Legacy effects of herbivory trampling on soil organic carbon via soil properties, plant biomass and functional traits

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Key words: Trampling intensity; stocking rate; lagged-time effect; Non-trophic interactions

Abstract
Herbivores are important for ecosystem biogeochemistry, including soil carbon pools. Non-trophic interactions between herbivores and soil processes have recently gained attention, but remain underexplored. They include both direct and indirect effects of herbivore behaviour and physical soil disturbance by herbivores (e.g., trampling) causing compaction, and therefore probably influence historical contingency; however, little empirical data on the persistent impact or legacy effect of trampling and subsequent drivers of shifts are available. To address the knowledge gaps described above, we investigated whether the soil organic C (SOC) is driven by the legacy effect of sheep trampling intensity (0, 40, 80 and 120 footsteps m^{-2}) in a typical steppe on the Loess Plateau. Cessation of trampling for two years, typical of historical trampling intensity, had positive effects on plant Shannon, Simpson, Pielou index, belowground biomass (BGB), soil available N (SAN), soil bulk density (SBD), community-weighted mean trait values of phosphorus (CWM_P) and SOC, but had negative effects on AGB, litter biomass (LB), CWM_C and soil moisture (SM). The effect of trampling increased with increased trampling intensity. LB, BGB, CWM_C, CWM_P, SBD, SAN and SM were the main drivers of trampling-mediated SOC. From the results of this study, trampling at 40 footsteps m^{-2} caused by sheep managed at a stocking rate of 2.7 sheep ha^{-1}. This appears to be compatible with rangeland adaptive management. Ecosystem function can be maintained with high stocking rates by providing adequate deferment to re-establish sufficient cover and allow natural processes to restore soil processes.

Introduction
Ungulate herbivores are crucial in shaping plant communities, soil nutrient dynamics and distribution, and the global carbon (C) cycle across terrestrial ecosystems. These complex herbivore-plant-soil interactions play an important role in ecosystem research and management. Although livestock tramples constantly, selective feeding and excrement returning have been long considered as primary mechanisms through which herbivores affect soil biogeochemistry, even though they defoliate and fertilize only occasionally. Yet, trampling is slowly becoming recognized as an important non-trophic force affecting soil biogeochemical cycles. Notably, we are currently lacking experimental research on herbivore trampling legacy effects on soils and ecosystem functioning. This essential knowledge gap hinders future developments in evaluating the temporary and persistent impacts of land use insensitivity on ecosystem functions and services.

To date, most studies of temporal changes have investigated grassland sites over the course of a single year or consecutive years along temporal development gradients. Such work provides limited information on the speed and magnitude of soil process to land-use change, especially as time lags in the response of soil properties to land-use intensification may be common. Recent reviews on herbivore effects on belowground carbon processes have argued that non-trophic impacts may in the long term exceed trophic effects in scale (Andriuzzi and Wall 2017; Andriuzzi and Wall 2018). To address the knowledge gaps described above, we investigated whether the soil organic C (SOC) is driven by the legacy effect of sheep trampling intensity (0, 40, 80 and 120 footsteps m^{-2}) in a typical steppe on the Loess Plateau. We propose the following assumptions: 1) Legacy effects of sheep trampling enhanced the SOC; 2) Changes in SOC will be associated with variations in the soil physical and chemical properties, plant above- below-ground biomass, and plant functional traits; 3) As trampling intensity increases, the positive legacy effects of trampling on SOC increases.

Methods
A long-term rotational grazing experiment with Tan-sheep (*Ovis aries*) was initiated in 2001 at Huanxian Grassland Agriculture Trial Station (HGATS, 37.14°N, 106.84°E, 1,650 m a.s.l) of Lanzhou University, which is located in Huan County, Gansu Province, China.

