



Light grazing reduces temporal variation in soil organic carbon in an alpine peatland: Perspectives from fungal communities

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ABSTRACT

Waterlogged alpine peatlands harbour substantial reserves of recalcitrant soil organic carbon (SOC) that is mainly decomposed by soil fungi. Even a slight fluctuation in peatland SOC can considerably alter C emissions, thereby impacting the future trajectory of climate change. These peatlands are often subject to yak grazing, which can affect ecosystem functions. However, how grazing regulates microbially mediated temporal variations in SOC in alpine peatlands remains largely unclear. Therefore, we conducted a field experiment on the Zoige Plateau to explore the effects of grazing on peatland soil C content and its association with soil fungal communities during different seasons (spring, summer, and autumn). Grazing significantly increased SOC in spring but not in the subsequent seasons. Furthermore, grazing significantly increased soil water contents in summer, dissolved organic carbon contents in autumn, and N-acetyl- β -D-glucosaminidase and leucine aminopeptidase activities in spring and autumn, but decreased phenol oxidase activity in spring and summer. Grazing significantly reduced fungal diversity at α and β scales. The coefficient of variation of SOC was significantly reduced by grazing, whereas similar trends were not observed for dissolved organic carbon or for dissolved organic and inorganic nitrogen. In the fenced area, the coefficient of variation of fungal species richness was the most important factor for predicting that of SOC. In the grazed area, coefficient of variation of soil $\text{NH}_4^+\text{-N}$ contributed the most to that of SOC. These findings underscore the pivotal role of fungal community in affecting SOC dynamics in alpine peatlands, which is crucial for understanding the ecological processes that maintain soil C cycling in alpine ecosystems.

1. Introduction

Alpine peatlands in the Qinghai-Tibet Plateau have accumulated substantial amounts of partially decomposed plant litter over centuries because of the anaerobic and cold environment, existing as a profound soil carbon (C) pool (Hugelius et al., 2020; Loisel and Gallego-Sala, 2022). The C stock in peatlands is estimated to be twice that in the world's forests (Loisel et al., 2021). Considering the high soil organic carbon (SOC) stock in peatlands, even minor fluctuations in SOC can substantially alter atmospheric CO_2 concentrations, thereby influencing the future trajectory of climate change (Nyaupane et al., 2024). Furthermore, waterlogged peatlands in alpine ecosystems display pronounced seasonality owing to the phase transition of soil water (Zhao and Hu, 2023). These temporal dynamics may considerably alter the soil physical structure (Hu et al., 2023), soil microbial community

composition (Ji et al., 2022), and further C cycling (Xiao et al., 2019). Therefore, exploring the dynamics of SOC in alpine peatlands is crucial for providing effective strategies to enhance C sequestration and maintain peatland function in a changing world.

According to the annual livestock data and model-derived stocking rate, most grasslands in the Qinghai-Tibetan Plateau are subjected to high livestock density that is almost equal to or even above their grassland carrying capacity (Zhang et al., 2021; Zhu et al., 2023). Livestock grazing activities strongly affect ecosystem functions and services. Foraging and trampling by livestock during grazing enriches rhizome grass and resistant grass species (Liu et al., 2015). This negatively affects primary production in alpine meadow and steppe ecosystems (Wang et al., 2020; Zhu et al., 2024). A shift in plant functional types changes the quantity and quality of C input into the soil, further affecting the microbial community in temperate grasslands (Wang et al.,

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2021; Zhou et al., 2024). These changes lead to substantial inconsistencies in soil SOC dynamics. For example, trampling by livestock can reduce microbial abundance and activity in grassland soils, thereby hindering the accumulation of microbial necromass and consequently reducing the SOC content (Du et al., 2024; Fan et al., 2020). While other studies found increases in SOC by grazing with moderate density in various types of grasslands (Serrano et al., 2024; Zhou et al., 2024). In peatlands with higher soil water, grazing effects on SOC are further affected by plant compensatory growth (Hamerlynck et al., 2023) and enhanced microbial nitrogen cycling genes (Ding et al., 2015). Although these studies have explored the various effects of grazing on SOC content, how grazing activities affect temporal variations in SOC as well as microbial processes in alpine peatlands remains largely unknown. Addressing this knowledge gap is crucial for understanding the ecological processes that maintain peatland structures and functions.

Microbially regulated ecological processes within alpine peatlands exhibit pronounced temporal dynamics that influence soil C sequestration (Broadbent et al., 2024). There exists a considerable uncertainty regarding the temporal variations in microbial properties. For example, a previous study on an alpine meadow found that soil microbial biomass was much higher in summer than in spring or winter (Wang and Hu, 2024). Contrastingly, soil microbial biomass peaked in late winter, followed by a temporal decrease during the snowmelt period in another study (Watanabe et al., 2019). Changes in soil microbial biomass can influence the SOC content by regulating the decomposition of organic matter (Du et al., 2024). In addition to microbial biomass, seasonal variations in the soil microbial community composition are critical for evaluating ecosystem functions and services. Seasonal factors, such as temperature and soil water table, can shrink or extend the niche breadth of certain microbes and further affect C metabolic functionality (Ji et al., 2022; Ma et al., 2022). Moreover, the soil microbial community is significantly altered in early spring or late winter with frequent freezing-thawing activities compared to the growing season (Ji et al., 2022). Changes in the microbial community during these periods enhance nutrient availability, thereby influencing primary production (Watanabe et al., 2019; Yang et al., 2019). Additionally, soil water content increases due to thawing in spring, leading to an enhancement of genes degrading labile C (Tang et al., 2023) and priming the breakdown of SOC (Kuzuyakov and Blagodatskaya, 2015). However, the interactive effects of grazing and season on soil microbial communities in alpine peatlands is far from clear. Thus, the effects of grazing on temporal variations in soil microbial communities must be identified to elucidate soil C dynamics in alpine peatlands.

