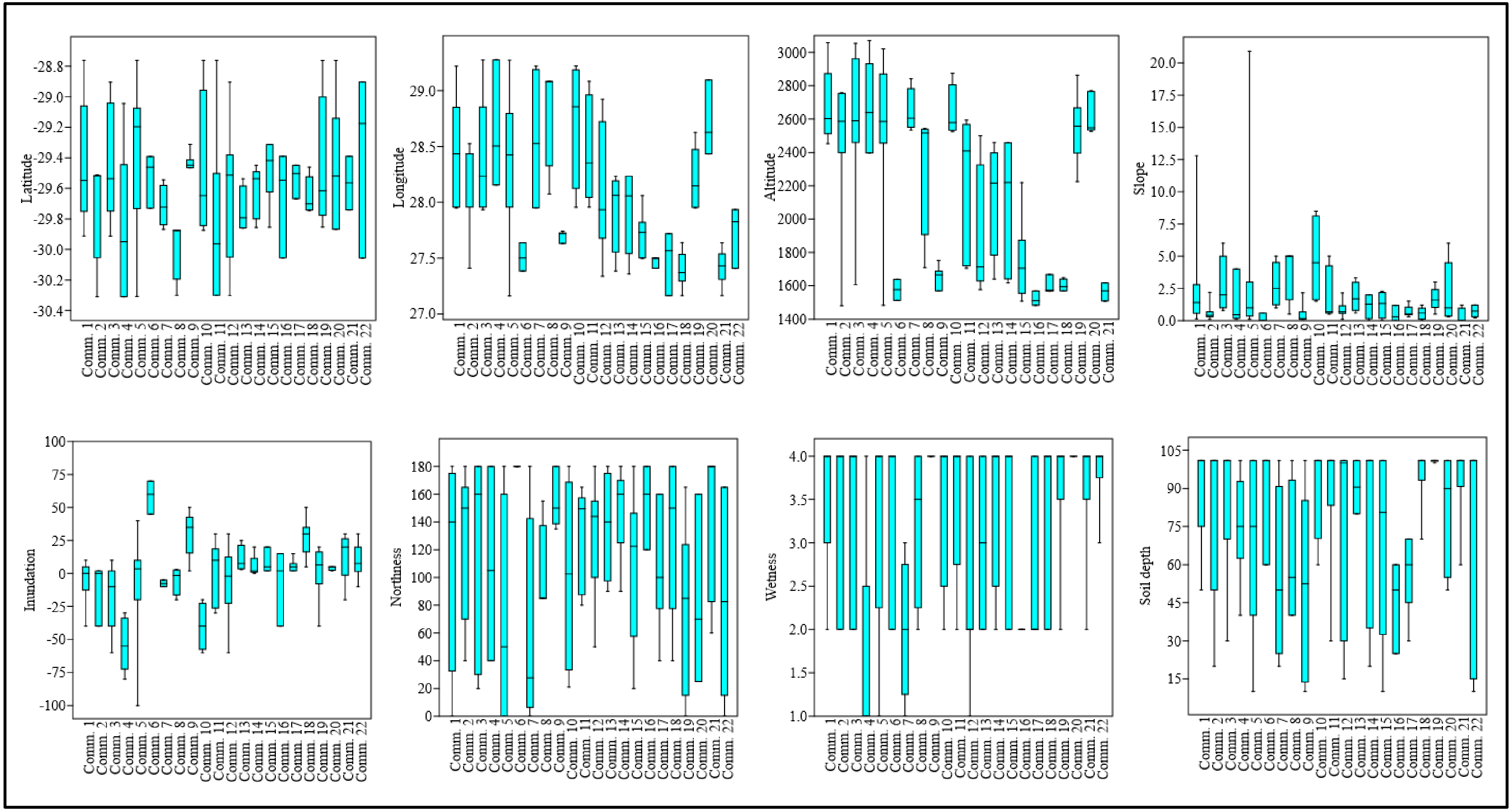

Figure 4.6: Boxplots for the comparison of the 22 Afromontane wetland plant communities in terms of environmental variables, with all plots and using the same classification presented in Figure 4.2

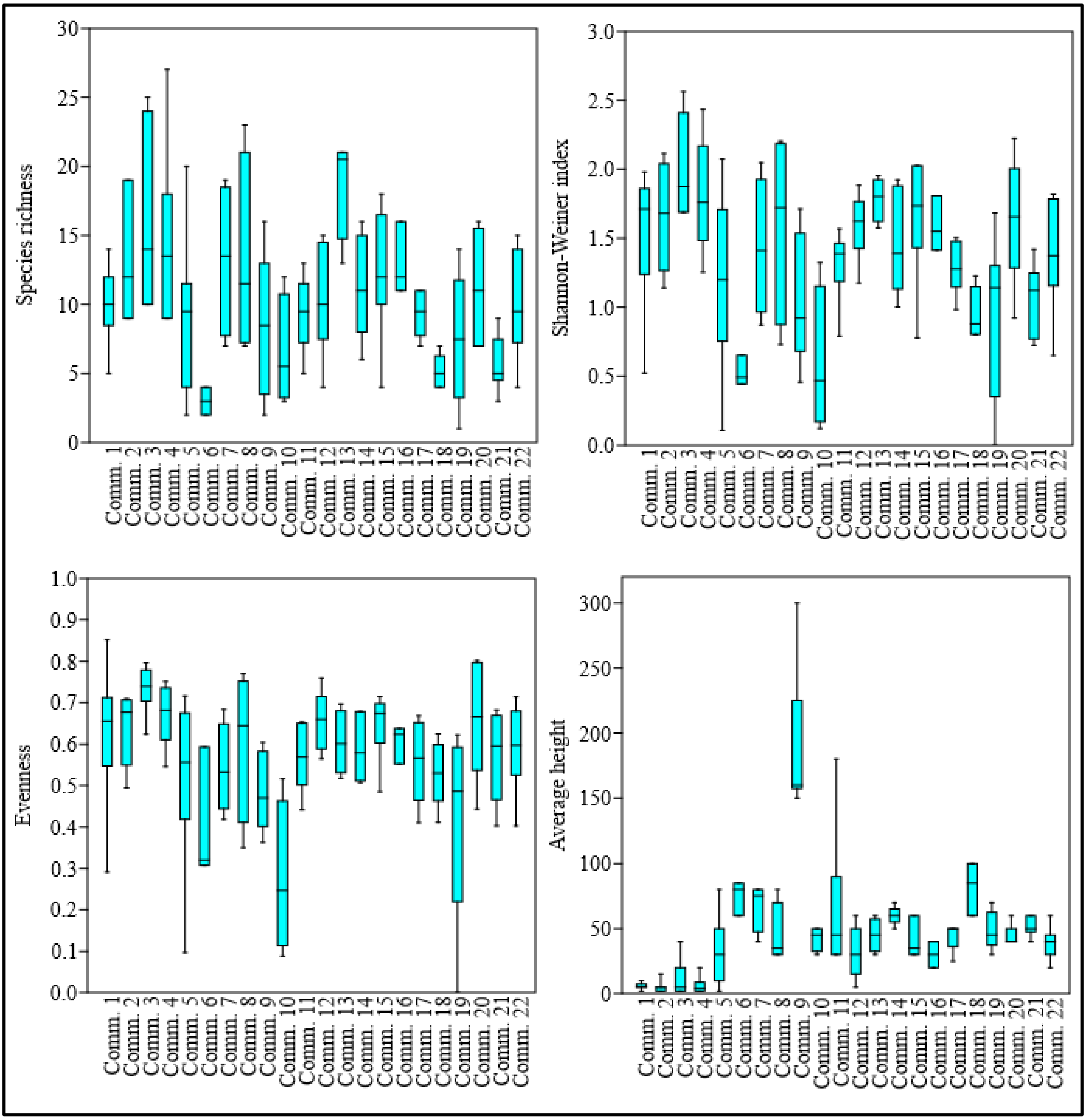

Figure 4.7: Boxplots for the comparison of the 22 Afromontane wetland plant communities in terms of average vegetation height, species richness, Shannon-Weiner index and evenness, with all plots and using the same classification presented in Figure 4.2

4.4. Discussion

The earliest studies on the palustrine wetlands of Lesotho were carried out in the early 1960s and 1970s (Guillarmod, 1962; van Zinderen Bakker & Werger, 1974). Since then, other studies conducted in the country (Meakins & Duckett, 1993; Grab & Deschamps, 2004; Du Preez & Brown, 2011) were mainly carried out on small areas, focusing on specific or a few wetlands. The current study has provided the most recent and more comprehensive assessment of the palustrine wetlands in the country by providing a classification and description of the wetland vegetation. The wetland vegetation has been classified into 22 communities, which are influenced mainly by spatial (longitude, latitude and landscape), topographic (altitude, aspect, and slope) and edaphic factors (soil parent material, inundation, peat, potassium, clay, total organic carbon, nitrogen, sulphur, electrical conductivity, calcium, soil depth, wetness, magnesium). The wetlands were occurring mainly in those areas where topography allows wetland conditions to develop (mostly in flat areas); mainly on the summit plateau and in the Lowlands. Nonetheless, it is noteworthy that there may be more communities in the country than the number reported here because only 150 plots from 30 wetlands were analysed in this study, although this forms an important starting point for documenting and classifying the wetland vegetation for Lesotho.

Despite Lesotho being entirely Afromontane, the study found a clear distinction between wetlands that are found in the Highlands and those in the Lowlands, in terms of diversity, species making up the communities and structure of the communities (Table 4.3). While the highland wetlands (types 1 to 4) are mainly south-facing, those in the Lowlands (type 5) are mainly north-facing. Vegetation changes can be observed with increasing northness, and differences exist between the north- and south-facing slopes because of distinct solar radiation patterns. The resulting ecological differences that include snow cover duration and moisture conditions between the moister and colder south-facing slopes and the drier and warmer north-facing slopes contribute to the observed differences in vegetation types (Nüsser, 2002). Indicators of wetland type 5 are typical lowland wetland plants. This wetland type is comparable to the most widespread and common type of wetlands in South Africa, the temperate grassy wetlands, (Sieben et al., 2014a). One of the highland wetland types (type 4) comprises wetlands that are found in the small high-altitude area underlain by sandstone and limited to the eastern edge of Lesotho (Sehlabathebe National Park). These wetlands are also located on very steep slopes. However, this wetland type was under-sampled in this study as it was represented by only two wetlands and nine vegetation plots. Despite the country’s high altitude (1388-3482 m a.s.l.) and rugged terrain, qualifying it to be entirely Afromontane (Carbutt & Edwards, 2015), some of the communities in the Lowlands also fit into the temperate grassy wetland vegetation of Sieben et al. (2017a) and the eastern temperate freshwater wetlands of Mucina and Rutherford (2006).

All the wetlands surveyed in the current study can broadly be classified as the freshwater wetland vegetation type of Mucina and Rutherford (2006), which is further divided into eastern temperate freshwater wetlands (AZf 3), Drakensberg wetlands (AZf 4) and Lesotho mires (AZf 5). The dominance of Poaceae, Asteraceae, Cyperaceae and Scrophulariaceae families observed in Lesotho has also been reported in the entire Maloti-Drakensberg region and the surrounding areas, although Asteraceae was the most dominant in the latter (Chapter 5). The current study also concurs with Sieben et al. (2017b) who report that Poaceae is the most common plant family in the South African wetlands, based on species richness. However, of the five most dominant plant families recorded in the current study, two (Asteraceae and Scrophulariaceae) have higher than average levels of endemism in the Maloti-Drakensberg region (Cowling & Hilton-Taylor, 1994). High levels of endemism in the high-altitude environments such as the Maloti-Drakensberg are attributed to the many small-scale microhabitats and a wide range of edaphic conditions that develop as a result of slope and aspect (Brand et al., 2019).

The five most common species in the study all represent different families. This implies that the wetland vegetation in the country is phylogenetically diverse and this is unlike the situation in South Africa where the five most common wetland plant species are all grasses (Poaceae) (Sieben et al., 2014a). The high altitude that characterises the greater part of Lesotho could account for this high diversity, and montane wetlands have been identified as some of the most species-rich in South Africa (Sieben et al., 2014a). While the high-altitude montane wetland communities in Lesotho are more diverse and are virtually never a monoculture, the lowland wetland communities are generally less diverse and sometimes monospecific communities. In lowland wetlands, it is common for just one or two species to dominate the entire wetland plant community (Boutin & Keddy, 1993; Sieben et al., 2010a). The trend of increasing diversity with altitude, also exhibited in the current study, is contrary to the decline in species richness with altitude, which has widely been recognised as a general law of ecology (Rosenzweig, 1995). However, the large number of species and communities recorded in this study generally reflects the high diversity of wetland habitats in the country, although the highest diversity is associated with higher altitudes. It is noteworthy that exceptions such as *Kniphofia caulescens* and *Carex cognata* communities usually exhibit lower diversity than other communities at such higher elevations. This suggests that the dominant species in these communities are so adapted to the harsh high-altitude conditions that they have developed a very large competitive effect on local resources and act as a habitat filter by excluding the less competitive species (Maire et al., 2012). It is also noteworthy that the Lowlands is the area subjected to more anthropogenic pressures that include cultivation, urbanisation and conversion to other forms of land use and this threatens the wetlands in this part of the country.

The higher species richness and diversity in the Highlands highlights that these wetland habitats are more heterogeneous than those in the Lowlands. This could be attributable, in part, to the fact that most of the dominant species in the high-altitude montane wetlands of the country are non-clonal (Table 4.3). Clonal plants are species that can reproduce vegetatively by sprouting from stolons or rhizomes, forming stands of individuals of that species (Song & Dong, 2002). Typical clonal plants include *Phragmites* and *Typha* spp that form dense rhizome mats and outcompete other non-clonal species. These findings corroborate Sieben et al. (2010b, 2017b) who suggest that, unlike lowland wetlands, high-altitude wetlands are unusual in that they are richer in species and particularly non-clonal species. Moreover, because the usually dominant wetland plants cannot cope well with the low temperatures characterising high-altitude environments, they cannot be as dominant as usual, leaving many vacant niches that then become available for colonisation by other plants (Sieben et al., 2010b). Furthermore, in wetland environments, the abundance of clonal plants is negatively associated with the overall plant species diversity, as well as with altitude (Song & Dong, 2002). The high diversity can also be attributed to the steep gradients in the landscape and harsh climatic conditions that create unique habitats in the mountains of Lesotho (Pooley, 2003). The high diversity can further be ascribed to the underlying basaltic parent material. The seepage water in these high-altitude wetlands is eutrophic as the underlying basalt is rich in nutrients (Mucina & Rutherford, 2006). This also influences floristic composition and community structure of the wetlands. These results are consistent with observations by Sieben et al. (2010a) who acknowledge the significant number of wetland community types in the montane areas of Lesotho. The high floristic diversity observed in the current study is also consistent with findings from the high-altitude montane wetlands of Alborz Mountains, Iran (Naqinezhad et al., 2009; Kamrani et al., 2011).

The ordination of the vegetation data for all plots reveals that the explanatory environmental variables supplied could explain only about 18.11% of the total variation. This highlights that the remaining variation could be explained by the environmental factors that were not included in the analysis, such as precipitation (assessed only indirectly through longitude) and wetland water quality. It may also be that plants colonise wetland habitats by chance (Chesson, 2000). However, the amount of variation explained in the ordination is comparable to similar studies in the wetlands of South Africa (Sieben et al., 2016c, 2017a). Moreover, Brand et al. (2013) highlight that substrate and hydrogeological conditions play a bigger role in influencing the floristic composition, structure and dynamics in high-altitude montane wetlands than microclimate. The inclusion of soil variables in the analysis increased the proportion of the total variation explained by the supplied variables from 18.11% to 65.40%. Thus, the inclusion of soil data in the analysis significantly improves wetland vegetation-environment assessments. The amount of variation explained in the ordination with soil data is significantly higher than that reported for the South African wetlands (Sieben et al., 2016c, 2017a). Nevertheless, the amount of variation explained after the inclusion of soil data could also have improved because the data set was smaller (30 vegetation plots).

While the second axis is positively associated with slope, it is negatively correlated with the wetness and soil depth. This implies that communities on the lower part of the ordination diagram are associated with wetter habitats with deeper soils, while those on the upper part are associated with steeper slopes. The former include communities such as *C. cognata–Juncus effusus* while the latter include communities such as *Merxmuellera macowanii,* which are often associated with hillslope seepages. The correlation between wetness and soil depth, which are both negatively correlated with slope, could be attributed to the soil deposition and water accumulation that is often consistent with fairly flat habitats. Altitude, longitude, slope, wetness, soil parent material, landscape, peat, inundation, aspect, soil depth and wetness are very important factors explaining the distribution and variation of the wetland vegetation in this study.

Abundance of peat is also strongly correlated with altitude and longitude. Because most of these Afromontane wetlands are often located on a slope at high altitudes, they are unique (Mucina & Rutherford, 2006; Sieben et al., 2014a). A temperature drop of 1 ℃ has been estimated for every 125 m gain in altitude in Lesotho and the Maloti-Drakensberg region (Pomela et al., 2000). Such steep environmental gradients over short distances (Körner et al., 2011) in Afromontane areas are associated with huge spatial variation in physical features and this results in remarkable variation in terms of species diversity and distribution (Kotze & O'Connor, 2000). Thus, increasing altitude corresponds with a decrease in temperature and an increase in rainfall (Mucina & Rutherford, 2006) and the greater part of Lesotho is generally much higher and colder than the surrounding areas (Sieben et al., 2014a). The hypoxia or anoxia in the wetlands, coupled with the low temperature and pH, often associated with these high-altitude wetlands reduces the rate of decomposition and favours the accumulation of organic matter and peat formation (Chatterjee et al., 2010; Gopal, 2016). Therefore, lower temperatures, higher rainfall and other environmental conditions associated with high altitudes also create habitats that can harbour unique vegetation (Sieben et al., 2014a).

Through its influence on temperature and rainfall, altitude is a suitable surrogate measure for climate in Lesotho and the Maloti-Drakensberg region, which represents an indirect gradient (Sieben et al., 2010a). The strong correlation between longitude and altitude can thus be explained by the fact that, altitude generally increases on moving from west to east in Lesotho and rainfall also increases with altitude, as well as with increasing longitude (Cowling & Hilton-Taylor, 1994; Mucina & Rutherford, 2006). The high altitudes of Lesotho are mainly associated with abundant orographic rainfall, which results in many springs and seepage zones (Mucina & Rutherford, 2006; Sieben et al., 2014a). The influence of altitude and wetness on high-altitude wetland vegetation has also been reported in South Africa (Kotze & O'Connor, 2000; Mucina & Rutherford, 2006; Sieben et al., 2010b, 2010b), southern Brazil (Rolon & Maltchik, 2006) and in Cumbria, UK (Jones et al., 2003). The importance of both altitude and slope gradients on the floristic composition of high-altitude montane wetlands has also been reported in Bulgaria, south-eastern Europe (Hájková et al., 2006) and in Alborz Mountains, India (Naqinezhad et al., 2009; Kamrani et al., 2011).

Although a negative correlation between altitude and wetness was observed in this study, altitude operates at a larger scale and wetness operates on a local scale. It is nevertheless noteworthy that while some communities are restricted to either the Highlands or Lowlands, others seem to have a wide ecological amplitude. These include *Eragrostis plana–Pennisetum sphacelatum*, *Eleocharis dregeana* and *Eragrostis planiculmis* communities. Furthermore, some species, such as *Ranunculus meyeri* Harv., occur at low abundances at lower altitudes but achieve greater cover at higher altitudes as they gain competitive advantage because of the lower temperatures that reduce the vigour of the usually more competitive species (Sieben et al., 2010b). Because some of the plant communities recorded in this study are restricted to the highest altitudes, occurring at the summit plateaus, there is a possibility that they may disappear in the face of climate change as they cannot migrate any further up (Lee et al., 2015; Bentley et al., 2019).

While high-altitude communities (e.g. *Limosella grandiflora–Haplocarpha nervosa*, *Agrostis bergiana* and *Cotula paludosa–R. meyeri* communities.) were also associated with soils that are high in total organic carbon, nitrogen and sulphur, the habitat soils for the low-altitude communities (e.g. *Cynodon incompletus*, *Eleocharis limosa*, *S. paludicola* and *E. dregeana* communities) were high in potassium and clay percentage. However, the negative correlation of potassium with altitude is contrary to Mucina and Rutherford (2006) who report that the high-altitude areas are associated with high potassium levels. In the current study, communities such as *C. cognata*¸ *Gunnera perpensa* and *E. plana–P. sphacelatum* were also associated with high soil magnesium, calcium and electrical conductivity. The importance of potassium, electrical conductivity and clay percentage in influencing high-altitude montane wetland vegetation is consistent with findings from a similar study on the wetlands of the Alborz Mountains, India (Kamrani et al., 2011). Because of the low temperature and basaltic parent material, the soils in the mountains of Lesotho are high in organic matter and generally nutrient-rich, with a high water-retention capacity (Mucina & Rutherford, 2006). However, the soils found in the Lowlands are considered generally nutrient-poor (Maro, 2011).

4.4.1 Conservation value and impacts of climate change

Some of the species encountered in this study are protected by law in Lesotho (Table 4.3), which highlights that they are threatened. The wetlands of Lesotho contribute significantly not only to biodiversity, but also provide a wide spectrum of ecosystem services, particularly in terms of water resources and livestock grazing. They are the headwaters of the five major economically important rivers in the country, namely, the Maliba-matšo, Senqu-Orange, Mohokare (Caledon), Makhaleng and Senqunyane, which also feed the LHWP dams (Department of Environment, 2014). They play a major role in sustaining the perennial flow of water and regulating the water quality of the rivers that flow to the Atlantic Ocean (Pooley, 2003). However, all the mountain areas in the country are drained through the Senqu-Orange River and its tributaries (Backéus & Grab, 1995), the most important and most developed shared river system in southern Africa. For South Africa, the water is tapped mainly through the LHWP. In fact, the Lesotho highlands water is of national importance to the South African population as a significant portion of the agriculture in the arid regions of the country is watered from the aqueducts from the dams on the Senqu-Orange River.

Because of their high carbon sequestration and storage capacity, the conservation of these wetlands can also play a role in mitigating global climate change. Peatlands are the second most important reservoir of carbon on earth, after oceans (Russi et al., 2013). Climate change predictions highlight that much of southern Africa will become drier (Mitchell, 2013). Basing on climate change modelling, by 2025, Namibia will probably experience problems of water quality and availability, Lesotho will be water stressed and South Africa will be facing absolute water scarcity (SADC, 2008). Thus, the conservation of these wetlands becomes indispensable.

The wetlands of Lesotho are a critical resource for livestock grazing, especially in summer when thousands of cattle, sheep and goats are seen grazing on these sensitive ecosystems (van Zinderen Bakker & Werger, 1974; Du Preez & Brown, 2011). In fact, much of the grazing in the mountains of Lesotho takes place within wetlands because they harbour the most palatable vegetation (Grab & Deschamps, 2004). The Basotho are now sometimes observed to keep their livestock in the mountains throughout the year. This is contrary to their tradition of mostly inhabiting the lowlands and taking their herds of livestock to the mountains in summer and returning them to the Lowlands during winter (Meakins & Duckett, 1993). Thus, the value of these wetlands as a grazing resource is increasingly becoming higher. The widespread degradation and loss of wetlands, because of grazing and trampling by cattle, sheep and goats, has been reported quite extensively since the 1960s (e.g. Guillarmod, 1962; van Zinderen Bakker & Werger, 1974; Backéus & Grab, 1995; Du Preez & Brown, 2011). Most of the communities described here are threatened by grazing and trampling except for the *M. macowanii* community, which is unpalatable. It is painfully unpleasant to walk through the community because of the sharp tips of the dominant *M. macowanii* (Stapf) Conert.

At least eight invasive alien species have been recorded in the wetlands and these include *Paspalum dilatatum* Poir., *Cirsium vulgare* (Savi) Ten., *Cyperus esculentus* L., *Hypochaeris radicata* L. and *P. clandestinum* Hochst. ex Chiov. While some of them occurred more frequently (e.g. *P. dilatatum* occurred in 16% of the plots and was the 11th most frequent species in the study), others occurred in relatively low frequencies (Appendix 4.2) but in large stands in a given wetland (e.g. *C. vulgare*). *Paspalum dilatatum* is the fourth most dominant wetland species in South Africa, occurring in 9.1% of all the wetland vegetation plots in the country's database (Sieben et al., 2014a). Invasive alien plants are not only among the major drivers of wetland degradation and loss in sub-Saharan Africa (Mitchell, 2013), but also use wetlands as corridors to penetrate even terrestrial plant communities (Mucina & Rutherford, 2006).

The wetlands are further threatened mainly by the economic development associated with damming, mining and infrastructure development. Thus, unsustainable utilisation of the water and other resources, as well as other anthropogenic activities, in the different catchments of the country would have an adverse effect on the wetlands and concomitantly diminish their capacity to supply the water resources. Nevertheless, montane wetlands generally remain less impacted than those in the Lowlands where human pressure is higher (Lee et al., 2015), although wetlands in general are among the most threatened ecosystems globally (Millennium Ecosystem Assessment, 2005b; Russi et al., 2013). Consequently, montane wetlands also serve as repositories and refugia for biodiversity and are also regarded as biodiversity hotspots (Chatterjee et al., 2010).

These wetlands can also potentially be threatened by climate change, which has been predicted to significantly alter the availability of water for individual montane wetlands and give rise to substantial shifts in the distribution and composition of wetlands in montane landscapes (Lee et al., 2015). Widespread ecological transitions are likely to occur at higher elevations because montane regions exhibit greater sensitivity to climate change (Ryan et al., 2014; Bentley et al., 2019). This will concomitantly give rise to widespread changes in the functioning of these wetlands and their delivery of ecosystem services. Projections have also indicated that climate change will cause potentially severe threats on peat forming wetlands (Essl et al., 2012; Lee et al., 2015). The Maloti-Drakensberg area has recently been reported to be highly vulnerable to climate change (Brand et al., 2019). In the Maloti-Drakensberg, environmental domains that are defined by climate variables are projected to change substantially as a result of climate change, particularly an increase in temperature and a concomitant decline in water availability (Brand et al., 2019). Most of the species in the Maloti-Drakensberg are already at the highest altitudes and they cannot shift any higher (Bentley et al., 2019). Furthermore, the pattern of increasing dominance of C_3 plants in communities with increasing altitude, which is evident in this study and consistent with the findings by Kotze and O'Connor (2000) in KwaZulu-Natal, South Africa, highlights a threat to the high-altitude communities because C_3 will likely be replaced with C_4 plants as the climate changes.

4.5. Conclusion

Given their important role in water resources, livestock grazing and harbouring rare and endemic species, as well as unique biodiversity, the wetlands described in the current study are of high conservation value in southern Africa, particularly in the face of increased water scarcity, climate change and unprecedented loss of biodiversity. Thus, the wetlands of Lesotho play a critical role in providing ecosystem services at the local, national and regional scales. As a result, the government of Lesotho and the Orange-Senqu River Commission (ORASECOM) have a responsibility in terms of scaling-up the efforts towards the protection of these wetlands for the sustainable provision of the benefits obtained from them. Because the wetland vegetation of a particular wetland can be used as a proxy for biodiversity of the wetland, understanding the wetland vegetation-environment patterns is important for the successful conservation planning of these ecosystems. Thus, the current study has provided baseline information, which can be useful for monitoring the wetland vegetation and concomitantly the wetlands, which are vital for the water resources of Lesotho, South Africa and Namibia.

CHAPTER 5: CLASSIFICATION, DESCRIPTION AND ENVIRONMENTAL FACTORS OF MONTANE WETLAND VEGETATION OF THE MALOTI-DRAKENSBERG REGION AND THE SURROUNDING AREAS

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Abstract

Classification and description of wetland vegetation provides an understanding of the wetland vegetation-environment relationships, as well as their spatial variation and information for water resource management and biodiversity conservation. In this study, the montane palustrine wetland vegetation types of the Maloti-Drakensberg region and surrounding areas are discussed based on a phytosociological approach. The montane subset of the National Wetland Vegetation Database of South Africa was selected and supplemented with the new data collected from the Lesotho component of the Maloti-Drakensberg region. This montane subset was collected using the Braun-Blanquet method for vegetation and recommended methods for wetland environmental data. The new vegetation data from Lesotho were collected using the same methods used for the historical data. The combined data were then analysed mainly by means of clustering and ordination techniques. Forty-two wetland plant communities were obtained from the cluster analysis and these were summarised into sixteen community groups. These community groups are diverse in terms of species richness and also exhibit significant variation along the altitudinal gradient, mainly due to variations in environmental conditions that include temperature, parent material and the amount of precipitation, among other factors. The ordination revealed that the variation in the wetland vegetation is mainly explained by altitude, longitude, latitude, nitrogen content, soil depth, inundation depth and electrical conductivity, but slope, pH, sodium content, total organic carbon, soil texture and degree of wetness are also important. In terms of species composition, high-altitude plant communities were distinctively different from those at low altitudes. Regarding distribution, montane wetland vegetation is more concentrated in the Maloti-Drakensberg region than the rest of the region, although some community groups also occurred in the lowlands of Lesotho and all the provinces of South Africa. The diversity exhibited by these wetlands, coupled with their restricted distribution at high altitudes, capacity to support endemic species, their role in water resources and provision of other ecosystem services, point to the high conservation value associated with these ecosystems.

Keywords: Biodiversity, Canonical ordination, Conservation, Maloti-Drakensberg, Montane palustrine wetlands, Plant community, Phytosociology, Vegetation classification.

5.1. Introduction

Freshwater palustrine wetlands are distinct ecosystems found in different landscapes across the globe (Mitsch & Gosselink, 2015) and can be considered as isolated "islands" within terrestrial environments. Despite being small ecosystem units in the landscape, they support vegetation that is unique and distinct from that of the surrounding terrestrial ecosystems (Sieben et al., 2017b). This distinction is attributable to the prolonged waterlogging that causes deficiency of oxygen (hypoxia) or its total absence (anoxia) in the wetland soil and consequently, chemical changes in soil characteristics (Mitsch & Gosselink, 2015).

Covering approximately 6% of the Earth's land surface, wetlands are among the most ecologically sensitive, yet also among the most productive and socio-economically valuable ecosystems worldwide (Junk et al., 2013; Mitsch & Gosselink, 2015). Wetlands contribute to the provision of ecosystem services because of their importance in the hydrological cycle and other services (Cronk & Fennessy, 2001; Mitsch & Gosselink, 2015). Given their role in supporting biodiversity, harbouring more than 40% of the world's species of all life forms (Hu et al., 2017) and forming the basis of extensive food chains that often extend beyond their boundaries, wetlands are important sites for conservation (Rolon & Maltchik, 2006).

Wetlands continue to be among the most threatened ecosystems globally (Russi et al., 2013; Junk et al., 2014). Unlike other areas where montane wetlands are less impacted in comparison to those in the lowlands (Lee et al., 2015), the wetlands in the Maloti-Drakensberg region are generally intensively utilised and degraded, with very high anthropogenic pressures, particularly in the highlands of Lesotho. However, montane wetlands are usually and generally repositories and refugia for biodiversity. Montane wetlands are also regarded as biodiversity hotspots (Chatterjee et al., 2010) and are among the most species-rich wetlands in South Africa (Sieben et al., 2014a).

Because a community of plants gives a characterisation of the habitat units within a wetland and provides a habitat for associated animals, detailed wetland vegetation descriptions of a given wetland ecosystem can be used as a proxy for biodiversity for that system (Sieben et al., 2017a). This would then serve as a good approximation of the conservation value of the ecosystem (Sieben et al., 2010a, 2016), although high-altitude wetlands are generally small and often not extensive enough to support key fauna of conservation concern. Within a single wetland, a large diversity of micro-habitats may occur and concomitantly, large differences in plant species composition may be observed (Mitsch & Gosselink, 2000). Given that it is common for just one or two plant species to dominate the wetland plant community, wetland plant communities can easily be differentiated and classified on the basis of their dominant species (Boutin & Keddy, 1993; Sieben et al., 2010a).

As a special type of freshwater palustrine wetlands, montane wetlands form an archipelago of isolated habitats embedded within terrestrial ecosystems in mountain areas (Mucina & Rutherford, 2006). They are located in the headwaters of major river basins, providing water for many transboundary rivers and playing a large role in the ecology and hydrology of downstream systems. Because of the ecosystem services they provide, they contribute to water, food and environmental security (Singha, 2011). They are often rich in endemics because many species remain isolated at high altitudes (Junk et al., 2013).

Much of the research on the montane palustrine wetlands of South Africa and Lesotho has been fragmented, focusing on small areas or affording wetlands only marginal attention in studies devoted to terrestrial vegetation (Sieben et al., 2010a, 2011). Studies that have attempted to classify and describe the high-altitude montane wetland vegetation of the Maloti-Drakensberg region (Sieben et al., 2010a, 2011; Brand et al., 2013; Janks, 2014; Brand et al., 2015) focused only on the South African side and omitted some wetland types, particularly on the Lesotho part of the region. A complete survey of the wetland vegetation of the Maloti-Drakensberg region and the surrounding areas is only feasible once the wetlands of Lesotho are included, since Lesotho accounts for almost two thirds of the Maloti-Drakensberg region (Pomela et al., 2000). The Maloti-Drakensberg region forms part of the Eastern Escarpment and comprises the Eastern Cape Drakensberg and Witteberge, the KwaZulu-Natal Drakensberg, the Lesotho Drakensberg (Maloti Mountains) and the eastern Free State (Carbutt & Edwards, 2004; Moore & Blenkinsop, 2006; Clark et al., 2011) (Figure 5.1). Moreover, the montane wetlands of Lesotho form the headwaters of one of the major international watercourses in southern Africa, the Senqu-Orange River and thus play a large role in the water resources of Lesotho, South Africa and Namibia.

The aim of the current study is to classify, describe and explore the vegetation-environment relationships of the vegetation of the montane palustrine wetlands of the Maloti-Drakensberg region and the surrounding areas using a phytosociological approach. This can be useful in informing wetland conservation planning as floristically-based approaches have been identified as powerful tools to classify wetland vegetation and identify indicators of environmental change (Mucina & Rutherford, 2006).

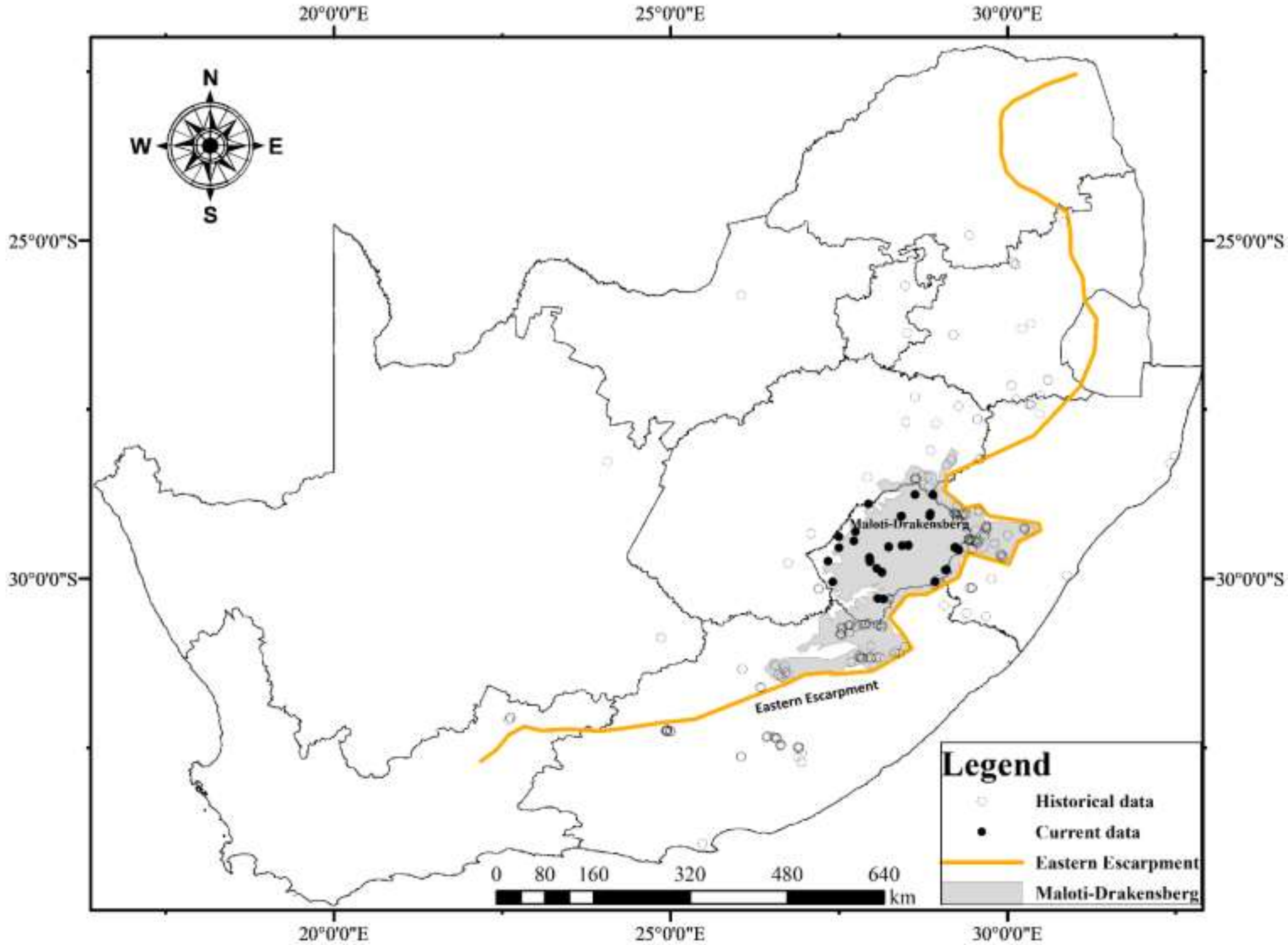

Figure 5.1: Map of the distribution of the vegetation plots included in the current study from the montane wetlands of the Maloti-Drakensberg region and surrounding areas.

5.2 Materials and Methods

5.2.1 Study design and data collection

The vegetation of the montane palustrine wetlands of the Maloti-Drakensberg region and surrounding areas was studied using two sets of data: (1) Historical wetland vegetation data from the South African part of the Maloti-Drakensberg region (Sieben et al., 2010a; Janks, 2014), representing 460 wetland vegetation plots. The selection of the plots to include in the analysis from the main database was on the basis of species composition, that is, those plots with species whose main distribution is associated with high altitudes in the Drakensberg. This dataset has been collated, together with other datasets from different types of wetlands in other parts of South Africa, into a central National Wetland Vegetation Database (Sieben et al., 2014a), (2) New vegetation data from the montane wetlands of the Lesotho part of the study area was collected by adding another 91 sample plots.

Both datasets were collected using the same methods, mainly the Braun-Blanquet method. The method involved placing plots in a stratified manner in the wetland. A 3 m × 3 m vegetation plot was placed randomly in each visually distinct and homogenous plant community of a wetland, where the species composition of the community was recorded by determining and identifying all the species present and estimating their cover using a cover-abundance scale with nine classes (van der Maarel, 1979; Omar et al., 2016). The same vegetation plot size was consistently used for both the historical and the newly collected data. The number of plots per wetland was dependent on the number of visually distinct and homogenous vegetation units in the system. Estimations of the average vegetation height in each plot were also made. The Braun-Blanquet method, as a protocol for collecting vegetation data, which has been used often in South Africa, has been in use for a long time, making effective plant community comparisons between current and historical data possible, as well as between different ecosystems (Sieben, 2011; Brown et al., 2013; Sieben et al., 2014a). The vegetation cover classes were later converted into percentage cover values following Omar et al. (2016).

