



Linking weed incidence to natural grassland vegetation patterns and environmental drivers in a smallholder crop-livestock system

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Abstract Natural grasslands surrounding cropping fields can act as reservoirs of plant species that influence weed establishment in cropping systems. Understanding these interactions is important for explaining changes in plant community assembly and vegetation composition across agricultural landscapes. This study compared species composition between manured maize (*Zea mays* L.) cropping fields and natural grasslands. Additionally, it identified

environmental factors that influence the distribution and assembly of vegetation in natural grasslands. The study was conducted in two agroecological regions (Highveld and Middleveld) of Eswatini. Transects in natural grasslands and maize cropping fields were used to sample plant species composition and density. Stacked-species Distribution Models (s-SDMs) were used to predict the assembly of natural grassland vegetation using climatic, soil, and socio-ecological variables. Weed species richness (S), diversity (H'), and dominance (D) were greater in manured maize fields than in natural grasslands. Model selection based on the Akaike information criterion (AIC) identified 10 factors explaining patterns in species abundance, richness, diversity, and dominance. Phosphorus influenced all diversity indices. Temperature, soil pH, and elevation influenced vegetation abundance, while soil texture affected vegetation abundance, richness, and diversity. About three-quarters of natural grasslands in the Highveld had the highest potential species richness, whereas more than half in the Middleveld had the lowest potential species richness. A combination of environmental variables influences the assemblage of plant species in grasslands, which, when grazed by cattle and introduced to maize cropping fields through uncured manure, may increase species richness and diversity, challenging weed management.

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Introduction

Natural grasslands support wildlife and livestock by providing food and facilitating nutrient cycling, promoting soil health, and conserving biodiversity. Over 80% of agricultural land is in natural grasslands, with approximately 70% in developing countries, where it supports livestock production (Boval & Dixon, 2012; Steinfeld et al., 2006). However, natural grassland communities are typically dynamic and respond to many interacting environmental factors, including climate and soil conditions, land use, and grazing intensity.

Natural grasslands exhibit high spatial and temporal heterogeneity (Berquer et al., 2021; Gabriel et al., 2005; Medeiros et al., 2016), and smallholder livestock farmers rely on this heterogeneity to provide feed for their grazing animals (Boval & Dixon, 2012). The type of livestock grazed influences vegetation through the selection of palatable species (Wang et al., 2019, 2021) as well as stocking rates, especially overstocking, which can also influence vegetation community structure by altering vegetation cover, dominance, and richness (Pizzio et al., 2016; Schmitz & Isselstein, 2020; Xiao et al., 2020).

Additionally, seed dispersal through livestock is an important driver of vegetation dynamics within the agricultural landscape. Seeds consumed by livestock during grazing may remain viable after passage through the digestive system and subsequently be deposited in manure (Harrington et al., 2011; Hogan & Phillips, 2011). Seed survival during digestion depends on several factors, such as seed viability, dormancy, and retention time (Rahimi et al., 2016; Rupende et al., 1998). In smallholder crop-livestock systems, the collection and application of uncured manure further facilitate the transfer of weed seeds into cultivated fields, and manure management practices are often insufficient to eliminate viable seeds (Concenço et al., 2011; Materechera, 2010; Materechera & Modiakgotla, 2006). Therefore, manure containing viable vegetation seeds, when applied to a cropping field, can increase seed abundance by introducing new seeds from grasslands into cultivated land. These weeds are undesirable as they compete for crop space, nutrients, and water, reducing yields and economic benefits for small-scale farmers.

Non-crop habitat plant diversity is shaped by surrounding grassland communities, ecotones, and other

uncultivated habitats within the heterogeneous landscape, and it influences weed germination in cropping fields (Gaujour et al., 2012). While many studies have explored how landscape heterogeneity influences weed composition and diversity in arable fields (Alignier et al., 2017; Gaba et al., 2010; Gabriel et al., 2005; Medeiros et al., 2016; Roschewitz et al., 2005), they have not accounted for the complex interactions of natural grassland vegetation patterns and their environmental factors that might affect weed occurrence and dispersal in cropping fields. In particular, the influence of vegetation existing in different cover types has not been specifically studied. This is especially important in systems where livestock graze on vegetation, as they may facilitate weed dispersal. A previous study conducted in the Highveld and Middleveld of Eswatini showed that fertiliser regimes significantly influence weed species composition and diversity in smallholder crop-livestock systems (Mncube et al., 2026). The study evaluated differences in weed flora under organic, inorganic fertilisation, and their combination, revealing higher species richness and diversity under the cattle manure regime than inorganic fertiliser alone. However, the environmental factors driving vegetation assembly in natural grasslands and how they differ from adjacent croplands remain poorly understood. The present study, therefore, extends this work by using stacked species distribution models to identify climatic, edaphic, and socio-ecological variables that shape grassland vegetation assemblages, providing an understanding of how grassland biodiversity may influence weed dispersal into cropping systems as well as the implications for weed management and sustainable crop production in smallholder systems.

This study investigated how soil texture, nutrition (Nitrogen, Phosphorus, Potassium, and pH), socio-ecological (elevation, slope, grazing pressure, land-cover, distance of grasslands from rivers, roads, and settlements, and topographic wetness index), and climatic factors may influence community assembly in natural grasslands utilised for cattle grazing in Eswatini. The study hypothesised that vegetation composition in maize cropping fields would be similar to natural grasslands due to seed dispersal by cattle manure. Specifically, diversity indices (i.e., species abundance, richness, diversity, and dominance) and species distribution models (SDMs) were used to understand vegetation patterns between natural

grasslands and maize (*Zea mays* L.) cropping fields in smallholder crop-livestock systems. The choice of diversity indices to measure community assembly influenced by environmental processes is important for analysing the composition of natural grasslands and comparing community assemblages between arable and non-arable land. Using species distribution models (SDMs) to predict optimal species sites based on observation data (species abundance) and environmental factors is a common analysis for identifying vegetation hotspots across the landscape. Moreover, species distribution models have been used to predict habitat suitability for plant species and habitat restoration (Palmer et al., 1997; Yang et al., 2013). Stacked-SDMs, where SDMs are first created for individual species and then combined, have been used to study spatial patterns of environmental suitability (Saarimaa et al., 2019; Ye et al., 2021) and to identify

suitable habitats for multiple species (Zellmer et al., 2019). In this study, stacked-SDMs were implemented to predict optimal locations for several natural grassland vegetation species.

