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High-altitude wetland vegetation of Bokong Nature Reserve in Matšeng Biosphere Reserve, Lesotho

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Bokong Nature Reserve (BNR) forms part of the core of the first and newly established Matšeng Biosphere Reserve in Lesotho. However, lack of baseline data makes it difficult to monitor the wetland vegetation in BNR. This study characterised the vegetation of the high-altitude montane palustrine wetlands of this area. Plant species composition was assessed using the Braun-Blanquet approach, and the height and cover of the vegetation were measured. Furthermore, environmental data were collected using standard methods. The data were analysed by determining species richness and calculating Shannon-Wiener diversity and evenness, as well as employing cluster analysis, canonical correspondence analysis and redundancy analysis. The results show that a total of 175 plant species from 102 genera and 40 families were encountered. The dominant plant families were Asteraceae, Poaceae and Cyperaceae. Hierarchical cluster analysis produced 10 plant communities in the range of 1–36 species per 3 m × 3 m plot. Important environmental factors influencing the wetland vegetation were longitude, altitude, latitude, soil sodium, inundation, soil texture, soil magnesium and soil phosphorus. The results indicate that the wetlands are not only in a relatively stable condition, but also support diverse vegetation and store a substantial amount of carbon, thus contributing to biodiversity conservation and climate change mitigation. Because the wetland vegetation determines the functioning of the system, which in turn influences the supply of ecosystem services, our findings form a baseline dataset for monitoring the BNR wetland vegetation, especially in the face of climate change.

Conservation implications: The BNR wetlands fall within the catchment of the Lesotho Highlands Water Project dams that are important for water resources in southern Africa. Furthermore, the wetlands are of international conservation value because they form part of the core of a UNESCO-declared man and biosphere reserve and play an important role in supporting biodiversity.

Keywords: biodiversity conservation; climate change; ecosystem service; Maloti-Drakensberg; Matšeng Biosphere Reserve; plant community; protected areas; water resources; wetland vegetation.

Introduction

Mountainous regions harbour high-altitude palustrine wetlands that play an important role in supporting biodiversity and in serving as water sources for downstream communities and ecosystems. Such wetlands are usually rich in endemics, because many species remain isolated at the high altitudes (Junk et al. 2013; Sharma, Chettri & Oli 2010; Sieben et al. 2021a). They are also important repositories for many threatened and rare high-altitude montane species (Jayachandran 2013). Furthermore, high-altitude palustrine wetlands supply many ecosystem services that sustain human life, including mitigating climate change impacts and contributing to water, food and environmental security (Singha 2011). Because they are located in headwaters, high-altitude montane palustrine wetlands are important to the ecology and hydrology of the local environment and downstream river systems and streams whose origins are in the mountains (Joyce, Simpson & Casanova 2016; Mitsch, Bernal & Hernandez 2015). These wetlands are also of international importance because they provide water for many transboundary rivers (Chatterjee et al. 2010) such as the Senqu-Orange River and the Limpopo River in southern Africa. Per unit area, wetland ecosystems provide services that are typically higher than those of terrestrial ecosystems, including forests (CBD Secretariat 2015; Ramsar Convention on Wetlands 2018).

Vegetation is the most conspicuous and ubiquitous feature in montane palustrine wetland systems, playing a key role in the functioning of these ecosystems (Cronk & Fennessy 2001).

Note: Additional supporting information may be found in the online version of this article as Online Appendix 1.

The composition of vegetation is influenced by, and influences, wetland hydrology and edaphic factors such as soil organic carbon and nutrient content (Mitsch & Gosselink 2015). Plants are the most widely recognised biotic indicator for the condition of a wetland (Chatanga & Sieben 2019; Collins 2005; DWAF 2004). Because wetland vegetation composition and structure are salient features that contribute towards forming habitats for animals, the description of plant communities is often used as a surrogate for wetland biodiversity (Sieben et al. 2016). The description of wetland habitats on the basis of their vegetation and the subsequent wetland classifications can play an important role in strategic planning for the conservation of palustrine wetlands (Mitsch & Gosselink 2015). Knowledge about the variation in wetland vegetation, coupled with an understanding of the major drivers of this variability is one of the key requirements for the successful management and conservation of wetlands.

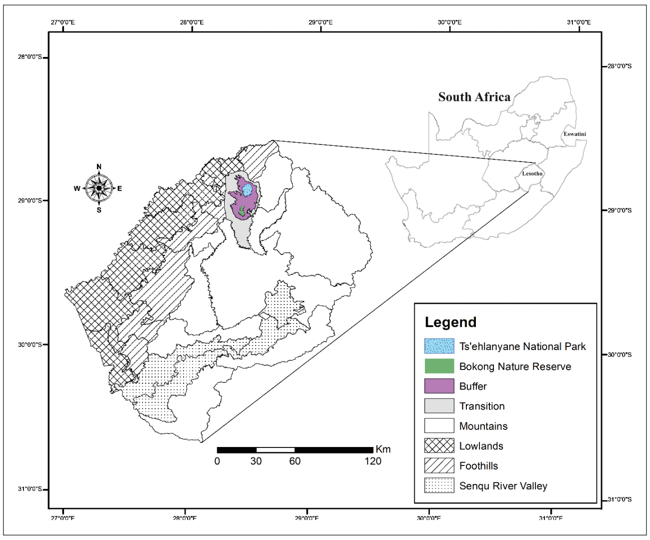


FIGURE 1: Map of Lesotho showing the location of Bokong Nature Reserve in Matšeng Biosphere Reserve and the agro-ecological zones.

