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Physicochemical properties of soils drive floristic richness of pastures in eastern Democratic Republic of Congo

Samy B. Bacigale^{1,2*} , Yannick Mugumaarhahama³, Valence B. Mutwedu³, Alphonse Z. Balezi⁴, Janvier B. Bashagaluke⁵, Benjamin B. Ncangu⁴, Leon N. Nabahungu², Dieudonné M. Katunga⁶, Kintche Kokou², Mathew G. Gicheha¹ and Isaac M. Osuga^{1*}

Abstract

Background The eastern Democratic Republic of the Congo (DRC) presents unique environmental conditions that shape pasture composition and productivity. However, overgrazing, deforestation, and recurrent bushfires have degraded the grasslands, threatening livestock productivity and biodiversity. Despite these challenges, little is documented on the dominant plant species and their ecological adaptations. By analysing the floristic diversity and soil properties across these regions, this study seeks to identify key constraints and opportunities for optimizing pasture management.

Results The findings revealed 209 plant species belonging to 49 botanic families where Poaceae, Fabaceae and Asteraceae were dominant. Annual grasses (40.7%) were dominant type over perennial grasses (29.3%) and shrubs (23.6%). The soils in the Ruzizi plain are mainly sandy and medium in nitrogen and very low in phosphorus, and are clayey and slightly acidic. The regions of Kabare and Kalehe have low phosphorus content and medium nitrogen content while those in Kalemie are mainly loamy besides being rich in silt and with relatively favorable pH for plant growth (5.5–6.5). The fidelity index (FI) of plant species revealed that the grazing lands in the Hinterland of Bukavu were characterized by 4 plant species including *Centella asiatica*, *Digitaria vestida*, *Sporobolus pyramidalis* and *Pennisetum clandestinum*, while the Ruzizi plain was characterized by 40 species with *Brachiaria ruziziensis*, *Sporobolus* sp., *Acacia spinoza* and *Stylosanthes scabra* being dominant; and Kalemie had 21 characteristic species among which *Hypparhenia* sp., *Parinaria* sp., *Costus* sp. and *Guizotia scabra* presented a FI > 0.65.

Conclusions These findings demonstrate that the floristic composition of grazing lands in eastern DRC is richly diverse and is mainly influenced by soil properties and agroecological conditions. Despite the high floristic richness observed in the study area, most of the plant species are increasers that have survived under disturbance conditions such as overgrazing and repeated bushfires, and therefore are not suitable for guaranteeing the optimum productivity of grazing animals. In the communal grazing system, common approaches are suggested for joint interventions between pasture users and relevant government departments. In the private grazing system, removal of increasers and introduction of improved grasses such as improved *Brachiaria* cultivars are suggested to achieve a balance among species diversity protection, cattle production, and soil quality management.

Keywords Agroecological zone, Grazing land, Pasture species, Soil properties, Cattle

*Correspondence:

Samy B. Bacigale
s.bacigale@cgiar.org

Isaac M. Osuga
isaac.osuga@jkuat.ac.ke

Full list of author information is available at the end of the article

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Introduction

In Africa, livelihoods are predominantly supported by rural setting activities, with more than 70% of the population engaging in rain-fed agriculture (Biteye 2016). Subsistent farming remains the most predominant livelihood activity and source of income of sub-Saharan African (SSA) rural households (Davis et al. 2017; Thornton et al. 2018). Most food production comes largely from fragmented pieces of land owned by smallholder farmers, making their production an important contributor in the continent's rural economy (Giller et al. 2021). The producers mainly practice mixed farming thus integrating cropping with livestock keeping. The livestock component is valuable in sustainable agriculture by providing meat, milk, manure, skin, and hair for increased productivity, profitability, and enterprise resilience which enhances the well-being and increased income for farmers in SSA (Mutwedu et al. 2015; Akilimali et al. 2017; Ayantunde et al. 2018, 2020; Mugumaarhahama et al. 2020).

In the Democratic Republic of the Congo (DRC), livestock contributes up to 9.2% of the gross domestic product (GDP) (National Investment Promotion Agency of DRC 2022) and plays an important function in the income and livelihood of the rural population (Mugumaarhahama et al. 2020). The DRC has 80 million hectares of arable land with the potential to sustain production of at least 100 million cattle, yet the current population is 2.4 million heads of cattle only (Miteyo et al. 2025). This implies that only 2.4% of the cattle production potential is being attained, which is not even sufficient to supply the country's red meat demand. Production is further aggravated by most farmers focusing on keeping small livestock such as poultry, pig, cavies, and rabbits (Maass et al. 2013; Mutwedu et al. 2015). Cattle and other ruminants are mainly grazed on communal grasslands (Mugumaarhahama et al. 2020). They are also supplemented on crop residues and agro-industrial byproducts when available mainly during dry seasons (Mutwedu et al. 2022). It is reported that the grazing material in the grasslands is mostly composed of weeds and less palatable plant species such as *Digitaria abyssinica*, *Cynodon dactylon*, *Sporobolus pyramidalis*, *Hypparhenia rufa*, *Commelina diffusa*, *Bidens pilosa*, *Conyza sumatrensis*, *Galinsoga ciliata* (Bacigale et al. 2014) which have low feeding quality. Besides the biophysical attributes, plant composition can vary based on production practices such as grazing and other economic activities reliant on the grasslands.

Rupprecht et al. (2016) reported that grazing can have numerous impacts on landscape structure. Their study findings indicated that grazing by large herbivores is a key factor shaping the composition and structure of the

vegetation and nutrient availability in savanna and steppe ecosystems. A work by Enyedi et al. (2008) demonstrated that plant species diversity may significantly decline when pasturing is abandoned. Veen et al. (2014) showed a changing plant composition under grazing exclusion in savanna landscapes and even deduced a co-evolutionary adaption of these ecosystems and herds of grazers. Feng et al. (2016) highlighted the importance of high floristic diversity in the generation of opportunities to select diverse diets from different strata which animals such as cattle can reach. The combinations of selected plants guarantee the acquisition of nutrients and secondary compounds that the animal needs for its nutritional and health maintenance (Li et al. 2024). However, underlying soil conditions may also determine plant community composition, vegetation structure and biomass ingredients and thus influence grazing intensity (Molina et al. 2024). Eni et al. (2012) revealed a positive interrelationship between soil organic matter and plant sizes and diversity, while Ma et al. (2020) realized that the content of N, P and K in the soil tended to affect the composition and distribution of plant species. The above information is scarce in DRC, but it is important to understand the reasons behind grassland degradation, especially in the eastern part of the country, so as to suggest appropriate interventions. It is, therefore, important to explore the composition of plant species on grazing lands in relation to soil physicochemical properties and the agroecologies in South-Kivu and Tanganyika provinces.

The South-Kivu and Tanganyika provinces are located in eastern DRC and have two contrasting agroecologies. The highlands around Bukavu city are characterized by rain-fed agriculture with livestock raised on zero-grazing or semi zero-grazing systems due to population pressure on land (Maass et al. 2012; Bacigale et al. 2014). On the other hand, the lowlands from Ruzizi plain to Kalemie territory along the Ruzizi River and Lake Tanganyika, are characterized by semi-aridity and pastoralism is the dominant livestock production system. The environment is fragile, characterized by the inadequate and erratic rainfall regime. The resultant resources (pasture and water) often lead to conflicts between livestock owners and crop farmers. The twin problems have negative spillovers on the management of grazing lands in the zone despite the area being predominantly supported by grazed livestock system (Bacigale et al. 2019; Mugumaarhahama et al. 2020). The dominant grazed feed resources are rarely documented (Bacigale et al. 2019). There is need to carry out research whose findings would provide such information for optimized grazed resources utilization and conservation. Besides, it is important to clarify the impact of the types of soil and ecologies in the eastern DRC as they influence the plant species distribution and productivity.

This study aimed to assess the floristic diversity of grazing lands in South-Kivu and Tanganyika provinces and their variation in different types of soils and ecologies.

Materials and methods

Study area

This study was conducted in four territories of the South-Kivu province, including Kalehe, Kabare, Walungu and Uvira, and in the Tanganyika province, the territory of Kalemie (Fig. 1).

The territories of Kalehe, Kabare and Walungu are often grouped in the same agro-ecological zone so-called the Hinterland of Bukavu. Kalehe is located within 2°16' 26" S latitude and 28°54' 58" E longitude at an elevation of 1655 m above sea level and an average temperature of 22.6 °C. The area is further characterized by clay soil and an average annual rainfall ranging between 1300 and 1680 mm. Kabare is located within 2°17' S latitude and 28°40' E longitude, with 19.2 °C as mean temperature per annum, 1608 mm mean rainfall per annum while the soil is mainly clayey. Walungu area is located within 2°37' S latitude and 28°40' E longitude and receives rainfall

of about 1500 mm per annum with a 22 °C mean temperature per annum. The soil in Walungu is mainly clay-sandy. Uvira is located within 3°20' S latitude and 29°30' E longitude, with an annual average rainfall of about 1600 mm and temperature averaging 25 °C per annum. The soil in Uvira is majorly sandy, while in some places it is sandy loam, and rarely clay and sandy (Bagula et al. 2022a, 2022b). Kalemie is located within 5°56' S latitude, 29°11' E longitude, and receives average rainfall of about 1090 mm per annum with an annual mean temperature at 28 °C (Data retrieved from NASA for 02/04/2018 to 23/12/2020).

