



Functional trait outperforms plant diversity in governing biomass production and allocation in semi—arid grasslands undergoing grazing exclusion

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ABSTRACT

Grazing exclusion is a key strategy for restoring degraded grasslands and enhancing their ecosystem services. Plant biomass production and allocation are critical indicators of restoration success, yet the mechanistic pathways by which plant functional traits and diversity regulate these dynamics under grazing exclusion remain unresolved. To address this, we measured aboveground (AGB) and belowground biomass (BGB) and root—to—shoot ratio (RSR) across a 27-year chronosequence in semi—arid grasslands of Songnen Plain, Northeast China, and investigated how plant functional traits and diversity (species and functional) regulate these processes. Results revealed temporally decoupled biomass peaks, with AGB peaking at 19 years (491.14 g m⁻²) and BGB peaking earlier at 15 years (1046.50 g m⁻²). Concurrently, RSR declined initially before stabilizing after 19 years, and plant diversity generally exhibited an opposite trend to biomass production. Principal component analysis identified key plant functional strategies under grazing exclusion, with PC1 partitioning resource-acquisitive traits (e.g., leaf area, LA) from conservative traits (e.g., leaf nitrogen content, LNC) and PC2 representing a defense axis dominated by traits such as leaf dry matter content (LDMC). Critically, correlation and variation partitioning analyses demonstrated that functional traits, rather than diversity, emerged as the dominant driver of biomass production and allocation. Structural equation modeling further revealed that grazing exclusion directly impacted AGB and allocation, and indirectly regulated them via species richness. Notably, grazing exclusion modulated biomass dynamics by altering functional traits (LA and LDMC) and LA—LNC trade-off. Additionally, LDMC—induced shifts in functional diversity (Rao's Q) contributed to biomass allocation adjustments. Our findings establish that biomass dynamics under grazing exclusion exhibit strong temporal patterns primarily driven by plant functional traits, delineating key mechanistic pathways. This framework provides a robust basis for assessing restoration success and strategically guides optimal management of semi—arid grasslands.

1. Introduction

Grasslands, covering approximately 30 % of the Earth's terrestrial surface, represent one of the most ecologically and economically important ecosystems worldwide (Bardgett et al., 2021; Bai and Cotrufo, 2022). These ecosystems rely on fundamental plant biomass production and allocation processes to maintain their ecosystem functions and service provision (Cao et al., 2024). Aboveground biomass (AGB) serves as a direct measure of forage productivity, while belowground biomass

(BGB) plays dual roles in supporting AGB production and facilitating substantial carbon sequestration in soils (Dijkstra et al., 2021; Ma et al., 2021). Furthermore, the root—to—shoot ratio (RSR) further serves as an important functional indicator, reflecting vegetation's adaptive responses to environmental stresses including drought and soil salinization (Sun et al., 2021; Guasconi et al., 2023). In the context of global environmental change, widespread grassland degradation has triggered significant reductions in biomass production. As a key restoration approach, grazing exclusion has demonstrated remarkable effectiveness

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in ecosystem restoration. Empirical evidence shows that eliminating grazing and trampling pressures leads to: (1) accelerated aboveground vegetation restoration, (2) improved soil physicochemical properties, and (3) enhanced root system development - collectively contributing to increased AGB and BGB (Denyer et al., 2010; Zhang et al., 2019). While short-term exclusion (≤ 10 years) generally promotes vegetation biomass restoration through grazing pressure release (Tai et al., 2021), the sustainability and long-term ecological outcomes of this practice require further investigation. Understanding the temporal dynamics of grassland biomass production and allocation patterns under different exclusion durations is therefore essential for evidence-based restoration assessment, duration-specific management optimization, and accurate prediction of ecosystem service restoration in degraded grasslands.

Functional traits serve as pivotal mediators of biomass production and allocation by directly regulating plant resource acquisition and partition strategies after grazing exclusion (Sun et al., 2024; Rehling et al., 2021). For instance, leaf area (LA) and specific leaf area (SLA) are strongly associated with photosynthetic efficiency, thereby influencing biomass accumulation (Liu et al., 2023; Künzi et al., 2025). Leaf dry matter content (LDMC), which indicates leaf tissue density, plays a critical role in organic matter retention and directly affects AGB levels (Zhang et al., 2023). At the community scale, community-weighted mean (CWM) trait values integrate plant functional responses to grazing exclusion (Feng et al., 2024). Furthermore, systematic analysis of plant functional trait strategies in resource allocation can be achieved through the leaf economics spectrum (LES) framework, which characterizes species along a continuum spanning 'fast' (resource-acquisitive) to 'slow' (resource-conservative) ecological strategies (Reich, 2014; Díaz et al., 2016). For example, the 'fast' strategy is characterized by high SLA, reflecting an ecological adaptation prioritizing rapid growth and transient resource utilization. In contrast, 'slow' strategists display low SLA, indicative of conservative resource allocation and prolonged tissue persistence (Wright et al., 2004). Beyond their role in resource acquisition, plant functional traits in grazing-managed grasslands additionally serve critical functions, such as defense (Díaz et al., 2016). Grazing exclusion has been shown to reorganize community-level LES, thereby altering biomass allocation patterns (Suding et al., 2015). Notably, key traits may demonstrate nonlinear responses along exclusion chronosequences, ultimately restructuring biomass allocation patterns through competitive exclusion and niche partitioning processes (Laliberté and Legendre, 2010). Despite these insights, current research remains constrained by its predominant focus on discrete restoration stages or static comparisons, resulting in significant knowledge gaps regarding the temporal trajectories of functional traits across exclusion gradients, and their mechanistic relationships with biomass allocation patterns.

Plant species diversity underpins ecosystem integrity, with its temporal dynamics playing a critical role in mediating grassland restoration outcomes under grazing exclusion. The effects of grazing exclusion on plant species diversity have been widely documented, yet current research reveals substantial inconsistencies. Some studies report enhanced species richness and community evenness following exclusion (Gao and Carmel, 2020; Liu et al., 2020), others demonstrate neutral or detrimental outcomes (Xiong et al., 2016; Song et al., 2020). These divergent findings likely stem from methodological and contextual differences across studies, particularly in geographic settings, exclusion duration, grassland types, and climatic regimes (Balvanera et al., 2006; Daleo et al., 2023). Traditional ecological theory suggests that grazing exclusion promotes diversity restoration through disturbance alleviation, subsequently facilitating biomass accumulation (Bai et al., 2007; Tilman et al., 2014). However, contemporary research identifies important temporal limitations to these diversity-mediated benefits. Short-term exclusion (< 10 years) typically enhances productivity through increased species richness (Fornara and Tilman, 2013), whereas prolonged exclusion often leads to competitive dominance by few species, ultimately disrupting diversity-productivity relationships (Suding

et al., 2015). This decoupling effect appears particularly strong in semi-arid grasslands (Garnier et al., 2004), where resource preemption by dominant species becomes more pronounced over time (Gough et al., 2000; Adler et al., 2011). Notably, comprehensive assessment of diversity effects on ecosystem functioning requires simultaneous consideration of both taxonomic and functional diversity dimensions. Functional diversity, reflecting the range and value of plant traits within communities, provides critical complementary information to species counts, offering mechanistic insights into ecosystem processes (Vandewalle et al., 2010; Bongers et al., 2021). As functional traits directly mediate plant-environment interactions (Díaz et al., 2007), their incorporation is essential for robust evaluation of biomass production and allocation patterns in restored grasslands.

Although the effects of plant functional traits and diversity on biomass production and allocation have been well-documented (e.g., Bai et al., 2007; Laliberté and Legendre, 2010), the sequential response mechanisms underlying community dynamics across prolonged grazing exclusion chronosequences remain poorly understood. This study investigated the semi-arid grasslands in China's Songnen Plain under different grazing exclusion durations (10, 15, 19, and 27 years) compared with actively grazing controls. We quantified biomass production and allocation patterns while analyzing their relationships with key plant functional traits and diversity metrics. Our investigation addresses three critical questions: (1) How does grazing exclusion duration affect temporal patterns of biomass production and allocation? (2) What are the relative contributions of functional traits, taxonomic and functional diversity in driving biomass dynamics? (3) Through what pathways do functional traits and diversity metrics mediate biomass production and allocation? The results will provide mechanistic insights into grassland restoration processes and inform evidence-based management strategies for semi-arid ecosystems.

