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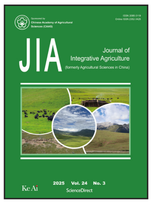

RESEARCH ARTICLE

Yak and Tibetan sheep mixed grazing enhances plant functional diversity in alpine grassland

Yuzhen Liu[1, 2, 3], **Xinquan Zhao**[4], **Xiaoxia Yang**[1, 2, 3], **Wenting Liu**[1, 2, 3], **Bin Feng**[1, 2, 3], **Shengnan Sun**[2], **Quanmin Dong**[1, 2, 3, 4#]

[1] *Academy of Animal Science and Veterinary Medicine, Qinghai University, Xining 810016, China*
[2] *Key Laboratory of Alpine Grassland Ecosystem in the Three-River-Source (Qinghai University), Ministry of Education, Xining 810016, China*
[3] *Qinghai Provincial Key Laboratory of Adaptive Management on Alpine Grassland, Qinghai University, Xining 810016, China*
[4] *State Key Laboratory of Plateau Ecology and Agriculture, Qinghai University, Xining 810016, China*

Highlights

- Mixed grazing at a 1:2 ratio enhances plant functional diversity.
- Grazing at moderate intensity increases species richness and β-diversity.
- Soil nitrogen, potassium, and bulk density drive functional diversity.

Abstract

The response of plant functional diversity to external disturbances not only effectively predicts changes in the ecosystem but it also reflects how plant communities use external environmental resources. However, research on how different herbivore assemblages affect plant functional diversity is limited. Therefore, this study systematically explored the effects of three typical herbivore assemblages (yak grazing, Tibetan sheep grazing, and mixed grazing by yaks and Tibetan sheep) on species richness, plant functional diversity, and soil physicochemical properties in alpine grasslands on the Qinghai-Tibet Plateau, China. This study further investigated the primary mechanisms driving the changes in plant functional diversity. The results indicate four key aspects of this system: (1) Grazing significantly enhanced plant functional diversity, particularly when the mixed grazing by yaks and Tibetan sheep was applied at a ratio of 1:2. This ratio showed the most substantial improvement in the functional dispersion index and Rao's quadratic entropy index. (2) Compared to enclosed treatments, grazing increased species richness and β-diversity, contributing to higher plant functional diversity. (3) Grazing treatments affected various plant traits, such as reducing plant community height and leaf thickness while increasing specific leaf area. However, the impact on plant functional diversity was most pronounced under the mixed grazing by yaks and Tibetan sheep at a ratio of 1:2. (4) Species α-diversity was positively correlated with plant functional diversity. Changes in plant functional diversity were primarily regulated by variations in soil physicochemical properties. Specifically, increases in soil available

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Yuzhen Liu, Mobile: +86-18709460225, E-mail: liuyzqhu@163.com; #Correspondence Quanmin Dong, Mobile: +86-13897473651, E-mail: qmdong@qhu.edu.cn

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nitrogen significantly promoted changes in plant functional diversity, while increases in soil available potassium and bulk density had a significant inhibitory effect on these changes. Long-term grazing significantly reduced the height of plant communities in alpine meadows, while a balanced mixture of yak and Tibetan sheep grazing, especially at a ratio of 1:2, enhanced plant functional diversity the most. This suggests that, under these conditions, the use of external environmental resources by the plant community is optimized.

Keywords: alpine grassland, adaptive management, herbivore assemblages, species diversity, functional diversity

1. Introduction

Species diversity and plant functional diversity within plant communities are vital components of ecosystems (Kuebbing *et al.* 2018). Species diversity reflects the abundance of biological resources, while plant functional diversity indicates the plants' adaptability to environmental changes and their ecological roles (Polley *et al.* 2020; Caram *et al.* 2023). Together, they shape the structural makeup of the plant communities. Species diversity provides the foundation for plant functional diversity by introducing various functional traits into the community (Suárez-Castro *et al.* 2022). Conversely, plant functional diversity influences species diversity through the distinct competitive advantages and survival strategies offered by different functional traits (Hu *et al.* 2014). However, previous studies have mainly focused on species diversity in ecosystems, while often overlooking plant functional diversity (Liu *et al.* 2016; Sanaei *et al.* 2023; Wang *et al.* 2024). Plant functional diversity exhibits stronger responses to external disturbances than species diversity (Mahaut *et al.* 2020). This difference underscores the limitations of assessing biodiversity's effects on ecosystem functions solely through species diversity, as this approach does not fully account for the impact of plant functional diversity on ecosystem resilience and functioning. Therefore, understanding how both species diversity and plant functional diversity are regulated under external disturbances is crucial for improving ecosystem management.

Grazing is the most common utilization practice in the alpine grasslands of the Qinghai-Tibet Plateau, and one of the main external disturbances to the ecosystem (Asner *et al.* 2004). In recent years, factors such as overgrazing and climate change have significantly degraded these grasslands (Chen *et al.* 2013; Dong *et al.* 2022). To mitigate this degradation, local governments have implemented contracting policies related to grassland responsibility, which involve allocating fenced-off areas to local herdsmen to prevent overgrazing (Sun *et al.* 2021). However, the implementation of these policies has also introduced new issues. Before their implementation, the alpine grasslands of the Qinghai-Tibet Plateau were subject to long-term mixed grazing by yaks and Tibetan sheep. After implementation, the presence of fences has led to the emergence of three different herbivore assemblages in what was once uniform grasslands: separate grazing by yaks, separate grazing by Tibetan sheep, and mixed grazing by both species.

Livestock grazing mainly affects grassland ecosystems through feeding, trampling, and the return of excrement (Liu Y *et al.* 2024). Due to the physiological differences among grazing livestock, different herbivore assemblages inevitably have different impacts on the grassland ecosystem, leading to the fragmented utilization of alpine grasslands, which is detrimental to their sustainable use (Liu Y *et al.* 2023). For example, grazing activities promote the miniaturization of plants, which significantly affects plant functional traits (Wang Z *et al.* 2021). However, due to the selective feeding characteristics of grazing livestock, yaks generally prefer to graze on Cyperaceae plants, so yak grazing has a more significant impact on the functional traits of Cyperaceae plants. In contrast, Tibetan sheep prefer to graze on Poaceae and forbs, so Tibetan sheep grazing significantly affects the functional traits of those plants (Feng *et al.* 2024). When both species graze together, the impact on plant functional traits varies with different assemblages, although the impacts of specific assemblages remain unknown. In addition, the selective feeding characteristics of grazing livestock can reduce the abundance of preferred forage species (Wang *et al.* 2011). Furthermore, yaks and Tibetan sheep have different activity frequencies, activity ranges, and excrement characteristics, which cause differences in soil physicochemical properties under different herbivore assemblages (Wang *et al.* 2018). Changes in these properties promote changes in plant community composition, thereby affecting the functional trait diversity of plant species. Since the selective feeding, trampling, and excrement return activities of grazing livestock under different grazing practices are closely related to plant functional traits (Cingolain *et al.* 2005), considering changes in functional diversity when determining which grazing practices are most beneficial for the sustainable use of alpine grasslands is an effective approach.