Bokong Nature Reserve (BNR) (1970 ha) and Tšehlanyane National Park (5600 ha) are the two protected areas that form the core of the recently declared and first man and biosphere reserve in Lesotho – Matšeng Biosphere Reserve (MBR) that is located in the northern part of the country (Figure 1). Situated in the highlands ecological zone in the Maloti-Drakensberg Mountains, the MBR was nominated by the United Nations Educational, Scientific and Cultural Organization (UNESCO) on 15 September 2021. The biosphere reserve is composed of three zones (UNESCO 2021): (1) core areas (7570 ha), which are strictly protected zones, contributing to the conservation of genetic, species, ecosystem and landscape diversity; (2) a buffer (31 050 ha), which surrounds the core areas, and is used for activities compatible with sound ecological practices that can foster scientific research, monitoring, education and training; and (3) a transitional zone (66 577 ha), which is where communities around the biosphere foster socio-culturally and ecologically sustainable economic and human activities (Figure 1). In terms of its altitude, BNR is one of the highest protected areas (nature reserves) in Africa, lying at the top of Mafika-Lisiu Pass and reaching altitudes that exceed 3000 metres above sea level. Although few wetlands exist in Tšehlanyane National Park (which is located at a lower altitude) because of its terrain, an extensive network of high-altitude palustrine wetland habitats occurs within BNR (Chatanga & Seleteng-Kose 2021). These BNR wetlands form part of the catchment of the Katse Dam, which is important for the Lesotho Highlands Water Project (LHWP). The LHWP is the largest international water transfer scheme in the world, which transfers fresh water from Lesotho to the most industrialised and densely populated Gauteng province of South Africa (Earle & Bazilli 2013). Compared to the wetlands in the rest of the catchment, the BNR wetlands represent a relatively minimally disturbed state.

Falling within the Katse Dam catchment, the BNR was established in 1992 as part of the LHWP. The 2021 declaration by UNESCO of the Man and Biosphere Reserve enhanced the protection of BNR. The wetland vegetation of BNR has, to date, been poorly studied with only two previous studies attempting to carry out vegetation assessment (Chatanga & Sieben 2019; Seleteng-Kose et al. 2021). Chatanga and Sieben (2019) assessed one wetland as part of a nationwide study, whereas Seleteng-Kose et al. (2021) conducted a study to inform the nomination process of MBR. The focus of the latter was on general biodiversity, paying only cursory attention to the wetland vegetation, wherein only five plant species were reported in the wetlands. The aim of the current study was to provide a comprehensive characterisation of the vegetation, including the vegetation–environment relationships, of the high-altitude montane palustrine wetlands within BNR. This study is valuable because it will provide the baseline data required for future monitoring of the wetlands. This will enable long-term monitoring of the plants that are regarded as characteristic of BNR wetlands, allowing the detection of significant changes that may occur in the wetlands. Information obtained will also be used in studies that quantify the effect of anthropogenic pressure on the wetlands outside the protected area within the Katse Dam catchment.

Research methods and design

Study area

The study was conducted in BNR in Leribe District, Lesotho. The following description of the study area was obtained from the BNR integrated management plan (MTEC 2021). The BNR occupies an area with an altitude range of 2600 m – 3200 m above sea level, making it one of the highest protected areas in Africa. Generally, there are two major seasons in Lesotho; summer (October to April) and winter (May to September). Because of its high altitude, BNR experiences extreme temperature and precipitation changes. Annually, BNR receives an average of 1200 mm – 1500 mm of rain, 80% of which falls during the summer season. Snowfall is also common during the winter season. In addition to the summer rain and winter snowfall, mist contributes up to 20% of the annual precipitation. Although there are no specific temperature records for BNR, data from similar areas in Lesotho show that they experience summer temperatures ranging 2°C – 22°C and winter temperatures between –3°C and 13°C. Strong and cold winds are common in winter, while warm winds are experienced from August to October. In terms of flora, BNR harbours unique vegetation known as the Drakensberg alpine tundra, which is restricted to the alpine belt of the Maloti-Drakensberg Mountains. The vegetation is characterised by the temperate plateau grasslands dominated by grass species of *Merxmuellera* and *Pentaschistis*, as well as low shrub heath communities dominated by species of *Erica* and *Helichrysum*.

Study design

A reconnaissance survey was conducted to get a sense of the distribution, extent and vegetation of the wetlands in BNR. Although most of the habitats in BNR have wetland characteristics, the study focussed on the four largest wetlands that were representative of the wetlands in the study area. Sampling was conducted in the wet (summer) season, during March 2022. A stratified random sampling approach based on vegetation types was adopted where 3 m × 3 m representative vegetation sampling plots were laid randomly in each visually distinct vegetation type. A total of 70 vegetation plots were laid in the observable distinctive and homogenous habitats of the wetlands (11 in the first wetland, 29 in the second, 20 in the third and 10 in the fourth wetland).

Collection of vegetation and environmental data

Species composition was determined in each plot by identifying all species present and estimating their cover using the Braun-Blanquet approach on a nine-class cover-abundance scale (Omar, Maroyi & Van Tol 2016; Van Der Maarel 1979). Average vegetation height in each plot was also estimated using a measuring tape, while the total vegetation cover was visually estimated. Botanical field guides (Pooley 1998, 2003; Van Oudtshoorn 2014) were used to help in identifying plant species during the field assessment. In addition to the plot-based data, as much of the wetland as possible was surveyed to record all plant species occurring in the wetland but not encountered in the plots. This provided an estimate of the total number of species occurring in each wetland. However, the latter provided information on the presence of the species in the wetlands but did not include the determination of their abundances.

Data about environmental variables (Table 1) were also collected in each plot. Soil samples were collected from the first 15 cm of the topsoil (which is the herbaceous vegetation rooting zone) at the centre of the plot using a Dutch soil auger. Soil depth was determined at the centre of each plot by driving the auger until the bed rock was hit or a depth of 120 cm was reached, which was the length of the auger. The same auger hole was used to determine water table depth. In the case of inundation, the water column depth was determined using a steel measuring tape. The soil samples were later air-dried for a minimum of 48 h until they were a constant weight. Dried soil samples were analysed for different variables (Table 1) (Stohlgren et al. 1998). The soil sample analyses were conducted by the Analytical Laboratory Services of the Institute for Commercial Forestry Research in Pietermaritzburg, South Africa. The methods of measurement of environmental and soil variables are summarised in Table 1.

