THE ECOLOGY AND PLANT FUNCTIONAL COMPOSITION OF THE AFROMONTANE PALUSTRINE WETLANDS IN LESOTHO

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ABSTRACT

The classification and description of wetland vegetation is important for biodiversity conservation and water resource management as it provides an understanding of the wetland vegetation-environment relationships and information to interpret spatial variation in plant communities. This study characterises the Afromontane palustrine wetlands of Lesotho in terms of plant communities, plant functional types and plant functional composition. Relationships of plant communities and functional traits were also explored. Vegetation, environmental and plant functional trait data were collected using the Braun-Blanquet method and standard methods. The data were analysed mainly by means of clustering, ordination and diversity analysis techniques. Twenty-two communities were produced by the classification of the Afromontane wetland vegetation and seven plant functional types, as well as seven functional communities were obtained from the classification. The wetland plant communities are 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, peat, potassium content, soil texture, total organic carbon, nitrogen, sulphur, electrical conductivity, calcium, soil depth, wetness, magnesium, aspect and latitude. Plant functional traits and functional composition of the communities were found to be broadly influenced by altitude, slope, longitude, soil parent material, landscape and inundation, and more finely by edaphic factors that include electrical conductivity, calcium, sodium, magnesium, nitrogen, organic matter, total organic carbon, clay percentage, pH, sand percentage and potassium. Regarding species composition and diversity, plant communities in the Highlands were more diverse and were distinctively different from those in the Lowlands. Although a few wetlands, particularly in the Highlands are still in their near-pristine condition, many wetlands in the country are showing severe signs of degradation. While some communities are either restricted to the Highlands or Lowlands, others exhibit a wide ecological amplitude and occur in both regions. The study further highlights the possibility of alterations in plant functional traits, types and functional composition in the face of environmental changes, including climate change. 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.

Keywords: Afromontane palustrine wetland, Biodiversity, Community-weighted mean, Conservation, Ecosystem function, Functional composition, Maloti-Drakensberg, Plant community, Plant functional type, Plant functional trait, Vegetation classification.

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1.0 INTRODUCTION

The Lesotho highlands represent a key water resource for both Lesotho and South Africa, and palustrine wetlands play a pivotal role in the water supply and hydroelectric power generation. A report from the Maloti Drakensberg Transfrontier Project (MDTP, 2007) highlighted that the montane wetlands of Lesotho, though rapidly degrading, are unique and play an important role in providing a sustainable supply of high quality water throughout the year. However, despite their uniqueness and importance, detailed vegetation surveys on these wetlands have been scarce and scattered (Sieben, 2011). Several of the developmental activities carried out in Lesotho, including diamond mining and damming as well as the associated infrastructure development, play a key role in the economy of the country, though at the expense of the ecological systems that support the water levels in these dams. Naturally, the geographical location and agro-ecology of Lesotho makes the country, and therefore its wetlands vulnerable to the effects of climatic change. The loss and degradation of wetlands curtail their ability to support biodiversity and to provide ecosystem services. With the eminent global climate change and the associated water shortages, the conservation of these wetlands becomes a key factor for the sustainable supply of water. Therefore, information from detailed studies on these wetlands plays a key role in conservation planning for these important ecosystems.

Palustrine wetlands are important for biodiversity conservation and for the livelihoods of human communities. Their ecosystem services per unit area are considered to be typically higher than those of other types of ecosystems (CBD Secretariat, 2015). Montane wetlands, in particular, are important in the ecology and hydrology of the local environment and downstream systems of rivers whose catchments are in these montane areas. Many montane wetlands are located in headwaters and are considered to be of international importance because they provide water for many transboundary rivers (Chatterjee et al., 2010) such as the well-known and important Orange-Senqu River in Southern Africa. Furthermore, montane wetland ecosystems are often rich in endemics because many species remain isolated at these high altitudes (Sharma et al., 2010). These wetlands, therefore, serve as repositories for high altitude biodiversity, and provide suitable habitats for rare and threatened montane species (Jayachandran, 2013). Considering their role in the hydrological cycle and other water-related ecosystem services, wetlands conservation is now a topical issue globally.

Environmental factors such as wetland size, geological substrate, altitude, land use, water chemistry and hydrological fluctuations are regarded as predictors for richness and composition of plant communities in wetlands (Rolon & Maltchik, 2006). Kotze and O'Connor (2000) and Sieben et al. (2010b, b) report that the degree of soil wetness is strongly related to the structural and functional features of a wetland. According to Brand et al. (2013), substrates (soil or bedrock) and hydrogeological conditions also have a greater influence on the floristic composition, structure and dynamics in high altitude montane wetlands than microclimate. Given that changes in altitude are associated with a tremendous spatial variation in physical features (Kotze & O'Connor, 2000; Sharma et al., 2010), a wide variation in wetland plant composition and diversity can be expected in Lesotho. In fact, Sieben et al. (2010a) acknowledge the significant number of wetland community types in Lesotho. Furthermore, high altitude montane wetlands of Lesotho are likely to be impacted more by climate change, coupled with anthropogenic activities such as livestock grazing and trampling, and developmental activities already occurring in these areas. Therefore, elucidating the pattern of wetland biodiversity across environmental gradients in Lesotho can support sound wetland conservation planning.

Because of the many types of environmental changes such as climate change and degradation that are expected to take place in wetland environments, Sieben et al. (2014) emphasise the need for an understanding of the link between plant community composition and the physical environment in wetlands. Given also that wetland vegetation is azonal (Sieben, 2011) and responds quickly to environmental changes (Cronk & Fennessy, 2001; Sieben et al., 2014), plant species occurring in wetlands are useful indicators of environmental conditions and ecological changes in these wetlands (Schulze et al., 2002; Sieben et al., 2014). Wetland condition determines the capacity of a wetland to support wildlife and to deliver ecosystem goods and services but this capacity, in many wetlands, is rapidly diminishing due to loss and degradation. Therefore, long term monitoring of the plants that are characteristic of specific wetland environments is important in order to detect any significant changes which could occur (Sieben et al., 2014). This therefore raises a need to determine characteristic species of specific wetland environments in order to establish a baseline for monitoring.

Despite their importance, wetlands are among the most threatened ecosystems globally (Millennium Ecosystem Assessment, 2005). More than 50% of the world's wetlands have already been lost since 1900, mainly due to anthropogenic factors (Rolon & Maltchik, 2006; Daryadel & Talaei, 2014). In addition, in excess of 50% of South Africa's wetlands have also been destroyed (Van Ginkel et al., 2011). Many wetlands in Lesotho are also indicating signs of degradation and probably many have been lost, though no study has quantified the degree of loss. With this loss of wetlands, human welfare is being threatened at a time of increasing water scarcity and demand (Daryadel & Talaei, 2014). The rapid degradation and loss of wetlands raise an urgent need for ecological studies aimed at understanding the patterns of biodiversity in these important but sensitive ecosystems to provide scientific support to biodiversity conservation programmes (Rolon & Maltchik, 2006). Furthermore, studies in montane wetlands can be useful in assessing the effect of climate change on biodiversity because mountains can represent unique areas for the detection of climatic change (Sharma et al., 2010).

The need for more detailed information on wetland vegetation to enhance monitoring, rehabilitation, management and conservation of wetlands has been emphasized (Mucina & Rutherford, 2006; Sieben, 2011). However, Sieben et al. (2014) highlight that there are neither current nor recent studies on the wetlands in Lesotho. Although many detailed studies have been carried out in South African wetlands, a detailed study on the wetlands in Lesotho is imperative. Given that environmental factors driving wetland community composition differ with geographical location and type of the wetland (Sieben et al., 2014), and wetlands exhibit remarkable diversity and uniqueness, wetland-specific and area-specific studies of wetlands are important (Macfarlane et al., 2008). Furthermore, because of the supreme importance of wetlands, Sieben et al. (2016) emphasise the need for more information about their species composition, ecology and distribution.

This study aims at characterising the Afromontane wetland vegetation of Lesotho by achieving the following objectives:

1. To classify and describe the plant communities
2. To determine the functional composition of the vegetation

The study will provide the much needed information for the proper conservation planning, and is therefore a key step towards identifying interventions to safeguard the ecosystem goods and services delivered by wetland ecosystems including sustainable water supply for Lesotho, South Africa and other downstream riparian countries. This study will also provide vital baseline information against which the success of management interventions and future environmental changes can be assessed. The information on the ecology and vegetation of the wetlands in Lesotho will be important for the proper conservation of these fragile and threatened but important ecosystems. Only about 4% of the wetlands in the Drakensberg area is statutorily conserved (Brand et al., 2013).

2.0 MATERIALS AND METHODS

2.1 Study Area

This study was carried out in Lesotho, a small mountainous enclave of South Africa. It is bounded by three of South Africa's provinces, namely, KwaZulu-Natal to the East, the Eastern Cape to the South, and the Free State to the North and West. Although the current study focuses on Lesotho, the description of the study area also covers the Maloti-Drakensberg biodiversity region in general because the greater proportion of Lesotho (about 70%) falls within this globally recognised hotspot (Cowling & Hilton-Taylor, 1994; Carbutt & Edwards, 2006; Kopij, 2006) and is known for high species endemism (Pomela et al., 2000). Lesotho also accounts for about 60% of this hotspot, with the remaining portion covered by the three South African provinces (Pomela et al., 2000). The Maloti-Drakensberg is one of the eight Southern African hotspots of botanical diversity, in terms of species richness and endemism (Cowling & Hilton-Taylor, 1994; Pooley, 2003).

The Lesotho part of the Maloti-Drakensberg biodiversity hotspot, called Maloti Mountains, forms the highlands of the country. Lesotho is the only country in the world that lies entirely above 1000 metres above sea level (m a.s.l.) (Ministry of Natural Resources, 2000). The highest mountain peak in Africa, south of Kilimanjaro is found in Lesotho, with a summit at an altitude of 3482 m a.s.l. at Thabana-Ntlenyana (Backéus & Grab, 1995; Mucina & Rutherford, 2006). The country has a wide altitudinal range (1388-3482 m a.s.l.) (Chakela, 1997; Pomela et al., 2000). Basing on Carbutt and Edwards (2015), who define the Afromontane region as the area occurring between ±1300 m and ±1800 m a.s.l. and alpine as the region from ±1800 to 3482 m a.s.l., the entire Lesotho qualifies to be at least Afromontane. Based on climate and elevation, Lesotho has been divided into four agro-ecological zones (AEZs): the Lowlands (below 1800 m a.s.l., Foothills (between 1800 and 2300 m a.s.l), Highlands (from 2300 to 3482 m a.s.l.) and Senqu River Valley (Pomela et al., 2000; Bureau of Statistics, 2009). Figure 1 presents the agro-ecological zones and the ten administrative districts of Lesotho.