Materials and methods

Study sites

The study was conducted for two cropping seasons in the Highveld (Mankayane; 26° 40' S, 31° 3' E) and the Middleveld (Luve; 26° 20' S, 31° 28' E) of Eswatini (Fig. 1). Mean temperatures at Mankayane were 20.9 and 18.4 °C in 2020/2021 and 2021/2022 and were 23.2 and 21.7 °C in 2020/2021 and 2021/2022 at Luve, respectively. Total rainfall during the study period was 904 mm (2020/2021)

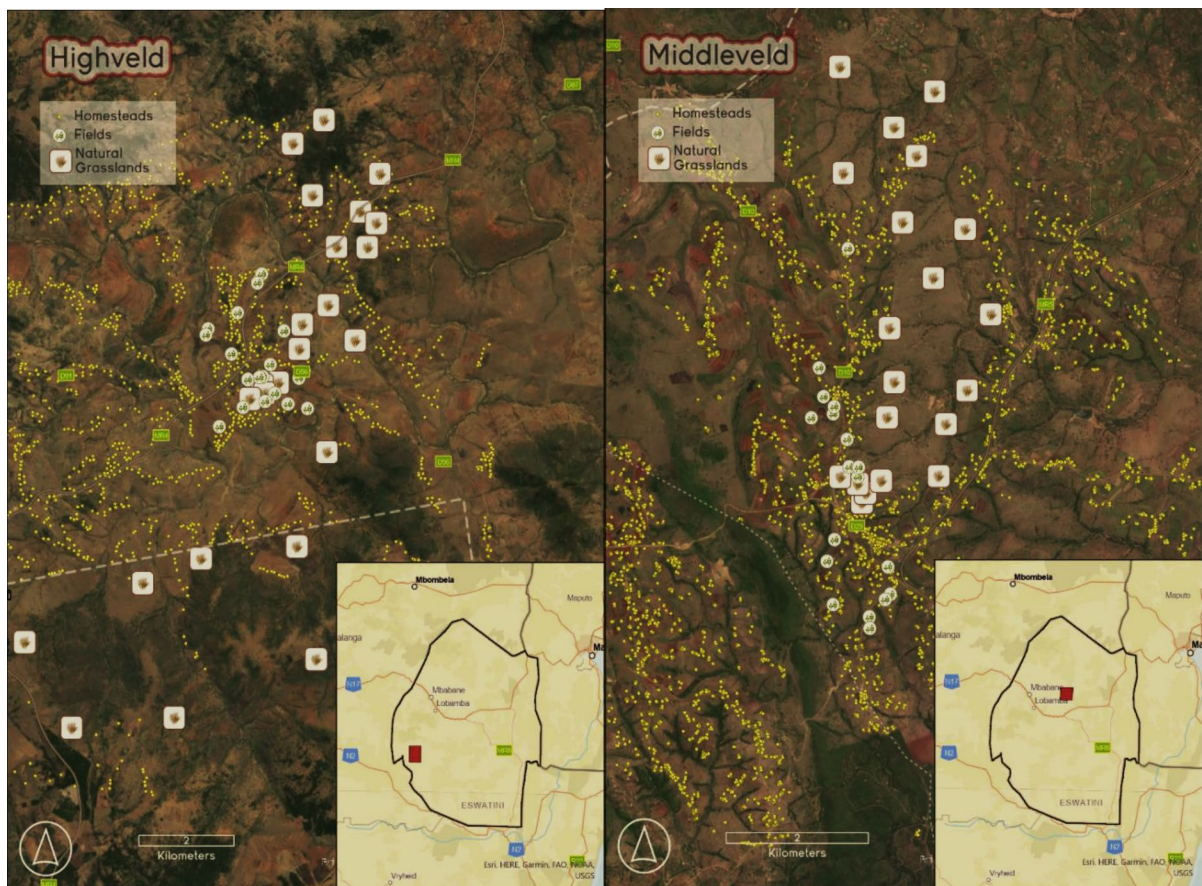


Fig. 1 The sampled regions Highveld (Mankayane) and Middleveld (Luve), as well as the sampled maize fields and natural grassland rangelands

and 780 mm (2021/2022) at Mankayane and 808 mm (2020/2021) and 505 mm (2021/2022) at Luve.

Soil analysis

For each study area, climatic factors, including temperature and total rainfall, were used to determine the grassland vegetation assemblage. Seven physical and chemical soil properties were also used to assess vegetation distribution in the natural grasslands (Table 1). A plot measuring 10 m×10 m was marked at the centre of each natural grassland. Soil samples were collected from 0 to 30 cm depth between April and May of each sampling season. A 5 cm diameter auger was used, and soil cores were taken at 1 m intervals following a zigzag sampling pattern, resulting in ten samples per natural grassland. The soil samples from each site were combined to create a composite mixture before testing. The soil was oven-dried at 72 °C for 48 h before being stored at room temperature until analysis. The hydrometer method was used to estimate the distribution of soil particle sizes, i.e., clay (%), silt (%), and sand (%) for each natural grassland site (Bouyoucos, 1936). Soil reaction (pH) was determined on a soil: water

V/V suspension using a ratio of 1:5 (Sonmez et al., 2008). The soil analysis procedures for nitrogen (N), phosphorus (P), and potassium (K) were performed according to Carter and Gregorich (2008). Nitrogen was determined using the Dumas procedure, which accounts for all forms of nitrogen available in the sample (Buckee, 1994; Dumas, 1826). The ammonium acetate acetic acid (AAAc) extraction technique was used to extract P and K cations. Phosphorus and K were measured using flame photometry.

