



# Effects of litter removal on grazing excluded grassland: A 5-year test with contrasting exclusion durations and topographic conditions

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## ABSTRACT

Litter removal is an important practice for the management of restored grasslands, while its effects on soils and plant communities remain unclear, mainly due to the variations with time and topographical conditions. To fill this knowledge gap, we compared the effects of litter removal on soils (moisture and net nitrogen mineralization) and plant communities (aboveground biomass, species diversity and temporal stability of the community and five functional groups) in different topographical scales (slope aspect and position) in the 10-year and 35-year grazing exclusion grasslands with a 5-year litter removal experiment. We found that soil moisture and net nitrogen mineralization, and plant community productivity were consistently lower in plots without litter in both 10-year and 35-year grazing exclusion grasslands than those in plots with litter. Litter removal significantly increased species diversity but decreased the temporal stability of community biomass in the 35-year grazing exclusion grassland, but not in the 10-year grazing exclusion grassland. The effects of litter removal on soil environments and plant communities varied with topographical conditions. Moreover, the temporal stability of community biomass after litter removal was largely determined by changes of the functional group asynchrony in the 10-year grazing exclusion grassland, but by functional group stability in the 35-year grazing exclusion grassland. Importantly, nitrogen mineralization mediated the mechanisms by which litter removal affected community stability. Our findings add novel evidence for the importance of litter management in regulating the ecological processes of grazer-excluded rangelands.

## 1. Introduction

Grasslands are one of the most important agricultural land uses, covering approximately 69 % of the global agricultural land area, and provide a wealth of fundamental ecological services (Kemp et al., 2013; Bardgett et al., 2021; Siebert et al., 2023). Grazing exclusion is an effective and economical approach to recover the ecological function of degraded grasslands by enhancing biodiversity, vegetation productivity, and soil moisture and nutrients, thereby contributing to the improvement of regional climate conditions (Kemp et al., 2013; Qiu et al., 2013; Wang et al., 2018; Hazhir et al., 2024). These changes trigger a positive effect on the increases in soil nitrogen (N) transformation and ecosystem stability (Qasim et al., 2017; Smith et al., 2020). However, recent studies indicate that both biodiversity and productivity in grassland ecosystems

decrease with the duration of grazing exclusion, mainly due to the increasing interspecific competition by the limited resource availability and the negative feedback from species-specific pathogens (Jing et al., 2014; Porensky et al., 2020; Souza et al., 2022). These negative changes (especially in the specific species or functional group) in turn affect the function and stability of the plant community, given that both aspects are closely coupled (Valencia et al., 2020; Schnabel et al., 2021; Eskelinen et al., 2022).

Grassland restoration often significantly accumulates plant litter in the ecosystem (Ruprecht et al., 2010; Zhang et al., 2022), while litter accumulation plays a key role in driving community succession and N cycling in restored grasslands (e.g., with grazing exclusion) (Xiong and Nilsson, 1999; Lamb, 2008; Loydi et al., 2013). On the one hand, litter accumulation facilitates plant community productivity and stability by

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improving soil moisture and nutrient retention to support seedling growth and species dominance effects (Weltzin et al., 2005; Montané et al., 2010; Hassan et al., 2021). On the other hand, litter accumulation reduces species diversity by inhibiting seed germination due to increasing physical and biological interference, impairing necessary germination cues and recruitment space (Foster and Gross, 1998; Patrick et al., 2008; Letts et al., 2015), and weakening the capacity of organic N turnover by exacerbating imbalances in nutrient stoichiometry caused by greater biocompetition (Hossain and Sugiyama, 2020; Du and Gao, 2021). For example, previous studies have shown that long-term plant litter accumulation (including artificial litter addition) can play a negative factor controlling plant community structure and composition by directly or indirectly affecting individuals and populations in grassland ecosystems (Foster and Gross, 1998; Amatangelo et al., 2008; Ruprecht and Szabó, 2012; Letts et al., 2015). A meta-analysis combining 3913 observations from 242 studies demonstrated that litter addition significantly decreased seedling establishment and density, and species richness (Zhang et al., 2022). Litter management is thus recommended for the sustainable management of litter accumulation ecosystems (Anderegg et al., 2022; Jessen et al., 2023; Chen et al., 2024a). However, results from current experiments suggest that the ecological effects of litter removal on the plant productivity and diversity and soil environment in grassland may be positive, negative or neutral, depending on grassland ecosystem type, climate and time of experiments (Jensen and Gutekunst, 2003; Amatangelo et al., 2008; Bansal et al., 2014; Yu et al., 2015; Zhang et al., 2019). Therefore, explicitly examining the effects of litter on soils and plants is urgently needed for the management of grazer-excluded grasslands.

Globally, slope-dominated mountain grasslands comprise 20 %–25 % of terrestrial ecosystems, corresponding to approximately 49 %–62 % of the total grassland area (Straffellini et al., 2024; Zhou et al., 2024), with 6 % of them located within rangelands (Olson et al., 2001). A key influencing factor in spatial heterogeneity of plant communities is topography, such as aspects and positions of slope, which strongly modulate the fine-scale and local-scale variations in microclimate and soil properties (Rezaei and Gilkes, 2005; Sanaei et al., 2019). Generally, the south-facing slope could maintain more stress-tolerant and light-demanding flora than the north-facing slope (Bennie et al., 2006), such as the higher abundance of annual and perennial grasses in the southern slope and higher presence of geophyte species in the northern slope in a mountainous rangeland (Farzam and Ejtehadi, 2017). In the semiarid shortgrass steppe of North America, aboveground net primary productivity (ANPP) was the highest sensitivity to precipitation in the lowland landscape due to higher resource availability (Hoover et al., 2021). In view of the intimate and complex role of topography in driving biotic-abiotic interactions through the enhancement of habitat heterogeneity and niche availability, ignoring topographic features would likely result in greater under- or over-estimation of landscape-level community function and composition (Stephenson et al., 2019; Hoover et al., 2021). Therefore, understanding how the effects of litter management vary with topographical factors is essential for optimizing grassland productivity and ecosystem sustainability in rangeland areas.