For each plot, in addition to the vegetation data, a standard protocol was used to systematically measure or assess information on a number of explanatory environmental variables that have been recommended for wetland habitats (Sieben, 2011; Sieben et al., 2014a). In at least one plot per wetland, a soil sample was collected from the top 15 cm of the soil (vegetation rooting zone) and later analysed for different soil variables. This was to provide additional explanatory variables for the vegetation-environmental analysis. The plot that would be chosen for soil sampling would be the one in the most widespread distinct community, representing the greatest proportion of the wetland. While the soil samples for the historical data were analysed by the Agricultural Research Council in Pretoria, the analyses for the newly collected soil samples were performed by the Analytical Laboratory Services of the Institute for Commercial Forestry Research in Pietermaritzburg, South Africa. However, the same methods were used for the soil sample analyses for both datasets (Table 5.1).

Two of the explanatory variables, hydrogeomorphic (HGM) unit and wetness (hydroperiod), will be discussed in greater detail here. The HGM type refers to the position of a wetland within a broader landscape and is influenced by the geomorphic setting (*geomorph*- characteristics) of the wetlands, the water source and the way in which water flows in, through and out of the wetland system (*hydro*- characteristics) (Ollis et al., 2013). However, local environmental conditions prevailing have a strong influence on the growth of the plants, making the hydroperiod an important determinant of plant growth in wetland habitats (Kotze et al., 1996). Hydroperiod refers to the depth, average frequency and duration of inundation in a wetland habitat substrate and can be determined by assessing the hydrogeomorphic features in the soil (Kotze et al., 1996; Moor et al., 2017).

A summary of the environmental and soil variables included in the study, as well as the methods used for their measurement or assessment, is presented in Table 5.1. Both vegetation and explanatory data were then entered into a spreadsheet from which they were imported into PC-Ord and CANOCO programmes for different analyses.

Table 5.1: Environmental variables that were measured or assessed and included in the analysis of montane wetland vegetation of the Maloti-Drakensberg region and surrounding areas

Variable	**Type of variable**	**Method of measurement/ assessment**	**Units**	**Abbreviations or categories used in the ordination diagrams**
HGM type	Categorical	Level 4 of the South African Wetland classification system (Ollis et al., 2013): Depression, Floodplain, Valleybottom without a channel, Valleybottom with a channel, Hillslope seepage feeding a watercourse, Hillslope seepage not feeding a watercourse	NA	Depression, VB-Unchannelled valleybottom, CVB-Channelled valleybottom, H-Hillslope seepage not feeding a watercourse, HW-Hillslope seepage feeding watercourse

Wetness	Index	Assessment of soil hydromorphic features following Kotze et al. (1996). Index: 1 –temporary, 2 – seasonal, 3 – semi-permanent, 4 – Permanent	NA	Wetness
Inundation depth/ water table depth[1]	Ratio	Assessed in the field based on standing water or water table depth	cm	Inundation
Slope	Ratio	GPS (Garmin *eTrex* 30x)	deg	Slope
Altitude	Ratio	GPS (Garmin *eTrex* 30x)	m	Altitude
GPS coordinates	Ratio	GPS (Garmin *eTrex* 30x)	deg	Longitude, latitude
Soil depth	Ratio	Soil augering	cm	Soil depth
Total organic carbon*	Ratio	Walkley_Black method	%mass	TOrg_C
Soil phosphorus*	Ratio	Bray 11 method	mg/kg	P
Soil nitrogen*	Ratio	Dumas method on the Leco Trumac CNS Analyzer	mg/kg	N
Major cations*	Ratio	Ammonium acetate extraction; measurement on plasma atomic absorption spectrometer	mg/kg	Ca, K, Mg, Na
Soil pH*	Ordinal	Water extraction	NA	pH
Electrical conductivity*	Ratio	Water extraction of soil; conductivity measured on filtrate using conductivity meter	uS/cm	EC
Soil texture*	Ratio	Gravimetric pipetting method	mass	%Clay, %Silt, %Sand

*Variables measured only on the plots where soil samples were collected.

[1]Inundation represents both inundation depth (positive) and water table depth (negative)

5.2.2 Data Analysis

To explore the ecological patterns in the vegetation of the Maloti-Drakensberg region and the surrounding areas, a number of multivariate statistical techniques were employed. Three main types of analyses were used for multivariate ecological community data analysis, namely hierarchical cluster analysis (HCA), Indicator species analysis (ISA) and canonical correspondence analysis (CCA).

5.2.2.1 Classification and Indicator Species Analysis

The plant community data were subjected to classification (cluster analysis) in order to obtain wetland plant communities in the study area. Cluster analysis classifies sites, species or variables based on similarity or dissimilarity (van Tongeren, 1995). Classification enables the identification, description and ecological interpretation of plant communities from vegetation data collected in the field, as well as an understanding of the vegetation-environment relationships (Clegg & O'Connor, 2012). Thus, hierarchical agglomerative cluster analysis was performed to identify homogenous montane wetland plant communities in the Maloti-Drakensberg region and the surrounding areas. PC-Ord, Version 6.0 (McCune & Mefford, 2011) was used for the classification. This clustering was performed on non-transformed percent plant cover data. A number of combinations of the similarity indices and linkage methods, available in PC-Ord, were tested and the combination of the Sørenson's (Bray-Curtis) similarity index and Ward's linkage method gave the best interpretable classification, in terms of clearly defined clusters. Thus, the Sørenson's (Bray-Curtis) similarity index was used in the cluster analysis as the measure of similarity and the linkage method was the Ward's method. The Ward's method produces clearly defined clusters (Pla et al., 2012). The names for plant communities and community groups were derived following the guidelines by Brown et al. (2013) for phytosociological surveys in southern Africa where the dominant plant species is used to name the community and, in cases of two species names used, the dominant one comes second while the first one (adjective) is either a codominant or a diagnostic species. However, in cases where there was no clear dominant, the name was derived from the description (structure and distribution) of the community.

Indicator species analysis (ISA) was used as a formalised criterion to determine the optimal number of clusters used in the final dendrogram. This was achieved by repeating the clustering algorithm with different numbers of clusters (Dufrêne & Legendre, 1997) and the number that produced the lowest average p-value of the indicator species was then used in the final dendrogram (Peck, 2010). Indicator species analysis was also used in the characterisation of different plant communities obtained from the final clusters. Species that were considered real indicators and thus listed for each cluster were those whose indicator values (IV) were greater than 20 and were also significant ($p \leq 0.05$) in the Monte Carlo permutation test (Dufrêne & Legendre, 1997; Sieben et al., 2016c). Indicator species analysis is often used to determine the species that are more likely to be found in a given cluster than others, thus testing the fidelity of an indicator species to a given community (Nüsser, 2002; Sieben et al., 2016c). The approach calculates a species indicator value by combining the species' relative abundance and its frequency of occurrence in various communities (Dufrêne & Legendre, 1997). Thus, the technique is useful for the identification of plant communities and community groups during vegetation classification. The ISA was also carried out in PC-Ord. In addition to the indicator species analysis, for each community group, median and range of species richness, as well as the mean vegetation height were determined for the vegetation plots. Plant communities and community groups were defined following earlier studies (e.g. Sieben et al., 2016c; 2017a). Community groups were defined using a similarity level (threshold) of 40%.

5.2.2.2 Ordination

Another critical feature of the analysis was the relationship between wetland plant community groups and environmental variables. Community groups were used in the ordination instead of the individual communities because of the large number of the communities. Therefore, the vegetation data and explanatory environmental variables, as well as the community groups obtained from the classification were subjected to canonical ordination (Ter Braak & Šmilauer, 1998) to explore the influence of environmental variables on wetland plant community groups. Log-transformed percent plant cover data were used for the ordination. Canonical ordination was performed using CANOCO, Version 5.11 (Ter Braak & Šmilauer, 1998). These analyses required detailed environmental data and were thus restricted to only those vegetation plots where soil samples had been collected. The type of ordination that was performed was a constrained canonical correspondence analysis (CCA). The statistical significance of the constrained ordination (relationship of communities with environmental variables) was tested using the unrestricted Monte Carlo permutation test, available in CANOCO (Ter Braak, 1995). The aim of canonical ordination is to detect the main pattern in the relations between the species or communities and the supplied environmental variables (Ter Braak, 1995).

The CCA was chosen for the analysis because the vegetation data were compositional and the gradient was greater than 4 units (Lepš & Šmilauer, 2003). The CCA detects patterns of variation in the species data that can be explained best by the supplied environmental variables (McGarigal et al., 2000). The relationships between species or communities and environmental variables can be shown in an ordination diagram by arrows for the explanatory variables, with lengths proportional to their importance in explaining the variation and directions representing their correlation with each axis (Ter Braak & Šmilauer, 1998). The angle between the arrows indicates the correlation between individual variables (Ter Braak, 1987; Velázquez, 1994).

5.3 Results

A total of 551 montane wetland vegetation plots (460 historical plots from South Africa and 91 new plots from Lesotho) were analysed in the current study for the Maloti-Drakensberg region and surrounding areas. The distribution of the 551 vegetation plots used in the analysis is presented in Figure 5.1, which also highlights the distribution ranges of the montane wetland vegetation within the Maloti-Drakensberg region and the surrounding areas, as well as in the

Eastern Escarpment. A total of 812 plant species from 86 families were encountered in the 551 montane wetland vegetation plots.

5.3.1 Classification

Hierarchical clustering produced 42 well-defined clusters (communities), which were then organised into 16 community groups (Figure 5.2). The indicator species and the associated indicator values, as well as the dominant species and distribution of the community groups in the study area are presented in Table 5.2. The synoptic table for the classification of this montane wetland vegetation is provided in Appendix 5.1.

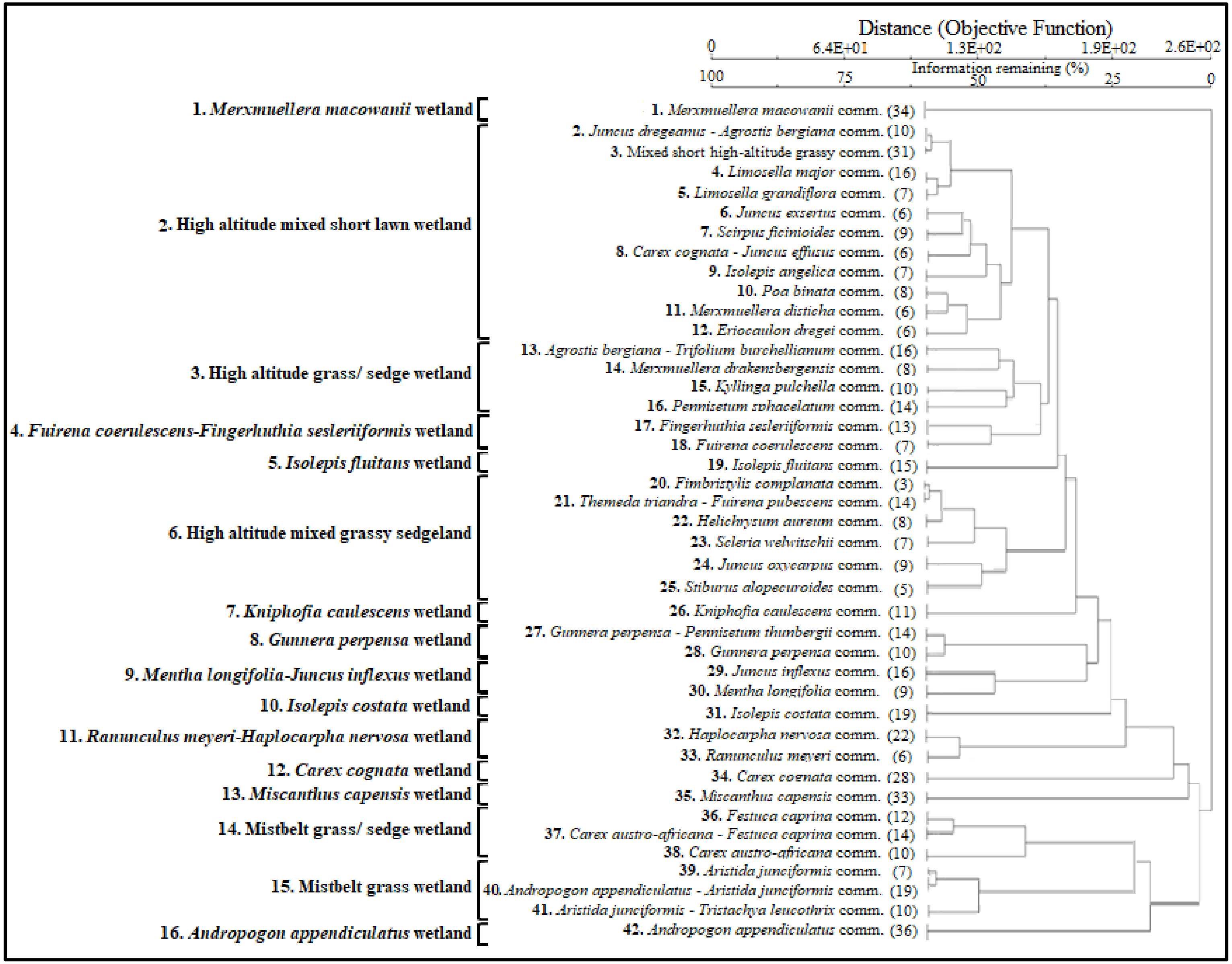

Figure 5.2: Dendrogram of the community groups and the plant communities of montane palustrine wetlands in the Maloti-Drakensberg region and surrounding areas. Numbers in brackets are the numbers of plots in that community. The left side of the dendrogram represents the 16 well-defined community groups into which the 42 plant communities have been organised.

Table 5.2: Indicator species for plant community groups of montane palustrine wetlands in the Maloti-Drakensberg region and the surrounding areas. Only species with indicator values of more than 20 and p-values less than 0.05 are presented and those with indicator values less 20 are only presented in cases where there are no species with values more than 20. All p-values less than 0.001 are given as < 0.001.

No.	No. of plots	Dominants	Distribution	Indicator species	Indicator value	P-value
1	34	*Merxmuellera macowanii*	EC, FS, KZN, LS	*Merxmuellera macowanii*	22.9	0.018
2	112	*Agrostis bergiana, Juncus dregeanus, Limosella major, Limosella longiflora, Restio sejunctus, Scirpus falsus, Limosella inflata, Ranunculus multifidus, Aponogeton junceus, Eleocharis dregeana, Schoenoxiphium lanceum, Juncus exsertus, Scirpus ficinioides, Carex cognata, Juncus effusus, Isolepis angelica, Poa binata, Merxmuellera disticha, Eriocaulon dregei*	EC, FS, KZN, LS, MP, WC	*Ranunculus baurii*	22.5	0.003
				Restio sejunctus	23.8	0.013
				Rhodohypoxis baurii	38.7	<0.001
				Limosella major	26.1	0.002
				Agrostis barbuligera	28.6	0.005
				Limosella grandiflora	49.2	<0.001
				Persicaria decipiens	23.2	0.010
				Wahlenbergia banksiana	23.4	0.009
				Juncus exsertus	80.8	<0.001
				Pseudognaphalium species	33.3	<0.001
				Senecio hypochoerideus	33.3	<0.001
				Scirpus ficinioides	92.0	<0.001
				Crassula gemmifera	23.8	<0.007
				Cynoglossum species	26.4	0.010
				Juncus effusus	86.9	<0.001
				Cotula hispida	25.7	<0.002
				Felicia uliginosa	23.5	0.010
				Helichrysum krookii	25.0	0.009
				Koeleria capensis	34.3	<0.001
				Poa binata	50.8	<0.001
				Helichrysum bellum	26.7	0.001
				Merxmuellera disticha	89.2	<0.001
				Rhodohypoxis milloides	33.3	<0.001
				Eriocaulon dregei	80.3	<0.001

3	48	*Trifolium burchellianum, Agrostis bergiana, Cotula paludosa, Isolepis angelica, Lobelia galpinii, Merxmuellera drakensbergensis, Kyllinga pulchella, Pennisetum sphacelatum*	EC, FS, KZN, LS, MP	*Agrostis bergiana*	20.9	0.005
				Cotula paludosa	30.5	<0.001
				Helichrysum odoratissimum	20.2	0.013
				Oxalis obtusa	20.0	0.018
				Satyrium bracteatum	21.4	0.017
				Gnaphalium filagopsis	20.0	0.014
				Kyllinga pulchella	25.5	0.010
				Pennisetum sphacelatum	21.0	0.002
4	20	*Fingerhuthia sesleriiformis, Fuirena coerulescens*	EC	*Fuirena coerulescens*	96.5	<0.001
				Lobelia flaccida	30.0	<0.001
5	15	*Isolepis fluitans, Limosella longiflora, Bryum* species, *Ranunculus meyeri*	EC, KZN, LS	*Agrostis subulifolia*	42.3	<0.001
				Bryum species	50.5	<0.001
				Senecio cryptolanatus	36.1	<0.001
				Thesium nigrum	20.1	0.020
6	46	*Fimbristylis complanata, Themeda triandra, Fuirena pubescens, Helichrysum aureum, Scleria welwitschii, Harpochloa falx, Juncus oxycarpus, Stiburus alopecuroides*	EC, FS, KZN, LP, MP	*Andropogon eucomus*	23.0	0.012
				Cyperus compressus	33.3	0.007
				Cyperus longus	23.8	0.007
				Cyperus prolifer	33.3	0.005
				Eleocharis acutangula	33.3	0.005
				Fimbristylis complanata	92.1	<0.001
				Nerine appendiculata	23.3	0.010
				Helichrysum kraussii	33.3	0.005
				Juncus lomatophyllus	42.3	<0.001
				Eragrostis planiculmis	33.3	0.006
				Nidorella species	40.6	<0.001
				Pycreus polystachyos	33.3	0.005
				Sorghastrum stipoides	33.3	0.005
				Vernonia natalensis	29.1	0.007
				Harpochloa falx	34.5	0.001
				Themeda triandra	21.4	0.004
				Helichrysum aureum	20.4	0.004
				Hypoxis species	38.6	<0.001
				Pennisetum macrourum	44.8	<0.001
				Scleria welwitschii	92.8	<0.001
				Nerine angustifolia	41.8	<0.001

				Stiburus alopecuroides	89.1	<0.001
				Bulbostylis contexta	20.1	0.014
7	11	*Kniphofia caulescens*	EC, KZN, LS	*Kniphofia caulescens*	21.7	0.004
8	24	*Gunnera perpensa, Pennisetum thunbergii, Kniphofia northiae*	EC, FS, KZN, LS, MP	*Pennisetum thunbergii*	19.1	0.032
				Satyrium hallackii	16.3	0.040
9	25	*Juncus inflexus, Mentha longifolia*	EC, KZN, NC, WC, LS	*Mentha aquatica*	18.4	0.031
				Nidorella auriculata	34.4	<0.001
10	19	*Isolepis costata*	EC, LS	*Isolepis costata*	29.8	0.002
11	28	*Haplocarpha nervosa, Ranunculus meyeri*	EC, KZN, LS	*Rorippa nasturtium*	18.2	0.031
				Haplocarpha nervosa	21.7	0.027
12	28	*Carex cognata*	EC, FS, GP, KZN, LS, NW	*Carex cognata*	23.7	<0.001
13	33	*Miscanthus capensis*	EC, FS, KZN, NC	*Miscanthus capensis*	23.4	0.032
				Rubus cuneifolius	20.2	0.022
				Polygonum hystriculum	41.7	<0.001
14	36	*Festuca caprina, Carex austro-africana, Andropogon appendiculatus, Pennisetum sphacelatum, Carex austro-africana, Isolepis inyangensis*	EC, FS, KZN, LS	*Wahlenbergia pallidiflora*	26.8	0.001
				Festuca caprina	23.7	0.018
				Carex austro-africana	21.6	0.008
				Schoenoplectus brachyceras	21.5	0.002
15	36	*Aristida junciformis, Andropogon appendiculatus, Tristachya leucothrix, Isolepis inyangensis*	EC, FS, KZN	*Scleria woodii*	21.6	0.009
				Senecio madagascariensis	23.8	0.007
				Ascolepis capensis	21.9	0.003
				Dierama pauciflorum	23.2	0.001
				Helichrysum epapposum	24.0	0.003
				Lobelia erinus	24.6	0.004
				Melasma scabrum	32.4	<0.001
				Commelina africana	32.6	<0.001
				Conyza albida	32.2	<0.001
				Gerbera viridifolia	70.0	<0.001
				Gladiolus papilio	47.4	<0.001
				Helictotrichon turgidulum	22.2	0.008
				Hesperantha baurii	40.6	<0.001
				Hypoxis parvifolia	60.0	<0.001
				Kniphofia ichopensis	50.0	<0.001
				Ledebouria cooperi	25.5	0.006
				Monocymbium ceresiiforme	35.1	0.001

				Panicum schinzii	50.0	<0.001
				Pycnostachys reticulata	71.1	<0.001
				Pycreus macranthus	30.5	<0.001
				Sebaea sedoides	42.9	<0.001
				Setaria pumila	55.1	<0.001
				Tritonia lineata	80.0	<0.001
				Tulbaghia natalensis	60.0	<0.001
16	36	*Andropogon appendiculatus*	EC, FS, KZN, MP	*Wahlenbergia undulata*	19.4	0.040

EC – Eastern Cape, FS – Free State, LS – Lesotho, KZN – KwaZulu-Natal, NC – Northern Cape, WC – Western Cape, NW – North West, LP – Limpopo, MP – Mpumalanga, GP – Gauteng

5.3.2 Description of the wetland plant communities

A brief description of the 16 community groups is provided. (See Table 5.2 for the full list of diagnostic species, their indicator values and the p-values). Most of the communities often exhibited signs of livestock grazing and trampling, except *Merxmuellera macowanii* community. It is noteworthy that most of the dominant species in the wetland vegetation in the study area are known to be non-clonal, for example, *Kniphofia caulescens, Gunnera perpensa, Haplocarpha nervosa, Isolepis fluitans* and *Carex cognata*, among other species.

1. *Merxmuellera macowanii* wetland

Merxmuellera macowanii wetland is a dense, medium to tall (40–100 cm high) tussock grassland, usually dominated by a single grass species (*M. macowanii*), which is also an indicator species of the community. The community is relatively low in species richness (ranging 1–22 species per 3 × 3 m plot) and at times, can be monospecific. This community is usually quite distinct within the surrounding landscape. It occurs at mid to high altitudes, ranging from 1500 to 3000 m above sea level (a.s.l.) and mostly in temporarily or seasonally wet slope seepage habitats, on shallow to deep (≥ 20 cm) peaty, loam or clay soils with slightly acidic conditions. Although this community is restricted to the Maloti-Drakensberg region, it is found throughout the region, in the Eastern Cape, Free State, KwaZulu-Natal and Lesotho.

2. High-altitude mixed short lawn wetland

High-altitude mixed short lawn wetland mostly occurs at mid to high altitudes (1300 to above 3200 m a.s.l.) but can also be found at lower altitudes. This is a heterogeneous group of communities found in different wetland types with varying degree of wetness but mainly in seasonally to permanently wet habitats. The communities mostly occur on shallow to deep (≥ 5 cm) soils with a variety of soil texture, including peat. They are open to dense, short to medium tall grasslands or sedgelands with high species richness, in the range of 2–44 per 3 × 3 m plot. The vegetation is dominated by grasses such as *Agrostis bergiana, Poa binata* and *Merxmuellera disticha* or sedges such as *Juncus dregeanus, J. exsertus, J. effusus, Eleocharis dregeana, Carex cognata, Isolepis angelica* and *Scirpus ficinioides.* The indicator species for these communities include *Rhodohypoxis baurii, Limosella major, L. grandiflora, J. exsertus, J. effusus, S. ficinioides, P. binata, M. disticha* and *Eriocaulon dregei.* Represented by 11 sub-communities, these communities have a wide distribution and are mostly found in the Eastern Cape, Free State, KwaZulu-Natal, Mpumalanga, Western Cape and Lesotho.

3. High-altitude grass/ sedge wetland

High-altitude grass/ sedge wetland is an open to dense and short to medium tall grassland or sedgeland, which occurs at mid to high altitudes (1300–3300 m a.s.l.) in temporarily to permanently wet zones of a variety of wetland types. This is also a heterogeneous group of wetland communities. There are four sub-communities in this main community. The soil, which is shallow to deep (≥ 5 cm), varies in texture and may include peat. These communities have species richness in the range of 2–19 per 3 × 3 m plot. They are characterised by species such as *Agrostis bergiana, Cotula paludosa, Satyrium bracteatum, Gnaphalium filagopsis* and *Kyllinga pulchella*. The dominants in this vegetation include *Agrostis bergiana*, the mat-forming *Trifolium burchellianum, C. paludosa, Merxmuellera drakensbergensis, Isolepis angelica, Lobelia galpinii, K. pulchella* and *Pennisetum sphacelatum.* These communities mostly occur in the Eastern Cape, Free State, KwaZulu-Natal, Mpumalanga and Lesotho.

4. *Fuirena coerulescens-Fingerhuthia sesleriiformis* wetland

Fuirena coerulescens-Fingerhuthia sesleriiformis wetland is an open to dense and short to medium tall grassland or sedgeland, dominated by the grass *Fingerhuthia sesleriiformis* and the sedge *Fuirena coerulescens*. This community has two sub-communities. These communities have a low number of species (2–15) per 3 × 3 m plot and is characterised by species such as *F. coerulescens* and *Lobelia flaccida*. Although the communities are mostly found at mid altitudes (1700–2100 m a.s.l.), they can also occur at lower altitudes. The communities are mainly associated with valleybottom or seepage wetlands, on shallow to medium deep (15-50 cm) peaty or clayey soils that are seasonally or permanently wet. This vegetation is mostly restricted to the Eastern Cape.

5. *Isolepis fluitans* wetland

Isolepis fluitans wetland is a dense and short sedgeland, which is dominated by *Isolepis fluitans, Limosella longiflora, Bryum* species and *Ranunculus meyeri.* The community has relatively low species richness, ranging 2–19 per 3 × 3 m plot. The indicator species for this community include *Agrostis subulifolia, Bryum* species, *Senecio cryptolanatus* and *Thesium nigrum.* The dominant sedge *Isolepis fluitans* forms lawn-like layer, which is often heavily grazed. The vegetation occurs at mid to high altitudes (1600–3000 m a.s.l.), mainly in the permanently inundated parts of depressions or seepage wetlands, on shallow to deep (10–80 cm) peaty soils. This community is common in the Eastern Cape, KwaZulu-Natal and Lesotho.

6. High-altitude mixed grassy sedgeland

High-altitude mixed grassy sedgeland is a heterogeneous group of wetland communities, dominated by species such as *Fimbristylis complanata*, *Themeda triandra, Fuirena pubescens*, *Helichrysum aureum, Scleria welwitschii, Harpochloa falx, Juncus oxycarpus* and *Stiburus alopecuroides.* The indicator species of these communities include *F. complanata, Cyperus compressus, Cyperus prolifer, S. alopecuroides, S. welwitschii, Pennisetum macrourum, H. falx* and *Juncus lomatophyllus.* There are six sub-communities in this main community. These communities are open to dense and short to tall grasslands or sedgelands with species richness ranging 4–22 per 3 × 3 m plot. They mainly occur at mid altitudes (1200–2300 m a.s.l.) in different wetland types with varying degree of wetness. The soils are shallow to moderately deep (20–60 cm), with varying texture, including peat. This vegetation is commonly found in the Eastern Cape, Free State, KwaZulu-Natal, Limpopo and Mpumalanga.

7. *Kniphofia caulescens* wetland

Kniphofia caulescens wetland is a conspicuous, dense and medium tall (30–50 cm) grassland, which is dominated and characterised by the geophyte *K. caulescens.* It has low species richness (2–13 per 3 × 3 m plot) but is a very attractive plant community. This wetland community is restricted to high altitudes (> 2200 m a.s.l.) and occurs mostly in seasonally to permanently wet valleybottom and valleyhead or hillslope seepage habitats, on deep (≥ 50 cm) peaty or loam soils. The community is restricted to the Maloti-Drakensberg region, in the Eastern Cape, KwaZulu-Natal and Lesotho. While this vegetation is relatively rare on the South African part of the Maloti-Drakensberg, it is still quite common in Lesotho where there are many high-altitude valleys.

8. *Gunnera perpensa* wetland

Gunnera perpensa wetland is dominated by species such as *G. perpensa, Pennisetum thunbergii* and *Kniphofia northiae.* There are two sub-communities in this community. The communities are conspicuous within their landscape. They are dense and short to medium tall grasslands that are characterised by *P. thunbergii and Satyrium hallackii.* These communities are usually species-rich, with species richness of 5–23 per 3 × 3 m plot. The vegetation is mostly found at mid to high altitudes (> 1300 m a.s.l.) in seasonally to permanently wet zones of seepage and valleybottom wetlands. The communities occur on medium to deep (≥ 30 cm) soils with varying texture, including peat. They are mostly found in the Eastern Cape, Free State, KwaZulu-Natal, Mpumalanga and Lesotho.

9. *Mentha longifolia-Juncus inflexus* wetland

Mentha longifolia-Juncus inflexus wetland is an open to dense and medium tall grassland or sedgeland, whose vegetation is dominated by *Mentha longifolia* and *Juncus inflexus*. The indicator species for these communities include *Mentha aquatica* and *Nidorella auriculata.* The species richness ranges 5-15 per 3 × 3 m plot and there are two sub-communities in this community. The communities are mostly found at mid to high altitudes (1300–2700 m a.s.l.) in temporarily, seasonally or permanently wet habitats of seepage or valleybottom wetlands on shallow to moderately deep (25–50 cm) clay or loam soils. They are mostly found in the Eastern Cape, KwaZulu-Natal, Northern Cape, Western Cape and Lesotho.

10. *Isolepis costata* wetland

Isolepis costata wetland is a dense and medium tall (30–70 cm) sedgeland, which is dominated and characterised by the sedge *I. costata*, with species richness in the range of 3–25 per 3 × 3 m plot. The community is mostly found at mid to high altitudes (1300–2700 m a.s.l.) in seasonally to permanently wet seepage or valleybottom wetlands, on shallow to deep (≥ 5 cm) soils of varying texture, including peat. It is mostly found in the Eastern Cape and Lesotho.

11. *Ranunculus meyeri-Haplocarpha nervosa* wetland

Ranunculus meyeri-Haplocarpha nervosa wetland is a dense and short to medium tall (2–40 cm), forb-dominated grassland. The dominant forbs are *H. nervosa and R. meyeri,* which are usually mat-forming and low creeping but become dominant among other forbs and grasses. Two sub-communities form this community. The communities, which have 3–20 species per 3 × 3 m plot, are characterised by *H. nervosa and Rorippa nasturtium.* They occur mostly at high altitudes (>1800 m a.s.l.), on shallow to deep (≥ 5 cm) peaty, clayey or loamy soils, in seasonally to permanently wet zones of depressions, valleyhead seepages or valleybottom wetlands. However, they can also occur at mid altitudes. These communities are commonly found in the Eastern Cape, KwaZulu-Natal and Lesotho.

12. *Carex cognata* wetland

Carex cognata wetland is a dense and medium tall (30–60 cm) sedgeland, which is dominated and characterised by *C. cognata*. It is a common sedgy community, with the number of species in the range of 1–14 per 3 × 3 m plot. This community occurs at mid to high altitudes (1300–3000 m a.s.l.) in the permanently wet zones of seepage or valleybottom wetlands, on shallow to deep (≥ 5 cm) peaty, clay or loam soils. It often occurs together with *Kniphofia caulescens* community. This community has a wide ecological amplitude and is among the most widespread in the study area. It is a high-altitude form of sedgeland, mostly found in the Eastern Cape, Free State, Gauteng, KwaZulu-Natal, North West and Lesotho.

13. *Miscanthus capensis* wetland

Miscanthus capensis wetland is dominated by a single large grass species (*M. capensis*) and characterised by *Rubus cuneifolius and Polygonum hystriculum*. The community is an open to dense and tall grassland, with 1–23 species per 3 × 3 m plot. It mostly occurs at mid to high altitudes (1300–2400 m a.s.l.) but can also occur at lower altitudes. The community is associated with shallow to moderately deep (20–60 cm) loam soils in temporarily or seasonally wet zones of different wetland types, including riverbanks. It is commonly found in the Eastern Cape, Free State, KwaZulu-Natal and Northern Cape.

14. Mistbelt grass/ sedge wetland

Mistbelt grass/ sedge wetland is dominated by species such as *Festuca caprina*, *Carex austro-africana*, *Andropogon appendiculatus*, *Pennisetum sphacelatum* and *Isolepis inyangensis*. Its indicator species include *Wahlenbergia pallidiflora*, *F. caprina*, *C. austro-africana* and *Schoenoplectus brachyceras*. This community is made up of three sub-communities. The communities are dense and short to tall (5–60 cm) grasslands or sedgelands, usually with high species richness (1–35 species per 3 × 3 m plot). They occur at mid to high altitudes (1200–3000 m a.s.l.), mostly in seepage or valleybottom wetlands and sometimes in riverbanks. The vegetation is associated with shallow to moderately deep (10–70 cm) clay, loam or peaty soils that are seasonally or permanently wet and is sometimes found on peaty soils. These communities are mostly found in the mistbelt, in the Eastern Cape, Free State, KwaZulu-Natal and the north-eastern part of Lesotho.

15. Mistbelt grass wetland

Mistbelt grass wetland is a dense and tall tufted grassland, whose dominants include *Aristida junciformis, Andropogon appendiculatus, Tristachya leucothrix* and *Isolepis inyangensis*. This community also comprises three sub-communities. These communities are characterised by species such as *Sebaea sedoides, Setaria pumila, Tritonia lineata, Tulbaghia natalensis, Panicum schinzii, Pycnostachys reticulata, Hesperantha baurii, Hypoxis parvifolia, Kniphofia ichopensis, Gerbera viridifolia* and *Gladiolus papilio*. These communities are usually rich in species, with species richness ranging from six to 22 per 3 × 3 m plot. The vegetation occurs at mid to high altitudes (1000–2400 m a.s.l.), mostly in seasonally or permanently wet zones of valleybottom wetlands or riverbanks, mainly on shallow to deep (20–60 cm) peaty, clay or loam soils. It is commonly found in the Eastern Cape, Free State and KwaZulu-Natal.

16. *Andropogon appendiculatus* wetland

Andropogon appendiculatus wetland is dominated by *A. appendiculatus* and characterised by *Wahlenbergia undulata*. It is an open to dense and tall tufted grassland, with species richness in the range of 2–23 per 3 × 3 m plot. It occurs at mid to high altitudes (1200–2300 m a.s.l.), mostly in seasonally or permanently wet zones of depressions, seepages or valleybottom wetlands. It is associated with deep (50–70 cm) clay, loam or, particularly peaty soils that are slightly acidic or neutral. This community is common and widespread throughout the mistbelt region. It is mostly found in the Eastern Cape, Free State, KwaZulu-Natal and Mpumalanga.

5.3.3 Ordination

Ninety-two of the 551 montane vegetation plots had detailed soil data. This subset of the vegetation plots represents 15 of the 16 wetland plant community groups identified from the classification presented in Figure 5.2 and only the *Isolepis fluitans* wetland (community group 5) was not represented in the subset because no soil sample had been collected from the plots representing this community. The CCA ordination diagram for only those vegetation plots with detailed soil data is presented in Figure 5.3 and the environmental variables included in the analysis account for 23.90% of the total variation. The model was significant ($F = 1.3$, $P = 0.002$) in the Monte Carlo permutation test. The results of the ordination for the entire dataset are not presented here because, without soil variables, the environmental variables included in the analysis explained a very low proportion (6.77%) of the total variation.

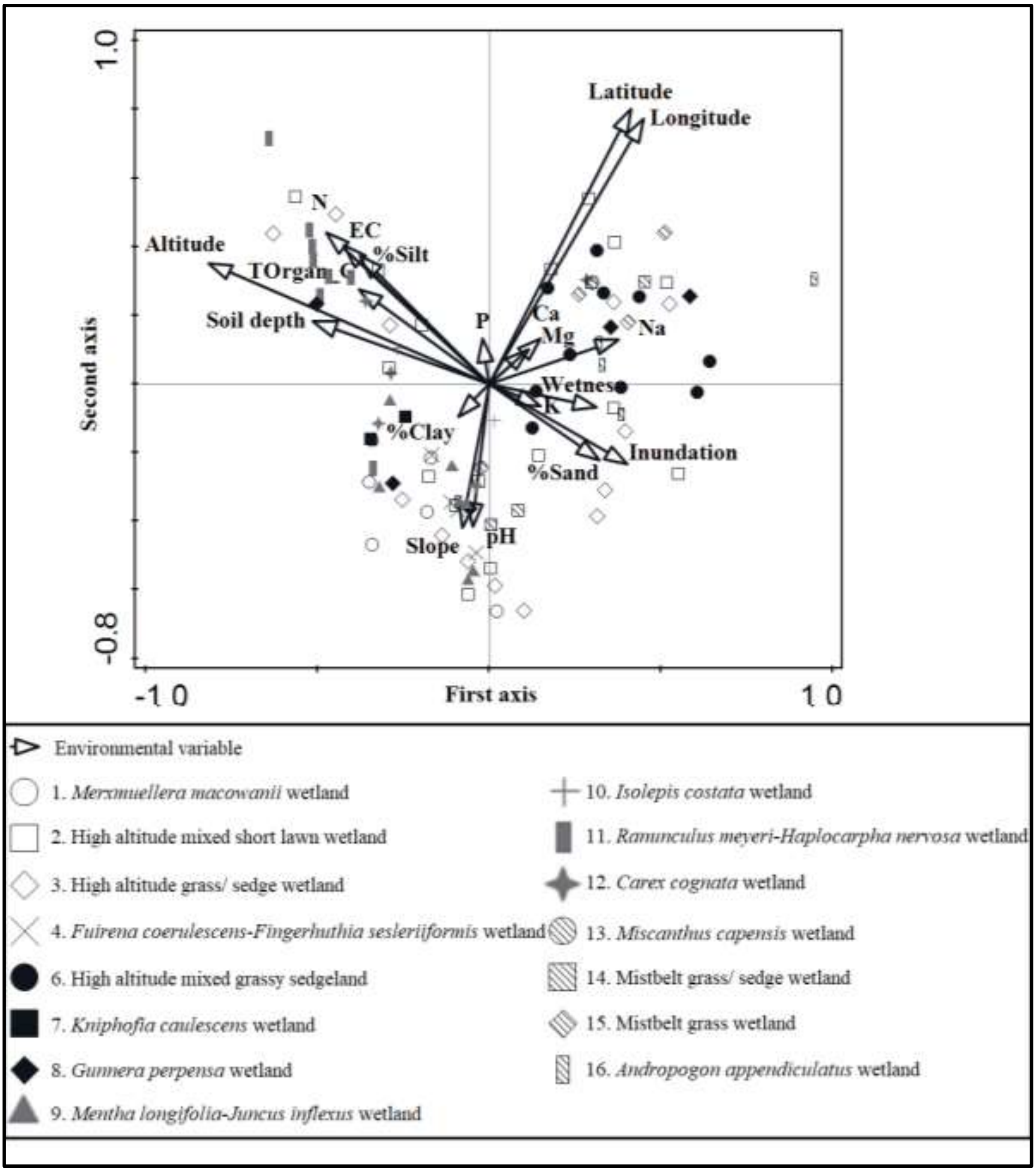

Figure 5.3: Canonical correspondence analysis ordination diagram for montane palustrine wetland plant community groups in the Maloti-Drakensberg region and surrounding areas, using plots with soil data and the same classification presented in Figure 5.2.