In early July 2016 and 2017, 24 plots (2 × 2 m) were established in the grazing exclusion area with a 0.5-m distance apart from each other. To determine how the temporary effects of herbivory trampling affect soil and plant variables, we tested four sheep trampling intensities: 0 (control), 40, 80, and 120 footsteps m^{-2} (corresponding to the stocking rates of G0, G2.7, G5.3, and G8.7, respectively) with six replicates for each trampling intensity. The replicates (24 in total) of different trampling intensities were randomly assigned to the 24 plots. To simulate Tan sheep trampling (*Ovis aries*), an artificial hoof was made. The hoof consisted of a casted hoof with a similar size (6.1 × 7.0 cm) and weight (36 kg) to that of a natural 2-yr-old Tan sheep, a hoof holder, and a control arm (Li et al. 2021). The pressure intensity of the hoof was 0.84 kg cm^{-2}. Preliminary tests showed that the stocking rates of G2.7, G5.3, and G8.7 constituted 40, 80, and 120 footsteps m^{-2}, respectively. The simulated trampling was carried out on June 21 to 30, July 21 to 30, and August 21 to 30 in 2016 and 2017. The duration of each trampling period was 10 d, and the interval between any two trampling periods was 20 d, which was similar to the rotational grazing experiment. In 2018, we stopped the simulated sheep treatment to assess the legacy effects of herbivory trampling on soil and plant parameters.

We randomly conducted plant community surveys in two quadrats (1 m × 1 m) in 2019 of each subplot to quantify plant aboveground biomass (AGB), and litter biomass (LB), determine the plant diversity index, measure CWM (community-weighted mean trait values) of plant C and phosphorus (P). After plant biomass was harvested, two soil cores were sampled in the same subplot at a depth of 0－40 cm using a 5-cm-diameter bucket auger and mixed into one sample. Soil composite samples were transported to the laboratory after the removal of roots and stones by determining the belowground biomass (BGB) being sieved by 0.25-mm mesh. Subsamples were kept at 4°C for soil abiotic properties analysis.

Results and Discussion

Legacy effects of herbivory trampling on plant diversity and functional traits

Increasing trampling intensity had no significant effects on species richness, plant Shannon index, Simpson index and LB (Fig. 1). However, trampling significantly increased Plelou index, BGB and CWM_P, but decreased AGB and CWM_C with an increase in intensity.

Legacy effects of herbivory trampling on soil physicochemical properties and SOC

Trampling significantly increased soil bulk density (SBD), available N (SAN) and SOC but decreased soil moisture (SM) as trampling intensity increased (Fig. 2). In the treatment where trampling was stopped for two years, trampling still had a positive effect on soil bulk density. This probably occurred because during the trampling exclusion period, the field experienced a dry year (2018) and then a wet year (2019), during which drought and rewetting can alter the chemical and physical soil structure. These changes in soil bulk density may alter nutrient mineralization and long-term C dynamics. The decreasing soil water permeability induced by increasing soil bulk density through historical trampling may have negative legacy effects on some components of soil food webs, which may inhibit C decomposition and enhance C storage.

Main predictors of historical trampling-mediated variances in SOC

LB, BGB, CWM_C, CWM_P, SBD, SAN and SM were the main drivers of trampling-mediated SOC (Fig. 3). SOC was significantly and positively correlated with CWM_P, SBD, and SAN, but negatively correlated with LB, CWM_C and SM (Fig. 4). Trampling promotes the incorporation of standing litter into the soil, which may decrease the negative effects of standing dead litter on SOC formation, further facilitating SOC formation. CWM of leaf P, as either a change or legacy effect, showed strong relationships with soil microbes, which are associated with general shifts in the quality and quantity of litter.