2. Materials and methods

2.1. Study area

The study was conducted in the western Songnen Plain (123°25'–123°40' E, 45°10'–45°20' N), a semi-arid region in north-eastern China (Fig. 1). The region experiences a temperate continental monsoon climate, with a mean annual temperature of 4.3°C. Seasonal temperature extremes range from -35°C in winter to 37°C in summer. Precipitation shows strong seasonality, with a mean annual of 380 mm (70 % concentrated in June–August), significantly lower than the mean annual evaporation (1761–1842 mm). The region receives abundant solar radiation ($5208 \text{ J cm}^{-2} \text{ yr}^{-1}$) with the mean annual sunshine duration of 2930 h, supporting a 132-day frost-free period. The predominant soils (meadow soil, saline meadow soil, light chernozem, and saline soil) are characterized by soil organic matter content ranging from 0.6 % to 2.0 %, salinity levels between 0.2 % and 1.5 %, and pH values from 7.5 to 10.6. The vegetation is predominantly typical meadow, with *Leymus chinensis* (Trin.) Tzvel. as the dominant species. Associated species include *Phragmites australis* (Cav.) Trin. ex Steud., *Lespedeza daurica* (Laxm.) Schindl., *Potentilla flagellaris* Willd. ex-Schlecht, *Calamagrostis epigeios* (L.) Roth, *Cleistogenes squarrosa* (Trin.) Keng, *Carex duriuscula* C. A. Mey., *Artemisia scoparia* Waldst. et Kit., and *Puccinellia scoparia* Waldst. et Kit., etc.

2.2. Experimental design and biomass measurement

This study employed the space-for-time substitution (chronosequence) approach to investigate long-term grazing exclusion effects. Field investigations and sampling were conducted in July 2021 across semi-arid grasslands representing a chronosequence of grazing exclusion durations. Sites were strategically selected to capture key stages of grassland restoration dynamics, specifically 10 years (GE10), 15 years (GE15), 19 years (GE19), and 27 years (GE27). The selection of these

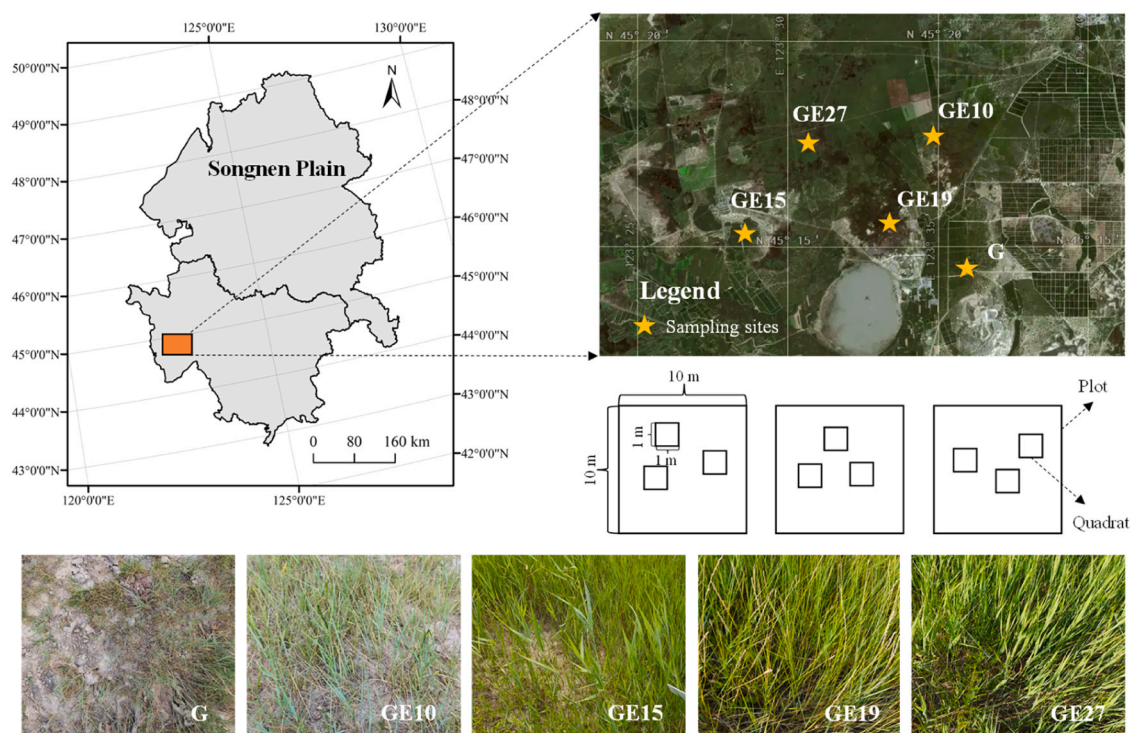


Fig. 1. Schematic diagram of study area location and experimental design. G, grazing site; GE10, 10-year grazing exclusion site; GE15, 15-year grazing exclusion site; GE19, 19-year grazing exclusion site; and GE27, 27-year grazing exclusion site.

time intervals was driven by the goal of encompassing critical phases of ecosystem response, from initial restoration through potential biomass accumulation periods to long-term stabilization. This design was informed by our preliminary observations (Gao et al., 2021) indicating that key productivity shifts typically occur within 10–20 years after exclusion. Additionally, the exact exclusion durations were determined based on verified historical management records maintained by the local grassland management bureau, which document the specific year exclusion was erected and enforced (1994 for GE27, 2002 for GE19, 2006 for GE15, 2011 for GE10). The integrity of exclusion and absence of grazing activity were confirmed during field surveys. An adjacent continuously grazing grassland (G; $0.5\text{--}1.0$ sheep $\text{ha}^{-1} \text{yr}^{-1}$) served as the control (0 year exclusion). The spatial arrangement is shown in Fig. 1.

In the grazing grasslands, vegetation is co-dominated by *Chloris virgata* Swartz and *L. chinensis*. However, following grazing exclusion, *L. chinensis* becomes monodominant, with compositae and leguminous species as the primary associates. All study sites were landscape-connected with homogeneous terrain, sharing consistent climatic, hydrological and edaphic conditions, and were originally dominated by *L. chinensis* prior to grazing interference. Vegetation survey was performed employing a nested plot-quadrat design. At each grassland site, we established three replicate plots ($10 \text{ m} \times 10 \text{ m}$), within which three quadrats ($1 \text{ m} \times 1 \text{ m}$) were randomly positioned (Fig. 1). This sampling scheme resulted in a total of 45 quadrats (5 sites \times 3 plots \times 3 quadrats) being examined. All vascular plant species occurring within the quadrats were systematically documented. For biomass determination, the aboveground components of all plant species were harvested at ground level. Belowground sampling was conducted using a 9-cm diameter auger to 30 cm depth. Root-soil composites were initially soaked in water for soil dispersion, followed by sequential filtration through 2 mm and 0.15 mm mesh sieves under continuous water flow to separate coarse and fine roots ($\leq 1 \text{ mm}$ diameter), respectively. All plant materials were dried to constant mass in an oven at 65°C for subsequent measurement of aboveground biomass

(AGB) and belowground biomass (BGB). The root-to-shoot ratio (RSR) was calculated as the ratio of BGB to AGB.

2.3. Measurement of plant functional traits

For each species within each quadrat, 4–5 representative individuals were selected, and 8–10 mature, undamaged leaves were collected from each individual. The leaves were immediately excised with clean scissors and placed between moistened filter paper to prevent desiccation. They were then sealed in labeled plastic bags and stored in a dark container to allow full hydration prior to saturated fresh weight (LFW) measurement. Leaf area (LA) was determined using a portable leaf area meter (Yaxin-1242, Beijing, China). The leaves were subsequently oven-dried at 65°C to constant mass to determine leaf dry weight (LW). Specific leaf area (SLA) was calculated as the ratio of LA to LW, and leaf dry matter content (LDMC) was calculated as the ratio of LW to LFW. Additional leaf samples were collected, dried at 65°C , and ground into a fine powder for elemental analysis. Leaf carbon content (LCC) and nitrogen content (LNC) were measured using an elemental analyzer (Vario EL Cube, Elementar, Germany), while leaf phosphorus content (LPC) was determined via the molybdenum-antimony spectrophotometric method (Cui et al., 2019). For species with insufficient biomass, samples were pooled by functional groups, and the mean trait values (LCC, LNC, and LPC) were assigned to all species within that group. Based on these measurements, the leaf carbon-to-nitrogen ratio (LCNR), nitrogen-to-phosphorus ratio (LNPR), and carbon-to-phosphorus ratio (LCPR) were calculated.

2.4. Data analysis

To quantify plant functional trait responses to grazing exclusion, we calculated community-weighted mean (CWM) values using the following formula:

$$CWM_j = \sum_{i=1}^S T_{ij} \times P_i \quad (1)$$

Where: CWM_j is the community weighted mean of plant functional traits j ; T_{ij} is the value of plant functional trait j for species i , and P_i is the density ratio of species i in the community.