In this study, we conducted a field experiment in an alpine peatland on the Zoige Plateau to explore the effects of grazing and seasons on the soil microbial processes. Soil fungi is the major group capable of producing oxidative enzymes and further decomposing recalcitrant C (Keiblinger et al., 2010; Liu et al., 2018). Given the high level of recalcitrant plant debris in alpine peatland soils (Chen et al., 2014; Hugelius et al., 2020), we evaluated the relationship between fungal community heterogeneity and temporal variation in SOC. We determined the soil C content, nutrient availability, enzyme activities and fungal community compositions during different seasons (spring, summer, and autumn) in fenced and grazed areas. Owing to technical errors, data from winter months were not included in the analyses. We aimed to address the following questions: (1) How does grazing affect soil properties, microbial enzymes and community composition in alpine peatlands across the seasons? (2) What are the temporal dynamics of peatland SOC and its major drivers?

2. Materials and methods

2.1. Site description and soil sampling

The study site is located in Hongyuan County (33.0946° N, 102.6577° E), Sichuan Province, China, which belongs to the Zoige

Plateau. The peatland type in our study site is a minerotrophic fen that receives water and nutrients from the surface or ground water (Chen et al., 2014; Loisel and Gallego-Sala, 2022). The mean annual precipitation and temperature is 698 mm and 2.4 °C, respectively. The elevation of this site is approximately 3470 m. The dominant plant species in this peatland include *Carex meyeriana*, *Carex tibetkobresia*, *Carex muliensis*, *Caltha scapose*, and *Sanguisorba filiformis*. The growing season of the plant species generally ranges from May to September.

Yak grazing at the study site has occurred at a density of 1.47 yak ha⁻¹, which is categorised as light grazing (Cao et al., 2004; Zhang et al., 2022). Enclosure management was established in 2018 to investigate the effects of grazing on changes in ecological processes in alpine peatlands. We sampled soil from the plots inside and outside the fenced area in the spring (April), summer (August), and autumn (October) of 2021. Each treatment (fenced and grazed) consisted of 10 sampling plots. The distance between each plot was at least 15 m. Soil samples were collected from five random locations in each plot using a coring auger (diameter: 6 cm; depth: 10 cm). The soil cores were then pooled together and sieved through a 2 mm mesh sieve to remove any apparent root debris and gravel. Soil samples for high-throughput sequencing and chemical analyses were stored at -80 °C and -20 °C, respectively.

2.2. Soil properties

The soil pH was determined using a pH meter (DZB-712; Rex Electric Chemical, Shanghai, China). Soil water content (SW) was determined by oven-drying at 105 °C to a constant mass. The dichromate oxidation method was used to estimate SOC content (Mebius, 1960). The chloroform fumigation-extraction method was used to measure the soil microbial biomass carbon (MBC) and nitrogen (MBN) (Vance et al., 1987). Soil extracts with 2 mol L⁻¹ KCl solution at a ratio of 1:5 (soil:water) were used to determine soil ammonium and nitrate nitrogen (NH₄⁺-N, NO₃⁻-N) concentrations through a flow injection analyser (QC8500; LACHAT, United States). The soil inorganic N content was calculated as the sum of NH₄⁺-N and NO₃⁻-N. Soil dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) were determined using a TOC/TN analyser (Multi N/C 2100; Analytik Jena, Germany). Moreover, dissolved organic N (DON) in the soil samples was calculated as the difference between the TDN and inorganic N (NH₄⁺, NO₃⁻).

2.3. Soil extracellular enzyme activity

Fresh soil samples were used for to analyse extracellular enzyme activity. The oxidative enzymes phenol oxidase (PHO) and peroxidase (POD) are responsible for eliminating polyphenolic and phenolic compounds that can restrict microbial C decomposition (Zhao et al., 2024). The hydrolytic enzymes N-acetyl-β-D-glucosaminidase (NAG) catalyses the hydrolysis of C-containing compounds of chitooligosaccharides whereas leucine aminopeptidase (LAP) catalyses the hydrolysis of leucine and other amino acid residues (German et al., 2011). Enzymatic activity was determined using the 96-well microplate method. Substrates of N-acetyl-glucosamine and L-Leucine-7-amino-4-methylcoumarin were used to measure the NAG and LAP, respectively (German et al., 2011). Substrate L-3,4-dihydroxyphenylalanine was used for POD and PHO (DeForest, 2009). Briefly, approximately 3 g of fresh soil samples was thoroughly mixed with 200 mL of 50 mmol L⁻¹ sodium acetate buffer (pH 5.5). Next, 200 μL of the supernatant and 50 μL of the substrate were added to 96-well microplates. The fluorescence intensity of the enzymes in 96-well microplates was quantified using a microplate reader (Varioskan Lux, Thermo Fisher Scientific, Waltham, MA, USA). The excitation wavelength was 365 nm. The emission wavelengths for hydrolases and oxidases were 365 and 450 nm, respectively. The enzyme activities are expressed as nmol or μmol h⁻¹ g⁻¹ dry soil.