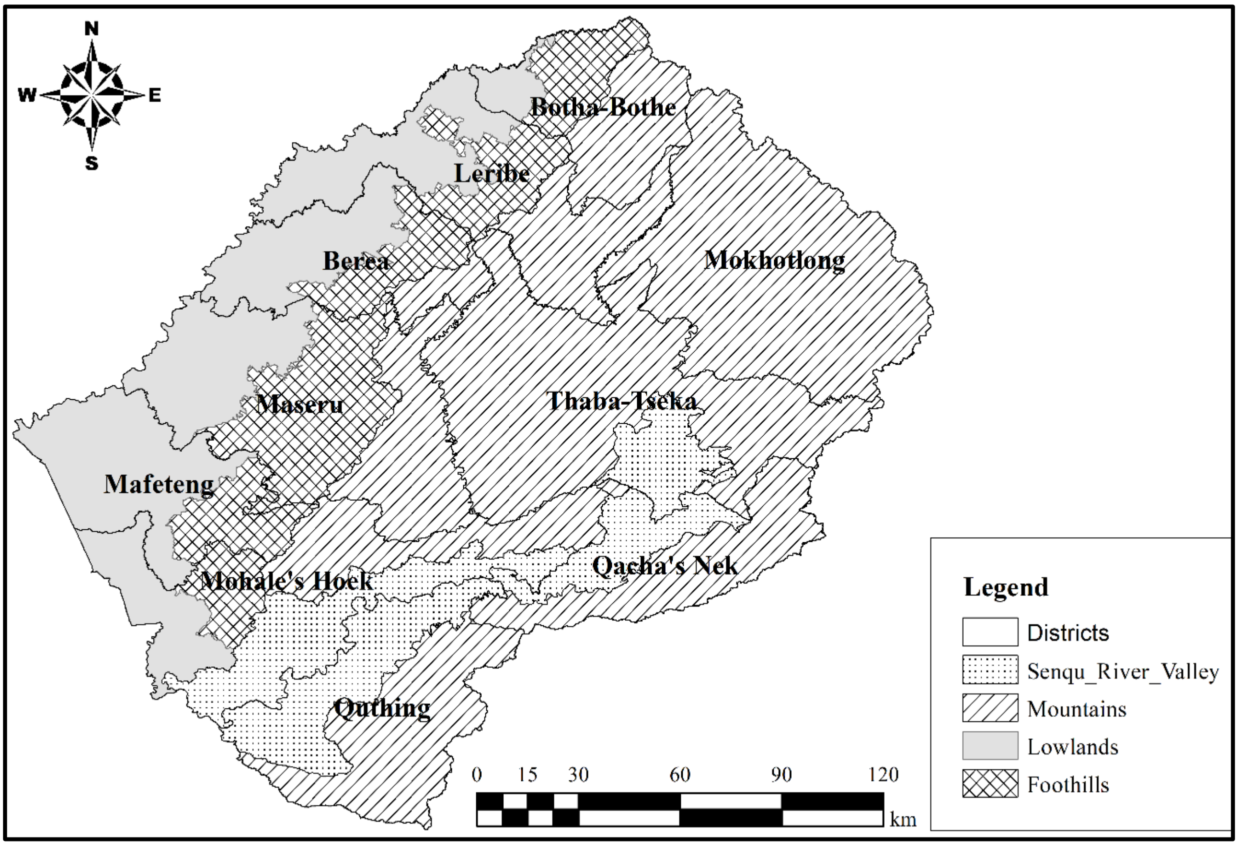

Figure 1: The four agro-ecological zones and the ten administrative districts of Lesotho

Lesotho has a temperate climate that is moderated by altitude (Kopij, 2006). 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. The country receives abundant orographic rainfall as warm moist air from the Indian Ocean cools down on rising over the high mountains (Sieben et al., 2010a). The rainfall, generally increasing eastwards, ranges from 500 mm to 2000 mm annually, with the Highlands receiving the highest amount and the Senqu-Orange River Valley the lowest (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). Spatially, the mean annual temperatures range from 15.2 ℃ in the Lowlands to 7 ℃ in the Highlands (Lesotho Meteorological Services, 2013). During winter, rainfall is rare, but heavy snowfalls frequently occur and the snow can persist on the ground for weeks or even months (Backéus & Grab, 1995; Pooley, 2003), especially on the south-facing slopes of the high mountains of the country.

Lesotho is characterised by high altitude flora and is covered entirely by the Grassland Biome of Southern Africa (Kopij, 2006; Mucina & Rutherford, 2006). Mucina and Rutherford (2006) broadly divide the Grassland Biome of Southern Africa into four bioregions (Drakensberg Grassland, Dry

Highveld Grassland, Mesic Highveld Grassland and the Sub-Escarpment Grassland). Lesotho is covered entirely by two of these bioregions: the Drakensberg Grassland Bioregion, which covers the higher altitude areas of the country, and the Mesic Highveld Grassland Bioregion which occurs in the lower altitude areas. The former bioregion accounts for the greater portion of the country. These two are the highest-lying bioregions of the biome, occurring at mean altitudes above 2000 m and above 1500 m a.s.l., respectively (Mucina & Rutherford, 2006). While the Mesic Highveld Grassland Bioregion mainly corresponds to the Lowlands of Lesotho and the lowest part of the Senqu River Valley, the Drakensberg Grassland covers the Highlands, Foothills and the upper Senqu River Valley (Pomela et al., 2000).

Within these bioregions is an archipelago of wetlands that host a wide range of species. The wetlands, locally known as *Mokhoabo* (in Sesotho Language), are a common feature in Lesotho, especially in the mountains. They form conspicuous patches across the country's landscape due to their distinct vegetation. Mucina and Rutherford (2006) classify the wetlands of the entire Lesotho into Eastern Temperate Freshwater wetlands (AZf 3), Drakensberg wetlands (AZf 4) and Lesotho mires (AZf 5), which occur at altitudes 750-2000 m, 1800-2500 m and 2500-3400 m a.s.l., respectively. The high altitude wetlands of Lesotho are unique among the Southern African wetlands (Backéus & Grab, 1995; Mucina & Rutherford, 2006).

2.2 Study design

The vegetation of the Afromontane palustrine wetlands of Lesotho was characterised using a phytosociological approach. The selection of wetlands for sampling was such that the entire country was spatially represented and as much variation in wetlands in the country was captured. An attempt was also made to include pristine/ near-pristine, as well as wetlands in protected areas such as national parks and nature reserves. Fieldwork, which commenced in February 2017 and ended in March 2018, was carried out during the wet (summer) season. A 3 m x 3 m representative sample plot was located randomly in each visually distinct and homogenous vegetation type of each wetland and different attributes were measured and recorded. This plot size has been recommended for grassy wetlands (Brown et al., 2013; Sieben et al., 2014) in Southern Africa. The location of representative 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 considered and sampled. A variety of attributes, both for vegetation and the environment was assessed in each plot.

2.3 Vegetation assessment

In each plot, the Braun-Blanquet method, a protocol often used for collecting vegetation data in South Africa (Sieben, 2011; Brown et al., 2013; Sieben et al., 2014), was used for vegetation assessment. Given the geographical location of Lesotho, adopting this method was logical and justified. Because this method has been in use for a very long time, it is possible to make comparisons between current and historical data (Brown et al., 2013), which allows for very effective plant community comparisons to be made. 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. Estimations of the proportion of the plot covered by vegetation and the average vegetation height were also made. In case of inundation, the average vegetation height was measured from the soil surface (Sieben, 2011). After assessing the plots in the visually distinct vegetation units, as much of the wetland would be surveyed in order to record species occurring within the wetland but outside the plots.

2.4 Assessment of explanatory variables and soil sampling and analysis

For each plot, in addition to the vegetation attributes, a standard protocol was also used to systematically measure or assess a number of explanatory environmental variables that have been recommended for wetlands (Sieben, 2011; Sieben et al., 2014). In at least one plot per wetland, a soil sample was collected from the top 15 cm of the soil using a soil auger and 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 hours and later analysed for different variables that have been recommended for wetlands (Sieben, 2011; Sieben et al., 2014). This was to provide additional explanatory variables for the vegetation-environment analysis. 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 presented in Table 1. While some variables were measured or assessed on site in all vegetation plots, additional ones (mainly soil variables and indicated with an asterisk in Table 1) were measured later and only on those plots where soil samples were collected.

Table 1: Environmental variables that were measured or assessed and included in the analysis of the vegetation of the Afromontane palustrine wetlands of Lesotho

Variable	**Type of variable**	**Method of measurement/ assessment**	**Units**	**Codes used in the ordination diagram**
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 – channeled valleybottom, H – Hillslope seepage not feeding a watercourse, HW – Hillslope seepage feeding watercourse
Landscape	Index	Assessed in the field: increasing urbanisation – 1 pristine, 2 – rural, 3 – urban	NA	Urban
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 on standing water or water table depth	cm	Inundation
Parent material[2]	Categorical	Assessment based on a geological map of Leketa et al. (2018)	NA	Basalt
Slope	Ratio	GPS (Garmin *eTrex* 30x)	degrees	Slope
Aspect[3]	Ratio	GPS (Garmin *eTrex* 30x)	degrees	North-fc
Altitude	Ratio	GPS (Garmin *eTrex* 30x)	metres	Altitude
GPS coordinates	Ratio	GPS (Garmin *eTrex* 30x)	degrees	Longitude, latitude
Soil depth	Ratio	Soil augering	cm	Soil depth
Presence/ 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*	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

*Variables with an asterisk were measured only on the plots where soil samples were collected.
[1]Inundation represents both inundation (positive) and water table depth (negative)
[2]The parent material in Lesotho is mainly basalt or sandstone
[3]Aspect was later categorised into North-facing (≤90º and >270º) and south-facing (>90º but ≤270º) during analysis.

2.5 Functional trait measurement and determination

A total of 57 plant species were collected for functional trait measurements and these were collected based on dominance (collectively covering potentially more than 50% of the plot) and frequency of occurrence in the study area (at least 10% of all the vegetation plots). In the wetlands, 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). For clonal plant species, an individual was defined as a ramet, the recognisably separately rooted above-ground unit (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013). A total of 12 important quantitative morphological functional traits (Table 2) were assessed on the species following the methods described by Sieben (2012) and Pérez-Harguindeguy et al. (2013).

Samples for plant leaf traits were collected as wet (spirit) collections. Ten leaves from representative specimens of each species were collected and placed in glass bottles containing 70% alcohol. For species without true leaves, the functional equivalent of a leaf was used (e.g. a stem or a portion of the stem) (Weiher et al., 1999). The leaves were later used for determining leaf length, leaf width, leaf area, specific leaf area (SLA) and leaf dry mass and the same leaves were used for all these traits. Leaf length, width and area were measured using a portable laser leaf area meter (CI-202, manufactured by CID Bio-Science Inc. USA). For needle-like leaves, leaf length was measured with a measuring tape and leaf width with a calliper and the product of the two then doubled (i.e. 2 x length x width) (Pérez-Harguindeguy et al., 2013). Ten mature whole plant individuals for each of the dominant species were also uprooted carefully to obtain as much of the underground parts as possible. The uprooted plants were carefully cleaned with water.

Table 2: Plant functional traits measured on the dominant and common plant species in the Afromontane palustrine 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	Planheig
Rooting depth	Ratio	Average maximum plant rooting depth	cm	Rootdept
Shoot biomass	Ratio	Average shoot dry weight	g	Shootmas
Root biomass	Ratio	Average below-ground dry weight	g	Rootmass
Total biomass	Ratio	Average total plant dry weight	g	Tdrymass
Root/shoot biomass ratio	Ratio	Average ratio of root to shoot dry weight		RSMratio
Leaf length	Ratio	Average of leaf length	cm	Leafleng
Leaf width	Ratio	Average of leaf width	cm	Leafwidt
Leaf length/ width ratio	Ratio	Average ratio of length to width of a leaf		LL/Wratio
Leaf area	Ratio	Average area of a leaf	cm^2	Leafarea
Leaf biomass	Ratio	Average leaf dry weight	g	Ldrymass
Specific leaf area	Ratio	Average ratio of dry weight of a leaf to its area	g/cm^2	Sleafare

Plant height was measured *in-situ* on 10 individual plants per species as recommended by Cornelissen et al. (2003) and Pérez-Harguindeguy et al. (2013). In the case of clonal species that share a single rootstock among several shoots, the overall measurement value was divided by the number of shoots. The rooting depth of the uprooted individuals was also measured. After taking the measurements, the samples were wrapped in a moist paper and packaged in air-tight plastic bags to keep them water saturated. The zipped plastic bags were stored in a cool box for transportation and later stored in a fridge at low temperature (about 4 °C) until analyses, as recommended by Cornelissen et al. (2003). After the measurements, whole plants were divided into above-ground and below-ground parts. The samples, including leaves were 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 an analytical balance. The weight of oven-dried specimens was also used to calculate total biomass and the root/shoot biomass ratio. SLA and leaf length to width ratio were derived from the measurements made on the leaf samples. The plant functional traits, methods of measurement or assessment and the codes used during the analyses are presented in Table 2.

2.6 Data Analysis

Species composition, explanatory environmental and plant functional trait data were captured in Microsoft Excel 2013 from which they were imported into PC-Ord and CANOCO programmes for different kinds of analyses. Prior to importing into these programmes for analysis, the Braun-Blanquet vegetation cover values were converted into percentage values. Three types of matrices were developed from the data; (1) plots x species abundance matrix, (2) plots x environmental variables matrix, and (3) species x traits matrix (using means). The fourth, community-weighted mean (CWM) trait (plots x traits) matrix (reflecting trait means per plot, weighted by species relative abundance), was developed and obtained by multiplying the plots x species abundance matrix by species x 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). For multivariate ecological community data analyses, five main types of analyses were employed, (1) Diversity analysis, (2) Hierarchical cluster analysis (HCA), (3) Indicator species analysis (ISA), (4) Canonical Redundancy Analysis (RDA), (5) Canonical Correspondence Analysis (CCA).

