



Different effects of grazing and nitrogen addition on ecosystem multifunctionality are driven by changes in plant resource stoichiometry in a typical steppe

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Abstract

Purpose Herbivore grazing and nitrogen (N) input may alter the multiple ecosystem functions (i.e., multifunctionality, hereafter) associated with carbon (C), N, and phosphorus (P) cycling. Most studies on variations in plant diversity, soil biotic or abiotic factors, and linkages to ecosystem functions have focused on grazing or N enrichment alone. Few studies have combined these two factors to explore the role of plant resource stoichiometry (C:N:P ratios) in ecosystem multifunctionality (EMF) control. Here, we evaluated the direct and indirect effects of stocking rate (0, 2.7, 5.3, and 8.7 sheep ha⁻¹) and N addition rate (0, 5, 10, and 20 g N m⁻² yr⁻¹) on a range of ecosystem functions and EMF via changing plant diversity, soil pH and plant

resource stoichiometry in a typical steppe on the Loess Plateau.

Results We found that increasing stocking rate and interaction between grazing and N addition significantly decreased EMF, while increasing N addition rate significantly promoted EMF. Grazing decreased soil NH₄⁺-N, soil NO₃⁻-N, aboveground biomass, and plant C, N, and P pools, but increased soil total N and P at 8.7 and 5.3 sheep ha⁻¹, respectively. N addition increased soil NH₄⁺-N, NO₃⁻-N, and total P. Plant aboveground biomass, and plant C, N, and P pools increased at the lower N addition rate (≤ 5 g N m⁻² yr⁻¹) under grazing. The structural equation models indicated that (1) EMF was driven by the direct effects of grazing and the indirect effects of grazing on plant resource stoichiometry and soil pH; (2) EMF increased with increasing N addition rates, but such positive response of EMF to increasing N addition rates was alleviated at high levels of plant resource stoichiometry and diversity; and (3) the indirect effects of plant diversity induced by grazing and N addition had moderate effects on EMF via the variations of plant resource stoichiometry.

Conclusions This study demonstrated grazing and N addition had contrasting effects on ecosystem multifunctionality in a typical steppe, and highlighted the capacity of plant diversity in balancing plant elements that serve as a key mechanism in the maintenance of EMF in response to intensive grazing and N enrichment.

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Introduction

Grassland ecosystems typically experience defoliation and eutrophication simultaneously due to the accumulation of herbivore excrement and atmospheric nitrogen (N) deposition (Stevens 2019; Borer et al. 2020). Growing evidence suggests that anthropogenic N input and the effects of herbivores together are altering global grassland ecosystem processes and functions, including productivity and biodiversity stability, and biogeochemical cycles (Cui et al. 2020; Zhang et al. 2021a; Zheng et al. 2021). So far, insufficient field evidence supports the interactive effects of grazing and N enrichment on multiple ecosystem functions (multifunctionality, EMF) in grasslands.

Biological and non-biological impacts of carbon (C), N, and phosphorus (P) cycles partly drive nutrient cycles and determine the limits of plant productivity (Daufresne 2021). Plant resource stoichiometry (C:N:P ratios) plays a key role in the interaction between primary producers and other trophic levels (e.g., herbivores) and is crucial for predicting the relative contribution of herbivores and litter pathways in ecosystems. There is mounting evidence that N enrichment causes increases in N concentration and N:P in plant tissues (Hu et al. 2020; Liu et al. 2020), which can affect trophic interaction and plant-mediated nutrient cycling. Although the effects of grazing or N enrichment on soil and plant C:N:P stoichiometry are well documented, few studies have been conducted to identify the interactions of grazing and N enrichment on the status of plant resource limitation and their linkages with ecosystem functions.

Biodiversity loss caused by herbivores or N enrichment can interfere or even decrease multiple ecosystem functions (Allan et al. 2015) by two mechanisms, i.e., directly loss of species functions and indirectly decline of resource utilization efficiency (Dib et al. 2020; Zhang et al. 2021a, b, 2022). Plant species diversity and aboveground biomass are usually promoted at a moderate stocking rate due to reduced resource contention and increased plant compensatory growth, but they may decrease at a high stocking rate because of the aggravating resource limitation

(i.e., nutrient availability) (Ren et al. 2018). With regard to N enrichment, a low N addition rate generally increases productivity and alleviates N availability limitation, and benefits fast-growing plant species (Zhou and Yang 2018). As the N addition rate increases, plant C:N and C:P decrease accompanied by species loss and diversity decline in grassland, in turn, causing noticeable impacts on ecosystem functions associated with C sequestration (Abbas et al. 2013; Guiz et al. 2018; Zheng et al. 2021). Therefore, the effects of biodiversity on ecosystem functioning are highly dependent on the stocking rate and N addition rate (Liu et al. 2021; Zhang et al. 2022).

Soil properties and processes are the major factors driving the EMF responses, theoretical mechanisms have been thoroughly developed, but experimental evidence is lacking. (Giling et al. 2019). Herbivores may impact soil properties and processes through trampling and excrement deposition (Li et al. 2021a, b), resulting in changes in EMF. For example, herbivore trampling may compact soil and restrain soil aeration, decreasing soil moisture and increasing soil pH (Yang et al. 2019). N-enrichment-induced decrease in soil pH is expected to influence the soil microbial activities and increase soil N and P availability, and thereby reduces N and P uptake by fine roots (Cui et al. 2020), which may alter multifunctionality resistance (Delgado-Baquerizo et al. 2020).

Grazing and N enrichment usually have either similar or converse effects on ecosystem structure and functions. For example, moderate stocking rate and N enrichment may increase soil N availability and plant N concentration (Li et al. 2019; Liu et al. 2020; Yang et al. 2018; Zhang et al. 2021a). Plant productivity generally increases with the increase in N addition rate (Liu et al. 2021; Zheng et al. 2021), but decreases with the increase in stocking rate (Zhang et al. 2022). Substantial literature evidence has shown that multi-functional performance is driven by eutrophication of grassland ecosystem or grazer activities, but the interaction of grazing and N enrichment on EMF is still vague. This restrains our ability to improve sustainable grassland management practices and to promote the ecosystem to delivery of multiple services and functions. The objective of our field study was to investigate the respective and integrated influence of stocking rate and N addition on EMF in a typical steppe. EMF is a comprehensive index derived by multiple ecosystem functions, such

as (a) aboveground biomass, (b) plant carbon pool, (c) plant nitrogen pool, (d) plant phosphorus pool, (e) soil organic carbon, (f) soil total nitrogen, (g) soil ammonium-nitrogen ($\text{NH}_4^+\text{-N}$), (h) soil nitrate-nitrogen ($\text{NO}_3^-\text{-N}$), and (i) soil total phosphorus. We hypothesize that (1) grazing and N addition will have contrasting effects on EMF by changes in soil abiotic properties, plant resource stoichiometry, and plant diversity; and (2) balanced N:P controls of grazing and N addition can maintain the ecosystem structure and function. Our study will provide experimental evidence about how herbivores' performance drives EMF under eutrophic conditions, and find a balance between maintaining plant production to meet the needs of livestock and improving other important ecosystem functions.

