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# Grazing effects on the relationship between plant functional diversity and soil carbon sequestration regulated by livestock species

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## Abstract

Grazing exerts a profound influence on both the plant diversity and productivity of grasslands, while simultaneously exerting a significant impact on regulating grassland soil carbon sequestration. Moreover, besides altering the taxonomic diversity of plant communities, grazing can also affect their diversity of functional traits. However, we still poorly understand how grazing modifies the relationship between plant functional diversity (FD) and soil carbon sequestration in grassland ecosystems. Here, we conducted a grazing manipulation experiment to investigate the effects of different grazing regimes (no grazing, sheep grazing (SG) and cattle grazing (CG)) on the relationships between plant FD and soil carbon sequestration in meadow and desert steppe. Our findings showed that different livestock species changed the relationships between plant FD and soil organic carbon (SOC) in the meadow steppe. SG decoupled the originally positive relationship between FD and SOC, whereas CG changed the relationship from positive to negative. In the desert steppe, both SG and CG strengthened the positive relationship between FD and SOC. Our study illuminates the considerable impact of livestock species on the intricate mechanisms of soil carbon sequestration, primarily mediated through the modulation of various measures of functional trait diversity. In ungrazed meadows and grazed deserts, maintaining high plant FD is conducive to soil carbon sequestration, whereas in grazed meadows and ungrazed deserts, this relationship may disappear or even reverse. By measuring the traits and controlling the grazing activities, we can accurately predict the carbon sequestration potential in grassland ecosystems.

***Keywords:*** grassland ecosystem, grazing management, plant diversity, plant functional traits, soil carbon sequestration

## 放牧对植物功能多样性与土壤固碳关系的影响受家畜物种调节

摘要：放牧对草地的植物多样性与生产力都具有深远影响，同时对调节草地功能固碳也有重要影响。此外，放牧除了会改变植物群落的分类多样性，还会影响其功能性状多样性。然而，放牧对草地生态系统

植物功能多样性与土壤固碳之间关系的影响尚不清楚。因此，我们进行了控制放牧实验，研究不同放牧制度(无牧、羊放牧和牛放牧)对草甸草原和荒漠草原植物功能多样性与土壤固碳功能之间关系的影响。研究结果表明，不同家畜物种改变了草甸草原植物功能多样性与土壤有机碳(SOC)之间的关系。羊放牧使植物功能多样性与土壤有机碳的正相关关系解耦，而牛放牧则使两者之间的关系由正变负。在荒漠草原，羊放牧与牛放牧均能加强植物功能多样性与土壤有机碳之间的正相关关系。我们的研究阐明了家畜物种对土壤固碳复杂机制的巨大影响，这种影响主要是通过调节植物功能性状多样性来实现的。在未放牧的草甸草原和放牧的荒漠草原中，保持较高的植物功能多样性有利于土壤固碳，而在放牧的草甸草原和未放牧的荒漠草原中，这种关系可能消失甚至逆转。通过测量植物功能性状和控制放牧家畜物种，我们可以更准确地预测草地生态系统的固碳潜力。

关键词：草地生态系统，放牧管理，植物多样性，植物功能性状，土壤固碳

## INTRODUCTION

Increasing evidence of global climatic warming as a result of rising levels of atmospheric $CO_2$ (Henry *et al.* 2018; Hoegh-Guldberg *et al.* 2019; Walker *et al.* 2020) has greatly stimulated the interest in soil carbon sequestration in natural ecosystems, particularly in grasslands (Conti *et al.* 2013). Grassland ecosystems store ~34% of the terrestrial carbon stock, with ~90% of their carbon stored belowground as root biomass and soil organic carbon (SOC). Therefore, they play a vital role in soil carbon sequestration (Bardgett *et al.* 2021; Rillig *et al.* 2015). Owing to its large size, small changes in the balance between inputs to and outputs from the soil carbon pool can have a significant impact on atmospheric $CO_2$ (Davidson and Janssens 2006; Liang *et al.* 2017). However, the direction and magnitude of management effects on soil carbon sequestration are context-specific, depending on factors such as climate, plant community composition and soil properties (Byrnes *et al.* 2018; Eze *et al.* 2018), so it is still an open question how they can be managed to store more carbon.

The two grassland types (i.e. meadow grassland in the higher rainfall zone and desert grassland in the lower rainfall zone) in northern China are quite different, with different climate types, plant community composition and soil properties. Livestock grazing is the most widespread management form in grasslands (Asner *et al.* 2004), particularly in northern China (Kemp *et al.* 2013), which is part of the largest remaining grasslands on Earth (i.e. the Eurasian steppe) (Wang *et al.* 2019). Grazing is therefore one of the most important factors that could change the soil carbon sequestration in grassland systems. Understanding the impacts of grazing livestock types under different management systems on SOC sequestration is a key to providing the most effective soil carbon management strategies (Khalil *et al.* 2019).