2.6.1 Classification

Cluster analysis is often used to classify sites, species or variables 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. To obtain vegetation typology of the Afromontane palustrine wetlands of Lesotho, agglomerative hierarchical cluster analysis was performed on vegetation data to identify homogenous plant communities in the wetlands. This would enable wetlands or plots that are similar in species composition, or species similar in functional traits to be grouped together with emphasis on the relationships between them (van Tongeren, 1995; McCune & Mefford, 2011).

For vegetation classification, the classification was performed twice; (1) grouping whole wetland units into wetland types based on plant species presence-absence data, (2) classifying species into communities, based on plot species composition and abundance data. PC-Ord, Version 6.0 was used for the classification (McCune & Mefford, 2011). The classification was performed with the Sørenson's (Bray-Curtis) similarity index and the Ward’s linkage method. The plant communities obtained were named following the guidelines by Brown et al. (2013).

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 types and plant communities obtained from the final clusters. Indicator species with indicator values (IV) greater than 20 and were significant ($p \leq 0.05$) in the Monte Carlo Permutation test were considered real indicators (Sieben et al., 2016) and were thus listed for each cluster. The ISA is often used to test the fidelity of a species to a given community. Monte Carlo Permutation test (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.

In the HCA, species or functionally similar vegetation plots can be grouped together. Hence, to obtain plant functional types (PFTs) and functional communities in the Afromontane palustrine wetlands in Lesotho, hierarchical agglomerative cluster analysis was also performed on the functional trait and CWM trait data to identify PFTs and functionally homogenous plant communities in the wetlands. This would enable plant species that are functionally similar or functionally similar vegetation plots to be grouped together, with emphasis on the relationships among them (van Tongeren, 1995; McCune & Mefford, 2011).

The classification was performed twice; (1) grouping plant species into PFTs on the basis of species functional trait data, and (2) classifying species into functional communities (FC) or assemblages, based on CWM of the 12 functional traits (Semenova & van der Maarel, 2000; McCune, 2015). While the first classification grouped plant species on the basis of similarity in their functional traits, the second classified plots based on their similarity in functional composition (CWM of the plant functional traits). PC-Ord, Version 6.0 was also used for the classification (McCune & Mefford, 2011), with the Sørenson's (Bray-Curtis) similarity index and the Ward's method as the measure of similarity and the linkage method, respectively.

2.6.2 Ordination

Another important feature of the analysis was the relationship between wetland plant communities and functional communities with explanatory variables. Thus, to examine the influence of environmental variables and gradients on wetland vegetation, the vegetation and explanatory variable data, as well as the plant communities obtained from the classification were subjected to canonical ordination (Ter Braak & Šmilauer, 1998). This was performed thrice: (1) Constrained Canonical Correspondence Analysis (CCA) on whole wetland units using species presence-absence data and environmental variables, (2) Constrained CCA on all vegetation plots using species abundance data and environmental variables, (3) Constrained CCA only on those vegetation plots where soil samples had been taken, using species abundance data and more detailed explanatory data. The canonical ordination was performed using CANOCO, Version 5.11 (Ter Braak & Šmilauer, 1998). The statistical significance of the constrained ordination was tested using the unrestricted Monte Carlo permutation test available in CANOCO (Ter Braak, 1995).

The CCA detects patterns of variation in the species data that can be explained best by the supplied explanatory 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). In the ordination diagram, each arrow points in the direction of the steepest increase of the explanatory variable with its length proportional to its importance in explaining the variation and the angle between the arrows indicates the correlation between individual variables (Ter Braak & Šmilauer, 1998).

To examine the influence of environmental variables on wetland plant functional traits and functional communities (assemblages), the CWM trait and explanatory variable data, as well as the plant functional communities obtained from the classification of CWM for the functional traits were subjected to canonical ordination (Ter Braak & Šmilauer, 1998). The CWM trait, environmental and soil data were log-transformed prior to the ordination analysis. Redundancy Analysis (RDA) was performed twice, based on the classification: (1) on all the vegetation plots, using CWM trait and environmental data, and (2) only on the subset of the vegetation plots where soil samples had been taken, using CWM trait and soil data. The canonical ordination was performed using CANOCO, Version 5.11 (Ter Braak & Šmilauer, 1998). The statistical significance of the constrained ordination was tested using unrestricted Monte Carlo permutation test (Ter Braak, 1995).

2.6.3 Plant species diversity analysis

Using species abundance data for each vegetation plot, Shannon-Weiner index (H'), species evenness index (E) and species richness, which are surrogates of species diversity, were also determined. The H' and E were calculated 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. $E = \frac{H'}{\ln S}$ where s is species richness.

For each community obtained from the classification, the means for these attributes and vegetation height were determined, as well as the median and range of species richness.

3.0 RESULTS

3.1 Plant species diversity analysis

Overall, 150 vegetation plots from 30 Afromontane palustrine wetlands in Lesotho were analysed in the current study. A total of 312 plant species belonging to 51 families occurred in the wetlands. Of the 312 species, 276 were encountered in the 150 plots and the remaining 36 species occurred within the wetlands but outside the plots. 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%). From these results, it can be observed that three (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 (Table 3), the number of species per 3 m x 3 m plot ranged from one to 27, with a median species richness of 10. The highest median number of species for whole wetland units (41.5) was recorded in the Highlands (Table 3). The five most frequently occurring species were *Ranunculus meyeri* (38.00%), *Trifolium burchellianum* (30.67%), *Haplocarpha nervosa* (24.67%), *Ranunculus multifidus* (20.00%) and *Pennisetum sphacelatum* (20,00%). Of all the species, 20.65% had a frequency of occurrence of at least 5% of all the plots, while 39.49% and 14.13% were so rare that they were encountered only once and twice, respectively.

3.2 Classification

3.2.1 Wetland types and plant communities

Cluster analysis for whole wetland units produced five well-defined clusters, one type of Lowland wetlands and four types of Highland wetlands (Figure 2). The environmental conditions of the wetland types, their indicator species and indicator values are presented in Table 3. Clustering using all the vegetation plots produced 22 distinct communities (Figure 3). Table 4 presents the 22 communities, their dominant species, indicator species and the associated indicator values.

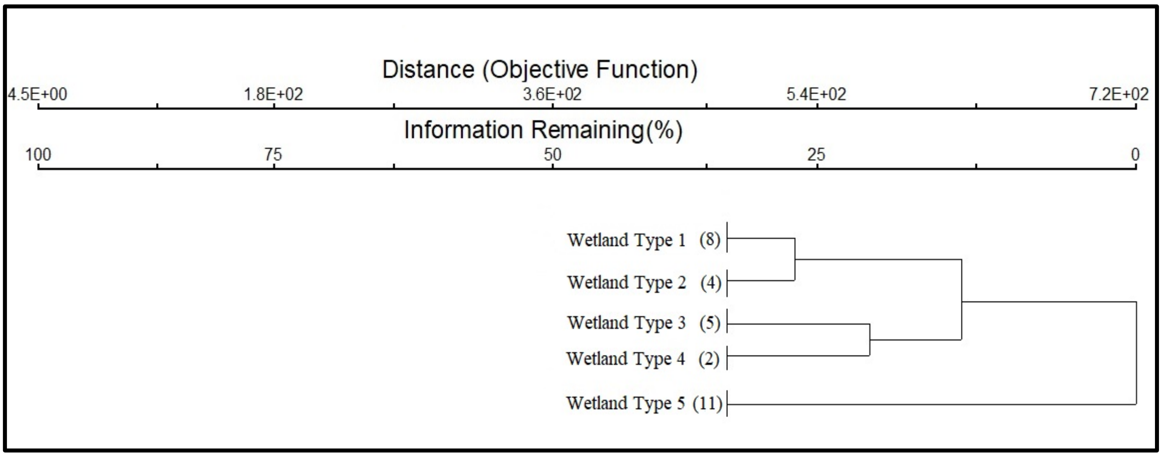

Figure 2: Dendrogram for the classification of the wetlands assessed in Lesotho. Numbers in brackets are the numbers of wetlands of that type

Table 3: Indicator species and environmental conditions for the Afromontane palustrine wetland types of Lesotho. Only species with indicator values of more than 20 and p-values less than 0.05 are presented.

Wetland Type	No. of wetlands	Species richness	Indicator species	Indicator value	p-value	Distribution and environmental conditions
Wetland Type 1	8	Median 28.5 (19-38)	*Cotula paludosa*	46.0	0.038	Occurs in the Highlands (from 2200 m a.s.l.), in high rainfall areas and are mostly seepage wetlands but valleybottom wetlands can also occur. Mostly on rich soils, underlain by basalt.
			Gymnopentzia bifurcata	37.5	0.046	
Wetland Type 2	4	Median 41.5 (40-53)	*Agrostis bergiana*	61.5	0.002	Occurs in the Highlands, from 2200 m a.s.l. Occurs in high rainfall areas and can be seepage or valleybottom wetlands. Mostly rich soils, underlain by basalt.
			Alchemilla colura	50.0	0.015	
			Anagallis hutonii	50.0	0.013	
			Aponogeton junceus	56.2	0.002	
			Berkheya multijuga	75.0	0.010	
			Carex monotropa	80.0	0.001	
			Dracoscirpoides ficinioides	59.2	0.019	
			Eumorphia sericea	75.0	0.009	
			Felicia rosulata	50.0	0.018	
			Isolepis angelica	53.3	0.005	
			Kniphofia caulescens	57.1	0.029	
			Koeleria capensis	56.2	0.030	
			Luzula africana	59.2	0.020	
			Moraea huttonii	50.0	0.015	
			Poa binata	54.8	0.006	
Wetland Type 3	5	Median 29 (23-45)	*Agrostis lachnantha*	61.5	0.001	Occurs in the Highlands, from 1700 m a.s.l. Found in high rainfall areas and are mostly valleybottom wetlands but seepages can also occur. Mostly rich soils, underlain by basalt.
			Mentha aquatica	46.0	0.039	
Wetland Type 4	2	Median 38.5 (36-41)	*Andropogon appendiculatus*	100.0	0.002	Occurs in the Highlands, from 2300 m a.s.l. in high rainfall areas and mostly on slope seepages. The soil is underlain by sandstone. This type of wetlands occurs in a protected area (Sehlabathebe National Park) in the eastern part of Lesotho
			Conyza pinnata	83.3	0.006	
			Cyrtanthus flanaganii	100.0	0.002	
			Geranium wakkerstroomianum	100.0	0.002	
			Lobelia erinus	56.9	0.044	
			Merxmuellera macowanii	63.5	0.021	
			Nidorella undulata	100.0	0.002	
			Pentaschistis natalensis	100.0	0.002	
			Rumex lanceolatus	52.0	0.027	
			Sebaea natalensis	83.3	0.006	
			Senecio isatideus	100.0	0.002	
Wetland Type 5	11	Median 26 (10-48)	*Cyperus fastigiatus*	63.6	0.010	Occurs mostly in the Lowlands (about 1400-1800 m.a.s.l). Occurs in less rainfall areas and are mostly valleybottom
			Echinochloa colona	45.5	0.039	
			Eleocharis limosa	54.5	0.041	
			Eragrostis plana	81.8	<0.001	
			Leersia hexandra	63.6	0.009	

Marsilea macrocarpa	72.7	<0.001	wetlands or depressions with mostly poor soils underlain by sandstone.
Panicum maximum	57.0	0.005	
Paspalum dilatatum	58.6	0.001	
Paspalum notatum	72.7	<0.001	
Schoenoplectus paludicola	54.5	0.039	

m.a.s.l. – metres above sea level.

