land

MDPI

Article

Fire, Herbivores, and Vegetation Type Shape Soil Biochemistry in Sodic Patches of a Semi-Arid Savanna Ecosystem

Siviwe Odwa Malongweni * and Johan van Tol

Department of Soil, Crop and Climate Sciences, Faculty of Natural Sciences, University of the Free State, Bloemfontein 9301, South Africa; vantoljj@ufs.ac.za
* Correspondence: 2016099166@ufs4life.ac.za

Abstract: In the Kruger National Park (KNP), the lower slopes of catenas have open patches referred to as sodic patches. Fire and herbivores are dominant mediators of vegetation in sodic patches. The effect of fire and herbivores on soil properties of sodic patches remains largely understudied. Moreover, the co-existence of trees and grasses and how they influence savanna soils is an important but poorly understood phenomenon in ecology. Therefore, the present study aimed to determine the influence of 20 years of fire, herbivores, vegetation type, and their interaction on soil biochemistry of sodic patches on the Nkuhlu exclosures in the Kruger National Park, South Africa. We found a higher main effect of fire on available phosphorus, cation exchange capacity, and soil organic matter. The presence of herbivores caused an increase in soil exchangeable cations (K^+, Ca^{2+}, Na^+, and Mg^{2+}), organic matter, cation exchange capacity, and microbial activity. Tree canopies had a higher effect on total nitrogen, exchangeable Ca and Mg, soil organic matter, and cation exchange capacity than open grassland zones. Our results indicate that changes in vegetation structure due to fire and herbivores and their secondary impact on soil properties should be taken into consideration in managing savannas. Moreover, fire and herbivores play an important role in the maintenance of vegetation type (trees and grasses) in sodic patches.

Keywords: canopy cover; grassland zone; grazing; Kruger National Park; sodic zone; soil properties; tree canopy

check for updates

Citation: Malongweni, S.O.; van Tol, J. Fire, Herbivores, and Vegetation Type Shape Soil Biochemistry in Sodic Patches of a Semi-Arid Savanna Ecosystem. *Land* **2022**, *11*, 1148. https://doi.org/10.3390/land11081148

Academic Editor: Krish Jayachandran

Received: 3 July 2022
Accepted: 22 July 2022
Published: 25 July 2022

1. Introduction

Fire and herbivores play a major role in determining the structure and dynamics of savanna ecosystems [1]. This is because they facilitate the co-existence of trees and grasses in this ecosystem. Fire causes a decline in the cover of woody vegetation by either killing or reducing trees to smaller size classes [2–5]. Similarly, browsing herbivores, particularly elephants and giraffes, reduce woody vegetation through tree toppling, snapping off branches, and bark stripping [2]. The combined effect of fire and herbivory on savannas led to the hypothesis that fire causes the decline in woody vegetation whereas herbivores inhibit recovery [3]. There is also a profound indirect effect of fire and herbivory on the tree-grass balance. Grass biomass removal through grazing leads to reduced fuel load, which makes fire less intense and, thus, less damaging to trees; consequently, grazing may result in an increase in woody vegetation [5].

Researchers claim that in the lower slopes of catenas in savannas, fire and herbivores have a severe impact towards the co-existence of trees and grasses [2,6]. In the Kruger National Park (KNP), the lower slopes of catenas have open patches referred to as sodic patches. Sodic patches are known to contain high levels of exchangeable sodium (Na) and a unique vegetation [2]. Moreover, sodic patches are ecologically important for nutrient accumulation, predator evasion, and wallowing, but they are often perceived as derelict lands because of vegetation denudation and low aesthetic quality. Mills et al. [6] claims that it is easy to distinguish the sodic zone from the savanna vegetation because trees are largely absent in the sodic zone yet are abundant in the surrounding vegetation. Since the sodic zone and adjacent savannas experience the same climate, it is possible that the marked differences in vegetation type are due to soil properties, with fire and herbivores potentially playing a modifying role [7]. Additionally, Mills et al. [6] suspects that the high sodium (Na) content in the soil of sodic patches may be stunting the growth of trees and/or attracting herbivores, which damage tree seedlings [6–8]. Moreover, it may be plausible that other soil nutrients affect the competitive outcome between trees and grasses in the sodic patches [2,6].

The effect of fire and herbivores on savanna structure and function is well documented in the literature [1,3,5]. The interactive effects of fire and herbivores and vegetation type on soil properties of sodic patches is often not the focus of investigation and has been less well studied in spite of their potential to influence savanna structure and function. Understanding the relationship between fire, herbivores, and vegetation diversity on sodic patches is critical to biodiversity conservation. Therefore, this study aimed to determine the influence of 20 years of fire, herbivores, vegetation type, and their interaction on soil biochemistry of sodic patches on the Nkuhlu exclosures in the Kruger National Park, South Africa.

2. Materials and Methods

2.1. Study Area

The study was conducted in the Nkuhlu long-term exclosures situated on the north bank of the Sabie river (24°59′10″ S, 31°46′24.6″ E), approximately 18 km downstream from Skukuza in Kruger National Park, South Africa (Figure 1). Elevation ranged between 208 m.a.s.l. next to the Sabie River up to 249 m.a.s.l. in the north-eastern corner of the study site (Figure 1). The Nkuhlu exclosures were built in 2001 as part of a large-scale, long-term exclusion experiment based on the removal of certain ecosystem drivers, namely fire and herbivory [9]. They are approximately 139 ha in size and divided into smaller units, each which is subjected to a different treatment of herbivory and fire. The mean annual rainfall is approximately 561 mm as measured at Skukuza, while the mean daily temperature is 21.9 °C, ranging from 5.6 °C in winter to average highs of 32.6 °C in summer [9]. The vegetation of the surrounding area of the Nkuhlu exclosure site is classified as 'Thickets of the Sabie and Crocodile Rivers' described by Gertenbach [10], and the vegetation type is referred to as *Acacia (Senegalia)* nigrescens—*Combretum apiculatum* association. The dominant woody species include *Combretum apiculatum*, *Grewia bicolor*, *G. flavescens*, *Dichrostachys cinerea*, *Euclea divinorum*, *Terminalia prunioides*, *Spirostachys africana*, *Vachellia (Acacia) grandicornuta*, and *Senegalia (Acacia) nigrescens* [9].

2.2. Experimental Design

The Nkuhlu exclosures consist of three herbivory treatments and two fire treatments. There was a total of five treatment combinations overall, namely (1) full exclosure: a fully fenced area to exclude all herbivores, divided into a burnt and unburnt plot; (2) partial exclosure: a partially fenced area excluding only elephant, and by virtue of their size giraffes, but allowing access to all other herbivores, divided into a burnt and unburnt plot; and (3) open access (a control site): an unfenced and unburnt area where all herbivores are permitted. These exclosures extend from within the river channel to the crest, in order to enclose the full sequence of terrain morphological features and their associated soils and vegetation. This allows for the study of the relationships of habitats along the topographic gradient, from the crest to within the river channel. The exclosures were subjected to controlled burning approximately every 5 years (October 2002, August 2007, June 2012, and October 2017) and to prevent fire from entering non-burn treatments, a firebreak had been created in both the partial and full exclosure [11]. In the present study, soil sampling took place in August 2021.