Data analysis

Plant diversity analysis

The data for both vegetation and environmental variables were captured in Microsoft Excel, and the Braun-Blanquet vegetation cover-abundance estimation values were converted into percentage cover (Mueller-Dombois & Ellenberg 1974; Omar et al. 2016; Van Der Maarel 1979). The frequency of occurrence of each plant species across all the plots was calculated. Dominance, in terms of the number of species encountered, of each plant family in BNR wetlands was also calculated by expressing the number of species of a given family as a fraction of the total number of species encountered. For each vegetation plot, plant species were listed, and species richness, Shannon-Wiener index of diversity (H') and evenness index (E) were determined (Ludwig & Reynolds 1988). The relative abundance of species i in each plot (p_i) was used in the calculation of H' and E, using the formulae (Ludwig & Reynolds 1988):

TABLE 1: Geographical and environmental variables assessed and included in the analysis of wetland vegetation of Bokong Nature Reserve wetlands.

Variable	Method of measurement or tool	Units	Abbreviations
Altitude	GPS device (Garmin eTrex 30x)	Metres	Altitude
GPS coordinates	GPS device (Garmin eTrex 30x)	Degrees	Longitude; Latitude
Soil depth	Soil augering (Dutch auger)	cm	Soil depth
Inundation depth or water table[a]	Depth of water column or depth of water table	cm	Inundation
Soil texture[b]	Gravimetric pipetting method	%	%Clay; %Silt; %Sand
Exchangeable acidity[b]	Titration method	mmol/100 g	Ex. Acid
Soil pH[b]	Water extraction	n/a	pH
Phosphorus[b]	Bray 11 method	mg/kg	P
Nitrogen[b]	LECO analysis	%	N
Sulphur[b]	LECO analysis	%	S
Loss on ignition[b]	Combustion	%	LOI
Total organic carbon[b]	Walkley-Black method	%	TOC
Major cations[b]	Ammonium acetate extraction; measurement on plasma atomic absorption spectrometer	cmol/kg	Ca; Mg; K; Na
Electrical conductivity (EC)[b]	Water extraction of soil; EC measured on filtrate using conductivity metre	uS/cm	EC

GPS, Global Positioning System; LECO, Laboratory Equipment Corporation; cmol, centimoles; uS, microsiemens.

[a], Inundation represents both inundation depth (positive) and water table depth (negative), following Chatanga and Sieben (2019).

[b], Variables analysed at the laboratory.

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

$E = \frac{H'}{\ln S}$ where *S* is the number of species.

While only the vegetation data were imported into PC-Ord 6.0 (Mjm Software Design, Gleneden Beach, OR, United States), both vegetation and environmental data were imported into Paleontological Statistics (PAST) 4.04 and CANOCO 5.15 (Microcomputer Power, Ithaca, NY, United States) programs for analyses.

Classification and indicator species analysis

To objectively determine the plant communities found in the palustrine wetlands of BNR, the vegetation abundance data were analysed using agglomerative hierarchical cluster analysis (HCA) and indicator species analysis (ISA) in the PC-Ord Program, version 6.0. The HCA classifies vegetation plots into statistically recognised communities on the basis of their similarities in species composition and abundance (McCune & Mefford 2011; Van Tongeren 1995). Given that plant species composition and abundance are determined by, and reflect their habitat, the classification and description of vegetation elucidate the vegetation–environment relationships and provide information for the interpretation of the spatial variation between plant communities (Clegg & O'Connor 2012). Various combinations of similarity indices and linkage methods that are available in the PC-Ord program were tested, and the Sørensen's Similarity Index and Ward's linkage method produced the best interpretable and clearly defined clusters. Thus, a combination of Sorensen Similarity Index and Ward's linkage method was used to produce the clusters, and the procedure for the classification and species indicator analysis followed Chatanga and Sieben (2019). The Sørensen (Bray-Curtis) similarity index is a good measure of distance for community data and remains sensitive in heterogeneous data sets, reducing the influence of outliers by giving them less weight (McCune & Mefford 2011).

By iteratively classifying the vegetation plots (each time with a different number of clusters and recording the average indicator species *p*-values), ISA was used to determine the number of clusters in the resulting dendrogram. The number of clusters that resulted in the lowest average *p*-value was taken to be the best in providing the number of communities (Peck 2010) present. From this analysis, species whose indicator values were greater than 20 and statistically significant ($p \leq 0.05$) in the Monte Carlo permutation test were recorded for each of the plant communities obtained. The plant species that were dominant in each of the resulting communities were determined from the species cover abundance data. Species that were considered dominant were those whose abundances were at least 38%, which correspond to Braun-Blanquet cover classes 3, 4 or 5. The communities were named using the two most dominant species of each plant community where the second most dominant species became the first part of the community name, while the most dominant became the second part of the name (Brown et al. 2013; Chatanga & Sieben 2019). The median and range for diversity indices (species richness, Shannon index and evenness) and averages for the height and cover of the vegetation were determined for each community obtained from the classification. Mann–Whitney pairwise tests (using Bonferroni corrected *p*- values) and boxplot analysis were then conducted in PAST 4.04 to compare the wetland plant communities obtained from the HCA in terms of their vegetation and all environmental attributes.

Ordination

To explore the plant community–environment relationships, the data on vegetation and environmental variables were analysed using canonical ordination. The main objective of conducting canonical ordination was to detect the major patterns in the relationships of communities and vegetation attributes with their environment (Ter Braak 1995). The canonical ordination was performed in CANOCO, Version 5.15 (Ter Braak & Šmilauer 2018). While plant community–environment relationships were assessed using canonical correspondence analysis (CCA), the relationship of the measures of plant diversity and structure with the environmental factors was explored using redundancy analysis (RDA). The CCA and RDA can be used to explore patterns of variation in data between species that can be best explained by the supplied explanatory variables (McGarigal, Cushman & Stafford 2000). Because the species abundance data were skewed (most values less than 30%), both CCA and RDA were performed on log-transformed percentage vegetation data. The CCA was chosen for ordination because the species abundance data were compositional, unimodal and the gradient was greater than four standard deviation units, while RDA was selected because the data on plant diversity and structure of the community (height and percentage cover) followed a linear regression model (Lepš & Šmilauer 2003; Ter Braak & Šmilauer 2018). The less significant explanatory variables were excluded by forward selection during ordination and the statistical significance of the relationship of communities with environmental variables was tested using the unrestricted Monte Carlo permutation test found in CANOCO with 499 runs (Ter Braak 1995).

