



# Impact of grazing on plant species and functional community structure in Tibetan alpine grasslands: Implications for plant diversity conservation



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## ABSTRACT

Understanding how grazing influences plant diversity and spatial distribution is essential for evaluating the ecological consequences of grassland restoration, especially in sensitive alpine ecosystems (e.g., Tibetan Plateau). This study assessed the impact of grazing on plant species and functional  $\alpha$ - and  $\beta$ -diversity using data from 16 paired grazed and fenced plots across a transect in Tibet. Overall, grazing led to a decline of 9.77% in species  $\alpha$ -diversity (Simpson index) and 11.50% in functional  $\alpha$ -diversity, while  $\beta$ -diversity decreased by 4.75% and 10.03%, respectively. According to the intermediate disturbance hypothesis, the current grazing intensity in Tibet might not be the optimal level. Spatially, grazing homogenized the latitudes and longitudes patterns of species and functional  $\alpha$ -diversity. Grazing often promoted  $\alpha$ -diversity at higher altitudes, but decreased it at lower altitudes. The difference in community composition between fencing and grazing conditions at the same site ( $\beta_{GF}$ ) varied with geographic location. There were differences in the spatial distribution patterns between species  $\beta_{GF}$  and functional  $\beta_{GF}$ , likely due to differing dominant factors. Therefore, fencing may be less effective in preserving biodiversity at relatively high elevations, but it can still be a feasible method at relatively low elevations. Functional diversity and  $\beta$ -diversity may be more sensitive than species diversity and  $\alpha$ -diversity, respectively, indicating more attention should be paid to functional  $\beta$ -diversity in terms of biodiversity conservation.

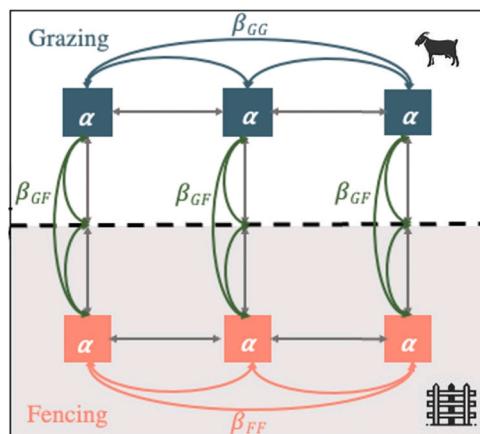
## 1. Introduction

Plant diversity is an essential foundation for maintaining ecological balance, human health, and economic development (Xu et al., 2025; Zhu et al., 2025). However, with the growth of the global population, plant diversity is increasingly disrupted by human activities (Wiens and Zelinka, 2024), leading to a gradual decline in plant diversity (Thomas, 2013). This decline presents significant challenges for maintaining ecological balance, ensuring food security, and protecting biological and medicinal resources (Liu et al., 2019). Grazing, as a major human activity on grasslands, has been demonstrated to affect biodiversity on a global scale (Milchunas and Lauenroth, 1993; Wang and Wesche, 2016; Xiang et al., 2023; Zhang et al., 2023). Plant diversity includes species diversity and functional diversity, both of which may respond differently to grazing or fencing, and these responses often vary across environmental gradients and habitat types (Cadotte et al., 2009; Wu et al., 2014). In addition, plant diversity can be described by  $\alpha$ -diversity

(within-community diversity) and  $\beta$ -diversity (between-community diversity), both of which are critical for understanding ecosystem resilience and recovery processes. These dimensions of diversity are particularly important in the context of grassland restoration, as they influence community assembly, ecosystem functioning, and long-term stability (Wang et al., 2024). The effects of grazing on plant diversity are influenced by factors such as grassland type, climate condition and Grazing strategies (periodic cold-season and warm-season grazing) (Wu et al., 2017a; Wu et al., 2017b; Munkhzul et al., 2021). These differences further contribute to the spatial patterns of plant diversity, namely  $\beta$ -diversity. Plant  $\beta$ -diversity refers to the differences in plant community composition at different locations under the same treatment (e.g., the differences between any two grazed sites,  $\beta_{GG}$  or between any two fenced sites,  $\beta_{FF}$ ) or the differences in community composition under different treatments at the same site (e.g., differences between grazed and fenced conditions for any one site,  $\beta_{GF}$ , which represents the changes caused by grazing) (Fig. 1). Plant species, particularly those

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**Fig. 1.** Schematic diagram of the experiment (with three replicates).  $\beta_{FF}$ ,  $\beta_{GG}$  and  $\beta_{GF}$  represent the  $\beta$ -diversity between fenced plots, between grazed plots, and between grazed and fenced plots, respectively.

with narrow geographical distributions, exhibit environmental dependency (Geng et al. 2012; Yang et al. 2024), contributing to the spatial patterns of plant diversity. Grazing not only affects species diversity but also alters the spatial structure of plant diversity through selective grazing by livestock and differential plant responses to grazing (Wu et al., 2014). These processes directly affect the success of passive and active restoration strategies in alpine grasslands.

To comprehensively study plant diversity conservation methods, it is necessary to consider plant diversity across different grazing habitats. Previous studies have explored the effects of grazing on plant species and functional  $\alpha$ -diversity and  $\beta$ -diversity (Letten et al., 2013; Chi et al., 2019), advancing conservation efforts. However, three important scientific questions remain to be addressed. First, it remains unclear whether taxonomic or functional diversity exhibits greater sensitivity to environmental disturbances (de Bello et al., 2006; Hanke et al., 2014), making it difficult to determine which biodiversity component should be prioritized for conservation efforts (de Bello et al., 2006; Hanke et al., 2014). Second, grazing demonstrates contrasting effects on plant diversity, with studies reporting increases (Pulungan et al., 2019) or decreases (Yang et al., 2014; Li et al., 2023), which may be related to climate and soil conditions. This phenomenon highlights the urgent need for mechanistic studies that disentangle grazing impacts across different ecological contexts and organizational levels (community vs. landscape). Third, understanding spatial patterns of  $\beta_{GF}$  is crucial for developing regional grazing management policies. However, whether  $\beta_{GF}$  exhibits distinct geographical patterns remains debated (Saccone et al., 2014; Kaufmann et al., 2021; Munkhzul et al., 2021). These discrepancies may stem from environmental heterogeneity or geographical distance effects. Therefore, further exploration is needed to understand grazing's overall effects on plant diversity and its impact on the spatial patterns of diversity. Addressing these uncertainties is essential for understanding how grazing shapes biodiversity patterns and, in turn, affects the ecological outcomes of grassland restoration. Clarifying the spatial responses of species and functional diversity to grazing will not only advance theoretical insights in plant diversity conservation but also provide a scientific basis for region-specific grassland management and restoration strategies.

Tibet is home to numerous unique species and rich plant diversity (Zeng et al., 2015; Bhatia and Srivastava, 2025). As one of China's major pastoral regions, Tibet's plant diversity exhibits significant species loss and community restructuring under grazing pressure (Dong and Sherman, 2015; Liu et al., 2018). These ecological dynamics make Tibet an ideal natural laboratory for investigating the broad-scale effects of grazing on plant diversity and its spatial patterns, especially in the context of ecological degradation and restoration. To quantify the

impact of grazing on plant diversity, Tibet has conducted numerous experimental and modeling studies (Wu et al., 2012; Wang et al., 2019; Huang and Fu, 2023), delving into the effects of grazing on species diversity and functional diversity (Niu et al., 2016). These studies not only provide a theoretical foundation for quantifying grazing's impacts on plant diversity but also offer valuable data for grassland degradation and restoration. However, despite this progress, two critical knowledge gaps remain that limit our understanding of how grazing influences ecological recovery trajectories. First, how grazing alters the spatial distribution patterns of plant  $\alpha$ -diversity remains an unresolved question (Li et al., 2024; Xu et al., 2024). Second, the dominant mechanisms governing plant diversity remain unclear (Bao et al., 2024; Zhang et al., 2024).

