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Medium-term interactive effects of herbivores and plant life form on the biochemistry of shallow sandy soils in a protected semi-arid savanna

Siviwe Odwa Malongweni[1*] and Johan van Tol[1]

Abstract
Savannas are characterized by the co-occurrence of two different plant life forms: grasses and trees. Herbivory plays a major role in the balance between grasses and trees in savanna ecosystems. The present study aimed to investigate the impact and interactions between long-term (i.e. 20 years) herbivory and/or its exclusion and plant life form on the soil biochemistry of a protected semi-arid savanna ecosystem in the Kruger National Park (KNP), South Africa. To study the effects of herbivory on soil properties, herbivore exclosures (fully fenced areas, partially fenced areas, and an unfenced area) were used in conjunction with plant life form (trees and grasses) were considered. Interaction effects of herbivory and plant life form on soil pH, electrical conductivity (EC), total nitrogen (TN), total carbon (TC), available phosphorus (available P), exchangeable cations (K^+, Na^+, Mg^{2+} and Ca^{2+}) cation exchange capacity (CEC), organic matter (OM) and total microbial activity were determined on savanna soils in the Nkuhlu exclosures, KNP. Exclosures where herbivores were present had significantly higher soil pH, The presence of herbivores caused an increase in soil pH, EC, exchangeable Na, CEC, and OM. The influence of the tree canopy was significantly more pronounced in elevating total C and N, exchangeable K^+, Mg^{2+} and Ca^{2+}, CEC and OM than observed in the open grassland zones across all exclosures. The two-way interaction between herbivory and plant life form resulted in significant decreases in TN, TC, exchangeable K, Na and Mg in open grassland areas outside of herbivore exclosures where large animals had direct access, as compared to areas within the exclosures which was protected from animal entry herbivory. This data can be used by national parks as an indicator to increase their knowledge of environmental issues relating to maintaining and preserving landscape features of savannas.

Keywords Browsers, Canopy cover, Grassland zone, Grazing, Herbivory, Kruger National Park, Soil properties, Tree canopy

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Introduction

Savanna ecosystems occupy approximately 20% of the earth's land surface and are characterized by the co-occurrence of grasses and trees or shrubs, which form an integral part of herbaceous layers, and the functioning of savanna systems (Sankaran et al. 2005; Ward et al. 2013). This co-occurrence of trees and grasses is governed by a complex set of interacting biotic and abiotic factors (Mapiye et al. 2008; Tabeni et al. 2014; Langevelde et al. 2003). Soil moisture, nutrient availability, light intensity, and temperature are some of the main abiotic factors that determine the growth of trees and grasses (Treydte et al. 2011). They also differ in their properties, which generates unique ways that plants compete for these resources. Ward et al. (2013) observed that grasses with their dense and shallow root system use water and nutrients from the topsoil, whereas trees are limited when it comes to the topsoil resources and have exclusive access to subsoil water and nutrients. Therefore, trees act as a nutrient pump taking up nutrients from deeper soil layers or from soil outside the canopy and depositing it under their canopy through litter fall or leaching i.e., bioturbation. This hypothesis suggests that soil moisture and nutrient concentrations are likely to be higher under the tree canopy than in open grasslands (Langevelde et al. 2003; Ward et al. 2013). This variation in moisture and nutrient concentration levels between trees and grasses is likely to cause variations in soil properties and processes as well (Preez et al. 2011; Eldridge et al. 2017; Holdo and Mack 2014). However, the effects of niche separation between savanna trees and grasses on soil properties and processes has been understudied. Therefore, a key challenge is to understand the relative contributions and interactions of savanna trees and grasses to soil functional heterogeneity.

Apart from variations in the above-mentioned abiotic conditions, there are other factors which also influence grass and woody biomass spatio-temporal changes within savannas (Holdo and Mack 2014; Langevelde et al. 2003; Ward et al. 2013). Numerous studies have attributed temporal and spatial variations in the grass and woody biomass of savannas to fire and herbivores in junction with catenal position (Janecke et al. 2020; Riddell et al. 2012; Sankaran and Hanan 2008; Osborne et al. 2018). The scope of this paper, however, is limited to the influence of herbivory and plant life form as influenced by catena processes amongst many other factors. We did not include fire in our study. This is because savanna fires in arid areas are not intense and severe enough to reduce vegetation and cause soil changes (Mwansa 2018). Moreover, semi-arid savannas are considered'fuel limited' (Smit and Archibald 2019). The hot and dry weather conditions cause grasses which serves as a fuel source to become patchy and dry because of drought (Starns et al. 2020). Herbivores impose their own effects on the structure and function of savannas (Eldridge et al. 2017). For instance, when herbivores aggregate at high densities in hotspots such as under trees, canopy-herbivore interactions result. These interactions may lead to biomass removal through grazing, debarking, and tree toppling (Langevelde et al. 2003; Ward et al. 2013). However, organic components of feces and urine from grazing herbivores can build soil organic matter reserves, resulting in soil having increased water-holding capacity, higher nutrient concentration levels, increased water-infiltration, and improved structural stability (Chamane 2012; Holdo and Mack 2014). On the contrary, trampling, a relatively understudied ecological process (Barthelemy 2016; Preez et al. 2011; Eldridge et al. 2017), may unfavourably affect soil hydrological properties by reducing rates of drainage to deeper layers. But generally, the role of herbivores on soil surrounding tree-grass communities remains largely unexplored.