Currently, most studies focus on the impacts of grazing intensity, nitrogen deposition, warming, and other factors on the plant functional diversity of alpine grassland plants (Komac *et al.* 2015; Zhang *et al.* 2021; Schuchardt *et al.* 2023). However, the research on how different herbivore assemblages affect plant functional diversity in alpine grassland is limited. Therefore, understanding the changes in plant functional diversity under different herbivore assemblages and their primary drivers is crucial for the sustainable use of alpine grasslands.

In this study, we hypothesize that: (1) mixed grazing by yaks and Tibetan sheep has more pronounced effects on plant species diversity and functional diversity in alpine grasslands compared to single-species grazing; and (2) mixed grazing by yaks and Tibetan sheep regulates changes in plant functional diversity by influencing plant species diversity and soil physicochemical properties. To verify these hypotheses, we conducted a grazing experiment with three different herbivore assemblages — yak grazing, Tibetan sheep grazing, and mixed grazing by yaks and Tibetan sheep in various proportions — under moderate grazing intensity in alpine grasslands on the Qinghai-Tibet Plateau. We systematically investigated and analyzed the changes in plant species diversity, plant functional diversity, and soil physicochemical properties under the different herbivore assemblages, aiming to provide insights for the sustainable use of alpine grasslands.

2. Materials and methods

2.1. Study site

The study area is located within Haiyan County, Qinghai Province, China, specifically on the Qinghai University Alpine Grassland-Livestock Adaptive Management Technology Platform at 36°56´N latitude and 100°53´E longitude, with an elevation of 3,038 m. This site is characterized by a cold and humid climate. The average annual temperature is 1.4°C, with seasonal fluctuations ranging from –24.8°C in winter to 12.5°C in summer, indicating the lack of a year-round frost-free period. Precipitation is concentrated mainly from June to September, with an average annual rainfall of 425 mm. The soil is categorized as Gelic Cambisol with an average thickness of 0.65 m (Liu Y *et al.* 2024). The dominant plant species in the alpine grassland comprise *Stipa sareptana*, *Kobresia humilis*, *Leymus secalinus*, *Carex aridula*, *Potentilla acaulis*, *Astragalus laxmannii* Jacq., and *Dracocephalum heterophyllum*.

2.2. Experimental design

In 2014, the experiment was conducted on alpine grassland with flat terrain, consistent environmental conditions, and a similar grazing history, based on moderate grazing intensity of 3.86 sheep units per ha. The effects of various herbivore assemblages on alpine grassland ecosystems were examined, including yak grazing (YG, 2,600 m^2), Tibetan sheep grazing (SG, 1,700 m^2), and mixed grazing by yaks and Tibetan sheep at ratios of 1:2 (MG 1:2, 4,300 m^2), 1:4 (MG 1:4, 6,000 m^2), and 1:6 (MG 1:6, 7,700 m^2). The control group was established within a fenced enclosure without any grazing (NG, 500 m^2), with each experimental treatment replicated three times. Table 1 presents detailed information on the experimental design. Prior to the start of the grazing experiment, grass production in the alpine meadows was assessed and the consumption rates of both yak and Tibetan sheep were determined to ensure a uniformly moderate grazing intensity across all experimental conditions. Grazing plot areas were adjusted based on the ratios of mixed yak and Tibetan sheep grazing. Moreover, grazing days were dynamically adjusted to sustain moderate grazing intensity throughout the grazing period, to account for the conditions in actual practice. Livestock were provided with sufficient drinking water during grazing, but no supplementary feed was given. Local herders provided the livestock for the experiment, which included 1.5-year-old male yaks weighing 100±5 kg and 1-year-old male Tibetan sheep weighing 30±2 kg, to minimize experimental errors.

2.3. Plant and soil sample collection

In October 2019, cages were installed in each treatment to prevent grazing by yaks and Tibetan sheep and

Table 1 Grazing experiment design

Treatment[1)]	Number of yaks	Number of Tibetan sheep	Area of plot (m^2)	Grazing intensity sheep units (no. ha^{-1})	Number of plots
YG	1	0	2.6×10^3	3.86	3
SG	0	2	1.7×10^3	3.86	3
MG 1:2	1	2	4.3×10^3	3.86	3
MG 1:4	1	4	6.0×10^3	3.86	3
MG 1:6	1	6	7.7×10^3	3.86	3
NG	0	0	0.5×10^3	3.86	3

[1)] YG, yak grazing; SG, Tibetan sheep grazing; MG 1:2, mixed grazing of yaks and Tibetan sheep at a ratio of 1:2; MG 1:4, mixed grazing of yaks and Tibetan sheep at a ratio of 1:4; MG 1:6, mixed grazing of yaks and Tibetan sheep at a ratio of 1:6; NG, grazing exclusion.

mitigate measurement errors. Within each plot, three 1 m×1 m×1 m cages were arranged diagonally, spaced more than 5 m apart. Nine cages were established per treatment, resulting in a total of 54 cages across all treatments. Vegetation surveys commenced in mid-August 2020. Quadrats measuring 50 cm×50 cm were placed at the center of each cage for the vegetation surveys. We recorded the frequency, cover, and height (averaged for 10 individuals of each species; for species with fewer than 10 individuals, all were measured), as well as the aboveground biomass of each species (harvested, oven-dried at 105°C to constant weight, and weighed using an analytical balance with a precision of 0.0001 g). Plant functional trait samples were then collected from the remaining area within the cages (Fig. 1). After collecting the plant samples, soil samples were taken from the 0–10, 10–20, and 20–30 cm soil layers within the clipped quadrats using a 100 cm^3 ring knife. These samples were used to determine soil bulk density (BD) and soil moisture (SM) content. Subsequently, soil samples from the same soil layers were collected using a 3.5 cm diameter soil auger, with three auger samples combined into one sample per quadrat. The collected soil samples were divided into two parts. One part was promptly transported to the laboratory and stored at –4°C to determine soil available nitrogen (AN), while the other part was air-dried, cleaned of excess impurities, and sieved to determine soil total nitrogen (TN), total phosphorus (TP), total organic carbon (TOC), available phosphorus (AP), available potassium (AK), and soil pH.