Ethical considerations

No ethical considerations were necessary for the study. However, because the study was conducted in a protected area, a research permit was sought and granted from the Department of Environment in Lesotho.

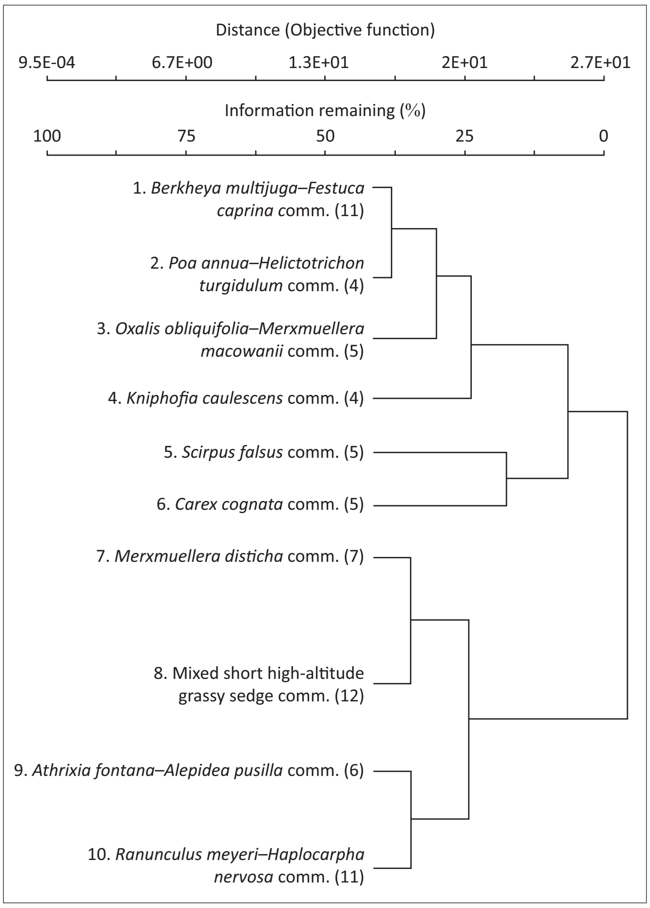
Results

A total of 175 plant species from 102 genera and 40 families were recorded in the high-altitude palustrine wetlands of BNR (Online Appendix 1 - Table 1–A1). Among them was one alien species (*Hypochaeris radicata*), which has naturalised in Lesotho. While 135 species were recorded in the vegetation sampling plots, 40 species were found to occur in the wetlands outside the plots (Online Appendix 1 - Table 1–A1). The 10 most frequently occurring species, on the basis of the proportion of plots in which they were recorded in the wetlands, were *Oxalis obliquifolia* (58.57%), *Senecio macrocephalus* (54.29%), *Athrixia fontana* (51.43%), *Merxmuellera disticha* (50.00%), *Alepidea pusilla* (45.71%), *Haplocarpha nervosa* (44.29%), *Festuca caprina* (42.86%), *Koeleria capensis* (38.57%), *Poa binata* (34.29%) and *Ranunculus meyeri* (34.29%) (Online Appendix 1 - Table 1–A1). The 10 most dominant plant families in terms of number of species encountered were Asteraceae (21.14%), Poaceae (16.00%), Cyperaceae (11.43%), Scrophulariaceae (5.71%), Crassulaceae (4.00%), Orchidaceae (3.43%), Iridaceae (2.86%), Asphodelaceae (2.29%), Campanulaceae (2.29%) and Ericaceae (2.29%). Species richness ranged from 1 (monospecific) to 36 (more diverse) ($\bar{x}$ = 14.49; CV = 47.32%) in the vegetation plots, although only a few plots were monospecific. Shannon-Wiener diversity was found to be in the range of 0–2.97 ($\bar{x}$ = 1.79; CV = 32.66%) per plot, while species evenness ranged from 0 to 0.86 ($\bar{x}$ = 0.69; CV = 15.47%). In terms of structure, the height of the vegetation was 2–70 cm ($\bar{x}$ = 33.71; CV = 58.10%), while its cover was 30% – 100% ($\bar{x}$ = 89.29; CV = 16.08%).

Hierarchical cluster analysis of the vegetation plots produced 10 distinctive wetland plant communities with median species richness ranging from 4 to 18 species per plot (Figure 2). Each of the 10 communities is characterised by dominant species, indicator species and the fidelity of the indicator species to the communities (Online Appendix 1 - Table 2–A1). The synoptic table for the communities, presented in Online Appendix 1 - Table 3–A1, shows that, while some of the species occur in almost all the vegetation plots, others occur in only a few or outside the plots. Furthermore, some species occur in all the plots in a given community. Online Appendix 1 - Figure 1–A1 presents the box and whisker plots comparing the 10 wetland plant communities in terms of species richness, Shannon-Wiener diversity, evenness, vegetation cover and vegetation height. The plant communities displayed clear variation with respect to height, cover and diversity; some are quite diverse (36 species) and others monospecific (Online Appendix 1 - Table 4–A1). Samples of the communities are also shown pictorially in Figure 3. Online Appendix 1 - Table 4–A1 further describes the 10 plant communities recorded in the BNR wetlands with respect to their dominant species, cover, height, species richness, Shannon-Wiener diversity, evenness and environmental factors. The 10 plant communities obtained in this study are associated with different environmental conditions in the wetlands (Online Appendix 1 - Table 4–A1 and Online Appendix 1 - Figure 2–A1). However, in terms of edaphic factors, only soil magnesium content showed significant differences for Mann–Whitney pairwise comparison and this was between the following: Communities 1 & 8 (p = 0.035), and 1 & 10 (p = 0.046).

