



Relative role of topographic position and soil edaphic factors on leaf nutrient concentrations of *Euryops floribundus* in semi-arid mountainous grassland landscapes

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Abstract The encroachment of shrub species into mountainous grasslands threatens global biodiversity and ecosystem stability. Shrub encroachment is influenced not only by the environmental characteristics of the region, but also by specific traits of the encroaching shrub species, such as leaf nutrient concentration. However, the topography-driven changes in the leaf nutrient concentration of encroaching shrub species in mountainous grasslands remain largely unexplored. Here we examined how landscape topography and selected soil edaphic properties influence the leaf nutrient composition of the encroaching shrub *Euryops floribundus* N.E. Br in three mountainous grassland sites in eastern South Africa. Each landscape site was surveyed and demarcated into three topographic positions: downslope, midslope, and upslope. In each topographic position per site, six 10 m x 10 m

plots were randomly selected to collect leaf samples from *Euryops floribundus*, along with soil samples taken from the topsoil layer. We found evidence that landscape topography, nutrient availability and associated chemistry of the soil influences leaf nutrient concentrations of the encroaching *Euryops floribundus*. Specifically, leaf phosphorus concentration in the downslope position was 33% higher compared to upslope position in Manzimdaka, and correlated to effective cation exchange capacity, exchangeable acidity and acid saturation of the soil. Leaf potassium concentration increased by 22% in downslope positions compared to upslope positions in Tsengiwe. A similar trend of leaf potassium content was observed in Manzimdaka, although a significant increase of 20% occurred between downslope compared to midslope positions. We also observed a 37% and 28% increase in leaf zinc concentration in downslope positions compared to upslope positions in Tsengiwe and Manzimdaka, respectively. Furthermore, leaf manganese was 63% lower in downslope positions compared to upslope positions in Upper Mnxe. This study provides valuable insights into the impact of landscape topography on the nutrient concentration of encroaching shrub species in mountainous grasslands. The examination of leaf nutrient traits along a topographic gradient will lead to improved understanding of plant strategies at local scales and give much needed insights into the ecological mechanisms that influence the dominance and persistence

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of *Euryops floribundus* monoculture stands in mountainous grasslands.

Keywords Landscape topography · Leaf nutrients · Shrub species · Shrub encroachment · Mountainous grasslands · Soil nutrients · *Euryops floribundus* N.E. Br

Introduction

Globally, shrub encroachment poses a serious threat to biodiversity and ecosystem stability of mountainous grasslands (Naito and Cairns 2011; Gartzia et al. 2014; Archer et al. 2017; Lerotholi et al. 2024). Shrub encroachment is a phenomenon wherein woody species expand into grass dominated landscapes (Van Auken 2009). The expansion of shrubs is primarily driven by several complex factors, including changes in climatic conditions, fire frequency, overgrazing by domestic livestock, and the rising levels of atmospheric carbon dioxide (Roques et al. 2001; Van Auken 2009; O’connor et al. 2014; Archer et al. 2017). However, landscape topography has also been identified as a significant factor influencing shrub encroachment in mountainous grasslands (Gartzia et al. 2014; Bora et al. 2021; Mekonnen et al. 2021; Soubry et al. 2022; Gxasheka et al. 2023). Landscape topography is a key factor affecting soil water and nutrient availability in mountainous ecosystems (Fu et al. 2004; Moeslund et al. 2013; Liu et al. 2020). Specifically, landscape gradients influence water movement and erosion dynamics, resulting in shallower upslope soils receiving and retaining less water and nutrients, while deeper downslope soils have the capacity to accumulate more water and nutrients (Lane et al. 1998; Hook and Burke 2000; Wernerehl and Givnish 2015; Yuan et al. 2019; Liu et al. 2020). Altogether, these landscape processes create heterogeneous soil conditions and variable soil nutrient availability that influence growth and patterns of encroaching shrub species.

Despite the significance of landscape topography on soil factors and the growth of encroaching shrub species, previous studies have mainly focused on examining the influence of topography on the structural characteristics of encroaching shrubs, including height, canopy cover, and stem density (Snyman 2012; Pule et al. 2018; Masibonge et al. 2019;

Dendoncker and Vincke 2020), but overlooking the influence of landscape topography on leaf nutrient concentration, which is crucial for plant growth, competitive ability and nutrient cycling. Therefore, understanding how landscape attributes influence the leaf nutrient concentration of encroaching shrub species is essential for a comprehensive understanding of the dynamics of shrub encroachment and the development of effective management practices in mountainous grasslands. Leaf nutrients in plants are generally essential for maintaining plant health, competitiveness, thus enhancing ecosystem productivity, and facilitating nutrient cycling (Reich 2005; Venterink and Güsewell 2010). Harper (1989) suggests that an increase in leaf nutrients serves as an adaptive feature employed by plants to thrive in various environments. For instance, increased leaf nutrient concentrations promote photosynthesis by providing essential elements required for chlorophyll production and enzyme activity (Liu et al. 2010; Marschner 2011; Swoczyna et al. 2022). Further, increased leaf nutrient concentration improves plant defense mechanisms, such as producing secondary metabolites, which enhance resistance against herbivores, pests, and pathogens (Herms and Mattson 1992; Cipollini et al. 2018).

Although leaf nutrient concentration is crucial for the growth and adaptability of woody plants, studies in mountainous regions have shown significant variations in leaf nutrient concentrations across different landscapes. Notably, Wu et al. (2007) observed higher concentration of nitrogen (N), phosphorus (P), and potassium (K) at lower (330 m to 400 m) elevations compared to higher (400 m to 480 m) elevations. Similarly, Drollinger et al. (2017) reported an increase in nitrogen (N), magnesium (Mg), potassium (K), and phosphorus (P) concentrations at lower elevations compared to higher elevations in Himalayas mountains, Nepal. In contrast, Köhler et al. (2006) found nuanced patterns, with certain nutrients remaining consistent while others decreased along an elevation gradient in Spain. Furthermore, In Asia, Du et al. (2017) reported a decline in nitrogen (N), sulphur (S), and potassium (K) concentrations at lower (546 m to 856 m) elevations, coupled with an increase in carbon (C), calcium (Ca), sodium (Na), iron (Fe), manganese (Mn), and copper (Cu) concentrations compared to higher (1105 m to 1323 m) elevations. In addition, these authors found no significant influence

of elevation gradients on phosphorus (P), magnesium (Mg), aluminum (Al), or zinc (Zn) concentrations. Such inconsistent findings reported in these studies likely stem from the specific woody plant species occurring in the different mountainous regions. In this context, Qin et al. (2022) suggested that individual plant species may exhibit unique strategies that modify leaf concentration in response to local and environmental conditions, highlighting the necessity for further research into the species-specific responses of leaf nutrient concentration along varying landscape ecosystems.

Here, we investigate leaf nutrient patterns of an encroaching shrub (*Euryops floribundus* N.E. Br) across different topographic positions in three semi-arid mountainous grassland landscape sites in eastern South Africa. *Euryops floribundus* is a rapidly growing, evergreen, multi-stemmed perennial shrub indigenous to the arid and semi-arid biomes of the Eastern Cape Province in South Africa. This shrub is expanding extensively and encroaching into communal grazing lands, forming large monoculture stands (Fig. 1), yet it remains unpalatable to livestock such as goats, sheep, and cattle (Masibonge et al. 2019; Ruwanza 2022; Gxasheka and Dlamini 2024). Additionally, there is no documented information available on the leaf nutrient composition of *Euryops floribundus*, neither in general nor across different topographic gradients. Therefore, we seek to address the following research questions: (1) How do leaf nutrient concentrations of the shrub *Euryops floribundus* vary across different topographic positions in mountainous grasslands? (2) Which edaphic factors contribute to the leaf nutrient patterns observed in *Euryops floribundus* across these landscape sites?

Material and Methods

Study area Description

We selected a study area within the communal grasslands in the vicinity of Cala, a town located within the Sakhisizwe Local Municipality in the Eastern Cape province of South Africa (Gxasheka and Dlamini 2024). On average, the area receives an annual rainfall of 500 mm and temperatures ranging from 22 °C in January to 12 °C in July (Table 1). The area has a semi-arid climate, with the majority

of precipitation occurring during the summer season (November to March) and minimal rainfall during the winter season (June to August). The woody layer is dominated by *Euryops floribundus* while the grass layer is dominated by *Aristida congesta*, *Elionurus muticus*, *Eragrostis chloromelas*, *Eragrostis plana*, *Heteropogon contortus*, *Sporobolus africanus*, and *Themeda triandra* (Table 1). Mudstones of the Karoo supergroup dominates the geology of the study area along with shallow and stony soil. The research area is a communal grazing land with no fences or management practices, such as rotational grazing, or prescribed burning. Specific quantitative information regarding stocking rates in the study area is not available. This lack of planned management is common in many communal grazing lands throughout South Africa, where livestock numbers are rarely monitored and grazing pressure varies extensively (Palmer and Bennett 2013). Despite this, the estimated long-term grazing capacity by the Department of Agriculture for our study area is about 8 hectares (ha) per Large Stock Unit (LSU) (DAFF 2018). Over the last three decades, the study area has been continuously used as grazing land for a variety of livestock including cattle, sheep, and goats, with no limits or constraints imposed on land management (Gxasheka 2013).

Site Selection and Leaf and Soil Sample Collection

In this study, we used a comprehensive approach to choose communal grazing sites, including drives with local extension personnel and community leaders, as well as extensive field observation to identify mountainous grazing lands encroached by *Euryops floribundus*. Based on our field surveys, we chose three grassland landscape sites by considering the proximity of nearby homesteads to the communal grazing areas, corresponding with our observations of the local distribution pattern of *Euryops floribundus* during field surveys. In Table 1, the selected sites are listed as follows: Tsengiwe, located less than 100 m from homesteads; Upper Mnxe, situated at an intermediate distance of 200–800 m from homesteads; and Manzimdaka, positioned more than 1600 m away from homesteads. Each landscape site was demarcated into three topographic positions, namely downslope, midslope, and upslope. At each topographic position, six plots (10 m x 10 m) were randomly established and spaced approximately 10