Janecke (2020) claims that differences caused by herbivory and plant life form are modified by catena. In soil science, a catena can be defined as a series where soils are derived from the same parent material but differ in soil type as you move along a hillslope (Borden et al. 2020). For example, shallow sandy soil occupies the crest of the Nkuhlu exclosures in KNP, but towards the lower-mid and foot-slope of the catena, clayey soils gradually appear despite the soil being derived from the same parent material, i.e., granite. The clay layer present towards the bottom of the slope serves as a less permeable barrier that often slows down and sometimes impedes the flow of water throughout the soil profile (Brady and Weil 2008; Janecke 2020; Coller 2013). Consequently, water seeps through (and easily evaporates) the saprolite on the surface. Sodium (Na) accumulates downslope of the seeps to create sodic sites because of the Na-releasing parent material, granite, and the fact that rainfall is insufficient to cause leaching of accumulated salts (Khomo and Rogers 2005; Theron 2020). Sodic sites are often associated with vegetation denudation and general land degradation due to extreme accumulation of salts. That is why the sodic zone is frequently viewed negatively despite it being a natural ecological process which serves important ecological functions. These functions include predator evasion strategies for herbivores because of their relative openness, wallowing points for animals during wet periods and as nutrient accumulation spots in the landscape (Janecke 2020; Khomo and Rogers 2005). Which is why Khomo and Rogers (2005) argue that sodic sites should not be viewed as degraded. They state that the natural processes that result in sodic sites need a better understanding to improve management of savanna ecosystems.

Because differences in vegetation distribution and attractiveness (preference) of herbivores to selected areas exist between the crest and foot-slope of the Nkuhlu exclosures, it is important to understand soil changes influenced by herbivory and plant life form along the catena. Therefore, this study aims to determine the influence of 20 years of herbivore exclusion and/or exposure, plant life form and their interaction on soil biochemistry of shallow sandy soil in a semi-arid savanna ecosystem in the Kruger National Park (KNP), South Africa. In a previous study, Malongweni and Tol (2022) evaluated the impact of these animal-plant life form interactions on sodic (clayey) soils on foot-slopes of the study area and did find that there were significant impacts of herbivory on soil organic matter (SOM), cation exchange capacity (CEC) and microbial activity. plant life form, on the other hand, brought about significant changes in total carbon (TC), total nitrogen (TN), exchangeable calcium (Ca) and magnesium (Mg) as well as SOM. Since herbivory and plant life form influence soil properties along the catena of Nkuhlu exclosures, it was deemed necessary to conduct a study that examines, compares, and contrasts changes in soil properties between the crest and foot-slope (sodic zone). In this study, we posit that the presence of herbivores, along with variations in plant life forms, will exert a significant influence on crucial soil biochemical properties. Specifically, we anticipate discernible effects on organic matter decomposition rates and nutrient cycling, potentially leading to notable repercussions on the overall functioning of the ecosystem.

By addressing these research questions, your study aims to contribute valuable insights into the complex interactions between herbivores, plant life forms, and soil properties within the specified ecosystem.

Methods

Study area

The study was carried out in the Nkuhlu exclosures (24°59′10″ S, 31°46′24.6″ E) which were constructed in 2001 in Skukuza, KNP for the purpose of developing an understanding of spatial and temporal heterogeneity patterns around the riparian zone, and how these are affected by fire and herbivory (Siebert and Eckhardt 2008). The area is a 139 ha semi-arid subtropical savanna which on an annual basis receives roughly 561 mm of rainfall with an average minimum and maximum temperature of 5.6 °C in winter to 32.6 °C in summer, respectively (Siebert and Eckhardt 2008). Gertenbach (1983) reported that the dominant species species in Nkuhlu exclosures consist of *Grewia bicolor*, *G. flavescens*, *Combretum apiculatum*, *Vachellia (Acacia) grandicornuta*, *Dichrostachys cinerea*, *Terminalia prunioides*, *Euclea divinorum*,*Spirostachys africana*, and *Senegalia (Acacia) nigrescens*.

Variation in soils is apparent along the catena in the Nkuhlu exclosures (Scogings 2011; Siebert and Eckhardt 2008). Shallow sandy soil directly overlying weathering rock can be found on the crest. According to the South African Soil Classification system, the soil found on the crest can be classified as Mispah and shallow Glenrosa and it qualifies as Leptosol in the World Reference Base (WRB) (Soil Classification Working Group 2018). Sandy to sandy loam soil can be found in the lower mid and foot-slope (Siebert 2008). This region is characterized by deep, Na-rich duplex soils and is sometimes referred to as the sodic zone. In the WRB, the sodic zone is classified as Luvisol whist it is Montagu or Oakleaf in the South African Soil Classification system (Scogings 2011; Siebert and Eckhardt 2008). The focus of this paper was restricted to the shallow soils of the crest. However, the results were compared to the findings of Malongweni and Tol (2022) who conducted a similar study on the foot-slope of the same exclosures.

Experimental design and soil sampling

The 139 ha exclosures are divided into three sections, namely (1) full exclosure: a 70 ha fully fenced area designed to exclude all animal entry, (2) partial exclosure: a partially fenced area of 44 ha where elephants, and, by virtue of size, giraffes, cannot enter but all other herbivores are allowed and (3) open access area: a 25 ha unfenced area where all animals are permitted to enter (Figs. 1, 2 and 3).

The full and partial exclosures include both burnt and non-burnt plots while the open access area exclusively comprises non-burnt plots without any fire treatment (Fig. 2). The burnt plots undergo controlled annual fires, however, the current study did not take fire into consideration and solely concentrated on the non-burnt plots which were not burnt for 20 years. At the sampling sites, data was collected for two plant life forms: trees and grasses. Samples collected beneath tree canopies represent trees, while data collected in open grassland zones represents grasses. Therefore, the study consisted of three herbivory treatments (open access area, partial and full exclosure) and two plant life forms (trees and grasses), thus resulting in a 3×2 factorial design (Fig. 3).

