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Influence of herbivores and trees on soil biochemical properties of a semi-arid savanna

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The study evaluates the interactive effects of mammalian herbivores and trees on soil biochemical properties of a semi-arid savanna ecosystem in South Africa. Composite soil samples were collected at three radial distances from a tree base, namely besides the tree trunk, canopy edge, and outside canopy, for two trees (*Combretum apiculatum* and *Grewia bicolor*), in the full exclosure and open access area in the Nkuhlu exclosures of Kruger National Park. We measured total nitrogen (TN), total carbon (TC), pH, available phosphorus (P), microbial activity, exchangeable cations (calcium [Ca^{2+}], magnesium [Mg^{2+}], sodium [Na^{+}] and potassium [K^{+}]) and cation exchange capacity (CEC). Result indicates that pH and Mg^{2+} in full exclosure were significantly higher than outside, whereas TN, TC, available P, microbial activity, K^{+} and CEC were lower. Under canopy samples had more pH, TN, TC, available P, K^{+} and Ca^{2+} than those collected from other sampling zones, mainly because of the effect of litter accumulation under the tree canopies. With the exceptions of CEC and microbial activity, the effects of the two tree species on soil nutrients were similar. Microbial activity was significantly high, whereas CEC was low under *G. bicolor* than *C. apiculatum*. The canopy edge of *G. bicolor* had the highest microbial activity, while the area outside the canopy of *C. apiculatum* had the lowest than all the other treatments. These results indicate that the presence of herbivores and woody species differentially affects the spatial distribution of the various nutrients, soil microbiota and other chemical properties depending on their radial distances from the tree base.

Conservation implications: It is ecologically unwise to completely eliminate trees and herbivores from savanna ecosystems, as they help to maintain soil fertility and biodiversity.

Keywords: *Combretum apiculatum*; exclosure; grazing; *Grewia bicolor*; herbivores; Kruger National Park; soil properties; tree canopy.

Introduction

Savanna ecosystems are characterised by a continuous grass matrix, interspersed with woody vegetation (trees and shrubs) of varying densities and height (Blentlinger & Herrero 2020). Grasses, trees and/or shrubs have distinct and sometimes contrasting effects on soil properties and processes. The effect of individual trees and grasses on savanna soils is well documented in the literature (Gallardo 2003; Holdo & Mack 2014; Malongweni & Van Tol 2022; Tuomi, Väisänen & Ylänne 2019). Numerous studies found that woody species improve the fertility of the soil under their canopies. For instance, Isichei and Muoghalu (1992) reported an increase in organic matter content beneath tree canopies compared to open grassland zones in an African savanna. This increase is attributed to lower soil temperatures, rainfall interception, alteration of soil moisture, litter accumulation, root exudation and enhanced pools of soil nutrients (C, N, P and cations) or a combination of these factors (Blank & Carmel 2012). Some studies have also demonstrated that savannas with different tree species vary in litter quality and root exudates, generating a divergence in soil properties, which may influence the soil biodiversity (Gallardo 2003; Tuomi et al. 2019).

In African savannas, acacias (*Acacia*), bushwillows (*Combretum*) and the many species of *Grewia* are the most common tree species (Siebert & Eckhardt 2008). They play a significant role in maintaining soil fertility and provide nutrition to herbivores. Herds of mammalian herbivores tend to aggregate under these woody species as they find them palatable (Seloana et al. 2018; Titcomb et al. 2021). Through plant consumption (browsing) and traffic, herbivores tend to possess distinct and sometimes contrasting direct and indirect effects on savanna soils and vegetation. For example, Holdo and Mack (2014) found that at sufficiently high densities, large herbivores can trample vegetation and compact soil thus leading to the loss of vegetation and soil degradation. Conversely, Liu et al. (2015) claim that grazing herbivores maintain and enhance vegetation and improve soil health. They achieve this by dispersing seeds of trees, fertilising soil with dung and reducing the size of competing plants. According to Tuomi et al. (2019), herbivore-induced changes in soil properties and processes in savanna ecosystems depend strongly on plant species and changes in litter quality and litter input quantity. Such indirect effects have, to our knowledge, not yet been broadly demonstrated for different types of tree species in savanna-grassland systems. Much work has been done on *Acacia*, and little is known about other species (Ludwig, De Kroon & Prins 2008). Therefore, research exploring the impact of tree species on savanna soil properties and ecosystem function is crucial and ignoring it is a critical oversight.