Materials and methods

Study site

This study was conducted in a typical temperate steppe based on the Huanxian Grassland Agriculture Trial Station of Lanzhou University in Huan County, Gansu Province, China (37.14°N, 106.84°E, 1,650 m a.s.l). The mean annual temperature is 7.8 °C and the mean annual precipitation is 289.8 mm, occurring mainly (>70%) from April to September (the growing season). The typical soil type is classified as loessal soils with sand texture. *Artemisia capillaris*, *Lespedeza davurica* and *Stipa bungeana* are the dominant species (Li et al. 2021a).

Experimental design

We carried out the experiments in a typical steppe (slope $\approx 5^\circ$) with similar plant community composition and soil condition. The experimental designs for long-term Tan-sheep (*Ovis aries*) grazing have been detailed previously (Li et al. 2021a, b), and thus were described briefly here. In 2001, four stocking rates (i.e., 0, 2.7, 5.3, and 8.7 sheep ha^{-1}) with three replicates were randomly set up in 12 paddocks (100 m \times 50 m for each paddock). For each stocking rate, Tan-sheep were allowed to graze in one of the three paddocks for 10 days during a 30-day rotation period from May to September. The N addition experiment had four N addition rates

(i.e., 0, 5, 10, and 20 $\text{g N m}^{-2} \text{yr}^{-1}$ for the CK, N5, N10, and N20, respectively) with three replicates for each treatment. In 2012, a fenced experimental cell (11 m \times 2 m) was randomly established in all grazing paddocks. In each fenced cell, four subplots (2 m \times 2 m) were set up and separated by 1-m walkways. The subplots were randomly treated with N addition rates. The N supplement was NH_4NO_3 dissolved in water and sprayed evenly on the plot twice a year in May (before grazing) and July (during the grazing period).

Plant and soil sampling

The aboveground biomass was collected by cutting aboveground vegetation from a quadrat (1 m \times 1 m) randomly placed in each subplot in all experimental cells in mid-August 2016. In each quadrat, plants of each species were identified, then washed and oven-dried at 65 °C for 48 h, and biomass was weighted. We calculated species relative abundance by using the aboveground biomass of each species accounting for the total aboveground biomass (AGB) in each subplot.

Two soil cores were sampled in the same experimental cells at a depth of 0–10 cm using a bucket auger (10 cm diameter). Soil samples were air-dried indoors and mixed thoroughly. Substances such as fine roots and spalls were removed by sieving ground soil through a 1-mm and then a 0.25-mm sieve.

Laboratory analysis

Soil moisture (SM) was measured as the weight loss through oven-drying at 105 °C for 48 h. The pH was measured using a PHS-3E pH meter (Leici, Shanghai, China). Soil $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ were extracted using 2 M KCl and measured using the colorimetric (Spectrophotometer Cary 60UV-Vis from Agilent, Alto, America). The C concentrations in plant and soil were analysed Walkley-Black titration method (Van Reeuwijk 2002). Plant and soil total N concentrations were determined following Kjeldahl digestion by an auto-Kjeldahl's apparatus (UDK149, VELP, Usmate Velate, Italy), while the total P concentrations were measured by the molybdenum blue colorimetry method (Sparks et al. 1996).

Plant measurements

We calculated species richness as the total number of species, and quantified species diversity in terms of the Shannon index (Shannon and Weaver 1949) and species evenness (Smith and Wilson 1996) as:

$$\text{Shannon index} = - \sum p_i \ln(p_i) \quad (1)$$

$$\text{Species evenness} = - \sum p_i \ln(p_i) / \ln R \quad (2)$$

where R is the number of species, p_i is species i relative abundance.

We calculated the community C, N, and P concentrations, and C:N, C:P, and N:P for each quadrat according to Garnier et al. (2007):

$$\text{Nutrient} = \sum p_i \times \text{nutrient}_i \quad (3)$$

where *Nutrient* is the total element value of the community in a quadrat, *nutrient_i* is the element value of species i .

Ecosystem multifunctionality index measurements

We measured nine functions as AGB, vegetation carbon density (VCD), vegetation nitrogen pool (VNP), vegetation phosphorus pool (VPP), soil organic carbon (SOC), soil total nitrogen (STN), soil total phosphorus (STP), and soil NH_4^+ -N and NO_3^- -N (Giling et al. 2019; Jing et al. 2015; Maestre et al. 2012). The VCD, VNP, and VPP were determined as the vegetation carbon, nitrogen, and phosphorus contents per unit of aboveground biomass. We used the averaging approach to evaluate EMF (Maestre et al. 2012; Byrnes et al. 2014; Meyer et al. 2018), i.e., calculating Z-scores of the nine functions before analysis, and considering the EMF as the average Z-scores of all nine functions measured in a treatment. We further supplemented the averaging approach using the threshold approach (i.e., calculating the number of functions beyond the given thresholds of 10%, 25%, 50%, 75%, and 90%) to give a sense of the extent to which grazing and N addition impact the number of functions provided at different levels (Byrnes et al. 2014; Zavaleta et al. 2010), details of which are provided in Supporting Information (Fig. S2).