The species diversity indices of plant community, including species diversity (H'), species richness (R), and species evenness (E), were represented by the Shannon–Wiener index, Patrick index, and Pileous index, respectively. They were calculated as follows:

$$H' = - \sum_{i=1}^S P_i \times \ln P_i \quad (2)$$

$$R = S \quad (3)$$

$$E = H' / \ln S \quad (4)$$

Where: H' is the species diversity index, R is the species richness index, E is the species evenness index, P_i is the density ratio of species i in the community, and S is the number of species observed in plant community.

To comprehensively assess the response of functional diversity to grazing exclusion, we employed three key indices: Rao's quadratic entropy (Rao's Q), functional richness (FR_{ic}), and functional evenness (FE_{ve}) which were based on the ten functional traits obtained in this study. The functional diversity indices were computed using the "FD" package in R 4.4.0 (Laliberté et al., 2014). These indices capture different dimensions of functional diversity, providing a holistic understanding of community functional structure.

We employed linear mixed models (LMMs) to assess differences in AGB, BGB, RSR, CWM values of plant functional trait, and species/functional diversity indices across grassland sites with differing grazing exclusion durations. All models incorporated "Plot" as a random intercept effect to control for spatial autocorrelation among sampling units within sites. Analyses were implemented in R 4.4.0 using the lme4 package for model fitting (Bates et al., 2015) and "lmerTest" for significance testing (Kuznetsova et al., 2017), assuming a Gaussian error distribution. Post hoc pairwise comparisons were performed via Tukey's Honestly Significant Difference (HSD) test, with significance thresholds set at $P < 0.05$. To evaluate the contributions of functional traits to plant ecological strategies, a principal component analysis (PCA) was conducted using the "prcomp" function, and variable loadings plot was generated with the "factoextra" package (Kassambara and Mundt, 2016). Prior to analysis, all traits were standardized to zero mean and unit variance to ensure scale invariance. The relationships between AGB, BGB, RSR and CWM traits, as well as diversity indices, were examined by Pearson correlation analysis using "corrplot" package (Wei et al., 2017), with statistical significance set at $P < 0.05$. Variables were log-transformed if necessary to improve the normality of the residuals. To quantify the relative contributions of plant functional traits, species diversity, and functional diversity to the variation in plant biomass production and allocation, a variation partitioning analysis (VPA) was performed using the "vegan" package (Oksanen et al., 2018).

Based on the LMMs, PCA, and correlation analysis results, the most significant functional traits, species diversity indices, and functional diversity indices were selected for subsequent structural equation modeling (SEM) analysis to reveal the pathways influencing biomass production and allocation. All selected variables were log-transformed, and we built a prior model based on prior knowledge of the effects and relationships among the selected variables. The prior model was developed with maximum likelihood estimation and was further trimmed by removing nonsignificant paths in a stepwise fashion until the model had an adequate fit. The fit of the model was assessed based on the chi-square (χ^2) test, degrees of freedom (DF), whole-model P value, root-mean-square error of approximation (RMSEA), and Akaike

information criterion (AIC). SEM was generated using AMOS 24.0 (Amos Development Corporation, Chicago).

3. Results

3.1. Grassland vegetation biomass production and allocation

LMMs demonstrated that grazing exclusion duration exerted significant effects on AGB, BGB, and RSR ($P < 0.001$; Fig. 2). The maximum AGB was observed at the GE19 site, reaching 491.14 g m⁻², which was 4.84 times greater than that at the G site (Fig. 2a). BGB was highest at the GE15 site (Fig. 2b), with a value of 1046.50 g m⁻², representing a 1.21-fold increase compared to the G site. In contrast, the RSR peaked at the G site (5.65) and subsequently declined progressively (Fig. 2c), reaching its minimum value of 1.76 at the GE19 site.

3.2. CWM values for plant functional traits

LMMs revealed that grazing exclusion duration exerted significant effects on all ten functional traits ($P < 0.001$; Fig. 3). The GE19 site exhibited the highest LA (785.84 mm²), surpassing other sites by 1.3–3.8 times (Fig. 3a). The G site showed the lowest LA (206.67 mm²), significantly lower than all exclusion sites ($P < 0.05$). LW increased progressively from G (22.76 mg) to GE19 (59.39 mg) along the exclusion chronosequence but declined at GE27 site (Fig. 3b). LDMC peaked at G (40.76 %) and fluctuated among exclusion sites (Fig. 3c). SLA rose sharply from G site (9.06 mm² mg⁻¹) to GE10 site (13.96 mm² mg⁻¹), followed by a gradual decline (Fig. 3d), indicating a rapid shift in plant resource acquisition strategies post-exclusion. GE15 site had the highest LCC (458.90 mg g⁻¹), significantly exceeding all sites except GE27 (445.20 mg g⁻¹) (Fig. 3e). The G site showed the lowest LCC (390.63 mg g⁻¹). GE10 exhibited the highest LNC (19.85 mg g⁻¹) (Fig. 3f), while mid-term exclusion sites (GE15: 10.91 mg g⁻¹; GE19: 10.11 mg g⁻¹) showed significantly lower values ($P < 0.05$). The G site exhibited the highest LPC (1.44 mg g⁻¹), significantly exceeding all grazing exclusion sites ($P < 0.05$), whereas no significant differences were detected among exclusion sites (Fig. 3g). GE15 (42.24) and GE19 (40.87) showed the highest LCNr (Fig. 3h), significantly exceeding other sites ($P < 0.05$), with GE10 being the lowest (21.39). GE27 (481.12) and GE15 (478.28) sites exhibited the highest LCPR (Fig. 3i), with G site showing the lowest value. GE10 site had the highest LNPR (19.93), significantly greater than G site (Fig. 3j), GE15, and GE19 sites ($P < 0.05$).

The cumulative contribution rate of the first two principal components (PC1 and PC2) in the PCA analysis was 75.67 %, effectively reflecting the plant functional strategies (Table 1; Fig. 4). PC1, explaining 49.24 % of the total variance, served as the dominant axis for functional traits, reflecting the core trade-offs in resource utilization strategies. In the positive direction of PC1, traits such as LA, LW, LCNr, and LCPR exhibited high loadings, while LNC and LPC showed significant negative loadings. This aligns with the LES, where the positive direction of PC1 represents a "fast investment–return" strategy characterized by high carbon storage and morphological expansion, while the negative direction corresponds to a "conservative" metabolic strategy prioritizing nitrogen and phosphorus partition. PC2 explained 26.43 % of the variance and was strongly associated with LDMC and LNPR in the positive direction, and with high LPC in the negative direction, reflecting a differentiation axis of "physical defensive" strategy.

Basing on the results of PCA LA, LNC, and LDMC were selected for subsequent correlation analysis and VPA to align with the three-dimensional species diversity and functional diversity indices. Specifically, LA (loading: 0.809) and LNC (loading: -0.912) anchor opposing ends of PC1, while LDMC (loading: 0.772) dominates PC2 as a key structural defense trait. We prioritized LDMC over higher-loading PC2 traits (e.g., LNPR: 0.906) to avoid redundancy with LNC and leverage its cross-cutting chemical defense role. Collectively, these traits were

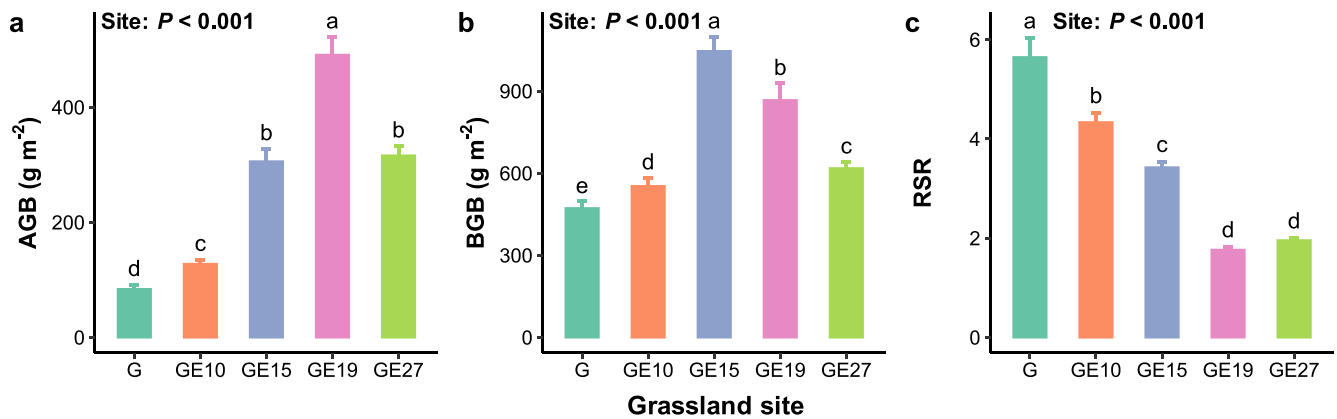


Fig. 2. AGB (a), BGB (b) and RSR (c) across the grassland sites. AGB, aboveground biomass; BGB, belowground biomass; RSR, root-to-shoot ratio. G, grazing site; GE10, 10-year grazing exclusion site; GE15, 15-year grazing exclusion site; GE19, 19-year grazing exclusion site; and GE27, 27-year grazing exclusion site. Different letters indicate statistically significant differences among grassland sites ($P < 0.05$).