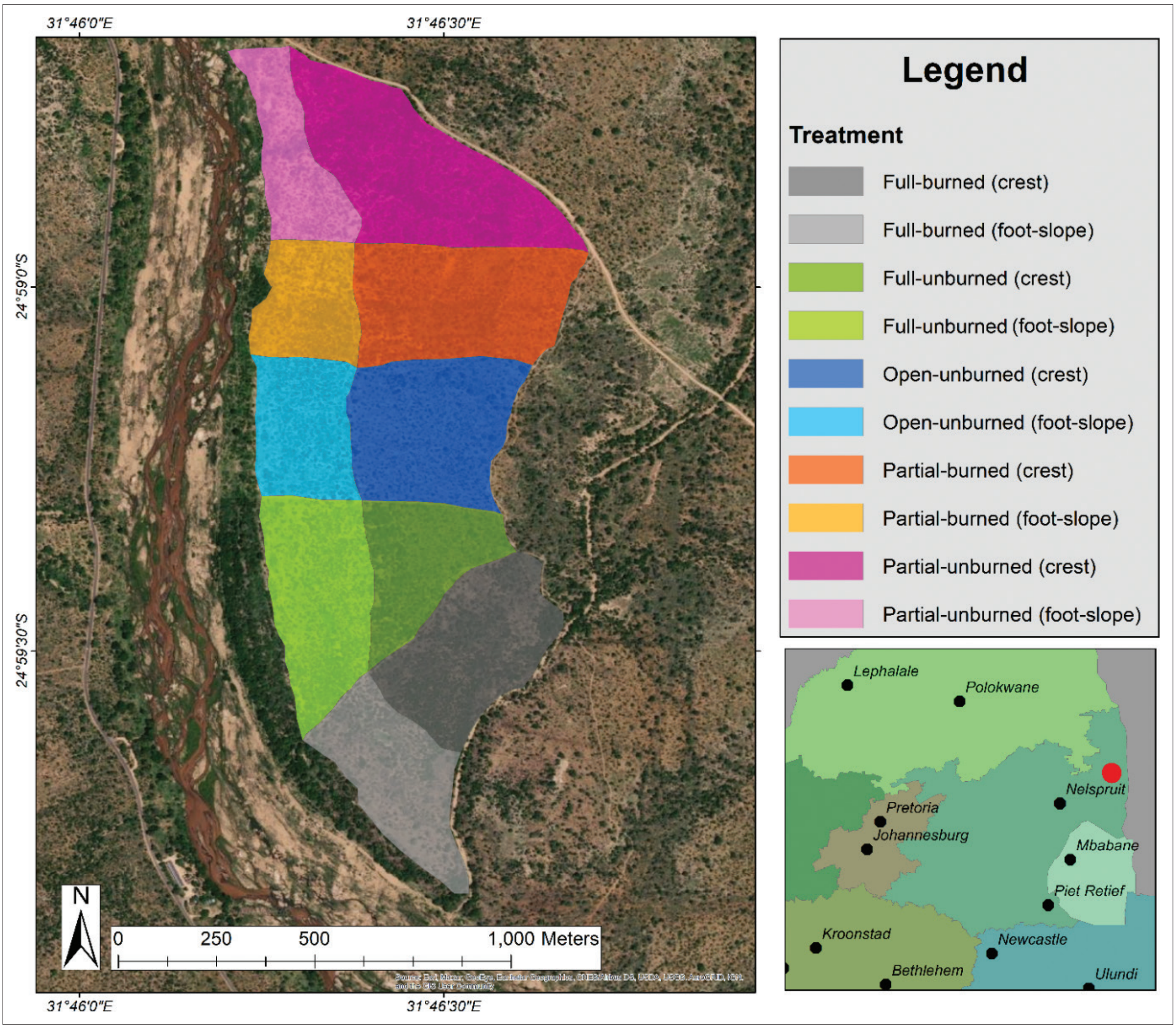
There is also a paucity of information, if any, assessing different dimensions of the interactive relationship between herbivory, tree species and soil properties in savannas (Siebert & Eckhardt 2008; Smit et al. 2010; Van Langevelde et al. 2003). The effects of herbivores and variations in tree species have been studied separately but rarely in combination or in relation to soil (Abdalla et al. 2018; Holdo & Mack 2014). Moreover, all the researchers used a single tree canopy spatial location as a limiting zone for comparative purposes and ignore the existence of projections that are smaller or bigger than tree canopies (i.e. radial distance-based projections, under the canopy, near to canopy and far from canopy). Most studies are short-term and are not highly structured to provide additional value for long-term outcomes. The main finding of these studies is that changes in herbivory influence vegetation structure and composition (Little et al. 2017). There is a need for studies investigating and addressing the medium to long-term effects of mammalian herbivores and trees on savanna soils and how effective exclosures and vegetative cover are in causing or influencing changes in savanna soils. Therefore, a better understanding of underlying mechanisms exploring the impact of different woody species and herbivores on savanna soil and ecosystem function is needed. In this article, we address the question whether the effects of vegetation species and herbivores affect soil properties in a semi-arid savanna. To help address this question, a study was undertaken to determine the individual and interactive effect of 20 years of herbivory (full exclosure and open access area), dominant tree species (*Combretum apiculatum* and *Grewia bicolor*) and radial distance-based canopy cover projections (under, besides and outside canopy) on the selected soil chemical (total nitrogen [TN], total carbon [TC], pH, EC, exchangeable calcium (Ca), magnesium (Mg), potassium (K) and sodium (Na), cation exchange capacity [CEC] and available phosphorus [P]) and biological properties (total microbial activity) of Nkuhlu exclosures in Kruger National Park.

Research methods and design

Study area description

The study was carried out in the Nkuhlu large-scale, long-term exclosures situated in the southeastern region of the Kruger National Park of South Africa (Figure 1), approximately 18 km from Skukuza (24°59′10″ S, 31°46′24.6″ E). The area receives approximately 550 mm of precipitation on an annual basis and the average temperature is 21.9 °C, with temperatures dropping and rising to an average of 5.7 °C and 32.6 °C during the winter and summer seasons, respectively. The exclosures were established in 2002 on the premise that by virtue of their size, large and tall mammalian herbivores (mainly elephants and giraffes) are the most significant drivers of change and maintenance in environments they inhabit (O'Keefe & Alard 2002; Scogings 2014). They cover roughly 139 ha of land that has been sub-divided into three separate units, namely: (1) full exclosure, a 70 ha fully fenced site where animal entry is prohibited, split into a burnt and unburnt plot (2) partial exclosure, a 44 ha partially fenced site where large and tall animals, particularly elephants and giraffes are not permitted, split into a burnt and unburnt plot (3)open access area (control site), a 25 ha unfenced area where all animals are allowed (Jonsson et al. 2010). No burning takes place in the control site.