Farmer practices

The cropping fields sampled in the study belonged to farmers who practiced integrated crop-livestock farming. Stratified sampling technique (Müller-Dombois & Ellenberg, 1974) was used to select 12 farmer-managed maize fields from Regional Development Areas (RDAs) in the main maize growing regions. The farmers employed two fertiliser regimes: manure only ($n=6$) and manure plus inorganic fertiliser ($n=6$). Cattle were allowed to graze randomly on communal natural grasslands, which received no maintenance, and stocking rates were not considered. Cattle were confined in kraals (an

Table 1 Summary of the 17 environmental drivers used to analyse natural grassland vegetation assemblages

Environmental factors	Data source
Climatic variables	
Rainfall (mm)	Daily recordings
Temperature (°C)	Daily recordings
Soil physical and chemical variables	
Clay (%)	Soil analysis
Silt (%)	Soil analysis
Sand (%)	Soil analysis
pH	Soil analysis
Nitrogen (%)	Soil analysis
Phosphorus (mg.kg ⁻¹)	Soil analysis
Potassium (mg.kg ⁻¹)	Soil analysis
Socio-ecological variables	
Grazing pressure (%)	Grassland observation
Elevation (m.a.s.l)	SRTM DEM
Slope (°)	SRTM DEM
Landcover	Landsat 8 OLI
Distance of grasslands from rivers (m)	OKACOM + Openstreet
Distance of grasslands from roads (m)	OKACOM + Openstreet
Distance of grasslands from settlements (m)	OKACOM + Openstreet
Topographic wetness index	SRTM DEM

enclosure for livestock) overnight, where manure accumulated during the non-cropping season; it was later removed and broadcast in the fields at a rate of 9 t.ha^{-1} before land preparation. The average nutrient availability in the manure was Nitrogen = 33 kg, Phosphorus = 55 kg, and Potassium 70 kg. Fields were prepared with a mouldboard plough followed by a disc harrow. The planted maize variety was SC 719 (Seed-Co®, Zimbabwe). The seeding rate was 25 kg.ha^{-1} , and the inter- and intra-row spacings were $0.9 \text{ m} \times 0.25 \text{ m}$, respectively. In the manure plus inorganic fertiliser fields, basal fertiliser [N: P: K, 2:3:2 (37%)] was applied at 500 kg.ha^{-1} in the Highveld and 400 kg.ha^{-1} in the Middleveld. Also, four weeks after maize emergence, Limestone Ammonium Nitrate [LAN (28%)] top dress was applied at 200 kg.ha^{-1} in the Highveld and 150 kg.ha^{-1} in the Middleveld. Early post-emergence (EPOST), Cyanazine (BLADEx®) at 900 g.kg^{-1} (90% wettable granule formulation) was applied to control weeds at the maize four-leaf stage. A PB-20 or PB-16 Knapsack sprayer (Jun Chong Co., Ltd., Kluang, Johor, Malaysia) was utilised and calibrated to achieve and maintain a 300 kPa pressure, with a spray volume of 200 L.ha^{-1} .

Manure weed seed bank

Manure was sampled for weed survival before broadcasting from piles placed in each field. The average number of piles per field was 53. Manure was sampled from each heap in the field using a 5 cm diameter auger, 10 cm into the heap. The top crusts of manure were removed, and all manure samples collected per field were mixed to form a composite mixture. Manure was kept in airtight sealable bags and was spread in germination plastic trays the following day. Each plastic tray, sized $30 \times 30 \times 10 \text{ cm}$, was filled with sterile dry sand to a depth of 4 cm. Manure samples from each field were evenly spread in each tray to a depth of 3 cm. The trays were perforated at the base to allow drainage. Trays were placed under natural light in a screen house for the maize growing period (20 weeks) and were watered daily to stimulate germination. Manure was turned using a hand fork to stimulate photoblastic weed seed germination. Germinated weeds were identified, counted, and removed from the trays.

Weed and grassland vegetation sampling

Weed sampling in cropping fields was conducted two months after herbicide application at maize growth stage R4 (maize dough stage). The sampling began on February 26th to April 4th, 2021, and March 2nd to April 14th, 2022. Three transects were marked in each maize field, two at the field edges marked vertically, and one at the field centre marked horizontally, with five $1 \times 5 \text{ m}$ quadrats, spaced at 1 m intervals (The relevé method, Minnesota Department of Natural Resources, 2013). A 25 m long transect was selected because field sizes ranged from $50 \times 50 \text{ m}$ to $100 \text{ m} \times 60 \text{ m}$. Natural grassland identification was conducted with assistance from farmers and extension officers. Twenty-four natural grasslands were identified in the Highveld, and 20 in the Middleveld (Fig. 1). Between the summer months of March and May, most plants, especially grass, have reached the reproductive stage, making identification easier. Therefore, natural grassland sampling was conducted from April 10th to May 5th, 2021, and from April 2nd to May 3rd, 2022. Four transects were marked in a North, South, East, and West direction from each natural grassland. Each transect was 100 m long, comprising five $5 \text{ m} \times 1 \text{ m}$ quadrats, at 20 m intervals. Sampling began at least 10 m from the habitat edge.

For both habitats, broadleaved plants of at least 10 cm height, grasses of at least 15 cm height, and stoloniferous grasses of at least 5 cm length were sampled. The number of species observed was recorded together with their total density. Density was the number of individuals per species within a transect. Identification of weeds (in cropping fields) and vegetation (in grasslands) was through species screening and identification through the Royal Botanic Gardens (Kew) and online databases, i.e., POWO (2022) and CABI (2022).

Environmental factors

The extent of vegetation removal by cattle, or grazing pressure, was determined by calculating the percent vegetation cover on the natural grassland (Eq. 1). Vegetation cover was determined by using the point intercept method (Drezner & Drezner, 2021), and the following formula was used to estimate the vegetation cover:

$$\text{Vegetation cover(\%)} = \frac{\sum \text{Total hits for each cover component per transect}}{\text{Total number of hits per transect} \times 100} \quad (1)$$

where cover components were vegetation, litter, gravel, stone, or bare ground.

The landcover categorization of the research areas was established using Landsat 8 OLI images sourced from the Google Earth Engine (GEE) platform. The images were procured in August 2021. Six socio-ecological variables derived from remote sensing were also used to estimate vegetation distribution patterns. The variables were elevation, slope, distance of natural grasslands from water bodies, roads, and settlements, and topographic wetness index (TWI) (Table 1). Elevation and slope were used to represent the influence of topography on vegetation distribution patterns. The Shuttle Radar Topography Mission (SRTM) Digital Elevation Model (DEM) with a spatial resolution of 90 m was used as the elevation layer. Slope was derived from the DEM in ArcGIS 10.7.

The digitised settlements and vector layers of water bodies and roads were used to calculate the Euclidean distance from settlements using ESRI ArcMap version.

9.1. Settlements within a 5 km radius of the study area were digitised in QGIS, using Google Earth imagery, zoomed to a resolution of 100 m. Vector layers for water bodies and roads were sourced from the OKACOM database and OpenStreetMap (www.openstreetmap.com). The coordinate system was first reprojected from a geographic coordinate system (WGS 84) to a projected system (WGS 84/UTM 35S), then resampled to a spatial resolution of 30 m.

