





Assessing environmental factors contributing to plant species richness in mountainous mesic grasslands



Authors:

Katlego K. Mashiane¹ 
 Abel Ramoelo² 
 Samuel Adelebu³ 
 Ernest Daemane³ 

Affiliations:

¹Department of Geography,
 Faculty of Natural and
 Agricultural Sciences,
 University of the Free State,
 Qwaqwa, South Africa

²Department of Geography,
 Geoinformatics and
 Meteorology, Faculty of
 Natural and Agricultural
 Sciences, University of
 Pretoria, Hatfield, South Africa

³Department of Geography,
 Faculty of Natural and
 Agricultural Sciences,
 University of the Free State,
 Bloemfontein, South Africa

Corresponding author:

Katlego Mashiane,
 2018711909@ufs4life.ac.za

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Southern African mountain ranges are characterised by rich and diverse plant species thriving in different habitats with pronounced endemic species. However, globally, biodiversity at the species level is deteriorating rapidly because of environmental change leading to habitat degradation and fragmentation. Mountainous grassland communities are particularly vulnerable to rapid ecosystem changes because of their specialised niches and sensitivity to global warming. Understanding the determinants of vegetation is necessary for effective and efficient management. This study aimed to determine significant environmental drivers influencing plant species richness in mountainous mesic grasslands. Topographical variables (slope and elevation) were derived by using a 30 m resolution Digital Elevation Model. Soil variables such as bulk density, silt fragments, pH, coarse fragments, soil organic carbon, sand and nitrogen were acquired from the International Soil Conference and Information Centre (ISCI), and species richness and diversity were derived from vascular plant species inventory data compiled using a field survey. Species richness was influenced by soil bulk density, and the interaction between elevation and soil bulk density; higher species richness was associated with lower bulk density and higher elevations. Similarly, species composition changed as edaphic factors and elevation changed.

Conservation implications: Species richness increased with soil bulk density, which decreased with elevation. Fire severity had little effect on species richness and diversity, which may indicate that management actions do not affect species. However, the impact of grazers still needs to be better understood at this time. Moreover, the strong positive relationship between species richness and diversity in this study shows that species richness can be used as a surrogate for diversity and conservation monitoring, especially in mesic highland grasslands.

Keywords: mountains; subalpine; edaphic; topography; protected grasslands.

Introduction

Plant diversity controls processes are pivotal to the functioning of ecosystems (Cardinale et al. 2011). However, species-level biodiversity is deteriorating rapidly because of global environmental change drivers such as climate change, pollution, invasive species and land-use changes (Hooper et al. 2012). It has been stressed that reduced species richness and concomitant changes in species composition could alter ecosystem services (Tilman, Reich & Isbell 2012). In addition, studies showed that reducing plant diversity in grasslands may lead to lower production of above-ground plant biomass (Tilman, Wedin & Knops 1996).

Modelling the distribution of mountainous species diversity is essential for identifying priority areas for conservation (Barros et al. 2015), mainly because of the sensitivity of these species to climate change (Picó & Van Groenendael 2007; White et al. 2012). For example, subtropical highland grasslands in Brazil are home to several endemic groups of plants (Iganci et al. 2011), and some taxa are represented by an island-like distribution (Lorenz-Lemke et al. 2010). Furthermore, in mountainous areas of Europe, plant diversity is increased by disturbance regimes such as grazing and soil erosion; as a result, the subalpine grasslands are mosaics comprising varying herbaceous communities (Armas-Herrera et al. 2020). This enhances species composition for grazing while restricting the expansion of unwanted species, that is, shrub encroachment. Understanding of biodiversity indicators and factors driving heterogeneity is crucial for conservation interventions and modelling future distributions in response to global change (Barros et al. 2015; Kuzemko et al. 2016).