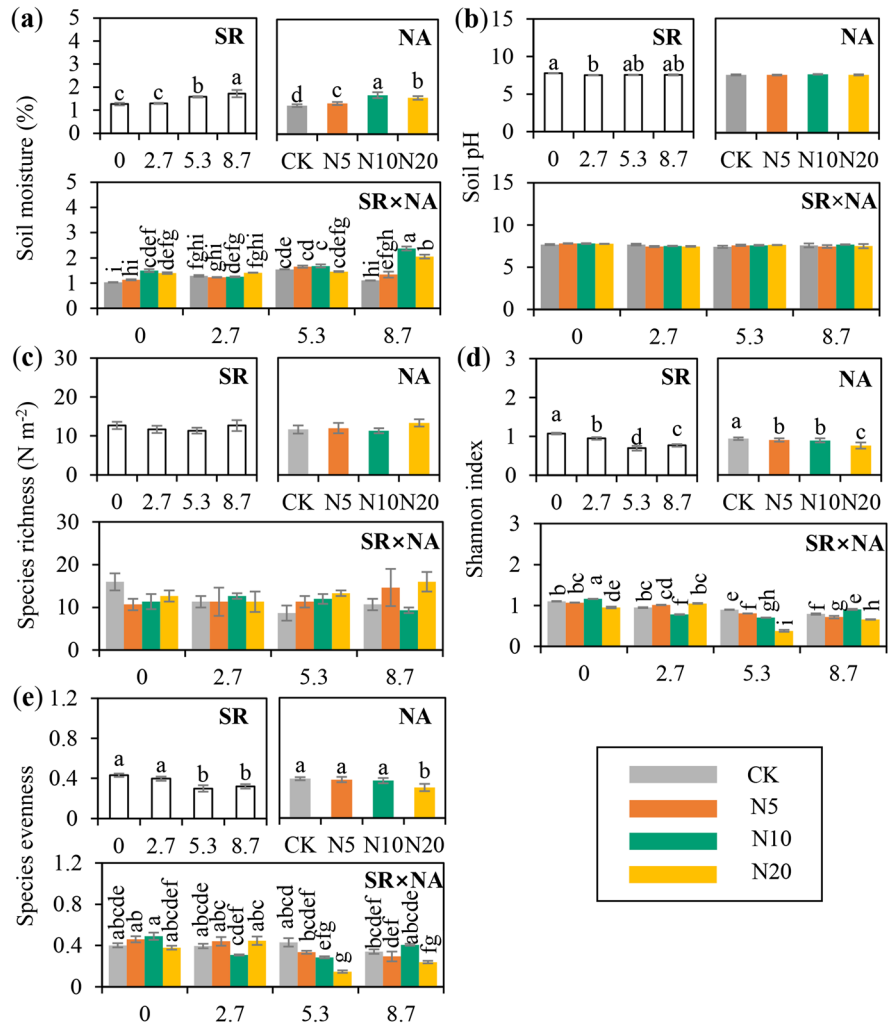
Statistical analysis

All statistical analyses were performed in SAS version 9.4 (SAS Institute Inc., Cary, NC, USA) and R version 4.1.0 (R Development Core Team 2021), with significance levels set at $P < 0.05$. We used a generalized linear mixed model (Proc GLIMMIX), with stocking rate, N addition, and their interaction as fixed factor, and subplot as the random effect to assess soil abiotic properties, plant species diversity, ecosystem functions, EMF, and soil and plant C:N:P stoichiometry (Figs. 1, 2, 3, and 4). We used the Tukey-Kramer adjustment for multiple comparisons.

We selected the main predictors of EMF from individual ecosystem attributes by using random forest analysis (“rfPermute” package), which was based on the percentage increase in the mean square error (Archer 2018; Breiman 2001; Cutler et al. 2007; Fig. 5). Spearman’s correlation analysis was used to assess how the selected main predictors of EMF from the random forest analysis correlated with EMF (Fig. 6). We also employed Spearman’s correlation analysis by using the “ggcor” package (Huang 2018) to estimate the relationships among ecosystem functions and attributes (Fig. 6).

Structural equation modeling (SEM) was used to analyze the causal pathways through which grazing and N addition influenced EMF. We presumed that grazing and N addition directly altered soil pH and soil stoichiometry, and shifts in these soil properties could affect Shannon index, plant stoichiometry, and consequently average EMF, and the number of functions beyond each given threshold (10%, 25%, 50%, 75%, and 90%). Specifically, linear regression was used to assess how community N:P (Fig. 7a) or Shannon index (Fig. 7b) correlated with EMF. We extracted the first principle component scores of principal component analysis (PCA) ordination of scores for plant and soil stoichiometry by using the “vegan” package (Oksanen et al. 2020). Soil stoichiometry was calculated as soil C:N, C:P, and N:P, and plant stoichiometry was estimated as plant C, N, P, C:N, C:P, and N:P (Table S1). The SEM was fit using the “piecewiseSEM” package (Lefcheck 2016). We operated hypothetical causal models including all possible pathways (Fig. S1) and promoted the model fit by progressively removing non-significant pathways and simplifying models, finally deriving final models (Fig. 7). We determined the model fit

Fig. 1 The effects of nitrogen addition, stocking rate (sheep ha⁻¹), and their interaction on ecosystem attributes: **a** Soil moisture, **b** Soil pH, **c** Species richness, **d** Shannon index, and **e** Species evenness. SR, stocking rate; NA, nitrogen addition. Nitrogen addition rates are: CK, 0 g N m⁻² yr⁻¹; N5, 5 g N m⁻² yr⁻¹; N10, 10 g N m⁻² yr⁻¹; and N20, 20 g N m⁻² yr⁻¹. Significant differences between means are indicated by uppercase letters based on Tukey-Kramer test (*P* < 0.05)



by d-separation tests and obtained AIC scores from Fisher's C statistics (Shipley 2013).

Results

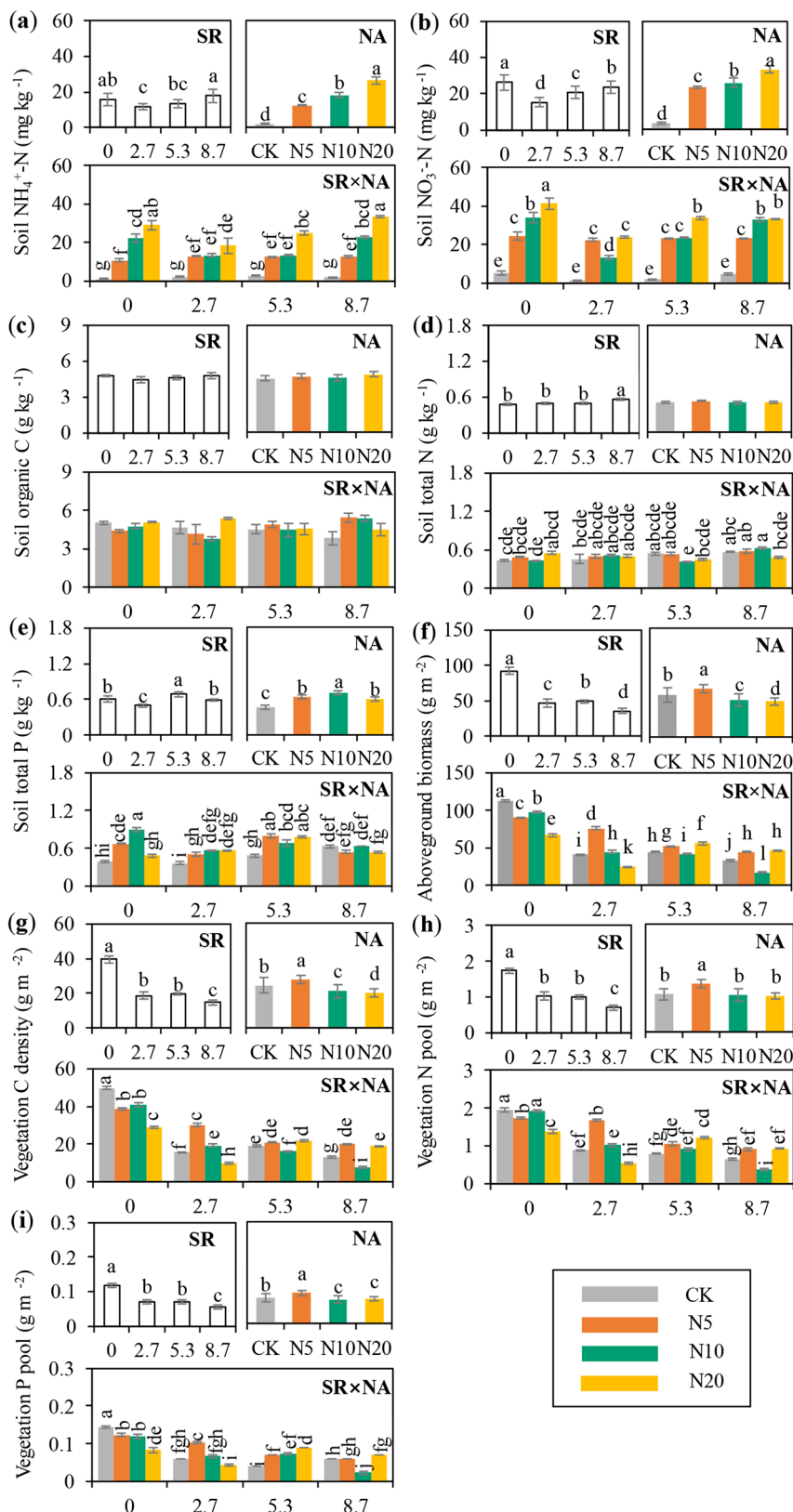
Ecosystem attributes, functions, and multifunctionality