There are many ways in which grazing can alter soil carbon sequestration in grassland. First, the often-low substrate quality of plant litter limits its own decomposition rates. In contrast, herbivore feces and urine provide a fast decomposition pathway by returning highly decomposable resources that are rich in plant-available nutrients, which can lead to significant changes in soil carbon sequestration (Bakker *et al.* 2004). Another pathway is trampling, which affects the fragmentation efficiency of deadfall and also modifies physical attributes such as bulk density and soil penetration resistance, and breaks up soil aggregates (Wen *et al.* 2016), which can influence soil carbon sequestration (Ball 2013). Finally, grazing also changes the floristic composition of plant communities through different mechanisms (Olff and Ritchie 1998). Plants adopt two main strategies (avoidance and tolerance) to deal with grazing (Díaz and Lavorel 2007; Díaz *et al.* 2007; Rota *et al.* 2017). On the one hand, plant resistance to grazing is related to avoidance traits, such as low plant height ($H$) and leaf area (LA) (Zheng *et al.* 2011). On the other hand, grazing-tolerant plants usually have traits such as large specific leaf area (SLA) or high leaf nitrogen concentration, to allow fast regrowth after defoliation. The effect of grazing on plant communities depends also on the type of grazer i.e. present (Díaz and Lavorel 2007). By their feeding behavior, livestock species vary in how they reduce the biomass of certain plant species, and in how they indirectly promote other, less grazed plant species. The functional traits of plants have been suggested to be key for understanding how different plant species drive SOC storage (Deyn *et al.* 2008),

**Table 1:** General information of every research site in this study

| Grassland type | Study site | Geographical location and altitude | MAT<br>MAP | Soil type |
|---|---|---|---|---|
| Meadow steppe | Bayan Wulagacha, Ewenki Banner, Inner Mongolia Autonomous Region | 48°34′ N, 119°55′ E<br>744 m | 0.4°C<br>352.1 mm | Dark chestnut soil |
| Desert steppe | Zhaohe Town, Damao Banner, Inner Mongolia Autonomous Region | 41°15′ N, 111°13′ E<br>1687 m | 4.7°C<br>251.8 mm | Light chestnut colored soil |

and can therefore be used as a bridge to understand the link between grazing and carbon sequestration.

It is usual to use community-weighted mean (CWM) and functional diversity (FD) to quantify the relationship between community-level plant functional traits and ecosystem functioning, such as carbon sequestration (Díaz *et al.* 2007). The CWM, i.e. the average trait value of a community accounting for effects of species abundance within communities (Mason *et al.* 2005). A significant effect of CWMs on ecosystem functions would thus indicate that ecosystem processes are largely driven by the traits of dominant species (Díaz *et al.* 2007; Garnier *et al.* 2004). The selection effect suggests that more diverse mixtures have a higher probability of containing a highly productive species, which may result in the higher productivity of a mixture if the species becomes dominant (Clark *et al.* 2019; Fargione *et al.* 2007). Likewise, any changes in CWM traits for plant species with different resource strategies may determine the magnitude and direction of community-level responses to grazing (Kichenin *et al.* 2013). Variation in functional traits within species is also key. The diversity of traits (FD) (Mason *et al.* 2005) can influence ecosystem processes, including carbon sequestration. Larger plants are also expected to shed more biomass in the form of leaf and woody litter per unit ground area and thus contribute directly to carbon accumulation in the standing litter and in the organic soil (Garnier *et al.* 2004; Lavorel and Grigulis 2012). Besides the identity, also the diversity of functional traits may affect SOC. The coexistence of plants with contrasting functional trait values should lead to a more complete use of resources by the community as a whole and thus to higher biomass production and higher carbon input into the soil, increasing both aboveground and soil carbon stocks (Conti *et al.* 2013). The complementarity effect suggests that niche differentiation in space and time, interspecific facilitation via habitat amelioration or resource enrichment, or reduced interspecific competition should lead to the greater acquisition of limiting resources and therefore to higher productivity (Tilman *et al.* 1997). It is likely that grazing can alter soil carbon sequestration by changing both the FD and dominance patterns of functional traits.

Importantly, the effects of grazing on SOC can also strongly vary depending on specific grazing management characteristics. There are different herbivore species, such as cattle and sheep, which differ in body size and have different foraging preferences. For example, sheep prefer soft, juicy plants with high nitrogen content and volatile odors. In contrast, cattle are not as selective in their foraging for plant species and prefer to feed on the dominant species with high biomass (Descombes *et al.* 2020a). As a result, sheep and cattle are likely to have different effects on plant communities, and thereby also on soil carbon storage.