Based on community survey data from 16 pairs of grazed and fenced plots in Tibet, this study aims to address the following key scientific questions: (1) Which is more sensitive to grazing: species diversity or functional diversity? (2) How does the overall impact of grazing on plant diversity? (3) What are the spatial distribution patterns of  $\beta_{GF}$ ? (4) In what ways does grazing shape the spatial distribution of  $\alpha$ -diversity? Addressing these questions will allow the quantification of grazing's impact on biodiversity from various perspectives such as functional diversity,  $\beta$ -diversity, and the enclosure effect, and help in formulating biodiversity conservation strategies.

## 2. Methods

### 2.1. Study area and sampling

In August 2021, an east-west transect ( $\sim 1100$  km) was established across the northern Tibetan Plateau ( $80.52^{\circ}\text{E}$ – $91.79^{\circ}\text{E}$ ,  $31.04^{\circ}\text{N}$ – $32.40^{\circ}\text{N}$ ; elevation: 4421–4870 m), strategically positioned  $> 10$  km from major roads to minimize traffic disturbance. Sixteen paired grazed-fenced sites were selected along accessible areas, with each pair separated by  $\geq 100$  m to avoid edge effects. At each site, three replicate quadrats ( $0.5 \times 0.5$  m for alpine meadows;  $1 \times 1$  m for alpine steppes) were systematically placed along 100-m sampling lines, maintaining 20-m intervals between replicates. This design yielded 96 soil samples and 96 plant samples (16 site pairs  $\times$  2 treatments  $\times$  3 replicates), encompassing 65 species (Table S1) and 398 individual plants analyzed for 20 functional traits. Climatically, the transect spanned mean annual temperatures (MAT) of  $-0.8^{\circ}\text{C}$  to  $0.8^{\circ}\text{C}$  and precipitation (MAP) of 93.7–530.9 mm (2000–2020 averages). Spatial distribution of sampling locations is shown in Figure S1.

### 2.2. Data collection

During the community survey, observations were made for each species' height, cover, frequency, and fresh weight. For plant height, the heights of five randomly selected plants for each species were measured, and the average of these measurements was recorded as the average plant height (AvePH), the maximum height among these five plants was recorded as the maximum plant height (MaxPH) (Eisenhauer et al., 2009). Fresh samples of each species were dried in a constant temperature oven at  $65^{\circ}\text{C}$  for 48 h to determine their dry weight. The plant water content (PWC) for each species was calculated based on the fresh and dry weights. For leaf traits, three intact leaves were randomly selected from each species in each subplot to measure leaf length (LL) and leaf width (LW). Additionally, ten leaves were randomly selected to measure leaf area (LA) and specific leaf area (SLA) (Shen et al., 2025). Leaf chemical composition was analyzed using various methods. Leaf total phosphorus content (LTP) was measured using the molybdenum-antimony resistance colorimetric method (MADAC), and leaf total nitrogen content (LTN) was determined using the Kjeldahl nitrogen determination method (Ding et al., 2025). Leaf malondialdehyde content (MDA) was measured using the TBA tri-wavelength colorimetric method. Enzyme activities in leaves were measured using

colorimetric methods for peroxidase (POD) and catalase (CAT). Superoxide dismutase (SOD) activity was determined using the NBT photo-reduction method, and ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) activity and RuBisCO activase (RCA) were measured using kit-based methods (Chen et al., 2024). Photosynthetic pigments, including chlorophyll a (Chl a), chlorophyll b (Chl b), and carotenoids, were measured using spectrophotometry (Yang et al., 2022b; Ding et al., 2025). After the plant community survey and plant sample collection, soil samples were collected from each subplot using a soil auger with a diameter of 5 cm. Soil samples were taken from two depths: 0–5 cm and 5–10 cm. For each subplot, three soil cores were randomly collected and thoroughly mixed to create a composite soil sample. Portions of the soil samples were stored in a freezer at -20 °C for the determination of soil moisture content, pH, ammonium nitrogen ( $\text{NH}_4^+$ -N), nitrate nitrogen ( $\text{NO}_3^-$ -N), and available phosphorus (AP). Other portions were air-dried in a shaded area for subsequent analysis of total nitrogen (TN), organic carbon (SOC), and total phosphorus (TP). All measurements were conducted using standard laboratory methods (Zhang et al., 2020).

Based on the monthly average temperature and precipitation data from 145 meteorological stations on the Tibetan Plateau, obtained from the China Meteorological Data Service Center (<http://www.nmic.cn>), spatial interpolation was performed using Anuspline software with a spatial resolution of 1 km × 1 km. Using these interpolated data, MAT and MAP for the period 2000–2020 were calculated using R 4.2.2 software. The specific MAT and MAP for each sampling site were extracted using the geographical coordinates of the field observation sites in R 4.2.2.

### 2.3. Statistical analyses

For each species in each subplot, the average of its relative cover, relative height, and relative frequency was calculated to determine the importance value of the species (IPV).

$$\text{IPV} = \frac{\text{relative height} + \text{relative cover} + \text{relative frequency}}{3} \quad (1)$$

Using these importance values, species  $\alpha$ -diversity (species richness and Simpson index) and  $\beta$ -diversity ( $\beta_{GG}$ ,  $\beta_{GF}$  and  $\beta_{FF}$ ; with  $\beta$ -diversity based on Bray-Curtis distance) were calculated for each subplot using the vegan package in R 4.2.2 software. Based on the observed functional trait data, functional dispersion (FDis) and Rao's quadratic entropy index (RaoQ) were computed using R 4.2.2 software. FDis quantifies functional richness, while RaoQ is analogous to the species Simpson index (Laliberte and Legendre, 2010). The formulas for calculating FDis and RaoQ are as follows:

$$\text{FDis} = \frac{\sum a_j z_j}{\sum a_j} \quad (2)$$

where  $a_j$  is the abundance of species  $j$ ,  $z_j$  is the distance of species  $j$  to the weighted centroid  $c$ , and  $s$  is the total number of species.

$$\text{RaoQ} = \sum_{i=1}^s \sum_{j=1}^s d_{ij} P_i P_j \quad (3)$$

where  $P_i$  and  $P_j$  represent the relative abundance of plant species  $i$  and  $j$  in a specific quadrant, and  $d_{ij}$  denotes the interspecies distance. The calculation method for  $d_{ij}$  is as follows:

$$d_{ij} = \frac{1}{n} \sum_{k=1}^n (X_{ik} - X_{jk})^2 \quad (4)$$

where  $X_{ik}$  and  $X_{jk}$  represent the function trait  $k$  of plant species  $i$  and  $j$  in a specific quadrant, respectively, and  $n$  represents the number of function traits.

Using the "comdistnt" function from the picante package (<https://github.com/skembel/picante>), the functional  $\beta$ -diversity of plant communities ( $\beta_{GG}$ ,  $\beta_{GF}$ , and  $\beta_{FF}$ ; with  $\beta$ -diversity based on Euclidean

distance) was calculated based on plant functional trait data. A two-way ANOVA was conducted to analyze the effects of grazing on soil environmental factors and plant functional/species  $\alpha$ -diversity. The "adonis2" function from the vegan package in R 4.2.2 software was used to quantify the effects of grazing and sampling sites on the species/functional composition of plant communities.

Regression analyses using the ggpmisc package (<https://github.com/cran/ggpmisc>) were performed to explore the relationships between the functional and species  $\alpha$ -diversity of plant communities and their latitude, longitude, and elevation. The "beta.div.comp" function from the adespatial package in R 4.2.2 software was used to quantify the relative influence of turnover (Repl), species/functional richness difference (RichDiff), and similarity processes on  $\beta_{GG}$ ,  $\beta_{GF}$  and  $\beta_{FF}$ .

Geographical distances were calculated using the "distm" function from the geosphere package (<https://github.com/rspatial/geosphere>). Regression analyses were conducted to examine the relationships between species and function  $\beta_{GG}/\beta_{FF}$  and geographical distance. The wilcox.test function from the stats package was used to test the differences between  $\beta_{GG}$  and  $\beta_{FF}$  (Field et al., 2012). A random forest model from the rfPermute package (<https://www.rdocumentation.org/packages/rfPermute/version/2.1.81>) was used to quantify the relative contributions of climate and soil environmental factors to  $\alpha$ -diversity and  $\beta_{GF}$ .

