



Forage nutrition quality and pools in Tibetan grasslands: Fencing effects, functional groups and yield-nutrition trade-offs



Yong Qin ^{a,b} , Peng Zhang ^c, Yuanpeng Zhu ^d, Xianzhou Zhang ^a, Gang Fu ^{a,*}

^a Lhasa Plateau Ecosystem Research Station, Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China

^b University of Chinese Academy of Sciences, Beijing 100049, China

^c State Key Laboratory of Simulation and Regulation of Water Cycle in River Basin, China Institute of Water Resources and Hydropower Research, Beijing 100048, China

^d Anhui Provincial Academy of Eco-Environmental Science Research, Hefei, 230061, China

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ABSTRACT

Few studies have comprehensively assessed the forage nutrition quality and pools among different plant functional groups across various grassland types and management practices. Moreover, the relationship between forage yield and nutrition quality remains controversial, hindering the development of effective grassland management strategies. This study investigated 37 paired fencing-grazing sites along an 1800-km transect on the Tibetan Plateau to systematically evaluate the variations of forage nutrition quality and pool at both community and functional group levels (graminae, sedge, edible forb and unpalatable forb) across alpine meadows, steppes and desert steppes. Fencing increased spatial average crude protein (CP) content of community by 7.90 %, while reducing crude ash (ASH) and water-soluble carbohydrate (WSC) contents by 6.20 % and 7.27 %, respectively. The CP, ASH, ether extract (EE), acid detergent fiber (ADF) and neutral detergent fiber (NDF) pools were increased by 13.15–29.48 %. The effects of fencing varied with the 37 sites. Fencing heterogenized the spatial pattern of community nutrition quality, but homogenized the CP content of sedge. Graminae provided the highest NDF. Sedges offered the highest CP and WSC, and moderate ADF, and EE. Edible forbs served the highest EE. Unpalatable forbs supplied the highest ASH. The relationships between forage yield and nutrition quality varied with functional groups and management types. Compared with the spatial heterogeneity method (based on the proportion of edible forage), the traditional mean value method may overestimate or underestimate the nutrition carrying capacity. Therefore, fencing generally improved forage crude protein content, at the expense of decreasing crude ash and water-soluble carbohydrate content. Contrary to expectations, sedges did not exhibit higher nutrition quality compared to other functional groups. The trade-offs between forage yield and nutrition quality did not always hold true. A fixed proportion of edible forage should not be used for the assessment of potential nutrition carrying capacity.

1. Introduction

Natural grasslands are a critical foundation for livestock production, with forage nutrition quality directly influencing animal health, growth performance, and productivity (Mikhailova et al., 2000; Seibert et al., 2021; Qin et al., 2024). However, natural grasslands have long been subjected to multiple pressures, including overgrazing, and biological invasions, resulting in degradation and declines in forage nutrition quality and productivity (Speed et al., 2013; Zhao et al., 2017; Zhu et al., 2024). Fencing, as an essential management tool, plays a significant role in maintaining the grassland-livestock balance and ensuring sustainable

utilization by controlling grazing, enabling rotational management, and protecting ecologically critical areas. It has also been shown to improve plant diversity, enhance soil quality, and promote microbial functions and nutrient cycling, thereby supporting forage nutrition restoration (Sitters et al., 2020; Zhang et al., 2023a; Ju et al., 2024). Numerous studies have assessed the protective effects of fencing on forage nutrition quality, providing a scientific basis for grassland conservation and management (Zha et al., 2022; Li and Fu, 2023). However, certain aspects of fencing effects require further exploration. First, the spatial patterns of forage nutrition quality under fencing versus grazing remain unclear. Fencing may lead to spatial homogenization of forage nutrition

* Corresponding author.

E-mail address: fugang@ignrr.ac.cn (G. Fu).

quality, potentially limiting livestock to access diverse resources (Tahmasebi et al., 2020; Xu et al., 2023; Qin et al., 2024). Second, there is still a controversy about whether the impact of fencing on the nutritional quality of forage has spatial heterogeneity. Existing studies have predominantly focused on single-point scales, emphasizing the overall effects of fencing, while systematic investigations into the spatial variability of fencing effects at regional scales are limited (Fu et al., 2022; Zhu et al., 2024). Third, the differential responses of various forage functional groups to fencing remain poorly understood. Differences in physiological traits, resource allocation strategies, and competitive relationships among functional groups may affect their response patterns to fencing (Gierus et al., 2012; Li et al., 2018). Therefore, it is necessary to further explore the spatial patterns of forage nutrition quality under fencing and grazing, as well as the spatial heterogeneity of fencing effects from a regional scale and functional group perspective.

The Tibetan Plateau, as the largest alpine grassland region globally, boasts abundant forage nutrition resources, playing a critical role in regional ecological stability and livestock development (Wang et al., 2023; Ding et al., 2024). Due to its vast and fragile alpine grassland ecosystems, the Tibetan Plateau is highly sensitive to both climatic variability and anthropogenic disturbances, making it a key region for studying the ecological effects of grassland management strategies such as grazing exclusion (Chen et al., 2016, 2018). However, the region has long faced challenges such as land degradation and declines in forage nutrition quality (Ma et al., 2017; Wang et al., 2022; Zhang and Fu, 2024), which severely limit the sustainable use of grassland resources. To address these issues, a large-scale fencing program, the “Retire Grazing to Restore Grasslands” project, was launched in 2003 on the Tibetan Plateau. This initiative has achieved remarkable success in improving grassland ecosystems (Zhang and Fu, 2024; Zhu et al., 2024). While substantial research has provided valuable data for grassland management and spatial optimization (Yao et al., 2019a; Zhang et al., 2023a), several critical scientific questions remain unresolved. First, most existing studies have emphasized the effects of fencing on forage yield, while overlooking forage nutritional quality. Nutrition quality is the fundamental criterion to evaluating the value of grassland resources and livestock production efficiency, which directly affects livestock growth and forage utilization (Zha et al., 2022). Second, the trade-off between forage yield and nutrition quality remains unclear. Although fencing can enhance forage yield, it may lead to a “nutritional dilution effect”, such as reductions in crude protein and ether extract contents and increases in fiber components (Tahmasebi et al., 2020; Zhang et al., 2023a; Zheng et al., 2024). These effects may also vary with fencing management and functional group characteristics. Third, the response mechanisms of alpine desert steppes in the western Tibetan Plateau to fencing remains poorly understood. Compared with the central alpine steppe and eastern alpine meadow, the western region, the western region exhibits distinct soil properties and plant communities, which may result in unique ecological sensitivities to fencing (Lu et al., 2015). Fourth, most studies have used CP as the sole indicator of forage quality, neglecting other critical nutrition components such as Ash (crude ash, minerals), EE (ether extract, energy reserves), WSC (water-soluble carbohydrates, rapid energy sources), ADF (acid detergent fiber, digestibility), and NDF (neutral detergent fiber, palatability). These indicators are equally essential for a comprehensive evaluation of forage quality (Dumont et al., 2015). Therefore, the above four key scientific issues urgently need to be further explored.

To evaluate the effects of fencing on forage nutrition quality across the Tibetan Plateau, this study selected a transect of 1800 km covering three grassland types (alpine meadows, alpine steppes and alpine desert steppes) and collected data from 37 paired fencing and grazing sites. The main goals of this study are to (1) compare the differences in forage nutrition quality and pools between fencing and grazing conditions, among four functional groups (graminae, sedge, edible forb and unpalatable forb) under the three grassland types; (2) investigate the relationship between forage yield and nutrition quality; and (3) compare

the differences between the fixed (spatial averaging method) and non-fixed (spatial heterogeneity method) edible forage proportion methods in quantifying nutritional carrying capacity. Based on previous studies, we made four hypotheses: (1) The effects of fencing on forage nutrition quality and pool varied with sites. (2) The nutrition quality of the sedges was higher than that of the other functional groups (e.g. forbs). (3) The relationships between forage yield and nutrition quality varied among plant functional groups and between fencing and grazing conditions. (4) Compared to the fixed value of edible forage proportion, the non-fixed edible forage proportion offered higher accuracy in quantifying the potential nutrition carrying capacity. Table 1

2. Materials and methods

2.1. Study area

Alpine meadows, steppes, and desert steppes of the Tibetan Plateau are the products of long-term natural evolution, with their species composition forming stable communities since the Holocene (about 11,700 years ago) (Wu et al., 2016). Currently, the alpine grasslands of the Tibetan Plateau are jointly influenced by climate change and human activities, with the impact of human activities gradually increasing (e.g., the transition from nomadic pastoralism to intensive grazing) (Chen et al., 2014). Human activities have three key historical turning points on the alpine grasslands of the Tibetan Plateau (Du et al., 2022). Before the industrialization period (pre-1950s), nomadic pastoralism, through seasonal migrations, formed a dynamic vegetation mosaic. During the collectivization period (1950s-1980s), the number of livestock increased dramatically, and continuous grazing pressure led to the degradation of

Table 1
A quick glossary.

Abbreviation	Full names
Nutrition index	
CP	crude protein
Ash	ash
EE	ether extract
WSC	water-soluble carbohydrates
ADF	acid detergent fiber
NDF	neutral detergent fiber
Geographic factors	
Lon	longitude
Lat	latitude
Ele	elevation
Climatic factors	
MAT	mean annual temperature
MAP	mean annual precipitation
MARad	mean annual radiation
Plant properties	
AGB	aboveground biomass
SD	species diversity
PD	phylogenetic diversity
FD	functional diversity
Soil properties	
SOC	soil total carbon
STN	soil total nitrogen
STP	soil total phosphorus
pH	pH
SBD	soil bulk density
SMC	soil moisture content
SAP	soil available phosphorus
NH ₄ N	soil ammonium nitrogen
NO ₃ N	soil nitrate nitrogen
Other	
Overall	all grassland type
AM	alpine meadows
AS	alpine steppes
AD	alpine desert steppes
β-FF	β values between fencing-fencing sites
β-GG	β values between grazing-grazing sites
β-FG	β values between fencing-grazing sites

some typical alpine grasslands into toxic weed communities. By the market economy period (post-1980s), the density of the road network increased, and the expansion of settlement areas interrupted traditional migration routes. The fragmentation of grasslands led to a sharp reduction in vegetation cover fluctuations in modern continuous grazing areas, significantly weakening the ecosystem's self-restoration capacity. This evolutionary trajectory reveals a non-linear relationship between human activities and the stability of grassland ecosystems.

The study area was located in the southwestern part of the Qinghai-Tibet Plateau, covering geographical coordinates from 26 °N to 36 °N latitude and 78 °E to 99 °E longitude. This region constitutes the main body of the Tibetan Plateau, with an average elevation exceeding 4000 m. The climate is cold, with an annual average temperature ranging from -2.8 °C to 11.9 °C and annual precipitation varying between 50 mm and 901 mm, decreasing trend from the southeast to the northwest. Due to the variation in water and heat conditions, the ecosystems in the region exhibit a distinct distribution pattern. From southeast to northwest, the dominant ecosystems include alpine meadows, alpine steppes, and alpine desert steppes, with alpine steppes being the most widespread. The area experiences varying livestock grazing pressures, with Tibetan sheep predominant in the western areas and yaks in the eastern areas. Grazing intensity is relatively high throughout the region, contributing to long-term overgrazing and subsequent degradation of large portions of natural grasslands on the Tibetan Plateau.

2.2. Field work and physicochemical analysis

A survey and sampling of plant communities were conducted between late July and mid-August 2023, during the peak biomass period. The study area spanned approximately 1800 km along a national highway, with sampling sites randomly distributed along this distance. The spatial straight-line distance between sampling sites was more than 30 km, with each site situated at least 1 km away from roads, water bodies, and villages. In total, 37 paired fencing-grazing sites were established (Fig. S1). For each paired fencing-grazing site, a 100 m transect was set up both inside and outside the fence, with five repeated quadrats taken along the transect. The quadrat size was 0.5 m × 0.5 m for alpine meadows and 1 m × 1 m for alpine steppes and alpine desert steppes.

We identified and recorded all plant species within each quadrat. Collected all aboveground green living plants by clipping at ground level for each species. Five soil subsamples at 0–20 cm were collected using a soil auger and mixed into a composite sample for each quadrat. We also collected soil samples for bulk density measurement using the ring-knife method at 0–20 cm. The longitude (Lon), latitude (Lat), and elevation (Ele) of each sampling site were also recorded using a global positioning system.