Here, we used a 4-year grazing experiment in the eastern Eurasian steppe to assess: (i) whether different livestock species have different effects on soil carbon sequestration in different grasslands; (ii) what is the relationship between plant functional trait diversity and SOC in different grassland types and (iii) how do different livestock species regulate this relationship. We consider these results in relation to factors affecting the sustainability of Eurasian grasslands and propose a management framework to help ensure the soil carbon sequestration capacity and potential of rangelands when grazed in grassland ecosystems by measuring plant functional traits as well as controlling grazing animal species in a simple way.

## MATERIALS AND METHODS

### Study site

This study was set on the eastern part of the steppe belt of Eurasia, from northeast to southwest in the main part of the northern steppe of China. The geographical range of the area was 41°15′–48°34′ N, 111°13′–119°55′ E and the altitude crossed from 744 to 1687 m. The study was divided across two areas: meadow steppe and desert steppe (Table 1). These two study areas showed obvious differences in precipitation and temperature. In the desert steppe, the mean annual precipitation (MAP) was 251.8 mm, and the mean annual temperature (MAT) was 0.4°C. In the meadow steppe, the MAP was 352.1 mm and the MAT was 4.7°C.

In this study, the plant species richness and aboveground productivity of the experimental plots of meadow grassland were higher, and *Stipa baicalensis*, *Leymus chinensis* and *Carex pediformis* were the dominant plant species. *Agropyrorn cristatum*, *Allium senescens*, *Caragana microphylla* and *Fitifolium sibiricum* were associated species. In the desert steppe, *Stipa krylovii* and *L. chinensis* were established as group species, and the main associated species were *Stipa breviflora*, *Aster altaicus* and *Cymbaria daurica*. All these plant species can be eaten by cattle and sheep.

## Experimental design

Prior to the experiment in 2012, the two research areas, which had the same historical background of grazing and similar vegetation within the areas, were enclosed to exclude livestock grazing. The overgrazing indicator ($C_4$ grasses) never exceeded the critical limit of 50%, and therefore had not been overgrazed in recent years. Within the enclosed areas, we set up a long-term grazing experiment in 2012 with a completely randomized block design. Following 1 year of enclosure, at two grassland types, the experiment was designed as a randomized complete block, with three blocks as replicates. Each replicate block was divided into three plots, which were assigned to three grazing treatments: NG, no grazing; SG, moderate sheep grazing; and CG, moderate cattle grazing. Meanwhile, each plot was enclosed with woven-wire fences (10 cm mesh size; 1.5 m high). Each plot size was calculated according to plant productivity and livestock foraging at each study site. The plot sizes of NG, SG and CG are the same, all 50 m by 50 m, 0.25 ha. The grazing herbivores selected were local common grazing livestocks: Urumqi sheep and Mongolian cattle. Each year, grazing occurred from June to August. The same grazing intensity was applied in all the grazing treatments to test the effects of herbivore species identity, and grazing was maintained at a moderate intensity (i.e. 3.34 sheep units per ha). We use the same set of cattle and sheep in all the grazing treatments, i.e. rotational grazing treatment to avoid the effects of using different individual animals in different treatments on grassland. The grazing experiment design was based on the method of rangeland carrying capacity calculation published by the agriculture industry standard NY/T 635-2015 (Ministry of Agriculture of The People's Republic of China).

## Field sampling

After 4 years of moderate grazing experiments, plant and soil samples were collected from all experimental plots in both grassland types in August 2016. Specifically, three blocks were selected in each type of grassland, and each block was divided into three plots, to which grazing treatments were randomized: NG, SG and CG. To mitigate the effects of grassland heterogeneity on plant and soil samples, the vegetation community survey was conducted using the sample strip method. In meadow grassland, two sample strips were set up in each plot to take 9 sample squares, and 9 plots (3 treatments, 3 block replications) totaled 81 sample squares. In desert grassland, 6 sample squares were set up in each plot, totaling 54 sample squares (again, samples were taken in 2 sample strips with 6 samples per sample plot, 3 treatments and 3 replications). Sample plots were all 50 cm × 50 cm in size, and the vegetation was surveyed to determine plant height, abundance and plant traits of each species (Supplementary Fig. S1). Subsequently, the plants were broken by harvesting method, and all the plants in the sample plots were cut (1 cm stubble), brought back to the laboratory and dried at 70°C for 48 h to determine the biomass. Soil samples are taken in sample plots where vegetation has been taken. The five-point sampling method was adopted, where a soil auger with a diameter of 2.5 cm was used to take out the soil at a depth of 10 cm, and the number of samples corresponded to the aboveground plant samples one by one. Since SOC is mainly concentrated in the shallow layer, and grazing-induced changes in SOC may be more likely to occur in the shallow soil layers, just the shallow samples were collected. Soil samples were sieved over 2 mm mesh to separate the coarse roots and other visible debris. Samples from the same depth were mixed, packed in polyethylene bags, immediately stored in a portable refrigerator (4°C) and transported to the laboratory for further analysis. Approximately 200 g of each soil sample was air-dried for the analysis of SOC concentration, which was determined using the dichromate oxidation method (Nelson and Sommers 1996).