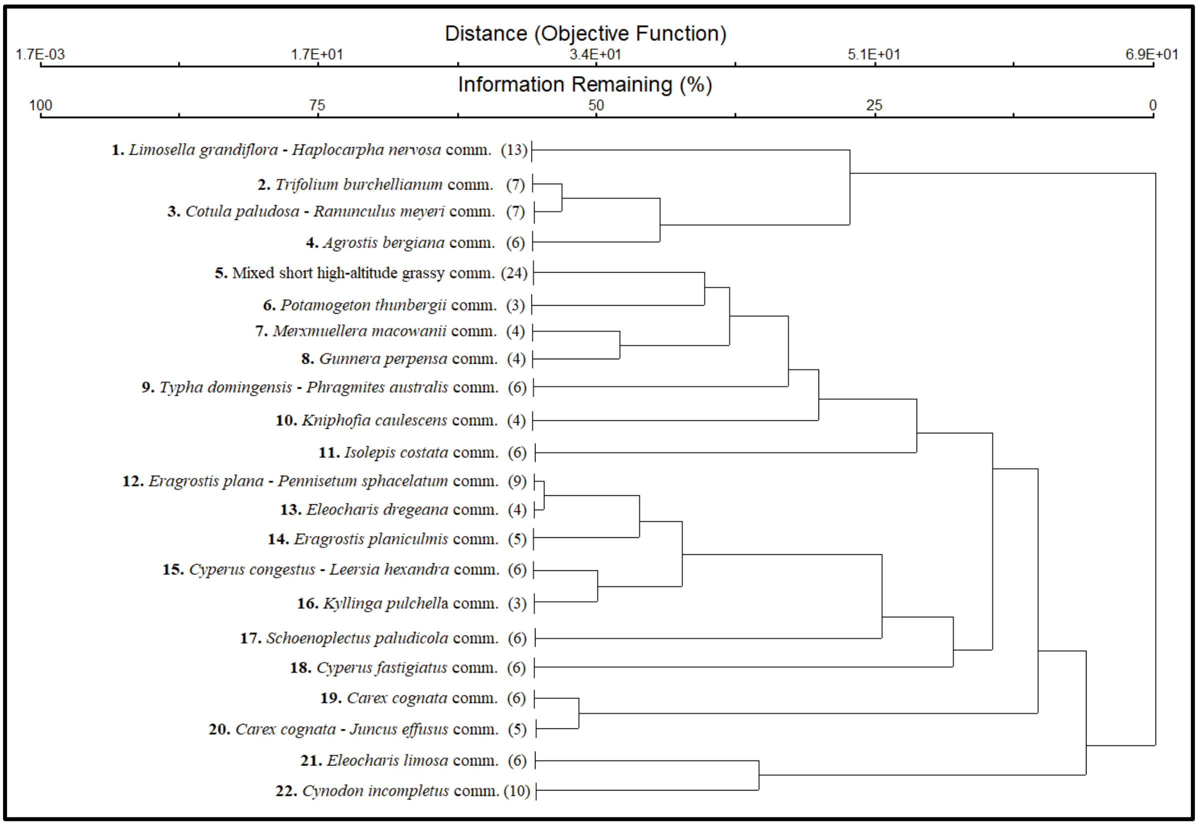

Figure 3: Dendrogram showing plant communities of the Afromontane palustrine wetlands of Lesotho. Numbers in brackets are the numbers of plots in that community

Table 4: Indicator species of the Afromontane palustrine wetland communities of Lesotho. Only species with indicator values of more than 20 and p-values less than 0.05 are presented.

No.	Comm.	Indicator species	Indicator value	P-value
1	*Limosella grandiflora -Haplocarpha nervosa* comm.	*Haplocarpha nervosa*	21.7	0.027
2	*Trifolium burchellianum* comm.	*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	0.480
		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
20	*Carex cognata - Juncus effusus* comm.	*Carex cognata*	23.0	0.033
		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	0.480
		Lepidium schinzii	21.7	0.041

3.2.2 Plant functional types and composition

The study classified a total of 57 wetland plant species from 40 genera and 21 families (Figure 4). These species were encountered in 120 vegetation plots in 30 wetlands. Cluster analysis on the basis of the 12 quantitative functional traits of all the 57 plant species produced seven well-defined clusters (PFTs) (Figure 4), while the classification of the 120 vegetation plots on the basis of CWM traits resulted in two major groups, which were divided into seven functional communities (Figure 5). The seven wetland PFTs are described in terms of their species and functional characteristics (Table 5) and the seven plant functional communities are described in terms of the dominant species, functional types occurring, structure and environmental conditions (Table 6). A functional type is represented by at least three and at most 10 plant families (Table 6). Species richness, Shannon-Weiner index and evenness index were mainly higher in high-altitude wetland functional communities (Table 6). Average height was generally greater in low-altitude wetland plant functional communities than in the high-altitude ones.

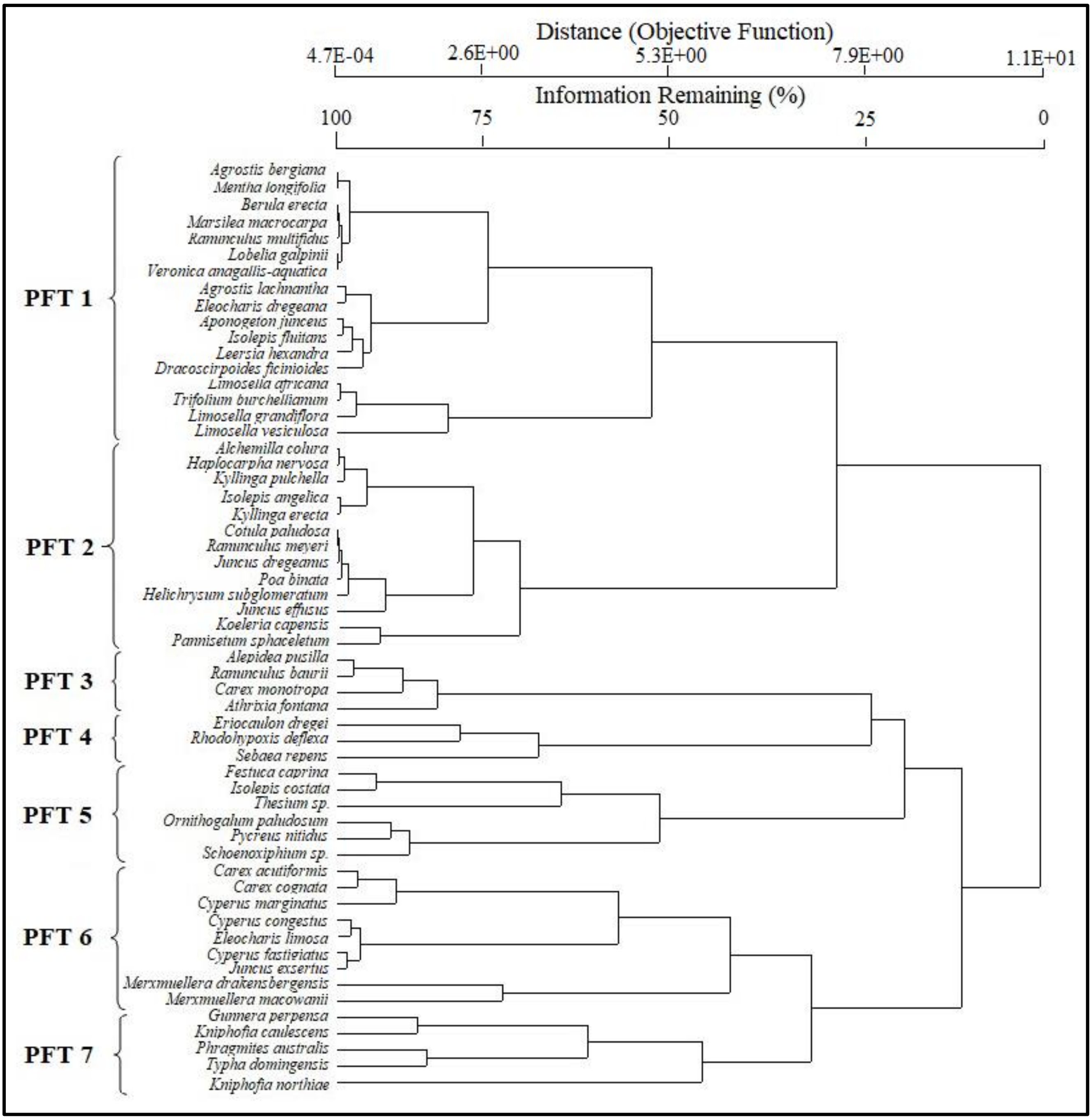

Figure 4: Functional classification of plant species of the Afromontane wetlands in Lesotho, based on 12 morphological quantitative traits. PFT represents plant functional type.

Table 5: Description of the plant functional types (PFTs) from the classification presented in Figure 4.

Functional type	Plant species	No. of species	No. of families represented	Growth form and other functional characteristics of the types
PFT 1	*Agrostis bergiana, Agrostis lachnantha, Aponogeton junceus, Berula erecta, Dracoscirpoides ficinioides, Eleocharis dregeana, Isolepis fluitans, Leersia hexandra, Limosella africana, Limosella grandiflora, Limosella vesiculosa, Lobelia galpinii Marsilea macrocarpa, Mentha longifolia, Ranunculus multifidus, Trifolium burchellianum, Veronica anagallis-aquatica*	17	10	Relatively small, medium tall graminoids and forbs (< 80 cm); short rooting depth (< 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
PFT 2	*Alchemilla colura, Cotula paludosa, Haplocarpha nervosa, Helichrysum subglomeratum, Isolepis angelica, Juncus dregeanus, Juncus effusus, Koeleria capensis, Kyllinga erecta, Kyllinga pulchella, Pennisetum sphacelatum, Poa binata, Ranunculus meyeri*	13	6	Relatively small, medium tall graminoids and forbs (< 60 cm); short rooting depth (< 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.
PFT 3	*Alepidea pusilla, Athrixia fontana, Carex monotropa, Ranunculus baurii*	4	4	Short small graminoids and forbs (< 40 cm); short rooting depth (< 20 cm); relatively small specific leaf area (30-100) and leaf length to width ratio; accumulates more biomass above the ground
PFT 4	*Eriocaulon dregei, Rhodohypoxis deflexa, Sebaea repens*	3	3	Short, small graminoids and forbs (< 15 cm); very short rooting depth (< 10 cm); very small specific leaf area (2-10) and very small leaf length to width ratio; accumulates more biomass above ground
PFT 5	*Festuca caprina, Ornithogalum paludosum, Isolepis costata, Pycreus nitidus, Thesium sp, Schoenoxiphium sp,*	6	4	Relatively small, medium tall graminoids and forbs (< 40 cm); relatively short rooting depth (< 25 cm); accumulates more biomass below ground; small specific leaf area (5-115) and a high leaf length to width ratio
PFT 6	*Carex acutiformis, Carex cognata, Cyperus congestus, Cyperus marginatus, Cyperus fastigiatus, Eleocharis limosa, Juncus exsertus, Merxmuellera drakensbergensis, Merxmuellera macowanii*	9	3	Tall sedges and tufted grasses (> 40 cm); shallow 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
PFT 7	*Gunnera perpensa, Kniphofia caulescens, Kniphofia northiae, Phragmites australis, Typha domingensis*	5	4	Tall reeds, perennial and large graminoids and large forbs (> 30 cm); shallow to deep rooting depth (> 10 cm); accumulates more biomass above ground; relatively high specific leaf area (50-300) and a relatively high leaf length to width ratio

Table 6: Description of the functional communities of the vegetation of the Afromontane wetlands in Lesotho from the classification presented in Figure 5.