Plant samples were dried at 105 °C for 30 min to deactivate enzymatic activity, followed by further drying at 70 °C to a constant weight. The dry weight of each plant species in each quadrat was recorded and divided by the quadrat area to calculate the aboveground biomass (AGB). We measured six plant functional traits (leaf area, specific leaf area, maximum height, leaf carbon, leaf nitrogen, and leaf phosphorus) for each species within each quadrat (Qin et al., 2025). These functional traits are key factors that influence how plants adapt to their growing environments. Together, they affect community functions such as productivity, competitiveness, and resource use efficiency. Analyzing these traits can help understand how plants adapt to different environmental conditions and reveal the ecological relationships between species in a plant community (Reich et al., 2018). For nutritional analysis, the following methods were employed: crude protein (CP) was determined using the Kjeldahl method; crude ash (ASH) was measured by the dry ashing method; ether extract (EE) was determined using the Soxhlet extraction method; water-soluble carbohydrates (WSC) were analyzed by the anthrone colorimetric method; acid detergent fiber (ADF) and

neutral detergent fiber (NDF) were measured using an automated fiber analyzer. For soil samples, visible plant roots and stones were removed before analysis. Soil properties were determined as follows: soil total carbon (STC) and total nitrogen (STN) were analyzed using an elemental analyzer; soil total phosphorus (STP) and available phosphorus (SAP) were measured using the molybdenum-antimony anti-spectrophotometric method; soil ammonium nitrogen (NH_4^+N) and nitrate nitrogen ($\text{NO}_3^- \text{N}$) were determined using the indophenol blue colorimetric method and hydrazine sulfate method, respectively; soil moisture content (SMC) and bulk density (SBD) were measured using the drying method and ring knife method, respectively; soil pH was determined using the potentiometric method.

2.3. Statistical analysis

All analyses were conducted in R version 4.4.1 (R Core Team, R Foundation for Statistical Computing, Vienna, Austria). The vegan, picante, and fd-packages were used for calculating species diversity (SD), phylogenetic diversity (PD), and functional diversity (FD) of plant communities, respectively. Meteorological data, including temperature, precipitation, and radiation records from 2000 to 2020, were obtained from the China Meteorological Administration (<http://data.cma.cn/>). These records were aggregated to calculate mean annual temperature (MAT), mean annual precipitation (MAP), and mean annual radiation (MARad) with spatially continuous climate data generated using ANUSPLIN software (The Australian National University) at a spatial resolution of 1 km. Finally, the values of MAP, MAT, and MARad were extracted for each study site.

Before the field study, we reviewed a large number of relevant studies (Wu et al., 2015) and engaged in in-depth discussions with local herders during our fieldwork. The calculation formula for forage nutrition content and pool of the community and its functional groups was as follows.

$$\text{NC}_{g,k} = \frac{\sum_{i=1}^n (\text{NC}_{i,k} \times \text{AGB}_i \times I_{g,i})}{\sum_{i=1}^n (\text{AGB}_i \times I_{g,i})} \quad (1)$$

$$\text{NP}_{g,k} = \sum_{i=1}^n (\text{NC}_{i,k} \times \text{AGB}_i \times I_{g,i}) \quad (2)$$

where $\text{NC}_{g,k}$: The weighted average value (%) of the k-th nutrition quality indicator for the community or functional group. $\text{NP}_{g,k}$: The nutrition pool of the k-th nutrition quality indicator for functional group or the community. $\text{NC}_{i,k}$: The content (%) of the k-th nutrition quality indicator for the i-th plant species. AGB_i : The aboveground biomass (g/m^2) of the i-th plant species. $I_{g,i}$: 1, if species i belong to a functional group; 1, for the entire community (all species are included); 0, otherwise. n: The total number of plant species in the community or functional group. g: community, gramineae, sedge, edible forbs, or unpalatable forbs. k: CP, ASH, EE, WSC, ADF or NDF.

The natural logarithm was used to measure the effect of fencing on an individual variable (Hedges et al., 1999).

$$\text{RR} = \ln \left(\frac{X_{\text{fencing}}}{X_{\text{grazing}}} \right) \quad (3)$$

where X_{fencing} represented the variable value under fencing conditions, X_{grazing} represented the variable value under grazing conditions, and RR represented the response ratio. When $\text{RR} > 0$, fencing had a positive effect on the variable; when $\text{RR} < 0$, fencing had a negative effect on the variable; and when $\text{RR} = 0$, fencing had no effect on the variable.

We collectively referred to the content of CP, ASH, EE, WSC, ADF, and NDF as nutrition content and the pool of CP, ASH, EE, WSC, ADF, and NDF as nutrition pool. The β value for nutrition content or pool represented the compositional differences of these indicators among different sampling sites. Specifically, it can be categorized into three cases: β between fencing-fencing sites ($\beta\text{-FF}$), β between grazing-grazing

sites (β -GG), and β between fencing-grazing sites (β -FG). The β values for both nutrition content and its pool were calculated using the Bray-Curtis dissimilarity formula, which applied to any of the three cases mentioned above.

$$\beta_{ij}^{NC} = 1 - \frac{2 \times \sum_{k \in NC} \min(x_{ik}, x_{jk})}{\sum_{k \in NC} (x_{ik} + x_{jk})} \quad (4)$$

$$\beta_{ij}^{NP} = 1 - \frac{2 \times \sum_{k \in NP} \min(y_{ik}, y_{jk})}{\sum_{k \in NP} (y_{ik} + y_{jk})} \quad (5)$$

where NC referred to the set of nutrition content indicators, and NP referred to the set of nutrition pool indicators. x_{ik} represented the value of sampling site i for the k-th nutrition content indicator, while y_{ik} represented the value of sampling site i for the k-th nutrition pool indicator. i indicated the sampling site, which belonged to either fencing or grazing sites. β_{ij}^{NC} denoted the Bray-Curtis dissimilarity between sampling sites i and j based on nutrition content (NC), and β_{ij}^{NP} denoted the Bray-Curtis dissimilarity between sampling sites i and j based on the nutrition pool (NP).

Since the forage within the fencing area was undisturbed by grazing, we calculated the nutrition carrying capacity (NCC) of alpine grasslands based on the crude protein pool (CPP) of the fencing area. Additionally, we employed both the spatial heterogeneity method and the mean value method for the edible forage proportion to calculate the NCC for each sampling site. The calculation formula was as follows.

$$NCC_i = \frac{CPP_i \times E_i \times U}{I \times D} \quad (6)$$

where NCC_i : The nutrition carrying capacity of the i-th sampling site (sheep/ha). CPP_i : The CP pool of the i-th sampling site (kg). E_i : The edible CP proportion of the i-th sampling site (either the actual value for each site or the mean value across all sites). U : The grassland utilization rate (fixed at 70%). I : The daily crude protein intake per sheep (0.0539 kg/d). D : The grazing duration (averaged at 365 days).

A linear mixed-effects model (LMM) was used to assess the effects of fencing on forage nutrition content, nutrition pools, and environmental variables across different grassland types (Table S1). In this model, the site was treated as a random factor and management type (fencing vs. grazing) was treated as a fixed factor (Zhang and Fu, 2024). To analyze the differences in nutrition content among functional groups (graminae, sedge, edible forb, and unpalatable forb) between sites, Tukey's Honest Significant Difference (HSD) multiple comparison test was used (Table. S2) (Goeman and Solari, 2022). The Wilcoxon rank-sum test was used to compare the β of nutrition content and its pools, specifically comparing β -FF, β -GG, and β -FG (Ng and Balakrishnan, 2004). Using the ggpmisc-package, we fitted the relationships between nutrition content, nutrition pool, and geographic factors (longitude, latitude, and elevation) under fencing and grazing conditions. We analyzed how the effects of fencing on each variable changed concerning geographic coordinates, and examined the relationships between the β values of nutrition content and its pools about geographic, climatic, and soil distances. Geographic distances were calculated using the geosphere-package, while climatic and soil distances were computed using Euclidean distance (Ju et al., 2024). A paired t-test was conducted to compare the differences between the two methods of calculating nutrition carrying capacity (Table. S3) (Grabchak, 2023). The vegan-package was employed to assess the relative contributions of various factors-geographic location (Lon, Lat, and Ele), climatic factors (MAT, MAP, and MARad), soil properties (SMC, SBD, pH, SOC, STN, STP, SAP, NH_4^+ N, and NO_3^- N), and plant diversity (SD, PD, and FD) to nutrition content and its pool (Fu et al., 2022). Finally, piecewise structural equation models (PSEM) were constructed under fencing, grazing conditions using the piecewiseSEM-package. This was done to explore the direct and indirect

relationships between environmental factors and response variables (Bollen and Davis, 2009).

3. Results

3.1. The overall effects of fencing on forage nutrition content and its pool in alpine grasslands

The effects of fencing on forage nutrition content and pools varied across functional groups and grassland types (Figs. 1–3). Fencing increased community crude protein (CP) content by 7.90 %, while crude ash (ASH) and water-soluble carbohydrates (WSC) contents decreased by 6.20 % and 7.27 %, respectively. Nutrition pools—including CP, ASH, ether extract (EE), acid detergent fiber (ADF), and neutral detergent fiber (NDF) increased by 13.15 %–29.48 %. Among functional groups, gramineae showed decreases in crude ash and water-soluble carbohydrates contents by 7.52 % and 11.70 %, respectively, with increases in acid detergent fiber and neutral detergent fiber contents by 2.72 % and 2.14 %. While their pools of crude protein, ether extract, acid detergent fiber, and neutral detergent fiber increased significantly by 25.26 %–42.80 %. Sedges exhibited increases in crude protein, ether extract, acid detergent fiber, and neutral detergent fiber contents by 3.03 %–10.47 %, while water-soluble carbohydrates content decreased by 6.97 %. The ether extract pool increased notably by 35.90 %. Edible forbs showed an increase in acid detergent fiber content by 3.89 %, while crude ash and water-soluble carbohydrates contents decreased by 4.89 % and 6.49 %, respectively. In contrast, unpalatable forbs displayed reductions in crude ash, acid detergent fiber, and neutral detergent fiber contents by 3.12 %–6.21 %, while their pools of crude protein and ether extract increased by 44.22 % and 63.39 %, respectively. The effects of fencing were particularly significant in alpine meadows and alpine desert steppes, where sedge ether extract content increased by 20.45 % and 18.94 %, respectively, and community crude protein pools rose by 31.87 % and 57.32 %. While no significant changes were observed in the alpine steppes.

The β -FF (β between fencing-fencing sites), β -GG (β between grazing-grazing sites), and β -FG (β between fencing-grazing sites) of forage nutrition content and pool showed variations across different grassland types and functional groups (Fig. 4). For nutrition content, β -FG was lower than β -FF and β -GG across the community, gramineae, sedges, edible forbs, and unpalatable forbs. For nutrition pools, a similar trend was observed with β -FG being lower than both β -FF and β -GG (e.g., Community: β -FF vs. β -GG vs. β -FG: 0.38 vs. 0.36 vs. 0.27). Moreover, β for both nutrition content and pools differed significantly among grassland types. For nutrition content, β differences at the community level were greater in alpine meadows and alpine desert steppes compared to alpine steppes.

3.2. Spatial patterns of forage nutrition content and its pool in alpine grasslands under fencing and grazing conditions

The spatial patterns of forage nutrition content and pool differed significantly between fencing and grazing conditions, with higher response rates in fencing conditions for nutrition content and pools of community, especially for crude protein, ether extract, water-soluble carbohydrates, and crude ash contents (Fig. 5, S2–S8). Notably, certain nutritional indicators of specific functional groups, such as crude protein content in sedges and ether extract content in unpalatable forbs, exhibited faster response rates under grazing conditions. In terms of differences in nutrition composition, the response rates of nutrition content and pool to geographic, climatic, and soil distances were mostly higher under fencing than under grazing. However, some functional groups, like nutrition pool of gramineae, showed higher response rates under grazing conditions.