The current study was conducted in the unburnt plots of full exclosure and control site. Nkuhlu exclosures are situated in sloping land that extends from the crest to the Sabie River channel, which is situated on the foot-slope and/or valley bottom (Janecke 2020; O'Keefe & Alard 2002). Soils within the crest and foot-slope vary between shallow sandy soil directly overlying hard granite rock and deep sandy to sandy loam Na-dominated soil, respectively (Khomo & Rogers 2005; Scogings et al. 2014). The World Reference Base (WRB) classifies the shallow sandy soil on the crest as Leptosol, while the South African system (Soil Classification Working Group [SCWG]2018) classifies them as Mispah and shallow Glenrosa. The deep, Na-rich duplex soil on the foot-slope can be classified as Luvisol in the WRB or Oakleaf and Montagu soils according to the South African Soil Classification system (Siebert & Eckhardt 2008). This paper will only consider the crest. According to Scogings, Hjältén and Skarpe (2011), the most common woody species throughout the Kruger National Park, including the crest of Nkuhlu exclosures include: (1) *C. apiculatum*, (2) *Combretum hereroense*, (3) *G. bicolor*, (4) *Grewia flavescens*, (5) *Dichrostachys cinerea* and (6) *Euclea divinorum*. This article only considers the *C. apiculatum* and *G. bicolor* species (Figure 2). These two species were selected on the basis that they are among the most abundant in the study area and the fact that their composition and vegetation structure is highly influenced by herbivory (Bakker et al. 2016). Most mammalian herbivores, particularly elephants and giraffes include substantial quantities of *C. apiculatum* and *G. bicolor* in their diets by ingesting large amounts as they find them palatable (Seloana et al. 2018). Also, elephants alter the composition and vegetative structure that influences soil properties by congregating under trees, stripping them off and discarding the leaves on the savanna floors.



Source: Adopted and Malongweni, S.O. & Van Tol, J., 2022, 'Fire, herbivores, and vegetation type shape soil biochemistry in sodic patches of a semi-arid savanna ecosystem', *Land* 11(8), 1148. https://doi.org/10.3390/land11081148

FIGURE 1: Study site location (red dot) in the Kruger National Park, South Africa, and map of the Nkuhlu exclosures showing the treatments where the field experiment was conducted.

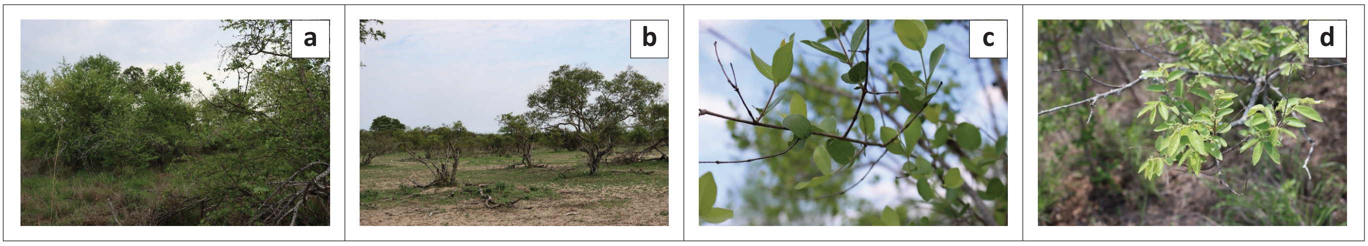


FIGURE 2: Typical patchy distribution of vegetation (a: full exclosure, b: Open access area [control site]) and woody species (c: *Combretum apiculatum*, d: *Grewia bicolor*) in Nkuhlu exclosure of the Kruger National Park, South Africa.

For each of these two tree species, soil samples were collected at three radial distances from the tree trunk namely: (1) Zone A, tree centre (beside tree trunk) – below canopy, besides the trunk of the tree; (2) Zone B, canopy edge – along the edge of the tree crown and (3) Zone C, outside canopy – open grassland zone or savanna patches in the inter-canopy space.

Experimental design

The experiment was a 3 × 2 × 2 factorial design with different combinations of two herbivore utilisations levels (open access and full exclosure), two woody species (*C. apiculatum* and *G. bicolor* species) and three sampling zones (under the canopy, edge of canopy and far from canopy). Five soil samples were collected from three points within each sampling site. As a result, each sampling area had three composite samples (replicates), each comprising five sub-samples randomly collected at a sampling depth of 10 cm. Therefore, a total of 36 samples were collected from Kruger National Park. Subsequently, the collected soil samples were air-dried, mechanically crushed and pulverised manually using a 2-mm sieve. Soils sampled for the purpose of microbial analysis were collected a sampling depth of 5 cm and immediately transferred into sampling bags and stored at approximately 4 °C in a cooler box filled with ice before passing them through a < 2-mm sieve. These soil samples were immediately analysed as Wallenius et al. (2010) reported that even short delays may impact the results.

Soil biochemical analyses

Dry combustion method using an automatic highly sensitive CN analyser was used to measure TN and TC (Bremner & Mulvaney 1982). Determination of pH of soil samples was carried out using a glass electrode pH meter at a soil-to-water ratio 1:2.5 (w/v) by mixing 5 g of air-dried soil with 25 mL deionised water (McLean 1982). The molybdenum blue method of Olsen and Sommers (1982) was used for measuring available P, and extraction was carried out using sodium bicarbonate ($NaHCO_3$). Ammonium acetate (NH_4Oac) was used for extracting exchangeable cations (Ca^{2+}, Mg^{2+}, K^+ and Na^+), which were quantified using the inductively coupled plasma spectrometer (ICP-MS). The values for these elements were used to calculate the cation exchange capacity (CEC). The fluorescein diacetate (FDA) hydrolysis method was used to measure total microbial activity in soil as described by Schnürer and Rosswall (1982).

Statistical analyses

Statistical analyses were completed with JMP statistical software (version 16.0, SAS Institute Inc.). Analysis of variance (ANOVA) was used to analyse treatment effects by assessing whether TC, TN, soil pH, exchangeable Ca, Mg, K and Na, CEC, available P and total microbial activity differed among the three treatments (exclosure, woody species and canopy cover based radial distance). Fischer's protected least significant difference was used for mean separation at an alpha level of 0.05.