## 3. Results

### 3.1. Overall impact of grazing on soil and plant communities

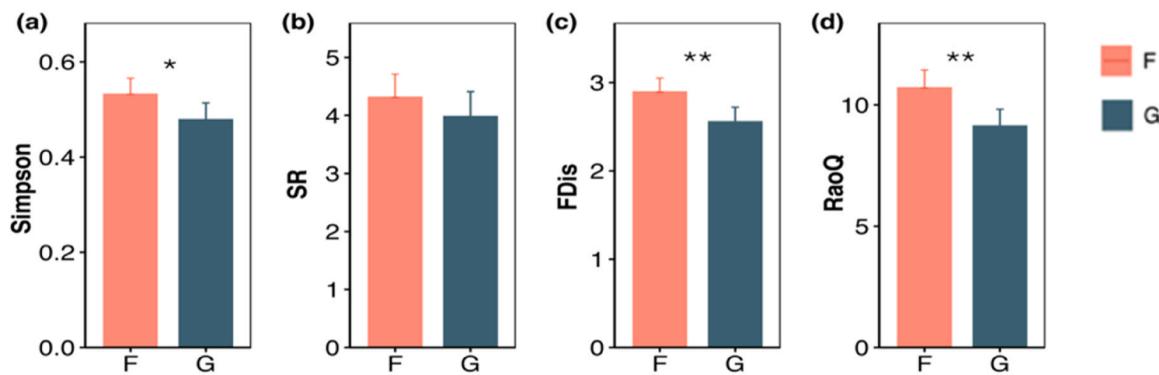
At a soil depth of 5–10 cm, grazing significantly reduced soil moisture (fenced: 8.27 %, grazed: 7.15 %,  $P < 0.001$ ) and slightly decreased soil organic carbon (SOC) levels (fenced: 1.17, grazed: 1.04,  $P < 0.1$ ) (Figure S2, Table S2). Compared with fenced plots, grazing reduced biodiversity indicators by 9.77 % for the Simpson index, 11.54 % for functional dispersion (FDis), and 14.24 % for Rao's quadratic entropy (RaoQ) (Fig. 2, Table S3). Grazing also caused compositional shifts in plant communities (Table 1), along with declines in both functional  $\beta$ -diversity (10.03 %) and species  $\beta$ -diversity (4.75 %) (Fig. 3a, c). In addition,  $\beta$ -diversity increased with geographic distance (Fig. 3b, d), and this spatial turnover was further intensified by grazing, particularly for species  $\beta$ -diversity (Fig. 3d).

The variations in functional  $\beta$ -diversity among sites were primarily driven by the functional similarity process, with grazing enhancing the relative influence of the functional replacement process (Fig. 4a). In contrast, species  $\beta$ -diversity among sites was mainly driven by species replacement, with grazing simultaneously reducing the relative influence of species replacement and species richness difference processes (Fig. 4b). The relative influence of the functional similarity process in regulating  $\beta_{GF}$  variation was greater than that of  $\beta_{FF}$  and  $\beta_{GG}$  (Fig. 4a). However, the relative influence of the species replacement process in regulating  $\beta_{GF}$  was less than that of  $\beta_{FF}$  and  $\beta_{GG}$  (Fig. 4b).

### 3.2. Geographic distribution patterns of plant diversity under fencing and grazing conditions

$\alpha$ -diversity showed a positive correlation with longitude, a negative correlation with latitude, and a unimodal pattern along the elevation gradient, increasing at mid-elevations and then declining. Grazing tended to homogenize the geographic (longitude and latitude) patterns of  $\alpha$ -diversity and altered its elevational distribution. Specifically, grazing increased species richness at elevations around approximately 4400–4450 m. However, in the mid-elevation range, grazing reduced multiple diversity metrics, including Rao's Q, FDis, species richness, and the species Simpson diversity index. In contrast, at higher elevations (e.g., >4750 m), grazing enhanced all of these diversity indicators (Fig. 5).

$\beta_{GF}$  exhibited a similar geographical distribution pattern as  $\alpha$ -diversity. However, species  $\beta_{GF}$  increased linearly with longitude, while functional  $\beta_{GF}$  first decreased and then increased with increasing



**Fig. 2.** Comparison of plant (a) species Simpson, (b) species richness (SR), (c) FDis and (d) RaoQ between fencing (F) and grazing (G) conditions across all the sampling sites. \*\* and \* indicated  $p < 0.01$  and  $p < 0.05$ , respectively.

**Table 1**

Two-way ANOVA of plant community composition for grazing treatments and sample sites.

	Grazing	Site	Grazing $\times$ Site
Species	2.34*	30.60***	2.21***
Function	-0.61	46.39***	2.34***

\* indicated  $p < 0.05$ .

\*\* indicated  $p < 0.001$ .

longitude. In terms of latitude, functional  $\beta_{GF}$  declined more rapidly, whereas the rate of change for species  $\beta_{GF}$  was faster with elevation (Fig. 6).

### 3.3. Drivers of plant diversity

MAP was the most critical environmental factor regulating changes in plant species and functional  $\alpha$ -diversity (Fig. 7). Grazing significantly altered the dominant environmental factors affecting plant diversity: For functional  $\alpha$ -diversity, grazing made soil pH at 5–10 cm depth the primary driving factor, while eliminating the influence of N.P at 0–5 cm depth and weakening the effect of MAP. For species  $\alpha$ -diversity, grazing removed the effect of N.P at 0–5 cm depth, making soil pH at 0–5 cm, pH at 5–10 cm, and MAT the key influencing factors, while reducing the explanatory power of MAP. Furthermore, the driving factors of plant  $\beta_{GF}$  showed significant differences: Species  $\beta_{GF}$  diversity was primarily influenced by AP, N.P, NH4.N, NO3.N, TN at 0–5 cm depth, along with AP, N.P, NH4.N, SOC, soil moisture content, MAP and MAT at 5–10 cm depth, with soil moisture content at 5–10 cm being the dominant factor. Functional  $\beta_{GF}$  diversity was jointly regulated by AP, N.P, NH4.N, TN, TP at 0–5 cm depth, and available N.P, NH4.N, soil moisture content, MAP and MAT at 5–10 cm depth, with MAT exhibiting the strongest explanatory power (Fig. 8).