The contributions of geographic location, climatic factors, soil properties, and plant diversity to explaining forage nutrition content and

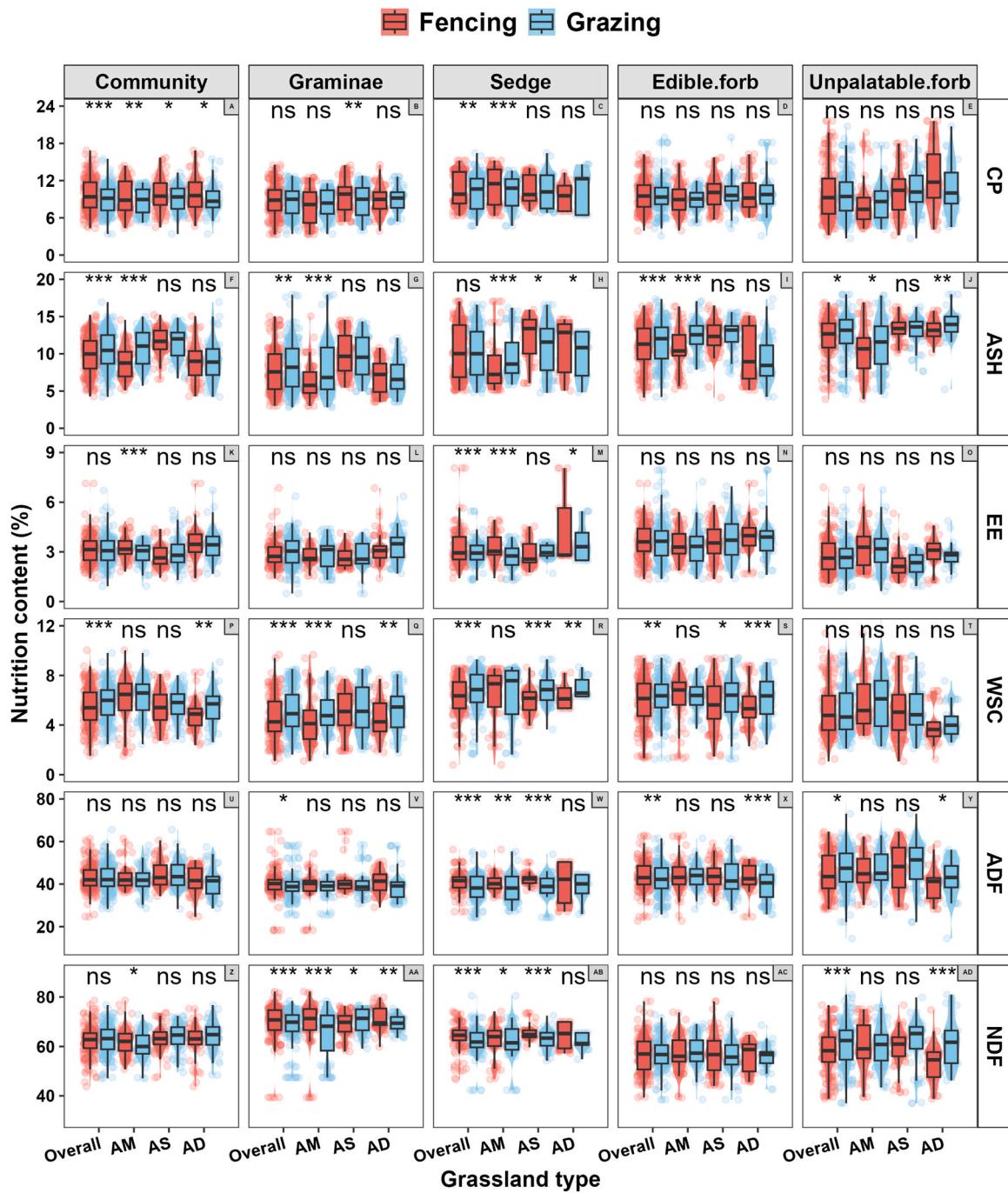


Fig. 1. Comparison of forage nutrition content under fencing and grazing across different grassland types: (A, F, K, P, U, Z) Community, (B, G, L, Q, V, AA) Graminae, (C, H, M, R, W, AB) Sedge, (D, I, N, S, X, AC) Edible forb, and (E, J, O, T, Y, AD) Unpalatable forb. "Overall" refers to all grassland types, with "AM" for alpine meadows, "AS" for alpine steppes, and "AD" for alpine desert steppes. Significance was tested using a linear mixed-effects model: *** $p < 0.001$, ** $0.001 < p < 0.01$, * $0.01 < p < 0.05$, ns: not significant.

pool differed between fencing and grazing conditions (Fig. 6, S9–S15), with distinct direct and indirect influence pathways (Fig. 7, S16–S22). For example, under grazing conditions, soil properties had a smaller impact on the β of nutrition content and pool compared to fencing conditions.

3.3. Spatial patterns of the effects of fencing on forage nutrition content and its pool in alpine grasslands

The effects of fencing on the nutrition content and pool varied with longitude, latitude, and elevation (Figs. S23–S29). For instance, as

longitude increased, the effect of fencing on community crude ash content and pool decreased, while its effect on community neutral detergent fiber content increased. As latitude increased, fencing had a stronger effect on community crude ash content but a weaker effect on sedge water-soluble carbohydrates content. With elevation, fencing had a stronger effect on community crude ash content but a weaker effect on sedge ether extract content, water-soluble carbohydrates content and pool. Regarding nutrition composition differences, the β -FG of community nutrition pools decreased with increasing longitude, while the β -FG of gramineae nutrition pools increased. Furthermore, even within the same grassland type, the impact of fencing on nutrition quality

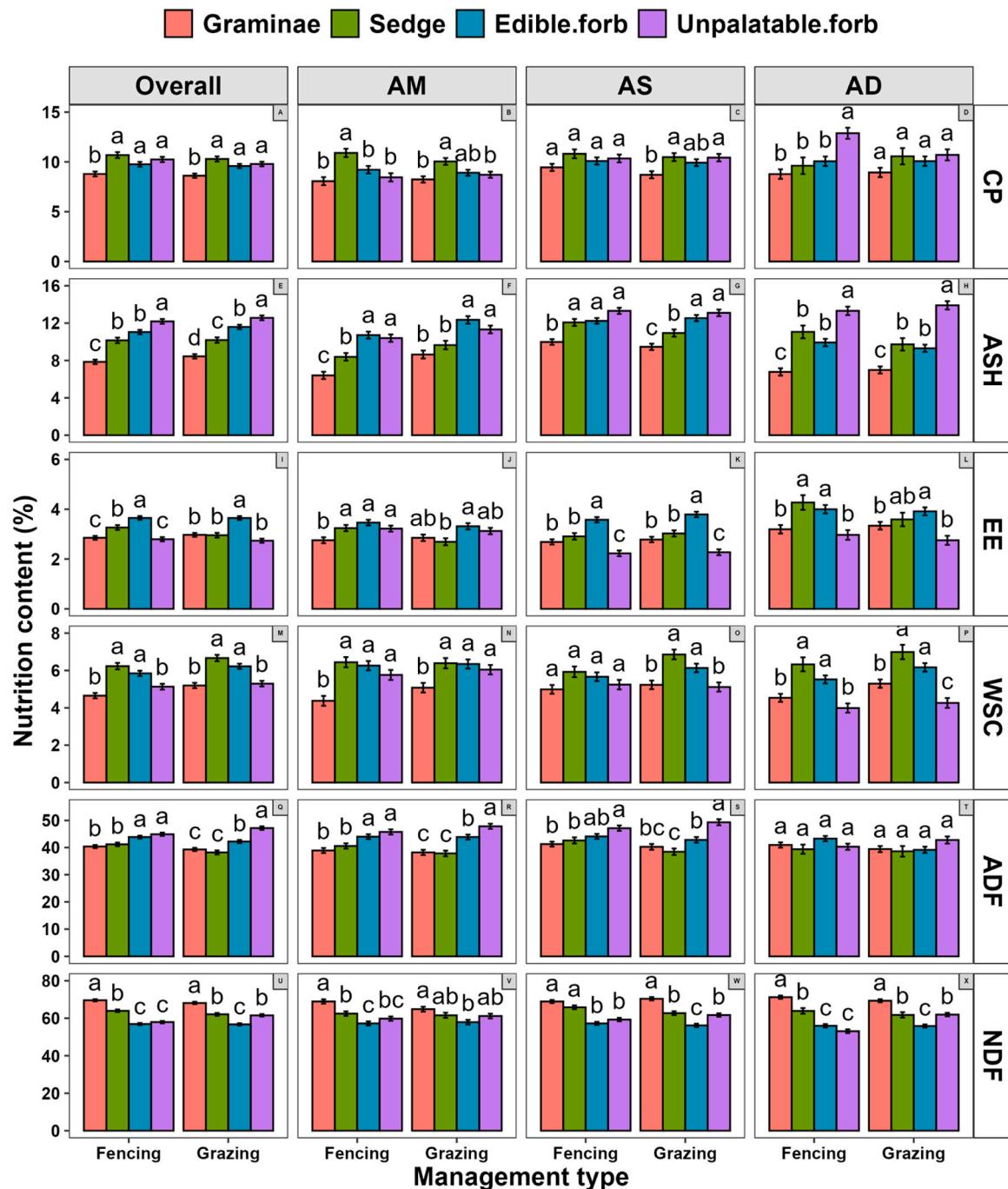


Fig. 2. Comparison of forage nutrition content in functional groups under fencing and grazing across different grassland types: "Overall" refers to all grassland types, with "AM" for alpine meadows, "AS" for alpine steppes, and "AD" for alpine desert steppes. Significance was tested using Tukey's HSD: no shared letters indicate significant differences.

varied with geographic location. For example, in alpine desert steppes, the effect of fencing on community crude protein content decreased as elevation increased.

The effects of fencing on nutrition content and pool were comprehensively regulated by geographic location, climatic factors, soil properties, and plant diversity (Fig. 6, S9–S15), with soil properties making the largest exclusive contribution. Geographic location, climatic factors, soil properties, and plant diversity not only directly influenced forage nutrition quality but also exerted indirect effects (Fig. 7, S16–S22).

3.4. Nutrition quality differences between functional groups

Significant differences in nutrition content were observed among functional groups (Fig. 2). Graminae provided high-quality structural fiber, with lower acid detergent fiber, crude protein, crude ash, ether extract, and water-soluble carbohydrates contents but higher neutral detergent fiber. Sedges exhibited balanced nutrition, characterized by higher crude protein, crude ash, and water-soluble carbohydrates contents but lower neutral detergent fiber. Edible forbs served as energy reserves, with higher ether extract, water-soluble carbohydrates, and acid detergent fiber contents but lower neutral detergent fiber. Unpalatable forbs were rich in minerals, with higher crude ash and acid

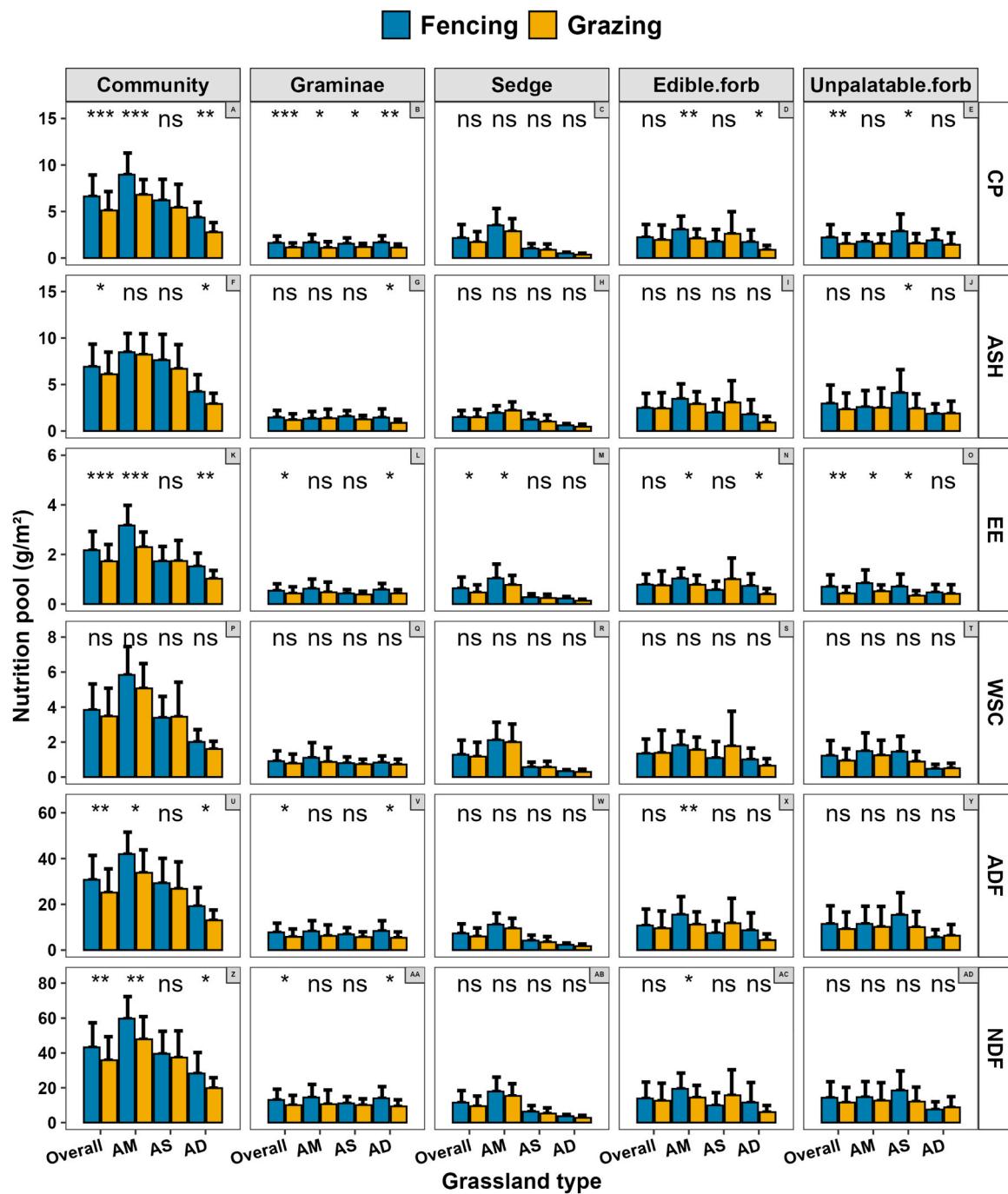


Fig. 3. Comparison of forage nutrition pool under fencing and grazing across different grassland types: (A, F, K, P, U, Z) Community, (B, G, L, Q, V, AA) Graminae, (C, H, M, R, W, AB) Sedge, (D, I, N, S, X, AC) Edible forbs, and (E, J, O, T, Y, AD) Unpalatable forbs. "Overall" refers to all grassland types, with "AM" for alpine meadows, "AS" for alpine steppes, and "AD" for alpine desert steppes. Significance was tested using a linear mixed-effects model: *** $p < 0.001$, ** $0.001 < p < 0.01$, * $0.01 < p < 0.05$, ns: not significant.

detergent fiber contents but lower ether extract and neutral detergent fiber. Additionally, grassland types and management practices influenced the differences in nutrition content among functional groups.