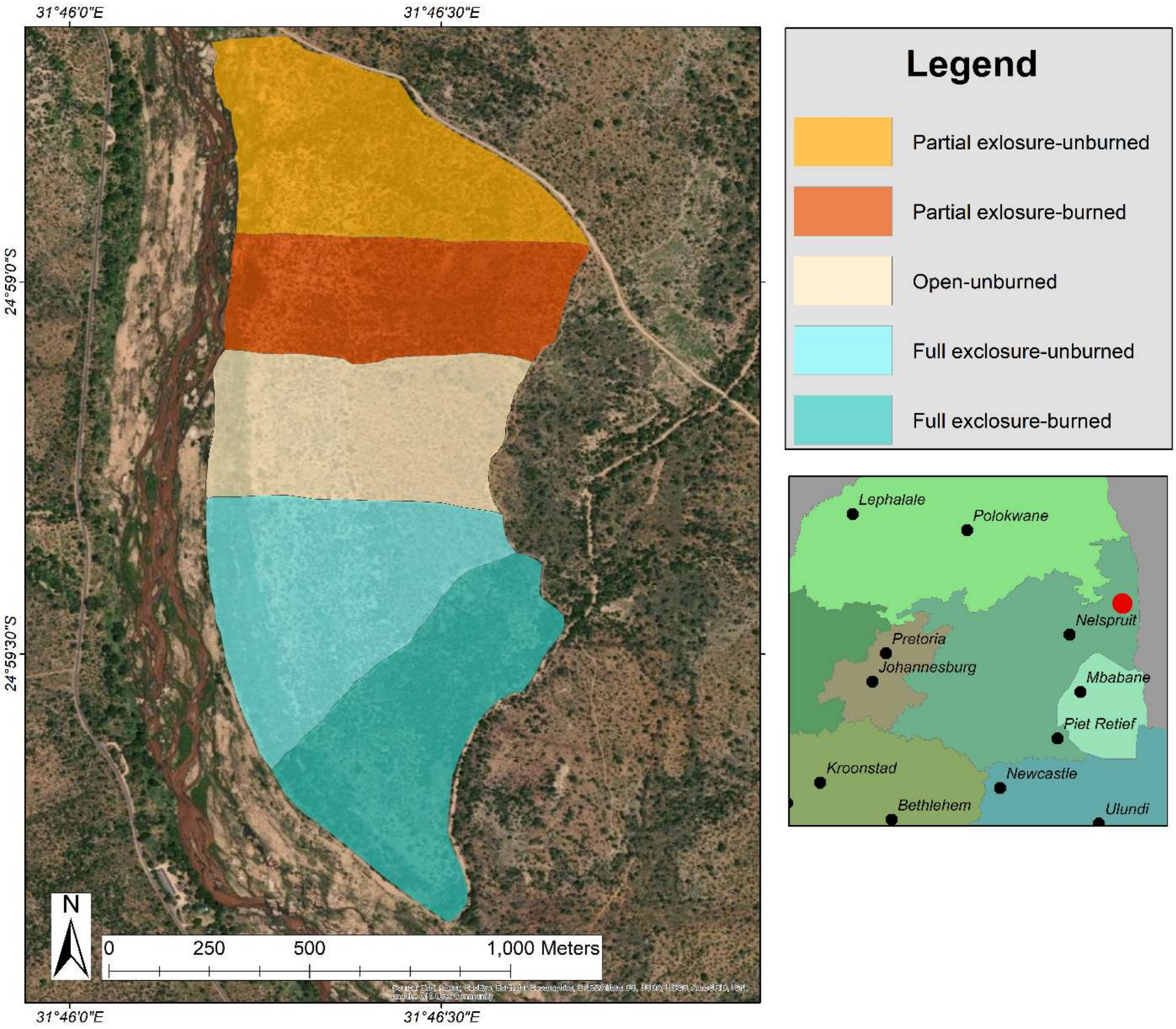


Figure 1. Location of study site (red dot) in the Kruger National Park, South Africa, and map of the Nkuhlu exclosures showing the treatments where the field experiment was conducted.

The experiment was a 3 × 2 × 2 factorial design with different combinations of three herbivore utilizations levels (open access, partial, and full exclosure), two fire treatments (burnt and unburnt plots), and two vegetation types (under tree canopies and open grassland zones). There were no burnt plots in the open access area, and this resulted in an unbalanced factorial design.

2.3. Soil Sampling

Soils of the Nkuhlu exclosure site vary between shallow sandy soil directly overlying weathering rock on the crests and deep, sand to sandy loam on the riparian zone of the Sabie River. The footslopes are characterized by deep, sodium-rich duplex soil [9,12]. The duplex soil on the footslopes consists primarily of sodic patches and is referred to as sodic zone. This paper will only consider the sodic zone. The sodic zone can be classified as Luvisol in World Reference Base (WRB) or Oakleaf and Montagu soils in the South African system [13].

There were two sampling areas within the sodic zone, and soil samples were collected from underneath tree canopies and in open grassland zones. Five soil samples (0–10 cm) were randomly collected from four points underneath the tree canopies and four points in the open grassland zones. Therefore, there was a total of eight sampling points. These five samples were then combined into one composite sample for each sampling point. As a result, a total of 40 samples were collected from KNP.

The collected samples were air-dried and pulverized manually using a 2 mm sieve to obtain uniform particle size for subsequent analysis at the Soil Science Laboratory of the University of Free State, South Africa. Soil samples intended for microbial analysis were sampled at 0–5 cm depth, placed in plastic bags, and put on ice (approximately 4 °C) before sieving (<2 mm). These samples were then analyzed as soon as possible because Wallenius et al. [14] observed that even short storage times could affect the results.

2.4. Soil Biochemical Analyses

Soil pH was measured using a glass electrode pH meter in 1:2.5 (w/v) soil–water ratio suspension using 5 g air-dried soil as described by McLean [15] and the International Institute of Tropical Agriculture [16]. Soil electrical conductivity (EC) was determined using the saturated soil paste method [17]. Total carbon and nitrogen were determined by the dry combustion method using an automatic highly sensitive CN analyzer [18]. Available P was extracted by $NaHCO_3$ and determined by the molybdenum blue method [19]. Exchangeable cations (Ca^{2+}, Mg^{2+}, K^+, and Na^+) were extracted using NH_4Oac and quantified on Inductively Coupled Plasma Spectroscopy. The values for these elements were used to calculate the cation exchange capacity (CEC). Soil organic matter (SOM) was determined using the mass loss on ignition (LOI) method [20]. The total microbial activity was determined using the fluorescein diacetate (FDA) hydrolysis method [21].