2.4. DNA extraction and high-throughput sequencing

Total genomic DNA was extracted from 0.2 g fresh soil samples using the Power Soil DNA kit (MoBio Laboratories) according to the manufacturer's instructions. The concentration and quality of the extracted DNA were assessed using a Nanodrop 3000 spectrophotometer (Nanodrop, Wilmington, DE, USA). The fungal ITS gene (V1 region) was amplified using the forward primer (5'-GCATCGATGAAGAACGCAGC-3') and reverse primer (5'-TCCTCCGCTTATTGATATGC-3').

PCR was performed as follows: Initial denaturation at 94 °C for 5 min, followed by 30 cycles of denaturation at 94 °C for 30 s, annealing at 52 °C for 30 s, extension at 72 °C for 30 s, and a final extension at 72 °C for 10 min. Each PCR reaction was set up in a 50 µL system containing 25 µL of 2× Premix Taq, 1 µL of each primer (10 µM concentration), 50 ng of template DNA, and Nuclease-free H₂O to bring the total volume to 50 µL. PCR amplifications were performed in triplicate for each soil sample to guarantee reproducibility. The amplicon library was loaded onto an Illumina MiSeq platform and sequenced using a 2 × 250 paired-end configuration (Shanghai Personalbio Technology Co., Ltd., Shanghai, China).

After quality filtering, 6,083,854 valid fungal sequences were identified. An average of $101,397 \pm 12,009$ sequence reads was obtained for all samples. Valid sequences were then processed to generate amplicon sequence variants (ASV) using UNOISE3 (Edgar, 2018). Taxonomic assignment for each representative sequence was conducted using BLAST, specifically targeting SILVA 138/18S_eukaryota (Bolyen et al., 2019). Rarefaction analyses indicated that the sequencing depth was sufficient to assess the effects of grazing on the soil microbial communities (Figure S1).

2.5. Statistical analysis

All statistical analyses were performed using R software (v.4.3.1; <http://www.r-project.org/>). Raw “Chloroplast” and “Mitochondria” sequences were filtered out from the microbial dataset. The ASV table was rarefied using the function ‘rarefy_even_depth’ in the package phyloseq to resample the dataset such that all the samples have the same library size before community analyses (McMurdie and Holmes, 2013). The natural log-transformed response ratio (ln-RR, effect size) was applied to evaluate the responses of soil properties to grazing under different seasons with the function “rma” in the “metafor” package (Viechtbauer, 2010). Seasonal variabilities in soil C and N content were measured using the coefficient of variation (CV), namely, the ratio of variance for a series of data to its mean (Tilman, 1999), for which smaller values represent greater stability. Student's t-tests were performed to explore the effects of treatment (fenced and grazed) on the CV values of the soil C and N content. The relationships between DOC and soil properties were determined through linear regression models.

The species richness index and β dispersion were used to characterise fungal α and β diversity in each plot, respectively. Multivariate dispersion of the fungal community was calculated as the average distance of group members to the group centroid with the function “betadisper” in vegan (Oksanen et al., 2022). Two-way analysis of variance (ANOVA) was performed to explore the effects of treatment (fenced and grazed) and season (spring, summer, and autumn) on fungal diversity and soil abiotic properties. Permutational multivariate ANOVA (PERMANOVA) was used to evaluate the effects of treatment and season on fungal community compositions with the function “adonis2” (Oksanen et al., 2022). The fungal community composition was determined at the phylum level. Fungal guilds and trophic modes of fungal ASVs were annotated using the FUNGuild tool (Nemergut et al., 2013).

The relationships between environmental variables and fungal community composition were determined using mantel tests across different seasons with the function “mantel” (Oksanen et al., 2022). Variations in the fungal community composition across different treatments were analysed through constrained redundancy analyses with the

function “rda” in the “vegan” package (Oksanen et al., 2022). Random forest analysis was used to evaluate the relative importance of environmental factors on fungal α and β diversity with the function “rfPermute” in the “rfPermute” package (Archer, 2022).

A multiple regression model was used to evaluate the effects of the CV values of the measured variables on those of SOC. According to Akaike's information criterion values, the final model included microbial variables of fungal species richness, MBC and MBN, and abiotic variables of pH, SW, NH₄⁺-N, and DON. The R² of the model was extracted with the function “glm.hp” in the package “glm.hp” (Lai et al., 2022). The relative importance of the individual factors in predicting the CV values of SOC was further determined. In addition, the relationship between the CV values of fungal α diversity and those of SOC was determined using a linear regression model.