2.4. Measurement of plant functional traits

In this study, seven dominant species from alpine meadows were selected for functional trait measurements. The species were *S. sareptana*, *K. humilis*, *L. secalinus*, *C. aridula*, *P. acaulis*, *A. laxmannii* Jacq., and *D. heterophyllum*. The primary traits measured were plant height (PH), individual plant weight (PW), specific leaf area (SLA), leaf thickness (LT), leaf dry matter content (LDMC), and the leaf carbon (LC), nitrogen (LN), and phosphorus (LP) contents. To measure plant height, 15 individuals of each species in the sampling area were selected and their natural heights were recorded, using the average value as the original data. The fresh weight of the leaves was then measured and a leaf area scanner (LI-3000C, Li-Cor, Lincoln, NE, USA) was used to determine leaf area. Leaf dry weight and individual plant weight were measured by drying the samples in an oven at 105°C to a constant weight. Specific leaf area was calculated as the ratio of leaf area to leaf dry weight. Leaf thickness was measured using a micrometer. Finally, the remaining leaves were dried to a constant weight to determine leaf moisture content, and then ground for the analysis of leaf carbon, nitrogen, and phosphorus contents using an atomic absorption spectrometer (Ren *et al.* 2018).

2.5. Measurement of soil physicochemical properties

SM was determined using the gravimetric method; BD was assessed through the ring knife method; TOC and TN were determined using an elemental analyzer (Element, Hanau, Germany); TP was assessed using the $HClO_4$-H_2SO_4 method (Wang J *et al.* 2021); AN was determined through a continuous-flow auto-analyzer (Alpkem, OI Analytical, USA); AP was determined using the sodium carbonate leaching-molybdenum-antimony anticolorimetric method; AK was determined through the ammonium acetate extraction-flame photometric method (Feng *et al.* 2024); and soil pH was measured using a pH meter (Metrohm 827, Herisau, Switzerland).

2.6. Data analysis

Calculation of species diversity The species diversity

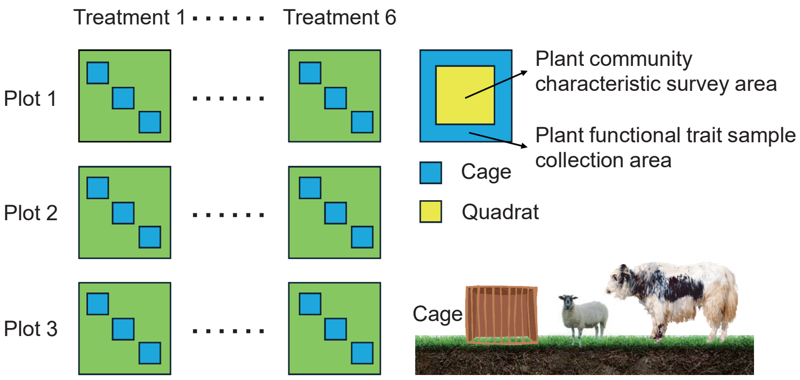

Fig. 1 Schematic diagram of sample collection.

calculation was performed using the "vegan" package. Five diversity indices: species richness (*R*), Shannon-Wiener index (*H*), Simpson index (*D*), Pielou index (*J*), and β-diversity, were calculated using the following formulas:

$$R=S \tag{1}$$

$$H=-\sum_{i=1}^{S}P_i\ln P_i \tag{2}$$

$$D=1-\sum_{i=1}^{S}P_i^2 \tag{3}$$

$$J=H/\ln S \tag{4}$$

$$\beta\text{-diversity}=\frac{j}{a+b-j} \tag{5}$$

where *S* represents the frequency of species occurrence within a plot; P_i denotes the proportion of individuals belonging to species *i* relative to the total number of individuals; β-diversity was quantified using the Jaccard index, where *a* and *b* represent the species counts in communities A and B respectively, and *j* represents the number of species shared by both communities (Liu *et al.* 2015; Ohara and Ushimaru 2015).

Calculation of functional diversity The functional diversity calculation was based on the "FD" package. The formula for calculating the functional richness index (*FRic*) is:

$$FRic=\frac{SFic}{Rc} \tag{6}$$

where *SFic* represents the niche occupied by the species in the community, and *Rc* represents the absolute value of the magnitude of trait *c* in the community.

The formulas for calculating functional evenness index (*FEve*) are:

$$FEve=\frac{\sum_{l=1}^{S-1}\left(PEW_l\frac{1}{S-1}\right)-\left(\frac{1}{S-1}\right)}{1-\frac{1}{S-1}} \tag{7}$$

$$PEW_l=\frac{EW_l}{\sum_{l-1}^{S-1}EW_l} \tag{8}$$

$$EW_l=\frac{d_{xy}}{P_x+P_y} \tag{9}$$

where *l* represents the index of the functional axes in the multidimensional functional space; *l* ranges from 1 to S−1; *S* is the total number of functional traits or dimensions considered; PEW_l represents the local weighted average evenness; EW_l represents the weighted average evenness; and P_x and P_y represent the relative densities of species *x* and species *y* in the plant community.

The formulas for calculating functional dispersion index (*FDis*) are:

$$FDis=\frac{\sum P_yZ_y}{\sum P_y} \tag{10}$$

$$C=[C_x]=\frac{\sum P_ym_{xk}}{\sum P_y} \tag{11}$$

where *C* represents the weighted centroid, P_y represents the relative density of species *y* in the plant community, Z_y denotes the weighted distance between species *y* and the weighted centroid, and m_{xk} represents the *k* th trait value of species *x*.

The formula for calculating the Rao's quadratic entropy index (*RaoQ*) is:

$$RaoQ=\sum_{i=1}^{S}\sum_{j=1}^{S}d_{ij}p_ip_j \tag{12}$$

where d_{ij} represents the functional trait distance between species *i* and species *j*, and p_i denotes the proportion of individuals of species *i* relative to the total population size.