Data collection

Botanical field survey to assess the floristic diversity

The data was collected during the period from November to December of the year 2022, corresponding to the major rainy season in the two provinces. Twenty-five grazing lands were selected based on their importance in cattle grazing, accessibility, security and representation of diverse socioeconomic and land-use contexts of the zone. Indeed, the Hinterland of Bukavu experiences

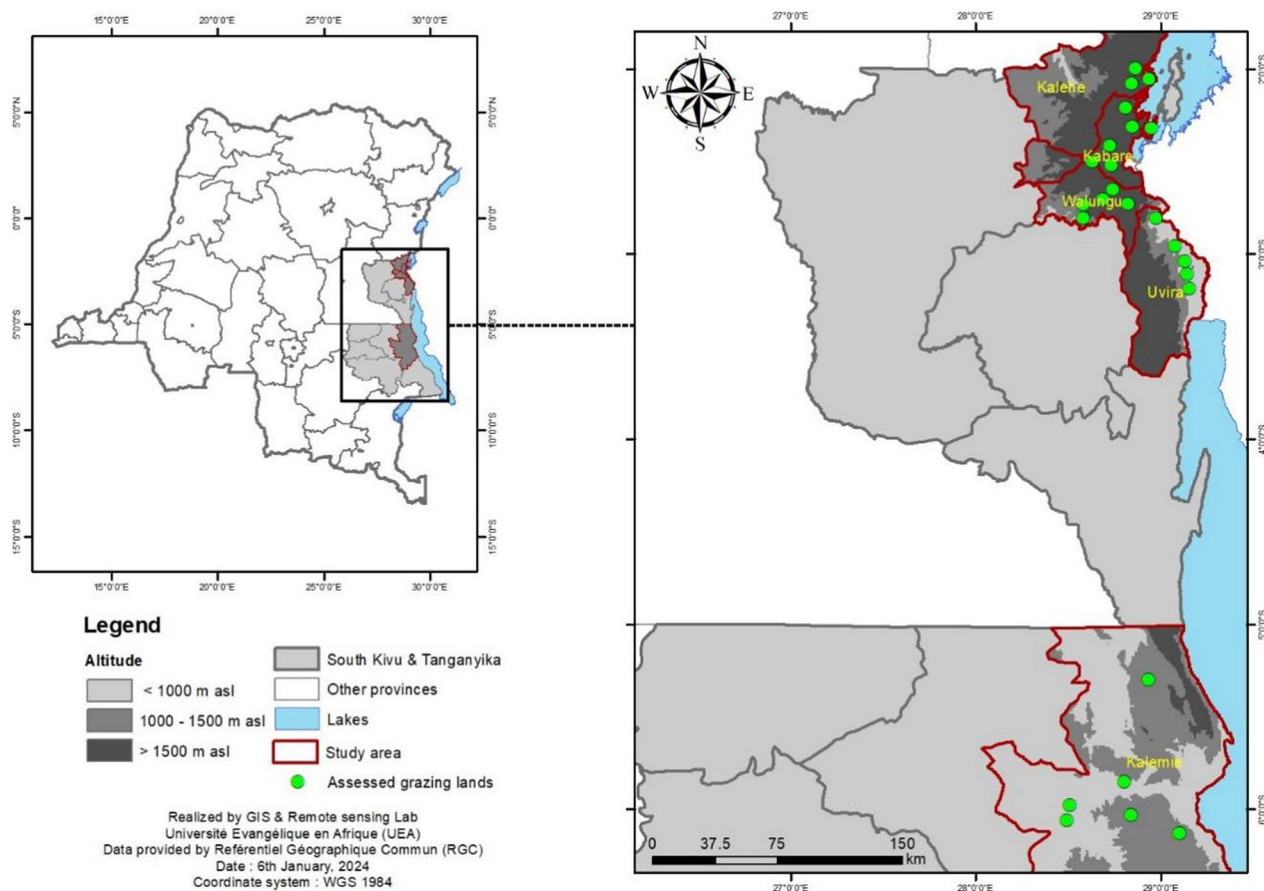


Fig. 1 Map showing the study area along the altitudes

high population pressure leading to land scarcity, competing agricultural activities and high grazing pressure on remaining grasslands. By comparison, the Ruzizi Plain is characterized by intensive transhumant grazing system and cross-border livestock trade with neighboring Burundi and Rwanda. The Kalemie Zone has moderate grazing intensity, although it is increasingly affected by agricultural expansion and human settlement. Based on the above ecological variabilities influencing grassland use and degradation in Eastern DRC, nineteen grazing lands were selected in four territories of the South-Kivu province (Kalehe: Bihama, Bogamanda, Munanira villages; Kabare: Cirunga, Miti, Kakondo, Mulumemunene, Mushunguri, Nyacibamba villages; Walungu: Nyandja, Cibeke, Cidorho, Muzinzi, Nyirundwe villages; Uvira: Katogota, Mutarule, Sange, Runingu and Kiliba villages) and six in one territory of the Tanganyika province (Kalemie: Kisondja, Kirimbi, Muganja, Lwanika, Kazaroho and Byaduniya villages). In each grazing land, three phytosociological plots measuring 7 m × 7 m were established perpendicularly to the slope. Within each plot, an inventory of all plant species and their botanical families was conducted, and the plants were assigned a cover-abundance coefficient that was later converted into quantity following Van der Maarel (1979). The biological and morphological types were determined for each plant species in the different plots. The plant species were identified in situ. However, non-identified species were coded and placed in an herbarium for later identification at the Research Center in Natural Sciences of Lwiro (CRSN/Lwiro). The fidelity index (FI) was then calculated to determine the plant species that characterize the grazing lands in each agroecology based of the degree of presence as described by Dufrene and Legendre (1997). This method has proven to be particularly useful in long-term environmental monitoring for conservation or ecological management (Cáceres et al. 2020).

Soil characterization

Soil samples were collected from topographically homogeneous sites that had similar types of vegetation. From each site, a single composite sample composed of four sub-samples from the center and three others from a direction of 120° were collected. Stratified sampling was used to collect four sub-samples in each stratum from heterogeneous sites. The stratum sampling followed the procedure described for homogeneous sites. In all cases, sampling was done at a depth of 20 cm (0–20 cm) using a probe as majority of herbaceous pasture species occupy the surface layers of the soil. From each grazing land, a portion of about 500 g was collected and placed in a specific bag for the chemical analysis of the necessary parameters at the soil laboratory of the International

Institute of Tropical Agriculture (IITA), the Olusegun Obasanjo campus in Bukavu, DRC. The soil pH, total nitrogen, phosphorus and texture were analyzed. Soil pH was determined by a digital pH-meter at 1:5 (solute:solution) ratio. Total nitrogen was determined by the Kjeldahl method (Okalebo et al. 2002). The available phosphorus was determined using the modified Olsen method (Okalebo et al. 2002), and the soil texture by the hydrometer method (Estefan et al. 2013).

Climatic characterization

The bioclimatic variables were retrieved from Worldclim (<https://www.worldclim.org>) and Africlim (https://www.york.ac.uk/environment/research/kite/_resources) databases (Platts et al. 2015; Fick and Hijmans 2017). The data was used to characterize climatic conditions that prevail in the studied grazing lands. The data consisted of environmental variables that were obtained from interpolations of monthly average precipitations and temperatures using datasets covering years 1986 to 2015. ArcGIS Desktop 10.7 was used for data extraction using coordinates of surveyed grazing lands in South-Kivu and Tanganyika provinces. Table 1 presents the bioclimatic data used in this study.

Statistical data analysis

The collected data was entered into Microsoft Excel for data cleaning and validation. All statistical analyses were performed using R version 4.0.5 as described below:

Floristic composition A descriptive analysis was carried out to determine the floristic composition with the forage species being grouped according to their botanical families for which the frequencies were determined. Moreover, the ordination by principal coordinates analysis (PCoA) was applied on a species by plots matrix to characterize the variation in the floristic composition of pastures using the Bray–Curtis dissimilarity matrix on square root transformed percent cover values. To detect similarity in floristic composition between grazing lands, PCoA was also applied to Bray–Curtis's dissimilarity matrix between centroids of individual groups, previously calculated on Euclidean distance space of one PCoA. Species present in less than 10% of the plots were not considered in the PCoA. For the fidelity index, the function `multipatt()` was used to depict the indicator species.

Soil properties and climatic conditions The territories of Kalehe, Kabare, Walungu, Uvira and Kalemie were compared based on different variables characterizing the soil and climatic conditions. Analysis of variance (ANOVA) was used after checking the conditions of normality and homoscedasticity. In cases where the

Table 1 Bioclimatic variables used to characterize climatic conditions in surveyed grazing lands

Variables	Units	Code	Source
Altitude	m		GPS
Annual mean temperature	°C	bio01	WorldClim
Mean diurnal range	°C	bio02	WorldClim
Isothermality (bio02/bio07) (×100)	%	bio03	WorldClim
Temperature seasonality (standard deviation × 100)	%	bio04	WorldClim
Maximum temperature of warmest month	°C	bio05	WorldClim
Minimum temperature of coldest month	°C	bio06	WorldClim
Temperature annual range (bio05–bio06)	°C	bio07	WorldClim
Mean temperature of wettest quarter	°C	bio08	WorldClim
Mean temperature of driest quarter	°C	bio09	WorldClim
Mean temperature of warmest quarter	°C	bio10	WorldClim
Mean temperature of coldest quarter	°C	bio11	WorldClim
Annual precipitation	mm	bio12	WorldClim
Precipitation of wettest month	mm	bio13	WorldClim
Precipitation of driest month	mm	bio14	WorldClim
Precipitation seasonality (coefficient of variation)	%	bio15	WorldClim
Precipitation of wettest quarter	mm	bio16	WorldClim
Precipitation of driest quarter	mm	bio17	WorldClim
Precipitation of warmest quarter	mm	bio18	WorldClim
Precipitation of coldest quarter	mm	bio19	WorldClim
Number of dry months	Month	llds	AfriClim
Annual moisture index	–	mi	AfriClim
Moisture index of arid quarter	–	miaq	AfriClim
Moisture index of moist quarter	–	mimq	AfriClim
Potential evapotranspiration	mm	pet	AfriClim

ANOVA validity conditions were not met, the Kruskal–Wallis test was used. In the case of significant differences between the territories, Tukey’s or Dunn’s test was used to separate homogeneous groups. In addition, Principal Component Analysis (PCA) was performed separately through Multiple Factor Analysis (MFA) on soil physicochemical and bioclimatic data to characterize soil properties and climatic conditions of pastures, respectively. Further, the MFA provided uncorrelated principal components (PC), which were used for clustering. The coordinates of the centroids of the territories on the axes obtained by MFA were used as input in the clustering algorithms. The MFA output, in the form of a reduced dataset based on the retained principal components, was subjected to a clustering analysis (CA) using the hierarchical clustering on principal components (HCPC) procedure to find clusters that maximize the differences between clusters while minimizing the variability within clusters.

Results

Characterization of soils in pastures

The main characteristics of soils of the studied grazing lands per territory are presented in Fig. 2 and summarized in Table 2.

The results demonstrate that soils in Uvira territory are sandier with a pH close to neutrality. They contain small amounts of clay and silt, but also mineral elements, mainly nitrogen and phosphorus.