In addition, the composition of grassland species is controlled by interacting environmental factors such as moisture regime, soil characteristics and other disturbances, including fire. Despite

interventions such as policy reform and increasing protected areas, most pressures on biodiversity are intensifying (Butchart et al. 2010; Hooper et al. 2012). As a result, biodiversity loss is accelerating, and thus, this loss of species could be detrimental to the ecosystem and its functions (Butchart et al. 2010; Meyer et al. 2018; Oliver et al. 2015). In addition, richness in grassland species is controlled by parameters that increase heterogeneity such as disturbances, management practices and topography (Zulka et al. 2014). Spatio-temporal studies of grassland vegetation are required to examine species' response to heterogeneity and ecosystem processes (Lundholm 2009).

Besides evidence supporting a positive relationship between environmental heterogeneity and species richness, some studies report negative and monotonous relationships (Lundholm 2009; Yang et al. 2015). Establishing heterogeneity-diversity relationships (HDRs) is fundamental for developing management strategies and abating biodiversity loss (Filibeck et al. 2019). For example, forage nutrition and spatiotemporal vegetation variations because of geographic rainfall gradients influence the occurrence of large mammals in Serengeti National Park, Tanzania (McNaughton 1985, 1988). Soil catena characteristics control species composition in sub-alpine grassland communities of Monte Perdido National Park in Spain (Armas-Herrera et al. 2020). Although potentially susceptible to global environmental change, the vegetation of temperate mountains in Southern Africa is influenced by ecological, physical and anthropogenic processes (Brown & Du Preez 2020). Information and studies on the mountains in southern Africa still need to be documented. Therefore, by intensifying research and monitoring in this region, information on the vegetation and resilience of this ecosystem would become available (Brown & Du Preez 2020). Studies that combine multiple datasets based on ecological traits are encouraged to better understand what determines spatial patterns of biodiversity at explicit scales (Barros et al. 2015).

Grassland ecosystems rank among the most threatened ecosystems in South Africa. Thus, conservation plans should be put in place to abate the loss of rare and endangered species. In mesic Afrotropical grasslands of southern Africa, vegetation is subjected to intense land-use activities such as grazing by livestock and wildlife (O'Connor 2008). The Golden Gate Highlands National Park (GGHNP) is a protected conservation area experiencing intense grazing by livestock and wild animals, with the potential to change the composition of grass species. The GGHNP is highly variable in topography and climate, which results in a complex mosaic of plant communities (Kay, Bredenkamp & Theron 1993). The existing monitoring programmes for grassland vegetation and data ought to be evaluated and analysed for effective conservation policies. The objective of the study was to determine significant environmental drivers influencing plant species richness in the mountainous mesic grasslands of GGHNP.