2.5. Statistical Analyses

Response variables were assessed for conformity to assumptions of normality and homogeneity of variance. We used log and logit transformations, as appropriate for individual variables, to improve normality and homogeneity of variance. We used three-way analysis of variance (ANOVA) to assess whether the response variables (soil pH, EC, total C, total N, available P, exchangeable cations, CEC, SOM, and total microbial activity) differed among fire and exclosure treatments, between the two types of vegetation (trees and grasses), or if there were interactive effects between fire, exclosure, and vegetation. For significant main effects and interactions, Fischer's protected least squares difference were used to separate the means. The effects were significant at probability less than 0.05. Statistical analyses were done using JMP version 16.0 Pro.

3. Results

3.1. Total Nitrogen (Total N)

The results of the study revealed a significant main effect of vegetation type on total N ($p < 0.05$; Figure 2a). Total N under tree canopies was significantly higher than in open grassland zones.

It was also noticed that exclosure and fire did not independently cause statistical changes in total N, nor were there any statistically significant interactions between exclosure, fire, and vegetation type (Figure 2b,c).

3.2. Total Carbon (Total C)

There was a significant main effect of vegetation type on total C, with areas under tree canopies having higher total C than open grassland zones (Figure 3a). With the exceptions of the open access area and the burnt plots of the full exclosure, the three-way interaction between exclosure, fire, and vegetation type resulted in higher total C under tree canopies than in open grassland zones.

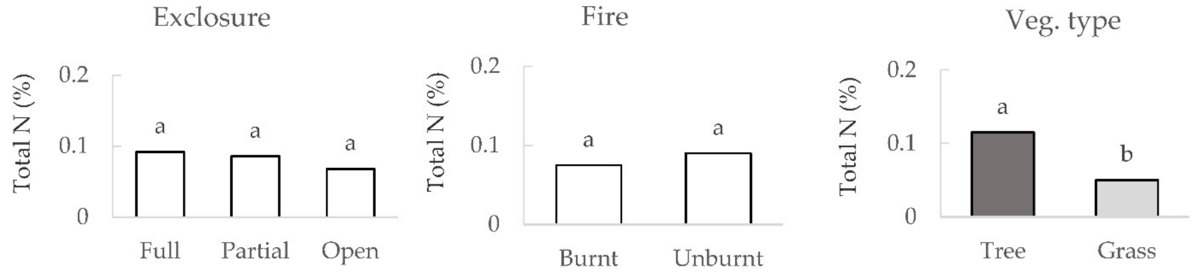
3.3. Soil pH and Electrical Conductivity (EC)

Exclosure, fire, and vegetation type did not independently nor interactively influence pH and electrical conductivity (Table 1).

Table 1. The main and interactive effect of herbivores, fire, and vegetation (veg.) type on soil pH and electrical conductivity (EC).

Factor	pH	EC (mS/m)
Exclosure		
Full	6.11 a	1.91 a
Partial	6.09 a	1.94 a
Open access	6.13 a	1.94 a
Fire		
Unburnt	6.12 a	1.68 a
Burnt	6.09 a	1.63 a
Niche		
Tree	6.01 a	1.76 a
Grass	6.07 a	1.80 a
Main effect	*p*-values and significance	
Exclosure	0.94 ns	0.29 ns
Fire	0.59 ns	0.25 ns
Niche	0.09 ns	0.79 ns
Interaction		
Exclosure × Fire	0.30 ns	0.15 ns
Exclosure × Niche	0.47 ns	0.78 ns
Fire × Niche	0.78 ns	0.35 ns
Exclosure × Fire × Niche	0.72 ns	0.20 ns

Means with different letter for the same factor within the column are significantly different ($p < 0.05$). ns = not significant.

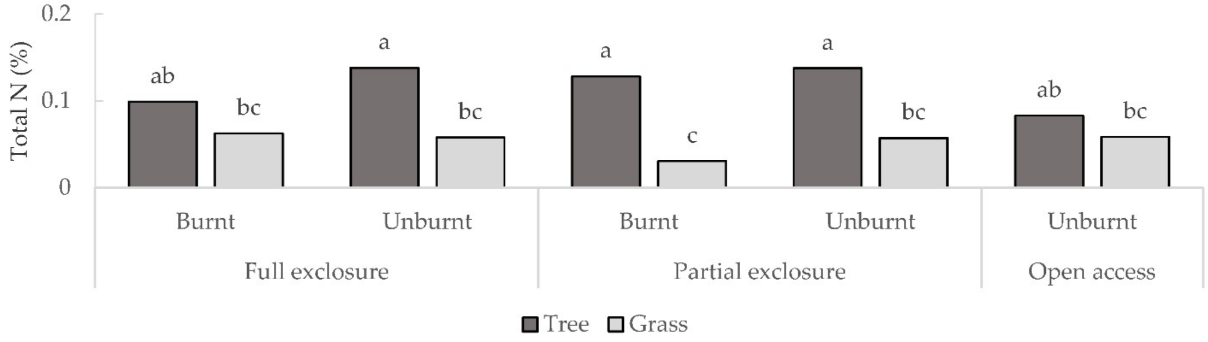


(**a**)

Factor	Total N
Exclosure X Fire	0.98 ns
Exclosure X Veg. type	0.17 ns
Fire X Veg. type	0.65 ns

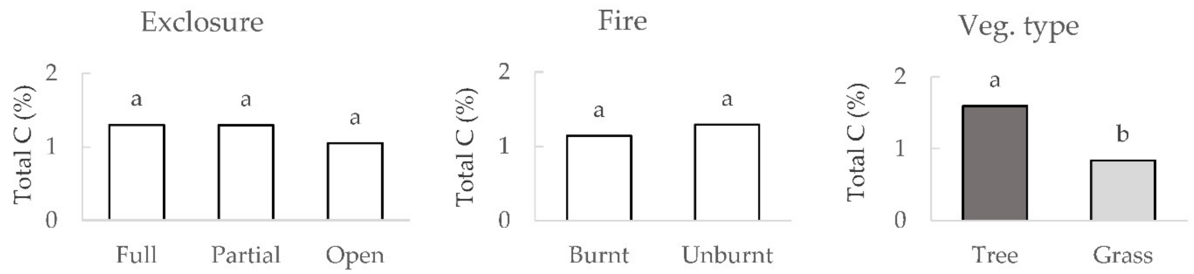
Values are *p*-value and significance: * $p < 0.05$, ns = not significant.

(**b**)



(**c**)

Figure 2. The main and interactive effect of herbivores, fire, and vegetation (veg.) type on total nitrogen (total N): (**a**) independent effect; (**b**) two-way interactive effect; (**c**) three-way interactive effect.

