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Effects of livestock grazing on the relationships between soil microbial community and soil carbon in grassland ecosystems

Hongwei Xu [a], Chengming You [a], Bo Tan [a], Lin Xu [a], Yang Liu [a], Minggang Wang [b], Zhenfeng Xu [a], Jordi Sardans [c d e], Josep Peñuelas [d e]

a National Forestry and Grassland Administration Key Laboratory of Forest Resources Conservation and Ecological Safety on the Upper Reaches of the Yangtze River & Forestry Ecological Engineering in the Upper Reaches of the Yangtze River Key Laboratory of Sichuan Province, Sichuan Agricultural University, Chengdu 611130, China

b The Key Laboratory for Silviculture and Conservation of Ministry of Education, College of Forestry, Beijing Forestry University, Beijing, China

c CSIC, Global Ecology Unit CREAF-CSIC-UAB, 08913 Bellaterra, Catalonia, Spain

d CREAF, 08913 Cerdanyola del Vallès, Catalonia, Spain

e Nonlinear Analysis and Applied Mathematics (NAAM)-Research Group, Department of Mathematics, Faculty of Science, King Abdulaziz University, P.O. Box 80257, Jeddah 21589, Saudi Arabia

Abstract

Livestock grazing of grassland ecosystems may induce shifts in microbe community traits and soil carbon (C) cycling; however, impacts of contrasting managed grazing regimes on soil C-microbe community trait relationships are unclear. Here, we conducted a global meta-analysis of 623 pairwise observations of grazing impacts on soil C cycling and microbe community traits under three grazing intensities (light, moderate, and high), durations (<5 years, 5–10 years, and >10 years), and livestock species assemblage (sheep, cattle, sheep+cattle). Grazing intensity and duration generally led to declines in content of soil organic carbon (SOC), total nitrogen, and total phosphorus, and soil respiration. In contrast to effects of high levels of grazing intensity, light and/or moderately intense grazing increased diversity of soil bacteria and fungi, while soil microbial biomass and enzyme activities were negatively related to grazing duration. Grazing by sheep reduced saccharase and acid phosphatase activity and soil microbial biomass content. Livestock grazing tended to induce linear SOC-microbe trait relationships, with no effects on microbe relations with nitrogen or phosphorus. Overall, our results indicate that global soil C cycling-soil microbe community trait relationships in grassland ecosystems intensify with livestock grazing and depend on grazing intensity, duration, and livestock species. These findings highlight the global importance of livestock grazing for soil C cycling in grasslands and the need to include these relationships in grassland ecosystem models to improve predictions of soil biogeochemical cycles under future management scenarios.

Keywords: grazing intensity; soil carbon cycling; grassland degradation; soil microbial activity; ecosystem function

1 Introduction

Grassland soils represent a key component of global carbon (C) cycling (Myrgiotis et al., 2021), given they account for about 10% of the global C pool (Dlamini et al., 2016). However, livestock grazing of grasslands affects multiple ecosystem processes (Davidson et al., 2017; Teague & Kreuter, 2020), where intensive and/or inappropriate grazing regimes have led to global-scale degradation (McSherry & Ritchie, 2013; Zhang et al., 2022a) and disruption of ecosystem function, including soil C cycling (López-Mársico et al., 2015; Montenegro-Diaz et al., 2022). Soil microbe communities are essential for the maintenance of ecosystem processes, including soil C cycling (Liu et al., 2015; Trivedi et al., 2016) that is known to be driven by soil microbe diversity (Qiu et al., 2021); for example, soil microbe diversity is positively associated with rates of litter decomposition and C cycling (Zhou et al., 2020), aboveground plant community function and soil quality, and overall ecosystem stability (Bardgett & van der Putten, 2014; van Elsas et al., 2012). Thus, understanding links between soil C cycling and microbe diversity is required to improve the management of grasslands to ensure sustainable ecosystem function.

