Contents lists available at ScienceDirect

Journal of Environmental Management

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

Research article

Long-term grazing improved soil chemical properties and benefited community traits under climatic influence in an alpine typical steppe

Yu-Wen Zhang [a], Ze-Chen Peng [a], Sheng-Hua Chang [a], Zhao-Feng Wang [a], Duo-Cai Li [b], Yu-Feng An [c], Fu-Jiang Hou [a,*], Ji-Zhou Ren [a]

[a] State Key Laboratory of Herbage Improvement and Grassland Agro-ecosystems, Key Laboratory of Grassland Livestock Industry Innovation, Ministry of Agriculture, College of Pastoral Agriculture Science and Technology, Lanzhou University, Lanzhou, Gansu, PR China
[b] Bureau of Quality and Technical Supervision Liangzhou Branch, Wuwei, Gansu, PR China
[c] Sunan Yugu Autonomous County Deer Farm, Zhangye, Gansu, PR China

ARTICLE INFO

ABSTRACT

Grazing and climate change both contribute to diversity loss and productivity fluctuations. Sensitive climate conditions and long-term grazing activities have a profound influence on community change, particularly in high-altitude mountain grassland ecosystems. However, knowledge about the role of long-term continuous grazing management on diversity, productivity and the regulation mechanisms in fragile grassland ecosystems is still rudimentary. We conducted a long-term grazing experiment on an alpine typical steppe in the Qilian Mountains to assess effects of grazing intensity on soil, diversity, productivity and the regulation mechanisms. Plants and soil were sampled along grazing gradients at different distances from the pasture entrance (0, 0.3, 0.6, 0.9, 1.2 and 1.5 km) under the non-growing (WP) and the growing season grazing pasture (SAP). The results revealed that community diversity and biomass did not change significantly on a time scale, while the concentration of soil organic carbon and total phosphorus increased significantly. Heavy grazing (0–0.3 km) decreased community diversity and biomass. Grazing increased soil chemical properties in heavy grazed areas of WP, while the opposite was recorded in SAP. Soil chemical properties explained the largest variances in community diversity and community biomass. The prediction model indicates that grazing in WP mainly affects community diversity through soil chemical properties, and promotes a positive correlation between community diversity and community biomass; in SAP, the direct effect of grazing gradients on community diversity and biomass is the main pathway, but not eliminating the single positive relationship between diversity and biomass, which means that diversity can still be used as a potential resource to promote productivity improvement. Therefore, we should focus on the regulation of soil chemical properties in WP, such as the health and quality of soil, strengthening its ability to store water, sequester carbon and increase nutrients; focus on the management of livestock in SAP, including providing fertilizer and sowing to increase diversity and production in heavily grazed regions and reducing grazing pressure through regional rotational grazing. Ultimately, we call for strengthening the stability and sustainability of ecosystems through targeted and active human intervention in ecologically sensitive areas to cope with future grazing pressures and climate disturbances.

1. Introduction

Grasslands, which constitute almost 40% of the terrestrial biosphere, provide habitat for a great diversity of animals and plants (Buisson et al., 2022). Large mammals graze nearly all natural grasslands, profoundly affecting the community diversity and productivity of grassland, and the processes are inextricably linked to climatic influences (Yu et al., 2019; Quéré and Mayot, 2022). Although extensive research on the effects of

climate and grazing on grassland diversity and productivity has been conducted using prediction models (He et al., 2022; Wei et al., 2020), there is still a lack of evidence from long-term continuous grazing experiments, especially the regulation effect of grassland systems on changes in soil properties. Therefore, it is imperative to investigate the regulatory process of long-term grazing on the diversity and biomass of grassland systems, which is of great importance for the management of grasslands to cope with the impact of climate factors.

In most cases, grazing and climate change have simultaneous, complex, and multichannel effects on grassland systems (He et al., 2022). The rise in temperature further affects the structure of the herbaceous understory by affecting the growth and distribution of alpine shrubs (Du et al., 2021). Meanwhile, plant traits strongly drive plant diversity through forage selection that affects herbivores. For example, large generalist herbivores such as cattle preferred nutrient-rich plant species of high forage quality with relatively thin and tall leaves, whereas shrubs, tall and armoured plants, as well as species rich in fibre, were avoided, thus having a direct impact on species diversity and distribution (Pauler et al., 2020). In addition, herbivores can directly affect the diversity and distribution of the plant community by carrying different seeds on their fur and spread them as they move from one place to the other (Auffret and Plue, 2014).

Certainly, climate factors and grazing intensity significantly affect the biomass of alpine grasslands (Liu et al., 2018; Du et al., 2021). Different grazing management measures, especially seasonal grazing, have a clear impact on the traits of plant litter and feces (Wu et al., 2016), and as the most important source of improving soil nutrients in pasture, litter and feces play a positive role in promoting community biomass (Ma et al., 2021).

The process of change in soil properties caused by climate and grazing is slow and profound (Wang et al., 2022). Long-term free grazing conditions will cause the soil properties and community traits of the paddock to have a very significant correlation with pasture management, including the distance from the water point and the frequency of grazing herd visits (Loke et al., 2021). However, the aboveground parts of plants are more susceptible to changes in climate conditions such as rainfall and livestock activities such as feeding compared to the positive effects of soil properties (Depauw et al., 2022). As a result, the response process of vegetation biomass in various areas of a paddock to climate conditions and grazing may be significantly different.

The relationship between diversity and productivity is the basis for our understanding of ecosystem function and sustainability (He et al., 2022). Research suggests that heavy grazing causes a negative relationship between plant diversity and productivity in an alpine grassland (Xiang et al., 2021), while the effects of livestock grazing on its relationship can be ignored in mountain grassland ecosystems (Liu et al., 2018). Meanwhile, multidimensional resource abundance can regulate the relationship between plant productivity and diversity, leading to the uncertainty in the relationship (Wang et al., 2022). Therefore, clarifying the mechanism that regulates diversity, productivity and their relationships is of great significance for the sustainable development of ecosystems, especially in climate sensitive mountain grassland ecosystems, and for reviewing current grazing management.

Mountain ecosystems represent a "bellwether of climate factor effects" (Jäschke et al., 2020). Over the past 50 years, the mean annual temperature on the Tibetan Plateau has climbed by 0.4 °C per decade, almost twice the rate of the global average (Zhu et al., 2020). The Qilian Mountains are located in the north of the Qinghai-Tibet Plateau, serving as an important ecological barrier in China and central Asia, and are highly sensitive and vulnerable to climate change due to their high altitude and variable climate conditions (Du et al., 2021). Grazing has become a very important and common land use type in alpine grassland ecosystems on the Tibetan Plateau (Hou et al., 2021). To be alert to the potential threat of climate change and long-term grazing to the diversity and productivity of the grassland ecosystem, we carried out a long-term continuous grazing experiment on the Qinghai-Tibet Plateau to investigate the soil and community traits at different grazing times (growing or non-growing season) and with distance from the pasture entrance (grazing gradient). Our work aims to address three hypotheses: 1) Long-term grazing strongly shapes the soil chemical properties and community traits of pastures at both temporal and spatial scales (grazing gradients); 2) the impact of grazing and soil chemical properties on community traits is more direct and intense compared to climate conditions; and 3) the continuous grazing pressure led to a positive feedback

relationship between diversity and biomass in pastures with a long grazing history. The ultimate goal of our work is to clarify the regulatory mechanisms of long-term grazing on community diversity and productivity in ecologically fragile and sensitive grasslands and provide land managers with a practical knowledge regarding vegetation distribution and its implication on soil chemical properties to address future grazing pressures and climate disturbances.