The distance between natural grasslands and water bodies, roads, and human settlements represented surface and groundwater availability to vegetation, the influence of cars, human and animal tracks on vegetation distribution, and an indication of housing and human population density. Topographic wetness index (TWI) was used to quantify water catchment and drainage by terrain. It was calculated using a digital elevation raster layer (DEM cell size = 30 m) in ArcGIS. Several tools within the program were used to calculate slope, flow direction, flow accumulation, tangent of slope, and ultimately TWI (Eq. 2) (Sørensen et al., 2006):

$$\text{TWI} = \ln(\text{Sca_scaled} / \text{tangent_slp}) \quad (2)$$

where

sca_scaled = (sca + 1 × cell size)

sca = flow accumulation tools (fd)

fd = flow direction tools (dem).

tangent_slp = con [slope > 0, (tan slope), 0.001]

slope = [slope(dem) × 1.57096] / 90].

Abundance and diversity measures

The effects of soil properties, climatic, and socio-ecological factors on community assembly were determined using species richness, abundance, diversity, and dominance indices. Species richness (S) was the total number of species per manured maize field or natural grassland (Eq. 3), while abundance was the number of individuals per species per sample. Shannon–Wiener (H') diversity index was used to determine species richness and composition of weed species in manured maize fields and natural grasslands (Eq. 4). Gini-Simpson (D) diversity index was used to measure the degree of dominance of individual weed and vegetation species in communities (Eq. 5). The diversity indices were determined using the following formulae (Legendre & Legendre, 1998):

$$S = \sum_{i=1}^s p_i^0 \quad (3)$$

$$H' = \sum_{i=1}^s p_i \ln p_i \quad (4)$$

$$D = 1 - \sum_{i=1}^s n_i(n_i - 1) / (N(N - 1)) \quad (5)$$

where s equals the number of species, p_i equals the ratio of individuals of species i , superscript 0 is the insensitivity to species frequencies, n is the number of individuals of one species, N = the total number of all individuals.

Statistical analyses

Weed and vegetation abundance data were square root transformed to equalize the contributions of the most common and rarest species (Maindonald & Braun, 2007). The Bray–Curtis similarity index was used to determine the similarity between sampled habitats (Clarke & Gorley, 2006). The composition of weed species and vegetation between habitats, agro-ecological zones, and seasons was compared using

Permutational Analysis of Variance (PERMANOVA) using 999 random permutations. Similarity Percentage (SIMPER; Clarke, 1993) analysis was used to calculate the contribution of each species to the dissimilarities between manured maize fields and natural grasslands. The species investigated had a dissimilarity greater than 2.5%.

Environmental data were tested for normality using the draftsman plot, then normalised and subjected to Euclidean distance matrix (Clarke & Gorley, 2006). Distance-based multivariate multiple regression (DistLM) was used to analyse how the 17 environmental factors influenced the abundance, richness, diversity, and dominance of natural grassland species between the study areas, and to identify any significant factors contributing to vegetation assembly. The Akaike information criterion (AIC) stepwise selection procedure was used to determine the optimal model, which included variables that explained species abundance, richness, diversity, and dominance. Least important variables that did not lower the AIC value by more than one point were removed. The AIC value was used to determine the most important factor. Analyses were conducted in PRIMER+PERMANOVA (Plymouth Marine Laboratory Routines in Multivariate Ecological Research, version 6: Plymouth Marine Laboratory, UK).

Mean species richness, diversity, and dominance between the manured maize fields and natural grasslands were compared using a generalised linear model (GLM), and post hoc pairwise comparisons with Least Squares Difference (LSD) correction for multiple pairs were employed. Analyses were conducted using the Statistical Package for Social Science (IBM SPSS Statistics version 28), and statistical significance was accepted at $p < 0.05$.

Modelling of species distribution

To determine the optimal habitat for each species, species distribution models were modelled using the “MaxEnt” (MaxEnt; version 3.4.4) package in R (R Core Team, 2022; version 3.4.3) (Phillips et al., 2006). The model approach enabled the development of habitat suitability for multiple species based on each species’ environmental factors. Species data were collected from natural grasslands using transects from 24 sites in the Highveld and 20 sites in the Middleveld.

The datasets for N, P, K, soil pH, temperature, rainfall, silt, sand, clay, and grazing pressure were used to create environmental layers in ArcGIS version 10.7 and were clipped to the extent of the sampling unit (bounding box). All data layers were projected to the WGS 84/UTM 35S coordinate system (to limit distortion) and were resampled to a spatial resolution of $0.05^\circ \times 0.05^\circ$ (Ye et al., 2020).

To determine the potential geographical distribution of each species, individual SDMs were developed first. The regularisation multiplier was set to 0.1 to avoid over-fitting of the dataset. The maximum number of background points allowed was 10,000. Hinge, linear, and quadratic features were used. Approximately 75% of the data was for training, while 25% for testing, with replicate runs set to 10. The Area Under the Receiving Operator Curve (AUC) was used to assess the model’s goodness-of-fit, and the model with the highest AUC value was considered the best performer. The AUC values for all species ranged from 0.89 to 0.99, indicating excellent model performance. Stacked-species distribution models (s-SDM) were constructed by combining individual SDMs, providing the potential geographical distribution pattern of species richness to the spatial scale of natural grasslands. This was done by adding individual SDMs (Calabrese et al., 2014).

Results

Vegetation and weed species richness and diversity

Forty-four natural grassland species were recorded, 36 at Mankayane and 30 at Luve. Of those, 10 species, including five grasses and two sedges, were found in the natural grasslands, while 34 species were common between the habitats (Supplementary Table S1). Additionally, 66 weed species were recorded from the manured maize fields. Furthermore, 44 weed species were recorded from manure, and 23 species were present in the manure, natural grasslands, and manured maize fields (Supplementary Table S1). Permutational analysis showed that a significant interaction between habitats (cropping fields and natural grassland) and agroecological zones (Highveld and Middleveld) produced the greatest variation in species composition and assembly (Pseudo F-value = 14.515, $p < 0.05$) (Supplementary Table S2).

Comparison of species diversity indices between manured maize fields and natural grasslands showed that vegetation species richness (S) was significantly different between habitats and agroecological zones ($F(136, 1) 21.541, p < 0.001$). Weed species richness was greater in the manured maize fields in the Middleveld compared to the Highveld and the natural grassland vegetation in both agroecological zones (Fig. 2a). Additionally, vegetation species richness was significantly different between vegetation habitats and seasons ($F(136, 1) 4.111, p < 0.043$). Further, weed species richness was greater in manured

maize fields than in natural grasslands in both seasons (Fig. 2b).

