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## Research article

### Grazing in a megagrazer-dominated savanna does not reduce soil carbon stocks, even at high intensities

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Recent studies suggest that wild animals can promote ecosystem carbon sinks through their impacts on vegetation and soils. However, livestock studies show that intense levels of grazing reduce soil organic carbon (SOC), leading to concerns that rewilding with large grazers may compromise ecosystem carbon storage. Furthermore, wild grazers can both limit and promote woody plant recruitment and survival on savanna grasslands, with both positive and negative impacts on SOC, depending on the rainfall and soil texture contexts. We used grazing lawns in one of the few African protected savannas that are still dominated by megagrazers (> 1000 kg), namely white rhinoceros *Ceratotherium simum*, as a model to study the impact of prolonged and intense wild grazing on SOC stocks. We contrasted SOC stocks between patches of varying grazing intensity and woody plant encroachment in sites across different rhino habitat types. We found no differences in SOC stocks between the most- and least grazed plots in any of the habitats. Intermediately grazed plots, however, had higher SOC stocks in the top 5 cm compared to most and least grazed plots, but only in the closed-canopy woodland habitat and not in the open habitats. Importantly, we found no evidence to support the hypothesis that wild grazing reduces SOC, even at high grazing intensities by the world's largest megagrazer. Compared to the non-encroached reference plots, woody encroached plots had higher SOC stocks in soils with low clay content and lower SOC stocks in soils with high clay content, although only in the top 5 cm. Accordingly, our study highlights that wild grazers may influence SOC indirectly through their impact on tree-grass ratios in grassy ecosystems. Our study thus provides important insights for future natural climate solutions that focus on wild grazer conservation and restoration.

Keywords: fire, grazing impact, rewilding, soil carbon, white rhinoceros, woody encroachment



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## Introduction

Large-bodied herbivores play crucial roles in ecosystem and Earth system functioning (Cromsigt et al. 2018, Schmitz et al. 2018, Hyvarinen et al. 2021, Malhi et al. 2022). Their impacts on vegetation, nutrient dynamics and fire regimes influence ecosystem carbon dynamics with consequences that potentially scale up to the global climate (Schmitz et al. 2014, 2018). Large-bodied grazers can for instance redistribute aboveground carbon into belowground pools through grazing-associated defoliation, trampling and dung deposition (Kristensen et al. 2022). They may also promote or hinder woody plant establishment (O'Connor et al. 2014, Voysey et al. 2021), thus influencing the quantity and quality of organic matter entering the soil through litter input and root exudation (Jackson et al. 2002, Li et al. 2016). In addition, grazers may reduce the intensity and frequency of fires, which may strongly affect carbon sequestration in fire-prone systems such as savannas and grasslands (Pellegrini et al. 2018, Li et al. 2021). Several authors have suggested that the restoration of wild animal populations (i.e. rewilding) may be an effective natural climate solution by accelerating the carbon uptake of ecosystems (Schmitz et al. 2014, Cromsigt et al. 2018, Mahli et al. 2022), also referred to as 'animating the carbon cycle' (Schmitz et al. 2018, 2023). Quantifying the impacts of large grazers on SOC is thus key to understanding and predicting how their management and restoration can contribute to natural climate solutions in wild grassland and savanna systems (Cromsigt et al. 2018).

Recent meta-analyses from livestock systems show that grazing intensity, grass community composition, and the interaction between rainfall and soil texture strongly mediate the magnitude and direction of grazing effects on SOC (McSherry and Ritchie 2013, Tang et al. 2019, Lai and Kumar 2020). According to these studies, high to intermediate intensities of livestock grazing generally reduce SOC. Moreover, low intensity grazing in C3 grasslands may increase SOC, while even intermediate grazing intensity in C4 grasslands was shown to increase SOC, possibly reflecting grazing-induced increases in the fine and shallow roots of C4 grasses (McSherry and Ritchie 2013, Abdalla et al. 2018). Increasing rainfall tends to reduce the negative livestock effects on SOC on clay soils, while amplifying them on sandy soils (McSherry and Ritchie 2013). Furthermore, grazing influences on SOC are generally thought to decline with increasing soil depth due to the decrease of grass root biomass with soil depth (Dijkstra et al. 2021).

Despite the booming literature on the effects of domestic grazers on SOC (McSherry and Ritchie 2013, Jiang et al. 2020, Lai and Kumar 2020), few studies have looked at the impacts of wild grazers on SOC (Forbes et al. 2019). Studies that do look at wild grazer impacts mainly focus on temperate grasslands, while tropical and subtropical savannas, particularly those that are dominated by megagrazers (> 1000 kg) remain understudied (Forbes et al. 2019, Hyvarinen et al. 2021). Given that wild grazers comprise a broader variety of species and functional groups with a larger variation in body

mass and digestive physiology (Hofmann 1989), their effects on SOC are likely to differ from those of domestic grazers. Recent syntheses suggest that wild grazers positively influence SOC input and its persistence (Kristensen et al. 2022, Malhi et al. 2022). Andriuzzi and Wall (2018), however, emphasized the high levels of uncertainty around the impacts of wild grazers on SOC, and highlighted how intense grazing may reduce SOC input under certain conditions and/or accelerate its loss. Furthermore, Sitters et al. (2020) and Wigley et al. (2020) reported contrasting results of herbivore effects on SOC stocks in the same East African savanna system. The former found that the inclusion of African savanna elephant *Loxodonta africana* reversed the negative effects of cattle grazing on SOC, while the latter reported an increase in SOC when elephants and other large herbivores were excluded. Thus, the net effects of, particularly intense, wild herbivory on SOC stocks remain unclear.

Megagrazers represent a special case of wild grazers, constituting a unique guild of terrestrial grass-eating mammals with a very large body size (> 1000 kg). Extant species include the white rhinoceros *Ceratotherium simum*, the greater one-horned rhino *Rhinoceros unicornis* and the common hippopotamus *Hippopotamus amphibius*. Due to their size, they avoid top-down population control by large carnivores and can tolerate low quality forage due to their low mass-specific metabolic rate (Owen-Smith 1988). As a result, they can strongly shape savanna grassland heterogeneity, as they reduce grass height and create and maintain so-called 'grazing lawns' (Verweij et al. 2006, Cromsigt and Olf 2008, Waldram et al. 2008, Cromsigt and te Beest 2014). Grazing lawns are functionally distinct grassland types, characterised by a specific community of grazing-tolerant, often prostrate-growing stoloniferous grass species of high nutritional quality (Hempson et al. 2015) that only develop following prolonged (at least 2–3 years) continuous grazing (Cromsigt and Olf 2008). Furthermore, these grazing lawns provide an open habitat with reduced predation risk, attracting a wide range of mammalian herbivores (Hempson et al. 2015, le Roux et al. 2018). Thus, these lawns present a natural grazing intensity contrast where the grazing lawn is used by herbivores at relatively high intensities for prolonged periods compared to the tall grassland adjacent to the lawn. Although a variety of large and medium-sized mammalian short-grass grazers use and maintain lawns, previous work has shown that megagrazers, such as white rhino (rhino from hereon), significantly increase the proportion of grazing lawns in the landscapes where they occur at functional densities (Waldram et al. 2008, Cromsigt and te Beest 2014), i.e. the minimum population density which results either in a change or persistence of a given ecosystem state or process.

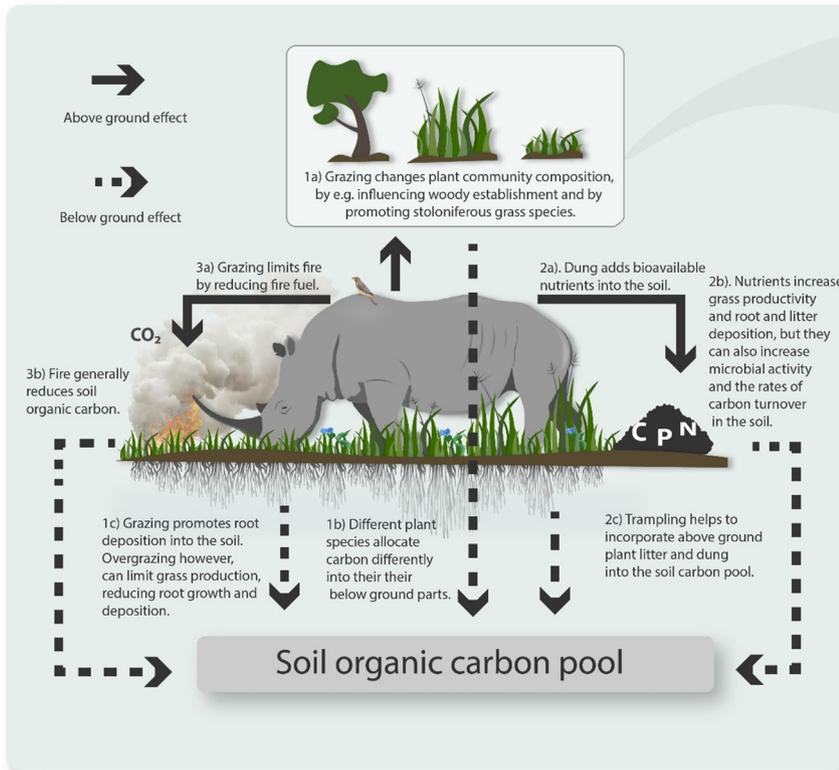
Grazing lawns also affect two other major drivers of SOC dynamics in savannas and grasslands: woody encroachment and fire. Megagrazers and other large, lawn-grazing herbivores kill and remove seedlings through trampling and browsing, thereby limiting woody plant establishment and recruitment on the lawns and adjacent areas (Hempson et al. 2015, Voysey et al. 2021). Others have highlighted that

grazing may also promote woody encroachment by removing grass biomass and thus reducing grass competition for woody plants (O' Connor et al. 2014, Case and Staver 2017). Based on a recent meta-analysis, woody encroachment can either increase or decrease SOC depending on the average rainfall of the system (Zhou et al. 2017). Woody encroachment effects on SOC tend to be negative in higher rainfall, but positive in lower rainfall areas (Jackson et al. 2002). Effects of woody encroachment also depend on the type of the encroaching woody species and on soil type; where positive effects on SOC are more likely for leguminous- compared to non-leguminous encroachers and on sandy soils compared to silty and clay soils (Jackson et al. 2002, Li et al. 2016). Grazing lawns further act as natural firebreaks, and the loss of rhino together with associated grazing lawns and other short grass patches, have been linked to increased fire extent and frequency at a landscape-scale (Waldram et al. 2008). Meta-analyses on fire impacts on SOC reveal that increasing fire frequency

and intensity reduce SOC stocks, the effect being mediated by rainfall seasonality, which possibly reflects the fire season (Pellegrini et al. 2018, Li et al. 2021). However, low intensity fires may promote SOC, likely through incorporation of partly-burnt plant biomass into the SOC pool (Findlay et al. 2022, Pellegrini et al. 2022) (Fig. 1A).

