

Grazing systems select leaf number as an indicator of ecosystem responses to climatic variability in salinized meadows

Yazhuan Sang^a, Lingxin Yi^a, Yang You^a, Xiongzhao He^b, Fujiang Hou^{a,*}

^a China-Kazakhstan Belt and Road Joint Laboratory on Grassland Ecological Restoration; Key Laboratory of Grassland Livestock Industry Innovation, Ministry of Agriculture and Rural Affairs; Engineering Technology Research Center for Ecological Restoration and Utilization of Degraded Grassland in Northwest China, National Forestry and Grassland Administration; College of Pastoral Agriculture Science and Technology, Lanzhou University, Lanzhou 730020, Gansu, China

^b School of Agriculture and Environment, College of Science, Massey University, Palmerston North, New Zealand

ARTICLE INFO

Keywords:

Ecological indicators
Grazing management
Leaf number
Functional traits
Air temperature
Salinized meadow

ABSTRACT

The degradation of salinized meadows under environmental change calls for reliable functional indicators to support adaptive grazing management. However, while plant functional traits mediate grazing effects, identifying those that can robustly indicate the coupling between environmental factors and productivity across different grazing systems remains unresolved. Through a four-year controlled grazing experiment in a salinized meadow, we evaluated whether grazing systems select leaf number (LN) as a functional indicator of environment-productivity linkages. By integrating structural equation modeling and random forest analysis, we disentangled the cascading network connecting climate, grazing, traits, diversity, and ecosystem functioning. Our results showed that rotational grazing enhanced community productivity through increased LN, whereas continuous grazing shifted the system toward a height-avoidance strategy. Air temperature emerged as the dominant climatic driver, promoting LN and productivity under rotational grazing, while precipitation played a secondary role. Across all grazing systems, LN was the most important predictor of aboveground biomass (relative importance: 18.4%), surpassing plant height and stem length. LN also showed a synergistic relationship with the Shannon-Wiener index ($P < 0.01$). These results demonstrate that grazing acts as a selector of ecological pathways rather than merely an intensity gradient. We therefore propose LN as a practical indicator linking grazing management to ecosystem responses under the interannual climatic variability, providing a trait-based tool for forecasting salinized meadow functioning.

1. Introduction

Plant community stability and ecosystem functioning are strongly driven by the abundance of dominant species and species diversity (Creed et al., 2009; Cao et al., 2024; Zhang et al., 2020a). Both natural and anthropogenic disturbances substantially restructure these properties, with grazing, one of the most direct forms of grassland utilization, acting as a pivotal driver (Sang et al., 2026a). However, current research largely frames grazing effects as a simple intensity gradient, wherein moderate grazing stimulated compensatory growth and diversity, whereas overgrazing triggered degradation (Manlike et al., 2020; Yan et al., 2015; Yuan et al., 2020). This perspective overlooks the potential for grazing systems themselves to act as ecological pathway selectors, capable of reconfiguring the intrinsic mechanistic networks through which plant communities respond to climate (Pacifi et al.,

2018; Zhang et al., 2025a). Grazing systems do not merely alter the magnitude of plant responses; rather, they determine whether signals are channeled through productive trait syndromes (e.g., leaf proliferation) or defensive syndromes (e.g., height avoidance), thereby selecting divergent ecological pathways. Moderate grazing has been shown to enhance compensatory plant growth, bolster soil nutrient uptake, and elevate diversity metrics, including the Shannon-Wiener index, species richness, and functional diversity (Ren et al., 2018; Wang et al., 2018). In contrast, overgrazing induced widespread grassland degradation (Manlike et al., 2020). Continuous grazing, characterized by uninterrupted defoliation without rest periods, often forces plants into defensive strategies such as stem elongation, thereby weakening the capacity of plants to respond to environmental signals through productive traits such as leaf proliferation (Sang et al., 2026a). Approximately 90% of China's natural grasslands have experienced varying degrees of

* Corresponding author.

E-mail address: cyhoufj@lzu.edu.cn (F. Hou).

<https://doi.org/10.1016/j.ecolind.2026.115495>

Received 16 May 2026; Received in revised form 4 September 2026; Accepted 9 September 2026

Available online 14 September 2026

1470-160X/© 2026 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

degradation, with 60% classified as severely degraded, primarily due to long-term overgrazing and climate change (Bai et al., 2014a). This degradation not only diminished biomass and diversity but also altered population structure and species composition (Fedrigo et al., 2022; Li et al., 2018). Consequently, whether continuous and rotational grazing select divergent mechanistic pathways remains an unresolved question.

Plant functional traits serve as a critical nexus linking environmental disturbances to ecosystem functioning (Jiang et al., 2023; Mahaut et al., 2020;), yet their application in grazing ecology remains limited. Existing studies have largely focused on two trait categories: defense-related traits (e.g., high leaf dry matter content, LDMC; low specific leaf area, SLA) that confer herbivore resistance by reducing palatability and increasing tissue toughness (Jaurena et al., 2012; Polley et al., 2022), and size-related traits (e.g., plant height) that reflect compensatory growth or avoidance strategies under varying grazing intensities (Wang et al., 2016; Zuo et al., 2018). While these traits explain static resistance syndromes or intensity-dependent responses, they share two critical limitations: LDMC and SLA require laboratory processing, limiting their utility for rapid field assessment; and none of them simultaneously capture the dynamic interplay between climatic drivers and grazing regimes in shaping ecosystem productivity (Polley et al., 2022; Roelofsen et al., 2014; Zheng et al., 2010; Zhao et al., 2021;). SLA, for instance, explains biomass variation across grazing intensities but reflects leaf-level resource economics rather than whole-plant investment in photosynthetic organs (Tuo et al., 2024; Zheng et al., 2010). These studies treated grazing as a continuous intensity gradient, neglecting how different grazing systems (e.g., rotational vs. continuous) may activate distinct trait-mediated pathways. How climatic factors regulate these pathways remains poorly understood. The biodiversity-ecosystem functioning relationship has received considerable attention: the mass ratio hypothesis posits that community productivity is primarily driven by dominant species traits (Cruz et al., 2010), while complementarity and selection effects link species diversity to productivity (Wang et al., 2024; Wang et al., 2025). Yet how grazing regimes modulate the coupling between dominant species traits and community diversity under climate variability is still unclear, and a simple, field-measurable indicator capable of capturing these interactions is lacking. To address this gap, we propose leaf number (LN) as a key functional indicator. LN directly proxies photosynthetic organ quantity, with changes reflecting plant carbon assimilation investment and biomass dynamics (Kovenock and Swann, 2018; Zhao et al., 2021). Unlike SLA or LDMC, LN is rapidly and non-destructively measured in the field, making it practical for adaptive management. Crucially, LN integrates both climatic signals (temperature and precipitation) and grazing pressure, whereas traits like plant height predominantly indicate avoidance strategies disconnected from climate-productivity linkages. This integrative capacity makes LN uniquely suited to test our hypothesis that grazing systems act as ecological pathway selectors, potentially shaping how climate signals propagate to community productivity.

Globally, salinized meadows cover approximately 1 billion hectares, with China accounting for about 100 million hectares, representing roughly 10% of the world's total salinized land area (Sang et al., 2026b; Zhang et al., 2026). The central-western Hexi Corridor region alone contains approximately 1.02 million hectares of such meadows. These ecosystems act as major global suppliers of animal products, fulfilling over 33% of worldwide demand, while holding substantial potential for conversion into high-quality croplands or pastures (Sang et al., 2026a). This study focuses on *Calamagrostis pseudophragmites*, the dominant species in salinized meadows. As a dominant species in salinized meadows, *C. pseudophragmites* exhibits strong salt-alkali tolerance and an extensive clonal rhizome system, playing a key role in maintaining community stability and productivity under saline conditions. The saline environment imposes unique stress pressures, potentially shaping the linkages among traits, environment, and grazing, which differ fundamentally from those in non-saline grassland. Therefore, we

propose and test the hypothesis that grazing systems function as ecological pathway selectors in salinized meadows. Specifically, we ask whether rotational grazing, compared to continuous grazing, selected for and reinforced a distinct trait-mediated productivity pathway centered on a key photosynthetic investment trait, leaf number (LN). We further ask whether LN served as a central functional hub that integrated environmental signals, grazing pressure, and diversity dynamics to predict ecosystem function, and whether this hub varied across grazing regimes. By integrating structural equation modeling and random forest analysis to decipher the full cascade from climate to grazing to traits to diversity to ecosystem functioning, we aim to construct a trait-based predictive management framework. Within this framework, leaf number emerges as a potential monitoring indicator, well suited for guiding adaptive grazing decisions in salinized meadows.

2. Materials and methods

2.1. Study area

The experiment was conducted at the Linze Pratacultural Research Station of Lanzhou University (100°02' E, 39°15' N, altitude 1400 m) in Linze County, Zhangye City, Gansu Province. This area is situated in the core region of the mountain-desert-oasis ecotone of the Hexi Corridor. The average precipitation and temperature are summarized in Fig. 1. The study area was categorized as a salinized lowland meadow subclass, with a typical saline soil type, and comprised an extensive integrated crop-livestock ecosystem (Hou et al., 2008). Historically, the study area was used for unregulated free-range grazing with no standardized intensity or rotation. Following its designation as a saline meadow improvement area, the site was converted into an integrated grass-livestock system with improved breeds (Small-tailed Han sheep, Simmental cattle, Holstein cows). In 2019, the site was fenced and grazing was excluded for one year prior to the experiment to establish a uniform baseline. The focal species of this study, *C. pseudophragmites*, was the dominant plant species in this salinized meadow (Sang et al., 2026b).