The first axis of the ordination has a negative correlation with altitude, soil depth and total organic carbon but is positively correlated with degree of wetness, sodium content, inundation depth and percentage sand (Figure 5.3). The plant community groups located on the left side of the ordination diagram occur at highest altitudes and are associated with a shallower water column and deeper soils while those on the right side occur on more inundated shallower soils with higher sodium levels. The degree of wetness and inundation depth are positively correlated but at the same time are both negatively associated with altitude and soil depth. However, it is noteworthy that inundation was assessed on one visit. Community groups on the left side of the ordination diagram, particularly Group 11, are associated with highest altitude areas with deep soils and high organic carbon levels. Groups 4, 7 and 9 have a relatively weak association with these factors. Those on the right side, especially groups 6, 14, 15 and 16, are associated with a higher degree of wetness and high levels of sodium, as well as more inundated sandy soils that are shallow. It is also noteworthy that the total organic carbon is strongly correlated with altitude, meaning that accumulation of peat in the wetland habitats increases with altitude in the study area. Thus, these high-altitude wetlands are good reservoirs of carbon.

The second axis is negatively associated with slope, pH and clay content but has a positive correlation with longitude, latitude, nitrogen content, electrical conductivity, silt content and phosphorus content (Figure 5.3). This means that plant community groups on the lower part of the ordination diagram are associated with steeper slope seepage habitats that have less acidic clay soils and these include groups such as 1, 4, 7, 9 and 13. Groups that include 11 and 15, which are mainly located on the upper part of the ordination diagram, are associated with less steep habitats, more acidic soils and higher phosphorus content, as well as increasing longitude and latitude, meaning that they mostly occur at the high-altitude escarpment in Lesotho and the KwaZulu-Natal border area. These communities are also associated with silt soils, rich in nitrogen, as well as high electrical conductivity.

Some groups of communities show an association with certain environmental conditions. Group 11 is strongly associated with high altitudes and high levels of nitrogen, electrical conductivity and total organic carbon, as well as deep silt soils. Group 1 is associated with slope seepages with less acidic soils. However, other groups exhibit a wide ecological amplitude as they occur on a wide range of environmental conditions and these include groups 2, 3, 8, 10 and 12. The ordination diagram also shows a very strong positive correlation of nitrogen content, electrical conductivity, total organic carbon content and silt percentage, which are in turn positively associated with altitude and soil depth but are all negatively correlated with inundation depth, percentage sand and wetness. Thus, the montane wetland plant community groups at very high altitudes also seem to be associated with deep soils and high levels of total organic carbon, nitrogen, silt and electrical conductivity. Most of the community groups occur mainly in the altitudinal range of 1300–3000 m a.s.l. While some groups are found exclusively at the highest altitudes, many have a wide altitudinal range and are widely distributed across the environmental gradients. Furthermore, the *Carex cognata* wetlands (community group 12) are more widespread than any other community group in the study area.

5.4 Discussion

Despite focusing on small areas, some of the earliest studies on the montane wetlands of the Maloti-Drakensberg region were conducted as far back as the early 1960s and 1970s (e.g. Guillarmod, 1962; van Zinderen Bakker & Werger, 1974). Since then, a number of studies covering some of the areas have been carried out in the region (e.g. Meakins & Duckett, 1993; Sieben et al., 2010a; Du Preez & Brown, 2011; Janks, 2014; Brand et al., 2015; Grundling et al., 2015). The current study has thus provided the most recent and complete assessment by providing a classification and description of the vegetation of the montane wetlands of the Maloti-Drakensberg region and surrounding areas.

All the wetlands surveyed in the current study fall in the Freshwater Wetland vegetation type of Mucina and Rutherford (2006). The distribution of the montane palustrine wetlands found in the current study is comparable to the distribution of the montane freshwater wetlands (AZf 4 and AZf 5) reported by Mucina and Rutherford (2006). The typical dominance of short grasses and sedges in these high-altitude montane wetlands observed in the current study was also reported earlier (Schwabe, 1995) and montane wetlands have been identified as some of the most species-rich in South Africa (Sieben et al., 2014a).

The large number of species recorded in the Maloti-Drakensberg region and the surrounding areas is a reflection of the high diversity of habitats in the montane wetlands in the region. The high species richness associated with high-altitude montane wetlands demonstrated in the current study is consistent with the findings from the high-altitude montane wetlands of Alborz Mountains, Iran (Kamrani et al., 2011). Sieben et al. (2010b) also reported a high diversity in the South African montane wetlands. By reporting the dominance of non-clonal species in the different communities of the high-altitude montane wetlands, the current study corroborates Sieben et al. (2010b, 2017b) who suggest that, contrary to lowland wetlands, montane wetlands are unusual in that they are characterised by less clonal dominants, higher species richness and higher functional diversity. In wetland environments, the abundance of clonal plants is negatively correlated with the overall plant species diversity, as well as with altitude (Song & Dong, 2002). Furthermore, because the usually dominant wetland plants cannot cope well with the low temperatures associated with high-altitude environments, they cannot be as competitive as usual, leaving many niches vacant, which become occupied by more forbs and rosette plants (Sieben et al., 2010b).

The CCA ordination reveals that the supplied environmental variables could explain only 23.90% of the total variation, highlighting that the rest of the variation could be explained by the environmental variables that were not included in the current study, such as micro-climate. Alternatively, it could be that the colonisation of wetland habitats by plants in the study area is by chance as explained by the lottery model of Chesson (2000). However, the amount of variation explained in the current study is comparable to other types of wetlands in South Africa (Sieben et al., 2016c, 2017a). Moreover, Brand et al. (2013) emphasise that substrates (soil or bedrock) and hydrogeological conditions have a greater influence on the floristic composition, structure and dynamics in high-altitude montane wetlands than micro-climate.

The ordination reveals that high-altitude wetlands generally have a shallower water column, perhaps because, unlike wetlands in the lowlands, high-altitude montane wetlands are usually located on hillslopes where the water tends to flow more than accumulate, which emphasises the uniqueness of these wetlands (Mucina & Rutherford, 2006; Sieben et al., 2014a). Furthermore, there is less water available because most of these wetland habitats are found on a lower-order stream or drainage line. They also tend to have smaller catchment areas than the wetlands in the lower-altitude areas. Moreover, such wetlands are fed by seepage, which means the water quality is very much determined by the geological substrate. The water in these wetlands is eutrophic because of the underlying basalt (van Zinderen Bakker & Werger, 1974). The negative correlation between the degree of wetness and soil depth can also be explained by the poor drainage associated with shallow soils.

The ordination diagram also highlights that altitude and wetness remain some of the most important factors explaining the variation in montane wetland vegetation in this region. However, while altitude operates on a larger scale, wetness operates at a local scale. The study area is generally much colder than the surrounding areas in the lowlands of Lesotho and South Africa (Sieben et al., 2014a). In the Maloti-Drakensberg Region, a temperature drop of 1 ℃ has been estimated for every 125 m gain in altitude (Pomela et al., 2000). Because of such steep environmental gradients over short distances (Körner et al., 2011), montane environments exhibit tremendous spatial variation in physical features, which translates into a large variation in terms of species diversity and distribution (Kotze & O'Connor, 2000). Lower temperatures and other environmental conditions associated with high-altitude montane areas create habitats that harbour unique plant communities (Sieben et al., 2014a).

In the Maloti-Drakensberg area, altitude has been identified as a suitable surrogate measure for climate and represents an indirect gradient, whose influence is through temperature and rainfall (Velázquez, 1994; Sieben et al., 2010a). The rainfall, which is mainly orographic in and around this area, results in many springs and seepage zones (Mucina & Rutherford, 2006; Sieben et al., 2014a). Altitude and wetness are strong predictors of montane wetland vegetation in South Africa (Kotze & O'Connor, 2000; Mucina & Rutherford, 2006; Sieben et al., 2010b), southern Brazil (Rolon & Maltchik, 2006) and in Cumbria, United Kingdom (Jones et al., 2003). Nonetheless, it is important to note that some community groups exhibit a wide ecological amplitude as they occur on a wide range of altitudes (about 1300–3000 m a.s.l.) and these include groups 2, 3, 9, 10, 12 and 14. Some species, such as *Ranunculus meyeri*, which have a wide ecological amplitude but occur at low cover at lower altitudes can achieve higher cover values at higher altitudes as they gain competitive advantage because of the lower temperatures that reduce the vigour of the usually competitive species (Sieben et al., 2010b). The influence of both altitude and slope gradients on the species composition of the vegetation in high-altitude montane wetlands has also been reported in Bulgaria, south-eastern Europe (Hájková et al., 2006) and in Alborz Mountains, India (Kamrani et al., 2011).

Rainfall in the Maloti-Drakensberg region and the surrounding areas increases with altitude, as well as with longitude (Cowling & Hilton-Taylor, 1994; Mucina & Rutherford, 2006). This explains the importance of longitude as an explanatory environmental variable for the vegetation in the Maloti-Drakensberg area as revealed on the ordination diagram. Thus, the occurrence of community groups 11 and 15 in the high-altitude escarpment in the eastern Lesotho and the KwaZulu-Natal border area implies that they require higher amount of rainfall. The negative correlation between altitude and wetness reported here was also found in the subtropical freshwater wetlands of South Africa (Sieben et al., 2016c). Overall, while altitude, longitude, latitude, nitrogen content, soil depth, inundation depth and electrical conductivity were the major factors explaining the variation in the montane wetland vegetation, slope, pH, sodium content, total organic carbon, soil texture and degree of wetness were also important variables. Moreover, the inclusion of edaphic variables in the analysis also significantly improved the proportion (from 6.77% to 23.90%) of the variation explained by the explanatory environmental variables supplied.

Given that some of the montane wetland plant communities occur at the summit plateaus, they are likely to disappear as wetland structure and function become altered and wetlands get lost in the face of climate change (Lee et al., 2015). Globally, wetlands are among the ecosystems most vulnerable to climate change and this susceptibility is amplified in montane wetlands (Lee et al., 2015) because of their high sensitivity to variations in rainfall and temperature (Chatterjee et al., 2010). Furthermore, widespread ecological transitions are likely to occur at higher altitudes as climate changes because montane regions exhibit greater sensitivity to climate change (Ryan et al., 2014). Hence, because climate change is expected to impact adversely on montane wetland vegetation (Joyce et al., 2016), climate change is one of the potential threats to the montane wetlands of the Maloti-Drakensberg. Climate change has been predicted to significantly alter the availability of water for individual montane wetlands, which will give rise to substantial future shifts in the distribution and composition of wetlands in montane landscapes (Lee et al., 2015). This will concomitantly give rise to widespread changes in the delivery of ecosystem services by these wetlands. Furthermore, climate change projections have indicated that the changing climate will cause potentially severe threats on peat forming wetlands (Essl et al., 2012; Lee et al., 2015). For example, more than 80% probability of montane wetland drying by 2080 has been predicted in Pacific Northwest, United States of America (Lee et al., 2015).

Furthermore, the study recorded some species (e.g. *Kniphofia caulescens* and *Ecomis bicolor)* and some genera (e.g. *Eumorphia* and *Rhodohypoxis*) that are endemic to the Maloti-Drakensberg region (Mucina & Rutherford, 2006), meaning that these taxa have a limited distribution. Thus, the documentation of montane wetland vegetation helps to inform sustainable conservation management plans, as well as to monitor changes in their biodiversity with time (Chatterjee et al., 2010). Despite being concentrated in the Maloti-Drakensberg region (Eastern Cape, eastern part of the Free State, western part of KwaZulu-Natal, south-western part of Mpumalanga and the Highlands of Lesotho), montane wetland vegetation occurs in the entire country of Lesotho and every province of South Africa, although the frequency declines with distance from the Maloti-Drakensberg region (Figure 5.1).

Montane wetlands in the Maloti-Drakensberg region and the surrounding areas offer a wide range of ecosystem services, especially regarding water resources and livestock grazing. The importance of these wetlands, particularly those on the Lesotho side, in the delivery of ecosystem services has been described in detail (Chapter 7). The wetlands are located in the headwaters of important catchments, which play a large role in regional and local water cycles.

The high-altitude peat forming wetlands in the Maloti-Drakensberg contribute immensely to the importance of this region as the key water reserve in southern Africa (Grundling et al., 2015). For South Africa, the water is tapped mainly through the Lesotho Highlands Water Project. Hence, the conservation of these montane wetlands is essential, especially with climate change predictions highlighting that much of southern Africa will become drier (Mitchell, 2013). According to the latest climatic models, by 2025, South Africa will be facing absolute water scarcity, Lesotho will be water stressed and Namibia is likely to experience water quality and availability problems (SADC, 2008). Because the current study also found that montane wetlands in the Maloti-Drakensberg are reservoirs of carbon, the conservation of these wetlands could also play a role in mitigating global climate change. The montane wetlands on the Lesotho part of the Maloti-Drakensberg region have been regarded for a long time as an important resource for livestock grazing (van Zinderen Bakker & Werger, 1974; Du Preez & Brown, 2011). In fact, much of the livestock grazing in the mountains of Lesotho takes place within wetlands, which harbour the most palatable vegetation (Grab & Deschamps, 2004).

Although much of the landscape at high altitudes, elsewhere, generally remains relatively undisturbed (Lee et al., 2015), the wetlands in the Maloti Drakensberg region are facing severe threats from overgrazing and concomitant soil erosion (Nüsser & Grab, 2002), coupled with economic development (diamond mining, damming and construction of infrastructure), particularly on the Lesotho part of the region. Thus, despite the high diversity and socio-economic value of these wetlands, the widespread degradation and loss of wetlands, mainly due to livestock grazing and trampling, has been reported quite extensively since the 1960s, especially in Lesotho (Guillarmod, 1962; van Zinderen Bakker & Werger, 1974; Meakins & Duckett, 1993; Backéus & Grab, 1995; Du Preez & Brown, 2011; Grundling et al., 2015). Thus, except for the *Merxmuellera macowanii* wetland community, most of the communities described in this study are threatened by grazing and trampling. The grass *M. macowanii* is unpalatable and has sharp tips, which makes it difficult to walk through the vegetation, and therefore cattle and other grazers avoid these areas (personal observation). Hence, because of their intensive utilisation and degradation, the wetlands assessed in this study might not reflect the natural potential of the vegetation but a secondary form of wetland vegetation. Nonetheless, these communities are reference types in the study area. Given the multiple threats they are facing, wetlands in the mountains are likely to change and if restoration of wetlands is to be attempted, it is useful to have such reference types, both for conservation planning and for restoration targets.

The current study has elucidated the montane wetland vegetation of a significant part of the high-lying Eastern Escarpment, which has been recognised for a long time for its contribution to biodiversity and the provision of ecosystem services in southern Africa (Carbutt & Edwards, 2004; Moore & Blenkinsop, 2006; Moore et al., 2009; Clark et al., 2011). The Eastern Escarpment, which includes some of the highest mountain summits south of Kilimanjaro, reaching over 3400 m a.s.l (Knight & Grab, 2015), hosts the most centres of plant endemism in southern Africa (Clark et al., 2011). It is also within this region that the large transboundary world heritage site (the Maloti-Drakensberg Park), covering part of South Africa and Lesotho, is situated. Therefore, the proportion of the study area under protection should be increased, particularly on the Lesotho part of the Maloti-Drakensberg.

Because of their role in water resources, livestock grazing and harbouring rare and endemic species, as well as unique biodiversity and restricted distribution in the region, the wetlands described in this study are of high conservation value in southern Africa. Plant species diversity of wetland plant communities can be used as a proxy for the diversity of other taxa within these specific wetland ecosystems. Therefore, the findings from the current study can provide important baseline information for comparing the wetland biodiversity of these wetlands in future and concomitantly, the montane wetlands of the Maloti-Drakensberg region and the surrounding areas, which underpin the water resources for Lesotho, South Africa and Namibia.

CHAPTER 6: VARIATION IN PLANT FUNCTIONAL COMPOSITION OF THE AFROMONTANE PALUSTRINE WETLANDS ALONG AN ALTITUDINAL GRADIENT IN LESOTHO

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Abstract

The understanding of montane wetlands and their ecology is essential for biodiversity conservation and sustainable delivery of ecosystem services. Plant functional traits provide information on species adaptations to specific environments and are considered the key mechanism by which species influence the functioning and subsequent provision of ecosystem services. This study characterises the Afromontane wetlands along the altitudinal gradient in Lesotho in terms of plant functional traits and composition. Wetland plant species are classified into functional types using their functional traits. Relationships of plant functional traits and functional types with environmental factors are also explored. Plant species composition was assessed using the Braun-Blanquet method and functional trait and environmental data were collected using protocols recommended in literature (Sieben, 2012; Pérez-Harguindeguy et al., 2013). The data were analysed using clustering and ordination techniques. Eight plant functional types were obtained from the functional classification of the wetland plant species. The functional types were dominated by C_3 plants, particularly in high-altitude wetlands. The wetland plant communities in Lesotho exhibit coexistence of species from different plant functional types, which highlights plant functional differentiation to exploit microhabitat heterogeneity. Both functional traits and functional composition of the communities were generally influenced by altitude, longitude and slope, and more locally by edaphic factors that include electrical conductivity, total organic carbon, nitrogen, clay percentage, potassium, magnesium and calcium. This highlights that spatial, topographic and edaphic conditions of a given site influence the functional traits and functional composition of a plant community as the plants have to adapt to the prevailing wetland conditions. The study highlights the possibility of alterations in plant functional traits, types and composition in the face of environmental alterations, including climate change. Because these wetlands support rich biodiversity and provide many ecosystem services, the current findings can contribute the information needed for biodiversity conservation planning and sustainable provision of wetland ecosystem services in Lesotho and beyond. The findings can help in predicting the impact of changes in biodiversity on ecosystem functioning and the subsequent delivery of ecosystem services.

Keywords: Community-weighted mean; Ecosystem function; Functional composition; Montane palustrine wetland; Photosynthetic pathway; Plant functional trait; Plant functional type

6.1 Introduction

Montane ecosystems are ecologically sensitive environments that offer unique habitat conditions for a great variety of plant and animal species (Du Preez & Brown, 2011). An understanding of the factors that determine the structure and functioning of these montane ecosystems is required, especially because today the focus in conservation has shifted from specific species and their habitats towards the networks of species and ecosystems (Ostfeld et al., 1997; Sieben & le Roux, 2017). Therefore, in the quest to better understand the functioning of ecosystems, plant functional traits are assessed and plant species can be categorised into functional types, based on similarities in their functional traits and role within an ecosystem (Smith et al., 1997). Plant functional traits refer to morphological, physiological and phenological attributes, measurable for individual plants, which can potentially influence individual plant fitness through their effects on survival, growth and reproduction (Violle et al., 2007; Garnier & Navas, 2012; Pérez-Harguindeguy et al., 2013). Functional traits can also affect the environment of the plants (Garnier & Navas, 2012) as the traits can modify ecosystem functioning. Plant functional types (PFTs) are groups of plant species that, because they tend to share certain key functional traits, have similar functioning at the organismal level, have similar responses to factors of the environmental and/or play similar roles in (or have similar effects on) ecosystems (Semenova & van der Maarel, 2000; Cornelissen et al., 2003). Given the correlation between plant functional composition and ecosystem functioning (Díaz & Cabido, 2001; Lavorel & Garnier, 2002), it may be possible for ecosystems that have similar functioning to be also similar in functional composition because they subject the plants to similar stresses (Sieben, 2012).

Functional traits and PFTs can be used to describe the attributes of plant communities (Keddy, 2010; Sieben, 2012; Moor et al., 2015). Plant functional traits also provide an understanding of how functional composition in general terms determines biodiversity, ecosystem processes and ecosystem services (Díaz & Cabido, 2001; Pérez-Harguindeguy et al., 2013). Thus, functional traits also enable the determination of how organisms interact with their environment (Violle et al., 2007; Garnier & Navas, 2012). The extent to which the traits of a species affect ecosystem properties and functioning depends on the abundance of the species in the community and this is described as the biomass ratio hypothesis (Gaucherand & Lavorel, 2007; Garnier & Navas, 2012).

Because functional traits can be used to determine PFTs, the latter provide an understanding of how plants are adapted to survive in particular environments (Sieben, 2012; Moor et al., 2015).

Plant functional types can also be useful for comparing the functioning of the same type of ecosystem located in different geographic locations or on different positions of an environmental gradient. Therefore, PFTs can also be valuable tools in predicting how changes in environmental factors would affect community composition and dynamics in wetlands (Boutin & Keddy, 1993; Sieben et al., 2014a). The functional classification of wetland plants can be based on a systematic measurement of different plant functional traits (Boutin & Keddy, 1993; Sieben, 2012; Sieben et al., 2014a). In such classifications, the composition of wetland vegetation in terms of the PFTs can be combined with vegetation structure and species diversity (Sieben et al., 2014a).

The occurrence of PFTs is related to environmental characteristics (Semenova & van der Maarel, 2000; Gaucherand & Lavorel, 2007). Research on the relationships of biodiversity to ecosystem functioning has revealed that functional composition is the major determinant of ecosystem processes (Gaucherand & Lavorel, 2007; Roscher et al., 2012; Zhang et al., 2015). Thus, the identification of important plant functional traits may provide a better understanding of the determinants of different ecosystem properties and processes (Roscher et al., 2012) and the subsequent ecosystem services (Sieben et al., 2017c). With the increasing demand for ecosystem services, the identification of species or groups of species that are critical in controlling the ecosystem properties responsible for ecosystem service delivery is needed for the conservation and sustainable supply of those services (de Bello et al., 2010). Wetland ecosystem services are fundamentally products of ecosystem properties and functioning, which in turn are significantly influenced by traits of the dominant species (Sieben, 2012; Moor et al., 2015; Zhang et al., 2015). However, the application of functional ecology in wetland vegetation studies is a more recent development, which is now attracting considerable attention (e.g. Sieben, 2012; Moor et al., 2015; Zhang et al., 2015; Lhotsky et al., 2016; Sieben & le Roux, 2017; Rebelo et al., 2018).

High-altitude montane wetlands are a special sub-division of freshwater palustrine wetlands that form an archipelago of isolated ecosystems embedded within terrestrial ecosystems in montane areas (Mucina & Rutherford, 2006). These wetlands are of high environmental, ecological and socio-economic importance as they provide a wide spectrum of crucial ecosystem services (Chatterjee et al., 2010). The most conspicuous and ubiquitous feature of montane palustrine wetlands, which also plays a fundamental role in their functioning, is the vegetation (Cronk & Fennessy, 2001; Sieben et al., 2010a; Gopal, 2016). Wetland vegetation consists of vascular plants, termed macrophytes, that are typically adapted to inundated or saturated conditions (Mitsch & Gosselink, 2015). The vegetation is not only influenced by, but also influences, the hydrology and edaphic factors in these ecosystems (Cronk & Fennessy, 2001; Mitsch & Gosselink, 2015). Because wetland vegetation responds quickly to changes in the local environment (Cronk & Fennessy, 2001; Sieben et al., 2014a), plant species occurring in wetlands can be used as indicators of conditions in the environment and ecological changes occurring in these ecosystems (Sieben et al., 2014a; Mitsch & Gosselink, 2015).

Given that plants need to disperse to new sites, become established and subsequently persist, all plant species face the primary challenges that include dispersal, establishment and continued existence (persistence) (Weiher et al., 1999). Persistence entails tolerating fluctuations in resource availability and the changes in the array of abiotic (e.g. pH, temperature and flooding) and biotic (e.g. competition and herbivory) conditions of a particular site (Weiher et al., 1999). Habitat filters refer to the biotic and abiotic factors that only permit species with particular traits to establish and persist in a particular location (Maire et al., 2012; Kraft et al., 2014; Li et al., 2018). Because wetland habitats require special adaptations, they support distinct plant trait combinations (Sieben, 2012). However, some species may exhibit dissimilar functional traits to reduce interspecific competition and coexist in a community, a process called niche differentiation or resource partitioning (Maire et al., 2012).

Plants occurring in montane palustrine wetlands have to either overcome or cope with the cold conditions, coupled with anoxia and low pH (Chatterjee et al., 2010; Gopal, 2016). In these montane environments, rapid changes in climate with altitude over relatively short horizontal distances are associated with dramatic changes in vegetation and hydrology (Sharma et al., 2010). This is because changes in altitude are associated with a tremendous spatial variation in physical features (Kotze & O'Connor, 2000). In the Maloti-Drakensberg area that includes Lesotho, altitude is a suitable surrogate measure for an ecological gradient, in terms of temperature and precipitation (Sieben et al., 2010b). Growth forms and types of metabolism are important strategies for plant adaptation to high-altitude wetland habitats because of the cold temperatures associated with such environments (Sieben et al., 2010b).

Lesotho has a network of wetlands across a number of environmental gradients, making it an ideal study area for assessing the relationships between functional traits and factors of the environment. The country is located in the interior parts of southern Africa and has a wide altitudinal range (1,388-3,482 m a.s.l.) over a relatively short horizontal distance (Pomela et al., 2000), which makes the entire country an Afromontane region (Carbutt, 2019). Altitude is an important environmental gradient in this country and has a substantial effect on vegetation (Kotze & O'Connor, 2000; Sieben et al., 2010b). Climate change is projected to adversely impact the wetlands and watersheds in the mountain landscapes of Lesotho (Bentley et al., 2019). Hence, because plant functional traits provide species adaptations to specific environments (Sieben et al., 2014a), understanding plant adaptations to their habitats in the Afromontane wetlands becomes critical for the conservation of biodiversity and supply of ecosystem services. Previous studies on the plant functional composition of wetlands along wetness and altitudinal gradients around this area (Kotze & O'Connor, 2000; Sieben et al., 2010b) were not based on actual measurement of plant traits and focused mainly on the neighbouring areas in South Africa.

The current study aims to characterise the montane wetlands in Lesotho in terms of plant functional traits, plant functional trait types and plant functional composition. It will do so by exploring plant trait-environment relationships along the range of wetland habitats that exist along the altitudinal gradient of the country. This will reveal the influence of environmental factors on plant functional traits and composition in high-altitude montane palustrine wetlands.

6.2 Materials and Methods

6.2.1 Assessment of vegetation and explanatory variables

In selecting wetlands for sampling, the focus was on near-pristine or pristine wetland systems, including the wetlands in protected areas, such as nature reserves and national parks. Sampling was conducted during the late summer (wet) season (February-March) in both 2017 and 2018. Details of the procedure for collecting vegetation and environmental data are provided in Chapter 4. A total of 120 vegetation plots from 30 wetlands were assessed in this study. In each wetland system, soil sampling was done in one plot that represented the most widespread plant community in the wetland. Thus, thirty of the 120 vegetation plots had detailed soil data. The different environmental variables that were recorded or assessed and incorporated in the analysis of plant functional composition in this study are presented in Table 6.1.

Table 6.1: Environmental variables that were measured or assessed and incorporated in the analysis of the functional composition of the vegetation of the Afromontane palustrine wetlands in Lesotho

Variable	Type of variable	Method of measurement/ assessment	Units	Abbreviations/ codes used in the ordination diagrams
Wetness	Index	Assessment of soil hydromorphic features[1]. Index: 1 – temporary, 2 – seasonal, 3 – semi-permanent, 4 – Permanent	NA	Wetness
Altitude	Ratio	GPS (Garmin *eTrex* 30x)	metres	Altitude
Slope	Ratio	GPS (Garmin *eTrex* 30x)	degrees	Slope
GPS coordinates	Ratio	GPS (Garmin *eTrex* 30x)	degrees	Longitude, latitude
Soil depth	Ratio	Soil augering	cm	Soil depth
Total organic carbon*	Ratio	Walkley_Black method	%mass	TOrg_C
Soil phosphorus*	Ratio	Bray 11 method	mg/kg	P
Soil nitrogen*	Ratio	Dumas method on the Leco Trumac CNS Analyzer	mg/kg	N
Soil sulphur*	Ratio	Dumas method on the Leco Trumac CNS Analyzer	mg/kg	S
Major cations*	Ratio	Ammonium acetate extraction; measurement on plasma atomic absorption spectrometer	mg/kg	Ca, K, Mg, Na
Soil pH*	Ordinal	Water extraction	NA	pH
Exchangeable acidity*	Ratio	Titration method	mmol/100g	Exch_aci
Electrical conductivity*	Ratio	Water extraction of soil; EC measured on filtrate using conductivity meter	uS/cm	Elec_con
Soil texture*	Ratio	Gravimetric pipetting method	%mass	%Clay, %Silt, %Sand

*Variables with an asterisk were measured only on the plots where soil samples were collected.

[1]Source: Kotze et al. (1996)

6.2.2 Functional trait measurement and determination

The plant functional traits, methods of measurement or assessment and the codes used during the analyses in this study are presented in Table 6.2. The functional trait measurements were made on 57 different plant species, selected on the basis of dominance (collectively covering potentially more than 50% of the plot) and frequency of occurrence in the study area (occurring in at least 20% of all the vegetation plots). Each of these plant species was collected as ten random mature individuals growing in areas receiving as much light as possible (Weiher et al., 1999; Cornelissen et al., 2003). For clonal plant species, an individual was defined as a ramet, recognized as a separately rooted above-ground unit (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013). However, for tufted species (mostly grasses and sedges), the whole tuft would be uprooted. A total of 11 quantitative morphological functional traits (Table 6.2) were assessed on the species following the methods described by Sieben (2012) and Pérez-Harguindeguy et al. (2013). The study focused on morphological traits. Seed traits were not considered because some plants did not have seeds at the time of data collection and many wetland plants are clonal, which makes their vegetative characters more important (Sieben, 2012).

Table 6.2: Plant functional traits measured on the dominant and common plant species in the Afromontane palustrine wetlands in Lesotho

Plant trait	**Scale**	**Method of measurement** (averages based on specimens from 10 mature plants)	**Units**	**Trait code**
Plant height	Ratio	Average plant height of vegetative parts	cm	P_Height
Rooting depth	Ratio	Average maximum plant rooting depth	cm	R_Depth
Shoot biomass	Ratio	Average shoot dry weight	g	S_Mass
Root biomass	Ratio	Average below-ground dry weight	g	R_Mass
Total biomass	Ratio	Average total plant dry weight	g	T_Mass
Root/shoot biomass ratio	Ratio	Average ratio of root to shoot dry weight	–	RS_Mratio
Leaf length	Ratio	Average of leaf length	cm	L_Length
Leaf width	Ratio	Average of leaf width	cm	L_Width
Leaf area	Ratio	Average area of a leaf	cm^2	L_Area
Leaf biomass	Ratio	Average leaf dry weight	g	L_Mass
Specific leaf area	Ratio	Average ratio of dry weight of a leaf to its area	cm^2/g	SLA

Ten mature whole plant individuals for each of the dominant species were uprooted carefully to obtain as much of the underground parts as possible and to prevent parts of the roots from remaining underground. The uprooted plants were carefully cleaned using water to remove the soil particles. Plant height and rooting depth were measured *in-situ* using a measuring tape as recommended by Pérez-Harguindeguy et al. (2013).

Ten leaves from representative specimens of each plant species were collected and placed in bottles containing 70% alcohol for the measurement of leaf traits. For species without true leaves, the functional equivalent of a leaf was used (e.g. a green stem or a portion of the stem) (Weiher et al., 1999). The leaves were later used for determining leaf length, leaf width, leaf area (size), specific leaf area (SLA) and leaf dry mass. Leaf length, width and area were measured using a portable CI-202 laser leaf area meter (manufactured by CID Bio-Science Inc. USA). For needle-like leaves, leaf length was measured with a measuring tape and leaf width with a Vernier calliper and the product of the two then doubled (i.e. 2 × length × width) to give leaf area (Pérez-Harguindeguy et al., 2013).

All the samples, including leaves were later placed in an oven at 70 ºC for at least 72 hours (Pérez-Harguindeguy et al., 2013). Plant biomass, including above-ground and below-ground biomass, was measured on the oven-dried specimens using AE 6801417 analytical balance (manufactured by Adam Equipment, UK). After the measurement of biomass, the plants were divided into above-ground and below-ground parts and the biomass (root/shoot) ratio was calculated. In the case of clonal species that share a single rootstock among several shoots, the overall above-ground and below-ground biomass was divided by the number of shoots. SLA was derived from the measurements made on the leaf samples.

6.2.3 Data Analysis

All datasets (functional traits, species composition and environmental data) were captured and imported into subsequent programmes for analysis, using percentage cover values (van der Maarel, 1979; Omar et al., 2016). Three types of matrices were developed from the data: (1) plots x species abundance matrix, (2) plots × environmental variables matrix, and (3) species × traits matrix (using means). The fourth, community-weighted mean (CWM) trait (plots × traits) matrix (reflecting trait means per plot, weighted by species relative abundance), was obtained by multiplying the plots × species abundance matrix by the species × traits matrix (Semenova & van der Maarel, 2000; McCune, 2015). The multiplication of the matrices was performed using PC-Ord, version 6.0 (McCune & Mefford, 2011). Three main types of analyses were then employed, namely, (1) Hierarchical cluster analysis (HCA), to classify functional groups of species based on functional trait data, (2) Constrained ordination (Redundancy Analysis – RDA), to find the correlation between community-weighted means and environmental variables, and (3) Canonical Correspondence Analysis (CCA), to reveal correlations between the occurrence of functional groups and environmental factors.

6.2.3.1 Classification

To obtain PFTs in the Afromontane palustrine wetlands in Lesotho, HCA was performed on the basis of similarity in plant functional traits (using species × traits matrix) (van Tongeren, 1995; McCune & Mefford, 2011). PC-Ord Version 6.0 was used for the cluster analysis (McCune & Mefford, 2011), with the use of Sørenson's (Bray-Curtis) similarity index and

Ward's method as the linkage method. A dendrogram was derived from this cluster analysis, which shows the relationships of the plant species on the basis of similarity in their functional traits.

To determine the plant functional composition of the wetlands, the plant species occurring in all the plots were allocated to the PFTs obtained from the classification. Those species that had not been collected for functional trait analysis were allocated to the PFTs a posteriori so that they could be included in the determination of functional composition of the plots (Díaz & Cabido, 2001; Sieben, 2012). This was done by using my knowledge of the species to allocate them into the different PFTs on the basis of their similarities in easily observable properties, such as height and growth form, to members of the PFTs. Species that could not fit well into the PFTs obtained from the cluster analysis were allocated to a separate PFT. These species represented a minor part of the total wetland vegetation cover (average of 5.56% of the vegetation plot).

6.2.3.2 Ordination

To examine the influence of environmental conditions on the abundance of certain traits and functional types, constrained canonical ordination was employed. The primary objective of performing constrained ordination was to detect the main patterns of variation in the species, functional trait or PFT data that could be explained by the supplied variables of the environment (McGarigal et al., 2000). In the ordination output, the total variation in the data set is given, which is the sum of all the eigenvalues of the axes. The relationships between plant functional traits or PFTs and environmental factors can be indicated in an ordination diagram by arrows for the explanatory variables, with lengths proportional to their relevance in explaining the variation and directions representing their correlation with the axes (Ter Braak & Smilauer, 1998). The canonical ordination was performed using CANOCO Version 5.11 (Ter Braak & Šmilauer, 1998) and only on the subset of the vegetation plots where soil samples had been taken.

Because the units of most of the functional traits were different, the CWM trait data were log-transformed prior to the ordination analysis. To explore the trait-environment relationships, the data from the CWM trait matrix (plots × traits matrix) were subjected to Redundancy Analysis (RDA) with the explanatory variable (plots × environmental variables matrix) data (Ter Braak & Šmilauer, 1998). For this, the RDA was used because the gradient of the response (CWM trait) data was small (less than four units), meaning that the response curve was linear (Lepš & Šmilauer, 2003).

For the assessment of the distribution and abundance of PFTs with respect to environmental factors, the data from the plant species abundance matrix (plots × species matrix) were also log-transformed and then subjected to CCA. The choice for CCA for the ordination was based on the fact that the response (species abundance) data were compositional and the gradient was greater than four units (Lepš & Šmilauer, 2003). The statistical significance of the constrained ordination (relationship of plant functional traits and PFTs with environmental factors) was tested using unrestricted Monte Carlo permutation test (Ter Braak, 1995).

6.3 Results

The cluster analysis classified the species into seven clusters (PFTs) (Figure 6.1). As explained in Section 6.2.3.1, the rest of the species occurring in the wetland vegetation plots were classified into the seven PFTs *a posteriori*. The eighth PFT was added, comprising species that could not fit well into the seven PFTs obtained from the classification and yet were similar to each other in terms of overall morphology. The PFTs are described in terms of their species, functional characteristics and environmental factors (Table 6.3). PFT1 was the most common in the study area, in terms of frequency of occurrence, followed by PFT2 and the least common was PFT3 (Table 6.3). Most of the wetland vegetation plots in this study exhibited coexistence of species from a number of PFTs. The dominant photosynthetic pathway of the PFTs in the study was C_3, particularly in the high-altitude wetlands.