2. Materials and methods

2.1. Study site

The experiment took place in Zhangye City, Gansu Province, China (99°32′N, 38°54′W). Mean annual precipitation is 170 mm/year. Annual temperature was 8.2 °C (https://en.tutiempo.net/climate, accessed March 20, 2023). According to the FAO world reference base, the soil in the study region is mainly composed of gelic leptosols. The vegetation in this area is characterized by the large cover of herbaceous plants (mainly *Poa poophagorum*, *Stipa purpurea* and *Leymus secalinus*), which are mountain grassland as cool temperate and slightly dry (Ren et al., 2008). Perennial biological species dominate the vegetation community. The forage began to become green in late April and entered the yellowing and withering period in early September.

2.2. Experimental design

Due to the limited number of pastures, it is difficult to establish accurate replicates in large-scale grazing trials. This research employs pseudo-replication and a space-for-time substitution constraint (Hurlbert, 1984). The pasture was set up in 1958 and fenced in 1991 for large-scale grazing. It uses a seasonal rotation of the same herd grazing pattern. Gansu wapiti is the type of animal studied in this study (*Cervus elaphus kansuensis*). Growing season grazing pasture (SAP) grazing takes place from May to August each year, and non-growing season grazing pasture (WP) grazing takes place from November to April. The animals are penned at night, herded during the day, and then released to wander at the study site. The ground near the pens is grazed more regularly than the paddocks further away. Because these management practices have been in place for many years, it may be possible to collect samples from locations at various distances from the pens to learn more about the long-term impact of grazing intensity on plant and soil (Zhang et al., 2022). Therefore, we take the concentration point in the area with the strongest grazing pressure as the starting point (0) and confirm the grazing and feeding routes of livestock through on-site investigations and inquiries with the herdsmen. We have combined the changes in vegetation and soil along the feeding route, such as significant changes in vegetation and representative uniform terrain changes, to set up six sampling points, which are 0, 0.3, 0.6, 0.9, 1.2 and 1.5 km, and marked with stones to facilitate the review of soil and plant sampling.

2.3. Field sampling and measurement

We rediscovered the marker points to obtain accurate gradient information during the sampling year. Therefore, we measured the long-term impact of 20 years of grazing on ecosystem properties, without capturing interference signals from the presence of pasture heterogeneity. Field sampling took place during the summer months (primarily July–August) of 1999 and 2019. Three 1 m × 1 m plots were chosen at random near the stone for each sampling point. In each plot, we measured the species abundance (number of species per m^2) and density (number of each plants per m^2), and we randomly selected 5 plants to measure the plant height (height from the ground to the plant top), crown width (crown diameter of the plant), and reproductive branch number (number of branches with seeds of the plant) of each species. The biomass of each plot's community was trimmed to a stubble height of 1 cm, sorted by species, dried to a consistent mass at 60 °C, and
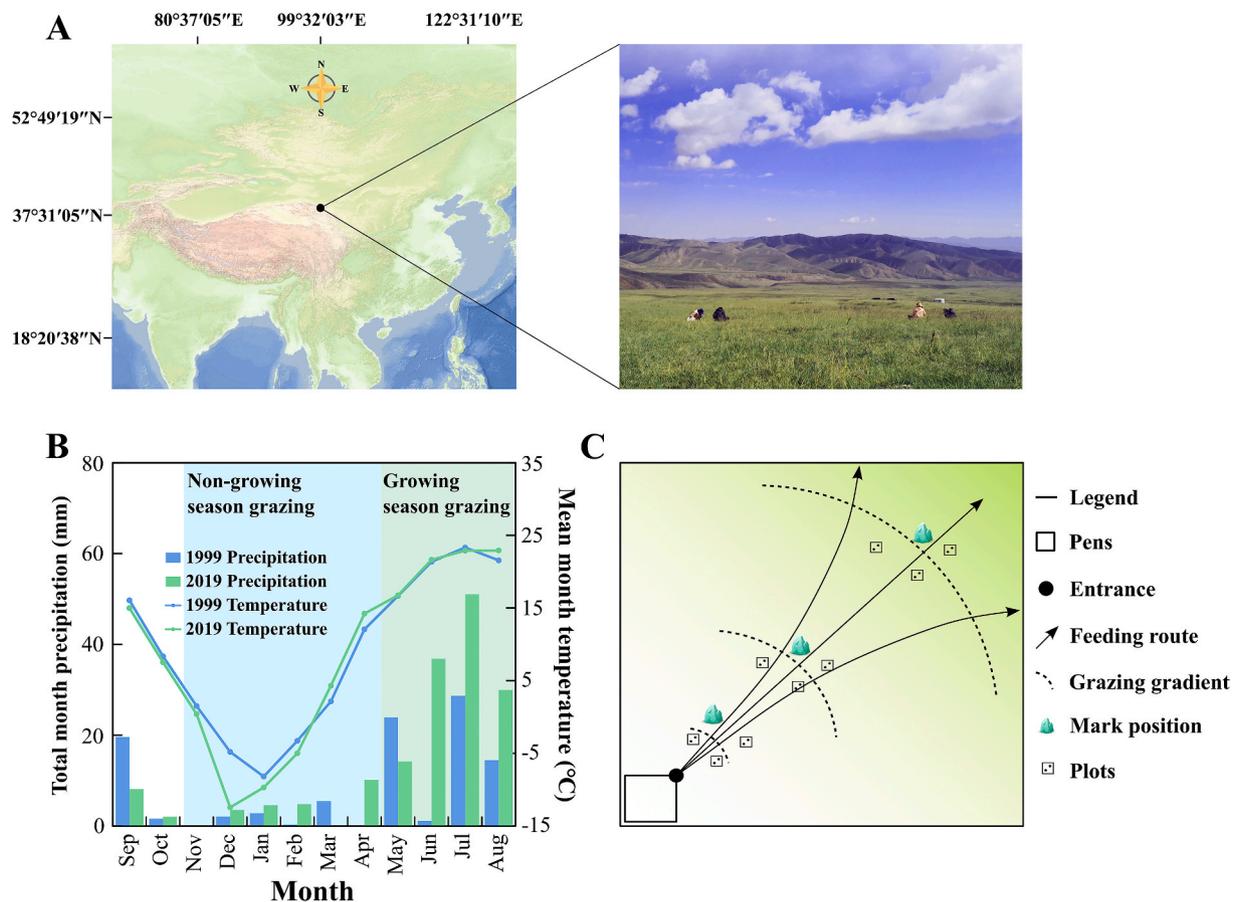
Fig. 1. Topographic map of the study site and sampling photos of the grazing pasture (A). Total month precipitation and mean month temperature from September 1998 to August 1999 and September 2018 to August 2019 (B). The concept diagram for experimental (C).

weighed. After removing the plant, we randomly selected two soil sampling spots in each plot and sampled to a depth of 10 cm with a soil auger. We mixed a composite sample and brought it back to the laboratory for it to dry naturally in the shade. Then we measured the soil available nitrogen concentration (AN, mg kg^{-1}) (Wang et al., 2013), soil Olsen-P concentration (AP, mg kg^{-1}) (Olsen et al., 1954), soil organic carbon concentration (OC, g kg^{-1}) (Nelson and Sommer, 1983), soil total nitrogen concentration (TN, g kg^{-1}) (Bremner and Mulvaney, 1982) and soil total phosphorus concentration (TP, g kg^{-1}) (Anderson and Ingram, 1989). (see Fig. 1).

2.4. Statistical analysis

The coefficient of variation (CV) was calculated by

$$CV = SD \div AVG \qquad (1)$$

Where *SD* is the standard deviation; and *AVG* is the mean of the data.

