Agriculture, Ecosystems and Environment 393 (2025) 109846

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Divergent responses of ecological functions to long-term herbivore exclusion in the Tibetan mountainous grasslands

Shuaihao Bai [a], Jingxue Zhao [a,*], Guangpeng Qu [b], Lihua Tian [c], Gao-Lin Wu [d]

[a] State Key Laboratory of Herbage Improvement and Grassland Agro-Ecosystems, and College of Ecology, Lanzhou University, Lanzhou 730000, China
[b] State Key Laboratory of Hulless Barley and Yak Germplasm Resources and Genetic Improvement, Institute of Grassland Science, Tibet Academy of Agricultural and Animal Husbandry Sciences Lhasa 850002, China
[c] Sichuan Zoige Alpine Wetland Ecosystem National Observation and Research Station, and College of Grassland Resources, Southwest Minzu University, Chengdu 610041, China
[d] Institute of Soil and Water Conservation, Northwest A & F University, Yangling, Shaanxi 712100, China

ARTICLE INFO

Keywords:
Alpine grasslands
Grazing exclusion
Ecosystem multifunctionality

ABSTRACT

Herbivore exclusion is a widespread practice used to restore and manage degraded grasslands on the Tibetan Plateau. However, experimental evidence for the long-term impacts of herbivore exclusion on ecosystem structure and functioning of mountainous grasslands is still largely lacking. Here, we examined long-term herbivore exclusion impacts on ecological functions across four typical grassland types (alpine screes, alpine meadow, alpine steppe, and swamp meadow) along an elevation gradient on the southern slope of Nyaiqentanglha Mountain. The results showed that long-term herbivore exclusion had divergent influences on ecosystem functioning of mountainous grasslands, with the EMF tended to decrease in swamp meadow and alpine steppe but increase in alpine meadow and alpine screes. In addition, herbivore exclusion tended to decrease the aboveground ecosystem multifunctionality (AEMF) but had a trend to increase the belowground ecosystem multifunctionality (BEMF). Path analysis of the structural equation model showed that herbivore exclusion regulated EMF and BEMF mainly through altering plant productivity and soil nutrients while influenced the AEMF primary by affecting plant diversity. These findings revealed that the impacts of long-term herbivore exclusion on multiple ecological functions greatly depended on plant diversity, productivity, and soil nutrients, with the mountainous grasslands mostly experiencing decrease trends on ecosystem multifunctionality. The findings also highlighted the fundamental importance of developing proper grazing management practice for protecting ecosystem multifunctionality in the widespread mountainous grasslands on the Tibetan Plateau.

1. Introduction

Mountainous grasslands comprise large area of the Tibetan Plateau (TP) and are crucial for the survival of herbivorous animals and livelihoods of herdsmen (Li et al., 2018; Zhu et al., 2023). Likewise, these mountainous grasslands are of vital importance in providing ecological functions including biodiversity conservation, water retention, carbon sequestration, and climate regulation (Bai and Cotrufo, 2022; Chen et al., 2022; Wang et al., 2022). Herbivorous grazing is the primary utilization measures for mountainous grasslands and the most pivotal economic activity for Tibetan herdsmen, linking economic use, conservation, and management for mountainous grasslands (Sun et al., 2020; Zhan et al., 2022). In the last decades, due to the gradually increased herbivorous grazing intensity, human activity disturbance, and rapid climate change, the Tibetan mountainous grasslands have experienced obvious degradation, which can significant affect ecological functions (Kuang and Jiao, 2016; Latif et al., 2019; Zhu et al., 2023). Thus, it is essential to promote sustainable development of animal husbandry while also preserving biodiversity and ecosystem functioning and sustainability in these mountainous grasslands.

Herbivore exclusion is a primary management practice used to restore degraded mountainous grasslands (Wu et al., 2010; Zhao et al., 2017). It has been shown to increase plant diversity, community productivity (Wang et al., 2017, 2021; Hou et al., 2019; Zhu et al., 2024), soil carbon sequestration (Yu et al., 2019; Dai et al., 2021), soil organic carbon fractions (Li et al., 2022), and soil respiration (Chen et al., 2016;

* Corresponding author.
E-mail address: zjx@lzu.edu.cn (J. Zhao).

https://doi.org/10.1016/j.agee.2025.109846
Received 7 January 2025; Received in revised form 10 March 2025; Accepted 1 July 2025
Available online 4 July 2025

Zhao et al., 2016a) in degraded mountainous grasslands. However, herbivore exclusion also can lead to loss of plant diversity and species richness (Altesor et al., 2005; Huang et al., 2022) and reduction of soil carbon and nitrogen cycling (Shang et al., 2017; Wu et al., 2017a). These inconsistent conclusions obtained by these previous studies should be mainly due to different herbivore exclusion durations and vegetation types (Wu et al., 2017b; Zhao et al., 2017). Herbivore exclusion usually has immediate effects within the first few years of implementation, but the recovery efficiency decreases with grazing prohibition duration increases (Wu et al., 2024). For example, recent studies have reported that short-term herbivore exclusion significantly improves soil and plant properties (Zhan et al., 2022). Long-term herbivore exclusion significantly hindered biodiversity conservation and productivity maintenance (Yu et al., 2024), but enhanced carbon and nitrogen sequestrations (Xiong et al., 2024; Fernández-Guisuraga et al., 2022). In addition, previous studies have proved that the long-term excessive herbivore grazing can have significant negative impacts on ecosystem functioning in mountainous grasslands by reducing biodiversity (Liu et al., 2023), productivity (Wang et al., 2022), and soil carbon and nutrients (Chen et al., 2022; Mipam et al., 2024). Thus, long-term herbivore exclusion is clearly detrimental to the sustainable recovery of degraded mountainous grasslands.

Mountainous grassland ecosystems can simultaneously provide and maintain multiple ecological functions (ecosystem multifunctionality, EMF). The EMF index can indicate the ability of mountainous grasslands to simultaneously provide and maintain both above- and belowground ecological functions, and critical for accurately implementing sustainable grassland management (Yang et al., 2023; Zhao et al., 2024). Currently, relevant information is limited in mountainous grassland ecosystems about on the impacts of long-term herbivore exclusion on the dynamics of the EMF. Also, regarding the effects of herbivore exclusion on EMF, conflicting results have been yielded, with positive (Liu et al., 2020; Zheng et al., 2023), neutral (Bi et al., 2018), and negative effects were reported according to studies around the world (Sun et al., 2020; Wu et al., 2024). This may be because EMF is driven by complex biotic and abiotic mechanisms (Wang et al., 2019). Nevertheless, most previous studies have focused on the changes of the multiple ecological functions under herbivore exclusion, with only a few studies are available to evaluate the variation of above- and belowground functions (Ma et al., 2022), which impede our ability to predict the consequences of long-term herbivore exclusion on ecological functions in mountainous grasslands.

Herbivore exclusion impacts on EMF may be differential with vegetation types (Yao et al., 2023) and elevations (Pan et al., 2017; Wang et al., 2023), due to the limitation of hydrothermal and nutrient conditions. For example, in semi-arid grasslands, herbivore exclusion can eliminate the ability of plant diversity to maintain multiple ecosystem functions (Wu et al., 2024) and exacerbate the negative impact of drought on EMF (Yu et al., 2024). On the contrary, in humid and fertile grasslands, long-term herbivore exclusion may not be conducive to maintaining the multiple ecological functions. On the mountainous TP, herbivore intensity, vegetation characteristics, and soil factors often vary together with elevation gradients (Wang et al., 2013; Zhao et al., 2016b), further complicating the relationship between herbivore and EMF. Despite these complexities, there is no consensus on the impact of herbivore exclusion on ecosystem multifunctionality in different mountainous grasslands.

In the present study, we hypothesize that long-term herbivore exclusion generally may have negative influences on the EMF and differentially impact above- and belowground ecological functions in mountainous grasslands. Here, we explored long-term herbivore exclusion impacts on ecological functions across four typical mountainous grassland types (swamp meadow, alpine steppe, alpine meadow, and alpine screes) along an elevation gradient of the southern slope of Nyaiqentanglha Mountain. The primary aims were: 1) to clarify the impact of long-term herbivore exclusion on EMF in mountainous grasslands, 2) to assess the responses of above- and belowground ecological functions to long-term herbivore exclusion, and 3) to distinguish the potential factors driving the impacts of herbivore exclusion on ecosystem functioning in the Tibetan mountainous grasslands. The findings of our study can help provide critical insights for the sustainable management of Tibetan mountainous grasslands under long-term herbivore exclusion.

2. Materials and methods

2.1. Study sites

The research was conducted from 2006 to 2020 along the southern slope of the Nyaiqentanglha Mountains in Damxung County, Xizang Autonomous Region, China (Fig. 1). This region has a plateau temperate semi-arid monsoon climate, with a humid and warm summer but a cold and dry winter. The annual mean temperature is 1.8 °C. Annually, the region receives an average of 442 mm of precipitation, with around 90 % of rain falling during the growing season (Wang et al., 2013). There are four distinct grassland communities distributed along the southern slope of the Nyaiqentanglha Mountains owing to varied environmental factors such as temperature and precipitation. With the elevation increasing, the grassland type gradually changes from swamp meadows (4300 m) dominated by *Kobresia tibetica* at the foot of the mountain to alpine steppes (4300 −4650 m) dominated by *Stipa capillacea* and alpine meadows (4700 −5210 m) dominated by *Kobresia pygmaea* at intermediate elevations, and finally to alpine screes (5210 −5600 m) at the top region of the mountain (Fig. 1). Pasture for livestock (yak and sheep) and wild herbivores is the main utilization measures for mountainous grasslands along the elevation gradient. Herbivore composition likely varied with elevation, with alpine screes primarily hosting blue sheep and occasionally yaks, while swamp meadows attracted Tibetan gazelle and grazing livestock such as yaks and sheep.