The formula for calculating the community-weighted mean (*CWM*) is:

$$CWM=\sum P_i\times trait_i \tag{13}$$

where P_i represents the relative contribution rate of species *i*, and $trait_i$ represents the trait value of species *i*.

Calculation of effect size To compare the changes in species diversity, plant functional diversity, and soil physicochemical properties under various treatments compared to the control, we quantified the effects of grazing treatments using response ratios. The formula for calculating the response ratio (*R*) is:

$$R=ln(T/C) \tag{14}$$

Additionally, we quantified the impacts of grazing treatments on species diversity, plant functional diversity, and soil physicochemical properties compared to the enclosure using the percentage change (*PC*). The calculation formula is:

$$PC\ (\%)=(e_R-1)\times100 \tag{15}$$

In the formula, *T* denotes the observed values of diversity, functional diversity, and soil physicochemical properties under grazing treatment, whereas *C* denotes the observed values under control conditions. *e* is the base of natural logarithms. A positive response ratio signifies an increase in the respective indicator's magnitude due to the treatment, while a negative response ratio indicates a reduction in the indicator's magnitude resulting from the treatment (Wei *et al.* 2023; Liu Y *et al.* 2024).

Selection of key variables and formulation of structural equation models Pearson correlation analyses were initially conducted on the species diversity and plant functional diversity indices using the "ggcor" package. Subsequently, principal component analysis (PCA) was employed to reduce the dimensions of these indices, and information from the first axis was retained for selecting essential soil physicochemical property indicators (Liu Y *et al.* 2023). PCA was executed using the "FactoMineR" package. The important physicochemical indicators affecting changes in plant species diversity and plant functional diversity were selected based on hierarchical partitioning using the "glmm.hp" package (Lai *et al.* 2022, 2023). Utilizing these results, the "PiecewiseSEM" package was employed to construct a composite variable structural equation model, aiming to further elucidate the primary mechanisms governing changes in plant functional diversity due to grazing activities. A model was deemed to pass the test if $P>0.05$ in the structural equation model. Lower values of Akaike information criterion (AIC) and Fisher's *C* indicate greater model interpretability (Lefcheck 2016).

3. Results

3.1. Effects of herbivore assemblages on changes in the soil physicochemical properties in alpine grasslands

Grazing activities predominantly impacted the topsoil in terms of soil physicochemical properties, most notably the available nutrients (Fig. 2; Appendices A and B). In the topsoil (0–10 cm), TN significantly increased compared to the enclosure treatment in all grazing treatments except MG 1:2 and MG 1:6. Specifically, YG, SG, and MG 1:4 showed increases of 12.36, 18.67 and 16.81%, respectively. Similarly, TP significantly increased compared to the enclosure treatment in all grazing treatments except MG 1:2, with increases in YG, SG, MG 1:4, and MG 1:6 of 5.87, 9.33, 5.35 and 10.45%, respectively. No significant effects on TOC or pH compared to the enclosure treatment were observed for any of the grazing treatments. However, all grazing treatments significantly increased AN, AP and BD while reducing AK. Additionally, SM increased significantly in treatments YG, SG, and MG 1:6 by 25.33, 7.71 and 27.20%, respectively (Fig. 2; Appendix C).

3.2. Effects of herbivore assemblages on changes in the species diversity in alpine grasslands

Compared to the enclosure treatment, all grazing treatments except MG 1:6 significantly increased species

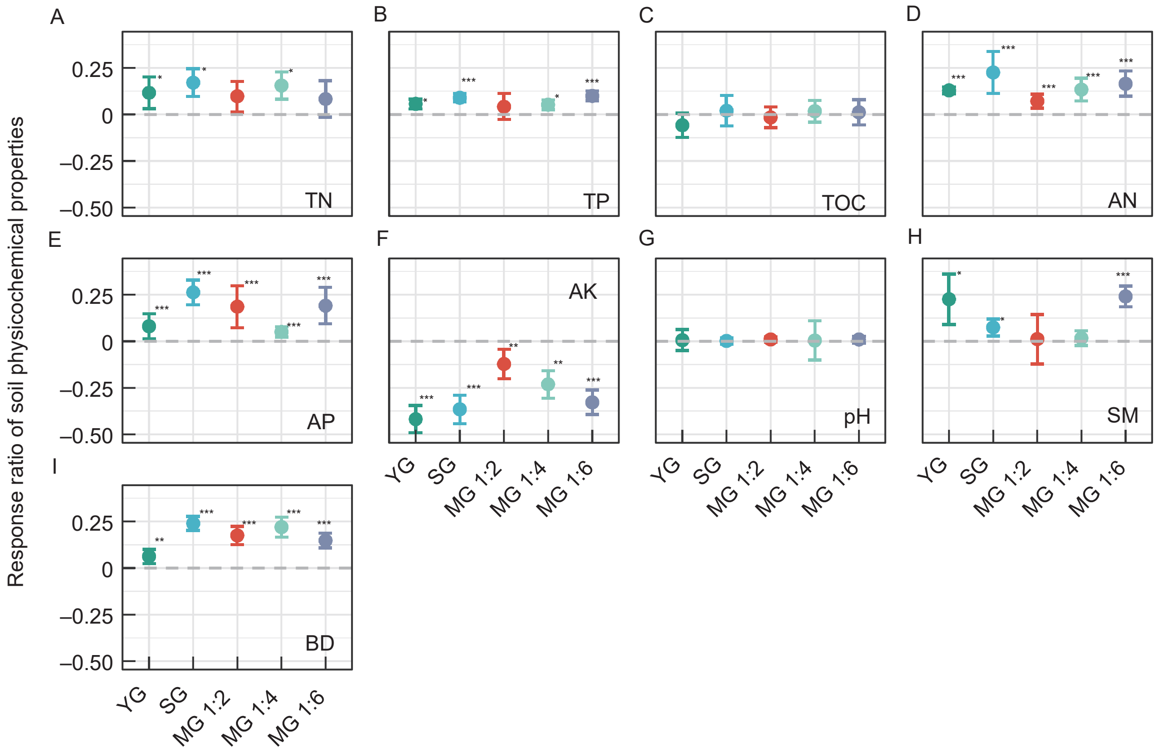

Fig. 2 Changes in soil physicochemical properties in the 0–10 cm soil layer under different herbivore assemblages. A, total nitrogen (TN). B, total phosphorus (TP). C, total organic carbon (TOC). D, available nitrogen (AN). E, available phosphorus (AP). F, available potassium (AK). G, soil pH (pH). H, soil moisture content (SM). I, soil bulk density (BD). YG, yak grazing; SG, Tibetan sheep grazing; MG 1:2, mixed grazing of yaks and Tibetan sheep at a ratio of 1:2; MG 1:4, mixed grazing of yaks and Tibetan sheep at a ratio of 1:4; MG 1:6, mixed grazing of yaks and Tibetan sheep at a ratio of 1:6; NG, grazing exclusion. *, $0.01<P<0.05$; **, $0.001<P<0.01$; ***, $P<0.001$. Values indicate the means with 95% confidence intervals. When the values intersect with 0, the treatment is considered to have no significant effect on the indicator compared to the control. When the values are greater than 0, the treatment is considered to have a significant positive effect on the indicator compared to the control, and *vice versa*. The horizontal dashed lines are zero lines.