There was a species diversity (H') interaction between vegetation habitats and agroecological zones ($F(136, 1) 6.026, p < 0.014$). Species diversity was greater in manured maize fields in the Middleveld than in the Highveld and the natural grasslands in both agroecological zones (Fig. 3).

Species dominance (D) was significantly different between habitats ($F(136, 1) 26.790, p < 0.001$) and was lower in the manured maize fields compared to the natural grasslands (Fig. 4a). Additionally, species dominance in the Highveld was considerably

Fig. 2 Mean ($\pm$ SD) weed species richness (S) between vegetation habitats and agroecological zones (a) and seasons (b). The different letters indicate post hoc pairwise differences

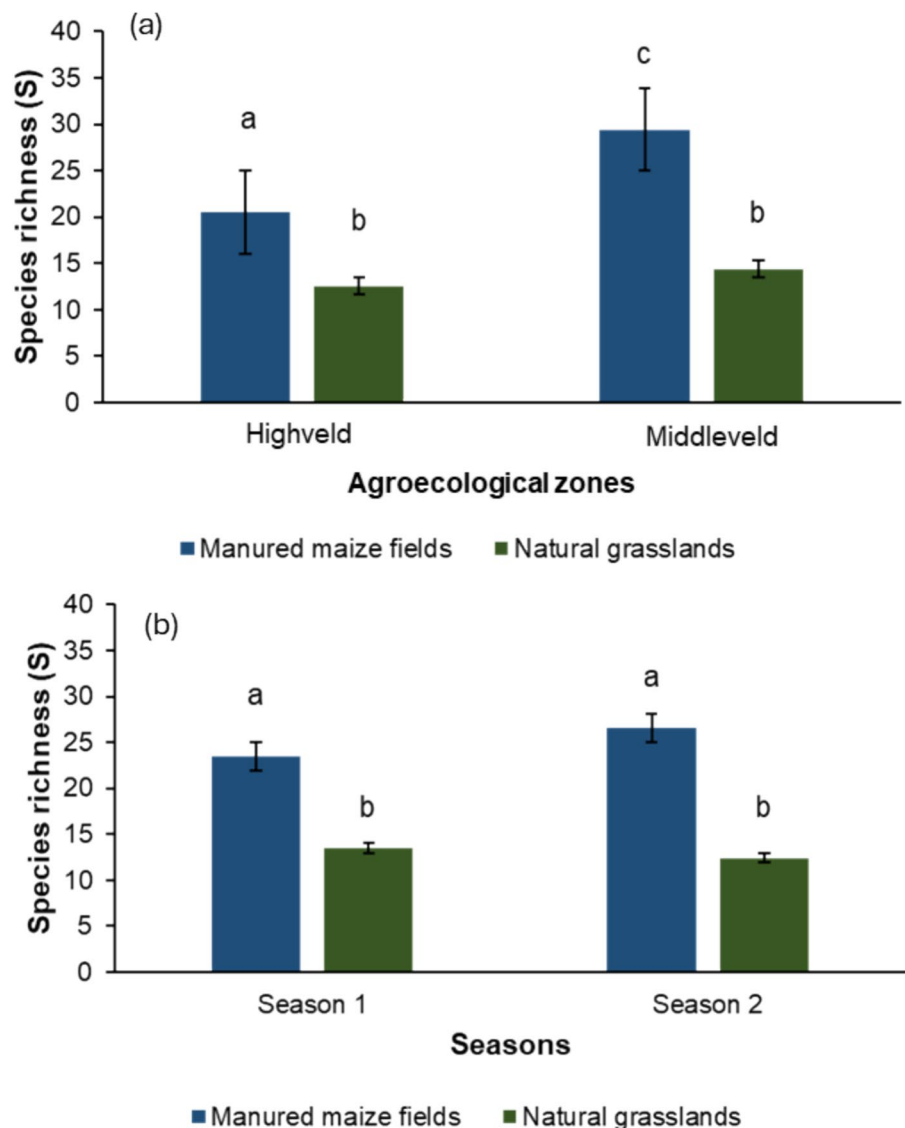
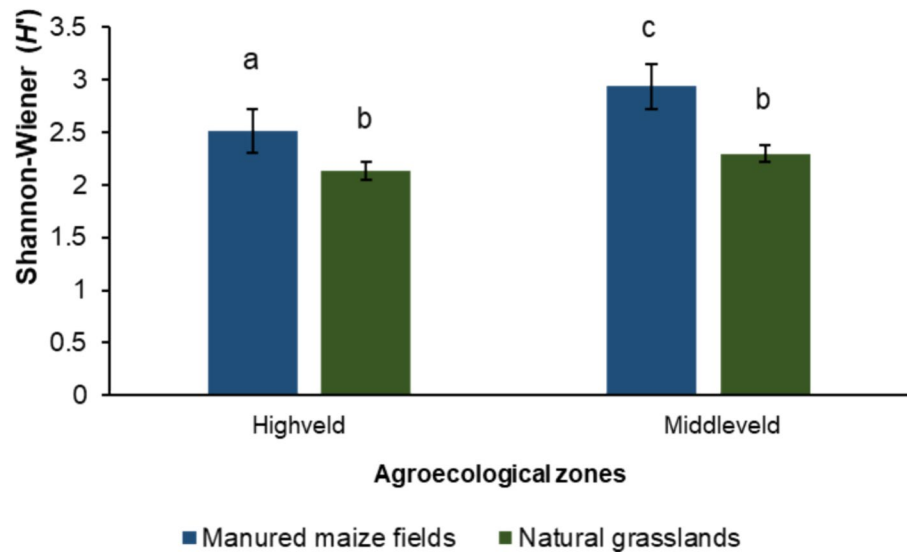


Fig. 3 Mean ($\pm$ SD) weed species diversity (H') between vegetation habitats and agroecological zones. The different letters indicate post hoc pairwise differences



lower compared to the Middleveld ($F(136, 1) 24.513$, $p < 0.001$) (Fig. 4b).

Similarity Percent (SIMPER) analysis across agroecological zones showed within average species similarity of 55% in manured maize fields, which was lower than in natural grasslands (58%) (Table 2). In the Highveld, within average species similarity was 54%, lower than the Middleveld (63%). The average species dissimilarity between manured maize fields and natural grasslands was 85%, which was greater than that of the agroecological zones (56%).