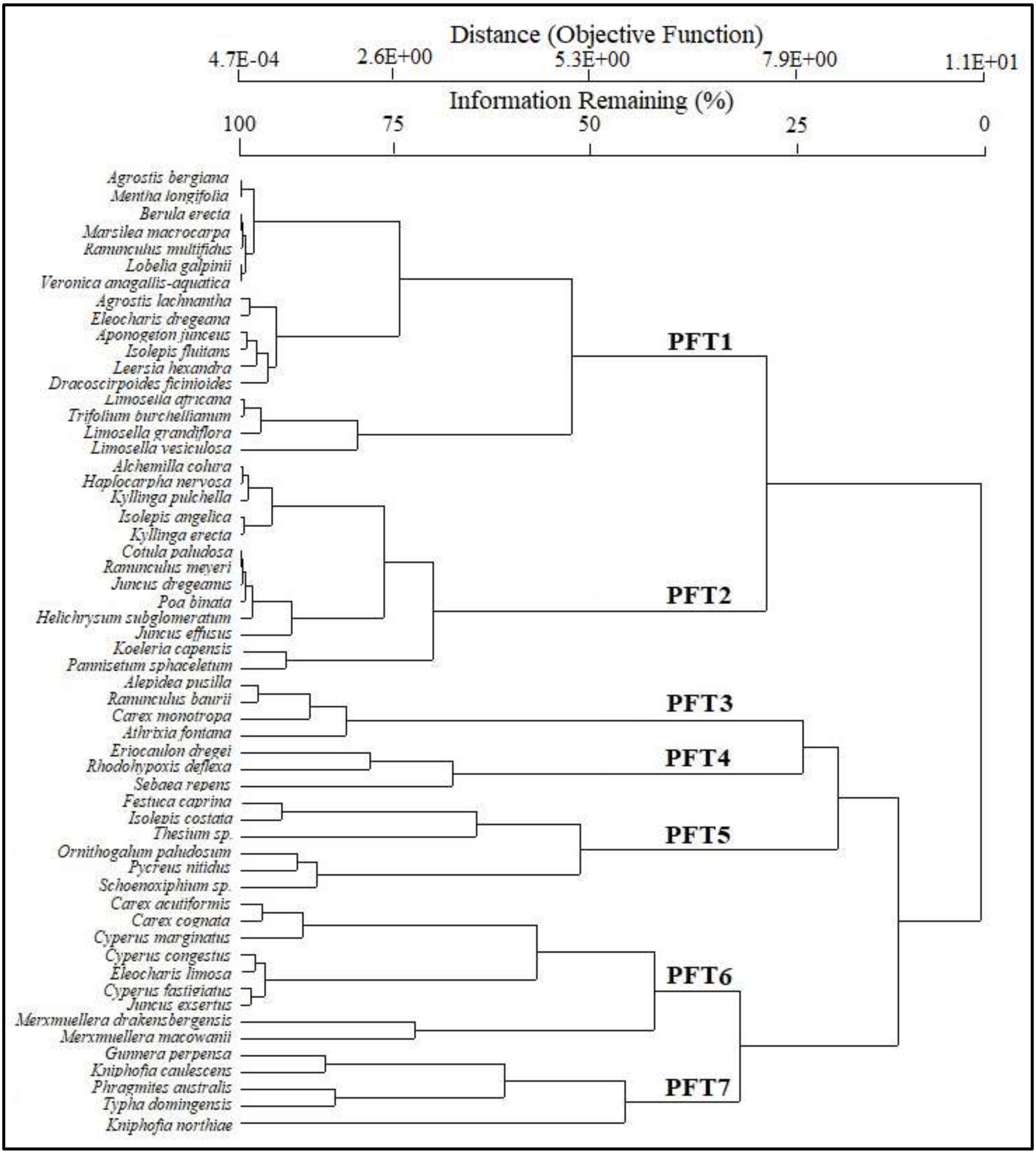

Figure 6.1: Functional classification dendrogram of plant species of the Afromontane palustrine wetlands in Lesotho, based on 11 morphological quantitative functional traits. PFT represents plant functional type.

Table 6.3: Description of the plant functional types (PFTs) obtained from the classification presented in Figure 6.1.

Plant Functional type	Plant species	No. of species	No. of families represented	Frequency (%) of PFT (n = 120 plots)	Growth form, other functional characteristics and environmental factors of the PFTs
PFT1	*Agrostis bergiana, A. lachnantha, Aponogeton junceus, Berula erecta, Dracoscirpoides ficinioides, Eleocharis dregeana, Isolepis fluitans, Leersia hexandra, Limosella africana, L. grandiflora, L. vesiculosa, Lobelia galpinii Marsilea macrocarpa, Mentha longifolia, Ranunculus multifidus, Trifolium burchellianum, Veronica anagallis-aquatica*	17	10	96.67	Relatively small, short to medium tall (< 80 cm) graminoids and forbs; mainly C_3 metabolism; shallow rooting (< 20 cm); accumulates more below-ground than above-ground biomass; very high specific leaf area (> 300) and a relatively high leaf length-to-width ratio. Exhibits a wide ecological amplitude in terms of environmental conditions. Although occurring mainly in high-altitude wetland habitats with varying soil texture and nutrient levels, this PFT also occurs in low-altitude wetlands.
PFT2	*Alchemilla colura, Cotula paludosa, Haplocarpha nervosa, Helichrysum subglomeratum, Isolepis angelica, Juncus dregeanus, J. effusus, Koeleria capensis, Kyllinga erecta, K. pulchella, Pennisetum sphacelatum, Poa binata, Ranunculus meyeri*	13	6	86.67	Relatively small, short to medium tall (< 60 cm) graminoids and forbs; has both C_3 and C_4 plants; shallow rooting (< 20 cm); accumulates more above-ground than below-ground biomass; high specific leaf area (100-300) and a relatively high leaf length-to-width ratio. Has a wide ecological amplitude in terms of environmental conditions. Despite being mainly associated with high-altitude wetland habitats with varying soil texture and nutrient levels, the PFT can also be found in low-altitude wetlands.
PFT3	*Alepidea pusilla, Athrixia fontana, Carex monotropa, Ranunculus baurii*	4	4	13.33	Short (< 40 cm) small graminoids and forbs; mainly C_3 metabolism; short rooting depth (< 20 cm); relatively low specific leaf area (30-100) and leaf length-to-width ratio; accumulates more biomass above-ground than below-ground. Found in high-altitude wetland habitats

					with sandy or silty shallow soils that are rich in nitrogen and sulphur but with low levels of electrical conductivity, calcium and magnesium.
PFT4	*Eriocaulon dregei*, *Rhodohypoxis deflexa*, *Sebaea repens*	3	3	35.83	Short (< 15 cm), small graminoids and forbs; mainly C_3 metabolism; very short rooting depth (< 10 cm); very low specific leaf area (2-10) and very small leaf length-to-width ratio; accumulates more above-ground than below-ground biomass. Occurs in high-altitude wetland habitats with sandy or silty shallow soils that are rich in nitrogen and sulphur but with low levels of electrical conductivity, calcium and magnesium.
PFT5	*Festuca caprina*, *Ornithogalum paludosum*, *Isolepis costata*, *Pycreus nitidus*, *Thesium* sp, *Schoenoxiphium* sp,	6	4	51.67	Relatively small, short (< 40 cm) graminoids and forbs; mainly C_3 metabolism; shallow rooting (< 25 cm); accumulates more below-ground than above-ground biomass; low specific leaf area (5-115) and a high leaf length-to-width ratio. Exhibits a wide ecological amplitude in terms of environmental conditions. Occurs in both high-altitude and low-altitude wetland habitats, with varying soil texture and nutrient levels but mainly in shallow soils with low levels of electrical conductivity, calcium and magnesium.
PFT6	*Carex acutiformis*, *Carex cognata*, *Cyperus congestus*, *C. marginatus*, *C. fastigiatus*, *Eleocharis limosa*, *Juncus exsertus*, *Merxmuellera drakensbergensis*, *M. macowanii*	9	3	64.17	Tall (> 40 cm) sedges and tufted grasses; both C_3 and C_4 plants; medium to deep rooting depth (> 10 cm); accumulates more below-ground than above-ground biomass; relatively high specific leaf area (40-300) and a very high leaf length-to-width ratio. Associated with a broad range of environmental conditions. Occurs in both high- and low-altitude wetland habitats, with varying soil texture and nutrient levels
PFT7	*Gunnera perpensa*, *Kniphofia caulescens*, *K. northiae*, *Phragmites australis*, *Typha domingensis*	5	4	26.67	Tall reeds, perennial and large graminoids and large forbs (> 30 cm tall); mainly C_3 metabolism; medium to deep rooting (> 10 cm); accumulates more above-ground than below-ground biomass; relatively high specific leaf area (50-300) and a relatively high leaf length-to-width ratio. Found in both high- and low-altitude wetland

					habitats with sandy or silty shallow soils that are rich in nitrogen, sulphur, calcium and magnesium with high levels of electrical conductivity.
PFT8*	–	–	–	44.17	This type has a mixture of growth forms and has both C_3 and C_4 plants; exhibits a wide ecological amplitude.

PFT – plant functional type.

Specific leaf area was measured as the ratio of leaf area to dry weight (cm^2/g)

*PFT 8 was not derived directly from the hierarchical agglomerative classification of plant species but was created by allocating species *a posteriori* to a new PFT to incorporate species that could not fit precisely into any of the seven PFTs.

The RDA ordination diagram (Figure 6.2) shows the plant functional trait-environment relationships. In this ordination of CWM functional traits, the environmental variables supplied accounted for 81.10% of this (first two ordination axes accounted for 77.17%). The permutation test indicated that the model was significant (F = 1.3, P = 0.002). The correlation of each environmental variable with each of the first four axes and the significance of the association are presented in Table 6.4.

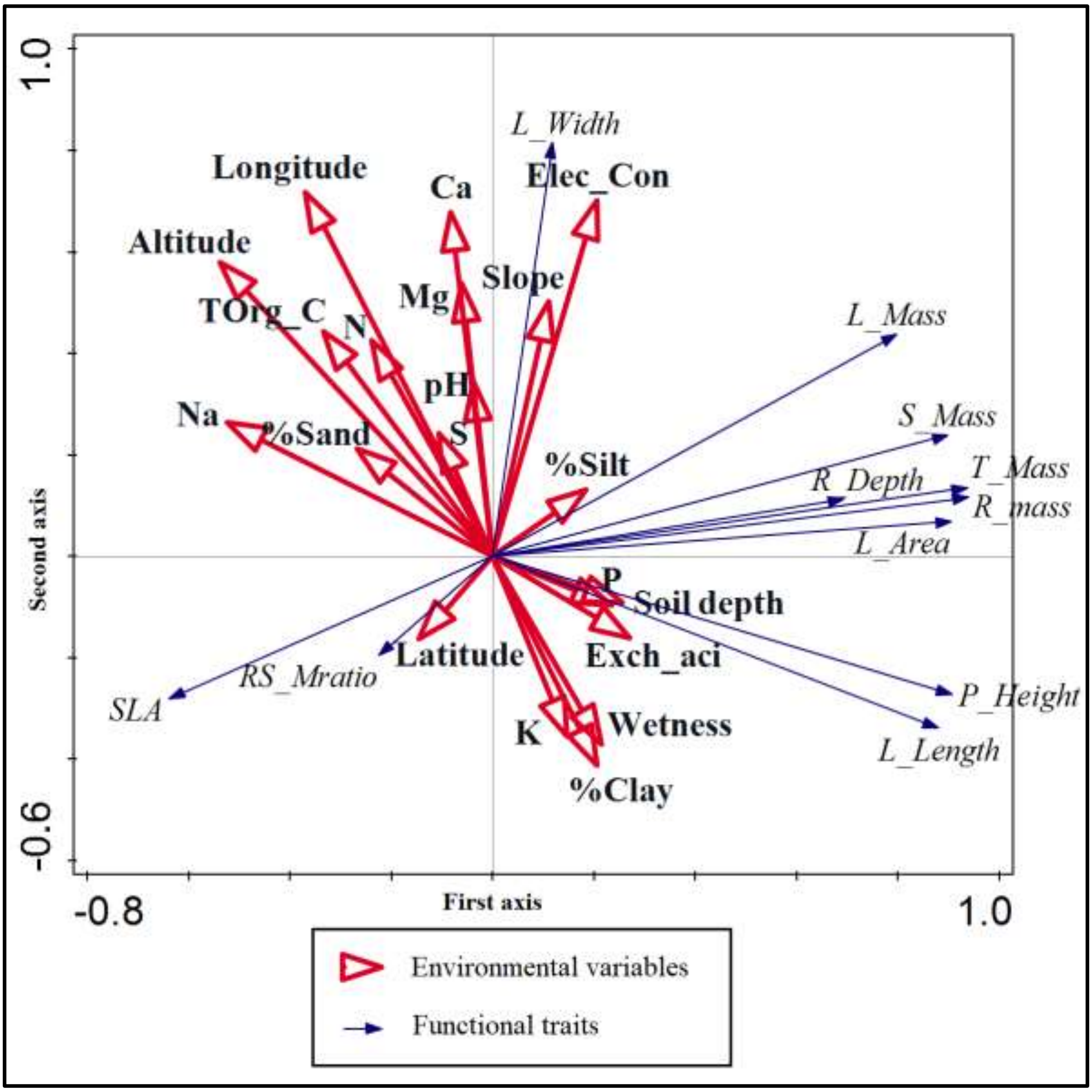

Figure 6.2: Redundancy analysis (RDA) ordination diagram for community-weighted mean functional traits and environmental variables of the Afromontane wetlands in Lesotho. See Tables 6.1 and 6.2 for the abbreviations of environmental variables and functional traits, respectively.

Table 6.4: Correlation matrix of environmental variables with the Redundancy ordination axes. The values are the product-moment correlation coefficients and significant variables are indicated with an asterisk. The permutation test on all the axes was significant (F = 1.3; P = 0.002).

	Axis 1	Axis 2	Axis 3	Axis 4	P-value
Longitude	-0.4631	0.5713	0.0082	0.2953	0.008*
Altitude	-0.5866	0.4259	0.1899	0.2680	0.002*
Soil depth	0.2496	-0.0326	-0.3995	-0.1399	0.238
Exchangeable acidity	0.3011	-0.0806	0.0381	0.1054	0.024*
Calcium	-0.2040	0.5981	-0.0172	-0.2828	0.11
Potassium	0.1758	-0.2783	0.0327	-0.5480	0.224
Magnesium	-0.1634	0.4623	-0.1511	-0.2561	0.13
Sodium	-0.5259	0.1622	0.0973	-0.0997	0.008*
Total organic carbon	-0.2854	0.3419	0.0966	0.0448	0.048*
Nitrogen	-0.3815	0.3412	0.0366	0.0535	0.044*
Electrical conductivity	0.0776	0.6464	-0.0870	0.0397	0.01*
%clay	0.2358	-0.3623	-0.1625	-0.2515	0.166
Slope	0.0230	0.4825	-0.1624	-0.0525	0.384
Wetness	0.2871	-0.2753	0.1329	0.0387	0.124

In terms of trait-environment relationships, community level SLA and root/shoot mass ratio showed a weak positive correlation with the factors altitude, sodium and percentage sand. Only leaf width was positively correlated with the second axis. While SLA and root/shoot mass ratio had a negative correlation with the first axis, the remaining functional traits showed a positive correlation. Plants with wide leaves were associated with high levels of soil electrical conductivity, magnesium and calcium, as well as with steeper slopes and low clay percentage, wetness and potassium. Tall and long-leafed species occurred in habitats with high clay percentage, wetness, potassium and exchangeable acidity and these were associated with the low-altitude wetlands in the western part of the country. These species were also deep-rooted, large-leafed and accumulated a large amount of both below and above-ground biomass. High SLA and root/shoot mass ratio were associated with sand soils high in total organic carbon, nitrogen and sodium, conditions that were associated with high-altitude wetlands in the eastern part of the country.

Figure 6.3 presents the CCA ordination of PFTs where 61.80% of the variation could be explained by the supplied explanatory variables. The Monte Carlo permutation test indicated that the model was significant (F = 3.9, P = 0.002). Clay percentage and potassium were positively correlated with the first axis, while altitude, longitude, total organic carbon, nitrogen, sulphur and slope had a negative correlation (Table 6.5). This means that the PFTs that are mainly on the right side of the ordination diagram were mainly associated with low-altitude wetland habitats with gentle slopes and clay soils that were rich in potassium but poor in nitrogen, total organic carbon and sulphur. The PFTs that are mainly on the left side of the ordination diagram (PFT3, PFT4 and PFT7) were associated with high-altitude wetland habitats with steep slopes and high levels of soil total organic carbon, nitrogen and sulphur. The second axis had a positive correlation with electrical conductivity, calcium, magnesium and soil depth, but was negatively correlated with latitude. Thus, while PFT7, which is located mainly on the upper part of the ordination diagram, was associated with deep soils that were high in electrical conductivity, calcium and magnesium levels, the two other PFTs (PFT3 and PFT4) which are located on the lower part, exhibited the opposite trend. The other PFTs, including PFT1, PFT2, PFT5, PFT6 and PFT8, occurred in a wide range of conditions in both high- and low-altitude wetland habitats. All the eight PFTs occurred in the high-altitude wetlands, with some being restricted to them and missing from the low-altitude wetlands. In addition to altitude, several other factors (e.g. longitude, electrical conductivity and total organic carbon) were among the most important predictors of both plant functional traits and PFTs.

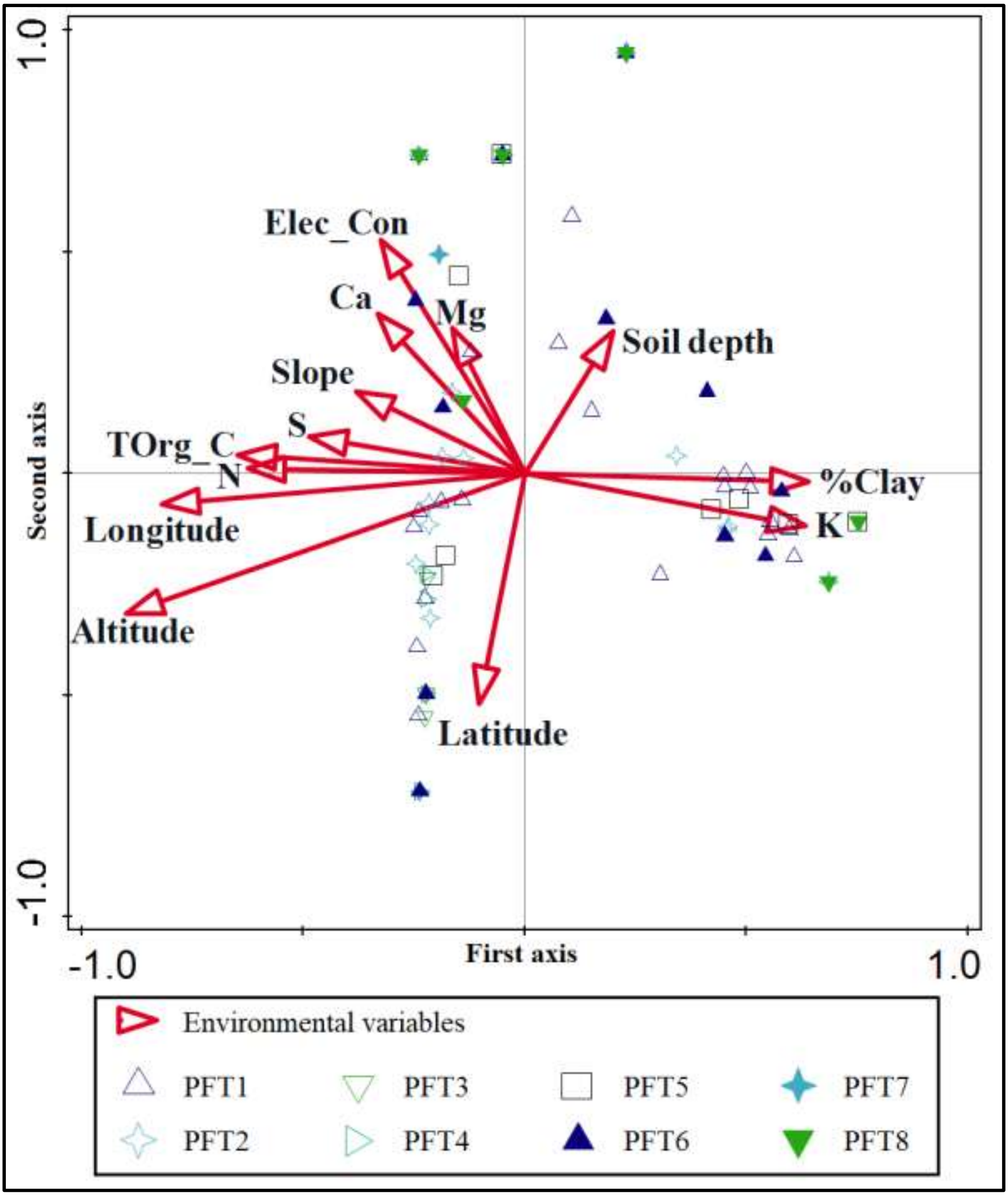

Figure 6.3: Canonical Correspondence Analysis (CCA) ordination diagram for plant functional types and environmental variables of the Afromontane palustrine wetlands in Lesotho, based on the classification presented in Figure 6.1. PFT stands for plant functional type. See Table 6.1 for the abbreviations of environmental variables.

Table 6.5: Correlation matrix of environmental variables with the canonical correspondence ordination axes. The values are the product-moment correlation coefficients and significant variables are indicated with an asterisk. The permutation test on all the axes was significant (F = 3.9; P = 0.002).

	Axis 1	Axis 2	Axis 3	Axis 4	P-value
Latitude	-0.1022	-0.5137	0.3999	0.0444	0.05*
Longitude	-0.8114	-0.0685	-0.0636	-0.0815	0.002*
Altitude	-0.8914	-0.3129	0.0688	-0.0322	0.002*
Soil depth	0.1968	0.3169	-0.3663	-0.0962	0.2
Calcium	-0.3295	0.3565	-0.0844	-0.1218	0.016*
Potassium	0.6270	-0.1168	-0.1647	0.0612	0.002*
Magnesium	-0.1613	0.3243	0.0143	-0.2659	0.156
Total organic carbon	-0.6409	0.0418	0.0055	-0.1006	0.004*
Nitrogen	-0.6195	0.0115	-0.0381	-0.1600	0.002*
Sulphur	-0.4822	0.0819	0.2741	-0.1060	0.062
Electrical conductivity	-0.3223	0.5210	0.2189	-0.0605	0.004*
%clay	0.6329	-0.0185	0.0634	-0.1333	0.004*
Slope	-0.3769	0.1832	-0.0471	-0.0127	0.3

6.4 Discussion

One important result of abiotic filtering is the typical change in species composition and their functional traits along environmental gradients (Kraft & Ackerly, 2014) and this is evident in the current study. The results of the ordination indicate differentiation of the vegetation along the altitudinal gradient and other factors of the environment in the Afromontane wetlands of Lesotho. The amount of variation explained in both ordination analyses (at least 61.80%), was higher than in other studies employing similar analyses, e.g. 13.5% (Roy et al., 2019) and 36.4% (Morandeira & Kandus, 2016). Both plant functional traits and PFTs were influenced by almost the same environmental factors that include altitude, longitude, electrical conductivity, total organic carbon, nitrogen, soil texture (particularly clay percentage), calcium, slope, potassium and magnesium.

In the current study, taxonomic diversity within PFTs was high as evidenced by the representation of at least three families in each PFT. This suggests the role of environmental filtering rather than phylogeny in wetland habitat colonisation and functional trait development (Reich et al., 2003; Roy et al., 2019). In environmental conditions with abiotic constraints such as in high altitudes, Dainese et al. (2015) suggest the possibility of evolutionary convergence of high-altitude plant species, where species with different evolutionary origins show similar functional adaptations to colder environments. There is evidence of variation in plant functional traits being strongly constrained by convergent evolution (Reich et al., 2003). The conditions of anoxia, low temperatures and low pH, which are associated with high-altitude wetland environments, tend to increase habitat filtering that species have to overcome in order to establish. This affects traits, including those that are related to the interception of light, such as SLA. However, the high taxonomic diversity within PFTs in the current study is contrary to Díaz and Cabido (1997) who report a lack of independence between PFTs and taxonomic affiliations because in their study, some functional types were dominated by a single plant family, a situation that is generally common in wetlands.

Prolonged waterlogging of the substrate, which causes anoxia in the soil and concomitant chemical changes, excludes a large variety of plants (Mitsch & Gosselink, 2015). Because of the effect of habitat filtering, dominant plant species in a community exhibit traits that are supported by habitat conditions (Maire et al., 2012). Grime (1998) highlights that, even in species-rich vegetation, most of the biomass is accounted for by only a small number of dominant species whose functional traits have an overriding influence in the community and its functioning. The biomass ratio hypothesis indicates that the degree to which the traits of a species influence ecosystem properties and functioning depends on the abundance of the species in the community (Gaucherand & Lavorel, 2007; Garnier & Navas, 2012). This implies that the resilience and resistance of ecosystems are greatly determined by the traits of the dominant plant species, where communities displaying the dominance of fast-growing plants tend to have low resistance and high resilience (Díaz & Cabido, 2001).

Some of the PFTs in this study exhibited a wide ecological amplitude and occurred in both high- and low-altitude wetland habitats. Thus, it is noteworthy that, although PFT1, PFT2, PFT3, PFT4 and PFT5 were mainly associated with high-altitude areas, some of the species (e.g. *Marsilea macrocarpa*, *Kyllinga erecta* and *K. pulchella*) from these PFTs occurred in low-altitude areas. At the same time, some of the species (*Gunnera perpensa*, *Merxmuellera drakensbergensis*, *M. macowanii*, *Kniphofia caulescens* and *K. northiae*) from the PFTs mainly associated with low-altitude areas actually occurred in high-altitude areas. While the high-altitude PFTs were mainly associated with hillslope seepages in high rainfall areas, low-altitude PFTs were mainly associated with valley bottom wetlands.

In this study, there was substantial variation in PFTs along environmental gradients, particularly along the altitudinal gradient. Thus, habitat filtering seems to be more pronounced at low altitudes where functional diversity was lower, while niche differentiation could be associated more with the high-altitude wetlands where functional diversity was higher. Semenova and van der Maarel (2000) report that many PFTs may co-exist in communities generally because complementary generative and vegetative pathways enable the plants to use different spatial and temporal ‘windows’ of their environment for growth and reproduction. Plant communities represent particular combinations of PFTs and thus each wetland vegetation plot in this study generally represented a number of PFTs, except in a few plots that were characterised by monodominance, particularly at low altitudes. This highlights plant functional diversity, particularly in the high-altitude montane wetlands. This is consistent with earlier findings where high-altitude montane wetlands have been reported to be unique in that they are characterised by higher functional diversity than those at low-altitudes (Kotze & O'Connor, 2000; Sieben et al., 2010b; 2017b). Thus, because it presents changes in climate and stresses, altitude represents an important gradient, which plays a large role in regulating species composition between wetlands through its effects on habitat diversity (Shimono et al., 2010). This implies that most wetland plant communities in the current study exhibit resource partitioning (complementarity) for coexistence. However, by finding not only plant species from different functional types coexisting in a community, but also species from the same functional type, the current study corroborates the two opposite niche-based deterministic processes: habitat filtering that predicts that most coexisting species should display similar traits; and niche differentiation that requires coexisting species to display dissimilar traits for coexistence (Maire et al., 2012).

In communities, some species are driven to converge toward an optimum trait value by habitat filtering and thus become functionally similar (Maire et al., 2012; Kraft & Ackerly, 2014) but others diverge (differentiate) to reduce interspecific competition and co-exist, thus becoming functionally dissimilar (Maire et al., 2012). Within competitive mixtures, the role of functional similarity has been emphasised for dominance, while functional dissimilarity improves species coexistence by reducing interspecific competition (Maire et al., 2012). The coexistence of different PFTs in this study suggests heterogeneity in the wetland habitats in the study area. Because the plants that are usually dominant in wetlands, such as clonal dominants (Boutin & Keddy, 1993), cannot cope well with the coldness that characterises high-altitude montane environments, they cannot achieve the usual dominance, leaving part of the niche space vacant, which then becomes available for colonisation by plants from other PFTs (Sieben et al., 2010b). In Lesotho, high-altitude areas are characterised by steep gradients over short distances

(Pooley, 2003; Körner et al., 2011) and these are associated with huge spatial variation in physical features, resulting in greater variation in terms of species (Kotze & O'Connor, 2000).

Higher SLA was associated high-altitude wetland habitats. While higher values of SLA are associated with rapid acquisition of resources, lower values are associated with a conservative strategy (Pla et al., 2012). Plant communities in high-altitude areas are dominated by species with a conservative attribute, while low-altitudes tend to select for species with an acquisitive attribute (Pla et al., 2012). This reflects the differences between plant species found in high-altitudes and those in low-altitude areas in terms of their role in ecosystem functioning. Hence, because plant functional composition is the main driver of ecosystem functioning (Roscher et al., 2012) and the subsequent ecosystem services (Sieben et al., 2017c), a variation is expected in the ecosystem services delivered most by high-altitude and low-altitude wetland ecosystems. The functioning of a species in an ecosystem is determined mainly by its capacity to capture and conserve resources, or to cope with competition and other environmental stresses (Lepš et al., 2006). This further implies that high SLA is associated with low temperatures and high rainfall in Lesotho. These results are consistent with Díaz and Cabido (1997) who found high SLA to be a common trait in the montane grasslands of central-western Argentina, where the altitude is comparable to that in Lesotho. The association of high SLA and low leaf dry mass with nutrient-rich soils found in this study is consistent with Gaucherand and Lavorel (2007) who report that fast-growing species in nutrient rich habitats usually exhibit both high SLA and low leaf dry matter content. Plants growing in nutrient-rich habitats tend to have increased resource acquisition. Because of their links to relative growth rate, these two traits indicate specific annual net primary productivity (Garnier et al., 2004).

The negative correlation between SLA and leaf dry matter content, evident in the current study (Figure 6.2), also occurs in cool-temperate herbaceous species (Pérez-Harguindeguy et al., 2013). SLA, as a proxy for relative growth rate, can also be an indicator of plant competitive ability (Weiher et al., 1999) and stress tolerance (Grime et al., 1997). While SLA is a good surrogate for the ability of a plant to use light efficiently, plant height is a good proxy for the ability to compete for light (Weiher et al., 1999). However, the pattern of high SLA being associated with high-altitude environments found in the current study is contrary to the reports of it being associated with low altitudes (Pla et al., 2012). This could be attributed to the fact that the high-altitude soils in Lesotho, which are associated with the basaltic parent material, are nutrient-rich while the sandstone-derived low-altitude soils are nutrient-poor (Mucina & Rutherford, 2006).

Competitive ability is strongly associated with plant height and above-ground biomass, while fecundity depends on above-ground vegetative biomass (Weiher et al., 1999). Thus, the negative association between root/shoot mass ratio and total biomass suggests that wetland plant species that accumulate less total biomass tend to allocate more of their resources towards root development and are characterised by reduced fecundity, a situation that is expected at high altitudes. The increase in plant rooting depth with increasing shoot mass and height highlights the need for a reliable supporting below-ground material when the shoot becomes large. The decrease in plant height (dwarfism) and leaf area with increasing altitude represents typical plant adaptations to the coldness associated with high-altitude montane environments (Sieben et al., 2010b; Dainese et al., 2015). The current study also confirms that cold stress and high radiation stress, often associated with high-altitude areas, tend to select for small leaves (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013).

Traits such as plant height, leaf size and root architecture that respond to changes in temperature or moisture availability, can also be used to predict how plant species respond to climate change (Garnier & Navas, 2012). Widespread ecological transitions are predicted to occur at high elevations as montane regions display greater sensitivity to climate change (Ryan et al., 2014). With climate change predictions indicating that a greater part of southern Africa will become drier (Mitchell, 2013) and that by 2025, Lesotho will be water stressed, changes in wetland plant species and functional composition are expected (SADC, 2008), with concomitant changes in ecosystem processes and functioning. The high-altitude wetland communities in the country, dominated mainly by PFT1, PFT2, PFT3 and PFT4 will likely experience significant reductions in their cover and abundance as the climate changes, resulting in changes to the overall wetland functioning and ecosystem service delivery. Furthermore, given that some of the wetland PFTs (e.g. PFT1) are associated with communities that mainly occur at the summit plateaus, they are likely to disappear altogether in the face of climate change (Lee et al., 2015). A recent study has also predicted community compositional changes in Lesotho because of the contraction in the range of montane plant species and the movement to higher altitudes as the climate changes (Bentley et al., 2019). The increasing dominance of C_3 photosynthetic pathway in wetland plant communities with increasing altitude in the study area (reported in Chapter 4), coupled with the dominance of this metabolism in most of the PFTs, evident in the current study, further highlights that the wetland vegetation in Lesotho faces a real threat as the climate changes, in terms of functioning.

This study has demonstrated variation in wetland plant functional traits and plant functional composition of communities along environmental gradients. The identification of groups of plants that are critical in controlling wetland ecosystem properties and functioning is important because functional composition is a good indicator of ecosystem health (Sieben, 2012; Roy et al., 2019). The impact of biodiversity changes on the delivery of ecosystem services can be assessed by identifying the vital characteristics of organisms that influence ecosystem processes and functions (de Bello et al., 2010). This is particularly so in Lesotho where the wetlands play a huge role in providing a wide spectrum of ecosystem services, including water resources, livestock grazing and crop cultivation (Chapter 7). Thus, this study can contribute to the information needed for biodiversity conservation planning and sustainable provision of wetland ecosystem services in the country and beyond.

CHAPTER 7: ECOSYSTEM SERVICES OF HIGH-ALTITUDE WETLANDS: INFLUENCE OF FUNCTIONAL TRAITS AND ENVIRONMENTAL DRIVERS IN THE LESOTHO AFROMONTANE PALUSTRINE WETLANDS

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Abstract

Although wetlands are among the most valuable ecosystems, condition and extent of wetlands is declining worldwide, to the detriment of ecosystem service delivery. This study assessed the ecosystem services provided by the Afromontane palustrine wetlands of Lesotho using the WET-EcoServices tool and explored the relationships of the services with environmental factors and plant functional traits using ordination techniques. Higher-altitude wetlands differed from the lower-altitude wetlands in the spectrum of services they deliver. These wetlands were mostly valued for carbon storage, provision of natural resources, streamflow regulation, maintenance of biodiversity and erosion control. Lower-altitude wetlands were valued for natural resources, cultivated foods, nitrate removal, phosphate trapping and streamflow regulation. The environmental factors mostly related to the delivery of ecosystem services were altitude, longitude (directly correlated with precipitation in the context of Lesotho), landscape, soil parent material, slope and soil depth. The delivery of several services was also correlated to plant functional traits, for example, carbon storage and maintenance of biodiversity were positively correlated with plant shoot mass, total plant biomass and rooting depth. The location and environmental characteristics of a given wetland within a catchment and the functional characteristics of the wetland's dominant plant species have an influence on the ecosystem services that it delivers. However, the level of threat to ecosystem services is high, especially in the lower-altitude wetlands. The threats, which are mainly anthropogenic, are mainly associated with crop cultivation, overgrazing and trampling by livestock and economic development. Thus, for sustainable provision of wetland ecosystem services, these Afromontane palustrine wetlands require urgent attention and up-scaling of the conservation efforts.

Keywords: carbon storage; ecosystem functioning; ecosystem service; montane palustrine wetland; plant functional trait; WET-EcoService

7.1 Introduction

Wetlands are among the most threatened and sensitive ecosystems, while simultaneously among the most important for biogeochemical cycles and provision of ecosystem services (Maltby & Acreman, 2011; Mitsch & Gosselink, 2015). While decreasing direct dependence on ecosystem services (ES) has been reported in developed countries, in the developing world many people still depend directly on wetland ES for their livelihoods (Maltby & Acreman, 2011; Gopal, 2016). Because of their high productivity and role in water filtration, wetlands have been described as “nature’s supermarkets” and “kidneys of the landscape”, respectively (Daryadel & Talaei, 2014; Mitsch & Gosselink, 2015). Wetlands have play a key role, directly or indirectly, in meeting all the 20 Aichi Biodiversity Targets for the Strategic Plan for Biodiversity 2011-2020 (CBD Secretariat, 2015), 75 indicators of the UN Sustainable Development Goals (SDGs), and the Paris Agreement on Climate Change (Ramsar Convention on Wetlands, 2018).

Wetland ES represent the benefits that people derive directly or indirectly from wetland ecosystems (Millennium Ecosystem Assessment, 2005b; Russi et al., 2013). Wetland ES are divided into four categories according to how they benefit society (Millennium Ecosystem Assessment, 2005b; Kotze et al., 2007; Russi et al., 2013; Mitsch & Gosselink, 2015). The four categories recognised are:

1. *Provisioning ES*, which are the tangible products (“goods”) that are delivered by the wetlands, e.g. food, fibre, freshwater, timber, natural medicines, land for cultivation and grazing for livestock;
2. *Cultural ES*, which are direct non-material benefits, including aesthetic, heritage and cultural-safeguarding values that people derive from wetland functions, e.g. spiritual enrichment, cognitive development, recreation and ecotourism, education and research, inspiration, cultural heritage, indigenous knowledge systems and aesthetics;
3. *Regulating ES*, which are indirect benefits obtained through the role of the wetlands in the regulation of ecosystem processes such as improving water quality, climate regulation, natural hazard regulation, sediment trapping, erosion control, flood reduction and streamflow regulation; and
4. *Supporting ES*, which entail the basic ecosystem processes that are required to sustain the ecosystem functions that enable wetlands to deliver the services in the other three categories. Supporting ES include biodiversity maintenance, primary production, pollination, soil formation and biogeochemical cycles.

Montane wetlands, in particular, are important in the ecology and hydrology of the local environment and the associated downstream systems (Mitsch et al., 2015; Joyce et al., 2016). Montane palustrine wetlands form an archipelago of freshwater wetlands found within terrestrial ecosystems in montane areas (Mucina & Rutherford, 2006). These wetlands are located in the headwaters of major river basins and provide water that feeds the baseflow of the rivers (Chatterjee et al., 2010). They function as simple reservoirs that store water during the wet periods and release it slowly thereafter, either through runoff or subsurface drainage (Chatterjee et al., 2010). Because of the low temperatures associated with high altitudes, resulting in low decomposition rates, montane wetlands have a capacity to store carbon and thus contribute to climate regulation (Mitsch et al., 2015; Joyce et al., 2016).

Wetland conservation and management requires an understanding of the determinants of the functioning of wetlands, their ES and value (Daryadel & Talaei, 2014; Mitsch & Gosselink, 2015; Irvine et al., 2016). A large body of research has confirmed that plant functional composition is the main driver of ecosystem processes (Garnier et al., 2004; Roscher et al., 2012; Zhang et al., 2015). Plant functional traits are considered the key mechanism by which plant species contribute to ecosystem properties (de Bello et al., 2010; Zhang et al., 2015). Thus, the identification of key plant functional traits (e.g. specific leaf area, biomass, height and rooting depth) may contribute to a better understanding of the determinants of ecosystem properties and processes (Roscher et al., 2012) and the subsequent ES (Garnier et al., 2004; de Bello et al., 2010; Sieben et al., 2017c).

In an attempt to aid informed decision-making and planning in wetland conservation, the WET-EcoServices tool was developed for assessing the services that individual palustrine wetlands provide (Kotze et al., 2007). This tool has been used in various studies to assess the ES delivered by wetlands (e.g. Arias-Hidalgo et al., 2013; Namaalwa et al., 2013; Rebelo et al., 2013, 2019). While these and other studies employed the WET-EcoServices tool on a few wetland systems (1-3), the current study is the first application of the method at a bioregional scale and is one of the few studies to explore the relationships between plant traits and ES.

The study of wetland ES in Lesotho is important because the country represents one large catchment whose services extend far beyond its boundaries. Thus, the aim of the current study is to assess the ES delivered by the Afromontane palustrine wetlands of Lesotho using the WET-EcoServices tool (Kotze et al., 2007) and to explore the relationships of the services with environmental factors and plant functional traits. The study also classifies the wetlands in terms of ecosystem service provision and compares the delivery of the services between the lower-altitude (1388 to 1800 m above sea level) and higher-altitude (above 1800 to 3482 m above sea level) wetlands. The study further assesses the level of threat to the delivery of the ES.

7.2 Study Area

This study was carried out in the country of Lesotho, which accounts for more than 60% of the Maloti-Drakensberg, spanning Lesotho and South Africa and representing a substantial part of the globally recognised Eastern Escarpment (Carbutt, 2019). Lesotho has an altitudinal range from about 1388 to 3482 m above sea level (a.s.l.) (Pomela et al., 2000). The entire Lesotho qualifies to be at least Afromontane, which Carbutt (2019) defines as occurring above 1300 m a.s.l. Owing to its altitude, the country provides a suitable area for studying ecosystem services provided by high-altitude montane palustrine wetlands. Lesotho as a country represents an entire catchment of the headwaters of the Senqu-Orange River. Directly and indirectly, Lesotho's wetlands are estimated to contribute about 30% of the total employment in the country and about 22% of its gross domestic product (Department of Environment, 2014). The indirect contribution is through the dams, hydropower generation and water provision to South Africa.