## Trait measurements

We focus in particular on four well-studied functional traits: one plant morphological trait (plant height) and three traits from the leaf economics spectrum (Shipley *et al.* 2006; Wright *et al.* 2004) that are directly relevant to forage quality (LA ($m^2$), SLA ($m^2$ $kg^{-1}$), LDMC (mg $g^{-1}$): leaf dry matter content). These traits can be important indicators of both species' performance and community functional response to grazing. We measured traits on all four species (*S. baicalensis*, *C. pediformis*, *Lespedeza bicolor* and *A. senescens*), which are present in every sample plot in the area (>70% average relative abundance share) (Cornelissen *et al.* 2003) and belong to the families *Poaceae*, *Tussilidae*, *Fabaceae* and *Liliaceae*, respectively, are very representative of the community. The four species in the desert steppe (*S. krylovii*, *L. chinensis*, *A. altaicus* and *C. daurica*), which are present in every sample plot in the area meet biomass and coverage requirements. Trait measurements were done before harvesting the plants for each species within a 0.5 m × 0.5 m quadrat in each plot. The height of each species was determined as the mean values of five randomly selected individuals. We randomly selected 5–10 intact individuals of the four species in our sample plots and chose more than 20 mature intact leaves for individual LA repeat measurements. Plant leaves were dried at 70°C for 48 h and weighed to calculate SLA and LDMC. For measurement of aboveground traits such as H, SLA and LDMC we refer to the method in previous work (Cornelissen *et al.* 2003).

### Community and soil measurements

We calculated the CWMs of plant height, LA, SLA and LDMC for each species in grazed and ungrazed plots in each site. We calculated FD for all traits, a measure of variation in trait values among species within a community. We quantified the FD of our study communities using four metrics (Villéger *et al.* 2008): CWM, functional divergence (FDiv), functional dispersion (FDis) and quadratic entropy of Rao (RaoQ) following the study (Díaz and Lavorel 2007) CWMs for each of the four plant functional traits were calculated as: $\mathrm{CWM} = \sum_{i=1}^{n} p_i \ \mathrm{trait}_i$ where $p_i$ is the relative abundance of species *i* in the community, and trait *i* is the trait value of species *i* (Lavorel *et al.* 2007). CWM represents the expected trait value of a randomly sampled individual from a community (Garnier *et al.* 2004) and is strongly driven by the trait values of the dominant species. FDiv was measured as the average distance from each species to the spatial center of gravity of the trait (Villéger *et al.* 2008). FDis is expressed as the weighted average distance in the multidimensional feature space of a single species to the weighted center of mass of all species (Villéger *et al.* 2008). RaoQ fulfills all *a priori* criteria and it surpasses other proposed indices, because it includes species abundances and more than one trait. All functional metrics were calculated using the statistical package FDiversity v. 2011 (Casanoves *et al.* 2011).

### Statistical analyses

All variables were log-transformed to fit the model requirements. We used linear mixed-effect models (LMMs) with grazing treatment as a fixed effect and block as a random effect to assess the impacts of grazing on SOC. Tukey tests were applied for the *post hoc* comparisons of grazing treatment effects, and were performed with the function *glht* in the '*multcomp*' package (Hothorn *et al.* 2008). To test for links between SOC and the different components of FD, we followed a stepwise model selection procedure, to select the best predictors of SOC in different grazing treatments. We put all the plant FD factors (CWM H, CWM LA, CWM SLA and CWM LDMC, FDiv, FDis and RaoQ) that can influence SOC into the model. The model with the lowest Akaike information criterion was selected as being the best. After fitting the final model, the Breusch–Pagan tests, value inflation factor and Durbin–Watson statistics were used to test for heteroscedasticity, multicollinearity and autocorrelation between residuals, respectively. LMMs were achieved using the function *lmer* from the package *lme4* (Bates *et al.* 2015). Analyses were performed with software R version 4.1.

## RESULTS

### Effects of different grazing treatments on SOC concentrations

According to the results of the LMMs, the variations in SOC concentrations in grassland ecosystems did not exhibit significant differences across different animal grazing treatments. (Fig. 1; Table 2).