Research methods and design

Study area

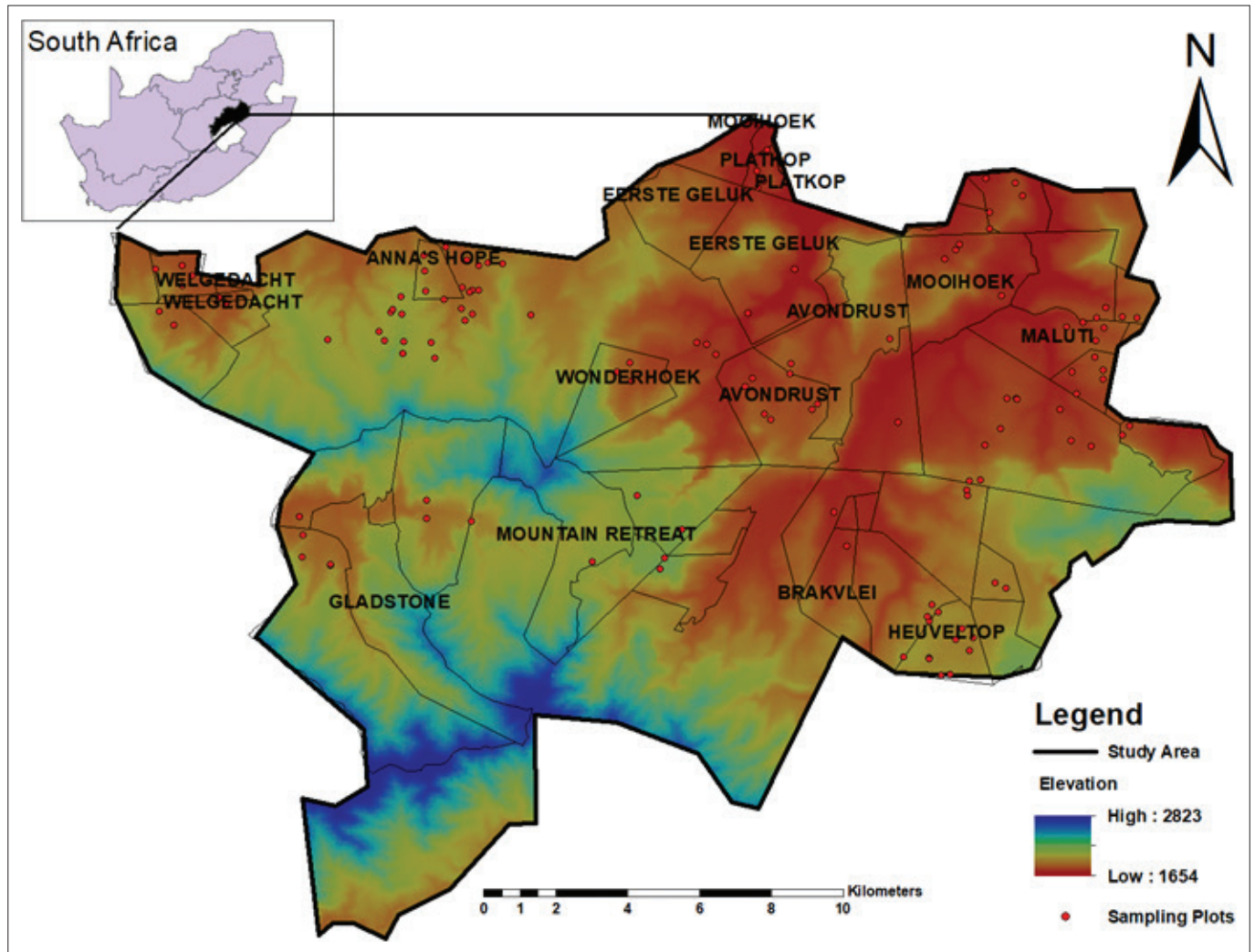
The study was conducted in GGHNP, situated in the north-eastern part of the Free State province, South Africa (Figure 1). The park covers 32758.35 ha and lies between 28°27' S – 28°37' S and 28°33' E – 28°42' E. The GGHNP is a mountainous grassland located at the foothills of the Drakensberg and forms part of the mesic highveld grassland with marked variation in geology and topography. The following soil types were identified in the study area: shallow rocky soils (Glenrosa and Mispah), deep soil along drainage lines (Oakleaf), well-developed sandy soils (Hutton and Clovelly), as well as Clayey structured soils (Milkwood and Tambakulu) (SANParks 2020). The Park has a rich geology divided into stratigraphic units; four sedimentary units (Tarkastad subgroup, Molteno, Elliot and Clarens formations) and an igneous Drakensberg group that dates 195–210 million years ago. Golden Gate Highlands National Park is characterised by summer rainfall, temperate summers and cold winters. The rainfall season stretches from September to April with a mean annual ranging from 1800 mm to 2000 mm (Kay et al. 1993). The GGHNP lies between 1654 m and 2829 m above sea level (Figure 1) and comprises the following grasslands units: Eastern Free State sandy grasslands (Gm 4), Basotho montane shrubland (Gm 5), Lesotho highveld basalt grassland (Gd 8) and Northern Drakensberg highveld (Gd5) (Mucina & Rutherford 2006).