We use the package 'vegan' (Oksanen et al., 2018) to calculate the community diversity index (Shannon-Wiener index). We use the JASP version 0.16.1 software to calculate the effect size (Hedges' *g*) and the 95% confidence interval to evaluate the change of variables after 20 years. Plant height and crown width may represent a trade-off between competitive ability and stress tolerance to some extent (Miller et al., 2019). Reproductive branch number may represent the investment of plants in reproduction distribution to extend their population to more open spaces (Wang et al., 2022). We used the plant height, crown width and number of reproductive branches of all species in the plot to jointly evaluate the functional diversity of the community. We analyze the community functional diversity index using the package 'FD', which includes the functional richness index (FRic), functional evenness index (FEve), functional divergence index (FDiv), functional dispersion index (FDis), and Rao's Q index (RaoQ) (Laliberté and Legendre, 2010). We also calculated the Spearman correlations between variables and community diversity (Shannon-Wiener index) and community biomass (total community biomass). We applied the multiple regression model by lm function in 'stats' package in R (Field et al., 2012) and the analysis of variance decomposition using the calc. relimp function in the package 'relaimpo' in R (Grömping, 2006) to estimate the importance of the variables. To quantify the pure and shared contributions of climate conditions (annual cumulative temperature, total annual precipitation and mean annual temperature), grazing gradients (longitude, latitude, altitude, and gradient), community functional diversity (FRic, FEve, FDiv, FDis and RaoQ) and soil chemical properties (AN, AP, OC, TN and TP) on community diversity (community species distribution) and community biomass (the biomass of gramineae, leguminosae, compositae and other families), variation partitioning analysis was performed using the package 'rdacca.hp' (Lai et al., 2022). We use the package 'plspm' (Tenenhaus et al., 2005) for partial least squares path modeling (PLS-PM) to explore the mechanism of variables on community diversity (Shannon-Wiener index) and community biomass (total community biomass). All data were tested for homogeneity of variances using Levene's test in the 'car' package (Fox and Weisberg, 2019) and subsequently normality was tested using the Shapiro–Wilk test. Logarithmic transformation was used to improve the normality when necessary. All analyzes were performed using R 4.1.2 (R Core Team, 2020).

3. Results

3.1. Grazing effects on community diversity and biomass

The community diversity under the WP and SAP does not show a discernible trend with the increasing grazing gradient, while the community biomass has an increasing trend. Community diversity and biomass under the SAP are generally lower than those in the WP (Table 1). By comparison, it was found that heavy grazing (0 km) significantly decreased community diversity. Overall, long-term grazing did not cause significant changes in community diversity and biomass, but it had a strong impact along with the grazing gradient (Table 1).

3.2. Grazing effects on community functional diversity index and soil chemical properties

The grazing had a discernible trend effect on the community functional diversity index with increasing gradients. In comparison, we did not find significant changes in the community functional diversity index

on a time scale (Supplementary Table S1).

WP has higher values of the soil chemical property than SAP. Growing season grazing increased the soil chemical property values along with the grazing gradients, while non-growing season grazing had no discernible effect. On the contrary, AP did not change significantly on the time scale, while other soil chemical properties showed an increasing trend overall (Supplementary Table S2).

3.3. Coefficient of variation with variables

The soil chemical properties have a lower CV value compared to the variables of the community, indicating that the soil chemical properties are relatively stable and the community is vulnerable to the impact of the external environment (Fig. 2A). The comparison results show that the CV values of different indexes have a downward trend in general (Fig. 2B).

Table 1
Effects of grazing on the community diversity and biomass.

Grazing pasture	Grazing gradient (km)	Community diversity	Community biomass (g m^{-2})	Effect size (Hedges' *g*)	
				Community diversity	Community biomass
WP	0	1.82 ± 0.07a	118.9 ± 15.5 ab	−1.47 (−3.29,0.47)ns	−0.38 (−1.97,1.27)ns
	0.3	1.96 ± 0.13a	114.9 ± 20.0 ab	−0.50 (−2.10,1.17)ns	0.36 (−1.28,1.96)ns
	0.6	1.98 ± 0.04a	110.6 ± 11.8 b	0.27 (−1.36,1.86)ns	0.86 (−0.89,2.52)ns
	0.9	1.69 ± 0.11a	134.5 ± 21.3 ab	−0.45 (−2.06,1.20)ns	0.21 (−1.41,1.80)ns
	1.2	2.02 ± 0.12a	149.1 ± 16.0 ab	1.39 (−0.52,3.18)ns	0.66 (−1.04,2.28)ns
	1.5	1.87 ± 0.10a	178.0 ± 25.5a	0.24 (−1.39,1.83)ns	1.31 (−0.57,3.08)ns
SAP	0	1.34 ± 0.10c	87.60 ± 8.40 b	−3.85 (−6.82,−0.79)*	1.02 (−0.77,2.71)ns
	0.3	1.91 ± 0.17 ab	87.00 ± 18.6 b	−0.36 (−1.96,1.28)ns	−0.41 (−2.01,1.24)ns
	0.6	1.63 ± 0.04bc	92.10 ± 6.70 ab	−2.73 (−5.10,−0.25)*	−0.16 (−1.75,1.46)ns
	0.9	1.51 ± 0.17bc	91.70 ± 10.0 ab	−0.99 (−2.67,0.79)ns	−0.77 (−2.41,0.95)ns
	1.2	1.56 ± 0.12bc	129.7 ± 8.70a	−1.36 (−3.15,0.54)ns	−1.45 (−3.26,0.48)ns
	1.5	2.14 ± 0.24a	127.5 ± 12.9a	−0.38 (−1.98,1.27)ns	−1.36 (−3.15,0.54)ns
Source of variation					
Grazing pasture (GP)		*	**		
Grazing gradient (GG)		*	**		
GP × GG		ns	ns		

Note: for each grazing pasture (GP), the means ± SE in a column followed by different lowercase letters are significantly different in the grazing gradient (GG), according to Duncan's test at *P* < 0.05. Results of two-way ANOVAs testing the single and interactive effects of GP and GG on the community functional diversity index in 2019, significance levels (*** < 0.001,** < 0.01,* <0.05, ns > 0.05). Effect size presented as Hedges' *g* and their 95% confidence intervals. Positive values of effect size indexed improvements in the 2019 from 1999. Negative effect size values are the opposite. Significant change effects are indicated with a *. The non-significant change effects are indicated with ns. Non-growing season grazing pasture (WP), growing season grazing pasture (SAP).
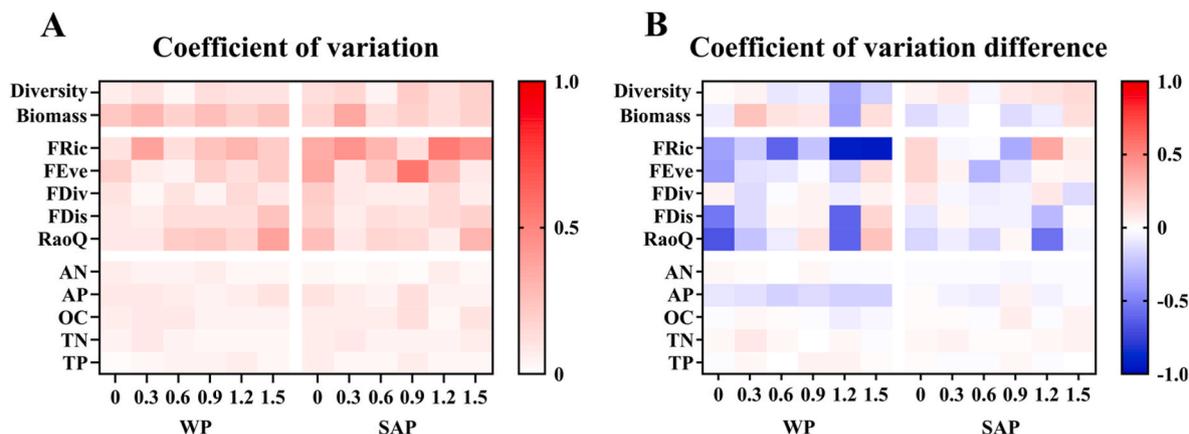
Fig. 2. Heat map estimated the different index heterogeneity in terms of the coefficient of variation (CV) along the grazing gradients in 2019 (A) and the CV difference (B). Non-growing season grazing pasture (WP), growing season grazing pasture (SAP), functional richness index (FRic), functional evenness index (FEve), functional divergence index (FDiv), functional dispersion index (FDis), Rao's Q index (RaoQ), soil available nitrogen concentration (AN), soil Olsen-P concentration (AP), soil organic carbon concentration (OC), soil total nitrogen concentration (TN) and soil total phosphorus concentration (TP).