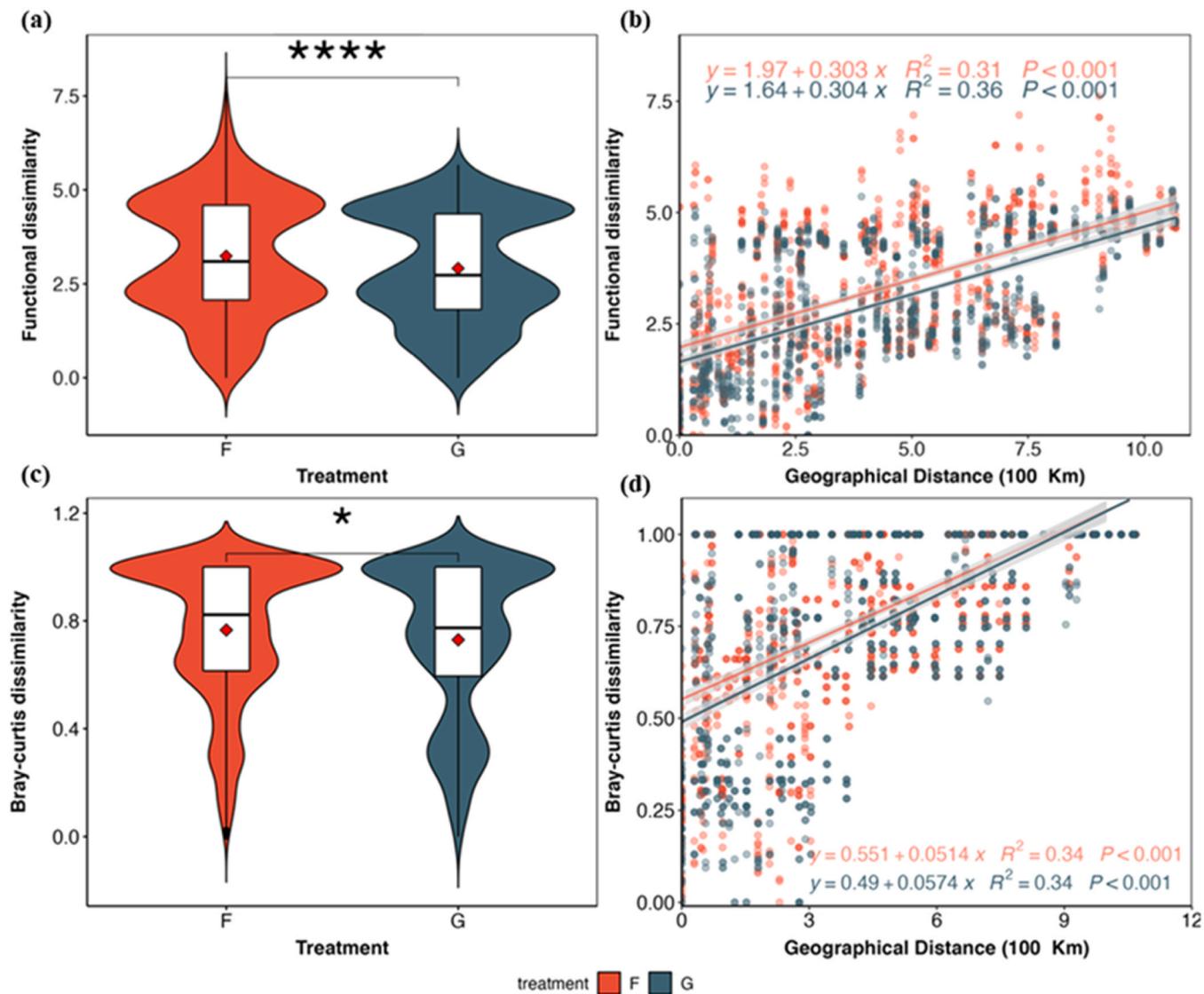
## 4. Discussion

The effects of grazing on plant functional structure diverged from its impact on species composition (Fig. 2, Table 1), which contrasts with earlier perspectives. Grazing may prioritize the selection of functional traits (such as plant height) rather than specific species. This could suggest that using a fractal structure for fencing to enhance edge effects may improve its protective effectiveness. This phenomenon can be attributed to several factors. Firstly, livestock grazing acted as a biological filter, favoring plant species with traits that conferred resistance to herbivores while disadvantaging those that were more susceptible, thus altering species community structure (Gatica et al., 2020). However, different species can possess similar functional traits, so changes in species structure due to grazing did not necessarily result in changes in

functional structure. Secondly, the relative contributions of the three processes (similarity, replacement, and richness difference) to species  $\beta$ -diversity were different from those of functional  $\beta$ -diversity (Qin et al., 2019; Pozzobom et al., 2021). Grazing reduced species  $\beta$ -diversity among sites by reducing the relative contribution of the processes of species richness difference and replacement but reduced functional  $\beta$ -diversity among sites by increasing the relative contribution of the functional replacement process (Fig. 3). For species  $\beta_{GF}$ , the replacement process had a larger impact than the richness difference process. In contrast, the richness difference and similarity processes played more substantial roles in driving functional  $\beta_{GF}$  (Fig. 4). This highlights that the dominant processes for species and functional composition were different, and their relative contributions also varied. Thirdly, the key environmental factors influencing plant community structure differed between functional and species dimensions. Even for the same environmental factors (e.g., soil moisture at 5–10 cm), their impact can vary between these two dimensions (Figs. 7–8). Therefore, functional diversity is at least as important as species diversity, and it is crucial to focus on the effects of grazing on functional diversity.

As geographic location changes,  $\beta_{GF}$  also varies. This phenomenon supports the conclusions of Munkhzul et al. (2021) and Cai et al. (2024) regarding the environmental dependency of grazing effects. It is therefore necessary to consider the context-specific impact of grazing on biodiversity and its corresponding conservation strategies. Additionally, the longitudinal patterns of plant functional and species  $\beta_{GF}$  differ (Fig. 6). This phenomenon can be attributed to several factors. Firstly, precipitation in Tibet increases from west to east (Ga et al., 2018; Zhang and Zhou, 2021). Areas with higher precipitation typically have denser vegetation and greater plant biomass (Gao et al., 2013; Bahadur et al., 2024). This indicates that more resources are available to support a greater number of plant species. Additionally, these regions often have higher livestock carrying capacity and human population density, resulting in greater grazing pressure (Yu et al., 2004). Secondly, the diversification of plant functional traits may be related to precipitation levels (Schwinning and Kelly, 2013; Wang and Wesche, 2016). In regions with moderate precipitation, plant functional traits may be relatively uniform, whereas in areas with extreme precipitation or drought, plant functional traits may become more diverse to adapt to these extreme conditions (Zuo et al., 2021). For example, plants in arid regions may evolve deep root systems or drought-resistant leaves, while plants in wetter areas may develop higher water-use efficiency. These adaptive strategies lead to different patterns of functional  $\beta_{GF}$  compared to species  $\beta_{GF}$ . Lastly, species and functional  $\beta_{GF}$  have different sensitivities to environmental factors (Forsyth and Gilbert, 2021; Barrere et al. 2023). For instance, soil moisture (which varies with longitude) has a greater impact on species  $\beta_{GF}$  than on functional  $\beta_{GF}$  (Fig. 8).

Overall, grazing reduces plant  $\alpha$ -diversity is consistent with the findings of previous studies by Schulz et al. (2019) and Cai et al. (2024). This reduction may be related to the following mechanisms. Firstly,