### The relationship between FD and SOC concentrations

We conducted a linear mixed model to assess how FD (CWMs and FDs) drives SOC content under different grazing practices (NG, SG and CG) both in meadow and desert. Within ungrazed meadow steppes, we found that SOC is significantly affected by two factors ($R^2 = 0.604$, $P < 0.001$): FDiv (positive) and

CWM of plant height (negative) (Table 3). Within meadow steppes grazed by sheep, the relationship between FDiv and SOC disappeared, while the relationship with CWM of plant height (negative) remained. Furthermore, SOC within sheep-grazed meadow steppe is also determined by CWM LA (negative) and CWM SLA (positive). CG changed the outcome of the model in an opposite way ($R^2 = 0.638$, $P < 0.001$). CG, although maintaining the relationship between FDiv and SOC, changed the direction of the slope (from positive to negative). Furthermore, within cattle-grazed areas, the relationship between SOC and CWM LA was positive, as opposed to the negative relationship in sheep-grazed meadow steppes (Table 3).

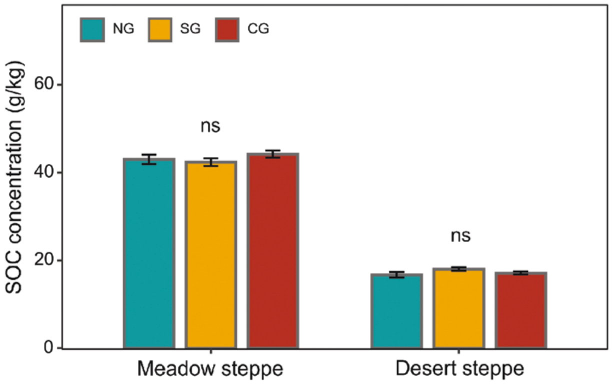

**Figure 1:** The effect of different species of livestock grazing in different grassland types on SOC. Letters "ns" indicate no significant differences among herbivore treatments.

In the desert steppe, we obtained different outcomes (Table 4). Different from meadow steppe, the relationship between FD and SOC was absent under the condition of NG, while only CWMs of traits were related to SOC ($R^2 = 0.597$, $P < 0.001$). Grazing changed these relationships, but only small differences in the drivers of SOC were found between cattle ($R^2 = 0.557$, $P < 0.001$) and sheep ($R^2 = 0.680$, $P < 0.001$) grazed areas. Within grazed desert steppes, two measures of FD, namely FDis and RaoQ were positively related to SOC, while SOC was negatively related to the CWM of plant height, CWM LDMC (only in cattle-grazed areas) and CWM LA (Table 4).

## DISCUSSION

In this study, we assessed how different livestock species affect SOC stocks, as well as the relationship between FD and SOC. Our findings indicate that different species livestock grazing practices have significant regulatory effects on plant FD and soil carbon sequestration. Furthermore, the type of grassland has a significant influence on the direction and intensity of the regulation.

In both meadow steppe and desert steppe, grazing regimes did not have an overall significant effect on the SOC concentration (Fig. 1; Table 2). This has similarities (Wigley *et al.* 2020; Ylänne *et al.* 2018) and contrasts (Abdalla *et al.* 2018; Jiang *et al.* 2020) with previous studies. Previous research has shown that the influence of grazing on SOC can be

**Table 2:** Results of LMMs testing the effect of treatment on SOC concentrations

| Grassland type | Model description | | | Est. | SE | df | *t* | Pr (>\|*t*\|) |
|---|---|---|---|---|---|---|---|---|
| Meadow steppe | Fixed effects | (Intercept) | | | | | | <0.0001 |
| | | SOC ~ treatment | | | | 81 | | 0.321 |
| | | | SG–NG | −0.920 | 1.217 | | −0.756 | 0.730 |
| | | | CG–NG | 0.930 | 1.217 | | 0.764 | 0.725 |
| | | | CG–SG | 1.850 | 1.217 | | 1.519 | 0.282 |
| | Random effects | (variance) Block | | | | | | |
| Desert steppe | Fixed effects | (Intercept) | | | | | | <0.0001 |
| | | SOC ~ treatment | | | | 54 | | 0.129 |
| | | | SG–NG | 1.271 | 0.628 | | 2.025 | 0.106 |
| | | | CG–NG | 0.412 | 0.628 | | 0.655 | 0.789 |
| | | | CG–SG | −0.860 | 0.628 | | −1.369 | 0.357 |
| | Random effects | (variance) Block | | | | | | |