In this study, we conducted a 5-year field experiment to investigate the effects of litter removal on soils and plants in both upper and lower positions of north and south slopes in semi-arid grasslands receiving the 10-year and 35-year grazing exclusion. We measured soil moisture and nitrogen, species richness, and productivity and temporal stability of plant community and five functional groups. We aimed to test the following hypotheses: (H1) litter removal will decrease soil N mineralization rates and mineral N concentrations because of increasing microbial N immobilization by intensifying soil moisture limitation (Dijkstra et al., 2015; Chen et al., 2024a,b); (H2) litter removal will enhance plant community productivity and stability via increasing species richness and diversity, as biodiversity will intensify functional group asynchrony and stability (Valencia et al., 2020; Van-Ruijven et al., 2020); (H3) the effects of litter removal on soils and plants will be

stronger in the long-term than the short-term grazing exclusion grassland due to the greater quantity and depth of litter accumulation (Loydi et al., 2013; Jessen et al., 2023); (H4) the effects of litter removal will vary with positions and aspects of slope due to differential allocation of resources and local-scale variability in the amount of litter accumulation (Table S1).

## 2. Materials and methods

### 2.1. Study site

The experiment was conducted in a semiarid grazing exclusion grassland in Yunwushan National Natural Grassland Reserve (106°24'–106°28'E, 36°13'–36°19'N), located in Guyuan City, Ningxia Hui Autonomous Region, Northwestern China. The area has a warm temperate semiarid climate, with an average annual rainfall of 440 mm, of which 60–80 % falls during the growing season (May–September), and an average annual temperature of 7°C with maximum and minimum temperatures in July (25°C) and January (−14°C). The annual evaporation ranges from 1330 to 1640 mm. The soil is a mountain gray-cinnamon soil, classified as a Calci-Orthic Aridisol in the Chinese taxonomic system, corresponding to a Haplic Calcisol in the FAO/UNESCO system (Liu et al., 2023). The topography of the study site is characterized as belonging to the tableland-gully area (Kong et al., 2022). The altitude varies from 1800 to 2100 m above sea level, and the slope inclinations of 5°–40°, and slope lengths of 80–450 m (ArcGIS 10.8, ESRI, USA). No agricultural activities had been carried out in the reserve since 1982. The predominant species in the area are *Stipa przewalskyi*, *Stipa grandis*, *Artemisia sacrorum* var. *messerschmidiana*, *Potentilla chinensis*, and *Medicago archiducis-nicolaii*.

### 2.2. Experimental design

To estimate the effects of litter removal on plant diversity, community productivity, stability and soil water and nitrogen dynamics in early and late stages of grazing exclusion, as well as their response to topographic properties. Previous studies showed that optimal grazing exclusion for degraded grassland in our study site is 15–20 years (Qiu et al., 2013), so we selected a 10-year and 35-year grazing exclusion grassland to present early and late stages of grazing exclusion, which were approximately 3 km apart, to conduct litter removal experiment in May 2019–2023. A sample transect was established in the south and north slopes of both 10-year and 35-year grazing exclusion grasslands. In each slope of the transect, we selected lower and upper positions to establish experimental plots. In each position of the selected slopes, three paired plots (3 m × 3 m) were randomly established. The paired plots were composed of a litter removal treatment and a control treatment. We totally had 48 plots (2 durations of grazing exclusion × 2 slope aspects × 2 slope positions × 2 litter treatments × 3 replicates) (Fig. S1). To ensure the comparability of the experimental results, each paired plot was selected according to the following two criteria, i.e., similar community composition, and litter quantity and thickness. The plant community in the paired plots in each slope position adequately represented the community characteristics at this location. In addition, the initial soil and litter accumulation properties at each position prior to litter removal are presented in Table S1. In the plots without litter, all litter was artificially removed from the plot using a rake one month before the start of the experiment, and then removed at the end of each growing season and before the start of the following growing season.

### 2.3. Field N mineralization and moisture measurement

The in-situ soil net N mineralization was measured from July to August each year using undisturbed buried core method, as previous results indicated that net N mineralization in this period could capture much of the variation in N mineralization during the growing season in

the study region (Wei et al., 2011; Kong et al., 2022; Hou et al., 2022). Briefly, a pre-prepared PVC core (internal diameter 5 cm and length 12 cm) was buried 10 cm into the below-ground in each plot and covered with a waterproof plastic film during the incubation periods. Meanwhile, a paired soil samples from the 0–10 cm were taken near the core to obtain the initial mineral N content. At the end of the incubation period (a month), soils in the incubation cores were taken back and transported to the laboratory in a cooled thermos box and stored at 4°C before analysis. This method is a standard method for long-term ecological research (Robertson et al., 1999), and has been widely used in field measurements (Risch et al., 2019). Soil mineral N in 10 g of fresh soil (including ammonium and nitrate) was extracted with a 2 mol L<sup>-1</sup> KCl after homogenization of each soil sample and was examined by an AutoAnalyzer-AA3 (Seal Analytical, Norderstedt, Germany). Soil moisture before and after soil incubation was determined by oven-drying the soils at 105°C to a constant weight. The rates of net ammonification and nitrification were calculated from the difference between initial and final contents of ammonium and nitrate during the incubation period for each plot. The net N mineralization was calculated by summing the net nitrification and ammonification in the incubation period (Wei et al., 2011).