3.5. Comparison of methods of calculating nutrition carrying capacity

The calculation results of nutrition carrying capacity (NCC) differed between the spatial heterogeneity method and the mean value method (Fig. 8, Table S3). The spatial heterogeneity method estimated the NCC at 1.74 sheep/ha, while the mean value method yielded 1.83 sheep/ha, a difference of 5.17 %. In areas with lower actual NCC ($NCC < 1$), the

mean value method overestimated the carrying capacity while in areas with higher actual NCC ($NCC > 2.3$), the mean value method underestimated the carrying capacity.

4. Discussion

4.1. The effects of fencing on forage nutrition content and pool in alpine grasslands

Our findings supported Hypothesis (1), which indicated that fencing increased the crude protein of plant community while decreasing crude

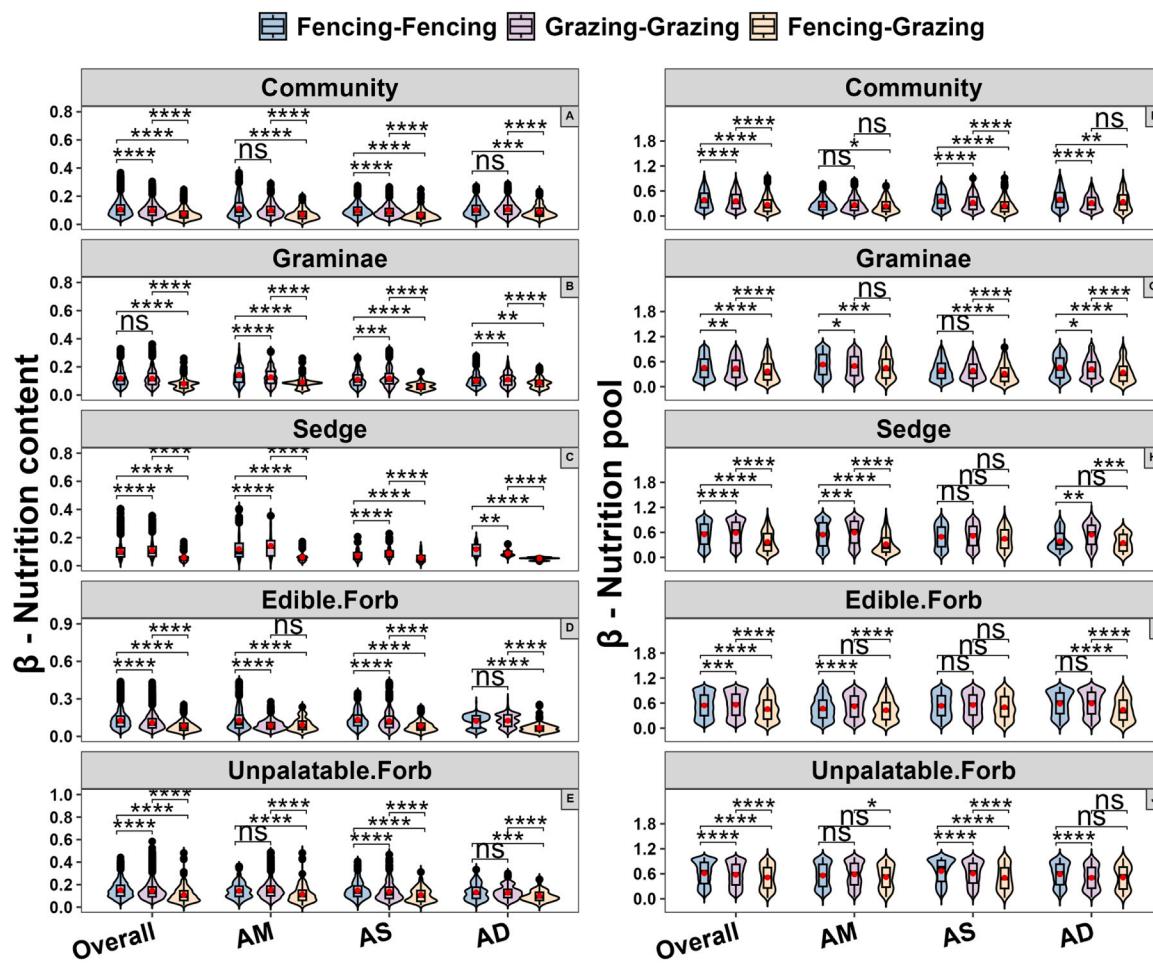


Fig. 4. The composition differences of forage nutrition content (A-E) and its pool (F-J) between fencing-fencing, grazing-grazing, and fencing-grazing conditions include: (A, F) Community, (B, G) Graminae, (C, H) Sedge, (D, I) Edible forb, and (E, J) Unpalatable forb. "Overall" refers to all grassland types, with "AM" for alpine meadows, "AS" for alpine steppes, and "AD" for alpine desert steppes. Significance was tested using the Wilcoxon rank-sum test. *** $p < 0.001$, ** $0.001 < p < 0.01$, * $0.01 < p < 0.05$, ns: not significant.

ash and water-soluble carbohydrates. This phenomenon can be attributed to several factors. First, fencing altered the proportions of plant functional groups. It increased the growth of high-crude protein forages like sedges, while reducing the growth of unpalatable, high-ash forbs (Cao et al., 2011; Yao et al., 2019a). Second, the stable growing conditions inside the fencing area changed the plants' metabolic allocation strategies, prioritizing protein synthesis to meet higher growth demands. This process reduced the investment in fast-regenerating tissues, leading to a decrease in the accumulation of secondary metabolites such as carbohydrates (Zha et al., 2022; Zhang et al., 2023a). Third, fencing may have altered the vertical distribution of plant root biomass, reducing the efficiency of phosphorus and potassium absorption from the upper soil layers, which in turn affected the crude ash content of forages. Fourth, fencing may increase the thickness of the litter layer, which can suppress the bioavailability of essential minerals like calcium and magnesium, thus affecting crude ash (Zhang et al., 2023a). Fifth, fencing can reduce soil disturbance caused by grazing. Under grazing conditions, livestock excrement's microbial decomposition may accelerate the cycling of trace soil nutrients and provide feedback to soil organic matter (Speed et al., 2013; Sitters et al., 2020). In contrast, fencing limits such microbial activity, possibly reducing nutrient cycling efficiency. Sixth, fencing can lower the surface albedo, which may increase soil temperature. This change accelerated the thermal decomposition of water-soluble carbohydrates and crude ash (Hambäck et al., 2014).

The effects of fencing on forage nutrition quality were related to

grassland types (Figs. 1–2), which could be explained by the following mechanisms. First, alpine meadows and desert steppes were significantly affected by fencing, which might be related to the differences in resource limitation and nutrient cycling between these two types of grasslands (Fig. 7, S16). The water content and soil nutrients in alpine meadows were relatively high. Fencing might promote the accumulation of soil nutrients and the absorption of elements such as nitrogen and phosphorus by plants by reducing grazing disturbance (Chen et al., 2021; Su et al., 2023), thereby improving nutrition quality. In contrast, the extreme resource scarcity in alpine desert steppes made plants highly sensitive to resource changes. Fencing may alter plant resource competition dynamics, impacting nutrition allocation (Eldridge et al., 2016; Hidalgo-Galvez et al., 2023). Second, differences in grazing intensity across grassland types may indirectly influence fencing effects. Alpine meadows, due to their higher plant biomass and nutrition productivity (Table S1, Fig. 3) and favorable climatic conditions, could experience higher grazing intensity (Wu et al., 2020), resulting in more pronounced effects of fencing in reducing grazing disturbances. Third, the selective pressures of grazing on plant functional traits (e.g., height, root distribution, and accumulation of defensive compounds) might vary among grassland types (Lu et al., 2015). Long-term high-intensity grazing in alpine meadows may drive plant evolution toward greater grazing tolerance (Yao et al., 2022), such as increasing fiber components to enhance mechanical resistance and reduce palatability, as well as decreasing carbohydrates to reduce attractiveness. Fourth, differences in livestock types across grassland types might further influence fencing

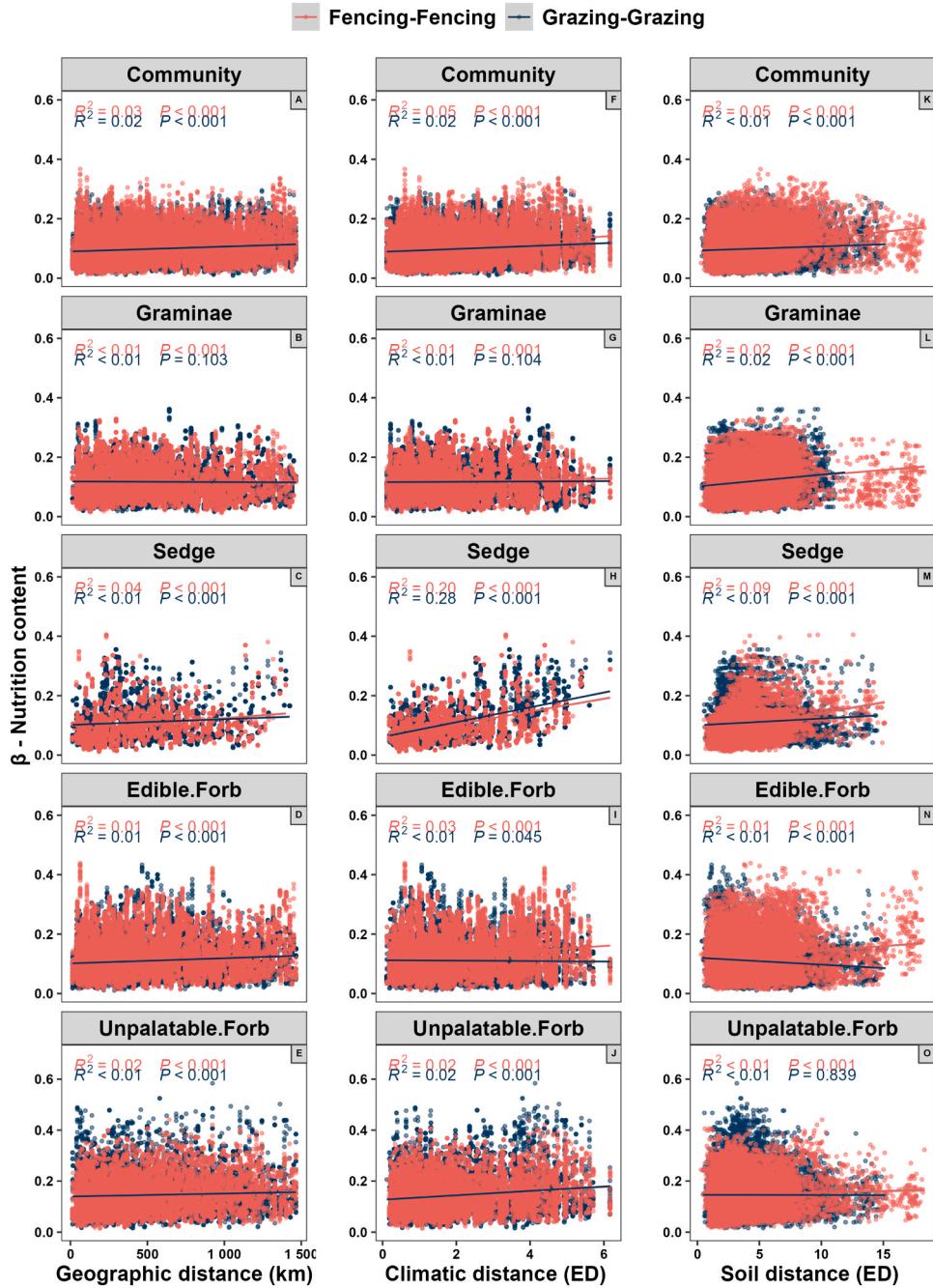


Fig. 5. The comparison of nutrition content composition differences along geographic, climatic, and soil distances under fencing-fencing and grazing-grazing conditions includes: (A, F, K) Community, (B, G, L) Graminae, (C, H, M) Sedge, (D, I, N) Edible forbs, and (E, J, O) Unpalatable forbs.

effects (Hool et al., 2020; Martin et al., 2020). In the central and eastern regions, alpine meadows and alpine steppes were primarily grazed by yaks with narrower dietary preferences, whereas alpine desert steppes in the west were mainly grazed by sheep with broader dietary preferences, resulting in distinct impacts on plant communities (Vaintrub et al., 2021). Fifth, there were significant differences in the composition of plant communities among different grassland types (Zhang et al., 2023b), and the responses of the forage nutrition quality of different functional groups to fencing varied (Figs. 1–2). The proportion of high-quality forage (such as sedges) in alpine meadows was relatively high (Table S1). Fencing might enable these plants to accumulate nutritional components more fully by restricting livestock disturbance.

