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WETLANDS IN THE DEVELOPING WORLD

Variation in Plant Functional Composition of the Afromontane Palustrine Wetlands Along an Altitudinal Gradient in Lesotho

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Abstract

Understanding montane wetlands and their functioning is essential for biodiversity conservation and sustainable provision of ecosystem services. Plant functional traits represent species adaptations to specific environments and are considered the key mechanism by which individual species contribute to the functioning and subsequent provision of ecosystem services. This study characterises the Afromontane palustrine wetlands along the altitudinal gradient in Lesotho in terms of plant functional traits and composition. Wetland plant species are classified into functional types (PFTs) using their functional traits. Relationships of plant functional traits and PFTs with environmental factors are also explored. Plant species composition was assessed using the Braun-Blanquet method, while functional traits and environmental factors were assessed using protocols recommended in the literature. The data were analysed using clustering and ordination techniques. Eight PFTs were obtained from the functional classification of the species. The PFTs were dominated by C_3 plants, particularly in high-altitude wetlands. The wetland plant communities in Lesotho exhibited the coexistence of species from different PFTs, highlighting functional differentiation to exploit microhabitat heterogeneity. Both functional traits and functional composition of communities were mainly influenced by altitude, longitude, slope and several edaphic factors. Because montane regions display greater sensitivity to changes in climate, alterations in wetland plant functional traits, PFTs and composition will possibly occur in the face of climate change. These alterations will result in modifications in montane wetland ecosystem functioning that include primary productivity and nutrient cycling, with subsequent changes in the delivery of ecosystem services.

Keywords Ecosystem function · Functional composition · Montane palustrine wetland · Photosynthetic pathway · Plant functional trait · Plant functional type

Introduction

Montane ecosystems are ecologically sensitive environments that offer unique habitat conditions for a great variety of plant and animal species (Du Preez and Brown 2011). High-altitude montane wetlands are a special type of freshwater palustrine wetlands that form an archipelago of isolated ecosystems embedded within terrestrial ecosystems in montane areas (Mucina and Rutherford 2006). These wetlands are of high environmental, ecological and socio-economic importance as they provide a wide spectrum of crucial ecosystem services (Chatterjee et al. 2010). Ecosystem services are the benefits that human beings derive directly or indirectly from ecosystem functions (Roscher et al. 2012; Sieben et al. 2017b).

The most conspicuous and ubiquitous feature of montane palustrine wetlands is the vegetation, which plays a fundamental role in the functioning of the wetlands (Cronk and Fennessy 2001; Sieben et al. 2010a; Gopal 2016). Wetland vegetation consists mostly of vascular plants, termed macrophytes, that are typically adapted to inundated or saturated soil conditions (Mitsch and Gosselink 2015). The vegetation is not only influenced by, but also influences, the hydrology and edaphic factors in these ecosystems (Cronk and Fennessy 2001; Mitsch and Gosselink 2015). Because wetland

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vegetation responds quickly to changes in the local environment (Cronk and Fennessy 2001; Sieben et al. 2014), plant species occurring in montane wetlands can be used as indicators of the conditions and changes occurring in these ecosystems (Sieben et al. 2014; Mitsch and Gosselink 2015).

Given that plants need to disperse to new sites, become established and subsequently persist, all plant species have specific adaptations in order to face these primary challenges (Weiher et al. 1999). For a plant to persist in an environment, it has to tolerate the fluctuations in resource availability and changes in the array of abiotic (e.g. pH, temperature and flooding) and biotic (e.g. competition and herbivory) conditions of a particular site (Weiher et al. 1999). The biotic and abiotic conditions of a habitat act as a filter that permits only species with particular traits to establish and persist (Maire et al. 2012; Kraft et al. 2014; Li et al. 2018). Because montane wetland habitats require special adaptations, they support distinct combinations of plant traits (Sieben 2012). However, some species may exhibit dissimilar functional traits to reduce interspecific competition and coexist in a community, a process called niche differentiation or resource partitioning (Maire et al. 2012).

Plants occurring in montane palustrine wetlands have to cope with the cold conditions, coupled with anoxia and low pH (Chatterjee et al. 2010; Gopal 2016). Steep changes in climate with altitude over relatively short horizontal distances are associated with equally steep changes in vegetation and hydrology (Sharma et al. 2010). Sieben et al. (2010b) highlight that, in the Maloti-Drakensberg area that includes Lesotho, altitude is a suitable surrogate measure for an ecological gradient, in terms of temperature and precipitation. The same authors also highlight that growth forms, such as mat-forming, and types of metabolism, such as C_3 photosynthetic pathway, are important strategies for plant adaptation to high-altitude wetland habitats because of the cold temperatures associated with such environments.

An understanding of the factors that determine the structure and functioning of these montane wetland ecosystems is required, especially because today the focus in conservation has shifted from specific species and their habitats towards the networks of species and ecosystems (Ostfeld et al. 1997; Sieben and le Roux 2017). In the quest to better understand the functioning of ecosystems, plant functional traits are assessed (Smith et al. 1997). Plant functional traits are morphological, physiological and phenological attributes that can be measured for individual plants and that potentially influence plant fitness though their effects on survival, growth and reproduction (Violle et al. 2007; Garnier and Navas 2012; Pérez-Harguindeguy et al. 2013).

Functional traits can also affect the environment of the plants (Garnier and Navas 2012), for example through the 'mass effect', where the physical environment is affected because a plant species may be present with a large number of individuals, all of which are performing a certain function. The extent to which the traits of a species affect ecosystem properties and functioning depends on the abundance of the species in the community, which is termed the biomass ratio hypothesis (Gaucherand and Lavorel 2007; Garnier and Navas 2012). It is assumed that similarities in plant functional traits reflect similar roles within the ecosystem (Smith et al. 1997). Hence, plants with similar combinations of functional traits can be grouped into plant functional types (PFTs), which are groups of species that have similar functioning at the organismal level and thereby respond in a similar way to environmental factors or have similar effects on ecosystems (Semenova and van der Maarel 2000; Cornelissen et al. 2003).