Across territories, soils present clear contrasts in terms of chemical and physical compositions. Soils in Kalehe and Walungu are highly acidic, while those in Kabare are moderately acidic and in Uvira and Kalemie soils have a pH close to neutrality. The soils of Kalehe and Kabare are more clayey with higher assimilable P content than the other territories where Olsen-P is very low. The N content in Kalehe, Kabare and Walungu are ranked as medium contrary to those from Uvira and Kalemie which are low. The soils in Kabare territory

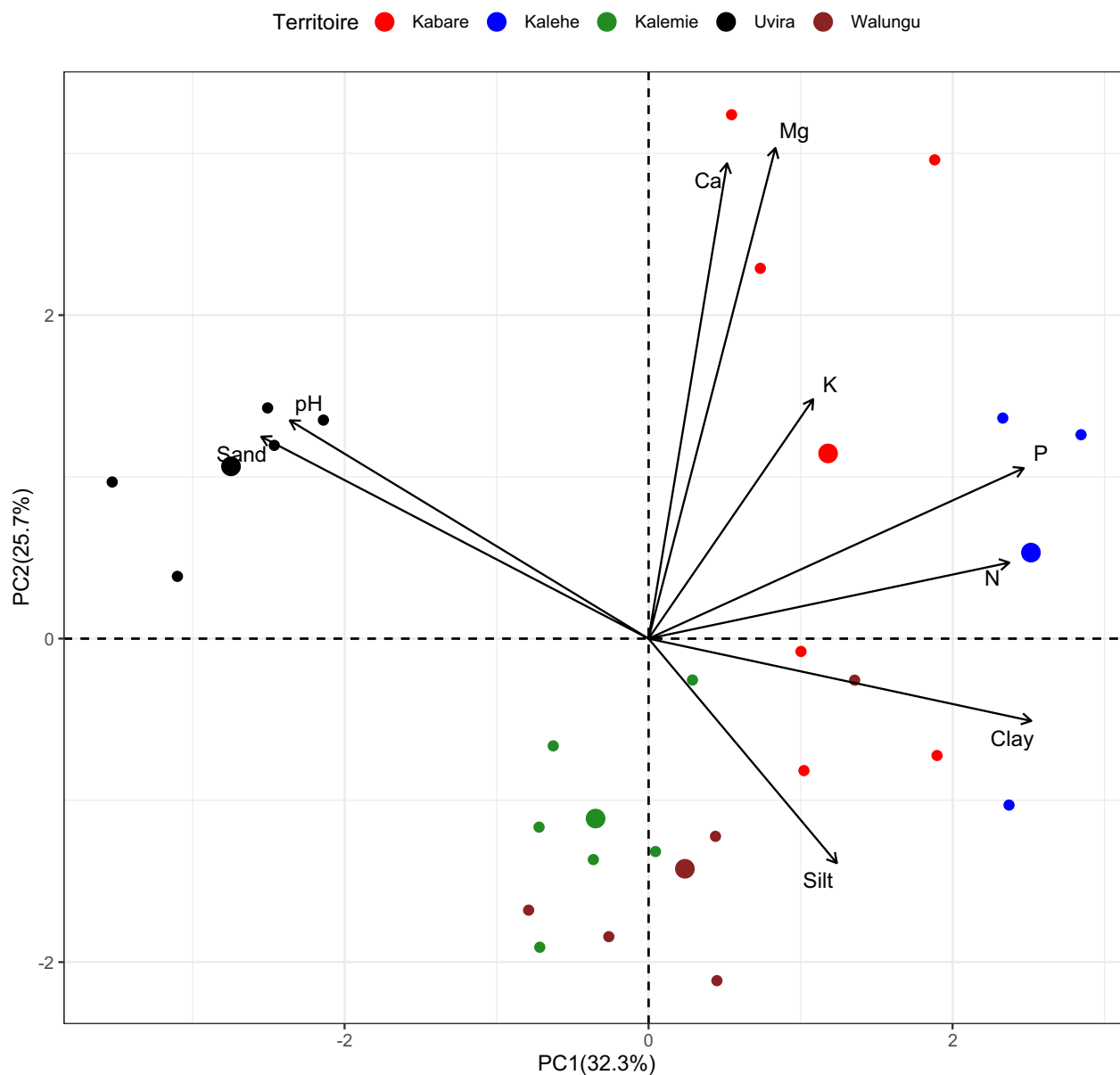


Fig. 2 Principal components analysis biplot with the soil characteristics of grazing lands

have the highest calcium and magnesium content. The soils found in most parts of Walungu and Kalemie territories are almost similar and are characterized by a higher silt content, though they are generally poorer in mineral elements (N, P, Ca and Mg). Results presented in Table 2 indicate that the potassium content did not differ significantly amongst the five territories. The soils samples from Kalehe territory had significantly higher total nitrogen and phosphorus than the other territories. The soil samples collected from Kabare had the highest calcium and magnesium contents.

Characterization of climatic conditions in the pastures

Figure 3 shows a clear distinction between the bioclimatic conditions in Uvira and Kalemie from those in other territories. The territories of Uvira and Kalemie are characterized by higher temperatures (annual mean temperature, mean diurnal range, temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, and mean temperature of coldest quarter), lowest isothermality and lowest precipitations (annual

Table 2 Soil properties of grazing lands in the five territories

Parameters	Kalehe	Kabare	Walungu	Uvira	Kalemie	Mean
pH	4.97 ± 0.18 ^c	5.74 ± 0.35 ^b	4.98 ± 0.19 ^c	6.56 ± 0.11 ^a	6.01 ± 0.19 ^b	5.65 ± 0.20
Total N (%)	0.51 ± 0.18 ^a	0.30 ± 0.08 ^b	0.32 ± 0.02 ^b	0.15 ± 0.11 ^c	0.14 ± 0.04 ^c	0.28 ± 0.09
Olsen-P (mg kg ⁻¹)	20.04 ± 4.75 ^a	13.19 ± 1.56 ^b	7.64 ± 8.81 ^c	5.13 ± 3.67 ^c	5.98 ± 1.84 ^c	10.40 ± 4.13
K (cmol kg ⁻¹)	0.72 ± 0.26 ^a	0.33 ± 0.16 ^a	0.28 ± 0.11 ^a	0.37 ± 0.17 ^a	0.44 ± 0.20 ^a	0.43 ± 0.18
Ca (cmol kg ⁻¹)	2.85 ± 1.10 ^b	7.17 ± 3.31 ^a	1.05 ± 0.74 ^b	4.01 ± 1.31 ^{ab}	2.08 ± 1.13 ^b	3.43 ± 1.52
Mg (cmol kg ⁻¹)	1.78 ± 1.07 ^b	3.25 ± 2.31 ^a	0.40 ± 0.30 ^c	1.50 ± 0.26 ^b	0.77 ± 0.35 ^c	1.54 ± 0.86
Clay (%)	34.88 ± 13.75 ^a	34.82 ± 11.95 ^a	28.50 ± 6.55 ^{ab}	14.34 ± 2.08 ^b	25.02 ± 7.06 ^{ab}	27.51 ± 8.28
Silt (%)	20.67 ± 3.06 ^{bc}	26.81 ± 7.17 ^b	23.00 ± 1.41 ^b	10.6 ± 4.34 ^c	37.59 ± 3.93 ^a	23.73 ± 3.98
Sand (%)	44.45 ± 10.97 ^b	38.38 ± 10.70 ^b	48.5 ± 5.47 ^b	75.06 ± 4.50 ^a	37.39 ± 4.62 ^b	48.76 ± 7.25
Slope (°)	14.2 ± 3.1 ^a	8.8 ± 6.7 ^{ab}	15.8 ± 3.5 ^a	0.4 ± 0.3 ^b	1.9 ± 1.1 ^b	8.22 ± 2.94
Dominant texture	Clay loam	Clay loam	Sandy clay loam	Sandy loam	Loam	-

Values with the same letter are statistically equal at the significance level $\alpha = 0.05$

precipitation, precipitation of wettest month, precipitation of driest month, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, precipitation of coldest quarter; annual moisture index, moisture index of arid quarter, and moisture index of moist quarter). These two territories also have the longest dry seasons and the highest levels of potential evapotranspiration.

Results presented in Fig. 3 and Table 3 broadly classify the 5 territories into two main groups with the climatic conditions of Kabare, Kalehe and Walungu being characterized by more precipitations (with the averages ranging from 1500 to 1800 mm) and lower daily temperatures (averages ranging from 17 to 19 °C); and those of Kalemie and Uvira being higher in daily temperatures (averages ranging from 22 to 24 °C) and lower precipitations (averages not exceeding 1200 mm). The other climatic parameters of temperature and precipitation also follow the same trend.

Figure 4 shows that the ecological conditions of grazing lands in Kabare, Kalehe and Walungu are homogeneous as defined by soil and climatic parameters. This is not the case for Kalemie and Uvira, which have heterogeneous ecological conditions. Kabare, Kalehe, and Walungu surround the city of Bukavu and are so-called “the Hinterland of Bukavu”.

Floristic richness of grazing lands in South-Kivu and Tanganyika provinces

The floristic investigations conducted on grazing lands in South-Kivu and Tanganyika provinces documented 209 plant species belonging to 49 botanical families (Supplementary file 1: Table S1). The most frequently identified botanical families (Fig. 5) in the three ecologies (Fig. 4) were Poaceae, Fabaceae and Asteraceae. However, plant families such Acanthaceae, Commelinaceae, Cyperaceae,

Euphorbiaceae, Lamiaceae, Malvaceae and Rubiaceae were also well represented in the three ecologies. Other families such as Amaranthaceae, Annonaceae, Apiaceae, Apocynaceae, Araceae, Araliaceae, Asparagaceae, Boraginaceae, Brassicaceae, Caryophyllaceae, Celastraceae, Chrysobalanaceae, Colchicaceae, Commelinaceae, Convolvulaceae, Crassulaceae, Dioscoreaceae, Geraniaceae, Hyacinthaceae, Hypericaceae, Juncaceae, Melastomataceae, Menispermaceae, Myrtaceae, Nephrolepidaceae, Onagraceae, Orchidaceae, Orobanchaceae, Oxalidaceae, Phyllanthaceae, Phytolacaceae, Plantaginaceae, Polygalaceae, Proteaceae, Pteridaceae, Sapindaceae, Solanaceae, Verbenaceae, Zingiberaceae were rarely represented on the studied grazing lands.

The morphological and biological characteristics of plant species identified on the grazing lands in South-Kivu and Tanganyika are summarized in Fig. 6. Results indicate that annual grasses are the most abundant across the grazing lands in the three ecologies, especially in the Hinterland of Bukavu. The perennial grasses were more observed in Kalemie than in Ruzizi plain and the Hinterland of Bukavu, while the shrubs were much abundant in the Ruzizi plain. Overall, trees and subtrees were comparatively less. No subtree was observed on the grazing lands in the Ruzizi plain. Therophytes were more abundant in the Hinterland of Bukavu and the Ruzizi. Proportionately, while they were equally represented with Phanerophytes in Kalemie. Also, Chamephytes and Hemicryptophytes were similarly equal in grazing lands of the Hinterland of Bukavu and Kalemie. Phanerophytes were the second most prevalent in the Ruzizi plain followed by Hemicryptophytes, Chamephytes and Geophytes.