Fencing heterogenized the spatial patterns of forage community nutrition quality while homogenizing the spatial patterns of nutrition

quality of certain functional groups (Fig. 5). This can be explained by several factors. On the one hand, fencing may make plant community growth more dependent on the spatial variation of natural environmental resources by reducing disturbances (Fig. 7, S16–S22). The gradient effects of longitude, latitude, and altitude directly may drive the significant differentiation of the composition of plant functional groups and the accumulation of nutritional components by influencing the distribution pattern of resources (Fu et al., 2022). For example, under fencing conditions, the contents of crude protein, ether extract, water-soluble carbohydrates, and crude ash in the community and their pool changes are significant, probably because these indicators may be directly affected by the gradients of light, water, and temperature, and fencing enhances the ability of plants to respond to environmental changes (Yao et al., 2019b). On the other hand, the heterogenizing effect

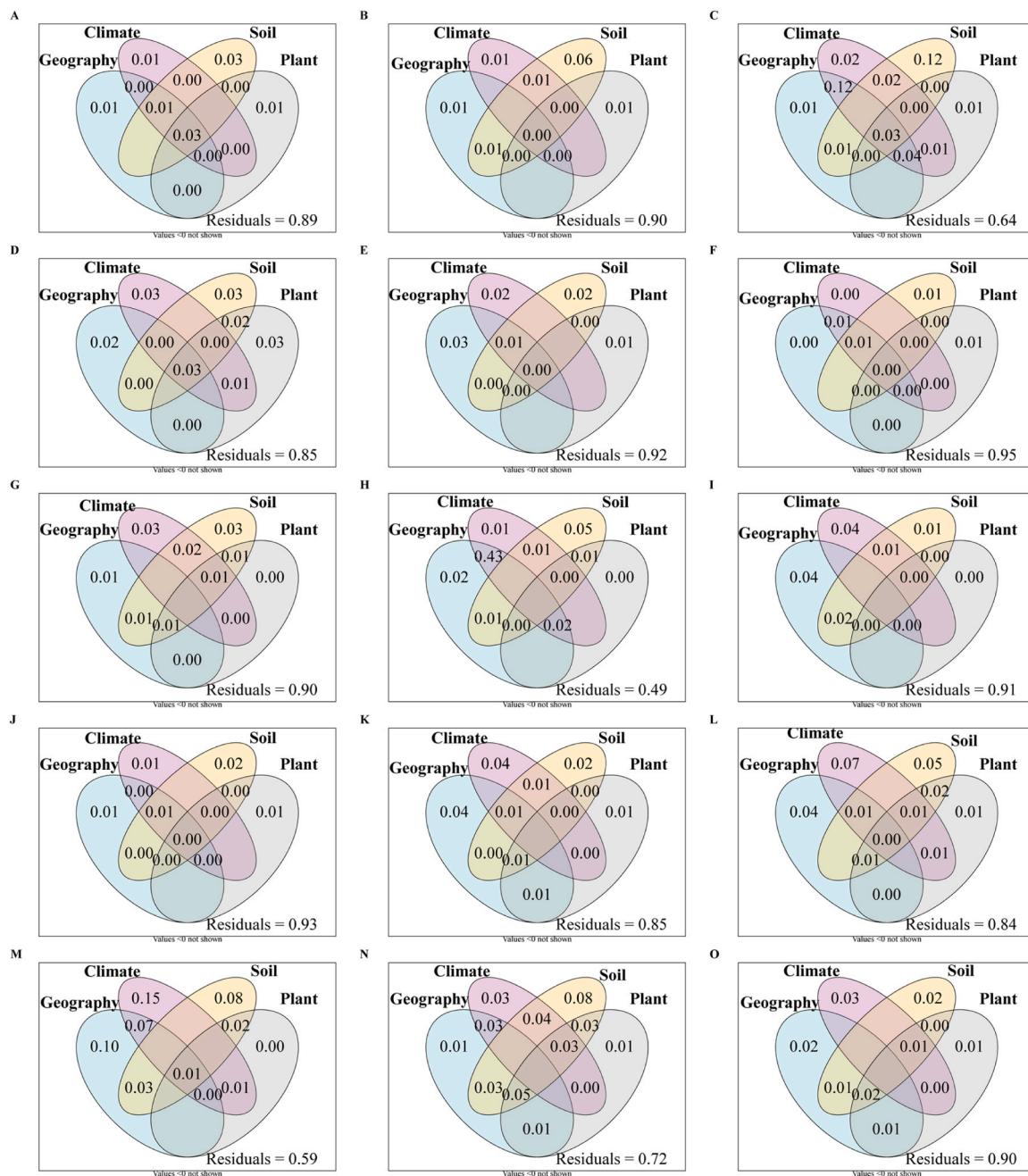


Fig. 6. The relative contribution of geographical location, climatic factors, soil properties, and plant diversities to the composition differences of forage nutrition content was analyzed under different conditions: (A-E) for fencing-fencing conditions, (F-J) for grazing-grazing conditions, and (K-O) for fencing-grazing conditions. The analysis is conducted at various levels, including: (A, F, K) at the Community level; (B, G, L) at the Graminae level; (C, H, M) at the Sedge level; (D, I, N) at the Edible forbs level; and (E, J, O) at the Unpalatable forbs level.

of fencing may also stem from the suppression of community composition dynamics caused by selective grazing and trampling behaviors of livestock (Bryant et al., 2017). Long-term grazing homogenized functional group proportions, over-utilizing high-quality plants and favoring grazing-resistant, low-quality plants (e.g., unpalatable forbs) (Venter et al., 2019), which may weaken community sensitivity to environmental gradients and lead to more uniform spatial patterns of nutrition quality. Third, fencing may result in localized homogenization of specific nutritional indicators within certain functional groups. For instance, the content of crude protein and water-soluble carbohydrates of sedges changed rapidly, probably because sedges preferentially allocated resources for the accumulation of proteins and soluble sugars under grazing disturbance (Zha et al., 2022) to enhance their

adaptability. Similarly, ether extract of unpalatable forbs showed higher response rates under grazing, which may be due to their strong grazing tolerance and resource allocation strategies (Gavier-Pizarro et al., 2010), prioritizing fat accumulation to enhance survival in nutrient-limited conditions. These localized homogenizing effects within functional groups and the overall heterogenizing trend created the complex dynamics of the effects of fencing on the spatial patterns of nutrition quality (Fu et al., 2022).

Fencing effects on forage nutrition content and pools had distinct spatial patterns (Figs. S23–S29). In high latitude and altitude regions, plant communities relied more on limited environmental resources for growth, with low temperatures, short growing seasons, and nutrient deficiencies prompting plants to prioritize resource allocation toward

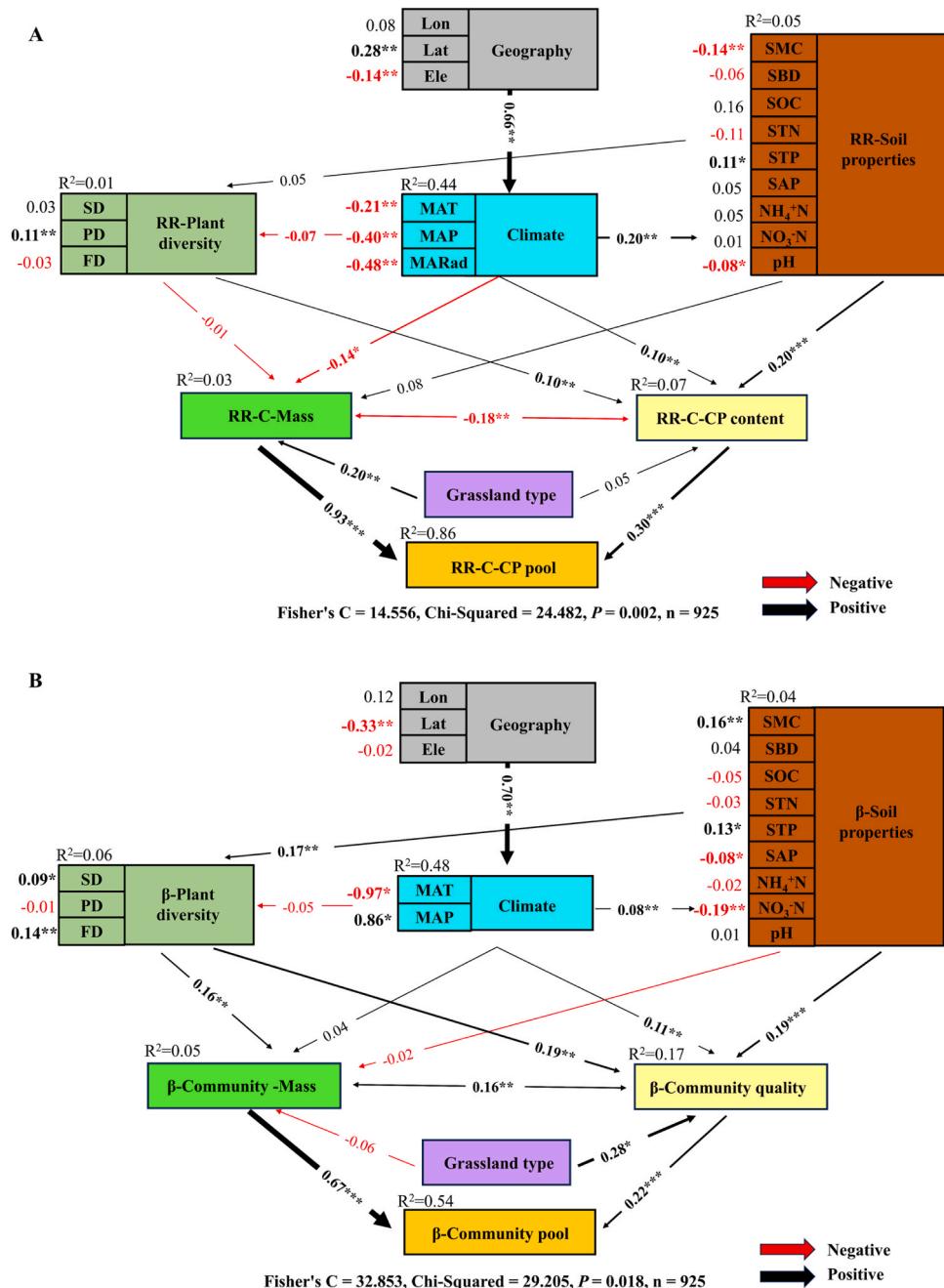


Fig. 7. The piecewise structural equation models (PSEM) analysis of crude protein (CP) and the composition differences of nutrition quality. (A) fencing effects on forage community CP content; (B) fencing effects on composition differences of nutrition quality of forage community CP. "RR" referred to fencing effects. The β value represented the compositional differences of nutrition quality or pool among different sites under fencing and grazing conditions. The red line indicates a negative correlation, and the black line indicates a positive correlation. *** $p < 0.001$, ** $0.001 < p < 0.01$, * $0.01 < p < 0.05$.

mineral accumulation (Yao et al., 2019a; Küsters et al., 2021) to meet basic survival needs and adapt to environmental stresses. This trend was particularly evident in the gramineae functional group, likely due to their higher environmental adaptability (Ren et al., 2016a). With increasing longitude (with an increase in precipitation), higher water availability likely reduced the plant demand for minerals (White et al., 2014), weakening the positive effect of fencing on crude ash content. In addition, regarding structural components, increased precipitation promoted plant growth and metabolism (Yoshihara et al., 2022), enhancing the impact of fencing on fiber content. This may be because plants allocated more resources to cell wall components to strengthen structural stability (Fu et al., 2022; Zhang et al., 2023a). As latitude increased, the effect of fencing on water-soluble carbohydrate content of

sedges weakened. Sedges, being a fencing-sensitive functional group (Fig. 2), faced limitations in radiation and nutrition availability, which restricted soluble sugar accumulation (Fig. S20). Similarly, as elevation increased, the impact of fencing on ether extract and water-soluble carbohydrates of sedges decreased, which might be related to resource scarcity and metabolic constraints. Under such conditions, sedges prioritized resource allocation toward survival-related compounds rather than energy storage (Zha et al., 2022). In addition, there were significant interactions between climatic conditions and grazing intensity on forage nutrition quality and their pools (Fig. 7). On the one hand, climate conditions could indirectly influence forage nutritional quality and its pool through their direct impact on grazing intensity (i.e. the ratio of aboveground biomass between fencing and grazing

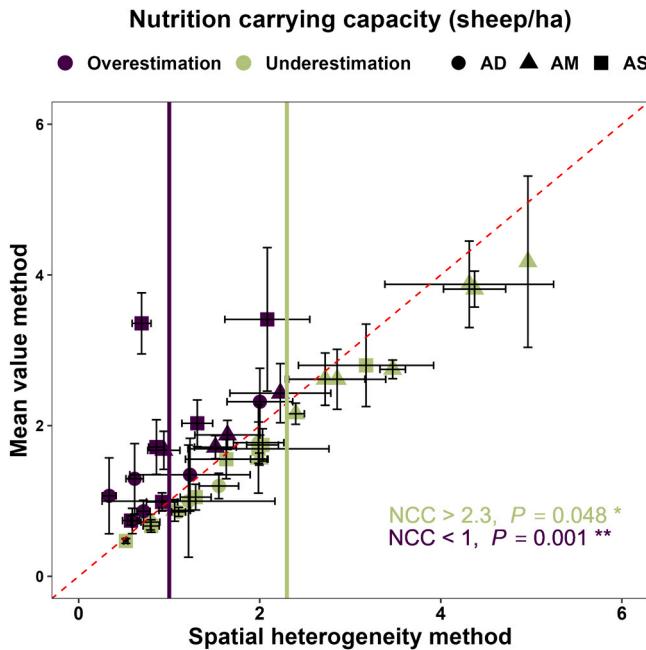


Fig. 8. The differences in results between the two methods of calculating nutrition carrying capacity were as follows: spatial heterogeneity method used the actual edible forage ratio for each sampling point, while the mean value method used the average edible forage ratio across all sampling points. Significance was tested using a paired *t*-test. "AM" refers to alpine meadows, with "AS" for alpine steppes, and "AD" for alpine desert steppes.

conditions). On the other hand, climate conditions can indirectly affect grazing intensity through their direct impact on soil properties and plant diversity.