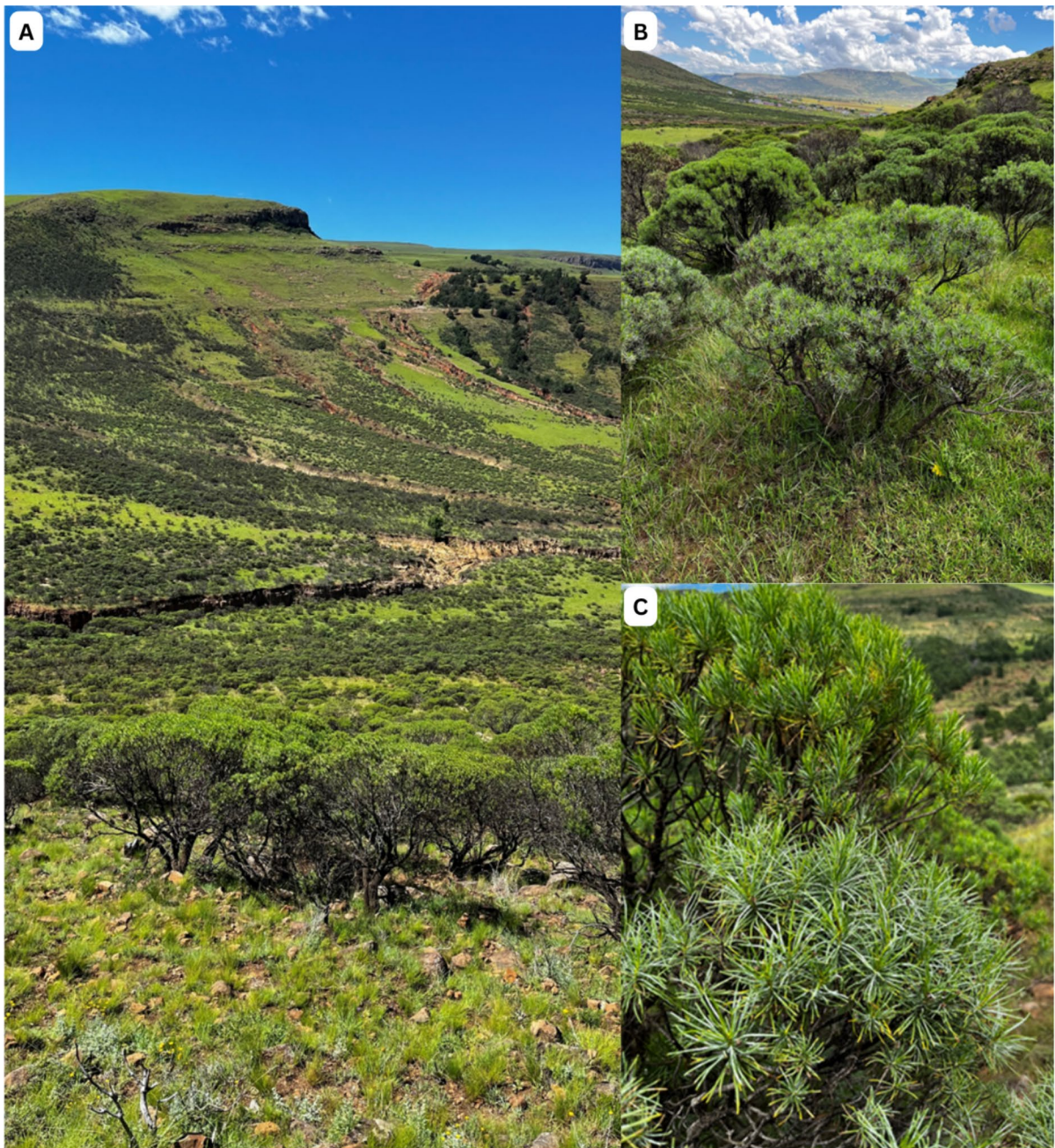


Fig. 1 **A** general view of *Euryops floribundus* encroachment across different landscapes. **B** Monoculture stand and **C** leaves of mature *Euryops floribundus*

m apart. In each 100 m² plot, we randomly selected seven mature and healthy *Euryops floribundus* individuals of approximately the same size (Wang et al. 2022). Subsequently, a uniform quantity of leaves of the shrub species was collected from the east, north,

west, and south sides of the crowns (Zeng et al. 2021). Finally, leaves from seven shrubs within each plot were mixed and placed in a one brown paper bag to form a composite sample. In the laboratory, the collected leaf samples were dried in the oven at 75 °C

Table 1 Geographical location of the three investigated sites in Eastern Cape Province, South Africa

Study site	Tsengiwe	Upper Mnxe	Manzimdaka
Landscape attributes			
GPS co-ordinates	S 31°35 '13.1"	S 31°31' 20.5"	S 31°33'48.9"
	E 27°38 '07.5"	E 27°35 '00.1"	E 27°42 '45.8"
Altitude (m.a.s.l)	1294.06 ±7.62	1313.72±4.69	1320.56±15.47
MAP (mm)	500	500	500
MAT (°C)	15.2	15.2	15.2
Distance from homestead (m)	< 100	200-800	> 1600
Soil properties			
Geology	Mudstone of Karroo supergroup	Mudstone of Karroo supergroup	Mudstone of Karroo supergroup
Clay (%)	31.61±1.5	39.78±2.13	41.56±1.68
Organic carbon (g/kg)	18.5±1.27	26.28± 1.14	26.39± 1.47
pH (KCl)	5.24±0.04	5.14±0.05	5.13±0.04
ECEC (cmol/L)	17.24±1.16	18.06±0.96	18.03±1.26
Exchangeable acidity(cmol/L)	0.1±0.01	0.06±0.01	1.76±1.15
Acid saturation (%)	0.5±0.12	0.06±0.06	6.06±3.69
Vegetation			
Vegetation type	Tsomo grassland	Tsomo grassland	Tsomo grassland
Shrub species	<i>Euryops floribundus</i>	<i>Euryops floribundus</i>	<i>Euryops floribundus</i>
Grass species	<i>Aristida congesta</i> , <i>Elionurus muticus</i>	<i>Aristida congesta</i> , <i>Elionurus muticus</i>	<i>Aristida congesta</i> , <i>Elionurus muticus</i>
	<i>Eragrostis chloromelas</i> , <i>Eragrostis plana</i>	<i>Eragrostis chloromelas</i> , <i>Eragrostis plana</i>	<i>Eragrostis chloromelas</i> , <i>Eragrostis plana</i>
	<i>Sporobolus africanus</i> , <i>Themeda triandra</i>	<i>Sporobolus africanus</i> , <i>Themeda triandra</i>	<i>Sporobolus africanus</i> , <i>Themeda triandra</i>

for 48 hours, followed by grinding into powder using a waring commercial laboratory blender. We also collected soil samples from the topsoil layer (0-10 cm) at the four corners and middle part of the plot to form a composite soil sample representing each plot. Soil samples were placed in labelled plastic bags, sealed, and transported to the laboratory for further processing.

Leaf and Soil Sample Analysis

Leaf material samples were analyzed for Calcium (Ca), Phosphorus (P), Potassium (K), Magnesium (Mg), Manganese (Mn), Copper (Cu), and Zinc (Zn) at the Plant Laboratory of the Department of Agriculture in Western Cape, South Africa. The analysis was conducted following Method 6.1.1 of the Agricultural Laboratory Association of Southern Africa (ALASA) (ALASA 1998). Before analyses of collected samples in the laboratory, the soils were air-dried and sieved through a 2-mm aperture metal

sieve to eliminate visible plant residues. Soil pH was measured using a glass electrode in a 1:2.5 ratio solution in 1 M KCl suspension (Dlamini et al. 2019). Exchangeable base cations, including Calcium (Ca) and Magnesium (Mg) were initially extracted using 1 M KCl solution, whereas Phosphorus (P), Potassium (K), Zinc (Zn), Manganese (Mn) and Copper (Cu) were extracted using an Ambic 2 extractant containing 0.25 M NH_4HCO_3 . The extracted cations were detected using inductively coupled plasma optical emission spectrometry (ICP-OES) with an Optima 7300DV spectrometer (Perkin Elmer, Inc., 2 Shelton, CT). The effective cation exchange capacity (ECEC) was determined by summing the KCl-extractable calcium (Ca), magnesium (Mg), acidity, and extractable potassium (K). Percentage acid saturation of the ECEC was calculated as $\text{extractable acidity} \times 100 / (\text{Ca} + \text{Mg} + \text{K} + \text{extractable acidity})$ (Dlamini et al. 2019). Soil organic carbon and clay content was estimated by the mid-infrared spectroscopy (MIRS) (Thomas et al. 2021; Ng et al. 2022).

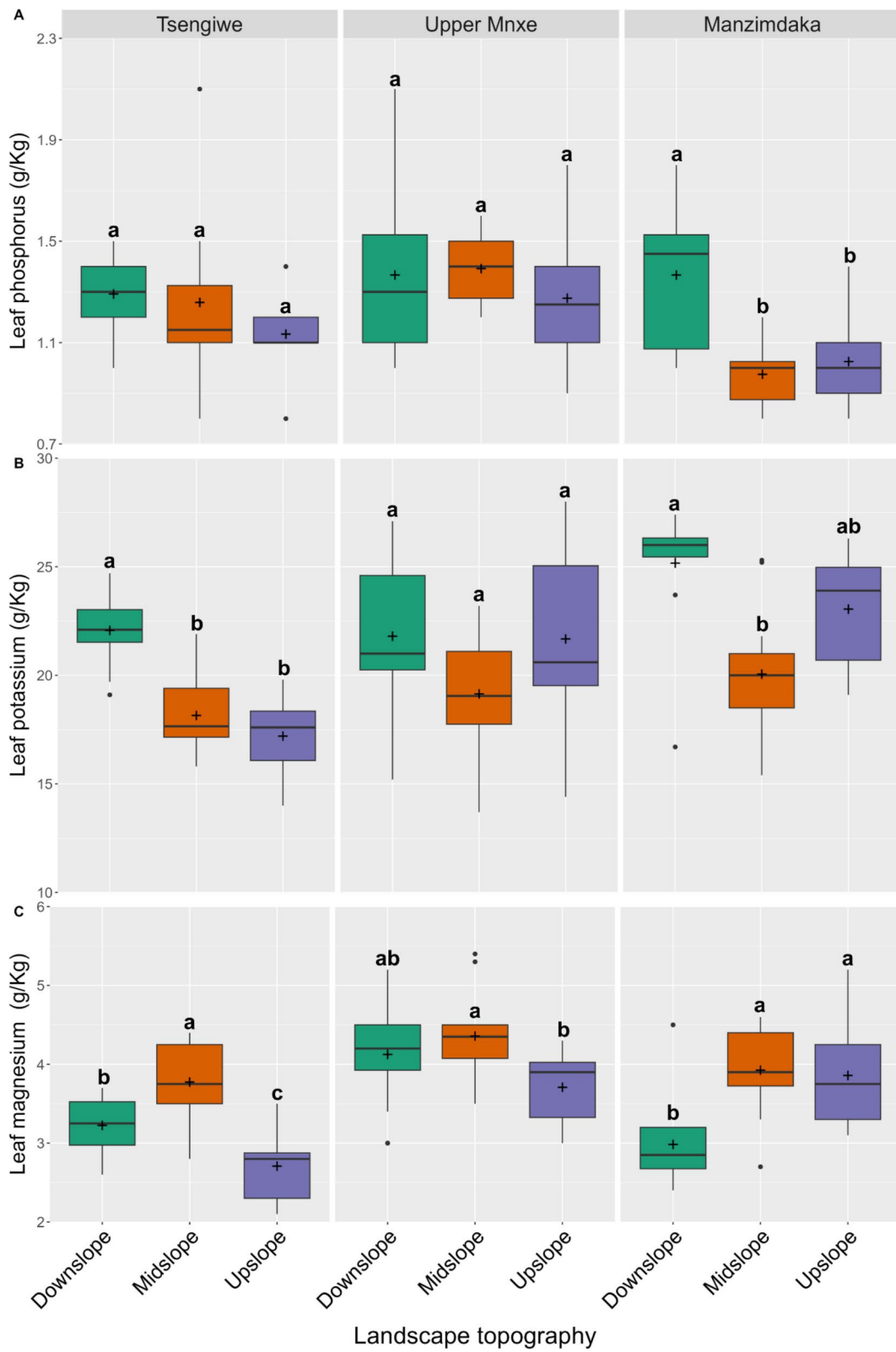


Fig. 2 Box plots showing the distribution of **A** Phosphorus, **B** Potassium and **C** Magnesium in *Euryops floribundus* leaves in Tsengiwe, Upper Mnxe and Manzimdaka. Box plot elements: box = values of 25th and 75th percentiles; horizontal line = median; symbol + = mean, whiskers = values of 5th and 95th percentiles. Black dots outside the whiskers represent the outliers. Different letters denote significant differences at $p \leq 0.05$ across the topographic positions.