3. Results

3.1. Effects of grazing on soil properties across different seasons

Grazing exerted a notable effect on soil properties across different seasons in the alpine peatlands (Fig. 1; Table S1; Figure S2). SW content was significantly enhanced by grazing in summer (Fig. 1). Grazing significantly increased SOC content during spring, whereas a similar increasing trend was not significant in summer or autumn (Fig. 1). It significantly enhanced the soil DON content in autumn (Fig. 1). Moreover, it significantly increased NAG and LAP activities in spring and autumn, while concurrently reducing PHO activity in spring and summer (Fig. 1). Soil pH, DOC, inorganic N, and POD showed no response to grazing across different seasons (Fig. 1).

3.2. Fungal diversity across different treatments and seasons

Grazing and season significantly influenced fungal α and β diversity in the alpine peatland. For α scale, grazing significantly reduced fungal species richness across all sampling seasons (Fig. 2a). In particular, fungal species richness was lowest in summer (Fig. 2a). For β scale, similar reductions in fungal β dispersion under the grazing treatment were observed across different seasons (Fig. 2b). The PERMANOVA results demonstrated significant changes in fungal community composition by grazing and season (Table S2). Ascomycota and Basidiomycota were the predominant fungal phyla (Figure S3). Furthermore, grazing markedly increased the abundance of symbiotrophic fungal guilds, which showed a significant seasonal pattern characterised by a peak in summer (Figure S4).

3.3. Relationship between fungal community and environmental factors

Significant relationships between fungal community composition and environmental variables were observed in the multivariate analyses (Figs. 3, S5). The first two ordination axes explained 11.27 % of the total variation in the RDA model ($F = 1.392$, $P < 0.001$) (Fig. 3a). Furthermore, the result of random forests showed that soil NO₃-N content was the most important factor affecting fungal community composition (Fig. 3b) and α diversity (Figure S6).

3.4. The CV values of SOC across different treatments and their drivers

We further evaluated the temporal variations in soil C and N contents in response to grazing in alpine peatlands. Grazing significantly reduced the CV value of SOC (Fig. 4). The observed pattern in SOC showed fewer fluctuations across different seasons in grazed areas than in fenced areas (Figure S2). However, similar outcomes were not achieved for DOC, DON, and inorganic N (Fig. 4). In the multiple regression models, microbial variables and abiotic factors explained 96.38 % and 3.62 % of the variation in the CV values of SOC in the fenced area, respectively (Fig. 5a). Additionally, fungal α diversity was the most important driver