The results of grazing and N application affecting ecosystem attributes, functions, and multifunctionality are summarized in Table 1. Increasing stocking rate and N addition rate significantly increased SM (Fig. 1a) but decreased the Shannon index and species evenness (Fig. 1d-e). Their significant interaction induced higher SM at N10 and N20 with a stocking

rate of 8.7 sheep ha⁻¹ (Fig. 1a) but lower Shannon index and species evenness at N10 and N20 with a stocking rate of 5.3 or 8.7 sheep ha⁻¹ (Fig. 1d-e). Soil pH and species richness were not significantly affected by grazing and N addition, except that soil pH was significantly lower at 2.7 sheep ha⁻¹ compared to control (Fig. 1b-c).

Increasing N addition rate significantly increased soil NH₄⁺-N and NO₃⁻-N, while increasing the stocking rate significantly decreased them, except that soil NH₄⁺-N had no significant difference between 0 and 8.7 sheep ha⁻¹ (Fig. 2a-b). STN was significantly greater at 8.7 sheep ha⁻¹ compared to control, but it was not significantly affected by N addition (Fig. 2d). Interaction of grazing and N addition induced significantly lower soil NH₄⁺-N and soil

Fig. 2 The effects of nitrogen addition, stocking rate (sheep ha⁻¹), and their interaction on ecosystem functions: **a** soil NH₄⁺-N, **b** Soil NO₃⁻-N, **c** Soil organic C, **d** Soil total N, **e** Soil total P, **f** Above-ground biomass, **g** Vegetation carbon density, **h** Vegetation nitrogen pool, and **i** Vegetation phosphorus pool. SR, stocking rate; NA, nitrogen addition. Nitrogen addition rates are: CK, 0 g N m⁻² yr⁻¹; N5, 5 g N m⁻² yr⁻¹; N10, 10 g N m⁻² yr⁻¹; and N20, 20 g N m⁻² yr⁻¹. Significant differences between means are indicated by uppercase letters based on Tukey-Kramer test (*P* < 0.05)



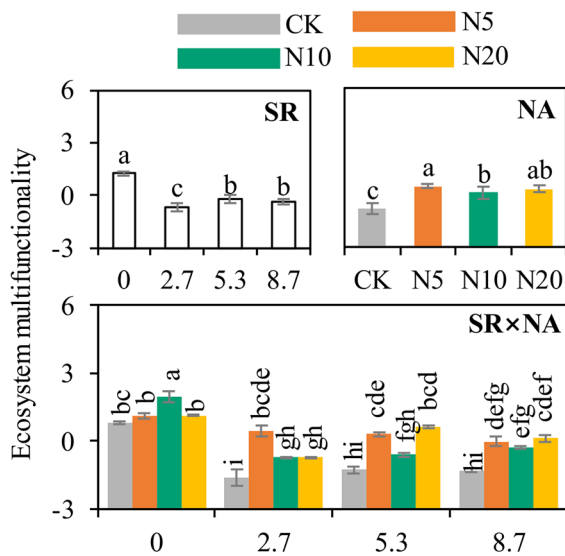


Fig. 3 The effects of nitrogen addition, stocking rate (sheep ha^{-1}), and their interaction on ecosystem multifunctionality. SR, stocking rate; NA, nitrogen addition. Nitrogen addition rates are: CK, $0 \text{ g N m}^{-2} \text{ yr}^{-1}$; N5, $5 \text{ g N m}^{-2} \text{ yr}^{-1}$; N10, $10 \text{ g N m}^{-2} \text{ yr}^{-1}$; and N20, $20 \text{ g N m}^{-2} \text{ yr}^{-1}$. Significant differences between means are indicated by uppercase letters based on Tukey-Kramer test ($P < 0.05$)

NO_3^- -N at N10 or N20 under grazing, while their significant interaction induced higher STN at N10 with a stocking rate of $8.7 \text{ sheep ha}^{-1}$ (Fig. 2a-b, d). STP was significantly higher at $5.3 \text{ sheep ha}^{-1}$ and lower at $2.7 \text{ sheep ha}^{-1}$ compared to control (Fig. 2e). Interaction of grazing and N addition led to significantly higher STP at N5 and N20 with a stocking rate of $5.3 \text{ sheep ha}^{-1}$ but lower STP at N10 in all grazed plots (Fig. 2e). Increasing the stocking rate significantly decreased AGB, VCD, VNP, and VPP, while N addition significantly increased AGB, VCD, VNP, and VPP at N5 and decreased them at N10 or N20 (Fig. 2f-i). Grazing and N addition had significant negative interaction effects on AGB, VCD, VNP, and VPP (Fig. 2f-i). SOC was not significantly affected by grazing and N addition (Fig. 2c).

Increasing the stocking rate significantly decreased EMF, while increasing N addition rate significantly promoted EMF, and their interaction was significantly negative (Fig. 3).