Statistical Analysis

All data analysis and graphics were conducted using R version 4.4.1 (R Core Team 2024). Before any analysis, the data were tested for normal distribution using the Shapiro-Wilk test and variance homogeneity using Levene's test. If non-normality was detected, the data were transformed accordingly to meet the assumptions of normality and equal variances. The data was then back-transformed for graphical presentation (Salekin et al. 2023). A one-way analysis of variance (ANOVA) was conducted to investigate the influence of landscape topography on the concentration of nutrients in the leaves (P, K, Ca, Mg, Mn, Cu, and Zn) of the encroaching shrub species on each landscape site. Results were deemed significant at $p \leq 0.05$. A post-hoc analysis was then performed using the Tukey test. To investigate factors influencing nutrient content in the leaves of *Euryops floribundus*, we conducted a principal component analysis (PCA) to examine the relationships between soil properties and leaf nutrients. This PCA analysis was carried out using the “FactoMineR” and “factoextra” packages (Kassambara and Mundt 2017). A permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) was performed to evaluate if there were significant differences regarding leaf nutrients and soil chemistry along the landscape topographic positions (downslope, midslope, and upslope) using the vegan package (Oksanen et al. 2024). In addition, we used the R packages “ggplot2”, “dplyr”, and “ggpubr” to visualise and manipulate data (Wickham 2016; Wickham et al. 2023a; Wickham et al. 2023b).

Results

Distribution of Leaf Macronutrients Across Landscape Topography

The macronutrient content of *Euryops floribundus* leaves varied across the landscape gradient within

three communal grazing sites (Fig. 2). Mean values are reported throughout the text, while both mean and median values are shown in the corresponding figures. Notably, leaf P content in the downslope position (1.37 g/kg) was 40% and 33% higher compared to the midslope (0.98 g/kg) and upslope (1.03 g/kg) positions, respectively in Manzimdaka ($p \leq 0.05$; Fig. 2 A). On the contrary, leaf P content did not differ significantly in the midslope and upslope topography of the landscape. In Tsengiwe, we observed no significant difference in leaf P content among the downslope (1.29 g/kg), midslope (1.26 g/kg), and upslope (1.13 g/kg) positions ($p > 0.05$; Fig. 2 A). Similarly, leaf P content did not significantly differ between the downslope (1.37 g/kg), midslope (1.39 g/kg), and upslope (1.28 g/kg) positions in Upper Mnxe ($p > 0.05$; Fig. 2 A). Leaf K content was significantly higher on the downslope (28% and 22%) (22.01 g/kg) compared to the midslope positions (18.15 g/kg) and upslope positions (17.20 g/kg) in Tsengiwe ($p < 0.05$; Fig. 2 B). Conversely, leaf K content did not vary significantly between the midslope and upslope positions. Leaf K content at Manzimdaka followed a similar pattern, with 20% greater in downslope position (25.17 g/kg) compared to midslope position (20.93 g/kg) ($p < 0.05$; Fig. 2 B). However, there was no significant difference in leaf K content between downslope and upslope (23.05 g/kg) positions as well as in the midslope and upslope positions. In Upper Mnxe, leaf K content did not differ significantly across the downslope (21.80 g/kg), midslope (19.14 g/kg), and upslope (21.68 g/kg) positions ($p > 0.05$; Fig. 2 B). In Tsengiwe, leaf Mg content was significantly higher in the downslope of the landscape (19 %) (3.23 g/kg) than upslope (2.71 g/kg) ($p < 0.05$; Fig. 2 C). On the contrary, leaf Mg was significantly lower on downslope (15 %) (3.23 g/kg) compared to midslope (3.78 g/kg) position. Furthermore, leaf Mg declined significantly by 28% upslope compared to midslope positions. Leaf Mg was significantly higher downslope (11%) (4.13 g/kg) compared to upslope (3.71 g/kg) positions in Upper Mnxe ($p < 0.05$; Fig. 2 C). However, leaf Mg did not differ between the downslope (4.13 g/kg) and midslope (4.36 g/kg) as well as between midslope and upslope positions. In Manzimdaka, leaf Mg was significantly lower downslope (23% and 24%) (2.98 g/kg) compared to midslope (3.93 g/kg) and upslope (3.86 g/kg) positions ($p < 0.05$; Fig. 2 C). Conversely, leaf

Mg did not differ significantly between midslope and upslope positions. In all landscape sites investigated, Ca concentration in leaves did not show significant differences across the landscape topography ($p > 0.05$; Table S1).

Changes in Leaf Micronutrient Distribution Across Topographic Positions

Concentration of Mn in the leaves of the *Euryops floribundus* varied with landscape position across the sites. On average, leaf Mn concentration declined by 63% and 55% downslope (34.0 mg/kg) and midslope (41.67 mg/kg) compared to the upslope position (93.08 mg/kg) in Upper Mnxe ($p < 0.05$; Fig. 3 A). However, leaf Mn content did not differ significantly between the downslope and midslope positions. In Tsengiwe and Manzindaka, leaf Mn was not significant across the topographic positions ($p > 0.05$; Fig. 3 A). Leaf content of Zn was significantly higher (35% and 37%) on the downslope (26.98 mg/kg) than on the midslope (20.01 mg/kg) and upslope positions (19.67 g/kg) in Tsengiwe ($p < 0.05$; Fig. 3 B). Conversely, leaf Zn did not differ significantly between midslope and upslope positions. Leaf Zn content at Manzindaka mirrored the trend observed at Tsengiwe, with a 28% increase in downslope (24.29 mg/kg) compared to both midslope (19.03 mg/kg) and upslope (19.04 mg/kg) positions ($p < 0.05$; Fig. 3 B). In contrast, there was no significant difference observed in leaf Zn content in midslope and upslope positions. In all three landscape sites, leaf Cu showed no significant variation across landscape topography ($p > 0.05$; Table S1).

Variation in Leaf Nutrient Distribution Across Landscape Topography

Landscape topography significantly influenced the macronutrients (P, K, and Mg) and the micronutrient (Zn) in *Euryops floribundus* leaves. Notably, Leaf P content was significantly higher on the downslope (18%) (1.34 g/kg) compared to the upslope position (1.14 g/kg) ($p < 0.05$; Fig. 4 A). On the contrary, leaf P content did not vary significantly between the downslope and midslope (1.21 g/kg) positions as well as in the midslope and upslope positions. Leaf K content in the downslope position (23.01 g/kg) was 19% and 11% higher compared to the midslope (19.41 g/

kg) and upslope (20.64 g/kg) positions, ($p \leq 0.05$; Fig. 4 B). However, leaf K content did not differ significantly in the midslope and upslope topographic positions. Leaf Mg was significantly lower downslope (14% and 15%) (3.44 g/kg) and upslope (3.43 g/kg) compared to midslope (4.02 g/kg) position ($p < 0.05$; Fig. 4 C). Conversely, leaf Mg concentration did not differ significantly in the downslope and upslope topographic positions. Leaf content of Zn was significantly higher (23% and 31%) on the downslope (26.0 mg/kg) than on the midslope (21.17 mg/kg) and upslope (19.78 g/kg) ($p < 0.05$; Fig. 4 D). Conversely, leaf Zn did not differ significantly between midslope and upslope topographic positions. Additionally, landscape topography did not significantly influence the concentrations of Ca, Mn and Cu in the leaves of *Euryops floribundus* ($p > 0.05$; Table S2).

Correlation Between Edaphic Soil Factors and Leaf Nutrients Variables of *Euryops floribundus*

The relationship between soil edaphic factors and leaf nutrients of the *Euryops floribundus* were visualized by PCA, with the first two axes explaining 46.7% of the variance in Tsengiwe (Fig. 5 A). There was a significant differentiation between downslope, midslope, and upslope along the first principal component (PC1) (PERMANOVA, $R^2=0.5199$, $p=0.001^{**}$). This axis accounted for 31.7% of the total variance and showed a positive relationship with soil manganese, soil phosphorus, soil potassium, leaf potassium, and leaf zinc in downslope and midslope positions (Fig. 5 A and D). The second principal component (PC2), which accounted for 15 % of the total variation showed a significant separation among downslope, midslope, and upslope position (PERMANOVA, $R^2=0.2971$, $p=0.005^{**}$). This axis reflected a positive correlation between soil copper content, soil clay content, and leaf magnesium in the midslope and upslope topographic positions. In Upper Mnxe, the first and second axes of the PCA explained 30.7% and 15.8% of the total data variation (Fig. 5 B). The PC1 revealed a positive correlation with soil copper, soil phosphorus, soil zinc and leaf potassium, while showing a negative correlation with soil calcium, soil effective cation exchange capacity (ECEC), and leaf magnesium (Fig. 5 B and D). However, the PCA showed no significant separation between downslope, midslope and upslope positions along