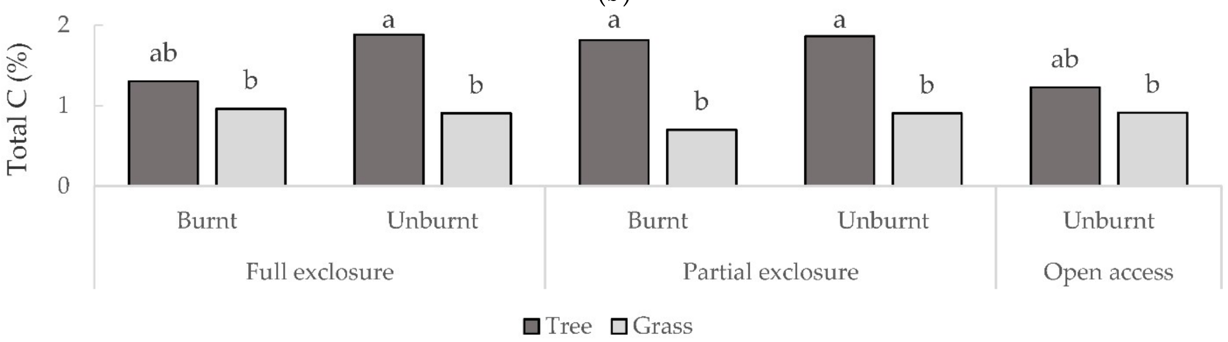


(**a**)

Factor	Total C
Exclosure X Fire	0.67 ns
Exclosure X Veg. type	0.12 ns
Fire X Veg. type	0.45 ns

Values are *p*-value and significance: * $p < 0.05$, ns = not significant.

(**b**)



(**c**)

Figure 3. The main and interactive effect of herbivores, fire, and vegetation (veg.) type on total Carbon (total C): (**a**) independent effect; (**b**) two-way interactive effect; (**c**) three-way interactive effect.

3.4. Available Phosphorus (Available P)

The results of the study revealed that fire had a significant main effect on available P ($p < 0.05$; Figure 4a); unburned plots had high available P relative to burnt plots. Exclosure and vegetation type did not independently cause statistical changes in available P, nor were there any significant interactions between exclosure and vegetation type, as well as between fire and vegetation type.

The two-way interaction between exclosure and fire had a significant influence on total P (Figure 4b). Moreover, it was observed that in the open access area and the unburnt plots on the full exclosure, available P under tree canopies was significantly high compared to open grassland zones (Figure 4c). Additionally, it was noticed that the burnt plots on the partial exclosure had the least amount of available P than all the other treatments.

3.5. Exchangeable Cations and Cation Exchange Capacity (CEC)

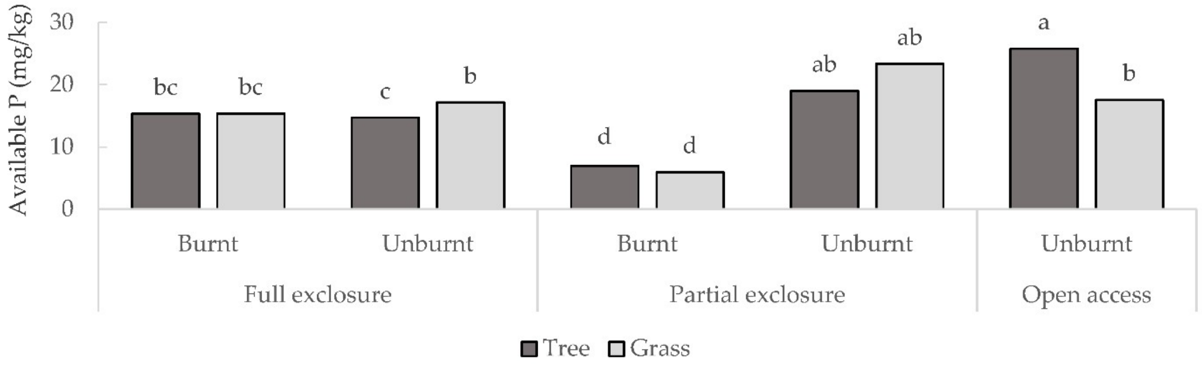
Data regarding exchangeable cations and CEC (Table 2) showed that exclosure, fire, and vegetation type had a significant influence on exchangeable cations and CEC. The full exclosure and open access area had a much higher concentration of exchangeable K than the partial exclosure. The open access area had the lowest concentration of exchangeable Ca, whereas the partial exclosure had the highest. Both the partial exclosure and control site had significantly higher concentration levels of exchangeable Na than the full exclosure. The partial exclosure had significantly higher exchangeable Mg than the control site and full exclosure. Furthermore, the open access area and the partial exclosure had significantly higher CEC than the full exclosure.

(**a**)

Factor	Available *P*
Exclosure X Fire	0.01 *
Exclosure X Veg. type	0.20 ns
Fire X Veg. type	0.43 ns

Values are *p*-value and significance: * $p < 0.05$, ns = not significant.

(**b**)



(**c**)

Figure 4. The main and interactive effect of herbivores, fire, and vegetation (veg.) type on available phosphorus (available P): (**a**) independent effect; (**b**) two-way interactive effect; (**c**) three-way interactive effect.

Table 2. The main and interactive effect of herbivores, fire, and vegetation (veg.) type on exchangeable cations and cation exchange capacity (CEC).

Factor	**Variable**				
	K (mg/kg)	**Ca (mg/kg)**	**Na (mg/kg)**	**Mg (mg/kg)**	**CEC**
		Exclosure			
Full	92.8 a	1316.6 ab	223.7 b	43.8 b	1.3 b
Partial	55.5 b	1409.7 a	323.3 a	58.5 a	2.1 a
Open access	102.316 a	934.7 b	340.8 a	42.1 b	2.1 a
		Fire			
Unburnt	84.6 a	1307.8 a	309.8 a	50.7 a	1.9 a
Burnt	72.4 a	1231.9 a	352.8 a	47.3 a	1.6 b
		Niche			
Tree	82.8 a	1523.8 a	289.2 a	57.3 a	1.9 a
Grass	77.9 a	1129.6 b	283.2 a	44.6 b	1.6 b
Main effect	***p*-value and significance**				
Exclosure	0.04 *	0.03 *	0.04 *	0.002 *	0.01 *
Fire	0.69 ns	0.09 ns	0.12 ns	0.14 ns	0.05 *
Niche	0.60 ns	0.05 *	0.37 ns	0.014 *	0.02 *

Table 2. *Cont.*

Factor	Variable				
	K (mg/kg)	Ca (mg/kg)	Na (mg/kg)	Mg (mg/kg)	CEC
		Interaction			
Exclosure × Fire	0.79 ns	0.38 ns	0.04 *	0.27 ns	0.46 ns
Exclosure × Niche	0.81 ns	0.93 ns	0.92 ns	0.14 ns	0.01 *
Fire × Niche	0.58 ns	0.49 ns	0.75 ns	0.96 ns	0.15 ns
Exclosure × Fire × Niche	0.62 ns	0.007 *	0.78 ns	0.86 ns	0.04 *

Means with different letter for the same factor within the column are significantly different ($p < 0.05$). * $p < 0.05$, ns = not significant.