richness and β-diversity. Specifically, the species richness increased by 16.96, 17.86, 22.32 and 14.29% under the YG, SG, MG 1:2, and MG 1:4 treatments, respectively, while β-diversity increased by 29.9, 12.41, 33.68 and 15.7%, respectively. In contrast, the MG 1:6 treatment notably reduced both the Shannon-Wiener index and the Pielou index by 16.27 and 20.66%, respectively. Additionally, none of the grazing treatments significantly affected the Simpson index (Fig. 3; Appendix D).

3.3. Effects of herbivore assemblages on changes in the plant functional diversity in alpine grasslands

Compared to the enclosure treatment, the YG, SG, MG1:2, MG1:4, and MG1:6 treatments significantly reduced CWM_{PH} by 35.77, 33.8, 43.97, 44.16 and 39.91%, and CWM_{LT} by 18.33, 16.72, 21.08, 18.69 and 20.10%, respectively. However, they also significantly increased CWM_{SLA} by 28.61, 22.55, 20.43, 21.81 and 19.11%, respectively. Moreover, CWM_{PW} increased notably only in the YG (23.01%) treatment, while CWM_{LDMC} decreased in both the YG (10.15%) and SG (10.40%) treatments but increased in the MG1:2 (10.31%) treatment. The grazing treatments had no significant effect on CWM_{LC}. The CWM_{LN} increased significantly only in the MG1:2 (7.91%) treatment, whereas CWM_{LP} decreased significantly only in the MG1:6 (10.77%) treatment. FRic increased significantly in all grazing treatments except for the YG treatment, while FEve remained unaffected. FDis and RaoQ displayed increasing trends solely in the MG1:2 treatment, increasing by 23.81 and 26.87%, respectively (Fig. 4; Appendix E).

3.4. Effects of soil factors on plant species diversity and functional diversity

Hierarchical partitioning analysis showed that AP, BD, AN, and SM were the primary physicochemical factors influencing species diversity changes, whereas AP, AK, AN, SM, and BD were the main factors driving changes in functional diversity (Fig. 5-A and B). Pearson correlation analysis revealed significant positive correlations between FDis and RaoQ with the Pielou, Simpson, and Shannon-Wiener indices. FEve exhibited significant positive correlations with the Pielou and Shannon-Wiener indices, while FRic displayed a significant positive correlation only with richness (Fig. 5-C).

3.5. Mechanisms of the effect of grazing regulation on functional diversity

The structural equation model analysis suggested that grazing activities exerted a primary influence on changes in species diversity and soil physicochemical properties, consequently indirectly impacting changes in functional

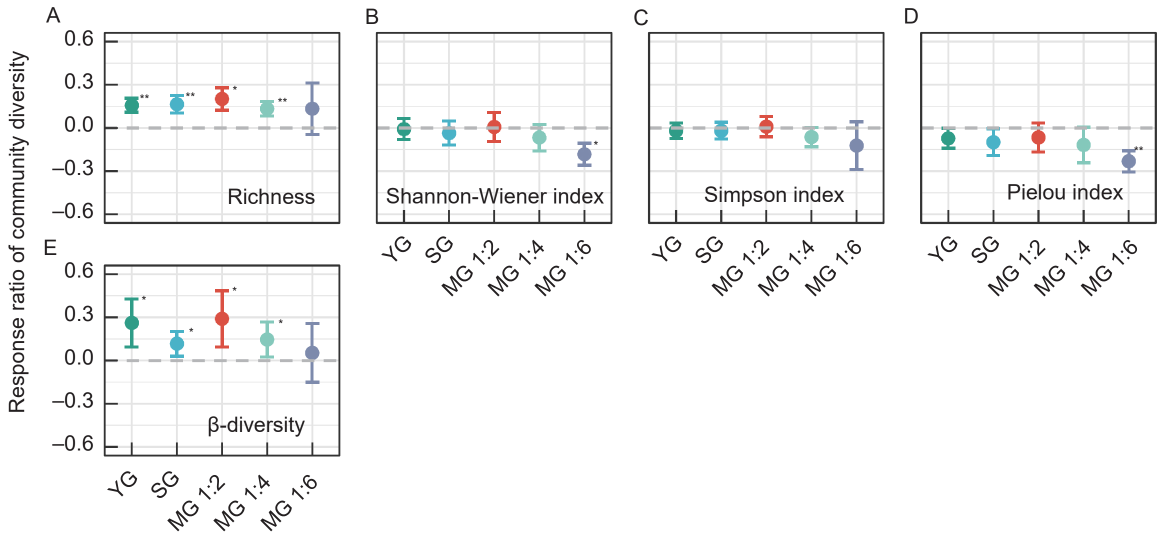

Fig. 3 Changes in species diversity under different herbivore assemblages. A, species richness. B, Shannon-Wiener index. C, Simpson index. D, Pielou index. E, β-diversity. YG, yak grazing; SG, Tibetan sheep grazing; MG 1:2, mixed grazing of yaks and Tibetan sheep at a ratio of 1:2; MG 1:4, mixed grazing of yaks and Tibetan sheep at a ratio of 1:4; MG 1:6, mixed grazing of yaks and Tibetan sheep at a ratio of 1:6; NG, grazing exclusion. *, $0.01<P<0.05$; **, $0.001<P<0.01$; ***, $P<0.001$. Values indicate the means with 95% confidence intervals. When the values intersect with 0, the treatment is considered to have no significant effect on the indicator compared to the control. When the values are greater than 0, the treatment is considered to have a significant positive effect on the indicator compared to the control, and *vice versa*. The horizontal dashed lines are zero lines.