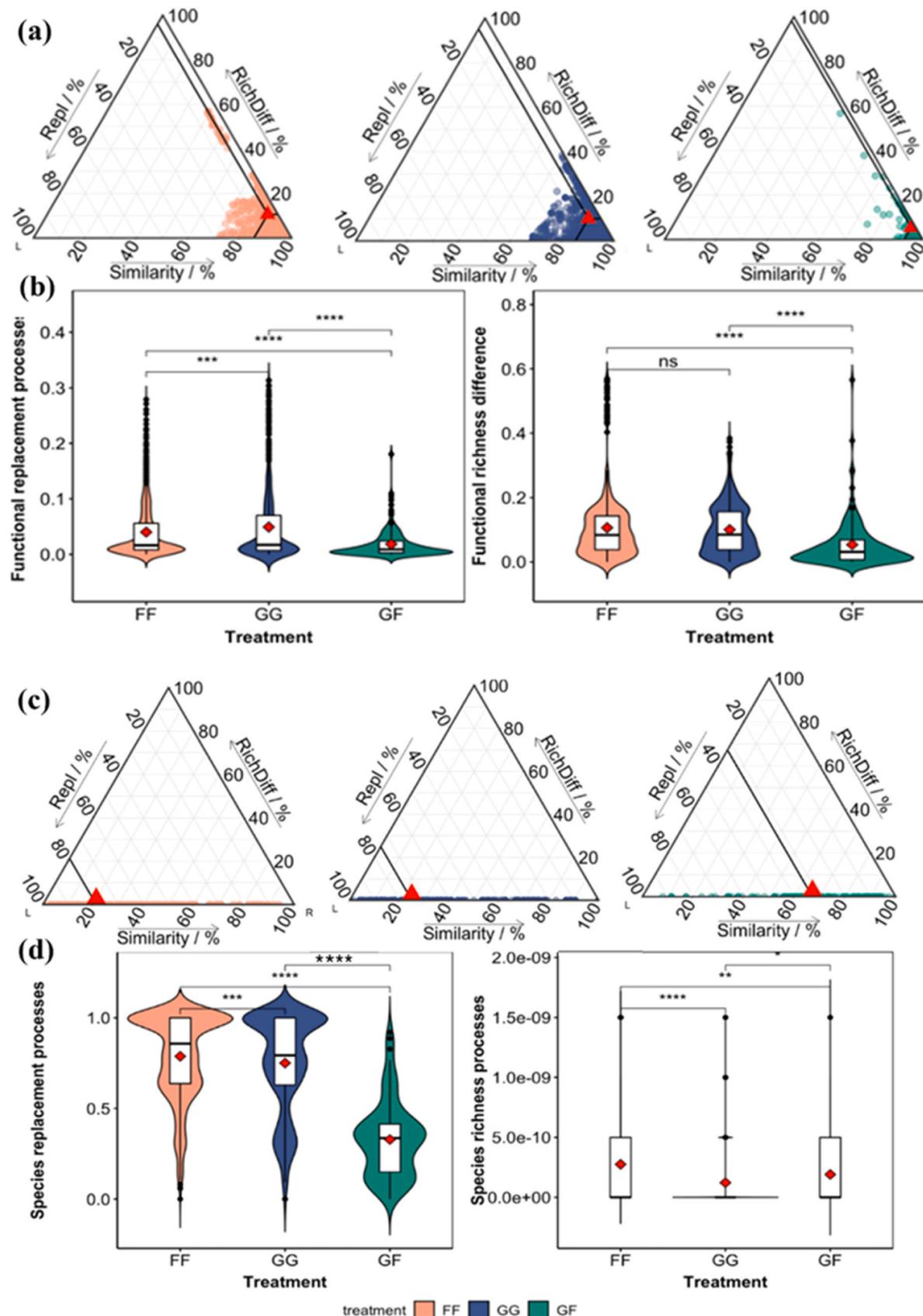


**Fig. 3.** The violin plots showed (a) functional dissimilarity and (c) species Bray-Curtis dissimilarity among any two of all the sampling sites under fencing (F) and grazing (G) conditions, respectively (\*\*\*( $p < 0.001$ ); \*,  $p < 0.05$  based on wilcoxon-test). Distance-decay curves showing (b) function dissimilarity and (d) species dissimilarity against geographic distances among sampling sites. Red and blue solid lines denoted linear regressions under fencing and grazing conditions, respectively.

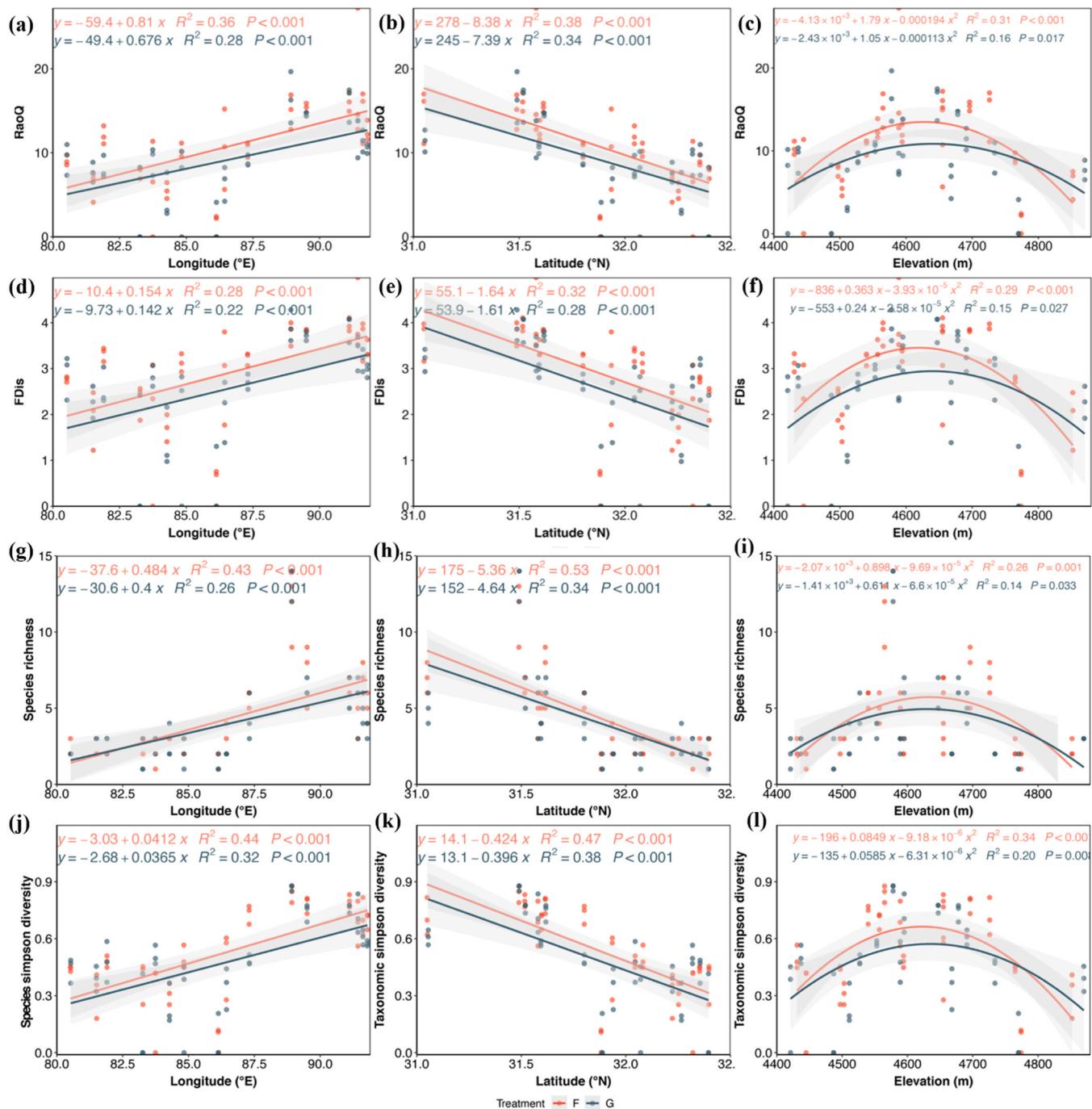
grazing can lead to a decrease in soil moisture at 5–10 cm depth (Figure S2), which can cause drought-intolerant plant species to struggle in drier soil conditions and subsequently decline. The reduction in soil moisture caused by grazing may also alter other soil physical and chemical properties (e.g., soil temperature, soil pore oxygen content). Secondly, grazing can increase soil compaction (Northup et al., 2010; Lai and Kumar, 2020), reduce soil permeability and aeration (Wang et al., 2020), thereby affecting root growth and soil microbial activity (Yang et al., 2019). Microbial activity, in turn, influences soil nitrogen and phosphorus availability, which can regulate plant growth. Additionally, grazing increases the extent of bare soil (Golodets and Boeken, 2006), exacerbating wind and water erosion of the soil. This soil compaction and erosion can lead to a reduction in soil organic matter, consequently affecting the cycling of crucial nutrients like nitrogen and phosphorus. Grazing may also increase soil salinity (Di Bella et al., 2015), particularly in arid regions, making the environment less favorable for the growth of certain plant species. Moreover, the  $\alpha$ -diversity of soil bacteria is closely related to plant  $\alpha$ -diversity, and grazing reduces the  $\alpha$ -diversity of soil bacteria (Zhang and Fu 2021a). Fifth, grazing imposes selective pressure on plant species (Oñatibia et al., 2020), with

those favored by livestock facing greater grazing pressure, while those not grazed benefit from increased environmental resources. This selective pressure can lead to a convergence in species importance values within the plant community. Finally, the impact of grazing on diversity is related to grazing intensity (Zheng et al., 2012; Zhang et al., 2018), and the grazing intensity in this study may be not at a moderate level.