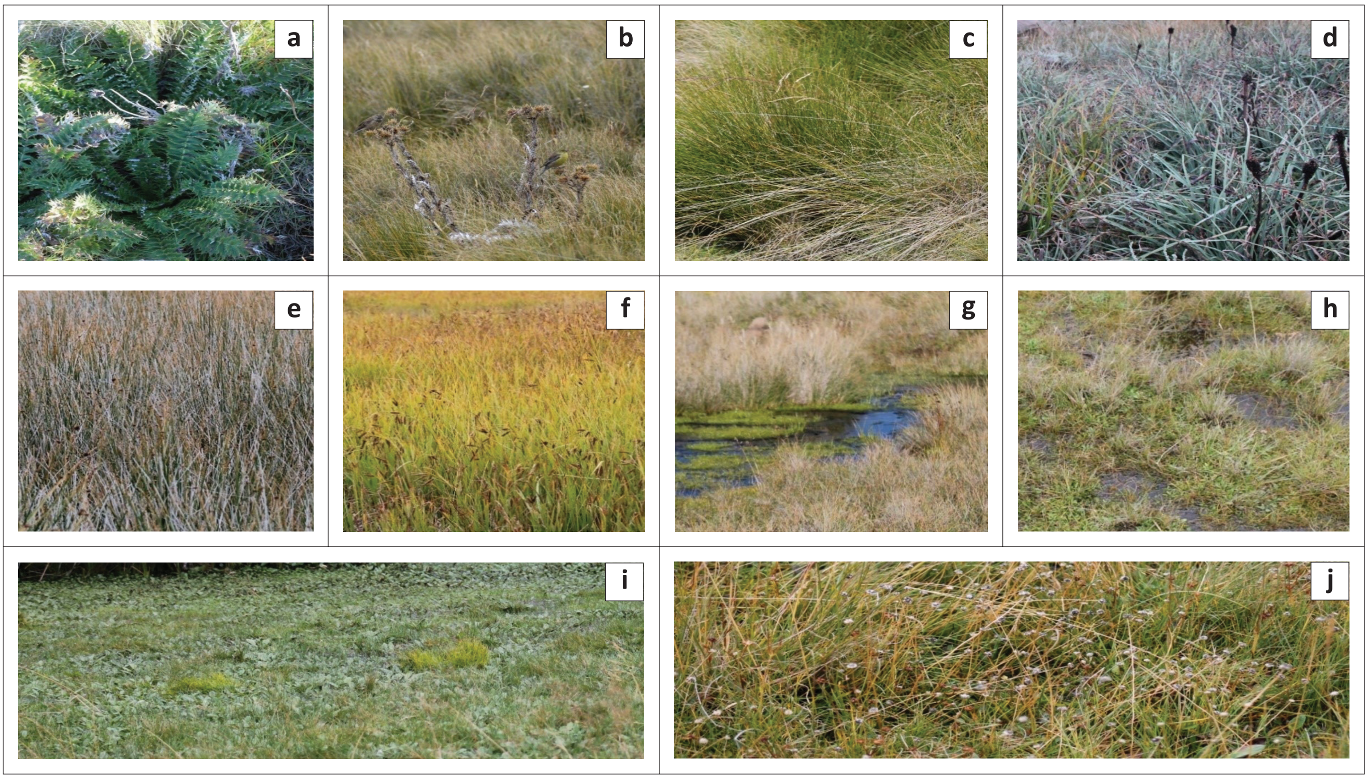
The altitudinal range of the wetland vegetation described in BNR is 2858 m – 3007 m above sea level (Online Appendix 1 - Table 5–A1). The depth of the soil in the BNR wetlands was in the range of 8 cm – 120 cm, while the textural properties of the top soil (at 0 cm – 15 cm below the soil surface) reflect a silt loam textural classification as indicated by the analysis of the size of the particles. The wetland soils were high in total organic carbon (TOC) (up to 27.16%), cations and electrical conductivity (EC) but low in total nitrogen (TN) and phosphorus (P). However, calcium (Ca) was much higher than the other base cations in these wetlands. The soil water regime was characterised by relatively uniform water table levels in the wetlands, and this was reflected by the low standard deviation for inundation. The inundation depth indicates that, while some wetland parts had a water column with a height of up to 30 cm above the ground, others had a water table 40 cm deep. The soil pH ranged from 5.05 to 6.22.

The total variation in the CCA ordination of the plant communities with all environmental variables (except nitrogen, exchangeable acidity and loss on ignition) was 7.97 and the environmental variables supplied accounted for 37.60% of this variation. The permutation test showed that the model was significant (F = 1.40, p < 0.01), meaning that the environmental variables were significantly related



Note: The number of plots for each community is given in brackets. 'Comm.' means community.

FIGURE 2: Dendrogram showing plant communities of the palustrine montane wetlands of Bokong Nature Reserve in Matšeng Biosphere Reserve, Lesotho.



Source: Photographs taken by K. Kobisi (19–29 March 2022)

FIGURE 3: Plant communities occurring in the palustrine wetlands of Bokong Nature Reserve in Lesotho. (a) *Berkheya multijuga–Festuca caprina* community; (b) *Poa annua–Helictotrichon turgidulum* community; (c) *Oxalis obliquifolia–Merxmuellera macowanii* community; (d) *Kniphofia caulescens* community; (e) *Scirpus falsus* community; (f) *Carex cognata* community; (g) *Merxmuellera disticha* community; (h) Mixed short high-altitude grassy sedge community; (i) *Athrixia fontana–Alepidea pusilla* community; (j) *Ranunculus meyeri–Haplocarpha nervosa* community.

to the community data. The first axis is positively correlated with longitude, percentage silt, phosphorus and potassium content but negatively related with altitude, latitude and percentage sand (Figure 4). Communities that are located on the right side of the y-axis of the ordination diagram (communities 2, 4, 5 and 6) are associated with lower-altitude wetland habitats that are on the eastern parts of BNR and have deep soils that are high in silt and phosphorus. Communities on the left side of the y-axis of the ordination diagram (communities 7, 8 and 10) are associated with sandy soils in higher-altitude wetland habitats that are located in the northern parts of BNR. The second axis of the ordination diagram can best be explained by sodium, inundation and magnesium. Thus, communities such as 1 and 3 are associated with wetland habitats that have a deeper water table and soils that are high in magnesium and low in sodium, sulphur, EC and clay content. However, communities 9 and 10 are associated with inundated soils that are high in sodium, sulphur, EC and clay content.