**Table 3:** Final models obtained from multiple linear regression analysis between SOC concentrations and FD components under different treatments within meadow steppes, using a stepwise ascending procedure

| Grazing treatment | Model form | Predictor variables | Slope | *P* | *N* | $R^2$ |
|---|---|---|---|---|---|---|
| NG | SOC = 1.845 + 1.651 FDiv − 0.556 CWM H | *Model* | | <0.001 | 25 | 0.604 |
| | | FDiv | + | 0.010 | | |
| | | CWM H | − | 0.001 | | |
| SG | SOC = 1.788 − 0.549 CWM H − 10.126 CWM LA + 0.426 CWM SLA | *Model* | | <0.001 | 25 | 0.483 |
| | | CWM H | − | 0.026 | | |
| | | CWM LA | − | 0.034 | | |
| | | CWM SLA | + | 0.043 | | |
| CG | SOC = 2.277 − 3.247 FDiv + 5.076 CWM LA | *Model* | | <0.001 | 25 | 0.638 |
| | | FDiv | − | <0.001 | | |
| | | CWM LA | + | 0.002 | | |

All multiple regression models were statistically significant ($P < 0.05$). $R^2$, regression adjusted coefficient for the multiple regression model; *N*, number of sites in the analyses; slope and *P* refer to individual predictor variables in the final model. Abbreviations: CWM H = community-weighted mean of height, CWM LDMC = community-weighted mean of leaf dry matter content, CWM LA = community-weighted mean of leaf area, CWM SLA = community-weighted mean of specific leaf area.

**Table 4:** Final models obtained from multiple linear regression analysis between SOC concentrations and FD components under different treatments within meadow steppes, using a stepwise ascending procedure

| Grazing treatment | Model form | Predictor variables | Slope | *P* | *N* | $R^2$ |
|---|---|---|---|---|---|---|
| NG | SOC = 1.131 − 0.201 CWM H + 0.159 CWM SLA − 4.224 CWM LDMC | *Model* | | <0.001 | 14 | 0.597 |
| | | CWM H | − | 0.023 | | |
| | | CWM SLA | + | 0.005 | | |
| | | CWM LDMC | − | 0.004 | | |
| SG | SOC = 0.761 + 0.526 FDis + 0.781 RaoQ − 0.127 CWM H − 1.430 CWM LDMC | *Model* | | 0.001 | 14 | 0.557 |
| | | FDis | + | 0.022 | | |
| | | RaoQ | + | 0.016 | | |
| | | CWM H | − | 0.023 | | |
| | | CWM LDMC | − | 0.025 | | |
| CG | SOC = 1.581 + 0.359 FDis + 0.160 RaoQ − 0.270 CWM H − 0.092 CWM LA − 0.3116 CWM LDMC | *Model* | | <0.001 | 14 | 0.680 |
| | | FDis | + | <0.001 | | |
| | | RaoQ | + | 0.002 | | |
| | | CWM H | − | <0.001 | | |
| | | CWM LA | − | 0.009 | | |
| | | CWM LDMC | − | 0.011 | | |

All multiple regression models were statistically significant ($P < 0.05$). $R^2$, regression adjusted coefficient for the multiple regression model; *N*, number of sites in the analyses; slope and *P* refer to individual predictor variables in the final model. Abbreviations: CWM H = community-weighted mean of height, CWM LDMC = community-weighted mean of leaf dry matter content, CWM LA = community-weighted mean of leaf area, CWM SLA = community-weighted mean of specific leaf area.

low at short time scales, due to the comparatively low precipitation in grassland ecosystems causing delayed effects (Lu *et al.* 2015; Post and Kwon 2000; Sollenberger *et al.* 2019). In these systems with a slow decomposition of standing litter, the formation of SOC takes long. Therefore, the change of soil carbon in a grassland system following short-term grazing treatment may be insufficient to achieve statistical significance. However, our results show that while different grazing regimes do not affect levels of SOC sequestration, grazing did modify the effects of plant communities on carbon storage (Tables 3 and 4). This is because grazing can affect plant functional traits (Deraison *et al.* 2015), and as a result plant litter traits (Rosenfield *et al.* 2020), with consequences for SOC input traits (Abdalla *et al.* 2018), which can eventually lead to SOC changes (Chang *et al.* 2018).