Livestock grazing of grasslands has been shown to reduce soil C pools by an average of 10.3% (Zhou et al., 2017), probably as a result of impacts on soil microbes. For example, livestock grazing has been shown to elicit profound effects on soil microbe diversity and activity (Hu et al., 2021; Traore et al., 2021), where magnitude of effects on diversity are negatively dependent on grazing intensity (Zhao et al., 2017; Zhang et al., 2022b), likely due to decreases in soil permeability under high levels of grazing that inhibit microbial metabolic activity (Joshua et al., 2007; Jeffery et al., 2009). Similarly, duration of grazing activity is negatively associated with soil microbe diversity (Li et al., 2020), due to higher levels of plant damage and soil trampling with increasing period of grazing (van der Heyde et al., 2017) that eventually lead to greater levels of soil erosion and nutrient loss (Kosmalla et al., 2022; Zhang et al., 2022a). Negative effects of increases in livestock grazing on global soil C pools have been attributed to decreases in plant species richness (Gao & Garmel, 2020) and biomass (Zhang et al., 2022a), greater levels of soil erosion, and reductions in soil moisture (Kosmalla et al., 2022; Mariappan et al., 2022) that reduce soil microbe activity and associated C flux and nutrient cycling (Allison & Treseder, 2008). Diversity and activity of soil microbe communities have been shown to couple positively with soil C stocks (Liu et al., 2015; Delgado-Baquerizo et al., 2020; Zhou et al., 2020); however, impacts of livestock grazing on this relationship in grasslands, including for microbial C-stocks, remain unclear (Cai et al., 2017; Eldridge et al., 2017; van der Weerden et al., 2020).

While global impacts of grazing on plant community dynamics, litter decomposition, soil nutrient and C cycling in grasslands have been studied (Zhou et al., 2017; Gao & Garmel, 2020; Filazzola et al., 2020), there is a lack of understanding of effects of grazing intensity and duration on soil microbe communities. Thus, we synthesized a global dataset of observations in a meta-analysis of (1) effects of grazing intensity and duration, and livestock species assemblage (sheep, cattle, a mixture of sheep and cattle) on soil nutrient content and soil microbe community traits (biomass, diversity, activity); and (2) variation in soil microbe links with soil C and nutrient content with grazing regime. Specifically, we tested the hypotheses that livestock grazing (1) reduces soil content of C, nitrogen (N), and phosphorous (P) and microbial biomass, diversity, and activity due to decreases in plant biomass and increases in soil erosion and water loss and (2) intensifies links between soil microbe community traits and soil C, N, P content.

2 Methods

2.1 Data compilation

Published peer-reviewed articles on responses of soil enzyme activities and microbe communities to grazing were compiled from Google Scholar (http://scholar.google.com/), Web of Science (http://apps.webofknowledge.com/), and CNKI (http://www.cnki.net/) on Feb 10, 2022 using the search terms (“grassland”) and (“grazing” or “grazed” or “grazer”) and (“soil microbial” or “soil bacteria” or “soil fungi” or “soil enzyme” or “soil respiration”). Articles were selected for inclusion in the meta-analysis if (1) livestock species assemblage and grazing intensity and duration were reported; (2) ungrazed control plots were included; (3) treatment means and sample sizes were provided; (4) studies comprised grazing treatments only; and, (5) studies included data for topsoil.

As a result, our dataset comprised 623 data points from 95 articles (Appendix Dataset S1) for 21 variables related to soil enzymes, microbe community traits, and physicochemical properties (Table S1). We extracted data from tables directly and from figures using GetData Graph Digitizer v. 2.24.

The dataset included longitude, latitude, mean annual temperature (MAT), mean annual precipitation (MAP) for the areas in which the studies were conducted, along with classification of grazing treatment duration (<5 years, 5–10 years, and >10 years) and intensity (light, moderate, high), and livestock species assemblage (sheep, cattle, sheep+cattle).

2.2 Meta-analysis

The natural logarithmic response ratio (RR) (Hedges et al., 1999; Powers et al., 2011) was used to evaluate soil enzyme and microbe responses to grazing:

$$RR=\ln\left(\frac{\overline{X_t}}{\overline{X_c}}\right)=\ln\overline{X_t}-\ln\overline{X_c} \tag{1}$$

where $\overline{X_t}$ and X_c are the treatment and control means for a variable, respectively.