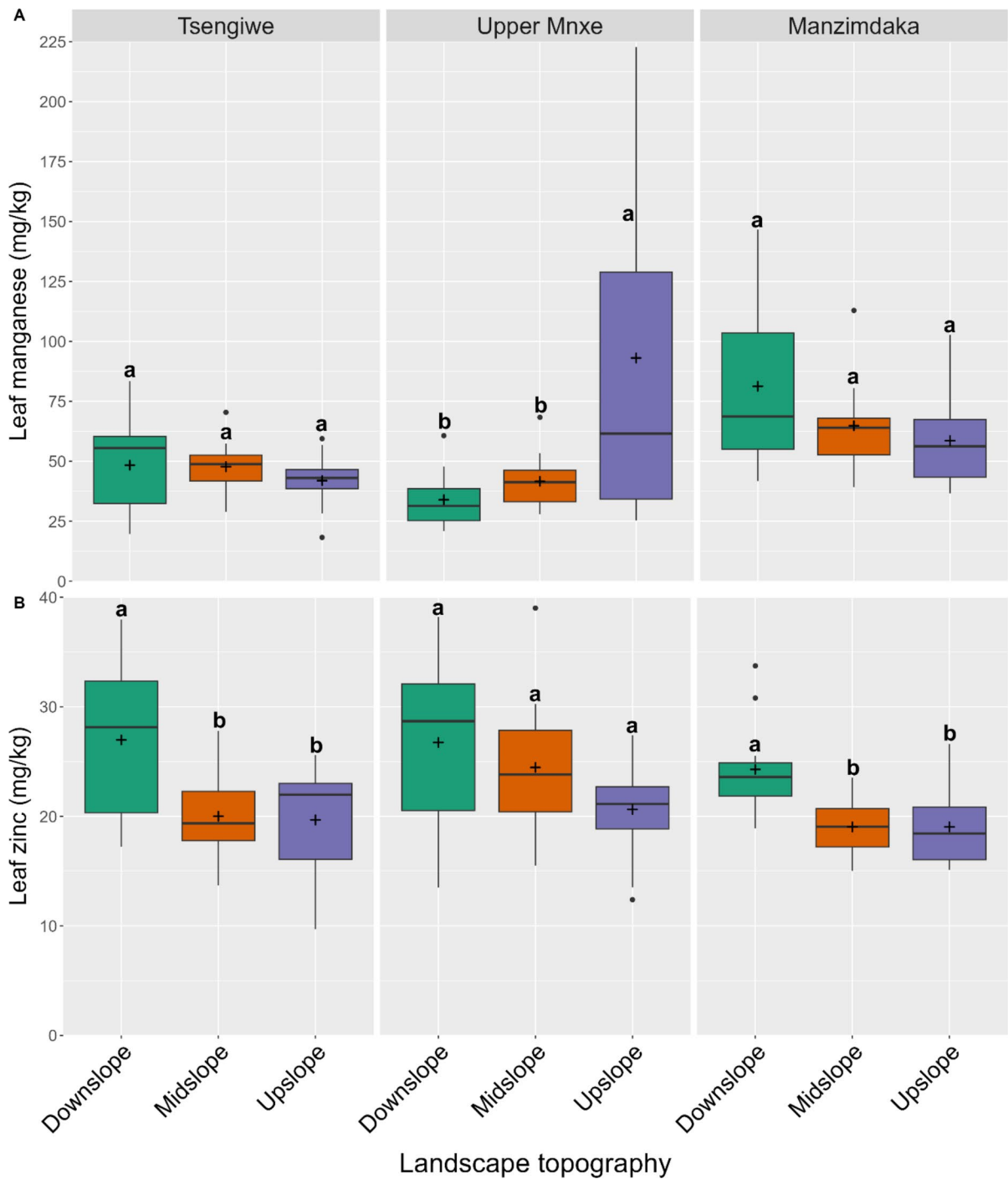
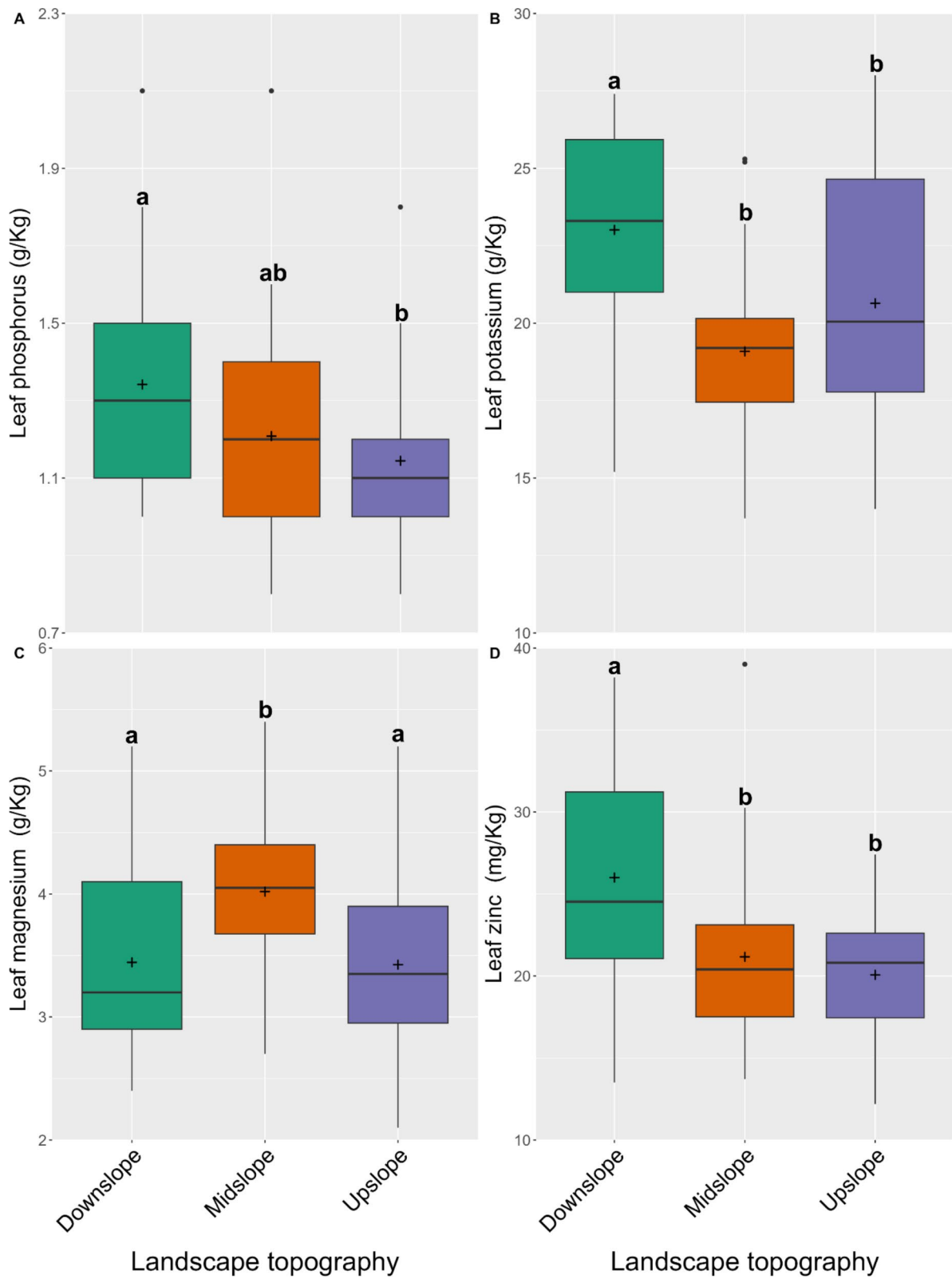


Fig. 3 Box plots showing the distribution of **A** Manganese and **B** Zinc in *Euryops floribundus* leaves in Tsengiwe, Upper Mnxe and Manzimdaka. For content details, see Fig. 2.



◀**Fig. 4** Box plots showing the distribution of **A** Phosphorus, **B** Potassium, **C** Magnesium and **D** Zinc in *Euryops floribundus* leaves across three sites. For content details, see Fig. 2.

the PC1 (PERMANOVA, $R^2=0.1541$, $p=0.067$). The PC2 showed a significant separation between downslope, midslope and upslope positions (PERMANOVA, $R^2=0.1732$, $p=0.047^*$). The parameters that were positively correlated with the second principal component were soil exchangeable acidity (EA), soil acid saturation (AS) and leaf manganese in the upslope position. In Manzimdaka, PC1 explained 28 % of the data variation and presented positive correlation loadings with soil EA, soil ECEC, soil AS, leaf phosphorus and leaf manganese (Fig. 5 C and D). Although, there was no significant separation between downslope, midslope and upslope positions along this axis (PERMANOVA, $R^2=0.1571$, 0.1732 , $p=0.053$). The PCA revealed that the downslope separates from midslope and upslope mainly along PC2 (16.5 % of variance explained), which was positively correlated with soil copper and leaf zinc (PERMANOVA, $R^2=0.4506$, 0.1732 , $p=0.001^{***}$).

Discussion

Influence of landscape topography and soil chemistry on leaf macronutrients of *Euryops floribundus*

Woody species segregate along landscape gradients often defined by topography and soil edaphic characteristics (Zuleta et al. 2020). Topography is a critical landform attribute that controls plant distribution and diversity patterns. Within landscape ecosystems, topographically driven hydrological variation is a key factor structuring the distribution of tree species (Zuleta et al. 2020). Soil properties mirror the effect of topography and define the patterns for woody plant growth and encroachment. As such, the proliferation of woody plant species in mountainous grasslands can be locally mediated by edaphic soil factors such as soil type (shallow vs. deep soils), chemical and physical soil properties (soil texture, cation availability) and soil depth (Dlamini et al. 2019; Gxasheka et al. 2023). In mountainous regions, landscape topography has been reported by some studies to influence soil nutrient availability (Rezaei and Gilkes 2005; Liu et al. 2020; Zhang et al. 2021). Work by Davies

et al. (2005) suggested that the variation in floristic composition is more strongly related to soil nutrient availability, particularly P and Mg. The nutrients inherent in the soil in turn, influence the concentration of macronutrients (e.g. P, K, Ca and Mg) within the leaves of the woody plants found along varying topographic positions (Drollinger et al. 2017; Wang et al. 2018; Liu et al. 2020).