The composition of forage nutrition quality showed greater differences among fencing sites compared to grazing sites (Fig. 4). This could be explained by the following reasons. First, fencing created more stable growth conditions for plants, but this stability may amplify microenvironmental differences between sites. Differences in soil fertility, microclimatic conditions, and plant diversity among different sites within the fencing area were likely to be more noticeable (Fig. 7), thus resulting in greater differences in nutrition composition. Second, the movement and selective grazing behavior of herbivores across grazing sites reduced differences in plant composition (Judy et al., 2015; Ringmark et al., 2019). Grazing imposed sustained selection pressure on plant communities, leading to more similar species composition and functional traits (Ruggieri et al., 2020), which ultimately diminished differences in nutritional components. Third, livestock preferentially grazed on high-nutritional value plants, such as sedges (Yao et al., 2019b), leading to a decrease in the biomass of these species. Meanwhile, grazing-tolerant with low-nutrition plants (e.g., those with high fiber and low soluble carbohydrate content) became dominant (Marchiori et al., 2012; Martins-Noguerol et al., 2023), making the forage nutrition components more consistent among grazing sites.

4.2. Nutrition quality differences between functional groups

Our results did not fully align with Hypothesis (2), which may be attributed to the following mechanisms. First, the resource-use efficiency (light, water, nutrients, etc.) of different functional groups determines their nutrition allocation and accumulation strategies (Yao et al., 2019b). For instance, gramineas adopted a strategy of high resource utilization efficiency (Pompeiano et al., 2013) and mainly accumulated structural carbohydrates (Fig. 2). This was beneficial for resisting herbivore grazing and at the same time enhanced drought tolerance and lodging resistance. In contrast, unpalatable forbs, with

lower resource-use efficiency, were more inclined to accumulate defensive compounds (e.g., secondary metabolites) (Kopp et al., 2020) to counter herbivore attacks. Second, differences in photosynthetic capacity among functional groups (Mathur et al., 2018) may directly influence their nutrition accumulation. Third, there were significant differences in the composition of rhizosphere and phyllosphere microbial communities among functional groups (Ling et al., 2022), and they may impact plant nutrition quality through mechanisms such as nitrogen fixation and resistance regulation. For example, unpalatable forbs (e.g., legumes such as *Astragalus* and *Oxytropis*) exhibit strong root nodule nitrogen fixation capabilities, enhancing their overall nitrogen accumulation. Fourth, differences in the allocation of nutrition and photosynthetic products across organs among functional groups may further amplify variations in nutrition quality (Tränkner et al., 2018). Graminae have a high proportion of stems (Ren et al., 2016b), and mainly accumulate cellulose, while sedges have a more balanced ratio of stems to leaves (Escudero and Hipp, 2013), enabling them to accumulate structural materials while enriching nutrition in leaves.

The differences in nutrition quality among functional groups were related to grassland types (Fig. 2). This could be explained by the following reasons. First, changes in resources such as climate and soil might regulate the differences in nutrition quality among functional groups (Lu et al., 2015). In alpine meadows with relatively abundant resources, the competition pressure among functional groups was relatively low (Liu et al., 2022) resulting in relatively small differences in nutritional quality. In alpine steppes with moderate resource availability, the competition between functional groups was likely more intense. In resource-scarce alpine desert steppes, these differences were further amplified (Xu et al., 2018). Second, the functional group composition varied across grassland types (Table S1). The relative importance value of sedges was highest in alpine meadows, while gramineas and edible forbs had the highest relative importance value in alpine desert steppes. Unpalatable forbs were most dominant in alpine steppes. Third, differences in phenology among grassland types may influence the accumulation period of nutrition (Ren et al., 2020). Alpine meadows had the earliest green-up and latest senescence, with the longest growing season, thus promoting facile nutrition accumulation. In contrast, alpine desert steppes experienced the latest green-up, earliest senescence, and the shortest growing season, limiting the time available for nutrition accumulation.

Fencing altered the differences in nutrition quality among functional groups (Fig. 2). This can be explained by several reasons. First, fencing created a more equitable and less competitive resource allocation environment for functional groups (Zhang et al., 2023a). Through feeding preferences and mechanical disturbances, grazing altered the competitive relationships among functional groups (Eldridge et al., 2016), reducing the nutrition quality of some groups (e.g., sedges and gramineas) while giving unpalatable forbs an advantage in fiber accumulation (Zha et al., 2022). Second, fencing may alter the species composition within functional groups (Bretzel et al., 2016), as different species exhibited varying nutrition quality. Third, fencing could influence the phenological traits of functional groups by altering the distribution of deposited litter. For example, litter within fencing areas may differentially affect the green-up period of functional groups (Stavi, 2020), and the temperature sensitivity of nutrition accumulation could vary among different functional groups. Fourth, the effects of fencing on compensatory growth may further explain changes in nutrition differences among functional groups (Song et al., 2020). After grazing, compensatory growth was usually accompanied by an improvement in nutrition quality (e.g., increased crude protein and reduced fiber components), and the compensatory growth abilities of different functional groups were different (Yao et al., 2019b).

4.3. Trade-offs between yield and nutrition quality

Our findings supported hypothesis (3) (Fig. S30). These inconsistent

relationships might be related to differences in resource allocation strategies among different functional groups (Zhang et al., 2023b). Sedges, with well-developed root systems and long-term adaptation to cold and humid environments (Yao et al., 2022), exhibited high resource-use efficiency. This allowed them to maintain high crude protein and ether extract while increasing yield, without sacrificing high-value nutrition for higher productivity. Graminae demonstrated a stronger trade-off relationship. With the increase in yield, they exhibited a strong trend of fibrosis to enhance mechanical strength and lodging resistance (Grant et al., 2014), but resulted in declines in crude protein and ether extract. Edible forbs, characterized by their highly nutritious leaves, typically had lower mineral accumulation capacity compared to deep-rooted plants (Bhatti et al., 2018). During rapid growth, the dilution effect on minerals may become more apparent, potentially leading to a decrease in crude ash. Unpalatable forbs contained higher levels of secondary metabolites, such as alkaloids and bitter glycosides (Zhao et al., 2010; Lu et al., 2012). These compounds were critical for stress tolerance and defense but require resource consumption, which may limit the accumulation of crude protein and ether extract.

Fencing weakened the trade-off between forage yield and the content of crude protein and ether extract (Figs. S30). This can be explained by several reasons. First, livestock tended to preferentially graze on the tender tissues of plants, which had relatively high-value nutritional components (Thomas et al., 2021). In contrast, under fencing conditions, due to the lack of selective grazing by livestock, the proportion of tender tissues in plants was relatively high. Second, plants tended to allocate carbon, nitrogen, and phosphorus preferentially to regenerative tissues under grazing conditions (Chen et al., 2021) to cope with repeated grazing. However, the lack of such pressure under fencing conditions might make the forage yield and nutrient allocation more balanced (Tahmasebi et al., 2020). Third, differences in functional group composition between fencing and grazing conditions, particularly the higher proportion of sedges within fencing areas (Table S1), and the trade-off relationship between the yield and nutrition quality of sedges was relatively weak, which might further weaken the overall trade-off characteristics. Fourth, grazing might increase the micro-environmental temperature by reducing vegetation cover (Maestre et al., 2022). Climate warming often led to an increase in forage yield and a decrease in crude protein and ether extract (Li et al., 2018; Xu et al., 2018), thereby strengthening the trade-off between yield and nutrition quality under grazing conditions.

4.4. Calculation of nutrition carrying capacity

The spatial heterogeneity method was found to more accurately reflect the potential status of grassland nutrition carrying capacity (Fig. 8). Its main advantage lay in that it fully took into account the spatial heterogeneity of the nutritional quality of grasslands. The resource distribution in grasslands was not uniform in space. There were significant differences in soil nutrients, precipitation, and vegetation communities among different sites. By calculating the proportion of edible forage for each site, the spatial heterogeneity method captured the details of local resource distribution. In low-nutrition regions, the spatial heterogeneity method identified resource-poor areas, avoiding the overestimation of nutrition carrying capacity and reducing the risk of grassland degradation caused by overgrazing. In high-nutrition regions, this method detected high-yield areas with high-quality forage, accurately reflecting their nutrition carrying capacity potential and avoiding the underutilization of resources. This sensitivity and precision made the results of the spatial heterogeneity method closer to reality, providing a more scientific and reliable basis for grassland management and sustainable utilization.

4.5. Limitations and perspectives

Although this study provided important insights into forage nutrition

quality in Tibetan Plateau grasslands, there were still some limitations. First, this study did not distinguish the differences between rotational and continuous grazing. For example, rotational grazing, by providing periodic vegetation recovery periods, may promote nutritional balance, whereas continuous grazing tends to lead to the decline of highly palatable species. Second, although rodents (such as plateau pika) and insects play key roles in fencing ecosystems, this study did not monitor the population dynamics of small animals, leading to an incomplete assessment of the overall impact of fencing on grass-livestock interactions. Third, the spatial heterogeneity of grazing intensity was not fully considered. Fourth, this study represented only one year of analysis and did not reveal the multi-year effects of fencing on forage nutrition. Fifth, although grazing is an integral part of natural ecological feedback cycles, this study did not fully account for the ecological adaptability of grazing. As a selective pressure in the millennia-long evolution of alpine grasslands, grazing has shaped plant community resilience and rapid regeneration strategies. Fencing management essentially decouples this co-evolutionary relationship—when the physical disturbances (e.g., feeding, trampling) and chemical regulation (e.g., manure feedback) by livestock are suddenly removed, the system is forced into a non-equilibrium transition process. Additionally, in terms of data analysis, high correlations among multiple independent variables may lead to unstable variance partitioning, thereby affecting the accuracy of variance partitioning analysis. In piecewise structural equation modeling, model design may face challenges of overfitting. Improper model selection, especially when dealing with multiple potential variables and pathways, could result in biased conclusions. Therefore, future studies should establish a multi-factor interaction model by integrating a four-dimensional framework: grazing system (rotational/continuous grazing) × fencing duration × small animal activity × climate fluctuations. We recommend combining long-term fixed-site observations with pastoralist interviews. For instance, monitoring rodent density, soil nematode communities, and plant secondary metabolite content along fencing gradients (e.g., a 1–15 year fenced plot sequence) could help identify ecological thresholds of fencing management. Additionally, stable isotope techniques (e.g., δ15 N tracing) could be introduced to analyze nutrient cycling pathways under different grazing intensities, providing theoretical guidance for the precise determination of nutritional carrying capacity standards.

5. Conclusions

Our findings challenged four persistent paradigms in grassland management. First, in light of the available evidence, it was observed that the implementation of fencing measures typically lead to a discernible enhancement in the crude protein content of forage community. This improvement, however, came at the cost of a reduction in both the crude ash and water-soluble carbohydrate content of forage community.

Moreover, contrary to initial expectations, the nutrition quality of sedges did not surpass that of the other functional groups present in the study area. This unexpected outcome challenged the preconceived notion regarding the superiority of sedges in terms of nutrition.

Third, the widely assumed principle of a necessary trade-off between forage yield and nutritional quality was found not to be universally applicable. There were instances where an increase in forage yield did not necessarily result in a corresponding decline in nutrition quality, and vice versa. This realization underscored the complexity of the relationship between these two important factors in forage production.