Variance (v) in RR of individual observations was calculated as:

$$v=\frac{\mathrm{S_t^2}}{\mathrm{n_t X_t^2}}+\frac{\mathrm{S_c^2}}{\mathrm{n_c X_c^2}} \tag{2}$$

where S_t and S_c are the treatment and control SDs, respectively, and n_t and n_c are treatment and control sample sizes, respectively. We calculated SD as either $\mathrm{SE}\sqrt{\mathrm{N}}$ or $\frac{\mathrm{mean}}{10}$, depending on reporting of SE in the studies.

We calculated weighted response ratios (RR_{++}), along with 95% bootstrap confidence intervals (CI) and SE ($S(RR_{++})$) using a random effects model:

$$RR_{++}=\frac{\sum_{i=1}^{m}\sum_{j=1}^{ki}W_{ij}RR_{ij}}{\sum_{i=1}^{m}\sum_{j=1}^{ki}W_{ij}} \tag{3}$$

$$95\%\mathrm{CI}=RR_{++}\pm1.96\mathrm{S}(RR_{++}) \tag{4}$$

$$S(RR_{++})=\sqrt{\frac{1}{\sum_{i=1}^{m}\sum_{j=1}^{ki}W_{ij}}} \tag{5}$$

There were no effects of grazing on response variables when 95% bootstrap CIs = 0; 95% bootstrap CIs >0 or <0 indicate grazing increases or decreases in soil enzyme activities and microbial community indices, respectively ($P < 0.05$).

We calculated the weighting factor (w) as:

$$w_{ij}=\frac{1}{\vartheta_i+\sigma^2} \quad (6)$$

where ϑ_i and σ^2 are variance of the data in the i-th study and the random variable common between studies, respectively.

We calculated *rr* as the proportional change (%) in RR_{++} of soil enzyme activity and microbe community trait responses to grazing as:

$$rr=[\exp(RR_{++})-1]\times 100\% \quad (7)$$

A random effects model was used to test *RRs* of soil enzyme activities and microbe community traits to grazing intensity and duration, and livestock species assemblage (sheep or goat, cattle or yak, and mixture of sheep or cattle or horse), based on the heterogeneity in group cumulative effect sizes (Q_M) (Gao et al., 2021; Xu et al., 2022a, b). Publication bias in *RR*s of grazing effects on variables (Fig. S1) was tested using the funnel method (Fig. S2) and biased variables were corrected using the trim and filled methods (Egger, 1997). Data processing and analysis were implemented in R v. 4.0.2 using the “metafor” package.

3 Results

3.1 Overall effects of grazing

There were contrasting effects of grazing on soil physicochemical properties, enzyme activity, and microbe community traits (Fig. 1), where there increases in bacteria diversity (1.0%) and richness (24.8%), fungi diversity (17.3%), phospholipid fatty acid (PLFA; 9.9%), and pH (2.2%) and decreases in activities of saccharase (SA; 31.1%), urease (UA; 7.0%), acid phosphatase (AP; 11.9%), soil basal respiration (SR; 15.4%), soil organic carbon (SOC; 10.1%), total soil nitrogen (TN; 10.2%), and total soil phosphorus (TP; 15.0%) (Fig. 1).

3.2 Effects of grazing intensity

Intensity of grazing led to contrasting effects on soil enzyme, microbe, and physicochemical parameters (Fig. 2; Table S2). Light and moderate grazing increased fungi diversity by 14.1 and 13.3%, respectively, and fungi richness by 17.0 and 13.1%, respectively. Moderate and high levels of grazing decreased soil activity of SA (28.3 and 27.9%, respectively), levels of SR (17.9 and 28.3%, respectively), and content of SOC (10.6 and 13.9%, respectively), TN (13.2 and 14.7%, respectively), and soil moisture (14.7% and 19.7%, respectively), and increased soil pH (2.4 and 1.4%, respectively). High levels of grazing decreased activities of AP (10.5%), microbial biomass carbon (MBC; 7.2%), microbial biomass nitrogen (MBN; 7.5%), arbuscular mycorrhizal fungi (AMF; 30.0%), and ratio of fungi to bacteria (F:B; 15.8%), and increased microbial metabolic quotient (qCO_2) by 42.2%.