In this study, we examined differences between leaf nutrient concentrations of *Euryops floribundus* shrub species located along different topographic positions and the inherent soil edaphic characteristics of mountainous grasslands in eastern South Africa. In the mountainous grassland landscape sites investigated, we posit that variations in soil nutrients along the topographic positions constrain the distribution of the *Euryops floribundus* and may thereby contribute to the variations in the concentrations of the leaf nutrients. We found that leaf P concentration was not significantly different in Tsengiwe and Upper Mnxe, but there were significant differences in the concentration of leaf P across the topographic positions at Manzimdaka, which is characterized by a slightly higher elevation of 1320 meters above sea (Table 1). Specifically, the *Euryops floribundus* located in downslope areas in Manzimdaka had a significantly higher concentration of leaf P compared to those shrubs found in the midslope and upslope topographic positions. A similar trend was also evident when data was pooled from all three landscape sites (Fig. 4 A). As reported here and in other parts of the world, leaf nutrient P concentrations can increase, decline or even stay consistent, with increasing elevation (Vitousek et al. 1988). Qin et al. (2022) observed higher leaf P concentration at lower elevations compared to higher elevations in the northeastern region of the Qinghai-Tibet Plateau, China. In the northeast part of Central Nepal, Drollinger et al. (2017) also observed a significant decrease in leaf P concentrations with increasing elevation. The leaf P patterns reported across varying landscapes could be attributed to the fact that elevation alters ecosystem properties, and subsequently the processes that regulate plant nutrient supply associated with soil nutrient availability (Mayor et al. 2017). At the landscape scale, topography can determine P redistribution across different topographic positions. The low leaf P concentrations from upslope and midslope positions at Manzimdaka could be linked to the lowest available P availability on the steepest slopes

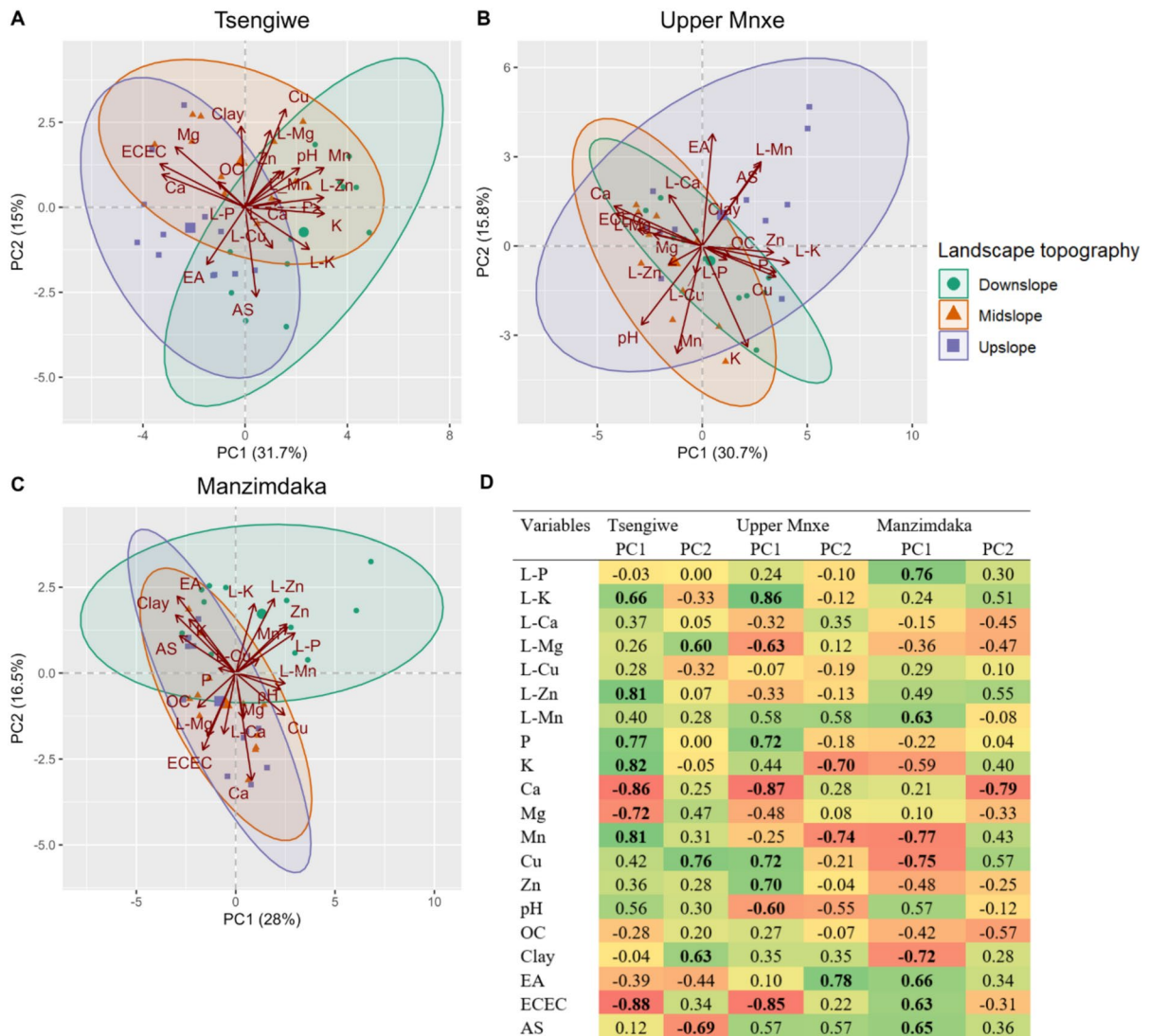


Fig. 5 Principal component analysis (PCA) showing relation between leaf nutrients and soil edaphic factors in **A** Tsengiwe, **B** Upper Mnxe and **C** Manzimdaka mountainous grassland positioned with regard to the first two components axes. Ellipses represent similarity at 95% confidence intervals for the three landscape topographical positions. Parameter abbreviations are as follows: L-P: phosphorus; L-K: potassium; L-Ca: leaf calcium; L-Mg: leaf magnesium; L-Cu: leaf copper; L-Zn: leaf zinc; L-Mn: leaf manganese; P: phosphorus; K: potassium; Ca: calcium; Mg: magnesium; Cu: copper; Zn: zinc;

Mn: manganese; EA: exchange acidity; ECEC: effective cation exchange capacity; AS: acid saturation; pH: pH; OC: organic carbon. **Note:** Loading values > 0.60 or < -0.60 are considered high correlations and are highlighted in bold. The colour gradient in Table D represents both the magnitude and the direction of the correlation coefficients among different variables in a PC component. A highly significant negative or positive correlation is represented by red and green colour gradients, and weak or near-zero correlations by a yellow gradient.

because of P removal by water flow and erosion (Dessalegn et al. 2014). In our study, soil chemistry, and in particular effective cation exchange capacity, exchangeable acidity and acid saturation of soil were the most important soil edaphic factors determining

leaf P concentration in the downslope positions of the mountainous grasslands. Phosphorus is the least available and least mobile of the plant macronutrients in most soils. That said, the positive relationship between the soil properties linked to the chemistry of

the soil suggests that their increase in the grassland soils is likely to increase P availability and uptake by *Euryops floribundus*, especially in areas located in downslope positions. Such changes in the chemistry of the soil are most likely because an increase in the effective cation exchange capacity increases the availability and mobility of P in the soil (Jones and Jacobsen 2005), and this change may make P to be more accessible for uptake by the shrub species. The prevalent acidic soil pH conditions at the three sites; Tsengiwe (soil pH = 5.24), Upper Mnxe (5.14) and Manzimdaka (5.13) and the varied growth patterns of the *Euryops floribundus* under these soil conditions suggest distinct mechanisms for P cycling and uptake in the studied mountainous grasslands. Soil pH is considered to be the “master variable” in the soil due to its profound impact on a myriad of chemical reactions that influence essential plant nutrients (Penn and Camberato 2019). Indeed, soil pH impacts sorption and desorption soil chemical processes that control P solubility. It appears that *Euryops floribundus* thrives under acidic soil conditions and its increased proliferation in low pH soils translates to greater P uptake even if P solubility is generally lower in acidic soils. This is because certain plant species develop the ability to adapt and survive in acidic soil conditions (Penn and Camberato, 2019). It is plausible that roots of *Euryops floribundus* may be colonized by arbuscular mycorrhizal fungi, which extend extensive mycelial networks into the soil. This symbiotic relationship is central to plant nutrient acquisition, as it increases the uptake of diffusion-limited nutrients such as P from the soil (Hacisalihoglu and Kochian 2003; Frew et al. 2025), consequently increasing the competitive ability of the species and promoting its expansion across the studied grassland landscapes. Going forward, we need to explore this probable root-mediated process to further elucidate the ecological interactions of *Euryops floribundus* in mountainous grassland landscapes.

In Tsengiwe and Manzimdaka, shrubs in downslope positions showed higher leaf K concentration compared to midslope and upslope positions. Also, the combined data from all three sites showed a similar pattern (Fig. 4 B). The higher leaf K concentrations in shrubs at the downslope positions was likely enhanced by soil nutrient availability, particularly of soil K. This inference is supported by the positive correlation between leaf K concentration and

soil macronutrients nutrients (K, P) as well as micronutrients (Cu and Mn). In line with our results, Wang et al. (2018) observed an increase in leaf K content at lower elevations in Southwestern, China. Similarly, Wu et al. (2007) documented higher leaf K concentrations on downslope positions compared to other slope positions in the southernmost region of Taiwan. Furthermore, Drollinger et al. (2017) reported higher leaf K concentrations at lower elevation sites compared to higher elevation sites in the northeast part of Central Nepal.

Although this study was not explicitly designed to evaluate the effects of grazing on shrub nutrients, the higher leaf macronutrient concentrations in downslope areas are likely associated with livestock grazing, particularly manuring associated with urine and dung deposition in overgrazed areas. In semi-arid mountainous landscapes, livestock predominantly prefer to graze in downslope areas than other landscape positions. For example, Raynor et al. (2021) found that downslope areas were grazed 120% more than upland areas by cattle. Similarly, Sigua et al. (2011) reported that cattle spent 40-50% of their grazing time in downslope areas. This spatial grazing pattern is linked to gentler topography and the availability of palatable forage compared to upland areas and the proximity to resources like homesteads and water access points (Gartzia et al. 2016; Hoogenboom et al. 2016; Masibonge et al. 2019; Yongdong et al. 2024). Consequently, this grazing preference leads to localised deposition of dung and urine which contribute to the enrichment of the soil nutrient pool (Haynes and Williams 1993; Schnyder et al. 2010; Sigua et al. 2011; Li et al. 2021), potentially increasing leaf nutrient content of downslope populations of *Euryops floribundus*. To support this perspective, a study conducted in China by Li et al. (2021) found that a mixture of dung and urine increased P content in plants compared to the control. Furthermore, this livestock preference for grazing downslope areas leads to overgrazing of palatable grasses and subsequent reductions to root biomass, photosynthetic capacity and weakens the ability to compete for soil nutrients (Briske and Richards 1994; García-Pausas et al. 2017; Getabalew and Alemneh 2019; Umuhoza et al. 2021; Yongdong et al. 2024). In this study, the unpalatable *Euryops floribundus* species may have the advantage to uptake more nutrients as the desirable grasses decline, increasing leaf nutrient content

which may promote growth and dominance. These findings suggest that downslope areas would benefit from specific management practices such as seasonal rest to encourage recovery of palatable grass species as well as controlling livestock grazing to redistribute nutrient-rich manure across the landscape.