It was also noticed that fire did not independently influence exchangeable cations, however, unburnt plots had significantly high CEC than burnt plots. Exchangeable Ca and Mg concentrations differed significantly between the two vegetation types. They were highest under tree canopies and lowest in open grassland zones, whereas exchangeable K and Na were not influenced by vegetation type.

3.6. Soil Organic Matter (SOM)

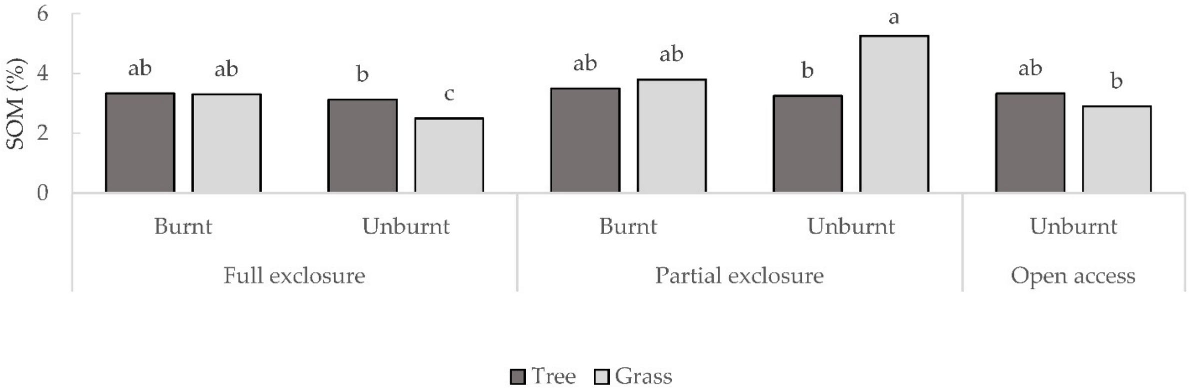
There were significant main and interactive effects of exclosure, fire and vegetation type on SOM ($p < 0.05$; Figure 5a–c). The full exclosure and control site (i.e., with higher herbivore biomass) had significantly low SOM compared to the partial exclosure. Burning resulted in a significant increase in SOM. Moreover, open grassland zones had significantly low SOM than areas under tree canopies (Figure 5a).

(**a**)

Factor	SOM
Exclosure X Fire	0.003 *
Exclosure X Veg. type	0.005 *
Fire X Veg. type	0.048 *

Values are p-value and significance: * $p < 0.05$, ns = not significant.

(**b**)



(**c**)

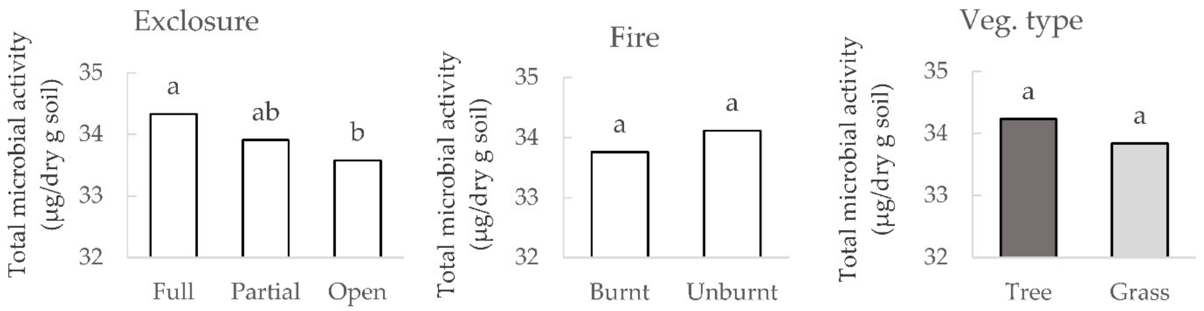
Figure 5. The main and interactive effect of herbivores, fire, and vegetation (veg.) type on soil organic matter (SOM): (**a**) independent effect; (**b**) two-way interactive effect; (**c**) three-way interactive effect.

It was also observed that in the unburnt plots of the partial exclosure, SOM under tree canopies was significantly low compared to open grassland zones (Figure 5c). Conversely, areas under tree canopies on the unburnt plots of the full exclosure had significantly high SOM than open grassland zones. Moreover, open grassland zones on the unburnt plot of the full exclosure had the lowest SOM compared to all the other treatments (Figure 5c).

3.7. Total Microbial Activity

Exclosure had a significant main effect on total microbial activity, with the full exclosure having the highest total microbial activity and the open access area having the lowest microbial activity. The partial exclosure was not significantly different from the full exclosure nor open access area.

On the control site, it was observed that areas under tree canopies had significantly higher total microbial activity than open grassland zones (Figure 6c).

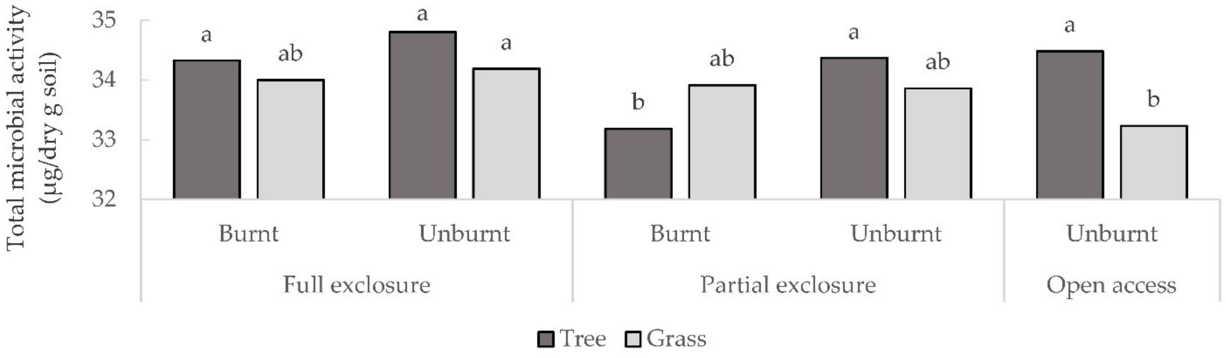


(**a**)

Factor	Total Microbial Activity (µg/dry g soil)
Exclosure X Fire	0.63 ns
Exclosure X Veg. type	0.25 ns
Fire X Veg. type	0.12 ns

Values are *p*-value and significance: * $p < 0.05$, ns = not significant.

(**b**)



(**c**)

Figure 6. The main and interactive effect of herbivores, fire, and vegetation (veg.) type on total microbial activity: (**a**) independent effect; (**b**) two-way interactive effect; (**c**) three-way interactive effect).