Given the correlation between plant functional composition and ecosystem functioning (Díaz and Cabido 2001; Lavorel and Garnier 2002), it is likely that ecosystems that have similar functioning are also similar in functional composition as they subject the plants to similar stresses (Sieben 2012). Functional traits can also be used to describe the attributes of plant communities (Sieben 2012; Moor et al. 2015) as they reflect how organisms interact with their environment (Violle et al. 2007; Garnier and Navas 2012). Functional composition is the major determinant of ecosystem processes (Gaucherand and Lavorel 2007; Roscher et al. 2012; Zhang et al. 2015) and therefore traits can provide an understanding of how functional composition generally underpins ecosystem processes and services (Díaz and Cabido 2001; Pérez-Harguindeguy et al. 2013).

Because functional traits can be used to determine PFTs, the latter provide an understanding of how plants are adapted to survive in particular environments (Sieben 2012; Moor et al. 2015). PFTs can also be useful for comparing the functioning of the same type of ecosystem located in different geographic locations or on different positions of an environmental gradient. For this reason, PFTs are valuable tools in predicting how changes in environmental factors would affect community composition and dynamics in ecosystems such as wetlands (Boutin and Keddy 1993; Sieben et al. 2014). This implies that knowledge of the PFTs can help to predict and interpret the changes that may happen in wetland ecosystems.

Currently, one way to make a case for conservation from an economic perspective is by considering ecosystem services. With the increasing demand for ecosystem services, the identification of species or groups of species that are critical in controlling the ecosystem properties responsible for the supply of ecosystem services is needed for the conservation and sustainable supply of those services (de Bello et al. 2010). Wetland ecosystem services are fundamentally products of ecosystem properties and functioning, which in turn are significantly influenced by traits of the dominant species (Sieben 2012; Moor et al. 2015; Zhang et al. 2015).

Lesotho has a network of wetlands across a number of environmental gradients, making it an ideal study area for assessing the relationships between functional traits and environmental factors. The country is an Afromontane region, located in the interior regions of southern Africa and it has a wide altitudinal range (1,388-3,482 m a.s.l.) over a relatively short horizontal distance (Pomela et al. 2000; Carbutt 2019). Altitude is an important environmental gradient in this country and it has a strong influence on vegetation (Kotze and O'Connor 2000; Sieben et al. 2010b). Climate change is likely to adversely affect the wetlands and watersheds in the mountain landscapes of the country as the warm climatic conditions of valleys are likely to shift upslope (Bentley et al. 2019).

Although there is a long history of studies focusing on the altitudinal gradient in plant ecology (Whittaker and Niering 1975), there is still no sufficient evidence of a particular trend in vegetation along the gradient (Rahbek 1995), which makes site-specific studies important. In an attempt to elucidate the vegetation trends along various environmental gradients, gradient analysis can be used, which allows multivariate analyses to be employed on vegetation data (Whittaker and Niering 1975; Whittaker 1978). Furthermore, assessments of vegetation changes with altitude and other environmental gradients in montane areas can be useful in assessing climate change impact on biodiversity because mountains are suitable areas for detecting climate change, as well as assessing its impacts (Sharma et al. 2010).

The current study aims to characterise the montane wetlands in Lesotho in terms of plant functional traits, PFTs and plant functional composition. It will do so by exploring plant trait-environment relationships across the range of wetland habitats that exist along the altitudinal gradient of the country. This will reveal the influence of environmental factors on plant functional traits and composition in high-altitude montane palustrine wetlands. Previous studies on the plant functional composition of wetlands along wetness and altitudinal gradients around this area (Kotze and O'Connor 2000; Sieben et al. 2010b) were not based on actual measurement of plant traits and focused mainly on the neighbouring areas in South Africa. An understanding of the adaptations (in the form of functional traits) and functional composition of the plants to their habitats in these Afromontane wetland environments is critical, both for the conservation of biodiversity and for the sustainable provision of ecosystem services.

Materials and Methods

Assessment of Vegetation and Explanatory Variables

In selecting wetlands for sampling, the focus was on near-pristine or pristine wetland systems, including the wetlands in protected areas, such as nature reserves and national parks. Sampling was conducted during the late summer (wet) season (February-March) in both 2017 and 2018. Details of the procedure used for collecting vegetation and environmental data are provided by Chatanga and Sieben (2019). Stratified random sampling approach was employed for vegetation assessment. A 3 × 3 m representative sample plot was placed randomly in each visually distinct and homogenous vegetation unit of each wetland. The number of plots assessed per wetland was dependent on the number of observable distinct and homogenous vegetation units in the wetland. The location of the 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 captured.

In each plot, the Braun-Blanquet approach (van der Maarel 1979; Brown et al. 2013; Sieben et al. 2014) was used for vegetation assessment. Species composition was recorded using the Braun-Blanquet cover-abundance scale (van der Maarel 1979; Omar et al. 2016). Estimations of the average vegetation height and the proportion of the plot under the aerial cover of the vegetation were also made. In case of inundation, the average vegetation height was estimated from the soil surface (Sieben et al. 2014). During the assessment, plant species were identified with the help of botanical field guides (Pooley 2003; Van Oudtshoorn 2014) and samples of the species that could not be identified in the field were collected and later taken to the herbarium at the National University of Lesotho for identification. A total of 118 vegetation plots from 30 wetlands were assessed in this study.

In addition to the vegetation assessment, a standard protocol was used in each plot to systematically measure or assess a number of environmental variables that are recommended for wetlands (Sieben et al. 2014). In each wetland system, soil sampling was conducted in one plot that represented the most widespread distinct plant community in the wetland. Thus, thirty of the 118 vegetation plots had detailed soil data. The depth of the soil in each plot was also determined by driving a soil auger until it reached the bed rock. The soil samples were packaged in air-tight bags and air-dried for at least 48 h (Stohlgren et al. 1998) before being analysed for different variables (Sieben et al. 2014) (Table 1). The soil sample analyses were performed by the Analytical Laboratory Services of the Institute for Commercial Forestry. The different environmental variables that were recorded or assessed and included in the analysis of plant functional composition in this study are presented in Table 1. While some variables were assessed onsite and on all the plots, others (indicated with an asterisk on Table 1) were measured later and only on the plots where soil samples were collected.