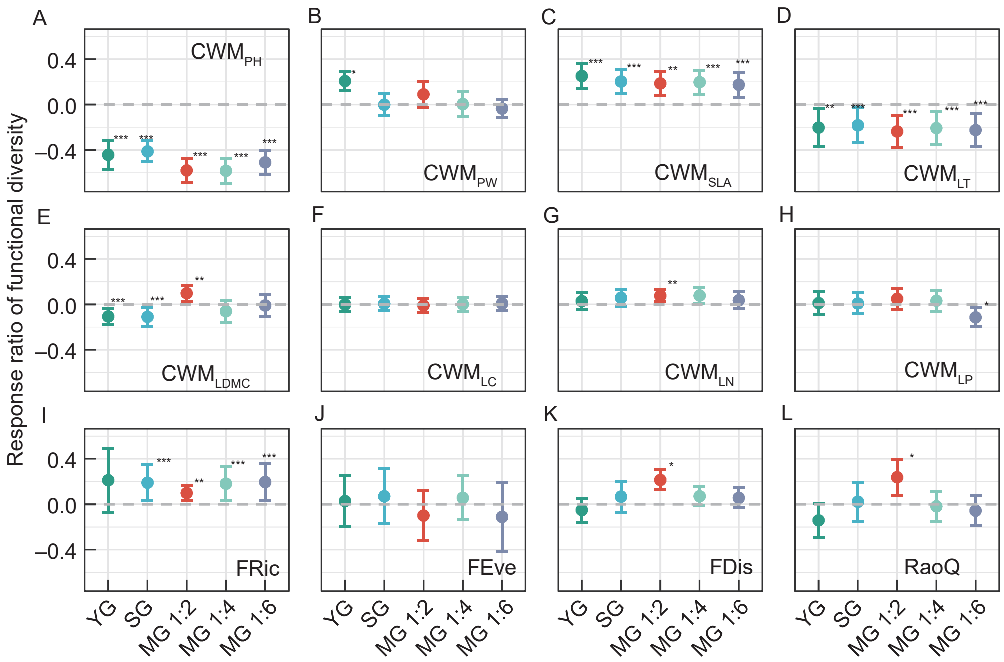

Fig. 4 Changes in functional diversity under different herbivore assemblages. A, plant height (CWM$_{PH}$). B, plant weight (CWM$_{PW}$). C, specific leaf area (CWM$_{SLA}$). D, leaf thickness (CWM$_{LT}$). E, leaf dry matter content (CWM$_{LDMC}$). F, leaf carbon content (CWM$_{LC}$). G, leaf nitrogen content (CWM$_{LN}$). H, leaf phosphorus content (CWM$_{LP}$). I, functional richness index (FRic). J, functional evenness index (FEve). K, functional dispersion index (FDis). L, Rao's quadratic entropy index (RaoQ). YG, yak grazing; SG, Tibetan sheep grazing; MG 1:2, mixed grazing of yaks and Tibetan sheep at a ratio of 1:2; MG 1:4, mixed grazing of yaks and Tibetan sheep at a ratio of 1:4; MG 1:6, mixed grazing of yaks and Tibetan sheep at a ratio of 1:6; NG, grazing exclusion. *, $0.01<P<0.05$; **, $0.001<P<0.01$; ***, $P<0.001$. Values indicate the means with 95% confidence intervals. When the values intersect with 0, the treatment is considered to have no significant effect on the indicator compared to the control. When the values are greater than 0, the treatment is considered to have a significant positive effect on the indicator compared to the control, and *vice versa*. The horizontal dashed lines are zero lines.

diversity. Grazing activities notably bolstered species diversity and soil physicochemical properties, thereby significantly amplifying functional diversity. Species richness and β-diversity served as the principal mediators for functional diversity changes *via* species diversity, while the soil physicochemical properties of AN, AK, and BD acted as the primary mediators (Fig. 6).

4. Discussion

4.1. Effects of herbivore assemblages on the soil physicochemical properties of alpine grassland

The physicochemical properties of soil are key ecological factors that regulate changes in vegetation diversity within alpine grassland ecosystems (Feng *et al.* 2024). During grazing, livestock affect these soil properties primarily through trampling and the return of excreta (Zhang *et al.* 2022). In this study, the key soil physicochemical factors driving changes in plant species diversity and plant functional diversity under different herbivore assemblages were AN, AP, AK, SM, and BD. These factors are closely related to the direct impacts of livestock on the grassland during grazing. Previous studies have indicated that Tibetan sheep exhibit higher grazing frequencies and larger ranges of activity, whereas yaks show the opposite behaviors (Pan *et al.* 2019). The variation in soil bulk density was significantly correlated with the trampling frequency of grazing livestock. When Tibetan sheep grazed, their higher trampling frequency led to the most noticeable increase in soil bulk density; while yaks, with their lower trampling frequency, caused the smallest increase in soil bulk density. When yaks and Tibetan sheep grazed together, their respective activity frequencies were notably reduced, resulting in a soil bulk density increase that fell between the levels observed when either yaks or Tibetan sheep grazed alone.

In terms of soil moisture content, grazing activities increased the soil moisture compared to enclosure treatments for two primary reasons. First, urine excreted by grazing livestock adds moisture to the alpine grasslands. Second, trampling by grazing livestock modifies the microtopography of the alpine grasslands, enhancing their water retention capacity. Changes in soil available

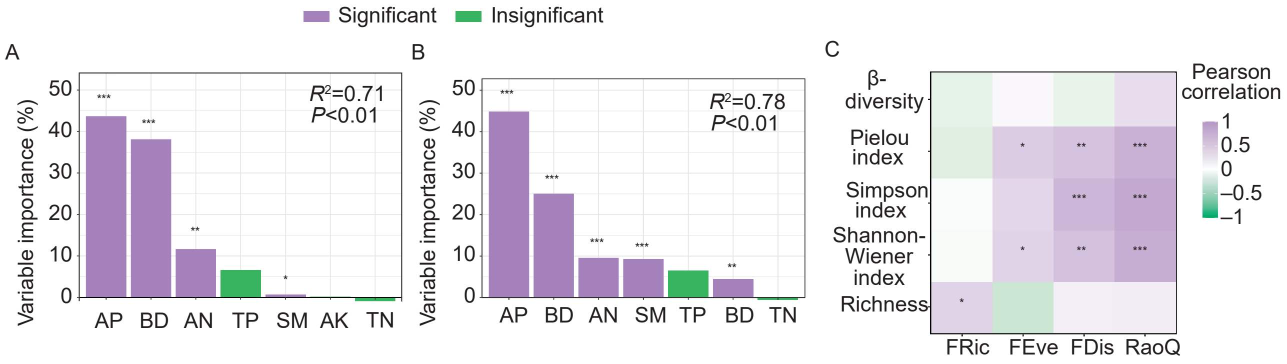

Fig. 5 The main physicochemical factors driving changes in plant species diversity (A) and plant functional diversity (B) under different herbivore assemblages, as well as changes in the correlation between species diversity and functional diversity (C). AP, available phosphorus; BD, bulk density; AN, available nitrogen; TP, total phosphorus; SM, soil moisture; AK, available potassium; TN, total nitrogen; FRic, functional richness index; FEve, functional evenness index; FDis, functional dispersion index; RaoQ, Rao's quadratic entropy index.