2.2. Experimental design

In 2006, herbivore exclusion experiment by fencing was established at four sites along the southern slope of the Nyaiqentanglha Mountains, corresponding to the four typical mountainous grassland types including alpine screes, alpine meadow, alpine steppe, and swamp meadow. Fences with a height of 2 m and a mesh size of 5 centimeters effectively excluded medium and large wild herbivores such as Tibetan gazelle *Procapra picticaudata* and blue sheep *Pseudois nayaur*, as well as grazing livestock including yaks and sheep, but did not prevent access of small mammals such as plateau pika *Ochotona curzoniae*. In each of the four sites, we set up a 20 m× 20 m herbivore exclusion (HE) plot and additionally set up a free herbivore (FH) plot 20 m away from the upper edge of the herbivore exclusion plot.

We acknowledge the issue of pseudo replication in the herbivore exclusion experiment. However, this is a common problem in long - term studies conducted in resource - constrained areas (Davies and Gray, 2015), especially in high - altitude regions where replicating such fences is challenging. To avoid the problem of pseudo replication as much as possible, we selected homogeneous areas of each grassland type after rigorous field surveys before the experimental design. This was to ensure that these areas could represent the main characteristics of the grassland type, such as altitude, slope, dominant species, endemic species, and soil properties. Moreover, these areas have maintained the typical characteristics of the grassland type through long - term monitoring (Wang et al., 2013; Zhao et al., 2016a; Deng et al., 2023). In addition, we set an interval of 3 m between the 1 × 1 m quadrats. This distance exceeds the overlapping radius of the root systems of the dominant species, minimizing the spatial autocorrelation between quadrats.

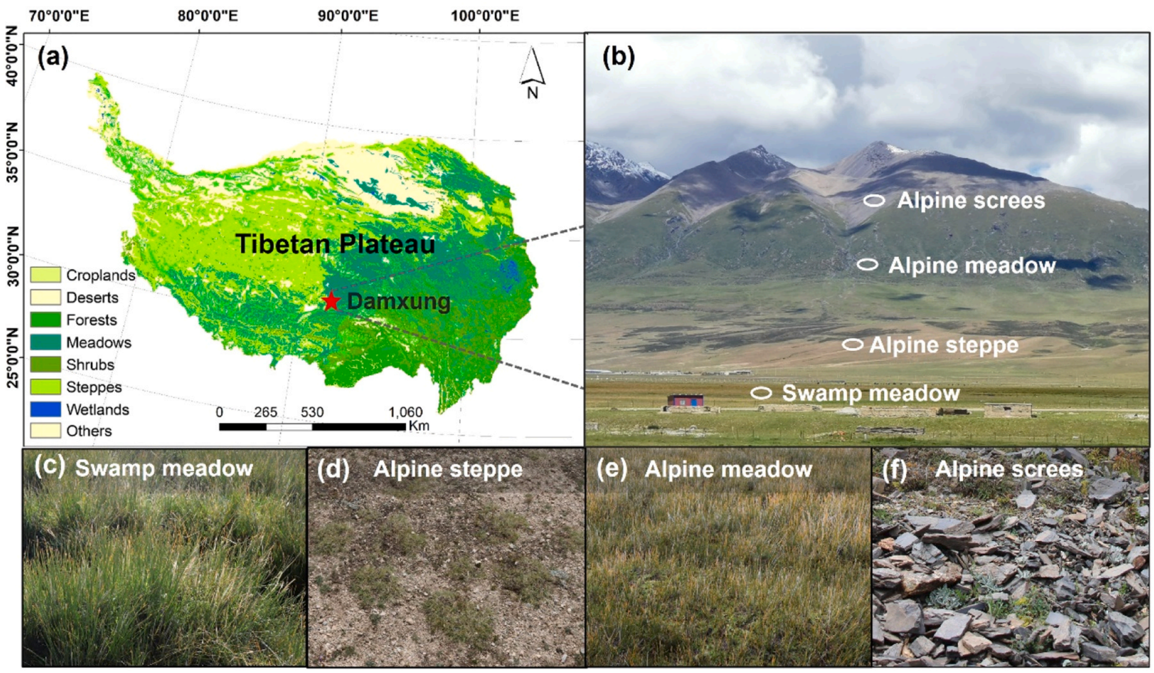

Fig. 1. Location of the present study sites was conducted on the Tibetan Plateau (a), of the four typical vegetation types selected along the slope of the Nyai-qentanglha Mountain (b), swamp meadow (c), alpine steppe (d), alpine meadow (e), and alpine screes (f).

2.3. Vegetation sampling

In 2020, after 14 years' herbivore exclusion, vegetation surveys and soil sampling were conducted in mid-August to capture peak growing-season conditions, when plant biomass and community structure stabilize (Wang et al., 2013). At each 20 m × 20 m plot, we set up five 1 m × 1 m sampling quadrats, with an interval of 3 m between neighboring quadrats. In total, 40 HE and FH quadrats were sampled from the four sites. In each quadrat, plant height, cover, and AGB (aboveground biomass) were measured and recorded. Then, we calculated the relative importance value (IV) of individual species and the plant diversity indexes using the following functions (Wu et al., 2009):

$$IV = (RH + RC + RB)/3$$

Where *RH*, *RC*, and *RB* mean the relative values of height, cover, and biomass of the *i*th species, respectively.

Species richness index (*S*): $S = R$

Shannon-Wiener diversity index (*H*): $H = -\sum \mathrm{P}i\ (1\mathrm{n}\ \mathrm{P}i)$

Evenness index (*E*): $E = H/1\mathrm{nS}$

where *R* and P*i* represent the total species number and the IV value of the *i*th species, respectively.

2.4. Soil sampling and analysis

At each quadrat, we obtained five soil samples (0–10 cm soil depth) and combined them into a mixed sample, with any noticeable root material and rocks removed. Soil samples were air-dried at room temperature, then passed through a 2 mm sieve before analyzing pH, soil organic carbon (SOC), light fraction organic carbon (LFOC), heavy fraction organic carbon (HFOC) total nitrogen (TN), total phosphorus (TP), inorganic nitrogen (NH_4^+−N and NO_3^-−N), and available phosphorus (AP). The SOC and TN contents were measured by a Vario EL III analyzer (Elementar, Germany). The LFOC content and the HFOC content were calculated by multiplying the light fraction mass concentration and the heavy fraction mass concentration with the carbon content in light fraction and heavy fraction respectively (Li and Wang, 2017). The contents of NO_3^-−N and NH_4^+−N were determined by an Auto Analyzer (Bran Luebbe, Germany). The TP content was measured through digestion with H_2SO_4 and $HClO_4$ (Yuan et al., 2012). The AP was determined after extracted soil with a 0.5 M $NaHCO_3$ solution and quantified by an ultraviolet spectrophotometer.

2.5. Ecosystem multifunctionality

To estimate the variations in multiple ecological functions across swamp meadow, alpine steppe, alpine meadow, and alpine screes, we calculated the EMF index as follows (Maestre et al., 2012):

$$EMF = \frac{1}{N}\sum_{i=1}^{N} f(x_i)$$

where *N* and $f(x_i)$ represent the number of individual functions and the standard deviation of all observations, respectively.

We further utilized the relative interaction intensity (*RII*) index to assess the extent of herbivore exclusion on ecological functions. This index was calculated using the following formula:

$$RII = (X_{HE} - X)/(X_{HE} + X)$$

X_{HE} and X represent the ecological function values in HE and FE plots, with the values greater than zero representing a positive effect and less than zero indicating a negative impact of the herbivore exclusion on ecological functions.

To make the EMF more accurate, we conducted a classification random forest analysis to identify which were the main predictors of the EMF index. The results showed that the factors which were significantly associated with EMF include: NH_4^+−N, *H*, SOC, *S*, TN, NO_3^-−N, and pH (Fig. S4). Based on the above calculation, the aboveground ecosystem multifunctionality (AEMF) index was calculated according to the *H* and *S*, and the belowground ecosystem multifunctionality (BEMF) index was calculated according to the NH_4^+−N, SOC, TN, NO_3^-−N, and pH.

2.6. Data analysis

The impacts of vegetation types and herbivore exclusion on plant community metrics (height, cover, AGB, *S*, *H*, and *E*) and soil properties (SOC, LFOC, HFOC, TN, NH_4^+−N, NO_3^-−N, TP, AP, and pH) were assessed using Two−way ANOVA in SPSS 27.0 (IBM SPSS Software Inc., Armonk, NY, USA). Structural equation model (SEM) was used to assess the impacts of herbivore exclusion, plant productivity and diversity as well as soil nutrients on EMF. Model fit was evaluated using χ^2 and RMSEA. The SEM model was developed using AMOS 26 (IBM SPSS, Inc.), and the vegetation map was generated in ArcGIS 10.8 (ESRI).