Functional Trait Measurement and Determination

Functional trait measurements were made on 57 different plant species, selected on the basis of dominance (collectively

Table 1 Environmental variables that were measured or assessed and incorporated in the analysis of the functional composition of the vegetation of the Afromontane palustrine wetlands in Lesotho

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

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

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

covering potentially 60% or higher in each plot). The average cover-abundance of these species in each plot was 82%. A species would be selected if it occurred with a cover-abundance of 8% or higher (Braun-Blanquet cover values of 2a, 2b, 3, 4 or 5) per plot in an average of more than 65% of all the vegetation plots in which it occurred. Traits from each of these plant species were measured from ten random mature individuals growing in open areas (Weiher et al. 1999; Cornelissen et al. 2003). For clonal plant species, an individual was defined as a ramet, which is a recognisable separate above-ground unit (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013). A total of eleven quantitative morphological functional traits were assessed on the species following the methods described by Sieben (2012) and Pérez-Harguindeguy et al. (2013). In addition to the quantitative traits, five qualitative functional traits were also considered: metabolism, growth form, leaf presence and position, leaf shape and root type. Table 2 lists the plant functional traits, their methods of measurement or assessment and the codes or categories that are used to represent them in later analyses. Seed traits were not considered because some plants did not have seeds at the time of data collection and many wetland plants are clonal, which makes their vegetative characters more important (Sieben 2012). The collected plants were uprooted carefully in order to do the least damage to the underground parts. For tufted species (mostly grasses and sedges), the whole tuft would be uprooted. The uprooted plants were carefully washed with water to remove the soil particles. Plant height and rooting depth were measured *in situ* using a measuring tape, as recommended by Pérez-Harguindeguy et al. (2013).

For the measurement of leaf traits, ten leaves from separate representative specimens of each species were collected and placed in bottles containing 70% alcohol. For species without true leaves, the functional equivalent of a leaf was used (e.g. a green stem or a portion of the stem) (Weiher et al. 1999). The leaves were later used for determining leaf length, leaf width, leaf area, specific leaf area (SLA) and leaf dry mass. Leaf area was measured using a portable CI-202 laser leaf area meter

Table 2 Plant functional traits measured on the dominant and common plant species in the Afromontane palustrine wetlands in Lesotho

Plant trait	Scale	Method of measurement or assessment (averages based on specimens from 10 mature plants)	Units	Trait code
Plant height	Ratio	Average plant height of vegetative parts	cm	P_Height
Rooting depth	Ratio	Average maximum plant rooting depth	cm	R_Depth
Shoot biomass	Ratio	Average shoot dry weight	g	S_Mass
Root biomass	Ratio	Average below-ground dry weight	g	R_Mass
Total biomass	Ratio	Average total plant dry weight	g	T_Mass
Root/shoot biomass ratio	Ratio	Average ratio of root to shoot dry weight	g/g	RS_Mratio
Leaf length	Ratio	Average of leaf length	cm	L_Length
Leaf width	Ratio	Average of leaf width	cm	L_Width
Leaf area	Ratio	Average area of a leaf	cm^2	L_Area
Leaf biomass	Ratio	Average leaf dry weight	g	L_Mass
Specific leaf area	Ratio	Average ratio of the area of a leaf to its dry weight	cm^2/g	SLA
Growth form	Nominal	Assessment growth form	–	Graminoid; forb
Metabolism	Nominal	Whether the plant is C3, C4 or parasitic	–	C_3; C_4; Parasitic
Presence and position of leaves	Nominal	Assessment of the presence of leaves and their position on the plant	–	Leafless; leaves at the base; leaves on the stem
Leaf shape	Nominal	Assessment of the shape of the leaves	–	Linear; lanceolate; oval; oblong
Root type	Nominal	Assessment of whether the plant has a tuft, taproot, stolon, rhizome or is annual	–	Tufted; annual, taproot; stolon; bulb; rhizomatous

(manufactured by CID Bio-Science Inc. USA). For needle-like leaves, leaf length was measured with a measuring tape and leaf width with a Vernier calliper and the product of the two was then doubled (i.e. 2 · length · width) to give leaf area (Pérez-Harguindeguy et al. 2013) as these leaves often consistently point upwards.

After initial measurements, all plant and leaf samples were placed in an oven at 70 °C for at least 72 h (Pérez-Harguindeguy et al. 2013). Plant biomass was measured on the oven-dried specimens using an AE 6,801,417 analytical balance (manufactured by Adam Equipment, UK). After measuring biomass, the plants were divided into above-ground and below-ground parts and the biomass (root/shoot) ratio was calculated. To get the total individual biomass for tufted and clonal species that share a single rootstock among several shoots, the overall below-ground biomass was added to the overall above-ground biomass and the sum divided by the number of shoots. SLA was derived from the measurements made on the leaf samples, by dividing the surface area of the leaf by its dry mass.

Data Analysis

The overall dataset consists of three matrices: (1) plots · species abundance matrix using percentage cover values, (2) plots · environmental variables matrix, and (3) species · traits matrix (using means of the trait values for each species). A fourth matrix (reflecting trait means per plot, weighted by species relative abundance (also referred to as community-weighted means (CWM)) was developed and obtained by multiplying the plots · species abundance matrix by the species · traits matrix (Semenova and van der Maarel 2000; McCune 2015). The multiplication of matrices was performed using PC-Ord, version 6.0 (McCune and Mefford 2011). A constancy table for the entire set of the community data was prepared (Appendix 1) following the guidelines by Jennings et al. (2009).

Classification

To classify the wetland plant species into functional groups (PFTs), agglomerative hierarchical cluster analysis (HCA) was performed on the basis of similarity in plant functional traits (using the species · traits matrix) (van Tongeren 1995; McCune and Mefford 2011). PC-Ord Version 6.0 was used for cluster analysis (McCune and Mefford 2011), with the use of Sørenson’s (Bray-Curtis) similarity index and Ward’s method as the linkage method. A dendrogram was derived from this cluster analysis, which is a tree diagram where the most similar species are proximate to each other on the same branch of the diagram.