Sampling design and field data collection

The researchers stratified GGHNP according to old crop farming fields that are distributed evenly, these sites have quadrats, were sampled in the study area. Data were collected in March 2019, April 2019 and May 2019 during the peak growing season. At each quadrat, all herbaceous plant species were identified to species level where possible. The 1 m × 1 m was gridded into 100 cells of 1 cm² each (representing 1% cover) and summed different land types and elevation (Figure 1). Golden Gate Highlands National Park was proclaimed in 1962 with additional proclamation of eight farms on the border of QwaQwa in 1989 (SANParks 2020). Vegetation sampling was undertaken in 30 m × 30 m plots placed purposively within homogeneous patches of grass communities. Each sampling plot was divided into four transects of 30 m. Within each 30 m transect, a nested 1 m × 1 m quadrat was sampled at 10 m intervals. In total 142 plots each with 16 quadrats, species cover was averaged per species from each plot.

Ancillary data acquisition and preparation

Chemical and physical properties of soil such as soil bulk density (BD), silt fragments (SF), pH, coarse fragments (CFs), soil organic carbon (SOC), sand (SD) and nitrogen of topsoil (15 cm) were downloaded from the International Soil Conference and Information Centre (<https://soilgrids.org>); the soil data were validated using ground data from across the globe (Hengl et al. 2017). Elevation data and Shuttle Radar Topography Mission (SRTM), Digital Elevation Model (DEM) at 30 m resolution were obtained from US Geological



Source: Mashiane, K., Ramoelo, A. & Adelabu, S., 2023, 'Diversifying modeling techniques to disentangle the complex patterns of species richness and diversity in the protected Afromontane grasslands', *Biodiversity and Conservation* 32, 1423–1436. <https://doi.org/10.1007/s10531-023-02560-8>

FIGURE 1: A map of the Golden Gate Highlands National Park study area (the park) with names of sampling sites, plots and elevation (metres above sea level [masl]).

Survey's EROS data centre (<https://earthexplorer.usgs.gov>). The slope was derived from a DEM using the Spatial Analyst Tool in ArcGIS 10.4. Fire severity data were acquired from a study conducted in the study area (Adagbasa, Adelabu & Okello 2018). The study estimated fire severity using the Normalized Burn Ratio (NBR) index by analysing pre and post fire season (April 2017–September 2017) from remote sensing images with burnt and unburnt pixels.

To prepare the data for analysis, the raster images were clipped to the extent of the study area and imported into R to extract pixel values representing environmental variables in each plot using the 'extract' function. The taxonomic composition of the vegetation and its cover were used to derive species richness and diversity for each plot. The former was determined by averaging the 1 m² quadrats to obtain mean plot species richness. Total species diversity was calculated using the Shannon–Wiener Index:

$$H' = -\sum p_i \ln p_i \quad [\text{Eqn 1}]$$

where p_i is the proportion of the species within the sampling unit, these units were averaged to obtain plot level value

of species diversity (alpha diversity), which was used as a predictor of species richness. The species richness and diversity were computed using 'vegan' and 'plyr' found in R statistical software packages (Oksanen 2017) by implementing the diversity and apply function for species diversity and richness, respectively.

Data analysis

The function 'stat.desc' (in pastecs package) in R was used to determine descriptive statistics of all the variables in this study. Exploratory analysis, that is, a correlogram, was used to test for intercorrelations and the relationships between biotic (species richness and diversity), abiotic (BD, SF, sand, soil pH, SOC, CF), fire severity, topographic data (elevation and slope) and an interaction of soil and topo-edaphic variables. Simple multiple linear regression was used to determine the influence of each environmental variable on species richness. To ensure that multicollinearity was low inflation factors (VIFs) were calculated and the variable with the highest VIF was removed. This was repeated until the VIF of all variables in the final model was at acceptable levels (VIF < 5). Hierarchical partitioning was used to estimate the contribution of each

explanatory variable in the multivariate linear models because the goal was to identify variables with strong direct influence. Hierarchical partitioning calculates all possible regression subsets and averages model improvements across all hierarchies, thus permitting a ranking of variables by their independent effects. This analysis was calculated using the R package 'hier.part'.

Permutational multivariate analysis of variance (PERMANOVA) was used to determine the influence of environmental predictor variables on species composition among different sites in Golden Gate Highlands National Park (GGHNP). Subsequently, environmental variables were fitted onto an ordination of species composition to determine variables that significantly affected species composition across 9 of 13 sites based on the ample species composition data > 5 species per quadrat. These relationships were displayed using non-metric multidimensional scaling (NMDS).

