Land Degradation & Development

WILEY

RESEARCH ARTICLE OPEN ACCESS

Grazing Affects Soil Organic Carbon Stocks Directly and Indirectly Through Herbaceous Species Diversity in Sahelian Savanna Ecosystems

Haftay Hailu Gebremedhn[1,2] | Simon Taugourdeau[2,3] | Sylvanus Mensah[4,5] | Lydie Chapuis-Lardy[6] | Torbern Tagesson[7] | Patricia Moulin[6] | Ousmane Ndiaye[2,8] | Aleksander Wieckowski[7] | Paulo Salgado[2,3]

[1]College of Agriculture and Environmental Sciences, Haramaya University, Dire Dawa, Ethiopia | [2]Dispositif Partenarial "Pôle Pastoralisme et Zones Sèches", Pôle de Recherche de Hann, ISRA, Dakar, Senegal | [3]SELMET, CIRAD, INRAE, Institut Agro Univ Montpellier, Montpellier, France | [4]Chair of Forest Growth and dendroecology, Albert-Ludwigs-Universität Freiburg, Freiburg im Breisgau, Germany | [5]Laboratoire de Biomathématiques et d'Estimations Forestières, Faculté des Sciences Agronomiques, Université d'Abomey Calavi, Cotonou, Benin | [6]Eco&Sols, Université de Montpellier, CIRAD, INRAE, IRD, Institut Agro Montpellier, Montpellier, France | [7]Department of Physical Geography and Ecosystem Science, Lund University, Lund, Sweden | [8]Institut Sénégalais de Recherches Agricoles, Centre de Recherches Zootechniques de Dahra, Dakar, Senegal

Correspondence: Haftay Hailu Gebremedhn (hailuhft418@gmail.com)

Received: 15 October 2024 | **Revised:** 26 January 2025 | **Accepted:** 4 March 2025

Funding: This work was supported by the New Zealand Government as part of the Global Research Alliance on Agricultural Greenhouse Gases initiative, the CaSSECS Project (Carbon Sequestration and Greenhouse Gas Emissions in (Agro) Sylvopastoral Ecosystems in the Sahelian CILSS States) (FOOD/2019/410-169), and the Formas Project (Dnr 2021-00644).

Keywords: grazing intensity | herbaceous biomass and species diversity | Senegal | soil organic carbon

ABSTRACT

The impact of livestock grazing on soil organic carbon (SOC) stocks in the Sahel has been poorly documented due to a lack of data from different grazing intensities. This study evaluated SOC stocks under four grazing intensities within 0–30 cm soil depth in dry savanna ecosystems of Senegal. It also examined possible indirect relationships between grazing and SOC through herbaceous species diversity, herbaceous biomass, and carbon–nitrogen ratio. Four sites representing high, moderate, light, and no grazing intensity levels were selected. Transect survey methods were used for sampling soil and vegetation data within each of the sites. Data were analyzed using mixed-effects models and piecewise structural equation modeling (pSEM). SOC stocks were significantly different among the four grazing intensities, and higher stocks were observed with increased intensity. Furthermore, high-intensity grazing was shown to reduce the carbon–nitrogen ratio by negatively affecting the diversity of herbaceous species, which indirectly promoted SOC stocks. In conclusion, this study found that increased grazing intensity promoted SOC stocks both directly and indirectly through herbaceous species diversity.

1 | Introduction

The Kyoto Protocol describes soil as an essential biospheric carbon dioxide (CO_2) sink (Keesstra et al. 2016). The soil organic carbon (SOC) stock is estimated to be about 800 GtC in the first 30 cm of soil and between 1500 and 2000 GtC in the first meter (IPCC 2016). However, this stock is dynamic, continually accumulating and decaying (Don et al. 2023). Increasing SOC stocks through sequestration activities depends on the sustainable implementation of carbon sequestration management practices. Therefore, quantifying changes in soil use and identifying best management practices are essential to increase SOC stocks (Minasny et al. 2017). Rangeland ecosystems are gaining increasing attention, as they are one of the land use types that can store additional carbon in soils and biomass (Paustian et al. 2019). Rangelands are estimated to contain over 20% of the global SOC (FAO 2023). Hence, effective rangeland management can help mitigate climate change and lower atmospheric CO_2 levels (Gebremedhn et al. 2022). Grazing management practices, in particular, play a crucial role in modifying the structure and function of ecosystems, thereby impacting SOC stocks (Noulèkoun et al. 2021; Pineiro et al. 2010). Therefore, understanding the effects of grazing at the ecosystem level has become a primary goal for the sustainability of rangeland livestock systems (Friedel et al. 2004).

Livestock grazing influences rangelands primarily through three mechanisms: plant defoliation from grazing, soil and litter trampling, and the deposition of animal waste, such as feces and urine (Hiernaux et al. 1999). While these actions have immediate impacts on vegetation and soil, their repeated occurrence over time can lead to long-term changes in the soil's capacity to sustain plant growth (Zhang et al. 2018).

However, generalizing the effects of rangeland grazing, particularly its impact on the carbon cycle, has been a challenge. Research on grazing intensity has shown inconsistent results. Some studies have found that high grazing intensity decreases SOC stocks (Golluscio et al. 2009; Yong-Zhong et al. 2005) or shows no significant change (Aynekulu et al. 2017; Steffens et al. 2008). Conversely, other studies have indicated that under certain grazing intensities, SOC stocks can increase (Reeder and Schuman 2002; Schuman et al. 1999). A meta-analysis by McSherry and Ritchie (2013) noted that the effects of grazing on SOC stocks depend on various factors such as mean annual precipitation, soil type, species composition, and soil depth. Furthermore, the sustainability of SOC stocks is influenced by other factors, including direct human activities and biogeochemical processes (Golluscio et al. 2009; Smith 2005). In Sub-Saharan Africa, carbon storage on a per hectare basis has been enhanced through the incorporation of animal manures, agroforestry, and rotational grazing in rangelands (Dondini et al. 2023). These factors, along with the inconclusive nature of the evidence, indicate the need for a further study on the role of grazing in impacting SOC stocks before implementing soil carbon sequestration programs in African rangelands.

Pastoralism is pivotal for the livelihood of people of the African Sahel, contributing significantly to overall food security and the local economy (De Haan et al. 2016). It also provides vital ecological services, including erosion protection, wildlife habitat, and carbon sequestration (Mbow et al. 2020; Umutoni et al. 2015). However, this dry savanna ecosystem is subject to various forms of land and vegetation degradation driven by external factors such as climate change, drought, and desertification (Le Houérou 2002; Tagesson et al. 2015). Livestock grazing is often considered one of the main causes of vegetation and soil degradation in the Sahel (Rasmussen et al. 2018).