2.2. Experimental design

The experiments were conducted according to the guidelines of experimental field management protocols (file No: 2010-1 and 2010-2) and were approved by the Animal Use and Care Committee of Lanzhou University. The experimental design, including plot layout, grazing system allocation, and animal management protocols, followed the procedures detailed in our previous publications (Sang et al., 2026a, 2026b). The experiment adopted a completely randomized design, with all grazing treatments replicated three times on plots that were topographically homogeneous, with consistent soil type and initial vegetation conditions. Replicate plots were randomly distributed across the study area. The experiment began in June 2020 and comprised two grazing systems, continuous and rotational, both conducted annually from mid-June to mid-September. For continuous grazing, 24 Simmental bulls (7 months old; initial body weight: 175 ± 1.74 kg) were divided into three groups of eight animals each. Each group grazed continuously in a $200 \text{ m} \times 300 \text{ m}$ plot at a stocking rate of 1.33 cattle/ha (moderate, C1.33) for a total of 90 days per year. For rotational grazing, another 24 Simmental bulls of the same age and body weight were divided into three groups of eight animals each. These groups were allocated to plots of $200 \text{ m} \times 200 \text{ m}$, $200 \text{ m} \times 100 \text{ m}$, and $200 \text{ m} \times 50 \text{ m}$, corresponding to stocking rates of 0.66, 1.33, and 2.66 cattle/ha, respectively (light, R0.66; medium, R1.33; and heavy, R2.66). Each stocking rate had three replicates. Rotational grazing consisted of three 10-day grazing periods, each followed by a 20-day rest interval. In addition, a $10 \text{ m} \times 10 \text{ m}$ non-grazing enclosure (NG) was established within each grazing land as a control.

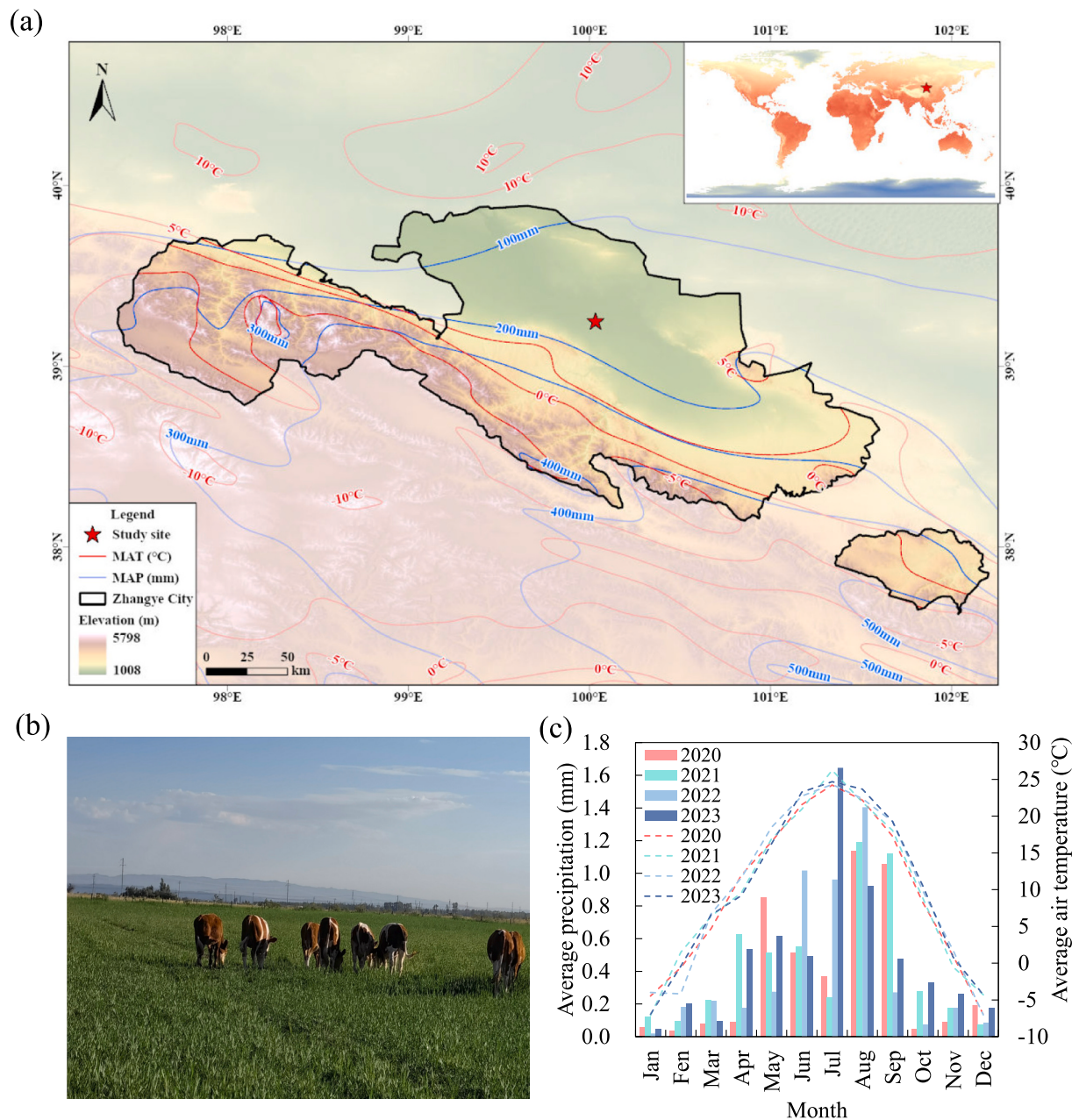


Fig. 1. The graph depicts the distribution of mean annual precipitation, mean annual temperature and elevation in the study site (a). Photograph of the grazing experimental plot in the study area (b). The average precipitation (column) and average air temperature (line) from 2020 to 2023 in the study area (c).

2.3. Sample acquisition

From 2020 to 2023, during the peak growing season of each growing season, four quadrats (1 m × 1 m) were randomly selected in each experimental plot. The plant height, stem length, leaf length, leaf width, and leaf number of *C. pseudophragmites* were measured in the field. Leaf number was recorded as the total number of fully expanded leaves per tiller. All plants within each quadrat were clipped at ground level, placed into paper envelopes, and transported to the laboratory. The fresh weight of the total community biomass was recorded. The stems and leaves of *C. pseudophragmites* were then manually separated from the rest of the community sample. The separated *C. pseudophragmites* and the remaining community biomass were placed into separate envelopes and oven-dried at 105 °C for 30 min for enzyme inactivation, followed by drying at 65 °C for 48 h to a constant weight, after which their dry weights were measured.

2.4. Calculation of indicators

The plant community species diversity indices calculated include species richness (SR), Shannon-Wiener index (SWI), and Pielou-evenness index (PEI) (Blaix et al., 2025).

$$SR = S$$

$$SWI = - \sum_{i=1}^S P_i \ln(P_i)$$

$$PEI = \frac{SWI}{\ln(S)}$$

where S is the number of plant species in each quadrat of the community, and P_i is the proportion of individuals of the i^{th} species to the total number of individuals of all species.

To quantify the relative contributions of each factor (e.g., grazing

treatment, year) and their interactions to the variation in each ecological indicator, a univariate general linear model (GLM) was applied using SPSS 26.0. For each response variable, a full factorial ANOVA model was fitted with all fixed factors and their interaction terms. The percentage contribution of each source of variation (each main effect and interaction) was calculated based on the Type III sum of squares, which represents the independent effect of a term after adjusting for all other terms in the model (Huang et al., 2024). The formula is:

$$\text{Contribution (\%)} = \frac{SS_{\text{Type III(term)}}}{SS_{\text{Corrected Total}}} \times 100$$

where $SS_{\text{Type III(term)}}$ is the Type III sum of squares for the given factor or interaction, and $SS_{\text{Corrected Total}}$ is the corrected total sum of squares obtained from the between-subjects effects table. Calculations were performed independently for each response variable. The contribution of the error term was similarly derived from the residual sum of squares. Because this method fully partitions the total variation into explained and unexplained components, the sum of the contributions from all factors, interactions, and the error term equals 100%, providing a complete representation of the relative influence of each source on the total variation.

2.5. Statistical analysis

SPSS 26.0 (IBM, USA) was used for statistical analysis. The effects of grazing, year, and their interaction on community aboveground biomass, dominant species aboveground biomass, and functional traits of the dominant species were analyzed using two-way ANOVA, followed by Tukey's post hoc test for multiple comparisons (Figs. 2, 3). Linear regression and nonlinear mixed models were used to determine the relationships between aboveground biomass (of the dominant species or the community) and species diversity under different grazing treatments (Fig. 4). Meteorological data were obtained from the China Agricultural Meteorological Database. A generalized linear mixed model with a Gaussian or gamma distribution was applied to assess the effects of dominant species functional traits, temperature, and precipitation on community characteristics, as well as to test the effects of community characteristics, temperature, and precipitation on functional traits of the

dominant species (Tables 2, 3). Principal component analysis (PCA) was performed to reduce the dimensionality of species diversity indicators. Based on correlation results, only dominant species plant height and leaf number were selected as representative indicators for subsequent inclusion in the structural equation model (SEM) (Fig. 5). Random forest analysis was conducted using the “randomForest” and “rfPermute” packages in the R Statistical Environment (version 4.3.3) (Fig. 6). Prism 8.0 (GraphPad Software, USA) and Origin (OriginLab, USA) were used for creating figures. Structural equation model analysis was performed using IBM SPSS Amos 21.0.

3. Results and analysis

3.1. Responses of aboveground biomass to grazing

Year and its interaction with grazing significantly affected AGB and DS-AGB ($P < 0.001$); grazing significantly affected DS-AGB (Fig. 2a, b). AGB and DS-AGB decreased gradually with increasing grazing duration (Fig. 2a, b). Year significantly affected RDF, with the highest value recorded in 2021 ($P < 0.001$) (Fig. 2c). Grazing and its interaction with year significantly affected DS-RDF, with a lower ratio observed under rotational grazing at the low stocking rate ($P < 0.001$) (Fig. 2d). The contribution rates of year to AGB, DS-AGB, RDF, and DS-RDF were 41.84%, 12.15%, 33.28%, and 6.85%, respectively (Fig. 2e). The contribution rates of grazing to these four indicators were 2.52%, 3.93%, 1.23%, and 8.62%, respectively (Fig. 2e). The contribution rates of the interaction between year and grazing to these four indicators were 15.93%, 15.02%, 6.71%, and 14.66%, respectively (Fig. 2e).