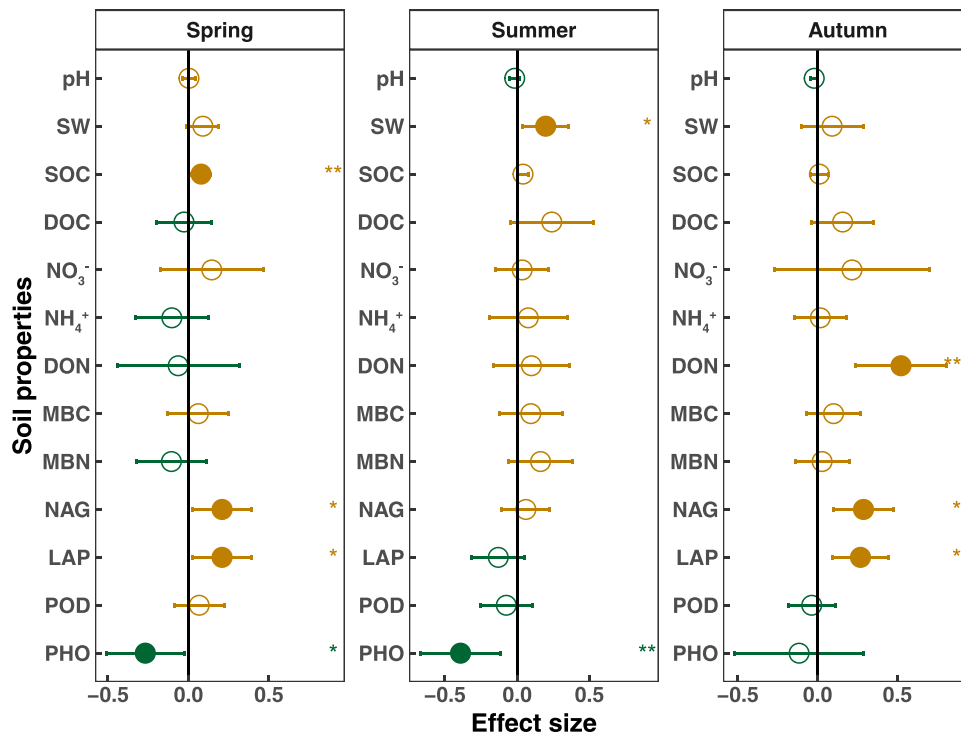


Fig. 1. Effects of grazing on soil properties across different seasons. Data are expressed as the estimated effect sizes of ln-RR, and error bars show the 95 % confidence intervals. ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$. SW, soil water content (%); SOC, soil organic carbon (g kg^{-1}); DOC, dissolved organic carbon (mg kg^{-1}); NO_3^- , soil NO_3^- (mg kg^{-1}); NH_4^+ , soil NH_4^+ (mg kg^{-1}); DON, dissolved organic nitrogen (mg kg^{-1}); MBC, microbial biomass carbon (mg kg^{-1}); MBN, microbial biomass nitrogen (mg kg^{-1}); NAG, N-acetyl- β -D-glucosaminidase ($\text{nmol g}^{-1} \text{h}^{-1}$); LAP, leucine aminopeptidase ($\text{nmol g}^{-1} \text{h}^{-1}$); POD, peroxidase ($\text{nmol g}^{-1} \text{h}^{-1}$); PHO, phenol oxidase ($\text{nmol g}^{-1} \text{h}^{-1}$).

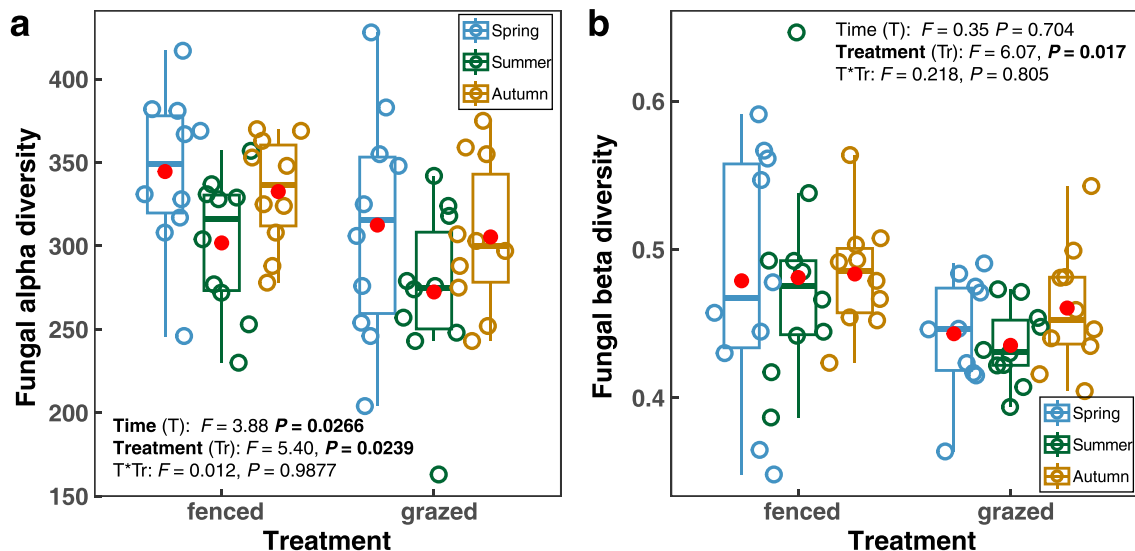


Fig. 2. Fungal α diversity (a) and β diversity (b) across different treatments and seasons. Statistical significance was determined using two-way ANOVA. The red solid point shows the mean value in each treatment.

of temporal variation of SOC in the fenced area (Figure S7a). In the grazed area, microbial variables and abiotic factors explained 67.09 % and 32.91 % of the variation, respectively (Fig. 5b). Soil $\text{NH}_4^+\text{-N}$ was the most important driver of temporal variation of SOC in the grazed area (Figure S7b). Furthermore, a statistically significant correlation between the CV values of SOC and those of fungal α diversity were observed in the fenced area, but not in the grazed area (Figure S8).

4. Discussion

4.1. Reductions in fungal diversity under grazing and their abiotic drivers

In this study, grazing exhibited a slight influence on soil properties compared with the season (Table S1; Fig. 1). These findings markedly differ from previous studies on alpine meadows (Fan et al., 2017; Wang et al., 2020), grasslands (Wang et al., 2021; Zhu et al., 2024), and arid