Functional community	No. of plots	Dominant species	PFTs from Figure 4 mainly represented	Species diversity			Community structure		Environmental conditions
				Species richness	Mean H'	Mean Evenness	Mean height (cm)	Mean cover (%)	
FC 1	24	*Isolepis angelica, Haplocarpha nervosa, Kyllinga pulchella, Eriocaulon dregei, Festuca caprina, Ranunculus multifidus, Rhodohypoxis deflexa, Ranunculus meyeri, Carex monotropa, Cotula paludosa, Juncus effusus, Alchemilla colura, Ranunculus baurii, Ornithogalum paludosum, Alepidea pusilla, Juncus exsertus, Agrostis lachnantha, Limosella Africana, Lobelia galpinii, Koeleria capensis, Helichrysum subglomeratum, Sebaea repens*	PFT 1, PFT 2, PFT 3 & PFT 4	Median 10.5 (5-27)	1.65	0.64	15.92	95.54	Occurs mainly above 2400 m a.s.l. on deep soils in either valleybottom wetlands or hillslope seepages
FC 2	30	*Trifolium burchellianum, Isolepis angelica, Agrostis bergiana, Marsilea macrocarpa, Haplocarpha nervosa, Isolepis fluitans, Poa binata, Limosella grandiflora, Juncus effusus, Helichrysum subglomeratum, Limosella Africana, Limosella vesiculosa, Aponogeton junceus, Leersia hexandra, Lobelia galpinii, Thesium sp., Juncus dregeanus, Dracoscirpoides ficinioides, Berula erecta*	PFT 1, PFT 2 & PFT 5	Median 9.5 (3-24)	1.48	0.62	15.37	85.53	Occurs mainly above 2400 m a.s.l. on deep soils in a variety of wetland types with varying degree of wetness
FC 3	27	*Eleocharis dregeana, Cyperus fastigiatus, Eleocharis limosa, Cyperus congestus, Pannisetum sphaceletum, Juncus effusus, Leersia hexandra, Ranunculus meyeri, Marsilea macrocarpa, Dracoscirpoides ficinioides, Agrostis lachnantha, Veronica*	PFT 1, PFT 2, & PFT 6	Median 10 (3-21)	1.45	0.61	49.63	94.70	Occurs mainly above 1500 m a.s.l. on deep soils in permanently wet habitats of mostly valleybottom wetlands

		anagallis-aquatica, Limosella vesiculosa, Kyllinga erecta							
FC 4	17	*Gunnera perpensa, Kniphofia caulescens, Dracoscirpoides ficinioides, Carex cognata, Carex acutiformis, Mentha longifolia*	PFT 1, PFT 6 & PFT 7	Median 7 (1-15)	0.95	0.42	51.76	91.94	Occurs mainly above 2400 m a.s.l. on deep soils in a variety of wetland types with varying degree of wetness
FC 5	9	*Isolepis costata, Cyperus marginatus, Ornithogalum paludosum, Veronica anagallis-aquatica, Festuca caprina, Schoenoxiphium sp., Pycreus nitidus, Thesium sp.*	PFT 5 & PFT 6	Median 11 (8-20)	1.60	0.63	57.78	96.00	Occurs from 1600 m a.s.l. on deep soils in either valleybottom wetlands or hillslope seepages with varying degree of wetness
FC 6	7	*Merxmuellera macowanii, Merxmuellera drakensbergensis, Isolepis costata, Athrixia fontana*	PFT 3, PFT 5 & PFT 6	Median 10(5-23)	1.42	0.55	57.14	87.86	Occurs mainly above 2500 m a.s.l. on moderately deep soils in temporary to seasonally wet hillslope seepages
FC 7	6	*Phragmites australis, Typha domingensis, Kniphofia northiae*	PFT 7	Median 9 (2-16)	1.06	0.47	175.00	91.33	Occurs from 1500 m a.s.l. in either valleybottom wetlands or hillslope seepage habitats with temporary or permanently wet and moderately deep soils

H' – Shannon-Weiner index, FC – functional community, PFT – plant functional type, a.s.l. – above sea level

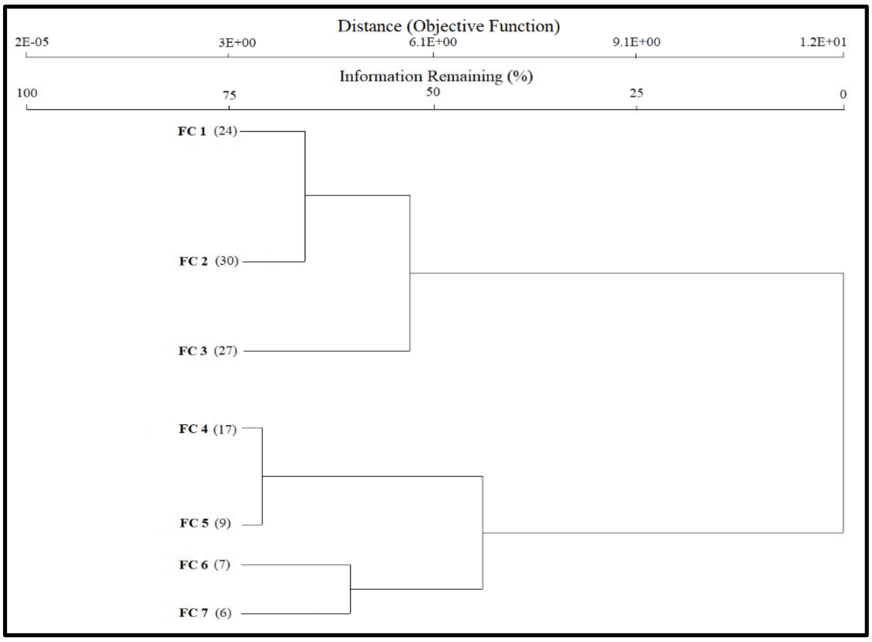

Figure 5: Functional classification of the vegetation of the Afromontane wetlands in Lesotho based on community-weighted means of 12 morphological quantitative traits. Numbers in brackets are the numbers of plots representing that functional community. FC stands for functional community.

3.3 Ordination

3.3.1 Wetland types and plant communities

The CCA ordination diagram for whole wetlands is presented in Figure 6. In this ordination, the total variation is 8.64 and the environmental variables supplied account for 49.6% of this. The first axis of the ordination is best explained by altitude, longitude, parent material and landscape. The wetlands located to the left side of the ordination diagram (Wetland types 1, 2 and 4) are high altitude near-pristine wetlands that are also associated with higher rainfall areas mainly underlain by basalt. Those on the right side (mainly Wetland Type 5) occur in lower altitude and are urban wetlands that are associated with lower rainfall areas mainly underlain by sandstone. The second axis is positively correlated with slope but negatively related with latitude, meaning that the wetlands on the upper part of the ordination diagram (Wetland type 3 and 4) are mainly slope seepages in the Highlands.

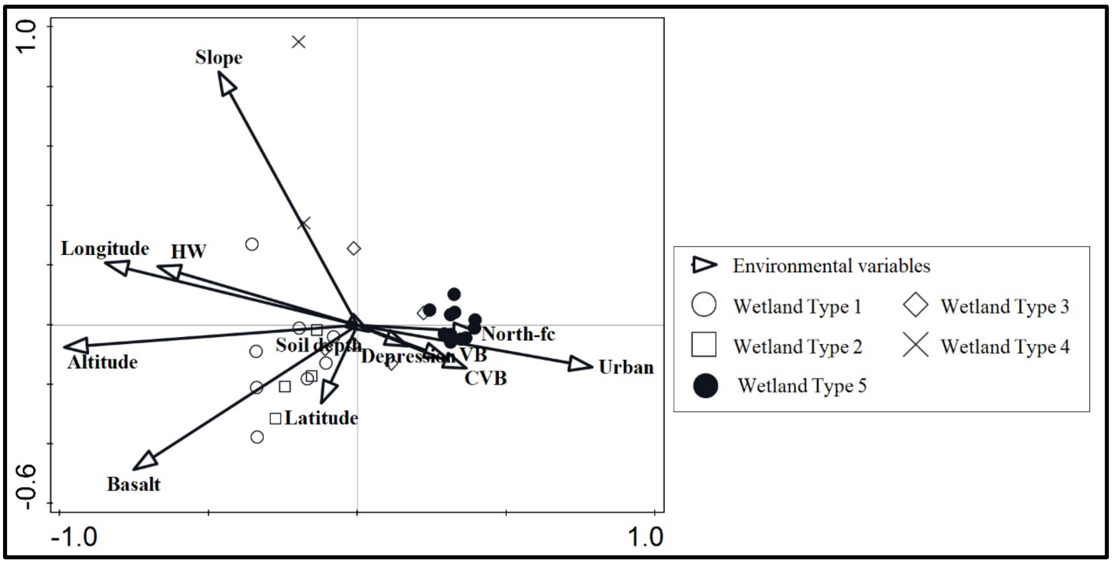

Figure 6: CCA ordination diagram showing Afromontane palustrine wetland types of Lesotho using the same classification presented in Figure 2

Figure 7 shows the CCA ordination diagram for all vegetation plots where the total variation is 25.483 and the explanatory variables supplied account for 18.11% of this. The first axis of the ordination is positively correlated with altitude, longitude, soil parent material and peat but negatively associated 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 urban wetlands in the western lowland areas of the country. 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 altitudes and these include communities 12, 13 and 14.

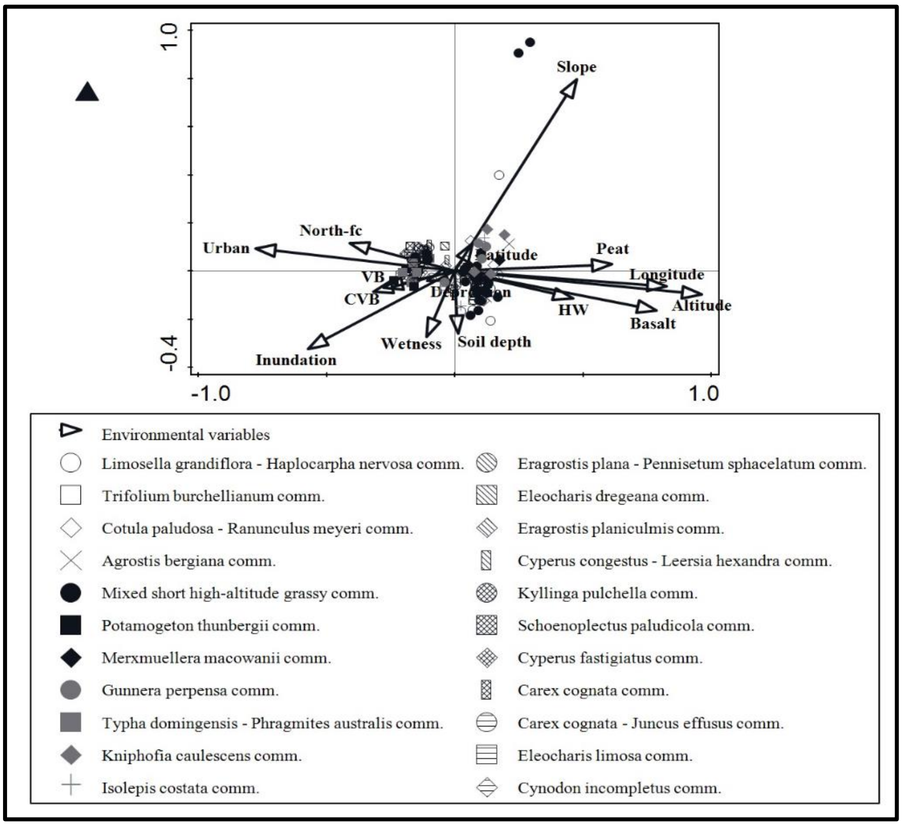

Figure 7: CCA ordination diagram showing plant communities in the Afromontane palustrine wetlands of Lesotho, with all plots and using the same classification presented in Figure 3.

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 3. Figure 8 presents the CCA ordination diagram for this subset of the vegetation plots. The total variation was 10.051 and 65.40% of this could be explained by the supplied explanatory variables. While the first axis is mainly explained by altitude, percentage clay, potassium, longitude, total organic carbon, nitrogen and sulphur, the second axis is best explained by electrical conductivity and latitude but calcium, soil depth and magnesium are also important factors. 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.

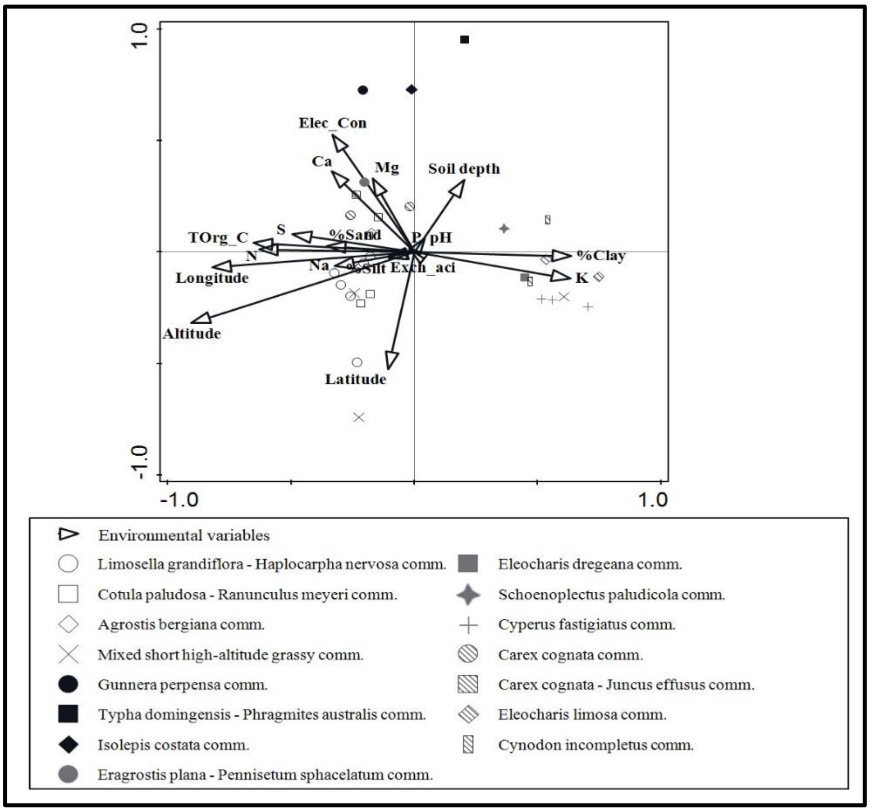

Figure 8: CCA ordination diagram showing plant communities in the Afromontane palustrine wetlands of Lesotho, with only plots with soil data and using the same classification presented in Figure 3

The description of the 22 wetland plant communities, including the structure, diversity and environmental conditions is presented in Table 7.