We found that the factors driving SOC differed between grazing regimes (Tables 3 and 4). Grazing livestock greatly affects plant functional traits as well as their FD (Ali and Agrawal 2012; Potter *et al.* 2022). The significant effect of grazing on functional traits underlies the effects of grazing on carbon sequestration. Our findings showed that the effect of grazing on CWM and FD is dependent on livestock species and on grassland type (Supplementary Table S1). The CWM SLA, CWM LDMC and FDiv responded significantly to grazing livestock species, e.g. meadow steppe CG reduced CWM SLA (Supplementary Fig. S2). The response of CWM H, CWM SLA and FDis to grazing was not only dependent on grazing livestock species but also on grassland type, e.g. CG in meadow grassland increased CWM H, whereas the effect of desert grassland grazing livestock species on CWM H was not significant (Supplementary Figs S2 and S3). Then, grazing moderated the relationship between functional traits and carbon sequestration. First, in ungrazed meadows steppe, SOC concentrations were mainly influenced by FDiv and CWM of plant height (Table 3). Specifically, as FDiv increased and CWM of plant height decreased, estimated SOC concentrations were predicted to increase (Table 3). In contrast, the FDiv also correlates significantly and negatively with SOC concentrations under CG in the meadow steppe (Table 3). The positive relationship between SOC and FDiv might have been caused by the niche complementary effects previously described for diversity–productivity relationships (Cont *et al.* 2013). The diversity of plant species and the divergence of traits, i.e., the coexistence of species with different trait values, allow plants to make full use of the resources in the environment (Streit *et al.* 2019). High diversity of plant traits facilitates the accumulation of biomass (Brandt *et al.* 2019; Niu *et al.* 2015) and thereby could result in the formation of more plant litter, which increases the carbon input to the soil and could thus increase the soil carbon stock (Conti *et al.* 2013). As two variables constitute

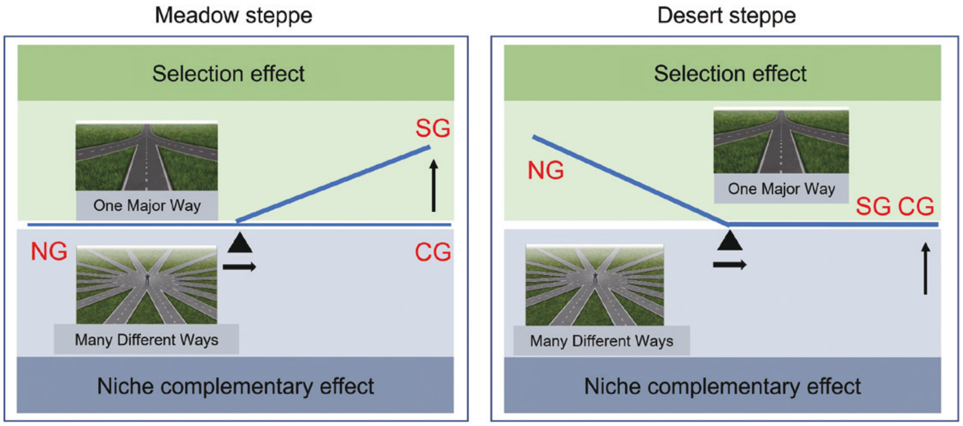

**Figure 2:** A framework for regulating the relationship between plant FD and soil carbon sequestration by different types of livestock grazing on different grassland types. The highways in the figure depict the ways in which soil carbon sequestration occurs: a wide road to a destination means that the higher the dominance of the dominant species in the community plays a greater role in carbon sequestration; multiple roads to a destination means that the greater the diversity and the greater the divergence of traits, the greater the carbon sequestration capacity of the community. The left figure indicates that the relationship between diversity and SOC in the ungrazed sample is consistent with a complementary ecological niche effect, with the CG sample continuing the mechanism relationship and the SG sample tending to shift to a selection effect mechanism. The right figure indicates that the relationship between diversity and SOC in the ungrazed samples is consistent with a selection effect, while the ecological niche complementarity effect is enhanced in the grazed samples.

changes in FDiv, differences in functional traits and differences in the relative abundance of species, the greater the heterogeneity of plant species as well as traits in the community, the more beneficial it is for soil carbon sequestration. This correlation between FDiv and SOC is consistent with the mechanism of niche complementarity (Fig. 2). Grazing livestock reversed the positive effect of FDiv on SOC into a negative relationship, while SG eliminated the relationship between FDiv and SOC (Table 3). During CG, differences between traits become smaller and heterogeneity between species tends to homogenize due to foraging (Liu *et al.* 2018). Meanwhile, leaf traits of foraged plants will tend to thicken and harden due to grazing avoidance effects and become less rapidly decomposed (García-Palacios *et al.* 2017). A potential reason for the negative relationship between FD and SOC under SG is that sheep feeding greatly reduces plant diversity (Liu *et al.* 2015). However, when plant diversity is no longer able to maintain SOC content, the traits of a few dominant species will affect SOC change. Therefore, the traits of LA, SLA and plant height were all important factors driving SOC under sheep feeding (Song *et al.* 2017).