Ethical considerations

This article followed all ethical standards for research without direct contact with human or animal subjects.

Results

Descriptive statistics

The maximum number of species recorded in a single plot was 17 and the lowest was 3. The highest record of species diversity was 2.45 while the lowest was 0.64 in GGHNP (Table 1). Out of the ecological variables, species richness had the highest coefficient of variation (38.9%) compared with fire severity (25.9%) and species diversity (24.7%) (Table 1). Among all edaphic variables, SOC showed the highest coefficient of variation (31.6%). Slope (80.4%) had the highest coefficient of variation out of the topographic variables when compared with elevation (5.72%) (Table 1).

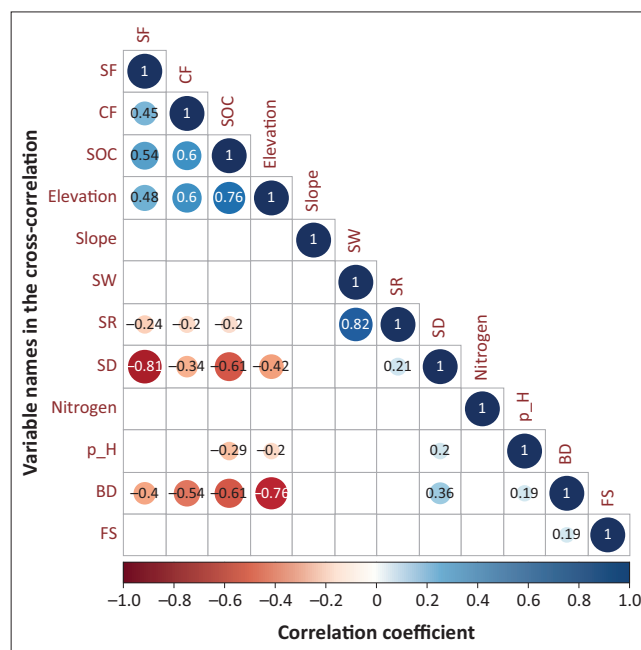
Relationship between species richness and environmental variables

There was a significantly negative relationship between grass species richness and SF, soil organic content and CF; however, there was a positive relationship between species richness and sand. Although significant, the other variables had a

weak relationship with species richness. Species diversity was not significantly related to topographical and soil variables (see Figure 2).

The multiple linear regression showed that species richness was positively and significantly associated with species diversity within the biotic-based model (Table 2). However, after removing species diversity, the model with abiotic variables showed soil BD as the only significant variable associated with species richness, albeit negatively. With the topo-edaphic-based model, interaction variables of elevation with BD, CF and sand fragments contributed significantly to variation. Only soil BD was positively associated with species richness.

Hierarchical partitioning showed species diversity as the variable having the highest independent effects followed by edaphic variables (Figure 3). The abiotic-based model exhibited silt fragments as the variable with the highest explanation of variation in species richness. The interaction



SR, species richness; SW, diversity; BD, bulk density; SF, silt fragments; SD, sand; p_H, pH; SOC, soil organic carbon; CF, coarse fragments; FS, elevation, slope, fire severity.

FIGURE 2: Correlogram for 142 herbage samples in the Golden Gate Highlands National Park.

TABLE 1: Descriptive statistics including species richness, species diversity, soil variables (list them), topographic variables (list them) and fire severity.

Variables	Units	Minimum	Maximum	Median	Mean	Standard deviation	Coefficient of variation
Species richness	S	3.00	17.00	9.00	8.97	3.49	38.91
Species diversity	H'	0.64	2.45	1.63	1.63	0.40	24.65
Bulk density	cg/cm ³	1199	1454	1388	1389	36.08	2.60
Silt fragments	g/kg	16.00	26.00	20.00	20.37	1.69	8.30
Sand	g/kg	44.00	59.00	54.00	54.08	2.56	4.74
Soil pH	pH ¹⁰	56.00	62.00	59.00	59.29	1.47	2.47
Soil organic carbon	dg/kg	8.00	41.00	13.00	13.09	4.13	31.55
Coarse fragments	cm ³ /dm ³	2.00	19.00	6.50	7.12	2.72	38.16
Elevation	masl	1686	2399	1842	1856	106.2	5.72
Slope	angle°	0.00	26.73	5.10	6.45	5.21	80.84
Fire severity	-	2.00	6.00	4.00	3.72	0.96	25.90
Nitrogen	cg/kg	196.0	334.0	231.0	234.2	19.95	8.52