3.2. Response of functional traits of dominant species to grazing

The PH significantly increased with grazing duration ($P < 0.01$), with the highest value observed in NG followed by R1.33 (Fig. 3a). Grazing and its interaction with year exerted a significant effect on SL, with longer stems in R1.33 in 2020 and NG in 2022 ($P < 0.001$; Fig. 3b). Year, grazing, and their interaction significantly affected LL, which significantly increased with grazing duration ($P < 0.05$), with longer leaves observed in NG (Fig. 3c). Both grazing and year significantly

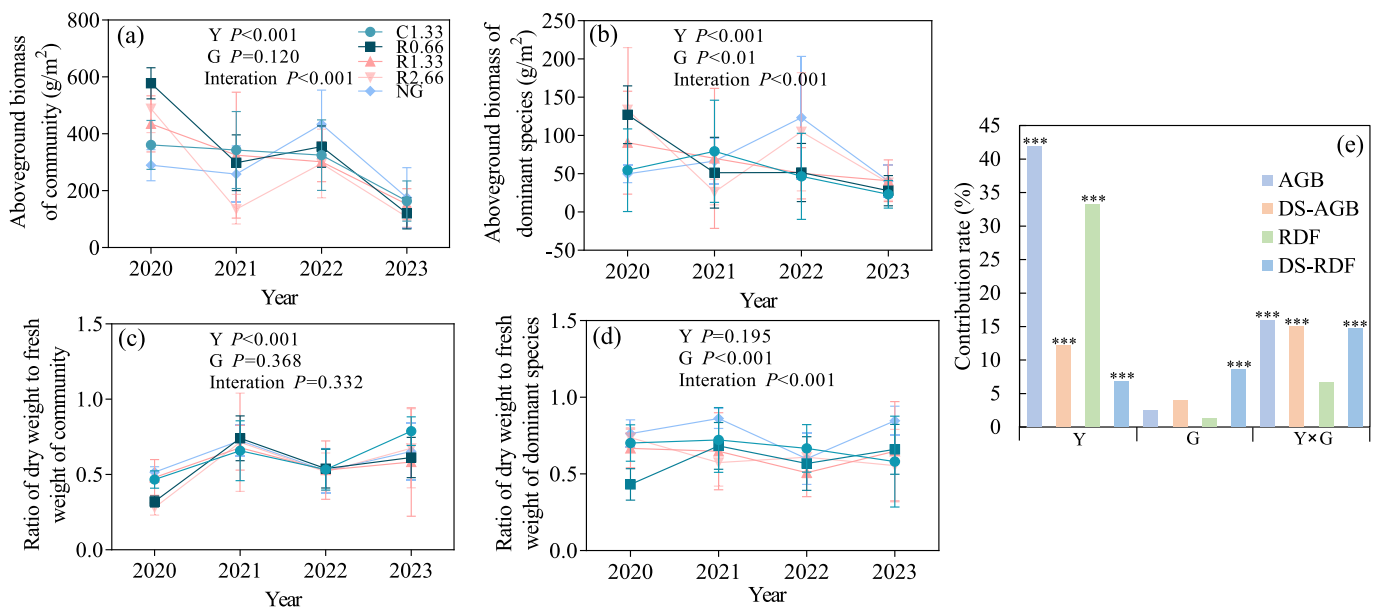


Fig. 2. Interannual variations (2020–2023) of (a) aboveground biomass of community (AGB), (b) aboveground biomass of dominant species (DS-AGB), (c) ratio of dry weight to fresh weight of community (RDF), and (d) ratio of dry weight to fresh weight of dominant species (DS-RDF) under different grazing treatments. Panel (e) presented the percentage contribution rates of grazing (G), year (Y), and their interaction ($Y \times G$) to the variation of each variable. Significance level: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

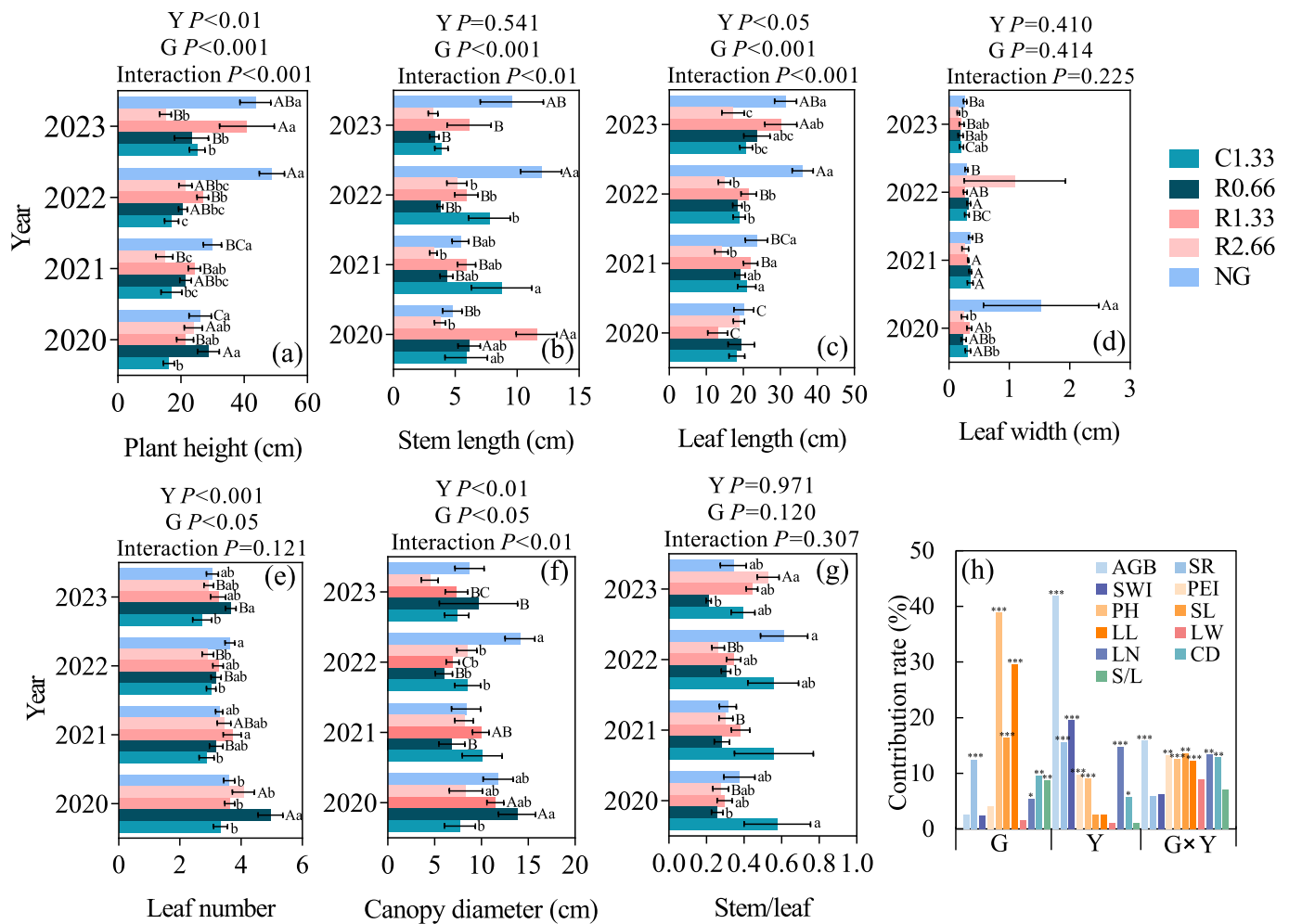


Fig. 3. Grazing (G), year (Y), and their interaction (G × Y) affecting the functional traits of dominant species (a–g), and their contributions to community structures and dominant species functional traits (h). SR, species richness; SWI, Shannon-Wiener index; PEI, Pielou evenness index; PH, plant height; SL, stem length; LL, leaf length; LW, leaf width; LN, leaf number; CD, canopy diameter; S/L, dry weight of stem and leaf ratio. Different lowercase letters represent the significant difference between grazing treatments ($P < 0.05$), and different uppercase letters represent the significant difference between years ($P < 0.05$). Significance level: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

influenced LN ($P < 0.05$), with the maximum LN observed in R0.66 (Fig. 3e). Grazing, year, and their interaction had significant effects on CD ($P < 0.05$), with the lowest value observed in R2.66 in 2023 and highest in R0.66 in 2020 (Fig. 3f). In contrast, grazing, year, and their interaction showed no significant impact on LW or S/L ($P > 0.05$), though the S/L was lowest in R0.66 (Fig. 3d, g). The contribution rate of grazing to PH of dominant species was the highest (38.89%), followed by LL (29.68%) (Fig. 3h). The contribution rate of annual variation to AGB was the highest (41.84%); while for the dominant species, the LN was the highest (14.75%) (Fig. 3h). The interaction between grazing and year contributed most to SL (13.61%), followed by LN (13.40%) (Fig. 3h).

3.3. Coupling and decoupling between aboveground biomass and species diversity of community and dominant species

SR was significantly affected by G ($P < 0.001$) and Y ($P < 0.001$), with no significant G × Y interaction ($P = 0.37$). SWI was significantly influenced only by Y ($P < 0.001$). PEI was significantly affected by G ($P < 0.01$), Y ($P < 0.001$), and their interaction ($P < 0.01$) (Table 1). AGB was positively correlated with that of DS-AGB and with DS-MC in all grazing treatments ($P < 0.001$) (Fig. 4Aa, c). The correlation between AGB and DS-RDF was positive in higher grazing treatments (C1.33, R1.33 and R2.66) but negative in lower grazing treatments (R0.66 and

NG) (Fig. 4Ab). In addition to these linear correlations, significant non-linear threshold responses were observed. Under R0.66, RDF showed a downward-opening quadratic relationship with DS-AGB ($P < 0.05$) (Fig. 4Ad). In contrast, under C1.33, an upward-opening quadratic relationship was found between RDF and DS-RDF ($P < 0.05$) (Fig. 4Ae). The species diversity indices (SR, SWI) were significantly positively correlated with DS-AGB in rotational grazing treatments (R0.66, R1.33, R2.66) and NG (Fig. 4Ba, b). Under C1.33 and R0.66, DS-RDF was significantly negatively correlated with SR, SWI, and PEI ($P < 0.05$), while under R1.33 and R2.66, significant positive correlations were observed for all three indices. In contrast, under NG, the response patterns diverged among indices: DS-RDF followed a significant downward-opening quadratic model with SR and SWI ($P < 0.05$), but showed significant positive correlation with PEI (Fig. 4Bd, e, f). The correlations between DS-MC and species diversity indices (SR, SWI and PEI) were significantly negative in C1.33 but positive rotational grazing treatments (Fig. 4Bg, h, i).