selected by their representativeness for different ecological strategies and physiological functions

3.3. Plant species diversity and functional diversity

LMMs revealed that exclusion duration had a significant effect on three plant species diversity metrics ($P < 0.01$; Fig. 5). H' was lowest in the GE15 site and reached its maximum in the GE19 site, with a value of 2.215 (Fig. 5a). G site had significantly higher R than all the other sites ($P < 0.05$) except GE19, with the lowest value observed in the GE15 site (Fig. 5b). Furthermore, E was relatively high in the GE10 (0.809) and G (0.793) sites (Fig. 5c), both of which were significantly higher than that of the GE15 site ($P < 0.05$).

LMMs revealed that exclusion duration significantly influenced Rao's Q ($P < 0.001$; Fig. 6a), G site showed significantly higher Rao's Q than all the other sites except GE10 site. However, exclusion duration had no significant effect on FR_{ic} or FE_{ves} , with no notable differences observed among sites ($P > 0.05$, Fig. 6b and c).

3.4. Contributions of plant traits and diversity to biomass production and allocation

Correlation analysis revealed AGB and BGB were significant positive correlated with LA ($P < 0.05$; Fig. 7). In contrast, both they exhibited significant negative correlations with LNC, LDMC and Rao's Q ($P < 0.05$). Additionally, BGB was significantly negatively correlated with H' , R , E , and FR_{ic} ($P < 0.05$). Meanwhile, the RSR was significant negative correlated with LA ($P < 0.05$) but positively correlated with LNC, LDMC, R , and Rao's Q ($P < 0.05$).

LA exhibited a significant negative correlation with LN and LDMC ($P < 0.05$). This result aligns with the opposite direction of LA and LNC along PC1 axis in PCA plot. In addition, there were also certain connections between functional traits and diversity. In particular, Rao's Q was negatively correlated with LA and positively correlated with LNC and LDMC ($P < 0.01$). Moreover, significant positive correlations were detected between species diversity (R) and functional diversity indices (Rao's Q and FR_{ic}) ($P < 0.01$).

VPA revealed that plant functional traits, species diversity, and functional diversity collectively explained 95.3 % of the variation in AGB, 87.9 % in BGB, and 82.9 % in RSR (Fig. 8). For AGB, plant functional traits alone contributed 66.1 % of the explanatory power, significantly surpassing the contributions of species diversity and functional diversity (Fig. 8a). For BGB, plant functional traits accounted for 47.8 % of the variation, species diversity accounted for 17.5 %, and the interactions of functional traits and diversity explained 18.5 % (Fig. 8b). In the case of RSR, plant functional traits again exhibited the highest

explanatory power (41.8 %), followed by the interaction between functional traits and species diversity, which accounted for 22.3 % (Fig. 8c).

3.5. Pathways of plant functional traits determining biomass allocation

Correlation analyses identified LA, LNC, and LDMC as key functional traits influencing AGB, BGB, and RSR, leading to their inclusion in SEM. Among diversity metrics, R correlated significantly with BGB and RSR, while maintaining positive associations with both H' and E . Additionally, Rao's Q demonstrated significant relationships with all biomass components and positive correlations with R , E , and FR_{ic} . These results justified the selection of R and Rao's Q as primary diversity variables for SEM analysis.

SEM elucidated the pathways through which grazing exclusion regulated grassland biomass allocation ($\chi^2 = 17.268$, $df = 11$, $P = 0.100$; RMSEA = 0.114; AIC = 85.268; Fig. 9). Grazing exclusion increased AGB ($\beta = 0.35$, $P < 0.001$), which subsequently suppressed RSR ($\beta = -0.80$, $P < 0.001$). It also exerted a direct negative effect on RSR ($\beta = -0.41$, $P < 0.001$). Through species richness (R), exclusion indirectly reduced AGB ($\beta = 0.17$, $P < 0.001$) but enhanced BGB ($\beta = -0.20$, $P < 0.05$), ultimately increasing RSR. Trait-mediated pathways revealed that exclusion increased LA ($\beta = 0.46$, $P < 0.001$) but decreased LDMC ($\beta = -0.41$, $P < 0.01$), collectively promoting AGB and BGB accumulation, thereby modulating RSR. Notably, the LA–LNC trade-off ($\beta = -0.31$, $P < 0.05$) emerged as a key driver of biomass allocation shifts. Furthermore, reduced LDMC, which lowered Rao's Q ($\beta = 0.29$, $P < 0.05$), ultimately contributing to decreased RSR ($\beta = 0.05$, $P < 0.05$).

4. Discussion

4.1. Threshold effects of grazing exclusion duration on plant biomass production

Our study revealed a decoupled temporal pattern in biomass responses to grazing exclusion: AGB peaked at 19 years of exclusion, while belowground biomass (BGB) reached its maximum earlier, at 15 years (Fig. 2). This asynchrony aligns with several studies in semi-arid grasslands but reveals critical nuances regarding optimal management duration (Hu et al., 2016; Wan et al., 2024). For instance, Deng et al. (2017) summarized that in the grasslands of northern China, AGB and BGB were still increasing after a 27-year grazing exclusion, but their rapid growth periods were < 3 years and < 6 years respectively. This divergence likely arises from site-specific thresholds: (1) Water competition intensifies as carrying capacity is exceeded (Ren et al., 2018;