However, there is hardly any scientific data from the Sahel obtained under controlled stocking conditions and over periods long enough to allow the effects to manifest. However, a grazing experiment at the Dahra site in Senegal offered an opportunity to study this impact on vegetation dynamics in Sahelian climatic conditions (Gebremedhn et al. 2023). The study found that grazing intensity had a negative indirect influence on total plant biomass due to its negative influence on species diversity. Changes in grazing intensity can therefore potentially affect the rangeland SOC stocks, but we know relatively little about the direct and indirect effects of grazing intensity on SOC stocks under Sahelian climatic conditions.

In this study, we analyzed the impact of grazing intensity on soil carbon stocks at three different soil depths and investigated the indirect effect through their interaction with herbaceous species diversity and biomass in four dry savanna ecosystems of Senegal. More specifically, we aimed to (i) determine the effects of grazing intensity on SOC stocks at different soil depths; (ii) examine the main effects and interactions of grazing intensity, herbaceous species diversity, and biomass on SOC stocks; and (iii) examine possible indirect relationships between grazing and SOC through herbaceous species diversity and biomass.

2 | Materials and Methods

2.1 | Site Description

The study was conducted at the Dahra research site (15°21′N, 15°28′W) in Senegal (Figure 1), which is in the western part of the Sahelian region. The site's average annual rainfall is 371 mm. The rainfall climatology includes a ~9-month-long dry season (October–July) and a ~3-month rainy season (July–October), which also represents the growing season (Agence Nationale de l'Aviation Civile et de la Météorologie, Senegal). The main soils are sandy and poorly fertile due to low buffer and exchange capacity, locally classified as Dior (Aubert and Newsky 1949) or as Arenosols (IUSS-WRB 2015).

Three percent of the site is covered with shrubs and trees (Rasmussen et al. 2011), most of which are *Balanites aegyptiaca*, *Vachellia tortilis*, and *Senegalia senegal* species. Its main ground vegetations are annual grasses (e.g., *Cenchrus biflorus*, *Eragrostis tremula*, *Aristida mutabilis*, and *Dactyloctenium aegyptium*) and forbs (e.g., *Diodella samentosa* and *Zornia glochidiata*) (Tagesson et al. 2015; Gebremedhn et al. 2023). Dahra is a pastoral site whose average livestock stocking rate, according to Assouma et al. (2018) estimate, ranges from 0.43 Tropical

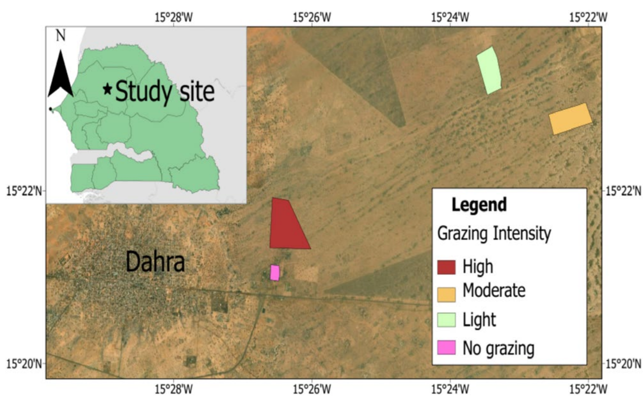

FIGURE 1 | Map of Senegal showing the location of the study area and the experimental sites. [Colour figure can be viewed at wileyonlinelibrary.com]

Livestock Unit (TLU)/ha during the wet season to 0.31 TLU/ha during the dry season.

2.2 | Plot Selection and Sampling Design

We used distance from settlements as an indicator of a difference in the level of grazing intensity (Gebremedhn et al. 2023). We assumed that sites near or surrounding settlements experience frequent livestock grazing and are therefore considered sites of high grazing intensity and that grazing intensity decreases with increasing distance from settlements. After we made a reconnaissance survey with the resource managers with extensive knowledge about the historical and current grazing practices in the study area, we selected areas representing four different levels of grazing intensity to assess their effects on SOC Stock. They are described as follows:

1. "High grazing" intensity: This site is located within the Centre de Recherche Zootechnique (CRZ) and is managed by the Institut Sénégalais de Recherche Agronomique (ISRA). The CRZ, established in 1950, is a controlled livestock area where cattle (*Bos taurus indicus*) have limited mobility. Its herd size dropped from 2203 heads in 1984 to 138 heads in 2022. The site encompasses 900 ha and experiences two grazing pressures: (i) year-round grazing by the CRZ's cattle, with no alternative feed sources, resulting in overgrazing during the prolonged dry season, poor animal condition, and death due to feed shortages; and (ii) seasonal grazing by cows, sheep (*Ovis aries*), goats (*Capra aegagrus hircus*), and horses (*Equus ferus caballus*) from pastoralists, who settle temporarily in the area to seek feed. These livestock move once local vegetation is depleted, but their stocking rates are unknown.
2. "Moderate grazing" intensity: This site is located approximately 10 km from the CRZ and represents typical communal grazing in the Sahelian Savanna. It supports pastoral systems where livestock (primarily cattle, goats, and sheep) graze year-round, with forage availability fluctuating seasonally. High biomass and better forage quality are present during the growing season and early dry season (August–December), while feed availability significantly decreases from January to May, prompting pastoralists to seek alternative grazing areas. The average stocking density per hectare at this site is also unknown.
3. "Light grazing" intensity: An enclosure covering about 20 ha, used primarily for grazing in the dry season (January–July), was selected to represent light grazing. This site has been fenced for about 5 years. This site was established adjacent to the moderate-grazing site. The objective of the enclosure was to assess grass species regeneration and forage productivity by restricting livestock access during the vegetation growth period. Similar to other grazing sites, cattle, goats, and sheep dominate grazing in the area during the dry season. However, due to animals occasionally entering and grazing within the enclosure, the stocking rate at this site could not be estimated.
4. "No grazing" site: An 18-year-old fenced area, covering around 0.32 ha, was chosen to represent the absence of grazing. This site was established in the center of the high-grazing-intensity area (i.e., within the CRZ settlement) and is primarily used for hay production, with grasses harvested once a year, usually in April.