3.4. The interrelationship between functional traits of dominant species and community characteristics

LN served as the strongest predictor for both AGB ($P < 0.001$) and RDF ($P < 0.001$), significantly outperforming SL and CD. AT was the primary factor influencing species diversity, while SWI was also

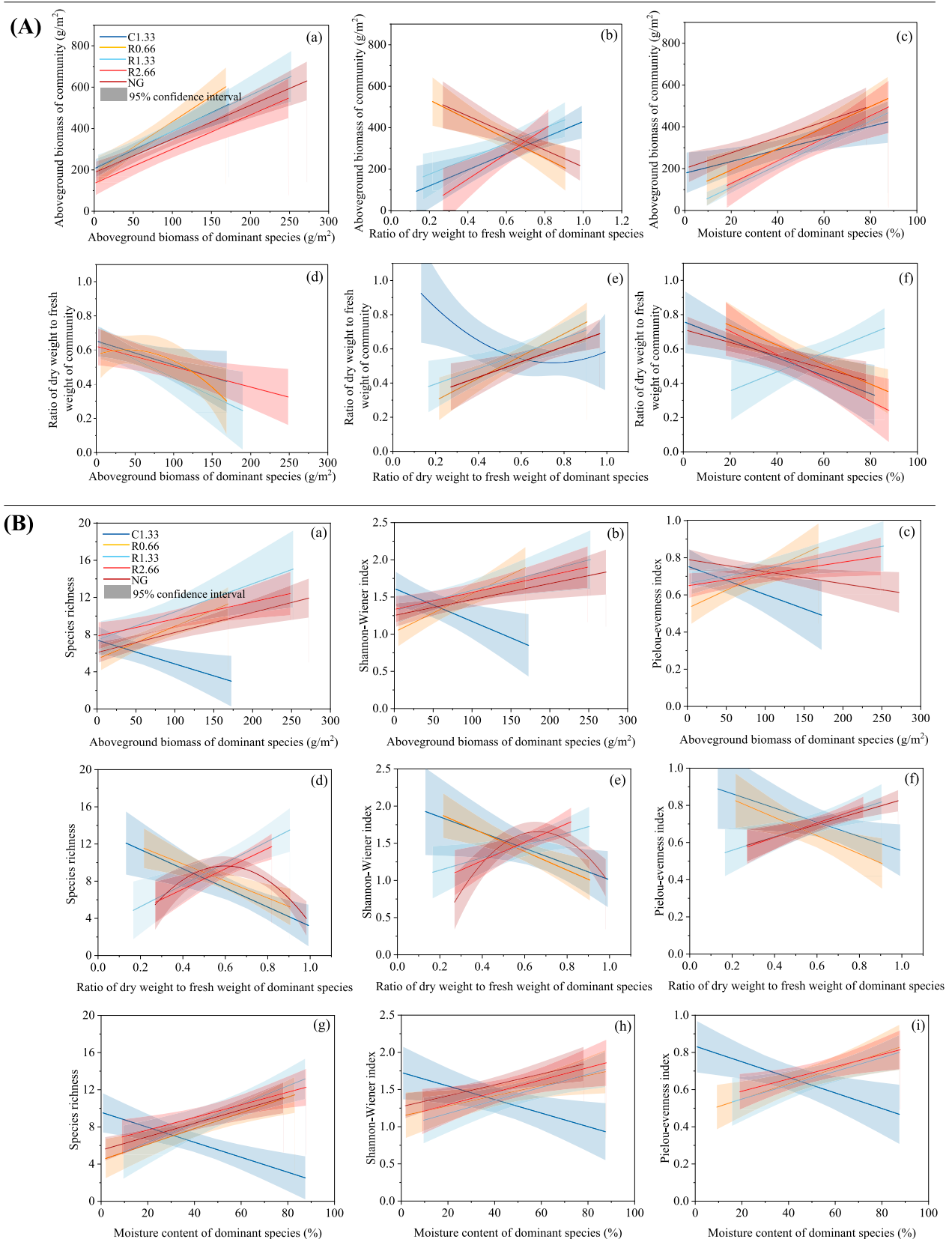


Fig. 4. Relationships between dominant species traits and community characteristics as well as species diversity indices. Panel A showed the relationships between dominant species traits and community characteristics. Panels (a–c) represented the relationships of DS-AGB, DS-RDF, and moisture content of dominant species (DS-MC) with AGB, respectively; panels (d–f) represented the relationships of DS-AGB, DS-RDF, and DS-MC with RDF, respectively. Panel B showed the relationships between dominant species traits and species diversity indices. Panels (a–c) represented the relationships of DS-AGB with SR, SWI, and PEI, respectively; panels (d–f) represented the relationships of DS-RDF with SR, SWI, and PEI, respectively; panels (g–i) represented the relationships of DS-MC with SR, SWI, and PEI, respectively. Shaded areas represented the 95% confidence intervals of the fitted lines.

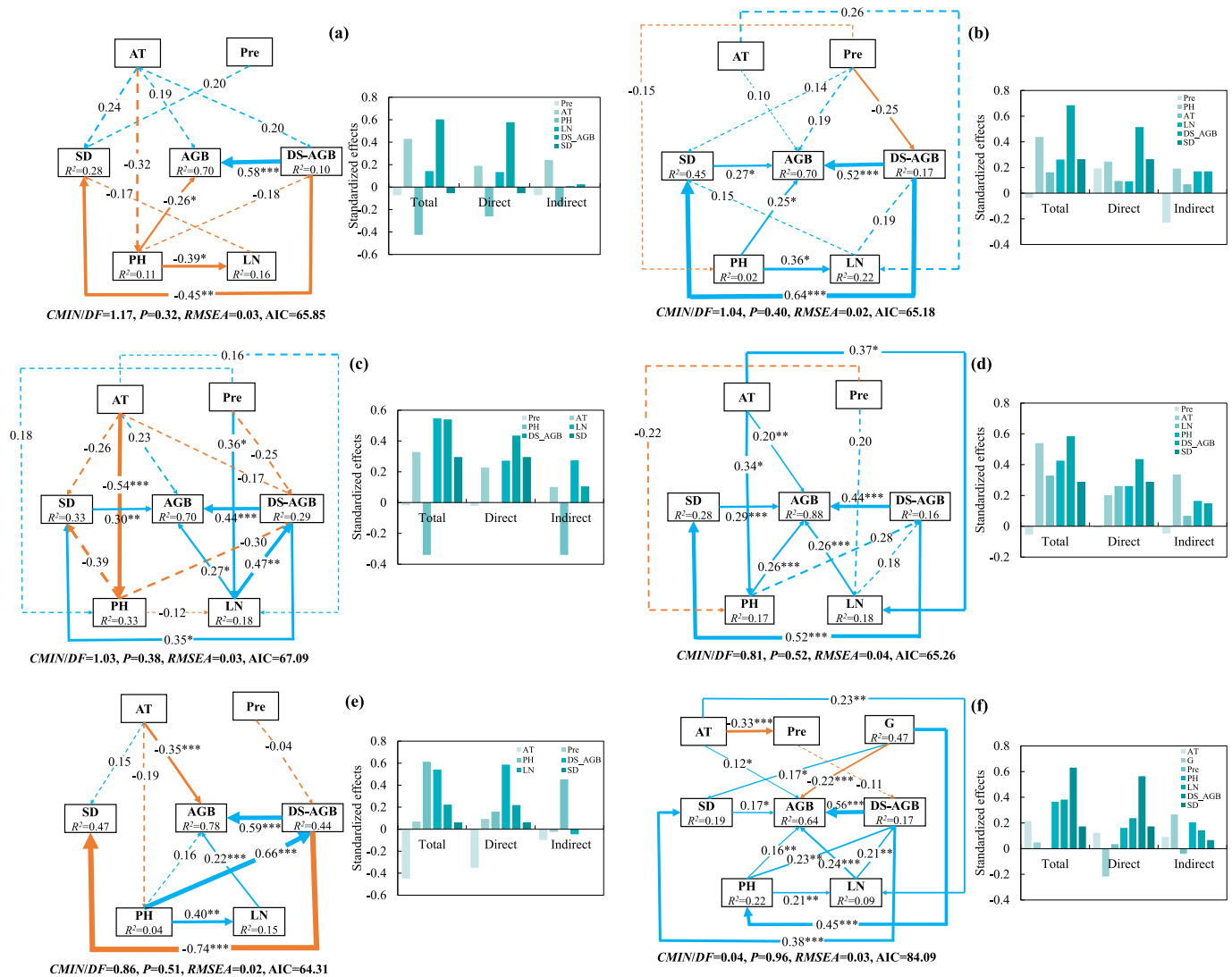


Fig. 5. The pathways and fluxes of environmental factors affecting community and dominant species biomass under (a) C1.33, (b) R0.66, (c) R1.33, (d) R2.66, (e) NG, (f) Overall conditions and the effects of various factors on AGB. Blue and orange arrows represent positive and negative relations, respectively. The arrows width indicates the strength of the relationships. Values adjacent to the arrows are standardized path coefficients. Solid lines represent significant correlations, while dashed lines indicate non-significant correlations. CMIN, DF, P , RMSEA and AIC denote model fit index, degrees of freedom, significance level, root mean square error of approximation, and Akaike information criterion, respectively. Significance level: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

significantly correlated with LN ($P < 0.01$). Pre had limited effects on community structure, and PH, LL, LW, and S/L had no significant predictive power (Table 2). Further analysis revealed that functional traits of the dominant species were jointly influenced by diversity indices and climatic factors: PH was affected by SWI, AT, and Pre; LN was predicted by AT and Pre; LW correlated with PEI and AT; SL was explained by both SWI and AT. CD, LN, and S/L showed exclusive correlations with AT, while SR had no significant associations with any functional traits (Table 3).

3.5. SEM analysis of functional traits of dominant species on community characteristic

Structural equation modeling (SEM) revealed that climatic factors regulate both the functional traits of dominant plant species and community structure. Under rotational grazing, AT enhanced both AGB and DS-AGB directly and indirectly by increasing LN of the dominant species, while DS-AGB and SD increased synergistically. In contrast, SD declined under NG and C1.33. Pre positively influenced AGB mainly by

promoting LN, though it could also directly suppress DS-AGB. Grazing reduced overall AGB, but indirectly promoted AGB accumulation by increasing PH of the dominant species. Across all treatments, DS-AGB consistently showed the strongest direct positive effect on AGB (effect size: 0.58, 0.52, 0.44, 0.44, 0.59 and 0.56). The primary indirect pathways varied with grazing treatments: AT was dominant under C1.33 and R2.66 (effect values: 0.24 and 0.34), Pre under R0.66 (−0.23), LN under R1.33 (0.28), and PH under NG (0.45). Comprehensive analysis indicated that the overall indirect effect of grazing was the largest (0.27) (Fig. 5).