We also found that grazing regimes can greatly affect the relationship between FD and SOC, not only depends on the dispersity of traits, but also on the proportion of dominant species (Orwin *et al.* 2018). Plant height has been considered as one of the most sensitive traits to grazing (Díaz and Lavorel 2007; Pakeman 2004). For meadow steppe, we found evidence, which SOC increased as the CWM of plant height increased when not grazed and when grazed by sheep (Table 3). Besides, grazing often tended to reduce the SLA of conservative and rapid resource utilization species (Hahn and Maron 2016). SLA is the most important trait for effective photosynthesis in plants and an important pathway for the synthesis of organic matter during carbon input (Wright *et al.* 2004). As the main source of SOC is organic matter synthesized by photosynthesis, so the importance of SLA cannot be overstated. The SLA of the plants decreases when CG, suggesting that the plants all exhibit a grazing avoidance strategy (Díaz *et al.* 2001). CG is less selective but has no significant effect on plant height, so under moderate grazing, CG changes the carbon input pattern of plants more by altering their leaf traits. At this point, SOC in the system is proportional to the SLA, so when the SLA increases, there is a corresponding increase in SOC (Table 3). However, changes in SLA do have a predictive effect on trends in SOC. In addition, the most important implication of the results is that part of the interpretation of FD and ecosystem soil carbon sequestration function can rely, in part, on the mechanism of selection effects, so when there is a greater variation in the ratio of LA of dominant species in the community, such species are more likely to develop dominance and reduce SOC in the environment (Fig. 2).

Some of the differences in plant communities and SOC that we observed among grazing treatments can be explained when looking at the characteristics of the different livestock species. Sheep tend to eat young, short plant species with rich leaf nitrogen content, while cattle tend to eat less selectively. SG can significantly change the related traits of plants, such as LA and plant height (Descombes *et al.* 2020b). This means that plots where SG had led to the local dominance of shorter-statured plants were associated with lesser carbon storage in plant and soil. This result is like the results reported by the previous study (Ruiz-Jaen and Potvin 2011) for natural tropical forests in Panama, and it is not surprising considering that height is a good predictor of the total biomass of the plants (Chave *et al.* 2005). Grazing affects grassland carbon sequestration by affecting plant height because plant biomass directly influences the amount of carbon contained in both the above- and belowground portions of the standing vegetation and can be incorporated into the soil as litter at senescence (Deyn *et al.* 2008; Lavorel and Grigulis 2012).

The moderating effect of livestock grazing on the relationship between FD and SOC was strongly dependent on grassland type. In meadow grasslands with high precipitation, SG and CG can be explained by the mechanisms of selection effects and niche complementarity effects, respectively (Fig. 2). In contrast, in desert grasslands with sparse precipitation and NG, only CWMs had a significant correlation with SOC, while there was no significant causal relationship between FD and SOC (Table 4). In the case of grazing (SG and CG), both FDis and RaoQ were positively related to SOC, which implied that the higher the dispersion of functional traits, the higher the carbon sequestration capacity of the plants in the community. The mechanism of livestock grazing on carbon sequestration in desert grassland ecosystems is consistent with a niche complementarity effect (Fig. 2). It is reasonable to infer that plants growing in desert grasslands are more likely to have conservative traits and themselves have a stronger grazing avoidance strategy. When plants suffer grazing disturbance, the plasticity of their functional traits tends to be in the direction of grazing avoidance (Krimmel and Pearse 2016). Plants have a narrower threshold of adaptability to the environment, and the pressure of grazing itself has been more than a minor difference in differences in grazing livestock, so that differences in grazing livestock species did not strongly influence the relationship between FD and SOC.

In other words, the lower divergence of plant functional traits, the higher the SOC concentrations in meadow steppe. On the contrary, the higher dispersion of plant functional traits, the higher the SOC concentrations in desert steppe. Because cattle will reduce the degree of divergence in meadow steppe. Rather than depending on dominant species alone to maintain soil carbon sequestration, not only sheep but also cattle, the increase in SOC is better augmented by the maintenance of a diversity of plant functional traits.

## CONCLUSIONS

We provided strong empirical evidence that livestock species can drive the intricate mechanisms of soil carbon sequestration, primarily mediated through the modulation of various measures of functional trait diversity. In ungrazed meadows and grazed deserts, maintaining high plant FD is conducive to soil carbon sequestration, whereas in grazed meadows and ungrazed deserts, this relationship may disappear or even reverse. We therefore suggest that managing above ground livestock species is important for conserving and promoting grassland soil carbon sequestration, and that the management should also consider local livestock species. In future research on the mitigation of global warming, attention should be paid to the concretization and diversification of grazing management in grassland ecosystems.

### *Supplementary Material*

Supplementary material is available at *Journal of Plant Ecology* online.

Figure S1: The design of experiment.

Figure S2: The effect of different livestock grazing on the community-weighted mean of plant traits in different grassland types.

Figure S3: The effect of different livestock grazing on the functional diversity in different grassland types.

Table S1: Summary of ANOVA analyzing the effects of livestock species on community-weighted mean of plant traits and functional diversity.

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