3. Results

3.1. Community structure and plant productivity following herbivore exclusion

The sedges had the highest IV value in swamp meadow and alpine meadow (Fig. 2a and c). Grasses had the highest importance value in alpine steppe (Fig. 2b), while forbs were dominant in alpine screes (Fig. 2d). Herbivore exclusion had positive effects on the height, cover, and AGB but negative impacts on plant diversity (*H*, *S*, and *E*) in mountainous grasslands, particularly in swamp meadow and alpine steppe (Fig. 3). The results indicated that herbivore exclusion could lead to an increase in plant productivity, while either enhance or reduce plant diversity. Specifically, the height, cover, and AGB of swamp meadow significantly increased after herbivore exclusion, while the *H*, *S*, and *E* significantly decreased (Fig. 3a). The effect values of increased height and decreased richness were the most significant (Fig. 3a). Herbivore exclusion also significantly increased the AGB of alpine steppe and alpine meadow (Fig. S2c), and the height of alpine meadow significantly increased (Fig. 3b and c). There were no significant differences in *H*, *S*, and *E* among alpine steppe, alpine meadow, and alpine screes. The interaction effect between vegetation types and herbivore exclusion (VT × HE) indicated that the combined influence significantly affected plant diversity and plant height, while having no significant impact on AGB and cover. herbivore exclusion had a significant impact on both plant diversity and productivity.

3.2. Herbivore exclusion impacts on the soil properties

Compared with swamp meadow and alpine steppe, herbivore exclusion created a greater positive impact on the soil physicochemical properties of alpine meadow and alpine screes (Fig. 3). There was no

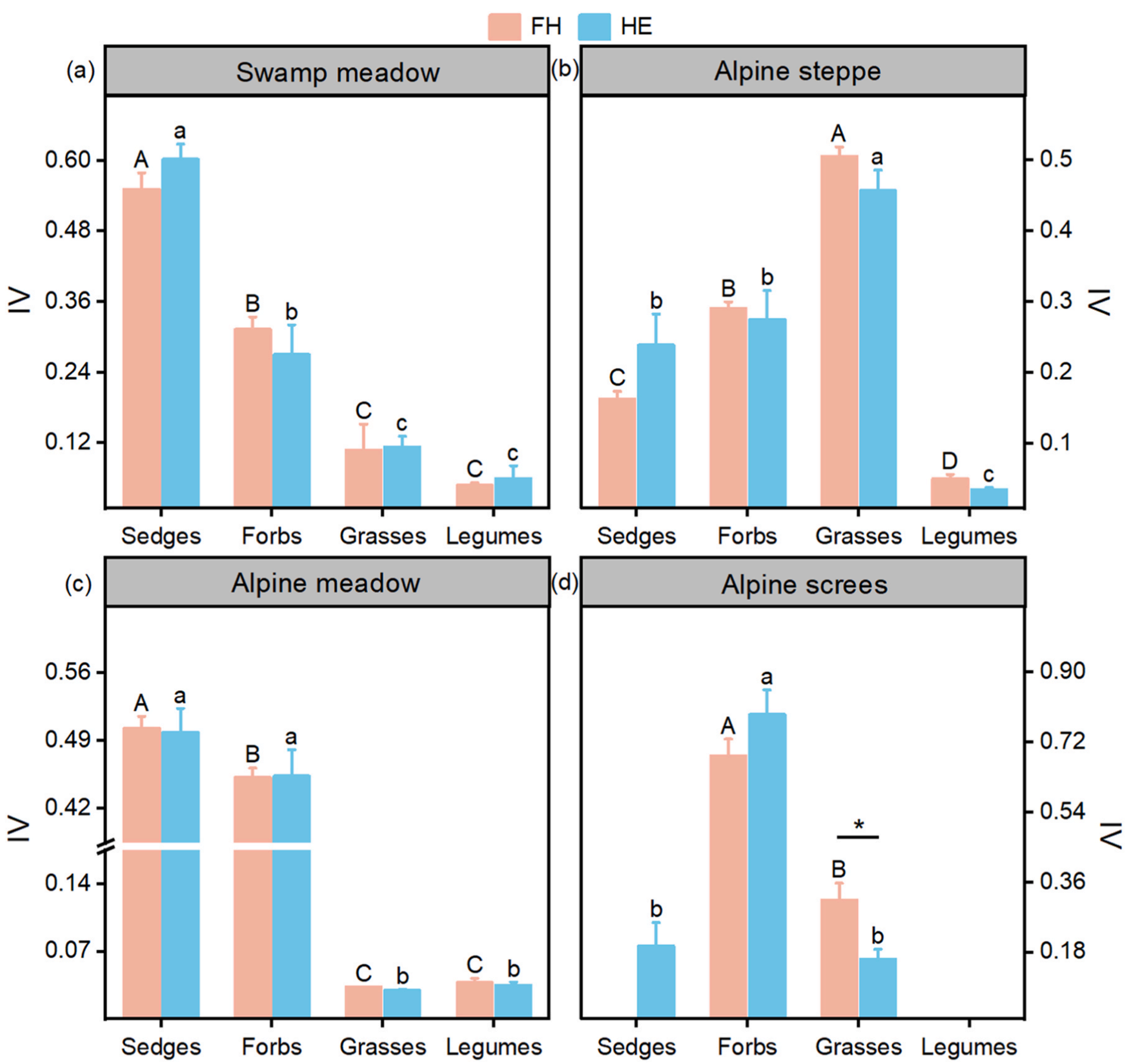

Fig. 2. Differences of the important value (IV) of the functional groups across vegetation types under free herbivore (FH) and herbivore exclusion (HE). Different letters indicate significant differences among functional groups. Asterisks represent the significant differences between the FH and HE treatments. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

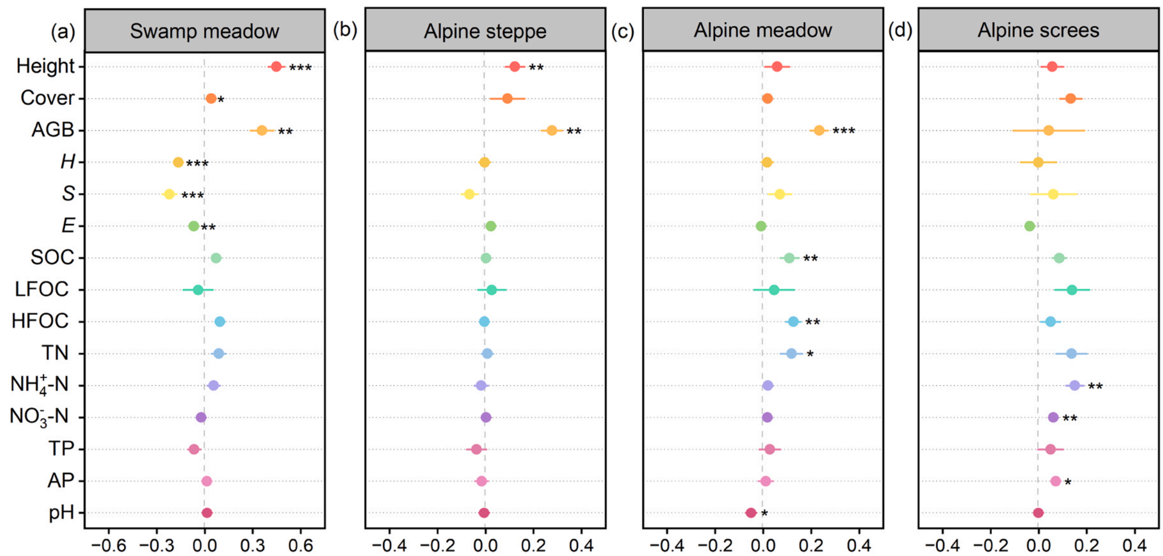

Fig. 3. Differences in plant and soil factors between the herbivore exclusion (HE) and free herbivore (FH) across vegetation types. Asterisks represent the significant differences between the FH and HE treatments. *H*, Shannon Wiener index; *S*, richness index; *E*, evenness index; Height, the height of plant; Cover, the cover of vegetation; AGB, aboveground biomass; SOC, soil organic carbon; LFOC, light fraction organic carbon; HFOC, heavy fraction organic carbon; TN, total nitrogen; NH_4^+-N, ammonia nitrogen; NO_3^--N, nitrate nitrogen; TP, total phosphorus; AP, available phosphorus; pH, soil pH * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

significant difference in soil physicochemical properties between free herbivore and herbivore exclusion treatments in the swamp meadow and alpine steppe ecosystems. Overall, herbivore exclusion had a trend to increase soil organic carbon in mountainous grasslands, with a significant rise of SOC content in alpine meadow. However, SOC, HFOC, TN, and pH in alpine meadow were significantly different, and NH_4^+−N, NO_3^-−N, and AP in alpine screes were significant rise (Fig. 3). Our results further suggested that the interaction of the grassland types and herbivore exclusion have little effect on soil physicochemical properties (Fig. S3).