We employed a transect survey to collect soil and vegetation data across these four sites. At the high-grazing intensity site, a 7 km east-to-west transect was established within the CRZ. Quadrats (1 m^2) were placed at 200 m intervals, yielding a total of 36 quadrats. In the moderate-grazing site, a 4 km transect was laid out with quadrats spaced 200 m apart, resulting in 21 quadrats. For the light-grazing site (enclosure), a 400 m transect was established, with 21 quadrats placed at 20 m intervals. Finally, in the no-grazing site, three parallel 80 m transects were established with quadrats spaced 10 m apart, yielding 21 quadrats. These sampling strategies were designed to ensure data collection covered the entire treatment area. The smaller quadrat intervals for the light- and no-grazing sites were due to their smaller size compared to the high- and moderate-grazing sites.

2.3 | Soil Sampling and Analysis

2.3.1 | Soil Collection

In each of the 1 m^2 quadrats, soil samples at three depths (0–10, 10–20, and 20–30 cm) were taken. Bulk density giving 297 samples (expressed in g cm^{-3}) for the three depths was determined using a 197-cm^3 core ring (5 cm diameter), after drying to a constant weight at a temperature of 65°C. The coarse fragments in these sandy soils were less than 1% and considered negligible. After oven-drying and sieving (2-mm mesh size), all samples were stored for carbon and nitrogen content analysis.

2.3.2 | Soil Carbon and Nitrogen Contents

To assess the SOC content, infrared spectrometry and chemical analysis were used according to the procedure previously applied to Senegalese sandy soil by Malou et al. (2021). The sieved soil samples ($n = 297$) were scanned to obtain their spectral signatures in the visible and near-infrared reflectance spectra (VisNIR) range (350–3500 nm) using a LabSpec 4 spectrophotometer (Analytical Spectral Devices, ASD, Boulder, CO, USA). Noise reduction and spectral enhancement were done with a Savitsky-Golay derivative transformation with an order of 1, a polynomial order of 2, and a smoothing window of 11 data points. The Kennard–Stone algorithm (Kennard and Stone 1969) was used in Unscrambler 10.5 (Camo Software, Oslo, Norway) to identify the most representative samples for building the model, using both laboratory measurements and the reflectance spectra. Thus, a subset of 102 soil samples was selected to run conventional laboratory analyses at the ISO9001:2015-certified IRD LAMA's laboratory in Dakar. The C (and N) concentrations were determined by dry combustion on 100-mg aliquots of soil (ground to < 0.2 mm), using an elemental analyzer (Thermo Finnigan Flash EA1112, Milan, Italy). These measurements were used as calibration ($n = 72$) and validation ($n = 30$) subsets. The coefficient of determination (R^2) between predictions and observations in the calibration subset reached 0.92. The performance of the validation model was additionally evaluated by the figures of merit commonly used in IR spectroscopy applied to soil (Barthès et al. 2019; Malou et al. 2021).

2.3.3 | SOC Stocks

The SOC stocks for each layer were calculated as follows:

$$\mathrm{SOC}_i \left(\mathrm{Mg\,C\,ha^{-1}}\right) = \mathrm{BD}_i \times \mathrm{d}_i \times \mathrm{OC}_i$$

where BD is the bulk density of the different soil depths ($i = 1$–3) ($\mathrm{g\,cm^{-3}}$); d is the thickness of the measured soil depth layer (0.1 m); and OC_i is the organic C content (in g $\mathrm{kg^{-1}}$ soil). The total SOC stocks for the 0–30 cm soil depth were calculated by summing the SOC for the three soil depth layers.

2.4 | Vegetation Collection and Related Parameters

In each of the 1 m^2 quadrats, species diversity and herbaceous biomass were also measured. Species diversity was quantified using the Shannon–Weiner diversity index (H), as outlined in Krebs (1999):

$$H' = -\sum_{i=1}^{s} p_i \ln p_i$$

where s represents the number of species, p_i is the proportion of individuals or abundance of the ith species, and *ln* refers to the natural logarithm based on e.

To estimate the aboveground herbaceous dry biomass (AHB), both live and dead aboveground materials were harvested from each 1 m^2 quadrat at the peak flowering stage. The fresh weight of the samples was recorded in the field. Subsequently, 30% of the samples from each quadrat were placed in paper bags for dry matter analysis. These samples were dried in an oven at 105°C for 48 h (Jagodziński et al. 2020), after which the dry weight was determined. Then, the total dry herbaceous biomass in each quadrat was calculated by multiplying the proportion of each dried sample's biomass by the weight of the total fresh biomass.

2.5 | Data Analysis

All statistical analyses were conducted using the R software, version 4.2.2 (R Core Team 2022). Mixed-effects models were employed to evaluate the effects of grazing intensity and soil depth on SOC stocks. This analysis was performed using the lmer function from the *lmerTest* R Package (Kuznetsova et al. 2017), with the plot included as a random grouping factor, allowing for the accounting of unknown effects. The response variable was log-transformed to comply with the normality assumption, which was tested using the Shapiro–Wilk statistic ($W = 0.97488$, p value $= 0.06439$). As we found no interaction between soil depth and grazing intensity, further analyses were considered for 0–30 soil depth. Next, we examined the main and interacting effects of grazing intensity, herbaceous species diversity, and biomass on SOC stocks at a depth of 0–30 cm by applying linear models.

To explore the potential indirect effects of grazing on SOC mediated by herbaceous species diversity and biomass, we utilized structural equation modeling (SEM). Prior to developing the SEM, we examined the correlation between species diversity and the carbon-to-nitrogen (C:N) ratio and found that increased species diversity was associated with a rise in the C:N ratio (see Figure S1). The analysis proceeded by first evaluating the effect of grazing intensity on species diversity, biomass, and soil C:N ratio. We then assessed the direct effect of species diversity, biomass, and soil C:N ratio on SOC stock. Grazing intensity was treated as an ordered categorical variable, with 0 representing no grazing, 1 for light grazing, 2 for moderate grazing, and 3 for heavy grazing intensity. The SEM was executed using the piecewise SEM (pSEM) function from the *piecewiseSEM* package (Lefcheck 2016). Model fit was assessed using Fisher's C statistic and the corresponding p value.

3 | Results

3.1 | Grazing Intensity Effects on SOC Stocks

SOC stocks were significantly different among different grazing intensities ($p < 0.005$) and varied according to soil depth ($p < 0.001$) (Table 1). Higher SOC stocks were observed in areas with increased grazing intensity (Figure 2a). Additionally, our results indicated a substantial decrease in SOC stocks with increasing soil depth across all grazing intensity levels (Figure 2b). However, we found no significant interaction between grazing intensity and SOC at the different soil depths (Table 1; Figure S2).