Based on random forest analysis, the influence weights of various factors on community structure characteristics differed significantly: LN was the most important predictor for AGB; RDF contributed the most to DS-AGB; while the SWI had the greatest influence on both SR and PEI. Furthermore, the strongest mutual importance was observed between AGB and RDF, as well as between PEI and the SWI (Fig. 6).

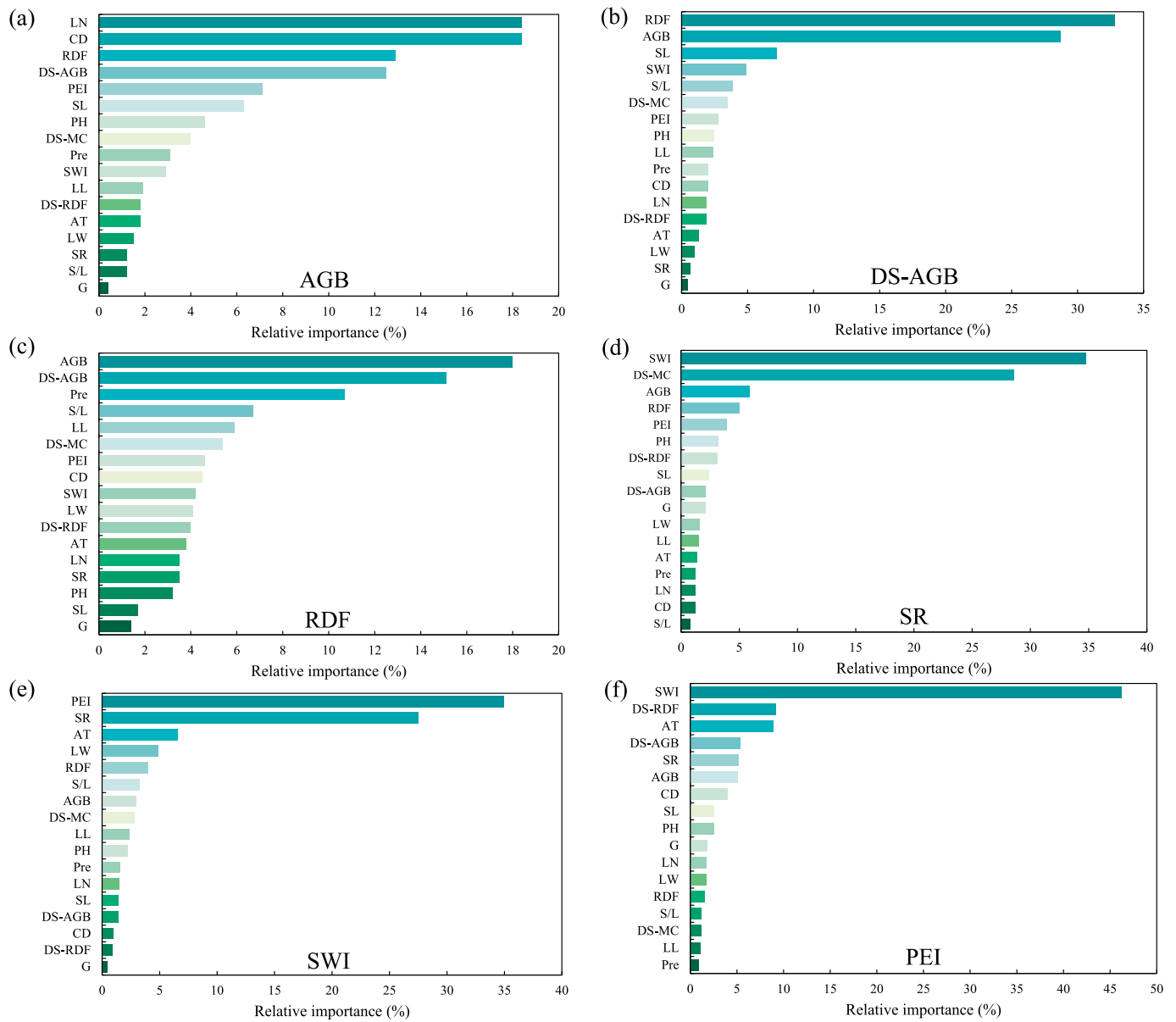


Fig. 6. The relative importance of climate, functional traits of dominant species and community structure to aboveground biomass of community (a), aboveground biomass of dominant species (b), ratio of dry weight to fresh weight of community (c), Species richness (d), Shannon-Wiener index (e) and Pielou-evenness index (f).

Table 1

Effects of grazing (G), year (Y), and their interaction (G × Y) on species diversity.

Indices	SR		SWI		PEI	
	F	P	F	P	F	P
G	5.51	< 0.001	0.67	0.62	3.28	< 0.01
Y	6.67	< 0.001	16.13	< 0.001	7.17	< 0.001
G × Y	1.09	0.37	1.27	0.25	2.35	< 0.01

4. Discussion

4.1. Mechanisms and regulation of community productivity driven by dominant species traits

The stability of ecosystem structure and function is closely linked to the abundance of dominant populations and species diversity (Lei et al., 2016; Zhang et al., 2025b). Our results demonstrated that the DS-AGB

Table 2

Parameter estimates of functional traits of dominant species on community structure.

Index	PH	LL	SL	CD	LW	LN	S/L	AT	Pre
AGB	0.41	-1.22	8.96**	5.33*	10.72	56.00***	21.36	1.88	-6.23
RDF	-0.003	0.006	0.003	-0.005	-0.084	-0.122***	-0.047	-0.007	0.011
SR	0.01	0.008	-0.03	0.12	-2.22	0.71	-0.45	0.22***	0.18
SWI	0.007	-0.004	0.0005	-0.001	0.04	0.13**	-0.04	0.04***	0.05
PEI	0.002	-0.002	-0.01	0.0004	0.02	0.04	-0.04	-0.02***	0.01

AT, Average air temperature; Pre: Average precipitation. Significance level: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Table 3

Parameter estimates of species diversity on functional traits of dominant species.

Index	SR	SWI	PEI	AT	Pre
PH	0.002	0.35*	0.30	0.11***	0.09*
LL	0.01	0.17	0.44	0.10***	0.08*
SL	0.005	0.44*	−0.89	0.07***	0.06
CD	0.02	0.21	−0.46	0.09***	0.07
LW	−0.04	0.29	−0.76*	−0.03***	0.01
LN	0.003	0.13	0.22	0.04***	0.02
S/L	0.002	−0.24	−0.14	−0.02***	−0.004

AT, Average air temperature; Pre: Average precipitation. Significance level: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

served as the strongest direct predictor of AGB (effect size: 0.44–0.59) and exhibited a highly significant positive correlation ($P < 0.001$). This finding corroborates the mass ratio hypothesis, indicating that community productivity is predominantly governed by dominant species owing to their substantial contribution to total biomass and superior ecological resource-use efficiency (Hou et al., 2023; Lisner et al., 2024; Takehiro and William, 2011). The peak community biomass observed at R0.66 stocking rate identifies a grazing intensity at which this driver's potential was maximized. Grazing intensity critically regulates community structure through two contrasting pathways. Light-to-moderate grazing stimulated compensatory growth in dominant species, thereby maintaining or even enhancing biomass (Guo et al., 2024; Kapas et al., 2020). Conversely, prolonged or heavy grazing reduced the abundance of dominant individuals, liberating niche resources and facilitating the proliferation of grazing-tolerant plants (Li et al., 2014; Strom, 2002). Notably, the highest species richness recorded under heavy grazing (R2.66) likely arises from a synergistic combination of preferential consumption of palatable species by livestock, the subsequent dominance of grazing-tolerant species, and increased micro-environmental heterogeneity driven by trampling and foraging, which amplified niche differentiation (Koerner et al., 2016; Zhang et al., 2020a).

RDF was negatively correlated with DS-AGB ($P < 0.05$), yet this relationship exhibited a critical threshold at R0.66 ($P < 0.001$). Initially, increasing DS-AGB led to higher water content (lower RDF) as plants expanded leaf area and enhanced water-holding capacity to support photosynthesis and transpiration (Wang et al., 2012; Zhang et al., 2021). However, upon approaching a community-level biomass threshold, compensatory growth depleted soil water and nutrients, triggering a shift toward dry matter accumulation (e.g., lignin synthesis) and reversing the RDF trend (Zhang et al., 2020b). This hydrological feedback loop serves to regulate a fundamental transition in plant functional strategy. Below the threshold, plants invest in water acquisition and carbon assimilation to support growth; once the threshold is exceeded, investment shifts toward structural reinforcement to withstand stress (Thakur et al., 2026; Zhang et al., 2025c). Accordingly, RDF is better understood not simply as a correlate of biomass, but as a diagnostic indicator that the ecosystem has transitioned from a productive to a conservative functional state. Light grazing may help maintain community stability by disrupting this trajectory before the threshold is reached (Zhang et al., 2020a). The positive correlation between AGB and DS-MC across stocking rates ($P < 0.01$) further underscores the pivotal role of plant hydration in post-grazing recovery and biomass accumulation (Zhang et al., 2023).

DS-MC and RDF represent ecological processes at different scales. DS-MC reflects the water status of the dominant species at the individual scale, whereas RDF represents a community-level aggregated trait of dry matter allocation. Therefore, their similar directional trends with diversity indices reflected consistent responses to the same underlying environmental gradients, such as grazing pressure and resource availability, rather than a contradiction between the two indicators. According to the mass ratio hypothesis, dominant species traits drive community functioning through their proportional biomass

contribution (Cruz et al., 2010; Hou et al., 2023), and community-level traits are essentially abundance-weighted aggregates of species traits, whose trajectories along environmental gradients may not parallel those of individual-scale traits (Lei et al., 2016). DS-MC reflected the physiological water status of *C. pseudophragmites* in response to groundwater fluctuations and microhabitat moisture, representing an individual-scale response trait. In contrast, RDF integrated the dry matter allocation strategies of all species in the community in response to grazing and climate, representing a community-scale aggregated trait (Jiang et al., 2023; Li et al., 2018). When grazing intensity and interannual climate jointly filtered species composition, individual-scale water status and community-scale dry matter allocation exhibited convergent directional responses to the same environmental gradients (Pavanetto et al., 2025; Zhao et al., 2021). The direction of the DS-MC diversity relationship reversed between continuous and rotational grazing in this study, further indicating that this association depended on grazing systems rather than reflecting an inherent contradiction between DS-MC and RDF.