In high-altitude regions, grazing promoted  $\alpha$ -diversity (Fig. 6, Figure S3), corroborating some previous research findings (Speed et al., 2013), against other studies (Wang et al., 2025). This partially suggests that biodiversity conservation measures (such as fencing) in high-altitude areas are effective and should be maintained in future conservation strategies. There are several possible reasons for this. Firstly, the distribution of wildlife in high-altitude areas is relatively sparse, and their range of activity is limited. Moderate grazing can aid in the dispersal and spread of plant species (Dai et al., 2019). The movement and foraging behavior of animals can facilitate seed dispersal, thereby increasing plant diversity. Secondly, ecological relocation policies may have further reduced human activities in high-altitude regions, especially grazing (Song et al., 2015). This reduction decreases plants' investment in defense and increases their investment in resource



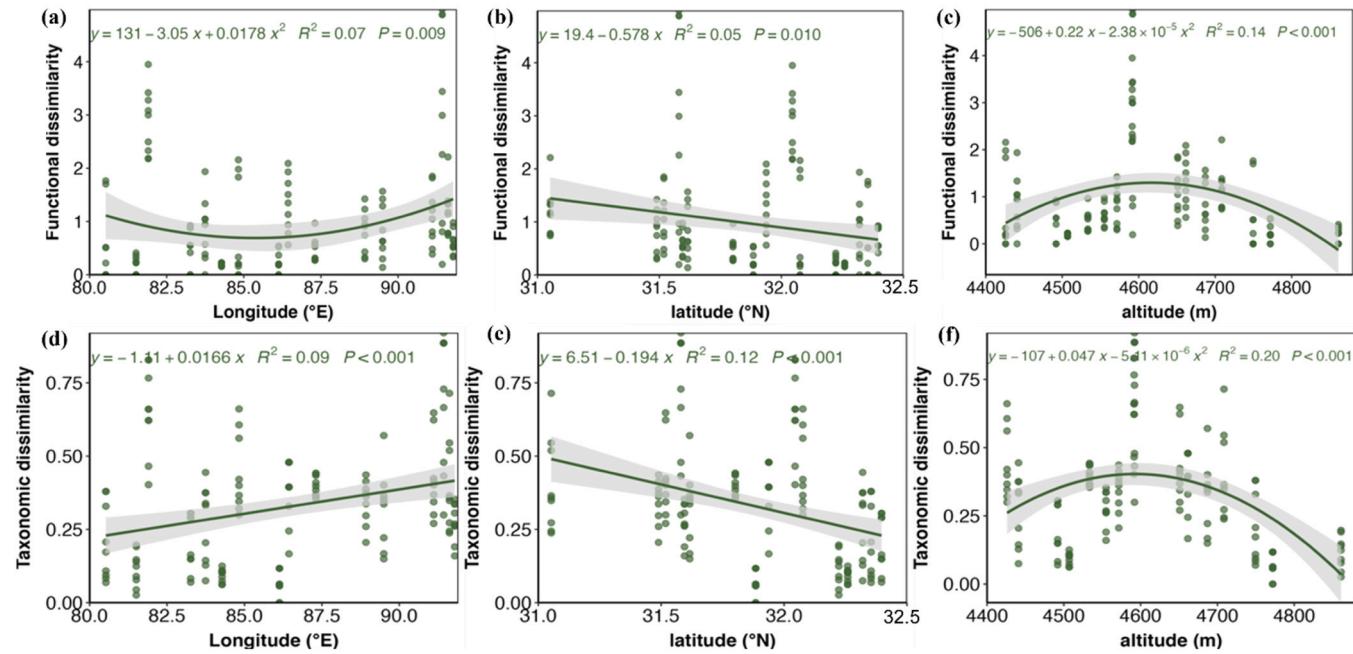
**Fig. 4.** Triangular sites of plant (a) function and (c) species  $\beta$ -diversity. Each point was determined by triplet values from the Similarity, replacement (Repl), and richness difference (RichDiff) processes. Mean values of Similarity, Repl, and RichDiff were indicated by the small red triangle. From left to right were  $\beta_{FF}$ ,  $\beta_{GG}$  and  $\beta_{GF}$ . Violin plots of (b) function and (d) species  $\beta$ -diversity. \*\*\*\*, \*\*\*, \*\* and \* indicated  $p < 0.001$ ,  $p < 0.005$ ,  $p < 0.01$  and  $p < 0.05$ , respectively. FF, GG and GF represented  $\beta_{FF}$ ,  $\beta_{GG}$  and  $\beta_{GF}$ , respectively.



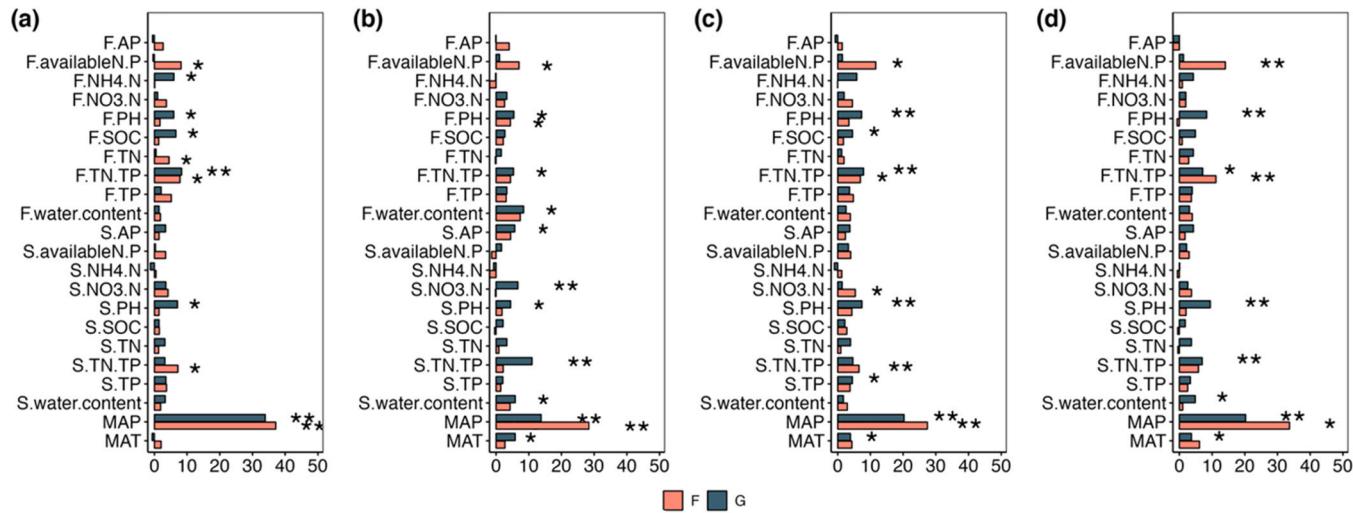
**Fig. 5.** (a) Variation trend of functional  $\alpha$ -diversity (RaoQ) along longitude under fencing or grazing conditions. (b) Variation trend of functional  $\alpha$ -diversity (RaoQ) along latitude under fencing or grazing conditions. (c) Variation trend of functional  $\alpha$ -diversity (RaoQ) along altitude under fencing or grazing conditions. (d) Variation trend of functional  $\alpha$ -diversity (FDis) along longitude under fencing or grazing conditions. (e) Variation trend of functional  $\alpha$ -diversity (FDis) along latitude under fencing or grazing conditions. (f) Variation trend of functional  $\alpha$ -diversity (FDis) along altitude under fencing or grazing conditions. (g) Variation trend of species  $\alpha$ -diversity (species richness) along longitude under fencing or grazing conditions. (h) Variation trend of species  $\alpha$ -diversity (species richness) along latitude under fencing or grazing conditions. (i) Variation trend of species  $\alpha$ -diversity (species richness) along altitude under fencing or grazing conditions. (j) Variation trend of species  $\alpha$ -diversity (Simpson diversity) along longitude under fencing or grazing conditions. (k) Variation trend of species  $\alpha$ -diversity (Simpson diversity) along latitude under fencing or grazing conditions. (l) Variation trend of species  $\alpha$ -diversity (Simpson diversity) along altitude under fencing or grazing conditions.