3.4. Main drivers controlling community diversity and biomass

We conducted correlation analysis and multiple linear regression to identify the correlation and relative importance of climate conditions, grazing gradients and soil chemical properties that affect community diversity and biomass. There was a significant positive correlation between FRic and community diversity and biomass in WP. In SAP, there was a significant correlation between climate conditions and community diversity and biomass. In addition, there was a significant correlation between grazing gradients and community biomass. Overall, the total factor explained 83% and 59% of the variation in community diversity and biomass in WP, respectively, and explained 78% and 71% of the variation in community diversity and biomass in SAP (Fig. 3).

Variation partitioning showed that soil chemical properties explained the largest variances in community diversity (i.e., 22.7% and 23.5% in WP and SAP, respectively) and community biomass (i.e., 21.6% and 22.5% in WP and SAP, respectively). The climate conditions are the second largest factors that explained the variances in community diversity (i.e., 18.6% and 13.4% in WP and SAP, respectively), while the CFD and grazing gradients are the second largest factors to explained the community biomass in WP and SAP, respectively (Fig. 4B and D).

3.5. Possible pathways driving community diversity and biomass

The PLS-PM identified potential drivers of community diversity and community biomass based on possible contributions of climate conditions, grazing gradients, CFD and soil chemical properties. The results showed that the climate conditions had a significant negative impact on the soil chemical properties in WP and SAP but a significant positive impact on community diversity. Grazing gradients strongly affect the

community traits in SAP (including CFD, community diversity and community biomass), while only controlling the community biomass in WP. It is worth noting that the soil chemical properties have a significant positive impact on community diversity and then promote community biomass in WP, while in SAP, through CFD, the soil chemical properties promote community diversity but do not further affect community biomass (Fig. 5A and B). Overall, community diversity and CFD promote community biomass in WP, while grazing gradients and climatic conditions promote community biomass in SAP (Fig. 5C and D). There is a significant positive correlation between community diversity and community biomass (Fig. 5E and F).

4. Discussion

4.1. Effects of long-term grazing on community traits and main drivers

The selection of forage by herbivores is a major driver of plant diversity in pasture vegetation (Pauler et al., 2020). Endo- and epizoochoric seed dispersal through ungulates can act as ecological filters and therefore affect species composition (Auffret and Plue, 2014). Regarding community diversity, we did not discover a significant change in grazing gradients in WP and SAP, and community diversity was lower in SAP than in WP (Table 1). Two mechanisms may support this phenomenon. The first is that there is a clear impact of plant traits on forage selection and that grazing during the growing season can increase extinction rates by extirpating subordinate or rare palatable species from the community, further decreasing community diversity (Pauler et al., 2020). Second, grazing can promote seed dispersal and increase seed sources (Auffret and Plue, 2014), which then increases the uncertainty of community composition and weakens the diversity
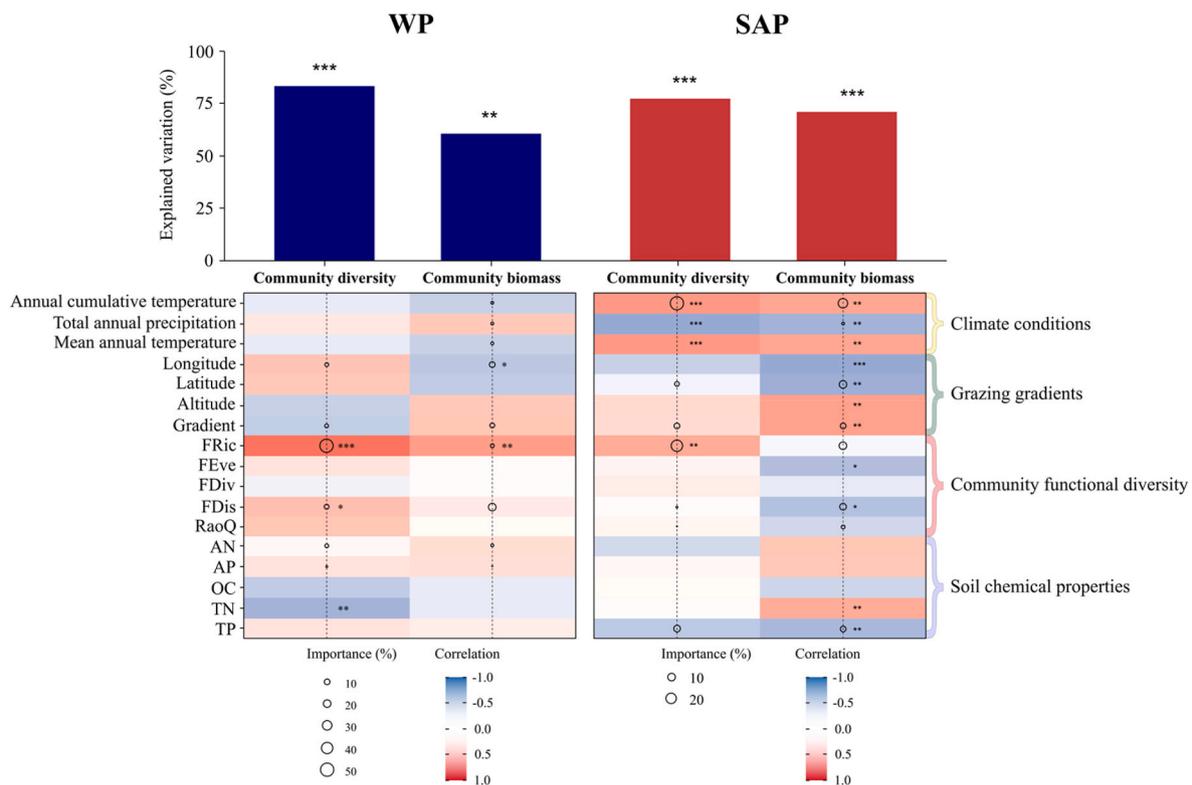
Fig. 3. Contributions of variables to community diversity and community biomass based on correlation and best multiple regression model. Circle size represents the variable importance (that is, proportion of explained variability calculated via multiple regression modeling and variance decomposition analysis). The * indicates the significance of multiple regression modeling, levels of significance (*** < 0.001,** < 0.01,* <0.05, ns > 0.05). Colors represent Spearman correlations. Non-growing season grazing pasture (WP), growing season grazing pasture (SAP), functional richness index (FRic), functional evenness index (FEve), functional divergence index (FDiv), functional dispersion index (FDis), Rao's Q index (RaoQ), soil available nitrogen concentration (AN), soil Olsen-P concentration (AP), soil organic carbon concentration (OC), soil total nitrogen concentration (TN) and soil total phosphorus concentration (TP).