The country is divided into four major agro-ecological zones: the Lowlands (1388-1800 m a.s.l.), Foothills (above 1800 to 2000 m a.s.l.), Highlands (2000-3482 m a.s.l.) and Senqu River Valley (1400-2000 m a.s.l.), which is the narrow strip flanking the Senqu River and penetrating deep into the Highlands (Pomela et al., 2000) (Figure 7.1). The Highlands, Foothills and the part of the Senqu River Valley lying above 1,800 m a.s.l. are generally considered the highlands of the country, while the remaining part of the Senqu River Valley and the Lowlands form the lowlands (Hughes & Hughes, 1992; Kopij, 2006; Grundling et al., 2015). In terms of vegetation, the highlands region is covered by the Drakensberg Grassland, while the lowlands region is covered by the Mesic Highveld Grassland (Mucina & Rutherford, 2006). While the highlands region is mainly underlain by basalt, the lowlands are dominated by sedimentary sandstone (Hughes & Hughes, 1992; Grundling et al., 2015). Within both regions are palustrine wetlands, locally known as *Mokhoabo*. Most of the higher-altitude wetlands are seepages at the source of river systems, and most of the lower-altitude wetlands are valley-bottom systems (van Zinderen Bakker & Werger, 1974).

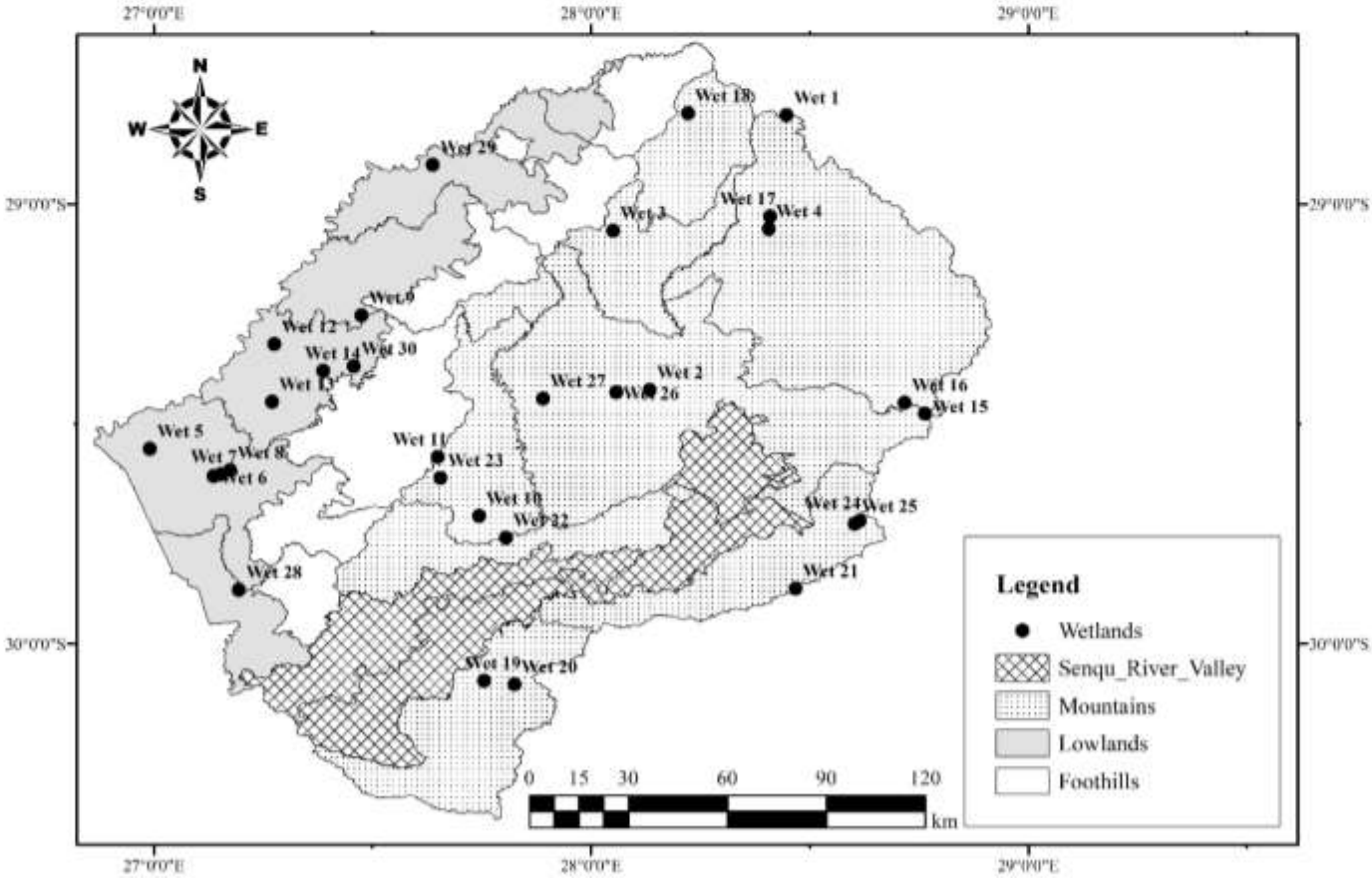

Figure 7.1: Map of Lesotho showing the distribution and location of the Afromontane palustrine wetlands assessed for ecosystem service delivery in the current study and the associated agro-ecological zones. Wet stands for wetland.

Lesotho has a temperate climate that is moderated by altitude (Kopij, 2006). The country receives abundant orographic rainfall, predominantly in summer (Sieben et al., 2010a). The rainfall, generally increasing eastwards due to rain-shadow effects, ranges from 500 mm to 2000 mm annually, with the highlands receiving a higher amount than the lowlands (Pomela et al., 2000; Pooley, 2003; Grundling et al., 2015). Generally, Lesotho's summers and winters have mean temperatures of 25 ℃ and 15 ℃, respectively (Pomela et al., 2000). During winter, rainfall is rare, but heavy snowfalls frequently occur in the mountains and the snow can persist on the ground for weeks or even months (Backéus & Grab, 1995; Pooley, 2003).

7.3 Materials and Methods

7.3.1 Study design

The two major regions of the country, which were used for the stratification in this study were the lowlands (1388 to 1800 m a.s.l.) and the highlands (above 1800 to 3482 m a.s.l.). Because the frequency of the wetlands is higher in the highlands than in the lowlands and the highlands cover more than 80% of the country's surface area, more wetlands were assessed in the former (19 wetlands) than in the latter (11 wetlands) (Figure 7.1).

7.3.2 Wetland ecosystem service assessment

The ES delivered by the wetlands of Lesotho were assessed in 30 wetlands and linked to explanatory factors in the highlands and lowlands regions. An attempt was made to cover the extent of variation in wetlands across the country, but focusing as much as possible on pristine / near-pristine systems, as well as wetlands in protected areas. Fieldwork was conducted during the rainy season period of February–March 2017 and 2018. The assessment was carried out using the WET-EcoServices tool (Kotze et al., 2007) at Level 2 (the rapid field-based level), which consists of a series of indicators that are scored on a scale of 0 (ecosystem service not provided) to 4 (maximum possible level of provision of the ecosystem service) and are supported by guidelines and rationales that help the user assess the importance of 15 different ES (Table 7.1). The tool assigns a score between 0 and 4 to each of the aspects that influence an ES being delivered and the score depends on the extent of the contribution of the aspect to the ES. Based on a number of aspects influencing a given ES, the tool then calculates an integrated score for each ES delivered by the wetland. A separate assessment of effectiveness, which is considered as the supply of a particular ES, and opportunity, which reflects the demand for the ecosystem service is calculated for all regulating services, except carbon storage and streamflow regulation (Kotze et al., 2007). The tool provides the formulae for calculating the effectiveness and opportunity scores. The effectiveness and opportunity scores are then combined into an overall importance score. The extent to which a service is supplied by a wetland based on the score is interpreted as low (< 0.5), moderately low (0.5–1.2), intermediate (1.3–2.0), moderately high (2.1–2.8) and high (>2.8) (Kotze et al., 2007).

This tool requires the wetlands to firstly be classified into hydrogeomorphic (HGM) units. The HGM type is the position of a wetland system within a wider landscape and is determined by the geomorphic setting of the wetland, the source of the water and the way in which the water enters, flows through and exits the wetland (Ollis et al., 2013). A separate assessment was made of the level of threat that a wetland faces, which is defined as the potential or impending pressures with a detrimental impact on the delivery of ES (Kotze et al., 2007). For this, the tool uses the same scoring system that it uses for the delivery of ecosystem service. This assessment would enable the comparison of wetlands in terms of the level of threat they face. However, it is noteworthy that the WET-EcoServices approach places a high level of reliance on proxies of ES rather than the direct measurement of the ecosystem processes and therefore has its limitations. Relative to pristine wetlands, the overall scores for degraded wetlands tend to be overestimated, especially for services such as flood attenuation (Rebelo et al., 2019).

Table 7.1: Ecosystem services included and assessed using the WET-EcoServices tool in the Afromontane palustrine wetlands of Lesotho. Adapted from Kotze et al. (2007)

Classification of ecosystem services		**Ecosystem services**		**Description**	**Abbreviations used in the ordination diagrams**
Indirect benefits	**Regulating and supporting benefits**	Flood attenuation		When the floodwaters in the wetland spread out and their flow slows down, the severity of floods is reduced downstream	Floodatt
		Streamflow regulation		Sustenance of streamflow during periods of low flow	Streamfl
		Water quality enhancement benefits	Sediment trapping	When the wetland traps and retains sediment carried by runoff waters	Sedmtrap
			Phosphate assimilation	Wetland removing phosphates contained in runoff waters	Phostrap
			Nitrate assimilation	Wetland removing nitrates contained in runoff waters	Nitrremo
			Toxicant assimilation	Wetland removing toxicants (e.g. metals, biocides and salts) contained in runoff waters	Toxicrem
			Erosion control	Controlling of erosion at the wetland, primarily through the protection offered by the wetland vegetation	Eroscont
		Carbon storage		Trapping of carbon in the wetland system, primarily as organic matter in the soil	Cstorage
		Biodiversity maintenance		By providing habitat and maintaining natural processes, a wetland contributes to maintaining biodiversity	Maintbio
Direct benefits	**Provisioning benefits**	Provision of water for human use		Wetlands supply water that is extracted directly and is used for domestic, agricultural or other purposes	Wsupp
		Provision of harvestable resources		Wetlands offer natural resources, including for livestock grazing, craft plants, medicinal plants, fish, etc.	Natreso
		Provision of cultivated foods		Wetlands provide areas that are favourable for food cultivation	Cultfoo
	Cultural benefits	Cultural heritage		Wetlands offer places of special cultural significance that are used for, e.g. baptism or gathering of culturally significant plants	Cultsign
		Tourism and recreation		Wetlands provide sites that are valuable for tourism and recreation, which are often associated with scenic beauty and abundance of birds	Tourrecr
		Education and research		Wetlands provide sites that are valuable for education and research	Eduresea

7.3.3 Assessment of vegetation and explanatory variables

In each wetland assessed, a 3 m × 3 m representative sample plot was placed randomly in each visually distinct and homogenous vegetation unit of the system (Brown et al., 2013; Sieben et al., 2014a). The number of sample plots per wetland depended on the number of observable distinct homogenous vegetation units in the wetland. The location of the sample plots in a randomly stratified manner in each distinctive vegetation unit of the wetland ensured that as much variation as possible in the wetland vegetation was captured. In each plot, the species composition, as well as the cover estimates of each species were assessed using the Braun-Blanquet cover-abundance scale and later converted into percentage cover values (van der Maarel, 1979; Omar et al., 2016). Additionally, estimations of vegetation structure were made, including the height and cover of all strata. The proportion of the wetland covered by each vegetation unit was also estimated. After vegetation assessment in the plots, as much of the wetland was surveyed in order to record species occurring outside the plots but within the wetland. This strategy would ensure a species list which is as complete as possible for the wetland system. In addition to the vegetation assessment in each plot, a standard protocol was also used to systematically measure or assess different variables of the environment that are recommended for wetlands (Sieben et al., 2014a) (Table 7.2).

Table 7.2: Environmental variables that were measured or assessed and incorporated in the analysis of the ecosystem services delivered by the Afromontane palustrine wetlands in Lesotho

Variable	Type of variable	Method of measurement/ assessment	Units	Code used in the ordination diagrams
HGM type	Categorical	Level 4 of the South African Wetland classification system (Ollis et al., 2013): Depression, Floodplain, Valleybottom without a channel, Valleybottom with a channel, Hillslope seepage feeding a watercourse, Hillslope seepage not feeding a watercourse	NA	D-Depression, V-unchannelled valleybottom, VC-channelled valleybottom, H-Hillslope seepage not feeding a watercourse, HW-Hillslope seepage feeding watercourse
Parent material[1]	Categorical	Assessment based on a geological map of Leketa et al. (2018)	NA	Basalt
Landscape	Index	Assessed in the field: increasing urbanisation: 1– pristine, 2 – rural, 3 – urban	NA	Urban
Aspect[2]	Ratio	GPS (Garmin *eTrex* 30x)	degrees	Northness
Altitude	Ratio	GPS (Garmin *eTrex* 30x)	metres	Altitude
Slope	Ratio	GPS (Garmin *eTrex* 30x)	degrees	Slope
GPS coordinates	Ratio	GPS (Garmin *eTrex* 30x)	degrees	Longitude, latitude
Soil depth[3]	Ratio	Soil augering	cm	Soil depth
Wetland size	ratio	Google Earth and its Earth Point tools (Earth Point, 2019)	ha	Area

[1]The parent material in Lesotho is mainly basalt and sandstone
[2]Aspect was assessed as northness during the analysis, with values ranging from 0 ^{o} to 180 ^{o}. For increasing northness, values in both the east and west of the compass were considered to increase towards the north, from 180 ^{o} to the 0 ^{o} point.
[3]Given that soil depth was measured per vegetation plot, the mean soil depth for the wetland system was used in the analysis.

7.3.4 Determination of plant functional traits

Fifty-seven plant species were collected for functional trait measurements and these were collected either because they were common in terms of frequency of occurrence in the study area (occurring in at least 10% of the vegetation plots) or because they were dominant (collectively covering potentially more than 50% of the plot). The collection of samples and measurement of functional traits were done randomly on 10 mature individuals growing in the most benign conditions (Weiher et al., 1999; Cornelissen et al., 2003). Quantitative leaf, root and whole-plant functional traits, derived from the lists suggested by Weiher et al. (1999) and Pérez-Harguindeguy et al. (2013) were assessed on the species, following the methods described by Sieben (2012) and Pérez-Harguindeguy et al. (2013). A total of 12 functional traits were assessed in the current study (Table 7.3).

Table 7.3: Plant functional traits measured on the dominant and common plant species in the Afromontane wetlands of Lesotho

Plant trait	**Scale**	**Method of measurement** (averages based on specimens from 10 mature plants)	**Units**	**Trait code**
Plant height	Ratio	Average plant height of vegetative parts	cm	S_Height
Rooting depth	Ratio	Average maximum plant rooting depth	cm	R_Depth
Shoot biomass	Ratio	Average shoot dry weight	g	S_Mass
Root biomass	Ratio	Average below-ground dry weight	g	R_Mass
Total biomass	Ratio	Average total plant dry weight	g	T_Mass
Root/shoot biomass ratio	Ratio	Average ratio of root to shoot dry weight	g/g	RS_Mratio
Leaf length	Ratio	Average of leaf length	cm	L_Length
Leaf width	Ratio	Average of leaf width	cm	L_Width
Leaf length/ width ratio	Ratio	Average ratio of length to width of a leaf	cm/cm	LL/W_Ratio
Leaf area	Ratio	Average area of a leaf	cm^2	L. Area
Leaf biomass	Ratio	Average leaf dry weight	g	L_Mass
Specific leaf area	Ratio	Average ratio of one sided area of a fresh leaf to its dry weight	cm^2/g	SLA

Leaf area was measured using CI-202 leaf area meter while length and biomass were measured with a measuring tape and AE 6801417 analytical balance, respectively.

7.3.5 Data Analysis

For each wetland system, the scores from the different indicators were used to calculate the overall scores of each ES using the Excel spreadsheets accompanying the WET-EcoServices tool (Kotze et al., 2007). To assess the supply and demand of specific ES wherever possible, the effectiveness and opportunity scores were also calculated separately for most of the regulating services (Kotze et al., 2008). The wetlands were classified into groups with similar capacity to deliver ES, using agglomerative hierarchical cluster analysis (HCA) in the Program PAST 3.20 (Hammer et al., 2001). Using HCA would enable groups of wetlands to have sub-groups, which would allow wetlands with higher similarity or dissimilarity to be determined. The similarity index used was Euclidean distance (one of the most common distance measures) and the linkage algorithm was the Ward's method. The percentage cover value of each plant species in each vegetation unit was multiplied by the proportion of that unit of vegetation in the wetland system. An estimate of the abundance of each of the plant species in the wetland system was then obtained by summing the new cover values of each species from all the vegetation units in the wetland. This resulted in a wetlands × species abundance matrix. Community-weighted plant functional trait means (CWM) for the wetlands (Garnier et al., 2004; McCune, 2015) were then calculated by means of multiplying the wetlands × species abundance matrix by the species × traits matrix (Semenova & van der Maarel, 2000; McCune, 2015) to get a CWM trait (wetlands × traits) matrix (reflecting trait means per wetland weighted by species relative abundance). The multiplication of the matrices was performed using PC-Ord 6.0 (McCune & Mefford, 2011). In addition, species richness and mean vegetation height and cover for each wetland were determined. The Shannon-Weiner and evenness indices were also calculated for each wetland.

The explanatory variables that were examined as having an influence on the delivery of ES included environmental variables and community-weighted functional traits. This examination was done by subjecting the data on ecosystem service delivery and explanatory variables to canonical ordination (Ter Braak & Šmilauer, 1998). Redundancy Analysis (RDA) was chosen because the response data were compositional and had a gradient less than four units long, which indicates that the dataset was heterogeneous (Lepš & Šmilauer, 2003). The RDA was performed in the program Canoco 5.11 (Ter Braak & Šmilauer, 1998), separately for three sets of explanatory variables: the environmental data (Table 7.2), the community-weighted plant functional traits (Table 7.3) and attributes of community structure (vegetation height and total cover) and measures of diversity. The statistical significance of this ordination was tested using an unrestricted Monte Carlo permutation test (Ter Braak, 1995). The total proportion of the variation explained by the supplied explanatory variables can be calculated as the sum of the canonical eigenvalues divided by the Total Inertia, which indicates the total variation in the dataset (Ter Braak, 1995). For all the wetlands in each of the two regions (lower-altitude and higher-altitude), an overall mean threat score was also calculated. To analyse the relationship between the level of threat to ES and altitude, a logistic regression model was performed in the program PAST 3.20 (Hammer et al., 2001). This model was chosen because the threat level (response variable) was a bounded variable.

7.4 Results

7.4.1 Ecosystem service delivery by the wetlands

In terms of mean scores for effectiveness, higher-altitude wetlands scored high for nitrate removal, toxicant removal and phosphate trapping, while the lower-altitude wetlands scored high for erosion control, flood attenuation and sediment trapping (Figure 7.2). Regarding mean opportunity scores, lower-altitude wetlands scored high for toxicant removal, nitrate removal, phosphate removal and sediment trapping and the higher-altitude wetlands had higher scores for flood attenuation and erosion control (Figure 7.2).

In terms of specific services, higher-altitude wetlands generally scored higher values for carbon storage, maintenance of biodiversity and streamflow regulation, while those in the lower-altitude areas consistently scored higher values for cultivated foods, phosphate trapping, nitrate removal, sediment trapping and toxicant removal (Figure 7.3). However, both higher-altitude and lower-altitude wetlands scored high for ES such as provision of natural resources, streamflow regulation, nitrate removal, erosion control, flood attenuation and water supply for human use.

The classification of the wetlands based on their capacity to deliver the 15 ES produced three groups of wetlands (Figure 7.4a). The group WC1 was entirely and exclusively made up of 13 higher-altitude wetlands while group WC2 exclusively comprised five lower-altitude wetlands. The last group (WC3) was made up of a mix of higher- and lower-altitude wetlands. Figure 7.4(b) shows the general profile of the three groups of wetlands in terms of their delivery of ES. The highest scores for WC1 were for carbon storage, streamflow regulation, maintenance of biodiversity, provision of natural resources and tourism and recreation, while WC2 scored highest for nitrate removal, phosphate trapping, toxicant removal and streamflow regulation. WC3 scored highest for cultivated foods, provision of natural resources and water supply for human use. This third group represents a group of wetlands at intermediate levels of ES demand and supply.

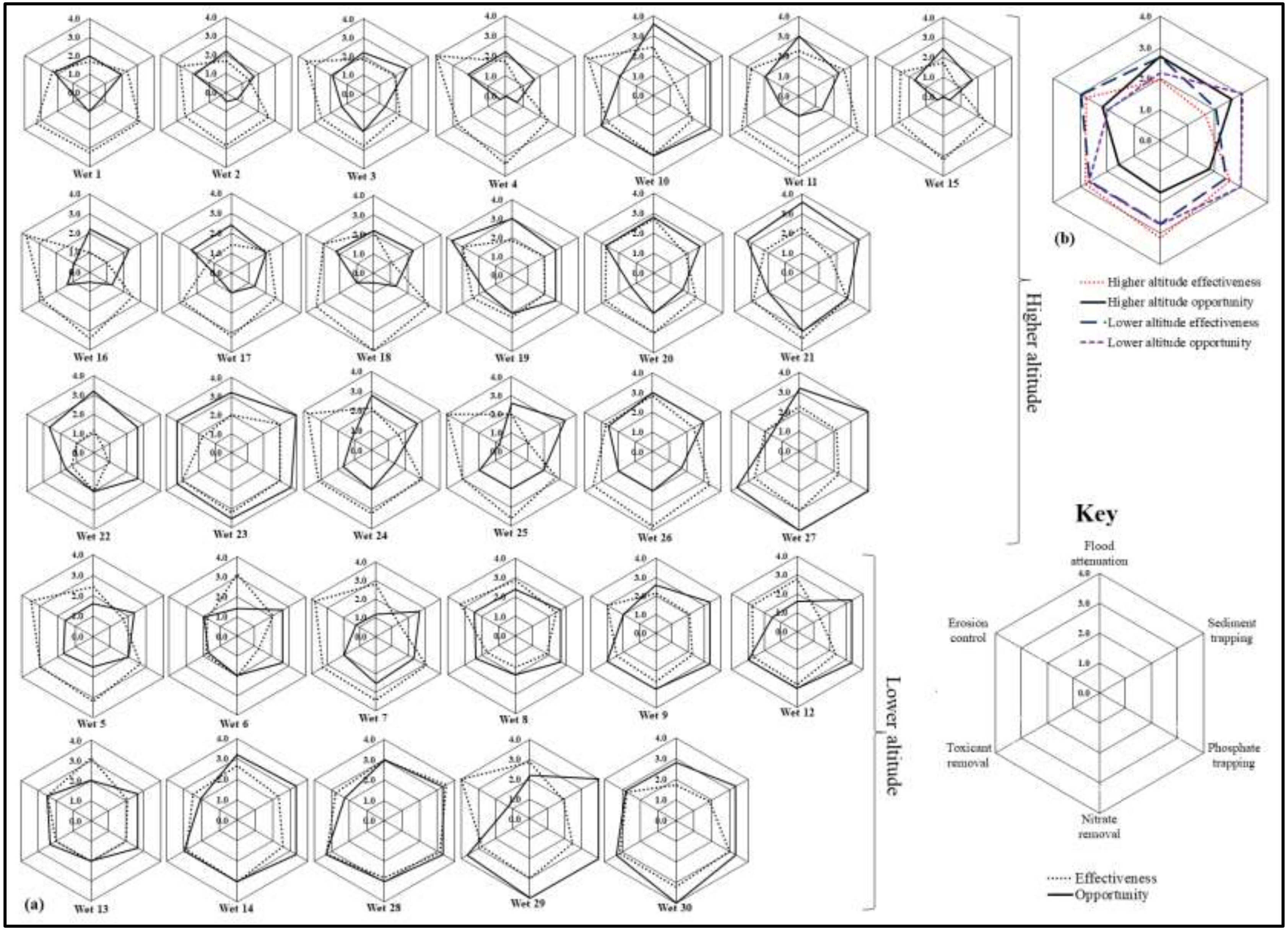

Figure 7.2: Radar graphs showing the effectiveness and opportunity of delivering six of the regulating ecosystem services by 30 Afromontane palustrine wetlands in Lesotho (a) and the radar graphs comparing higher-altitude and lower-altitude wetlands in terms of their mean scores of effectiveness and opportunity of ecosystem service delivery (b). Effectiveness reflects the supply of (capacity of the wetland to deliver) a particular ecosystem service, while opportunity reflects the demand for (level of opportunity afforded to the wetland to deliver) the ecosystem service (Kotze et al., 2008). Wet stands for wetland. The location of each wetland in the country is indicated on the map in Figure 7.1.

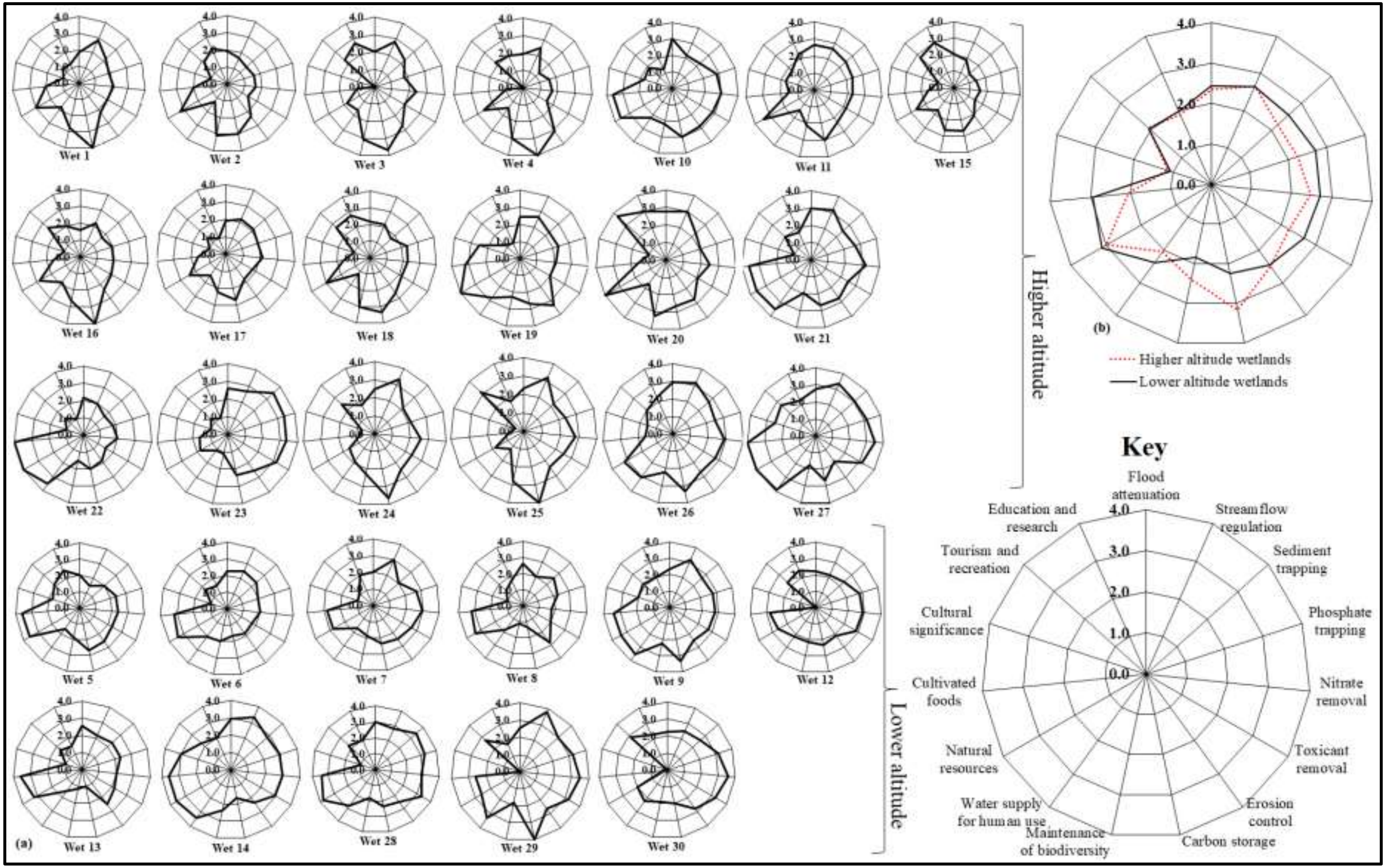

Figure 7.3: Radar graphs showing the overall extent of delivery of 15 ecosystem services by 30 Afromontane palustrine wetlands in Lesotho (a) and the radar graphs comparing higher-altitude and lower-altitude wetlands in terms of ecosystem service delivery (b). Wet stands for wetland. The location of each wetland in the country is indicated on the map in Figure 7.1.

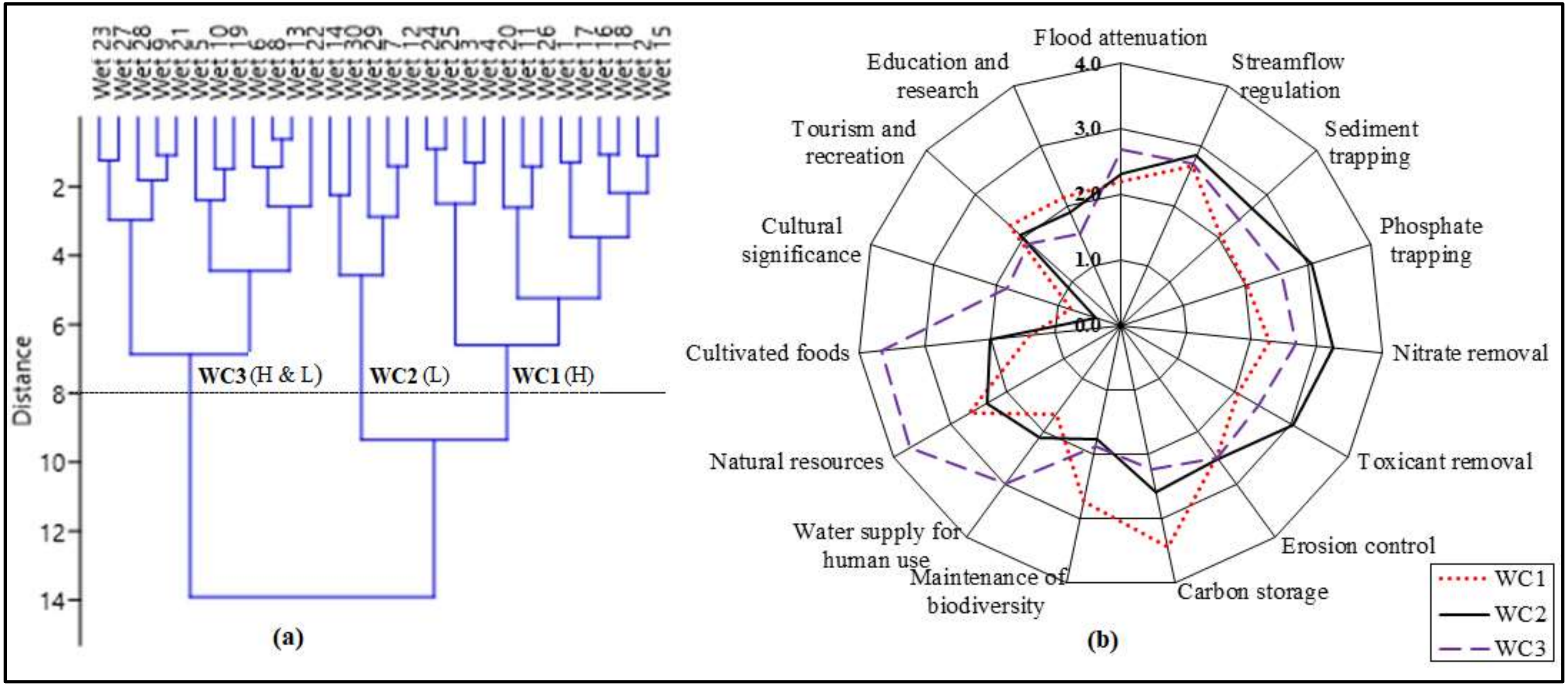

Figure 7.4: Dendrogram of the Afromontane palustrine wetlands assessed in Lesotho in terms of ecosystem service provision (a) and the radar graphs comparing the resulting wetland groups in terms of ecosystem service provision (b). Wet stands for wetland and WC for wetland cluster. H stands for high-altitude, while L stands for low-altitude. The location of each wetland in the country is indicated on the map in Figure 7.1

7.4.2 Ordination

In the ordination of wetland ES with environmental variables and groups of wetlands (Figure 7.5), the environmental variables supplied accounted for 60.87% of this; the first two ordination axes accounted for 56.60%. The model was significant ($F = 2.2$, $P = 0.008$) in the Monte Carlo permutation test. The relationships between ES and explanatory variables are shown by arrows representing explanatory variables, with lengths proportional to their relevance in explaining the variation and directions representing their correlation with the axes and other variables. The ES are also represented, as response variables and illustrated by different types of arrows. The most important factors explaining the variation in ES scores were altitude, longitude (corresponding with a dry-to-wet gradient from west to east), landscape (pristine-rural-urban) and soil parent material.

The first axis of the ordination diagram was positively correlated with latitude and aspect but negatively correlated with soil depth. Wetlands located on the right side of the ordination diagram are more north-facing, while those on the left side are more south-facing. The second axis was negatively correlated with altitude, longitude and slope. Wetlands located on the lower part of the ordination diagram (i.e. all of WC1 and some of WC3) are mainly higher-altitude hillslope seepage wetlands underlain by the basaltic parent material in the eastern part of the country. These wetlands are associated with ES such as biodiversity maintenance, carbon storage and tourism and recreation. The wetlands located on the upper part of the ordination diagram (all of WC2 and some of WC3) are mostly valley-bottom wetlands with deep soils and gentle slopes and underlain by sandstone at lower altitudes. The lower altitudes are also the more urbanised areas of the country. The wetlands were associated with provision of cultivated foods, phosphate trapping, water supply, toxicant removal, nitrate removal, sediment trapping and flood attenuation, which were negatively correlated with altitude, longitude and wetland area but associated with sandstone parent material.

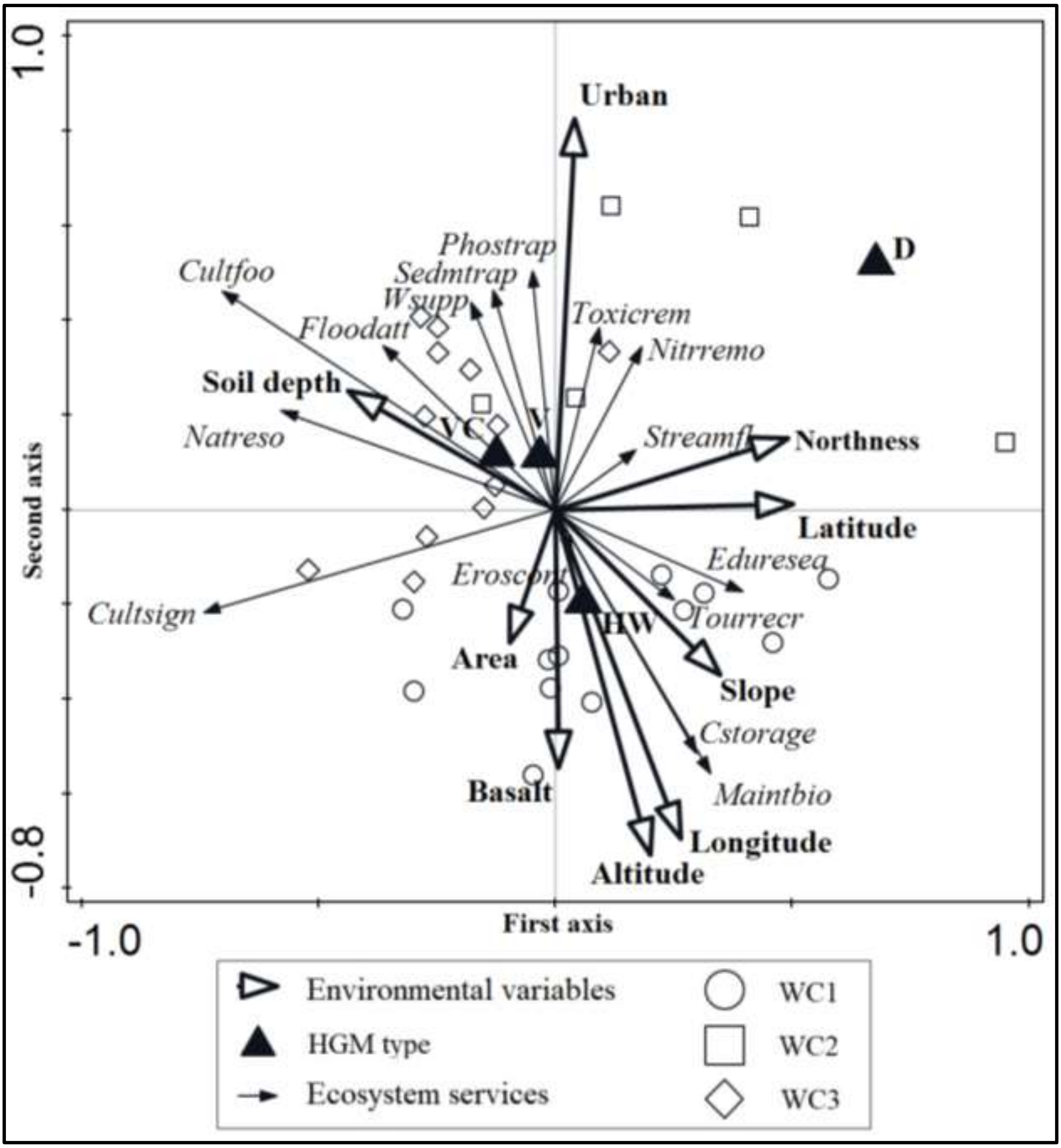

Figure 7.5: Redundancy analysis ordination diagram for ecosystem services, environmental variables and groups (based on the classification presented in Figure 7.4a) of the Afromontane palustrine wetlands in Lesotho. Wet stands for wetland and WC for wetland cluster. See Tables 7.1 and 7.2 for the abbreviations of environmental variables and ecosystem services, respectively.