In contrast to other macronutrients (P and K), leaf Mg concentration of the shrubs showed an unclear pattern, both at the site level and in the pooled data from the three investigated landscape sites. This unclear trend suggests that the underlying edaphic factors that drive leaf Mg concentration in *Euryops floribundus* differ depending on the landscape topography at the investigated sites. Notably, we observed higher leaf Mg concentration in the shrubs situated at the downslope position compared to those at the upslope position, but it was lower than that of the shrubs at the midslope position in Tsengiwe. This indicates a gradient of increasing Mg uptake from upslope to downslope position, with midslope position showing the highest concentration of leaf Mg. This observed concentration of leaf Mg can be explained by the positive correlation established between leaf Mg and soil micronutrients (Mg and Cu) as well as soil clay content in the midslope position (Fig. 5 A and D). Both topography and soil texture interactively affect water conditions and nutrients (Itoh et al. 2003). As reported by Hirai et al. (1997), soil fertility generally increases with increasing clay content, and as such the positive correlation of these soil edaphic factors suggests that clayey soils are mostly found in the midslope and downslope positions at Tsengiwe where they retain soil Mg and Cu, and this probably enhances the concentration of the leaf Mg taken up by the *Euryops floribundus*. In line with our findings of higher leaf Mg concentrations in lower topographic positions, Macek et al. (2012) found that leaf Mg concentrations were higher at lower elevations than at higher elevations in the northwest Himalayas of India. In the northeastern United States, Friedland et al. (1988) also observed that leaf Mg concentrations were higher at lower elevations as opposed to higher elevations. Furthermore, Müller et al. (2016) reported that leaf Mg concentrations were higher in lower elevations than higher elevations in Rolwaling Himal, Nepal. Contrary to Tsengiwe, leaf Mg content at downslope position was not significantly different compared to midslope and upslope

positions, although midslope was greater than upslope in Upper Mnxe. The higher leaf Mg content aligns with the expected trend of favourable soil conditions from upslope to midslope positions (Alonso-Amelot 2008; Guzman et al. 2019). In support of this view, we revealed a positive correlation between leaf Mg content and soil Cu and clay content (Fig. 5 B and D) suggesting that an increase in these soil properties increases the concentration of Mg in the leaves of the *Euryops floribundus* located on the midslope position. In addition, the absence of significant differences of leaf Mg content at downslope and midslope positions suggests relative uniformity in the uptake of Mg by shrub species as they encroach the different topographic positions. In Manzimdaka, leaf Mg concentration was lower downslope compared to midslope and upslope positions. This pattern can be attributed to the strong negative correlation between leaf Mg content and soil Ca downslope (Fig. 5 C and D). The negative relationship suggests that as Ca content increases in the soil, the uptake of Mg by the *Euryops floribundus* decreases. This observation was also observed in other studies elsewhere (Metson 1974; Gransee and Führs 2013; Sun et al. 2013) which reported that an increase of exchangeable Ca in the soil may hinder the uptake of Mg by plants, thus potentially explaining the lower leaf Mg concentration. To accurately capture the soil edaphic factors, a detailed soil survey accompanied by intensive soil classification in the mountainous grassland sites is needed to fully understand the mechanisms by which they operate and their effects on the woody plant structure of *Euryops floribundus*. For example, a detailed survey of soils by Hirai et al. (1997) in Serawak, Malaysia revealed that soils located at the base of mature *Dryobalanops lanceolata* trees had higher amounts of exchangeable Ca, Mg and K and available P than soils under *Dryobalanops aromatica* trees.

Leaf Micronutrients of *Euryops floribundus* Across Different Landscape Topography

Leaf micronutrients are required in small quantities, and they play a pivotal role in facilitating optimal metabolic processes during plant growth (Hagen-Thorn and Stjernquist 2005; Marschner 2011; Gupta

et al. 2016; Pandey 2018). In this study, we observed a consistent pattern of increasing leaf Zn content from upslope to downslope positions across the three studied landscape sites. Notably, these observed patterns were significantly pronounced at Tsengiwe and Manzimdaka sites. This same trend was also noticeable in the combined data from all three sites (Fig. 4 D). The explanation for these leaf nutrient patterns is linked to our finding that leaf Zn concentrations are influenced by different soil properties in the downslope positions of these sites (Fig. 5). Specially, leaf Zn content was positively correlated with soil nutrients (P, K, Mn) in Tsengiwe site (Fig. 5 A and D). This positive correlation suggests that an increase in P, K, and Mn in the soil influences the uptake and accumulation of Zn content in shrubby leaves of *Euryops floribundus*. Surprisingly, leaf Zn content was not explained by any of the measured soil properties including Zn concentration in the soil at Manzimdaka site. Other studies (Russell and Van Moort 1981; Wu et al. 2007) have also noted that leaf Zn content were not correlated with soil properties, including soil Zn content in Australia and Taiwan. In our study, the higher leaf Zn levels are attributed to the presence of deep, coarse-textured soils occurring in downslope positions, which facilitate the penetration of shrub roots for Zn absorption. The main taproot and many thinner roots of *Euryops floribundus* observed in the field probably increases the root surface area, facilitating extensive exploration of the soil, thus increasing the availability of Zn (Hacisalihoglu and Kochian 2003). Additionally, this process may be enhanced by proteins and amino acids in the root tissue that bind with Zn, increasing the storage of Zn and facilitating its absorption (Hamzah Saleem et al. 2022). In this study, we also observed that landscape topography did not significantly affect leaf Mn content in Tsengiwe and Manzimdaka, except at Upper Mnxe. Specifically, we found significantly lower leaf Mn content in the downslope position compared to the upslope position at the Upper Mnxe grassland site. This observed trend in leaf Mn content suggests that *Euryops floribundus* may adapt its nutrient uptake in response to certain landscape conditions. Supporting this observation, Du et al. (2017) found that plants may dynamically and synergistically modify their nutrient concentration in response to environmental changes. Similar findings regarding leaf Mn were also reported elsewhere by Martin et al. (2020),

who observed an increase in leaf Mn along an elevational gradient. Additionally, Drollinger et al. (2017) reported a decrease of foliar N, Mg, K and P nutrient concentrations with increasing elevation and an increase in folia Mn concentrations, which was linked to the strong accumulation of Mn in leaves caused by very high acidic soil conditions, that allow for solubilization and availability of Mn for plant uptake.

Conclusion

In this study, we investigated how landscape topography influences the leaf nutrient content of the encroaching shrub *Euryops floribundus* in mountainous grassland sites. We observed significant variations in leaf macro- and micronutrient concentrations of *Euryops floribundus* across different topographic positions in the sites investigated. Specifically, the findings showed a consistent trend of decreasing leaf P concentration from upslope to downslope positions in Manzimdaka. Multivariate analysis revealed that soil properties such, effective cation exchange capacity, soil exchange acidity, and soil acid saturation had a strong influence on the concentration of leaf P. Similarly, we found a decline in leaf K concentration from upslope to downslope positions in Tsengiwe and Manzimdaka, with multivariate analysis showing that the availability of soil K increases the leaf K content in *Euryops floribundus* shrubs found in downslope areas. Conversely, the pattern of leaf Mg concentration across landscape topography was unclear, suggesting site-specific variations in the mechanisms by which *Euryops floribundus* absorbs Mg from the soil. Furthermore, we found contradictory trends in leaf micronutrient concentrations, with Zn concentration declining from upslope to downslope positions in Upper Mnxe and Mn concentration decreasing from downslope to upslope positions in Tsengiwe and Manzimdaka. Overall, the observed spatial variations in leaf nutrient concentrations in our study suggests a remarkable adaptability of *Euryops floribundus* to diverse landscape conditions, with a particularly pronounced accumulation of leaf nutrients evident in downslope areas of the studied mountainous grasslands. Consequently, this adaptability is most likely contributing greatly to its proliferation as it encroaches the grasslands. While this study focused on the influence of landscape topography

on the leaf nutrient content of *Euryops floribundus*, future research should look into the coupled effect of soil microbial communities and soil properties on the leaf nutrient stoichiometry and structural traits of encroaching shrub species across elevational gradients. Understanding these interactions is crucial for gaining insight into the nutrient acquisition strategies employed by encroaching shrub species like *Euryops floribundus* in mountainous grasslands.

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Authors' Contributions The experiment was designed and planned by MG and PD. MG conducted the field sampling, entered the data into MS Excel, and performed the statistical analyses. MG drafted the initial manuscript, while PD provided feedback on the earlier versions. All authors have read and approved the final manuscript.

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Data Availability The data for the current study will be made available upon reasonable request.

Declarations

Conflict of Interests The authors declare that they have no competing interests.

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References

- ALASA (1998) Method 6.1.1: dry ashing. In: Palic, D. (ed.) Handbook of feeds and plant analysis. ALASA, Pretoria, South Africa.
- Alonso-Amelot ME (2008) High altitude plants, chemistry of acclimation and adaptation. *Studies in Nat Prod Chem* 34: 883–982. [https://doi.org/10.1016/S1572-5995\(08\)80036-1](https://doi.org/10.1016/S1572-5995(08)80036-1)
- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26(1): 32–46. <https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x>
- Archer SR, Andersen EM, Predick KI, Schwinning S, Steidl RJ, Woods SR (2017) Woody plant encroachment: causes and consequences. *Rangeland systems: Processes, management and challenges* 25–84.
- Bora Z, Angassa A, Wang Y, Xu X, You Y (2021) Effect of elevation on the density and species composition of encroacher woody plants in Borana rangeland, southern Ethiopia. *Environ Manag* 67(6):1075–1087. <https://doi.org/10.1007/s00267-021-01458-x>
- Briske DD, Richards JH (1994) Plant responses to defoliation: A physiological, morphological and demographic evaluation. In Bedunah DJ & Sosebee RE (Eds.), *Wildland plants: Physiological ecology and developmental morphology* (pp. 635–710). Society for Range Management.
- Cipollini D, Walters D, Voelckel C (2018) Costs of resistance in plants: from theory to evidence. *Annu. Plant Rev Online* 263–307. <https://doi.org/10.1002/9781119312994.apr0512>
- Davies SJ, Tan S, LaFrankie JV, Potts MD (2005) Soil-related floristic variation in a hyperdiverse dipterocarp forest in Lambir Hills, Sarawak. In: Roubik DW, Sakai S, Hamid A (eds) *Pollination ecology and the rain Forest diversity*. Sarawak Studies. Springer-Verlag, New York, pp 22–34
- Dendoncker M, Vincke C (2020) Low topographic positions enhance woody vegetation stability in the Ferlo (Senegalese Sahel). *J Arid Environ* 175:104087 <https://doi.org/10.1016/j.jaridenv.2019.104087>
- Department of Agriculture, Forestry and Fisheries (DAFF) (2018) Conservation of Agricultural Resources Act: Long-term grazing capacity map for South Africa 2017. Government gazette, No.41870. https://www.gov.za/sites/default/files/gcis_document/201808/41870gon898r.pdf (accessed 13 March 2025).
- Dessalegn D, Beyene S, Ram N, Walley F, Gala TS (2014) Effects of topography and land use on soil characteristics along the toposequence of Ele watershed in southern Ethiopia. *Catena* 115:47–54. <https://doi.org/10.1016/j.catena.2013.11.007>
- Dlamini P, Mbanjwa V, Gxasheka M, Tyasi L, Sekhohola-Dlamini L (2019) Chemical stabilisation of carbon stocks by polyvalent cations in plinthic soil of a shrub-encroached savanna grassland, South Africa. *Catena* 181:104088.
- Drollinger S, Müller M, Kobl T, Schwab N, Böhner J, Schickhoff U, Scholten T (2017) Decreasing nutrient concentrations in soils and trees with increasing elevation across a treeline ecotone in Rolwaling Himal, Nepal. *J. Mt. Sci* 14:843–858. <https://doi.org/10.1007/s11629-016-4228-4>
- Du B, Ji H, Peng C, Liu X, Liu C (2017) Altitudinal patterns of leaf stoichiometry and nutrient resorption in *Quercus*