Community diversity

Community biomass
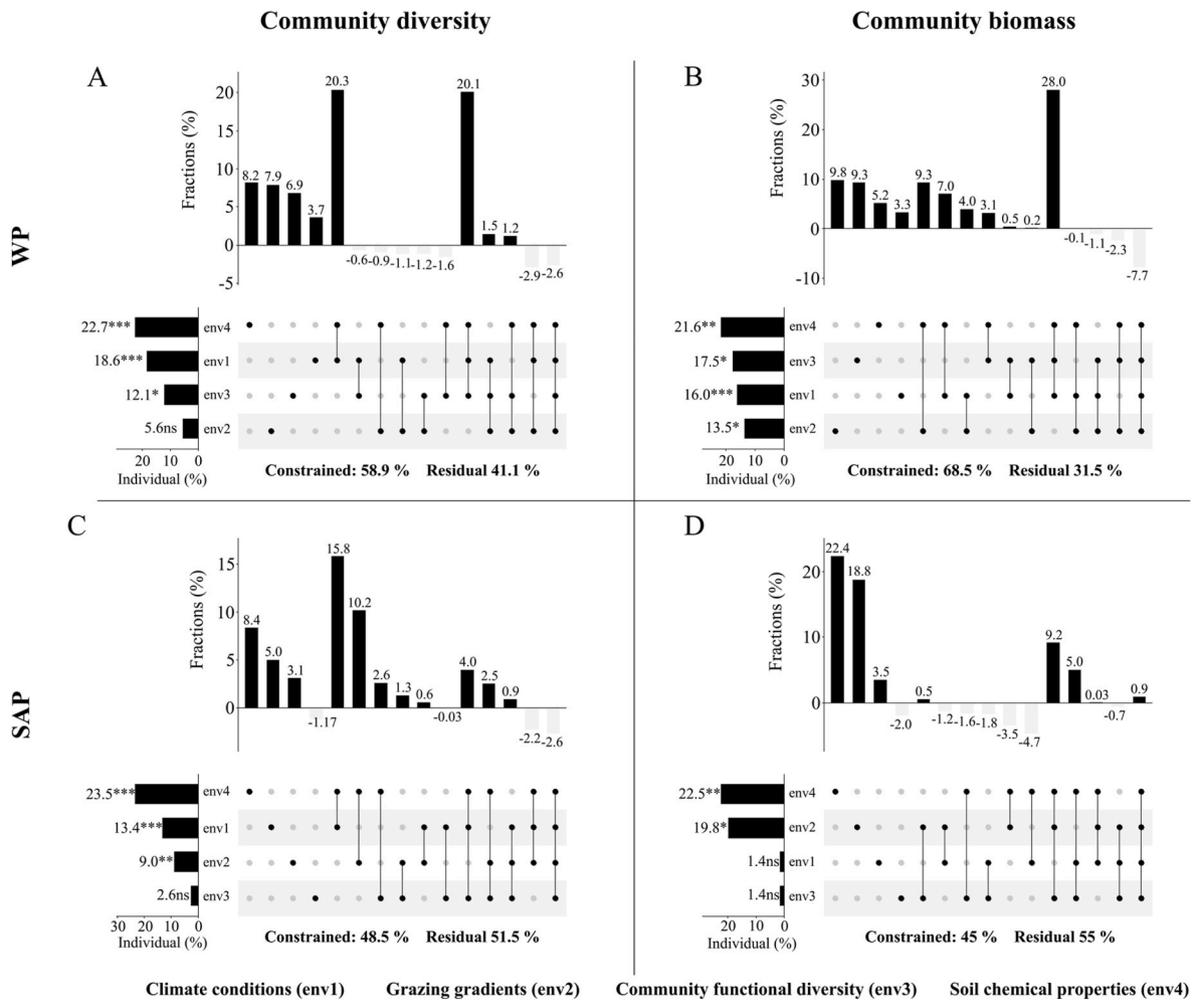
Fig. 4. UpSetView plots of variation partitioning results to show the pure and shared contributions of climate conditions (annual cumulative temperature, total annual precipitation and mean annual temperature), grazing gradients (longitude, latitude, altitude, and gradient), community functional diversity (functional richness index (FRic), functional evenness index (FEve), functional divergence index (FDiv), functional dispersion index (FDis) and Rao's Q index (RaoQ)) and soil chemical properties (soil available nitrogen concentration (AN), soil Olsen-P concentration (AP), soil organic carbon concentration (OC), soil total nitrogen concentration (TN) and soil total phosphorus concentration (TP)). The numbers in the graphs are the percentage of variance explained by the corresponding environmental factors. The dot matrix and the corresponding bar above it show the values of shared and exclusive contributions. Negative values due to adjustment of R-squared mean negligible contributions and are not shown in the graph, but they are included in the computation of the total contribution of each variable category which were shown on the edge of the dot matrix. Residuals represent the percentage unexplained by these variables. Non-growing season grazing pasture (WP), growing season grazing pasture (SAP).

difference between different grazing gradients.

The WP effects on community biomass that we observed were higher than the SAP (Table 1). The most intuitive differences between WP and SAP are the temperature, precipitation, and disturbance periods, as they influence plant regrowth (Liu et al., 2021). During the growing season, although the deposition of dung and urine in the higher soil temperature and moisture can accelerate nutrient availability and promote plant growth, the disturbance caused by livestock can lead to a temporary or permanent decrease in plant reproduction and regeneration, leading to lower vegetation biomass (Tian et al., 2021). However, non-growing season grazing through livestock trampling leads to the reduction of litter and shallow placement of seeds, which is conducive to germination the following year and further promotes plant growth (Quan et al., 2015).

Functional traits directly link the performance of organisms with the environment and are used to scale up effects on the overall structure, function, and diversity of ecosystems (Carboni et al., 2021). In comparison, we did not find that the community diversity, community biomass and community functional diversity indexes had a significant change in time scale (Tables 1 and Supplementary Table S1). Plants may

not be sensitive to grazing in alpine grassland systems with long evolutionary histories of herbivory because most plants are perennials that dominate throughout high altitudes, and their respective traits are adaptive to alpine climates as well as to grazing (Jäschke et al., 2020).