Results for plant species fidelity index (FI) in different ecologies are presented in Supplementary file 1: Table S2. The grazing lands from the Hinterland of Bukavu, the

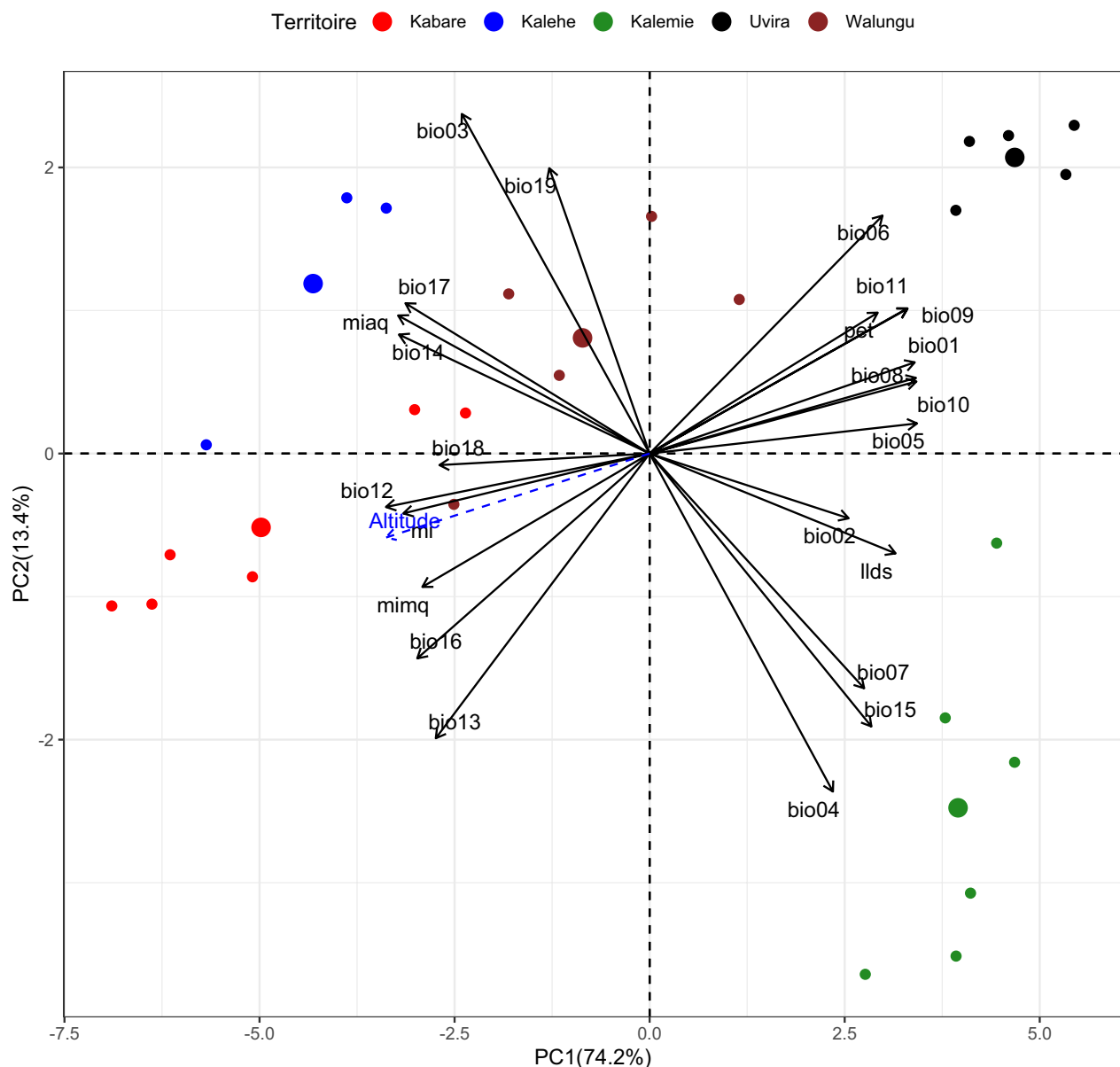


Fig. 3 Principal components analysis biplot with the climatic conditions prevailing in the grazing lands

Ruzizi plain and Kalemie are respectively characterized by 4, 40 and 21 plant species. The four species with the highest FI for the Hinterland of Bukavu were *Centella asiatica*, *Digitaria vestida*, *Sporobolus pyramidalis* and *Pennisetum clandestinum*. In the Ruzizi plain, the four species with the highest FI were *Brachiaria ruziziensis*, *Sporobolus* sp., *Acacia spinosa* and *Stylosanthes scabra*, while in Kalemie, they were *Hypparhenia* sp., *Parinaria* sp., *Costus* sp. and *Guizotia scabra*.

The plant species identified in the Hinterland of Bukavu, Ruzizi plain (Uvira) and Kalemie ecologies

are presented in Fig. 7, Fig. 8 and Fig. 9, respectively. Figure 7 for the Hinterland of Bukavu ecology shows slight heterogeneity among the grazing lands of Kabare, Kalehe, and Walungu territories. The grazing lands of Kabare and Kalehe are more similar in terms of plant species than those of Walungu. In terms of vegetation, *Sporobolus pyramidalis* is more abundant in Walungu while *Pennisetum clandestinum* is abundant in Kabare and Kalehe. *Digitaria vestida* and *Paspalum conjugatum* are found across the territories in the Hinterland of Bukavu. There was observed little plant diversity in the Hinterland of Bukavu.

Table 3 Bioclimatic characteristics of the territories of Kalehe, Kabare, Walungu, Uvira (in South-Kivu province) and Kalemie (in Tanganyika province)

Parameters	Kalehe	Kabare	Walungu	Uvira	Kalemie	Mean
Altitude (m)	1910.7 ± 207.6 ^a	2167 ± 312.1 ^a	1565.6 ± 274.8 ^b	785.7 ± 10.2 ^d	1048.3 ± 231.6 ^c	1495.5 ± 207.26
Annual mean temperature (°C)	16.8 ± 1.2 ^c	15.5 ± 1.7 ^c	19.1 ± 1.6 ^b	24.3 ± 0.3 ^a	22.1 ± 1.0 ^a	19. ± 1.2
Mean diurnal range (°C)	10.0 ± 1.2 ^{ab}	9.3 ± 1.3 ^c	10.6 ± 0.4 ^{ab}	10.6 ± 0.8 ^{ab}	11.7 ± 0.4 ^a	10.4 ± 0.8
Isothermality (100 × BIO2/BIO7)	91.7 ± 2.1 ^a	89.7 ± 1.7 ^a	88.6 ± 1.7 ^a	84.6 ± 1.2 ^b	73.2 ± 2.7 ^c	85.6 ± 1.9
Temperature seasonality (100 × SD)	25.8 ± 4.4 ^d	29.6 ± 4.6 ^d	34.4 ± 7.7 ^c	50.3 ± 7.5 ^b	90.4 ± 20.2 ^a	46.1 ± 8.9
Maximum temperature of warmest month (°C)	22.1 ± 1.7 ^{bc}	20.6 ± 2.3 ^c	25.1 ± 1.8 ^b	30.2 ± 0.8 ^a	29.5 ± 1.2 ^a	25.5 ± 1.6
Minimum temperature of coldest month (°C)	11.3 ± 0.7 ^{bc}	10.3 ± 1.1 ^c	13.2 ± 1.5 ^b	17.7 ± 0.2 ^a	13.6 ± 1.2 ^b	13.2 ± 0.9
Temperature annual range (°C)	10.9 ± 1.1 ^{bc}	10.3 ± 1.2 ^c	11.9 ± 0.6 ^{bc}	12.5 ± 1.0 ^b	16.0 ± 0.4 ^a	12.3 ± 0.9
Mean temperature of wettest quarter (°C)	16.8 ± 1.3 ^{bc}	15.6 ± 1.6 ^c	18.8 ± 1.6 ^b	24.0 ± 0.2 ^a	22.1 ± 0.9 ^a	19.5 ± 1.1
Mean temperature of driest quarter (°C)	16.6 ± 1.3 ^{cd}	15.3 ± 1.8 ^d	18.9 ± 1.4 ^{bc}	24.1 ± 0.4 ^a	21.0 ± 1.2 ^b	19.2 ± 1.2
Mean temperature of warmest quarter (°C)	17.0 ± 1.1 ^d	15.8 ± 1.7 ^d	19.5 ± 1.6 ^c	25.0 ± 0.4 ^a	22.9 ± 0.9 ^b	20.0 ± 1.2
Mean temperature of coldest quarter (°C)	16.5 ± 1.3 ^c	15.2 ± 1.8 ^c	18.8 ± 1.5 ^{bc}	23.9 ± 0.3 ^a	20.8 ± 1.3 ^b	19.1 ± 1.3
Annual precipitation (mm)	1781.0 ± 165.9 ^a	1849.8 ± 84.0 ^a	1533.8 ± 101.2 ^b	895.2 ± 15.1 ^d	1154 ± 45.1 ^c	1442.8 ± 82.3
Precipitation of wettest month (mm)	214.3 ± 18.2 ^{ab}	232.7 ± 14.4 ^a	194.8 ± 13.4 ^b	134.0 ± 2.2 ^c	199.2 ± 14.2 ^b	195.0 ± 12.5
Precipitation of driest month (mm)	37.7 ± 2.3 ^a	27.8 ± 2.0 ^b	18.0 ± 2.7 ^c	5.0 ± 1.1 ^d	2.8 ± 1.6 ^d	18.3 ± 1.9
Precipitation seasonality (CV)	39.0 ± 2.3 ^e	46.9 ± 1.2 ^d	51.9 ± 1.4 ^c	61.8 ± 0.5 ^b	76.0 ± 4.7 ^a	55.1 ± 2.0
Precipitation of wettest quarter (mm)	586.0 ± 55.2 ^{ab}	630.7 ± 22.0 ^a	554.0 ± 33.9 ^{bc}	356.4 ± 5.7 ^d	510.0 ± 29.4 ^c	527.4 ± 29.3
Precipitation of driest quarter (mm)	178.0 ± 8.2 ^a	126.7 ± 7.3 ^b	87.6 ± 10.0 ^c	35.0 ± 1.4 ^d	16.2 ± 6.4 ^e	88.7 ± 6.7
Precipitation of warmest quarter (mm)	493.3 ± 126.6 ^a	378.7 ± 11.2 ^a	402.8 ± 84.9 ^a	138.6 ± 40.0 ^b	232.3 ± 64.3 ^b	329.1 ± 65.4
Precipitation of coldest quarter (mm)	302.7 ± 146.9 ^{ab}	235.3 ± 29.0 ^{ab}	380.2 ± 231.1 ^a	234.8 ± 105.7 ^{ab}	51.7 ± 21.0 ^b	240.9 ± 106.7
Number of dry months	1.0 ± 0.5 ^c	1.5 ± 0.8 ^c	3.0 ± 0.2 ^b	5.0 ± 0.1 ^a	4.7 ± 0.8 ^a	3.0 ± 0.5
Annual moisture index	124.3 ± 10.1 ^{ab}	157.3 ± 27.8 ^a	110.6 ± 20.9 ^b	57.3 ± 0.6 ^d	82.5 ± 6.0 ^c	106.4 ± 13.1
Moisture index of arid quarter	54.0 ± 1.0 ^a	46.8 ± 7.3 ^a	28.8 ± 4.9 ^b	7.0 ± 0.4 ^c	4.0 ± 2.3 ^d	28.1 ± 3.2
Moisture index of moist quarter	159.7 ± 13.0 ^{ab}	204.7 ± 37.6 ^a	151.6 ± 28.4 ^{ab}	95.0 ± 1.0 ^c	133.8 ± 10.4 ^b	149.0 ± 18.1
Potential evapotranspiration (mm)	1397.7 ± 51.4 ^c	1221.7 ± 151.7 ^c	1503.0 ± 141.1 ^{bc}	1730.0 ± 6.2 ^a	1542.2 ± 50.4 ^b	1478.9 ± 80.2

Values with the same letter are statistically equal at the significance level $\alpha = 0.05$

Figure 8 presents the results for plant species found in the Ruzizi plain (Uvira). It is evident that the dominant types in Katogota differ from those in Mutarule-Sange and Runingu-Kiliba ecologies. For example, Mutarule-Sange and Runingu-Kiliba are abounded by plant species such as *Stylosanthes scabra*, *Commelina diffusa* and *Kyllinga bulbosa* while *Euphorbia hirta*, *Sida acuta*, *Spermacoce princeae* and *Brachiaria ruziensis* are the most abundant in the Katogota area. There was observed huge plant diversity within the Ruzizi plain as compared to the Hinterland of Bukavu.