3.3. Changes in ecosystem functioning following herbivore exclusion

There were significant differences in the EMF of herbivore exclusion and free herbivore among different mountainous grasslands, and the EMF and BEMF indexes of the swamp meadows were greater than other three types of grasslands. Herbivore exclusion had inconsistent impacts on the EMF of the four typical mountainous grasslands, which had hindered us to draw general conclusions. We found that herbivore exclusion reduced the EMF of swamp meadow and tended to reduce that of alpine steppe while tended to increase the EMF of alpine meadow and alpine screes (Fig. 4d). In general, herbivore exclusion tended to

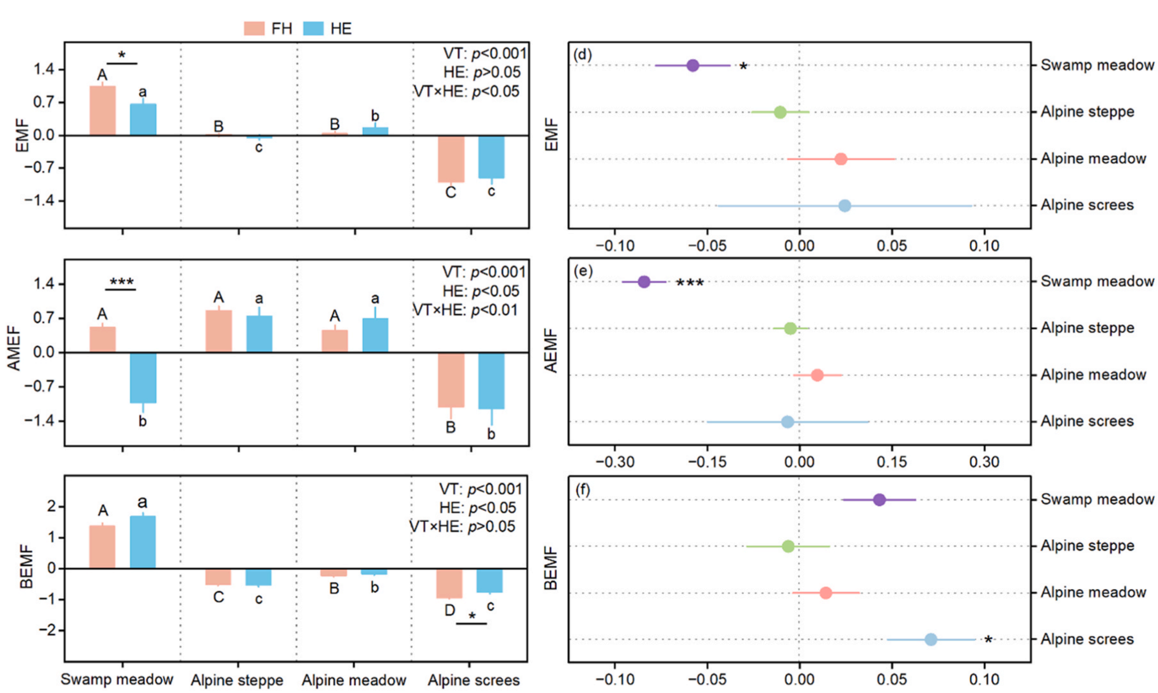

Fig. 4. Changes of ecosystem multifunctionality (EMF), aboveground ecosystem multifunctionality (AEMF), belowground ecosystem multifunctionality (BEMF) indexes across different vegetation types under free herbivore (FH) and herbivore exclusion (HE)(a-c). Differences in EMF, AEMF, and BEMF indexes between HE and FH treatments across different vegetation types (d-f).

decrease the AEMF but had a trend to increase the BEMF. However, the impact of herbivore exclusion on the AEMF and BEMF indices varies greatly between different grassland types. Herbivore exclusion decreased the AEMF of swamp meadow while showing an increasing trend in BEMF (Fig. 4e and f). In contrast, herbivore exclusion tended to increase both AEMF and BEMF of alpine meadow, resulting in an overall enhancement of EMF, while the opposite effect was observed in alpine steppe (Fig. 4d–f). Notably, herbivore exclusion primarily improved the BEMF of alpine screes, thereby enhancing the EMF (Fig. 4d and f).

3.4. Relationships of aboveground and belowground characteristics with EMF, AEMF, BEMF

We conducted a comprehensive analysis of the correlations between EMF, AEMF, and BEMF with various vegetation and soil factors. Our results indicated that AGB exhibited significant correlations SOC, TN, AP, and pH. Additionally, EMF was significantly correlated with *H*, *S*, Height, Cover, AGB, SOC, LFOC, HFOC, TN, NH_4^+–N, NO_3^-–N, AP, and pH. Furthermore, EMF, AEMF, and BEMF indexes were significantly correlated with Cover, AGB, and pH. The AEMF index was significantly correlated with *H*, *S*, Cover, AGB, and pH. While the BEMF index was significantly correlated with *E*, Height, Cover, AGB, SOC, LFOC, HFOC, TN, NH_4^+–N, NO_3^-–N, AP, and pH (Fig. 5). The structural equation model revealed that herbivore exclusion indirectly regulated EMF and BEMF through plant productivity and soil nutrients, while directly influencing AEMF by productivity (Fig. 6). In the total impact on EMF and BEMF, the contribution of vegetation productivity and soil nutrients was much higher than other indicators (Fig. 6d and f), while in AEMF, the contribution of plant diversity was higher (Fig. 6e). Therefore, we concluded that long-term herbivore exclusion had divergent impacts on the AEMF and BEMF in mountainous grasslands, which were highly depended on plant diversity and productivity as well as soil nutrients.

4. Discussion

4.1. Ecological individual functions responses to herbivore exclusion

Along the elevation gradients, we found that herbivore exclusion tended to positively affect plant height, coverage, and aboveground biomass in the four mountainous grassland types, which are consistent with the previous findings (Yan and Lu, 2015; Lian et al., 2024; Tan et al., 2024; Zhu et al., 2024). In mountainous grasslands, dominant species were excellent forage species feed herbivores, accounting for most of community productivity. Due to the selective feeding of herbivores, long-term herbivore exclusion tended to increase the dominance and abundance of dominant species (Fig. S1), which could translate into greater community biomass in mountainous grasslands (Liu et al., 2020). This shift amplified their competitive advantage over rare species, resulting in the decline of plant diversity of the grassland community (Liu et al., 2019a, 2020, 2023). Also, herbivore exclusion induced accumulation of plant litter would also affect the use of light by different functional groups, resulting in a decrease in plant diversity (Zou et al., 2016). Due to the lack of light and nutrient availability, some less competitive dwarf plants in the lower strata of the community were less dense or even disappear from the plant community (Li et al., 2018). Therefore, in line with previous studies (Kelemen et al., 2013; Zhu et al., 2021), our results suggested that the plant diversity conservation could be facilitated by maintaining herbivores grazing in swamp meadow, whereas other grasslands showed negligible response to herbivore exclusion. On the other hand, after long-term herbivore exclusion, increases in plant height and litter accumulation reduced soil transpiration and made soil moisture more easily conserved (Wu et al., 2014; Deng

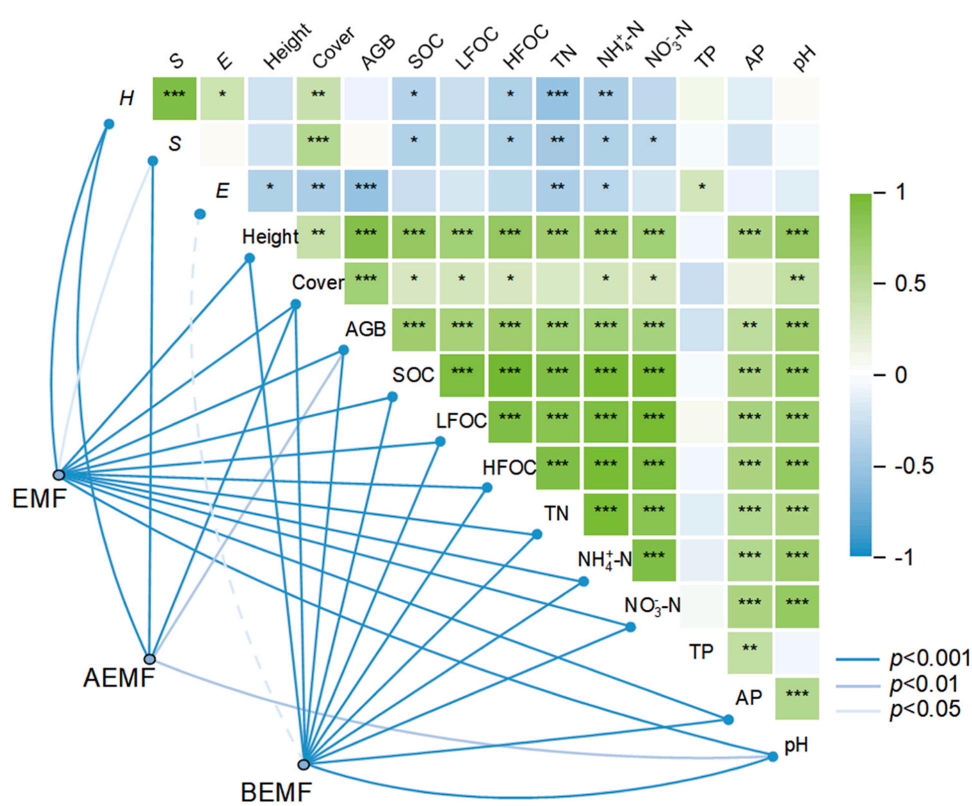

Fig. 5. Correlation coefficients between the vegetation characteristics, soil properties, and ecosystem multifunctionality (EMF), aboveground ecosystem multifunctionality (AEMF), and belowground ecosystem multifunctionality (BEMF). *H*, Shannon Wiener index; *S*, richness index; *E*, evenness index; Height, the height of plant; Cover, the cover of vegetation; AGB, aboveground biomass; SOC, soil organic carbon; LFOC, light fraction organic carbon; HFOC, heavy fraction organic carbon; TN, total nitrogen; NH_4^+-N, ammonia nitrogen; NO_3^--N, nitrate nitrogen; TP, total phosphorus; AP, available phosphorus; pH, soil pH (significance: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$).