4. Discussion

4.1. Herbivores

The results of our study revealed that the most prominent soil changes influenced by herbivores in the sodic patches of Nkuhlu exclosures were SOM content, concentration of exchangeable cations, CEC, and microbial activity. The partial exclosure had the highest SOM content, whereas there were no significant differences in SOM content between the full exclosure and open access area. Increases in SOM in the partial exclosure could be due to dung and urine deposition [22]. Dung and urine enhance substrate decomposition and mineralization rate, thus increasing SOM. The reductions in SOM in the open access area may be a consequence of soil compaction due to the trampling, pawing, and wallowing action by large herbivores [23]. Sodic patches are often associated with overgrazed, trampled vegetation and according to Tuomi et al. [22] and van Coller [24], the presence of large herbivores in the sodic zone, particularly elephants, cause soil compaction, decreased soil porosity, increased bulk densities, and decreased organic matter.

In our study, we also observed that the effect of exclosure on the concentration of exchangeable cations (K, Ca, Na and Mg) and CEC were herbivore-specific, in that they were significantly high in the partial exclosure, whereas there were no significant differences between the full exclosure and open access area where large and tall animals were permitted. Higher exchangeable cations in the partial exclosure are due to higher SOM content. Organic matter has been shown to provide much of the cation exchange capacity of surface soils in savanna soils [24].

It was also noticed that the presence of large and tall herbivores caused significant reductions in soil microbial activity. Our results support the previous findings that herbivore size and population density regulate the structure and function of microbial community [25]. This is because an increase in herbivore size and population density leads to soil compaction. Herbivore-mediated soil compaction can destroy the network of tunnels and pores used by soil organisms such as earthworms and microbes, thus resulting in low microbial activity and diversity [26].

4.2. Fire

In general, fire had a significant effect on soil organic matter. Highest soil organic matter content was observed in burnt plots than unburnt plots. Burnt plots had high organic matter content because fire tends to increase soil fertility by chemically converting nutrients bound in dead plant tissues and the soil surface to more available forms [27]. Mehdi et al. [28] and MacKenzie et al. [29], who found a loss of organic matter after occurrence fire, disagree with these findings. According to Mehdi et al. [28] and MacKenzie et al. [29], fire consumes organic matter and converts it into ash during the burning process. Moreover, fire destroys organic matter through volatilization. Heydari et al. [30] found that frequent fires reduce the thickness of the organic layer of the soil profile and suppresses soil organic C mineralization rates due to loss of microbial biomass since fire destroys microbes. In our study, however, we found that fire did not affect total microbial activity. This could be because South African savannas are poor in nutrients, and nutrient-poor savannas tend to have low-intensity fires that are not hot enough to affect soil organisms [31].

Available phosphorus was significantly higher in unburnt than in burnt plots. Fire caused a loss of available P through volatilization and/or pyro-mineralization. This agrees with Mehdi et al. [28], who reported a decrease in total and available soil P following the fire in Zagros forests, western Iran. Mehdi et al. [28] claim that this is because burning very rapidly transforms the organic P present in biomass and soil organic matter into inorganic P.

CEC showed a similar trend to available P in that it was significantly lower in burnt plots than in unburnt plots. Loss of CEC can be attributed to thermal destruction of soil organic matter during the burning process [32]. Soil CEC decreases have been reported in a variety of environments affected by burning. For instance, Yildiz et al. [33] observed up to 40% reductions in CEC of pine forest soils in Turkey two weeks after burning. On the other hand, Ulery et al. [32] reported that CEC of severely burned soil can be up to 82% lower than the unburned soil.

4.3. Vegetation Type

Areas under tree canopies had higher total N and C than open grassland zones. Similar observations have been reported by Isichei and Muoghalu [34]. This may be caused by litter deposition under tree canopies. Litter decomposes, and the decomposition process results in the gradual C and N enrichment of residue decomposing material [35].

Soil organic matter showed a similar trend to total N and C, and it was higher under tree canopies than in the open. Organic matter accumulation under tree canopies may be a result of nutrient inputs from litter-fall and its slower rate of mineralization under tree canopies due to reduction in temperature there. Additionally, leachates from tree canopies and nutrient transport by tree roots from the rooting zone to tree canopies may also be a source of higher soil organic matter under tree canopies. Higher soil organic matter under tree canopies may account for higher CEC in the soil of our study. This is because, in addition to being a dependable source of plant nutrients, soil organic matter has been shown to improve the cation exchange capacity of soils. This is because organic matter components of soil have negatively charged sites on their surfaces which adsorb and hold cations by electrostatic force [36].

Based on the results of our study, soils under tree canopies were found to have significantly higher concentration of exchangeable Ca and Mg than those in open grassland zones. Similar observations have been reported by Isichei and Muoghalu [34], who found that soils under tree canopies had significantly higher levels of organic matter, calcium, magnesium, potassium, total exchangeable cations, cation exchange capacity, and pH than those in open grasslands.

Microbial activity followed the same thread as total N and C, exchangeable Ca and Mg, SOM, and CEC in that it was higher under tree canopies than in open grassland zones. This is because increased plant residue inputs in areas surrounding the trees provide more substrate for soil microorganisms, thus resulting in a more active and more abundant microbial community [37].

4.4. Fire, Herbivores, and Vegetation Type Interaction

Soil properties, particularly exchangeable Ca, CEC, and total C, were influenced by the interactive effect of fire, exclosure, and vegetation type. Burning and herbivores in conjunction with canopy cover increased soil organic C, and this is because fire and trees tend to attract birds and grazers which deposit their droppings, dung, and urine beneath canopies. Herbivores, particularly grazing herbivores, are attracted to the recently burned areas due to the flush of green growth and higher quality forage following a fire [3,24]. According to Chamane [3], herbivores can alter C inputs to the soil by changing the quantity and quality of organic inputs (e.g., litterfall, herbivore dung). Therefore, the low soil total C content in the open grassland zones of unburnt plot in the full exclosure might be a consequence of herbivore exclusion and absence of trees. Similar findings have been reported by van Langevelde et al. [5], who noticed that the interaction between fire and herbivory provides a mechanistic explanation for observed discontinuous changes in soil properties between trees and grass vegetations.

The interaction between fire, exclosure, and vegetation type significantly increased soil CEC. Liang et al. [38] and Khanna et al. [39] also reported a subsequent increase in cation exchange capacity. These reporters claim that this increase is due to animal waste deposition and the release of oxides from the combustion of organic matter during the burning process.

Burning and herbivory largely influenced soil fertility in the sodic zone. The absence of fire in conjunction with the exclusion of herbivores resulted in a decrease in total C content. The open grassland zones on the unburnt plot of the full exclosure had the lowest SOM content than all the other treatments. This is because even though sodic patches are often referred to as nutrient hotspots, no animals were permitted to enter inside the full exclosure, whereas herbivores were able deposit their waste in the open access area and partial exclosure, thus increasing SOM. Moreover, elephants may also enhance soil fertility by promoting the dominance of C4 plants relative to C3 plants [40–42]. This is because the diet of extant elephants is dominated by C3 browsers, although some elephants have a significant C4 grass component in their diet. C4 plants form soil organic carbon that has higher $\delta 13C$ values than that formed by the C3 plants. According to van Coller [23] and Sandhage-Hofmann et al. [40], toppling of trees by elephants, remaining browsing material, and decomposition of roots could result in an even higher soil organic matter in the sodic zone where herbivores are permitted.