#### 2.4. Vegetation measurements and harvesting

The plant aboveground biomass, species richness and plant coverage were measured in each plot at the time of peak standing biomass (from 20 August to 1 September). Specifically, a 50 × 50 cm quadrat was randomly established in each of all plots. Species richness was quantified by the total number of species per plot (50 × 50 cm square). The relative cover of individual plant species was assessed in each plot using a frame with 25 grids (each grid 10 × 10 cm) placed above a 50 × 50 cm quadrat (Eskelinen et al., 2022; Xu et al., 2022), and the aboveground plant was clipped at the base to harvest their net primary productivity. We classified biomass into five functional groups (grass, forb, legume, sedge, and subshrub) according to similarities in growth forms, functional traits, and responses to environmental factors of plant species (Lavorel et al., 1997; Lavorel and Garnier, 2002; Bai et al., 2004; Suding et al., 2008). Grass, characterized by perennial rhizome or bunchgrasses growth, belongs to competitive species. Forb, characterized by annual seed plants, belongs to ruderal species. Legume, characterized by annual or perennial herbaceous plants with nitrogen-fixing functions, belongs to competitive species. Sedge, characterized by perennial grass-like plants, belongs to tolerant species. Subshrub, characterized by perennial herbaceous plants with basal woody stems, belongs to tolerant species. Aboveground dry biomass was determined separately after 72 h oven drying (65°C). The aboveground net primary productivity (ANPP) was estimated using the peak aboveground biomass of the plant community.

The temporal stability of the community and each functional group was quantified as the ratio of temporal mean biomass ( $\mu$ ) to its temporal standard deviation ( $\sigma$ ) in each plot over the 5-year experiment (2019–2023) (Tilman et al., 2006). The species richness was defined as the total number of species in each plot. The species diversity (Shannon-Wiener index) was calculated by relative cover of each species per plot (Biswas and Mallik, 2010; Eskelinen et al., 2022).

We calculated functional group asynchrony and stability to assess the stability of the community. The functional group asynchrony was quantified as the community-level asynchrony index (Chen et al., 2024a), and was calculated as:

$$\text{Asynchrony} = 1 - \frac{\sigma^2}{\left(\sum_{i=1}^n \sigma_{fi}\right)^2}$$

where  $\sigma^2$  is the temporal variance in community biomass, and  $\sigma_{fi}$  is the temporal standard deviation in the annual biomass of functional group  $i$

in a community with  $n$  functional group. Asynchrony ranges between 0 (complete synchrony) and 1 (complete asynchrony). The higher functional group asynchrony can increase community stability by decreasing variation in community-level biomass.

The functional group stability was calculated as (Schnabel et al., 2021):

$$\text{Functional group stability} = \frac{\mu}{\sum_{i=1}^n \sigma_{fi}}$$

where  $\mu$  is the temporal mean biomass.

#### 2.5. Statistical analysis

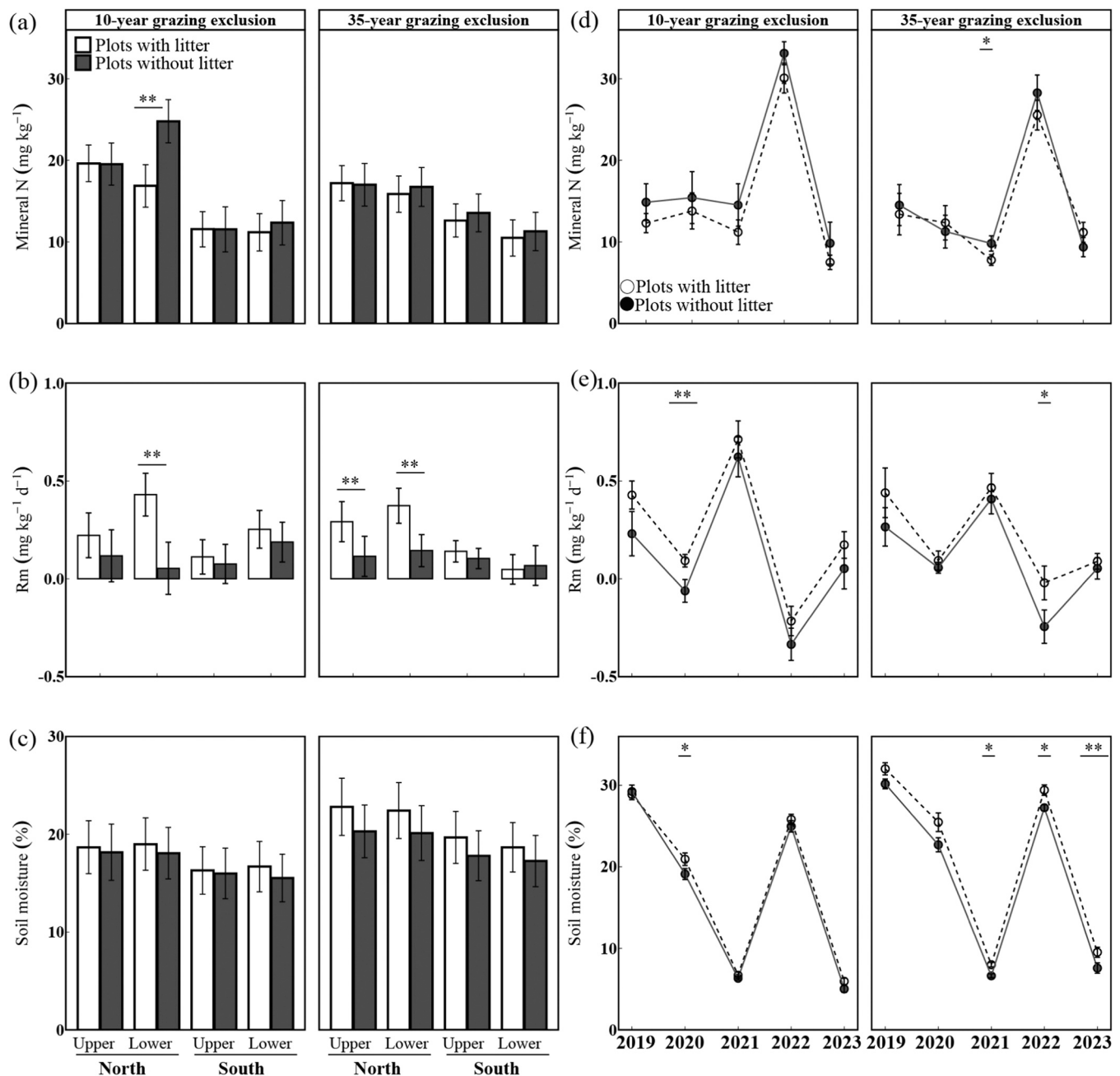
Prior to statistical tests, plant and soil metrics were log-transformed to meet the assumptions of normality and homogeneity of variance. The multivariate analysis of variance (MANOVA) was performed to assess the effects of litter removal, topography, experimental year and their interactions on metrics of soils (e.g., moisture, mineral N content, and net N mineralization rates), plant community (e.g., ANPP, species diversity and stability) and the five functional groups (biomass and stability of each group of grass, forb, legume, sedge, and subshrub) in the 10-year and 35-year grazing exclusion grassland, respectively. The *t*-test was used to examine differences between plots with and without litter. Regression model was used to determine how plant species diversity, stability and asynchrony of five functional groups, and soil moisture, mineral N concentrations and net N mineralization rates related to plant community stability. Furthermore, a structural equation model (SEM) was used to explore the pathways through which litter removal affected community biomass stability. We first built a complete conceptual model that included all possible pathways based on our prior knowledge of the experiment, and then sequentially removed non-significant pathways until an optimal model was obtained (Fig. S2, Table S2). The goodness of the overall model fitting was evaluated using the chi-square ( $\chi^2$ ), degrees of freedom (df) and probability level (*P*-values). All analyses were performed in R (version 4.3.2), with the 'vegan' package for calculating Shannon-Wiener index, the 'ggplot2' package for plotting all regression figures, and the 'lavaan' package for SEM.