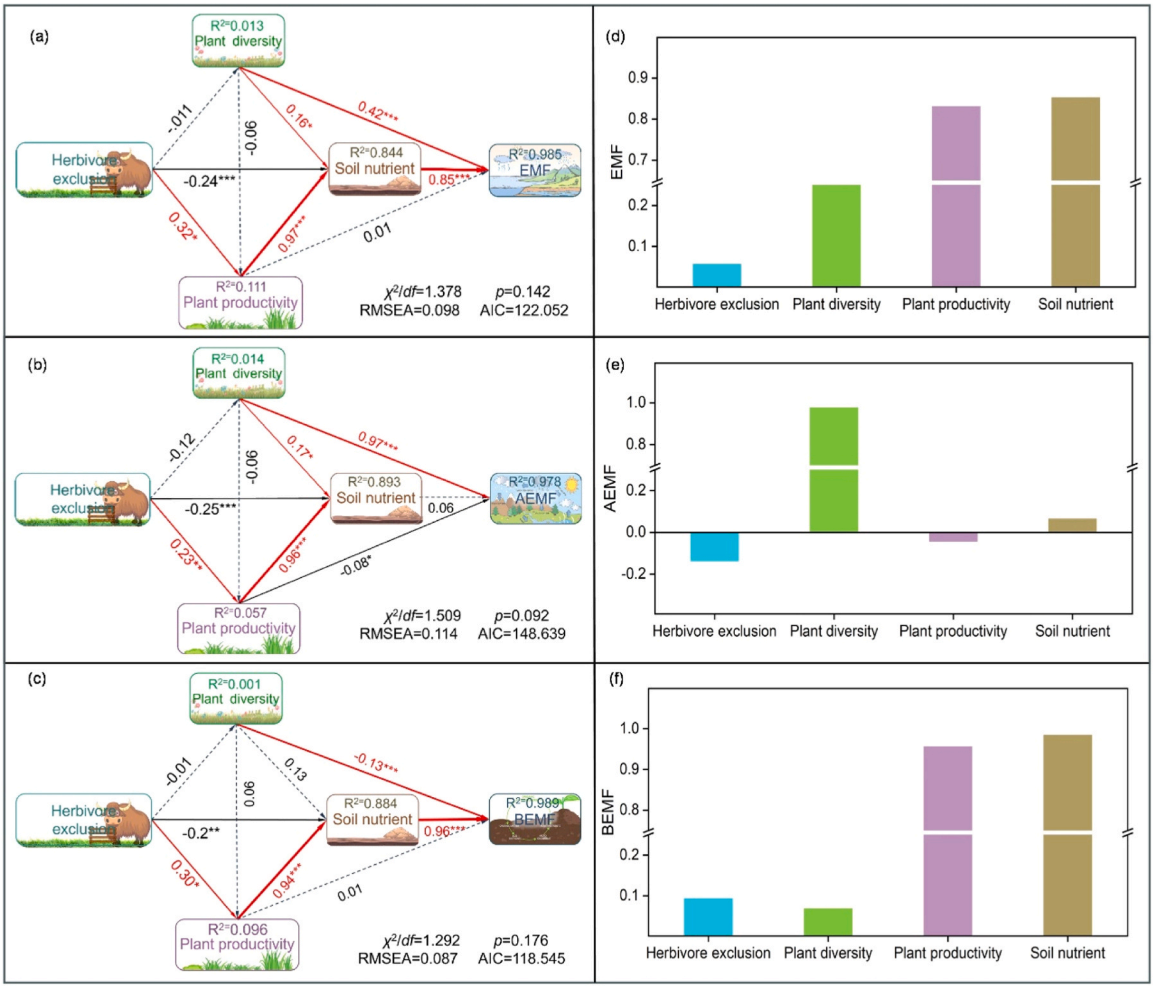

Fig. 6. Structural equation models depicting direct and indirect effects of herbivore exclusion, plant diversity, plant productivity, and soil nutrient on the EMF. Black and red arrows indicate positive and negative effects, respectively. Dashed arrows indicate insignificant effects. Numbers besides the arrows represent standardized path coefficients (significance: $*p < 0.05$; $**p < 0.01$; $***p < 0.001$), proportional to the arrow thickness. The proportion of variance explained (R^2) appears alongside the variables, and goodness-off statistics are shown below each model. Standardized total effects derived from the structural equation models depicted. Numbers along the bars represent the standardized total effect values.

et al., 2017), ultimately beneficial for plants sensitive to water stress. Herbivore exclusion had been shown effective in improving soil carbon and nitrogen contents of the overgrazed mountainous grasslands (Li et al., 2018; Zhao et al., 2019). The low soil physicochemical base of alpine meadow and alpine screes led to significant changes in soil physicochemical properties after herbivore exclusion (Fig. 3). The present study found that long-term herbivore exclusion generally increased the SOC and TN contents across the four mountainous grassland types. However, the magnitude of the stimulation impacts varied with grassland types and climatic factors. One possible reason for the stimulation of SOC and TN contents was that herbivore exclusion induced increase in AGB significantly increase plant litter and root exudate inputs, which led to increases in soil carbon and nitrogen stocks (Li et al., 2018; Gebregergs et al., 2019). In addition, herbivore exclusion led to improvements in soil physical properties thereby promote SOC and TN accumulations (Wang et al., 2016; Bai et al., 2020; Wu et al., 2021). The increased plant cover under herbivore exclusion could protect soil aggregate structure and reduce soil surface exposure to wind erosion, thereby reducing soil C and N losses (Mekuria et al., 2007; He et al., 2008; Deng et al., 2017; Li et al., 2022). Therefore, herbivore exclusion was an effective measure for carbon and nitrogen sequestration of mountainous grasslands.

4.2. Differential responses of ecosystem multifunctionality to herbivore exclusion

Our findings provided solid empirical evidence that long-term impacts of herbivores exclusion on the ecosystem multifunctionality in mountainous grasslands substantially

depend on vegetation types, with swamp meadow and alpine steppe undergoing negative impacts but alpine meadow and alpine screes experiencing positive effects on the EMF. Our results also provided field experimental evidence that long-term herbivores exclusion had divergent impacts on the above- and belowground ecological functions in mountainous grasslands, which highly depended on plant diversity and productivity as well as soil nutrients (Jing et al., 2015; Yu et al., 2024). It was well noted that plant diversity played a critical role in regulating grassland ecosystem functioning (Wang et al., 2024), and we also revealed positive relationships between plant diversity and AEMF in mountainous grasslands. The results showed that herbivore exclusion generally decreased AEMF of mountainous grasslands especially in swamp meadows, mainly driven by declines in plant diversity (Fig. 3 and Fig. 4). However, this decrease pattern in AEMF was reversed in alpine meadow with high grazing intensity. The response of light availability to herbivore exclusion was related to plant diversity and aboveground biomass in swamp meadows. In the early stage of herbivore exclusion, rapid increase of the vegetation cover and plant productivity were the main reasons for the significantly improved AEMF (Liu et al., 2022). However, after long-term herbivore exclusion, limited light and soil resources could lead to the disappearance of some plant species (Sun et al., 2020), which in turn would lead to the decline of plant diversity and ultimately result in a decrease in the AEMF. We also identified light limitation induced decline in plant diversity as a mechanism through which herbivores exclusion reduced AEMF in swamp meadows. In swamp meadow site with greater vegetation cover and plant biomass, herbivore exclusion decreased light availability more than in alpine meadow and alpine screes sites with lower vegetation cover and plant biomass. Although we found that the EMF responses to herbivore exclusion depended on grassland types, the mechanisms by which herbivore exclusion promoted BEMF were the same regardless of grassland types. The herbivore exclusion induced increase in soil nutrients was primary reason for the improvement of the BEMF in mountainous grasslands, particularly those communities in harsh environments with resource depletion and low productivity.

4.3. Uncertainties and implications

In addition to plant diversity, soil biodiversity, such as soil microbial and fauna diversity, could also alter ecological functions particularly that influencing carbon and nutrient biogeochemical cycles (Jing et al., 2015; Hu et al., 2021). The present herbivores exclusion experiment was carried out in the four typical mountainous grasslands spanning large climatic and elevation gradients, where soil biodiversity could presumably differ across grassland types (Delgado-Baquerizo et al., 2016). However, the diversity of soil microbial and fauna were not determined in the present experiment. In future, it would be worthy of further study on how soil biodiversity, in addition to climatic changes and grazing disturbances, affect ecological functions in mountainous grasslands. Our findings showed that long-term herbivore exclusion did not fully restore the ecological functions of degraded mountainous grasslands, and even negatively altered the ecosystem functioning of some grassland communities. Specifically, our results suggested that long-term herbivores exclusion could increase the risk of the loss of plant diversity and reduction of ecosystem functions. There were several possible interpretations of these findings. First, recovery of ecological functions in harsh environment including alpine screes and alpine meadows might require longer timeframes (Prach and Walker, 2011). Second, complete recovery of ecosystem functioning by herbivore exclusion could be impossible as grazing and climate change caused stable degraded states resulted in decline in seed banks, nutrients stocks, and altered other ecological processes (Li et al., 2018; Liu et al., 2020). Thus, to avoid the degradation of mountainous grasslands under severe climate change and intensity anthropogenic activities, we call for developing proper grazing management practice for different mountainous grasslands and combining with artificial ecological restoration to adapt to future warmer climate on the TP.