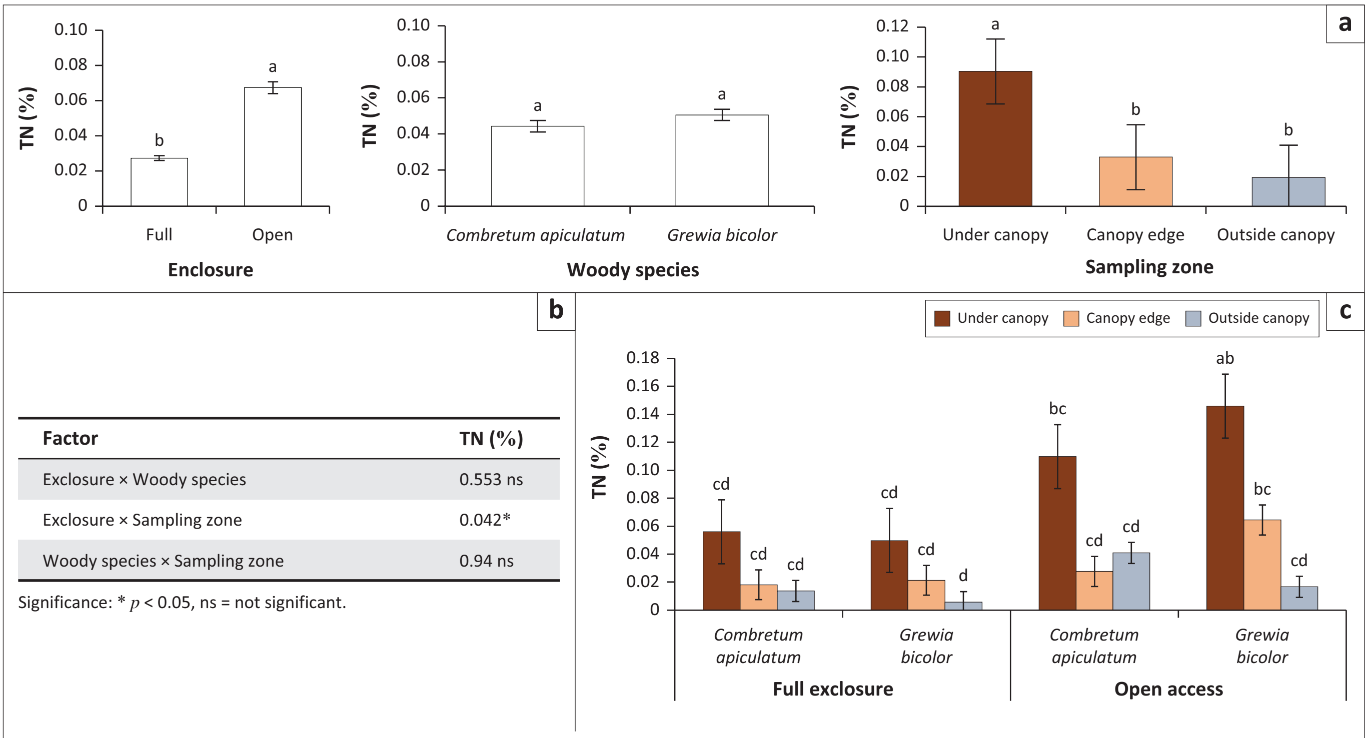
Ethical considerations

Ethical clearance to conduct this study was obtained from the University of the Free State Environment and Biosafety Research Ethics Committee (no. UFS-ESD2021/0192/21]).

Results

Total carbon and total nitrogen

The results of the study revealed that there were statistically significant differences in TN and TC ($p < 0.05$; Figure 3a and Figure 4a) among the different exclosures and sampling zones, with the open access area and samples under tree canopy having higher TN and TC than the other treatments. Samples collected under tree canopies had significantly higher TN and TC than those collected along the edge of the tree crown and in open grassland zones (Figure 3a and Figure 4a). However, there were no significant differences in TN and TC between samples collected on the edge as well as away from canopy. The two species did not independently cause statistical changes in total N.

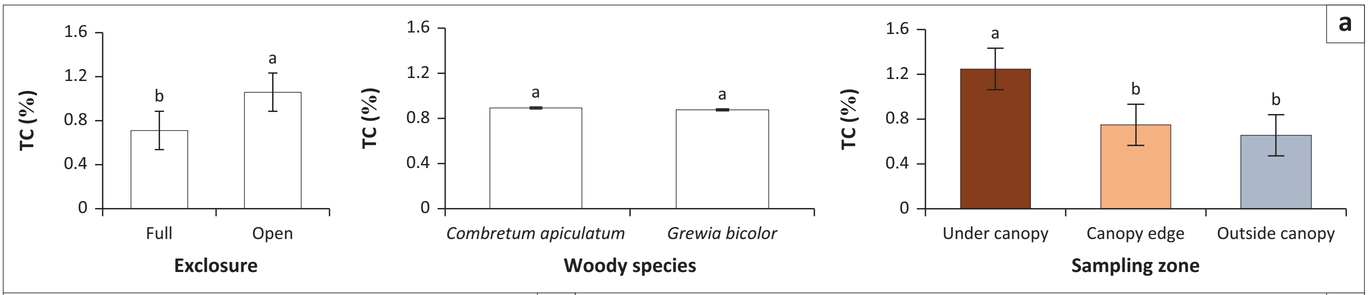


Factor	TN (%)
Exclosure × Woody species	0.553 ns
Exclosure × Sampling zone	0.042*
Woody species × Sampling zone	0.94 ns

Significance: * $p < 0.05$, ns = not significant.

TN, total nitrogen.

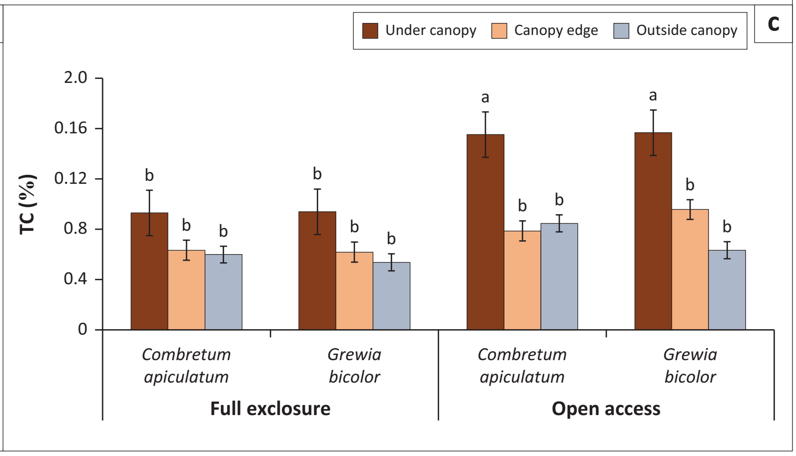
FIGURE 3: The main and interactive effect of herbivores, woody species and sampling zone on soil TN (a: independent effect, b: two-way interactive effect and c: three-way interactive effect).



b

Factor	TC (%)
Exclosure × Woody species	0.075ns
Exclosure × Sampling zone	0.040*
Woody species × Sampling zone	0.757ns

Significance: * $p < 0.05$, ns = not significant.