competition, breaking the competition-defense trade-off and resulting in a homogeneous plant community structure (Viola et al., 2010). Moderate grazing reintroduces selective pressure, breaking this homogeneity and promoting plant diversity. Thirdly, livestock generally prefer to forage in lower-altitude areas (Roath and Krueger, 1982), where grazing pressure is higher due to greater human presence and denser pasturelands (Hameed et al., 2022). In lower-altitude areas, pastures are

repeatedly grazed, with shorter recovery times, placing more stress on plants. In contrast, high-altitude pastures can have longer growth and recovery periods and are rarely grazed repeatedly (Gou et al., 2020). This altitude-related grazing intensity distribution allows plants in high-altitude areas more time to recover, thus increasing  $\alpha$ -diversity. Fourth, grazing typically leads to a decrease in soil organic carbon (SOC) and total nitrogen (TN) content. In low-altitude, humid grassland areas,



**Fig. 6.** (a-c) Variation trend of function  $\beta_{GF}$  (function dissimilarity) along longitude, latitude, and altitude, respectively; (d-e) Variation trend of species  $\beta_{GF}$  (taxonomic dissimilarity) along longitude, latitude, and altitude, respectively.

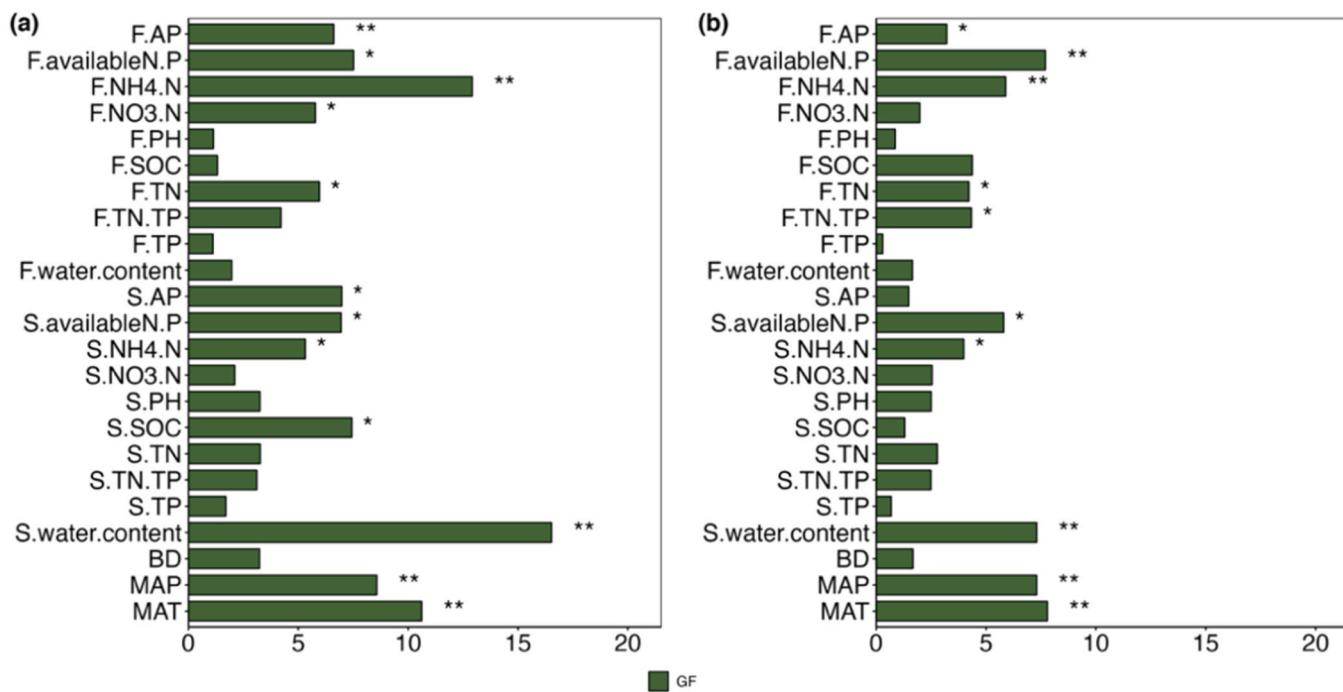


**Fig. 7.** Driving factors of plant  $\alpha$ -diversity were analyzed using a random forest model (ntree = 500, nrep = 1000). The subfigures represent: (a) species Simpson index, (b) species richness, (c) functional diversity (FDis), and (d) RaoQ. The factors included 0–5 cm/5–10 cm soil layer ammonium nitrogen (F.NH4.N/S.NH4.N), 0–5 cm/5–10 cm soil layer nitrate nitrogen (F.NO3.N/S.NO3.N), 0–5 cm/5–10 cm soil layer soil moisture (F.water.content/S.water.content), 0–5 cm/5–10 cm soil layer total nitrogen (F.TN/S.TN), 0–5 cm/5–10 cm soil layer total phosphorus (F.TP/S.TP), 0–5 cm/5–10 cm soil layer organic carbon (F.SOC/S.SOC), 0–5 cm/5–10 cm soil layer pH (F.PH/S.PH), 0–5 cm/5–10 cm soil layer rapidly available phosphorus (F.AP/S.AAP), 0–5 cm/5–10 cm soil layer available N:P (ammonium nitrogen + nitrate nitrogen)/available phosphorus, F. available N:P/S.available N:P. F. indicated 0–5 cm soil layer, and S. indicated 5–10 cm soil layer.

this effect may be offset by increased plant productivity (Wang and Wesche, 2016). In high-altitude regions, grazing has a minor impact on soil moisture at the 5–10 cm depth (Figure S4). These smaller changes reduce plant drought stress, allowing more plant species to coexist, thereby increasing  $\alpha$ -diversity.

Overall, grazing reduces plant  $\beta$ -diversity (Fig. 3a, c), indicating an increase in biological homogeneity, which could further lead to the loss of landscape diversity. This also emphasizes that, alongside the consideration of  $\alpha$ -diversity protection, maintaining  $\beta$ -diversity is an important factor in biodiversity conservation that should not be overlooked. The primary reasons for this phenomenon include at least the following. Firstly, grazing reduces the impact of the processes of species

turnover and species richness difference on plant species  $\beta$ -diversity, while increasing the impact of the species similarity process on plant species  $\beta$ -diversity (Fig. 4). Although grazing enhances the impact of functional turnover on plant functional  $\beta$ -diversity, plant functional  $\beta$ -diversity is still dominated by the similarity process (accounting for approximately 80%). Secondly, grazing directly affects plants through foraging and trampling, which interferes with the dispersal process of plant species to some extent, altering the structure and distribution of original plant populations (Lezama and Paruelo, 2016), thereby limiting species dispersal. Thirdly,  $\beta$ -diversity is closely related to  $\alpha$ -diversity (Jost, 2007; Hou et al., 2025), indicating that the reduction in  $\alpha$ -diversity caused by grazing may also lead to a decrease in  $\beta$ -diversity.



**Fig. 8.** Main driving factors of plant  $\beta_{GF}$  based on the random forest model ( $n_{tree}=500$ ,  $n_{rep}=1000$ ). The subfigures represented: (a) species  $\beta_{GF}$ , (b) function  $\beta_{GF}$ . The factors included 0–5 cm/5–10 cm soil layer ammonium nitrogen (F.NH4.N/S.NH4.N), 0–5 cm/5–10 cm soil layer nitrate nitrogen (F.NO3.N/S.NO3.N), 0–5 cm/5–10 cm soil layer soil moisture (F.water.content/S.water.content), 0–5 cm/5–10 cm soil layer total nitrogen (F.TN/S.TN), 0–5 cm/5–10 cm soil layer total phosphorus (F.TP/S.TP), 0–5 cm/5–10 cm soil layer organic carbon (F.SOC/S.SOC), 0–5 cm/5–10 cm soil layer pH (F.PH/S.PH), 0–5 cm/5–10 cm soil layer rapidly available phosphorus (F.AP/S.AP), 0–5 cm/5–10 cm soil layer available N:P (ammonium nitrogen + nitrate nitrogen)/available phosphorus, F. indicated 0–5 cm soil layer, and S. indicated 5–10 cm soil layer.