3.3 Effects of grazing duration

Short-term grazing (0–5 years) increased soil activity of AP by 14.6% and bacteria richness by 21.3%, and decreased AMF content by 36.0%, F:B by 13.4%, and soil moisture by 10.7%. Medium (5–10 years) and longer term (>10 years) grazing decreased SR (16.1 and 21.5%, respectively), content of SOC (9.7 and 15.0%, respectively), TN (6.7 and 20.0%, respectively), and TP (9.5 and 15.7%, respectively), and increased soil pH (3.5 and 1.7%, respectively). Grazing for >10 years decreased activities of SA (36.2%), AP (12.1%), and UA (11.5%), soil content of microbial biomass

C (MBC; 15.0%), MBN (17.7%), TN (20.0%), and TP (15.7%), and SR (21.5%) (Fig. 3; Table S2). Grazing duration was negatively correlated with RRs of AP, MBC, MBN, SR, and SOC, and positively correlated with RRs of AMF (Fig. S3).

3.4 Effects of livestock species assemblage

Livestock species led to contrasting effects on soil enzyme, microbe, and physicochemical parameters (Fig. 4; Table S2). Grazing by sheep led to decreases in activity of SA (30.7%) and AP (5.7%), soil content of MBC (5.2%) and AMF (30.1%), GP:GN (4.7%), and SR (15.6%), and increased soil pH(1.7%). Grazing by cattle led to decreases in UA activity (15.7%) and soil content of MBN and microbial biomass P (MBP) (6.8 and 28.0%, respectively), while sheep and cattle grazing decreased SR (15.6 and 14.9%, respectively), and content of SOC (11.1 and 8.5%, respectively), soil TN (11.9 and 6.8%, respectively), soil TP (10.2 and 8.4%, respectively), and soil moisture (12.7 and 7.2%, respectively).

3.5 Effects of climate

Mean annual precipitation (MAP) was positively related to RRs of MBC and MBN and mean annual temperature (MAT) was positively related to RRs of UA activity, soil content of MBC and MBN, fungi diversity, and PLFA content (Fig. 5).

3.6 Relationships between soil nutrient content and microbe traits under contrasting grazing regimes

Overall, RRs of SOC content were positively related to RRs of SA and AP activity, soil content of MBC, MBN, and MBP, SR, bacteria and fungi diversity, and PLFA content (Fig. S4). Under high levels of grazing, RRs of SOC content were positively related to RRs of SA activity, and bacteria and fungi diversity, while under moderate and high levels of grazing, SOC RRs were positively related to RRs of UA activity, soil content of MBC, MBN, and MBP, and SR; relationships with SOC were stronger under the high levels of grazing (Fig. 6). There were positive relationships between RRs of SOC content and RRs of SA activity, fungi diversity, and MBN content under longer-term grazing (>10 years), RRs of AP activity and bacteria diversity under medium term grazing (5–10 years), and RRs of soil content of MBC and MBN, and SR under short-term (0–5 years) and longer-term grazing (Fig. S5).

Overall, RRs of soil TN content were positively related to RRs of activity of AP, soil content of MBC, MBN, and MBP, SR, and bacteria diversity (Fig. S6). Under moderate and high levels of grazing, RRs of soil TN content was positively related to RRs of soil MBC content and SR, RRs of AP activity under all three levels of grazing and longer-term grazing (>10 years) (Fig. S7).

Overall, RRs of soil TP content were positively related to RRs of SA and UA activity, soil MBP content, and SR (Fig. S8). Under high levels of grazing, soil TP content RRs were positively related to SA activity RRs, while under light and high levels of grazing and short-term grazing (0–5 years), soil TP content RRs were positively related to soil MBP content RRs; soil TP content RRs were positively related to RRs of SR under moderate and high levels of grazing (Fig. S9).