### 3. Results

#### 3.1. Effects of litter removal on soil moisture, N mineralization and availability

Litter removal (LR) significantly decreased soil moisture, with 4.1 % and 7.5 % reduction in 10-year and 35-year grazing exclusion grasslands, respectively ( $P < 0.010$  for LR). The effect of litter removal on soil moisture was independent of positions and aspects of slope in both grasslands. However, such effect depended on experimental years in the 35-year grazing exclusion grassland (Table S3), with significant reduction in the last 3 years of the experiment, but not in the first two years (Fig. 1f).

Litter removal reduced the rates of net N mineralization, with 56.0 % and 49.5 % reduction in 10-year and 35-year grazing exclusion grasslands, respectively ( $P < 0.05$  for LR). The effect of litter removal on N mineralization was not influenced by slope positions and experimental years in both grasslands ( $P > 0.100$  for their interactions). For the 35-year grazing exclusion grassland, the effects of litter removal on N mineralization varied with slope aspects (Table S3), with a significant reduction in both upper and lower positions in the north slope, but not in the south slope (Fig. 1b). For the 10-year grazing exclusion grassland, soil N mineralization was affected by the interactions of litter removal and slope aspect with slope position ( $P = 0.052$ ) and with experimental year ( $P = 0.029$ ). The significant reduction in N mineralization was



**Fig. 1.** Effects of litter removal on soil mineral nitrogen concentrations (Min-N, a, d), net nitrogen mineralization rates ( $R_m$ , b, d) and moisture (c, f). a-c: Effects of litter removal at lower and upper positions of north and south slopes in the 10-year (GE10y) and 35-year (GE35y) grazing exclusion grasslands ( $n = 15$ ), and the values were averaged across 5 experimental years. d-f: Effects of litter removal from 2019 to 2023 in the 10-year and 35-year grazing exclusion grasslands ( $n = 12$ ), and the values were averaged across aspects and positions of slope for each experimental year. Error bars are standard errors of the means. Asterisks indicate statistical significance based on the paired *t*-test (\*,  $P < 0.1$ ; \*\*,  $P < 0.05$ ; \*\*\*,  $P < 0.01$ ).

observed in the lower position of north slope (Fig. 1b), and in the second year of experiment (Fig. 1e).

The concentrations of mineral N were not affected by litter removal or its interaction with experimental years and slope positions and aspects in the 35-year grazing exclusion grassland, but were affected by interaction of litter removal with slope aspects and positions in the 10-year grazing exclusion grassland. The concentrations of mineral N in soil were significantly increased by litter removal in the lower position of north slope, but was not affected in other positions (Fig. 1a).

### 3.2. Effects of litter removal on the biomass and diversity of plant community

The aboveground net primary productivity (ANPP) was reduced by litter removal in both 10-year (-12.9 %) and 35-year (-7.8 %) grazing exclusion grasslands (Table 1). For the 10-year grazing exclusion grassland, litter removal significantly reduced ANPP in the lower position of north slope and the upper position of south slope ( $P = 0.038$  for  $LR \times SA \times SP$ , Fig. 2a). For the 35-year grazing exclusion grassland, litter removal only significantly reduced ANPP in the upper position of south slope ( $P = 0.016$ , Fig. 2a).

The effects of litter removal on the biomass of five functional groups



**Table 1**

ANOVA results (*P* values) for the effects of litter removal (LR), slope aspect (SA), slope position (SP) and experimental years (Y) on the aboveground net primary productivity (ANPP), species richness and Shannon-Wiener index of plant community, and the biomass of five functional groups (grass, forb, legume, sedge, and subshrub) in the 10-year and 35-year grazing exclusion grasslands, respectively, over the 5 years from 2019 to 2023.