In our study, we did not consider exclosures as replicates. This is because they are large and clearly distinct systems from different vegetation types and subject to different management regimes (Thoresen et al. 2021; Holdo and Mack 2014). This design has been critiqued as 'pseudoreplication' by Hulbert (1984), but, Oksanen (2001) asserts its legitimacy, given the common constraints faced in ecological research. Thoresen et al. (2021) claims that Nkuhlu exlosures encompass different vegetation types and are subject to varying management regimes, making them inherently unique. While the exclosures within our sites were not replicated due to established protocols from decades past, we counterbalance this in our site layout by following approaches taken by Thoresen et al. (2021) as well as Holdo and Mack (2014). This was achieved by deliberately ensuring that there is enough spatial separation between our sampling points. Doing this prevents the samples from being influenced by localized or site-specific factors that could bias

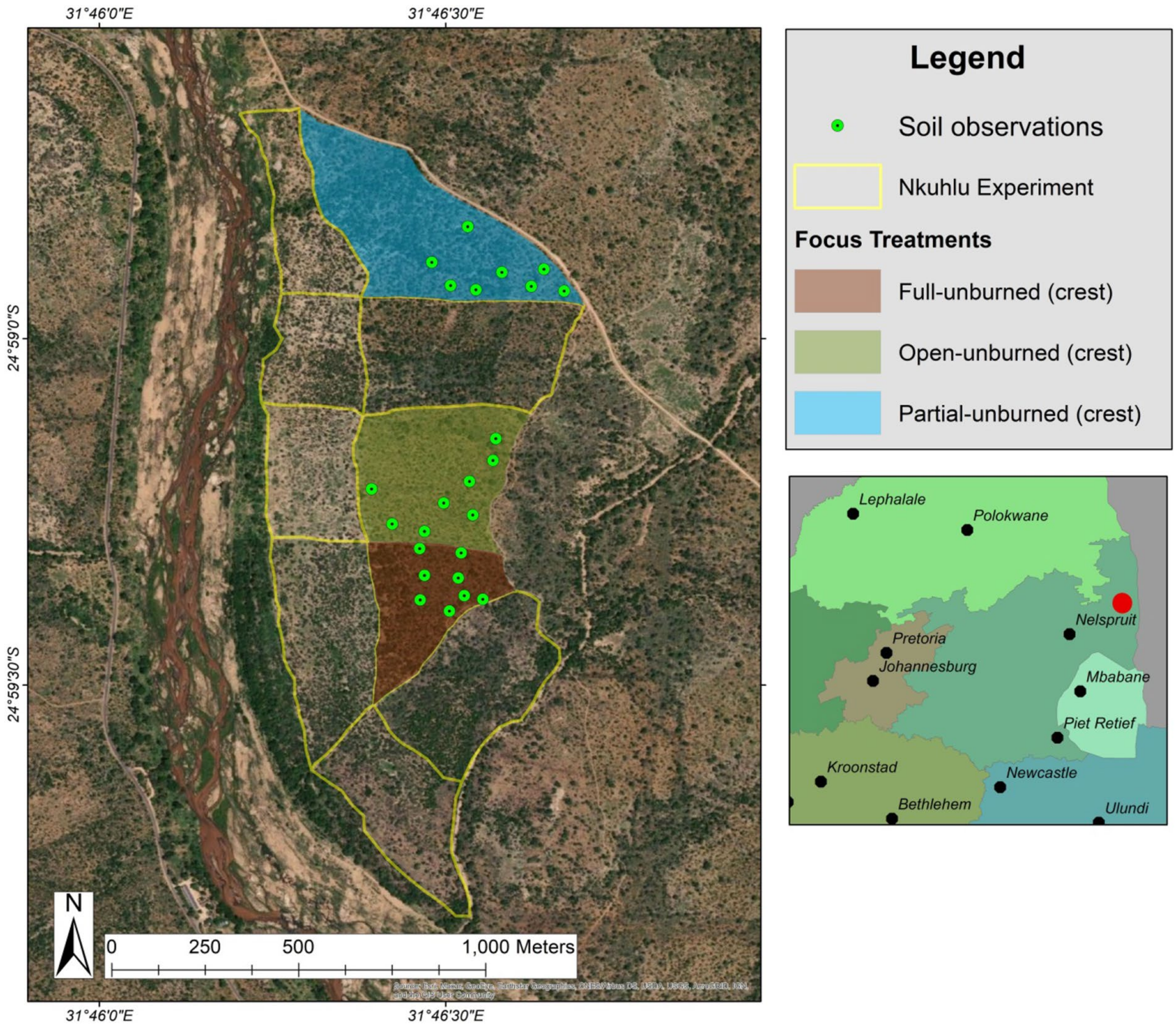


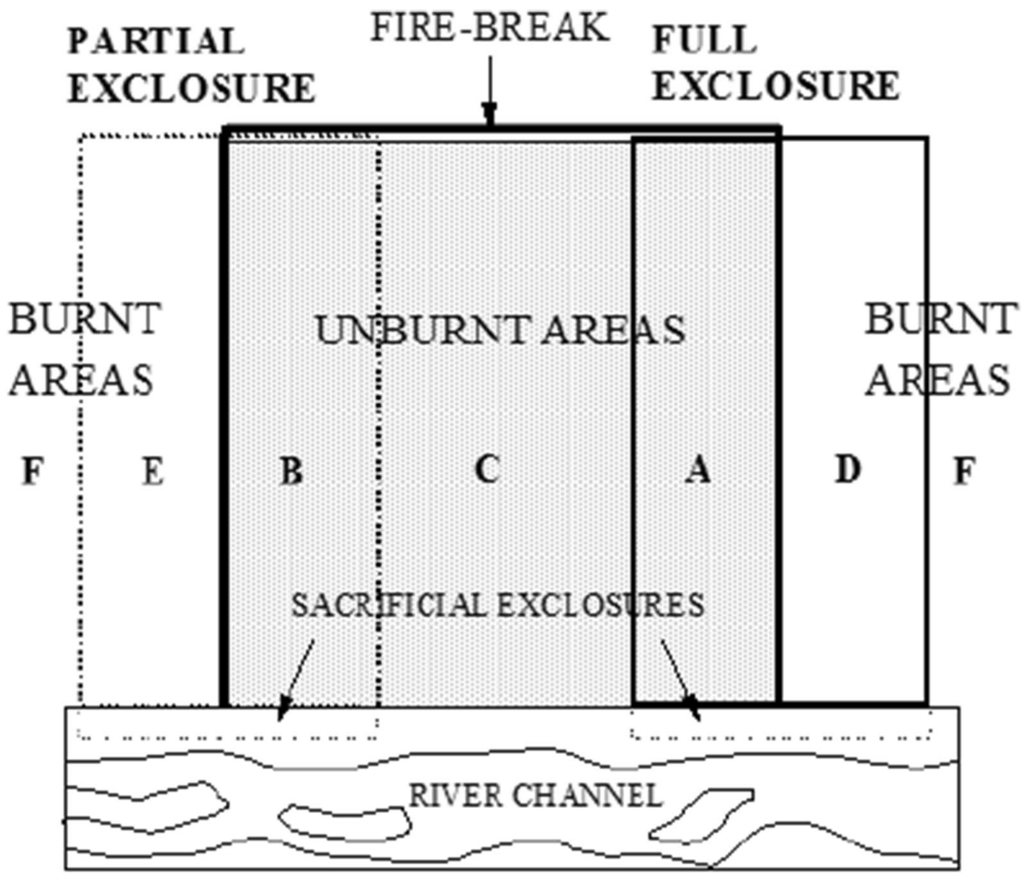
Fig. 1 Location of study area (red dot) within the Kruger National Park in South Africa and map of the Nkuhlu exclosures indicating the locations of the sample plots as well as sample points within each plot (green dots). This study focused only on the crest positions and unburnt plots (adopted from Malongweni and van Tol 2022)

our results. Moreover, it allowed us to capture a broader representation of the environmental conditions present within the study area.

Samples intended for total microbial analysis were promptly sieved on-site at the Nkuhlu exclosures, placed in plastic sample bags and then stored in a cooler box filled with ice throughout the soil sampling period. During transportation to the laboratory, they were maintained in a refrigerated compartment powered by a vehicle. Upon arrival at the laboratory, they were analyzed as soon as possible. Once at the lab, the soil samples collected for the analysis of other soil properties under investigation (excluding total microbial activity) were air-dried at room temperature for about a week, and then passed through a 2 mm sieve to obtain uniform particle size for subsequent analysis.

Data collection

Laboratory analyses were performed for total carbon (TC), total nitrogen (TN), pH, electrical conductivity (EC), available phosphorus (available P), exchangeable cations (Na^{+}, K^{+}, Mg^{2+} and Ca^{2+}), cation exchange capacity (CEC), soil organic matter (SOM), and total microbial activity. TC and TN were determined using the dry combustion method of Bremner and Mulvaney (1982). A pH meter was used for measuring pH using a 1:2.5 soil–water ratio suspension (McLean 1982). The saturated soil paste method was used for determining



FIRE TREATMENT	HERBIVORE UTILIZATION		
	NONE	BY "SMALLER' HERBIVORES ONLY	UNRESTRICTED