As shown in Fig. 9, species found in Kisondja ecology included *Afromomum* sp., *Kyllinga bulbosa*, *Mariscus flabelliformis*, *Pteridium aquilinum* and *Solenostemone* sp. In Lwanika, species such as *Guizotia scabra*, *Acanthospermum hispidum*, *Harungana madagascariensis* and *Sporobolus pyramidalis* were particularly abundant.

Figure 10 presents the plant species distribution as they correlate with soil physicochemical parameters and agroecological zones. Species like *Cynodon plecostachys*, *Hydrocotyle manii*, *Kyllinga erecta* and *Sida*

acuta have strong correlation with high levels of calcium, magnesium and potassium in the soil, mostly in the Kabare area. By contrast, *Trifolium purseglovei*, *Pennisetum clandestinum*, *Vigna vexilata*, *Centella asiatica*, *Kyllinga bulbosa*, *Digitaria vestida*, *Geranium* sp. and *Solenostemone* sp. are much linked with soils of Kalehe which are rich in phosphorus and sodium. However, *Paspalum conjugatum*, *Panicum brevifolium*, *Dyschoriste radicans* and *Harungana madagascariensis* show a marked affinity for clayey-silt soils in the ecology of Kalehe, Kabare and Walungu. In the Ruzizi plain (Uvira) where soils are sandy with pH close to neutrality, plants species like *Acacia spinoza*, *Trifolium usambarense*, *Brachiaria ruziensis*, *Sporobolus pyramidalis*, *Parthenium hysterophorus*, *Commelina* sp., *Indigofera erecta*, *Themeda triandra*, *Cassia mimosoides*, *Stylosanthes scabra* and *Hypparhenia rufa* seem to prosper. Kalemie ecology is characterized by silty soils like Walungu, and both have *Imperata cylindrica*, *Hypparhenia cymbaria* and *Hypparhenia* sp. in common, but species like *Costus* sp., *Parinari* sp., *Brachiaria* sp. and *Guizotia scabra* are much associated

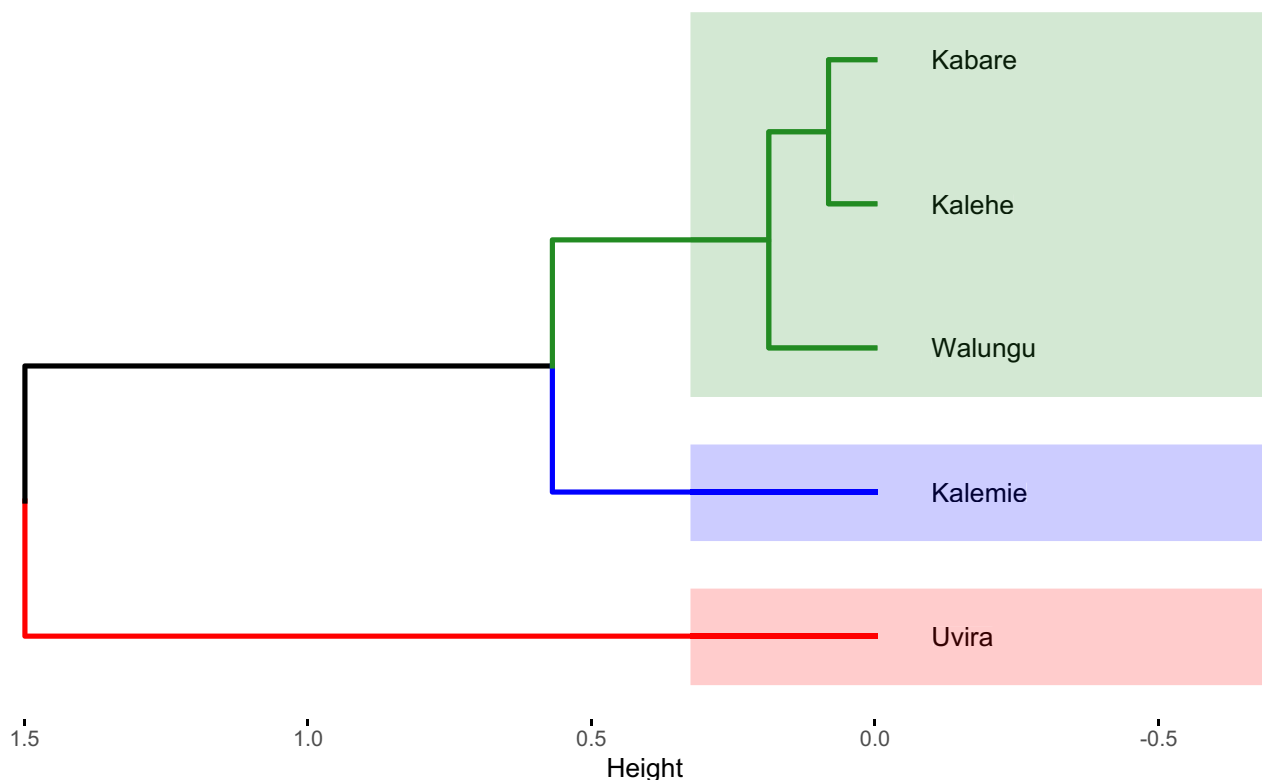


Fig. 4 Dendrogram showing the clustering of territories based on the soil properties and climatic conditions

with Kalemie ecology only. Finally, *Spermacoce princae* is located centrally on the biplot and should, therefore, have a high ecological plasticity.

Discussion

In eastern DRC, cattle are traditionally grazed on natural grasslands (Mugumaarhahama et al. 2021). This implies that there is critical need to assess factors that influence the productivity of the grassland ecosystems. This would be necessary in production and profitability optimization of grassland grazed production systems where plant species are the main source of feedstuffs. Quality and quantity of the feedstuffs are determined by production and composition of the palatable plant materials which depend largely on the edaphoclimatic factors. It is therefore important to assess the soil factors, the climatic conditions and to inventory the plant species on the grazing lands in the eastern DRC. This study considered the territories in South-Kivu and Tanganyika provinces, which are among the most important in cattle production in eastern DRC.

The results of the current study demonstrated that the soils in the Ruzizi plain and Kalemie zones, which are in low altitude, are sandier with a pH close to neutrality. They tend to be acidic and clayey with higher P content

in the Hinterland of Bukavu,, which is in high altitude. Several researchers have found that physicochemical parameters of soils depend on elevation. Kamal et al. (2023) found that silt content decreased, and clay content increased with altitude, while sand content showed inconsistent variation in the Swat River Catchment in Pakistan. On contrast, Badia et al. (2016) found that increasing elevation decreases significantly the pH, base saturation, exchangeable potassium, and fine silt-sized particles, while it increases organic matter, C/N ratio, soil aggregate stability, and coarse sand-sized particles. The soil in the Ruzizi plain (Uvira) where pastures are heavily grazed (Mugumaarhahama et al. 2021), are exposed to soil degradation by impairing the physical structure of soils and hinder water infiltration and root deepening and expose soils to potential erosions (Pulido et al. 2016). The soils of Kalehe and Kabare have higher nitrogen and phosphorus than other sites, showing that they have potential to boost vegetation productivity as demonstrated by Simpson et al. (2014).

The territories of Uvira and Kalemie which are at low altitude were found to have higher temperatures, lower isothermality, lower precipitations, longer dry seasons and the higher levels of potential evapotranspiration compared to Kalehe, Kabare and Walungu which are

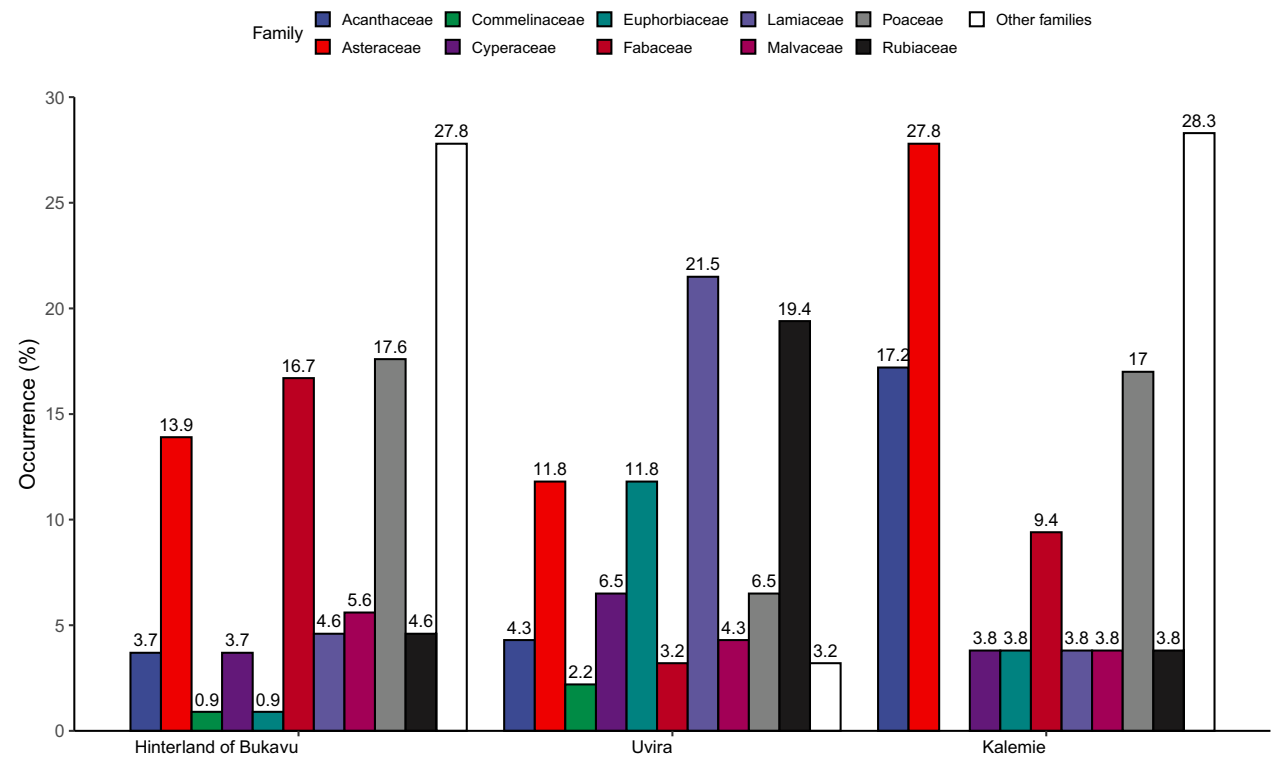


Fig. 5 Presentation of botanical families identified on the grazing lands in South-Kivu and Tanganyika provinces. The Hinterland of Bukavu includes the territories of Kalehe, Kabare and Walungu which surround the Bukavu City