	ANPP	Richness	Shannon	Grass	Forb	Legume	Sedge	Subshrub
<b>10-year grazing exclusion</b>								
LR	<b>0.0063</b>	0.2110	0.1931	0.2385	0.7265	<b>0.0008</b>	0.2919	0.4949
SA	<b>0.0002</b>	< <b>0.0001</b>	< <b>0.0001</b>	0.0039	0.2828	< <b>0.0001</b>	< <b>0.0001</b>	0.5102
SP	< <b>0.0001</b>	0.6090	0.9109	< <b>0.0001</b>	0.2327	<b>0.0010</b>	0.5368	<b>0.0011</b>
Y	<b>0.0010</b>	<b>0.0185</b>	<b>0.0027</b>	<b>0.0545</b>	< <b>0.0001</b>	< <b>0.0001</b>	< <b>0.0001</b>	<b>0.0476</b>
LR×SA	0.3491	0.1870	0.4834	0.2174	0.8366	0.1943	<b>0.0040</b>	0.1493
LR×SP	0.3809	0.6543	0.3922	0.4558	0.3725	0.2491	0.6646	0.2458
LR×Y	0.4606	0.6343	0.8859	0.8413	0.3300	0.2209	0.3199	0.2742
SA×SP	0.1412	0.5169	0.4594	<b>0.0018</b>	< <b>0.0001</b>	< <b>0.0001</b>	0.2904	0.0078
SA×Y	<b>0.0542</b>	0.1416	<b>0.0917</b>	0.8651	0.7752	<b>0.0010</b>	0.4807	<b>0.0744</b>
SP×Y	<b>0.0086</b>	0.3109	0.2863	0.7247	0.4838	0.3312	0.5398	0.4269
LR×SA×SP	<b>0.0378</b>	0.5362	0.9560	0.6448	0.4525	<b>0.0049</b>	<b>0.0368</b>	<b>0.0870</b>
LR×SA×Y	0.6838	0.9547	0.9042	0.6613	0.7023	0.4964	0.1974	0.5490
LR×SP×Y	0.6783	0.9185	0.8669	0.5233	0.6762	0.3136	0.8017	0.2430
SA×SP×Y	0.4084	0.3128	0.4809	0.4661	0.3330	<b>0.0219</b>	0.9442	0.8494
LR×SA×SP×Y	0.4715	0.9872	0.9277	0.9510	0.9754	0.6744	0.8683	0.5915
<b>35-year grazing exclusion</b>								
LR	<b>0.0289</b>	< <b>0.0001</b>	< <b>0.0001</b>	<b>0.0474</b>	< <b>0.0001</b>	0.4253	<b>0.0211</b>	0.2106
SA	< <b>0.0001</b>	< <b>0.0001</b>	< <b>0.0001</b>	<b>0.0073</b>	<b>0.0013</b>	0.1040	<b>0.0205</b>	0.8543
SP	<b>0.0008</b>	<b>0.0005</b>	<b>0.0515</b>	0.5319	<b>0.0962</b>	0.1040	<b>0.0645</b>	<b>0.0164</b>
Y	<b>0.0101</b>	< <b>0.0001</b>	< <b>0.0001</b>	0.7961	0.4206	<b>0.0178</b>	<b>0.0800</b>	<b>0.0066</b>
LR×SA	0.1583	0.8297	0.9995	0.5181	<b>0.0552</b>	0.7637	0.7423	0.6883
LR×SP	0.3437	0.6512	0.7642	0.1742	<b>0.0291</b>	0.7637	0.5816	0.9015
LR×Y	0.8685	0.3603	0.8877	0.4688	<b>0.0378</b>	0.2139	0.4419	0.7878
SA×SP	<b>0.0001</b>	< <b>0.0001</b>	< <b>0.0001</b>	< <b>0.0001</b>	< <b>0.0001</b>	<b>0.0074</b>	<b>0.0736</b>	<b>0.0259</b>
SA×Y	0.9398	<b>0.0416</b>	0.2432	0.5221	<b>0.0455</b>	0.1899	0.3090	0.1099
SP×Y	0.6605	0.4851	0.8455	0.7663	0.3811	0.1899	0.2268	0.8823
LR×SA×SP	0.2925	<b>0.0423</b>	0.2030	0.1526	<b>0.0651</b>	0.4253	0.1553	0.1436
LR×SA×Y	0.8802	0.8128	0.9996	0.4806	0.7841	0.4158	0.9135	0.8915
LR×SP×Y	<b>0.0318</b>	0.5962	0.8945	0.8116	0.9270	0.4158	0.8042	<b>0.0751</b>
SA×SP×Y	0.4018	0.4694	0.1833	0.6890	0.5140	<b>0.0178</b>	0.4582	0.2565
LR×SA×SP×Y	0.9920	0.3687	0.5177	0.2172	0.1753	0.2139	0.6509	<b>0.0279</b>

Bold values indicate statistical significance. All the models used log<sub>10</sub> values for the response variables.

varied with the time of grazing exclusion. For the 10-year grazing exclusion grassland, litter removal solely increased legume biomass, but did not affect others when averaged across slopes and experimental years. However, the effects of litter removal on biomass of sedge, legume, and subshrub varied with aspects and positions of slope (Table 1). The sedge biomass at the lower position was reduced by litter removal in north slope, but increased in south slope (Fig. 3i). The legume biomass was increased by litter removal at the lower position of north slope and upper position of south slope (Fig. 3g). The subshrub biomass was decreased by litter removal in the upper position of north slope, but not affected in other positions (Fig. 3k).

For the 35-year grazing exclusion grassland, litter removal decreased grass biomass (-12.6 %, *P* = 0.047), and increased sedge (+63.5 %, *P* = 0.021) and forb biomass (+65.8 %, *P* < 0.001), but did not change subshrub and legume biomass when averaged across all the variations (*P* > 0.100 for LR, Table 1). The effects of litter removal on grass and sedge biomass were consistent with aspects and positions of slope and with experimental years (*P* > 0.100 for their interactions), but the effects on forb biomass were significantly varied with these factors. Litter removal significantly increased forb biomass in both positions of north slope and the upper position of south slope (Fig. 2e). Litter removal increased forb biomass in 2019 and 2023 but not in other experimental years when averaged across aspects and positions of slope (Fig. 2f).