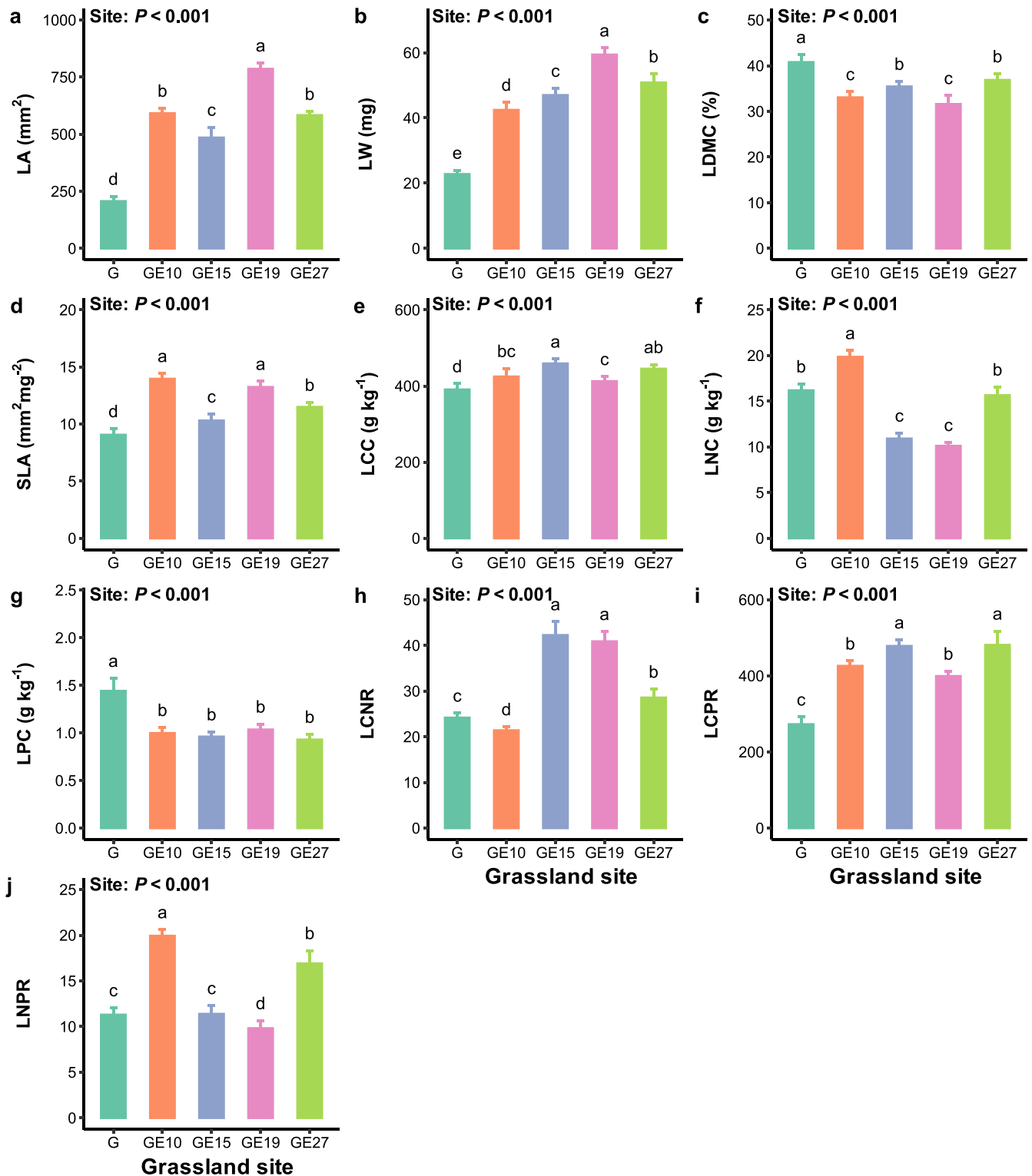


Fig. 3. CWM traits across the grassland sites. LA, leaf area (a); LW, leaf weight (b); LDMC, leaf dry matter content (c); SLA, special leaf area (d); LCC, leaf carbon content (e); LNC, leaf nitrogen content (f); LPC, leaf phosphorus content (g). LCNR, leaf carbon—to—nitrogen ratio (h); LNPR, leaf nitrogen—to—phosphorus ratio (i); LCPR, leaf carbon—to—phosphorus ratio (j); G, grazing site; GE10, 10—year grazing exclusion site; GE15, 15—year grazing exclusion site; GE19, 19—year grazing exclusion site; and GE27, 27—year grazing exclusion site. Different letters indicate statistically significant differences among grassland sites ($P < 0.05$).

Michalet et al., 2023), (2) Nutrient depletion triggers negative plant-soil feedbacks (Chen et al., 2021), and (3) the dominance of superior grass species significantly enhanced, but Senescence dominates in aging perennial communities (Osem et al., 2006; Cislighi et al., 2019). Critically, our site's soda saline-alkali soil conditions (pH > 8.5, salt content

> 0.8 %) likely lowered resilience, accelerating resource limitation effects compared to less degraded systems.

In this study, BGB reached its peak at 15 years of grazing exclusion, while AGB reached its peak at 19 years of exclusion, indicating that BGB reached the threshold before AGB. This is inconsistent with the result of

Table 1
PCA loadings of plant functional traits.

Plant functional traits	Principal analysis component			
	PC1	PC2	PC3	PC4
LA	0.809	−0.311	0.253	0.423
LW	0.793	−0.271	0.193	0.505
SLA	−0.378	0.198	−0.786	0.393
LDMC	−0.088	0.772	0.443	−0.019
LCC	0.749	0.446	−0.115	−0.235
LNC	−0.912	0.219	0.176	0.206
LPC	−0.770	−0.606	0.125	0.029
LCNR	0.916	−0.242	−0.197	−0.182
LCPR	0.777	0.585	−0.103	0.023
LNPR	−0.248	0.906	0.051	0.248
Variation explained %	49.24	26.43	10.26	7.82

Notes: LA, leaf area; LW, leaf dry weight; SLA, specific leaf area; LDMC, leaf dry matter content; LCC, leaf carbon content; LNC, leaf nitrogen content; LPC, leaf phosphorus content; LCNR, leaf carbon-to-nitrogen ratio; LNPR, nitrogen-to-phosphorus ratio; and LCPR, carbon-to-phosphorus ratio.

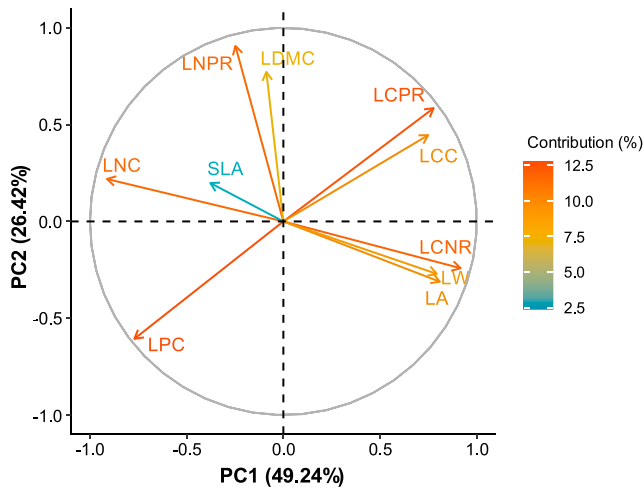


Fig. 4. PCA variable loadings plot. LA, leaf area; LW, leaf dry weight; SLA, specific leaf area; LDMC, leaf dry matter content; LCC, leaf carbon content; LNC, leaf nitrogen content; LPC, leaf phosphorus content; LCNR, leaf carbon-to-nitrogen ratio; LNPR, nitrogen-to-phosphorus ratio; and LCPR, carbon-to-phosphorus ratio.

previous studies that BGB lags behind AGB (Hu et al., 2016). It is traditionally believed that although AGB has decreased, there is still a certain amount plant litter return, thereby enriches soil nutrient content (and improves water retention and infiltration capacity, creating favorable conditions for root development and promoting BGB accumulation (Schleuss et al., 2020; Du and Gao, 2021). However, the asynchrony of our results likely reflects differential resource allocation strategies, where belowground organs exhibit preferential and rapid responses to resource availability changes, while aboveground biomass responds more slowly due to lag effects in community succession dynamics (Poorter et al., 2012). Moreover, the well-developed rhizome system of *L. chinensis* leads to excessive root proliferation under prolonged grazing exclusion (>15 years), ultimately compromising soil aeration and hydraulic conductivity. These adverse edaphic conditions subsequently constrain fine root respiration, nutrient uptake efficiency, and ultimately limit belowground biomass accumulation (Schönbach et al., 2011; Cheng et al., 2016). This pattern underscores the importance of considering temporal factors in grazing exclusion management strategies to optimize ecosystem benefits.

Regarding RSR in our results, it peaked in grazed sites and reached its minimum after 19 years of grazing exclusion (Fig. 2c). This pattern aligns with the resource optimization theory proposed by Koevoets et al. (2016), which posits that plants in resource-limited grasslands (e.g., grazed systems) preferentially allocate biomass to root systems to enhance water and nutrient acquisition efficiency. As grazing exclusion progresses to an appropriate duration, the plant community reaches a relatively stable stage of restoration, leading to a decreasing trend in RSR (Ma et al., 2021; Guasconi et al., 2023; Michalet et al., 2023). However, a notable fluctuation in RSR is observed between GE19 and GE27, indicating that prolonged grazing exclusion without proper utilization may disrupt the balance of biomass allocation. Therefore, when implementing grazing exclusion measures, it is crucial to tailor the duration and management strategies to specific ecological conditions.

4.2. Response of plant functional strategies to grazing exclusion duration

Our results demonstrate that grazing exclusion significantly increased LA and LW, particularly in the 19-year excluded grassland (Fig. 3a and b). These traits showed strong positive loadings on PC1 (Table 1), identifying them as key drivers of plant community functional changes during early-stage ecosystem restoration. Consistent with the leaf economics spectrum theory (Wright et al., 2004), the observed LA and LW increases in our study reflect an "acquisition-oriented" strategy, where plants rapidly exploit newly available resources (e.g., light, nutrients) through morphological plasticity during initial exclusion periods. Contrastingly, LNC was significantly lower in exclusion sites than