NOT BURNT	A	B	C
BURNT	D	E	F (Reference)

Fig. 2 Schematic layout and treatments to be applied to the exclosure sets (adopted from O'Keefe and Alard 2002)

EC as described by Corwin and Yemoto (2017). Available P was measured using the Olsen extraction method. Exchangeable Na^{+}, K^{+}, Mg^{2+} and Ca^{2+} were extracted using NH_4OAc and quantified on Inductively Coupled Plasma Spectroscopy. The values for these elements were used to calculate the CEC. SOM was determined using the Loss on ignition (LOI) method (Nelson and Sommers (1996). Total microbial activity was determined using the fluorescein diacetate (FDA) hydrolysis method as described by Schnürer and Rosswall (1982).

Statistical analyses

Statistical analyses were conducted using JMP statistical software (version 16.0, SAS Institute Inc.). Analysis of variance (ANOVA) was employed to evaluate treatment effects, specifically assessing differences in soil pH, EC, TN, TC, available P, exchangeable Ca, Mg, K and Na, CEC, SOM, and total microbial activity among the two treatments (exclosure and plant life form). Mean separation was determined using Fischer's protected least significant difference at a significance level of 0.05.

Fig. 3 View of plant life form distribution and impact of herbivory on biomass accumulation in the herbaceous layer (trees and grasses) within the Nkuhlu exclosures (left: fully fenced Nkuhlu exclosure to exclude all herbivores, center: semi-fenced exclosure to prohibit the entry of large and tall herbivores (i.e. elephants and giraffes) and permit the entry of smaller herbivores, right: unfenced control site where all herbivores are permitted).There were two sampling areas within the crest in each exclosure, namely, underneath tree canopies and within open grassland zones. Five sub-samples were randomly collected during the spring season of 2021. Sampling locations were typically more than 50 m apart. The samples were obtained to a depth of 10 cm using a soil sampling auger at four locations, including points underneath tree canopies and within open grassland zones, respectively. The sub-samples were combined into a single composite sample for each sampling point to give a total of 24 samples collected from KNP. The composite samples were carefully placed in plastic sampling bags and then transported to the laboratory for further analysis

Results

Soil pH and electrical conductivity (EC)

Exclosures and plant life form independently influenced soil pH on the crest of the Nkuhlu exclosures (Table 1). The full exclosures had significantly higher pH than the open access area and partial exclosures ($p < 0.05$). Moreover, areas under tree canopy had much higher pH than open grassland zones. The exclusion of herbivores led to a notable decrease in EC. The interaction between herbivores and plant life form did not yield statistically significant changes in pH an EC.