4.2. Plant trait adaptation and resource trade-offs under grazing disturbance

Plant functional traits offer a fundamental framework for elucidating plant adaptation to herbivory (Funk et al., 2017). In this study, PH increased significantly with grazing duration ($P < 0.01$), embodying a classic grazing-avoidance strategy. By allocating resources to vertical growth, dominant species minimized foraging risk and enhanced light interception within the more open canopies induced by grazing (Li et al., 2020a; Zhang et al., 2020a). This response was not merely an intensity-dependent reaction but was fundamentally shaped by grazing regime structure: continuous grazing imposed uninterrupted defoliation without rest intervals, forcing stable resource allocation to stem elongation, whereas rotational grazing provided periodic recovery windows that reduced the necessity for sustained defensive investment (Kapas et al., 2020; Li et al., 2020b). Mechanistically, this response may be associated with mechanical damage, which has been shown to trigger jasmonic acid synthesis and upregulate stem elongation genes in grazing-adapted species (Cao et al., 2024; Feki et al., 2025; Hou et al., 2021). Similarly, grazing-induced increases in LL, which peaked at R1.33 ($P < 0.05$), reflected a leaf-prioritized strategy to offset biomass loss through expanded photosynthetic area (Bai et al., 2014a, 2014b; Shen et al., 2019). At moderate grazing intensity (R1.33), improved resource availability and enhanced plant sensitivity to environmental cues likely facilitated compensatory leaf elongation (Li et al., 2020b; Shen et al., 2025; Sang et al., 2026b).

Grazing pressure forced plants into fundamental trade-offs in resource allocation. Analysis of contribution rates revealed a clear dichotomy, grazing exerted the strongest influence on PH as a direct response to selective pressure, whereas interannual climate variation primarily modulated traits such as LN by regulating tillering capacity in response to precipitation and temperature (Li et al., 2015; Wang and Wang, 2015). Under continuous grazing, this climatic regulation of LN was overridden by sustained defoliation pressure, preventing climate signals from propagating to productivity through leaf traits. In contrast, rotational grazing allowed compensatory resources to be channeled into leaf proliferation and tillering, enabling temperature and precipitation to drive LN expansion and reinforcing the climate–productivity cascade (Huxley et al., 2023; Zhao et al., 2021). The most pronounced interaction between grazing and year was observed for SL, followed by LN. This indicates that sustained grazing drives a long-term strategic reallocation, favoring investment in stem biomass over tiller and leaf production (He et al., 2021; Niinemets, 2020). This shift is exacerbated by long-term grazing, which potentially reduces soil nitrogen and phosphorus availability, forcing plants to optimize resources for fewer, more efficient leaves (Sang et al., 2026a, 2026b; Yu et al., 2021).

The contrast between grazing-induced stem elongation and climate-

driven leaf proliferation illustrated how grazing systems acted as ecological pathway selectors (Orwin et al., 2018). Under continuous grazing, the absence of rest intervals drove a defensive syndrome characterized by stem elongation. Under rotational grazing, periodic recovery windows permitted a resource-acquisition syndrome characterized by leaf proliferation. In this context, “pathway selector” describes how grazing system structure determines whether climatic signals propagate through leaf number or are overridden by defensive height investment, thereby directing ecosystem functioning along divergent trajectories. Crucially, because LN integrates climatic signals and couples with diversity, it emerges as the informative functional indicator of ecosystem response under interannual climatic variability, in contrast to PH. Collectively, these phenotypic adjustments, whether trade-offs, functional switches, or compensation, ultimately converge to fulfill the core functions of survival, growth, and reproduction under disturbance.

4.3. Integration of multi-dimensional driving forces: Ecosystem function prediction model based on dominant species traits

The interplay between plant functional traits and aboveground biomass sheds light on how functional composition governs ecosystem functioning (Schaller et al., 2016; Zhang et al., 2023). The system dependent reshaping of trait syndromes extended beyond productivity to community diversity: grazing significantly affected SR and PEI, with a significant grazing-year interaction on PEI, indicating that grazing actively reshaped community diversity structure even under interannual climatic variation, and that PEI was particularly sensitive to the interplay between grazing management and climatic variation. This confirms that grazing acts not merely as a disturbance gradient but as a selective force modulating the trajectory of community reorganization across years. We integrated structural equation modeling and random forest analysis to disentangle the multidimensional drivers of ecosystem functioning in a salinized meadow. Our results identified LN of the dominant species as the strongest predictor of both AGB and RDF ($P < 0.001$). Mechanistically, this primacy stems from LN serving as a proxy for the number of photosynthetic organs; changes in LN directly mirror plant investment strategies in carbon assimilation, thereby positioning it as a central hub linking environmental drivers to productivity formation (Kovenock and Swann, 2018; Zhao et al., 2021). Under rotational grazing, we observed a distinct causal pathway from AT to LN to AGB, which encapsulates the ecological tenet of energy input fueling structural investment for productivity output. Within this framework, accumulated AT promotes LN growth, while rotational grazing facilitates compensatory growth via moderate disturbance (Huxley et al., 2023). Further analysis highlighted the predominant role of AT over Pre in regulating ecosystem function. This divergence likely arose because salinized meadows are water-limited; precipitation exhibited threshold-dependent effects, where moderate drought relief stimulated growth, but excess moisture impaired it by altering soil salinity dynamics (Liu et al., 2024). In contrast, AT acted as a consistent energy source that simultaneously modulated diversity and traits, rendering it a more robust predictor (Huxley et al., 2023; Pavanetto et al., 2025).

In the biological dimension, we detected a functional decoupling between diversity and dominance. Although SWI correlated significantly with LN ($P < 0.01$), its influence manifested through micro-environmental stabilization and interspecific interactions that supported trait expression (Cao et al., 2024; Zhang et al., 2020a). In the disturbance dimension, grazing acted as a pathway selector, exerting the largest indirect effect (0.27) while differentially activating pathways across regimes. Specifically, this indirect effect operated by reshaping resource allocation priorities: continuous grazing overrides climatic signals and forces defensive height investment, whereas rotational grazing decouples grazing pressure from climatic signals, allowing LN to integrate temperature and diversity dynamics. This reflects a reshaping of energy allocation: light grazing fostered trait expression via resource

release, whereas heavy grazing triggered a strategic shift in defensive investment (Bai et al., 2014a, 2014b; Niinemets, 2020; Shen et al., 2019).

Building on these insights, we propose a trait mediated predictive framework in which LN operated as an integrative hub linking environmental factors, diversity, and productivity. By contrast, PH reflects a grazing induced defensive pathway and therefore lacks the capacity to integrate environmental signals. Within this framework, rotational grazing during warm years reinforces the trait-LN-productivity cascade, whereas continuous heavy grazing forces a shift toward a height avoidance strategy, eroding LN's integrative role and compromising ecosystem resilience. These mechanisms clarify why LN, rather than PH, constitutes a diagnostic indicator for grazing management in salinized meadows.

5. Conclusions

Grazing systems functioned as ecological pathway selectors in the salinized meadow, with rotational grazing reinforcing a trait-mediated productivity pathway from air temperature to LN to AGB, whereas continuous grazing shifted the system toward a height-avoidance strategy. Leaf number of the dominant species *C. pseudophragmites* emerged as the most robust predictor of community productivity and was positively coupled with Shannon–Wiener diversity, confirming its role as an integrative hub linking climate, diversity, and productivity. These findings establish LN as a practical, field-measurable indicator for monitoring ecosystem responses to grazing and climate variability. By linking trait-based monitoring to grazing system selection, this study provides a mechanistic framework for adaptive grazing management and targeted restoration of degraded salinized meadows. Nevertheless, future research should integrate leaf economics spectrum traits, microbial community dynamics, and soil nutrient cycling through multisite, long-term observations to further validate the generality of these findings and extend the trait-based predictive framework.

CCRediT authorship contribution statement

Yazhuan Sang: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Lingxin Yi:** Investigation. **Yang You:** Investigation. **Xionghao He:** Writing – review & editing, Supervision. **Fujiang Hou:** Writing – review & editing, Methodology, Funding acquisition, Formal analysis, Conceptualization.

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.

Acknowledgments

This study was supported by the National Key Research and Development Program (2025YFE0212000), Innovation Platform Plan Program of Gansu Province (26JDWA001), Program for Innovative Research Team of Ministry of Education (IRT_17R50).

Data availability

The authors do not have permission to share data.

References

- Bai, X., Cheng, J., Zheng, S., Zhan, S., Bai, Y., 2014b. Ecophysiological responses of *Leymus chinensis* to nitrogen and phosphorus additions in a typical steppe. *Chinese J. Plant Ecol.* 38 (2), 103–115. <https://doi.org/10.3724/SP.J.1258.2014.00010>.