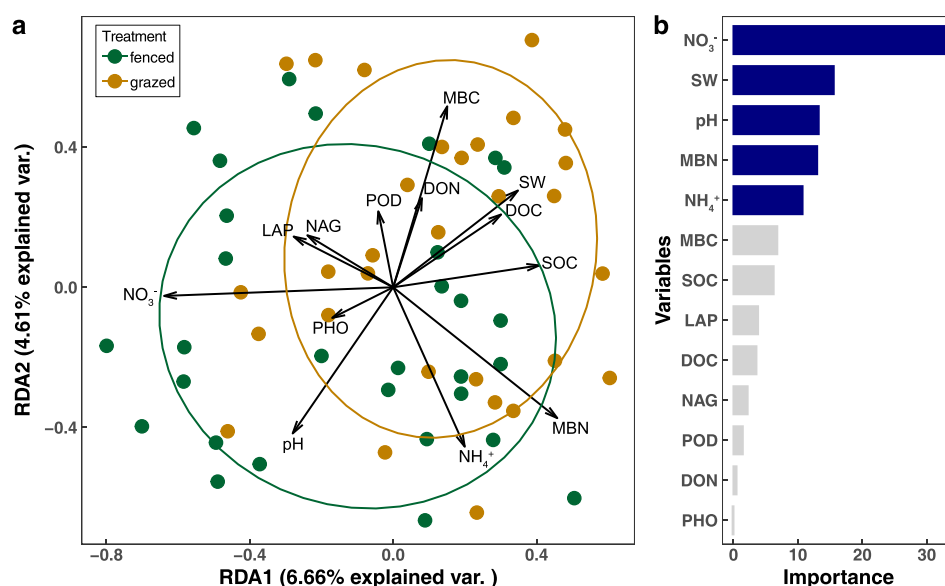


Fig. 3. Relationship between fungal community composition and environmental variables. (a) Ordination diagrams of redundancy analyses based on the fungal communities and predictor variables across different treatments. (b) A random forest model of the importance of environmental factors on the first constrained axis of fungal community composition. Blue and grey bars indicate significant variables and nonsignificant variables, respectively.

steppes (Liu et al., 2015; Usman et al., 2024). This indicates stronger environmental changes across different seasons owing to alterations in air temperature (Broadbent et al., 2024). In an alpine peatland with a high water table, grazing effects on soil properties are buffered through the positive responses of plant compensatory growth (Zhou et al., 2022) and enhanced N cycling genes (Ding et al., 2015) caused by higher soil water content. In addition, the short duration of the fencing treatment (3 years) and the lower grazing density (1.47 yak ha⁻¹) could lead to the slight effect of grazing on soil properties in the alpine peatlands.

We observed a significant reduction in soil fungal diversity across different seasons under grazing conditions (Fig. 2). This result considerably differs from those reported in meadow and steppe grasslands, wherein fungal α diversity exhibited no significant responses to grazing (Jiang et al., 2024; Zhou et al., 2024). Grazing exerts various effects on microbial processes through mechanisms such as defoliation and trampling (Liu et al., 2015). Defoliation caused by aboveground foraging directly decreases photosynthesis and reduce their selection effect on soil fungi, which may lead to homogeneous fungal communities. Furthermore, trampling can impair soil microbial diversity owing to its adverse effects on the soil physical structure, such as a decreased number of soil pores and increased bulk density (Hiltbrunner et al., 2012). Thus, grazing may lead to a reduced fungal species richness in alpine peatlands. Similarly, grazing significantly reduced β diversity, leading to a simplified and homogeneous fungal community in the alpine peatland. Trampling via hoof action can homogenise the soil matrix by reducing soil pores and filling depressions (Wang et al., 2021). A compacted soil environment is not conducive to the growth of specific fungi with a low ability to adapt to grazing (Usman et al., 2024; Xun et al., 2018). Therefore, the grazing-induced decrease in soil heterogeneity likely resulted in a homogeneous fungal community in the alpine peatlands.

We further identified the soil nitrate content as the most important environmental factor driving fungal diversity (Fig. 3). One reason for this is that soil microbial communities in the studied Zoige peatlands typically experience a limited N availability (Luo et al., 2021; Xue et al., 2021). In addition, nutrient availability can regulate microbial diversity through the proliferation of fast-growing microbial taxa and inhibition of other taxa (Kang et al., 2024). We also observed a low level of N availability during the growing season (Figure S2), suggesting high

nutrient uptake and further competition between the plant and microbial communities.

The season also considerably affected fungal diversity and enzyme activities in the alpine peatland. The observed lower fungal α diversity in summer was possibly attributed to the stronger recruitment of specific fungi by plant whose biomass reaches its peak in summer (Fan et al., 2017). The higher abundance of symbiotrophic fungi in summer (Figure S3) in our study may support the peak biomass through mutualistic symbiosis (Frey, 2019), which contributes to plant-derived C sequestration in peatland soils. Higher enzyme activities and significant correlations between fungal communities and soil properties were observed in spring, when there was great soil heterogeneity through seasonal freeze-thaw dynamics (Broadbent et al., 2024). This indicates that soil microbes remain active in early spring, which is a critical timepoint in element cycling owing to the phase changes of soil water in alpine ecosystems (Hugelius et al., 2020). Considering the significant seasonal changes, microbial processes during these time points should be given special attention in future research on alpine peatlands.

4.2. Relationships between fungal communities and peatland soil C dynamics

In the studied alpine peatlands, we found a significant increase in SOC under light grazing in spring, however, no changes were observed in the subsequent seasons (Fig. 1). The effect of light grazing density on SOC in our study substantially differs from previous studies, wherein overgrazing activities resulted in a substantial loss of SOC in alpine grasslands (Wang et al., 2020; Zhang et al., 2024) and arid steppes (Usman et al., 2024). In alpine peatlands, inhibiting activity of phenol oxidase under anaerobic conditions suppresses the degradation of organic matter owing to the accumulation of phenolic compounds (Fenner and Freeman, 2011; Zhao et al., 2024). In the present study, phenol oxidase activity was reduced under grazing conditions, which plays a role in the accumulation of SOC during early spring. No significant increase in SOC was observed under grazing in subsequent growing seasons, which could be attributed to the physical disruption of SOC resulting from the trampling caused by livestock grazing (Abdalla et al., 2024).