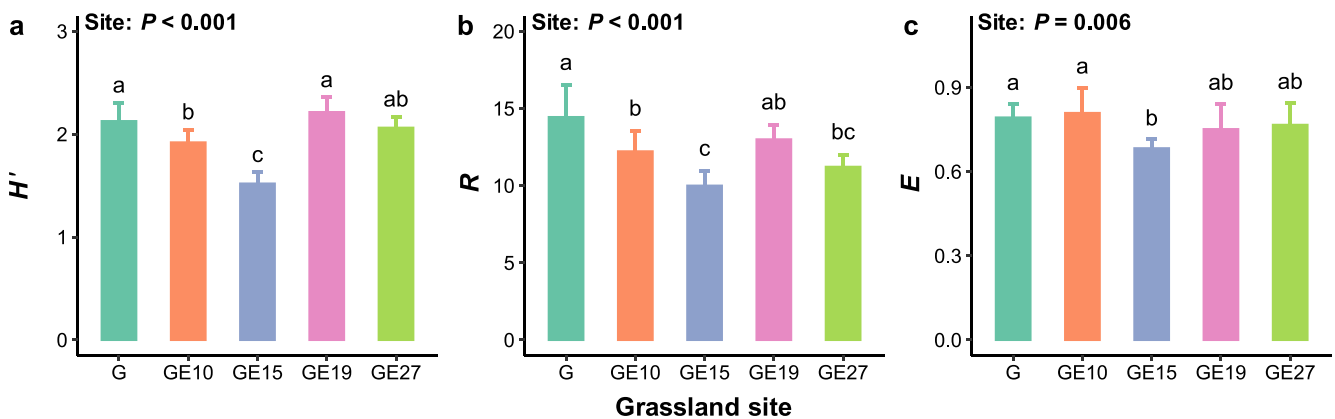


Fig. 5. Plant species diversity indices of H' (a), R (b), and E (c) across the grassland sites. H' , species diversity index; R , species richness index; E , species evenness index. G, grazing site; GE10, 10-year grazing exclusion site; GE15, 15-year grazing exclusion site; GE19, 19-year grazing exclusion site; and GE27, 27-year grazing exclusion site. Different letters indicate statistically significant differences among grassland sites ($P < 0.05$).

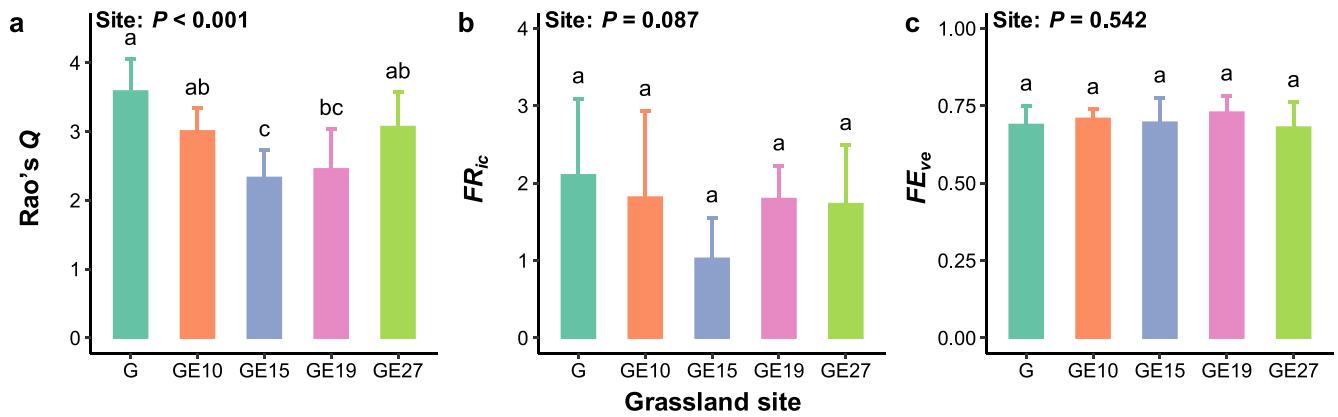


Fig. 6. Plant functional diversity indices of Rao's Q (a), FR_{ic} (b), and FE_{ve} (c) across the grassland sites. Rao's Q , Rao's quadratic entropy; FR_{ic} , functional richness index; FE_{ve} , functional evenness index; G, grazing site; GE10, 10-year grazing exclusion site; GE15, 15-year grazing exclusion site; GE19, 19-year grazing exclusion site; and GE27, 27-year grazing exclusion site. Different letters indicate statistically significant differences among grassland sites ($P < 0.05$).

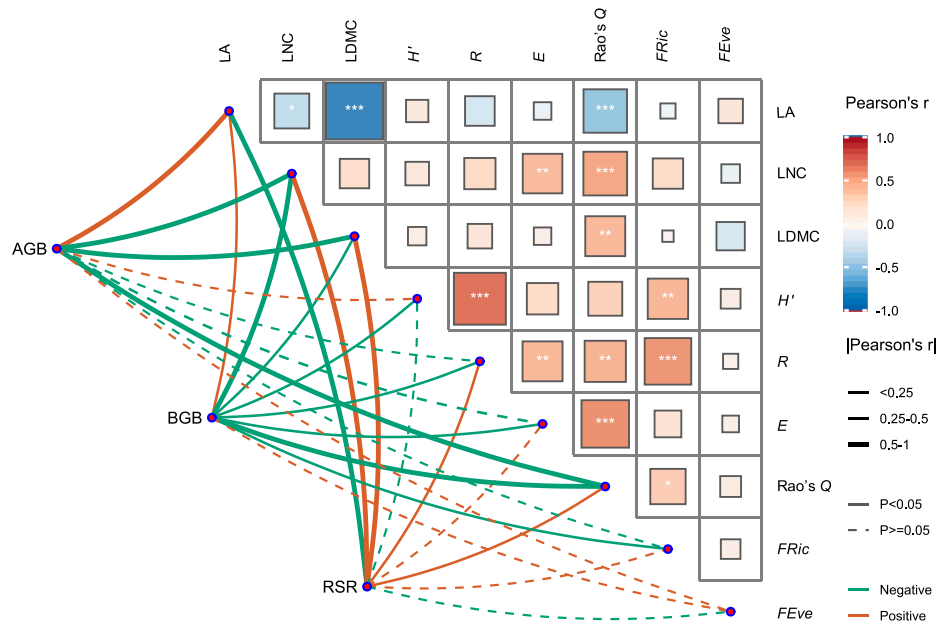


Fig. 7. Correlations between plant functional traits, species diversity, functional diversity and biomass production and allocation. AGB, aboveground biomass; BGB, belowground biomass; RSR, root-to-shoot ratio; LA, leaf area; LNC, leaf nitrogen content; LDMC, leaf dry matter content; H' , species diversity index; R , species richness index; E , species evenness index; Rao's Q , Rao's quadratic entropy; FR_{ic} , functional richness index; and FE_{ve} , functional evenness index. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

in grazed areas (Fig. 3f), exhibiting a strong negative loading on PC1 (Table 1). This pattern challenges the conventional "high nitrogen—high light" linear hypothesis (Evans, 1989), suggesting a strategic shift toward nitrogen conservation post-exclusion. Instead of maintaining high nitrogen investment, plants appear to compensate through form adaptation (e.g., LA expansion) to sustain photosynthetic capacity (Díaz et al., 2016), demonstrating a trade-off between structural and biochemical investment strategies.

Beyond the traditional unidimensional "acquisition—conservation" trade-off (Wright et al., 2004), our analysis identified a secondary independent axis of functional variation (PC2) primarily driven by LDMC (Table 1). This reveals that semi-arid grassland plants employ multidimensional functional strategies in response to grazing exclusion, ultimately sustaining ecosystem service functions (Osem et al., 2006; Sun et al., 2024). With diminished herbivory pressure, plants preferentially invest in photosynthetic tissues (e.g., mesophyll cells) rather than structural components (e.g., cell wall lignification) (Poorter et al.,

2009). Plants simultaneously downregulate physical defense traits (lower LDMC) and optimize nutrient-use efficiency (e.g., via LNPR modulation) to enhance competitive growth. Such adaptive reorganization reflects a strategic shift in the trade-off between "defense—competition" following grazing exclusion and aligns with the "stress—tolerant strategy" (Grime, 1977), wherein reduced abiotic/biotic stress favors resource reallocation toward productivity.