Total nitrogen (TN) and total carbon (TC)

There was a significant main effect of plant life form on TN and TC ($p < 0.001$; Table 1). TN under tree canopies was significantly higher than TN in open grassland zones. Also, the 2-way interaction between exclosures and plant life form was significant for TN and TC ($p < 0.05$).

Available phosphorus (P)

The influence of exclosure was seen between the open (16.9 mg/kg) and partial exclosure (8.8 mg/kg) which were significantly ($p < 0.01$; Table 1) different from each other, and full exclosure (12.9 mg/kg) was similar to both the open and partial exclosure. Plant life form did not independently cause statistical changes in available P nor were there any significant interactions between exclosure, and plant life form.

Soil organic matter (SOM) and total microbial activity

There were no significant main nor interactive effects of exclosure and plant life form on SOM and total microbial activity (Table 2).

Exchangeable cations and cation exchange capacity (CEC)

Data regarding exchangeable cations and CEC ($p < 0.01$; Table 3) showed that exclosure had a significant influence on exchangeable Na, with the control site having

Table 1 The main and interactive effects of herbivory and plant life form on soil chemical properties [pH, electrical conductivity (EC), total nitrogen (TN), total carbon (TC) and available phosphorus (available P)]

Factor	Variable				
	pH	EC (mS/m)	TN (%)	TC (%)	Available P (mg/kg)
			Mean(± SE)		
Exclosure					
Full	6.01 (± 2.54)[a]	1.52 (0.122)[b]	0.07 (± 0.0136)[a]	1.13 (± 0.0136)[a]	12.9 (± 3.529)[ab]
Partial	5.77 (± 1.97)[b]	1.76 (0.147)[a]	0.09 (± 0.0136)[a]	1.25 (± 0.0136)[a]	8.8 (± 3.645)[b]
Open	5.76 (± 2.09)[b]	1.69 (0.143)[a]	0.05 (± 0.041)[a]	0.96 (± 0.014)[a]	16.9 (3.529)[a]
Veg. type					
Tree	6.07 (± 2.82)[a]	1.66 (0.107)[a]	0.1 (± 0.0117)[a]	1.40 (± 0.0117)[a]	14.3 (± 3.0377)[a]
Grass	5.71 (± 2.05)[b]	1.64 (0.102)[a]	0.04 (± 0.0107)[b]	0.83 (± 0.0107)[b]	10.9 (± 2.592)[a]
Main effect	*p*-values				
Exclosure	0.0351[*]	0.046[*]	0.0688 [ns]	0.1686 [ns]	0.03701[**]
Veg. type	0.0211[*]	0.077 [ns]	0.0001[**]	0.0002[**]	0.2923 [ns]
Interaction					
Exclosure x Veg. type	0.068 [ns]	0.233 [ns]	0.01[*]	0.0133[*]	0.7715 [ns]

Means with different letter [a, b] for the same factor within the column are significantly different (signification codes: **$p < 0.01$, *$p < 0.05$, ns = not significant). SE is the standard error

Table 2 The main and interactive effect of herbivory and plant life form on soil biological properties (soil organic matter (SOM) and total microbial activity)

Factor	Variable	
	SOM (%)	Total microbial activity (µg/g dry soil)
	Mean(± SE)	
Exclosure		
Full	3.0 (± 0.444)[a]	33.8 (± 0.228)[a]
Partial	3.0 (± 0.444)[a]	33.5 (± 0.249)[a]
Open	2.7 (± 0.458)[a]	33.6 (± 0.236)[a]
Veg. type		
Tree	2.8 (± 2.861)[a]	33.7 (± 0.196)[a]
Grass	3.0 (± 3.208)[a]	33.5 (± 0.18)[a]
Main effect	*p*-values	
Exclosure	0.6163 [ns]	0.954 [ns]
Veg. type	0.5112 [ns]	0.481 [ns]
Interaction		
Exclosure x Veg. type	0.8723 [ns]	0.249 [ns]

Means with different letter [a, b] for the same factor within the column are significantly different (signification codes: **$p < 0.01$, *$p < 0.05$, ns = not significant). SE is the standard error

much higher concentration of exchangeable Na than the partial and full exclosures. The interaction between exclosure and plant life form also had a significant influence on exchangeable K ($p < 0.05$). The concentration of exchangeable K, Mg and Ca were on average higher under tree canopies compared to open grassland zones, whereas exchangeable Na was not influenced by plant life form. CEC was not independently and interactively influenced by either exclosure or plant life form (Table 3).

Significant interactions

The variables which were interactively influenced by exclosure, and plant life form include TN, TC, exchangeable K, Na and Mg (Fig. 4). Except for the open access area, the area under tree canopy had higher TN and TC than open grassland zones in all the exclosures (Fig. 4A and B). The area under tree canopy in the open access area had higher exchangeable K than all the other treatments whereas the open grassland zone in the partial exclosure had the lowest (Fig. 4C). Crown cover in the control site resulted in significantly higher exchangeable Na than the other exclosures. However, plant life form did not cause any significant changes in exchangeable K in all the exclosures (Fig. 4D).

The open grassland zone of the full exclosure had the lowest Mg while in the open and partial exclosure there were no differences (Fig. 4E). The area under tree canopies in the partial exclosure had significantly higher Mg than the full and open exclosure. Plant life form influenced exchangeable Mg only in the full and partial exclosure and not in the open access area, with areas under tree canopies having significantly higher exchangeable Mg than open grassland zones, respectively (Fig. 4E).