Litter removal significantly increased species richness (+32.9 %, *P* < 0.001) and Shannon-Wiener index in the 35-year grazing exclusion (+20.1 %, *P* < 0.001), but not in the 10-year grazing exclusion. Additionally, the effects of litter removal on species richness in the 35-year grazing exclusion grassland varied with positions and aspects of the slope (Table 1). The species richness was significantly increased by litter removal in the lower position of north slope, and in the both positions of south slope in the 35-year grazing exclusion grassland (Fig. 4).

### 3.3. Effects of litter removal on temporal stability of plant community

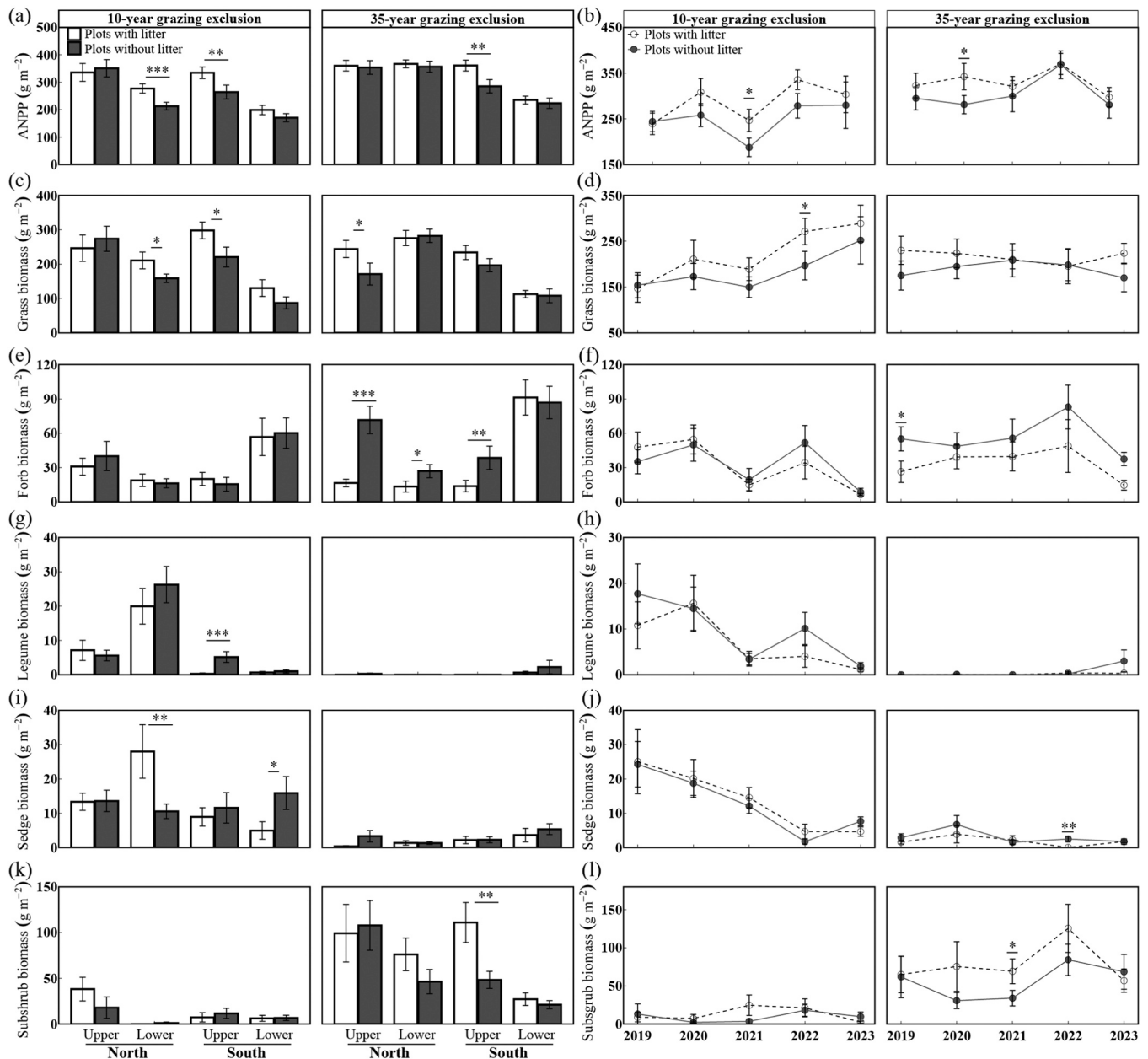
Litter removal significantly decreased the temporal stability of plant community biomass (-25.8 %) and functional group asynchrony (-10.4 %) in the 35-year grazing exclusion grassland (Table 2), but not in the 10-year grazing exclusion grassland. Additionally, these effects were consistent in the aspects and positions of slope and experimental years as suggested by the lack of the significant interactions of litter removal with these factors (Table 2).

The effects of litter removal on temporal stability of five functional groups also varied with the time of grazing exclusion. For the 10-year grazing exclusion grassland, litter removal increased temporal stability of legume biomass (*P* < 0.100 for LR), and that such effect was dependent on aspects and positions of slope (*P* < 0.100 for LR×SA×SP), with a significant increase in the upper position of south slope (Fig. 3d). The effect of litter removal on subshrub stability also varied with aspects and positions of slope (Table 2), with significantly reduced stability in the upper position of north slope (Fig. 3f).

For the 35-year grazing exclusion grassland, litter removal significantly increased the temporal stability of forb and sedge biomass (*P* < 0.100 for LR). Additionally, the effects on forb stability varied with aspects and positions of slope (*P* = 0.041 for LR×SA×SP), with significantly increased stability in the lower position of north slope and the both positions of south slope, but lower stability in the upper position of north slope (Fig. 3c).