4 Discussion

4.1 Effects of grazing intensity on soil C cycling and microbe traits

Our meta-analysis provides direct evidence for degradation of grassland soils and a reduction in grassland ecosystem stability by intense levels of livestock grazing. We found reductions in SOC and soil microbial biomass content, and activity of enzymes under increasing grazing pressure, whereas, light and moderate grazing intensity tended to increase microbe diversity (Fig. 7), likely as a result of the belowground reallocation of plant biomass (root growth) by low-intensity grazing that improves and maintains soil moisture content and supports higher levels of soil microorganism abundance (Wilson et al., 2018; Mipam et al., 2019). Livestock grazing has been shown to aggravate water and wind erosion of soil C content, due to changes in soil structure (Zhou et al., 2017), and intense levels of grazing, which tend to decrease plant diversity and cover, soil aeration, and water permeability, due to foraging and trampling effects (Jeffery et al., 2009), limit the contribution of soil microorganisms to ecosystem function, such as in soil C cycling, due to negative impacts on environmental conditions (Birgander et al., 2014; McSherry et al., 2013). We found that moderately intense grazing increased F:B ratios, whereas under high levels of grazing, ratios decreased, indicating contrasting dominance of fungi and bacteria under moderate and high levels of grazing, respectively (Xun et al., 2018), likely due to the greater sensitivity of soil fungi to disturbance than bacteria (Tolkkinen et al., 2015); for example, fungal hyphae are particularly vulnerable to intense grazing (Tordoff et al., 2011).

4.2 Effects of grazing duration on soil C cycling and microbe traits

We found that RRs of SOC decreased with grazing duration, supporting previous meta-analyses (Tang et al., 2019; Zhou et al., 2017). Soil enzyme activity RRs and soil microbial biomass are reduced under longer-term grazing duration (>10 years), likely as a result of prolonged decreases in the return of plant-based organic matter to the soil (Zhang et al., 2022a) and negative impacts of trampling on soil erosion and associated increases in nutrient losses, including C, and decreases in soil moisture content that limit availability of resources required for microbial growth (Van Syoc et al., 2022). Although our analysis showed that grazing for >10 years leads to increases in the diversity of bacteria and fungi, this finding requires verification, due to a lack of data for sites grazed for 5–

10 years; however, it is likely that large variations in soil, vegetation, and climate conditions of the global-scale dataset may partly explain such response patterns (Wilson et al., 2018; Li et al., 2020). Our results provide clear evidence that effects of grazing on soil C and microbe communities largely depend on grazing duration, where 10 years may represent a critical threshold for impacts of livestock grazing on soil enzyme activity and microbial biomass and overall grassland soil ecosystem stability. We suggest, however, that soil fungi and bacteria diversity and evenness responses to grazing duration should be investigated further.

4.3 Effects of livestock species assemblage on soil C cycling and microbe traits

Livestock species is a key driver of grazing effects on soil microbe community traits (van der Weerden et al., 2020; Traore et al., 2021). Indeed, we found negative effects of sheep grazing on SOC and MBC content, enzyme activity (SA and AP), and AMF abundance were greater than for grazing by cattle, likely due to contrasting dietary preferences. For example, large grazers, such as cattle, tend to consume plants of greater palatability and use their tongue and teeth to remove higher level vegetation (Pruszenski & Hernandez, 2020), whereas smaller grazers, such as sheep, tend to use teeth to nibble vegetation close to ground-level (Li et al., 2021; Song et al., 2017); this difference results in a larger foraging area under sheep grazing than under cattle (Rook et al., 2004), with greater impacts on soil C and microbe community traits. Similarly, differences in organic inputs between grazing species affect soil properties: larger amounts of manure under cattle grazing that alleviate associated reductions soil nutrients and soil moisture (Cai et al., 2017) may explain the lower negative effects of cattle grazing we found in this study and could slow the reductions in soil C content and microorganism activity.

4.4 Effects of climate on soil C cycling and microbe traits

Regional climate factors, such as temperature and precipitation, contribute to element cycling and nutrient availability, and soil microbe community structure and function in grassland ecosystems (McDaniel et al., 2013; Wang et al., 2021; Yang et al., 2021). However, we found no evidence for relationships between SOC content RRs and MAP or MAT, possibly because most of the studies included in our meta-analysis were conducted in areas of relatively low precipitation and temperature where there are low accumulation levels of SOC, indicating that disturbance from grazing may be a stronger driver of grassland soil C turnover, particularly in dry and cold regions, such as tundra, than local climate conditions. In contrast, we found that MAP was positively related to RRs of microbial biomass (MBC and MBN) and MAT was positively related to UA activity, soil microbial biomass content, fungi diversity, and PLFA content under grazed conditions, where shifts from negative to positive relationships with increasing MAP and MAT occurred at critical threshold points of c. 500 mm and 5 ℃, respectively. It is possible that these trends in relationship are explained by accelerated rates of litter decomposition rate with increasing MAP and MAT (González & Seastedt, 2001; Pillay et al., 2021) that provide a positive feedback for soil microbe community foraging of nutrients (Ren et al., 2018) and/or changes in soil physicochemical properties driven by temperature and precipitation patterns lead to shifts in soil microbe communities (Zhou et al., 2020; Tang et al., 2022).