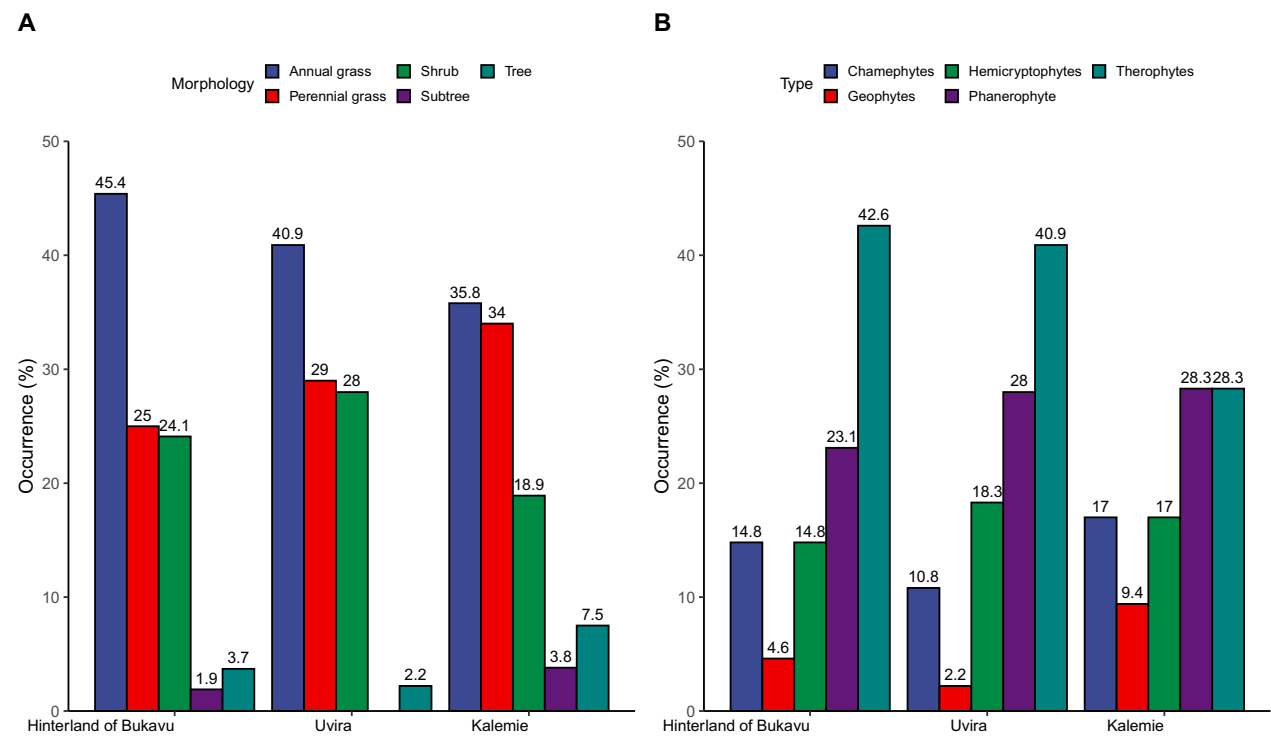


Fig. 6 Morphological type (A) and biological type (B) of plant species identified in the South Kivu and Tanganyika pastures

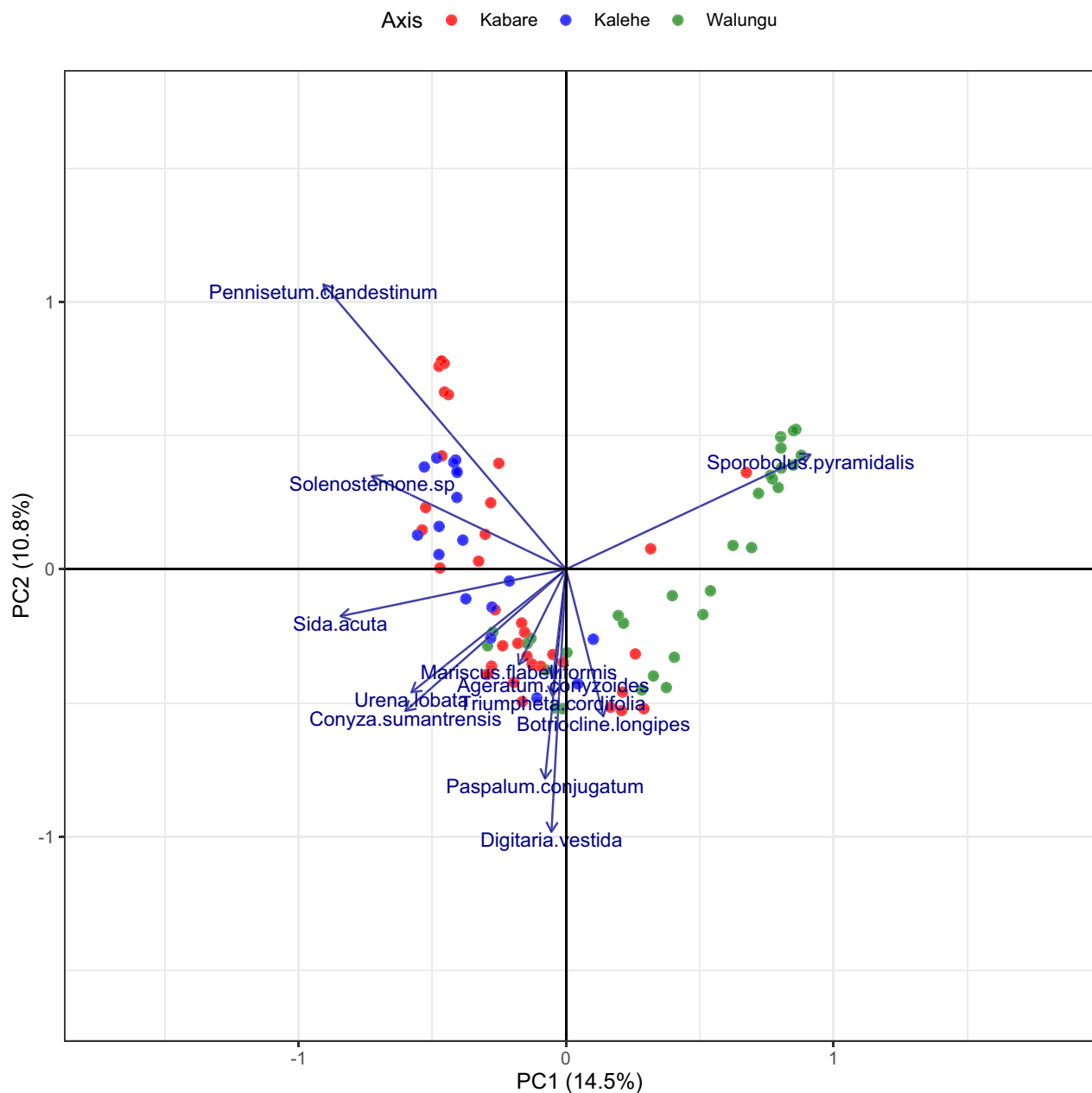


Fig. 7 Biplots of the principal coordinates analysis (PCoA) obtained using data from grazing lands in the Hinterland of Bukavu only: Species projection

in the highlands. Similar situation was found by other authors (You et al. 2008; Veuille 2011) who emphasized that that most climatic parameters are influenced by the altitude. Indeed, mountains generate distinct climates different from those of low elevations (Beniston 2006). This is due to dynamic and thermodynamic processes which modify synoptic weather systems and create regional-scale atmospheric circulation regimes that

generate wind systems, cloudiness and precipitation patterns (Barry 2008).

A total of 209 plant species were identified in the study areas which were grouped into 49 botanical families. Generally, three botanical families (Fabaceae, Poaceae and Asteraceae) were dominantly plentiful in the study territories. The findings match what Teague et al. (2011) reported that five botanical families (Fabaceae, Poaceae, Asteraceae, Rubiaceae and Orchidaceae) are numerically

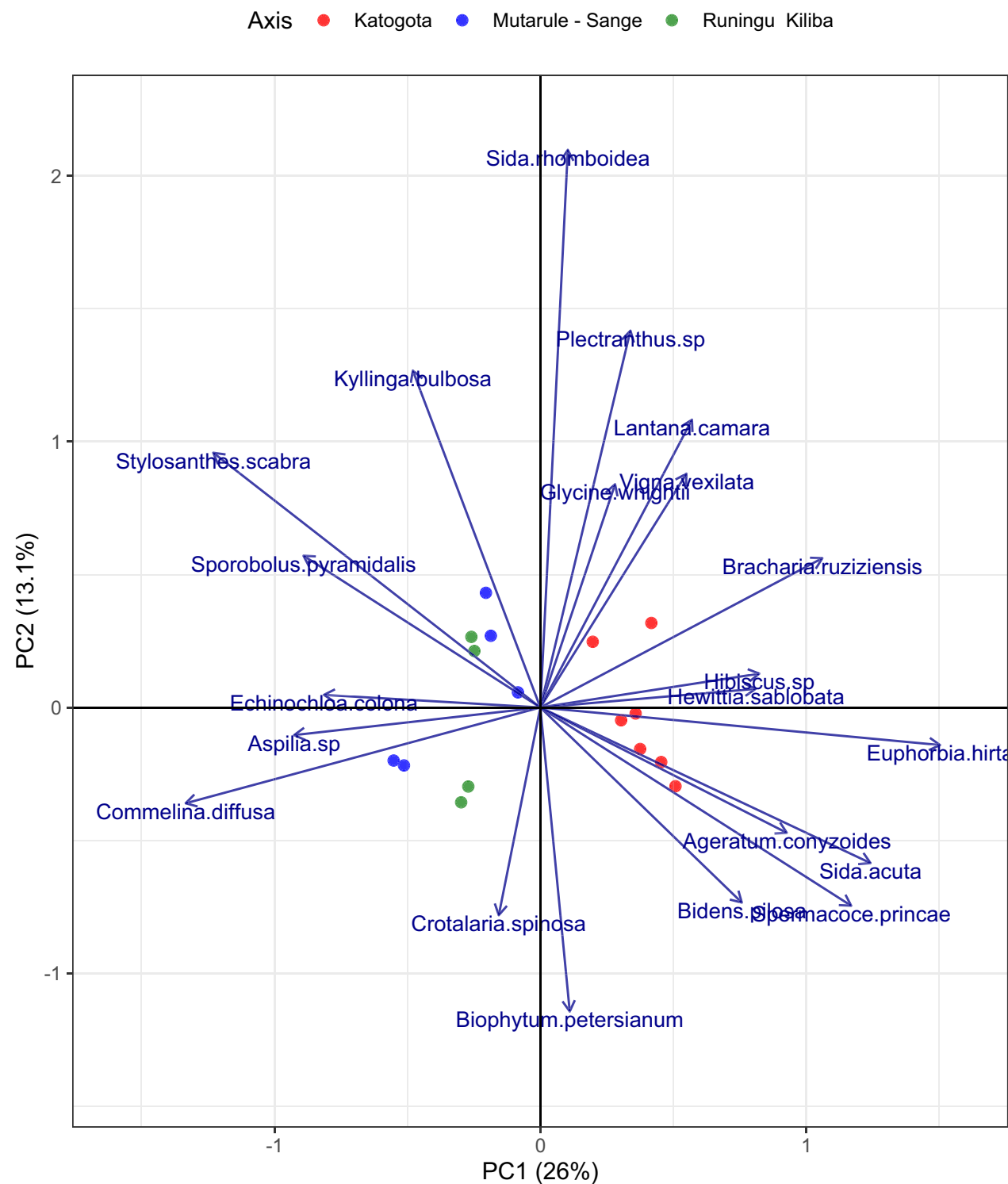


Fig. 8 Biplots of the principal coordinates analysis (PCoA) obtained using data from grazing lands of the Ruzizi plain (Uvira) only: Species projection