Soil and plant C:N:P stoichiometry

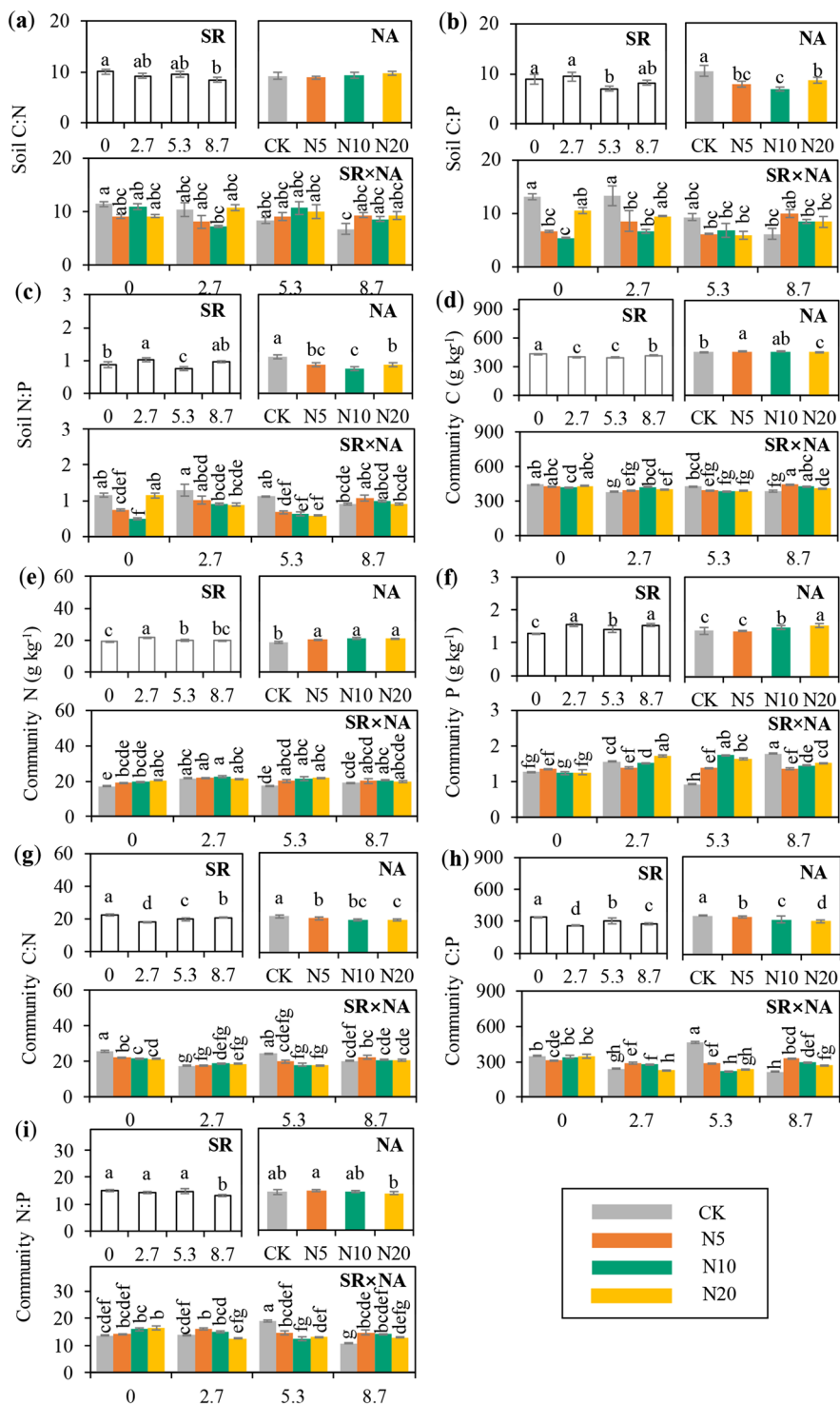
Increasing stocking rate and N addition rate, and their interaction significantly decreased soil C:N and C:P, community C:N and C:P but increased community N and P, except that soil C:N was not significantly affected by N addition (Fig. 4a-b, e-h). Soil N:P was significantly higher at $2.7 \text{ sheep ha}^{-1}$ but lower at $5.3 \text{ sheep ha}^{-1}$ compared to control, while it significantly decreased as N addition rate increased (Fig. 4c). Interaction of grazing and N addition induced higher soil N:P at N10 but lower at N20 in grazed plots (Fig. 4c). Community C significantly decreased with an increase in stocking rate, while it was significantly greater at N5 and lower at N20 compared to control (Fig. 4d). Interaction of grazing and N addition induced lower community C at N5, N10, and N20 at $5.3 \text{ sheep ha}^{-1}$ (Fig. 4d). Community N:P was significantly lower at $8.7 \text{ sheep ha}^{-1}$ than other grazing treatments, while N addition had no significant effect on community N:P compared to control. Their interaction induced significantly lower community N:P at N10 or N20 under grazing (Fig. 4i).

Relationships between soil and plant stoichiometry, individual ecosystem functions and attributes, and EMF

The random forest model identified plant Shannon index, soil pH, SM, and most soil and plant stoichiometric values as significant predictors of EMF (Fig. 5). We also found significant correlations between soil and plant stoichiometry, individual ecosystem functions and attributes, and EMF (Fig. 6). For instance, soil pH, SM, Shannon index, and plant stoichiometry (Community C, N, P, C:N, C:P, and N:P) were generally correlated with the aboveground plant functions (AGB, VCD, VNP, and VPP). Soil pH and plant stoichiometry (Community C, N, P, C:N, C:P, and N:P) were generally correlated with EMF. Soil stoichiometry (e.g. soil C:N or N:P) was significantly correlated with EMF and individual ecosystem functions (e.g. soil C, N, P, NH_4^+ -N, and NO_3^- -N).

Soil stoichiometry was driven by the increased C:N, C:P, and N:P. Plant stoichiometry was primarily driven by increases in community C, C:N, C:P, and N:P and decreases in community N and

Fig. 4 The effects of nitrogen addition, stocking rate (sheep ha⁻¹), and their interaction on soil and plant C:N:P stoichiometry: **a** soil C:N, **b** Soil C:P, **c** Soil N:P, **d** Community C, **e** Community N, **f** Community P, **g** Community C:N, **h** Community C:P, and **i** Community N:P. SR, stocking rate; NA, nitrogen addition. Nitrogen addition rates are: CK, 0 g N m⁻² yr⁻¹; N5, 5 g N m⁻² yr⁻¹; N10, 10 g N m⁻² yr⁻¹; and N20, 20 g N m⁻² yr⁻¹. Significant differences between means are indicated by uppercase letters based on Tukey-Kramer test (*P* < 0.05)



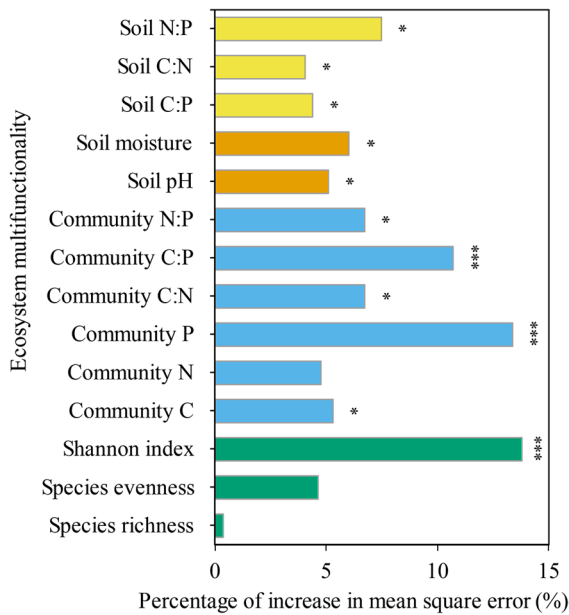


Fig. 5 Random forests showing mean predictor importance of soil and plant stoichiometry, ecosystem attributes on ecosystem multifunctionality. Significance levels of each predictor are: * $P < 0.05$ and *** $P < 0.01$

P (Table S1). SM had a weak relationship with EMF and soil stoichiometry did not significantly influence other ecosystem attributes directly (Fig. 6), though they were significantly affected by stocking rate, N addition, and their interaction. Hence, we removed soil moisture and stoichiometry to obtain the final model (Fig. 7).