4.5 Links between SOC content and soil microbe traits under contrasting grazing regimes

An important finding in our study is that, while livestock grazing often induced a linear relationship between microbe community traits and SOC content, there was no similar effect on relationships with soil TN or TP. These results indicate that microbe communities may be more active in C cycling than in N or P cycling under grazing pressure, possibly because grazing livestock tend to prefer non-legume taxa, such as the Poaceae and Cyperaceae, to leguminous species that are a major source of soil N content in grasslands (Franche et al., 2009; Li et al., 2019). Thus, it is likely that while most livestock grazing of grasslands may have limited impacts on soil N derived from leguminous plants (Song et al., 2017; Li et al., 2021), there could be a decrease in microbial activity that may lead to weakened relationships between soil TN and microorganisms. Likewise, the combination of continuous leaching and losses of P from livestock-grazed grasslands soils (Vadas et al., 2015) and slow soil gains in P from rock weathering may lead to a decoupling of P cycling and microbial activities. Thus, a consequence of livestock grazing of grassland may increase the dependence of soil C cycling on microbial activities, with no impact on the relationships of N and P with microorganisms. Furthermore, we found that such dependence of SOC content on microbe traits tended to be stronger under moderate and high levels of grazing than under low intensity grazing, that led to the subsequent increase in other soil processes, including UA activity, soil microbial biomass content, and soil respiration, indicating that SOC-microbial activity relationships intensify with grazing intensity. Given the key role of microbe community traits in soil C cycling (Delgado-Baquerizo et al., 2020), grazing-mediated impacts on SOC-microbe relationships may operate through effects on plant productivity and litter decomposition (Liu et al., 2015; Eldridge et al., 2017; López-2015 Mársico et al., 2015).

Negative effects of grazing on plant growth and cover tend to increase with grazing intensity (Tang et al., 2019; Wang & Tang, 2019; Montenegro-Diaz et al., 2022), reducing the return of C and nutrients to the soil via litter decomposition (Traore et al., 2021) that then decrease food source availability for soil microbes (Eldridge et al., 2017), leading to microbial nutrient limitation (Van Syoc et al., 2022) and lower levels of SOC conversion (McSherry et al., 2013; McBride et al., 2020).

Similarly, intense levels of grazing may inhibit microbial growth and function in soil C cycling (Van Syoc et al., 2022; Tang et al., 2021), due to effects of higher soil temperatures and levels of water evaporation (Rehschuh et al., 2022) following greater exposure of the soil surface to solar radiation (Niu et al., 2014), while livestock trampling increases soil erosion (Kosmalla et al., 2022) and soil microbe mortality and/or migration (Joshua et al., 2007; Qiu et al., 2021) that adversely influences microbe growth and associated ecosystem C processes (Malik & Bouskill, 2022; Mariappan et al., 2022).

5 Conclusions

Our meta-analysis indicates that global grassland soil content of C, N, and P, and microbial biomass, along with microbe diversity and activity are sensitive to livestock grazing. Grazing intensity and duration tend to be negatively related to soil content of C, N, and P, enzyme activities, soil microbial biomass content, and levels of soil respiration. In contrast to high levels of grazing intensity, light and moderately intense grazing increase soil bacteria and fungi diversity. Most importantly, grazing intensity, rather than grazing duration, strengthens SOC-microbial trait relationships, while there were no such effects on relationships with soil TN or TP. Our findings highlight the importance of livestock grazing in soil microbe-mediated C processes and we suggest these relationships should be accounted for in grassland ecosystem C-cycling models.

Acknowledgements

Author contributions

Conflict of interest statement

The authors declare no conflicts of interest.

Data availability statement

The data supporting the findings of this study are available in Supplementary Dataset 1.