Hluhluwe-iMfolozi Park (HiP), South Africa, remains one of the last strongholds of white rhino with populations at functionally relevant densities, whereas populations in other core areas have significantly declined under the current poaching crisis (Nhleko et al. 2022). HiP is also known for its extensive grazing lawns that occur across the Park's strong rainfall, fire frequency and soil texture gradients (Cromsigt et al. 2017a). The size and spatial distribution of grazing lawns in the park varies from a few to hundreds of meters in diameter, and can thus occur in small patches or more uniformly across hectares (Cromsigt et al. 2017a). Because rhino and buffalo *Syncerus caffer* have constituted more than 75% of grazer biomass in

### (A) Mechanisms



### (B) Hypotheses

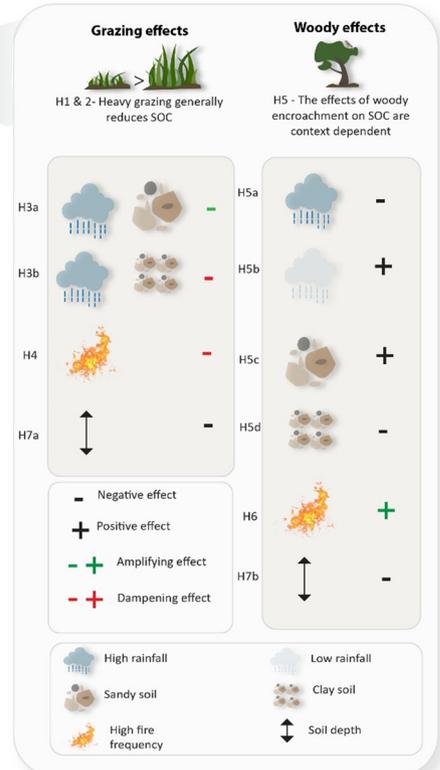


Figure 1. A conceptual framework illustrating (A) the mechanisms and (B) hypotheses for megagrazer impacts on soil organic carbon stocks (SOC). (A) Megagrazers can influence SOC through (1a) changing plant community composition and (1b) subsequently influencing how plants allocate carbon into their below ground parts. (1c) Grazing also promotes root deposition into the soil. (2a) Dung adds nutrients and labile carbon into the soil, (2b) which in turn can increase microbial activity and carbon turnover in the soil. (2c) Trampling helps to incorporate above ground plant litter and dung into the below ground SOC pool. Finally, because (3a) grazing competes with fire for grass biomass, grazing reduces the occurrence of fire, and (3b) fire associated carbon emissions. (B) We hypothesized that (H1&2) heavy grazing generally reduces SOC, (H3a) increasing rainfall amplifies the negative effects of grazing on SOC on sandy soils, but (H3b) dampens them on clay soils, and that (H4) increasing fire frequency dampens the negative effects of grazing on SOC. We also hypothesized that woody encroachment reduces SOC with (H5a) high rainfall and on (H5c) clay soils and increases SOC at (H5b) low rainfall and (H5d) on sandy soils. We further hypothesized that (H6) the positive woody effects on SOC to amplify with increasing fire frequency. We finally hypothesized the strongest grazing and woody encroachment effects on SOC in the top layer (0–5 cm) and the weakest effects in the bottom layer (15–30 cm).

the park for the last 3–4 decades (le Roux et al. 2017, 2018), and because buffalo are tall grass grazers that do not use grazing lawns, rhino are the predominant grazer on HiP's grazing lawns (Kleynhans et al. 2011). Thus, HiP and its grazing lawns make a convenient model to study the effects of consistent long-term grazing by megagrazers on SOC under a range of environmental conditions. HiP has also experienced long-term woody encroachment of its savanna grasslands (Wigley et al. 2010) and offers strong encroachment contrasts in addition to the grazing intensity gradients.

In addition to grazing lawns, rhino also use tall grass resources, where their habitat use is generally driven by seasonality. During the wet season, rhino concentrate on open grazing lawns occurring in the valley bottoms in HiP (Perrin and Brereton 1999, Shrader and Perrin 2006). At the beginning of the dry season, rhino increase their use of the closed-canopy tamboti *Spirostachys africana* woodland grazing lawns likely because the shaded grass remains greener for longer into the dry season. During the late dry season, when grazing lawns no longer yield sufficient biomass, rhino increase their use of grasslands on the hill slopes, dominated by palatable tall grasses such as *Themeda triandra* (Owen-Smith 1988). The use of this hillslope habitat is particularly high during the dry seasons of dry years, when rhino can spend 80–90% of their time there (Owen-Smith 1988). Rhino use this habitat much less during normal rainfall years when they focus on grazing lawns for at least half of their time (Arsenault and Owen-Smith 2011). During relatively wet years, rhino may even focus on open and woodland grazing lawns throughout the year (Shrader and Perrin 2006). Therefore, these three different rhino habitats reflect variation in the intensity of use by rhino: high- (open lawn habitat), medium- (woodland lawn habitat) and low-intensity of use (hill slope habitat).

In this study, we utilized the grazing lawns of HiP to investigate the effects of long-term, high intensity megagrazer-dominated grazing on SOC stocks and investigated if and how woody encroachment and fire frequency, both indirectly influenced by grazing lawn presence, further shape SOC stocks. Within each habitat, we expected 1) the most heavily grazed patches to have lower SOC stocks compared to nearby least-grazed patches. Within the open lawn and woodland lawn habitats, we expected 2) intermediately grazed grazing lawn edges to have higher SOC stocks compared to the most intensely grazed parts of the lawns and to least grazed areas next to the lawns. Across all habitats, we expected 3) increasing rainfall to reduce negative grazing effects on SOC on clay soils, while amplifying them on sandy soils. Across all habitats, we expected 4) SOC to decline with increasing fire frequency. Because grazing lawns and other intensely grazed patches are expected to burn less than adjacent tall grassland (Waldram et al. 2008), we further expected increasing fire frequency to reduce the SOC difference between the most grazed and least-grazed patches across habitats. In areas with low rainfall and coarse-textured soils, we expected 5) tall grass patches encroached by woody vegetation to have higher SOC stocks compared to nearby non-encroached tall grass patches and the opposite trend in areas with high rainfall and fine

textured soils. Across habitats, we also expected 6) increasing fire frequency to reduce the negative effects and increase the positive effects of woody encroachment on SOC. Finally, we expected 7) the strongest effects of grazing and woody encroachment in the top 5 cm soil, and the weakest in the lowest 15–30 cm soil (Fig. 1B).

## Material and methods

### Study area

Hluhluwe iMfolozi Park (HiP) (28°26'31"S, 32°13'46"E) covers ~960 km<sup>2</sup> in the north of the KwaZulu-Natal Province of South Africa. Elevation varies between 45 and 750 m a.s.l., with the highest areas in the north, and the lowest-lying valleys where the White and Black Mfolozi rivers meet in the south. Summer rainfall dominates, with 75% of the rain falling between October and March. Rainfall however varies strongly within the park, increasing with elevation, and from the southwest to the northeast. Around 550 mm year<sup>-1</sup> falls in the lower-lying southwestern parts, while the northern hills receive around 1000 mm/year on average (Howison et al. 2017). Fire is an integral part of the ecosystem, and is actively managed through prescribed burning, with an average fire return interval of 2–4 years (Archibald et al. 2017). However, spontaneous fires also occur regularly in the park, these increasing in frequency with rainfall (Archibald et al. 2017). The soil types and geology in the park are heterogenous, including strong variation in soil clay content (Howison et al. 2017).

HiP supports a mix of C4 grasses and C3 woody plants where Afromontane forests and grasslands cover hillslopes and summits above 250–300 m, while the lower lying areas support savanna grasslands and woodlands with varying tree and grass cover (Staver et al. 2017). These grasslands and woodlands are characterised by a mosaic of heavily-utilized grazing lawns and less intensely grazed tall grassland (Cromsigt and Olf 2008). Moreover, HiP has experienced strong woody thickening for at least four decades, resulting in a patchwork of grassland areas that remain open versus grassland areas that have been heavily encroached by predominately the leguminous *Dichrostachys cinerea* and *Vachellia karroo* (Wigley et al. 2010). Well-utilized grazing lawns in the park have shown very little woody encroachment compared to the surrounding tall grassland during the last decades (Voysey et al. 2021). HiP is one of the few places globally that still supports near intact mega- and large herbivore communities as well as large predator communities (Cromsigt et al. 2017b).

### Study design

We performed field sampling between October 2019 and March 2020, which coincided with higher than average annual rainfall (Howison et al. 2017). We selected 16 sites along rainfall, fire frequency and soil clay content gradients (Table 1, Fig. 2 for descriptions). Six sites were located in the open lawn habitat that rhino concentrate on during the wet

season and early dry season, five sites in the woodland lawn habitat that rhino focus on during the dry season and five sites in the hill slope habitat that rhino use during the late dry season, and especially in dry years.

To explore the effects of grazing on SOC stocks, we located natural grazing contrasts within each site based on either the presence of grazing lawns (in the open lawn and woodland lawn habitats) or on signs of grazing based on strong reductions in grass height and dung accumulation (in the hill slope habitat, which did not have grazing lawns). In the open lawn and woodland lawn habitats, we compared: (A) the center of the grazing lawn (the most grazed), (B) the edge of the grazing lawn representing a mosaic of lawn and non-lawn grass (intermediately grazed) and (C) the tall grassland outside the grazing lawn (the least grazed). In the hill slope habitat, which only contained tall grass, we considered patches with low grass biomass and higher dung accumulation to represent higher grazing intensity (the most grazed) compared to the immediately surrounding areas with high grass biomass and no dung accumulation (the least grazed). We refrained from adding a third grazing contrast level in this habitat, as the grazing intensity gradient did not allow for this. Thus, the open lawn and woodland lawn habitats each contained three grazing contrasts and the hillslope habitat only two.

To explore the effects of woody encroachment on SOC stocks, we included an additional woody-encroached tall grassland plot at each site to compare to the least grazed

tall grassland plots (plot D in Fig. 2). We selected woody-encroached grassland plots with common shrub encroachers in HiP (especially *Dicrostachys cinerea*) that were 1.5–2.0 m tall. Tall grass plots and woody-encroached plots consisted of similar grass biomass, grass species and amount of dung (Supporting information). We thus assumed the grazing impact to be similar, and minimal, for these two treatments and the main difference to be woody encroachment. We only added the woody-encroached plot to the open lawn habitat and the hillslope habitat sites, as the woodland lawn habitat did not have encroached areas.

In all 16 sites, we laid out one 2.5 × 2.5 m plot for each grazing and woody-encroachment level, resulting in four plots in each open lawn site, three in each woodland lawn site (no woody-encroached plot) and three in each hillside site (no intermediately-grazed plot). The distance between sites ranged between 0.25 and 37 km. The distance between sampling plots within each site was minimized (< 25 m between plots) to reduce variation in soil properties between plots and to allow for using 'site' as a blocking variable. In open lawn and woodland lawn habitats, we placed our sampling plots in areas without a visible slope, whereas in the hill slope habitat, plots were aligned along the slope contour, to reduce potential confounding effects of water runoff or other slope effects on SOC. We furthermore avoided areas with clear signs of termite presence and other disturbances such as wallows, latrines and large (> 1 m<sup>2</sup>) patches of bare ground.

Table 1. Proportion (%) of plots containing each grass and woody species and average soil clay content, fire frequency, rainfall pH and bulk density per habitat (For the environmental variables, standard deviations are expressed in brackets, and the letter in the superscript indicates significant differences ( $p < 0.1$ ) between the habitats,  $n = 54$ ).