5. Conclusion

Our findings provided solid empirical evidence that long-term impacts of herbivores exclusion on ecosystem functioning depend on grassland types, with most mountainous grasslands experiencing negative impacts on ecosystem multifunctionality. Additionally, our results also revealed that long-term herbivores exclusion had divergent impacts on above- and belowground ecological functions in mountainous grasslands, which were highly depended on plant diversity and productivity as well as soil nutrients. Thus, developing proper grazing management practice was critical for protecting the ecosystem multifunctionality in widespread mountainous grasslands on the TP. Our results also highlighted that long-term herbivores exclusion could increase the risk of plant diversity loss and reduction of ecosystem functions. To avoid the degradation of mountainous grasslands under severe climate change and intensity anthropogenic activities, we call for adjusting domestic herbivory numbers and developing proper grazing management practice for different mountainous grasslands to adapt to future warmer climate on the TP.

CRediT authorship contribution statement

Shuaihao Bai: Data curation, Software, Writing – original draft, Investigation, Visualization. **Guangpeng Qu:** Formal analysis, Funding acquisition, Conceptualization, Methodology. **Jingxue Zhao:** Writing – review & editing, Conceptualization, Resources, Data curation, Funding acquisition. **Lihua Tian:** Formal analysis, Software, Conceptualization. **Gao-Lin Wu:** Methodology, Validation, Supervision, Project administration.

Declaration of Competing Interest

The authors declare no competing financial interests.

Acknowledgements

This research was funded by the National Natural Science Foundation of China (32230068 and 42071058) and Grassland Degradation Restoration Project (GZFCG2023-17620).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109846.

Data availability

Data will be made available on request.

References

Altesor, A., Oesterheld, M., Leoni, E., Lezama, F., Rodríguez, C., 2005. Effect of grazing on community structure and productivity of a Uruguayan grassland. Plant Ecol. 179, 83–91. https://doi.org/10.1007/s11258-004-5800-5.

Bai, Y.F., Cotrufo, M.F., 2022. Grassland soil carbon sequestration: current understanding, challenges, and solutions. Science 377, 603–608. https://doi.org/10.1126/science.abo2380.

Bai, Y.F., Ma, L., Degen, A.A., Rafiq, M.K., Kuzyakov, Y., Zhao, J.X., Zhang, R., Zhang, T., Wang, W.Y., Li, X.G., Long, R.J., Shang, Z.H., 2020. Long-term active restoration of extremely degraded alpine grassland accelerated turnover and increased stability of soil carbon. Glob. Change Biol. 26, 7217–7228. https://doi.org/10.1111/gcb.15361.

Bi, X., Li, B., Fu, Q., Fan, Y., Ma, L.X., Yang, Z.H., Nan, B., Dai, X.H., Zhang, X.S., 2018. Effects of grazing exclusion on the grassland ecosystems of mountain meadows and temperate typical steppe in a mountain-basin system in Central Asia's arid regions, China. Sci. Total Environ. 630, 254–263. https://doi.org/10.1016/j.scitotenv.2018.02.055.

Chen, H., Ju, P.J., Zhu, Q., Xu, X.L., Wu, N., Gao, Y.H., Feng, X.J., Tian, J.Q., Niu, S.L., Zhang, Y.J., Peng, C.H., Wang, Y.F., 2022. Carbon and nitrogen cycling on the Qinghai–Tibetan Plateau. Nat. Rev. Earth Environ. 3, 701–716. https://doi.org/10.1038/s43017-022-00344-2.

Chen, J., Zhou, X.H., Wang, J.F., Hruska, T., Shi, W.Y., Cao, J.J., Zhang, B.C., Xu, G.X., Chen, Y.Z., Luo, Y.Q., 2016. Grazing exclusion reduced soil respiration but increased its temperature sensitivity in a Meadow Grassland on the Tibetan Plateau. Ecol. Evol. 6, 675–687. https://doi.org/10.1002/ece3.1867.

Dai, L.C., Fu, R.Y., Guo, X.W., Du, Y.G., Lin, L., Zhang, F.W., Li, Y.K., Cao, G.M., 2021. Long-term grazing exclusion greatly improve carbon and nitrogen store in an alpine meadow on the northern Qinghai-Tibet Plateau. Catena 197, 104955. https://doi.org/10.1016/j.catena.2020.104955.

Davies, G.M., Gray, A., 2015. Don't let spurious accusations of pseudoreplication limit our ability to learn from natural experiments (and other messy kinds of ecological monitoring). Ecol. Evol. 5, 5295–5304. https://doi.org/10.1002/ece3.1782.

Delgado-Baquerizo, M., Maestre, F.T., Reich, P.B., Jeffries, T.C., Gaitan, J.J., Encinar, D., Berdugo, M., Campbell, C.D., Singh, B.K., 2016. Microbial diversity drives multifunctionality in terrestrial ecosystems. Nat. Commun. 7, 10541. https://doi.org/10.1038/ncomms10541.

Deng, L., Shangguan, Z.-P., Wu, G.-L., Chang, X.-F., 2017. Effects of grazing exclusion on carbon sequestration in China's grassland. Earth Sci. Rev. 173, 84–95. https://doi.org/10.1016/j.earscirev.2017.08.008.

Deng, Z.H., Zhao, J.X., Ma, P.F., Zhang, H.Z., Li, R.C., Wang, Z., Tang, Y.H., Luo, T.X., 2023. Precipitation and local adaptation drive spatiotemporal variations of aboveground biomass and species richness in Tibetan alpine grasslands. Oecologia 202, 381–395. https://doi.org/10.1007/s00442-023-05401-1.

Fernández-Guisuraga, J.M., Fernández-García, V., Tárrega, R., Marcos, E., Valbuena, L., Pinto, R., Monte, P., Beltrán, D., Huerta, S., Calvo, L., 2022. Transhumant sheep grazing enhances ecosystem multifunctionality in productive mountain grasslands: a case study in the Cantabrian mountains. Front. Ecol. Evol. 10. https://doi.org/10.3389/fevo.2022.861611.

Gebregergs, T., Tessema, Z.K., Solomon, N., Birhane, E., 2019. Carbon sequestration and soil restoration potential of grazing lands under exclosure management in a semi-arid environment of northern Ethiopia. Ecol. Evol. 9, 6468–6479. https://doi.org/10.1002/ece3.5223.

He, N.P., Yu, Q., Wu, L., Wang, Y.S., Han, X.G., 2008. Carbon and nitrogen store and storage potential as affected by land-use in a Leymus chinensis grassland of northern China. Soil Biol. Biochem. 40, 2952–2959. https://doi.org/10.1016/j.soilbio.2008.08.018.

Hou, D.J., He, W.M., Liu, C.C., Qiao, X.G., Guo, K., 2019. Litter accumulation alters the abiotic environment and drives community successional changes in two fenced grasslands in Inner Mongolia. Ecol. Evol. 9, 9214–9224. https://doi.org/10.1002/ece3.5469.

Hu, W.G., Ran, J.Z., Dong, L.W., Du, Q.J., Ji, M.F., Yao, S.R., Sun, Y., Gong, C.M., Hou, Q. Q., Gong, H.Y., Chen, R.F., Lu, J.L., Xie, S.B., Wang, Z.Q., Huang, H., Li, X.W., Xiong, J.L., Xia, R., Wei, M.H., Zhao, D.M., Zhang, Y.H., Li, J.H., Yang, H.X., Wang, X.T., Deng, Y., Sun, Y., Li, H.L., Zhang, L., Chu, Q.P., Li, X.W., Aqeel, M., Manan, A., Akram, M.A., Liu, X.H., Li, R., Li, F., Hou, C., Liu, J.Q., He, J.-S., An, L.Z., Bardgett, R.D., Schmid, B., Deng, J.M., 2021. Aridity-driven shift in biodiversity–soil multifunctionality relationships. Nat. Commun. 12, 5350. https://doi.org/10.1038/s41467-021-25641-0.

Huang, M., Sang, C., Zhao, J.X., Degen, A.A., Chen, X.P., Zhang, T., Bai, Y.F., Li, S.S., Wang, W.Y., Shrestha, N., Shang, Z.H., 2022. Grazing exclusion altered the pattern of the soil seed bank but not the aboveground vegetation along an altitudinal gradient in alpine grassland. Land Degrad. Dev. 33, 3901–3913. https://doi.org/10.1002/ldr.4432.

Jing, X., Sanders, N.J., Shi, Y., Chu, H.Y., Classen, A.T., Zhao, K., Chen, L.T., Jiang, Y.X., He, J.-S., 2015. The links between ecosystem multifunctionality and above- and belowground biodiversity are mediated by climate. Nat. Commun. 6, 8159. https://doi.org/10.1038/ncomms9159.

Kelemen, A., Török, P., Valkó, O., Miglécz, T., Tóthmérész, B., 2013. Mechanisms shaping plant biomass and species richness: plant strategies and litter effect in alkali and loess grasslands. J. Veg. Sci. 24, 1195–1203. https://doi.org/10.1111/jvs.12027.

Kuang, X.X., Jiao, J.J., 2016. Review on climate change on the Tibetan Plateau during the last half century. J. Geophys. Res. Atmos. 121, 3979–4007. https://doi.org/10.1002/2015JD024728.