After the clustering was conducted, the species that had been excluded from collection and measurement of functional traits were allocated to the PFTs a posteriori so that they could be included in the determination of functional composition of the plots (Díaz and Cabido 2001 ; Sieben 2012). This was done by using our knowledge of the species to allocate them into the different PFTs on the basis of their similarity to other species that were allocated on the basis of traits. Species that could not fit well into the PFTs obtained from the cluster analysis were allocated to a separate PFT. These species represented a minor part of the total wetland vegetation cover (average of 5.6%).

Ordination

To examine the influence of environmental conditions on the abundance of traits and functional types, constrained canonical ordination was employed. The primary objective of constrained ordination was to detect the main patterns of variation in the species, functional trait or PFT data that could be explained by the supplied environmental variables (McGarigal et al. 2000). In the ordination output the sum of all the eigenvalues is calculated, which is a measure of the total variation in the data. The canonical ordination was performed using CANOCO Version 5.11 (Ter Braak and Šmilauer 1998) on the subset of the vegetation plots where soil samples had been taken in order to get a complete range of possible explanatory variables. Forward selection was used to exclude the less important environmental variables.

The CWM trait data were subjected to Redundancy Analysis (RDA), which is a recommended ordination method when the response data have a linear response model (Lepš and Šmilauer 2003). This was done to explore the trait-environment relationships by using the CWM trait matrix (plots · traits matrix) as response variables and the environmental variables (plots · environmental variables matrix) as explanatory variables (Ter Braak and Šmilauer 1998).

For the assessment of the distribution and abundance of PFTs with respect to environmental factors, a matrix of plots by abundance of each PFT was used in the ordination. The data in this plots · PFTs matrix were subjected to Constrained Canonical Correspondence Analysis (CCA). The choice for CCA for the ordination was based on the fact that the response (species abundance) data were compositional and had a unimodal response curve (Lepš and Šmilauer 2003). The statistical significance of the constrained ordination (relationship of CWM plant functional traits and PFTs with environmental variables) was tested using an unrestricted Monte Carlo permutation test (Ter Braak 1995).

Results

The cluster analysis resulted in a classification that divided the species into seven clusters (PFTs) (Fig. 1). The additional (eighth) PFT comprised species that could not fit well into the seven PFTs and, on average, these species accounted for 5.6% of each vegetation plot. Table 3 describes the PFTs in terms of their species and their functional characteristics. PFT1 was the most common in the study area, in terms of frequency of occurrence, followed by PFT2 and the least common was PFT3. Most of the wetland vegetation plots had a combination of different PFTs.

Figure 2 presents the RDA ordination diagram and it shows the trait-environment relationships. In this ordination of CWM functional traits, the environmental variables supplied accounted for 90.2% of the total variation. The permutation test indicated that the model was significant (F = 1.3, P = 0.002). The correlation of each environmental variable with each of the first four axes and the significance of the association are presented in Table 4. The first axis of the ordination was negatively correlated with altitude, total organic carbon, sodium and nitrogen. The second axis was positively correlated with electrical conductivity, calcium, longitude (dry-to-wet gradient in the context of Lesotho), magnesium and slope but had a negative correlation with clay percentage, wetness and potassium.

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

Figure 3 presents the CCA species ordination diagram whereby species are allocated to PFTs. In this ordination, the supplied explanatory variables explained 61.80% of the total variation in the response data. The Monte Carlo permutation test indicated that the model was significant (F = 3.9, P = 0.002). Clay percentage and potassium were positively correlated with the first axis, while altitude, longitude, total organic carbon, nitrogen, sulphur and slope had a negative correlation with the same axis (Table 5). This means that the PFTs that are positioned on the right side of the ordination diagram were associated with low-altitude wetland habitats with gentle slopes and clay soils. The PFTs that are mainly on the left side of the ordination diagram (PFT3, PFT4 and PFT7) were associated with high-altitude wetland habitats with steep slopes. The second axis had a positive correlation with electrical conductivity, calcium, magnesium and soil depth but was negatively correlated with latitude. Thus, while PFT7, which is located mainly on the upper part of the ordination diagram, was associated with deep soils that were high in electrical