3.2 | Main and Interaction Effects of Grazing Intensity, Herbaceous Diversity, and Biomass on SOC Stocks

There was a significant interaction between herbaceous diversity and grazing intensity on SOC stocks ($p = 0.038$; Table 2). In particular, SOC was positively associated with herbaceous species diversity in the high grazing sites, while it was negatively associated with light grazing sites (Figure 3). On no and moderate grazing sites, we found no significant relationship between

TABLE 1 | Result of the mixed effects models testing main effects and interactions of grazing intensity, and depth on soil carbon.

	numDF	denDF	F	p
Grazing intensity	3	58	4.60232	0.0059
Soil depth	1	31	49.20136	< 0.0001
Grazing intensity: soil depth	3	31	1.59559	0.2104

diversity and SOC (Figure 3). Herbaceous biomass did not influence SOC, nor did it show a significant interaction with grazing intensity (Table 2).

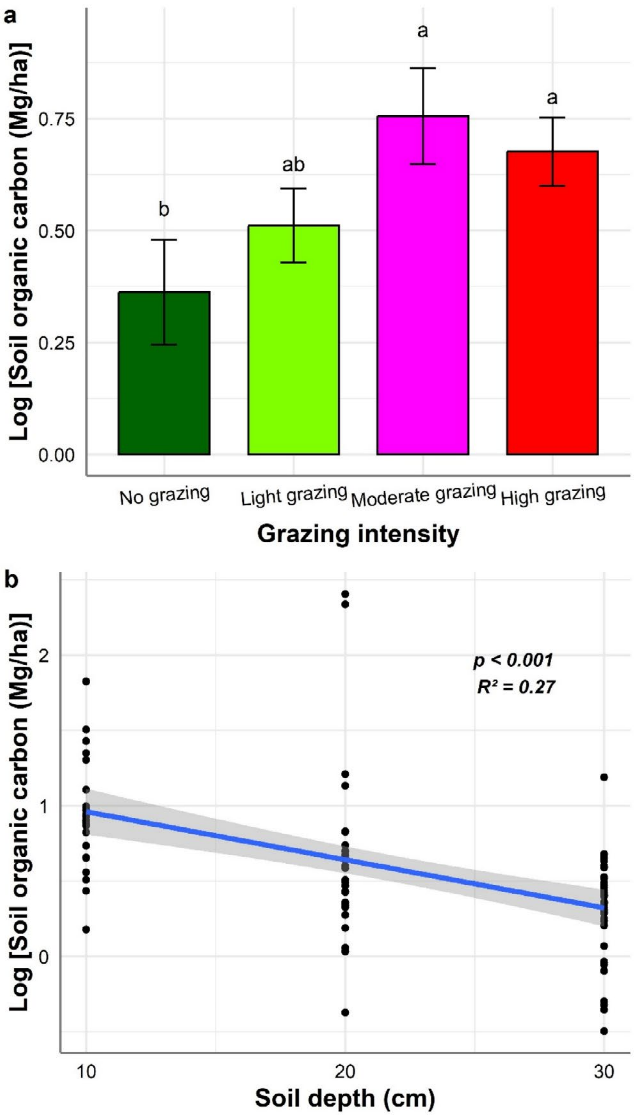

FIGURE 2 | Variations of soil organic carbon across levels of grazing intensity (a) and soil depth (b). Summary statistics and significance are given in Table 1. In (a), bar plots show means ± standard error, with letters denoting comparison between grazing intensity levels. [Colour figure can be viewed at wileyonlinelibrary.com]

3.3 | Direct and Indirect Influence of Grazing Intensity on the SOC Stocks and the C:N Ratio

The SEM explained 21% of the variance in SOC and showed a good fit to the data ($p > 0.05$; Figure 4). Grazing intensity had a significant direct negative impact on both herbaceous species diversity and biomass (Table 3). Additionally, increased grazing intensity in Sahelian savanna ecosystems reduced the C:N ratio by negatively affecting species diversity ($\beta = -0.54 \times 0.345 = -0.19$; Table 3; Figure 4). This, in turn, indirectly promoted SOC stock due to the relationship between the C:N ratio and SOC ($\beta = -0.19 \times -0.41 = 0.08$ Table 3; Figure 4).

4 | Discussion

We found significantly higher SOC stocks in areas subjected to high grazing intensity levels. The highest amount of feces was also observed in these areas, and this could contribute to the larger SOC stock. In line with this, Dungait et al. (2009) noted that the mass presence of feces in heavily grazed sites could result in the accumulation of SOC stocks. Furthermore, our research showed a strong decrease in SOC between 10 cm and 30 cm depths across all grazing intensity levels. Grazing animals promote the formation of litter-derived SOC in the topsoil, as heavy trampling during prolonged dry seasons could disrupt the sandy soil (Bikila et al. 2016). However, the high carbon stocks in the top 0–10 cm layer are less stable than SOC deeper in the soil, because soil microorganisms are more active in the topsoil due to the higher temperature and humidity (Jackson et al. 2017; Chen et al. 2020).

In contrast to the present findings, higher grazing intensity is generally expected to result in greater SOC loss due to increased removal of photosynthetic tissue and subsequent respiration of assimilated carbon by grazers, which reduces potential carbon inputs to soil organic matter (Gebremedhn et al. 2022; Phukubye et al., Phukubye et al. 2022; Yuan and Hou 2015). McSherry and Ritchie (2013) noted that the balance between the positive and negative effects of grazing on SOC stocks depends on various factors, including climate, soil characteristics, and grass type. For example, they observed that in soils with higher clay content, grazing tends to have a more pronounced negative effect on SOC under higher precipitation conditions. Conversely, in coarser soils with a higher proportion of sand and lower clay content, grazing showed the opposite trend. Similarly, Conant and Paustian (2002) reported that SOC losses decreased with

TABLE 2 | Analysis of variance table resulting from multiple linear model testing for the main and interaction effects of grazing intensity, herbaceous diversity, and biomass on SOC.