Our SEM indicated grazing ($\beta = -0.328$, standardized path coefficients, $P < 0.05$), and N addition ($\beta = 0.404$, $P < 0.05$) directly influenced EMF (Fig. 7). We found that grazing had a significant and negative effect on EMF by reducing soil pH. Although significant direct effects of grazing and N addition on plant stoichiometry were not found, their indirect effects of grazing and N addition on plant stoichiometry via the Shannon index were significant, which resulted in negative effects on EMF. Furthermore, given that community N:P was the important metric of plant stoichiometry, we found that the relationship between EMF and community N:P was curvilinear (U) whereas the curvilinear relationship between EMF and Shannon index was inverted (inverted U) (Fig. 7a-b). Similar effects of grazing

and N addition on EMF were observed over the 50%, 75%, and 90% thresholds (Fig. S2).

Discussion

Multiple functions are critical to assessing ecosystem impacts of N addition and grazing

We found that plant and soil showed different resource-acquisition strategies in response to N enrichment and grazing, as indicated by synergies or trade-offs between ecosystem functions. Ecosystem multifunctionality decreased with increasing stocking rates, probably due to the negative responses of most functions to stocking rates, such as soil NO_3^- -N, AGB, VCD, VNP, and VPP (Fig. 2b, f-i). However, soil NH_4^+ -N, STN, and STP significantly increased at 5.3 or 8.7 sheep ha^{-1} (Fig. 2a, d, e), probably due to livestock excrement return at higher stocking rates (Li et al. 2021a), maintaining the ecosystem performance.

Grazing animals usually increase SOC by returning excrement and decreasing decomposition due to trampling-induced anaerobic conditions (Li et al. 2021a, b; Yang et al. 2019). However, livestock also decreases soil C pool by decreasing litter input but activating soil microbes mediating soil C turnover (Frank et al. 2018; Wang et al. 2017). According to our previous studies, trampling has no significant effect on SOC, while excrement deposition under grazing activity may further increase exogenous SOC accumulation (Li et al. 2021a, b). Therefore, it is highly likely that the persistent C stock resulted from contrasting effects of reduced litter input and excrement return (Fig. 2c). Concerning the decreases in soil NH_4^+ -N (Fig. 2a; Schrama et al. 2013) and STP, and increases in community N and P at 2.7 sheep ha^{-1} (Fig. 2d, e), these findings suggest that low stocking rate cessation may not benefit typical steppe nutrient cycles.

Besides water, nitrogen is one of the primary limiting factors of biodiversity and productivity in arid and semi-arid grasslands (Wang et al. 2020). In N-limited systems, N fertilization has direct positive effects on ecosystem multifunctionality by enhancing soil available N (Fig. 2a-b), which can be readily acquired and utilized by plants. It is well documented that increasing N applications lead to higher soil N conditions (Mao et al. 2020; Liu et al. 2021), thus the

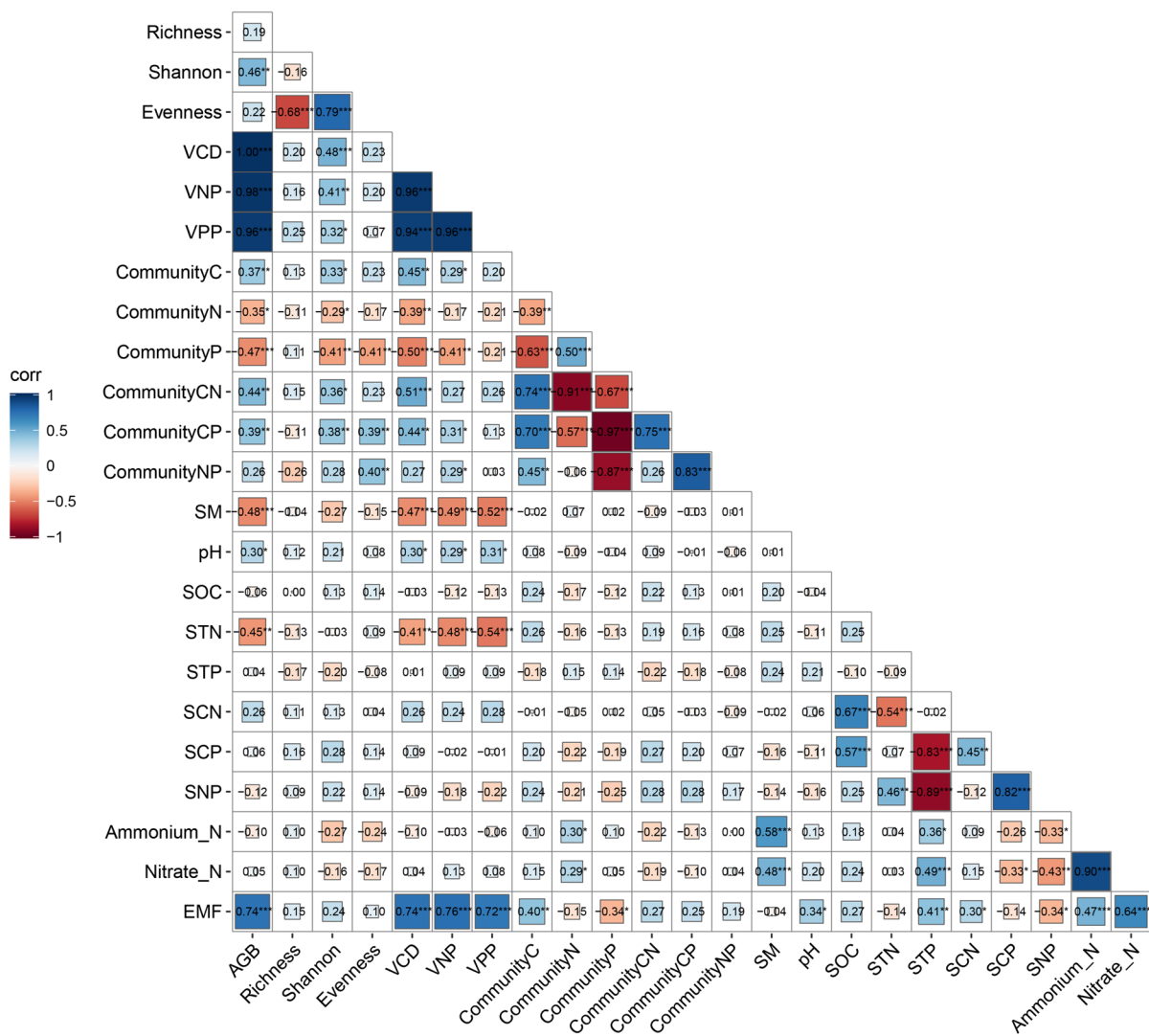


Fig. 6 Scatterplots matrices for the important predictors for 9 individual functions, soil and plant stoichiometry, ecosystem attributes, and ecosystem multifunctionality. The triangular matrix shows the pairwise relationships among variables. Blue and red squares indicate significant positive and negative correlations, respectively. Significance levels are: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. AGB, aboveground biomass; Richness, plant species richness; Shannon, plant Shannon index; Evenness, plant species evenness; VCD, vegetation carbon density; VNP, vegetation nitrogen pool; VPP, vegetation phos-

phorus pool; CommunityC, Community carbon concentration; CommunityN, Community nitrogen concentration; CommunityP, Community phosphorus concentration; CommunityCN, Community C:N; CommunityCP, Community C:P; CommunityNP, Community N:P; SM, soil moisture; pH, soil pH; SOC, soil organic carbon; STN, soil total nitrogen; STP, soil total phosphorus; SCN, soil C:N; SCP, soil C:P; SNP, soil N:P; Ammonium-N, soil $\text{NH}_4^+\text{-N}$; Nitrate-N, soil $\text{NO}_3^-\text{-N}$; EMF, ecosystem multifunctionality