- Bai, Y., Huang, J., Zheng, S., Pan, Q., Zhang, L., Zhou, H., Xu, H., Li, Y., Ma, J., 2014a. Drivers and regulating mechanisms of grassland and desert ecosystem services. *Chinese J. Plant Ecol.* 38 (2), 93–102. <https://doi.org/10.3724/SP.J.1258.2014.00009>.
- Blaix, C., Chabrierie, O., Alard, D., Catterou, M., Diquelou, S., Dutoit, T., Lacoux, J., Loucougaray, G., Michelot-Antalik, A., Pacé, M., Tardif, A., Lemauiel-Lavenant, S., Bonis, A., 2025. Forage nutritive value shows synergies with plant diversity in a wide range of semi-natural grassland habitats. *Agric. Ecosyst. Environ.* 347, 108369. <https://doi.org/10.1016/j.agee.2023.108369>.
- Cao, F., Li, W., Jiang, Y., Gan, X., Zhao, C., Ma, J., 2024. Effects of grazing on grassland biomass and biodiversity: a global synthesis. *Field Crop Res.* 306, 109204. <https://doi.org/10.1016/j.fcr.2023.109204>.
- Creed, R.P., Cherry, R.P., Pflaum, J.R., Wood, C.J., 2009. Dominant species can produce a negative relationship between species diversity and ecosystem function. *Oikos* 118 (5), 723–732. <https://doi.org/10.1111/j.1600-0706.2008.17212.x>.
- Cruz, P., De Quadros, F.L.F., Theau, J.P., Frizzo, A., Jouany, C., Duru, M., Carvalho, P.C. F., 2010. Leaf traits as functional descriptors of the intensity of continuous grazing in native grasslands in the south of Brazil. *Rangel. Ecol. Manage.* 63, 350–358. <https://doi.org/10.2111/08-016.1>.
- Fedrigio, J.K., Ataide, P.F., Azambuja, J.C.R., Bertoncelli, P., Nabinger, C., 2022. Deferment associated to contrasting grazing intensities affects root/shoot biomass allocation in natural grasslands. *Appl. Veg. Sci.* 25 (3), e12671. <https://doi.org/10.1111/avsc.12671>.
- Feki, K., Kamoun, H., Ben Romdhane, A., Tounsi, S., Harrabi, W., Salhi, S., Mhadhi, H., Trovato, M., Brini, F., 2025. *PvPR10-3* expression confers salt stress tolerance in *Arabidopsis* and interferes with jasmonic acid and ABA signaling. *Plant* 14 (19), 3092. <https://doi.org/10.3390/plants14193092>.
- Funk, J.L., Ames, G.M., Butterfield, B.J., Cavender-Bares, J., Firm, J., Laughlin, D.C., Sutton-Grier, A.E., Williams, L., Wright, J., 2017. Revisiting the Holy Grail: using plant functional traits to understand ecological processes. *Biol. Rev.* 92 (2), 1156–1173. <https://doi.org/10.1111/brv.12275>.
- Guo, T., Guo, M., Pang, Y., Sun, X., Ryo, M., Liu, N., Zhang, Y., 2024. Ungulate herbivores promote beta diversity and drive stochastic plant community assembly by selective defoliation and trampling: from a four-year simulation experiment. *J. Ecol.* 112 (9), 1992–2006. <https://doi.org/10.1111/1365-2745.14370>.
- He, Q., Jiang, K., Hou, W., Zhao, Y., Sun, X., Wang, L., Zou, Y., Zhu, Z., Zhang, H., 2021. Grazing alters species relative abundance by affecting plant functional traits in a Tibetan subalpine meadow. *Ecol. Evol.* 11 (16), 11028–11037. <https://doi.org/10.1002/ece3.7891>.
- Hou, F., Nan, Z., Xie, Y., Li, X., Lin, H., Ren, J., 2008. Integrated crop-livestock production systems in China. *Rangeland J.* 30 (2), 221–231. <https://doi.org/10.1071/RJ08018>.
- Hou, F., Jia, Q., Lou, S., Yang, C., Ning, J., Li, L., Fan, Q., 2021. Grassland agriculture in China—a review. *Front. Agric. Sci. Eng.* 8 (1), 35–44. <https://doi.org/10.15302/J-FASE-2020378>.
- Hou, G., Shi, P., Zhou, T., Sun, J., Zong, N., Song, M., Zhang, X., 2023. Dominant species play a leading role in shaping community stability in the northern Tibetan grasslands. *J. Plant Ecol.* 16, 3. <https://doi.org/10.1093/jpe/rtac110>.
- Huang, X., He, M., Li, L., Guo, Z., Hou, F., 2024. Grazing and precipitation addition interactions alleviate dominant species overgrowth and promote community productivity and biodiversity in a typical steppe. *Eur. J. Agron.* 161, 127370. <https://doi.org/10.1016/j.eja.2024.127370>.
- Huxley, J.D., White, C.T., Humphries, H.C., Weber, S.E., Spasojevic, M.J., 2023. Plant functional traits are dynamic predictors of ecosystem functioning in variable environments. *J. Ecol.* 111 (12), 2597–2613. <https://doi.org/10.1111/1365-2745.14197>.
- Jaurena, M., Lezama, F., Cruz, P., 2012. Perennial grasses traits as functional markers of grazing intensity in basaltic grasslands of Uruguay. *Chilean J. Agric. Res.* 72 (4), 541–549. <https://doi.org/10.4067/S0718-58392012000400013>.
- Jiang, S., Zhang, J., Tang, Y., Li, Z., Liu, H., Wang, L., Wu, Y., Liang, C., 2023. Plant functional traits and biodiversity can reveal the response of ecosystem functions to grazing. *Sci. Total Environ.* 899 (15), 165636. <https://doi.org/10.1016/j.scitotenv.2023.165636>.
- Kapas, R.E., Plue, J., Kimberley, A., Cousins, S.A.O., 2020. Grazing livestock increases both vegetation and seed bank diversity in remnant and restored grasslands. *J. Veg. Sci.* 31 (6), 1053–1065. <https://doi.org/10.1111/jvs.12956>.
- Koerner, S.E., Avolio, M.L., La Pierre, K.J., Wilcox, K.R., Smith, M.D., Collins, S.L., 2016. Nutrient additions cause divergence of tallgrass prairie plant communities resulting in loss of ecosystem stability. *J. Ecol.* 104 (5), 1478–1487. <https://doi.org/10.1111/1365-2745.12312>.
- Kovenock, M., Swann, A.L.S., 2018. Leaf trait acclimation amplifies simulated climate warming in response to elevated carbon dioxide. *Global Biogeochem. Cycles* 32 (10), 1437–1448. <https://doi.org/10.1029/2018GB005883>.
- Lei, L., Kong, X., Zhou, Z., Li, G., 2016. Plant functional traits, functional diversity, and ecosystem functioning: current knowledge and perspectives. *Biodivers. Sci.* 24 (8), 922–931. <https://doi.org/10.17520/biods.2015295>.
- Li, W., Li, X., Zhao, Y., Zheng, S., Bai, Y., 2018. Ecosystem structure, functioning and stability under climate change and grazing in grasslands: current status and future prospects. *Curr. Opin. Environ. Sustain.* 33, 124–135. <https://doi.org/10.1016/j.cosust.2018.05.008>.
- Li, X., Hou, X., Wu, X., Sa, R., Ji, L., Chen, H., Liu, Z., Ding, Y., 2014. Plastic responses of stem and leaf functional traits in *Leymus chinensis* to long-term grazing in a meadow steppe. *Chinese J. Plant Ecol.* 38 (5), 440–451. <https://doi.org/10.3724/SP.J.1258.2014.00040>.
- Li, X., Liu, Z., Wang, Z., Wu, X., Li, X., Hu, J., Shi, H., Guo, F., Zhang, Y., Hou, X., 2015. Pathways of *Leymus chinensis* individual aboveground biomass decline in natural semiarid grassland induced by overgrazing: a study at the plant functional trait scale. *PLoS ONE* 10 (5), e0124443. <https://doi.org/10.1371/journal.pone.0124443>.
- Li, Y., Gong, J., Liu, M., Hou, X., Ding, Y., Yang, B., Zhang, Z., Wang, B., 2020a. Defense strategies of dominant plants under different grazing intensity in the typical temperate steppe of Nei Mongol, China. *Chin. J. Plant Ecol.* 44 (6), 642–653. <https://doi.org/10.17521/cjpe.2019.0329>.
- Li, Y., Dong, S., Gao, Q., Zhang, Y., Liu, S., Ganjurjav, H., Hu, G., Wang, X., Yan, Y., Wu, H., Gao, X., Li, S., Zhang, J., 2020b. Rotational grazing promotes grassland aboveground plant biomass and its temporal stability under changing weather conditions on the Qinghai-Tibetan plateau. *Land Degrad. Dev.* 31 (17), 2662–2671. <https://doi.org/10.1002/ldr.3596>.
- Lisner, A., Segrestin, J., Konečná, M., Blazek, P., Janíková, E., Applová, M., Svancárová, T., Leps, J., 2024. Why are plant communities stable? Disentangling the role of dominance, asynchrony and averaging effect following realistic species loss scenario. *J. Ecol.* 183–1841. <https://doi.org/10.1111/1365-2745.14364>.
- Liu, H., Yin, D., He, P., Cadotte, M.W., Ye, Q., 2024. Linking plant functional traits to biodiversity under environmental change. *Biol. Divers.* 1, 22–28. Doi: <https://doi.org/10.1002/bod2.12004>.
- Mahaut, L., Fort, F., Violle, C., Freschet, G.T., 2020. Multiple facets of diversity effects on plant productivity: species richness, functional diversity, species identity and intraspecific competition. *Funct. Ecol.* 34 (1), 287–298. <https://doi.org/10.1111/1365-2435.13473>.
- Manlike, A., Sawut, R., Zheng, F.L., Li, X., Abudukelimu, R., 2020. Monitoring and analysing grassland ecosystem service values in response to grassland area changes—an example from Northwest China. *Rangeland J.* 42 (3), 179–194. <https://doi.org/10.1071/RJ20014>.
- Niinemets, Ü., 2020. Leaf trait plasticity and evolution in different plant functional types. *Annu. Plant Rev. Online* 3 (4), 473–521. <https://doi.org/10.1002/9781119312994.apr0714>.
- Orwin, K.H., Mason, N.W.H., Jordan, O.M., Lambie, S.M., Stevenson, B.A., Mudge, P.L., 2018. Season and dominant species effects on plant trait-ecosystem function relationships in intensively grazed grassland. *J. Appl. Ecol.* 55 (1), 236–245. <https://doi.org/10.1111/1365-2664.12939>.
- Pacifici, M., Visconti, P., Butchart, S.H.M., Watson, J.E.M., Cassola, F.M., Rondinini, C., 2018. Species' traits influenced their response to recent climate change. *Nat. Clim. Chang.* 8, 8, 750–750. Doi: <https://doi.org/10.1038/s41558-018-0229-3>.
- Pavanetto, N., Tordoni, E., Petruzzellis, F., Maccherini, S., Nardini, A., Beccari, E., Ricotta, C., Rocchini, D., Conti, L., Fanfarillo, E., Castello, M., Bacaro, G., 2025. Effect of climate extremes and grazing on functional traits of a grassland community: insights from a 20-year experiment. *Ann. Bot.* 136 (1), 129–139. <https://doi.org/10.1093/aob/mcaf059>.
- Polley, H.W., Collins, H.P., Fay, P.A., 2022. Community leaf dry matter content predicts plant production in simple and diverse grassland. *Ecosphere* 13 (5), e4076. <https://doi.org/10.1002/ecs2.4076>.
- Ren, H., Eviner, V.T., Gui, W., Wilson, G.W.T., Cobb, A.B., Yang, G., Zhang, Y., Hu, S., Bai, Y., 2018. Livestock grazing regulates ecosystem multifunctionality in semi-arid grassland. *Funct. Ecol.* 32 (12), 2790–2800. <https://doi.org/10.1111/1365-2435.13215>.
- Roelofs, H.D., van Bodegom, P.M., Kooistra, L., Witte, J.P.M., 2014. Predicting leaf traits of herbaceous species from their spectral characteristics. *Ecol. Evol.* 4 (6), 706–719. <https://doi.org/10.1002/ece3.932>.
- Sang, Y., You, Y., Xie, K., Hou, G., Yi, L., 2026a. Organ-specific nutritional divergence in reed under rotational grazing: leaf quality optimization vs. stem functional enhancement in salinized meadows. *J. Agric. Food Res.* 27, 102901. <https://doi.org/10.1016/j.jafr.2026.102901>.
- Sang, Y., You, Y., Xie, K., Yi, L., Hou, F., 2026b. Medium grazing intensity balances soil-driven trade-offs between ecosystem stability and livestock production in salinized meadows. *Plant Soil* 1–20. <https://doi.org/10.1007/s11104-026-08953-2>.
- Schaller, J., Roscher, C., Hillebrand, H., Weigelt, A., Oelmann, Y., Wilcke, W., Ebeling, A., Weisser, W.W., 2016. Plant diversity and functional groups affect Si and Ca pools in aboveground biomass of grassland systems. *Oecologia* 182, 277–286. <https://doi.org/10.1007/s00442-016-3647-9>.
- Shen, H., Dong, S., Li, S., Xiao, J., Han, Y., Yang, M., Zhang, J., Gao, X., Xu, Y., Li, Y., Zhi, Y., Liu, S., Dong, Q., Zhou, H., Yeomans, J.C., 2019. Grazing enhances plant photosynthetic capacity by altering soil nitrogen in alpine grasslands on the Qinghai-Tibetan plateau. *Agric. Ecosyst. Environ.* 280, 161–168. <https://doi.org/10.1016/j.agee.2019.04.029>.
- Shen, Y., Fang, Y., Oelmann, Y., Vancov, T., Chen, H., Du, Z., Chang, S., Cai, Y., 2025. Livestock excretion alleviates soil microbial carbon and phosphorus limitations relative to trampling and defoliation in an alpine meadow. *Agr. Ecosyst. Environ.* 389, 109687. <https://doi.org/10.1016/j.agee.2025.109687>.
- Strom, S., 2002. Novel interactions between phytoplankton and microzooplankton: their influence on the coupling between growth and grazing rates in the sea. *Hydrobiologia* 480 (1–3), 41–54. <https://doi.org/10.1023/A:1021224832646>.
- Takehiro, S., William, K.L., 2011. Dominant species, rather than diversity, regulates temporal stability of plant communities. *Oecologia* 166, 761–768. <https://doi.org/10.1007/s00442-011-1916-1>.
- Thakur, D., Rathore, N., Jandová, V., Münzbergová, Z., Dolezal, J., 2026. Shift from acquisitive to conservative plant strategies with increasing drought and temperature extremes in an alpine shrub. *Ann. Bot.* 137 (1), 125–139. <https://doi.org/10.1093/aob/mcaf211>.
- Tuo, H., Ghanizadeh, H., Ji, X., Yang, M., Wang, Z., Huang, J., Wang, Y., Tian, H., Ye, F., Li, W., 2024. Moderate grazing enhances ecosystem multifunctionality through leaf traits and taxonomic diversity in long-term fenced grasslands. *Sci. Total Environ.* 957, 177781. <https://doi.org/10.1016/j.scitotenv.2024.177781>.