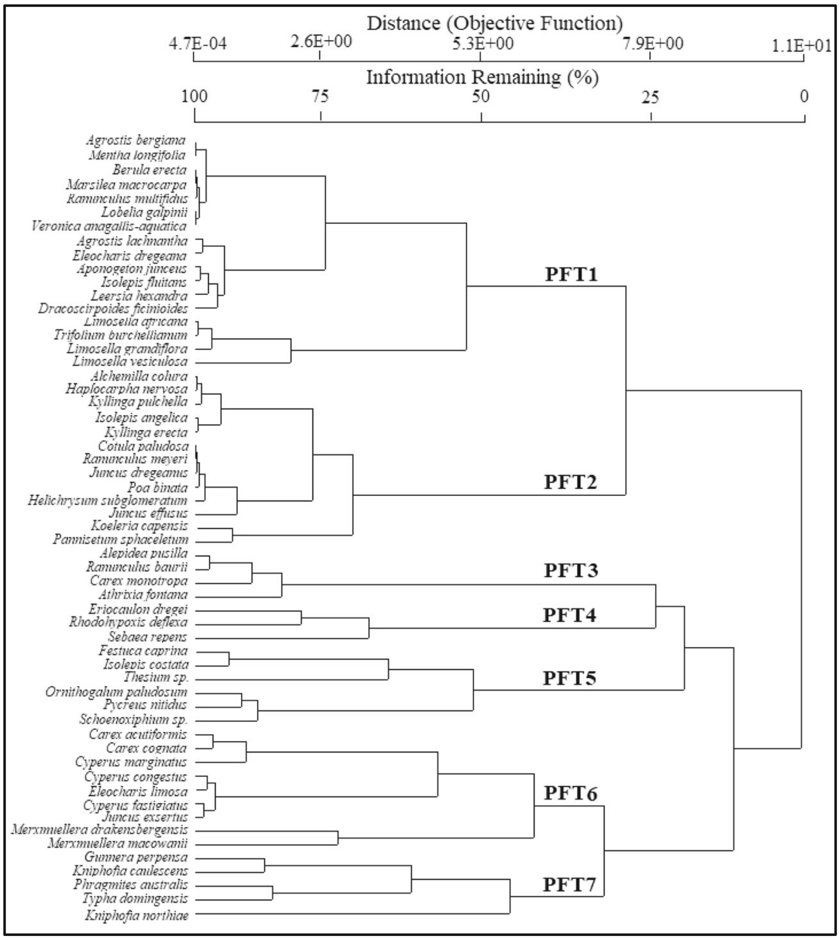

Fig. 1 Functional classification dendrogram of plant species of the Afromontane palustrine wetlands in Lesotho, based on morphological quantitative and qualitative functional traits. PFT represents plant functional type

conductivity, calcium and magnesium levels, the two other PFTs (PFT3 and PFT4) which are located on the lower part exhibited the opposite trend. All eight PFTs have been observed in the high-altitude wetlands, with some (PFT3, PFT4 and PFT7) being restricted to them and missing from the low-altitude wetlands. In addition to altitude, several other factors (e.g. longitude, electrical conductivity, total organic carbon and clay percentage) were among the most important predictors of both plant functional traits and PFTs.

Discussion

Influence of the Altitudinal Gradient

The ordination indicates that vegetation units can be differentiated on the basis of functional traits and composition along the altitudinal and other environmental gradients. The amount of variation explained in both ordination analyses (at least 61.80%), was high compared to other studies employing similar analyses (Morandeira and Kandus 2016; Roy et al. 2019). Both plant functional traits and PFTs were found to be influenced by almost the same environmental factors.

Most of the PFTs in this study exhibited a wide ecological tolerance and occurred in both high- and low-altitude wetland habitats. Thus, it is noteworthy that, although PFT1, PFT2, PFT3, PFT4 and PFT5 were mainly associated with high-altitude areas, some of the species from these PFTs occurred in low-altitude areas. At the same time, some of the species from the PFTs mainly associated with low-altitude areas actually occurred in high-altitude wetlands. While the high-altitude PFTs were mainly associated with hillslope seepages in high rainfall areas, low-altitude PFTs were mainly associated with valley bottom wetlands.

In this study, there was substantial variation in PFTs along environmental gradients, particularly along the altitudinal gradient. Thus, habitat filtering seems to be more pronounced at low altitudes where functional diversity was lower, while niche differentiation could be associated more with the high-altitude wetlands where functional diversity was higher. Semenova and van der Maarel (2000) report that many PFTs may co-exist in communities generally because complementary generative and vegetative pathways enable the plants to use different spatial and temporal 'windows' of their

Table 3 Description of the plant functional types (PFTs) from the classification presented in Fig. 1

Plant Functional type	Examples of plant species	No. of species	No. of plant families represented	Frequency (%) of PFT (n = 118 plots)	Growth form, other functional characteristics and environmental factors of the PFTs
PFT1	*Agrostis bergiana, A. lachnantha, Aponogeton junceus, Berula erecta, Dracoscirpoides ficinioides, Eleocharis dregeana, Isolepis fluitans, Leersia hexandra, Limosella africana, L. grandiflora, L. vesiculosa, Lobelia galpinii Marsilea macrocarpa, Mentha longifolia, Ranunculus multifidus, Trifolium burchellianum, Veronica anagallis-aquatica*	17	10	96.67	Relatively small, short to medium tall (< 80 cm) graminoids and forbs; mainly C_3 metabolism; shallow rooting (< 20 cm); accumulates more below-ground than above-ground biomass; very high specific leaf area (> 300) and a relatively high leaf length-to-width ratio. Tolerates a wide variety of environmental conditions. Mainly occurs in high-altitude habitats with varying soil texture and nutrient levels but can also occur in low-altitude wetlands.
PFT2	*Alchemilla colura, Cotula paludosa, Haplocarpha nervosa, Helichrysum subglomeratum, Isolepis angelica, Juncus dregeanus, J. effusus, Koeleria capensis, Kyllinga erecta, K. pulchella, Pennisetum sphacelatum, Poa binata, Ranunculus meyeri*	13	6	86.67	Relatively small, short to medium tall (< 60 cm) graminoids and forbs; has both C_3 and C_4 plants; shallow rooting (< 20 cm); accumulates more above-ground than below-ground biomass; high specific leaf area (100–300) and a relatively high leaf length-to-width ratio. Tolerates a wide range of environmental conditions. Mainly associated with high-altitude habitats with varying soil texture and nutrient levels but can also be found in low-altitude wetlands.
PFT3	*Alepidea pusilla, Athrixia fontana, Carex monotropa, Ranunculus baurii*	4	4	13.33	Short (< 40 cm) small graminoids and forbs; mainly C_3 metabolism; shallow rooting depth (< 20 cm); relatively low specific leaf area (30–100) and leaf length-to-width ratio; accumulates more biomass above-ground than below-ground. Found in high-altitude wetland habitats with sandy or silty shallow soils rich in nitrogen and sulphur but low levels of electrical conductivity, calcium and magnesium.
PFT4	*Eriocaulon dregei, Rhodohypoxis deflexa, Sebaea repens*	3	3	35.83	Short (< 15 cm), small graminoids and forbs; mainly C_3 metabolism; very short rooting depth (< 10 cm); very low specific leaf area (2–10) and very small leaf length-to-width ratio; accumulates more above-ground than below-ground biomass. Occurs in high-altitude habitats with sandy or silty shallow soils rich in nitrogen and sulphur but low electrical conductivity, calcium and magnesium.
PFT5	*Festuca caprina, Ornithogalum paludosum, Isolepis costata, Pycreus nitidus, Thesium sp, Schoenoxiphium sp,*	6	4	51.67	Relatively small, short (< 40 cm) graminoids and forbs; mainly C_3 metabolism; shallow rooting (< 25 cm); accumulates more below-ground than above-ground biomass; low specific leaf area (5-115) and a high leaf length-to-width ratio. Occurs in both high and low-altitude habitats, with varying soil texture and nutrient levels but shallow soils, low in electrical conductivity, calcium and magnesium.
PFT6	*Carex acutiformis, Carex cognata, Cyperus congestus, C. marginatus, C. fastigiatus, Eleocharis limosa, Juncus exsertus, Merxmuellera drakensbergensis, M. macowanii*	9	3	64.17	Tall (> 40 cm) sedges and tufted grasses; both C_3 and C_4 plants; medium to deep rooting (> 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. Occurs in both high and low-altitude habitats, with varying soil texture and nutrient levels