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Table and figure captions

Fig. 1 The response ratios of soil enzyme activities, microbial parameters, and chemical properties to grazing. Notes: dots with error bars denote overall means and 95% confidence intervals (CI). Numbers in parentheses indicates sample sizes. *indicates that grazing significantly affected soil properties. SA, saccharase enzyme. UA, urease enzyme. AP, acid phosphatase. MBC, microbial biomass carbon. MBN, microbial biomass nitrogen. MBP, microbial biomass phosphorus. SR, soil basal respiration. qCO_2, microbial metabolic quotient. Bacteria D, bacterial diversity index. Bacteria R, bacterial richness index. Fungi D, fungal diversity index. Fungi R, fungal richness index. AMF, arbuscular mycorrhizal fungi. PLFA, Total phospholipidfatty acid. F:B, fungi to bacteria ratio. GP:GN, Gram-positive bacteria to Gram-negative bacteria ratio. SOC, soil organic carbon. TN, soil organic nitrogen. TP, soil organic phosphorus.

Fig. 2 Effects of grazing intensity on soil enzyme activities, microbial parameters, and chemical properties. Notes: dots with error bars denote overall means and 95% confidence intervals (CI). Numbers in parentheses indicates sample sizes. *indicates that grazing significantly affected soil properties. LG, light grazing. MG, moderate grazing. HG, heavy grazing. AP, acid phosphatase. SA, saccharase enzyme. UA, urease enzyme. MBC, microbial biomass carbon. MBN, microbial biomass nitrogen. MBP, microbial biomass phosphorus. SR, soil basal respiration. qCO_2, microbial metabolic quotient. Bacteria D, bacterial diversity index. Bacteria R, bacterial richness index. Fungi D, fungal diversity index. Fungi R, fungal richness index. AMF, arbuscular mycorrhizal fungi. PLFA, Total phospholipidfatty acid. F:B, fungi to bacteria ratio. GP:GN, Gram-positive bacteria to Gram-negative bacteria ratio.

Fig. 3 Effects of grazing duration on soil enzyme activities, microbial parameters, and chemical properties. Notes: dots with error bars denote overall means and 95% confidence intervals (CI). Numbers in parentheses indicates sample sizes. *indicates that grazing significantly affected soil properties. AP, acid phosphatase. SA, saccharase enzyme. UA, urease enzyme. MBC, microbial biomass carbon. MBN, microbial biomass nitrogen. MBP, microbial biomass phosphorus. SR, soil basal respiration. qCO_2, microbial metabolic quotient. Bacteria D, bacterial diversity index. Bacteria R, bacterial richness index. Fungi D, fungal diversity index. Fungi R, fungal richness index. AMF, arbuscular mycorrhizal fungi. F:B, fungi to bacteria ratio. PLFA, Total phospholipidfatty acid. GP:GN, Gram-positive bacteria to Gram-negative bacteria ratio.

Fig. 4 Effects of herbivore assemblage on soil enzyme activities, microbial parameters, and chemical properties. Notes: dots with error bars denote overall means and 95% confidence intervals (CI). Numbers in parentheses indicates sample sizes. *indicates that grazing significantly affected soil properties. AP, acid phosphatase. SA, saccharase enzyme. UA, urease enzyme. MBC, microbial biomass carbon. MBN, microbial biomass nitrogen. MBP, microbial biomass phosphorus. SR, soil basal respiration. qCO_2, microbial metabolic quotient. Bacteria D, bacterial diversity index. Bacteria R, bacterial richness index. Fungi D, fungal diversity index. Fungi R, fungal richness index. AMF, arbuscular mycorrhizal fungi. F:B, fungi to bacteria ratio. PLFA, Total phospholipidfatty acid. GP:GN, Gram-positive bacteria to Gram-negative bacteria ratio.

Fig. 5 Relationships of (a) mean annual precipitation (MAP) with the response ratio of acid phosphatase (AP), microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN); (b) mean annual temperature (MAT) with the response ratio of urease enzyme (UA), microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), fungi diversity index (Fungi D) and Phospholipidfatty acid (PLFA).

Fig. 6 Relationships between microbial diversity and soil organic carbon (SOC) with grazing intensity. Notes: *, *p*<0.05. **, *p*<0.01. ***, *p*<0.001. SA, saccharase enzyme. MBC, microbial biomass carbon. MBN, microbial biomass nitrogen. MBP, microbial biomass phosphorus. SR, soil basal respiration. Bacteria D, bacterial diversity index. Fungi D, fungal diversity index.