SIMPER identified 15 dominant discriminating weed species, each contributing an abundance of 2.5% or more to the observed differences between vegetation habitats across the agroecological zones (Table 3).

Relationship between environmental variables and diversity indices

Results from multivariate multiple regression showed that 10 of the 17 environmental variables strongly influenced vegetation species abundance (Adjusted $R^2=0.73$, $AIC=281.77$) and species dominance (D) (Adjusted $R^2=0.79$, $AIC=-45.54$) in the natural grasslands. Species diversity (H') (Adjusted $R^2=0.67$, $AIC=59.52$) and species richness (S) (Adjusted $R^2=0.54$, $AIC=144.83$) were moderately influenced by environmental factors.

Based on AIC values, elevation was the most important predictor explaining species abundance, while temperature was the least important (Table 4). The distance of natural grasslands from roads was the principal predictor explaining both species dominance (D) and richness (S). Sand content was the most significant predictor explaining species diversity (H').

Vegetation species distribution

The final stacked-SDM showed that, on a grid scale with a spatial resolution of $0.05^\circ \times 0.05^\circ$, the potential species richness of each grid ranged from low potential (0 species) to high potential (8 species). In the Highveld, approximately 75% of the sampled natural grasslands had the highest potential species richness, while in the Middleveld, more than 50% had the lowest potential species richness (Fig. 5).

Discussion

The study compared vegetation species composition between manured maize fields and natural grasslands grazed by cattle. The study also determined environmental drivers influencing natural grassland vegetation patterns and their effects on weed occurrence in manured maize fields. The results indicated significant dissimilarities in species composition between maize cropping fields and natural grassland across

Fig. 4 Mean ($\pm$ SD) weed species dominance (D) between vegetation habitats (a) and agroecological zones (b). The different letters indicate post hoc pairwise differences

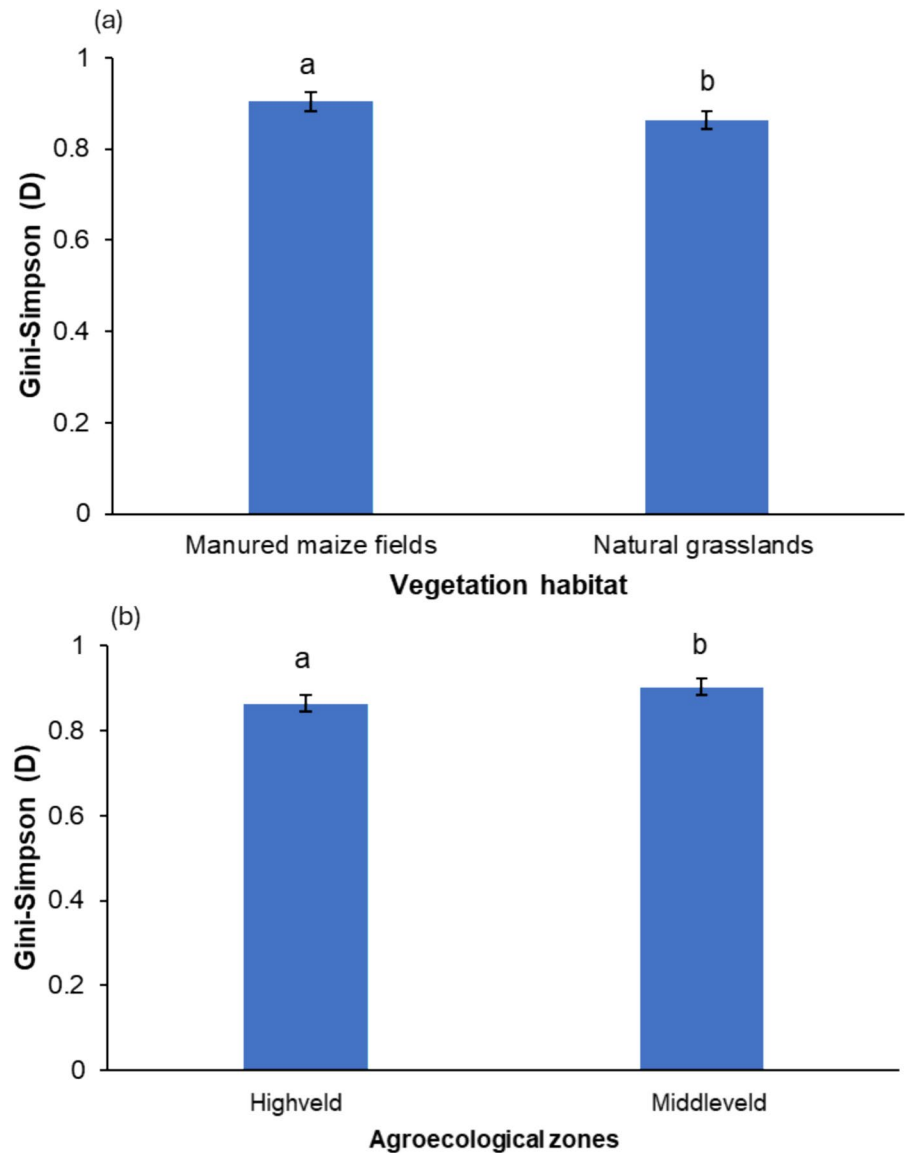


Table 2 Within similarity and between dissimilarity of species between vegetation habitats and agroecological zones

Vegetation habitat	Average similarity (%)	Fertiliser regimes pairwise	Average dissimilarity (%)
Manured maize fields (MMF)	55	MMF & GP	85
Grassland pastures (GP)	58		
Study areas			
Highveld (Hd)	54	Hd & Md	56
Middleveld (Md)	63		

Table 3 SIMPER analysis on weed species contributing more than 2.5% between vegetation habitats and agroecological zones

Weed species	Pairwise comparisons
<i>Xanthium strumarium</i>	4.6
<i>Eleusine indica</i>	4.2
<i>Ipomoea indica</i>	4.1
<i>Sida rhombifolia</i>	4.1
<i>Commelina benghalensis</i>	4.0
<i>Cynodon dactylon</i>	3.8
<i>Bidens pilosa</i>	3.4
<i>Digitaria sanguinalis</i>	3.3
<i>Paspalum distichum</i>	3.3
<i>Amaranthus hybridus</i>	3.3
<i>Richardia scabra</i>	3.2
<i>Oxalis latifolia</i>	3.1
<i>Tagetes minuta</i>	2.9
<i>Hibiscus cannabinus</i>	2.8
<i>Corchorus olitorius</i>	2.7