- variabilis in the Baotianman Mountains, China. *Plant Soil* 413:193–202. <https://doi.org/10.1007/s11104-016-3093-9>
- Frew A, Powell JR, Heuck MK, Alborno FE, Birnbaum C, Dearnaley JD, Egidi E, Finn L, Kath J, Koorem K, Oja J, Öpik M, Vahter T, Vasar M, Watts-Williams S, Zheng Y, Aguilar-Trigueros CA (2025) AusAMF: The Database of Arbuscular Mycorrhizal Fungal Communities in Australia. *Glob Ecol Biogeogr* 34(7): e70090. <https://doi.org/10.1111/geb.70090>
- Friedland AJ, Hawley GJ, Gregory RA (1988) Red spruce (*Picea rubens* Sarg.) foliar chemistry in northern Vermont and New York, USA. *Plant Soil* 105:189–193.
- Fu BJ, Liu SL, Chen LD, Lü YH, Qiu J (2004) Soil quality regime in relation to land cover and slope position across a highly modified slope landscape. *Ecol Res* 19:111–118.
- García-Pausas, J, Montané F, Rios AI, Taull M, Rovira P, Casals P (2017) Are soil carbon stocks in mountain grasslands compromised by land-use changes? In: Catalan J, Ninot JM, Aniz M (eds) High mountain conservation in a changing world. Springer Nature, Cham, pp 207–230. https://doi.org/10.1007/978-3-319-55982-7_9
- Gartzia M, Alados CL, Perez-Cabello F (2014) Assessment of the effects of biophysical and anthropogenic factors on woody plant encroachment in dense and sparse mountain grasslands based on remote sensing data. *Prog Phys Geogr* 38(2):201–217. <https://doi.org/10.1177/030913331452>
- Gartzia M, Fillat F, Pérez-Cabello F, Alados CL (2016) Influence of agropastoral system components on mountain grassland vulnerability estimated by connectivity loss. *PLoS One* 11(5): e0155193.
- Getabalew M Alemneh T (2019) Factors affecting the productivity of rangelands. *J. Plant Sci. Agric. Res* 3(1): 19.
- Gransee A, Fühns H (2013) Magnesium mobility in soils as a challenge for soil and plant analysis, magnesium fertilization and root uptake under adverse growth conditions. *Plant Soil* 368:5–21. <https://doi.org/10.1007/s11104-012-1567-y>
- Gupta N, Ram H, Kumar B (2016) Mechanism of Zinc absorption in plants: uptake, transport, translocation and accumulation. *Rev Environ Sci Biotechnol* 15:89–109. <https://doi.org/10.1007/s11157-016-9390-1>
- Guzman CD, Hoyos-Villada F, Da Silva M, Zimale FA, Chirinda N, Botero C, Vargas AM, Rivera B, Moreno P, Steenhuis TS (2019) Variability of soil surface characteristics in a mountainous watershed in Valle del Cauca, Colombia: Implications for runoff, erosion, and conservation. *J Hydrol* 576: 273–286. <https://doi.org/10.1016/j.jhydrol.2019.06.002>
- Gxasheka M (2013). *Euryops floribundus* Encroachment in Eastern Cape Communal Rangelands: Indigenous and Scientific Understanding of Effects on Range Ecology, and Food Security (Masters dissertation, University of Fort Hare).
- Gxasheka M, Dlamini P (2024) Slope aspect of a mountainous grassland landscape shapes the structure of an encroaching shrub (*Euryops floribundus* NE Br): insights from communal grazing sites located at varying distances from rural homesteads. *Community Ecol* 1–17. <https://doi.org/10.1007/s42974-024-00182-w>
- Gxasheka M, Gajana CS, Dlamini P (2023) The role of topographic and soil factors on woody plant encroachment in mountainous rangelands: A mini literature review. *Heliyon* 9 <https://doi.org/10.1016/j.heliyon.2023.e20615>
- Hacisalihoglu G, Kochian LV (2003) How do some plants tolerate low levels of soil zinc? Mechanisms of zinc efficiency in crop plants. *New Phytol* 159(2): 341–350. <https://doi.org/10.1046/j.1469-8137.2003.00826.x>
- Hagen-Thorn A, Stjernquist I (2005) Micronutrient levels in some temperate European tree species: a comparative field study. *Trees* 19:572–579. <https://doi.org/10.1007/s00468-005-0416-5>
- Hamzah Saleem M, Usman K, Rizwan M, Al Jabri H, Alsafan M (2022) Functions and strategies for enhancing zinc availability in plants for sustainable agriculture. *Front Plant Sci* 13:1033092. <https://doi.org/10.3389/fpls.2022.1033092>
- Harper JL (1989) The value of a leaf. *Oecologia* 80:53–58.
- Haynes RJ, Williams PH (1993) Nutrient cycling and soil fertility in the grazed pasture ecosystem. *Adv Agron* 49: 119–199.
- Hermes DA, Mattson WJ (1992) The dilemma of plants: to grow or defend. *Q Rev Biol* 67:(3): 283–335.
- Hirai H, Matsumira H, Hirotani H, Sakurai K, Ogino K, Lee HS (1997) Soils and the distribution of *Dryobalanops aromatica* and *D. lanceolata* in mixed dipterocarp forest – a case study at Lambir Hills National Park, Sarawak, Malaysia. *Tropics* 7: 21–33. <https://doi.org/10.3759/tropics.7.21>
- Hoogendoorn C J, Newton PCD, Devantier BP, Rolle BA, Theobald PW, Lloyd-West CM (2016) Grazing intensity and micro-topographical effects on some nitrogen and carbon pools and fluxes in sheep-grazed hill country in New Zealand. *Agric Ecosyst Environ* 217: 22–32.
- Hook PB, Burke IC (2000) Biogeochemistry in a shortgrass landscape: control by topography, soil texture, and microclimate. *Ecology* 81(10): 2686–2703. [https://doi.org/10.1890/0012-9658\(2000\)081\[2686:BIASLC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[2686:BIASLC]2.0.CO;2)
- Itoh A, Yamakura T, Ohkubo T, Kanzaki M, Palmiotto PA, LaFrankie JV, Ashton PS, Lee HS (2003) Importance of topography and soil texture in the spatial distribution of two sympatric dipterocarp trees in a Bornean rainforest. *Ecol Res* 18:307–320. <https://doi.org/10.1046/j.1440-1703.2003.00556.x>
- Jones C, Jacobsen J (2005) Plant nutrition and soil fertility. *Nutrient management module*, 2(11): 1–11.
- Kassambara A, Mundt F (2017) Package ‘factoextra’. Extract and visualize the results of multivariate data analyses, 76(2). <https://piyanit.nl/wp-content/uploads/2020/10/factoextra.pdf/> (accessed 22 March 2024).
- Köhler L, Gieger T, Leuschner C (2006) Altitudinal change in soil and foliar nutrient concentrations and in microclimate across the tree line on the subtropical island mountain Mt. Teide (Canary Islands). *Flora Morphol Distrib Funct Ecol* 201(3): 202–214. <https://doi.org/10.1016/j.flora.2005.07.003>
- Lane DR, Coffin DP, Lauenroth WK (1998) Effects of soil texture and precipitation on above-ground net primary productivity and vegetation structure across the Central Grassland region of the United States. *J Veg Sci* 9(2): 239–250. <https://doi.org/10.2307/3237123>
- Lerotholi N, Seleteng-Kose L, Odenya W, Chatanga P, Mapeshoane B, Marake MV (2024) Impact of mechanical shrub