Stoloniferous grass species	Open lawn habitat (%)	Woodland lawn habitat (%)	Hill slope habitat (%)
<i>Digitaria longiflora</i>	50	0	13
<i>Sporobolus nitens</i>	21	13	0
<i>Panicum coloratum</i>	29	0	0
<i>Urochloa mosambicensis</i>	13	0	0
<i>Dactyloctenium australe</i>	0	87	0
Bunch type grass species			
<i>Eragrostis superba</i>	29	0	27
<i>Eragrostis curvula</i>	13	7	47
<i>Bothriochloa insculpta</i>	13	0	0
<i>Panicum maximum</i>	38	73	0
<i>Themeda triandra</i>	4	0	67
<i>Sporobolus pyramidalis</i>	21	0	27
<i>Setaria sphacelata</i>	0	0	20
<i>Digitaria eriantha</i>	0	0	20
<i>Cymbopogon excavatus</i>	0	0	27
Woody plant species			
<i>Dicrostachys cinerea</i>	25	0	33
<i>Vachellia nilotica</i>	4	0	7
<i>Vachellia tortilis</i>	4	0	0
<i>Vachellia grandicornuta</i>	4	0	0
<i>Vachellia robusta</i>	4	0	0
Environmental variables			
Soil clay content (%)	35 ( $\pm 10$ ) <sup>a</sup>	17 ( $\pm 4$ ) <sup>b</sup>	51 ( $\pm 15$ ) <sup>c</sup>
Fire frequency	1 ( $\pm 1$ ) <sup>a</sup>	1 ( $\pm 1$ ) <sup>a</sup>	7 ( $\pm 2$ ) <sup>b</sup>
Rainfall (mm year <sup>-1</sup> )	562 ( $\pm 45$ ) <sup>a</sup>	581 ( $\pm 34$ ) <sup>a</sup>	712 ( $\pm 47$ ) <sup>b</sup>
pH	5.3 ( $\pm 0.5$ ) <sup>a</sup>	5.6 ( $\pm 0.4$ ) <sup>b</sup>	4.9 ( $\pm 0.2$ ) <sup>c</sup>
Bulk density 0–30 cm (g cm <sup>-3</sup> )	1.29 ( $\pm 0.18$ ) <sup>a</sup>	1.27 ( $\pm 0.16$ ) <sup>a</sup>	1.10 ( $\pm 0.23$ ) <sup>b</sup>

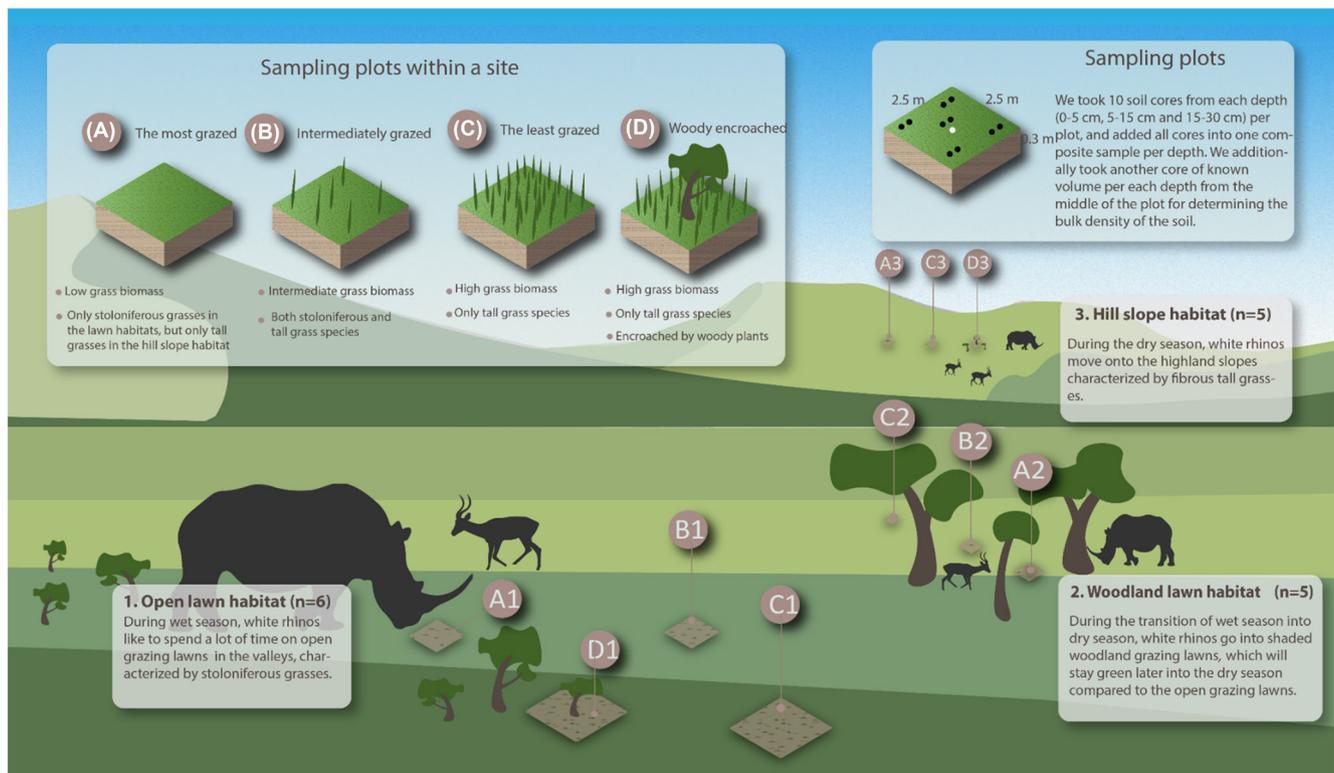


Figure 2. An illustration of the field sampling design. We used grazing lawns of Hluhluwe-iMfolozi Park as a natural model to study mega-grazer impacts on soil organic carbon (SOC) stocks. We wanted to better understand how grazing contrasts, woody encroachment and grazing intensity influenced SOC stocks. Therefore, we sampled soil in three rhino habitats, two with and one without grazing lawns. We sampled six sites in open lawn, five sites in woodland lawn and five in hill slope habitats. In open and woodland lawn habitats, we sampled each site for (A) most grazed, (B) intermediately grazed, (C) least grazed plots. In hillslope habitat we only sampled (A) most grazed and (C) least grazed plots (see text for details). We additionally sampled sites in open lawn and hill slope habitats for (D) woody encroached plots.

### Plot characteristics

We recorded the following variables at each plot: the coordinates, the percentage grass, forb and dung cover (as visual estimate of aerial cover, for dung the cover was estimated for each herbivore species separately), the percentage of stoloniferous grass cover from total grass cover, grass height and aboveground grass biomass with a Disc pasture meter (DPM) (Bransby and Tainton 1977). In all sites and habitats, the most-grazed plots were characterized by low grass sward height (< 7 cm), dominance of stoloniferous grass species (> 75%) (only in open lawn and woodland lawn habitats) and relatively high presence of grazer dung. The intermediately-grazed plots were characterized by medium sward height (7–50 cm), a combination of stoloniferous and tall grass species and moderate numbers of other signs of grazing such as grazer dung. The least-grazed plots were characterized by high sward height (> 50 cm), dominance of tall grass species (> 75%), and absence of grazer dung. Moreover, we selected the woody encroached plots in the open lawn and hill slope habitats to resemble the least grazed plots within the same site in terms of the vegetation and dung parameters (except for the presence of woody leguminous shrubs (1.0, 5–2.0 m tall) on the woody encroached plots).

In order to support our grazing intensity classification into three factorial levels (most, intermediately and

least grazed), we conducted a principal component analysis (PCA) in base R where we included six field parameters that are informative of grazing presence of intensity: 1) grass cover, 2) grass biomass and 3) bare ground cover, which are related to grazing levels because defoliation and trampling by grazers reduce grass sward height, which negatively influences the first two variables, and increase bare ground cover. Grazing lawns, which only form under prolonged intense grazing (Cromsigt and Olf 2008), are characterized by 4) stoloniferous grasses and sometimes high 5) forb prevalence. Therefore, the presence of stoloniferous grasses and forbs is indicative of high levels of grazing in HiP. Finally, 6) the presence of short grass grazer dung, such as impala and wildebeest, informs about the utilization of the grassland by short grass grazers (Cromsigt et al. 2009). It is however important to note that rhinos defecate in latrines which are often located outside of grazing lawns (Owen-Smith 1988). Therefore, we could not use dung counts to compare the relative usage of grazing lawns by rhinos and other short grass grazers. For the PCA, we scaled and centered all the aforementioned variables and additionally log-transformed the grass biomass variable (Supporting information). Our PCA revealed that the most grazed plots differed from intermediately and least grazed plots in terms of the field parameters included in the analysis. However, intermediately grazed and least grazed plots did not differ significantly from each other

(Supporting information). Furthermore, contrasting to our expectations, the woody encroached plots had higher grass cover and grass biomass compared to the least grazed plots (Supporting information).

We further identified all grass and woody species on the plots, and ran a non-metric multidimensional scaling (NMDS) analysis with Bray–Curtis distance in R using the package ‘vegan’ ([www.r-project.org](http://www.r-project.org), Oksanen et al. 2022). We did this to characterize the differences in the grass species composition in each habitat and each sampling plot (Supporting information). Our analysis shows that only the most-grazed grazing lawn plots grouped together in terms of grass species composition, whereas the intermediately- and least-grazed plots did not group in any habitat. This reflects the fact that the grazing lawns in our study tended to have more similar grass composition across sites within each habitat, while the tall grassland plots nearby the grazing lawns and in the hillslope habitat varied much more in species composition across sites, but within the same habitat.

### Soil sampling and processing

Soil samples were collected from three successive depths (0–5, 5–15 and 15–30 cm) at 10 points distributed across the plot (Fig. 2) using a Beater auger (4 cm diameter). Samples were pooled per depth category per plot and were stored in plastic bags. Moreover, at the center of each plot and for each depth, we took separate samples of known volume (with a soil sample ring) for the determination of bulk density per depth increment. To determine the stone-mass adjusted bulk density (bulk density from hereon) of each sampling plot per depth, we first oven-dried the bulk density samples at 105°C until constant mass and recorded the dry mass of the samples. We then sieved the oven-dried samples through a 2 mm sieve. We separated the remaining stones from other debris (mostly plant litter) from the sieve and recorded the mass of the stones. We calculated bulk density as:

$$BD = \frac{DM - SM}{V}$$

Where DM = dry mass of the unsieved sample, SM = total mass of stones in the sample and V = volume of the unsieved sample. This allowed us to remove the contribution of stone mass to the soil bulk density, which effectively led us to treat the volume stones occupied in our samples as empty pore spaces (see for instance Shrestha et al. 2004). Unfortunately, ~ 40% of the bulk density samples were displaced from our storage before measuring the stone mass (but after measuring dry mass). Thus, we measured stone mass for ~ 60% of the samples, representing all soil depths and treatments. We filled the missing stone mass values for the remaining 40% of samples with a gap-filling method (Supporting information for a detailed explanation). We derived bulk density values for the 0–30 cm profile by taking the weighted mean of the 0–5, 5–15 and 15–30 cm bulk density values per plot.