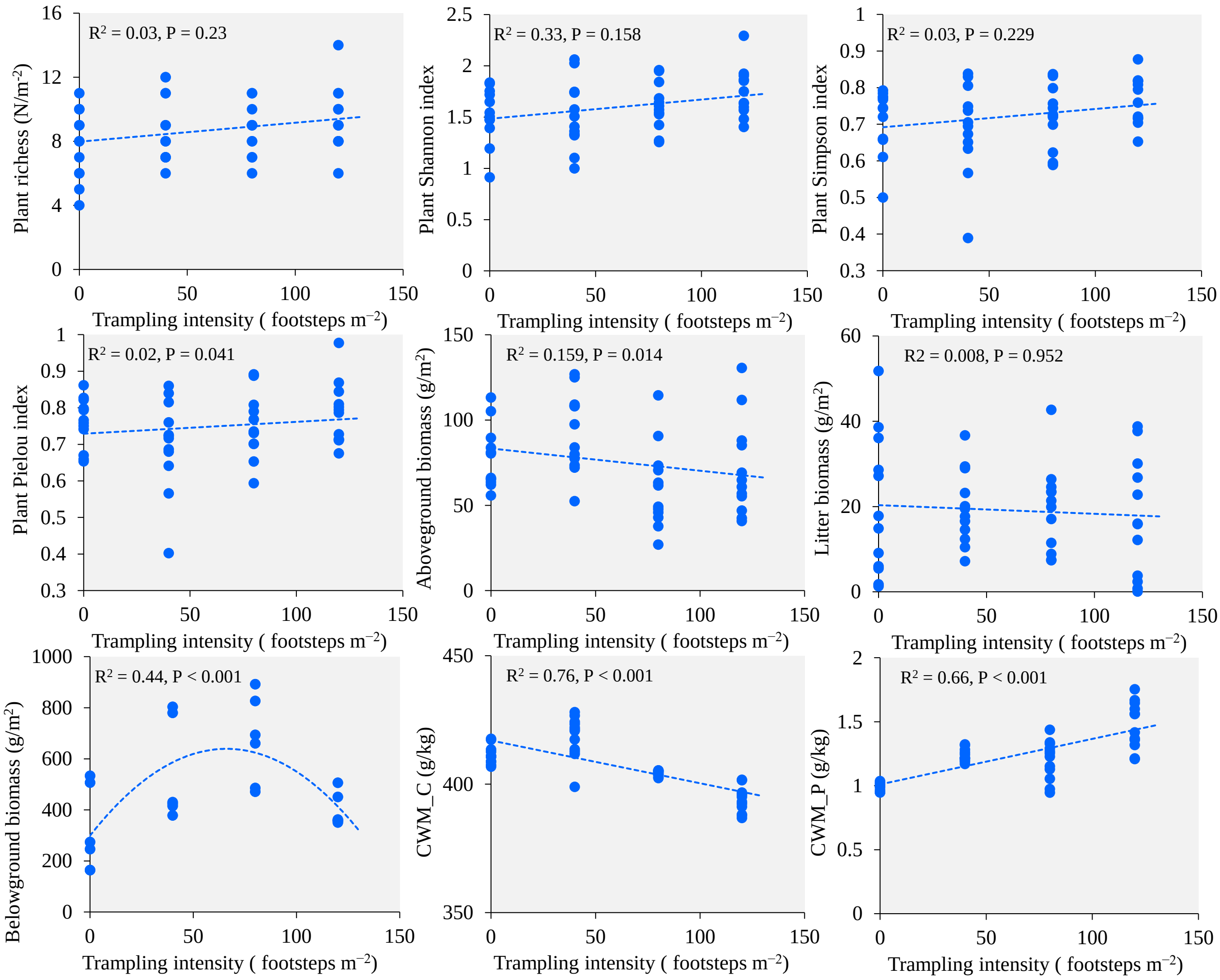

Fig. 1 Legacy effects of herbivory trampling on plant diversity and functional traits

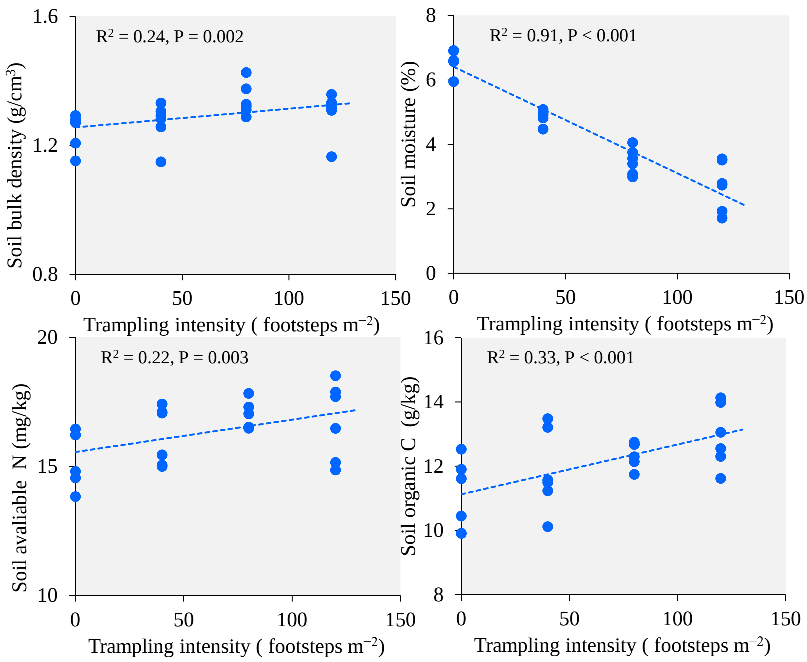

Fig. 2 Legacy effects of herbivory trampling on soil physicochemical properties and SOC