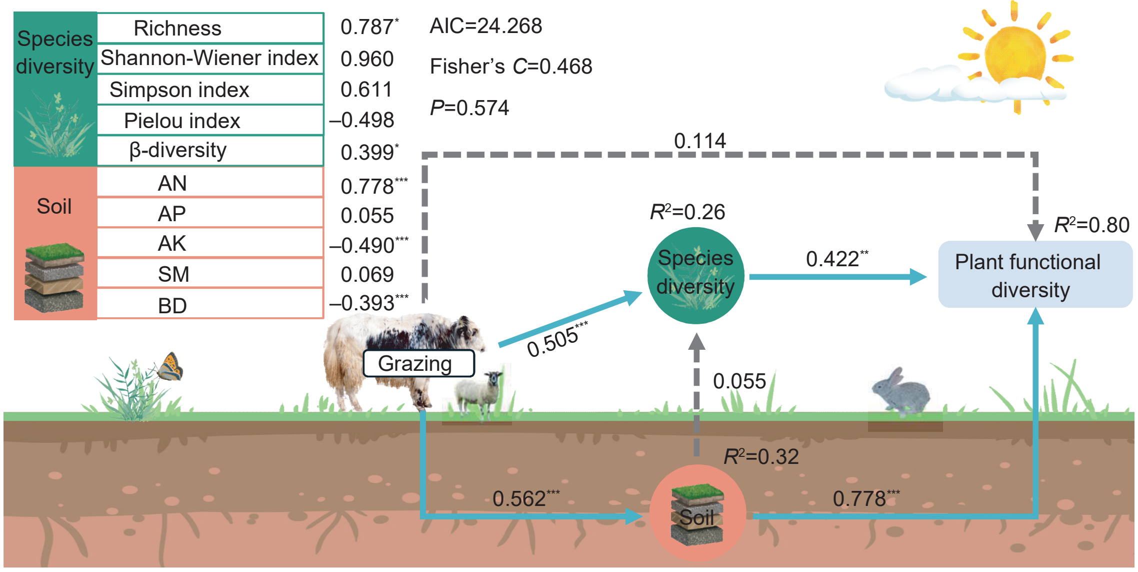

Fig. 6 The principal mechanism through which grazing activities influence plant functional diversity. AN, available nitrogen; AP, available phosphorus; AK, available potassium; SM, soil moisture; BD, bulk density. *, $0.01<P<0.05$; **, $0.001<P<0.01$; ***, $P<0.001$.

nitrogen are primarily driven by the return of excreta from grazing livestock. Tibetan sheep produce small, easily decomposable dung with a high nitrogen content, whereas yaks produce large, less decomposable dung with a low nitrogen content (Liu *et al.* 2016). Consequently, the increase in soil available nitrogen was greater during grazing by Tibetan sheep compared to yaks. When yaks and Tibetan sheep grazed together in a ratio of 1:2, the increase in available nitrogen was the lowest, indicating a significant suppression of their respective activity frequencies. However, as the proportion of Tibetan sheep in the mixed grazing assemblage increases, this suppression effect diminishes. Under natural conditions, soil available phosphorus primarily originates from mineralization and leaching processes (Liu J *et al.* 2024). Grazing livestock activities can reduce vegetation cover and disrupt biological soil crusts, enhancing mineralization and leaching. This leads to a significant increase in the soil available phosphorus content in grazed grasslands, with the pattern of its variation among the treatments in this study aligning with that of soil bulk density. Available potassium mainly comes from the release of soil parent material, and it is highly soluble and easily lost due to external disturbances (Whalen 2023). Consequently, grazing activities significantly reduced the available potassium content. However, mixed grazing notably suppresses the activity frequencies compared to yaks or Tibetan sheep alone. When yaks and Tibetan sheep grazed together in a ratio of 1:2, the reduction in available potassium was minimal. As the proportion of Tibetan sheep in the mixed grazing assemblages increased, this suppression effect gradually diminished, resulting in a greater reduction in the available potassium content.

4.2. Effects of herbivore assemblages on the species diversity of alpine grassland

This study found that grazing activities significantly increased species richness and β-diversity compared to enclosure measures, which can be primarily attributed to the selective foraging behaviors of grazing livestock. Enclosure measures effectively mitigated the disruptive impact of grazing livestock, promoting a more uniform growth environment for alpine grassland vegetation and leading to conditions of singular resource limitation. Within this altered environment, graminoid vegetation gradually gained a competitive advantage due to its efficient resource utilization, catalyzing a shift in vegetation community structure from heterogeneous assemblies to a dominant monotypic community of graminoid species (Lu *et al.* 2021). This shift largely accounts for the declines in species richness and β-diversity observed under enclosure conditions. Moderate grazing intensities led to noticeable differentiation and trade-offs among vegetation life forms and reproductive strategies, with different herbivore assemblages selectively foraging and depositing excreta. According to the resource ratio/heterogeneity hypothesis posited by Tilman (1982), the coexistence of multiple limiting resource ratios in heterogeneous environments promotes niche diversification, thereby enhancing species richness and β-diversity. In this study, as the proportion of Tibetan sheep in mixed grazing scenarios increased, the enhancements of species richness and β-diversity due to grazing activity progressively diminished, eventually disappearing entirely at a yak to Tibetan sheep ratio of 1:6. This phenomenon is primarily attributable to the differing feeding preferences of these two types of grazing livestock. Yaks prefer bulk consumption, favoring the abundant Cyperaceae vegetation, while Tibetan sheep prioritize nutrient-rich forage, preferring Poaceae species with elevated nitrogen contents (Pan *et al.* 2019). In mixed grazing scenarios with a low proportion of Tibetan sheep, the livestock effectively meet their nutritional requirements through selective feeding. However, as the proportion of Tibetan sheep increases, the livestock frequently shift forage, incurring higher feeding costs and reducing their inclination towards selective feeding (Wang *et al.* 2010a, b). This explains why grazing activity failed to increase species richness in the MG 1:6 treatment.