Fig. 7 Conceptual framework of the effects of grazing on soil enzyme activity and microbial community. Notes: Gray means insignificant. “-” indicate grazing intensity and duration had negative effects on soil enzyme activity and microbial community. “+” indicate grazing intensity and duration had positive effects on soil enzyme activity and microbial community.

Table S1. 25 variables included in this study.

Table S2 Effect test summary of grazing intensity, grazing duration and herbivore assemblage on each response variable under the random effects model.

Fig. S1 Frequency distribution of the response ratios of acid phosphatase (AP), saccharase enzyme (SA), urease enzyme (UA), microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), microbial biomass phosphorus (MBP), soil basal respiration (SR), microbial metabolic quotient (qCO_2), bacterial diversity index (Bacteria D), bacterial richness index (Bacteria R), fungal diversity index (Fungi D), fungal richness index (Fungi R), arbuscular mycorrhizal fungi (AMF), fungi to bacteria ratio (F:B), Gram-positive bacteria to Gram-negative bacteria ratio (GP:GN), soil organic carbon (SOC), total nitrogen (TN) and total phosphorus (TP).

Fig. S2 The funnel plot of the response ratios of acid phosphatase (AP), saccharase enzyme (SA), urease enzyme (UA), microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), microbial biomass phosphorus (MBP), soil basal respiration (SR), microbial metabolic quotient (qCO_2), bacterial diversity index (Bacteria D), bacterial richness index (Bacteria R), fungal diversity index (Fungi D), fungal richness index (Fungi R), arbuscular mycorrhizal fungi (AMF), Phospholipidfatty acid (PLFA), fungi to bacteria ratio (F:B), Gram-positive bacteria to Gram-negative bacteria ratio (GP:GN), soil organic carbon (SOC), total nitrogen (TN) and total phosphorus (TP).

Fig. S3 Relationships of grazing duration with the response ratio of acid phosphatase (AP), microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), soil basal respiration (SR), fungal diversity (Fungi D) and arbuscular mycorrhizal fungi (AMF).

Fig. S4 Relationships of the response ratio of different individual observations with soil organic carbon (SOC). Notes: AP, acid phosphatase. SA, saccharase enzyme. MBC, microbial biomass carbon. MBN, microbial biomass nitrogen. MBP, microbial biomass phosphorus. SR, soil basal respiration. Bacteria D, bacterial diversity index. Fungi D, fungal diversity index.

Fig. S5 Relationships between microbial diversity and soil organic carbon (SOC) with grazing duration. Notes: *, $p<0.05$. **, $p<0.01$. ***, $p<0.001$. SA, saccharase enzyme. UA, urease enzyme. AP, acid phosphatase. MBC, microbial biomass carbon. MBN, microbial biomass nitrogen. SR, soil basal respiration. Bacteria D, bacterial diversity index. Fungi D, fungal diversity index.

Fig. S6 Relationships of the response ratio of different individual observations with soil total nitrogen (TN). Notes: AP, acid phosphatase. MBC, microbial biomass carbon. MBN, microbial biomass nitrogen. MBP, microbial biomass phosphorus. SR, soil basal respiration. Bacteria D, bacterial diversity index.

Fig. S7 Relationships between microbial diversity and soil total nitrogen (TN) with grazing intensity (a) and duration (b). Notes: *, $p<0.05$. **, $p<0.01$. ***, $p<0.001$. AP, acid phosphatase. MBC, microbial biomass carbon. SR, soil basal respiration.

Fig. S8 Relationships of the response ratio of different individual observations with soil total phosphorus (TP). Notes: SA, saccharase enzyme. UA, urease enzyme. MBP, microbial biomass phosphorus. SR, soil basal respiration.

Fig. S9 Relationships between microbial diversity and soil total phosphorus (TP) with grazing intensity (a) and duration (b). Notes: *, $p<0.05$. **, $p<0.01$. SA, saccharase enzyme. AP, acid phosphatase. MBP, microbial biomass phosphorus. SR, soil basal respiration.