Latif, A., Ilyas, Sana, Zhang, Y.J., Xin, Y.Q., Zhou, L., Zhou, Q., 2019. Review on global change status and its impacts on the Tibetan Plateau environment. J. Plant Ecol. 12, 917–930. https://doi.org/10.1093/jpe/rtz038.

Li, W., Liu, Y.Z., Wang, J.L., Shi, S.L., Cao, W.X., 2018. Six years of grazing exclusion is the optimum duration in the alpine meadow-steppe of the north-eastern Qinghai-Tibetan Plateau. Sci. Rep. Uk. 8, 17269. https://doi.org/10.1038/s41598-018-35273-y.

Li, J.W., Shangguan, Z.P., Deng, L., 2022. Free particulate organic carbon plays critical roles in carbon accumulations during grassland succession since grazing exclusion. Soil Tillage Res. 220, 105380. https://doi.org/10.1016/j.still.2022.105380.

Li, J.P., Wang, W., 2017. Spatial patterns of soil organic carbon fractions and their control in temperate grasslands of China. Acta Ecol. Sin. 37, 140–147. https://doi.org/10.1016/j.chnaes.2017.06.006.

Lian, T.H., Li, Y.N., Wang, X., Xiang, S., Liu, Y.Z., Sun, S.C., 2024. Effect of grazing exclusion on plant communities varies over time in a Tibetan alpine meadow. Ecol. Eng. 209, 107420. https://doi.org/10.1016/j.ecoleng.2024.107420.

Liu, J.K., Bian, Z., Zhang, K.B., Ahmad, B., Khan, A., 2019a. Effects of different fencing regimes on community structure of degraded desert grasslands on Mu Us desert, China. Ecol. Evol. 9, 3367–3377. https://doi.org/10.1002/ece3.4958.

Liu, M., He, W., Zhang, Z.C., Sun, J., Cong, N., Nie, X.W., Wang, Y.F., Zhang, L., Yang, B., Chen, Y.C., Zhou, H.K., Shao, X.Q., Wang, Y.X., 2022. Mutual feedback between above- and below-ground controls the restoration of alpine ecosystem multifunctionality in long-term grazing exclusion. J. Clean. Prod. 333, 130184. https://doi.org/10.1016/j.jclepro.2021.130184.

Liu, X., Ma, Z.W., Huang, X.T., Li, L.H., 2020. How does grazing exclusion influence plant productivity and community structure in alpine grasslands of the Qinghai-Tibetan Plateau? Glob. Ecol. Conserv 23, e01066. https://doi.org/10.1016/j.gecco.2020.e01066.

Liu, M.X., Yin, F.L., Xiao, Y.D., Yang, C.L., 2023. Grazing alters the relationship between alpine meadow biodiversity and ecosystem multifunctionality. Sci. Total Environ. 898, 165445. https://doi.org/10.1016/j.scitotenv.2023.165445.

Ma, Y.H., Tian, L.H., Qu, G.P., Li, R.C., Wang, W.W., Zhao, J.X., 2022. Precipitation Alters the Effects of Temperature on the Ecosystem Multifunctionality in Alpine Meadows. Front. Plant Sci. 12. https://doi.org/10.3389/fpls.2021.824296.

Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., García-Gómez, M., Bowker, M.A., Soliveres, S., Escolar, C., García-Palacios, P., Berdugo, M., Valencia, E., Gozalo, B., Gallardo, A., Aguilera, L., Arredondo, T., Blones, J., Boeken, B., Bran, D., Conceição, A.A., Cabrera, O., Chaieb, M., Derak, M., Eldridge, D.J., Espinosa, C.I., Florentino, A., Gaitán, J., Gatica, M.G., Ghiloufi, W., Gómez-González, S., Gutiérrez, J.R., Hernández, R.M., Huang, X., Huber-Sannwald, E., Jankju, M., Miriti, M., Monerris, J., Mau, R.L., Morici, E., Naseri, K., Ospina, A., Polo, V., Prina, A., Pucheta, E., Ramírez-Collantes, D.A., Romão, R., Tighe, M., Torres-Díaz, C., Val, J., Veiga, J.P., Wang, D., Zaady, E., 2012. Plant Species Richness and Ecosystem Multifunctionality in Global Drylands. Science 335, 214–218. https://doi.org/10.1126/science.1215442.

Mekuria, W., Veldkamp, E., Haile, M., Nyssen, J., Muys, B., Gebrehiwot, K., 2007. Effectiveness of exclosures to restore degraded soils as a result of overgrazing in Tigray, Ethiopia. J. Arid. Environ. 69, 270–284. https://doi.org/10.1016/j.jaridenv.2006.10.009.

Mipam, T.D., Jiang, A., Jing, L.H., Zhang, S.H., Yi, W., Zhao, C., Ai, Y., Tian, L.M., 2024. Divergent Effects of Grazing Intensity on Soil Nutrient Fractions in Alpine Meadows. Land Degrad. Dev. 35, 5192–5199. https://doi.org/10.1002/ldr.5289.

Pan, Y., Wu, J.-X., Luo, L.-M., Tu, Y.-L., Yu, C.-Q., Zhang, X.-Z., Miao, Y.-J., Zhao, Y., Yang, J.-L., 2017. Climatic and geographic factors affect ecosystem multifunctionality through biodiversity in the Tibetan alpine grasslands. J. Mt. Sci. 14, 1604–1614. https://doi.org/10.1007/s11629-016-4242-6.

Prach, K., Walker, L.R., 2011. Four opportunities for studies of ecological succession. Trends Ecol. Evol. 26 (3), 119–123. https://doi.org/10.1016/j.tree.2010.12.007.

Shang, Z.H., Cao, J.J., Guo, R.Y., Henkin, Z., Ding, L.M., Long, R.J., Deng, B., 2017. Effect of Enclosure on Soil Carbon, Nitrogen and Phosphorus of Alpine Desert Rangeland. Land Degrad. Dev. 28, 1166–1177. https://doi.org/10.1002/ldr.2283.

Sun, J., Liu, M., Fu, B.J., Kemp, D., Zhao, W.W., Liu, G.H., Han, G.D., Wilkes, A., Lu, X.Y., Chen, Y.C., Cheng, G.W., Zhou, T.C., Hou, G., Zhan, T.Y., Peng, F., Shang, H., Xu, M., Shi, P.L., He, Y.T., Li, M., Wang, J.N., Tsunekawa, A., Zhou, H.K., Liu, Y., Li, Y.R., Liu, S.L., 2020. Reconsidering the efficiency of grazing exclusion using fences on the Tibetan Plateau. Sci. Bull. 65, 1405–1414. https://doi.org/10.1016/j.scib.2020.04.035.

Tan, Y.C., Chen, Z., Liu, W.W., Yang, M.Y., Du, Z.L., Wang, Y.F., Bol, R., Wu, D., 2024. Grazing exclusion alters denitrification N_2O/ ($N_2O + N_2$) ratio in alpine meadow of Qinghai-Tibet Plateau. Sci. Total Environ. 912, 169358. https://doi.org/10.1016/j.scitotenv.2023.169358.

Wang, L., Delgado-Baquerizo, M., Wang, D.L., Isbell, F., Liu, J.S., Feng, C., Liu, J.S., Zhong, Z.W., Zhu, H., Yuan, X., Chang, Q., Liu, C., 2019. Diversifying livestock promotes multidiversity and multifunctionality in managed grasslands. Proc. Natl. Acad. Sci. U. S. A. 116, 6187–6192. https://doi.org/10.1073/pnas.1807354116.

Wang, K.B., Deng, L., Ren, Z.P., Li, J.P., Shangguan, Z.P., 2016. Grazing exclusion significantly improves grassland ecosystem C and N pools in a desert steppe of Northwest China. Catena 137, 441–448. https://doi.org/10.1016/j.catena.2015.10.018.

Wang, Z.-P., Han, S.-J., Zheng, Y.-H., Zhang, X.-M., Wu, H.-H., Cui, J.-F., Xiao, C.-W., Han, X.-G., 2021. Fencing facility affects plant species and soil organic carbon in temperate steppes. Catena 196, 104928. https://doi.org/10.1016/j.catena.2020.104928.

Wang, Z., Luo, T.X., Li, R.C., Tang, Y.H., Du, M.Y., 2013. Causes for the unimodal pattern of biomass and productivity in alpine grasslands along a large altitudinal gradient in semi-arid regions. J. Veg. Sci. 24, 189–201. https://doi.org/10.1111/j.1654-1103.2012.01442.x.

Wang, Y.F., Lv, W.W., Xue, K., Wang, S.P., Zhang, L.R., Hu, R.H., Zeng, H., Xu, X.L., Li, Y. M., Jiang, L.L., Hao, Y.B., Du, J.Q., Sun, J.P., Dorji, T., Piao, S.L., Wang, C.H., Luo, C. Y., Zhang, Z.H., Chang, X.F., Zhang, M.M., Hu, Y.G., Wu, T.H., Wang, J.Z., Li, B.W., Liu, P.P., Zhou, Y., Wang, A., Dong, S.K., Zhang, X.Z., Gao, Q.Z., Zhou, H.K., Shen, M. G., Wilkes, A., Miehe, G., Zhao, X.Q., Niu, H.S., 2022. Grassland changes and adaptive management on the Qinghai–Tibetan Plateau. Nat. Rev. Earth Environ. 3, 668–683. https://doi.org/10.1038/s43017-022-00330-8.