In this study, we found a significant relationship between fungal

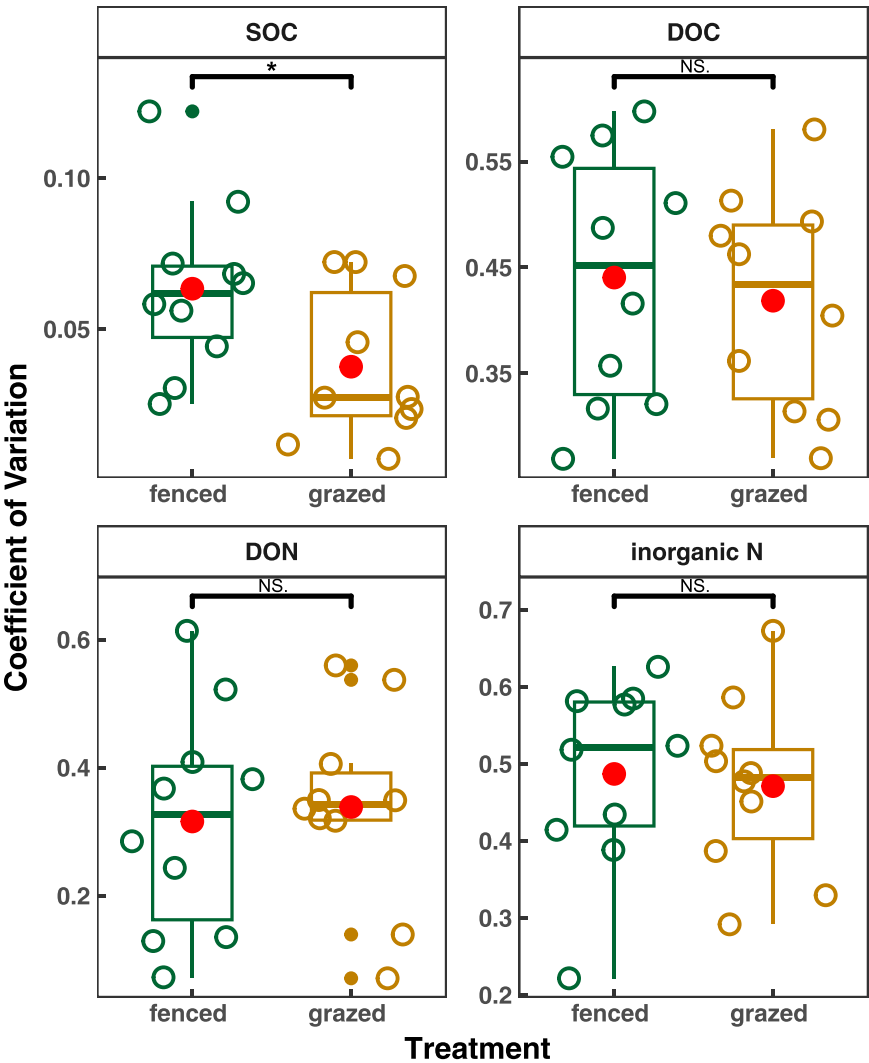


Fig. 4. The coefficients of variation (CV) in soil C and N contents under different treatments. The red point shows the mean CV value in each treatment. Statistical significance was determined using an independent sample *t*-test. ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; NS., not significant. inorganic N, inorganic nitrogen content which is the sum of soil NO_3^- and NH_4^+ contents.

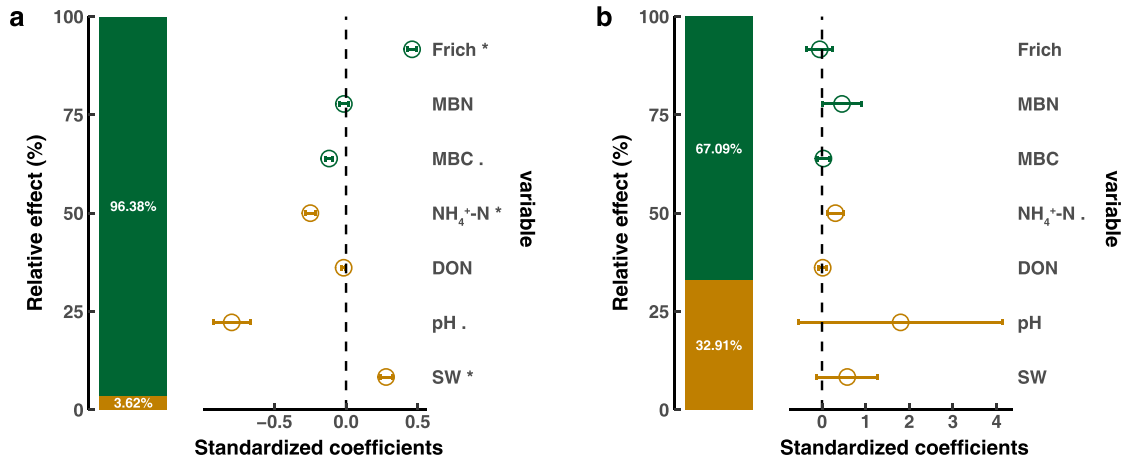


Fig. 5. Relative effects of the CVs of multiple predictors on those of SOC in the fenced (a) and grazed (b) areas. The figure shows the parameter estimates of the model's predictors and their 95 % CIs. The relative importance of each predictor is expressed as the percentage of explained variance. ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ., $P < 0.1$. Frich, fungal species richness.