Table 7: Description and environmental conditions of plant communities in the Afromontane palustrine wetlands of Lesotho

No.	Plant community	No. of plots	Dominants	Community structure	Species richness	Mean H'	Mean evenness	Environmental conditions
1	*Limosella grandiflora - Haplocarpha nervosa* comm.	13	*Haplocarpha nervosa, Limosella grandiflora*	Dense, short (2-10 cm) forb-dominated grassland	Median 10 (5-14)	1.54	0.64	Mostly high altitudes (> 2400 m a.s.l.). Found in seepage or valleybottom habitats, often on peaty or clay permanently wet soils that are deep (≥ 50 cm)
2	*Trifolium burchellianum* comm.	7	*Trifolium burchellianum Cotula paludosa Lobelia galpinii*	Open to dense, short (2-15 cm) forb-dominated grassland	Median 12 (9-19)	1.67	0.64	Mostly high altitudes (> 2400 m a.s.l.). Occurs on shallow to deep (≥ 20 cm) seasonally to permanently wet peaty or clay loam soils, mostly in seepage or valleybottom wetlands
3	*Cotula paludosa - Ranunculus meyeri* comm.	7	*Cotula paludosa Ranunculus meyeri*	Dense, short to medium tall (2-40 cm) forb-dominated grassland	Median 14 (10-25)	2.02	0.73	Restricted to high altitudes (> 2400 m a.s.l.) but can also occur in mid altitude areas. Occurs mostly in seepages on shallow to deep (≥ 20 cm) peaty or clay loam soils in seasonally to permanently wet zones

4	*Agrostis bergiana* comm.	6	*Agrostis bergiana Trifolium burchellianum Helichrysum subglomeratum*	Dense, short (2-20 cm) grassland dominated by graminoids	Median 13.5 (9-27)	1.81	0.67	Restricted to high altitudes (> 2400 m a.s.l.). Found mostly in seepages or depressions on shallow to deep (≥ 40 cm) peaty or clay loam soils. Can occur on a range of wetness degree
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	Median 9.5 (2-20)	1.23	0.55	Wide altitudinal range (1400 to above 3000 m a.s.l.) on shallow to deep (≥ 10 cm) soils of varying texture but can also be associated with peat. Can occur on a range of wetness degree in seepage or valleybottom wetlands.
6	*Potamogeton thunbergii* comm.	3	*Potamogeton thunbergii*	Short to medium tall (30-80 cm) community; low evenness	Median 3 (2-4)	0.53	0.41	Mostly mid altitudes (1400-1800 m a.s.l.) but can also occur at high altitudes. Occurs on shallow (20-40 cm) permanently inundated clay or clay loam soils in depressions or valleybottom wetlands
7	*Merxmuellera macowanii* comm.	4	*Merxmuellera macowanii*	Dense, medium tall (40-80 cm) tussock grassland; low evenness	Median 13.5 (7-19)	1.43	0.54	Mostly high altitudes (> 2500 m a.s.l.). Occurs on shallow to deep (≥ 20 cm) peaty or clay soils, mostly in temporarily or seasonally wet zones of seepage or valleybottom wetlands
8	*Gunnera perpensa* comm.	4	*Gunnera perpensa*	Dense, medium tall (30-60 cm) conspicuous forb-dominated community	Median 11.5 (7-23)	1.59	0.60	Mostly high altitudes (>2200 m a.s.l.) but can also occur at lower altitudes. Occurs on shallow to deep (≥ 20 cm) peaty, loam or clay soils that are slightly acidic and high in electrical conductivity, mostly in seasonally to permanently wet zones of seepage or valleybottom wetlands
9	*Typha domingensis - Phragmites australis* comm.	6	*Typha domingensis Phragmites australis*	Dense, tall (150-300 cm) reedland; low evenness.	Median 8.5 (2-16)	1.04	0.48	Mostly mid altitudes (1400-1800 m a.s.l.). Found in valleybottom wetlands on shallow to deep (≥ 10 cm), seasonally or permanently wet peaty or clay soils, usually rich in nutrients and high in electrical conductivity
10	*Kniphofia caulescens* comm.	4	*Kniphofia caulescens*	A conspicuous dense, medium tall (30-50 cm) grassland.	Median 5.5 (3-12)	0.60	0.27	Restricted to high altitudes (> 2500 m a.s.l.). Occurs mostly on seasonally to permanently wet seepage or valleybottom wetland habitats, in deep (≥ 50 cm) peaty or loam soils
11	*Isolepis costata* comm.	6	*Isolepis costata*	Dense, medium tall (30-60 cm) sedgeland	Median 9.5 (5-13)	1.31	0.57	Mostly high altitudes (> 1700 m a.s.l.). Occurs mostly in seasonally to permanently wet zones of seepage or valleybottom wetlands, on

								shallow to deep (≥ 30 cm) peaty or clay soils.
12	*Eragrostis plana - Pennisetum sphacelatum* comm.	9	*Eragrostis plana Pennisetum sphacelatum Paspalum dilatatum Eleocharis dregeana*	Open to dense, short to medium tall (5-60 cm) grassland, dominated by graminiods	Median 10 (4-15)	0.59	0.66	Mid to high altitudes (1400 – 2600 m a.s.l.), mostly in seepage or valleybottom wetlands. Occurs on shallow to deep (≥ 15 cm) temporarily or seasonally wet clay or clay loam soils that are associated with high electrical conductivity
13	*Eleocharis dregeana* comm.	4	*Eleocharis dregeana*	Dense, medium tall (30-60 cm) sedgeland	Median 20.5 (13-21)	1.78	0.60	Mid to high altitudes (1600 – 2600 m a.s.l.), mostly in valleybottom wetlands. Occurs on deep (≥ 80 cm) temporarily or seasonally wet clay or clay loam soils.
14	*Eragrostis planiculmis* comm.	5	*Eragrostis planiculmis Schoenoplectus decipiens*	Dense, medium tall (50-80 cm) grassland dominated by graminoids	Median 11 (6-16)	1.48	0.59	Mid to high altitudes (1400 – 2600 m a.s.l.), mostly in valleybottom wetlands but can also occur in depressions. Occurs on shallow to deep (≥ 20 cm) temporarily or seasonally wet clay or clay loam soils
15	*Cyperus congestus - Leersia hexandra* comm.	6	*Cyperus congestus Leersia hexandra*	Open to dense, medium tall (30-60 cm) sedgeland	Median 12 (4-18)	1.66	0.65	Mostly mid altitudes (1400 – 2400 m a.s.l.). Occurs on shallow to deep (≥ 10 cm) seasonally or permanently wet clay or clay loam soils, mostly in valleybottom wetlands though it can also occur in depressions.
16	*Kyllinga pulchella* comm.	3	*Kyllinga pulchella*	Dense, short (20-40 cm) sedgeland that occurs in small patches	Median 12 (11-16)	1.59	0.60	Mostly mid altitudes (1400 – 1800 m a.s.l.). Occurs in valleybottom wetlands or depressions, on shallow to deep (5-60 cm) seasonally or permanently wet sand or clay loam soils
17	*Schoenoplectus paludicola* comm.	6	*Schoenoplectus paludicola*	Open to dense, short (25-50 cm) sedgeland	Median 9.5 (7-11)	1.23	0.56	Mostly mid altitudes (1400 – 1800 m a.s.l.). Found in valleybottom wetlands on shallow to deep (30-70 cm) clay or clay loam soils that are seasonally or permanently wet
18	*Cyperus fastigiatus* comm.	6	*Cyperus fastigiatus*	Open to dense, medium to tall (60-100 cm) sedgeland	Median 5 (4-7)	0.95	0.53	Mostly mid altitudes (1400 – 1800 m a.s.l.). Occurs in valleybottom wetlands or depressions on deep (≥70 cm) seasonally or permanently wet clay or clay loam soils that is slightly acidic or neutral.
19	*Carex cognata* comm.	6	*Carex cognata*	Dense, medium tall (30-70 cm) sedgeland; low evenness	Median 7.5 (1-14)	0.94	0.41	Mostly high altitudes (>2200 m a.s.l.). Found mostly in seasonally to permanently wet zones of seepage or valleybottom wetlands. Occurs on shallow to deep (≥ 100 cm)

								peaty or clay soils that are high in electrical conductivity
20	*Carex cognata - Juncus effusus* comm.	5	*Juncus effusus Carex cognata*	Dense, medium tall (30-70 cm) sedgeland	Median 11 (7-16)	1.65	0.67	Mostly high altitudes (> 2400 m a.s.l.). Found in seepage or valleybottom wetlands, mostly on permanently wet habitats. Occurs on shallow to deep (≥ 50 cm) peaty or clay soils.
21	*Eleocharis limosa* comm.	6	*Eleocharis limosa*	Dense, medium tall (40-80 cm) sedgeland	Median 5 (3-9)	1.06	0.57	Mostly in mid altitudes (1400 – 1800 m a.s.l.). Found in depressions or valleybottom wetlands. Occurs on deep (≥60 cm) seasonally or permanently inundated clay or clay loam soils
22	*Cynodon incompletus* comm.	10	*Cynodon incompletus Cyperus marginatus Eleocharis limosa, Cyperus rotundus*	Dense, short to medium tall (20-70 cm) sedgy grassland	Median 9.5 (4-15)	1.40	0.60	Occurs mostly in mid altitudes (1400 – 1800 m a.s.l.) in valleybottom wetlands. Occurs on shallow to deep (≥10 cm) seasonally or permanently inundated clay or clay loam soils

Comm. – community, **H'** – Shannon-Weiner index

3.3.1 Wetland plant functional traits, types and communities

In the RDA ordination for all wetland vegetation plots (Figure 9), the total variation was 1363.918 and the environmental variables supplied accounted for 25.56% of this. The first axis of the ordination is mainly explained by the soil parent material. Communities located on the right side of the ordination diagram (FC 3, FC 5 and FC 7) are mainly found in valleybottom wetlands that are underlain by sandstone. The remaining communities are mainly associated with a variety of wetland types underlain by basalt, but occasionally sandstone. The second axis was positively correlated with altitude, slope and longitude but negatively related to inundation, soil depth, wetness and North-facing aspect. While the communities located mainly on the upper part of the ordination diagram (FC 1, FC 4 and FC 6) are associated with hillslope seepages in high altitude and high rainfall areas, those located mainly on the lower part (FC 3 and FC 7) are associated with inundated deep soils in low altitudes. The FC 2 and FC 5 occur in a wide range environmental conditions.

The ordination diagram (Figure 9) also shows the plant community-functional trait-environment relationships. While SLA and root to shoot mass ratio showed a positive correlation with soil depth and North-facing aspect, they were negatively correlated with slope. Leaf width, rooting depth, leaf dry mass, shoot mass, root mass and total dry mass were positively correlated with slope. Plant height, leaf area, leaf length and leaf length to width ratio were positively associated with landscape, inundation and wetness but negatively related with altitude and longitude. The communities on the right of the ordination diagram were also associated with high values of all the functional traits except root to shoot mass ratio and SLA, and those on the right side exhibited the opposite relationships. Unlike communities on the upper part of the diagram, those on the lower part were associated with high SLA.