Wang, Y., Sun, J., Lee, T.M., 2023. Altitude dependence of alpine grassland ecosystem multifunctionality across the Tibetan Plateau. J. Environ. Manag. 332, 117358. https://doi.org/10.1016/j.jenvman.2023.117358.

Wang, X., Xu, Z.W., Lü, X.T., Wang, R.Z., Cai, J.P., Yang, S., Li, M.-H., Jiang, Y., 2017. Responses of litter decomposition and nutrient release rate to water and nitrogen addition differed among three plant species dominated in a semi-arid grassland. Plant Soil 418, 241–253. https://doi.org/10.1007/s11104-017-3288-8.

Wang, B.Z., Yang, X.H., Zhu, Y.J., Tu, Y., Wang, D.Y., Indree, T., 2024. Plant diversity mediates the response of ecosystem multifunctionality to climate factor in Eastern Eurasian Steppe. Glob. Ecol. Conserv. 50, e02827. https://doi.org/10.1016/j.gecco.2024.e02827.

Wu, G.-L., Dong, W., Yu, L., Ding, L.-M., Liu, Z.-H., 2017a. Warm-season grazing benefits species diversity conservation and topsoil nutrient sequestration in alpine meadow. Land Degrad. Dev. 28, 1311–1319. https://doi.org/10.1002/ldr.2536.

Wu, G.-L., Du, G.-Z., Liu, Z.-H., Thirgood, S., 2009. Effect of fencing and grazing on a Kobresia-dominated meadow in the Qinghai-Tibetan Plateau. Plant Soil 319, 115–126. https://doi.org/10.1007/s11104-008-9854-3.

Wu, J.S., Feng, Y.F., Zhang, X.Z., Wurst, S., Tietjen, B., Tarolli, P., Song, C.Q., 2017b. Grazing exclusion by fencing non-linearly restored the degraded alpine grasslands on the Tibetan Plateau. Sci. Rep. 7, 15202. https://doi.org/10.1038/s41598-017-15530-2.

Wu, S.K., Hao, J., Diao, H.J., Su, Y., Kuan, H.D., Wang, C.H., Zhao, X., 2024. Short-term grazing diminished ecosystem multifunctionality of grassland in northern China. Plant Soil 505, 829–844. https://doi.org/10.1007/s11104-024-06711-w.

Wu, G.-L., Liu, Z.-H., Zhang, L., Chen, J.-M., Hu, T.-M., 2010. Long-term fencing improved soil properties and soil organic carbon storage in an alpine swamp meadow of western China. Plant Soil 332, 331–337. https://doi.org/10.1007/s11104-010-0299-0.

Wu, X.W., Wang, Y.C., Sun, S.C., 2021. Long-term fencing decreases plant diversity and soil organic carbon concentration of the Zoige alpine meadows on the eastern Tibetan plateau. Plant Soil 458, 191–200. https://doi.org/10.1007/s11104-019-04373-7.

Wu, T.-N., Wu, G.-L., Wang, D., Shi, Z.-H., 2014. Soil-hydrological properties response to grazing exclusion in a steppe grassland of the Loess Plateau. Environ. Earth Sci. 71, 745–752. https://doi.org/10.1007/s12665-013-2476-y.

Xiong, D.P., Shi, P.L., Sun, Y.L., Wu, J.S., Zhang, X.Z., 2024. Effects of grazing exclusion on plant productivity and soil carbon, nitrogen storage in alpine meadows in northern Tibet, China. Chin. Geogr. Sci. 24, 488–498. https://doi.org/10.1007/s11769-014-0697-y.

Yan, Y., Lu, X.Y., 2015. Is grazing exclusion effective in restoring vegetation in degraded alpine grasslands in Tibet, China? PeerJ 3, e1020. https://doi.org/10.7717/peerj.1020.

Yang, Y.-S., Zhang, F.-W., Xie, X.-R., Wang, J.-B., Li, Y.-N., Huang, X.-T., Li, H.-T., Zhou, H.-K., 2023. Effects of long-term grazing exclusion on vegetation structure, soil water holding capacity, carbon and nitrogen sequestration capacity in an alpine meadow on the Tibetan Plateau. J. Mt. Sci. Engl. 20, 779–791. https://doi.org/10.1007/s11629-021-7232-2.

Yao, Z.Y., Shi, L.N., He, Y.C., Peng, C.J., Lin, Z.R., Hu, M.-A., Yin, N., Xu, H.K., Zhang, D.G., Shao, X.Q., 2023. Grazing intensity, duration, and grassland type determine the relationship between soil microbial diversity and ecosystem multifunctionality in Chinese grasslands: a meta-analysis. Ecol. Indic. 154, 110801. https://doi.org/10.1016/j.ecolind.2023.110801.

Yu, L.F., Chen, Y., Sun, W.J., Huang, Y., 2019. Effects of grazing exclusion on soil carbon dynamics in alpine grasslands of the Tibetan Plateau. Geoderma 353, 133–143. https://doi.org/10.1016/j.geoderma.2019.06.036.

Yu, L.F., Sun, W.J., Zhang, H.Y., Cong, N., Chen, Y., Hu, J.J., Jing, X., 2024. Grazing exclusion jeopardizes plant biodiversity effect but enhances dryness effect on multifunctionality in arid grasslands. Agr. Ecosyst. Environ. 363, 108883. https://doi.org/10.1016/j.agee.2024.108883.

Yuan, J.Y., Ouyang, Z.Y., Zheng, H., Xu, W.H., 2012. Effects of different grassland restoration approaches on soil properties in the southeastern Horqin sandy land, northern China. Appl. Soil Ecol. 61, 34–39. https://doi.org/10.1016/j.apsoil.2012.04.003.

Zhan, T.Y., Zhao, W.W., Feng, S.Y., Hua, T., 2022. Plant community traits respond to grazing exclusion duration in Alpine Meadow and Alpine Steppe on the Tibetan Plateau. Front. Plant Sci. 13.. https://doi.org/10.3389/fpls.2022.863246.

Zhao, J.X., Li, X., Li, R.C., Tian, L.H., Zhang, T., 2016a. Effect of grazing exclusion on ecosystem respiration among three different alpine grasslands on the central Tibetan Plateau. Ecol. Eng. 94, 599–607. https://doi.org/10.1016/j.ecoleng.2016.06.112.

Zhao, J.X., Li, R.C., Li, X., Tian, L.H., 2017. Environmental controls on soil respiration in alpine meadow along a large altitudinal gradient on the central Tibetan Plateau. Catena 159, 84–92. https://doi.org/10.1016/j.catena.2017.08.007.

Zhao, J.X., Luo, T.X., Li, R.C., Li, X., Tian, L.H., 2016b. Grazing effect on growing season ecosystem respiration and its temperature sensitivity in alpine grasslands along a large altitudinal gradient on the central Tibetan Plateau. Agr. For. Meteor. 218-219, 114–121. https://doi.org/10.1016/j.agrformet.2015.12.005.

Zhao, J.X., Sun, F.D., Tian, L.H., 2019. Altitudinal pattern of grazing exclusion effects on vegetation characteristics and soil properties in alpine grasslands on the central Tibetan Plateau. J. Soil Sediment 19, 750–761. https://doi.org/10.1007/s11368-018-2056-6.

Zhao, J.X., Yang, W., Tian, L.H., Qu, G.P., Wu, G.-L., 2024. Warming differentially affects above- and belowground ecosystem functioning of the semi-arid alpine grasslands. Sci. Total Environ. 914, 170061. https://doi.org/10.1016/j.scitotenv.2024.170061.

Zheng, J.H., Zhang, B., Zhang, F., Zhao, T.Q., Wang, Q., Han, G.D., Zhao, M.L., 2023. Effects of fencing on near-term ecosystem multifunctionality in a typical steppe in Inner Mongolia. Agr. Ecosyst. Environ. 342, 108238. https://doi.org/10.1016/j.agee.2022.108238.

Zhu, Q., Chen, H., Peng, C.H., Liu, J.X., Piao, S.L., He, J.-S., Wang, S.P., Zhao, X.Q., Zhang, J., Fang, X.Q., Jin, J.X., Yang, Q.E., Ren, L.L., Wang, Y.F., 2023. An early warning signal for grassland degradation on the Qinghai-Tibetan Plateau. Nat. Commun. 14, 6406. https://doi.org/10.1038/s41467-023-42099-4.

Zhu, Y.J., Delgado-Baquerizo, M., Shan, D., Yang, X.H., Eldridge, D.J., 2021. Grazing impacts on ecosystem functions exceed those from mowing. Plant Soil 464, 579–591. https://doi.org/10.1007/s11104-021-04970-5.

Zhu, J.T., Zhang, Y.J., Wu, J.S., Zhang, X.Z., Yu, G.R., Shen, Z.X., Yang, X., He, Y.L., Jiang, L., Hautier, Y., 2024. Herbivore exclusion stabilizes alpine grassland biomass production across spatial scales. Glob. Change Biol. 30, e17155. https://doi.org/10.1111/gcb.17155.

Zou, J.R., Luo, C.Y., Xu, X.L., Zhao, N., Zhao, L., Zhao, X.Q., 2016. Relationship of plant diversity with litter and soil available nitrogen in an alpine meadow under a 9-year grazing exclusion. Ecol. Res. 31, 841–851. https://doi.org/10.1007/s11284-016-1394-3.