Table 4 Relative effect of environmental factors on diversity components

Diversity index	Environmental variable	Performance in the model	
		AIC	p-value
Abundance	Elevation	281.77	0.007
	Clay	283.30	0.002
	Silt	285.90	0.007
	Phosphorus	288.54	0.003
	Distance from water bodies	290.69	0.001
	pH	294.34	0.001
	Temperature	306.38	0.001
D	Distance from roads	−38.03	0.004
	Phosphorus	−29.70	0.001
	Distance from water bodies	−9.65	0.001
H'	Sand	60.86	0.004
	Distance from water bodies	68.14	0.002
	Phosphorus	80.91	0.001
S	Distance from roads	144.83	0.030
	Sand	147.70	0.002
	Phosphorus	156.61	0.001

agroecological zones. Broadleaved weeds were the main contributors to these dissimilarities, as they are well-adapted to cultivated maize fields (Sharma & Rayamajhi, 2022).

The natural grasslands in the Highveld and Midlelved had lower species richness and diversity than the manured maize fields in both study areas. This could be attributed to the dominance of grazing-tolerant species in grasslands and to habitat fragmentation caused by human activities, such as land cultivation, which affects seed dispersal and species composition (Gaujour et al., 2012). Grazing selects certain species through defoliation, trampling, and nutrient recycling from cattle manure, resulting in the dominance of prolific species with rapid growth and tolerance to grazing pressure (Bullock et al., 2001; Jawuoro et al., 2017; Narantsetseg et al., 2018; Rahmanian et al., 2020). Conversely, maize fields experience frequent disturbance, nutrient enrichment, and reduced interspecific competition, promoting opportunistic nutrient-responsive weeds. The co-occurrence of vegetation species between the two habitats and manure suggests that grasslands are also a source of propagules that could be easily dispersed by cattle, increasing weed abundance and richness in manured maize fields, when uncured manure is applied.

The study also found that environmental factors influenced vegetation patterns in grazed natural grasslands. Elevation, clay, silt, P, soil pH, the distance of natural grasslands from water bodies and roads, temperature, and sand were critical in the assemblage of natural grasslands. Elevation, which is interdependent with other environmental conditions, such as soil type, soil nutrition, soil pH, temperature, rainfall, and drainage, all of which affect vegetation germination and growth, was the main driver for vegetation abundance (Pei et al., 2018; Zou et al., 2021). Highly elevated areas with increased rainfall, such as Man-kayane, vegetation species tolerant of moist disturbed environments, including *Convolvulus arvensis*, *Cyperus esculentus*, *Sida rhombifolia*, and *Cynodon dactylon*, may dominate (Holm et al., 1977). Conversely, lower-elevation areas, such as Luve, may be dominated by drought and extreme (high) temperature-tolerant species, e.g., *Erigeron canadensis* and *E. sumatrensis* (Florentine et al., 2021; Ghosh et al., 2025). The distance of natural grasslands from water bodies was a predictor of species abundance, diversity, and dominance. These results corroborate Tsheboeng's

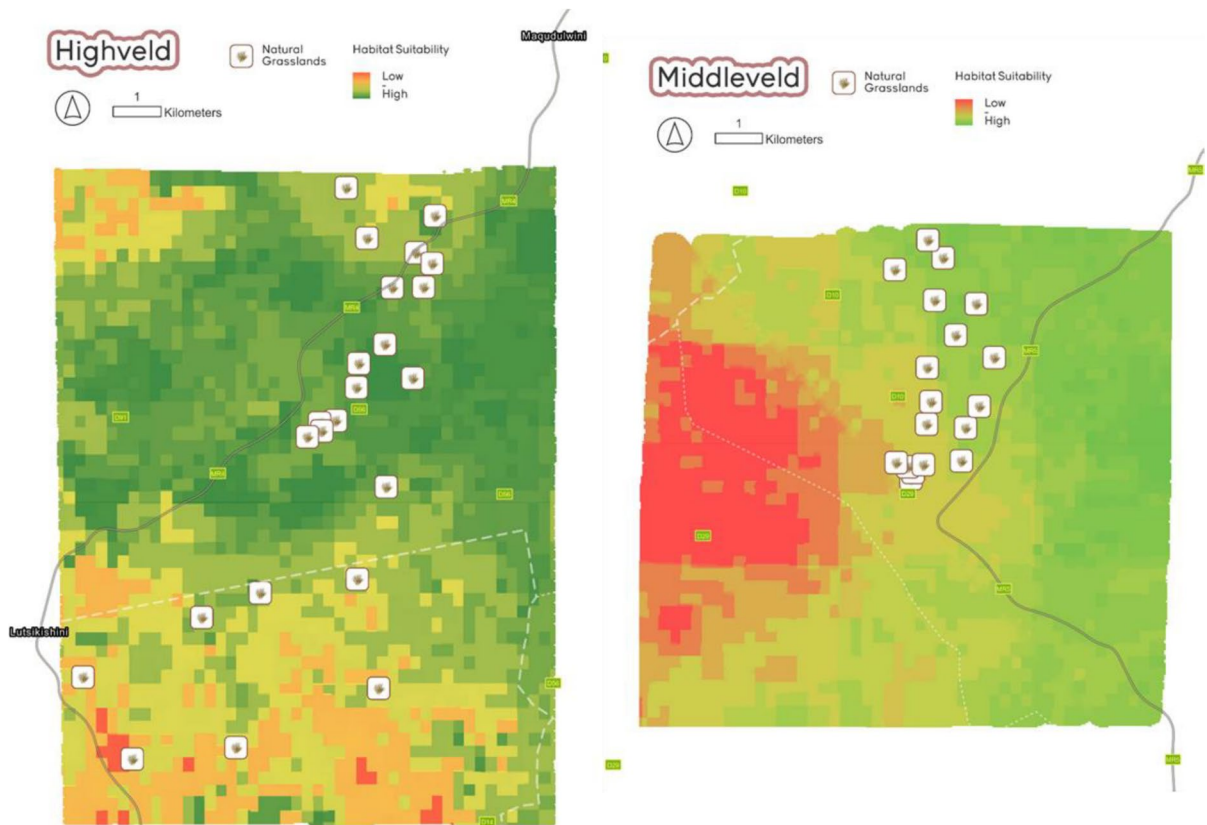


Fig. 5 Distribution pattern of potential species richness in the Highveld (Mankayane—left) (36 species) and in the Middleveld (Luvuvhu—right) (30 species)

(2018) findings that species vary with increasing distance, indicating that species germinate and establish along the groundwater depth gradients to which they have adapted. Areas near bodies experience higher grazing pressure, creating piospheres where hardy species, such as *Cynodon dactylon*, dominate near the water source, whereas climax species may be farther from it (Egeru et al., 2015; Jaweed et al., 2018; Jawuoro et al., 2017). Similarly, proximity to roads may increase species richness and abundance by enhancing dispersal through wind, water, animals, and human activity (Root-Bernstein & Svenning, 2018; Zeng et al., 2011).