### Soil organic carbon (SOC) analyses

Before SOC analysis, all samples were dried at 45°C to constant mass and sieved through to 2 mm. Therefore, all particulate matter > 2 mm, including most roots, was excluded from further analyses. Fine roots < 2 mm, however, could pass the sieve and were thus included in the processed samples. Soil analyses were conducted by the soil fertility laboratory of the KwaZulu-Natal Department of Agriculture and Rural Development Analytical Services in South Africa. The samples were analyzed for total carbon (TC) through the automated Dumas dry combustion method as described in Manson et al. (2020) using a LECO CNS analyzer. Clay percentage was estimated using the mid-infrared reflectance method (Manson et al. 2020). We determined the inorganic carbon (IC) content at the Utrecht University Geolab in the Netherlands by thermogravimetric analysis with a LECO TGA701 thermogravimetric analyzer using the specific thermal range of > 600°C, which represents the temperature range for the decomposition of IC (Edmondson et al. 2015). More specifically, we obtained IC content by multiplying the proportional mass lost at > 600°C by the TC estimates derived from the Dumas dry combustion method. We then calculated TC and IC density by multiplying TC and IC content with the bulk density, and derived SOC density by subtracting IC density from TC density. Finally, we transformed the SOC density (kgC m<sup>-3</sup>) into SOC stocks (tC ha<sup>-1</sup>) for each sample from a particular depth profile by:

$$SOC\ stock(d) = \frac{SOCd \times D \times 10000}{1000}$$

Where, SOCd = soil organic carbon density for a particular depth profile (i.e. 0–30, 0–5, 5–15, 15–30 cm) (kg m<sup>-3</sup>) and D = depth interval (i.e. 0.3, 0.05, 0.10, 0.15 m). We used SOC stock values (tC ha<sup>-1</sup>) for all our analyses. The value in the numerator signifies the number of square meters per hectare, and the value in the denominator signifies the number of kilograms within a tonne. From here on, when we use ‘SOC’, we refer to SOC stocks unless otherwise specified.

### Environmental variables

We extracted long-term rainfall values for each site (ranging between 519 and 769 mm year<sup>-1</sup>) from Howison et al. (2017), who derived the rainfall data by spatially extrapolating long-term average rainfall from 1935 to 2010 between various recording stations in the park using elevation as a covariate. We further extracted medium-term (15 years) fire frequencies from MODIS Burned Area Monthly Global 500 m product for 2004–2018 using Google Earth Engine JavaScript API (Gorelick et al. 2017). Fire frequencies varied from 0 to 12 times over the 15 year period. To test how environmental variables differed between each habitat, we used linear models in base R with rainfall, fire frequency, soil clay content, bulk density and soil pH in the entire 0–30 cm profile as separate responses and habitat type as the predictor

variable. Pairwise significant differences for the habitat are reported in Table 1.

### Statistical analysis

We had two main question subsets. Our first subset asked whether SOC differed overall and in each habitat separately (Q1) between the extreme grazing contrasts (i.e. within-site comparison of the most intensely versus the least intensely

grazed plots) (Q1.1), the woody encroachment contrast (i.e. within-site comparison of the woody-encroached versus the least grazed plots) (Q1.2) and among the grazing intensity classifications (i.e. within site comparisons of the most, intermediately and least grazed plots) (Q1.3). Because of the unbalanced design, with some plot contrasts missing for some habitats, each question only included the habitats that contained the plot contrasts relevant for the particular question (Fig. 3). Our second question subset asked whether and how

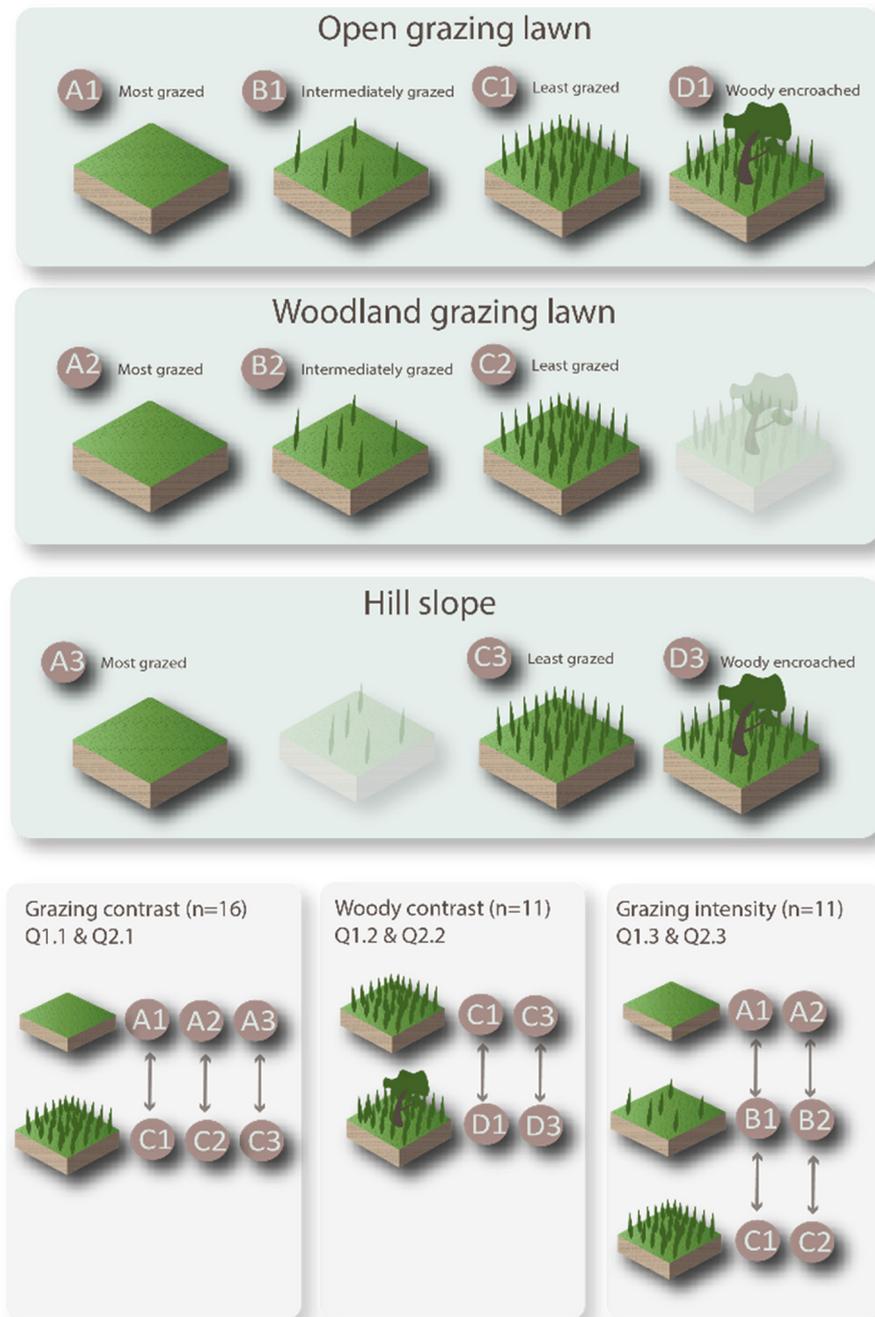


Figure 3. An illustration of the combination of grazing and woody encroachment contrasts at each rhino habitat sampled, and which combinations were used for each particular research question.

rainfall, fire frequency and soil clay content explained the effect magnitude and direction of grazing contrasts (Q2.1), woody encroachment (Q2.2) and grazing intensity (Q2.3) on SOC. For both question subsets, we first performed all analyses for the entire 0–30 cm profile, and then for each depth interval separately (0–5, 5–15 and 15–30 cm).

For the first question subset, we used generalized linear mixed effect models from the 'nlme' package in R (lme,

[www.r-project.org](http://www.r-project.org)). Using SOC as the response variable, we built full models using the following predictors: for Q1.1, Q1.2 and Q1.3 we included treatment (grazing contrasts, woody encroachment contrasts and grazing intensity classifications respectively), habitat and their interaction as predictors. For all models from question subset 1, site was the blocking variable i.e. the random effect. We report the model output for Q1 in Table 2, 3. For Q1.1, Q1.2 and Q1.3,

Table 2. ANOVA table output from the statistical analysis on the effect of habitat and treatment (extreme grazing contrasts (Q1.1), woody encroachment contrasts (Q1.2) and grazing intensity classifications (Q1.3)) on soil organic carbon (SOC) stocks. Analyses were conducted for the entire profile (0–30 cm) and for each depth interval separately. Lme() indicates generalized linear mixed effects models.

Question	Response	Predictors	Depth	Type of model	Fixed effect	F-value	p-value
Q1.1	SOC	Grazing contrast × Habitat	0–30 cm	lme()	(Intercept)	239.793	< <b>0.001</b>
					grazing contrast	0.005	0.944
					habitat	10.348	<b>0.002</b>
	SOC	Grazing contrast × Habitat	0–5 cm	lme()	grazing contrast:habitat	0.705	0.512
					(Intercept)	92.371	< <b>0.001</b>
					grazing contrast	0.711	0.421
	SOC	Grazing contrast × Habitat	5–15 cm	lme()	habitat	1.034	0.385
					grazing contrast:habitat	2.194	0.168
					(Intercept)	126.871	< <b>0.001</b>
	SOC	Grazing contrast × Habitat	15–30 cm	lme()	grazing contrast	0.052	0.825
					habitat	12.076	<b>0.001</b>
					(Intercept)	79.993	< <b>0.001</b>
Q1.2	SOC	Woody contrast × Habitat	0–30 cm	lme()	grazing contrast:habitat	0.231	0.798
					grazing contrast	0.009	0.925
					habitat	3.821	<b>0.055</b>
	SOC	Woody contrast × Habitat	0–5 cm	lme()	grazing contrast:habitat	0.111	0.896
					(Intercept)	249.593	< <b>0.001</b>
					woody contrast	2.110	0.190
	SOC	Woody contrast × Habitat	5–15 cm	lme()	habitat	16.109	<b>0.004</b>
					woody contrast:habitat	0.028	0.873
					(Intercept)	34.025	<b>0.000</b>
	SOC	Woody contrast × Habitat	15–30 cm	lme()	woody contrast	3.512	0.110
					habitat	0.001	0.980
					woody contrast:habitat	0.005	0.946
Q1.3	SOC	Grazing intensity × Habitat	0–30 cm	lme()	(Intercept)	205.863	< <b>0.001</b>
					woody contrast	2.386	0.183
					habitat	39.450	<b>0.000</b>
	SOC	Grazing intensity × Habitat	0–5 cm	lme()	woody contrast:habitat	0.005	0.947
					(Intercept)	87.277	< <b>0.001</b>
					woody contrast	0.282	0.632
	SOC	Grazing intensity × Habitat	5–15 cm	lme()	habitat	3.230	0.110
					woody contrast:habitat	0.992	0.393
					(Intercept)	138.026	< <b>0.001</b>
	SOC	Grazing intensity × Habitat	15–30 cm	lme()	grazing intensity	0.131	0.878
					habitat	4.527	0.062
					grazing intensity:habitat	0.558	0.582
SOC	Grazing intensity × Habitat	0–5 cm	lme()	(Intercept)	136.716	< <b>0.001</b>	
				grazing intensity	1.822	0.192	
				habitat	0.017	0.899	
SOC	Grazing intensity × Habitat	5–15 cm	lme()	grazing intensity:habitat	5.941	<b>0.011</b>	
				(Intercept)	109.721	< <b>0.001</b>	
				grazing intensity	0.713	0.505	
SOC	Grazing intensity × Habitat	15–30 cm	lme()	habitat	0.952	0.355	
				grazing intensity:habitat	0.208	0.814	
				(Intercept)	60.840	< <b>0.001</b>	
SOC	Grazing intensity × Habitat	0–5 cm	lme()	grazing intensity	0.040	0.961	
				habitat	4.490	<b>0.063</b>	
				grazing intensity:habitat	0.333	0.722	

Table 3. Summary table output from the statistical analysis on the effect of the interaction between habitat and treatment (extreme grazing contrasts, woody encroachment contrasts and grazing intensity classifications) on soil organic carbon (SOC) stocks. Each line represents the estimate of the difference between the most grazed and the least grazed plots (Q1.1), woody encroached and least grazed reference plots (Q1.2) and between most and intermediately grazed as well as most and least grazed plots within a habitat/soil depth (Q1.3). The levels of habitat differ between questions because each question addressed different habitat combinations. Analyses were conducted for the entire profile (0–30 cm) and for each depth interval separately. Lme() indicates generalized linear mixed effects models.