Table 3 (continued)

Plant Functional type	Examples of plant species	No. of species	No. of plant families represented	Frequency (%) of PFT (n = 118 plots)	Growth form, other functional characteristics and environmental factors of the PFTs
PFT7	*Gunnera perpensa, Kniphofia caulescens, K. northiae, Phragmites australis, Typha domingensis*	5	4	26.67	Tall reeds, perennial and large graminoids and large forbs (> 30 cm tall); mainly C_3 metabolism; medium to deep rooting depth (> 10 cm); accumulates more above-ground than below-ground biomass; relatively high specific leaf area (50–300) and a relatively high leaf length-to-width ratio. Found in both high and low-altitude habitats with sandy or silty shallow soils high in nitrogen, sulphur, calcium, magnesium and electrical conductivity.
PFT8[a]	*Persicaria amphibia, P. decipiens, Polygonum attenuatum, P. aviculare, Potamogeton thunbergii, Rorippa nasturtium-aquaticum*	–	–	44.17	This type has a mixture of growth forms and has both C_3 and C_4 plants; occurs in a wide range of environmental conditions.

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

[a] PFT8 was not derived directly from the agglomerative hierarchical classification of plant species but was created by allocating species a priori to a new PFT to incorporate species that could not fit precisely into any of the seven PFTs

environment for growth and reproduction. Plant communities represent particular combinations of PFTs and each vegetation plot was found to represent a number of PFTs, with the exception of some plots at low altitudes that were characterised by monodominance. This is consistent with earlier findings where high-altitude montane wetlands have been reported to be characterised by higher functional diversity than those at low-altitudes (Kotze and O'Connor 2000;

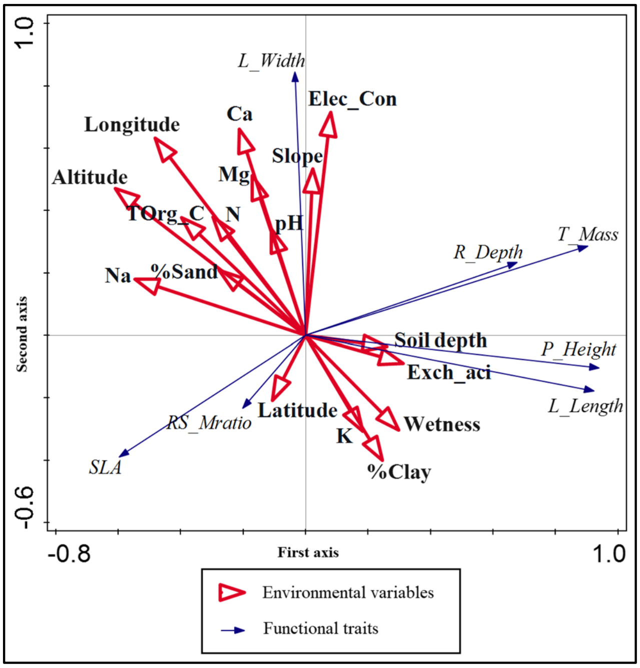

Fig. 2 Redundancy analysis (RDA) ordination diagram for community-weighted mean functional traits and environmental variables of the Afromontane palustrine wetlands in Lesotho. See Tables 1 and 2 for the abbreviations of environmental variables and functional traits, respectively

Table 4 Correlation matrix of environmental variables with the first four Redundancy ordination axes

	Axis 1	Axis 2	Axis 3	Axis 4
Longitude	-0.4631*	**0.5713****	0.0082	0.2953
Altitude	**-0.5866****	0.4259*	0.1899	0.2680
Soil depth	0.2496	-0.0326	-0.3995*	-0.1399
Exchangeable acidity	0.3011*	-0.0806	0.0381	0.1054
Calcium	-0.2040	**0.5981****	-0.0172	-0.2828
Potassium	0.1758	-0.2783	0.0327	**-0.5480****
Magnesium	-0.1634	0.4623*	-0.1511	-0.2561
Sodium	**-0.5259****	0.1622	0.0973	-0.0997
Total organic carbon	-0.2854	0.3419*	0.0966	0.0448
Nitrogen	-0.3815*	0.3412*	0.0366	0.0535
Electrical conductivity	0.0776	**0.6464****	-0.0870	0.0397
%clay	0.3358*	-0.3623*	-0.1625	-0.2515
Slope	0.0230	0.4825*	-0.1624	-0.0525
Wetness	0.2871	-0.3075*	0.1329	0.0387

The values are the product-moment correlation coefficients and significant variables are indicated with an asterisk (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). The permutation test on all the axes was significant (F = 1.3; P = 0.002)