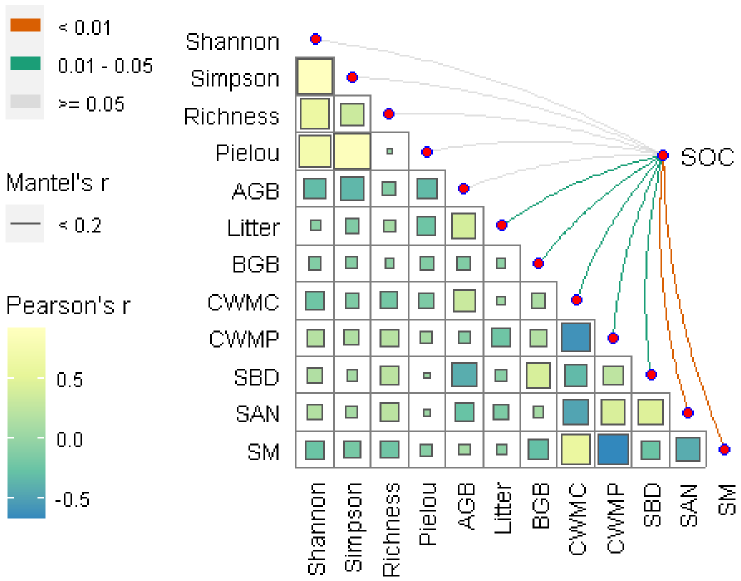

Fig.3 Mantel test for the correlation of the predictors with SOC

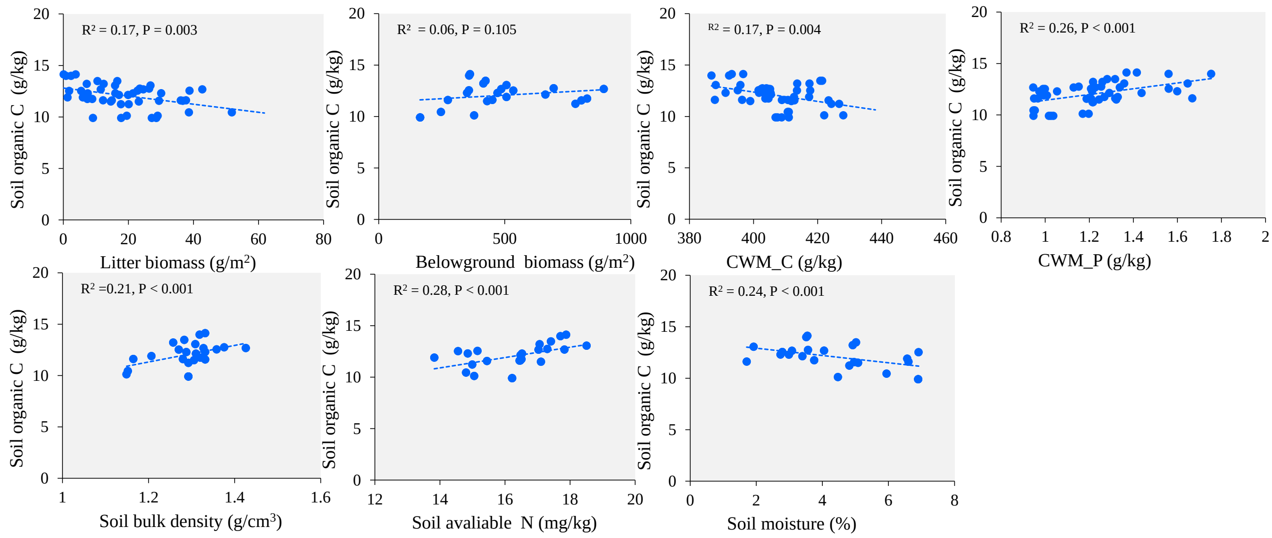

Fig.4 Linear correlations between predictors and SOC

Conclusions and/or Implications

In the current study, we found that trampling significantly increased SOC mainly via changes in SBD, SAN, SM, BGB, LB, CWM_C and CWM_P. From the results of this study, trampling at 40 footsteps m^{-2} caused by sheep managed at a stocking rate of 2.7 sheep ha^{-1} will be compatible with rangeland adaptive management.

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