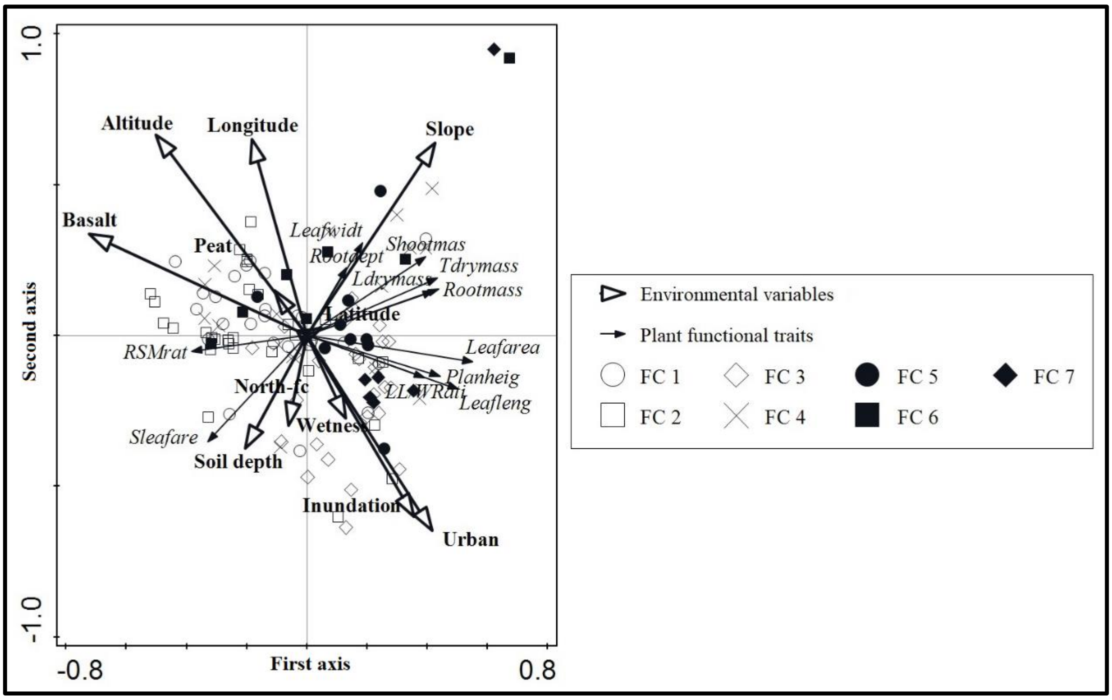

Figure 9: RDA ordination diagram for plant functional communities, community-weighted mean functional traits and environmental variables of the Afromontane wetlands of Lesotho, based on the classification presented in Figure 5 and using the whole dataset. FC stands for functional community.

See Table 1 and 2 for the abbreviations of environmental variables and functional traits, respectively.

The wetland vegetation plots with detailed soil data represented six of the seven functional communities in Figure 5; only FC 6 was not represented because it had no soil sample. The RDA ordination for this subset of the vegetation plots (Figure 10) had a total variation of 234.198 and 81.52% of this could be explained by the supplied explanatory variables. While the first axis was positively correlated with soil depth, silt percentage, soil exchangeable acidity and phosphorus content, it was negatively related with sodium content and percentage of sand. Communities that are mainly on the right side of the ordination diagram (FC 3, FC 4 and FC 7) were associated with silty and deep soils that are high in exchangeable acidity and rich in phosphorus. Those on the left side (FC 1 and FC 2) were associated with sandy soils with high sodium content. FC 5 tends to occur at the intermediate levels of the above-mentioned environmental conditions.

The second axis of the ordination diagram was positively correlated with soil electrical conductivity, calcium, magnesium, nitrogen, total organic carbon, organic matter, pH and sulphur but was negatively associated with clay percentage and potassium. Communities FC 3 and FC 5 are mainly on the lower part of the ordination diagram and are associated with clayey soils with high potassium content. Those communities mainly on the upper part of the ordination diagram (FC 4 and FC 7) are associated with soils that are high in electrical conductivity, pH, magnesium, calcium, nitrogen, organic carbon, sulphur and organic matter. Nonetheless, FC 1 and FC 2 can occur on a wide range of soil conditions.

Figure 10 also shows community-functional trait-soil conditions relationships. Leaf width had a strong positive association with electrical conductivity, calcium and pH, while leaf length to width ratio was positively related with exchangeable acidity, phosphorus, clay percentage and potassium but negatively correlated with sodium, sand percentage, nitrogen, organic matter and total organic carbon. Unlike the communities on the left side of the ordination diagram, those on the right side were associated with high values of all the traits except SLA, leaf width and root to shoot mass ratio. The communities on the upper part are associated with wide leaves, small root to shoot mass ratio and leaf length to width ratio while the opposite relationship is exhibited by those communities on the lower part.

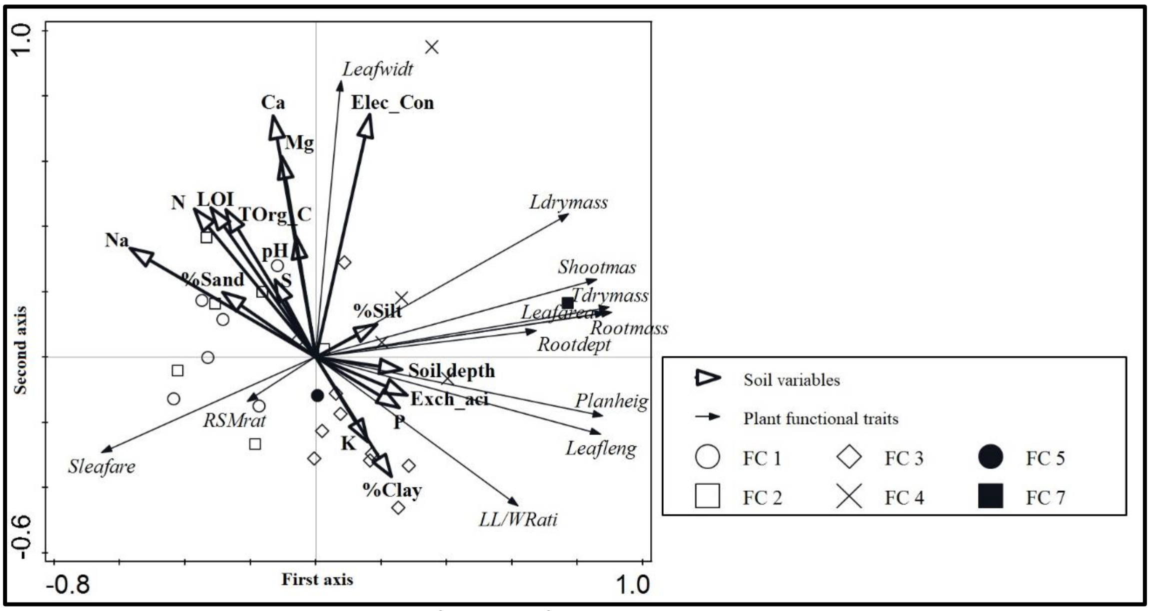

Figure 10: RDA ordination diagram for plant functional communities, community-weighted means of plant functional traits and soil properties of the Afromontane wetlands of Lesotho, based on the classification presented in Figure 5 and using only the subset with soil data. FC stands for functional community.
See Table 1 and 2 for the abbreviations of soil variables and functional traits, respectively.

4.0 DISCUSSION

4.1 Wetland plant communities and their description

The earliest studies on the palustrine wetlands of Lesotho were carried out as far back as the early 1960s and 1970s (Guillarmod, 1962; van Zinderen Bakker & Werger, 1974). Since then, other studies have been conducted in the country (e.g. Meakins & Duckett, 1993; Grab & Deschamps, 2004; Du Preez & Brown, 2011), although they were mainly carried out on small areas, focusing on specific or a few wetlands. The current study has thus provided the most recent and comprehensive assessment of the Afromontane palustrine wetlands of the entire country by providing a classification and description of the wetland vegetation. The wetland vegetation of Lesotho has been classified into 22 communities, which are influenced mainly by altitude, longitude, slope, soil parent material, landscape, inundation, peat, Potassium content, clay content, total organic Carbon, Nitrogen, Sulphur, electrical conductivity, Calcium, soil depth, wetness, Magnesium, aspect and latitude.

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 the current study concurs with Sieben et al. (2017b) who reports 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).

The five most common species in the Afromontane wetlands of Lesotho 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., 2014). However, 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., 2014). While *Cotula paludosa* - *Ranunculus meyeri* and *Agrostis* *bergiana* communities are the most diverse in terms of species richness, Shannon-Weiner index and evenness, *Potamogeton thunbergii*, *Carex cognata*, *Eragrostis plana–Pennisetum sphacelatum, Eleocharis limosa*, *Typha domingensis–Phragmites australis* and *Cyperus fastigiatus communities* are the least diverse and sometimes monospecific communities. Thus, the Afromontane wetland vegetation in Lesotho is generally quite diverse, although the highest diversity was recorded at high altitudes. This trend is contrary to the decline in species richness with altitude, which has been widely recognized as a general law of ecology (Rosenzweig, 1995). The high altitude communities that record lower diversity than other communities at such elevations are those that sometimes form monospecific stands, such as *Kniphofia caulescens* and *Carex cognata* communities.

The large number of species and communities recorded in this study reflects the diversity of wetland habitats in the country. However, the highest species richness recorded in the Highlands type of wetlands highlights that these wetlands are more diverse than the Lowland ones (Table 3) and this could be attributable, in part, to the lower anthropogenic pressure that is often associated with the Highlands. The high diversity in these high altitude wetlands is consistent with observations by Sieben et al. (2010a) who acknowledge the significant number of wetland community types in the montane areas of the country. This diversity can also be attributed to the steep gradients in the landscape and harsh climatic conditions (Pooley, 2003) that create unique habitats in such areas. The high floristic diversity observed in the Afromontane wetlands of the country is also consistent with the findings from the high altitude montane wetlands of Alborz Mountains, Iran (Naqinezhad et al., 2009; Kamrani et al., 2011).

The current study also found that most of the dominant species in the high altitude montane wetlands are non-clonal. Sieben et al. (2010b, 2017b) 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 have been found to be negatively associated with the overall plant species diversity, as well as with altitude (Song & Dong, 2002).

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 species composition. While the former types (Type 1 to 4) are mainly South-facing, the latter (Type 5) is mainly North-facing. Indicators of Wetland type 5 are typical Lowland wetland plants and these include *Cyperus fastigiatus, Eleocharis limosa, Eragrostis plana, Leersia hexandra, Paspalum dilatatum, Paspalum notatum* and *Schoenoplectus paludicola* (Table 3). This wetland type is comparable to the most widespread and common type of wetlands in South Africa, the Temperate Grassy Wetlands (Sieben et al., 2014). Wetland type 4 comprises high altitude 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.

The ordination of the vegetation data for all plots reveal 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 study. It may also be that plants colonise wetland habitats by chance (Chesson, 2000). However, the amount of variation explained in this ordination is comparable to the Temperate grassy wetlands and Subtropical freshwater wetlands of South Africa (Sieben et al., 2016, 2017a). Moreover, Brand et al. (2013) observe 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 ordination diagram also highlights that altitude, longitude, soil parent material, slope, inundation, landscape and peat are the most important factors explaining the variation in the wetland vegetation.

The CCA ordination diagram in Figure 7 reveals that high altitude wetland communities are generally associated with a shallower water column. These include *Kniphofia caulescens, Gunnera perpensa, Agrostis bergiana, Merxmuellera macowanii, Trifolium burchellianum, Limosella grandiflora–Haplocarpha nervosa, Carex cognata, Cotula paludosa–Ranunculus meyeri, Carex cognata–Juncus* *effusus* and Mixed short high altitude grassy communities. Perhaps, the shallower water column is because, contrary to the wetlands in lowlands, high altitude montane wetlands are usually hillslope seepages where the water tends to flow more than accumulate (Mucina & Rutherford, 2006; Sieben et al., 2014). Furthermore, high altitude wetlands tend to have smaller catchments than those in the lower altitude areas. This may also explain the observed negative correlation between slope and inundation. The opposite applies to the lower altitude communities. These include *Typha domingensis–Phragmites australis, Potamogeton thunbergii, Cynodon incompletus, Eleocharis limosa, Cyperus fastigiatus, Schoenoplectus paludicola, Kyllinga pulchella, Cyperus congestus–Leersia hexandra and Eragrostis plana–Pennisetum sphacelatum* communities. Most of these communities are also associated with urban areas in the western part of the country. The Lowlands are subjected to more anthropogenic pressures that include cultivation, urbanisation and conversion to other forms of land use.

Some of the communities, particularly those 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), which are not necessarily classified as montane. This is despite the country's high altitude (1388-3482 m a.s.l.) and rugged terrain, qualifying it to be entirely montane (Carbutt & Edwards, 2015). Such communities include *Eleocharis dregeana, Typha domingensis–Phragmites australis, Cyperus congestus–Leersia hexandra, Eragrostis planiculmis, Cyperus fastigiatus, Eragrostis plana–Pennisetum sphacelatum* and *Potamogeton thunbergii.* However, *Cynodon incompletus* recorded in the current study has not been recorded previously by these earlier studies.