TN, total nitrogen.

FIGURE 4: The main and interactive effect of herbivores, woody species and sampling zone on soil TC (a: independent effect, b: two-way interactive effect and c: three-way interactive effect).

The two-way interaction between exclosure and sampling zone had a significant effect on TN and TC (Figure 3b and Figure 4b). For *G. bicolor* in the open access site, it was observed that samples collected under canopy had high TN; however, there were no significant differences between the samples under canopy and those along the edge of the tree crown, as well as between the canopy edge and the open grassland zone. For both woody species, it was also observed that the samples collected under tree canopies in the control site (i.e. with higher herbivore biomass) had the higher TC than all the other treatments (Figure 4c).

Exclosure, woody species and sampling zone did not interactively cause statistical changes in TN for all *C. apiculatum* treatments and *G. bicolor* in the full exclosure, but samples outside canopy of *G. bicolor* in the full exclosure had significantly lower TN than the canopy edge of *G. bicolor* and the canopy of *C. apiculatum* in the open access area (Figure 3c). Herbivory, tree species and canopy-based radial distance did not interactively cause statistically significant differences in TC in the full exclosure, but samples collected under canopy of both species in the control site had higher TC than those sampled in the full exclosure (Figure 4c).

Soil pH

Soil pH of all the sampling areas showed that they are slightly acidic. However, exclosure and sampling zone had a significant main effect on soil pH ($p < 0.05$; Table 1). The full exclosure resulted in significantly higher pH than the control site where herbivores were permitted. Areas under tree canopies had significantly lower pH than tree crown edges and open grassland zones. There were no significant differences in pH between samples collected on the edge of canopy and those collected in the open grassland zone. Woody species also did not have a significant effect on soil pH.

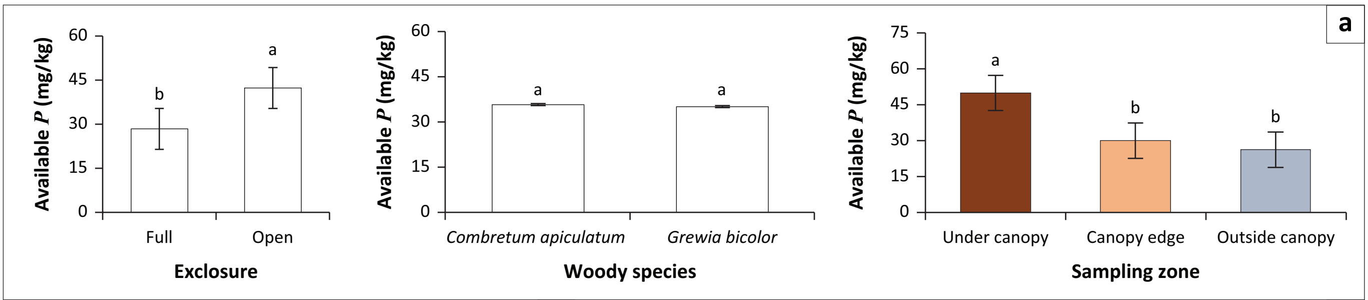
Exchangeable cations and cation exchange capacity

Data regarding exchangeable cations revealed that there were statistical differences in exchangeable K and Mg between the open access area and full exclosure (Table 1). The open access had higher exchangeable K and lower exchangeable Mg than the full exclosure. Exchangeable Na and Ca were not statistically influenced by exclosure. Woody species did not have a significant effect on exchangeable cations (Ca^{2+}, Mg^{2+}, Na^{+} and K^{+}). Sampling zone caused significant changes on exchangeable K and Ca but not Na and Mg, with samples collected under tree canopy having higher exchangeable K and Ca than both the area on the edge and outside of canopy. There were, however, no differences in exchangeable K and Ca between samples on the edge of canopy and those sampled far away from the crown. Cation exchange capacity was significantly affected by exclosure and woody species but not the sampling zone, with the open access area having higher CEC than the full exclosure. Furthermore, *G. bicolor* had significantly lower CEC than *C. apiculatum*. We also found that the two-way interaction between exclosure and woody species had a significant influence on exchangeable Mg and CEC but not exchangeable Ca, Na and K. Additionally, exchangeable K and Ca were significantly influenced by the two-way interaction between exclosure and sampling zone but not on other exchangeable cations and CEC. The interaction between woody species and sampling zone as

TABLE 1: The main and interactive effect of herbivores, woody species and sampling zone on pH, exchangeable cations and cation exchange capacity.

Factor	pH	K (mg/kg)	Ca (mg/kg)	Na (mg/kg)	Mg (mg/kg)	CEC
Variable						
Exclosure						
Full	6.2a	64.2b	1117.5a	304.2a	259.3a	1.6b
Open access	5.9b	99.1a	1305.7a	291.4a	150.6b	2.8a
Woody species						
Combretum apiculatum	6.1a	75.1a	1236.1a	296.1a	201.9a	2.6a
Grewia bicolor	6.1a	88.2a	1187.1a	299.5a	208.1a	1.8b
Sampling zone						
Under canopy	5.9b	113.3a	1506.3a	278.8a	201.1a	2.3a
Canopy edge	6.2a	74.3b	1066.5b	312.4a	204.6a	2.2a
Outside canopy	6.2a	57.3b	1062.1b	302.3a	209.2a	2.1a
***p*-value**						
Main effect						
Exclosure	0.043*	0.046*	0.512ns	ns	0.0001*	0.045*
Woody species	0.5914ns	0.23ns	0.599ns	0.103ns	0.25ns	0.049*
Sampling zone	0.048*	0.0005*	0.0008*	0.336ns	0.752ns	0.426ns
Interaction						
Exclosure × Woody species	0.480ns	0.575ns	0.429ns	0.374ns	0.003*	0.013*
Exclosure × Sampling zone	0.966ns	0.006*	0.042*	0.249ns	0.708ns	0.425ns
Woody species × sampling zone	0.861ns	0.630ns	0.180ns	0.683ns	0.485ns	0.659ns
Exclosure × Woody species × Sampling zone	0.964ns	0.753ns	0.580ns	0.949ns	0.497ns	0.328ns