Question	Response	Predictors	Depth	Model type	Fixed effect	Estimate	SE	DF	t-value	p-value
Q1.1	SOC	Grazing contrast × Habitat	0–30 cm	lme()	Intercept	114.906	14.506	13.000	7.921	< <b>0.001</b>
					Least grazed	-15.283	17.670	13.000	-0.865	0.403
					Woodland lawn	-48.396	21.516	13.000	-2.249	<b>0.043</b>
					Hillslope	28.567	21.516	13.000	1.328	0.207
					Least grazed:woodland lawn	21.659	26.209	13.000	0.826	0.424
					Least grazed:hillslope	29.739	26.209	13.000	1.135	0.277
					Intercept	13.133	2.003	12.000	6.556	< <b>0.001</b>
					Least grazed	-2.679	2.268	9.000	-1.181	0.268
					Woodland lawn	-5.906	2.971	12.000	-1.988	<b>0.070</b>
					Hillslope	1.034	3.419	12.000	0.303	0.767
SOC	Grazing contrast × Habitat	5–15 cm	lme()	Least grazed:woodland lawn	5.138	3.246	9.000	1.583	0.148	
				Least grazed:hillslope	-2.471	3.960	9.000	-0.624	0.548	
				Intercept	30.368	5.877	12.000	5.168	< <b>0.001</b>	
				Least grazed	-2.003	4.956	9.000	-0.404	0.696	
				Woodland lawn	-4.336	8.502	12.000	-0.510	0.619	
				Hillslope	32.545	9.447	12.000	3.445	<b>0.005</b>	
				Least grazed:woodland lawn	1.874	6.751	9.000	0.278	0.788	
				Least grazed:hillslope	5.176	7.639	9.000	0.680	0.515	
				Intercept	72.581	13.533	11.000	5.363	< <b>0.001</b>	
				Least grazed	-7.553	19.568	10.000	-0.386	0.708	
Q1.2	SOC	Woody contrast × Habitat	0–30 cm	lme()	Woodland lawn	-39.329	20.073	11.000	-1.959	<b>0.076</b>
					Hillslope	2.675	23.440	11.000	0.114	0.911
					Least grazed:woodland lawn	11.598	28.259	10.000	0.410	0.690
					Least grazed:hillslope	12.439	32.797	10.000	0.379	0.712
					Intercept	104.420	13.552	8.000	7.705	< <b>0.001</b>
					Woody encroached	-17.688	16.463	7.000	-1.074	0.318
					Hillslope	60.207	20.373	8.000	2.955	<b>0.018</b>
					Woody encroached:hillslope	4.177	25.169	7.000	0.166	0.873
					Intercept	11.140	2.335	8.000	4.771	<b>0.001</b>
					Woody encroached	-2.122	1.393	6.000	-1.523	0.179
SOC	Woody contrast × Habitat	0–5 cm	lme()	Hillslope	-0.006	3.733	8.000	-0.002	0.999	
				Woody encroached:hillslope	0.160	2.270	6	0.070	0.946	
				Intercept	28.924	5.302	8.000	5.456	<b>0.001</b>	
				Woody encroached	-6.008	7.498	5.000	-0.801	0.459	
				Hillslope	37.162	7.952	8.000	4.673	<b>0.002</b>	
				Woody encroached:hillslope	-0.823	11.756	5.000	-0.070	0.947	
				Intercept	65.064	11.500	8.000	5.658	<b>0.001</b>	
				Woody encroached	-16.883	15.153	3.000	-1.114	0.346	
				Hillslope	15.598	18.734	8.000	0.833	0.429	
				Woody encroached:hillslope	23.782	23.878	3	0.996	0.393	

(Continued)

Table 3. Continued.

Question	Response	Predictors	Depth	Model type	Fixed effect	Estimate	SE	DF	t-value	p-value
Q1.3	SOC	Grazing intensity × Habitat	0–30 cm	lme()	Intercept	114.906	14.587	18.000	7.877	< <b>0.001</b>
					Intermediately grazed	-18.248	17.961	18.000	-1.016	0.323
					Least grazed	-15.283	17.961	18.000	-0.851	0.406
					Woodland lawn	-48.396	21.636	9.000	-2.237	<b>0.052</b>
					Intermediately grazed:woodland lawn	26.402	26.641	18.000	0.991	0.335
					Least grazed:woodland lawn	21.659	26.641	18.000	0.813	0.427
					Intercept	13.133	1.861	17.000	7.057	< <b>0.001</b>
					Intermediately grazed	-2.697	2.320	17.000	-1.162	0.261
					Least grazed	-2.621	2.453	17.000	-1.068	0.300
					Woodland lawn	-5.906	2.760	9.000	-2.140	<b>0.061</b>
SOC	Grazing intensity × Habitat	5–15 cm	lme()	Intermediately grazed:woodland lawn	11.825	3.441	17.000	3.436	<b>0.003</b>	
				Least grazed:woodland lawn	5.080	3.532	17.000	1.438	0.169	
				Intercept	32.174	4.644	16.000	6.928	< <b>0.001</b>	
				Intermediately grazed	-4.108	4.821	16.000	-0.852	0.407	
				Least grazed	-3.873	5.128	16.000	-0.755	0.461	
				Woodland lawn	-6.143	6.648	9.000	-0.924	0.380	
				Intermediately grazed:woodland lawn	-0.358	6.921	16.000	-0.052	0.959	
				Least grazed:woodland lawn	3.744	7.137	16	0.524	0.607	
				Intercept	72.581	13.688	16.000	5.303	< <b>0.001</b>	
				Intermediately grazed	-14.425	17.975	16.000	-0.802	0.434	
SOC	Grazing intensity × Habitat	15–30 cm	lme()	Least grazed	-6.552	18.956	16.000	-0.346	0.734	
				Woodland lawn	-39.329	20.303	9.000	-1.937	<b>0.085</b>	
				Intermediately grazed:woodland lawn	22.569	27.662	16.000	0.816	0.427	
				Least grazed:woodland lawn	10.597	27.332	16.000	0.388	0.703	

the number of sample points (replicates) was 32, 33 and 22 respectively.

For the second question subset, we tested whether and how rainfall, fire frequency and soil clay content influenced the effects of grazing contrasts (Q2.1), woody encroachment (Q2.2) and grazing intensity (Q2.3) on SOC. For this analysis, we first averaged the clay values across all plots per site and thus used only one soil clay content value per site. We did this because we also only had one rainfall and fire frequency value per site. For Q2.1 and Q2.2, we calculated  $\Delta$ SOC as the difference in SOC between the plot contrasts, i.e. SOC from the most intensely grazed minus SOC from the least grazed plots for Q2.1 (A plots minus C plots in Fig. 2), and SOC from the woody encroached plots minus SOC from the least grazed tall grass plots for Q2.2 (D plots minus C plots in Fig. 2). The calculation of  $\Delta$ SOC yielded a single value per site and as such we used linear models in base R (lm, [www.r-project.org](http://www.r-project.org)) to answer Q2.1 and Q2.2. Because there was strong multicollinearity between rainfall and fire frequency (VIF=131.46), we considered them in separate models. Multicollinearity was calculated when including all predictors. Thus, for each predictor we built two full models, one with rainfall, soil clay content and their interaction as predictors, and another with fire frequency, soil clay content and their interaction as predictors. For Q2.3, we continued using SOC as the response and analyzed the influence of environmental variables on grazing intensity effects on SOC using a lme with site ID set as random effect. Here, we included each environmental variable (i.e. clay content and alternating fire frequency and rainfall as explained above) in interaction with the grazing intensity classification. For all Q2 models, we performed a stepwise elimination procedure to select the best candidate model. The selection was based on the AICc criterion. We report the model output for each best candidate model in Table 4. We checked model assumptions and, where heteroscedasticity was present, we applied weights (Supporting information for model structures). For Q2.1, Q2.2 and Q2.3, the number of sample points (replicates) was 32, 33 and 22 respectively.

## Results

### Characteristics of the habitats, sites and sampling plots

The three rhino habitats were characterized by distinct abiotic features and plant communities. The hill slope habitat had significantly higher rainfall, fire frequency and soil clay content compared to open lawn (rainfall:  $\beta=149.500$ ,  $p < 0.001$ ; fire frequency:  $\beta=5.833$ ,  $p < 0.001$ ; soil clay content:  $\beta=14.000$ ,  $p < 0.001$ ) and woodland lawn habitat (rainfall:  $\beta=130.600$ ,  $p < 0.001$ ; fire frequency:  $\beta=6.200$ ,  $p < 0.001$ ; soil clay content:  $\beta=32.300$ ,  $p < 0.001$ ). The hillslope habitat had lower bulk density and pH compared to open lawn (bulk density:  $\beta=-0.188$ ,  $p=0.012$ ; pH:  $\beta=-0.393$ ,  $p=0.005$ ) and woodland lawn habitat (bulk density:  $\beta=-0.170$ ,  $p=0.047$ ; pH  $\beta=-0.658$ ,  $p < 0.001$ ) respectively. The open

lawn habitat had higher soil clay content ( $\beta=18.200$ ,  $p < 0.001$ ) but lower pH ( $\beta=-0.264$ ,  $p=0.059$ ) than the woodland lawn habitat, but the two habitats did not differ in terms of rainfall ( $\beta=18.900$ ,  $p=0.396$ ), fire frequency ( $\beta=0.367$ ,  $p=0.777$ ) or bulk density ( $\beta=0.0175$ ,  $p=0.958$ ). In open lawn habitat, *Digitaria longiflora* and *Panicum coloratum* dominated the grazing lawn plots, while *Eragrostis superba* and *Panicum maximum* dominated the least-grazed plots (Table 1, Supporting information). In the woodland lawn habitat, *Dactyloctenium australe* dominated the grazing lawns while *Panicum maximum* dominated the least grazed plots. Intermediately-grazed plots in both open lawn and woodland lawn habitats hosted a combination of grass species from the lawns and the least grazed plots. *Themeda triandra* and *Eragrostis curvula* dominated both the most- and least-grazed plots in the hill slope habitat. *Dichrostachys cinerea* dominated woody-encroached plots in both open lawn and hill slope habitats and hosted similar grass species composition as the least-grazed plots in these habitats (Table 1 for details about the abiotic template and plant species composition in each habitat).

### The effects of environmental variables on SOC

Rainfall, fire frequency and soil clay content were all strongly correlated with SOC across habitats (Fig. 4). Instead of the hypothesized linear relationship between SOC and fire frequency, our relative goodness-of-fit test (AICc) supported a quadratic relationship between the variables. As such we modelled fire frequency quadratically. SOC increased with rainfall ( $\beta=0.107$ ,  $p=0.003$ ) and soil clay content ( $\beta=0.887$ ,  $p < 0.001$ ), while SOC first increased and then declined with fire frequency ( $\beta=-0.810$ ,  $p < 0.001$ ). Furthermore, hillslope habitat had more SOC compared to open lawn habitat ( $\beta=49.01$ ,  $p < 0.001$ ), and open lawn habitat had more SOC compared to woodland lawn habitat ( $\beta=28.13$ ,  $p=0.010$ ) (Fig. 5).