Table 3 The main and interactive effect of herbivory and plant life form on soil chemical properties (exchangeable cations and CEC)

Factor	Variable				
	Na (mg/kg)	K (mg/kg)	Mg (mg/kg)	Ca (mg/kg)	CEC (cmol(+)/kg)
	Mean(±SE)				
Exclosure					
Full	273.85 (±25.353)[b]	48.44 (±7.225)[a]	26.67 (±5.095)[a]	1022.58 (±183.09)[a]	1.85 (±0.138)[a]
Partial	278.65 (±25.348)[b]	40.26 (±7.38)[a]	35.23 (±5.0499)[a]	1088.25 (±183.032)[a]	2.03 (±0.136)[a]
Open	378.65 (±26.185)[a]	56.169 (±7.462)[a]	21.41 (±5.262)[a]	1086.17 (±189.05)[a]	2.11 (±0.143)[a]
Veg. type					
Tree	318.49 (±21.821)[a]	60.71 (±6.218)[a]	36.95 (±4.385)[a]	1266.11 (±157.579)[a]	2.02 (±0.119)[a]
Grass	302.4 (19.999)[a]	35.86 (±5.699)[b]	18.6 (±4.019)[b]	665.22 (±144.424)[b]	1.98 (±0.109)[a]
Main effect	*p*-values				
Exclosure	0.004[**]	0.0776 [ns]	0.0629 [ns]	0.0726 [ns]	0.399 [ns]
Veg. type	0.512 [ns]	0.0039[**]	0.0013[***]	0.002[***]	0.617 [ns]
Interaction					
Exclosure x Veg. type	0.017[*]	0.043[*]	0.0281[*]	0.1 [ns]	0.683 [ns]

Means with different letter [a, b] for the same factor within the column are significantly different (signification codes: **p < 0.01, *p < 0.05, ns = not significant). SE is the standard error

Discussion

Herbivores

The influence of herbivores resulted in higher EC and lower pH, which contradictsi Malongweni and Tol (2022), who found that herbivores did not influence soil pH or EC on the sodic zone of Nkuhlu exclosures. This is because soils in the foot-slope are characterized by a high base status and pH, which is associated with limited leaching (Janecke 2020). In the present study, In the present study, it is conceivable that the exclusion of herbivores in the full exclosure may have led to a potential decrease in soil EC due to the absence of animal urine, which is known to contribute to increases EC levels (Allen et al. 2020).

EC revealed a negative correlation with pH in that it was higher in instances where pH was low. This could be attributed to the fact that herbivores usually have extreme base excretion and high urinary pH because they are normally adapted to alkali-rich nutrition (Kiwull-Schöne et al. 2008).

Data regarding SOM and microbial activity showed that the exclusion of herbivores did not cause any significant changes in SOM and microbial activity within the crest of Nkuhlu exclosures. However, Malongweni and Tol (2022) observed that the full exclosure and control site had low SOM compared to the partial exclosure within the sodic zone. They explained reductions in soil organic matter in the open access area of the foot-slope by suggesting that it is a consequence of soil compaction due to the trampling, pawing, and wallowing action caused by large herbivores. When comparing total microbial activity and SOM results of this study to that of Malongweni and Tol (2022), the foot-slope had much higher total microbial activity and soil organic matter than the crest. These differences may be associated with changes in gradient and thus water flow patterns. Differences in elevation and water flow patterns can lead to the transportation of dissolved salts and other suspended substances such as organic matter from the crest to the foot-slope. These results correspond with the assertions of Janecke et al. (2020); Coller et al. (2013) who reported gradual increases in alluvial deposits and moisture downslope.

In our study, available P was found to be nearly two folds higher in the open access area than in the partial exclosure. Meanwhile, the sodic zone didn't show any significant differences in terms of P in the different exclosures. However, overall available P on sodic zone was 24%, 36% and 18% higher for the full exclusure, partial exclosure and control site than the crest, respectively (Malongweni and Tol 2022). Similar observations have been reported by Grant and Scholes (2006) who found that sodic sites revealed up to twice as much N and P concentrations than that found on the crest. Indicating that slope may indeed play an important role in determining soil changes over time in savannas.

The only cation which was significantly influenced by herbivory is exchangeable Na, with the open access area having higher concentration than both the full and partial exclosure. CEC was not influenced by herbivory. Whereas Malongweni and Tol (2022) reported that the presence of herbivores in the sodic zone caused significant changes in all exchangeable cations (Na, K, Mg, Ca) and CEC. On the crest, higher concentration of