WP has higher values of soil chemical properties than SAP, and SAP increased soil chemical properties along with grazing gradients, whereas WP is the opposite (Supplementary Table S2). This may be due to the growing season and the higher intensity of grazing, which promote the flow of nutrients from soil-vegetation-livestock interactions, thus reducing the values of soil chemical properties (Sun et al., 2014). In the non-growing season, the community structure may be dominated by plant absorption and utilization and maintain relative stability between different gradients (Herben et al., 2022). In contrast, AP did not change significantly on the time scale, while other soil properties showed an increasing trend overall (Supplementary Table S2). This may be mainly related to the mobilization process of soil phosphorus (P). Because P is difficult to move in the soil, its process is mainly related to the direct physicochemical activation of soil minerals by roots (Wen et al., 2021), so the distribution of roots in the soil layer may dominate AP. Meanwhile, we found a little change in community diversity on the time scale,
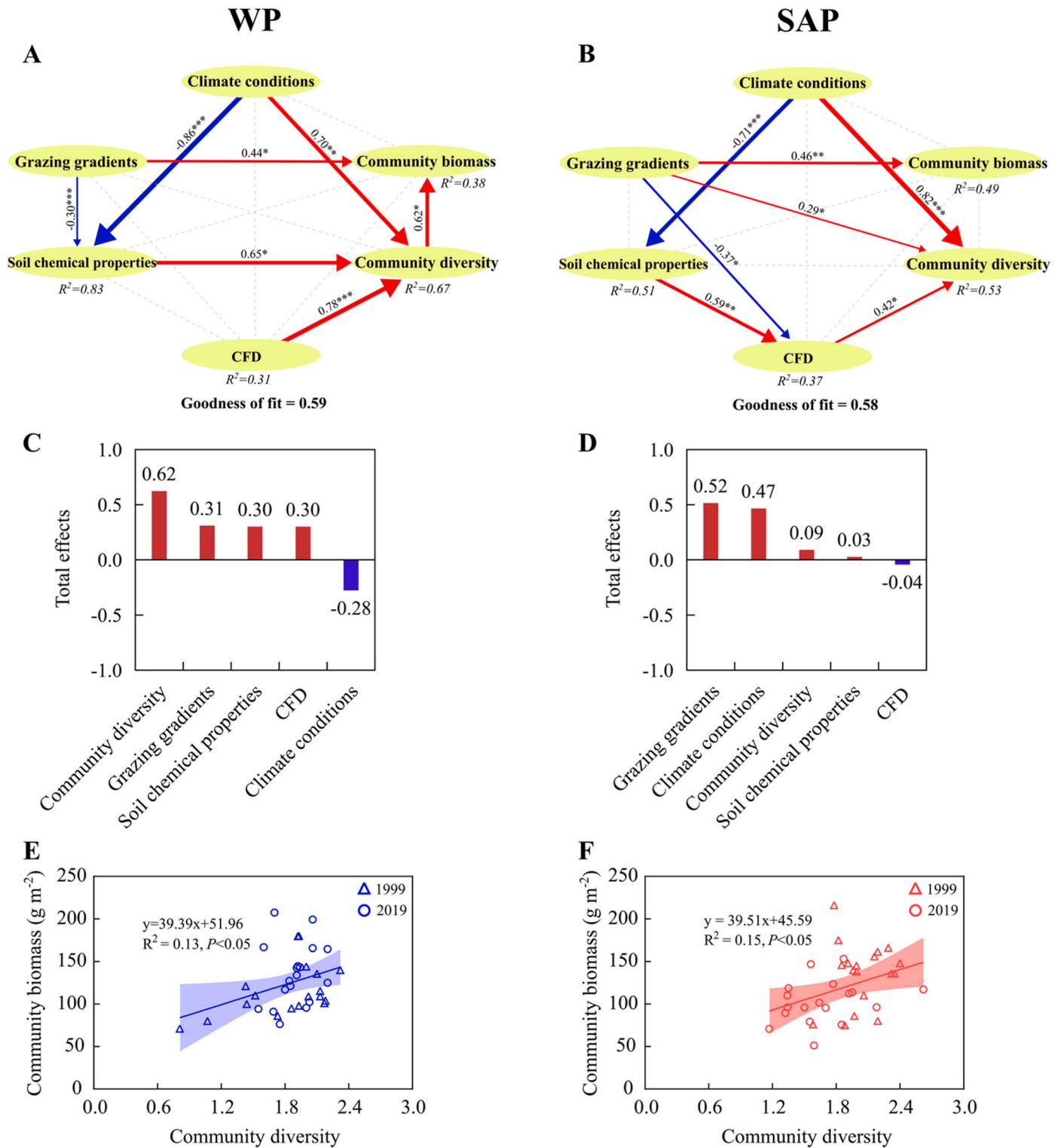
Fig. 5. Partial least squares path modeling (PLS-PM) results for the impact path of variables on community diversity and biomass of non-growing season grazing pasture (WP) and growing season grazing pasture (SAP) (A and B), as well as the standardised total effect (C and D). Relationships between community diversity and community biomass in WP (E) and SAP (F), respectively. Solid red arrows indicated the positive effects; the solid blue arrows indicated the negative effects; the gray dotted line indicated no effect path; and the numbers on the arrows indicated the effect size. Climate conditions included annual accumulated temperature, annual precipitation and annual mean temperature; grazing gradients included longitude, latitude, altitude and gradient; community functional diversity (CFD) included functional richness index (FRic), functional evenness index (FEve), functional divergence index (FDiv), functional dispersion index (FDis) and Rao's Q index (RaoQ); soil chemical properties included soil available nitrogen concentration (AN), soil Olsen-P concentration (AP), soil organic carbon concentration (OC), soil total nitrogen concentration (TN) and soil total phosphorus concentration (TP).

which can also be used to speculate that a stable community may have a stable root-layer system, thus indicating a stable AP.

The CV value of soil chemical properties is generally lower than that of community variables, and the CV values of these variables have a trend of decreasing over time (Fig. 2A and B). Because the factors controlling the change in soil chemical properties and community variables are fundamentally different, it usually leads to time and spatial asynchrony in the above- and below-ground responses to grazing (Bloor et al., 2020).

4.2. Regulation mechanism of community diversity and biomass

Variation partitioning showed that the soil chemical properties explained the largest variances in community diversity and community biomass (Fig. 4). Normally, the formation of above-ground dry matter is mainly related to the activation of the soil macronutrients (N and P) in plant rhizosphere processes (Wen et al., 2021). For example, Gramineae, Leguminosae and Compositae plants can strengthen their absorption of soil macronutrients to ensure growth through strategies that alter root morphology, microbial interactions and root exudates in the same soil environment, respectively, which will further affect community diversity and biomass (Herben et al., 2022; Wen et al., 2021). In addition, climate conditions are the second main factor explaining the variation in community diversity (Fig. 4A and C). Rising temperatures can affect the species composition and adaptive potential of pollination types, which in turn directly affect community diversity (Zhu et al., 2020, Fig. 3). Seasonal and interannual rainfall variation and temperature control soil biogeochemical processes, and higher temperature levels will promote substantial soil C losses and increase the availability of soil inorganic N, which will further induce changes in community diversity by affecting the competitiveness of different species (Giese et al., 2011; Hartley et al., 2021, Fig. 5A and B). Notably, with regard to livestock, forage selection by herbivores is an important driver of community diversity in SAP (Pauler et al., 2020, Fig. 4C; Fig. 5B), but the function of forage selection is weakened due to grasses dying in the non-growing season and even to selecting some species that avoid eating in the growing season (Tian et al., 2021); thus, the grazing gradient in WP has no significant impact on community diversity (Fig. 4A).

The PLS-PM prediction model indicates that in WP, grazing gradients and soil chemical properties have a high total effect on community biomass (Fig. 5C), which may be due to livestock excreta that are produced during the non-growing season of grass and cannot be timely utilized by roots. However, feces will gradually decompose over time, further changing the soil properties under different gradients and effecting community diversity (Aarons et al., 2015; Zhang et al., 2022, Fig. 5A). However, in SAP, the largest factor on community biomass is grazing gradient, and the total effects of community diversity, soil chemical properties and CFD are greatly weakened (Fig. 5D). However, the path shows that soil chemical properties have a significant positive impact on community diversity through CFD. It may be because in SAP, livestock excreta have a high level of available nutrients that match the growth period of plants and have a significant impact on plant traits, such as height and crown diameter, leading to changes in the competitiveness of species and thereby affecting community composition and diversity (Sitters et al., 2017; Aarons et al., 2015, Fig. 3). In addition, it is worth noting that community diversity in WP has a significant positive impact on community biomass, while the relationship has disappeared in SAP (Fig. 5A and B), but it does not eliminate the individual contribution of diversity to biomass (Fig. 5F), which means that diversity can still be used as a potential resource to promote productivity improvement.