The RDA ordination diagram of plant diversity and community structure measures with environmental factors is presented in Figure 5. The total variation in the RDA ordination of plant diversity and community structure measures with explanatory variables was 63.80, and the explanatory variables included accounted for 51.30% of the total variation. The permutation test demonstrated that the model was statistically significant ($F = 2.40$, $p < 0.01$), and that all the assessed environmental conditions influenced plant diversity and community structure in the BNR wetlands. Measures of plant diversity (richness, Shannon-Wiener and evenness) were positively correlated with altitude, latitude, soil pH and percentage sand. Higher wetland plant diversity is associated with higher altitudes in the northern and western parts of BNR. Higher wetland vegetation cover is associated with lower altitude habitats with deep clayey soils that are higher in TOC and EC in the eastern parts of the BNR. Taller wetland vegetation is associated with habitats that have less inundated soils that are high in magnesium and Ca but low in sodium content.

Discussion

The montane palustrine wetlands in the Maloti-Drakensberg area are reported to produce unique habitats because they are located on slopes, which makes them distinct from wetlands in other areas (eds. Mucina & Rutherford 2006). These palustrine wetlands in the high-altitude areas of Lesotho are reported to exhibit habitat heterogeneity, and consequently harbour high plant diversity (Chatanga & Sieben 2020). This study provides a comprehensive assessment of the high-altitude montane palustrine wetlands of BNR by describing and classifying the wetland vegetation as well as determining the vegetation–environment relationships. This is important because it provides baseline information about wetland vegetation, which will enable future monitoring. Furthermore, it provides a sense of the extent to which the system can

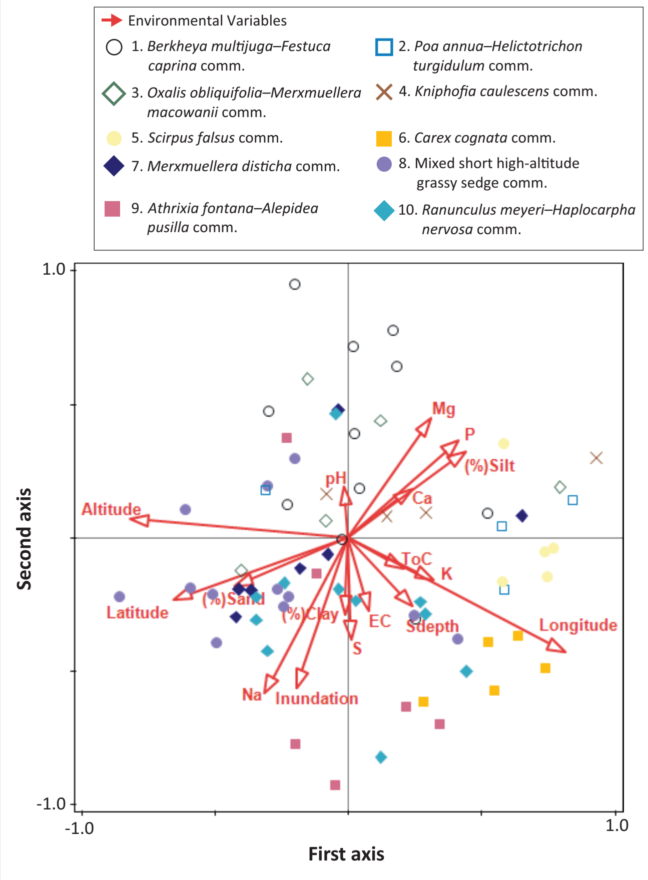


FIGURE 4: Canonical correspondence analysis ordination diagram showing plots (N = 70) and their communities described by the species composition (species descriptors are not represented) in the montane palustrine wetlands of Bokong Nature Reserve in Matšeng Biosphere Reserve, Lesotho, using the same classification presented in Figure 2. Environmental variables are given as explanatory variables.

supply ecosystem services because vegetation determines the functioning of the system, which in turn influences the wetland capacity to supply ecosystem services (Cronk & Fennessy 2001; Gopal 2016).

The current study identified a total of 175 plant species in four wetlands, which is much higher than what was recorded by Seleteng-Kose et al. (2021), who focussed on the general biodiversity of the entire MBR. They reported the existence of only five notable plant species in the wetlands without further details on the other wetland plant species. Interestingly, the current study that focussed on the core part of the MBR, did not record two of the species reported by Seleteng-Kose et al. (2021). These species, *Gunnera perpensa* L. and *Mentha aquatica* L., may have been recorded in the buffer or transitional zones of the MBR. Although the current study area was smaller, the difference in the reported number of species could be because the study by Seleteng-Kose et al. (2021) was a rapid-assessment while the current study was more comprehensive. The number of species (1–36) recorded in our vegetation plots highlights a high number of plant species that are supported by the BNR wetlands. Although only a few vegetation plots were monospecific, the majority exhibited higher species diversity, resulting in high beta diversity for the BNR wetlands.

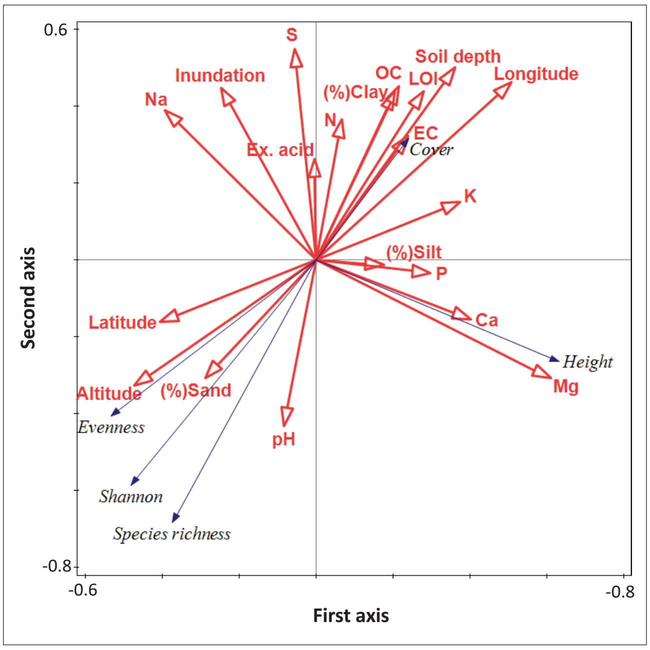


FIGURE 5: Redundancy analysis ordination diagram of plots (N = 70, not represented) described by measures of species diversity and vegetation structure of the montane palustrine wetlands of Bokong Nature Reserve in Matšeng Biosphere, Lesotho, based on the classification presented in Figure 2. Environmental variables are explanatory variables.