- Wang, C., Wang, S., 2015. A review of research on responses of leaf traits to climate change. *Chinese J. Plant Ecol.* 39 (2), 206–216. <https://doi.org/10.17521/cjpe.2015.0020>.
- Wang, H., Li, X., Pang, C., 2025. Contrasting effects of short- and long-term grazing exclusion on plant diversity in humid grasslands. *Agric. Ecosyst. Environ.* 381, 109420. <https://doi.org/10.1016/j.agee.2024.109420>.
- Wang, J., Wen, X., Zhao, F., Fang, Q., Yang, X., 2012. Effects of doubled CO₂ concentration on leaf photosynthesis, transpiration and water use efficiency of eight crop species. *Chinese J. Plant Ecol.* 36 (5), 438–446. <https://doi.org/10.3724/SP.J.1258.2012.00438>.
- Wang, J., Zhong, M., Wu, R., Dong, Q., Wang, K., Shao, X., 2016. Response of plant functional traits to grazing for three dominant species in alpine steppe habitat of the Qinghai-Tibet Plateau, China. *Ecol. Res.* 31, 515–524. <https://doi.org/10.1007/s11284-016-1360-0>.
- Wang, M., Xu, Z., Song, J., Liu, X., Jiao, X., 2018. Effects of different mowing treatments and stubble heights on the compensatory growth and quality of lettuce (*Lactuca sativa* L.). *J. Hortic. Sci. Biotech.* 93 (5), 537–544. <https://doi.org/10.1080/14620316.2017.1413426>.
- Wang, M., Zhang, C., Chen, S., Zhang, Y., Yu, T., Xue, X., Wu, L., Zhou, W., Yun, X., Yan, R., Bai, K., 2024. Moderate grazing increased carbon, nitrogen and phosphorus storage in plants and soil in the Eurasian meadow steppe ecosystem. *Sci. Total Environ.* 914, 169864. <https://doi.org/10.1016/j.scitotenv.2023.169864>.
- Yan, R., Xin, X., Yan, Y., Wang, X., Zhang, B., Yang, G., Liu, S., Deng, Y., Li, L., 2015. Impacts of differing grazing rates on canopy structure and species composition in Hulunber Meadow Steppe. *Rangel. Ecol. Manage.* 68 (1), 54–64. <https://doi.org/10.1016/j.rama.2014.12.001>.
- Yu, R., Zhang, W., Fornara, D.A., Li, L., 2021. Contrasting responses of nitrogen: phosphorus stoichiometry in plants and soils under grazing: a global meta-analysis. *J. Appl. Ecol.* 58, 5, 964–975. Doi: <https://doi.org/10.1111/1365-2664.13808>.
- Yuan, J., Li, H., Yang, Y., 2020. The compensatory tillering in the forage grass *Hordeum brevisubulatum* after simulated grazing of different severity. *Front. Plant Sci.* 11, 792. <https://doi.org/10.3389/fpls.2020.00792>.
- Zhang, J., Shen, X., Mu, B., Shi, Y., Yang, Y., Wu, X., Mu, C., Wang, J., 2021. Moderately prolonged dry intervals between precipitation events promote production in *Leymus chinensis* in a semi-arid grassland of Northeast China. *BMC Plant Biol.* 21 (1), 147. <https://doi.org/10.1186/s12870-021-02920-y>.
- Zhang, J., Chen, J., Huang, Y., Jiang, L., Zheng, Z., Zhou, H., Wang, H., Liu, H., 2025c. Extreme warming coordinately shifts root and leaf traits of Alpine plants toward conservatism. *Ecosyst. Health Sustain.* 11, 0350. <https://doi.org/10.34133/ehs.0350>.
- Zhang, P., Seabloom, E.W., Foo, J., MacDougall, A.S., Harpole, W.S., Adler, P.B., Hautier, Y., Eisenhauer, N., Spohn, M., Bakker, J.D., et al., 2025b. Dominant species predict plant richness and biomass in global grasslands. *Nat. Ecol. Evol.* 9 (6). <https://doi.org/10.1038/s41559-025-02701-y>.
- Zhang, W., Li, R., Sun, Y., Sun, Z., Wang, S., Liu, J., Li, Y., Xu, L., Zhao, Y., 2026. Effects of salinity management practices on the soil organic carbon stock in China's salinized soils: a meta-analysis. *Catena* 269, 110146. <https://doi.org/10.1016/j.catena.2026.110146>.
- Zhang, Y., Zhu, J., Shen, R., Wang, L., 2020a. Research progress on the effects of grazing on grassland ecosystem. *Chin. J. Plant Ecol.*, 2020, 44, 553–564. Doi: [10.17521/cjpe.2019.0314](https://doi.org/10.17521/cjpe.2019.0314).
- Zhang, Y., Ganjurjav, H., Dong, S., Gao, Q., 2020b. Excessive plant compensatory growth: a potential endogenous driver of meadow degradation on the Qinghai-Tibetan plateau. *Ecosyst. Health Sustain.* 6 (1), 1816500. <https://doi.org/10.1080/20964129.2020.1816500>.
- Zhang, Y., Jin, B., Zhang, X., Wei, H., Chang, Q., Huang, F.Q., Liu, W., Lv, Y., Xu, Q., Sun, G., Cheng, H., 2023. Grazing alters the relationships between species diversity and biomass during community succession in a semiarid grassland. *Sci. Total Environ.*, 887, 164155. Doi: <https://doi.org/10.1016/j.scitotenv.2023.164155>.
- Zhang, Y., Peng, Z., Wang, Z., Chang, S., An, Y., Li, D., Hou, F., Ren, J., 2025a. Plant community-dominating species can sustain population biomass by modifying and strengthening their own growth traits to deal with long-term grazing. *Agric. Ecosyst. Environ.* 391, 109744. <https://doi.org/10.1016/j.agee.2025.109744>.
- Zhao, S., Zhang, T., Yue, P., Lv, P., Hu, Y., Medina-Roldán, E., Zuo, X., 2021. Increased grazing intensities induce differentiation of the relationships between functional traits and aboveground plant biomass in shrub- and grass-dominated community in desert steppe. *Ecological Research* 36 (4), 590–602. <https://doi.org/10.1111/1440-1703.12219>.
- Zheng, S., Ren, H., Lan, Z., Li, W., Wang, K., Bai, Y., 2010. Effects of grazing on leaf traits and ecosystem functioning in Inner Mongolia grasslands: scaling from species to community. *Biogeosciences*, 7, 1117–1132. Doi: [10.5194/bg-7-1117-2010](https://doi.org/10.5194/bg-7-1117-2010).
- Zuo, X., Zhang, J., Lv, P., Wang, S., Yang, Y., Yue, X., Zhou, X., Li, Y., Chen, M., Lian, J., Qu, H., Liu, L., Ma, X., 2018. Effects of plant functional diversity induced by grazing and soil properties on above- and belowground biomass in a semiarid grassland. *Ecol. Indic.* 2 (93), 555–561. <https://doi.org/10.1016/j.ecolind.2018.05.032>.