ns, not significance; K, potassium; Ca, calcium, Na, sodium, Mg, magnesium; CEC, exchangeable cations and exchange capacity.
Means with different letters for the same factor within the column are significantly different ($p < 0.05$).
* $p < 0.05$.



b

Factor	TN (%)
Exclosure × Woody species	0.075ns
Exclosure × Sampling zone	0.040*
Woody species × Sampling zone	0.756ns

Significance: * $p < 0.05$, ns = not significant.

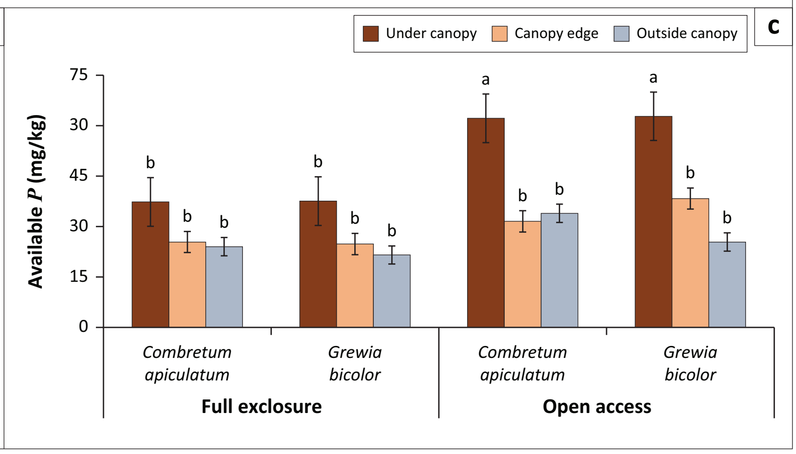


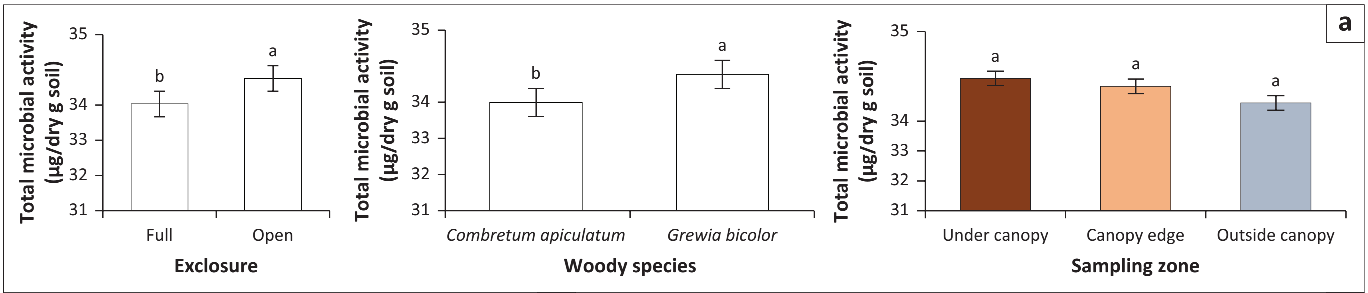
FIGURE 5: The main and interactive effect of herbivores, woody species and sampling zone on soil available P (a: independent effect, b: two-way interactive effect and c: three-way interactive effect).

well as the three-way interaction between exclosure, woody species and sampling zone did not cause any statistical changes in exchangeable cations and CEC.

Available phosphorus

Exclosure had a significant main effect on available P ($p < 0.05$; Figure 5a), with the open access area having higher available P than full exclosure. All the samples collected besides the tree trunk had high available P relative to other sampling zones. Species did not independently cause statistical changes in available P, nor were there any significant interactions between species and exclosure, as well as between species and sampling zone.

The two-way interaction between exclosure and sampling zone caused statistical changes in available P, with areas under *C. apiculatum* and *G. bicolor* in the open access area



b

Factor	Total microbial activity
Exclosure × Woody species	0.022*
Exclosure × Sampling zone	0.513ns
Woody species × Sampling zone	0.313ns

Significance: * $p < 0.05$, ns = not significant.

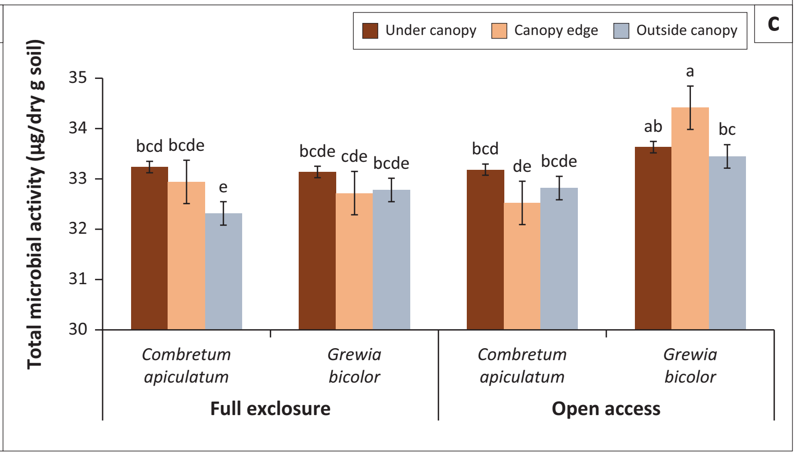


FIGURE 6: The main and interactive effect of herbivores, woody species and sampling zone on total microbial activity (a: independent effect, b: two-way interactive effect and c: three-way interactive effect).

having much higher available P than all the other treatments (Figure 5b and c). In the full exclosure, it was observed that the interaction between exclosure, woody species and sampling zone did not have any influence on availability. In the open access area, the canopy edge of G. bicolor had significantly higher available P than the area outside of canopy, however, there were no statistical differences in available P between the canopy edge and area under canopy as well as between the area under canopy and the open grassland zone.