5. Conclusions

Fire and herbivores highlighted the intricate changes in soil properties between tree and grass vegetations in the savanna ecosystems in the Kruger National Park, South Africa. Fire, herbivores, and vegetation type resulted in varying and sometimes opposing effects on soil biochemical properties. The effect was more evident in the case of SOM, exchangeable Ca and Mg, total N and C, CEC, Available P, and microbial activity. On the other hand, contrary to our expectations, fire, herbivores, and vegetation type did not have a significant effect on soil pH and electrical conductivity. It can further be concluded that open grasslands had poorer soil conditions than areas under tree canopies, when the total N and C, exchangeable Ca and Mg, CEC, and SOM were considered. All of these were significantly higher under tree canopies than in open grassland zones. Therefore, changes in vegetation structure due to fire and large herbivores and their secondary impact on soil properties should be taken into consideration in managing savannas. Moreover, although sodic patches are often associated with overgrazed, trampled vegetation, and fire, herbivores play an important role in the maintenance of vegetation (trees and grasses) richness in these nutrient hotspots.

Author Contributions: S.O.M. wrote the manuscript and processed the data; J.v.T. provided effective supervision. All authors have read and agreed to the published version of the manuscript.

Funding: This paper was funded by The Department of Environment, Forestry and Fisheries in South Africa as part of the Natural Resource Management Programme.

Institutional Review Board Statement: 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).

Data Availability Statement: Not applicable.

Acknowledgments: We wish to thank SANParks for allowing us to carry out this study at the Kruger National Park. We acknowledge Kaya Mrhubata, Tercia Strydom, Velly Ndlovu and the rest SANParks staff for their help. The authors would also like to acknowledge Elmarie Kotze, and Eddie Smit for their assistance in the collection and handling of the soil samples.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Venter, Z.S.; Hawkins, H.; Cramer, M.D. Implications of Historical Interactions Between Herbivory and Fire for Rangeland Management in African Savannas. *Ecosphere* **2017**, *8*, e01946. [CrossRef]
2. Janecke, B.B. Vegetation Structure and Spatial Heterogeneity in the Granite Supersite, Kruger National Park. *Koedoe—Afr. Prot. Area Conserv. Sci.* **2020**, *62*, 1–12. [CrossRef]
3. Chamane, S.C. Effect of Fire Frequency on Herbivore Distribution and Behaviour in the Kruger National Park, South Africa. Master's Thesis, University of KwaZulu-Natal, Pietermaritzburg, South Africa, 2012.
4. Smit, I.P.J.; Asner, G.P.; Govender, N.; Kennedy-Bowdoin, T.; Knapp, D.E.; Jacobson, J. Effects of Fire on Woody Vegetation Structure in African Savanna. *Ecol. Appl.* **2010**, *20*, 1865–1875. [CrossRef]
5. Van Langevelde, F.; van de Vijver, C.A.D.M.; Kumar, L.; van de Koppel, J.; de Ridder, N.; van Andel, J.; Skidmore, A.K.; Hearne, J.W.; Stroosnijder, L.; Bond, W.J.; et al. Effects of Fire and Herbivory on the Stability of Savanna Ecosystems. *Ecology* **2003**, *84*, 337–350. [CrossRef]
6. Mills, A.J.; Strydom, T.; Allen, J.L.; Baum, J. Pedoderm Chemistry in Sodic Patches on Savannah Hillslopes in the Southern Kruger National Park, South Africa. *Afr. J. Ecol.* **2021**, *59*, 1070–1074. [CrossRef]
7. Gibson, D.J.; Hulbert, L.C. Effects of Fire, Topography and Year-to-Year Climatic Variation on Species Composition in Tallgrass Prairie. *Vegetatio* **1987**, *72*, 175–185. [CrossRef]
8. Alard, G.F. A Comparison of Grass Production and Utilization in Sodic and Crest Patches on a Semi-Arid Granitic Savanna Catena in the Southern Kruger National Park, South Africa. Master's Thesis, Faculty of Science, University of the Witwatersrand, Johannesburg, South Africa, 2009.
9. Siebert, F.; Eckhardt, H.C. The Vegetation and Floristics of the Nkhuhlu Exclosures, Kruger National Park. *Koedoe—Afr. Prot. Area Conserv. Sci.* **2008**, *50*, 126–144. [CrossRef]
10. Gertenbach, W.P.D. Landscapes of the Kruger National Park. *Koedoe* **1983**, *26*, 9–121. [CrossRef]