### 3.4. Biological and environmental factors influencing biomass temporal stability

The removal of litter significantly altered the relationships of biomass temporal stability to biological and environmental factors. For

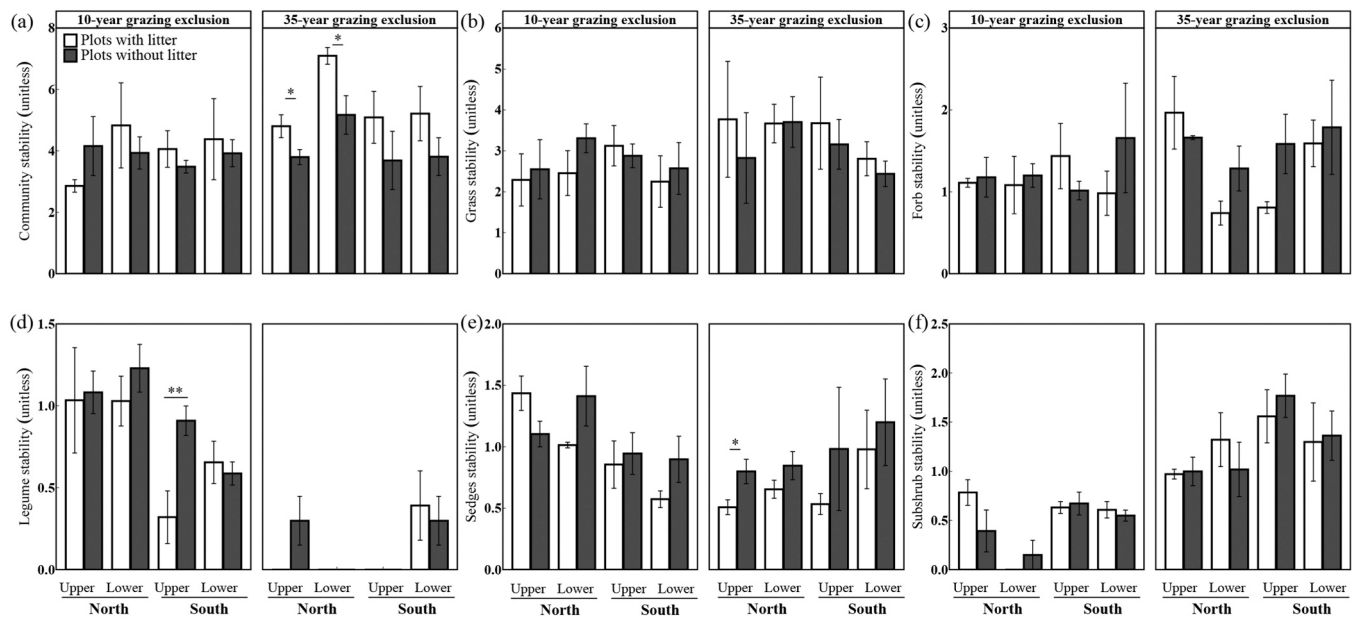


**Fig. 2.** Effects of litter removal on above-ground net primary productivity (ANPP) of grassland community (a) and the biomass of five functional groups (c, e, g, i, k) at lower and upper positions of north and south slopes in the 10-year (GE10y) and 35-year (GE35y) grazing exclusion grasslands. The values were averaged across 5 experimental years. Error bars are standard errors of the means ( $n = 15$ ). Effects of litter removal on above-ground net primary productivity of grassland community (b) and the biomass of five functional groups (d, f, h, j, l) from 2019 to 2023 in the 10-year (GE10y) and 35-year (GE35y) grazing exclusion grasslands. The values were averaged across aspects and positions of slope for each experimental year. Error bars are standard errors of the means ( $n = 12$ ). Asterisks indicate statistical significance based on the paired *t*-test (\*,  $P < 0.1$ ; \*\*,  $P < 0.05$ ; \*\*\*,  $P < 0.01$ ).

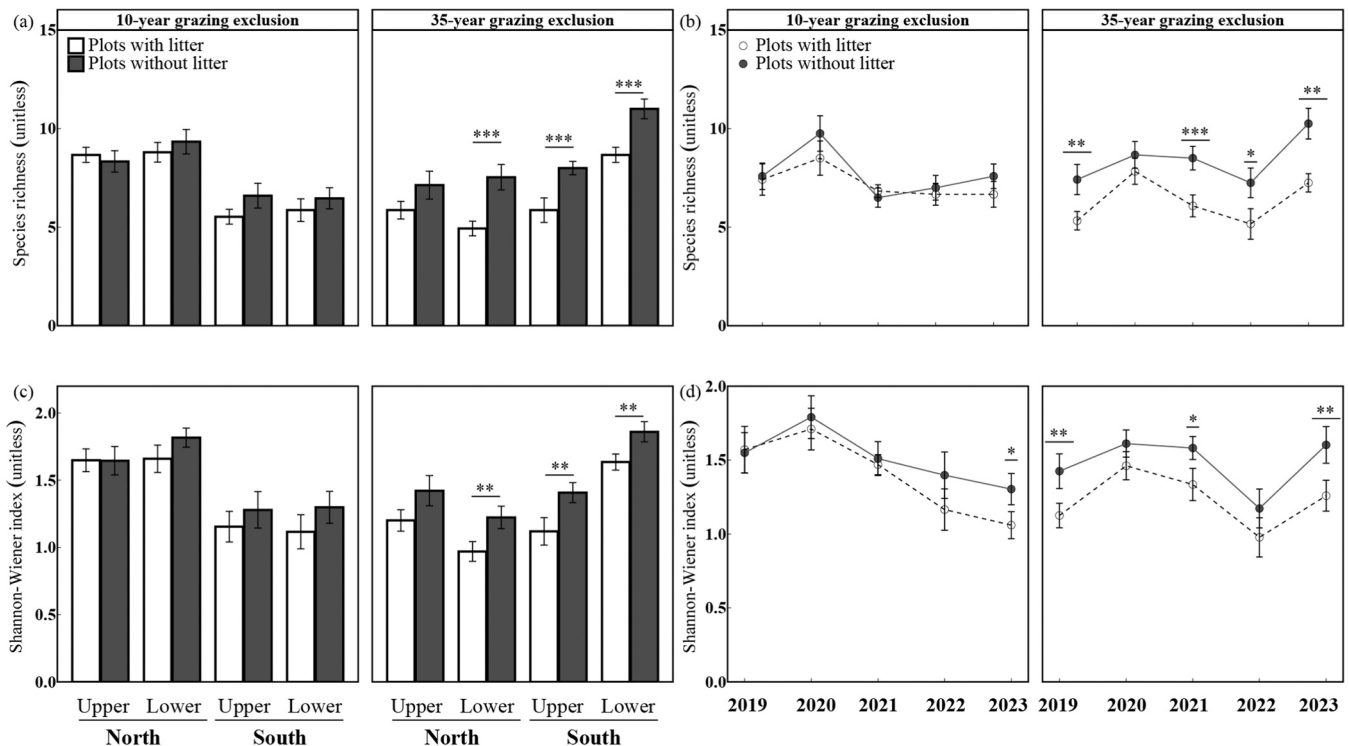
the plots with litter, the temporal stability of community biomass was significantly positively correlated with N mineralization ( $P = 0.005$ ), the temporal stability of subshrub ( $P = 0.012$ ), and functional group asynchrony ( $P = 0.001$ ), but negatively correlated with the temporal stability of legume ( $P = 0.063$ ) (Figs. S1–S3). However, for the plots without litter, the temporal stability of community biomass was significantly positively correlated with soil N mineralization ( $P = 0.009$ ) and moisture ( $P = 0.042$ ), the temporal stability of grass ( $P = 0.037$ ) and forb ( $P = 0.029$ ), and functional group stability ( $P = 0.002$ ) and asynchrony ( $P = 0.067$ ).