The contribution (48.57%) of the three most dominant families (Asteraceae, Poaceae and Cyperaceae) to the total number of species recorded in the wetlands (n = 175) is comparable to their contribution in the entire Lesotho (53.50%) reported by Chatanga and Sieben (2019). The dominance of the four families (Asteraceae, Poaceae, Cyperaceae and Scrophulariaceae) found in this study is also in line with the findings from the Ramsar site Letšeng-la-Letsie wetland (Kahlolo et al. 2021) and many other wetlands in Lesotho (Chatanga & Sieben 2019), as well as with the entire Maloti-Drakensberg region (Brand, Collins & Du Preez 2015; Brand, Du Preez & Brown 2013; Chatanga et al. 2019; Kotze & O'Connor 2000). Together, these results confirm that these four plant families are the most dominant in the Maloti-Drakensberg region. Our findings also concur with Carbutt and Edwards (2006) who reported that Asteraceae and Scrophulariaceae are the most dominant and fourth-most dominant families in the Maloti-Drakensberg region. Although the most dominant plant family was Asteraceae and Poaceae was second, the latter has been reported to be the most dominant in wetland ecosystems (Kotze & O'Connor 2000; Sieben, Mtshali & Janks 2014a). However, sedges (Cyperaceae) tend to be generally associated with the wetter parts of the wetland systems, while grasses (Poaceae) become more predominant towards the drier end of the wetland wetness gradient (Sieben et al. 2010).

The wetland vegetation of BNR has been classified into 10 plant communities whose distribution is mainly influenced by longitude, altitude, latitude, soil sodium content, inundation, soil magnesium content, soil phosphorus content and soil texture. This is in line with Sieben et al. (2021b), who reported that these environmental factors are important drivers of plant species diversity in wetlands. The plant communities recorded in this study exhibited clear variation in terms of species diversity and vegetation structure. Longitude, altitude, soil magnesium content, soil sulphur content, inundation, soil sodium content, TOC, soil pH, soil texture and latitude are important determinants of plant diversity and structure. This concurs with the findings from Letšeng-la Letsie Ramsar site, also in the Lesotho part of the Maloti-Drakensberg Mountains, where the same factors were found to be important drivers of wetland plant diversity and structure (Kahlolo et al. 2021). The current results are also consistent with findings from South Africa where the most important factors explaining the variation in species composition at the wetland scale were found to be soil texture, sodium content, organic carbon content, wetness and electric conductivity (Sieben et al. 2021b). The influence of inundation on wetland species composition and diversity, reported in this study, has also been recently reported in Togo (Folega et al. 2023).

The high species richness in BNR wetlands demonstrates the high diversity of habitats occurring in the area and this is also consistent with earlier findings that palustrine wetlands in high-altitude montane areas exhibit habitat heterogeneity, and thus harbour high biodiversity (Chatanga & Sieben 2019, 2020). Wetland plants exhibit remarkable diversity within and across wetlands (Sieben et al. 2014a). Within a single wetland, various plant communities can occur together across different habitats (Sieben, Mtshali & Janks 2014b) because the wide variety of habitats in the wetland gives rise to many distinct vegetation types (Sieben 2011). Higher species diversity is known to result in higher productivity and stability of ecological communities (Mitsch & Gosselink 2015). In addition to the large wetlands assessed in the current study, many other habitats in BNR have wetland characteristics and support wetland vegetation. This implies that there could be more wetland plant species in these habitats that were not documented in the current study.

The diversity of wetland vegetation in BNR is also consistent with the situation in the Maloti-Drakensberg Mountains in general (Chatanga et al. 2019) where some of the species (e.g. *Kniphofia caulescens*) are known to be endemic to the Maloti-Drakensberg region (eds. Mucina & Rutherford 2006). In their study covering South Africa, Lesotho and Eswatini, Sieben et al. (2021a) reported that endemic wetland plant species are concentrated in the Maloti-Drakensberg region, which includes the current study area. Because of their high altitude and protection status, the montane wetlands in BNR potentially serve as repositories and refugia for high-altitude wetland vegetation in the Maloti-Drakensberg region (Chatanga et al. 2019). This suggests that the wetlands in BNR have a high conservation value. Results of the current study further indicate that the vegetation and thus the wetlands in BNR are in a relatively stable condition. A balanced and stable community is critical for the natural functioning of wetland systems, and is regarded as an indicator of good ecosystem health (Mitsch & Gosselink 2015).

The wetland vegetation in BNR also provides habitat for the Sloggett's ice rat (*Otomys sloggetti*), which is endemic to Southern Africa, particularly South Africa and Lesotho (Seleteng-Kose et al. 2021). Although the condition of the BNR wetlands is good, there are signs of degradation because of burrowing by these ice rats, whose population has been reported by Mokotjomela, Schwaibold and Pillay (2009) and Grab (2012) to be on the increase in the Lesotho mountains, possibly on account of climate change and limited predation pressure. Given that Mokotjomela et al. (2009) reported that the damage caused by the ice rat in wetlands surpasses the impact of grazing and trampling by livestock, their impact may be more evident in future in the BNR wetlands as these wetlands are relatively inaccessible to livestock because of their protected status. The case of ice rats in these wetlands and their vegetation can be considered an ecological conundrum in that, whereas they are endemic and therefore require conservation, they can become a threat to wetlands when their population is unsustainably high. This would suggest the need for studies to ascertain whether they qualify as wetland ecosystem engineers and to assess their effects on plant species diversity and structure.