Fourthly, the recovery times of different plants after grazing disturbances are inconsistent. Some plants may recover quickly once grazing stops, while others may require a longer period to recover. This inconsistency in recovery times can lead to both short-term and long-term changes in plant communities, thereby affecting  $\beta$ -diversity. Fifthly, grazing reduces the water-use efficiency of plants (Han et al., 2018), meaning plants may become more reliant on limited water resources. This stress usually weakens the growth and reproductive abilities of plants, especially those with lower water-use efficiency, leading to species homogenization and functional trait convergence. Sixthly, vegetation destruction and habitat fragmentation (Li et al., 2021) make previously continuous vegetation more fragmented, reducing interactions between species and thereby lowering plant diversity. Habitat fragmentation also affects seed dispersal and plant regeneration.

Grazing homogenized the latitudinal and longitudinal patterns of  $\alpha$ -diversity in the Tibetan region (Fig. 5). This suggests that the choice of protection zones based on latitude and longitude should be reconsidered, as traditional latitudinal and longitudinal protection patterns may be less effective in grazing systems. This was likely due to the following mechanisms. Firstly, grazing homogenized the latitudinal and longitudinal patterns of soil moisture at 5–10 cm depth, one of the primary environmental factors driving  $\alpha$ -diversity (Figure S4). The reduction in plant roots and litter input decreased the organic matter in the soil, which in turn affected the soil's water retention capacity and nutrient supply, narrowing the ecological niches of plant populations (Derner and Schuman, 2007; Li et al., 2022). Secondly, herders tended to settle and graze on grasslands where plants grow vigorously. More intensive grazing exacerbated the loss of plant  $\alpha$ -diversity, meaning that grazing had a greater negative impact on the eastern and southern parts of Tibet, where water conditions are better and  $\alpha$ -diversity is higher (Shi et al., 2022). Thirdly, grazing altered the structure and function of soil microbial communities, which further affected soil fertility and plant diversity (Zhang and Fu 2021b). Fourthly, the impacts of grazing on alpine

grasslands differed between alpine meadows and alpine steppes (Wang et al., 2019). In the eastern alpine meadows and western alpine steppes of Tibet, grazing had different effects on soil and plant diversity. As the altitude decreased from west to east, changes in annual precipitation and mean annual temperature also influenced the extent of grazing impacts (Fig. 7). Fifthly, the spatial heterogeneity of grazing affected that of plants. When the spatial heterogeneity of grazing was weaker than that of plants, grazing reduced plant spatial heterogeneity (Adler et al., 2001). Therefore, setting up enclosures should be beneficial for the recovery and enhancement of plant  $\alpha$ -diversity, especially in environments more conducive to plant growth.

Functional  $\beta$ -diversity between grazing and fencing conditions was smaller than functional  $\beta$ -diversity among sites (Table 1). This can be attributed to the following mechanisms. Firstly, compared to  $\beta_{GF}$ , the processes of functional turnover and functional richness difference among sites have larger proportions (Fig. 4). Secondly, functional  $\beta$ -diversity among sites is primarily shaped by long-term climate change and geological activities (Hofmann et al. 2017). Specifically, due to differences in climate and terrain, Tibet has gradually developed different vegetation types from east to west, including alpine meadows, alpine steppes, and alpine desert steppes. These natural processes lead to strong variations in functional  $\beta$ -diversity among sites, while  $\beta_{GF}$  is merely the result of short-term human activities. Thirdly, functional  $\beta$ -diversity among sites contains the differences in plant community composition among different types of grasslands. However,  $\beta_{GF}$  does not contain these differences among grassland types.

Grazing alters plant species composition but does not significantly affect functional composition (Table 1). Grazing alters plant species composition but does not significantly affect functional composition (Table 1). This warns that using species composition as the core indicator may overestimate the actual ecological risks of grazing. Priority should be given to protecting functionally unique species, even if their species abundance is low. This phenomenon may be attributed to the

decline in the abundance of palatable plant species, as livestock selectively graze on these plants (Pandit et al., 2024). However, in high-altitude regions where ecological niches are relatively narrow, functional convergence occurs among different plant species (He et al., 2006; Ferrara et al., 2024), maintaining the stability of functional composition. Unpalatable weeds were not directly affected by grazing and continued to perform their ecological functions, thereby contributing to the stability of the ecosystem's functional composition. In overgrazed grasslands, unpalatable weeds also provide a biotic refuge for other plant species (Callaway et al., 2000; Cheng et al., 2014), reducing the negative impact of grazing on species diversity. Furthermore, some unpalatable weed species may have medicinal value, such as the anticancer properties of *Plantago* (Wen et al., 2023). Although unpalatable weeds may have adverse effects on grassland livestock farming, they play a significant role in maintaining the stability of grassland ecosystem functions and biodiversity. Future research should further explore the role of unpalatable weeds in biodiversity conservation within grazing areas, which is of critical theoretical and practical importance for the maintenance and sustainable use of grassland ecosystems.

This study found that grazing activities in Tibet led to a decline in local biodiversity. According to the Intermediate Disturbance Hypothesis, biodiversity typically reaches its maximum under moderate levels of disturbance, with both excessive and insufficient disturbance negatively impacting the ecosystem (Connell, 1978). Specifically, the current grazing intensity in Tibet, whether too high or too low, has resulted in the loss of both ecosystem function and species diversity. Overgrazing not only disrupts the natural recovery ability of grassland vegetation (Yang et al., 2022a) but may also exacerbate soil erosion and the decline of biological populations (Blanco et al., 2017). On the other hand, light grazing may lead to intensified interspecies competition (Sun et al., 2021). Therefore, to effectively protect and restore biodiversity in Tibet, it is urgently necessary to adjust grazing intensity to ensure management within the range of moderate disturbance. Through the scientifically sound control of grazing intensity, a balance can be achieved between species competition and coexistence in the grassland ecosystem, promoting the healthy growth of vegetation and maintaining the stability of biodiversity. Moreover, adjusting grazing intensity will also help improve the ecological resilience of grasslands, allowing them to better adapt to the challenges posed by climate change and human activities, thus laying a solid foundation for the protection of biodiversity in Tibet's grasslands.

## 5. Conclusion

This study highlights four key findings that have important implications for biodiversity conservation, at least in alpine ecosystems. 1) Grazing reduced both species and functional  $\alpha$  and  $\beta$  diversity, with a more pronounced decline in functional diversity. This suggested that prioritizing the protection of functional diversity could yield better conservation outcomes. 2) Grazing effects on plant  $\alpha$ -diversity and community composition varied spatially, indicating that fencing did not always lead to the restoration of plant diversity (e.g., at relatively high latitudes). 3) Grazing homogenized  $\alpha$ -diversity across latitudes and longitudes, which indicates that fencing played an important role in restoring the differences of  $\alpha$ -diversity between sites in the natural state. 4) Functional  $\beta_{FF}$  or  $\beta_{GG}$  was higher than the Functional  $\beta_{GF}$ , suggesting that geographical differences may outweigh the impact of grazing on functional diversity. Therefore, fencing may not be suitable for relatively high elevations, and alternative biodiversity conservation strategies should be considered. Prioritizing functional  $\beta$ -diversity is essential for effective biodiversity conservation.

## CRediT authorship contribution statement

**Rang Ding:** Writing – review & editing, Writing – original draft.

**Haorui Zhang:** Writing – review & editing, Writing – original draft. **Tianyu Li:** Writing – review & editing, Writing – original draft. **Gang Fu:** Writing – review & editing, Writing – original draft.

## 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.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109838.

## Data availability

Data will be made available on request.

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