N addition-exacerbated competition for light rather than soil N may be the key mechanism for decreasing in AGB, VCD, VNP, and VPP within no-grazed plots (Fig. 2f-i; Borer et al. 2014; Stevens et al. 2015). Meanwhile, most N addition rates increased AGB, VCD, VNP, and VPP under grazing, probably due to

the combined effects of herbivores' selective feeding and nutrient limitations (Li et al. 2017; Zheng et al. 2021). Contrary to the increase in SOC mentioned in previous N addition studies (Liu et al. 2020; Li et al. 2021a), we found that N enrichment did not significantly influence SOC (Fig. 2c) due to the promoting

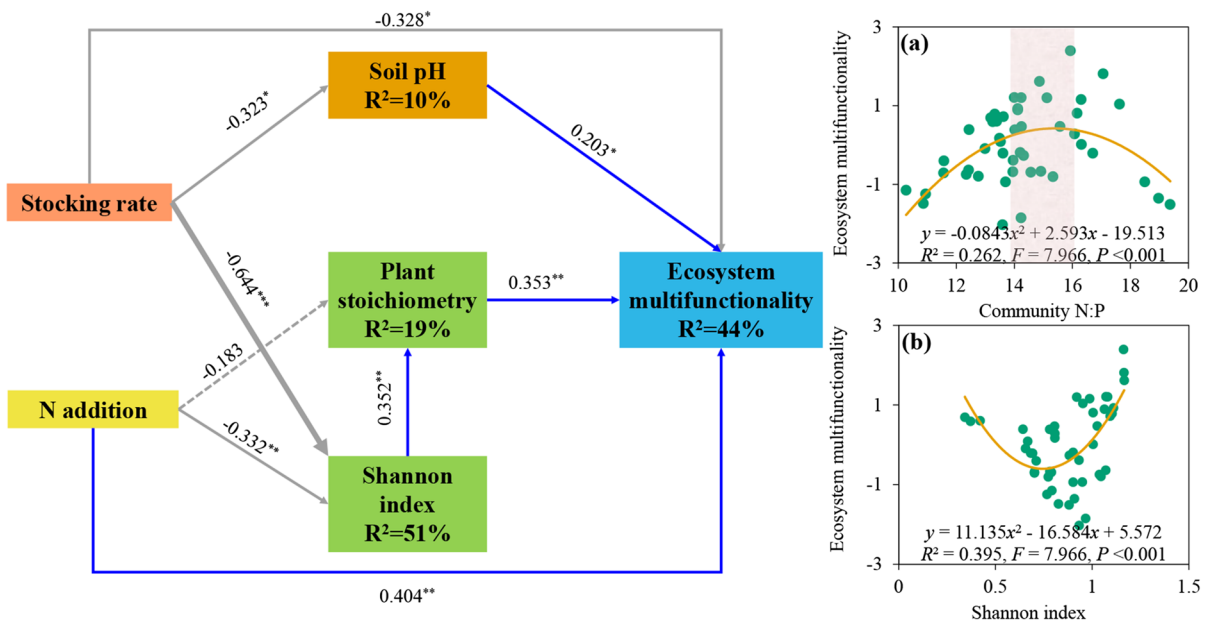


Fig. 7 The final structural equation model of effects of stocking rate, N addition on ecosystem multifunctionality through soil pH, plant stoichiometry (community C, N, P, C:N, C:P, and N:P), and Shannon index. AIC=61.98, BIC=118.117, Fisher's C=1.98, $P=0.986$, $df=10$. Solid and dashed arrows indicate significant and non-significant pathways, respectively. Blue and grey arrows indicate significant ($*P<0.05$, $**P<0.01$, and $***P<0.001$) positive and negative pathways,

respectively. Arrow width is proportional to the strength of the relationship. Numbers at arrows are standardized path coefficients. The proportion of variance explained (R^2) appears alongside response variable in the model. The relationship between ecosystem multifunctionality and community N:P **a** and Shannon index **b**. Yellow Lines are fitted lines from linear regressions

net export of C in soil induced by soil microbes (Li et al. 2021a). In summary, N application may not be always constructive for maintaining constant multifunctionality, because N enrichment also has multiple cascading and negative effects on ecosystem functioning, including biodiversity loss (Zhang et al. 2021a), saturation and emission (Chen et al. 2019), and long-term N addition-induced soil acidification (Bobbink et al. 2010).

Indirect effects of N addition and grazing on ecosystem multifunctionality

Grazing could indirectly affect the ecosystem multifunctionality in several ways, for example, through the changes in biological and non-biological factors, such as soil pH (Cui et al. 2020), and above- and below-ground biodiversity (Delgado-Baquerizo et al. 2020; Maestre et al. 2012; Zhang et al. 2022). A previous study reported a positive effect of grazing on soil pH in grazed grassland on the arid and

semi-arid grassland (Cui et al. 2020), we show that grazing significantly increased EMF by decreasing soil pH (Fig. 1b), probably because root exudate stimulated by grazing may lead to a decrease in soil pH, thus promote soil available nutrients (e.g., soil $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$; Fig. 6) for plant by activating microbial activity and turnover (Yang et al. 2018), which consequently increased plant above-ground functions (e.g., AGB, VCD, VNP, and VPP; Fig. 6) and EMF.

In addition to the direct negative effects of grazing on EMF, our SEM results further confirm that dramatic changes in EMF under grazing are largely due to variations of plant stoichiometry caused by decreasing plant diversity. Plant species loss, and alterations in composition and structure have been reported to decrease plant C:nutrient (Abbas et al. 2013), which may be attributed to decreases in biomass production and associated C stocks induced by competitive relaxation via species partitioning of light (Abbas et al. 2013; Liu et al. 2021). Our study

Table 1 Model summaries describing the responses of soil property, ecosystem multifunctionality, ecosystem function, soil stoichiometry, and plant nutrient and stoichiometry to stocking rate (SR) and N addition (NA) and their interaction (SR*NA)