Despite we categorize traits based on established frameworks linking high LA to rapid resource acquisition, high LNC to conservation of nitrogen-rich tissues, and high LDMC to structural defense (e.g., Grime's CSR, Leaf economics spectrum), we acknowledge that trait expression and functional strategies exist along continua and can be context-dependent. The magnitude and specific combination of these traits ultimately define a plant's position within the multidimensional trait space, as captured by our PCA and Rao's Q analyses. Our categorization serves to interpret the primary functional axes revealed by PCA and the nature of correlations with biomass within the context of this study

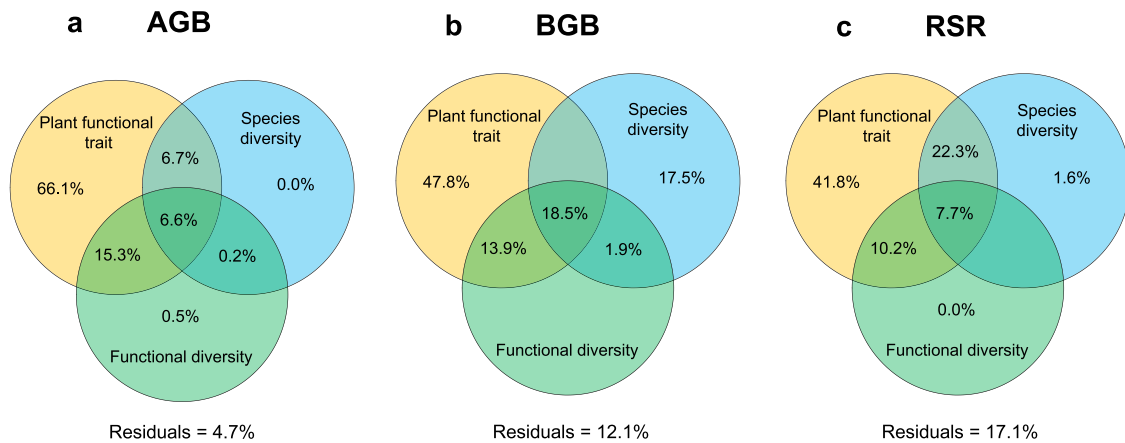


Fig. 8. Venn diagram showing the contributions of plant functional traits, species and functional diversity on AGB (a), BGB (b), and RSR (c). AGB, aboveground biomass; BGB, belowground biomass; RSR, root-to-shoot ratio. Non-positive contributions are not shown.

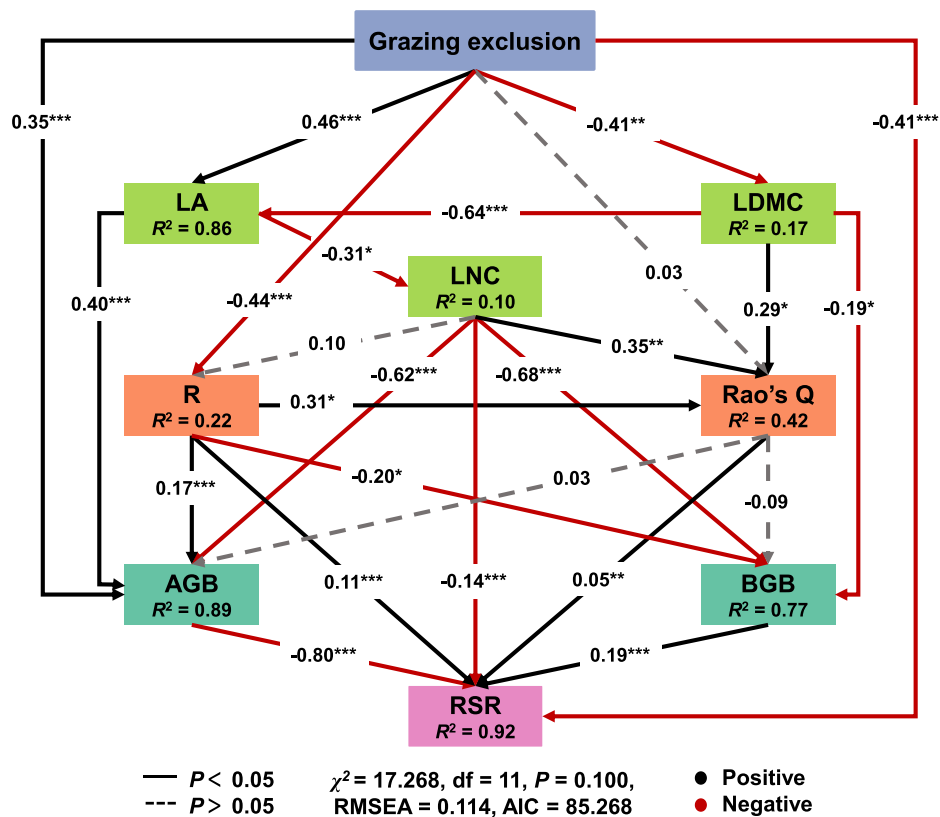


Fig. 9. Structural equation modeling (SEM) for pathways of plant functional traits and diversity on biomass allocation. LA, leaf area; LNC, leaf nitrogen content; LDMC, leaf dry matter content; R, species richness; Rao's Q, Rao's quadratic entropy; AGB, aboveground biomass; BGB, belowground biomass; and RSR, root-to-shoot ratio. Solid arrows indicate significant pathways (black = positive, red = negative); dashed arrows show non-significant pathways. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

system.

4.3. The nonlinear response of plant diversity to grazing exclusion duration

Our results show that the plant species diversity indices (H' , R , and E) exhibited a unimodal trend along the grazing exclusion chronosequence, initially declining before recovering. Specifically, the grazing grassland maintained relatively high diversity, whereas the 15-year exclusion displayed the lowest values (Fig. 5). This phenomenon mainly occurs because during the initial exclusion period (0–10 years), fast-growing,

highly dispersive annuals and short-lived perennial herbs (typically r-strategists) still maintain a substantial presence in the community. Grazing exclusion triggered marked shifts in community structure, favoring the dominance of certain species (Gao et al., 2021). As grazing exclusion continues, slow-growing but highly competitive perennial plants (typically K-strategists), particularly species with dense root systems, tall canopies, and efficient resource acquisition traits for light, water and nutrients, become increasingly dominant. These species may include native dominants (e.g., *L. chinensis*) or those exhibiting exceptional performance during ecosystem restoration (Cheng et al., 2016). As dominant species expanded, they competitively excluded others,

reducing overall species richness (Song et al., 2025). Prolonged exclusion (>15 years) drives community restructuring through enhanced spatial heterogeneity, soil amelioration, competitive regime shifts, and stronger niche partitioning, ultimately promoting coexistence of diverse species including late-successional taxa (Song et al., 2020; Michalet et al., 2023). Notably, E exhibited less variability than H' and R , likely because while dominant species expansion reduced richness, the remaining species achieved more uniform abundance distributions due to intensified resource competition.

Among all functional diversity indices analyzed in our study, only Rao's Q exhibited significant spatial variation across grassland sites. Notably, this index followed a distinct unimodal response pattern, reaching its minimum value in grasslands subjected to 15 years of grazing exclusion (Fig. 6). This pattern likely reflects the ecological succession following grazing exclusion. During the initial phase of restoration (e.g. <15 years of grazing exclusion), the plant community typically exhibits high functional diversity, comprising various species with distinct ecological characteristics (e.g., annuals and perennials, shallow-rooted and deep-rooted plants). However, as restoration progresses beyond 15 years, functional diversity declines due to the gradual convergence of dominant species toward specific functional types (particularly tall perennial grasses). With continued grazing exclusion, niche differentiation among coexisting species promotes greater variability in functional trait ranges and combinations (Liu et al., 2019), ultimately leading to the restoration of functional diversity. The transitional decline in Rao's Q suggests a potential reduction in community resilience during intermediate succession stages (Peco et al., 2017). For practical grassland restoration, we recommend implementing moderate disturbance regimes (e.g., rotational mowing) after 15 years of exclusion. Such management could enhance trait diversity by controlling dominant species expansion, and facilitating the establishment of functionally distinct species. This balanced approach would optimize both productivity and ecosystem stability (Guasconi et al., 2023). Notably, FR_{ic} and FE_{ve} showed limited variation across sites. In semi-arid ecosystems, this stability may arise from widespread niche overlap in resource acquisition strategies among species (Silvertown et al., 2015), and substantial functional redundancy where multiple species perform similar ecosystem functions (Sasaki et al., 2009; Pan et al., 2016). This redundancy likely buffers the system against biodiversity loss while maintaining functional stability.

4.4. Effects of plant functional traits and diversity on biomass production and allocation

The correlation analysis and VPA results in our study underscore the pivotal role of plant functional traits in regulating biomass production and allocation (Figs. 7 and 8). This dominance can be primarily attributed to the critical role of functional traits in driving vegetation biomass accumulation in grazing exclusion grasslands, as they directly regulate resource use efficiency, niche differentiation, and biomass allocation strategies (Díaz et al., 2016). Specifically, traits associated with the LES (e.g., LA and LNC) determine plant light capture efficiency and resource allocation patterns (Reich, 2014), serving as key physiological mechanisms underlying biomass accumulation. In semi-arid ecosystems, essential ecosystem functions are often sustained by a limited set of dominant traits. This functional redundancy implies that shifts in species diversity may not necessarily lead to significant changes in ecosystem functioning (Pan et al., 2016). Moreover, long-term grazing exclusion has altered community structure, enabling dominant species (e.g., *L. chinensis*) to expand clonally and form near-monoculture populations (Gao et al., 2021). Under these conditions, ecosystem functions are largely dictated by the trait composition of the dominant species rather than overall community diversity. For instance, our results revealed a positive correlation between both AGB and BGB with LA, whereas a significant negative correlation was observed with LNC and LDMC (Fig. 7). These findings align with the earlier discussion. A larger LA

enhances transpiration-driven water potential, thereby facilitating more efficient water and nutrient uptake and transport, which ultimately promotes AGB accumulation (Hu et al., 2024). Conversely, elevated LNC and LDMC reflect greater resource allocation to structural tissues (e.g., cell wall thickening and defense compounds), which constrains plant growth and reduces biomass production (Poorter et al., 2009; Setia et al., 2012; Lambers, 2022). Such resource allocation strategies ultimately lead to significant modifications in biomass allocation between above- and belowground compartments.