4.3. Effects of herbivore assemblages on the plant functional diversity of alpine grassland

The adjustments in community functional traits denote the adaptability of vegetation communities to environmental changes (Fan *et al.* 2023; Liu Z *et al.* 2023). This study found that all grazing treatments significantly reduced CWM_{PH} and CWM_{LT}, but significantly increased CWM_{SLA}. Grazing activities typically stunt plant growth and reduce leaf thickness, primarily due to prolonged livestock grazing. Livestock prefer taller plants for grazing (Dumont *et al.* 2007), leading to their gradual shortening, while frequent trampling by livestock provides a competitive advantage to shorter plants (Hempson *et al.* 2015). The significant increase in CWM_{SLA} indicates that moderate grazing intensity, regardless of herbivore assemblages, drives vegetation communities to shift towards species with faster growth rates and better resource acquisition abilities, reflecting the strong adaptability of the alpine grassland plant communities. Yak grazing significantly increased CWM_{PW}, primarily because yaks feed on the dominant sedge species. This reduces competitive pressure on the remaining plant species, allowing them to acquire more resources (such as light, water, and nutrients), leading to an increase in CWM_{PW}. This study found that CWM_{LDMC} significantly declined under the YG and SG treatments, whereas it increased significantly under the MG 1:2 treatment. This suggests that an optimal mixed grazing ratio promotes the accumulation of leaf dry matter in the vegetation communities, although this reduces palatability (De La Riva *et al.* 2016). This phenomenon is closely linked to the selective grazing behavior of the livestock. Compared to grazing by yaks or Tibetan sheep alone, mixed grazing by yaks and Tibetan sheep had a more uniform impact on the grassland vegetation communities. The marked increase in CWM_{LDMC} under the MG 1:2 treatment indicates that the vegetation exhibits avoidance traits, effectively reducing livestock foraging intensity. The increase in CWM_{LN} under the MG 1:2 treatment follows a similar rationale, which is consistent with the research findings of Feng *et al.* (2024). Except for the YG treatment, all other grazing treatments significantly increased FRic, indicating that grazing enhances functional diversity by increasing trait variation within the plant communities (Zuo *et al.* 2021). This effect is linked to the nutrient return pathways from different livestock excreta. Larger-bodied yaks produce low-nitrogen, less decomposable excreta, while smaller-bodied Tibetan sheep produce high-nitrogen, more decomposable excreta (Liu *et al.* 2016). The combination of these two types of excreta results in diverse nutrient recycling patterns, which support a broader range of plant species and create suitable ecological niches. The significant increases in FDis and RaoQ under the MG 1:2 treatment indicate that niche differentiation among species in alpine grasslands is most effective when yaks and Tibetan sheep graze together in this ratio. This finding suggests that the 1:2 ratio is an ideal grazing practice for alpine grasslands.

4.4. Main pathways by which grazing activities regulate changes in plant functional diversity

The correlation analysis revealed that species richness is significantly positively correlated only with FRic, while FDis and RaoQ are significantly positively correlated with the Pielou, Simpson, and Shannon-Wiener indices. This suggests that the increase in species richness under various herbivore assemblages, along with species differentiation, is a key factor for enhancing plant functional diversity in alpine grasslands (Mahaut *et al.* 2020). The structural equation model analysis indicated that grazing activities primarily influence plant species diversity and soil physicochemical properties directly, which in turn indirectly affects plant functional diversity. Grazing significantly enhances species diversity and soil physicochemical properties, thereby greatly increasing plant functional diversity. Specifically, species richness and β-diversity are the main factors regulating functional diversity through the changes in species diversity, while soil available nitrogen, available potassium, and bulk density regulate functional diversity through changes in soil physicochemical properties. Further analysis showed that although changes in soil physicochemical properties do not significantly impact species diversity, they significantly improve plant functional diversity. Additionally, the regulatory effect of soil physicochemical properties on plant functional diversity changes is stronger than that of species diversity. This indicates that in the alpine grassland ecosystem, changes in species diversity are mainly influenced directly by grazing activities, with top-down regulation dominating the plant species diversity changes. In contrast, plant functional diversity changes are primarily influenced indirectly by changes in soil physicochemical properties, with down-top regulation dominating the plant functional diversity changes.

In summary, moderate grazing intensity significantly enhances plant functional diversity in alpine grasslands by altering soil physicochemical properties and species diversity. This finding provides a better understanding of the mechanisms of the impact of grazing on alpine grassland ecosystems and scientific evidence for their sustainable management.

5. Conclusion

Under moderate grazing intensity, grazing by various herbivore assemblages significantly increased species richness and β-diversity in alpine grassland. However, as the proportion of Tibetan sheep increased in the mixed grazing treatment, this enhancement gradually weakened and completely disappeared when yaks and Tibetan sheep were mixed-grazed at a ratio of 1:6. Grazing activities resulted in the stunting and thinning of plant communities in alpine grassland but increased the specific leaf area, indicating a transition towards species with faster growth rates and better resource acquisition capabilities, demonstrating good adaptability. In alpine grasslands, grazing activities mainly affected the availability of nutrients and soil bulk density of the topsoil (0–10 cm), with no significant impacts on the subsoil (20–30 cm). The α-diversity of alpine grassland plant communities showed a significant positive correlation with functional diversity, but the functional diversity of plant communities was mainly influenced by changes in available nitrogen, available potassium, and soil bulk density, indicating that soil physicochemical properties play a major role. An appropriate ratio of mixed grazing by yaks and Tibetan sheep helps to enhance the functional diversity of alpine grassland plant communities, with the most significant effect observed at a ratio of 1:2. Thus, in terms of plant functional diversity, mixed grazing by yaks and Tibetan sheep at a ratio of 1:2 represents one of the ideal forms of adaptive management for alpine grasslands on the Qinghai-Tibet Plateau.

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Declaration of competing interests

The authors declare that they have no conflict of interest.

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