Last, it was evident that relying on a fixed proportion of edible forage as a sole metric for assessing the potential nutrition carrying capacity was an oversimplified approach. Such a method failed to account for the diverse and dynamic nature of forage composition and quality, as well as the intricate interactions between different functional groups. A more comprehensive and flexible approach was required to accurately evaluate the nutrition carrying capacity of an area, taking into consideration

the various factors that influence forage quality and availability. This may involve a more detailed analysis of forage composition, as well as an assessment of the ecological and environmental factors that impact forage production and quality over time.

CRediT authorship contribution statement

Yuanpeng Zhu: Writing – review & editing, Writing – original draft. **Peng Zhang:** Writing – review & editing, Writing – original draft. **Gang Fu:** Writing – review & editing, Writing – original draft. **Xianzhou Zhang:** Writing – review & editing, Writing – original draft. **Yong Qin:** 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.2025.109828](https://doi.org/10.1016/j.agee.2025.109828).

Data availability

Data will be made available on request.

References

- Bhatti, S.S., Kumar, V., Sambyal, V., Singh, J., Nagpal, A.K., 2018. Comparative analysis of tissue compartmentalized heavy metal uptake by common forage crop: A field experiment. *Catena* 160, 185–193. <https://doi.org/10.1016/j.catena.2017.09.015>.
- Bollen, K.A., Davis, W.R., 2009. Two Rules of Identification for Structural Equation Models. *Struct. Equ. Model. A Multidiscip. J.* 16 (3), 523–536. <https://doi.org/10.1080/10705510903008261>.
- Bretzel, F., Vannucchi, F., Romano, D., Malorgio, F., Benvenuti, S., Pezzarossa, B., 2016. Wildflowers: From conserving biodiversity to urban greening A review. *Urban For. Urban Green.* 20, 428–436. <https://doi.org/10.1016/j.ufug.2016.10.008>.
- Bryant, R.H., Miller, M.E., Greenwood, S.L., Edwards, G.R., 2017. Milk yield and nitrogen excretion of dairy cows grazing binary and multispecies pastures. *Grass Forage Sci.* 72 (4), 806–817. <https://doi.org/10.1111/gfs.12274>.
- Cao, J., Holden, N.M., Lü, X.T., Du, G., 2011. The effect of grazing management on plant species richness on the Qinghai-Tibetan Plateau. *Grass Forage Sci.* 66 (3), 333–336. <https://doi.org/10.1111/j.1365-2494.2011.00793.x>.
- Chen, J., Luo, Y., Xia, J., Zhou, X., Niu, S., Shelton, S., et al., 2018. Divergent responses of ecosystem respiration components to livestock exclusion on the Qinghai Tibetan Plateau. *Land Degrad. Dev.* 29 (6), 1726–1737. <https://doi.org/10.1002/ldr.2981>.
- Chen, X.P., Zhang, T., Guo, R.Y., Li, H.Y., Zhang, R., Degen, A.A., et al., 2021. Fencing enclosure alters nitrogen distribution patterns and tradeoff strategies in an alpine meadow on the Qinghai-Tibetan Plateau. *Catena* 197. <https://doi.org/10.1016/j.catena.2020.104948>.
- Chen, B.X., Zhang, X.Z., Tao, J., Wu, J.S., Wang, J.S., Shi, P.L., et al., 2014. The impact of climate change and anthropogenic activities on alpine grassland over the Qinghai-Tibet Plateau. *Agric. For. Meteor.* 189, 11–18. <https://doi.org/10.1016/j.agrformet.2014.01.002>.
- Chen, J., Zhou, X., Wang, J., Hruska, T., Shi, W., Cao, J., et al., 2016. Grazing exclusion reduced soil respiration but increased its temperature sensitivity in a Meadow Grassland on the Tibetan Plateau. *Ecol. Evol.* 6 (3), 675–687. <https://doi.org/10.1002/ece3.1867>.
- Ding, R., Qin, Y., Li, T.Y., Fu, G., 2024. Exploring spatiotemporal dynamics in temporal stability of soil carbon, nitrogen, phosphorus, and pH in Tibetan grasslands. *Geoderma* 451. <https://doi.org/10.1016/j.geoderma.2024.117062>.
- Du, C.J., Zhou, G.Y., Gao, Y.H., 2022. Grazing exclusion alters carbon flux of alpine meadow in the Tibetan Plateau. *Agric. For. Meteor.* 314. <https://doi.org/10.1016/j.agrformet.2021.108774>.
- Dumont, B., Andueza, D., Niderkorn, V., Lüscher, A., Porqueddu, C., Picon-Cochard, C., 2015. A meta-analysis of climate change effects on forage quality in grasslands: specificities of mountain and Mediterranean areas. *Grass Forage Sci.* 70 (2), 239–254. <https://doi.org/10.1111/gfs.12169>.
- Elbridge, D.J., Poore, A.G.B., Ruiz-Colmenero, M., Letnic, M., Soliveres, S., 2016. Ecosystem structure, function, and composition in rangelands are negatively affected by livestock grazing. *Ecol. Appl.* 26 (4), 1273–1283. <https://doi.org/10.1890/15-1234>.
- Escudero, M., Hipp, A., 2013. Shifts in Diversification Rates and Clade Ages Explain Species Richness in Higher-Level Sedge Taxa (*Cyperaceae*). *Am. J. Bot.* 100 (12), 2403–2411. <https://doi.org/10.3732/ajb.1300162>.
- Fu, G., Wang, J., Sun, W., 2022. Response of forage nutritional quality to climate change and human activities in alpine grasslands. *Sci. Total Environ.* 845. <https://doi.org/10.1016/j.scitotenv.2022.157552>.
- Gavier-Pizarro, G.I., Radeloff, V.C., Stewart, S.I., Huebner, C.D., Keuler, N.S., 2010. Housing is positively associated with invasive exotic plant species richness in New England, USA. *Ecol. Appl.* 20 (7), 1913–1925. <https://doi.org/10.1890/09-2168.1>.
- Gierus, M., Kleen, J., Loges, R., Taube, F., 2012. Forage legume species determine the nutritional quality of binary mixtures with perennial ryegrass in the first production year. *Anim. Feed Sci. Technol.* 172 (3–4), 150–161. <https://doi.org/10.1016/j.anifeedsci.2011.12.026>.
- Goeman, J.J., Solari, A., 2022. Comparing Three Groups. *Am. Stat.* 76 (2), 168–176. <https://doi.org/10.1080/00031305.2021.2002188>.
- Grabchak, M., 2023. How Do We Perform a Paired *t*-Test When We Don't Know How to Pair? *Am. Stat.* 77 (2), 127–133. <https://doi.org/10.1080/00031305.2022.2115552>.
- Grant, K., Kreyling, J., Dienstbach, L.F.H., Beierkuhnlein, C., Jentsch, A., 2014. Water stress due to increased intra-annual precipitation variability reduced forage yield but raised forage quality of a temperate grassland. *Agric. Ecosyst. Environ.* 186, 11–22. <https://doi.org/10.1016/j.agee.2014.01.013>.
- Hambäck, P.A., Inouye, B.D., Andersson, P., Underwood, N., 2014. Effects of plant neighborhoods on plant–herbivore interactions: resource dilution and associational effects. *Ecology* 95 (5), 1370–1383. <https://doi.org/10.1890/13-0793.1>.
- Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* 80 (4), 1150–1156. <https://doi.org/10.2307/177062>.
- Hidalgo-Galvez, M.D., Matías, L., Cambrollé, J., Gutiérrez, E., Pérez-Ramos, I.M., 2023. Impact of climate change on pasture quality in Mediterranean dehesas subjected to different grazing histories. *Plant Soil* 488 (1–2), 465–483. <https://doi.org/10.1007/s11104-023-05986-9>.
- Hool, N., Schüpbach-Regular, G., Thomann, B., 2020. Livestock management and veterinary services for cattle and pigs in Switzerland. *Schweiz. Arch. Tierheilkd.* 162 (5), 293–306. <https://doi.org/10.17236/sat00258>.
- Ju, W., Fang, L., Shen, G., Delgado-Baquerizo, M., Chen, J., Zhou, G., et al., 2024. New perspectives on microbiome and nutrient sequestration in soil aggregates during long-term grazing exclusion. *Glob. Change Biol.* 30 (1). <https://doi.org/10.1111/gcb.17027>.
- Judy, J.V., Jenkins, K.H., Klopfenstein, T.J., Stalker, L.A., Volesky, J.D., 2015. Effects of stocking rate on forage nutrient composition of Nebraska Sandhills upland range when grazed in early summer. *J. Anim. Sci.* 93 (9), 4343–4349. <https://doi.org/10.2527/jas.2015-9185>.
- Kopp, T., Abdel-Tawab, M., Mizraikoff, B., 2020. Extracting and Analyzing Pyrrolizidine Alkaloids in Medicinal Plants: A Review. *Toxins* 12 (5). <https://doi.org/10.3390/toxins12050320>.
- Küsters, J., Pötsch, E.M., Resch, R., Gierus, M., 2021. The effect of summer water stress on the nutritive value of orchard grass (*Dactylis glomerata L.*) in permanent grassland under increased temperature and elevated atmospheric CO₂. *Ecol. Indic.* 125. <https://doi.org/10.1016/j.ecolind.2021.107566>.
- Li, S.W., Fu, G., 2023. Impacts of Anthropogenic Activities and Climate Change on Forage Nutrition Storage in Tibetan Grasslands. *PlantsBasel* 12 (14). <https://doi.org/10.3390/plants12142735>.
- Li, C.Y., Peng, F., Xue, X., You, Q.G., Lai, C.M., Zhang, W.J., et al., 2018. Productivity and Quality of Alpine Grassland Vary With Soil Water Availability Under Experimental Warming. *Front. Plant Sci.* 9. <https://doi.org/10.3389/fpls.2018.01790>.
- Ling, N., Wang, T.T., Kuzavkov, Y., 2022. Rhizosphere bacteriome structure and functions. *Nat. Commun.* 13 (1). <https://doi.org/10.1038/s41467-022-28448-9>.
- Liu, Y.F., Zhang, Z.C., Liu, Y., Cui, Z., Shi, J.J., Wang, Y.L., et al., 2022. Shrub encroachment enhances the infiltration capacity of alpine meadows by changing the community composition and soil conditions. *Catena* 213. <https://doi.org/10.1016/j.catena.2022.106222>.
- Lu, H., Wang, S.-S., Zhou, Q.-W., Zhao, Y.-N., Zhao, B.-Y., 2012. Damage and control of major poisonous plants in the western grasslands of China - a review. *Rangel. J.* 34 (4), 329–339. <https://doi.org/10.1071/rj12057>.
- Lu, X.Y., Yan, Y., Sun, J., Zhang, X.K., Chen, Y.C., Wang, X.D., et al., 2015. Carbon, nitrogen, and phosphorus storage in alpine grassland ecosystems of Tibet: effects of grazing exclusion. *Ecol. Evol.* 5 (19), 4492–4504. <https://doi.org/10.1002/ee.3173>.
- Ma, Z.Y., Liu, H.Y., Mi, Z.R., Zhang, Z.H., Wang, Y.H., Xu, W., et al., 2017. Climate warming reduces the temporal stability of plant community biomass production. *Nat. Commun.* 8. <https://doi.org/10.1038/ncomms15378>.