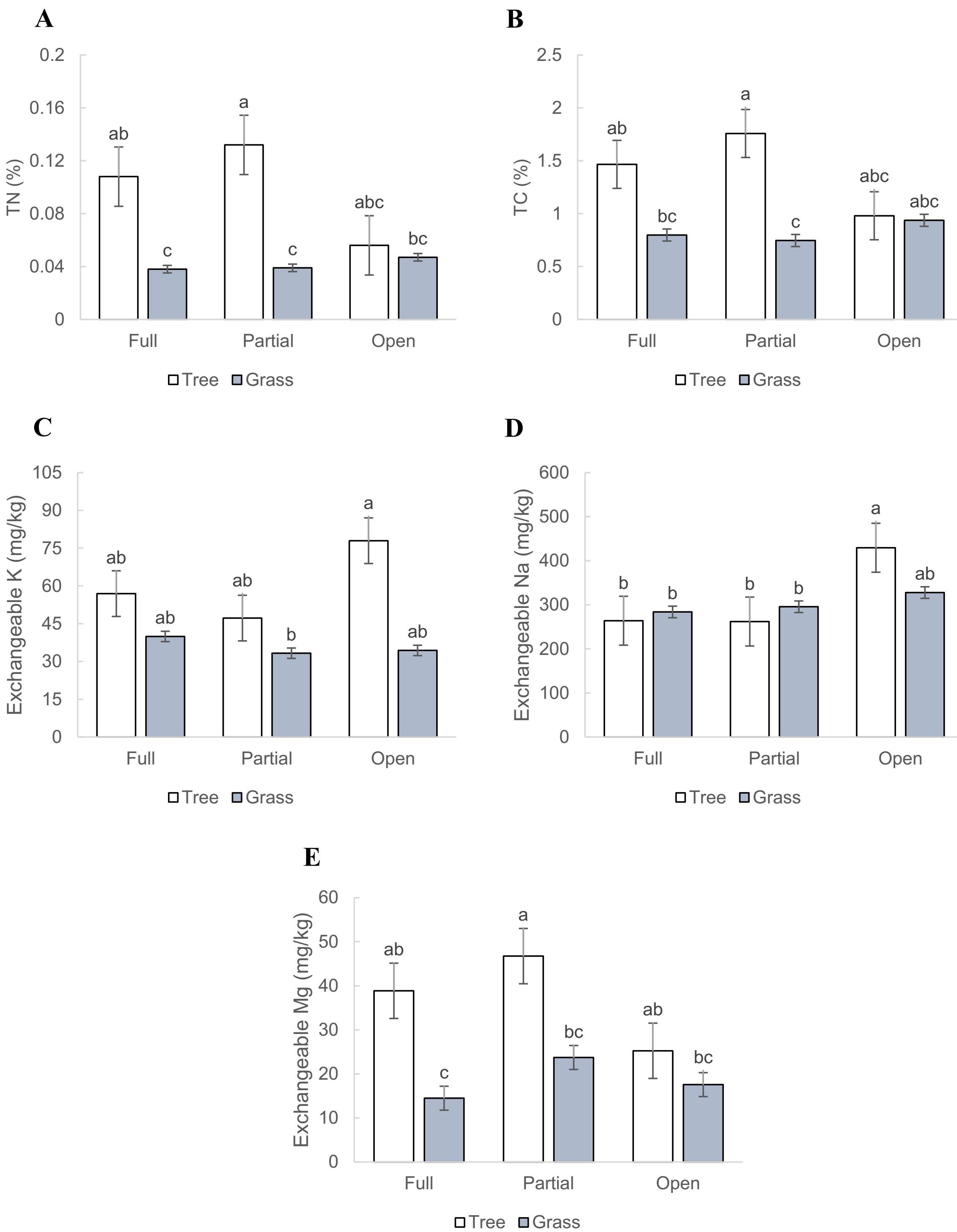


Fig. 4 Mean differences for the significant 2-way interactive effect of herbivory and plant life form on chemical properties (**A**: TC, **B**: TN, **C**: exchangeable K, **D**: exchangeable Na and **E**: exchangeable Mg)

exchangeable Na in exclosures where animal entry was permitted is possibly related to the Na concentrations in urine of organic matter accumulation from both plant residues and animal waste (urine and dung deposits).

Significant changes in only exchangeable Na on the crest and in other exchangeable cations and CEC in the sodic zone may be due to transitions caused by geology and differences in elevation between the crest and footslope and how elevation interacts with herbivores to promote biodiversity. Herbivores are attracted to the sodic zone because it contains more nutritious vegetation, predator vigilance, dietary salts or anti-acidosis minerals, water in ephemeral depressions and green foliage at wet seep areas than the crest and other surrounding areas. Researchers found that herbivores help to maintain the diversity of plant species and promote biodiversity by creating openings in the vegetation, which allows for the growth of new plants (Huntly 1991; Olff and Ritchie 1998). Additionally, their foraging behaviors play a role in dispersing the seeds of diverse plant species, fostering the development of new trees and shrubs. (Henley and Cook 2019; Kerley and Landman 2006; Khomo and Rogers 2005; McConkey et al. 2018). Reports published by the African Conservation Foundation (ACF) estimate that elephants are responsible for the growth of up to 60% of the woody plants in some regions.

Plant life form

There were significant differences in soil properties between grasses and trees. More SOM was added to soils under the trees simply because there is more abundant biomass. Also, slower rate of mineralization under tree canopies due to reduced soil temperature (shade) may have caused these areas to have higher levels of SOM than open grassland zones (Isichei and Muoghalu 1992; Toro-Manríquez et al. 2019). TC and TN were also higher under tree canopies because decomposition processes result in gradual C and N enrichment (Holdo and Mack 2014). Malongweni and Tol (2022) also observed similar changes in SOM, TN, and TC, whereby they were significantly higher under tree canopies than open grassland zones. pH and exchangeable cations were also high under tree canopies except for Na. According to Brady and Weil (2008) cations tend to increase with soil pH due to the greater negative charge that develops on organic matter and clay minerals such as kaolinite due to deprotonation of functional groups as pH increases.

The differences in soil properties between grasses and trees can also be attributed to the type of herbivore (Treydte et al. 2011). In our study and that of Malongweni and Tol (2022) for example, it was observed that in the open access area there were fewer trees, and some were toppled by the larger herbivores. Holdo and Mack (2014) found that larger herbivores can change the vegetation structure through trampling and toppling-over of trees. On the contrary, the full exclosure had large trees and dense canopies which are more closed and cast more shadows (Fig. 2).

According to Ludwig et al. (2004), in open grasslands, grasses face high solar radiation and temperatures and lower water and nutrient availability in the soil than beneath large trees. Some authors have described an enhanced soil respiration under the canopy compared to the open grassland (Toro-Manríquez et al. 2019; Uribe et al. 2015), related to a higher soil C and N content, despite lower soil temperature, while others reported increased CO_2 exchange rates in the open grassland, due to higher herbaceous biomass and light availability, as main drivers of CO_2 uptake (Hussain et al. 2009; Treydte et al. 2011).