	SR		NA		SR*NA	
	F	P	F	P	F	P
Soil properties						
Soil moisture	113.24	< 0.001	113.99	< 0.001	44.8	< 0.001
Soil pH	5.71	0.003	0.52	0.669	1.17	0.348
Plant diversity						
Species richness	0.65	0.588	1.31	0.291	2.26	0.045
Shannon index	755.22	< 0.001	249.14	< 0.001	183.31	< 0.001
Species evenness	46.95	< 0.001	28.40	< 0.001	20.64	< 0.001
Ecosystem functions						
Soil NH ₄ ⁺ -N	10.77	< 0.001	988.54	< 0.001	14.82	< 0.001
Soil NO ₃ ⁻ -N	64.52	< 0.001	774.24	< 0.001	11.37	< 0.001
SOC	0.97	0.422	1.08	0.371	3.55	0.004
STN	13.42	< 0.001	2.16	0.113	8.20	< 0.001
STP	61.30	< 0.001	112.48	< 0.001	36.93	< 0.001
AGB	2280.09	< 0.001	393.03	< 0.001	379.83	< 0.001
VCD	1778.07	< 0.001	289.39	< 0.001	264.52	< 0.001
VNP	730.73	< 0.001	126.07	< 0.001	143.57	< 0.001
VPP	730.91	< 0.001	119.32	< 0.001	226.06	< 0.001
EMF	127.52	< 0.001	59.03	< 0.001	11.05	< 0.001
Soil stoichiometry						
Soil C:N	4.98	0.006	1.48	0.24	5.42	< 0.001
Soil C:P	7.55	< 0.001	15.22	< 0.001	10.30	< 0.001
Soil N:P	33.77	< 0.001	44.41	< 0.001	20.25	< 0.001
Plant nutrients and stoichiometry						
Community C	126.82	< 0.001	10.11	< 0.001	56.80	< 0.001
Community N	29.62	< 0.001	23.19	< 0.001	4.60	< 0.001
Community P	152.36	< 0.001	70.19	< 0.001	148.64	< 0.001
Community C:N	84.80	< 0.001	23.79	< 0.001	19.24	< 0.001

Table 1 (continued)

	SR		NA		SR*NA	
	F	P	F	P	F	P
Community	214.70	<0.001	64.13	<0.001	191.44	<0.001
C:P						
Community	21.03	<0.001	7.05	<0.001	34.14	<0.001
N:P						

SOC, soil organic C; STN, soil total nitrogen; STP, soil total phosphorus; VCD, vegetation carbon density; VNP, vegetation nitrogen pool; VPP, vegetation phosphorus pool; EMF, ecosystem multifunctionality

supports that the resistance and resilience of species-poor communities to grazing are lower than those of species-rich communities (Zhang et al. 2022); however, our results also show that low plant diversity supported relative high EMF (Fig. 7), probably because low plant C:nutrient ratios caused by changes in plant communities may rapidly translate nutrients into soil and microorganisms through litter decomposition. Increasing stocking rate exacerbating the relationship between plant diversity and EMF is consistent with results previously found in rangeland (Baert et al. 2018., Zhang et al. 2022), yet our results expanded this conclusion by revealing that the capacity of plant diversity in balancing plant resource stoichiometry serves as a crucial mechanism in maintaining EMF.

Excessive N can decrease soil pH, and consequently, decrease EMF (Cui et al. 2020). However, we did not observe the direct correlations between soil pH and EMF under N addition. This may be attributable to insufficient N applied over the study period to significantly affecting soil pH in the study site. Plant resource stoichiometry also plays a significant role in mediating EMF under N addition. Increased N availability can decrease C:N but increase N:P in leaves both through plant nutrient reallocation and plant community composition changes (Fig. 4g, h; Sardans et al. 2017). Contrary to the effects of grazing, our results confirm that EMF was more likely affected by the positive direct effect of N addition, instead of its negative indirect effects through plant stoichiometry induced by the Shannon index (Fig. 7). On the one hand, N enrichment may directly enhance soil available N (Fig. 2a-b), which can be readily acquired and utilized by plants. By comparison, grazing has positive but lag effects on grassland through livestock feeding, trampling, and excrement (Li et al. 2021a, b). Moreover, in the reviewed grazing-EMF literature, few studies consider livestock production as EMF in grass-livestock interaction systems. Hence, the negative effects of grazing on EMF are overestimated. On the other hand, although both N enrichment and grazing reduce plant diversity, the inherent mechanisms are different (Fig. 1d). A previous study has reported that N addition greatly increases intraspecific trait variation which is beneficial for the light competition and fast growth of plants, and consequently decreases species diversity (Zheng et al. 2021). As for grazing, soil moisture and nutrients rather than light are the

major limiting factors for plant diversity and productivity (Zheng et al. 2021).

Implications for rangeland management under global change

Our findings provide significant implications for the restoration and management of grasslands under different global change scenarios. First, our results show that grazing significantly decreased EMF, and N addition had a positive effect on EMF, indicating that grazing management and fertilization supplementation could be considered together to improve ecosystem functioning. Moreover, future experiments should be carried out to elucidate the multiple and contrasting effects of grazing and N addition considering the effects of atmospheric N deposition.

Second, our study suggests that plant stoichiometry is critical in EMF maintenance. We reveal that the EMF increased with community N:P under N limitation of plant growth, while decreased under P limitation of plant growth, with a tipping point of community N:P being 15.38, which indicates that balanced plant N:P ($14 < N:P < 16$, Koerselman and Meuleman 1996) is conducive to regulating the optimal rangeland management. In current study, a low stocking rate (2.7 sheep ha⁻¹) did maintain plant species richness, species evenness, SOC, and STN, but directly reduced plant diversity, AGB, and EMF. However, a low stocking rate of 2.7 sheep ha⁻¹ with N addition rate of 5 g N m⁻² yr⁻¹ could improve grassland resources utilization and have less negative influences on ecosystem functions and EMF. Hence, the optimal grassland management practices should be a stocking rate of 2.7 sheep ha⁻¹ with N addition rate of 5 g N m⁻² yr⁻¹, considering the strategies of both grazing tolerance and conservative resource utilization. In addition, in order to understand and ensure the continued supply of ecosystem services, the livestock production index could be further included in EMF.

Third, results of this study suggest that high species diversity could weaken the negative effect of grazing on EMF. Thus, reseeding multiple and high-quality forage could be conducive to restore degraded grassland.

Conclusions

The study provides important application and insight into maintaining EMF through N addition and grazing management in grassland ecosystems. Our results show that N addition and grazing have contrasting effects on EMF in a typical steppe. The reduction of EMF is mainly mediated by the response of plant resource stoichiometry to decreasing plant diversity induced by grazing and N addition, indicating that plant species will develop optimal resource-use strategies to meet herbivores' control or environmental changes. N supplementation at the low rate of 5 g N m⁻² yr⁻¹ with a low stocking rate of 2.7 sheep ha⁻¹ could maintain the most important ecosystem functions, such as C and N storage.

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Author contributions Fujiang Hou, Lan Li, Xiumin Zhang, Junqi Hu, and Mengyuan Wang contributed to the study's conception and design. Lan Li and Zhen Wang prepared materials and collected data. Lan Li, and Xiong Z. He analysed the data. Lan Li wrote the first draft of the manuscript and all authors revised the manuscript. All authors approved the final manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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Different effects of grazing and nitrogen addition on ecosystem multifunctionality are driven by changes in plant resource stoichiometry in a typical steppe

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