5. Conclusions

In this study, CFD, community diversity and community biomass did not change significantly on the time scale, while soil chemical properties

showed an overall increase trend. On the spatial scale, heavy grazing decreased FRic, community diversity, and community biomass. And WP grazing increased the soil chemical properties in heavy grazing area, while it opposite in SAP. Variation partitioning showed that soil chemical properties explained the largest variances in community diversity (i. e., 22.7% and 23.5% in WP and SAP, respectively) and community biomass (i.e., 21.6% and 22.5% in WP and SAP, respectively). Through the prediction model, we believe that the impact of grazing in WP is mainly through regulating soil chemical properties to affect community diversity and promote a positive correlation between community diversity and community biomass; In SAP, grazing plays a leading role in strong direct interference with community diversity and biomass, but it can still further improve system productivity through positive relationships between diversity and biomass. These results suggest that we should start with the soil chemical properties of WP and start with the grazing management of SAP to deal with the issues of diversity and productivity. Therefore, we recommend more precise and dynamic management of herbivores, vegetation, and soil. For example, in WP, we should pay attention to the health and quality of the soil and strengthen its ability to conserve water, sequester carbon and increase nutrients to enhance ecological and agronomic benefits; in SAP, we should reduce grazing pressure through regional rotational grazing. According to the heavily grazed areas, appropriate measures, such as enclosure to promote the utilization of high soil chemical properties by plant roots in WP and fertilization to supplement lacking soil chemical elements, benefit plant growth in SAP. Ultimately, we hope to enhance the stability and sustainability of ecosystems in ecologically fragile and sensitive areas to cope with future grazing pressures and climate disturbances.

CRediT authorship contribution statement

Yu-Wen Zhang: Conceptualization, Data curation, Software, Visualization, Writing - original draft, Writing - review & editing. **Ze-Chen Peng:** Investigation. **Sheng-Hua Chang:** Investigation. **Zhao-Feng Wang:** Investigation. **Duo-Cai Li:** Investigation. **Yu-Feng An:** Investigation. **Fu-Jiang Hou:** Conceptualization, Methodology, Project administration, Funding acquisition, Data curation, Investigation, Resources, Supervision, Validation, Writing - review & editing. **Ji-Zhou Ren:** Conceptualization, Methodology, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2023.119184.

References

Aarons, S.R., Gourley, C.J.P., Hannah, M.C., 2015. Between and within paddock soil chemical variability and forage production gradients in grazed dairy pastures[J].

Nutrient Cycl. Agroecosyst. 102 (3), 411–430. https://doi.org/10.1007/s10705-015-9714-5, 2015.

Anderson, J.M., Ingram, J.S.I., 1989. Tropical Soil Biology and Fertility. CAB international, Wallingford, p. 171.

Auffret, A.G., Plue, J., 2014. Scale-dependent diversity effects of seed dispersal by a wild herbivore in fragmented grasslands[J]. Oecologia 175, 305–313. https://doi.org/10.1007/s00442-014-2897-7, 2014.

Bloor, J.M.G., Tardif, A., Pottier, J., 2020. Spatial heterogeneity of vegetation structure, plant N pools and soil N content in relation to grassland management[J]. Agronomy 10 (5), 716. https://doi.org/10.3390/agronomy10050716, 2020.

Bremner, J.M., Mulvaney, C.S., 1982. Nitrogen-JANSSON, SL 1958. Tracer studies on nitrogen total. Methods of Soil Analysis 2, 595–624. Part.

Buisson, E., Archibald, S., Fidelis, A., Fidelis, A., Suding, K.N., 2022. Ancient grasslands guide ambitious goals in grassland restoration[J]. Science 377 (6606), 594–598, 2022. https://doi.org/10.1126/science.abo4605.

Carboni, M., Livingstone, S.W., Isaac, M.E., Cadotte, M.W., 2021. Invasion drives plant diversity loss through competition and ecosystem modification[J]. J. Ecol. 109 (10), 3587–3601. https://doi.org/10.1111/1365-2745.13739, 2021.

Depauw, L., Hu, R., Dhungana, K.S., Govaert, S., Meeussen, C., Vangansbeke, P., Strimbeck, R., Graae, B.J., Frenne, P.D., 2022. Functional trait variation of Anemone nemorosa along macro-and microclimatic gradients close to the northern range edge [J]. Nord. J. Bot. 2022 (4), e03471 https://doi.org/10.1111/njb.03471, 2022.

Du, J., He, Z.B., Chen, L.F., Lin, P.F., Zhu, X., Tian, Q.Y., 2021. Impact of climate change on alpine plant community in Qilian Mountains of China. Int. J. Biometeorol. 65 (11), 1849–1858. https://doi.org/10.1007/s00484-021-02141-w.

Field, A., Miles, J., Field, Z., 2012. Discovering Statistics Using R. Sage publications, London.

Fox, J., Weisberg, S., 2019. An R Companion to Applied Regression, third ed. Sage, Thousand Oaks, CA.

Giese, M., Gao, Y.Z., Lin, S., Brueck, H., 2011. Nitrogen availability in a grazed semi-arid grassland is dominated by seasonal rainfall[J]. Plant Soil 340, 157–167. https://doi.org/10.1007/s11104-010-0509-9, 2011.

Grömping, U., 2006. Relative importance for linear regression in R: the package relaimpo. J. Stat. Software 17, 1–27, 2006.

Hartley, I.P., Hill, T.C., Chadburn, S.E., Hugelius, G., 2021. Temperature effects on carbon storage are controlled by soil stabilisation capacities. Nat. Commun. 12 (1), 1–7. https://doi.org/10.1038/s41467-021-27101-1.

He, M., Pan, Y.H., Zhou, G.Y., Barry, K.E., Fu, Y.L., Zhou, X.H., 2022. Grazing and global change factors differentially affect biodiversity-ecosystem functioning relationships in grassland ecosystems. Global Change Biol. 28 (18), 5492–5504. https://doi.org/10.1111/gcb.16305.

Herben, T., Šašek, J., Balšánková, T., Hadincová, V., Krahulec, F., Krak, K., Pecháčková, S., Skálová, H., 2022. The shape of root systems in a mountain meadow: plastic responses or species-specific architectural blueprints?[J]. New Phytol. 235 (6), 2223–2236. https://doi.org/10.1111/nph.18132, 2022.

Hou, F.J., Jia, Q.M., Lou, S.N., Yang, C.T., Ning, J., Li, L., Fan, Q.S., 2021. Grassland agriculture in China—a review. Front. Agr. Sci. Eng 8 (1), 35–44. https://doi.org/10.15302/J-FASE-2020378.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments [J]. Ecol. Monogr. 54 (2), 187–211. https://doi.org/10.2307/1942661, 1984.

Jäschke, Y., Heberling, G., Wesche, K., 2020. Environmental controls override grazing effects on plant functional traits in Tibetan rangelands[J]. Funct. Ecol. 34 (3), 747–760. https://doi.org/10.1111/1365-2435.13492, 2020.

Lai, J.S., Zou, Y., Zhang, J.L., Peres-Neto, P.R., 2022. Generalizing hierarchical and variation partitioning in multiple regression and canonical analyses using the rdacca. hp R package[J]. Methods Ecol. Evol. 13 (4), 782–788. https://doi.org/10.1111/2041-210X.13800, 2022.

Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91, 299–305. https://doi.org/10.1890/08-2244.1.

Liu, J.J., Liu, D.T., Xu, K., Gao, L.M., Ge, X.J., Burgess, K.S., Cadotte, M.W., 2018. Biodiversity explains maximum variation in productivity under experimental warming, nitrogen addition, and grazing in mountain grasslands[J]. Ecol. Evol. 8 (20), 10094–10112. https://doi.org/10.1002/ece3.4483, 2018.