Phosphorus was the only predictor explaining all the diversity components assessed. Phosphorus enrichment may extend the occurrence of species adaptable to high P availability and restrict those adapted to low P concentrations (van Dobben et al., 2017). Species such as *Paspalum distichum*, which absorbs P quickly, could grow and become prolific,

thereby dominating the grassland and reducing species richness and diversity (Holm et al., 1977; Tilman et al., 1997). The results corroborate those of Merunková and Chytrý (2012), who reported low species richness due to the dominance of P-tolerant species. Additionally, P-adapted species, when consumed by cattle, may transfer phosphorus to manure and ultimately to the field (Yoshitake et al., 2014; Zhao et al., 2022), thereby further promoting the dominance of arable phosphophilous weeds. Other soil properties, including pH and texture, further contributed to vegetation patterns. Soil pH could have influenced vegetation species abundance by providing nutrients and organic matter (Bhandari & Zhang, 2019). Acidic soils in the Highveld may support acid-tolerant species such as *Richardia scabra* for germination, growth, and reproduction (Mavungu-nidze et al., 2016). The results corroborate the findings of Michalcová et al. (2011), who reported that soil pH was a major driver of species composition in

natural grasslands. The effects of soil textural particles, including clay and silt, explained species abundance, while sand predicted species richness and diversity. This can be attributed to soil texture directly influencing root penetration and nutrient availability by controlling water and nutrient retention (Case & Staver, 2018; Robinson et al., 2018; Tripolskaja et al., 2021). Fine-textured soils may promote weed abundance by retaining water and nutrients, facilitating plant growth, while sandy soils may limit diversity and richness (Anaba et al., 2020; Azizi et al., 2021; Tramontini et al., 2013). However, the results contradict those of Gupta et al. (2022), who reported that natural vegetation was disassociated with soil texture.

Temperature determined vegetation abundance in natural grasslands, influencing plant germination and growth rate, especially during the warm spring–summer season (Farooq et al., 2021; Guo et al., 2020; Khaeim et al., 2022). Additionally, temperature controls the rate of nutrient mineralisation in the soil, which supports vigorous plant growth and seed production (Carbutt et al., 2013; Wang et al., 2020). Therefore, natural grasslands in warmer regions such as the Middleveld and Luve can lead to prolific seed production, increasing the volume of seeds consumed by cattle. Some weed species, such as *Echinochloa crus-galli* with hard seed coats and *Amaranthus hybridus* with small seeds, may escape digestion and composting (Blackshaw & Rode, 1991; Šarapatka et al., 1993). *Amaranthus hybridus* was present in the manure and contributed to the dissimilarities observed between the habitats and agroecological zones, indicating its ability to survive digestion. Additionally, weeds such as *Xanthium strumarium* and *Setaria verticillata* may attach themselves to cattle fur and be deposited in the kraal at night, thereby contributing to the richness and abundance of weeds in manure. Thus, farmers in areas such as Luve may need to enhance manure composting and implement integrated weed management strategies to reduce weed seeds in the soil.

The species distribution modelling further highlighted spatial differences between the agroecological zones. In the Highveld, particularly at Mankayane, the northern grasslands showed high potential species richness, with more than eight species. Additionally, Mncube et al. (2026) reported that maize fields in crop-livestock systems in the Highveld were highly heterogeneous, with high species richness.

This increased richness possibly reflects the introduction of a range of species through grazing and manure application. However, higher weed species richness does not necessarily signify greater crop loss, as diverse communities may reduce the dominance of highly competitive species and promote niche differentiation (Adeux et al., 2019; Storkey & Neve, 2018). Consequently, farmers in the Highveld may experience shifts in weed species composition rather than negative impacts of increased diversity. Conversely, the Middleveld had low potential species richness, greater dominance by a few species, and low evenness, indicating a homogeneous system. Such systems may contain persistent and competitive species, thereby negatively impacting maize production. For example, *Xanthium strumarium*, the greatest contributor to the observed dissimilarities between natural grasslands and maize cropping fields, may dominate these fields, resulting in significant yield losses (Karimmojeni et al., 2021). Therefore, weed management strategies should be adapted to local field conditions with emphasis on targeting dominant and competitive species rather than reducing overall species richness. Integrating improved manure management with site-specific selective weed control approaches may enhance crop productivity while maintaining beneficial plant diversity in smallholder crop-livestock systems.

Conclusion

The study demonstrated that differences in vegetation composition between the two habitats are driven by environmental adaptability. It identified 10 of 17 environmental factors influencing the assembly of natural grassland species and their subsequent impact on weed species incidence post-manure application in maize fields. These factors affected species richness and dominance, providing farmers with insights into potential vegetation and weed populations resulting from manure, thereby aiding in effective weed management. Effective integrated weed management would include composting manure to inhibit weed seed survival, monitoring soil pH, managing phosphorus application, and approaches that consider both landscape vegetation and field-level weed management to mitigate weed invasions.

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Author contributions TLM, EEP, HRM, and PJP conceptualised, conceived, and designed the study. TLM analysed the data and interpreted the results. TLM drafted the manuscript. EEP, PJP, JTR, HRM, and PNM critically revised and edited the manuscript.

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Data availability Data is available upon request from the corresponding author.

Declarations

Ethical standards This research was conducted in accordance with Stellenbosch University's ethical research policy. Permission to conduct the study was granted by the University Research Ethics Committee (REC:FESCAGRI-2020-18829) prior to data collection. Farmers participating in the study were sent a consent form via a link via WhatsApp messaging or by email. The consent form requested their participation in the study and permission to access their fields. Sensitive information, such as personal contact details, was kept separate and accessed only by the author. The natural grasslands were accessed with permission from the Ministry of Agriculture of the Kingdom of Eswatini and with the help of extension officers.

Competing interests The authors declare no competing interests.

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