Total microbial activity

The results of the study revealed significant main and interactive effects of exclosure and species on total microbial activity ($p < 0.05$; Figure 6a, Figure 6b and Figure 6c). The control site (i.e. with higher herbivore biomass) had significantly higher microbial activity compared to the full exclosure (i.e. herbivores not permitted). Sampling zone did not cause any significant changes in microbial activity. However, *G. bicolor* had significantly higher microbial activity than *C. apiculatum* (Figure 6a). The interaction between exclosure and woody species caused statistical changes in total microbial activity. The canopy edge of *G. bicolor* in the open access area had higher microbial activity than all the sampling zones of both *C. apiculatum* and *G. bicolor* in the full exclosure.

It was also noticed that all the samples collected under and on the edge of *G. bicolor* crown in the open access area had higher microbial activity than the area outside of canopy, with areas under canopy being not significantly different from canopy edge and the open grassland zone not being significantly different from the area under canopy (Figure 6c). Samples collected in outside the canopy of the *C. apiculatum* tree had the lowest microbial activity; however, it was not significantly different from other treatments, except for samples collected under *C. apiculatum* in both the full exclosure and open access area as well as all the sampling zones of *G. bicolor* in the control site.

Discussion

Effect of herbivory on soil biochemical properties

Our experimental study revealed that, with the exceptions of exchangeable Ca and Na, herbivory resulted in prominent changes in all the biochemical properties under investigation, indicative of the crucial role played by animals in maintaining savanna ecosystem function. The exclusion of herbivores caused significant increases in soil pH and exchangeable Mg, while the presence of herbivores led to significant increases in TN and TC, available P, microbial activity, exchangeable K and CEC. Our results coincide with the findings of Abdulahi et al. (2006) who reported higher TN, organic matter and soil P status in herbivore grazing sites of an African savanna in Eastern Ethiopia. The increase in TN and C, available P, microbial activity, CEC and exchangeable K could be attributed to the continuous deposition of animal excreta (Malongweni & Van Tol 2022). In this regard, in the full exclosure where the entry of herbivores is prohibited, soil improvement is a result of nutrient returns from litterfall. However, in the open access area (i.e. where herbivores are permitted), there will be higher nutrient returns because of defoliation, debranching of trees by browsing herbivores and the deposition of animal excrement into the soil (Abdulahi et al. 2016; Holdo & Mack 2014; Mordelet, Abbadie & Menaut 1993).

The results of the study also indicated that herbivore exclusion increased soil pH and exchangeable Mg. These results correspond with the findings of Abdulahi et al. (2016) who reported significantly higher values of soil pH and Mg in grazing sites of a semi-arid Ethiopian savanna. Abdulahi et al. (2016) claim that the increase was likely because of higher levels of CEC. Cation exchange capacity of the soil generally increases with soil pH because of a higher proportion of hydroxide (OH^-) ions present in the soil (Brady & Weil 2022). Although a high soil pH is likely to cause an increase in CEC, the results of our study indicated an inverse relationship between pH and CEC, with the full exclosure having a significantly lower pH and high CEC than the open access area. Nonetheless, higher CEC in the full exclosure was accompanied by a high concentration of exchangeable Mg. This may be caused by a decrease in the number of hydrogen (H^+) ions caused by soil pH increases.

Effect of woody species on soil biochemical properties

The main influence of the two tree species did not result in any changes in most of the soil properties under investigation in our study. Significant changes were only observed in soil microbial activity and CEC, with *G. bicolor* having a significantly higher microbial activity compared to *C. apiculatum*. This could be because in Kruger National Park and many other semi-arid African savannas, *G. bicolor* is considered one of the most important forages during the dry season (Chira & Kinyamario 2009; Le Houerou 1980; Siebert & Eckhardt 2008). Mammalian herbivores tend to congregate around it as they find it more palatable than *C. apiculatum* (Baumer 1983; Brink 2007; Le Houerou 1980). During grazing, large herds of plant eaters deposit significant amounts of urine and dung under the *G. bicolor* canopy. Dung and urine harbour constituents that promote microbial activity (Holdo & Mack 2014). According to Chira and Kinyamario (2009), *G. bicolor* is particularly enjoyed by elephants. Elephants tend to break down *G. bicolor* tree branches when foraging. But this species is known to resprout rapidly. New leaves are often of better quality than the previously browsed leaves because the N and P content of new leaves is often higher. Also, the number of leaves increases after defoliation. Improved forage quality and a higher number of leaves promote microbial activity because of better and higher nutrient returns (Schroder 2021).

Despite having a high microbial activity, *G. bicolor* had significantly lower CEC than *C. apiculatum*. These results do contradict the finding of Juhos et al. (2021) who reported a strong linear correlation between CEC and microbial activity. According to Juhos et al. (2021), linear correlation between CEC and microbial activity is governed by soil organic matter. Soils with high organic matter tend to also have high CEC because organic matter components of soil have negatively charged sites on their surface and these sites attract and exchange positively charged cations (Brady & Weil 2022). *G. bicolor* does well on rich, shallow sandy soils, occasionally on red clays (Brink 2007), whereas *C. apiculatum* commonly occurs in sandy soils but disappears completely on clayey soils (Gertenbach 1983). In the opinion of Brady and Weil (2022), increasing the clay content of a sandy soil will help increase its CEC. However, despite *C. apiculatum* not being able to grow in clayey patches on the crest of the Nkuhlu exclosures in the Kruger National Park, soil samples collected at a radial distance from its canopy had much higher CEC than corresponding *G. bicolor*.