### The effects of grazing and woody encroachment on SOC stocks

There were no significant differences in SOC in any of the soil depths overall between the most- and the least-grazed plots (Q1.1), between woody-encroached and the least-grazed plots (Q1.2) nor at different grazing intensities (Q1.3) (Table 2, Fig. 6). Intermediately-grazed plots had more SOC compared to most- and least-grazed plots in the top 5 cm in the woodland lawn habitat (Q2.2) (Table 2, 3, Fig. 7). Furthermore, neither soil clay content, rainfall nor fire frequency influenced the effect of grazing contrasts (Q3.1) or grazing intensity classifications (Q3.3) on SOC stocks (Table 4). Soil clay content did affect the difference in SOC between woody-encroached and the least-grazed plots (Q2.2;  $\beta=-0.153$ ,  $p=0.032$ ), but only in the top 5 cm (Table 4). At low clay content, the woody-encroached plots had more SOC than the not-encroached least-grazed grassland plot, while at high clay content, the least-grazed plots had more

Table 4. Summary table output for the best candidate models after stepwise elimination on the effect of the different environmental variables (rainfall, soil clay content and fire frequency) on extreme grazing contrasts (Q2.1), woody encroachment contrasts (Q2.2) and grazing intensity classifications (Q2.3) on soil organic carbon (SOC) stocks. Predictors of the full model indicate the terms that were included in the full model before step-wise elimination, and fixed effects indicate the terms in the best candidate model that scored the lowest AICc score. Rainfall and fire frequency were not simultaneously included in any model because of high multicollinearity. Models that included rainfall are unhighlighted and models including fire frequency are highlighted in grey. Analyses were conducted for the entire profile (0–30 cm) and for each depth interval separately. Significant p-values are marked in bold. Im() indicates linear models and Lme() indicates generalized linear mixed effect models.

Question	Contrast	Response	Predictors full model	Depth	Model type	Fixed effect	Estimate	S.E	t-value	p-value
Q2.1	Grazing contrast	$\Delta$ SOC	Rainfall $\times$ Clay	0–30 cm	Im()	Intercept	9.657	27.190	0.355	0.728
						Clay	-0.284	0.752	-0.378	0.712
	Grazing contrast	$\Delta$ SOC	Fire $\times$ Clay	0–30 cm	Im()	Intercept	9.657	27.190	0.355	0.728
						Clay	-0.284	0.752	-0.378	0.712
	Grazing contrast	$\Delta$ SOC	Rainfall $\times$ Clay	0–5 cm	Im()	Intercept	-0.826	3.02598	-0.273	0.790
						Clay	0.052	0.098	0.529	0.607
	Grazing contrast	$\Delta$ SOC	Fire $\times$ Clay	0–5 cm	Im()	Intercept	-0.826	3.02598	-0.273	0.790
						Clay	0.052	0.098	0.529	0.607
	Grazing contrast	$\Delta$ SOC	Rainfall $\times$ Clay	5–15 cm	Im()	Intercept	11.098	12.166	0.912	0.378
						Clay	-0.483	0.331	-1.459	0.168
Q2.2	Grazing contrast	$\Delta$ SOC	Fire $\times$ Clay	5–15 cm	Im()	Intercept	11.098	12.166	0.912	0.378
						Clay	-0.483	0.331	-1.459	0.168
	Grazing contrast	$\Delta$ SOC	Rainfall $\times$ Clay	15–30 cm	Im()	Intercept	-1.521	26.314	-0.058	0.955
						Clay	0.083	0.674	0.123	0.904
	Grazing contrast	$\Delta$ SOC	Fire $\times$ Clay	15–30 cm	Im()	Intercept	-1.521	26.314	-0.058	0.955
						Clay	0.083	0.674	0.123	0.904
	Woody contrast	$\Delta$ SOC	Rainfall $\times$ Clay	0–30 cm	Im()	Intercept	30.364	34.003	0.893	0.398
						Clay	-1.096	0.812	-1.349	0.214
	Woody contrast	$\Delta$ SOC	Fire $\times$ Clay	0–30 cm	Im()	Intercept	30.364	34.003	0.893	0.398
						Clay	-1.096	0.812	-1.349	0.214
Q2.2	Woody contrast	$\Delta$ SOC	Rainfall $\times$ Clay	0–5 cm	Im()	Intercept	4.315	2.393	1.803	0.109
						Clay	-0.153	0.059	-2.603	<b>0.032</b>
	Woody contrast	$\Delta$ SOC	Fire $\times$ Clay	0–5 cm	Im()	Intercept	4.315	2.393	1.803	0.109
						Clay	-0.153	0.059	-2.603	<b>0.032</b>
	Woody contrast	$\Delta$ SOC	Rainfall $\times$ Clay	5–15 cm	Im()	Intercept	9.316	14.831	0.628	0.550
						Clay	-0.415	0.346	-1.199	0.270
	Woody contrast	$\Delta$ SOC	Fire $\times$ Clay	5–15 cm	Im()	Intercept	9.316	14.831	0.628	0.550
						Clay	-0.415	0.346	-1.199	0.270
	Woody contrast	$\Delta$ SOC	Rainfall $\times$ Clay	15–30 cm	Im()	Intercept	16.03	33.818	0.474	0.648
						Clay	-0.483	0.748	-0.646	0.536
Q2.2	Woody contrast	$\Delta$ SOC	Fire $\times$ Clay	15–30 cm	Im()	Intercept	16.03	33.818	0.474	0.648
						Clay	-0.483	0.748	-0.646	0.536

(Continued)

Table 4. Continued.

Question	Contrast	Response	Predictors full model	Depth	Model type	Fixed effect	Estimate	S.E	t-value	p-value
Q2.3	Grazing intensity	SOC	Grazing intensity × Rainfall + Grazing intensity × Clay	0–30 cm	lme()	Intercept	92.908	11.564	8.035	< 0.001
						Intedmediately grazed	-6.248	12.969	-0.482	0.635
						Least grazed	-5.438	12.969	-0.419	0.679
Grazing intensity	SOC	Grazing intensity × Fire + Grazing intensity × Clay	0–30 cm	lme()	Intercept	84.762	14.273	5.938	< 0.001	
					Intedmediately grazed	-6.974	17.151	-0.406	0.689	
					Least grazed	-16.582	17.151	-0.966	0.346	
Grazing intensity	SOC	Grazing intensity × Rainfall + Grazing intensity × Clay	0–5 cm	lme()	Intedmediately grazed:fire	8.146	9.110	0.894	0.394	
					Least grazed:fire	0.727	10.947	0.066	0.947	
					Intercept	11.143	10.947	1.017	0.322	
Grazing intensity	SOC	Grazing intensity × Rainfall + Grazing intensity × Clay	0–5 cm	lme()	Intercept	10.448	1.517	6.886	< 0.001	
					Intedmediately grazed	2.678	2.103	1.273	0.218	
					Least grazed	-0.336	2.157	-0.155	0.878	
Grazing intensity	SOC	Grazing intensity × Fire + Grazing intensity × Clay	0–5 cm	lme()	Intercept	10.448	1.517	6.886	< 0.001	
					Intedmediately grazed	2.678	2.103	1.273	0.218	
					Least grazed	-0.336	2.157	-0.155	0.878	
Grazing intensity	SOC	Grazing intensity × Rainfall + Grazing intensity × Clay	5–15 cm	lme()	Intercept	29.237	3.251	8.992	< 0.001	
					Intedmediately grazed	-4.126	3.312	-1.245	0.228	
					Least grazed	-1.955	3.420	-0.571	0.574	
Grazing intensity	SOC	Grazing intensity × Fire + Grazing intensity × Clay	5–15 cm	lme()	Intercept	23.173	3.292	7.039	< 0.001	
					Intedmediately grazed	-1.744	4.325	-0.403	0.692	
					Least grazed	-2.978	4.532	-0.657	0.520	
Grazing intensity	SOC	Grazing intensity × Fire + Grazing intensity × Clay	15–30 cm	lme()	Intercept	5.880	2.043	2.878	0.018	
					Intedmediately grazed:fire	-2.198	2.716	-0.809	0.430	
					Least grazed:fire	0.735	2.771	0.265	0.794	
Grazing intensity	SOC	Grazing intensity × Rainfall + Grazing intensity × Clay	15–30 cm	lme()	Intercept	54.704	10.654	5.134	0.001	
					Intedmediately grazed	-3.842	13.278	-0.289	0.775	
					Least grazed	-2.117	13.278	-0.159	0.875	
Grazing intensity	SOC	Grazing intensity × Fire + Grazing intensity × Clay	15–30 cm	lme()	Intercept	53.145	14.149	3.756	0.002	
					Intedmediately grazed	-6.074	17.862	-0.340	0.738	
					Least grazed	-12.584	18.477	-0.681	0.505	
Grazing intensity	SOC	Grazing intensity × Rainfall + Grazing intensity × Clay	15–30 cm	lme()	Intedmediately grazed:fire	1.559	9.031	0.172	0.866	
					Least grazed:fire	2.293	11.206	0.204	0.840	
					Intercept	9.314	11.449	0.813	0.427	

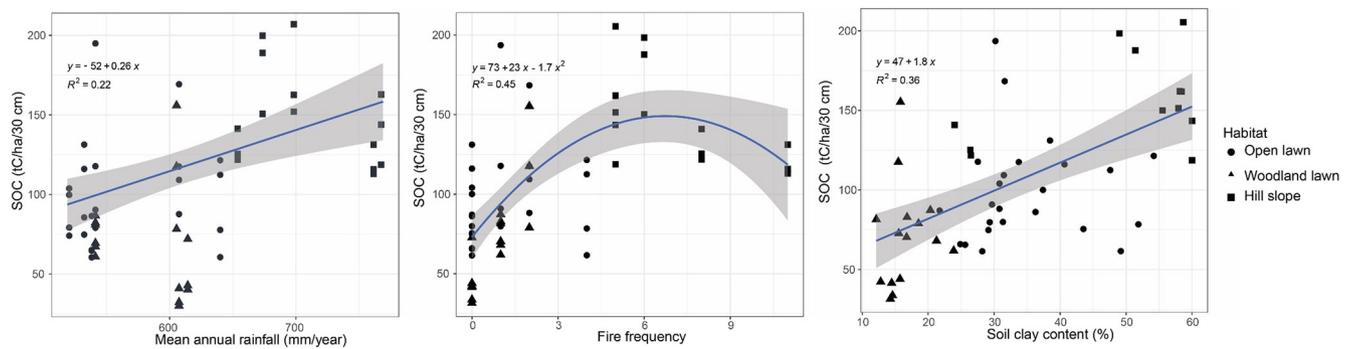


Figure 4. The relationships between SOC (tC/ha/30 cm depth) and environmental variables per habitat: mean annual rainfall, fire frequency and soil clay content.

SOC than the woody-encroached plot. Rainfall or fire frequency did not influence woody encroachment impacts on SOC (Table 4).