	Df	Sum Sq.	Mean Sq.	F	Pr (>F)
Shannon diversity	1	1.3343	1.33435	8.42	0.0055
Grazing intensity	3	0.5835	0.1945	1.23	0.3094
Herbaceous biomass	1	0.0077	0.00768	0.049	0.8266
Shannon diversity: grazing intensity	3	1.4358	0.47861	3.02	0.0382
Grazing intensity: herbaceous biomass	3	0.1652	0.05507	0.35	0.7910
Residuals	50	7.9206	0.15841		

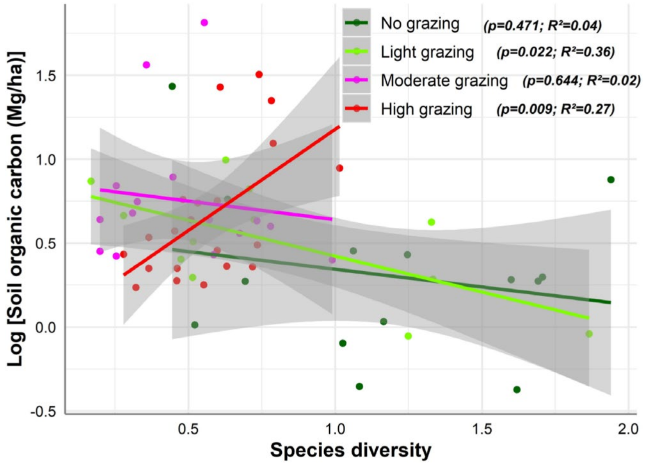

FIGURE 3 | Interaction effects of grazing intensity and herbaceous diversity on soil organic carbon. [Colour figure can be viewed at wileyonlinelibrary.com]

reduced grazing intensity in drier areas, whereas significant SOC stocks were observed in wetter regions. The current study experiences a prolonged dry season with only 3 months of rain annually. Therefore, in these semi-arid areas, intense grazing may promote the formation of SOC by facilitating the decomposition of standing plants and the incorporation of litter into the soil through high trampling. Additionally, the significant presence of fecal matter in heavily grazed sites could contribute to the accumulation of SOC stocks on the soil surface.

Regarding methodological approaches, Bernoux et al. (2005) outlined two methods for assessing changes in SOC: diachronic and synchronic. The diachronic approach involves measuring SOC changes over time on the same field plot, providing precise data on carbon sequestration. However, a baseline data set and long-term monitoring are required to capture changes exceeding the uncertainty of measurements. These requirements were not feasible within the time constraints and scope of our study. Consequently, we employed the synchronic approach,

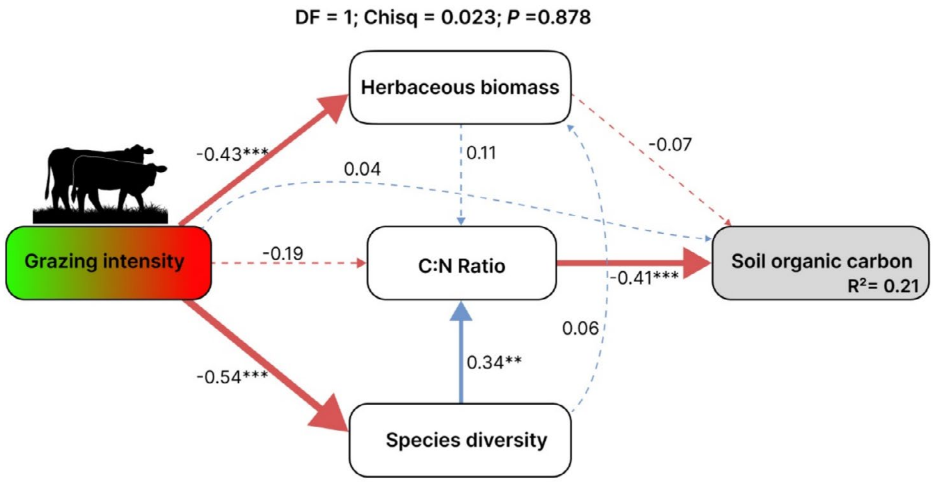

FIGURE 4 | Structural equation model depicting the interconnected pathways among grazing intensity, species diversity, herbaceous biomass, soil C:N ratio, and SOC. Arrows indicate the hypothesized causal relationships. Standardized path coefficients and their corresponding significance levels can be found in Table 3. Red arrows denote negative impacts, while blue arrows signify positive effects. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 3 | Summary of the structural equation model testing the interrelated paths between grazing intensity, herbaceous diversity (Shannon index), biomass, C:N ratio, and soil carbon stock (SOC).

Response variable	Predictor	est. std	SE	*Z*	*p*	ci. lower	ci. upper
Herbaceous biomass	Shannon diversity	0.057	0.133	0.427	0.669	−0.204	0.318
Herbaceous biomass	Grazing intensity	−0.432	0.12	−3.594	< 0.001	−0.668	−0.197
Shannon diversity	Grazing intensity	−0.537	0.084	−6.415	< 0.001	−0.701	−0.373
C:N ratio	Shannon diversity	0.345	0.123	2.803	0.005	0.104	0.586
C:N ratio	Grazing intensity	−0.189	0.136	−1.385	0.166	−0.456	0.078
C:N ratio	Herbaceous biomass	0.109	0.122	0.9	0.368	−0.129	0.348
SOC	Grazing intensity	0.038	0.136	0.278	0.781	−0.228	0.304
SOC	Herbaceous biomass	−0.066	0.128	−0.516	0.606	−0.318	0.186
SOC	C:N ratio	−0.41	0.117	−3.504	< 0.001	−0.64	−0.181

Abbreviations: est. std, standardized estimate; SE, standard error.

which compares SOC stocks across plots subjected to different grazing intensities at a single time point. While this method is practical and cost-effective, it assumes that reference plots represent baseline conditions and attribute SOC differences solely to grazing effects. This assumption can be influenced by confounding factors such as historical land-use changes, erosion, or site-specific variations. Although we minimized these potential biases by selecting plots with similar soil types, topography, and management histories, we acknowledge that the synchronic approach introduces greater uncertainty compared to the diachronic method. Future studies incorporating diachronic designs or long-term datasets are essential to validate and enhance the understanding of grazing effects on SOC dynamics. Species diversity and SOC stocks were inversely correlated with increasing grazing intensity. While species diversity declined with increasing grazing intensity (Gebremedhn et al. 2023), SOC stocks increased (Figure 2). Furthermore, we found a significant interaction effect between grazing intensity and the diversity of species on SOC stocks. This suggests that the effect of species diversity on SOC stocks depends on the level of grazing intensity. Specifically, a positive correlation between SOC stocks and species diversity was observed in plots with high grazing intensity, whereas SOC stocks tended to decrease in the three lower grazing intensity plots (Figure 3).