Liu, C.L., Li, W.L., Xu, J., Wei, W., Xue, P.F., Yan, H.P., 2021. Response of soil nutrients and stoichiometry to grazing management in alpine grassland on the Qinghai-Tibet Plateau. Soil Tillage Res. 206, 104822 https://doi.org/10.1016/j.still.2020.104822.

Loke, P.F., Kotzé, E., Preez, C.C.D., Twigge, L., 2021. Cross-rangeland comparisons on soil carbon dynamics in the pedoderm of semi-arid and arid South African commercial farms[J]. Geoderma 381, 114689. https://doi.org/10.1016/j.geoderma.2020.114689, 2021.

Ma, Z.W., Zeng, Y.F., Wu, J., Zhou, Q.P., Hou, F.J., 2021. Plant litter influences the temporal stability of plant community biomass in an alpine meadow by altering the stability and asynchrony of plant functional groups. Funct. Ecol. 36 (1), 148–158. https://doi.org/10.1111/1365-2435.13935.

Miller, J.E.D., Li, D.J., LaForgia, M., Harrison, S., 2019. Functional diversity is a passenger but not driver of drought-related plant diversity losses in annual grasslands. J. Ecol. 107 (5), 2033–2039. https://doi.org/10.1111/1365-2745.13244.

Nelson, D.W., Sommer, L.E., 1983. Total carbon, organic carbon, and organic matter. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), Methods of Soil Analysis. American Society of Agronomy and Soil Science Society of American, Madison, pp. 1–129.

Oksanen, J.F., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2018. Community ecology package. R package version, 2, 5-2.

Olsen, S.R., Cole, C.V., Watanabe, F., Dean, L.A., 1954. Estimation of Available Phosphorus in Soils by Extraction with Sodium Bicarbonate, vol. 939. USDA Circular No., USA, p. 19.

Pauler, C.M., Isselstein, J., Suter, M., Berard, J., Braunbeck, T., Schneider, M.K., 2020. Choosy grazers: influence of plant traits on forage selection by three cattle breeds. Funct. 34 (5), 980–992. https://doi.org/10.1111/1365-2435.13542.

Quan, Q., He, N.P., Zhang, Z., Zhang, Y.H., Gao, Y., 2015. Nitrogen enrichment and grazing accelerate vegetation restoration in degraded grassland patches. Ecol. Eng. 75, 172–177. https://doi.org/10.1016/j.ecoleng.2014.11.053.

Quéré, C.L., Mayot, N., 2022. Climate change and biospheric output[J]. Science 375 (6585), 1091–1092, 2022. https://www.science.org/doi/10.1126/science.abo1262.

Ren, J.Z., Hu, Z.Z., Zhao, J., Zhang, D.G., Hou, F.J., Lin, H.L., Mu, X.D., 2008. A grassland classification system and its application in China. Rangel. J. 30 (2), 199. https://doi.org/10.1071/RJ08002.

Sitters, J., Beest, M.T., Cherif, M., Giesler, R., Olofsson, J., 2017. Interactive effects between reindeer and habitat fertility drive soil nutrient availabilities in arctic tundra[J]. Ecosystems 20, 1266–1277. https://doi.org/10.1007/s10021-017-0108-1, 2017.

Sun, J., Wang, X.D., Cheng, G.W., Wu, J.B., Hong, J.T., Niu, S.L., 2014. Effects of grazing regimes on plant traits and soil nutrients in an alpine steppe, Northern Tibetan Plateau[J]. PLoS One 9 (9), e108821. https://doi.org/10.1371/journal.pone.0108821, 2014.

Tenenhaus, M., Vinzi, V.E., Chatelin, Y.M., Lauro, C., 2005. PLS path modeling[J]. Comput. Stat. Data Anal. 48 (1), 159–205. https://doi.org/10.1016/j.csda.2004.03.005, 2005.

Tian, L., Bai, Y.F., Wang, W.W., Qu, G.P., Deng, Z.H., Li, R.C., Zhao, J.X., 2021. Warm- and cold-season grazing affect plant diversity and soil carbon and nitrogen sequestration differently in Tibetan alpine swamp meadows. Plant Soil 458 (1), 151–164. https://doi.org/10.1007/s11104-020-04573-6.

Wang, S.X., Wang, X.A., Guo, H., Fan, W.Y., Lv, H.Y., Duan, R.Y., 2013. Distinguishing the importance between habitat specialization and dispersal limitation on species turnover[J]. Ecol. Evol. 3 (10), 3545–3553. https://doi.org/10.1002/ece3.745, 2013.

Wang, L., Jing, Y.Y., Xu, C.L., Yu, X.J., 2022. Effect of Grazing Treatments on Phenotypic and Reproductive Plasticity of Kobresia humilis in Alpine Meadows of the Qinghai-Tibet Plateau[J]. Front. Environ. Sci. 10. https://doi.org/10.3389/fenvs.2022.903763, 2022.

Wang, Y.F., Du, J.Q., Pang, Z., Liu, Y.L., Xue, K., Hautier, Y., Zhang, B., Tang, L., Jiang, L. L., Ji, B.M., Xu, X.L., Zhang, J., Hu, R.H., Zhou, S.T., Wang, F., Che, R.X., Wang, D., Zhou, C.T., Cui, X.Y., Eisenhauer, N., Hao, Y.B., 2022. Unimodal productivity–biodiversity relationship along the gradient of multidimensional resources across Chinese grasslands. Natl. Sci. Rev. 9, nwac165. https://doi.org/10.1093/nsr/nwac165.

Wei, D., Zhao, H., Zhang, J.X., Qi, Y.H., Wang, X.D., 2020. Human activities alter response of alpine grasslands on Tibetan Plateau to climate change[J]. J. Environ. Manag., 110335 https://doi.org/10.1016/j.jenvman.2020.110335, 2020, 262.

Wen, Z.H., White, P.J., Shen, J.B., Lambers, H., 2021. Linking root exudation to belowground economic traits for resource acquisition. New Phytol. 233 (4), 1620–1635. https://doi.org/10.1111/nph.17854.

Wu, G.L., Wang, D., Liu, Y., Ding, L.M., Liu, Z.H., 2016. Warm-season Grazing Benefits Species Diversity Conservation and Topsoil Nutrient Sequestration in Alpine Meadow. Land Degrad. Dev. 28 (4), 1311–1319. https://doi.org/10.1002/ldr.2536.

Xiang, M.X., Wu, J.X., Wu, J.J., Guo, Y.J., Lha, D., Pan, Y., Zhang, X.Z., 2021. Heavy grazing altered the biodiversity–productivity relationship of alpine grasslands in Lhasa River Valley, Tibet. Frontiers in Ecology and Evolution 455. https://doi.org/10.3389/fevo.2021.698707.

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.

Zhang, Y.W., Peng, Z.C., Chang, S.H., Wang, Z.F., Li, D.C., An, Y.F., Hou, F.J., Ren, J.Z., 2022. Growing season grazing promotes the shallow stratification of soil nutrients while non-growing season grazing sequesters the deep soil nutrients in a typical alpine meadow. Geoderma 426, 116111. https://doi.org/10.1016/j.geoderma.2022.116111.

Zhu, J.T., Zhang, Y.J., Yang, X., Chen, N., Li, S.P., Wang, P.D., Jiang, L., 2020. Warming alters plant phylogenetic and functional community structure. J. Ecol. 108 (6), 2406–2415. https://doi.org/10.1111/1365-2745.13448.