communities and SOC dynamics in alpine peatlands (Figs. 5, S8). Given the large soil C reserves in alpine peatlands, even a minor dynamic in SOC can substantially alter C emissions (Loisel et al., 2021; Nyaupane et al., 2024). Therefore, the lower seasonal variation in SOC may be beneficial for C storage in alpine peatland under the low grazing density (Ren et al., 2024). The novel finding is noteworthy, as previous studies have typically emphasised the effects of grazing patterns on SOC stock (Usman et al., 2024; Wang et al., 2020), but not on intra-annual variations. The intra-annual variation in SOC is likely associated with the critical role of fungal communities. Generally, soil fungi are the primary producers of oxidative enzymes, thereby exhibiting a greater ability to decompose recalcitrant SOC (Liu et al., 2018). Decomposed recalcitrant C is preferentially incorporated into fungal biomass (Keiblinger et al., 2010). Therefore, within the fenced areas, the high seasonal changes in plant growth could increase the temporal variations in fungal species richness in the natural alpine peatland (Wang et al., 2022; Zheng et al., 2023), leading to the pronounced seasonal dynamics of SOC. However, the key role of fungal diversity on SOC dynamics was replaced by soil ammonia content in grazed areas. This is possibly attributed to the dung and urine return caused by livestock grazing (Liu et al., 2015). In this study, grazing led to homogeneous fungal communities and stable oxidase activities (Figs. 2, S9, S10), which would cause the decreased contribution of microbial processes to SOC dynamics under grazing. These findings elucidate intra-annual SOC dynamics and their potential drivers under grazing, which are critical for balancing the trade-off between adaptive grazing and C cycling in alpine peatlands.

For the dissolved part, the peatland soil DOC increased with the season and suppressed microbial enzyme activity (Figures S2, S11). In alpine peatlands, water-saturated soil is accompanied by the accumulation of DOC in pore spaces (Prijac et al., 2022). Vegetation productivity is a major driver of DOC production when the capacity of water movement in peatlands is low (Tfaily et al., 2018). This is why soil DOC increased with season. We further observed more acidic soil conditions during the season (Figure S2), which resulted in the release of metal ions from mineral-bound organic C and an increase in DOC (Li et al., 2022). Additionally, DOC is rich in a complex mixture of phenolic compounds that can act as microbial enzyme inhibitors and suppress microbial enzyme activity (Hájek and Urbanová, 2024).

Overall, our findings provide a solid foundation for future large-scale evaluation concerning the effects of various grazing strategies on SOC dynamics and their drivers. However, the absence of data from winter months may have resulted in the loss of valuable information about SOC. Therefore, further in-depth analyses of inter-annual variations in SOC through continuous multiple-year monitoring within alpine peatlands would not only verify, but also broaden the conclusions drawn from the present study. In addition, our study infers the grazing effects on SOC through dichotomous field manipulations in which SOC responses are compared between “presence” or “absence” of grazing. However, future studies disentangling the relationship between SOC dynamics, soil microbial community and grazing patterns, including intensity, duration, and frequency (Stanley et al., 2024), will yield more valuable insights into how grazing management affects alpine peatland SOC dynamics.

5. Conclusion

Waterlogged peatland is crucial for mitigating progressive climate change owing to their strong capacity as C sinks; however, they are experiencing significant livestock grazing activities. In this study, we conducted a field experiment in an alpine peatland to explore the effects of grazing on peatland soil C content across different seasons and their associations with the soil fungal community structure. Grazing significantly reduced fungal diversity at α and β scales across different seasons. Microbial variables explained the higher variation in SOC dynamics than abiotic variables, with fungal α diversity as the most important driver of the temporal dynamics of SOC in natural peatlands. However, the key role of fungal diversity on SOC dynamics was replaced by soil ammonia

content in grazed areas. Grazing led to homogeneous fungal communities and stable oxidase activities, causing the reduced contribution of microbial processes to SOC dynamics. This study is among the first to underscore the pivotal role of fungal community heterogeneity in enhancing SOC dynamics within alpine peatlands. Grazing-induced SOC dynamics provide novel insights into optimal management to balance the trade-off between adaptive grazing and C sequestration.

CRedit authorship contribution statement

Huai Chen: Resources, Supervision, Conceptualization, Writing – review & editing, Funding acquisition, Project administration. **Jianliang Liu:** Writing – review & editing, Conceptualization, Funding acquisition, Supervision, Validation. **Yang Li:** Methodology, Data curation, Software, Formal analysis, Visualization, Funding acquisition, Writing – original draft, Investigation, Conceptualization. **Li Tang:** Methodology, Resources, Validation, Investigation. **Xinya Huang:** Methodology, Resources, Validation, Investigation.

Declaration of Competing Interest

All authors consent to the publication of this manuscript and declare no competing interests.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109848.

Data availability

The data is open in GSA of NGDC.

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