In the ordination of wetland ES with community-weighted plant functional traits (Figure 7.6), 38.69% of the total variation was explained by the supplied explanatory variables (functional traits). The Monte Carlo permutation test indicated that the model was significant ($F = 1.7$, $P = 0.024$). Most of the plant functional traits were important in explaining the variation in the ES scores. Shoot mass, total plant biomass, rooting depth, root mass and leaf width were positively correlated with the first axis, which had a negative correlation with specific leaf area (SLA). The second axis had a positive correlation with leaf area, plant height, leaf length and leaf mass, which were also positively correlated with phosphate trapping, toxicant removal, nitrate removal, sediment trapping, flood attenuation, tourism and recreation, erosion control, streamflow regulation, and education and research. Specific leaf area had a positive correlation with cultivated foods, provision of natural resources, water supply and cultural significance. Carbon storage and maintenance of biodiversity were positively correlated with shoot mass, total plant biomass, rooting depth, root mass and leaf width, which were negatively correlated with SLA and root-to-shoot mass ratio. Shoot mass, total plant biomass, rooting depth, root mass and leaf width had a positive correlation with tourism and recreation, streamflow regulation, erosion control and education and research. However, these traits had a weak positive correlation with most of the regulatory services. It is noteworthy that the provision of cultivated foods had a strong and negative correlation with the maintenance of biodiversity and carbon storage.

There was a strong positive correlation between the regulating services (e.g. phosphate trapping, nitrate removal, toxicant removal, streamflow regulation, sediment trapping and carbon storage) and the measures of vegetation structure (vegetation height and cover) and species richness (Appendix 7.1). Flood attenuation, tourism and recreation, water supply and erosion control were also positively correlated with vegetation height, vegetation cover and species richness. Maintenance of biodiversity, provision of natural resources and cultivated foods were positively correlated with Shannon-Weiner and evenness indices.

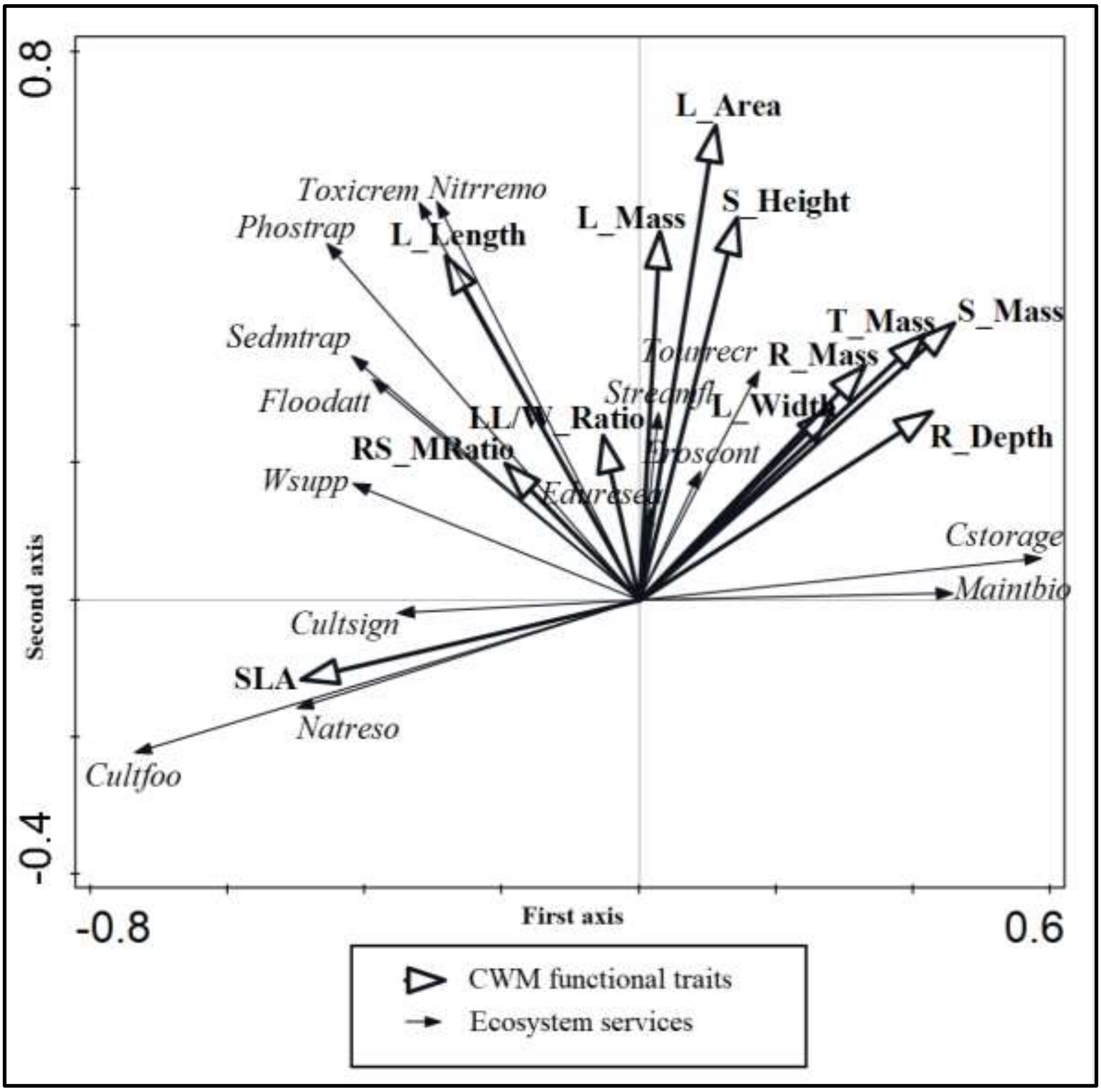

Figure 7.6: Redundancy analysis ordination diagram for ecosystem services and community-weighted plant functional traits of the Afromontane palustrine wetlands in Lesotho. CWM stands for community-weighted mean. See Tables 7.2 and 7.3 for the abbreviations of ecosystem services and plant functional traits, respectively.

The delivery of ES is threatened in almost all the wetland systems assessed and the level of threat significantly decreases with increasing altitude (Figure 7.7). The mean threat score for the lower-altitude wetlands was 3.7 (high) and the higher-altitude wetlands had a mean threat score of 1.8 (intermediate). While 72.73% of the lower-altitude wetlands recorded the highest possible threat score, only 10.53% of the higher-altitude wetlands recorded this level of threat.

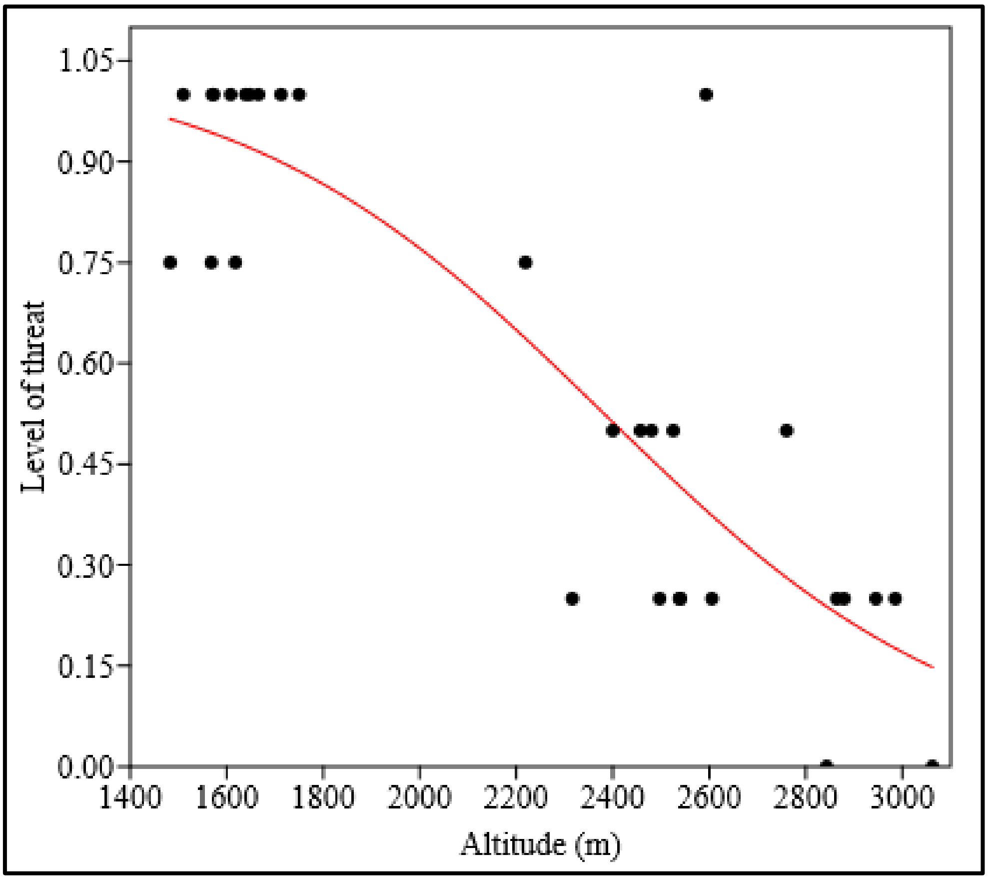

Figure 7.7: Relationship between level of threat to the delivery of ecosystem services and altitude in the Lesotho Afromontane palustrine wetlands. The level of threat was assessed using the WET-EcoServices (Kotze et al., 2008). Threat level = 1.05626 / (1 + 0.0018076*exp(0.0026539*altitude)

7.5 Discussion

Higher-altitude wetlands differed from the lower-altitude ones in the ES they deliver best. This is evidenced by the formation of one cluster (WC1), consisting entirely of higher-altitude wetlands and another (WC2), consisting entirely of lower-altitude wetlands. In the mixed group WC3, the higher-altitude wetlands are those that, although located in the mountains, are found within the proximity of villages or have been affected by road construction. This subjects them to a comparable level of ecosystem service demand and threat to those in lower-altitude areas.

The higher mean scores for the lower-altitude wetlands in terms of opportunity for toxicant removal, nitrate removal, phosphate removal and sediment trapping is consistent with the higher human pressure and the associated intense cultivation and use of fertilisers in the lowlands of Lesotho. In terms of mean effectiveness scores for nitrate removal, toxicant removal and phosphate removal, higher-altitude wetlands were better because of the higher vegetation cover that is associated with these wetlands, a factor that promotes uptake of these chemicals (Rebelo et al., 2019). This is unlike the lower-altitude wetlands that scored higher for effectiveness in erosion control, flood attenuation and sediment trapping, services that are usually enhanced as the gradient of the wetland becomes less steep in the lowlands.

7.5.1 Relationship between ecosystem services and environmental variables

Lower-altitude wetlands play an important role for cultivated crops because of the high human population density, coupled with the warmer climate and the wetlands' gentle slopes associated with the lowlands, which are favourable for cultivation. The main crops of the country (maize and sorghum) are C_4 plants that do not grow well in the cold higher-altitude areas (Department of Environment, 2014). The wetlands in Lesotho provide water for livestock drinking and domestic use, especially in the lowlands. This increases the demand for water, and thereby the pressures on lower-altitude valley-bottom wetlands, which are of importance for this service, just as in South Africa (Rebelo et al., 2019).

The gentle slopes, coupled with tall vegetation, associated with lower-altitude wetlands, tend to enhance the capacity of wetlands to deliver regulating ES, such as phosphate trapping, nitrate removal, sediment trapping and toxicant removal (Figure 7.2b and 7.3b), all of which concomitantly facilitate crop cultivation because of enriched soils. Approximately, half of the lowlands zone has been cultivated (Pomela et al., 2000), and an additional part has come under urbanisation, meaning that wetlands in this zone have generally lost much of their natural vegetation cover. Thus, the role of wetlands in the delivery of regulating ES, such as sediment trapping, erosion control and flood attenuation, is critical in the lowlands. This is because the lowlands is a zone that is highly susceptible to erosion because of dispersive soils and is characterised by a severely eroded landscape (Grab & Deschamps, 2004). The regulating services (phosphate trapping, toxicant removal, nitrate removal, sediment trapping and flood attenuation), which scored highest in the less steep lower-altitude valley-bottom wetlands, were also positively correlated. This is because the delivery of all these services is largely enhanced by the same factors: gentle slope conditions, surface roughness and vegetation cover. Sieben et al. (2017c) have highlighted that valley-bottom wetlands have the potential to deliver all of the regulating services listed above. By providing for sedimentation, nutrient uptake and denitrification processes, palustrine wetlands enhance water quality for downstream users, as well as reducing siltation in downstream aquatic systems. Furthermore, wetlands reduce the severity of floods downstream and the associated potential damage, an effect that is enhanced by the presence of vegetation (Kotze et al., 2007). Sather and Smith (1984) report a 60–65% reduction in flood peaks in watersheds with at least 15% wetland area.

Because the ecological integrity of the wetlands in the catchment areas influences the quality and quantity of water in the downstream watercourses by supporting perennial runoff with low sediment loads (Kotze et al., 2007; Chatterjee et al., 2010), the conservation of these wetlands is necessary. This will ensure a sustained optimum functioning of the wetlands and concomitantly the services they deliver (Wilson et al., 2013).

Two of the three highest scoring ES in this study were provisioning services (provision of natural resources and cultivated foods). This is mainly because Lesotho is characterised by high levels of poverty and the majority of the people are highly dependent on subsistence agriculture for livelihoods (Government of Lesotho, 2014). Wetlands are also considered a critical grazing resource for communal livestock in Lesotho (Du Preez & Brown, 2011) and much of the grazing in the montane areas occurs in wetlands, which support the most palatable vegetation (Grab & Deschamps, 2004). Wetlands double the carrying capacity of grasslands (Lannas & Turpie, 2009). Because of their high productivity and ability to retain water throughout the year, wetlands also have a good potential for year-round cultivation and grazing (Lannas & Turpie, 2009; Irvine et al., 2016).

The importance of higher-altitude wetlands for carbon storage was also indicated by the positive association between carbon storage and altitude. The anoxia caused by waterlogging, coupled with low temperatures in higher-altitude wetlands, reduces decomposition rates and concomitantly favour organic matter accumulation and peat formation (Chatterjee et al., 2010; Gopal, 2016). These conditions are optimal for the sequestration and storage of carbon, which is an important ecosystem service as it helps in stabilising the climate (Mitsch & Gosselink, 2015). The contribution of wetlands to carbon storage is disproportionate to their worldwide coverage, making them the most space efficient carbon sink globally. A recent review found that wetlands are undervalued in terms of their role in the fight against climate change (Moomaw et al., 2018). However, wetlands can also become a source of carbon by emitting large amounts of methane as they become degraded (Mitsch & Gosselink, 2015).

Support for biodiversity was an important ES in this study, particularly in the higher-altitude wetlands. By providing habitats for a numerous organisms, supporting food chains and influencing ecosystem functioning, biodiversity is an all-encompassing ecosystem service. Wetland ES derive from the interactions of different biodiversity components with their explanatory variables (Gopal, 2015). Thus, wetland biodiversity has a strong and direct relationship with ecosystem functioning and stability, which in turn is positively related to ecosystem service delivery (Pinto et al., 2014).

7.5.2 Relationship of ecosystem services and plant functional traits

Functional traits of plant species play a critical role in influencing ecosystem service delivery as they are related to the ES delivered by a wetland (Zhang et al., 2015) and a large number of species, coupled with high evenness, means that there is potentially a wide range of traits playing a role in ES. The current study found that carbon storage was positively correlated with shoot mass, total plant biomass, rooting depth and leaf width. These functional traits are associated with high photosynthetic rate, which implies a high carbon dioxide intake. Specific leaf area was also strongly and positively correlated with cultivated foods, provision of natural resources and cultural significance. Because specific leaf area is positively correlated with tissue nitrogen content (Díaz & Cabido, 1997; Pla et al., 2012) and negatively with the concentration of defensive compounds in plant tissues, plant communities with high specific leaf area could be associated with high nutritional quality and thus could exhibit a high carrying capacity for animals (Díaz & Cabido, 1997). Furthermore, streamflow regulation was positively correlated with plant height and leaf attributes (area, mass and length), which could indicate the discharge of sub-surface water to the surface, a factor important for streamflow regulation (Kotze et al., 2007).

Plants are the primary determinants of most of the regulating and provisioning services delivered by wetlands, including enhancement of water quality, erosion control, carbon sequestration, medicinal plants, livestock grazing, aesthetic beauty and crafts/construction material (Sieben et al., 2017c). In the current study, regulating services such as flood attenuation, phosphate trapping, nitrate removal, sediment trapping, toxicant removal, streamflow regulation and erosion control were positively correlated with plant shoot height, leaf traits (mass, area and length) and root-to-shoot mass ratio. This is probably because of the dependence on the extent of vegetation cover (Kotze et al., 2007), and this delivery is enhanced when the plants are deeply and extensively rooted (Rebelo et al., 2019). Furthermore, functional traits have been considered the key mechanism by which species contribute in influencing ecosystem properties (de Bello et al., 2010; Zhang et al., 2015), which give rise to the ES.

The positive correlation between most of the regulating services and measures of vegetation structure (vegetation height and cover), as well as plant species richness is consistent with earlier findings on the role of vegetation in ES (Kotze et al., 2007). This is because taller vegetation leads to higher surface roughness, which slows down water flow and this is critical for many ES in wetlands. In addition, bigger plants lead to advantages for the plants themselves such as higher productivity, which is also important for carbon sequestration and nutrient uptake. Nevertheless, the weak relationship of most regulating services with the shoot mass, total plant biomass, rooting depth, root mass and leaf width and their positive correlation with vegetation height, vegetation cover and species richness could suggest that plant community attributes are more important than individual species attributes for the delivery of most regulating ecosystems services. Thus, the reported influence of the traits of dominant plant species on wetland ES (Sieben, 2012; Zhang et al., 2015) appears to be true for some services but less so for others (e.g. most regulating services). This is also consistent with the fact that some services are nearly entirely dependent on plant functional traits whereas others are co-dependent on HGM units and vegetation structure (Sieben et al., 2017c).

7.5.3 Threats to wetland ecosystem service delivery

The negative correlation of cultivated foods with the maintenance of biodiversity and carbon storage, evident in the current study, highlights the trade-offs of agriculture (monoculture and drainage of wetlands) on supporting and regulating services of wetlands (Sil et al., 2016). Ecosystem service trade-offs, which occur when an increase in the use of one ES results in a reduced provision of another service, have been reported between provisioning and regulating services (Sil et al., 2016). This trade-off then emphasises the need and importance of “wise use”, which is regarded as the most effective way to protect and use wetland resources in developing countries where funding is limited (Wang et al., 2008). The most significant goals of the Ramsar Convention include the prevention of global wetland loss and the conservation of the remaining wetlands through their wise use (Daryadel & Talaei, 2014). The over-utilisation of wetland provisioning ES by human beings often has an adverse effect on ecosystem functioning and the delivery of supporting and regulating services (Pinto et al., 2014). As people get some benefits from the wetlands they can also subject the systems to degradation, which highlights a conflict between some ES use and wetland conservation. Wetland degradation happens when people subject the provisioning resources of a wetland to over-exploitation. It can also occur when people consider ‘disservices’ more than services, for example, when they drain wetlands to plant maize, instead of adjusting and planting the types of crops that do well in wetland environments.

Because the condition of a wetland determines its capacity to deliver provisioning and other ES, this capacity can potentially diminish due to degradation. Such degradation can have significant adverse consequences for water resources (Chatterjee et al., 2010). The wetlands in the lower-altitude areas of Lesotho are subjected to more anthropogenic pressures, including cultivation, livestock grazing, urbanisation and conversion to other forms of land use (Backéus & Grab, 1995; Pomela et al., 2000; Department of Environment, 2014). Thus, the level of threat to wetland ES delivery is much higher in the lowlands (mean score of 3.7) than in the mountains (mean score of 1.8). However, at higher altitudes degradation is also on the increase because of livestock grazing and economic development (mining and construction of infrastructure and dams). On top of that, wetlands seem to experience positive feedback mechanisms, which involve ice rats (*Otomys sloggetti)*. The more degraded a wetland becomes, the higher the chances of encroachment by ice rats, which will further degrade the system (Grab & Deschamps, 2004) and promote encroachment by terrestrial vegetation. Substantial invasion by alien plant species has also been observed in these wetlands (Chapter 4).

Overgrazing and trampling by livestock have been implicated in the degradation and loss of wetlands in Lesotho (e.g. van Zinderen Bakker & Werger, 1974; Backéus & Grab, 1995; Grundling et al., 2015). The Basotho way of life is underpinned by the principle that all land and natural resources are strictly communal and open access (Mokuku et al., 2004) and this results in the over-utilisation of the land, which leads to most wetlands being over-utilised, even in the Ramsar site of Letšeng-la-Letsie Wetland (Grundling et al., 2015). This is a good example of the "tragedy of the commons." Additionally, several developmental activities carried out in the country impact negatively on the wetlands, and these include mining and damming, as well as associated infrastructure development (Grundling et al., 2015). The activities have also involved construction of roads through mountain passes at altitudes above 3000 m a.s.l., which threatens the montane ecosystems in those areas, including wetlands (Meakins & Duckett, 1993; Department of Environment, 2014). Roads passing some of the adjacent wetlands result in the alteration of the hydrology in the wetlands, especially where the roads are located upland of the wetland system and the drainage system (e.g. culverts) of the road concentrates runoff into the wetland, delivering sediments and eroding the system. While many areas in the mountains were historically inaccessible and thus considered "protected" by their remoteness, the development and the concomitant increased accessibility and human population density have dramatically increased the threats to higher-altitude ecosystems.

Climate change is likely to affect these wetlands as it will cause potentially severe threats on the peat-forming wetlands (Lee et al., 2015). Ryan et al. (2014) have reported that higher altitudes are likely to experience widespread ecological changes because mountain regions display higher sensitivity to climate change. It has been predicted that climate change will substantially alter water availability for individual montane wetlands and this will lead to significant shifts in the composition and distribution of wetlands in mountain landscapes in the future (Lee et al., 2015). Furthermore, a recent model has predicted significant shifts in species distribution ranges as the climate changes in the Maloti-Drakensberg (Bentley et al., 2019). Chapter 4, which reports a pattern of increasing dominance of C_3 plants in wetland communities with increasing altitude in Lesotho, also highlights a threat to the higher-altitude communities because C_4 plants will likely replace C_3 species as the climate changes.

7.6 Conclusion

Given that wetland ecosystem service assessment is considered the primary step toward promoting the protection of wetlands (Wondie, 2018), the current study provides invaluable information that can be used for conservation planning and decision/policy making regarding the systems. By applying the WET-EcoServices tool in Lesotho, this study has provided information on wetland ES at a bioregional scale. Understanding the distribution of ES across landscapes is vital for planning the conservation of the associated ecosystems for the sustainable provision of the services. This can be done by prioritising certain wetlands for rehabilitation and protection based on the ES they deliver best. This is particularly relevant for a country, such as Lesotho, which is located in a major catchment in southern Africa and is the headwaters of rivers whose downstream is characterised by major industrially developed areas. Because the major ecosystem services delivered by mountains (e.g. climate regulation, water supply, support for biodiversity and support for tourism and recreation) (Sil et al., 2016), also reported in the current study, go beyond national and regional borders, land use changes have implications at a much larger scale than the country. The role of these wetlands, especially for water resources and livestock grazing, creates a strong economic argument for their conservation. The successful conservation of the wetlands in Lesotho requires an integrated approach. It is important to reduce grazing pressure on the wetlands in Lesotho by, for example, strengthening *maboella*, in consultation with the communities. *Maboella* is a sustainable traditional grazing system in Lesotho where rangelands are given time to rest and recover before they are utilised again.

We recommend that both effectiveness and opportunity scores should be reported when using the WET-EcoServices tool. Although the tool assists in assessing particular wetlands for comparative purposes, it was not designed to give a single overall measure of value or importance of a wetland system (Kotze et al., 2007). Therefore, I further recommend a direct measurement of the ecosystem processes that give rise to ES. This should also include a further examination of plant functional traits in relation to direct measures of ecosystem processes.

CHAPTER 8: GENERAL CONCLUSIONS AND RECOMMENDATIONS

8.1 Major research findings

Effective planning for the conservation of biodiversity and sustainable provision of ecosystem services for humanity relies fundamentally on the availability of information on biodiversity patterns (including diversity, structure and distribution). This information is still limited for many ecosystems, particularly in most southern African countries. Wetland ecosystems, particularly in montane environments are not spared from this lack of information. Widespread loss and degradation of wetlands has been reported globally, with more than half of the world's natural wetlands lost since 1900, mainly due to anthropogenic factors, with the greatest loss experienced in developing countries (UNWWAP, 2003; Rolon & Maltchik, 2006; Maltby & Acreman, 2011; Russi et al., 2013; Daryadel & Talaei, 2014; Davidson, 2014). Because they are not fully understood, montane wetlands are often degraded for short-term gains, despite being key to water, food and environmental security (Singha, 2011). The Afromontane wetlands of Lesotho are degrading rapidly (MDTP, 2007; Turpie et al., 2014a,b). Given the role of these montane wetlands in supporting biodiversity and supplying ecosystem services, gathering information on the ecology and the subsequent conservation of these ecosystems is indispensable. This has a potential to promote the conservation and wise use of these ecosystems and the concomitant sustainable provision of wetland ecosystem services.

The primary aim of this thesis was to classify the vegetation and assess the vegetation-environment relationships, plant functional composition and ecosystem services of the Afromontane palustrine wetlands of Lesotho. The study also explored the montane wetland vegetation of the entire Maloti-Drakensberg region, where more than 60% of the region is accounted for by Lesotho. The focus was on examining the plant communities and exploring the vegetation-environment relationships in the Afromontane palustrine wetlands in Lesotho and in the Maloti-Drakensberg. In an attempt to explore how wetland plants are adapted to their environment (high-altitude wetlands) and their link to ecosystem functioning, the study further characterised the Afromontane palustrine wetlands of Lesotho using a functional ecology approach and investigated the influence of environmental factors on plant functional traits and composition. Lastly, the study assessed the delivery of ecosystem services by these Afromontane palustrine wetlands and investigated the relationship of the ecosystem services to environmental variables and functional traits, as well as the level of threat to the delivery of ecosystem services by these ecosystems. Given the importance of montane wetlands for ecosystem service provision and the confirmed relationships between biodiversity and ecosystem functioning (Roscher et al., 2012; Zhang et al., 2015), it was prudent not only to classify and explore the wetland vegetation, but also to assess the functional composition of the plant communities and the subsequent ecosystem services delivered by the wetlands in Lesotho. Therefore, this section briefly summarises the major findings (Chapter 4 – 7) of the study in relation to the objectives and research questions outlined in Section 1.3 of Chapter 1 (General introduction) of this thesis.

Chapter 4 presents the classification, description and environmental factors of the Afromontane wetland vegetation in Lesotho using a phytosociological approach. This characterisation of the vegetation of the palustrine wetlands of Lesotho was achieved by means of cluster analysis and ordination. The classification of the wetland vegetation produced 22 communities, which were quite diverse in terms of the number of species. In terms of species composition and diversity, plant communities in the highlands exhibited higher diversity and were distinctively different from those in the lowlands. While some communities occur in a wide range of ecological conditions, others are restricted to either the highlands or the lowlands. High-altitude plant communities were also mainly dominated by C_3 species, while those at lower altitudes mainly displayed the dominance of C_4 plants. Variation in wetland vegetation was mainly related to spatial, topographic and edaphic factors.

Chapter 5 primarily aimed at classifying, describing and exploring the vegetation-environment relationships of the vegetation in the montane palustrine wetlands of the Maloti-Drakensberg region and the surrounding areas using a phytosociological approach. Clustering and canonical ordination techniques were also used in characterising the vegetation. Forty-two montane wetland plant communities were obtained from the classification and these were summarised into 16 major vegetation types (community groups). The community groups were quite diverse in terms of species richness and also exhibited substantial variation along the altitudinal gradient, largely due to variations in the conditions of the environment that include altitude, temperature, parent material and the amount of precipitation, among other factors. The variation in the wetland vegetation was mainly determined by altitude, longitude, latitude, nitrogen content, soil depth, inundation depth and electrical conductivity, but slope, pH, sodium content, total organic carbon, soil texture and wetness were also important. Although some community groups also occurred in the lowlands of Lesotho and in all the provinces of South

Africa, montane wetland vegetation was more concentrated in the Maloti-Drakensberg than the rest of the study area.

The main aim of Chapter 6 was to explore the key plant functional traits and classify the wetland plant species on the basis of their functional traits, as well as to determine the functional composition and trait-environment relationships of the Afromontane wetland vegetation in Lesotho. Clustering and ordination techniques were employed for data analysis. This does not only give insights into the adaptations that plants have developed to survive in these montane wetland environments (Sieben, 2012; Moor et al., 2015), but also provides an understanding of how functional composition in general terms underpins ecosystem processes and ecosystem services (Díaz & Cabido, 2001; Pérez-Harguindeguy et al., 2013). The study unveiled eight plant functional types in the wetland vegetation, which were dominated by plants with C_3 photosynthetic pathway, particularly in the high-altitude wetlands. The wetland communities exhibited coexistence of species from different plant functional types, which highlights plant functional differentiation to exploit microhabitat heterogeneity. Both plant functional traits and functional composition of the communities were broadly influenced by altitude, longitude and slope, and more finely by edaphic factors that include electrical conductivity, total organic carbon, nitrogen, clay percentage, potassium, magnesium and calcium.

Chapter 7 mainly focused on assessing the ecosystem services provided by the Afromontane palustrine wetlands of Lesotho using the WET-EcoServices tool (Kotze et al., 2007) and exploring the relationships of the services with environmental factors and plant functional traits using ordination techniques. The study also classified the wetlands in terms of ecosystem service provision and compared the delivery of the services between the higher- and lower-altitude wetlands and also assessed the level of threat to the delivery of the ecosystem services by these ecosystems. Although the wetlands were all important for ecosystem service delivery, there was notable variation between higher- and lower-altitude wetlands in the services they deliver most. The higher-altitude wetlands scored highest for carbon storage, provision of natural resources, streamflow regulation, maintenance of biodiversity and erosion control, while natural resources, cultivated foods, nitrate removal, phosphate trapping and streamflow regulation scored highest in the lower-altitude wetlands. The most important environmental factors influencing the delivery of wetland ecosystem services in Lesotho were altitude, longitude, landscape, soil parent material, slope and soil depth. Plant functional traits were also correlated with the delivery of ecosystem services and specific leaf area, total dry mass, shoot mass, root mass, rooting depth and plant height were the most important traits influencing ecosystem service delivery. Nevertheless, the study also found that the supply of ecosystem services is threatened, with the level of threat higher in lower-altitude than in the higher-altitude wetlands. The threats are mainly associated with anthropogenic factors that include crop cultivation, overgrazing and trampling by livestock and economic development.

8.2 Concluding remarks

The current study focused on exploring the vegetation types of the Afromontane wetlands in Lesotho and the Maloti-Drakensberg region and assessing and investigating the functional composition and ecosystem services provided by the Afromontane palustrine wetlands of the former. The diversity exhibited by the Afromontane wetlands in Lesotho and the Maloti-Drakensberg, coupled with their restricted occurrence at high elevations, support for endemic species, their importance for water resources and delivery of other ecosystem services, demonstrates the high conservation value of these ecosystems in southern Africa, especially in the face of escalating water scarcity and demand, climate change and biodiversity loss. The study has demonstrated variation in wetland vegetation, including plant functional traits and functional composition of communities, as a result of the influence of environmental gradients and edaphic factors. The findings of this study also suggests that both convergent evolution and niche differentiation jointly play a role in determining plant functional composition and distribution in high-altitude montane palustrine wetlands. Thus, some plant functional traits may converge while others diverge. For example, plant root traits may possibly display convergence due to soil wetness, while traits related to the shoots may exhibit convergence, reflecting niche partitioning with regards to light harvesting. Given the increasing anthropogenic pressures, coupled with climate change, that often result in environmental alterations in different landscapes, the understanding of functional traits that enable plant adaptation in montane wetland environments can play a critical role in the conservation of wetlands and the associated vegetation. The study has also highlighted the possibility of alterations in plant functional traits, types and functional composition in Lesotho in the face of environmental alterations, including climate change. Furthermore, the Afromontane wetlands of Lesotho are not only important for Lesotho, but also for the Senqu-Orange River riparian countries (South Africa and Namibia). The study has demonstrated that environmental factors and functional traits are important determinants for the ecosystem services delivered by montane wetlands.

The current study has further demonstrated the value of montane palustrine wetlands in delivering ecosystem services for humanity. By their geographical position in the landscape, montane wetlands play a critical role in the provision of important ecosystem services, particularly biodiversity conservation, water resources, provision of natural resources, climate change mitigation and other regulatory services. They also influence the delivery of ecosystem services by other ecosystems, such as lotic (flowing) and lacustrine (non-flowing) freshwater systems located downstream. Through their influence on the hydrology of the landscape and downstream, montane wetlands also play a role in influencing the provision of ecosystem services by terrestrial ecosystems. Hence, montane wetlands deliver ecosystem services at the local, regional and even the global scale.

Understanding the distribution of ecosystem services across landscapes is vital for planning the conservation of the associated ecosystems for the sustainable provision of the services. This is particularly relevant for a country such as Lesotho, which is located in a major catchment in southern Africa and is the headwaters of rivers whose downstream is characterised by major industrially developed areas. Because the major ecosystem services delivered by mountain ecosystems (e.g. support for biodiversity, water supply, climate regulation and support for tourism and recreation) (Sil et al., 2016), evident in the current study, go beyond national and regional borders, land use changes have implications at a much larger scale than the country itself. Furthermore, because of their location in high-altitude montane areas, montane wetlands face a real threat of climate change, to the detriment of biodiversity, climate change mitigation, water resources and provision of other ecosystem services. Thus, montane wetland conservation is indispensable and should be set as a priority in Lesotho and in other landscapes.

Directly or indirectly, wetlands play a critical role in meeting all the 20 Aichi Biodiversity Targets for the Strategic Plan for Biodiversity 2011-2020 (CBD Secretariat, 2015), are central for sustainable development and are valuable tools against climate change (Ramsar Convention on Wetlands, 2018). This indicates the invaluable contribution of wetlands to ecosystem service provision. It is the publication of the of the United Nations Millennium Ecosystem Assessment report (2005b) that increased the popularity of the concept of ecosystem services worldwide. Since then, the concept has drawn a lot of attention and is gaining more popularity. Many organisations, such as the Ecosystem Services Partnership (ESP) (2008) and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) (2012) have been set up (to mention only a few) and more publications have been produced by various authors (Table 2.1). To that effect, the IPBES has recently introduced and recommended a new but related concept, the notion of “nature’s contributions to people (NCP)”, arguably and mainly, to capture the full range of values of nature (IPBES, 2018). The IPBES (2019) has also published one of the most recent global assessment reports on the contribution of nature to society. It is nonetheless noteworthy that in their recent assessment of the difference between the older “ecosystem services” concept and this newly coined “nature’s contributions to people”, Kadykalo et al. (2019) conclude that the latter concept is not necessarily a paradigm shift as claimed but is rather complementary to the former. The contribution of nature to humanity has become so popular that it is now one of the most topical issues globally. It is acknowledged that “nature underpins the quality of life by providing basic life support for humanity (regulating), as well as material goods (material) and spiritual inspiration (non-material)” (IPBES, 2019). This nature entails all ecosystems, including wetlands. However, the value of the services provided by wetlands for nature and society are underestimated during policy and decision making processes (Ramsar Convention on Wetlands, 2018).

The current study can be valuable to wetland scientists, biodiversity conservationists, wetland managers, water resource managers and planners and vegetation ecologists in southern Africa. About 70% of Lesotho falls in the Maloti-Drakensberg and accounts for more than 60% of the region and this also makes the study important in wetland biodiversity conservation. By employing the WET-EcoServices method at a bioregional scale and exploring the relationships between plant functional traits and ecosystem services, the current study also contributes specifically to the expansion of the application of the tool and to the ecosystem service assessment methods in general. Wetland ecosystem service assessment is considered the primary step toward promoting the protection of wetlands (Wondie, 2018). Because the wetlands in the study area support rich biodiversity and provide many ecosystem services, this study can contribute valuable information needed for biodiversity conservation planning and decision/policy making regarding the systems, as well as for sustainable provision of wetland ecosystem services in Lesotho and beyond. This is mainly because the understanding of montane wetlands, their ecology and conservation is important for the conservation of biodiversity and sustainable supply of ecosystem services. Thus, the findings from the current study can also contribute the baseline information, which can be important in monitoring the wetland vegetation and subsequently the sustainable provision of wetland ecosystem services in Lesotho and beyond.

Afromontane wetland plant communities display variation that is related to spatial, topographic and edaphic factors. The characteristics of the species making up the communities are related to the ecosystem processes and functioning, as well as the subsequent delivery of ecosystem services by the wetlands. The review of literature and the results of all the field surveys in the current study can thus be summarised into one conclusion: “All conservation efforts directed towards biodiversity and the environment in general point to one goal: sustaining the provision of ecosystem services for nature and humanity.” Therefore, conserving biodiversity and ecosystems underpins and perpetuates the existence of the humankind.

8.3 Recommendations and implications for wetland management

The current study has demonstrated that the Afromontane palustrine wetlands of Lesotho and the Maloti-Drakensberg are diverse and that they play an important role in the provision of ecosystem services. Lesotho entirely lies in the catchment of the Senqu-Orange River and is considered the “water factory” of southern Africa. This places Lesotho, as a major and important water catchment, at the focal point of the water resources in southern Africa. Nonetheless, the wetlands in Lesotho that underpin the water resources are facing serious threats, which are mainly associated with crop cultivation, overgrazing and trampling by livestock, and economic development. Therefore, based on the current results, the study recommends urgent action (e.g. regulating the use of wetlands and rehabilitating those that have been degraded) and up-scaling of concerted efforts toward the conservation of wetlands in Lesotho and the Maloti-Drakensberg for the conservation of biodiversity and sustainable supply of ecosystem services, including water provision for Lesotho itself, South Africa and Namibia. The wetland conservation and management should also be mainstreamed across both public and private sectors and this will ensure participation from all sectors, with a potential for a coordinated approach. The role of these wetlands, especially for water resources, livestock grazing and support for biodiversity, creates a strong economic argument for their conservation.

8.4 Research needs

On the basis of the research findings and limitations of the current study, the following research needs have been identified:

- Despite that in excess of 50% global wetland loss has been reported, information on the loss of wetlands in Lesotho is limited. Hence, the determination of the historic and current coverage, location of palustrine wetlands in Lesotho, as well as an estimation of the loss of wetlands in the country is essential to inform conservation planning.

- For purposes of conservation planning, an assessment of the responses of individual dominant plant species to environmental gradients and factors in the Afromontane palustrine wetlands of Lesotho is essential as this can provide information on the optimum environmental conditions for the species in the wetlands.
- Given that many wetlands in Lesotho are showing signs of severe degradation, an assessment of the condition (health) of the different wetlands in the country should be carried out and this can provide insights into the extent of degradation of the wetlands and concomitantly, the extent to which the delivery of ecosystem services has been compromised. This can be achieved by using tools such as the WET-Health (Macfarlane et al., 2007).
- A direct measurement of the ecosystem processes that give rise to ecosystem services can provide further insights into the functioning of these wetlands and subsequently provide more information for conservation planning. This should also include a further assessment of plant functional traits in relation to the direct measures of ecosystem processes. The direct measurement would address the major limitation of the WET-EcoServices approach – the high level of reliance on proxies of ecosystem services rather than the direct measurement of the ecosystem processes.
- Given the heterogeneity in the Lesotho wetland habitats, inter-population trait variation would be expected. Thus, it would be important to assess the inter-population variation within wetland species to account for intraspecific trait variation that can develop due to genetic diversity or environmental plasticity. This is in part because, while some plant functional traits exhibit negligible intraspecific variation in response to site conditions (e.g. SLA), others respond strongly to environmental variation (e.g. plant height) (Lavorel et al., 2008).
- To improve the justification for the conservation of these wetlands to both decision makers and local communities, the actual quantification and monetary valuation of the ecosystem services delivered by the wetlands should be conducted.