Sanford et al. (1982) claim that large trees would be effective in temperature amelioration and mineral cycling which is contrary to our findings. Levels of total N and C between the trees and grasses in the open access were insignificant while the full and partial exclosure had significant differences between the grasses and trees. This is because browsers such as giraffes and elephants break tree branches, debark trees, and sometimes even push them over. This then decreases the number of trees present and canopy diameter of trees (Holdo and Mack 2014). The trees fall and/or are sometimes dragged by elephants to the grassland zones. This then leads to more homogeneous distribution of litterfall in inter-canopy spaces and less surface cover by the branches and crowns of trees. Denser canopy cover in the full and partial exclosure enables less light to reach the ground and this profoundly impacts community structure and ecosystem functions in savannas. Therefore, differences in TC and TN between trees and grasses may be a function of changes in vegetation structure through herbivory.

Herbivores, and plant life form interaction

In the partial exclosure, areas under tree canopies had much higher TN, TC, and exchangeable Mg than open grassland zones, whereas the presence of large herbivores in the control site did not cause any significant changes in these properties. This is because barely any herbaceous vegetation remained in the open access area (Fig. 2). Malongweni and Tol (2022) argued that this is because as elephants and giraffes make their way through the park and forage for food, they thin-out trees thus dramatically reducing the vegetation density of wherever they go. This causes grasses to have an advantage over the consumed (and sometimes broken) trees as they are more likely to gain better access to water and light on account of elephants and giraffes thinning and toppling the surrounding vegetation (Chamane 2012; Janecke 2020; Kohi 2013; Treydte et al. 2011; Langevelde et al. 2003). Water and light play a primary role in the formation of the morphological, chemical, and biological properties of soil (Janecke 2020). Numerous researchers claim that sub-canopy shaded habitats are not only important for thermal regulation of animals, but also are preferred areas of grazing because large woody plants change the availability of resources to the herbaceous layer by mostly creating patches of higher nutrition and moisture under the canopies of especially large trees (Treydte et al. 2011). Siebert and Eckardt (2008) reported a high number and density of big trees in the full exclosures of the Nkuhlu exclosures where herbivores are excluded. They also observed that the foot slope had larger and more nutritious trees than the crest. The proximity to the river may also play a role in the presence of big trees because of the higher probability of sub-surface water and alluvial deposits.

Areas under tree canopy in the open access area had greater concentration of exchangeable Na than treatments in all the other exclosures. Wheelock (1980) and Weir (1972) hypothesised that African elephants consume soils, tree barks and wood ash which has been proven to be rich in Na. In a study conducted in west Zimbabwe, Weir (1972) observed many elephants in rivers with high Na content and smaller numbers from water supplies with lower Na content. That being the case, elephants serve as Na reservoirs throughout their lifespan. The larger and longer lived the elephant, the more Na it stores. Elephants' faecal material and dead remains return the stored Na back into the soil, thereby improving the concentration of exchangeable Na (Holdo et al. 2002; Wheelock 1980). Exchangeable K was only found to be two folds higher under three canopies in the control site than in the open grassland of the partial exclosure. Meanwhile, the full exclosure did not show any significant difference in terms of exchangeable K. Trees that were initially thinned by elephants and giraffes tend to have higher K concentration during the flush of new leaves (Kohi 2013; Ward 1966). Kohi (2012) claims that new leaves can have about three times more K than the older ones. Malongweni and Tol (2022) on the other hand observed no significant two-way interactive effect of exclosure and plant life form towards exchangeable cations, TC, TN, microbial activity and SOC on the sodic patches of the Nkuhlu exclosures. Climate (together with geology) may play a role in these insignificant changes (Janecke 2020). Climate, particularly temperature and moisture, has a direct impact on soil physio-biochemical processes such as mineralization and/or accumulation of organic matter contents (Scholtz et al. 2014). These reactions are largely driven by the microbial composition of the soil, which, in turn, is also directly influenced by the climate. Due to the lower rainfall in the KNP, as well as the clay layer that occurs on the foot-slope of Nkuhlu exclosures, water flow is slower. (Janecke et al. 2020; Siebert and Eckhardt 2008).

Conclusion

The presence of herbivores had a significant impact on soil properties compared to areas where no herbivores were allowed. This is especially true with respect to pH, EC, available P, and exchangeable Na. We also found that some soil properties, especially TN, TC, CEC and SOM were not affected by herbivores. Moreover (and surprisingly), herbivores and plant life form did not independently nor interactively affect total microbial activity. It can further be concluded that open grasslands had poorer soil conditions than areas under tree canopies, when pH, TN, TC, exchangeable cations (K^+, Mg^{2+} and Ca^{2+}) were considered. All of these were significantly higher under tree canopies than in open grassland zones. Except for exchangeable Na, the size and height of herbivores does not influence soil conditions, rather the presence or absence of herbivores. Intriguingly, our findings suggest that the size and height of herbivores did not emerge as decisive factors influencing soil properties; rather, it was the mere presence or absence of herbivores that played a pivotal role. These insights are invaluable for ecosystem management, offering a deeper understanding of the intricate environmental dynamics within the Kruger National Park's landscape. They provide essential knowledge for conservation efforts and landscape preservation initiatives.

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Author contributions
SOM wrote the main manuscript text and processed the data, JVT provided effective supervision. All authors reviewed the manuscript.

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Availability of data and materials
The data supporting the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate
The animal study protocol was approved by the Environment & Biosafety Research Ethics Committee of UNIVERSITY OF THE FREE STATE (protocol code: UFS-ESD2021/0192/21, date of approval: 9 December 2021).

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Competing interests
The authors declare no competing interests.

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