term of elevation and BD was more pronounced as the variable with the strongest direct influence on species richness.

Grass species composition was significantly related to the environmental predictors, that is, BD, SF, sand fragments, pH and elevation. Annashope communities were associated with low sand and pH values. Maluti and Heuveltop (Figure 4) communities separated from the other sites and thrived on soils with high BD.

Discussion

In this study, species richness was not significantly related to any of the topographic variables. Although a positive HDR was expected, these are common but not universal. A meta-analysis conducted by Lundholm (2009) found positive HDRs to be mostly lacking. The lack of a relationship may have been because of the low levels of topographic variation across the sites. For instance, the variation in elevation range

was very low, this may be a result of our sampling technique of 'stratified random', which used old farming lands as a stratum and not elevation. The full mountain range in GGHNP has highly variable and unique topography, which results in diverse habitats (Kay et al. 1993). Therefore, stratification based on elevation maybe important for testing positive HDR of mountainous areas. The variations in mountain topography create micro-environmental conditions that influence habitat heterogeneity and fragmentation (Brown & Du Preez 2020; Gaury & Devi 2017). Consequently, these micro-habitats harbour and shelter a diversity of species serving as essential biodiversity hotspots, providing ecosystem services such as pollination and controlling biological invasion (Zulka et al. 2014). Studies investigating the influence of elevational gradients on species composition would be a boon for conservation management.

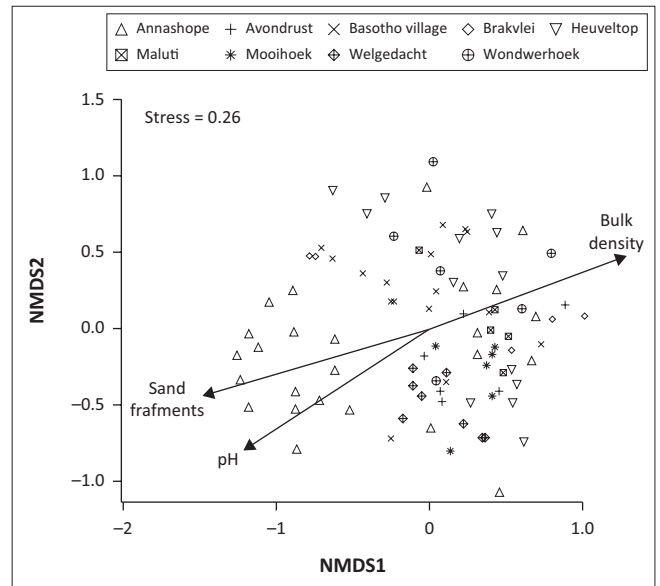
A model incorporating species diversity and a set of environmental variables performed well in predicting species

TABLE 2: Herbaceous species richness versus biotic, abiotic and topo-edaphic variables.

Variables	Biotic			Abiotic		
	<i>b</i>	<i>t</i>	VIF	<i>b</i>	<i>t</i>	VIF
Species diversity	+	16.64*	1.08	n/a	n/a	-
Bulk density	-	-0.65	2.78	-	-2.24*	2.68
Silt fragments	-	-1.10	3.64	-	-1.08	3.63
Sand fragments	+	0.005	3.94	-	-0.02	3.95
pH	-	-1.25	1.27	+	0.20	1.26
Soil organic content	-	-0.97	3.75	-	-0.94	3.74
Coarse fragments	-	-0.44	2.02	-	-1.25	2.01
Elevation	+	0.38	3.82	-	-0.45	3.81
Slope	+	0.02	1.04	+	0.59	1.04
Fire severity	-	-2.01	1.17	-	-0.52	1.16
Nitrogen	-	0.35	1.04	-	-0.49	1.04
Topo-edaphic						
Elevation_Bulk density	+	177*	1.32	-	-	-
Elevation_Silt fragments	-	-13.04	1.87	-	-	-
Elevation_Coarse fragments	-	-0.61	2.08	-	-	-
Elevation_Sand fragments	-	-13.63	1.21	-	-	-
Slope_Bulk density	-	-0.61	1.31	-	-	-