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Appendix 4.1: Wetland Vegetation Survey - Field Dataform

Releve number:	2	Date:	2/2/2017	Area / Study:	Thaba-Tseka
Surveyor(s):	PC, ES	Latitude:	29° 30' 43.5" S	Wetland name:	Thaba-Tseka
		Longitude:	28° 31' 30.3" E	Slope:	2.1830°
Plot size (m^2):	3x3	Altitude (m):	2498	Aspect:	North-facing (30.0°)

Vegetation structure:

Layer: 1	Cover: 95%	Av. Height: 5 cm	Dominants:	Growth form
				Small forbs
			Trifolium burchellianum	
			Cotula paludosa	
Total cover: 95%				

Wetland and habitat description:

HGM Unit: Valley head seepage with channel	Hydroperiod:	Permanent	Water velocity:	
Landscape setting:	Inundation depth:	Soil surface (0 cm)	Salinity:	
Urban/Rural/Pristine: Pristine	Groundwater table:	0 cm	Water source:	Seepage
Disturbance: Grazing and trampling	pH:			
	Conductivity:		Geology:	Basalt

Soil description:

Texture of top soil: Peat	Mottling present:	No	Soil sample taken:	
Colour of top soil: Black	Soil depth:	>1m	yes/no	No
Soil form: Champaigne	Deep layer:	sand loam at 60 cm		

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
Chrysocoma ciliata		+	(dead)				
Cotula paludosa		3					
Festuca caprina		+					
Gnaphalium sp		r					
Haplocarpha nervosa		+					
Isolepis angelica		1					
Juncus inflexus		r					
Kyllinga pulchella		2a					
Limosella grandiflora		+					
Limosella major		2a					
Lobelia galpinii		2a					
Moss sp		1					
Pennisetum sphacelatum		2a					
Poa binata		1					
Ranunculus meyeri		1					
Ranunculus multifidus		1					
Rumex lanceolatus		1					
Senecio polyodon		+					
Trifolium burchellianum		4					
				Total number of species:	**19**		

Notes: A road cuts across the wetland

Appendix 4.2: Species encountered in the palustrine wetlands of Lesotho, their photosynthetic pathways and frequency of occurrence in the sample plots

Species name	Authority	Family	Metabolism (C3/ C4)	%Frequency (n = 150)
Agrostis bergiana	Trin.	Poaceae	C3 grass	12.67
Agrostis eriantha	Hack.	Poaceae	C3 grass	2.67
Agrostis lachnantha	Nees	Poaceae	C3 grass	19.33
Agrostis sabulicola	Klokov	Poaceae	C3 grass	1.33
Agrostis sp	L.	Poaceae	C3 grass	1.33
Agrostis subulifolia	Stapf	Poaceae	C3 grass	0.67
Alchemilla colura	Hilliard	Rosaceae	C3	0.67
Alectra pumila	Benth.	Scrophulariaceae	C3	0.67
Alepidea pusilla	Weim.	Apiaceae	C3	3.33
Algae sp				0.67
Alternanthera nodiflora	R.Br.	Amaranthaceae	C4	0.67
Alternanthera sessilis	(L.) R.Br. ex DC.	Amaranthaceae	C4	3.33
Anagallis huttonii	Harv.	Primulaceae	C3	1.33
[a]*Anagallis* sp	L.	Primulaceae	C3	0.00
Androcymbium sp	Willd.	Colchicaceae		0.67
Andropogon appendiculatus	Nees	Poaceae	C4 grass	2.67
Andropogon eucomus	Nees	Poaceae	C4 grass	0.67
Aponogeton junceus	Lehm. ex Schltdl.	Aponogetonaceae	C3	13.33
Arctotis sp	L.	Asteraceae	C3	0.67
Athrixia fontana	MacOwan	Asteraceae	C3	6.67
Berkheya cirsiifolia	(DC.) Roessler	Asteraceae	C3	0.67
Berkheya multijuga	(DC.) Roessler	Asteraceae	C3	1.33
Berula erecta	(Huds.) Coville	Apiaceae	C3	5.33
Brachiaria eruciformis	(Sm.) Griseb.	Poaceae	C4 grass	3.33
Bromus catharticus	Vahl	Poaceae	C4 grass	3.33
Bulbine narcissifolia	Salm-Dyck	Asphodelaceae		0.67
Bulbostylis humilis	(Kunth) C.B.Clarke	Cyperaceae	C4 sedge	0.67
Bulbostylis sp	Kunth	Cyperaceae	C4 sedge	1.33
Calaver sp		Asteraceae	C3	0.00
Carex acutiformis	Ehrh.	Cyperaceae	C3 sedge	0.67
Carex cognata	Kunth	Cyperaceae	C3 sedge	12.00
Carex glomerabilis	V.I.Krecz.	Cyperaceae	C3 sedge	4.00
Carex monotropa	Nelmes	Cyperaceae	C3 sedge	5.33
Carex sp 1	L.	Cyperaceae	C3 sedge	2.00
Carex sp 2	L.	Cyperaceae	C3 sedge	2.67
Catalepis gracilis	Stent & Stapf	Poaceae	C4 grass	2.00
Cerastium arabidis	E.Mey. ex Fenzl	Caryophyllaceae	C3	8.00
Cerastium sp 1	L.	Caryophyllaceae	C3	0.67
Cerastium sp 2	L.	Caryophyllaceae	C3	0.67
Bryophyte sp 1				0.67
Bryophyte sp 2				0.67
[a]Bryophyte sp 3				0.00
Chironia purpurascens	(E.Mey.) Benth. & Hook.f.	Gentianaceae		0.67
Chrysocoma ciliata	L.	Asteraceae	C3	1.33
Cineraria dieterlenii	E.Phillips	Asteraceae	C3	2.67
Cineraria sp	L.	Asteraceae	C3	1.33
Cirsium vulgare	(Savi) Ten.	Asteraceae	C3	2.00
[a]*Conium chaerophylloides*	Eckl. & Zeyh.	Apiaceae	C3	0.00
[a]*Conopodium* sp	W.D.J.Koch	Apiaceae		0.00
[a]*Convolvulus ulosepalus*	Hallier f.	Convolvulaceae		0.00
Conyza albida	Spreng.	Asteraceae	C3	1.33
Conyza pinnata	Kuntze	Asteraceae	C3	4.00
Cotula hispida	Harv.	Asteraceae	C3	4.67
Cotula paludosa	Hilliard	Asteraceae	C3	19.33
Crassula lanceolata	Endl.	Crassulaceae	C3	0.67
Crassula natalensis	Schönland	Crassulaceae	C3	4.00
Crassula natans	Thunb.	Crassulaceae	C3	0.67
Crassula sp	L.	Crassulaceae	C3	0.67

Crassula tuberella	Toelken	Crassulaceae	C3	0.67
Craterocapsa sp	Hilliard & B.L.Burtt	Campanulaceae		0.67
Crepis sp	L.	Asteraceae	C3	0.67
Cynodon dactylon	(L.) Pers.	Poaceae	C4 grass	2.00
Cynodon incompletus	Nees	Poaceae	C4 grass	10.00
Cynodon nlemfuensis	Vanderyst	Poaceae	C4 grass	2.00
[a]*Cynoglossum austroafricanum*	Hilliard & B.L.Burtt	Boraginaceae	C3	0.00
Cyperus congestus	Vahl	Cyperaceae	C4 sedge	12.00
Cyperus esculentus var esculentus	L.	Cyperaceae	C4 sedge	0.67
Cyperus fastigiatus	Willd. ex Kunth	Cyperaceae	C4 sedge	9.33
Cyperus marginatus	Thunb.	Cyperaceae	C4 sedge	5.33
Cyperus rotundus	L.	Cyperaceae	C4 sedge	4.67
Cyperus semitrifidus	Schrad.	Cyperaceae	C4 sedge	2.00
Cyperus sp	L.	Cyperaceae	C4 sedge	0.67
Cyrtanthus breviflorus	Harv.	Amaryllidaceae	C3	0.67
Cyrtanthus flanaganii	Baker	Amaryllidaceae	C3	2.00
[a]*Cyrtanthus* sp	Aiton	Amaryllidaceae	C3	0.00
Cysticapnos pruinosa	(Bernh.) Lidén	Papaveraceae		0.67
Denekia capensis	Thunb.	Asteraceae	C3	3.33
Digitaria eriantha	Steud.	Poaceae	C4 grass	2.00
Digitaria ternata	(A.Rich.) Stapf	Poaceae	C4 grass	1.33
[a]*Disa versicolor*	Rchb.f.	Orchidaceae		0.00
Disperis wealii	Rchb.f.	Orchidaceae	C3	0.67
Dracoscirpoides ficinioides	(Kunth) Muasya	Cyperaceae	C3 sedge	4.00
[a]*Dracoscirpoides* sp	Muasya	Cyperaceae		0.00
Echinochloa colona	(L.) Link	Poaceae	C4 grass	4.67
Echinochloa crus-galli	(L.) P.Beauv.	Poaceae	C4 grass	0.67
Echinochloa jubata	Stapf	Poaceae	C4 grass	0.67
Echinochloa stagnina	P.Beauv.	Poaceae	C4 grass	1.33
Eleocharis dregeana	Steud.	Cyperaceae	C3 sedge	16.00
Eleocharis limosa	(Schrad.) Schult.	Cyperaceae	C4 sedge	16.67
[a]*Eleocharis monotropa*	R.Br.	Cyperaceae		0.00
[a]*Eleusine coracana*	(L.) Gaertn.	Poaceae	C4 grass	0.00
Epilobium capense	Buchinger ex Krauss	Onagraceae	C3	0.67
Epilobium hirsutum	L.	Onagraceae	C3	2.00
Epilobium salignum	Hausskn.	Onagraceae	C3	2.00
Equisetum ramosissimum	Desf.	Equisetaceae		0.67
Eragrostis caesia	Stapf	Poaceae	C4 grass	1.33
[a]*Eragrostis capensis*	Trin.	Poaceae	C4 grass	0.00
Eragrostis curvula	(Schrad.) Nees	Poaceae	C4 grass	2.67
Eragrostis plana	Nees	Poaceae	C4 grass	14.67
Eragrostis planiculmis	Nees	Poaceae	C4 grass	10.00
Erica alopecurus	Harv.	Ericaceae	C3	1.33
Eriocaulon dregei	Hochst.	Eriocaulaceae	C3	4.67
Eumorphia sericea	J.M.Wood & M.S.Evans	Asteraceae	C3	2.67
[a]*Euphorbia cyparissias*	L.	Euphorbiaceae	C3	0.00
Euphorbia ericoides	Lam.	Euphorbiaceae	C3	0.67
Felicia rosulata	Yeo	Asteraceae	C3	1.33
Felicia uliginosa	(J.M.Wood & M.S.Evans) Grau	Asteraceae	C3	0.67
Fern sp		Fern		0.67
Festuca caprina	Nees	Poaceae	C3 grass	5.33
Fingerhuthia sesleriiformis	Nees	Poaceae	C4 grass	4.67
Fuirena ecklonii	*Nees*	Cyperaceae		1.33
Fuirena pubescens	(Lam.) Kunth	Cyperaceae	C3 sedge	0.67
[a]*Fuirena* sp	Rottb.	Cyperaceae	C3 sedge	0.00
Galium capense	Thunb.	Rubiaceae	C3	1.33
Galium sp	L.	Rubiaceae	C3	0.67
Geranium multisectum	N.E.Br.	Geraniaceae	C3	0.67
Geranium sp 1	L.	Geraniaceae	C3	0.67
[a]*Geranium* sp 2	L.	Geraniaceae	C3	0.00
Geranium wakkerstroomianum	R.Knuth	Geraniaceae	C3	0.67
Geum capense	Thunb.	Rosaceae	C3	0.67
[a]*Geum* sp	L.	Rosaceae	C3	0.00

Geum urbanum	L.	Rosaceae	C3	1.33
[a]*Gladiolus saundersii*	Hook.f.	Iridaceae		0.00
Gnaphalium filagopsis	Hilliard & B.L.Burtt	Asteraceae	C3	2.00
Gnaphalium sp 1	L.	Asteraceae	C3	1.33
Gnaphalium sp 2	L.	Asteraceae	C3	0.67
Grass sp		Poaceae		0.67
Gunnera perpensa	L.	Gunneraceae	C3	8.67
Gymnopentzia bifurcata	Benth.	Asteraceae	C3	2.00
[a]*Gymnopentzia* sp	Benth.	Asteraceae	C3	0.00
Haplocarpha nervosa	Beauverd	Asteraceae	C3	24.67
Helichrysum adenocarpum	DC.	Asteraceae	C3	0.67
Helichrysum aureum	(Houtt.) Merr.	Asteraceae	C3	0.67
Helichrysum flanaganii	Bolus	Asteraceae	C3	2.67
Helichrysum infaustum	J.M.Wood & M.S.Evans	Asteraceae	C3	0.67
Helichrysum lingulatum	Hilliard	Asteraceae	C3	0.67
Helichrysum montanum	DC.	Asteraceae	C3	0.67
Helichrysum rugulosum	Less.	Asteraceae	C3	0.67
Helichrysum sp	Mill.	Asteraceae	C3	0.67
Helichrysum sp 1	Mill.	Asteraceae	C3	1.33
Helichrysum sp 2	Mill.	Asteraceae	C3	0.67
[a]*Helichrysum* sp 3	Mill.	Asteraceae	C3	0.00
Helichrysum subglomeratum	Less.	Asteraceae	C3	4.00
Helichrysum trilineatum	DC.	Asteraceae	C3	2.00
Helictotrichon longifolium	(Nees) Schweick.	Poaceae	C3 grass	0.67
Helictotrichon turgidulum	(Stapf) Schweick.	Poaceae	C3 grass	4.00
Hemarthria altissima	(Poir.) Stapf & C.E.Hubb.	Poaceae	C4 grass	0.67
Hemarthria sp	R.Br.	Poaceae	C4 grass	0.67
[a]*Hesperantha coccinea*	(Backh. & Harv.) Goldblatt & J.C.Manning	Iridaceae		0.00
Hesperantha sp	Ker Gawl.	Iridaceae		0.67
Hordeum capense	Thunb.	Poaceae	C3 grass	3.33
Hypochaeris radicata	L.	Asteraceae	C3	3.33
Hypoxis argentea	Harv. ex Baker	Hypoxidaceae		0.67
[a]*Isoetes* sp	L.	Isoetaceae		0.00
Isolepis angelica	B.L.Burtt	Cyperaceae	C3 sedge	20.00
Isolepis cernua	(Vahl) Roem. & Schult.	Cyperaceae	C3 sedge	0.67
Isolepis costata	Hochst. ex A.Rich.	Cyperaceae	C3 sedge	10.67
Isolepis fluitans	(L.) R.Br.	Cyperaceae	C3 sedge	4.67
[a]*Isolepis* sp 1	R.Br.	Cyperaceae	C3 sedge	0.00
Isolepis sp 2	R.Br.	Cyperaceae	C3 sedge	3.33
Juncus dregeanus	Kunth	Juncaceae	C3 sedge	2.67
Juncus effusus	L.	Juncaceae	C3 sedge	5.33
Juncus exsertus	Buchenau	Juncaceae	C3 sedge	10.00
Juncus inflexus	L.	Juncaceae	C3 sedge	2.00
Juncus oxycarpus	E.Mey. ex Kunth	Juncaceae	C3 sedge	2.67
Kniphofia brachystachya	(Zahlbr.) Codd	Asphodelaceae	C3	0.67
Kniphofia caulescens	Baker	Asphodelaceae	C3	6.67
Kniphofia northiae	Baker	Asphodelaceae	C3	2.00
Koeleria capensis	Nees	Poaceae	C3 grass	7.33
Kyllinga erecta	Schumach.	Cyperaceae	C4 sedge	1.33
Kyllinga pauciflora	Ridl.	Cyperaceae	C4 sedge	1.33
Kyllinga pulchella	Kunth	Cyperaceae	C4 sedge	15.33
Lactuca inermis	Forssk.	Asteraceae	C3	3.33
Leersia hexandra	Sw.	Poaceae	C3 grass	14.67
Lepidium schinzii	Thell.	Brassicaceae		0.67
Lepidium sp	L.	Brassicaceae		1.33
Limosella africana	Glück	Scrophulariaceae	C3	8.00
[a]*Limosella capensis*	Thunb.	Scrophulariaceae	C3	0.00
[a]*Limosella capensis*	Nees	Poaceae	C4 grass	0.00
[a]*Limosella capensis*	Bolus	Crassulaceae	C3	0.00
Limosella grandiflora	Benth.	Scrophulariaceae	C3	8.00
Limosella inflata	Hilliard & B.L.Burtt	Scrophulariaceae	C3	0.67
Limosella longiflora	Kuntze	Scrophulariaceae	C3	0.67
Limosella major	Diels	Scrophulariaceae	C3	8.00
Limosella vesiculosa	Hilliard & B.L.Burtt	Scrophulariaceae	C3	6.67

Litanthus pusillus	Harv.	Hyacinthaceae		1.33
Lobelia erinus	L.	Campanulaceae	C3	3.33
Lobelia galpinii	Schltr.	Campanulaceae	C3	14.67
Luzula africana	Drège	Juncaceae		2.00
[a]*Lycopodium* sp	L.	Lycopodiaceae		0.00
Marsilea macrocarpa	C.Presl	Marsileaceae	C3	15.33
Melica decumbens	(L.) Weber	Poaceae		0.67
Mentha aquatica	L.	Lamiaceae	C3	6.67
Mentha longifolia	(L.) L.	Lamiaceae	C3	4.00
Merxmuellera disticha	(Nees) Conert	Poaceae	C3 grass	1.33
Merxmuellera drakensbergensis	(Schweikerdt) Conert	Poaceae	C3 grass	1.33
Merxmuellera guillarmodiae	Conert	Poaceae	C3 grass	0.67
Merxmuellera macowanii	(Stapf) Conert	Poaceae	C3 grass	6.00
Merxmuellera sp	Conert	Poaceae	C3 grass	0.67
Mimulus gracilis	R.Br.	Scrophulariaceae		0.67
Monopsis decipiens	(Sond.) Thulin	Campanulaceae		0.67
Moraea huttonii	(Baker) Oberm.	Iridaceae		0.67
Moraea sp	Mill. ex L.	Iridaceae		0.67
Moss sp 1				2.67
Moss sp 2				2.00
Moss sp 3				0.67
Moss sp 4				0.67
Myosotis semiamplexicaulis	DC.	Boraginaceae		0.67
Myosotis sp	L.	Boraginaceae		0.67
Nasturtium officinale	R.Br.	Brassicaceae	C3	0.67
Nidorella undulata	(Thunb.) Sond.	Asteraceae	C3	3.33
Oenothera rosea	Aiton	Onagraceae	C3	2.00
Ornithogalum paludosum	Baker	Hyacinthaceae	C3	4.67
Oxalis obliquifolia	Steud. ex A.Rich.	Oxalidaceae	C3	6.00
Oxalis sp	L.	Oxalidaceae	C3	0.67
Panicum maximum	Jacq.	Poaceae	C4 grass	11.33
Papaver aculeatum	Thunb.	Papaveraceae		0.67
Papaver sp	L.	Papaveraceae		0.67
Paspalum dilatatum	Poir.	Poaceae	C4 grass	16.00
[a]*Paspalum distichum*	L.	Poaceae	C4 grass	0.00
Paspalum notatum	Flugge	Poaceae	C4 grass	13.33
Pennisetum clandestinum	Hochst. ex Chiov.	Poaceae	C4 grass	2.67
Pennisetum sphacelatum	(Nees) T.Durand & Schinz	Poaceae	C4 grass	20.00
Pennisetum thunbergii	Kunth	Poaceae	C4 grass	0.67
Pentaschistis airoides	(Nees) Stapf	Poaceae	C3 grass	0.67
Pentaschistis galpinii	(Stapf) McClean	Poaceae	C3 grass	1.33
Pentaschistis natalensis	Stapf	Poaceae	C3 grass	0.67
Pentaschistis sp 1	(Nees) Spach	Poaceae	C3 grass	0.67
[a]*Pentaschistis* sp 2	(Nees) Spach	Poaceae	C3 grass	0.00
Pentzia cooperi	Harv.	Asteraceae	C3	1.33
Persicaria amphibia	(L.) Delarbre	Polygonaceae	C3	1.33
Persicaria decipiens	(R.Br.) K.L.Wilson	Polygonaceae	C3	4.67
[a]*Persicaria lapathifolia*	(L.) Delarbre	Polygonaceae	C3	0.00
Peucedanum thodei	T.H.Arnold	Apiaceae		2.67
Phragmites australis	(Cav.) Trin. ex Steud.	Poaceae	C3 grass	2.67
Plantago lanceolata	L.	Plantaginaceae		0.67
Poa annua	L.	Poaceae	C3 grass	0.67
Poa binata	Nees	Poaceae	C3 grass	9.33
Poa pratensis	L.	Poaceae	C3 grass	0.67
Poa sp	L.	Poaceae	C3 grass	0.67
Polygonum attenuatum	R.Br.	Polygonaceae	C3	3.33
Polygonum aviculare	L.	Polygonaceae	C3	1.33
Potamogeton pusillus	L.	Potamogetonaceae	C3	0.67
Potamogeton sp	L.	Potamogetonaceae	C3	0.67
Potamogeton thunbergii	Cham. & Schltdl.	Potamogetonaceae	C3	5.33
Pselutagraph sp		Cyperaceae		0.67
Pseudognaphalium luteoalbum	(L.) Hilliard & B.L.Burtt	Asteraceae	C3	14.67
Pseudognaphalium undulatum	(L.) Hilliard & B.L.Burtt	Asteraceae	C3	0.67
Pycreus niger	(Ruiz & Pav.) Cufod.	Cyperaceae	C4 sedge	2.00
Pycreus nitidus	(Lam.) J.Raynal	Cyperaceae	C4 sedge	1.33

Ranunculus baurii	MacOwan	Ranunculaceae	C3	2.00
Ranunculus meyeri	Harv.	Ranunculaceae	C3	38.00
Ranunculus multifidus	Forssk.	Ranunculaceae	C3	16.67
Rhodohypoxis deflexa	Hilliard & B.L.Burtt	Hypoxidaceae	C3	11.33
Rorippa nasturtium	Beck	Brassicaceae	C3	3.33
Rorippa nasturtium-aquaticum	(L.) Hayek	Brassicaceae	C3	2.67
Rorippa nudiuscula	Thell.	Brassicaceae	C3	0.67
Rumex acetosella	L.	Polygonaceae	C3	0.67
Rumex lanceolatus	Thunb.	Polygonaceae	C3	14.00
Rumex rhodesius	Rech.f.	Polygonaceae	C3	0.67
Rumex sp 1	L.	Polygonaceae	C3	0.67
[a]*Rumex* sp 2	L.	Polygonaceae	C3	0.00
Rumex steudelianus	Meisn.	Polygonaceae	C3	1.33
[a]*Rumex woodii*	N.E.Br.	Polygonaceae	C3	0.00
Samolus sp	L.	Primulaceae		0.67
Scabiosa columbaria	L.	Dipsacaceae	C3	1.33
Scabiosa sp	L.	Dipsacaceae	C3	0.67
Schkuhria pinnata	(Lam.) Kuntze ex Thell.	Asteraceae	C3	2.00
Schkuhria sp	Roth	Asteraceae	C3	0.67
Schoenoplectus corymbosus	(Roem. & Schult.) A.Raynal	Cyperaceae	C3 sedge	1.33
Schoenoplectus decipiens	(Nees) J.Raynal	Cyperaceae	C3 sedge	7.33
Schoenoplectus paludicola	(Kunth) Palla	Cyperaceae	C3 sedge	14.67
Schoenoxiphium caricoides	C.B.Clarke	Cyperaceae	C3 sedge	0.67
Schoenoxiphium filiforme	Kük.	Cyperaceae	C3 sedge	0.67
Schoenoxiphium sp	Nees	Cyperaceae	C3 sedge	0.67
Scirpus falsus	C.B.Clarke	Cyperaceae	C3 sedge	1.33
Scirpus ficinioides	Kunth	Cyperaceae	C3 sedge	2.67
Sebaea natalensis	Schinz	Gentianaceae	C3	2.00
Sebaea repens	Schinz	Gentianaceae	C3	0.67
Sebaea sp 1	Sol. ex R.Br.	Gentianaceae	C3	0.67
Sebaea sp 2	Sol. ex R.Br.	Gentianaceae	C3	1.33
Selago galpinii	Schltr.	Scrophulariaceae		0.67
Senecio asperulus	DC.	Asteraceae	C3	1.33
Senecio burchellii	DC.	Asteraceae	C3	5.33
Senecio erubescens	Aiton	Asteraceae	C3	2.67
Senecio harveianus	MacOwan	Asteraceae	C3	0.67
Senecio inornatus	DC.	Asteraceae	C3	2.67
Senecio isatideus	DC.	Asteraceae	C3	1.33
Senecio macrocephalus	DC.	Asteraceae	C3	4.00
Senecio polyodon	DC.	Asteraceae	C3	13.33
[a]*Senecio* sp	L.	Asteraceae	C3	0.00
Senecio tenuiflorus	(DC.) Sch.Bip.	Asteraceae	C3	0.67
Setaria pallide-fusca	(Schumach.) Stapf & C.E.Hubb.	Poaceae	C4 grass	3.33
Sonchus nanus	Sond. ex Harv.	Asteraceae	C3	0.67
[a]*Sonchus* sp	L.	Asteraceae	C3	0.00
Sporobolus africanus	(Poir.) A.Robyns & Tournay	Poaceae	C4 grass	1.33
[a]*Sutera caerulea*	(L.f.) Hiern	Scrophulariaceae		0.00
Taraxacum officinale	F.H.Wigg.	Asteraceae	C3	10.00
Tetraria cuspidata	C.B.Clarke	Cyperaceae	C3 sedge	0.67
Thesium sp	L.	Santalaceae		5.33
Trifolium africanum	Ser.	Leguminosae/ Fabaceae	C3	0.67
Trifolium burchellianum	Ser.	Leguminosae/ Fabaceae	C3	30.67
Trifolium repens	L.	Leguminosae/ Fabaceae	C3	2.00
Trifolium sp	L.	Leguminosae/ Fabaceae	C3	0.67
Typha domingensis	Pers.	Typhaceae	C3	6.00
Ursinia sp	Gaertn.	Asteraceae	C3	3.33
[a]*Utricularia* sp	L.	Lentibulariaceae		0.00
Verbena bonariensis	L.	Verbenaceae	C3	3.33
Veronica anagallis-aquatica	L.	Scrophulariaceae	C3	12.00
Vulpia sp	C.C.Gmel.	Poaceae	C3 grass	1.33
[a]*Walafrida densiflora*	Rolfe	Scrophulariaceae		0.00
Xanthium sp	L.	Asteraceae	C3	0.67

[a]Species with a frequency of zero were encountered in the wetland systems but outside the vegetation plots.

Appendix 4.3: Dominance of plant families in terms of the proportion (%) of the number of species encountered

Family	%Dominance (percentage of species)
Poaceae	20.19
Asteraceae	19.23
Cyperaceae	14.10
Scrophulariaceae	4.17
Polygonaceae	3.85
Brassicaceae	1.92
Crassulaceae	1.92
Juncaceae	1.92
Apiaceae	1.60
Gentianaceae	1.60
Iridaceae	1.60
Asphodelaceae	1.28
Campanulaceae	1.28
Geraniaceae	1.28
Leguminosae/ Fabaceae	1.28
Onagraceae	1.28
Rosaceae	1.28
Charophytes	1.28
Moss	1.28
Amaryllidaceae	0.96
Boraginaceae	0.96
Caryophyllaceae	0.96
Papaveraceae	0.96
Potamogetonaceae	0.96
Primulaceae	0.96
Ranunculaceae	0.96
Amaranthaceae	0.64
Dipsacaceae	0.64
Euphorbiaceae	0.64
Hyacinthaceae	0.64
Hypoxidaceae	0.64
Lamiaceae	0.64
Orchidaceae	0.64
Oxalidaceae	0.64
Rubiaceae	0.64
Aponogetonaceae	0.32
Colchicaceae	0.32
Convolvulaceae	0.32
Equisetaceae	0.32
Ericaceae	0.32
Eriocaulaceae	0.32
Gunneraceae	0.32
Isoetaceae	0.32
Lentibulariaceae	0.32
Lycopodiaceae	0.32
Marsileaceae	0.32
Plantaginaceae	0.32
Santalaceae	0.32
Typhaceae	0.32
Verbenaceae	0.32
Fern	0.32

Appendix 4.4: Synoptic table for the wetland vegetation in Lesotho, based on species fidelity. The diagnostic species listed (with dark-shaded values) are only those species that gave indicator values greater than 20 and p-values less than 0.05 following indicator species analysis in PC-Ord. The species are ranked in decreasing order of the values of the phi coefficient. Empty spaces in part (a) indicate absence of the species, while in part (b) dashes indicate a negative fidelity. Negative fidelity means that a species is absent in the vegetation unit but frequent outside. The synoptic table was prepared following Brown et al. (2013). Where a community has no listed species, it means that no species was found to be an indicator from the species indicator analysis.

(a) Percentage frequency

Community	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Number of plots	13	7	7	6	24	3	4	4	6	4	6	9	4	5	6	3	6	6	6	5	6	10
Number of diagnostic species in the community	1	2	1	5	0	1	2	5	3	1	3	0	6	2	2	4	1	1	2	2	1	2
Diagnostic species for community 1																						
Haplocarpha nervosa	92	86	71	50	13		25	50		25		11							17	40		
Diagnostic species for community 2																						
Isolepis angelica	57	77	43	33	21						17											
Trifolium burchellianum	77	100	90	100	21		75				17	22	50	60	17	33				40		20
Diagnostic species for community 3																						
Festuca caprina	15	14	25		13			14														
Diagnostic species for community 4																						
Helichrysum subglomeratum			14	83																		
Cotula hispida		14		67			25													20		
Poa binata	23	29	14	83	8							11										
Catalepis gracilis				33								11										
Agrostis bergiana	15	14	43	83	21		25					11								20		
[1]Diagnostic species for community 5																						

(b) phi coefficient X 1000

Community	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Number of plots	13	7	7	6	24	3	4	4	6	4	6	9	4	5	6	3	6	6	6	5	6	10
Number of diagnostic species in the community	1	2	1	5	0	1	2	5	3	1	3	0	6	2	2	4	1	1	2	2	1	2
Diagnostic species for community 1																						
Haplocarpha nervosa	483	240	240	199	-	-	-	97	-	-	-	-	-	-	-	-	-	-	-	66	-	-
Diagnostic species for community 2																						
Isolepis angelica	117	749	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trifolium burchellianum	274	569	237	280	-	-	140	-	-	-	-	-	53	99	-	-	-	-	-	21	-	-
Diagnostic species for community 3																						
Festuca caprina	138	88	651	-	139	-	-	145	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Diagnostic species for community 4																						
Helichrysum subglomeratum	-	-	116	826	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cotula hispida	-	101	-	600	-	-	160	-	-	-	-	-	-	-	-	-	-	-	-	135	-	-
Poa binata	146	146	38	519	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Catalepis gracilis	-	-	-	457	-	-	-	-	-	-	-	164	-	-	-	-	-	-	-	-	-	-
Agrostis bergiana	25	-	201	434	107	-	61	-	-	-	-	-	-	-	-	-	-	-	-	41	-	-
[1]Diagnostic species for community 5																						

Diagnostic species for community 6																																														
Potamogeton thunbergii		8					100			33									17	17					32	-	-	-	-	602	-	-	254	-	-	-	-	-	-	-	-	103	103			
Diagnostic species for community 7																																														
Senecio macrocephalus						8		50	25			17													-	-	-	-	97	-	389	177	-	-	132	-	-	-	-	-	-	-	-	-	-	-
Oxalis obliquifolia			14			17		50			25	17													-	77	-	-	119	-	307	-	-	132	92	-	-	-	-	-	-	-	-	-	-	-
Diagnostic species for community 8																																														
Cineraria dieterlenii									75		25														-	-	-	-	-	-	-	743	-	229	-	-	-	-	-	-	-	-	-	-	-	-
Nidorella undulata									75		25	17													-	-	-	-	-	-	-	661	-	200	152	-	-	-	-	-	-	-	-	-	-	-
Gunnera perpensa		15		14					100			67	22												74	-	44	-	-	-	-	537	-	-	300	122	-	-	-	-	-	-	-	-	-	-
Scirpus ficinioides									50							17						17			-	-	-	-	-	-	-	486	-	-	-	-	-	-	177	-	-	-	-	-	177	-
Peucedanum thodei									50		25	17													-	-	-	-	-	-	-	486	-	229	177	-	-	-	-	-	-	-	-	-	-	-
Diagnostic species for community 9																																														
Phragmites australis										67															-	-	-	-	-	-	-	-	811	-	-	-	-	-	-	-	-	-	-	-	-	-
Typha domingensis						4				100		17							17						-	-	-	-	-	-	-	-	808	-	92	-	-	-	-	-	-	92	-	-	-	-
Schoenoplectus corymbosus										50															-	-	-	-	-	-	-	-	569	-	-	-	-	-	-	-	-	-	-	-	-	-
Diagnostic species for community 10																																														
Kniphofia caulescens						8			25		100	33									20				-	-	-	-	29	-	-	122	-	619	218	-	-	-	-	-	-	-	-	99	-	-
Diagnostic species for community 11																																														
Juncus oxycarpus									25			50													-	-	-	-	-	-	-	229	-	-	600	-	-	-	-	-	-	-	-	-	-	-
Isolepis costata		15		14					100			100	22								20				47	-	26	-	-	-	-	345	-	-	591	95	-	-	-	-	-	-	-	56	-	-
Pentzia cooperi												33													-	-	-	-	-	-	-	-	-	-	569	-	-	-	-	-	-	-	-	-	-	-
[1]**Diagnostic species for community 12**																																														
Diagnostic species for community 13																																														
Panicum maximum				14		4							11	75		50		17	17				60		-	-	-	-	-99	-	-	-	-	-	-	-	724	-	249	-	34	34	-	-	-	157

Fingerhuthia sesleriiformis				14		4								75	40										-	-	101	-	116	-	-	-	-	-	-	-	476	356	-	-	-	-	-	-	-	-
Fuirena ecklonii														50											-	-	-	-	-	-	-	-	-	-	-	-	460	-	-	-	-	-	-	-	-	-
Polygonum aviculare														50											-	-	-	-	-	-	-	-	-	-	-	-	460	-	-	-	-	-	-	-	-	-
Brachiaria eruciformis													11	50		33									-	-	-	-	-	-	-	-	-	-	-	109	430	-	341	-	-	-	-	-	-	-
Digitaria eriantha														50									10		-	-	-	-	-	-	-	-	-	-	-	-	365	-	-	-	-	-	-	-	-	214
Diagnostic species for community 14																																														
Bromus catharticus				14										25	40						20				-	-	135	-	-	-	-	-	-	-	-	-	200	379	-	-	-	-	-	172	-	-
Hordeum capense				14										25	40								10		-	-	135	-	-	-	-	-	-	-	-	-	200	379	-	-	-	-	-	-	-	172
Diagnostic species for community 15																																														
Cyperus congestus						4				67			22	25	20	67		33	17			17	10		-	-	-	-	29	-	-	-	356	-	-	134	-	66	389	-	240	29	-	-	46	29
Leersia hexandra				14						67			11		20	67	67	50	50			33	10		-	-	-	-	-	-	-	-	229	-	-	-	-	28	300	210	204	204	-	-	108	-
Diagnostic species for community 16																																														
Andropogon eucomus																	33								-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	573	-	-	-	-	-	-
Potamogeton pusillus																	33								-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	573	-	-	-	-	-	-
Trifolium africanum																	33								-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	573	-	-	-	-	-	-
Conyza albida													11				33								-	-	-	-	-	-	-	-	-	-	-	215	-	-	-	399	-	-	-	-	-	-
Diagnostic species for community 17																																														
Schoenoplectus paludicola			14			4				50			11		20	33	67	100	17			17	30		-	-	-	-	-	-	-	-	204	-	-	-	-	-	108	210	492	-	-	-	-	116
Diagnostic species for community 18																																														
Cyperus fastigiatus						4	33						11	25	20		33		100			33			-	-	-	-	-	118	-	-	-	-	-	-	89	68	-	118	-	636	-	-	168	-
Diagnostic species for community 19																																														
Carex cognata						13		25	25			33		50						100	60				-	-	-	-	-	-	66	66	-	-	134	-	194	-	-	-	-	-	553	274	-	-
Agrostis eriantha						8														33					-	-	-	-	154	-	-	-	-	-	-	-	-	-	-	-	-	-	389	-	-	-

Diagnostic species for community 20																																														
Juncus effusus		8		14																17	100				-	-	88	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	103	782	-	-
Pennisetum thunbergii																					20				-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	302	-	-
Diagnostic species for community 21																																														
Persicaria amphibia																						33			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	569	-
Diagnostic species for community 22																																														
Cynodon incompletus			14	14		4							11				33						100		-	32	32	-	-	-	-	-	-	-	-	-	-	-	-	111	-	-	-	-	-	802
Lepidium schinzii																							30		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	307

[1]No diagnostic species were obtained following indicator species analysis in PC-Ord.