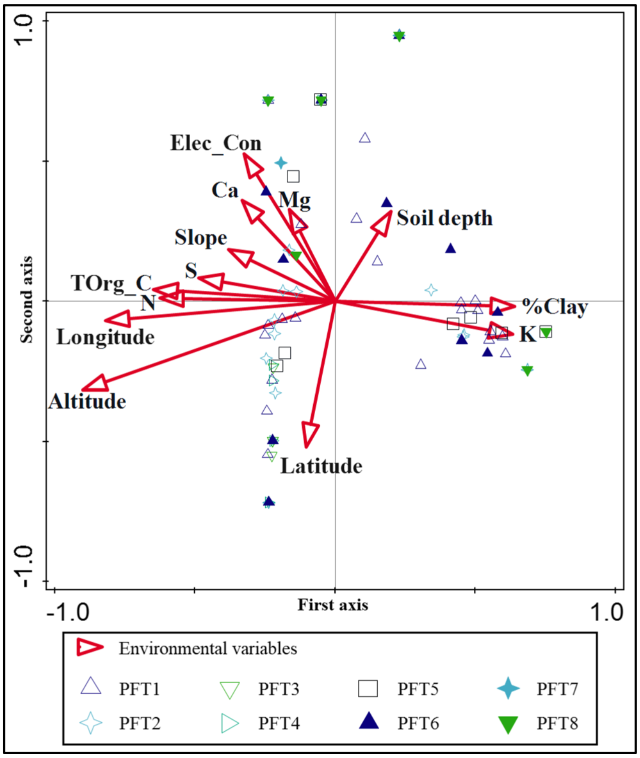

Fig. 3 Canonical Correspondence Analysis (CCA) ordination diagram for plant functional types and environmental variables of the Afromontane palustrine wetlands in Lesotho, based on the classification presented in Fig. 1. PFT stands for plant functional type. See Table 1 for the abbreviations of environmental variables

Sieben et al. 2010b). Therefore, altitude represents an important gradient, which plays a large role in regulating species composition between wetlands through its effects on habitat diversity (Shimono et al. 2010).

Table 5 Correlation matrix of environmental variables with the first four canonical correspondence ordination axes

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

The values are the product-moment correlation coefficients and significant variables are indicated with an asterisk (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). The permutation test on all the axes was significant ($F = 3.9$; $P = 0.002$)

The coexistence of different PFTs at high altitudes suggests heterogeneity in the wetland habitats in these montane areas. Because clonal dominants that are usually prominent in wetlands (Boutin and Keddy 1993) occur less prominently in high-altitude montane environments, they cannot achieve the usual dominance, leaving part of the niche space vacant, which then becomes available for colonisation by plants from other PFTs (Sieben et al. 2010b). In Lesotho, high-altitude areas are characterised by steep gradients over short distances (Pooley 2003) and these are associated with large spatial variation in physical features, resulting in an increase in niches available for different species (Kotze and O'Connor 2000). Furthermore, although the two components of ecosystem stability (resilience and resistance) are difficult to measure, the presence of species belonging to different PFTs can be considered to imply high resilience and resistance. While resistance is the capacity of an ecosystem to maintain its fundamental structure and functioning in the face of a disturbance, resilience is the ability of an ecosystem to rebound (recover) after a disturbance within a specific period of time (Díaz and Cabido 2001; Maestas et al. 2016). By contributing to the redundancy of important ecosystem functions, species with different requirements and tolerances (i.e. representing different PFTs) provide "insurance" to the ecosystem, thus increasing resilience of the system (Walker et al. 1999; Díaz and Cabido 2001). Díaz and Cabido (2001) also report that the resilience and resistance of ecosystems can be determined by the traits of the dominant plant species, where communities dominated by fast-growing plants tend to have high resilience and low resistance.

Higher SLA was found to be associated with high-altitude wetland habitats. While higher values of SLA are associated with rapid acquisition of resources, lower values are associated with a conservative strategy (Pla et al. 2012). Plant communities in high-altitude areas have been reported to be dominated by species with a conservative attribute, while low altitudes tend to select for species with an acquisitive attribute (Pla et al. 2012). This reflects the contrast between plant species found in high- and low-altitude areas in terms of their role in ecosystem functioning. Because differences in functional types lead to differences in ecosystem services (Roscher et al. 2012; Sieben et al. 2017b), a variation is expected in the ecosystem services delivered most by high-altitude and low-altitude wetland ecosystems. The functioning of a species in an ecosystem is determined mainly by its capacity to capture and conserve resources, or to cope with competition and other environmental stresses (Lepš et al. 2006). This further implies that high SLA can be associated with low temperatures and high rainfall in Lesotho, conditions that characterise most of the areas. These results are consistent with Díaz and Cabido (1997) who found that high SLA also was a common trait in the montane grasslands of central-western Argentina, where the altitudinal range is comparable to that in Lesotho. Because of their links to relative growth rate, SLA and leaf dry mass have been reported to indicate specific annual net primary productivity (Garnier et al. 2004).

The negative correlation between SLA and leaf dry matter content, evident in the current study (Fig. 2), also occurs in cool-temperate herbaceous species (Pérez-Harguindeguy et al. 2013). Specific leaf area, as a proxy for relative growth rate, can also be an indicator of the competitive ability (Weiher et al. 1999) and stress tolerance (Grime et al. 1997) of a plant species. While SLA is a good surrogate for the ability of a plant to use light efficiently, plant height is a good proxy for the ability to compete for light (Weiher et al. 1999). However, the pattern of high SLA being associated with high-altitude environments found in the current study is contrary to the reports of it being associated with low altitudes (Pla et al. 2012). This is probably found because the high-altitude soils in Lesotho, which are associated with the basaltic parent material, are nutrient-rich while the sandstone-derived low-altitude soils are nutrient-poor (Mucina and Rutherford 2006). Hence, the altitudinal gradient in the context of Lesotho is actually a composite gradient as it also reflects a contrast in substrate. The association of high SLA and low leaf dry mass with nutrient-rich soils found in this study is consistent with Gaucherand and Lavorel (2007) who report that fast-growing species in nutrient rich habitats usually exhibit both high SLA and low leaf dry matter content. Plants growing in nutrient-rich habitats tend to have increased resource acquisition.