At lower grazing intensities, higher species diversity may lead to increased plant competition for nutrients and water, potentially enhancing mineralization and nutrient cycling. This intensified nutrient cycling could stimulate microbial activity, resulting in increased microbial respiration and accelerated organic matter decomposition, ultimately reducing SOC stocks (Bardgett and Wardle 2003; Yang et al. 2021). Additionally, diverse plant communities often produce more heterogeneous and lower-quality litter, characterized by a higher C:N ratio and lower decomposition rates (Cotrufo et al. 2015; Hobbie 2015; Prescott 2010). While this might initially slow the breakdown of organic matter, it can also lead to reduced substrate use efficiency by soil microbes, as they expend more energy to process complex organic materials. This inefficiency could limit the accumulation of microbial-derived SOC, which is a key contributor to long-term soil carbon sequestration (Cotrufo et al. 2015).

Under lower grazing intensities, reduced herbivory may further limit the input of easily decomposable organic material, such as dung and urine, which are significant sources of labile SOC (Miller-Goodman 2002). This lack of labile carbon could constrain microbial activity, especially in plots with high species diversity where competition for resources is more intense (Bardgett and Wardle 2003). As a result, the potential for SOC stocks is reduced. In contrast, under high grazing intensity, the combination of increased species diversity and greater inputs of labile organic matter may promote SOC storage despite the negative effects of grazing on biomass production (Chen et al. 2020). Furthermore, the bivariate analysis revealed that grazing intensity had a significant direct negative effect on both herbaceous species diversity and biomass. Unlike herbaceous biomass, an increase in species diversity led to an increase in the C:N ratio. Additionally, the C:N ratio had a negative correlation with the SOC stocks. In line with this finding, a meta-analysis by Zhou et al. (2019) noted that a low C:N ratio promotes SOC stocks due to the high decomposition rates (high litter turnover). This suggests that an increase in grazing intensity reduces the C:N ratio due to its negative impact on species' diversity. Thus, grazing intensity indirectly promotes SOC stocks by reducing species diversity and altering nutrient cycling. This showed the important role of grazing intensity in shaping savanna SOC storage both directly and indirectly through herbaceous species diversity (Pineiro et al. 2010; Sanaei et al. 2023).

5 | Conclusions

In conclusion, this study highlights the significant influence of grazing intensity on SOC stocks in the semi-arid savanna ecosystems of Senegal. SOC stocks increased both directly and indirectly through increased herbaceous species diversity in areas with higher grazing intensity. This finding revealed important correlations between grazing intensity, herbaceous species diversity, and the C:N ratio, and demonstrated that grazing intensity indirectly promoted SOC stock by reducing species' diversity and altering nutrient cycling.

Author Contributions

Haftay Hailu Gebremedhn designed the study and drafted the paper. Sylvanus Mensah and Haftay Hailu Gebremedhn performed the data analyses. All authors contributed to writing, interpreting the results, and discussing the research objectives.

Acknowledgements

This research was supported by the New Zealand Government as part of the Global Research Alliance on Agricultural Greenhouse Gases initiative, as well as through funding from the CaSSECS Project (Carbon Sequestration and Greenhouse Gas Emissions in (Agro) Sylvopastoral Ecosystems in the Sahelian CILSS States) (FOOD/2019/410-169). Torbern Tagesson considers this research as part of his Formas Project (Dnr 2021-00644). The authors deeply thank the technical staff of the IRD facilities (LAMA & IESOL) in Dakar for their assistance. We thank all the staff of CRZ (*Centre de Recherche Zootechnique*) and the community for their assistance during field data collection. Open access publishing facilitated by AgResearch Ltd, as part of the Wiley - AgResearch Ltd agreement via the Council of Australian University Librarians.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

Assouma, M. H., P. Lecomte, P. Hiernaux, et al. 2018. "How to Better Account for Livestock Diversity and Fodder Seasonality in Assessing the Fodder Intake of Livestock Grazing Semi-Arid Sub-Saharan Africa Rangelands." *Livestock Science* 216: 16–23. https://doi.org/10.1016/j.livsci.2018.07.002.

Aubert, G., and B. Newsky. 1949. "Note on the Vernacular Names of the Soils of the Sudan and Senegal." In *Proceedings 1st Commonwealth Conference on Tropical and Subtropical Soils (Communication No. 46)*, 107–109. Commonwealth Bureau of Soil Science Technical. https://

horizon.documentation.ird.fr/exl-doc/pleins_textes/pleins_textes_5/b_fdi_12-13/16042. Accessed 2 April 2021.

Aynekulu, E., W. Mekuria, D. Tsegaye, et al. 2017. "Long-Term Livestock Exclosure Did Not Affect Soil Carbon in Southern Ethiopian Rangelands." *Geoderma* 307: 1–7. https://doi.org/10.1016/j.geoderma.2017.07.030.

Bardgett, R. D., and D. A. Wardle. 2003. "Herbivore-Mediated Linkages Between Aboveground and Belowground Communities." *Ecology* 84: 2258–2268. https://doi.org/10.1890/02-0274.

Barthès, B. G., E. Kouakoua, M. Clairotte, et al. 2019. "Performance Comparison Between a Miniaturized and a Conventional Near Infrared Reflectance (NIR) Spectrometer for Characterizing Soil Carbon and Nitrogen." *Geoderma* 338: 422–429. https://doi.org/10.1016/j.geoderma.2018.12.031.

Bernoux, M., C. Feller, C. C. Cerri, V. Eschenbrenner, and C. E. P. Cerri. 2005. "Soil Carbon Sequestration." In *Soil Erosion and Carbon Dynamics*, 13–22. CRC Press.

Bikila, N. G., Z. K. Tessema, and E. G. Abule. 2016. "Carbon Sequestration Potentials of Semi-Arid Rangelands Under Traditional Management Practices in Borana, Southern Ethiopia." *Agriculture, Ecosystems and Environment* 223: 108–114. https://doi.org/10.1016/j.agee.2016.02.028.

Chen, X., H. Y. H. Chen, C. Chen, et al. 2020. "Effects of Plant Diversity on Soil Carbon in Diverse Ecosystems: A Global Meta-Analysis." *Biological Reviews* 95: 167–183. https://doi.org/10.1111/brv.12554.

Conant, R. T., and K. Paustian. 2002. "Potential Soil Carbon Sequestration in Overgrazed Grassland Ecosystems." *Global Biogeochemical Cycles* 16: 90-91–90-9. https://doi.org/10.1029/2001gb001661.

Cotrufo, M. F., J. L. Soong, A. J. Horton, et al. 2015. "Formation of Soil Organic Matter via Biochemical and Physical Pathways of Litter Mass Loss." *Nature Geoscience* 8: 776–779. https://doi.org/10.1038/ngeo2520.