- Maestre, F.T., Le Bagousse-Pinguet, Y., Delgado-Baquerizo, M., Eldridge, D.J., Saiz, H., Berdugo, M., et al., 2022. Grazing and ecosystem service delivery in global drylands. *Science* 378 (6622), 915–920. <https://doi.org/10.1126/science.abq4062>.
- Marchiori, E., Sturaro, E., Ramanzin, M., 2012. Wild red deer (*Cervus elaphus L.*) grazing may seriously reduce forage production in mountain meadows. *Ital. J. Anim. Sci.* 11 (1). <https://doi.org/10.4081/ijas.2012.e9>.
- Martin, G., Barth, K., Benoit, M., Brock, C., Destruel, M., Dumont, B., et al., 2020. Potential of multi-species livestock farming to improve the sustainability of livestock farms: A review. *Agric. Syst.* 181. <https://doi.org/10.1016/j.agsy.2020.102821>.
- Martins-Noguerol, R., Moreno-Pérez, A.J., Pedroche, J., Gallego-Tévar, B., Cambrollé, J., Matías, L., et al., 2023. Climate change alters pasture productivity and quality: Impact on fatty acids and amino acids in Mediterranean silvopastoral ecosystems. *Agric. Ecosyst. Environ.* 358. <https://doi.org/10.1016/j.agee.2023.108703>.
- Mathur, S., Jain, L., Jajoo, A., 2018. Photosynthetic efficiency in sun and shade plants. *Photosynthetica* 56 (1), 354–365. <https://doi.org/10.1007/s11099-018-0767-y>.
- Mikhailova, E.A., Bryant, R.B., Cherney, D.J.R., Post, C.J., Vassenev, I.I., 2000. Botanical composition, soil and forage quality under different management regimes in Russian grasslands. *Agric. Ecosyst. Environ.* 80 (3), 213–226. [https://doi.org/10.1016/s0167-8809\(00\)00148-1](https://doi.org/10.1016/s0167-8809(00)00148-1).
- Ng, H.K.T., Balakrishnan, N., 2004. Wilcoxon-type rank-sum precedence tests. *Aust. N. Z. J. Stat.* 46 (4), 631–648. <https://doi.org/10.1111/j.1467-842X.2004.00358.x>.
- Pompeiano, A., Guglielminetti, L., Bargiacchi, E., Miele, S., 2013. Responses in chemical traits and biomass allocation of *Arundo donax L.* to deficit resources in the establishment year. *Chil. J. Agric. Res.* 73 (4), 377–384. <https://doi.org/10.4067/s0718-58392013000400008>.
- Qin, Y., Lian, T.Y., Zhang, X.Z., Fu, G., 2024. Reshaping the spatiotemporal patterns of temporal stability of forage nutrition quality in alpine grasslands of the Qinghai-Tibet Plateau: Spatial homogeneity, overall decline and localized increases. *Sci. Total Environ.* 954. <https://doi.org/10.1016/j.scitotenv.2024.176404>.
- Qin, Y., Sun, W., Li, S.W., Xu, L.H., Zhang, X.Z., Fu, G., 2025. Uncovering the multi-fencing effects: Changes in plant diversity across dimensions and spatio, and the relationship between diversity and stability. *J. Environ. Manag.* 373. <https://doi.org/10.1016/j.jenvman.2024.124019>.
- Reich, P.B., Sendall, K.M., Stefanek, A., Rich, R.L., Hobbie, S.E., Montgomery, R.A., 2018. Effects of climate warming on photosynthesis in boreal tree species depend on soil moisture. *Nature* 562 (7726), 263–267. <https://doi.org/10.1038/s41586-018-0582-4>.
- Ren, H.Y., Han, G.D., Lan, Z.C., Wan, H.W., Schnbach, P., Gierus, M., et al., 2016a. Grazing effects on herbage nutritive values depend on precipitation and growing season in Inner Mongolian grassland. *J. Plant Ecol.* (006) 009. <https://doi.org/10.1093/jpe/rtw011>.
- Ren, H.Y., Han, G.D., Schoenbach, P., Gierus, M., Taube, F., 2016b. Forage nutritional characteristics and yield dynamics in a grazed semiarid steppe ecosystem of Inner Mongolia, China. *Ecol. Indic.* 60, 460–469. <https://doi.org/10.1016/j.ecolind.2015.07.027>.
- Ren, S.L., Li, Y.T., Peichl, M., 2020. Diverse effects of climate at different times on grassland phenology in mid-latitude of the Northern Hemisphere. *Ecol. Indic.* 113. <https://doi.org/10.1016/j.ecolind.2020.106260>.
- Ringmark, S., Skarin, A., Jansson, A., 2019. Impact of Year-Round Grazing by Horses on Pasture Nutrient Dynamics and the Correlation with Pasture Nutrient Content and Fecal Nutrient Composition. *Animals* 9 (8). <https://doi.org/10.3390/ani9080500>.
- Ruggieri, A.C., Cardoso, A.D., Ongarotto, F., Casagrande, D.R., Barbero, R.P., Brito, L.D., et al., 2020. Grazing Intensity Impacts on Herbage Mass, Sward Structure, Greenhouse Gas Emissions, and Animal Performance: Analysis of *Bracharia* Pastureland. *Agron. Basel* 10 (11). <https://doi.org/10.3390/agronomy10111750>.
- Seibert, R., Donath, T.W., Moser, G., Laser, H., Grünhage, L., Schmid, T., et al., 2021. Effects of long-term CO₂ enrichment on forage quality of extensively managed temperate grassland. *Agric. Ecosyst. Environ.* 312. <https://doi.org/10.1016/j.agee.2021.107347>.
- Sitters, J., Wubs, E.R.J., Bakker, E.S., Crowther, T.W., Veen, G.F.C., 2020. Nutrient availability controls the impact of mammalian herbivores on soil carbon and nitrogen pools in grasslands. *Glob. Change Biol.* 26 (4), 2060–2071. <https://doi.org/10.1111/gcb.15023>.
- Song, C.L., Rohr, R.P., Vasseur, D., Saavedra, S., 2020. Disentangling the effects of external perturbations on coexistence and priority effects. *J. Ecol.* 108 (4), 1677–1689. <https://doi.org/10.1111/1365-2745.13349>.
- Speed, J.D.M., Austrheim, G., Mysterud, A., 2013. The response of plant diversity to grazing varies along an elevational gradient. *J. Ecol.* 101 (5). <https://doi.org/10.1111/1365-2745.12133>.
- Stavi, I., 2020. On-Site Use of Plant Litter and Yard Waste as Mulch in Gardening and Landscaping Systems. *Sustainability* 12 (18). <https://doi.org/10.3390/su12187521>.
- Su, J.S., Xu, F.W., Zhang, Y., 2023. Grassland biodiversity and ecosystem functions benefit more from cattle than sheep in mixed grazing: A meta-analysis. *J. Environ. Manag.* 337. <https://doi.org/10.1016/j.jenvman.2023.117769>.
- Tahmasebi, P., Manafian, N., Ebrahimi, A., Omidiour, R., Faal, M., 2020. Managing Grazing Intensity Linked to Forage Quantity and Quality Trade-off in Semiarid Rangelands. *Rangel. Ecol. Manag.* 73 (1), 53–60. <https://doi.org/10.1016/j.rama.2019.08.011>.
- Thomas, D.T., Flohr, B.M., Monjardino, M., Loi, A., Llewellyn, R.S., Lawes, R.A., et al., 2021. Selecting higher nutritive value annual pasture legumes increases the profitability of sheep production. *Agric. Syst.* 194. <https://doi.org/10.1016/j.agsy.2021.103272>.
- Tränkner, M., Tavakol, E., Jáklí, B., 2018. Functioning of potassium and magnesium in photosynthesis, photosynthate translocation and photoprotection. *Physiol. Plant* 163 (3), 414–431. <https://doi.org/10.1111/ppl.12747>.
- Vaintrub, M.O., Levit, H., Chincarini, M., Fusaro, I., Giammarco, M., Vignola, G., 2021. Review: Precision livestock farming, automats and new technologies: possible applications in extensive dairy sheep farming. *Animal* 15 (3). <https://doi.org/10.1016/j.animal.2020.100143>.
- Venter, Z.S., Hawkins, H.J., Cramer, M.D., 2019. Cattle don't care: Animal behaviour is similar regardless of grazing management in grasslands. *Agric. Ecosyst. Environ.* 272, 175–187. <https://doi.org/10.1016/j.agee.2018.11.023>.
- Wang, Y.F., Lv, W.W., Xue, K., Wang, S.P., Zhang, L.R., Hu, R.H., et al., 2022. Grassland changes and adaptive management on the Qinghai-Tibetan Plateau. *Nat. Rev. Earth Environ.* 3 (10), 668–683. <https://doi.org/10.1038/s43017-022-00330-8>.
- Wang, Y.F., Xue, K., Hu, R.H., Ding, B.Y., Zeng, H., Li, R.J., et al., 2023. Vegetation structural shift tells environmental changes on the Tibetan Plateau over 40 years. *Sci. Bull.* 68 (17), 1928–1937. <https://doi.org/10.1016/j.scib.2023.07.035>.
- White, S.R., Cahill, J.F., Bork, E.W., 2014. Implications of Precipitation, Warming, and Clipping for Grazing Resources in Canadian Prairies. *Agron. J.* 106 (1), 33–42. <https://doi.org/10.2134/agronj2013.0085>.
- Wu, J.P., Gong, X.Y., Yao, X.X., Casper, D.P., 2020. Plant communities responding to grazing pressure by sheep in an Alpine meadow. *Transl. Anim. Sci.* 4 (2), txaa075. <https://doi.org/10.1093/tas/txaa075>.
- Wu, J.S., Wurst, S., Zhang, X.Z., 2016. Plant functional trait diversity regulates the nonlinear response of productivity to regional climate change in Tibetan alpine grasslands. *Sci. Rep.* 6. <https://doi.org/10.1038/srep35649>.
- Wu, J.S., Yang, P.W., Zhang, X.Z., Shen, Z.X., Yu, C.Q., 2015. Spatial and climatic patterns of the relative abundance of poisonous vs. non-poisonous plants across the Northern Tibetan Plateau. *Environ. Monit. Assess.* 187 (8). <https://doi.org/10.1007/s10661-015-4707-z>.
- Xu, Z.Y., Hu, Z.H., Jiao, S., Bell, S.M., Xu, Q., Ma, L.L., et al., 2023. Depth-dependent effects of tree species identity on soil microbial community characteristics and multifunctionality. *Sci. Total Environ.* 878 (000), 12. <https://doi.org/10.1016/j.scitotenv.2023.162972>.
- Xu, W., Zhu, M.Y., Zhang, Z.H., Ma, Z.Y., Liu, H.Y., Chen, L.T., et al., 2018. Experimentally simulating warmer and wetter climate additively improves rangeland quality on the Tibetan Plateau. *J. Appl. Ecol.* 55 (3), 1486–1497. <https://doi.org/10.1111/1365-2664.13066>.
- Yao, X.X., Jianping, W., Xuyin, G., 2019a. Precipitation and seasonality affect grazing impacts on herbage nutritive values in alpine meadows on the Qinghai-Tibet Plateau. *J. Plant Ecol.* (6). <https://doi.org/10.1093/jpe/rtz027>.
- Yao, X.X., Li, C.H., Ahmad, A.A., Tariq, A., Degen, A.A., Bai, Y.F., 2022. An increase in livestock density increases forage nutritional value but decreases net primary production and annual forage nutritional yield in the alpine grassland of the Qinghai-Tibetan Plateau. *Front. Plant Sci.* 13. <https://doi.org/10.3389/fpls.2022.1020033>.
- Yao, X.X., Wu, J.P., Gong, X.Y., Lang, X., Wang, C.L., Song, S.Z., et al., 2019b. Effects of long term fencing on biomass, coverage, density, biodiversity and nutritional values of vegetation community in an alpine meadow of the Qinghai-Tibet Plateau. *Ecol. Eng.* 130, 80–93. <https://doi.org/10.1016/j.ecoleng.2019.01.016>.
- Yoshihara, Y., Aoki, R., Kinugasa, T., Sasaki, T., 2022. Predicted effects of simulated ambient warming and moisture on forage nutrient quality and community composition in Mongolian arid grassland. *Rangel. J.* 44 (3), 159–164. <https://doi.org/10.1071/rj220207>.
- Zha, X.J., Tian, Y., Ou, Z., Fu, G., 2022. Response of forage nutrient storages to grazing in alpine grasslands. *Front. Plant Sci.* 13. <https://doi.org/10.3389/fpls.2022.991287>.
- Zhang, G.Y., Dai, E.F., Dawa, Q.D., Luo, B., Fu, G., 2023a. Effects of Climate Change and Fencing on Forage Nutrition Quality of Alpine Grasslands in the Northern Tibet. *PlantsBasel* 12 (18). <https://doi.org/10.3390/plants12183182>.
- Zhang, M.N., Delgado-Baquerizo, M., Li, G.Y., Isbell, F., Wang, Y., Hautier, Y., et al., 2023b. Experimental impacts of grazing on grassland biodiversity and function are explained by aridity. *Nat. Commun.* 14 (1). <https://doi.org/10.1038/s41467-023-40809-6>.
- Zhang, G.Y., Fu, G., 2024. Changes in soil organic carbon, total nitrogen and total phosphorus in 2000–2020 and their driving mechanisms in Tibetan alpine grasslands. *Glob. Planet. Change*, 104484. <https://doi.org/10.1016/j.gloplacha.2024.104484>.
- Zhao, B.Y., Liu, Z.Y., Lu, H., Wang, Z.X., Sun, L.S., Wan, X.P., et al., 2010. Damage and Control of Poisonous Weeds in Western Grassland of China. *Agric. Sci. China* 9 (10), 1512–1521. [https://doi.org/10.1671/2927\(09\)60242-x](https://doi.org/10.1671/2927(09)60242-x).
- Zhao, F., Ren, C., Shelton, S., Wang, Z., Pang, G., Chen, J., et al., 2017. Grazing intensity influence soil microbial communities and their implications for soil respiration. *Agric. Ecosyst. Environ.* 249, 50–56. <https://doi.org/10.1016/j.agee.2017.08.007>.
- Zheng, Y., Hu, Z., Jian, J., Chen, J., Osborne, B.B., Zhou, G., et al., 2024. Tree functional group mediates the effects of nutrient addition on soil nutrients and fungal communities beneath decomposing wood. *Plant Soil.* 510, 797–813. <https://doi.org/10.1007/s11104-024-06959-2>.
- Zhu, J.T., Zhang, Y.J., Wu, J.S., Zhang, X.Z., Yu, G.R., Shen, Z.X., et al., 2024. Herbivore exclusion stabilizes alpine grassland biomass production across spatial scales. *Glob. Change Biol.* 30 (1). <https://doi.org/10.1111/gcb.17155>.