While the second axis is positively correlated 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 *Carex 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 have been observed to be very important factors explaining the distribution of wetland vegetation.

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., 2014). A temperature drop of 1 °C 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). Much of Lesotho is generally much higher and colder than the surrounding areas (Sieben et al., 2014). The hypoxia or anoxia in the wetlands, coupled with the low temperature and pH, often associated with these high altitude wetlands reduce the rate of decomposition and favour 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., 2014).

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., 2014). 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, b), southern Brazil (Rolon & Maltchik, 2006) and in Cumbria, United Kingdom (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).

The negative correlation between altitude and wetness observed in this study was also found in the subtropical freshwater wetlands of South Africa (Sieben et al., 2016). However, altitude operates on a larger scale and wetness operates at a local scale. It is nevertheless noteworthy that while some communities are restricted to either the Highlands or Lowlands, others seem to have wide ecological amplitude and occur in both regions. These include *Eragrostis plana–Pennisetum sphacelatum*, *Eleocharis dregeana* and *Eragrostis planiculmis* communities. Furthermore, some species, such as *Ranunculus meyeri*, have been reported to occur at low cover 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 competitive species (Sieben et al., 2010b).

The ordination for the plots with soil data (Figure 8) indicates that the explanatory variables supplied account for 65.40% of the total variation. This implies that 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, including soil data in the analysis significantly improves wetland vegetation-environment assessments. The amount of variation explained in this ordination is significantly higher than that reported for the South African wetlands (Sieben et al., 2016, 2017a, 2017d). In this ordination, 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 (Figure 10). Thus, communities on the right side of the ordination diagram, which are mainly confined to the Lowlands and the western parts of the country, are associated with high levels of clay and potassium. These include *Eleocharis dregeana, Schoenoplectus paludicola*, *Typha domingensis–Phragmites australis, Cynodon incompletus* and *Eleocharis limosa* communities. Those on the left side, which are mainly high altitude and located in the eastern part of the country, are associated with total organic carbon, nitrogen, sulphur, percentage sand and longitude. These include *Limosella grandiflora–Haplocarpha nervosa, Cotula paludosa–Ranunculus meyeri, Agrostis bergiana, Gunnera perpensa, Isolepis costata, Carex cognata, Carex cognata–Juncus effusus* and *Eragrostis plana–Pennisetum sphacelatum* communities.

The second axis is negatively correlated with latitude and positively correlated with electrical conductivity, soil depth, magnesium and calcium content. This implies that the communities on the upper part of the ordination diagram are associated with deep soils and high levels of calcium, electrical conductivity and magnesium. These include *Schoenoplectus paludicola*, *Typha domingensis–Phragmites australis, Isolepis costata, Gunnera perpensa, Eragrostis plana–Pennisetum sphacelatum, Carex cognata* and *Carex cognata–Juncus effusus* communities.

Most of the species that are dominant in the communities recorded in the current study have been reported to occur in the AZf 3, AZf 4 and AZf 5 wetlands (Mucina & Rutherford, 2006). The high altitude peat forming wetlands of Lesotho have been widely acknowledged as unique ecosystems that are not found elsewhere in the world, whose vegetation is distinctive (van Zinderen Bakker & Werger, 1974; Backéus & Grab, 1995; Sieben et al., 2010a). Because some of the plant communities recorded in this study are restricted to the highest altitudes, occurring at the summit plateaus, they are likely to disappear in the face of climate change as they cannot migrate any further up (Lee et al., 2015). Additionally, the study has also recorded some Maloti-Drakensberg endemic species (e.g. *K. caulescens* and *Ecomis bicolor)* and genera (e.g. *Eumorphia* and *Rhodohypoxis*), as well as species (e.g. *H. nervosa*) endemic to the Grassland Biome (Mucina & Rutherford, 2006). The current study also affirms earlier studies that recognise *Merxmuellera drakensbergensis, Carex cognata, K. caulescens, Gunnera perpensa, Isolepis fluitans, I. angelica, Andropogon appendiculatus, Pennisetum sphacelatum* and *H. nervosa* as wetland plant species occurring in Lesotho (Mucina & Rutherford, 2006; Du Preez & Brown, 2011).

The Afromontane wetlands of Lesotho 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 Lesotho Highlands Water Project (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, most of the mountain areas are drained through the Senqu-Orange River (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.

With climate change predictions highlighting that much of southern Africa will become drier (Mitchell, 2013), the conservation of these Afromontane wetlands is becoming more important. 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). Furthermore, 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)

For a long time, the Afromontane wetlands of Lesotho have been considered a critical resource for livestock grazing, especially in summer when thousands of livestock units are seen grazing on these sensitive ecosystems (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 because they harbour the most palatable vegetation (Grab & Deschamps, 2004). The Basotho, who mostly inhabit the lowlands and traditionally took their herds of livestock to the mountains in summer and returned to the lowlands during winter (Meakins & Duckett, 1993), are now sometimes observed to keep their livestock in the mountains throughout the year. Thus, the value of these wetlands as a grazing resource is increasingly becoming higher. Nevertheless, while few wetlands in the country, particularly in the Highlands, are still in their near-pristine condition, many of them are showing signs of severe degradation. The widespread degradation and loss of wetlands, mainly due to livestock grazing and trampling, 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 *Merxmuellera macowanii* dominated community, which is unpalatable. The sharp tips of *M. macowanii* make it difficult to walk through the community.

4.2 Wetland plant functional traits, types and composition

The results of the ordination indicate observable functional differentiation of the vegetation along gradients and other factors of the environment in the Afromontane wetlands of Lesotho. The amount of variation explained in both CWM redundancy analyses (25.56 % and 81.52%), was higher than in other studies employing similar analyses, e.g. 13.5% (Roy et al., 2019) and 36.4% (Morandeira & Kandus, 2016). The plant functional traits and functional communities were found to be influenced mainly by environmental factors such as altitude, longitude, slope, soil parent material, landscape, inundation, soil depth, electrical conductivity, calcium, sodium, magnesium, nitrogen, total organic carbon, organic matter, pH and soil texture. Species diversity was generally higher in functional communities associated with high-altitude and more pristine wetland habitats than in the low-altitudes.

By obtaining only seven PFTs from 57 dominant plant species, this study concurs with Díaz and Cabido (1997) who used 24 functional traits and distinguished only eight PFTs from 100 dominant plant species in Argentina. Morandeira and Kandus (2016) recorded 10 PFTs in a floodplain in South America. In the current study, phylogenetic diversity was high within PFTs as evidenced by the representation of at least three families in each PFT. This could suggest 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 the study area. Furthermore, in environmental conditions with more 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. However, the current findings are contrary to Díaz and Cabido (1997) who report lack of independence between PFTs and taxonomic affiliations because in their study, some functional types were absolutely dominated by one plant family..

It appears that variation in plant functional traits has been constrained by convergent evolution (Reich et al., 2003), a situation that would be expected in wetlands, particularly high altitude wetlands. Apart from anoxia, the low temperatures and low pH, which are often associated with high altitude wetland environments tend to increase habitat filtering that species have to overcome in order to establish in the high altitude montane wetland habitats. This affects traits, including those that are related to interception of light, such as SLA.

Notwithstanding the above results, plant communities represent particular combinations of PFTs and thus each functional community in this study was found to represent a number of PFTs. Except for FC 7, each functional community represented at least two PFTs. This is consistent with Kleyer (1999) who found that some of the vegetation samples were comprising species from up to 12 different PFTs. This implies that most wetland plant communities in the current study are functionally diverse and exhibit resource partitioning (complementarity) for co-existence. Semenova and van der Maarel (2000) report that many PFTs may co-exist because complementary generative and vegetative pathways enable the plants to use different spatial and temporal 'windows' of their environment for growth and reproduction. However, by finding not only plant species from different functional types co-existing in a community, but also species from the same functional type, the current study corroborate the two opposite niche-based deterministic processes: habitat filtering that predicts that most co-existing species should exhibit similar traits; and niche differentiation that requires that co-existing species display dissimilar traits to coexist (Maire et al., 2012). In communities, some species are forced 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 has been reported to improve species coexistence by reducing interspecific competition (Maire et al., 2012).

Species diversity was generally higher in high-altitude communities than in low-altitude ones. Because the plants that are usually dominant in wetlands 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 other plants (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). Furthermore, high-altitude montane wetlands have been reported to be unusual in that they are characterised by higher functional diversity than low-altitude ones (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 great effects on habitat diversity (Shimono et al., 2010).

The influence of environmental factors on plant functional traits and functional composition observed in this study further highlights the role of habitat filtering (Roy et al., 2019) in the functional composition and structure of wetland communities. High-altitude communities (e.g. FC 1 and FC 2) were found to be associated with lower SLA (Figures 9 & 10). Because SLA is positively related to relative growth rate (Pérez-Harguindeguy et al., 2013), it is plausible for high-altitude plants to exhibit lower SLA because the cold conditions in these areas result in low growth rate. This pattern highlights that communities at high-altitudes are dominated by species with a conservative attribute, while those at low-altitudes tend to select for species with an acquisitive attribute (Pla et al., 2012). This also reflects the differences between plant species found in high-altitudes and those in low-altitude areas in terms of their role in ecosystem functioning. 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 (Leps et al., 2006). This could further imply that low SLA is associated with low temperatures and high rainfall, conditions that characterise the high-altitude areas of Lesotho. Díaz and Cabido (1997) found high SLA to be a dominant trait in the montane grasslands of central-western Argentina, where the high altitude is comparable with the low-altitude areas in Lesotho. This, coupled with the pattern in the current study, could suggest that SLA exhibit a bell-shaped relationship with altitude.

The high SLA, demonstrated by the low-altitude communities, highlights the importance of such communities for animal grazing, which is one of the key ecosystem services required in Lesotho. Because SLA has been reported to be positively associated with tissue nitrogen content (Díaz & Cabido, 1997; Pla et al., 2012) and negatively with the concentration of defensive compounds in plant tissues, these low-altitude communities could be associated with high nutritional quality and thus could exhibit a high carrying capacity for grazing animals (Díaz & Cabido, 1997). Nevertheless, animal gazing in Lesotho mainly occurs in the high-altitude areas because of the availability of grazing land. Although the SLA and leaf dry mass showed a weak association with soil nutrient content in this study, Gaucherand and Lavorel (2007) report that fast-growing species in nutrient rich habitats usually exhibit both high SLA and low leaf dry matter content. Because of their links to relative growth rate, these two traits have been reported to indicate specific annual net primary productivity (Garnier et al., 2004). In cool-temperate herbaceous species, SLA has been reported to be negatively related with leaf dry matter content (Pérez-Harguindeguy et al., 2013) and this has been evident in the current study (Figures 9 and 10). 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).

SLA, as an important 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 higher values of SLA are associated with rapid acquisition of resources, lower values are associated with conservative strategy (Pla et al., 2012). Weiher et al. (1999) also highlight that competitive ability is strongly associated with plant height and above-ground biomass, while fecundity depends on above-ground vegetative biomass. Thus, the negative association between root to shoot mass ratio and total biomass traits 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.

The decrease in plant height (dwarfism) and leaf area with increasing altitude indicates classical plant adaptations to the coldness associated with high altitude montane environments (Sieben et al., 2010b; Dainese et al., 2015). The current study also seems to confirm 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). Some high-altitude communities that exhibited low species diversity were those that are usually characterised by monodominance.

Traits, such as leaf size, plant height and root architecture that respond to changes in temperature or moisture availability, can be used to predict plant species responses to climate change (Garnier & Navas, 2012). Therefore, with climate change predictions highlighting that much 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. For example, the high-altitude communities may experience the dominance of species with higher SLA and reduced species diversity as climate changes. The low-altitude PFTs will be expected to advance up to high altitudes at the expense of the high-altitude PFTs (Díaz & Cabido, 1997). Furthermore, given that some of the wetland PFTs (e.g. PFT 1) 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).

5.0 CONCLUSION

Given their 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, biodiversity loss and climate change. With the increasing demand for ecosystem services, the identification of groups of plants that are critical in controlling the wetland ecosystem properties responsible for the provision of ecosystem services is important because functional composition is a good indicator of ecosystem health or underlying ecosystem properties (Sieben, 2012; Roy et al., 2019). De Bello et al. (2010) observe that the impact of biodiversity changes on the delivery of ecosystem services can be assessed by identifying the vital characteristics through which organisms affect ecosystem processes and functions. 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 systems. Thus, the 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.

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