- removal on encroached mountain rangelands in Lesotho, southern Africa. *Afr J Ecol* 62(1):13203. <https://doi.org/10.1111/aje.13203>
- Li L, Zhang J, He XZ, Hou F (2021) Different effects of sheep excrement type and supply level on plant and soil C: N: P stoichiometry in a typical steppe on the loess plateau. *Plant Soil* 462:45–58.
- Liu F, Yang W, Wang Z, Xu Z, Liu H, Zhang M, Liu Y, An S, Sun S (2010) Plant size effects on the relationships among specific leaf area, leaf nutrient content, and photosynthetic capacity in tropical woody species. *Acta Oecol*:36(2), 149–159. <https://doi.org/10.1016/j.actao.2009.11.004>
- Liu R, Pan Y, Bao H, Liang S, Jiang Y, Tu H, Nong J, Huang W (2020) Variations in soil physico-chemical properties along slope position gradient in secondary vegetation of the hilly region, Guilin, Southwest China. *Sustainability* 12(4):1303. <https://doi.org/10.3390/su12041303>
- Macek P, Klimeš L, Adamec L, Doležal J, Chlumská Z, de Bello F, Dvorský M, Řeháková K (2012) Plant nutrient content does not simply increase with elevation under the extreme environmental conditions of Ladakh, NW Himalaya. *Arct Antarct Alp Res* 44(1): 62–66. <https://doi.org/10.1657/1938-4246-44.1.62>
- Marschner H. ed (2011) *Marschner's mineral nutrition of higher plants*. Academic press.
- Martin RE, Asner GP, Bentley LP, Shenkin A, Salinas N, Huaypar KQ, Pillco MM, Ccori Álvarez FD, Enquist BJ, Diaz S, Malhi Y (2020) Covariance of sun and shade leaf traits along a tropical forest elevation gradient. *Front Plant Sci* 10:1810. <https://doi.org/10.3389/fpls.2019.01810>
- Masibonge G, Tefera S, Mota L (2019) Invasion of *Euryops florbundus* in degraded South African communal grassland: Unpacking the invasion relationship with elevation, soil properties, the quality and quantity of the herbaceous layer. *Afr J Ecol* 58(1):69–79. <https://doi.org/10.1111/aje.12642>
- Mayor JR, Sanders NJ, Classen AT, Bardgett RD, Clement JC, Fajardo A, Lavorel S, Sundqvist MK, Bahn M, Chisholm C, Cieraad (2017) Elevation alters ecosystem properties across temperate treelines globally. *Nature* 542(7639):91–95. <https://doi.org/10.1038/nature21027>
- Mekonnen ZA, Riley WJ, Berner LT, Bouskill NJ, Torn MS, Iwahana G, Breen AL, Myers-Smith IH, Criado MG, Liu Y, Euskirchen ES, Goetz SJ, Mack MC, Grant R F (2021) Arctic tundra shrubification: a review of mechanisms and impacts on ecosystem carbon balance. *Environ Res Lett* 16(5):053001. <https://doi.org/10.1088/1748-9326/abf28b>
- Metson AJ (1974) Some factors governing the availability of soil magnesium: A review. *N Z J Exp Agric* 2(3):277–319. <https://doi.org/10.1080/03015521.1974.10427689>
- Moeslund JE, Arge L, Bøcher PK, Dalggaard T, Ejrnæs R, Odgaard MV, Svenning JC (2013) Topographically controlled soil moisture drives plant diversity patterns within grasslands. *Biodivers Conserv* 22:2151–2166. <https://doi.org/10.1007/s10531-013-0442-3>
- Müller M, Schickhoff U, Scholten T, Drollinger S, Böhner J, Chaudhary RP (2016) How do soil properties affect alpine treelines? General principles in a global perspective and novel findings from Rolwaling Himal, Nepal. *Prog Phys Geogr* 40(1):135–160. <https://doi.org/10.1177/0309133115615802>
- Naito AT, Cairns DM (2011) Relationships between Arctic shrub dynamics and topographically derived hydrologic characteristics. *Environ. Res. Lett.* 6(4), 045506. <https://doi.org/10.1088/1748-9326/6/4/045506>
- Ng W, Minasny B, Jeon SH, McBratney A (2022) Mid-infrared spectroscopy for accurate measurement of an extensive set of soil properties for assessing soil functions. *Soil Secur* 6: 100043. <https://doi.org/10.1016/j.soisec.2022.100043>
- Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Solymos P, Stevens MHH, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista HBA, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill MO, Lahti L, McGlinn D, Ouellette MH, Ribeiro Cunha E, Smith T, Stier A, Ter Braak CJF, Weedon J (2024) vegan: Community Ecology Package (Version 2.6-6.1). <https://cran.r-project.org/package=vegan>
- O'Connor TG, Puttick JR, Hoffman MT (2014) Bush encroachment in southern Africa: changes and causes. *Afr J Range Forage Sci* 31(2):67–88. <https://doi.org/10.2989/10220119.2014.939996>
- Palmer AR, Bennett JE (2013) Degradation of communal rangelands in South Africa: towards an improved understanding to inform policy. *Afr J Range Forage Sci* 30(1-2): 57–63. <https://doi.org/10.2989/10220119.2013.779596>
- Pandey (2018) Role of Plant Nutrients in Plant Growth and Physiology. In: Hasanuzzaman M, Fujita M, Oku H, Nahar K, Hawrylak-Nowak B. (eds) *Plant Nutrients and Abiotic Stress Tolerance*. Springer, Singapore. https://doi.org/10.1007/978-981-10-9044-8_2
- Penn CJ, Camberato JJ (2019) A critical review on soil chemical processes that control how soil pH affects phosphorus availability to plants. *Agriculture* 9(6):120. <https://doi.org/10.3390/agriculture9060120>
- Pule HT, Tjelele JT, Tedder MJ (2018) The effects of abiotic factors in South African semi-arid grassland communities on *Seriphium plumosum* L density and canopy size. *Plos one* 13(8): 0202809. <https://doi.org/10.1371/journal.pone.0202809>
- Qin Y, Liu W, Zhang X, Adamowski JF, Biswas A (2022) Leaf stoichiometry of *Potentilla fruticosa* across elevations in China's Qilian Mountains. *Front Plant Sci* 13:814059. <https://doi.org/10.3389/fpls.2022.814059>
- R Core Team (2024) The R Project for Statistical Computing. Available from: [https:// www.r- proje ct. org/](https://www.r-project.org/)
- Raynor EJ, Gersie SP, Stephenson MB, Clark PE, Spiegel SA, Boughton RK, Bailey DW, Cibils A, Smith BW, Derner JD, Estell RE, Nielson RM, Augustine DJ (2021) Cattle grazing distribution patterns related to topography across diverse rangeland ecosystems of North America. *Rangel Ecol Manag* 75: 91–10310.1016/j.rama.2020.12.002
- Reich PB (2005) Global biogeography of plant chemistry: filling in the blanks. *New Phytol* 168(2). <https://doi.org/10.1111/j.1469-8137.2005.01562.x>
- Rezaei SA, Gilkes RJ (2005) The effects of landscape attributes and plant community on soil chemical properties in rangelands. *Geoderma* 125(1-2): 167–176. <https://doi.org/10.1016/j.geoderma.2004.07.010>
- Roques KG, O'Connor TG, Watkinson AR (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density

- dependence. *J Appl Ecol* 38(2): 268–280. <https://doi.org/10.1046/j.1365-2664.2001.00567.x>
- Russell DW, Van Moort JC (1981) Biogeochemistry and pedogeochemistry of the White Spur area, near Rosebery, Tasmania. *Economic Geol* 76(2): 339–349. <https://doi.org/10.2113/gsecongeo.76.2.339>
- Ruwanza S (2022) Expansion by native shrub *Euryops floribundus* affects soil and vegetation in Machubeni communal land, South Africa. *Sci Afr* 16: p.e01134. <https://doi.org/10.1016/j.sciaf.2022.e01134>
- Salekin S, Hossain MN, Alam MA, Limon SH, Rahman MS (2023) Inter-specific competition between seeds and seedlings of two congeneric tropical trees. *Community Ecol* 24(3):333–342. <https://doi.org/10.1007/s42974-023-00165-3>
- Schnyder H, Locher F, Auerswald K (2010) Nutrient redistribution by grazing cattle drives patterns of topsoil N and P stocks in a low-input pasture ecosystem. *Nutr Cycl Agroecosys* 88: 183–195.
- Sigua GC, Coleman SW, Albano J, Williams M (2011) Spatial distribution of soil phosphorus and herbage mass in beef cattle pastures: effects of slope aspect and slope position. *Nutr Cycl Agroecosys* 89:59–70.
- Snyman HA (2012) Habitat preferences of the encroacher shrub, *Seriphium plumosum*. *S Afr J Bot* 81: 34–39. <https://doi.org/10.1016/j.sajb.2012.05.001>
- Soubry I, Robinov L, Chu T, Guo X (2022) Mapping shrub cover in grasslands with an object-based approach and investigating the connection to topo-edaphic factors. *Geocarto Int* 37(27):16926–16950. <https://doi.org/10.1080/10106049.2022.2120549>
- Sun X, Kay AD, Kang H, Small GE, Liu G, Zhou X, Yin S, Liu C (2013) Correlated biogeographic variation of magnesium across trophic levels in a terrestrial food chain. *PLoS one*. 8(11): p.e78444. <https://doi.org/10.1371/journal.pone.0078444>
- Swoczyna T, Kalaji HM, Bussotti F, Mojski J, Pollastrini M (2022) Environmental stress-what can we learn from chlorophyll a fluorescence analysis in woody plants? A review. *Front Plant Sci* 13: 1048582. <https://doi.org/10.3389/fpls.2022.1048582>
- Thomas CL, Hernandez-Allica J, Dunham SJ, McGrath SP, Haeefe SM (2021) A comparison of soil texture measurements using mid-infrared spectroscopy (MIRS) and laser diffraction analysis (LDA) in diverse soils. *Sci Rep* 11(1): p.16. <https://doi.org/10.1038/s41598-020-79618-y>
- Umuhoza J, Jiapaer G, Yin H, Mind'je R, Gasirabo A, Nzarabinda V, Umwali ED (2021) The analysis of grassland carrying capacity and its impact factors in typical mountain areas in Central Asia -A case of Kyrgyzstan and Tajikistan. *Ecol Indic* 131:108129.
- Van Auken OW (2009) Causes and consequences of woody plant encroachment into western North American grasslands. *J Environ Manag* 90(10):2931–2942. <https://doi.org/10.1016/j.jenvman.2009.04.023>
- Venterink HO, Gusewell S (2010) Competitive interactions between two meadow grasses under nitrogen and phosphorus limitation. *Funct Ecol* 24(4):877–886. <https://doi.org/10.1111/j.1365-2435.2010.01692.x>
- Vitousek PM, Matson PA, Turner DR (1988) Elevational and age gradients in Hawaiian montane rainforest: foliar and soil nutrients. *Oecologia* 77: 565–570. <https://doi.org/10.1007/BF00377275>
- Wang H, Su H, Biswas A, Cao J (2022) Leaf stoichiometry of *Leontopodium leontopodioides* at high altitudes on the northeastern Qinghai-Tibetan Plateau, China. *J Arid Land* 14(10): 1124–1137. <https://doi.org/10.1007/s40333-022-0033-9>
- Wang R, Wang X, Jiang Y, Cerdà A, Yin J, Liu H, Feng X, Shi Z, Dijkstra FA, Li MH (2018) Soil properties determine the elevational patterns of base cations and micro-nutrients in the plant–soil system up to the upper limits of trees and shrubs. *Biogeosciences* 15(6):1763–1774. <https://doi.org/10.5194/bg-15-1763-2018>
- Wernerehl RW, Givnish TJ (2015) Relative roles of soil moisture, nutrient supply, depth, and mechanical impedance in determining composition and structure of Wisconsin prairies. *Plos One*. 10(9): e0137963. <https://doi.org/10.1371/journal.pone.0137963>
- Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.
- Wickham H, Çetinkaya-Rundel M, Golemund G (2023b) R for data science: Import, tidy, transform, visualize, and model data, (2nd ed.,). Sebastopol: O'Reilly.
- Wickham H, François R, Henry L, Müller K, Vaughan D (2023a) dplyr: A Grammar of Data Manipulation. R package version 1.1.4. <https://dplyr.tidyverse.org>.
- Wu CC, Tsui CC, Hsieh CF, Asio VB, Chen ZS (2007) Mineral nutrient status of tree species in relation to environmental factors in the subtropical rain forest of Taiwan. *Forest Ecol Manag* 239(1–3): 81–91. <https://doi.org/10.1016/j.foreco.2006.11.008>
- Yongdong W, Fenetahun Y, Yuan Y, Chukwuka O, Ibrahim Y, Xinwen X (2024) Effects of land-use intensity on vegetation dynamics across elevation in Savanna Grassland, Southern Ethiopia. *Nat Conserv* 79:126598.
- Yuan ZQ, Fang C, Zhang R, Li FM, Javaid MM, Janssens IA (2019) Topographic influences on soil properties and aboveground biomass in lucerne-rich vegetation in a semi-arid environment. *Geoderma* 344:137–143. <https://doi.org/10.1016/j.geoderma.2019.03.003>
- Zeng Q, Liu Y, Yang J, Chen Y, Ma L, An S (2021) Nutrients of green and senesced leaves of a *Robinia pseudoacacia* plantation along a latitudinal gradient on the Loess Plateau, China. *J For Res* 32(6):2499–2506. <https://doi.org/10.1007/s11676-020-01273-w>
- Zhang Q, Wang Z, Yao Y, Kong W, Zhao Z, Shao M, Wei X (2021) Effects of slope morphology and position on soil nutrients after deforestation in the hilly loess region of China. *Agric Ecosyst Environ* 321:107615. <https://doi.org/10.1016/j.agee.2021.107615>
- Zuleta D, Russo SE, Barona A, Barreto-Silva JS, Cardenas D, Castaño N, Davies SJ, Detto M, Sua S, Turner BL, Duque A (2020) Importance of topography of tree species habitat distributions in terra firme forest in the Colombian Amazon. *Plant Soil*. 450:133–149. <https://doi.org/10.1007/s11104-018-3878-0>

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