## Discussion

While low levels of grazing may promote SOC, studies from livestock systems show that intense grazing generally reduces SOC (McSherry and Ritchie 2013, Tang et al. 2019, Lai and Kumar 2020). This has raised concerns that rewilding with large grazers may negatively affect soil carbon storage (Andriuzzi and Wall 2018). In our study system, one of the last remaining protected areas dominated by wild megagrazers, we found no evidence for this as SOC stocks did not differ among the extreme grazing contrasts we tested and were no lower in intensely grazed grazing lawns than in nearby less intensely grazed grassland. The biggest driver of SOC in our study was habitat, with major SOC level differences between the three habitats (Fig. 5). The hillslope grassland had about double the SOC of the woodland habitat with the open lawn habitat having intermediate SOC levels. This reflects the difference in clay content in the soils of these different habitats, with the hillslope grassland having the highest clay content (~ 51%), the open lawn habitat intermediate clay content (~ 35%) and the woodland lawns a relatively low clay content (~ 17%). Clay content is a major driver of variation in SOC (McSherry and Ritchie 2013). We did find more SOC in the top 5 cm in the intermediately grazed plots compared to most and least grazed plots, but only in the closed woodland lawn habitat. Furthermore, woody encroached plots had higher SOC in soils with low clay content and lower SOC in soils with high clay content compared to not encroached least grazed plots but only in the top 5 cm.

### Grazing-related effects on SOC stocks

Contrary to our hypotheses, SOC did not vary between the extreme grazing contrasts in any rhino habitat and rainfall, fire frequency and soil clay content did not affect this. The intermediately-grazed plots however did have more SOC in the top 5 cm in compared to most and least-grazed plots,

but only in the closed woodland lawn habitat. This is despite the fact that our PCA revealed that the intermediately grazed plots did not differ from the least grazed plots in terms of the grazing-related field parameters (Supporting information). This finding, however, confirms our original prediction that intermediate grazing would have the highest SOC levels, although we only found this for one habitat.

Other recent studies from African savannas reported that wild herbivores either increase or decrease SOC (Sitters et al. 2020, Wigley et al. 2020). Sitters et al. (2020) found that 20 years of cattle, or cattle + medium- and small-sized wild herbivore, grazing reduced SOC relative to control plots but that the inclusion of elephants reversed the negative effects of grazing on SOC. While cattle and wildlife grazing reduced SOC by ~ 7–10 tC ha<sup>-1</sup> compared to the control within the top ~ 15 cm of soil, the inclusion of elephant increased SOC by ~ 5–8 tC ha<sup>-1</sup> (Sitters et al. 2020). Using carbon isotopes they showed that the additional SOC was largely tree-derived and thus they suggested that elephants' tree toppling habits were likely responsible for increasing SOC stocks. In the same study system, although at much sandier soils, Wigley et al. (2020) showed that large herbivore exclusion (including elephants) on average resulted in an increase of ~ 21 tC ha<sup>-1</sup> within the top 30 cm of the soil. The authors particularly stressed the importance of grass-derived SOC in their study, reporting that the exclusion of herbivores resulted in higher grass biomass buildup, which contributed SOC through higher root biomass and greater amounts of litter. In our study system, the intensely grazed grazing lawns have predictably low above ground biomass, likely reducing the amount of carbon to be returned to the soil through litterfall. However, high grazing pressure on productive grasslands may also boost grass productivity and stimulate carbon allocation to below ground parts, both of which will contribute to SOC accumulation (Wilson et al. 2018). It is thus possible that these contrasting impacts may have led to a net neutral effect of the extreme grazing contrasts on SOC stocks in our study.

It is important to note that unlike the two studies from Laikipia district, we did not have an experimental control that excluded large grazers completely. Therefore, we could not compare grazing contrasts to the absence of large mammal

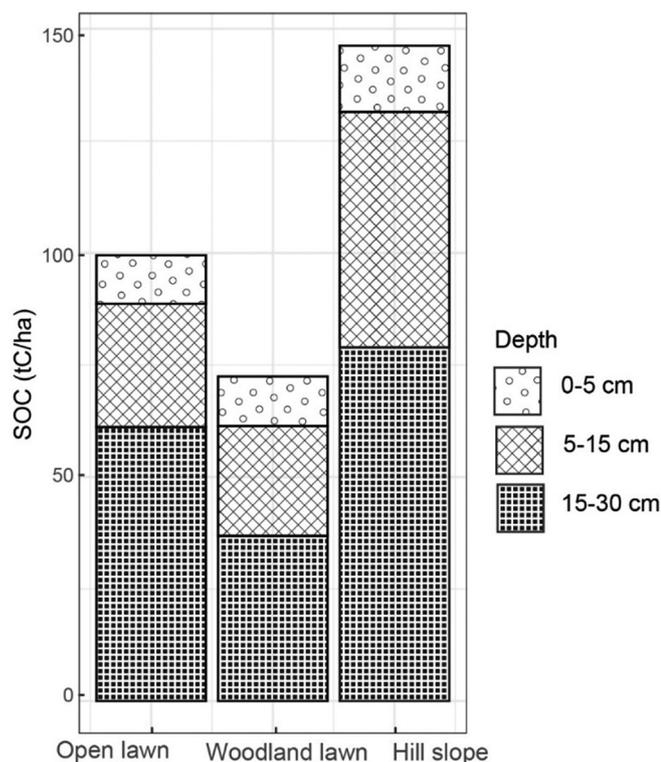


Figure 5. Mean soil organic carbon (SOC) stocks ( $\text{tC ha}^{-1}$ ) per habitat and depth.

grazing. In this respect, it is relevant to compare the SOC stocks in our grazed sites with those of ungrazed controls of [Sitters et al. \(2020\)](#) and [Wigley et al. \(2020\)](#) (Supporting information). Their sites had contrasting soil clay content, such that soils in [Wigley et al. \(2020\)](#) had relatively low clay content of 15% and soils in [Sitters et al. \(2020\)](#) had relatively high clay content of 52%. From a soil texture point of view, their findings would thus be most comparable with our woodland lawn habitat ([Wigley et al. \(2020\)](#)) and hillslope grassland habitat ([Sitters et al. \(2020\)](#)). The soils in our woodland lawn habitat stored  $\sim 70 \text{ tC ha}^{-1}$  in their top 30 cm, with no difference between the most and least grazed plots. This is more than the  $\sim 60 \text{ tC ha}^{-1}$  of the ungrazed controls of [Wigley et al. \(2020\)](#) in the top 30 cm. Furthermore, within the top 15 cm, the hillslope habitat in our study area stored  $\sim 50 \text{ tC ha}^{-1}$ , with no difference between the most and least grazed plots. This is more than the  $\sim 20 \text{ tC ha}^{-1}$  in the ungrazed controls of [Sitters et al. \(2020\)](#) in the top 15 cm. Accordingly, SOC levels in our grazed system were higher, not lower, than the ungrazed controls of these other two African studies on SOC and wildlife grazing. Importantly, the average grazer biomass in HiP amounts to  $\sim 8 \text{ t km}^{-2}$  ([le Roux et al. 2017](#)), which is  $\sim 3\text{--}5 \text{ t km}^{-2}$  more than the total grazer biomass (including livestock) in Laikipia district in Kenya ([Georgiadis et al. 2007](#)) where [Sitters et al. \(2020\)](#) and [Wigley et al. \(2020\)](#) conducted their studies. Thus, average grazing pressure is high in our system, particularly on the heavily frequented grazing lawns. Despite this, we found no evidence of reduced SOC, even on these intensely used grazing lawns.

Contrasting to the limited number of studies on wild grazer impacts on SOC, there is a large number of studies available on livestock impacts. These livestock studies show that the likelihood that grazing will increase or decrease SOC depends on grazing intensity and environmental context. For instance, [Lai and Kumar \(2020\)](#) in their synthesis of 287 studies found that high and medium livestock grazing intensities reduced SOC and light grazing increased it. [McSherry and Ritchie \(2013\)](#) furthermore reported that livestock grazing effects on SOC shifted from negative to positive with decreasing rainfall and increasing soil clay content. In our study, we found no impact of rainfall or soil clay content on the direction or magnitude of grazing effects on SOC. The discrepancy between our findings and the livestock studies alludes to the potential differences in the way wild grazers and livestock use the landscape and resources. The more diverse functional groups, body sizes and digestive physiologies of wild grazers compared to domestic grazers ([Hofmann 1989](#)) allow them to use a larger diversity of plants and plant parts, which can further translate into more heterogeneous impact on vegetation and soil overall. Moreover, wild herbivores, particularly in large protected areas with a heterogeneous environmental template, can easily move from areas where resources become seasonally limiting, to areas, where resources remain more abundant ([Venter et al. 2015](#)). On the other hand, livestock are typically confined within smaller areas, possibly exerting larger overall grazing pressure on the vegetation at similar grazer densities. Smaller fenced reserves that do confine wild grazer populations, particularly in areas with a homogenous abiotic template, may have more similar grazing impacts on SOC as in livestock systems ([Mills et al. 2020](#)). Overall, the differences between wild and domestic grazers complicate the direct comparison of grazing intensities between domestic and wild systems, even if density estimates are comparable.

### The effects of woody encroachment on SOC

In contrast to our expectations, the woody encroached grassland plots did not consistently have higher SOC values than the not encroached plots. However, we did find the expected relationship between soil clay content and the impacts of woody encroachment on SOC in the top 5 cm. At low soil clay content woody encroached plots had higher SOC stocks (compared to the nearby tall grassland plot) whereas at high soil clay content woody encroached plots had lower SOC stocks than the grassland plot. These results align with the global meta-analysis by [Li et al. \(2016\)](#) that found SOC content to increase under woody shrub encroachment in sandy and sand loamy soils, and to decrease in silty and clay soils. This can be explained by the differing capacity of above ground organic matter to mix into sandy and clay soils respectively: the top part of clay soils hardens more than those of sandy soils during dry periods, thus potentially hampering the mixing of above ground litter into the soil especially in the late wet and dry seasons.

Although we did not find any effect of rainfall, [Jackson et al. \(2002\)](#) reported that woody invasion of grassland in North

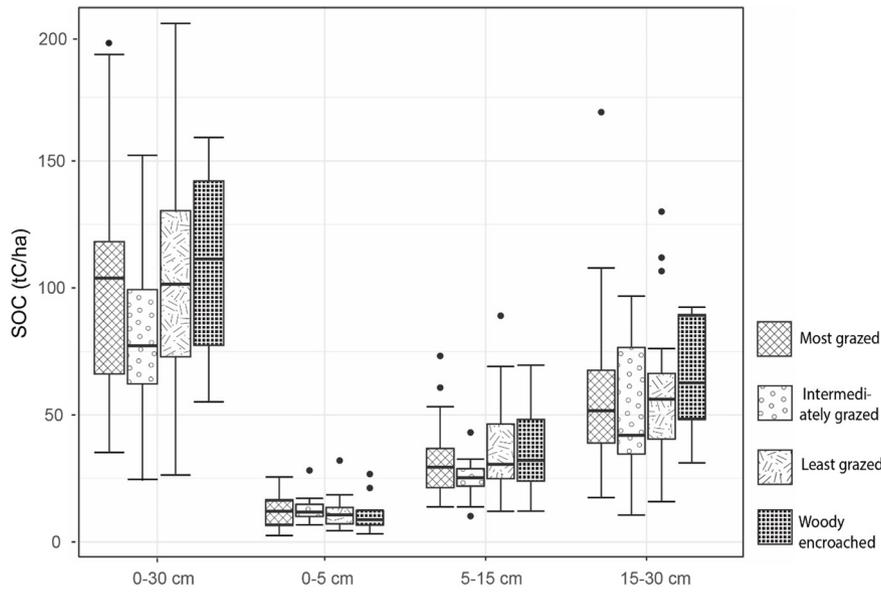


Figure 6. Boxplots showing the difference in soil organic carbon (SOC) stocks ( $tC\ ha^{-1}$ ) between plot contrasts per soil depth.