Weiher et al. (1999) highlight that competitive ability is strongly associated with plant height and above-ground biomass. Thus, the negative association between root/shoot mass ratio and total biomass suggests that wetland plant species that accumulate less total biomass tend to allocate more of their resources towards root development and are characterised by reduced fecundity, a situation that is expected at high altitudes. The increase in plant rooting depth with increasing shoot mass and height highlights the need for a reliable supporting below-ground material when the shoot becomes large, which occurs at lower altitudes. Nonetheless, in wetlands rooting depth is often constrained by anoxic conditions and most wetland plants at high altitudes are small. The decrease in plant height (dwarfism) with increasing altitude represents typical plant adaptations to the coldness associated with high-altitude montane environments (Sieben et al. 2010b; Dainese et al. 2015). The current study also confirms that cold stress and high radiation stress, often associated with high-altitude areas, tend to select for small leaves (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013). In spite of increasing SLA with increasing altitude, most likely explained by more nutrient-rich soils at higher altitudes, typical high-altitude adaptations (lower plant height and smaller leaves) were observed in parallel.

Habitat Filtering and Niche Differentiation

One important result of abiotic filtering is the change in species composition and community averaged functional traits along environmental gradients (Kraft and Ackerly 2014) and this is evident in the current study. In this study, taxonomic diversity within PFTs was high as evidenced by the representation of at least three families in each PFT. This suggests the role of environmental filtering rather than phylogeny in wetland habitat colonisation and functional trait development (Reich et al. 2003; Roy et al. 2019). Dainese et al. (2015) suggest the possibility of evolutionary convergence of high-altitude plant species, whereby species with different evolutionary origins show similar functional adaptations to colder environments. There is evidence of variation in plant functional traits being strongly constrained by convergent evolution (Reich et al. 2003). The conditions of anoxia, low temperatures and low pH, which are associated with high-altitude wetland environments, tend to increase habitat filtering that species have to overcome in order to establish. This affects traits, including those that are related to the interception of light, such as SLA. The high taxonomic diversity within PFTs in this study contradicts the findings of Díaz and Cabido (1997) in Argentina as they report a lack of independence between PFTs and taxonomic affiliations. In the Andes, some functional types were dominated by a single plant family (Díaz and Cabido 1997).

Prolonged waterlogging of the substrate, which causes anoxia in the soil and concomitant chemical changes, excludes a large range of plant species (Mitsch and Gosselink 2015). Because of the effect of habitat filtering, dominant plant species in a community exhibit traits that are supported by habitat conditions (Maire et al. 2012). Grime (1998) highlights that, even in species-rich vegetation, most of the biomass is accounted for by only a small number of dominant species whose functional traits have an overriding influence in the community and its functioning. The biomass ratio hypothesis states that the degree to which the traits of a species influence ecosystem properties and functioning depends on the abundance of the species in the community (Gaucherand and Lavorel 2007; Garnier and Navas 2012).

In communities, some species are driven to converge toward an optimum trait value by habitat filtering and thus become functionally similar (Maire et al. 2012; Kraft and 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). Most of the wetland plant communities in the current study exhibit resource partitioning for coexistence. 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 corroborates the two opposite niche-based deterministic processes: habitat filtering that predicts that most coexisting species should exhibit similar traits; and niche differentiation that requires coexisting species to display dissimilar traits for coexistence (Maire et al. 2012). However, the latter process is more dominant than the former in the study area as evidenced by most of the vegetation plots displaying a combination of different PFTs.

Conservation Implication and Impact of Climate Change

Traits such as leaf size, plant height and root architecture that respond to changes in temperature or moisture availability can also be used to predict how plant species respond to climate change (Garnier and Navas 2012). Widespread ecological transitions are predicted to occur at high elevations as montane regions display greater sensitivity to climate change (Ryan et al. 2014). With climate change predictions indicating that a greater part of southern Africa will become drier (Mitchell 2013) and that by 2025, Lesotho will become water stressed (SADC 2008), changes in wetland plant species and functional composition are expected, with concomitant changes in ecosystem processes and functioning. The high-altitude wetland communities in the country, currently dominated mainly by PFT1, PFT2, PFT3 and PFT4, will likely experience significant reductions in their cover and abundance as the climate changes, resulting in changes to the overall wetland functioning (e.g. primary productivity and nutrient cycling) and ecosystem service delivery. Furthermore, given that some of the wetland PFTs are associated with communities that mainly occur at the summit plateau, they may disappear altogether in the face of climate change (Lee et al. 2015). A recent study has also predicted community compositional changes in Lesotho because of the contraction in the range of montane plant species and the movement to higher altitudes as the climate changes (Bentley et al. 2019). The dominance of C_3 photosynthetic pathway, currently characterising the high-altitude wetland plant communities in the study area (Chatanga and Sieben 2019), coupled with the dominance of this metabolism in most of the PFTs (evident in the current study), further highlights that the montane wetland vegetation in Lesotho faces a real threat as the climate changes, in terms of functioning. The abundance of C_3 plants will decrease with climate change as they will likely be replaced with C_4 plants, particularly for graminoids.

This study has demonstrated variation in wetland plant functional traits and functional composition of communities along environmental gradients, which are spatial, topographic and edaphic. The identification of groups of plants that are critical in controlling the functioning of wetland ecosystems is important because functional composition is a good indicator of ecosystem health (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 of organisms that influence the ecosystem processes. This is particularly so in Lesotho where the wetlands play a large role in providing a wide spectrum of ecosystem services, including water resources, livestock grazing, biodiversity conservation and crop cultivation (Chatanga 2019). In terms of biodiversity conservation and water resources, these montane wetlands are not only important locally (in Lesotho) but are also of international importance as they are located in the catchment of one of the most important and shared transboundary river systems in southern Africa (the Senqu-Orange River). This river is important for Lesotho, South Africa and Namibia. The wetlands also support the Lesotho Highlands Water Project (LHWP) dams that supply freshwater to Gauteng, the most industrialised and populated province of South Africa. The LHWP is the largest international water transfer scheme in the world (Meakins and Duckett 1993; Earle and Bazilli 2013).

The situation described above indicates that the wetlands in Lesotho play an important role in water resources, biodiversity conservation and the provision of other ecosystem services in southern Africa. This highlights that these wetlands have a high conservation value in the region, especially in the face of increasing water scarcity, biodiversity loss and climate change. Thus, given that functional composition is the major determinant of ecosystem processes, this study can contribute to the information needed for biodiversity conservation planning and sustainable provision of wetland ecosystem services in the country and beyond.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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