higher in their global distribution. Although legumes have limited adaptation ability in marginal soils and changing environment, the Fabaceae family are largely

present in tropical environments due to their rooting systems (Saikia et al. 2020). Evidently, members of the Poaceae family (monocotyledons) were abundantly and

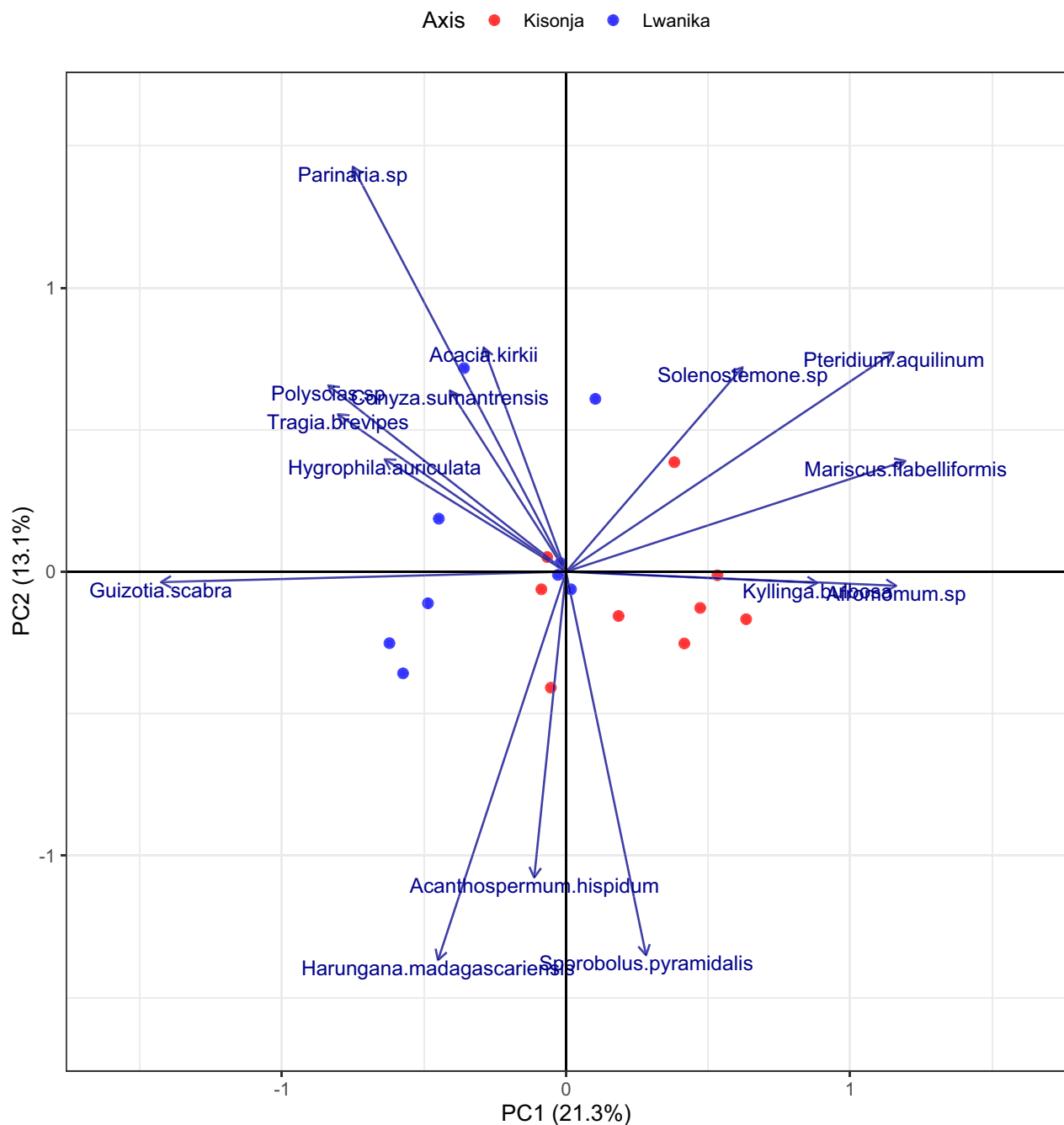


Fig. 9 Biplots of the principal coordinates analysis (PCoA) obtained using data from grazing lands of Kalemie only: Species projection

well distributed in the study area. The family has been noted to adapt to a range of pH (Keshavarzi 2020). The grasses can thrive in diverse climatic conditions including those characterized by high precipitations and temperatures due their ratio of root biomass to above-ground phytomasse (Roybal and Butterfield 2018). Dempewolf et al. (2008) reported that the Asteraceae family plants are diverse and represent about 10% of all flowering

plants. This is due to their ability to evolve into CAM photosynthesis while harboring the ability to transition to C4 photosynthesis (Siniscalchi et al. 2021) and the candidate genes present in most plants that allow them to survive in extreme climatic conditions (Palazzesi et al. 2022).

Many studies carried out in different parts of the world (Rusinovci et al. 2014; Corlett 2016; Avdiu et al. 2018;

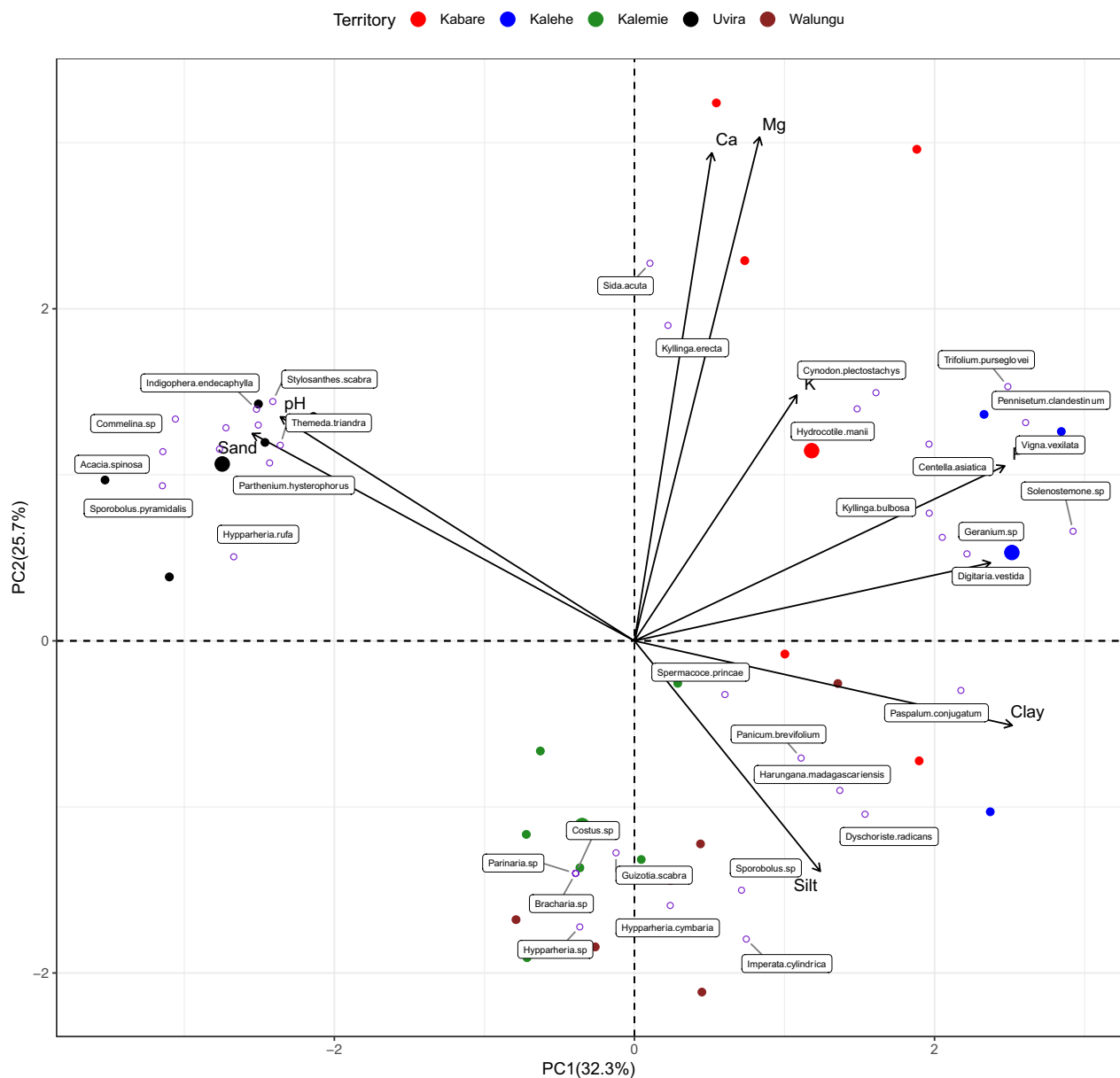


Fig. 10 Biplot resulting from the PCA carried out on data of the physicochemical characteristics of soils and the abundance-dominance of plant species on grazing lands of five territories including Kabare, Kalehe, Kalemie, Uvira and Walungu. Plant species represented by *purple dots* were added as additional variables in order to examine the correlation between their abundance-dominance value with soil properties and better understand their spatial and ecological distribution across these territories

Baderhekuguma et al. (2019) indicate high floristic diversity which is in agreement with the results of the current study. The diversity is higher in the Ruzizi plain (Uvira) and Kalemie zones where bush fire is practiced by herders during dry seasons. The use of fire to increase floristic diversity as well as management pathway has been used for generations; however, Burkle et al. (2015) noted that this can also result in emergence and multiplication of undesirable pasture species and forbs. Plant species such

as *Digitaria abyssinica*, *Sporobolus pyramidalis*, *Cynodon dactylon*, *Galinsoga ciliata*, *Parthenium hysterophorus*, *Conyza canadensis* and *Bidens pilosa* were observed in the current study. These are mainly found in or near arable lands and are considered as weeds. Their presence indicates the proximity of the studied grazing lands to arable fields (Rodrigues et al. 2023). An alternative explanation would be conversion of previous fallow lands to grasslands. Furthermore, weeds invade neighboring

areas, mainly sections of low sward density (Ens et al. 2015) common on the outskirts of grazing lands. The high plant diversity observed in this study is a pointer to differences in the abiotic factors such as the type and fertility of soil as highlighted by Harrison and Bardgett (2009) and climatic conditions (Harrison 2020). This underlines the significance of assessing the soil properties in the current study.