America increased SOC in drier areas, while reducing it in wetter areas. Mureva et al. (2021) confirmed these patterns in South African savannas, where woody colonization of grassland increased SOC by 24–27% at 300–350  $mm\ year^{-1}$  rainfall and reduced it by 26% at rainfall of 1500  $mm\ year^{-1}$ . The

lack of an effect of rainfall in our study could be due to the fact that HiP mostly experiences rainfall between 550 and 1000  $mm\ year^{-1}$ , and therefore our analysis omitted the low and high ends of the rainfall spectrum where Mureva et al. (2021) found woody encroachment to either increase or decrease SOC.

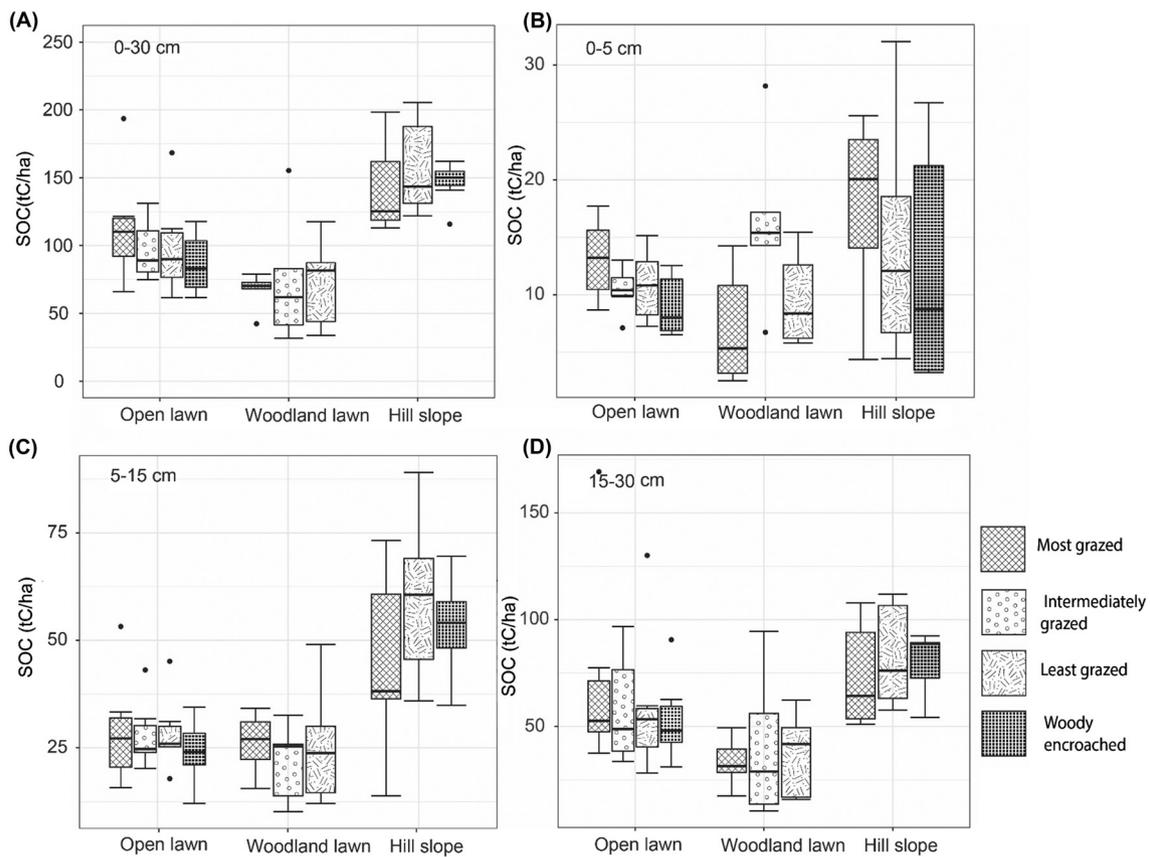


Figure 7. Boxplots showing the difference in soil organic carbon (SOC) stocks ( $tC\ ha^{-1}$ ) between plot contrasts per habitat and soil depth.

Furthermore, it is important to note that our PCA revealed that the woody encroached plots had higher PC1 values compared to the least grazed reference plots (Supporting information). This means that the effects of woody encroachment on SOC stocks in our study may have been confounded by the lower grass cover and biomass in the reference (least grazed) plots compared to the woody encroached plots. This is particularly relevant for sites with low clay content where woody encroached plots had more SOC compared to least grazed reference plots. Unfortunately, our data does not allow us to quantify the contribution of grasses to the higher SOC stocks on the woody encroached plots. However, future studies can utilize stable C isotopes to quantify the relative contributions of C4 grasses and C3 woody plants to SOC stocks (Jackson et al. 2002), therefore providing more confidence to the SOC contributions of woody plants even with reference plots differing in grass cover and biomass.

### Wild grazer contributions to climate change mitigation

There still remains considerable uncertainty around wild herbivore impacts on SOC, which obscures the potential of trophic rewilding's contributions to natural climate solutions. Voysey et al. 2021 found in HiP that medium sized browsers that visited grazing lawns due to the reduced predation risk provided by the openness of the lawns contributed to the reduction in woody plant recruitment on and surrounding grazing lawns. This, together with our results on the effects of woody encroachment on SOC leads us to hypothesize that megagrazers can influence SOC indirectly through mediating woody plant cover. Therefore, direct grazer impacts (i.e. defoliation, trampling, dunging) may not represent the total impacts of grazers on SOC.

Furthermore, most studies on megaherbivore impacts and carbon stocks focus on elephant impacts on above ground carbon stocks (Marshall et al. 2012, Berzaghi et al. 2019, Davies and Asner 2019). A recent perspective highlights the importance of quantifying a diversity of carbon pools to better understand how herbivory impacts long-term carbon storage (Kristensen et al. 2022). As an example, Sandhage-Hofmann et al. (2021) demonstrated that elephants were able to compensate for most above ground carbon losses by increasing carbon stocks below ground. This is important, because it shows that research focusing solely on the above ground impacts may under or over-estimate herbivore impacts on overall ecosystem carbon storage (Sandhage-Hofman et al. 2021, Kristensen et al. 2022). Moreover, studies are beginning to demonstrate that a focus on total SOC stocks alone fails to consider the effects of long-term carbon storage, which also leads to under- or overestimation of climate change mitigation potential (Lehmann and Kleber 2015, Lehmann et al. 2020). This is because particulate and mineral-associated SOC turn over at vastly different rates (Lavelle et al. 2020). Thus, even when grazing does not affect total SOC stocks, it can still influence long-term carbon storage by altering the

particulate/mineral carbon balance (Kristensen et al. 2022). Thus, in order to gain a more comprehensive understanding of how wild grazers can contribute to long-term carbon storage, it is imperative that future studies consider both direct and indirect effects of wild grazing on the diversity of carbon pools that turn over at different rates.

### Methodological considerations

While HiP's grazing lawns allowed us to test the effect of naturally occurring grazing contrasts and woody encroachment on SOC, it did not allow us to establish causality between grazing and woody encroachment impacts on SOC. Although grazing lawns can remain in short statured state for decades (Cromsigt et al. 2017a), many grazing lawns are dynamic and may gradually move in space depending on the spatial patterns of grazing on the lawn. In our study, this could have led to a situation where our least grazed plots adjacent to the grazing lawns have, in fact, been in a grazing lawn state for instance 5–10 years earlier. While we would still expect to see grazing impact on the top 5 cm of the soil, this dynamic history of the lawn could have at least partially obscured the grazing contrasts between the most and least grazed plots in our study and especially for the deeper soil levels. Furthermore, it is important to point out that our low sample size per habitat (five to six sites within one habitat) could have further obscured the impact of grazing on such a heterogenous variable as SOC stocks.

While higher sample size could reveal trends that we were unable to detect, future studies can also benefit from carefully implemented long-term enclosure experiments, where exclusion of megagrazers on and surrounding grazing lawns can be compared to controls without megagrazer exclusion. This would further help to disentangle some of the mechanisms behind direct (i.e. grass defoliation, trampling, dunging) and indirect grazing impacts (i.e. changes in vegetation structure) on SOC.

When preparing bulk soil samples for SOC estimations, sieving through < 2 mm is a widely used method in grazing and soil carbon studies (Sitters et al. 2020, Wigley et al. 2020). However, it may lead to a bias where grasses with relatively high production of fine roots such as stoloniferous lawn grasses show higher SOC stocks compared to grasses that invest more in the production of large roots such as tall bunch grasses. On the other hand, we derived our bulk density estimates from the bulk soil from which stones were removed. The mass of the bulk density samples thus potentially includes organic matter such as roots and leaves. Because such organic matter is likely to be less dense than the bulk soil, this method may underestimate the mass per volume bulk density estimates and thus our SOC stock values. While these two caveats are likely to bias SOC stock estimates in opposite directions, they seem to be important and should be addressed in future sampling designs that compare SOC stocks under grassland types that differ in fine root production.

## Conclusion

Large-bodied herbivores are important for ecosystem functioning and global carbon cycling. However, studies from livestock systems show that intense grazing can reduce SOC, raising uncertainties about the effects of wild grazers on the climate change mitigation potential of systems with high levels of concentrated grazing such as megagraser-dominated savannas. Here, we found no evidence to support the hypothesis that wild grazing reduces SOC even at high intensities, although our study does support the notion that woody encroachment, which can be mediated by grazing, can either increase or decrease SOC depending on soil texture. Therefore, the overall impact of large grazers on carbon sequestration is still obscure, masked in particular by differences in above-ground and below-ground impacts, between domestic and wild grazers and between direct and indirect impacts. Furthermore, in addition to direct grazing-related impacts, our study suggests that wild grazers may affect SOC indirectly through their impact on tree-grass ratios, an aspect that needs further attention in natural climate solutions for determining appropriate grazing intensities to optimize SOC storage.

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## Author contributions

**Olli Hyvarinen:** Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Resources (lead); Software (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Mariska te Beest:** Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Investigation (equal); Methodology (equal); Resources (equal); Supervision (equal); Validation (equal); Visualization (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Elizabeth le Roux:** Conceptualization (equal); Data curation (supporting); Formal analysis (equal); Investigation (equal); Methodology (equal); Resources (equal); Supervision (equal); Validation (equal); Writing – original draft (equal). **Graham**

**I. H. Kerley:** Conceptualization (equal); Investigation (equal); Methodology (equal); Resources (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Nicola Findlay:** Conceptualization (supporting); Data curation (supporting); Investigation (supporting); Methodology (supporting); Resources (equal); Validation (supporting); Writing – original draft (supporting). **Walter D. C. Schenkeveld:** Conceptualization (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (equal); Resources (equal); Validation (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Victor Trouw:** Data curation (supporting); Formal analysis (supporting); Methodology (supporting); Writing – original draft (supporting). **Joris P. G. M. Cromsigt:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (lead); Resources (equal); Supervision (lead); Validation (equal); Visualization (supporting); Writing – original draft (equal); Writing – review and editing (equal).

## Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.qnk98sfn7> (Hyvarinen et al. 2023).

## Supporting information

The Supporting information associated with this article is available with the online version.

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