Appendix 5.1: Synoptic table for the montane wetland vegetation of the Maloti-Drakensberg region and surrounding areas

Community Group	**1**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**3**	**3**	**3**	**3**	**4**	**4**	**5**	**6**	**6**	**6**	**6**	**6**	**6**	**7**	**8**	**8**	**9**	**9**	**10**	**11**	**11**	**12**	**13**	**14**	**14**	**14**	**15**	**15**	**15**	**16**
Community	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**
Number of plots	**34**	**10**	**31**	**16**	**7**	**6**	**9**	**6**	**7**	**8**	**6**	**6**	**16**	**8**	**10**	**14**	**13**	**7**	**15**	**3**	**14**	**8**	**7**	**9**	**5**	**11**	**14**	**10**	**16**	**9**	**19**	**22**	**6**	**28**	**33**	**12**	**14**	**10**	**7**	**19**	**10**	**36**
N0. of species in the community	**157**	**137**	**182**	**111**	**53**	**38**	**72**	**47**	**57**	**56**	**43**	**38**	**67**	**58**	**78**	**103**	**72**	**47**	**49**	**27**	**105**	**48**	**50**	**20**	**23**	**44**	**99**	**83**	**61**	**49**	**90**	**85**	**47**	**64**	**138**	**105**	**38**	**61**	**60**	**80**	**25**	**124**
Merxmuellera macowanii	100	42	3			17	14																				14	30	13	11	21		17	4	3							
Ranunculus baurii		82	6									40																10				5										
Restio sejunctus	3	60																																		8						
Rhodohypoxis baurii		80	3									57		13					7																							
Limosella major				74				47	14				19			7					7										21	23					7			11		
Agrostis barbuligera					69																																					
Limosella grandiflora	3		3		71	17			29	38		17	19																			18										3
Persicaria decipiens			6	6	69																							10						4								3
Wahlenbergia banksiana					69																								6													
Juncus exsertus			3	13	44	100			34						10	7	8	14	13		7										5	5	17	4				10				
Pseudognaphalium sp.						73																																				
Senecio hypochoerideus						73																																				
Scirpus ficinioides		50	3				100							13					7		7					18	14							7		8						
Crassula gemmifera				6			59																									5										
Cynoglossum sp.							59																													8						
Juncus effusus					14			100								7	8										7	10			5	5	17	4	6	8	21			16		
Cotula hispida	3	17	6	6			29	17		90	17		38						53													9										
Felicia uliginosa			3							60																																
Helichrysum krookii										55																																
Koeleria capensis	6	33	13						14	100	67	77	19				23		53		14		14			18		20				9			9	25				5		3
Poa binata	12	25	10				43			98	33		44		10	14			40			13				9		10				23		4		17						3
Helichrysum bellum										25	70								40																							
Merxmuellera disticha		8	3							60	100								13								7									17						
Rhodohypoxis milloides											53																															
Eriocaulon dregei		17	3					33			33	100							7					56	40						5	14				8						31
Agrostis bergiana	6	50	23	6				17				33	74	25	10	14	8	14	7							9		10			11	18	17			8						

Cotula paludosa	3		10					33					66			7										9						27	33									
Helichrysum odoratissimum	6													55																												
Oxalis obtusa														55																	5											
Satyrium bracteatum		8												55																												
Gnaphalium filagopsis															50																											
Kyllinga pulchella			13			17	14						6		100	14					7												17									3
Pennisetum sphacelatum			32	6	29		14	17					13			100	31	29			7	25	29				14	30	13	44		5	17	7	9	17	71	10	14	26	70	11
Fuirena coerulescens				6												14	8	100																		17						
Lobelia flaccida s. flaccida				6											10	14	8	87												11					3	8			14			6
Agrostis subulifolia										38	33								87								7					5										
Bryum sp.										13	17								73													5										
Senecio cryptolanatus										38	50								63																							
Thesium nigrum										25	33								47																							
Andropogon eucomus															10					43																						
Cyperus compressus																				63																						
Cyperus longus						17									10	7		14		53							21				5			4	3			10				
Cyperus prolifer																				57																						
Eleocharis acutangula																				63																						
Fimbristylis complanata				13											10					100	14	13		11																		6
Nerine appendiculata																				53			14																			
Helichrysum kraussii																				53																						
Juncus lomatophyllus				13					29					13						77											5					8						
Eragrostis planiculmis	3		3	6	14	33	14									14	23	14			14	100	14						6	67			17	7	3	8			14	5		8
Nidorella sp.																				58																						
Pycreus polystachyos																				53																						
Sorghastrum stipoides																				53																						
Vernonia natalensis			3																	63																						
Harpochloa falx	3									25										33	87	25													3		21					
Themeda triandra		8	6				14										15				80	80	29					30							9				43			3
Helichrysum aureum	12	17	6	13	29				14								8	29	7		21	83	71		20				6		5				3	8			14	16	40	6
Hypoxis sp.																					14	70																				3
Pennisetum macrourum			3																		14	70													3							
Scleria welwitschii					14																7	38	100																			

Nerine angustifolia																							74																		11
Stiburus alopecuroides				6			14									7								56	100				6							17			14			44
Bulbostylis contexta																									40																	
Kniphofia caulescens	3	58						17			33	33		13					7							100		20	6		16	14	33	11								
Pennisetum thunbergii	3			13		17		33								7		14	7		7	25	29				49	10		11	5	5						10	14			3
Satyrium hallackii s. hallackii																											34															
Mentha aquatica			6				14		14								8										21	10	31	43	11			14	6			30				
Nidorella auriculata	9			6														14									7	10	13	64					12							
Isolepis costata	6		6	19	14	17		17						13		7	23		13								50	10	25		100	9	17	4			14			11		3
Rorippa nasturtium-aquaticum			3																														37									
Haplocarpha nervosa	15	25	10	19	14		14	33	14	25	17	50	75	25		7	8	14	7							18	21		6		21	100	67	7		8						3
Carex cognata	9	8	6				14	67						13					7							18	7	10		11	21	5	17	100			29	30		11		3
Miscanthus capensis	6						14										15										7		6						100			10				
Rubus cuneifolius																																			45							
Polygonum hystriculum																																			62			10				
Wahlenbergia pallidiflora																																					66			11		
Festuca caprina	12	58	10		14		43			50	33		13	38		7	8	29			29	25				9	7			11	16	18	17	4		100	93		14	32		
Carex austro-africana	3				14																						14								3		93	100		32		
Schoenoplectus brachyceras																																		11				50				3
Scleria woodii																					7		14																69	5		
Senecio madagascariensis																					7																		59			
Ascolepis capensis																							14					10									14			62		17
Dierama pauciflorum		33																																			14			67		
Helichrysum epapposum																																					36			78		
Lobelia erinus	3	42	3	6	29				14						10	7					14	13					7	10									29	10		89		
Melasma scabrum																																					7			57		
Commelina africana			3												10						50	13	29		20				6						9				29	21	70	3
Conyza albida	3														10					33	7						7		6						15						50	
Gerbera viridifolia																																									70	
Gladiolus papilio																					14		14																29	5	70	3
Helictotrichon turgidulum	6	8	16		29		29	17							10		15				36	13					7	20	6		5				3			10	14		70	

Hesperantha baurii s. baurii							14												13				14													8					50	
Hypoxis parvifolia																																									60	
Kniphofia ichopensis																																									50	
Ledebouria cooperi																						38			20														14	5	50	6
Monocymbium ceresiiforme			3																		7		29																		80	
Panicum schinzii																																									50	
Pycnostachys reticulata																											7		6					21						5	90	8
Pycreus macranthus																					7	75	14	11	40											8			29	11	70	6
Sebaea sedoides																				33																					50	
Setaria pumila															10												7								3			20			60	
Tritonia lineata																																									80	
Tulbaghia natalensis																																									60	
Wahlenbergia undulata																	8																									46
Andropogon appendiculatus	9	17	23	13	57			33	14						10	29	23	14		33	71	88	43	100	40		7	20							3	17	71	10	57	74	70	100
Aristida junciformis s. galpinii	3			13												7				33	71	63	57											4	6		29	10	100	100	80	
Fingerhuthia sesleriiformis			10	6		50			29								100	43	7		7						14	10		11	16		17			8		10		5		3
Gunnera perpensa	6		16		43	33										21										9	86	100	13	33	37	5			12		14	10				
Isolepis angelica	3	25	10	13	29	17	29		100			17	56	13		7	15											10	13		11	55	17									6
Isolepis fluitans	6	50		6		17	14	33		25	33	17							100								21				16	18	17	7						5		3
Juncus inflexus				19	14	17			14				19			14	15		7								7	20	100	78	16	5		4	3							
Mentha longifolia s. capensis	6			6																								10	13	100	5	5			9							3
Merxmuellera drakensbergensis												17		100													7		6		11											
Ranunculus meyeri	9	42	6	56	43		14	67	43		50		69		30	29	15	29	60		7					55	21	10	19	11	47	77	100	29								
Trifolium burchellianum	9	25	26	6	29		14	33		25	33	17	100		10	14			20							9					5	55	33									
Tristachya leucothrix																					43	25																	43		90	
Agrostis lachnantha	15	8	16	19	86	50	43	17	43				13		20	43	31	43	13		14					45	14	60	56	44	21	27	17	36	3		7			16	80	6
Kyllinga erecta				13	29			17	14						10	7		29			7								6		5										80	6
Limosella longiflora										50	80								73													5		4								
Juncus oxycarpus		17		13								17					8		7		7	13	29	78	20		14	10			32	5				8	43		14	68		36
Monopsis decipiens	3			13								17									36	25	14	78	40														29	5		39

Athrixia fontana	3	50	10						14	13	67	50	6	13					47							9						9				8						
Ornithogalum paludosum	3	17					14			13	67	50	13	13					13							9						9	17			8						
Isolepis inyangensis					57			17								7						13	14											4			64	10	14	58		
Eragrostis capensis		8	3												10						21	63	14		20												21		14	42		
Digitaria setifolia																				33	29	50	57																29	5		3
Juncus dregeanus	3	50		31	57	17	14	17	14					13		14		43	20		7	13					7	20	13	11	42	27					36			11		3
Ranunculus multifidus			13	31	29			50	57	13			31	13		21	31	43								18	7	30	38	33	16	14	17	14	3	8	7			5		6
Bryum argenteum										25	50								13																							
Fuirena pubescens			6												10						36	50	43		20			10							3				14	16	50	6
Lobelia galpinii		17	6		14			33	14		33	17	50						13								7					18	17									
Pycreus cooperi					29																7																50		29	32		8
Veronica anagallis-aquatica	6		6	6		50			14						10		8											20	31	11	5	9	17	11								
Bulbostylis schoenoides		17		6	14																29	25	29													8			43	16		17
Juncus bufonius				6					43					13			15	14											6		5	5				8						
Cerastium arabidis	6	42	3		29					38	17		19	13					27							18	7						17									
Senecio polyodon		42	3	13				33	14	13		17	38			7			7		7	13	14								11	9	17	4	3		21	10		26		8
Cyperus denudatus																14						38	14	22	40									11					14	5		36
Eragrostis plana	3		10	6	29								6		40	14	8				14	13	14					10											14			6
Leersia hexandra				25				17							40	14					7						7	10						11								3
Paspalum dilatatum	3		13	19									6		40	21					7	13	29				7							7				20				3
Oxalis depressa	24		3			17								38		14	8	14													5											
Tetraria sp.										38	17																												14			
Eleocharis dregeana			13	31		17							6			36	8	14			7					9	14	30	25		11	5	33	7	3		36	10				3
Senecio harveianus			3				14			13			6		20	7										18									3		36			11		
Agrostis eriantha			3									17											14	33	20									7		8				11		11
Alchemilla colura		25	10																	33			14																			3
Alepidea pusilla		17	3								17	33	6	13					7													9				8						
Anagallis hutonii	3	33		6	14	17											8										14					5				17						
Andropogon schirensis												17												33																		19
Berkheya speciosa s. speciosa							14													33															3							
Carex monotropa		33	13						14	13	17	17							20													5										

Cineraria geraniifolia	3					33																							6													
Convolvulus ulosepalus																				33									6						3							
Epilobium capense	18	8				17	29		14									14								9	7	10	19	33	32	5	33	7	3	8						3
Festuca sp.		8																		33	7																					
Hemarthria altissima			3	6											10					33					20			10						4				10				3
Isolepis cernua	3		3	6		33											15	29									21	10	6	22						8						3
Limosella africana	3		3				14		14			33	13																		5	14	17			8						
Luzula africana		33	6				14			25				13																		5				17						
Pseudognaphalium luteoalbum		8	13	25		33		17	29						20	21	23		7		7						14	10	6	11	11		17	11	6				14	21		8
Rhodohypoxis rubella		17									17	33		13					7																							
Rumex lanceolatus	3	8		6		17		33					13		20			14									14		6		5		17	11				10				
Schkuhria sp.	6	25								25	33	17																							6	8			14			
Schoenoxiphium filiforme	3	33					14				17	33		13																		5										
Sebaea repens		8					14			13	33	17																				9			3							
Senecio inaequidens	6		3	13		33								13	10	14		29													11											
Setaria sphacelata															10	7				33	7							10							9							8
Sonchus nanus		8	3							13	33	17									21															17			14			
Taraxacum officinale			6	6				33		13			19			7					7												17									
Typha capensis																				33							7							4								
Wurmbea elatior		33	3							13								14																		8						
Xyris capensis				6																33											5											
Scabiosa columbaria	3	8	3					17																												17	14			32		
Urginea macrocentra	6	8																																	3		14			32		
Carex glomerabilis	6		6			17	14						13			7	31									9		20	31	22		9	17		3	8						3
Arundinella nepalensis			3	19					14												7	13												7	24	25		30				6
Carex acutiformis			6	6		17	14		14							14											7	30			11	5			6	8						
Helichrysum cooperi	3													13							7							10	6		5				9		29	30		26		
Marsilea macrocarpa			3												30																											
Schoenoplectus paludicola													6		30	7												10														
Trifolium africanum				13		17			29						30	14	23	14									7	10		11		5		4								
Cotula sp.				13		17			29					25					13							9					11		17									3
Epilobium salignum													6															20						7			29	10		11		
Helichrysum mundtii			3	6																	29							10											14			
Hypochaeris radicata	3		3	6	29			17					13		10						14								6													

Leucosidea sericea	3		3		29											7														11					6							3
Lobelia angolensis															10																								29			
Ornithogalum ornithogaloides	6	17	3				29							13																						8						
Phragmites australis			3																								29								3			10				3
Poa pratensis	6								29								23										7	10	6	22		5			3							
Schoenoxiphium sparteum	3	8							29					25			8	14									7			11		5			3	17						3
Sebaea macrophylla	6								29								8	14									7	20	6	11	5				3							
Senecio erubescens	18	8	3	6	29				14								23					25				18		10	19	11	16	5		7		8			14	5		3
Xyris gerrardii					14																		14																29	11		
Cyrtanthus breviflorus	3										17	17		13								13	14					10			5					8	14			26		
Alchemilla capensis														25			8				7										5											3
Berkheya multijuga		17	6				14			25																	7								3	8						
Bulbostylis humilis		8	3											25	10																											
Chironia krebsii					14				14																						5					25			14	21		
Conyza pinnata	6		6				14														14	25					14	10			11		17		6				14			
Eragrostis curvula			6				14								10	7	8				14	25			20		7								15					5		11
Erica alopecurus	3	25	3								17			25																		5										
Helichrysum cymosum s. calvum		25	3				14							13																						8						
Helichrysum flanaganii	3		3							25	17		13																													
Helichrysum subglomeratum		8	10				14						25																													
Merxmuellera sp.							14			25	17	17																														
Oxalis obliquifolia	9	17	3				14						6	13	10											18	7				5				9	25						
Pentaschistis galpinii	3									25																9																
Pentzia sp.			3							25	17			13	10																	5							14			
Rhodohypoxis deflexa	3	17	6		14		14	17	14			17	25																		5	18	17									
Senecio discodregeanus	3	25					14																													8						
Senecio macrocephalus	6	25					14							25													7				5					8						
Limosella vesiculosa	3	17										17	6													9						23	17									
Argyrolobium tuberosum				6										13							7			22	20												14			11		8
Helichrysum pilosellum																					14			22	20														14			11
Heliophila carnosa																								22																		11
Holcus lanatus																								11						22						8						

Oxalis smithiana	9		3													7											7			22					3							
Vulpia bromoides				13																										22	5											
Digitaria eriantha																					21		14																			
Ledebouria sp.				6																	21	13	14																14	11		3
Gerbera ambigua		8																																			7			21		
Aponogeton junceus		8	13	6	14			17					6		10				20								7					14		4						5		
Cheilanthes quadripinnata																											7								6			20				
Cirsium vulgare				6																									6						6			20				3
Crassula dependens															20	7																5										
Crassula natans			6	6		17			14	13					10				20											11	5											
Crassula vaillantii			3	13		17																						20	19		5	5										
Cyperus fastigiatus															10																							20				
Disa rhodantha																									20																	11
Eleocharis limosa				6											20																											
Eragrostis caesia			10	6			14						13		20																					8			14			
Eragrostis chloromelas			10				14								20		8								20					11					3					5		3
Eragrostis patentissima																									20															5		
Mariscus congestus			6	6	14																	13					7	10	13		5				12			20				3
Nidorella agria		8	3							13																	14	20														
Pentaschistis densifolia	3								14																			20	13			9										
Peucedanum thodei			6																							9	14	20			5											
Schizochilus zeyheri		8																						11	20																	6
Senecio gerrardii																									20																	11
Berula erecta				13													8										7		19		16							10				
Denekia capensis	6							17					19													9									12	8						3
Isolepis sp.								17					19																			5										
Thesium sp.			10						14				19																				17									
Deschampsia cespitosa										13			6													18						9										
Papaver aculeatum																7										18										8						
Alepidea natalensis		17	6																																							
Alepidea setifera																								11																		17
Axonopus affinis																																	17									
Bromus catharticus							14	17	14								8													11			17	4								3
Carex sp.		8						17																																		
Cerastium sp.																																	17									

Colpodium drakensbergense																																	17									
Crassula peploides		17																	13																							
Crassula tuberella		8																														5	17									
Cyperus schlechteri		17																																								
Cyrtanthus flanaganii			3					17																							5											
Felicia filifolia s. *filifolia*						17																																				3
Felicia sp.		8									17	17																				5										
Ficinia cinnamomea																												10								17						
Helichrysum anomalum														13																						17						
Helichrysum tenuiculum						17																																				
Helichrysum trilineatum	3		6								17																															
Helichrysum witbergense											17																															
Hesperantha tysonii		17																																								
Hordeum capense																																	17									
Isoetes sp.	3					17																														8						
Kniphofia brachystachya								17																																		
Ludwigia palustris								17																																		
Moraea alticola		8					14			13	17			13																		5										
Pentaschistis natalensis								17																																		
Polygonum meisnerianum								17								14					7							10												5		
Pycreus niger				6				17								7															5					8						
Pycreus nigricans								17																																		
Pycreus nitidus				13			14	17															14								5											
Romulea luteoflora											17	17																														
Rorippa nasturtium			3																														17									
Schoenoplectus decipiens			3			17								13	10		15													11				4								
Scirpus falsus		17																									7							4								
Sebaea marlothii		17								13									13																							
Sebaea natalensis	3		3					17																																		
Sebaea sp.	3											17																														
Senecio barbatus	3	17																																		8						
Senecio cathcartensis		8										17																				5										
Senecio isatideus			3					17															14												6							

Senecio natalicola		8									17	17							7							9																
Senecio qathlambanus												17																														
Senecio sp.																																	17									
Sisymbrium capense						17																																				
Stiburus conrathii		17																				13																				
Tetraria cuspidata		8						17																																		
Tulbaghia sp.		17																																								
Ursinia alpina											17																															
Watsonia sp.																																	17									
Xanthium sp.		17	3	6						13																				11						8				5		3
Hesperantha lactea																																								16		
Hypoxis filiformis																																					7			16		
Rhynchospora brownii					14																													11		8				16		3
Cotula heterocarpa															10	7	15	14																								
Cynodon transvaalensis																	15																									
Marsilea sp.																7	15																									
Senecio inornatus	6		13							13							8											10							15			10				3
Pseudognaphalium undulatum	15															7											7								3							3
Acalypha punctata																					7		14												9	8						
Agrostis sp.							14																									5										
Alchemilla elongata	3								14					13																	11											
Alepidea amatymbica		8	6						14																																	
Algae					14																																					
Alloteropsis semialata s. semialata																					14															8						
Amaranthus hybridus																		14																								
Anagallis sp.							14																																			
Anagallis tenuicaulis				13																																			14			
Andropogon amethystinus	3						14																																			
Asclepias sp.					14																																					
Bulbine sp.				6			14																																14			
Bulbostylis sp.	3				14																											5										
Carpha glomerata																		14																								
Cineraria dieterlenii																										9	14	10														
Cliffortia linearifolia	6		3						14																						5					8						3
Cotula microglossa																		14																								

Crassula setulosa							14																																			
Cyperus marginatus							14							6			7	8											6	11				4	3			10				6
Cyperus sp.	3														10	7	8	14	7																							
Dierama dracomontanum							14																																			
Digitaria monodactyla																																							14			
Diheteropogon amplectens																					7		14													8			14			
Elegia spathacea																		14																								
Eleusine coracana			3				14							13																												
Epilobium tetragonum s. tetragonum									14																																	
Eragrostis racemosa																					14		14												3	8				5		
Eriospermum ornithogaloides							14																																			
Euryops annae									14																																	
Festuca costata		8					14																												3	8						
Ficinia compasbergensis									14																			10														
Fimbristylis sp.																								11															14			
Fuirena ecklonii	3																										1 4			11	5				3							
Geranium harveyi	3								14																						5											
Geranium multisectum		8	3				14										8										7		6		5	5		7		8						
Geum capense	3	8	6				14			13																																
Gnaphalium confine	9			6					14									14																								
Gymnopentzia sp.																																							14			
Helichrysum auronitens	3		3						14					13			8														5					8						
Helichrysum lingulatum									14																																	
Helichrysum miconiifolium																																							14			
Helichrysum simillimum	3																						14								5	5							14	5		
Helichrysum umbraculigerum	3				1 4																														6							
Helictotrichon longifolium										13																9													14			
Heteropogon contortus																					7		14					10											14			
Hirpicium armerioides																					14																					
Hypoxis argentea																7							14				7													5		
Hypoxis longifolia				6																	7	13	14								5											
Isolepis setacea																		14																								

Juncus punctorius	3								14																				6													
Juncus tenuis					14										10														6													
Kniphofia northiae																											14				5					8						
Kniphofia thodei																					7		14																			
Kyllinga pauciflora																14												10														3
Lepidium schinzii																		14			7																					
Lidbeckia sp.																																							14			
Lobelia thermalis																	8	14												11								10				
Lolium perenne																	8	14																								
Mariscus keniensis																											14															
Merxmuellera stereophylla							14																																			
Mimulus gracilis															10	14			7								7											10				
Mohria rigida							14																																			
Monsonia brevirostrata							14																																			
Moraea spathulata									14																																	
Nidorella anomala																																					14	10				
Nidorella undulata	3																									9	14	10			5											
Panicum ecklonii					14																																		14			
Panicum sp.				6														14																	3	8						
Panicum subalbidum			6		14																																					
Pelargonium grossularioides	9								14							7															5											3
Pentaschistis airoides							14						6																													
Plantago lanceolata															10	7	8	14																								3
Plantago sp.									14																																	
Polygonum aviculare	3															7	8	14																								
Prunella vulgaris					14																																					
Psammotropha mucronata		8																																					14			
Pseudognaphalium oligandrum					14																																					
Pycreus sp.				6																		13		11															14			
Rabdosiella calycina																							14																			
Rumex crispus			3		14										10															11				4								
Satyrium longicauda		8																					14																			
Satyrium sp.														13									14																			
Scleria bulbifera																							14																			
Scleria sp.																					14															8			14			

Sebaea rehmannii																																							14	5		
Selago densiflora																					14																					
Senecio affinis	3				14																								6													
Senecio gregatus			6													7										9										8			14			
Senecio juniperinus	3								14					13															6		5											
Senecio parascitus							14																																			
Setaria nigrirostris																							14																			
Setaria sp.																		14																								
Sium repandum	3								14							7																										
Solanum sp.							14																																			
Sonchus dregeanus																	8	14																								
Spergularia media																		14																								
Stachys sp.																					14																					
Tetrachne dregei							14									7																										
Trachypogon spicatus			3																		7															8			14			14
Trichodesma africanum																							14																			
Ursinia nana s. nana							14																																			
Urtica urens							14																																			
Xerophyta viscosa							14																																			
Arctotis sp.														13																												
Berkheya sp.			3							13							8													11		5										
Centella asiatica				13											10	7																										
Cerastium capense				13													8									9																
Cineraria sp.														13													7															
Conyza chilensis																						13																				
Crassula natalensis										13																	7															
Diascia barberae										13																																
Disa versicolor																						13																				
Euphorbia cyparissias														13																												
Gazania krebsiana s. krebsiana		8	3							13																																
Helichrysum adenocarpum			3							13																																
Isolepis diabolica				13																																						
Isolepis prolifera				13																																						
Lepidium sp														13													7															
Limosella inflata			10							13																						5										

Litanthus pusillus													13																													
Lobelia preslii										13																																
Loudetia densispica																					7	13																				
Myosotis sp.														13																												
Papaver sp.														13																												
Passerina montana		8								13																									3							
Schoenoxiphium lanceum	3			13												7	8														5											3
Scleranthus sp.																						13																				
Sebaea grandis																						13																				
Sebaea pleurostigmatosa														13																		5										
Sebaea thomasii														13																	5											
Senecio asperulus	6		3											13													7															3
Senecio striatifolius																						13																				
Senecio tanacetopsis		8												13																												
Sporobolus africanus		8								13					10	7																								5		
Sporobolus fimbriatus				13																																						
Stachys aethiopica														13																												
Utricularia livida		8		13																																						
Artemisia afra			3																																12							
Alternanthera nodiflora		8																												11												
Arctotis arctotoides	6		3													7					7					9				11					3	8						
Conium fontanum	6																													11	5											
Conyza podocephala			6																											11								10				
Cyperus esculentus var esculentus																								11			7															6
Euryops sp.																														11												
Helichrysum splendidum		8	6													7												10		11	5				6							3
Picris echioides																													6	11												
Scirpoides dioecus																														11												
Polygonum plebeium																																		11						5		
Pycreus unioloides																																		11						5		6
Eumorphia sericea		8	3																												11					8						
Pentzia cooperi																															11											
Stachys natalensis																																					7			11		
Afrotysonia glochidiata	3																											10														

Alchemilla sp.				6																								10														
Alternanthera sessilis															10																											
Aristida sp.																												10														
Aster squamatus																																						10				
Berkheya macrocephala		8																										10														
Berkheya purpurea		8	3																									10														
Cheilanthes viridis																												10														
Ciclospermum leptophyllum																7																						10				3
Cineraria lyratiformis																																						10				
Cliffortia nitidula s. nitidula																																						10				
Cotula nigellifolia																												10														
Crinum bulbispermum																																						10				
Cymbopogon plurinodis	3		3													7																						10				
Cynodon dactylon															10																											
Cynodon incompletus			3	6									6		10																					8						
Cyperus distans																												10														
Cyperus rotundus			3										6		10																											3
Cyperus semitrifidus			3	6											10																											
Digitaria longiflora															10																											
Diplachne fusca															10																											
Echinochloa crus-galli															10																											
Erodium cicutarium															10																											
Euphorbia natalensis		8																									7	10														
Festuca scabra															10		8										7															3
Galium capense	3	8	3																									10							3			10				3
Geranium pulchrum			3																																			10				
Gomphocarpus fruticosus																																						10				
Haplocarpha scaposa																7																						10				
Hibiscus trionum																7											7	10							3							3
Hyparrhenia hirta			3																																6			10				
Imperata cylindrica																																			3			10				
Ipomoea crassipes															10																											

Isolepis pellocolea		8	3																									10														
Jamesbrittenia pristisepala															10																											
Kniphofia linearifolia	3																											10							3					5		
Lipocarpha micrantha																																						10				
Melolobium burchellii																																						10				
Mentha longifolia		8		6																														4				10				
Microchloa caffra															10						7																					
Monsonia sp.															10																											
Myosotis afropalustris																											7	10														
Oenothera indecora s. indecora																											7								3			10				
Oenothera rosea	3		3																								7								9			10				6
Panicum hymeniochilum																												10							3							
Panicum maximum			3	6											10																											3
Paspalum urvillei															10																				9							
Pennisetum clandestinum			3										6		10																											
Persicaria attenuata s. africana																												10														
Persicaria lapathifolia																																		4				10				
Phalaris arundinacea																																						10				
Polygonum attenuatum															10																											
Potamogeton pusillus															10																											
Pteridium aquilinum																																			6			10				
Pulicaria scabra																																						10				
Rubus ludwigii s. ludwigii			6																								7								3			10				
Rubus rigidus	3																											10							3							
Rumex rhodesius																										9	7	10								8						
Schkuhria pinnata															10	7																										
Schoenoxiphium sp.															10																											
Senecio rhomboideus															10																											
Zantedeschia aethiopica																																			3			10				
Carpha filifolia		8	10																																							
Catalepis gracilis			10													7																										

Berkheya cirsiifolia																										9																
Carex subinflata																										9																
Cliffortia paucistaminea																																			9							
Cymbopogon validus																																			9							
Cysticapnos pruinosa																										9																
Disperis wealii		8	6																							9																
Geranium schlechteri	3																									9																
Helichrysum albo-brunneum			3																							9																
Hyparrhenia dregeana																																			9							
Ajuga ophrydis	3																				7											5				8						
Alepidea longifolia																																				8						
Aster erucifolius		8																																								
Berkheya rosulata																																				8						
Bromus leptoclados		8																																								
Cineraria geifolia																																				8						
Cotula socialis		8																																								
Disa crassicornis		8																																								
Disa fragrans		8																																								
Eragrostis sp.				6																																8						
Erica aestiva																																				8						
Eumorphia prostrata		8																																								
Felicia rosulata		8	3																																							
Felicia wrightii		8																																								
Galium sp.																																				8						
Geranium robustum	3	8																																								
Geum urbanum		8																																		8						
Gladiolus varius																																										8
Gnaphalium limicola		8																																								
Gnidia sp.		8																																								
Helichrysum callicomum																					7															8						
Helichrysum cephaloideum		8														7																										
Helichrysum griseolanatum		8																																								
Helictotrichon sp.																																				8						
Hypericum lalandii			6	6												7																				8				5		

Kniphofia porphyrantha																																				8						
Kniphofia triangularis s. *triangularis*	3																																			8						
Lithospermum papillosum	3	8																																								
Merxmuellera stricta		8																																								
Moraea albicuspa		8																																		8						
Moraea inclinata																																				8						
Pentaschistis aurea		8																																								
Pentaschistis oreodoxa		8																																								
Pentaschistis praecox		8																																								
Persicaria serrulata		8																																								
Pimpinella reenensis																																				8						
Pseudoschoenus inanis																																				8						
Rorippa nudiuscula			3																																3	8						
Satyrium parviflorum																																				8						
Scabiosa sp.																																				8						
Schoenoplectus sp.																																				8						
Sebaea sp. 1		8																																								
Sebaea thodeana																																				8						
Senecio othonniflorus																																				8						
Senecio purpureus				6																											5					8						
Senecio scitus		8																																								
Stachys rugosa		8																																		8						
Urginea sp.		8																																								
Utricularia sp.		8																																								
Wahlenbergia krebsii s. *krebsii*	3	8																																	3					5		
Zaluzianskya microsiphon		8																																								
Agrostis montevidensis																	8																									
Fuirena hirsuta																	8																									
Gymnopentzia bifurcata	3		3										6				8																									
Helictotrichon hirtulum	3																8																									6
Jamesbrittenia filicaulis																	8																									
Lepidium africanum s. *divaricatum*																	8																									
Lobelia dregeana																	8																									

Nidorella resedifolia s. resedifolia																	8																									
Oxalis imbricata																	8														5											
Selago albida	3																8																									3
Alepidea sp.																					7																					
Anthoxanthum ecklonii																7																								5		
Berkheya radula																7																										
Bulbostylis oritrephes																					7																					
Calpurnia villosa																7																										
Chironia sp.																7																										
Chrysocoma ciliata													6			7																										
Clutia affinis																7																										
Conyza bonariensis																7																										3
Conyza sp.																					7														3							
Cotula dielsii																7																										
Crabbea acaulis																					7																					
Crassula nemorosa																											7															
Cyperus congestus			3													7																										
Cyperus rupestris																					7																					
Digitaria diagonalis																					7																					
Diospyros lycioides s. lycioides																7																										
Dissotis canescens																											7															
Echinochloa colona			3										6			7																										
Elionurus muticus																					7														3							
Epilobium hirsutum	3																																	7								
Equisetum ramosissimum																					7						7															3
Garuleum woodii																7																										
Geranium wakkerstroomianum	3																										7															
Geum sp.																											7															
Gladiolus sp.																					7																					
Gnaphalium sp.													6			7																										
Helichrysum coriaceum																					7																					
Helichrysum rugulosum																					7																					
Hermannia coccocarpa																					7																					
Hermannia depressa																					7																					

Hesperantha coccinea	3															7																										
Hibiscus micranthus																					7																					
Ilex mitis																											7															
Kniphofia multiflora																											7															
Kyllinga melanosperma																											7															
Laurembergia repens s. brachypoda				6												7																										
Melica decumbens																											7															
Myosotis semiamplexicaulis																											7															
Oxalis semiloba s. uhehensis																					7																					
Poa sp.																7																										
Polygala amatymbica																					7																					
Rhus pyroides																7																										
Rumex acetosella	6																				7																					
Rumex steudelianus																											7															
Sacciolepis chevalieri																7																										3
Sacciolepis sp.																					7																					
Salvia disermas																					7																					
Schoenoplectus corymbosus																											7							4								
Sebaea micrantha																					7																					
Senecio glutinosus			3													7					7																					3
Senecio polelensis																																					7					
Sutera caerulea																					7																					
Tagetes minuta																7																										
Thelypteris confluens																											7								3							3
Trifolium repens																7																										
Trifolium sp.																					7																					
Tulbaghia leucantha																					7																					
Verbena bonariensis																7											7							4	6							3
Xyris natalensis																7					7																					
Poa annua													6						7										6			5										
Senecio burchellii			6																																							
Agrostis sabulicola			3										6																													
Alectra picta				6																																						
Alectra pumila				6																																						

Androcymbium sp.													6																													
Brachiaria serrata				6																																						
Chenopodium phillipsianum																													6													
Conium chaerophylloides				6																																						
Crassula inanis				6																														4								
Crassula lanceolata													6																													
Cynodon nlemfuensis				6																																						
Cynoglossum austroafricanum				6																																						
Dactylis glomerata																													6													
Digitaria argyrograpta				6																																						
Digitaria ternata				6																																						
Eragrostis gummiflua													6																													
Eragrostis lehmanniana																													6													
Eriocaulon sp.				6																																						
Grass sp.													6																													
Helichrysum infaustum													6																													
Helichrysum montanum													6																													
Hemarthria sp.													6																													
Juncus exsertus s. lesuticus				6																												5										
Lobelia sp.				6																																						3
Polypogon viridis			3																										6													
Potamogeton sp.				6																																						
Pselutagraph sp.													6																													
Schoenoplectus muriculatus				6																																						
Senecio hastatus				6																																						
Sonchus asper s. asper																													6													
Sonchus oleraceus				6																									6													
Sporobolus ludwigii																													6													
Trifolium angustifolium				6																																						
Utricularia gibba				6																																						
Vulpia sp.	3												6																													
Walafrida densiflora	3												6																			5		4								
Clutia katharinae	3																																		6							

Conyza obscura																																			6							
Euphorbia epicyparissias	6																																		6							
Salix mucronata s. woodii																																			6							
Schoenoxiphium rufum																																			6							
Stachys grandifolia	3																																		6							3
Wahlenbergia grandiflora	3																																		6							
Geranium baurianum	6		3																																							
Ornithogalum tenuifolium s. tenuifolium	6																																									
Rubus pinnatus	6																																									
Brachiaria sp.																																								5		
Buchnera dura																																								5		
Crepis sp.																															5											
Eulalia villosa																																								5		
Hypoxis rigidula																																								5		
Medicago polymorpha																															5											
Nasturtium officinale																															5											
Rumex woodii	3																														5											
Scilla natalensis																																								5		
Senecio achilleifolius																															5											
Senecio bupleuroides																																								5		
Typha domingensis																															5			4								
Commelina sp.																																5										
Erica frigida																																5										
Lagarosiphon muscoides																																5										
Merxmuellera guillarmodiae																																5										
Potamogeton thunbergii																																5		4								
Samolus sp.																																5										
Hydrocotyle verticillata																																		4								
Phragmites mauritianus																																		4								
Pycreus mundii																																		4								
Ursinia sp.																																		4								
Acalypha schinzii			3																																							
Agrimonia procera			3																																							
Alepidea acutidens	3		3																																							

Brachiaria eruciformis			3																																							
Chironia purpurascens			3																																							
Craterocapsa sp.			3																																							
Crocosmia paniculata			3																																							
Erica woodii			3																																							
Euphorbia ericoides			3																																							
Fuirena sp.			3																																							
Geranium sp.			3																																							
Glinus sp.			3																																							
Helichrysum glomeratum			3																																							
Helichrysum herbaceum			3																																							
Helichrysum sp. 2			3																																							
Hesperantha sp.			3																																							
Lactuca dregeana			3																																							
Lycopodium sp.			3																																							
Moraea huttonii			3																																							
Myosotis arvensis			3																																							
Oenothera stricta			3																																							
Paspalum notatum			3																																							
Pelargonium alchemilloides			3																															3							
Pelargonium capituliforme			3																																							
Salvia repens			3																																							
Schoenoxiphium caricoides			3																																							
Setaria pallide-fusca			3																																							
Solanum nigrum			3																																							
Acacia mearnsii																																			3							
Agapanthus campanulatus																																			3							
Buddleja salviifolia																																			3							
Bulbine narcissifolia																																			3							
Cephalaria natalensis																																			3							
Cycnium racemosum																																			3							
Cynoglossum lanceolatum																																			3							
Diclis rotundifolia																																			3							
Erica anomala																																			3							
Erica evansii																																			3							

Eriosema salignum																																			3							
Eucomis bicolor																																			3							
Gladiolus saundersii																																			3							
Helichrysum argyrophyllum																																			3							
Helichrysum natalitium																																			3							
Ischaemum fasciculatum	3																																		3							
Kniphofia ensifolia s. ensifolia																																			3							
Lessertia perennans	3																																		3							
Limosella capensis																																			3							
Myrothamnus flabellifolius																																			3							
Ophioglossum vulgatum																																			3							
Panicum aequinerve																																			3							
Pelargonium dispar																																			3							
Phygelius aequalis																																			3							
Plectranthus grallatus	3																																		3							
Polygala virgata																																			3							
Rhus dentata																																			3							
Rhus discolor																																			3							
Schistostephium crataegifolium																																			3							
Sebaea filiformis																																			3							
Senecio arabidifolius																																			3							
Senecio retrorsus																																			3							
Solanum mauritianum																																			3							
Valeriana capensis																																			3							
Vernonia hirsuta																																			3							
Crassula sp.	3																																									
Cyrtanthus sp.	3																																									
Eucomis autumnalis s. autumnalis	3																																									
Galium spurium s. africanum	3																																									
Hebenstretia dura	3																																									
Helichrysum nudifolium	3																																									
Helichrysum sp.	3																																									

Hypericum aethiopicum s. aethiopicum	3																																										
Lasiospermum bipinnatum	3																																										
Leonotis ocymifolia	3																																										
Moraea sp.	3																																										
Oxalis sp.	3																																										
Pentaschistis sp.	3																																										
Selago galpinii	3																																										
Senecio napifolius	3																																										
Senecio tenuiflorus	3																																										
Sonchus sp.	3																																										
Sutera patriotica	3																																										
Sutera rotundifolia	3																																										
Alectra sessiliflora																																											3
Argyrolobium harveyanum																																											3
Conopodium sp.																																											3
Crepis hypochoeridea																																											3
Kniphofia sp.																																											3
Limosella sp.																																											3
Monopsis sp.																																											3
Oenothera tetraptera																																											3
Persicaria amphibia																																											3
Pycreus intactus																																											3
Rhynchosia sp.																																											3
Trifolium pratense																																											3

Appendix 7.1: Redundancy analysis ordination diagram for ecosystem services and measures of diversity, functional diversity and vegetation structure of the Afromontane palustrine wetlands in Lesotho. See Tables 7.2 and 7.3 for the abbreviations of ecosystem services and plant functional traits, respectively. Totcover stands for total cover, Avheight stands for average vegation height and Sp_richness stands for species richness.