De Haan, C., E. Dubern, B. Garancher, and C. Quintero. 2016. *Pastoralism Development in the Sahel: A Road to Stability?* World Bank. https://doi.org/10.1596/24228.

Don, A., F. Seidel, J. Leifeld, et al. 2023. "Carbon Sequestration in Soils and Climate Change Mitigation—Definitions and Pitfalls." *Global Change Biology* 30, no. 1: e16983. https://doi.org/10.1111/gcb.16983.

Dondini, M., M. Martin, C. De Camillis, et al. 2023. "Global Assessment of Soil Carbon in Grasslands–From Current Stock Estimates to Sequestration Potential." In *FAO Animal Production and Health Paper No. 187*. FAO. https://doi.org/10.4060/cc3981e.

Dungait, J. A. J., R. Bol, I. D. Bull, and R. P. Evershed. 2009. "Tracking the Fate of Dung-Derived Carbohydrates in a Temperate Grassland Soil Using Compound-Specific Stable Isotope Analysis." *Organic Geochemistry* 40, no. 10: 1210–1218. https://doi.org/10.1016/j.orggeochem.2009.08.001.

FAO. 2023. "Global Assessment of Soil Carbon in Grasslands." Food and Agriculture Organization of the United Nations. Animal Production and Health/Paper 187. https://doi.org/10.4060/cc3981en.

Friedel, M. H., G. C. Stuart-Hill, and D. Walsh. 2004. "What Engages the Interest of Land Managers in Rangeland Monitoring?" *African Journal of Range & Forage Science* 21: 89–100. https://doi.org/10.2989/10220110409485839.

Gebremedhn, H. H., T. Z. Kelkay, Y. Tesfay, et al. 2022. "Carbon Stock and Change Rate Under Different Grazing Management Practices in Semiarid Pastoral Ecosystem of Eastern Ethiopia." *Land* 11, no. 5: 639. https://doi.org/10.3390/land11050639.

Gebremedhn, H. H., O. Ndiaye, S. Mensah, and C. Fassinou. 2023. "Grazing Effects on Vegetation Dynamics in the Savannah Ecosystems of the Sahel." *Ecological Processes* 12, no. 1: 12–54. https://doi.org/10.1186/s13717-023-00468-3.

Golluscio, R. A., A. T. Austin, G. C. García Martínez, M. Gonzalez-Polo, O. E. Sala, and R. B. Jackson. 2009. "Sheep Grazing Decreases Organic Carbon and Nitrogen Pools in the Patagonian Steppe: Combination of Direct and Indirect Effects." *Ecosystems* 12: 686–697. https://doi.org/10.1007/s10021-009-9252-6.

Hiernaux, P., C. L. Bielders, C. Valentin, A. Bationo, and S. Fernández-Rivera. 1999. "Effects of Livestock Grazing on Physical and Chemical Properties of Sandy Soils in Sahelian Rangelands." *Journal of Arid Environments* 41: 231–245. https://doi.org/10.1006/jare.1998.0475.

Hobbie, S. E. 2015. "Plant Species Effects on Nutrient Cycling: Revisiting Litter Feedbacks." *Trends in Ecology & Evolution* 30: 357–363. https://doi.org/10.1016/j.tree.2015.03.015.

IPCC. 2016. *2016 Refinement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories*, edited by E. C. Buendia, K. Tanabe, A. Kranjc, et al. Intergovernmental Panel on Climate Change (IPCC). https://www.ipcc-nggip.iges.or.jp/public/2016rf/index.html.

IUSS Working Group WRB. 2015. *World Reference Base for Soil Resources 2014, Update 2015: International Soil Classification System for Naming Soils and Creating Legends for Soil Maps*. FAO.

Jackson, R. B., K. Lajtha, S. E. Crow, G. Hugelius, M. G. Kramer, and G. Piñeiro. 2017. "The Ecology of Soil Carbon: Pools, Vulnerabilities, and Biotic and Abiotic Controls." *Annual Review of Ecology, Evolution, and Systematics* 48: 419–445. https://doi.org/10.1146/annurev-ecolsys-112414-054234.

Jagodziński, A. M., M. K. Dyderski, K. Gęsikiewicz, and P. Horodecki. 2020. "Consequences of Different Sample Drying Temperatures for Accuracy of Biomass Inventories in Forest Ecosystems." *Scientific Reports* 10: 1–8. https://doi.org/10.1038/s41598-020-73053-9.

Le Houérou, H. N. 2002. "Man-Made Deserts: Desertization Processes and Threats." *Arid Land Research and Management* 16, no. 1: 1–36. https://doi.org/10.1080/153249802753365296.

Keesstra, S. D., J. Bouma, J. Wallinga, et al. 2016. "The Significance of Soils and Soil Science Towards Realization of the United Nations Sustainable Development Goals." *Soil* 2, no. 2: 111–128. https://doi.org/10.5194/soil-2-111-2016.

Kennard, R. W., and L. A. Stone. 1969. "Computer Aided Design of Experiments." *Technometrics* 11, no. 1: 137–148. https://doi.org/10.1080/00401706.1969.10490666.

Krebs, C. J. 1999. *Ecological Methodology*. Addison Wesley Longman Inc.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. "lmerTest Package: Tests in Linear Mixed Effects Models." *Journal of Statistical Software* 82: 1–26. https://doi.org/10.18637/JSS.V082.I13.

Lefcheck, J. S. 2016. "piecewiseSEM: Piecewise Structural Equation Modelling in r for Ecology, Evolution, and Systematics." *Methods in Ecology and Evolution* 7: 573–579. https://doi.org/10.1111/2041-210X.12512.

Malou, O. P., P. Moulin, T. Chevallier, et al. 2021. "Estimates of Carbon Stocks in Sandy Soils Cultivated under Local Management Practices in Senegal's Groundnut Basin." *Regional Environmental Change* 21, no. 3: 301–315. https://doi.org/10.1007/s10113-021-01790-2.

Mbow, C., M. Halle, R. El Fadel, and I. Thiaw. 2020. "Land Resources Opportunities for a Growing Prosperity in the Sahel." *Current Opinion in Environment Sustainability* 48: 85–92. https://doi.org/10.1016/j.cosust.2020.11.005.

McSherry, M. E., and M. E. Ritchie. 2013. "Effects of Grazing on Grassland Soil Carbon: A Global Review." *Global Change Biology* 19: 1347–1357. https://doi.org/10.1111/gcb.12144.