The amount of soil carbon is higher in the BNR wetlands ($\bar{x}$ = 10.87%, but up to 27.16%) than in Letseng-la-Letsie ($\bar{x}$ = 4.00%), a wetland that is also in the Maloti-Drakensberg Mountains but at a lower altitude and subjected to open access communal utilisation (livestock grazing and trampling) (Kahlolo et al. 2021). This substantial difference is possibly because of peat accumulation resulting from anoxia caused by waterlogging, coupled with low temperatures in BNR, that reduce decomposition rates and thus enhance organic matter accumulation (Chatterjee et al. 2010; Gopal 2016). These wetlands have optimal conditions enabling them to sequester and store carbon, which is a critical ecosystem service for stabilising climate (Mitsch & Gosselink 2015). These results are consistent with earlier findings where one of the wetlands in BNR was reported to be important for carbon storage, maintenance of biodiversity and streamflow regulation (Chatanga et al. 2020). High carbon stocks suggest that the wetlands are still in a stable condition and have experienced limited anthropogenic influence and degradation (Mitsch & Gosselink 2015). Nonetheless, it is important to note that, while high-altitude montane wetlands in good condition are important carbon sinks, they can easily become carbon sources if degraded, releasing their stored carbon (Mitsch & Gosselink 2015). This underscores the importance of careful monitoring. Wetlands are critical in mitigating climate change, although they have been reported to be undervalued in terms of the role they play in the fight against climate change (Moomaw et al. 2018).

Because species occurring in high-altitude wetland habitats are already at the coldest habitable environment, they cannot migrate any further in the case of temperatures becoming too high for their ecological tolerance (Bentley, Robertson & Barker 2019; Brand, Scott-Shaw & O'Connor 2019; Ryan et al. 2014). It has been predicted that high-altitude montane palustrine wetland plant communities in Lesotho are likely to experience substantial reductions in abundance and cover as the climate changes (Bentley et al. 2019; Brand et al. 2019; Chatanga & Sieben 2020), which will result in alterations in the wetland ecosystems. A number of dominant species in BNR wetland plant communities have been found to be restricted to the high-altitude habitats of Lesotho and are likely to experience substantial reductions in their abundance and cover in the face of climate change, or may disappear altogether (Bentley et al. 2019; Brand et al. 2019; Chatanga & Sieben 2020). This will cause changes that will result in alterations in the overall functioning of the wetlands. These may include communities 4, 8, 9 and 10 that are dominated by species restricted to the summit plateau. Species at potential risk include *Alepidea pusilla*, *Athrixia fontana*, *Cotula paludosa*, *Eriocaulon dregei*, *Festuca caprina*, *Haplocarpha nervosa*, *Kniphofia caulescens*, *Kniphofia northiae*, *Koeleria capensis*, *Limosella africana*, *Limosella vesiculosa*, *Lobelia galpinii*, *Poa binata*, *Ranunculus baurii*, *Ranunculus meyeri* and *Trifolium burchellianum* (Chatanga & Sieben 2020).

Availability of water in individual wetlands is also likely to be altered following climate change, which will lead to shifts in wetland conditions in different regions, particularly high-altitude areas (Lee et al. 2015). Mofutsanyana et al. (2020) predicted that, with a warming climate, wetlands in Southern Africa will shrink because of reduced water availability, resulting in lower water levels and a lower water table, thus reducing the extent and degree of wetness in wetland habitats, resulting in wetland vegetation being replaced with terrestrial vegetation. Reduced water supply will result in increased mortality of obligate wetland plant species and enhanced establishment and growth of terrestrial plant species, leading to a shift in wetland plant species composition. Encroachment by terrestrial species implies that invasive alien plant species are likely to invade and establish in the affected wetlands. As a result, the capacity of these wetlands to deliver ecosystem services will be curtailed. All of these factors underscore the necessity to manage and conserve the wetlands in BNR to ensure their stability. Sieben et al. (2021a) indicated that high-altitude montane wetlands should be afforded a high conservation priority with respect to plant species richness, not only in Southern Africa, but across the globe.

Conclusion

This study identified 175 plant species from 102 genera and 40 families in the high-altitude palustrine wetlands of BNR. The most dominant plant families were Asteraceae, Poaceae and Cyperaceae. Ten wetland plant communities were produced from HCA. Important environmental factors influencing the wetland vegetation included longitude, altitude, latitude, soil sodium, inundation, soil texture, soil magnesium and soil phosphorus. While most wetlands in Lesotho are communal, open access and consequently often over utilised, the wetlands in BNR are among the few in the country that are formally and effectively protected. Although the wetlands and plant communities reported in this study are in a relatively good condition, they could soon be threatened by the burrowing of ice rats, a threat that is likely to be exacerbated by climate change. While the wetland vegetation assessed in this study faces a possible threat limited to climate change and potentially ice rats because of their protected status, the rest of the wetland vegetation in Lesotho faces both natural and anthropogenic pressures, including overgrazing and livestock trampling. The other protected wetland vegetation is found in Sehlabathebe National Park in Qacha's Nek District.

Because the wetlands described in this study are protected and still in a relatively stable condition, being subjected to limited anthropogenic influence, their vegetation serves as the primary wetland vegetation at such high altitudes, making their conservation critical for biodiversity conservation and climate change mitigation and adaptation. Given that the wetlands and their vegetation occur in a UNESCO-declared man and biosphere reserve, and provide important ecosystem services (e.g. support for biodiversity, water supply, climate regulation, and tourism and recreation) that go beyond national and regional boundaries, the wetlands described in this study are of high scientific and international conservation value. The plant communities described in this study, along with their species diversity and structure, form a baseline for monitoring the status of Lesotho's high-altitude wetland ecosystems in the face of potential ice rat damage and climate change. These findings can inform conservation planning and management efforts in the BNR wetlands. We recommend future studies on the dynamics of ice rats in the BNR wetlands and assessment of their impact on vegetation, including their preferred plant species in the wetlands.

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Competing interests

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

Authors' contributions

P.C. led the conceptualisation of the study, and data analysis. M.W.P. and K.M.P. helped in conceptualising the study. All authors assisted in conducting fieldwork and writing the article.

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Data availability

The datasets generated during the current study are available from the corresponding author, P.C., on reasonable request.

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