It is evident from the findings that differences exist in soil profile in the studied territories which partially explain the variety of plant species found in corresponding ecologies. Soils in Kalemie territory are mainly loamy where *Parinaria* sp., *Hypparhenia* sp. and *Guizotia scabra* are abundant while those from the Hinterland of Bukavu are characterised by high content in macro-elements such as phosphorus and nitrogen which tend to favour species like *D. vestida*, *C. asiatica* and *P. clandestinum* more thus influencing their presence. The Ruzizi plain (Uvira) is majorly sandy which favours *S. scabra*, *B. ruziziensis* and *Commelina* sp. plant species. Previous studies have reported the influence of soil type on plant diversity (Han et al. 2022; Amegnaglo et al. 2018). Pittarello et al. (2020) reported that pasture species richness of Italian alpine grasslands was mainly affected by environmental factors rather than management regimes. It has been pointed out that the diversity of environments in tropical zones affects pasture productivity through a complex interconnection of factors such as climate, soil quality, plant species diversity and management practices (Kampmann et al. 2008). Plant species adapted to silty and clayey soils normally have a root system that is tolerant of waterlogging and able to efficiently extract nutrients from the soil (Brady et al. 2005). For example, *Paspalum conjugatum* is an herbaceous species used for wetland grazing, while *Dychrostachys cinerea* is highly tolerant of a wide range of edaphic conditions and has a role in nitrogen fixation. These plants can serve as biological indicators for soils with good water retention capacity but susceptible to compaction (Riefner and Boyd 2007). However, most plant species adapted to sandy soil have developed remarkable adaptation mechanisms. This is the case of *Acacia* sp. and *B. ruziziensis* which have a deep root system that enables them to extract water from deeper soil profile (Silva et al. 2016). *Trifolium usambarense* was frequently observed on sandy soils poor in other nutrients since it can fix atmospheric nitrogen, which in part compensates for the scarcity of nutrients in its environment (Griffith et al. 2000). *Spermacoce princeae* was found to be plastic to all ecologies in this study since it has the capability of living in acid-sandy, acid-clayey, or acid-loamy soils and can tolerate a wide

variation in pH values and nutrients availability (Zhou et al. 2022), but *Imperata cylindrica* was strictly found to be linked with degraded soils in Walungu and Kalemie. This plant species is reported to tolerate poor acid soils and tolerate drought under the tropics (MacDonald 2004). Molina et al. (2024) reported that vegetation structure is normally influenced by nutrient and moisture availability, which vary with soil types. In addition, nutrient–nutrient interactions, which influence nutrient availability to plants, are directly affected by soil pH. In this study, Kalemie and Ruzizi plain soils had pH values close to neutrality compared to the soils in the Hinterland of Bukavu which were acidic. Gillespie et al. (2022) reported that soil acidity has an impact on the plant species diversity, reducing with lower pH. Most pasture species with good nutritional value such as perennial ryegrass, cocksfoot, valuable herbs and legumes, grow well on moderately acidic soils (Poozesh et al. 2010). At low soil pH, important elements such as P, Mg and Ca become less available to many plants (Barrow and Hartemink 2023).

The findings from this study have shed light on the plant species available for grazing in the studied territories. The research has further highlighted biophysical and management factors that influence the abundance and distribution of the plant species. This information is necessary in designing programs aimed at increasing grazed livestock production and efficient resource utilization for sustainability. It is important to note that higher floristic diversity does not necessarily imply higher livestock production since not all plant materials are available to the grazing livestock due to differences in palatability and access. This view is expounded in the study by Yulianto et al. (2016) who noted that floristic richness of grazing lands does not necessarily imply a conducive environment for grazing animals. Furthermore, heavy grazing, which is common in transhumant and nomadic systems, such as the Ruzizi plain and Kalemie zones, results in higher increaser plant species which are of negative value in grazed systems (Chen et al. 2022). Most increaser species are woody or have antinutritional factors and volatile secondary compounds such as terpenes which strengthen their defence mechanism in the invasion success (Wolf et al. 2011) and accumulated more (hemi)cellulose, insoluble sugars and lignin (Pooter and Bergkotte 1992) preventing them to be selected by grazing animals. South-Kivu and Tanganyika provinces are characterized by high temperatures and variable rainfall which has significant influence on pasture species availability. Rain scarcity can lead to water stress, reducing the growth of desirable plant species (Huang et al. 2024). In addition, intermittent rainfall in Ruzizi plain and Kalemie zones

often induce prolonged droughts or floodings, directly impacting the availability of water and nutrients in the soil, thus affecting pasture growth (Renne et al. 2006). These climatic characteristics negatively impact the available grazing materials which directly lead to overgrazing. Baring the ground because of the overgrazing increases soil erosion, thus reducing its capacity to support plant growth and subsequently pasture productivity (Greenwood and McKenzie 2001).

Results from the current study clearly indicate that the soils of grazing lands in the Hinterland of Bukavu are more degraded than those of Ruzizi plain (Uvira) and Kalemie. In the highlands of Bukavu, the high human population exerts pressure on the available land, with more of the rich soil being used for crop production. This leaves lesser grazing lands implying higher grazing intensity which results in the emergence of increaser plant species and decreased pasture regeneration (Bilotta et al. 2007) and a subsequent reduction in livestock and land productivity. This is evidenced by the high productivity of privately owned livestock enterprises in Kabare and Kalehe territories where improved pasture species such as the *P. clandestinum* were introduced, managing increaser plants, and ensuring the required stocking rates. Stavi et al. (2009) demonstrated that unsustainable livestock grazing alters the cycles of soil carbon, nitrogen and other nutrients in grassland ecosystems by the interactions between plants and the soil.

The current study suggests that interventions should be oriented to improve soil pH and desirable forage diversity of pastures in the Hinterland of Bukavu. Since the private grazing system dominates in this zone (Azine et al. 2025), farmers should consider liming the pastures once per year to reduce acidity and therefore increase assimilation of soil nutrients by plants. The management practices suggested by Liu et al. (2025) are applicable in this ecology to sustain healthy pastures and enhance profitability in the grazing system. Given the increasing human population in the zone, part of animals should be on cut-and-curry system to reduce the grazing pressure on pastures. However, in areas dominated by communal grazing, such as the Ruzizi plain and Kalemie where the physical properties of soils are degraded, rotational grazing is often suggested (Regreening Africa 2022). The method enables restoration of desirable plant species which do not tolerate overgrazing and trampling. The case of ‘village planning’ method in Tanzania helped to resolve land use conflicts while significantly reducing overgrazing and bushfires on grasslands (Nyamhanga et al. 2025). Several authors have suggested co-creation of management and conservation measures involving the priorities of pastoralists and those

of government entities (Flintan and Cullis 2010; Call and Jagger 2017).

Proposals have been made on how to improve grazed land productivity and plant diversity by introducing plant types from other regions characterized by the same climatic and biophysical conditions. Establishment and utilization of *Brachiaria* hybrids have been tested in different grazed systems in the world with positive outcomes on soil properties and animal productivity (Gracindo et al. 2014; Ruggieri et al. 2020). Based on the findings of the current study for climatic and biophysical conditions of the grazed lands in South-Kivu and Tanganyika provinces, the *Brachiaria* hybrids and *P. clandestinum* are good forages with potential to increase livestock productivity in eastern DRC and they have plastic adaptation to be suggested across ecologies.

Conclusion

This study revealed a huge diversity of plant species on grazing lands which varied with the soil types and agroecological zones. Grazing lands in the hinterland of Bukavu where soils are mostly clayey, acidic, with high contents of phosphorus and nitrogen were characterized, as per the analysis of fidelity index (FI), by four species only including *Centella asiatica*, *Digitaria vestita*, *Sporobolus pyramidalis* and *Pennisetum clandestinum*. For the Ruzizi plain (Uvira), where soils are sandier with the lowest contents of nitrogen and phosphorus, grazing lands were characterized by 40 species dominated by *Brachiaria ruzizienensis*, *Sporobolus* sp., *Acacia spinoza* and *Stylosanthes scabra*. In Kalemie, where soils are rich in silt, 21 plant species are faithful to grazing lands and dominated by *Hypparhenia* sp., *Parinari* sp., *Costus* sp. and *Guizotia scabra*. However, despite the high floristic richness observed in South-Kivu and Tanganyika provinces, most of the plant species are increasers that have survived under disturbance conditions such as overgrazing and repeated bushfires, and therefore are not suitable for guaranteeing the productivity of grazing animals. From a long-term perspective, management of grazing lands in eastern DRC would depend on ongoing grazing system. In the communal grazing system, common approaches are suggested for joint interventions between pasture users and relevant government departments. By contrast, in the private grazing system, removal of increasers and introduction of improved grasses such as improved *Brachiaria* cultivars are suggested to achieve a balance among species diversity protection, cattle production, and soil quality management.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-025-00663-4>.

Additional file 1.

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Author contributions

SBB, AZB, JBB, MGG and IMO conceived the study. SBB, VBM, AZB, JBB, BBN and DMK conducted field research. SBB, YM, VBM and BBN cleaned and analyzed the data and drafted the manuscript. All authors contributed to the revision of manuscript and approved the final version of manuscript.

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Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

All authors agreed and approved the manuscript for publication in *Ecological Processes*.

Competing interests

The authors declare no competing financial interests.

Author details

¹Department of Animal Sciences, Jomo Kenyatta University of Agriculture and Technology (JKUAT), Nairobi, Kenya. ²International Institute of Tropical Agriculture (IITA), Bukavu, Democratic Republic of the Congo. ³Department of Animal Sciences, Université Evangélique en Afrique (UEA), Bukavu, Democratic Republic of the Congo. ⁴Department of Biology, Université Officielle de Bukavu (UOB), Bukavu, Democratic Republic of the Congo. ⁵Department of Soil Sciences, Université Catholique de Bukavu (UCB), Bukavu, Democratic Republic of the Congo. ⁶Programme National de Recherche Sur l'élevage (PNRE), Institut National Pour l'Etude et la Recherche Agronomiques (INERA), Mulungu, Democratic Republic of the Congo.

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