Miller-Goodman, M. S. 2002. "Grassland Ecophysiology and Grazing Ecology." *Crop Science* 42: 981. https://doi.org/10.2135/cropsci2002.0981.

Minasny, B., B. P. Malone, A. B. Mcbratney, et al. 2017. "Geoderma Soil Carbon 4 Per Mille." *Geoderma* 292: 59–86. https://doi.org/10.1016/j.geoderma.2017.01.002.

Noulèkoun, F., E. Birhane, H. Kassa, et al. 2021. "Grazing Exclosures Increase Soil Organic Carbon Stock at a Rate Greater Than "4 per 1000" Per Year Across Agricultural Landscapes in Northern Ethiopia." *Science of the Total Environment* 782: 146821. https://doi.org/10.1016/j.scitotenv.2021.146821.

Paustian, K., E. Larson, J. Kent, E. Marx, and A. Swan. 2019. "Soil C Sequestration as a Biological Negative Emission Strategy." *Frontiers in Climate* 1: 1–11. https://doi.org/10.3389/fclim.2019.00008.

Phukubye, K., M. Mutema, N. Buthelezi, P. Muchaonyerwa, and C. Cerri. 2022. "On the Impact of Grassland Management on Soil Carbon Stocks: A Worldwide Meta-Analysis." *Geoderma Régional* 28: e00479. https://doi.org/10.1016/j.geodrs.2021.e00479.

Pineiro, G., J. M. Paruelo, M. Oesterheld, and E. G. Jobbágy. 2010. "Pathways of Grazing Effects on Soil Organic Carbon and Nitrogen." *Rangeland Ecology & Management* 63: 109–119. https://doi.org/10.2111/08-255.1.

Prescott, C. E. 2010. "Litter Decomposition: What Controls It and How Can We Alter It to Sequester More Carbon in Forest Soils?" *Biogeochemistry* 101: 133–149. https://doi.org/10.1007/s10533-010-9439-0.

R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.r-project.org/.

Rasmussen, K., M. Brandt, X. Tong, et al. 2018. "Does Grazing Cause Land Degradation? Evidence From the Sandy Ferlo in Northern Senegal." *Land Degradation & Development* 29: 4337–4347. https://doi.org/10.1002/ldr.3170.

Rasmussen, M. O., F. M. Göttsche, D. Diop, et al. 2011. "Tree Survey and Allometric Models for Tiger Bush in Northern Senegal and Comparison With Tree Parameters Derived From High Resolution Satellite Data." *International Journal of Applied Earth Observation and Geoinformation* 13: 517–527. https://doi.org/10.1016/j.jag.2011.01.007.

Reeder, J., and G. Schuman. 2002. "Influence of Livestock Grazing on C Sequestration in Semi-Arid Mixed-Grass and Short-Grass Rangelands." *Environmental Pollution* 116: 457–463. https://doi.org/10.1016/S0269-7491(01)00223-8.

Sanaei, A., E. J. Sayer, Z. Yuan, et al. 2023. "Grazing Intensity Alters the Plant Diversity–Ecosystem Carbon Storage Relationship in Rangelands Across Topographic and Climatic Gradients." *Functional Ecology* 37: 703–718. https://doi.org/10.1111/1365-2435.14270.

Schuman, G. E., J. D. Reeder, J. T. Manley, R. H. Hart, and W. A. Manley. 1999. "Impact of Grazing Management on the Carbon and Nitrogen Balance of a Mixed-Grass Rangeland." *Ecological Applications* 9: 65–71. https://doi.org/10.1890/1051-0761(1999)009[0065:IOGMOT]2.0.CO;2.

Smith, P. 2005. "An Overview of the Permanence of Soil Organic Carbon Stocks: Influence of Direct Human-Induced, Indirect and Natural Effects." *European Journal of Soil Science* 56: 673–680. https://doi.org/10.1111/j.1365-2389.2005.00708.x.

Steffens, M., A. Kölbl, K. U. Totsche, and I. Kögel-Knabner. 2008. "Grazing Effects on Soil Chemical and Physical Properties in a Semiarid Steppe of Inner Mongolia (P.R. China)." *Geoderma* 143: 63–72. https://doi.org/10.1016/j.geoderma.2007.09.004.

Tagesson, T., R. Fensholt, I. Guiro, et al. 2015. "Ecosystem Properties of Semiarid Savanna Grassland in West Africa and Its Relationship with Environmental Variability." *Global Change Biology* 21, no. 1: 250–264. Portico. https://doi.org/10.1111/gcb.12734.

Umutoni, C., A. A. Ayantunde, and B. Faso. 2015. "Evaluation of Feed Resources in Mixed Crop-Livestock Systems in Sudano-Sahelian Zone of Mali in West Africa." *International Journal of Livestock Research* 5, no. 8: 27. https://doi.org/10.5455/ijlr.20150813090546.

Yang, F., Z. Zhang, A. Barberán, Y. Yang, S. Hu, and H. Guo. 2021. "Nitrogen-Induced Acidification Plays a Vital Role Driving Ecosystem Functions: Insights From a 6-Year Nitrogen Enrichment Experiment in a Tibetan Alpine Meadow." *Soil Biology and Biochemistry* 153: 108107. https://doi.org/10.1016/j.soilbio.2020.108107.

Yong-Zhong, S., L. Yu-Lin, C. Jian-Yuan, and Z. Wen-Zhi. 2005. "Influences of Continuous Grazing and Livestock Exclusion on Soil Properties in a Degraded Sandy Grassland, Inner Mongolia, Northern China." *Catena* 59: 267–278. https://doi.org/10.1016/j.catena.2004.09.001.

Yuan, H., and F. Hou. 2015. "Grazing Intensity and Soil Depth Effects on Soil Properties in Alpine Meadow Pastures of Qilian Mountain in Northwest China." *Acta Agriculturae Scandinavica Section B Soil and Plant Science* 65: 222–232. https://doi.org/10.1080/09064710.2014.992940.

Zhang, M., X. Li, H. Wang, and Q. Huang. 2018. "Comprehensive Analysis of Grazing Intensity Impacts Soil Organic Carbon: A Case Study in Typical Steppe of Inner Mongolia, China." *Applied Soil Ecology* 129: 1–12. https://doi.org/10.1016/j.apsoil.2018.03.008.

Zhou, G., S. Xu, P. Ciais, et al. 2019. "Climate and Litter C/N Ratio Constrain Soil Organic Carbon Accumulation." *National Science Review* 6, no. 4: 746–757. https://doi.org/10.1093/nsr/nwz045.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.