Our results demonstrate a significant negative correlation between BGB and diversity indices (H' , R , and E ; Fig. 7), indicating that prolonged grazing exclusion reduces species diversity through belowground resource competition. The development of dense root networks associated with high BGB may obstruct soil pores, impairing oxygen diffusion and water infiltration (Klump and Soussana, 2009). This hypoxic microenvironment particularly disadvantages non-dominant species, further contributing to diversity loss. While moderate grazing maintains microhabitat heterogeneity by controlling dominant species through herbivory and trampling (Cheng et al., 2016), long-term exclusion eliminates these regulatory mechanisms, exacerbating competitive exclusion. It is noteworthy that the results demonstrate an increase in AGB alongside a decrease in species diversity, particularly during the first 15 years of grazing exclusion (Figs. 2 and 5). However, no significant relationship between AGB and species diversity was observed across the entire exclusion chronosequence (Fig. 7). This absence of correlation may arise because the simultaneous decline of both variables after 15 years of exclusion could induce a positive biomass-diversity relationship. Statistically, this later positive correlation counterbalances the initial negative correlation observed within the first 15 years, resulting in a double-threshold characteristic for the overall biomass-diversity relationship. The underlying mechanisms can be attributed to competitive exclusion driving the initial negative correlation during the first 15 years of exclusion (Gao et al., 2021), followed by niche differentiation promoting synergistic shifts between AGB and diversity thereafter (Michalet et al., 2023). Additionally, external factors such as interannual precipitation variability (e.g., drought and flood events) may disrupt succession dynamics, thereby amplifying fluctuations in the biomass-diversity relationship (Kigel et al., 2021). Interestingly, Rao's Q showed contrasting relationships that were negative with both AGB and BGB but positive with RSR in our study (Fig. 7). This pattern suggests that grazing exclusion promotes functional homogenization and niche overlap among species, intensifying competition for resources. In such conditions, plants appear to prioritize aboveground allocation of photosynthetic assimilates (Freschet et al., 2015). Although plant diversity exhibits some influence on biomass production and allocation patterns in our study, its direct effects appear relatively minor compared to the predominant role of functional traits (Fig. 8). These findings underscore the complex interactions among functional traits, species dynamics, and ecosystem processes in shaping biomass allocation strategies under long-term grazing exclusion (Hanisch et al., 2020).

4.5. Influencing pathways of biomass production and allocation

Through our preceding analyses, we have elucidated both the direct effects of grazing exclusion on increasing AGB while reducing RSR, as well as its indirect effects mediated by species richness and functional traits. The positive effect of R on AGB demonstrated by SEM ($\beta = 0.17$, $P < 0.001$; Fig. 9) appears inconsistent with both the non-significant correlation observed in bivariate analysis and the dynamic patterns across the grazing exclusion chronosequence. This apparent discrepancy arises because SEM evaluates multivariate causal pathways, revealing that the R -AGB relationship exhibits dynamic fluctuations due to alternating ecological processes: competitive exclusion dominates in early stages of grazing exclusion, while niche differentiation prevails during intermediate stages (Wang et al., 2018). Crucially, SEM analysis

in our study confirms an underlying positive effect of species richness on biomass production, with this fundamental relationship being partially masked by stronger negative pathways (e.g., those mediated by functional traits) at different successional stages. Moreover, the synchronous decline in both *R* (caused by dominant species monopolization under prolonged grazing exclusion) and AGB ultimately accentuates this latent positive relationship in the long term (Song et al., 2020).

Particularly noteworthy is the indirect pathway through which the LA–LNC trade-off influences biomass production and allocation in this study (Fig. 9). This trade-off reflects plants' functional strategy to optimize resource allocation between photosynthetic efficiency (LA) and structural investment (LNC) under varying environmental conditions (Keep et al., 2021). In the initial stages of grazing exclusion, when soil nitrogen availability remains limited due to prior grazing pressure (Mudge et al., 2017), plants preferentially allocate resources to expand LA. This adaptive response maximizes light capture to compensate for nitrogen limitations, thereby enhancing photosynthetic capacity (Lemaire et al., 2007). The optimal balance between LA and LNC represents a critical physiological equilibrium where plants achieve maximum resource use efficiency. When these traits are proportionally balanced, plants can simultaneously optimize light and nitrogen utilization, leading to peak photosynthetic performance and consequently maximal biomass production (Monson et al., 2022). These findings underscore the sophisticated adaptive mechanisms plants employ to modulate trait combinations for optimal growth and biomass allocation in response to environmental constraints.

Another significant pathway in our results involves grazing exclusion reducing LDMC, which subsequently increases Rao's *Q* and ultimately decreases RSR (Fig. 9). This process operates through two key mechanisms: First, in the resource-abundant environment created by grazing exclusion (with increased nutrient availability and reduced light competition), plant communities shift toward homogeneous rapid-growth strategies characterized by low LDMC (Freschet et al., 2015). This functional convergence diminishes niche differentiation and limits the coexistence of species employing divergent ecological strategies. Second, low-LDMC species (e.g., *L. chinensis*) gain competitive dominance through their rapid resource acquisition capacity, progressively excluding conservative, high-LDMC species (e.g., drought-adapted Asteraceae) from the community (Díaz et al., 2016). This competitive exclusion reduces functional diversity (Rao's *Q*), potentially compromising ecosystem stability and resilience—particularly in terms of biomass allocation patterns (Walker et al., 2023). These findings highlight a critical trade-off in grassland management: while grazing exclusion enhances biomass production, the concomitant reduction in functional diversity may undermine the ecosystem's capacity to maintain balanced biomass allocation and respond to environmental fluctuations. This balance between productivity and functional maintenance warrants careful consideration in sustainable grassland management practices. Although this study advances our understanding of grassland biomass dynamics, it did not account for root trait variations. Future research should explicitly quantify how grazing exclusion mediates biomass production and ecosystem service provision through coupled aboveground–belowground trait interactions.

5. Conclusion

Our study reveals a critical temporal decoupling in grassland biomass restoration under grazing exclusion where BGB peaks earlier (15 years) than AGB (19 years), highlighting distinct restoration trajectories and the presence of threshold effects. This finding necessitates careful optimization of exclusion duration to maximize restoration outcomes, as long-term implementation beyond peak restoration stages may lead to suboptimal biomass yields. Crucially, we fundamentally redefine the mechanisms driving grassland restoration by establishing plant functional traits as the core regulators of biomass dynamics, surpassing the explanatory power of species or functional diversity.

Multidimensional trait strategies, represented by PCA axes integrating resource acquisition–conservation (PC1: LA vs. LNC) and structural defense (PC2: LDMC), directly govern biomass production and allocation thresholds. While grazing exclusion exerts direct effects on biomass, it also indirectly influences outcomes by modulating species richness, and more importantly regulating trait expression (e.g., LA, LDMC), trait–trait relationships (e.g., the LA–LNC trade-off), and subsequently functional diversity (Rao's *Q*). Consequently, we propose moving beyond diversity-centric frameworks towards a trait-based management paradigm. Optimizing exclusion strategies requires tailoring practices to local contexts and specific timelines, informed by monitoring key functional traits linked to biomass targets. Integrating trait selection and manipulation into restoration frameworks offers an evidence-based pathway to maximize sustainable biomass yield, improve resource allocation efficiency, and ultimately enhance grassland resilience under global change pressures.

CRedit authorship contribution statement

Shouzheng Tong: Supervision. **Hongyuan Ma:** Project administration, Funding acquisition. **Yang Gao:** Software, Investigation, Funding acquisition. **Zhongnan Wang:** Methodology. **Jian Liu:** Investigation. **Yuqi Zhang:** Resources, Investigation. **Yu An:** Writing – review & editing, Software, Investigation.

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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Data availability

The authors do not have permission to share data.

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