Effect of canopy cover on soil biochemical properties

Our results show that the TN, TC, available P and exchangeable Ca and K of the savanna soils were much higher under trees than at the canopy edge and open grassland zones. However, there were no differences between soil samples collected on the edge of canopy, and these collected outside the tree canopy. Several other researchers have reported similar higher values in soil properties under tree canopies than in open grassland as found in this study (Aweto & Dikinya 2003; Holdo & Mack 2015; Isichei & Moughalu 1992; Malongweni & Van Tol 2022). Higher TN, TC, available P and exchangeable Ca and K under the canopies of the two tree species is presumably because of the effect of litter addition to soil under the canopies, which has resulted in improved fertility in soil under the canopies relative to levels in soil outside the canopies (Aweto & Dikinya 2003; Isichei & Moughalu 1992). It could also be a consequence of microclimatic conditions under tree crowns, such as lower temperatures, reduced light availability and higher soil moisture or combinations of the above. The consequence of temperature reductions under tree canopies is a slower rate of mineralisation (Holdo & Mack 2014; Mordelet et at. 1993). Moreover, reductions in light availability through shade often increase soil nutrient concentrations (Ludwig et al. 2008). Also, as soil samples under the canopy were collected besides the tree trunk, the higher concentration of tree roots near the base of the trees may have had the effect of promoting the build-up of nutrients in that area (Holdo & Mack 2014; Isichei & Moughalu 1992; Malongweni & Van Tol 2022). Tree roots naturally decay on their own thus resulting in improved soil nutrition. 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 TN and TC under tree canopies (Malongweni & Van Tol 2022).

This study also revealed that there were no differences in pH between samples collected on the canopy edge and those collected outside canopy; however, these two canopy positions had significantly higher pH than the area next to the tree trunk under the tree crown. It is possible that without crown cover, nutrients on the canopy edge and outside canopy were easily leached from the soil during rainfall. This result supports the assertion of Brady and Weil (2022) that high pH is often caused by excess leaching. Furthermore, since the soil on the edge and outside the tree canopies dries out more because it is exposed to direct solar radiation and this results in the shrinkage of clay colloids, thereby increasing soil pH (Aweto & Dikinya 2003).

Interactive effect of herbivory, woody plant species and canopy cover on soil biochemical properties

The interactive effects of exclosure, woody species and sampling zone had a significant effect on all studied properties except exchangeable Na. Areas under canopy for both *G. bicolor* and *C. apiculatum* species in the open access area resulted in significant increases in TC as well as available P. These results reinforce previous findings from other studies as well as our own work on canopy-herbivory interactions in Kruger National Park (Holdo & Mack 2014; Ludwig et al. 2004; Malongweni & Van Tol 2022). Increases in TC and available P caused by the three-way interaction between herbivores, woody species and sampling zone could be primarily caused by herbivore excreta as well as the effect of tree litter on soil organic matter (Holdo & Mack 2014; Malongweni & Van Tol 2022). Organic matter production by litterfall and animal waste and its slow rate of mineralisation under canopies is because of reductions in temperatures there (Isichei & Moughalu 1992). It could also be because of direct biotic effects of trees such as nutrient transport by plant roots from rooting zone to tree canopies (Schroder 2021).

All the trees in the full exclosure had higher pH than those in the open access area, with the canopy edge having the highest pH than other sampling zones. These results contradict the assertion of Ndlela and Schimidt (2016) that mammalian herbivores cause an increase in soil pH of savannas because their excreta, particularly urine, is alkaline. In our study, the reason why the presence of herbivores resulted in a significant decrease in soil pH within the open access area is unclear and we found no evidence to support it.

We also found that *G. bicolor* in the open access area had significantly higher microbial activity than other treatments, with the canopy edge having the highest activity. However, there were no significant differences in microbial activity between soil samples collected under canopies and those collected on the edge of the tree crown. This could be because *G. bicolor* regrows quickly after defoliation and/or after being consumed by herbivores (Chira & Kinyamario 2009). This leads to the growth of more leaves, with better quality and greater canopy width. This leads to higher nutrient returns and reduced evaporation losses from the crown-covered surface, which then make the soil prone to microbial metabolism (Chira & Kinyamario 2009; Isichei & Moughalu 1992; Schroder 2021).

In the open access area, the sampling zone besides the tree trunk of both woody species had higher exchangeable K and Ca compared to the full exclosure (other sampling zones). This could be because of urine and dung deposition into the soil from grazing herds of herbivores that congregate under trees. Herbivore excreta improves exchangeable K and Ca by increasing the organic matter content. According to Brady and Weil (2022), organic matter contains several essential nutrients, including K and an increase in soil organic matter content increases the number of colloidal sites for the exchange of cations. This is why from the results of our experiment, it was observed that CEC in the open access area, particularly under tree crown, had much higher CEC than the sampling zones away from canopy and in the full exclosure.

Conclusion

From the findings of our study, it can be concluded that the retaining scattered woody plants in a semi-arid savanna of the Kruger National Park have been effective in improving of soil nutrient enrichment and the areas under woody plants were in a better condition than the open grassland zones. This is especially true with regard to soil TN, TC, available P, as well as exchangeable K and Ca, which are significantly higher under tree canopies compared to areas outside canopy. It can be also concluded that the herbivores play an important role in improving and maintaining soil fertility in savanna ecosystems; hence the control site caused significant increases in TN, TC, available P, microbial activity, CEC and exchangeable K compared to the full exclosure where the entry of herbivores was prohibited. Similarly, this study confirmed that both woody *G. bicolor* and *C. apiculatum* species had a positive effect on soil fertility enrichment. This is especially true with regard to soil microbial activity and CEC. Therefore, herbivory and woody species are necessary in promoting improved soil health and sustaining soil biodiversity in savanna ecosystems.

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Competing interests

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

Authors' contributions

Both authors contributed to the conception and design of the study. Material preparation, data collection and analysis were performed by S.O.M. J.v.T. supervised the project. The final manuscript has been read and approved by both authors.

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Data availability

The data sets generated during the current study are available from the corresponding author upon reasonable request.

Disclaimer

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