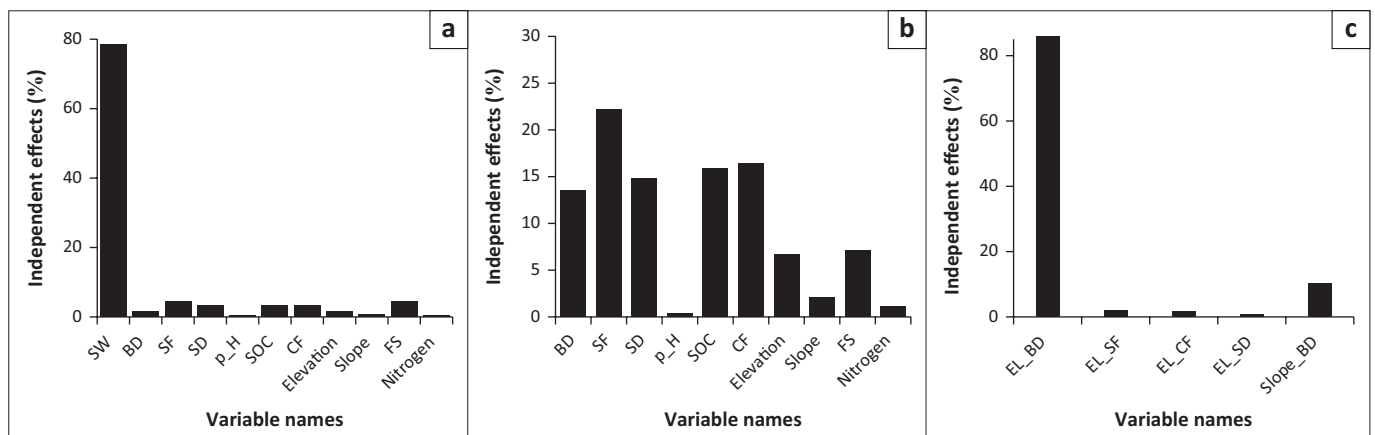
b, sign of the regression coefficient, *t*, test statistic; VIF, variable inflation factor; n/a, not applicable.

*, $p < -0.05$.



Note: based on Bray–Curtis dissimilarity scores, after Wisconsin double standardisation.

FIGURE 4: Non-metric multidimensional scaling ordination of Golden Gate Highlands National Park, grass species composition at different sites.



SW; species diversity; BD, bulk density; SF, silt fragments; SD, sand fragments; SOC, soil organic content; CF, coarse fragments; pH, pH; FS, fire severity; EL, elevation; and slope.

FIGURE 3: Hierarchical partitioning regression analysis for herbaceous species richness of (a) biotic-based (b) abiotic-based and (c) topo-edaphic-based variables.

richness. In addition, species diversity was strongly related to species richness in Spearman's correlation analysis. The results highlight the importance of incorporating biotic variables in establishing HDRs, which require an understanding of individual species' response to gradients of spatial environmental heterogeneity factors (Lundholm 2009). For example, local patterns in soil moisture seem to be affected by topography through more mechanisms than other topographically controlled factors and with a strong influence on plant diversity. Lundholm (2009) suggests that species diversity allows for compartmentalisation and complementary resource use because no single species can fully exploit the conditions of the entire ecosystem, a concept known as niche differentiation (Tilman 1999). Therefore, species richness is merely the number of species in an ecosystem, while diversity considers the evenness; thus, considering species diversity and richness as independent and dependent variables helps to understand their influence on the GGHNP ecosystems' resilience.