11. O'Keefe, T.; Alard, G. Effects of Herbivores and Fire on Riparian and Upland Savanna Ecosystems: Field Operations Manual for Herbivore and Fire Exclosures on the Sabie and Letaba Rivers in the Kruger National Park, South African National Parks, Skukuza. 2002. Available online: https://www.sanparks.org/parks/kruger/conservation/scientific/exclosures/Exclosure_Field_Manual.pdf (accessed on 10 January 2022).
12. Scogings, P.F.; Hjältén, J.; Skarpe, C. Secondary Metabolites and Nutrients of Woody Plants in Relation to Browsing Intensity in African Savannas. *Oecologia* **2011**, *167*, 1063–1073. [CrossRef]
13. Soil Classification Working Group (SCWG). *Soil Classification—A Taxonomic System for South Africa*; Agricultural Research Council: Pretoria, South Africa, 2018.
14. Wallenius, K.; Rita, H.; Simpanen, S.; Mikkonen, A.; Niemi, R. Sample Storage for Soil Enzyme Activity and Bacterial Community Profiles. *Microbiol. Methods* **2010**, *81*, 48–55. [CrossRef] [PubMed]
15. McLean, E.O. Soil pH and Lime Requirement. In *Methods of Soil Analysis Part 2: Chemical and Microbiological Properties*, 2nd ed.; Page, A.L., Miller, R.H., Keeney, D.R., Eds.; American Society of Agronomy, Inc.: Madison, WI, USA, 1982; Volume 9, pp. 199–224.
16. International Institute of Tropical Agriculture (IITA). *Selected Methods for Soil and Plant Analysis*; Manual Series No. 1; International Institute of Tropical Agriculture: Ibadan, Nigeria, 1979.
17. Corwin, L.D.; Yemoto, K. Salinity: Electrical Conductivity and Total Dissolved Solids. *Soil Sci. Soc. Am.* **2017**, *84*, 1442–1461. [CrossRef]
18. Bremner, J.M.; Mulvaney, C.S. Nitrogen-total. In *Methods of Soil Analysis—Part 2*, 2nd ed.; American Society of Agronomy: Madison, WI, USA, 1982; pp. 595–624.
19. Olsen, S.R.; Sommers, L.E. Determination of Available Phosphorus. In *Method of Soil Analysis. Part 2: Chemical and Microbiological Properties*, 2nd ed.; Miller, R.H., Keeney, D.R., Eds.; ASA: Madison, WI, USA, 1982; pp. 403–427.
20. Nelson, D.W.; Sommers, L.E. Total Carbon, Organic Carbon, and Organic Matter. In *Methods of Soil Analysis, Part 3—Chemical Methods*; American Society of Agronomy, Inc.: Madison, WI, USA, 1996; pp. 961–1009.
21. Schnürer, J.; Rosswall, T. Fluorescein Diacetate Hydrolysis as a Measure of Total Microbial Activity in Soil and Litter. *Appl. Environ. Microbiol.* **1982**, *43*, 1256–1261. [CrossRef] [PubMed]
22. Tuomi, M.; Väisänen, M.; Ylänne, H. Stomping in Silence: Conceptualizing Trampling Effects on Soils in Polar Tundra. *Funct. Ecol.* **2021**, *35*, 306–317. [CrossRef]
23. Van Coller, H.; Siebert, F.; Siebert, S.J. Herbaceous Species Diversity Patterns Across Various Treatments of Herbivory and Fire Along the Sodic Zone of the Nkuhlu Exclosures, Kruger National Park. *Koedoe—Afr. Prot. Area Conserv. Sci.* **2013**, *55*, 1–6. [CrossRef]
24. Ubuoh, E.A.; Ejekwolu, C.C.; Onuigbo, I.V. The effect of Burnt and Un-burnt Land on Soil Physicochemical Characteristics in Ekeya-Okobo Local Government Area, Akwa Ibom State, Nigeria. *Appl. Sci. Environ. Manag.* **2017**, *21*, 923–929. [CrossRef]
25. Stevens, B.M.; Sonderegger, D.L.; Johnson, N.C. Microbial Community Structure Across Grazing Treatments and Environmental Gradients in the Serengeti. *Soil Ecol. Lett.* **2022**, *4*, 45–56. [CrossRef]
26. Van Klink, R.; Schrama, M.; Nolte, S.; Bakker, P.; WallisDeVries, M.F.; Berg, M.P. Defoliation and Soil Compaction Jointly Drive Large-Herbivore Grazing Effects on Plants and Soil Arthropods on Clay Soil. *Ecosystems* **2015**, *18*, 671–685. [CrossRef]
27. Schoch, P.; Binkley, D. Prescribed Burning Increased Nitrogen Availability in A Mature Loblolly Pine Stand. *For. Ecol. Manag.* **1986**, *14*, 13–22. [CrossRef]
28. Mehdi, H.; Ali, S.; Ali, M.; Mostafa, A. Effects of Different Fire Severity Levels on Soil Chemical and Physical Properties in Zagros Forests of Western Iran. *Folia For. Pol. Ser. A* **2012**, *54*, 241–250.
29. MacKenzie, M.D.; DeLuca, T.H.; Sala, A. Forest Structure and Organic Horizon Analysis Along a Fire Chronosequence in the Low Elevation Forests of Western Montana. *For. Ecol. Manag.* **2004**, *203*, 333–343. [CrossRef]
30. Heydari, M.; Rostamy, A.; Najafi, F.; Dey, D.C. Effect of Fire Severity on Physical and Biochemical Soil Properties in Zagros Oak (*Quercus brantii* Lindl.) Forests in Iran. *J. For. Res.* **2017**, *28*, 95–104. [CrossRef]
31. Nghalipo, E.; Joubert, D.; Throop, H.; Groengroeft, A. The Effect of Fire History on Soil Nutrients and Soil Organic Carbon in a Semi-arid Savanna Woodland, Central Namibia. *Afr. J. Range Forage Sci.* **2018**, *36*, 9–16. [CrossRef]
32. Ulery, A.L.; Graham, R.C.; Goforth, B.R.; Hubbert, K.R. Fire Effects on Cation Exchange Capacity of California Forest and Woodland Soils. *Geoderma* **2017**, *286*, 125–130. [CrossRef]
33. Yildiz, O.; Esen, D.; Sarginci, M.; Toprak, B. Effects of Forest Fire on Soil Nutrients in Turkish Pine (*Pinus burtia*, Ten) Ecosystems. *Environ. Biol.* **2010**, *31*, 11–13.
34. Isechei, A.O.; Muoghalu, J.I. The Effects of Tree Canopy Cover on Soil Fertility in a Nigerian Savanna. *Trop. Ecol.* **1992**, *8*, 329–338. [CrossRef]
35. Holdo, R.M.; Mack, M.C. Functional Attributes of Savanna Soils: Contrasting Effects of Tree Canopies and Herbivores on Bulk Density, Nutrients and Moisture Dynamics. *Ecology* **2014**, *102*, 1171–1182. [CrossRef]
36. Brady, N.C.; Weil, R.R. *The Nature and Properties of Soils*, 14th ed.; Prentice-Hall: Upper Saddle River, NJ, USA, 2008.
37. Eisenhauer, N.; Beßler, H.; Engels, C.; Gleixner, G.; Habekost, M.; Milcu, A.; Partsch, S.; Sabais, A.C.W.; Scherber, C.; Steinbeiss, S.; et al. Plant Diversity Effects on Soil Microorganisms Support the Singular Hypothesis. *Ecology* **2010**, *9*, 485–496. [CrossRef]
38. Liang, B.; Lehmann, J.; Solomon, D.; Kinyangi, J.; Grossman, J.; O'Neill, B.; Skjemstad, J.O.; Thies, J.; Luizao, F.J.; Peterson, J.; et al. Black Carbon Increases Cation Exchange Capacity on Soils. *Soil Sci. Soc. Am.* **2006**, *70*, 1719–1730. [CrossRef]

39. Khanna, P.K.; Raison, R.J.; Falkiner, R.A. Chemical Properties of Ash Derived from Eucalyptus Litter and its Effects on Forest Soils. *For. Ecol. Manag.* **1994**, *66*, 107–125. [CrossRef]
40. Sandhage-Hofmann, A.; Linstädter, A.; Kindermann, L.; Angombe, S.; Amelung, W. Conservation with Elevated Elephant Densities Sequesters Carbon in Soils Despite Losses of Woody Biomass. *Glob. Chang. Biol.* **2021**, *27*, 4601–4614. [CrossRef] [PubMed]
41. Allen, J.A.; Setälä, H.; Kotze, D.J. Dog Urine Has Acute Impacts on Soil Chemistry in Urban Greenspaces. *Front. Ecol. Evol.* **2020**, *8*, 615979. [CrossRef]
42. Cook, G.D. The Fate of Nutrients During Fires in A Tropical Savanna. *Aust. J. Ecol.* **1994**, *19*, 359–365. [CrossRef]