Soil BD was the only variable negatively affecting species richness within the abiotic-based model and the results of the topo-edaphic-based model showed that elevation and BD jointly affected species richness. This is not surprising because the mountain soil is affected by topography and thus influences local terrestrial plant diversity patterns (Moeslund et al. 2013). Edaphic features such as soil BD can impair or amplify water loss and spatial accumulation patterns (Moeslund et al. 2013). As such, the extent to which portions of a landscape capture or retain water and nutrient resources is an essential determinant of vegetation patterns (Moeslund et al. 2013). This emphasises the role of topographically controlled edaphic features on landscapes in GGHNP. This could indicate that soil with a lower BD can be vital for plant biodiversity in grassland terrestrial plant species. The results suggest that stable landscapes at high elevations harbour niche species diversity. Mid and foot-slope catena are often the recipients of all upslope water and nutrient resources. This causes enrichment that either limits or enhances species richness and diversity, depending on soil quality (McNaughton 1985). Steep slopes are prone to soil erosion, a disturbance could either promote the growth of early-succession species or preclude disturbance-intolerant species in mountainous grassland ecosystems (Armas-Herrera et al. 2020; Filibeck et al. 2019).

Species composition was significantly related to the environmental predictors of soil variables and elevation. The ordination showed that species composition turned over along sand, pH and BD gradients. This is consistent with the results of Armas-Herrera et al. (2020), who suggested that grassland vegetation mosaics are maintained by soil-plant feedbacks, especially in subalpine grassland communities where soil disturbances and inevitable succession drive plant co-existence. This finding emphasises the importance of soil drainage in maintaining species diversity in African Mountain vegetation (Brown & Du Preez 2020). A species composition shift will likely occur associated with increasing soil resources such as water and nutrients. As defined by particle size, soil texture, is important for controlling soil-plant relationships, especially seedling germination and

establishment. Soil texture especially, silt and clay content, strongly influences the establishment of many plant species (Fair, Peters & Lauenroth 2001).

The risk of species extinction because of global environmental change is imminent, propelling the modelling and identification of conservation hotspots (Barros et al. 2015). Subtropical highland grasslands have co-evolved with climate and specific microhabitat conditions (Iganci et al. 2011). Changes in climatic conditions may lead to environmental changes in microhabitats with dire consequences for species diversity, especially in mountainous grasslands, which are sensitive and thus susceptible to environmental changes. The conservation of topographically controlled soils that support and enhance plant diversity can be crucial for maintaining grassland plant communities. In fact, McNaughton (1985) showed that the resilience for grass species to environmental changes will likely depend on their physiological traits in rangelands. Monitoring aspects of biodiversity, that is, richness and diversity as well as species composition are critical for managing ecosystem functions and services for rangelands. These parameters of diversity are crucial for determining carrying capacity and stocking rates to ensure sustainable management of natural resources.

Conclusions

The research corroborates the fact that drivers of species diversity in grassland communities are multidimensional by nature (Shoemaker et al. 2020). This is evident by the variations in importance and direction of multiple environmental drivers and their influence on species richness. To understand community dynamics, the incorporation of biotic and abiotic factors is beneficial (Shoemaker et al. 2020). The notion that diverse habitats, which are influenced by unique and heterogeneous topography in mountainous biomes, enhance species composition should be investigated. These habitats could be meta-populations fragmented into islands of similar species composition. The research shows that slope and soil interactions are important influencers of species richness in this montane grassland, particularly slope and BD. Soil conservation practices such as revegetation and erosion control blankets on bare soil should therefore be a priority, especially in mesic mountainous grasslands where the soil is prone to erosion and nutrient leaching.

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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

All authors conceived and designed the research. K.K.M. conducted the fieldwork, analysed the data and wrote the article. All authors reviewed and edited the manuscript.

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Data availability

Data used in the analysis for the results are available upon request.

Disclaimer

The views and opinions expressed in this article are those of the authors and do not necessarily reflect the official policy or position of any affiliated agency of the authors.

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