The results from Structural Equation Model (SEM) suggested that the pathways through which litter removal affected plant community varied with the time of grazing exclusion (Fig. 6). For the 10-year grazing

exclusion grassland, litter directly increased functional group asynchrony, and indirectly affected functional group asynchrony and diversity via decreasing soil N mineralization. Litter removal also directly affected community stability via functional group asynchrony. However, litter removal did not have direct or indirect effects on functional group stability. For the 35-year grazing exclusion grassland, litter removal indirectly affected functional group stability by reducing soil N mineralization, and indirectly affected community stability via changing N mineralization and functional group stability. These results further highlighted that soil N mineralization played an important role in regulating the effects of litter removal on plant community in this grazing excluded grasslands.



**Fig. 3.** Effects of litter removal on the temporal stability of the biomass of grassland community (a) and five functional groups (b–f) at lower and upper positions of north and south slope in the 10-year (GE10y) and 35-year (GE35y) grazing exclusion grasslands. The values were calculated across 5 experimental years. Error bars are standard errors of the means ( $n = 3$ ). Asterisks indicate statistical significance based on the paired  $t$ -test (\*,  $P < 0.1$ ; \*\*,  $P < 0.05$ ; \*\*\*,  $P < 0.01$ ).



**Fig. 4.** Effects of litter removal on species richness (a, b) and Shannon-Wiener index (c, d). a and c: Effects of litter removal at lower and upper positions of north and south slope in the 10-year (GE10y) and 35-year (GE35y) grazing exclusion grasslands ( $n = 15$ ), and the values were averaged across 5 experimental years. b and d: Effects of litter removal from 2019 to 2023 in the 10-year and 35-year grazing exclusion grasslands ( $n = 12$ ), and the values were averaged across aspects and positions of slope for each experimental year. Error bars are standard errors of the means. Asterisks indicate statistical significance based on the paired  $t$ -test (\*,  $P < 0.1$ ; \*\*,  $P < 0.05$ ; \*\*\*,  $P < 0.01$ ).

#### 4. Discussion

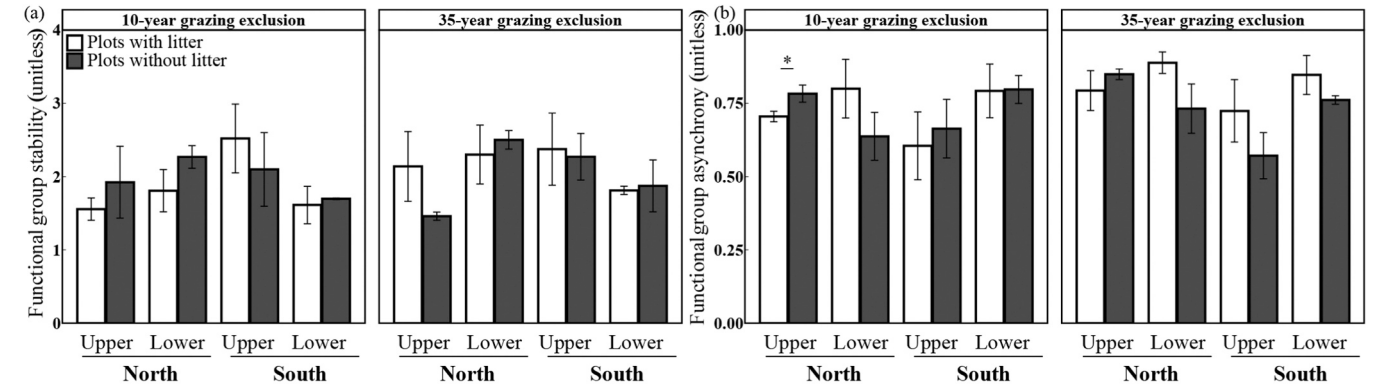
In this study, we conducted a 5-year experiment to examine how litter removal affects soils and plant communities in litter accumulated ecosystems and how these effects vary with topographic scales and

grazer exclusion duration. We found that litter removal consistently decreased soil N mineralization in both 10-year and 35-year grazing exclusion grasslands, supporting our hypotheses that litter removal would decrease soil N cycling (H1). However, litter removal decreased plant community productivity, rejecting our hypothesis that litter

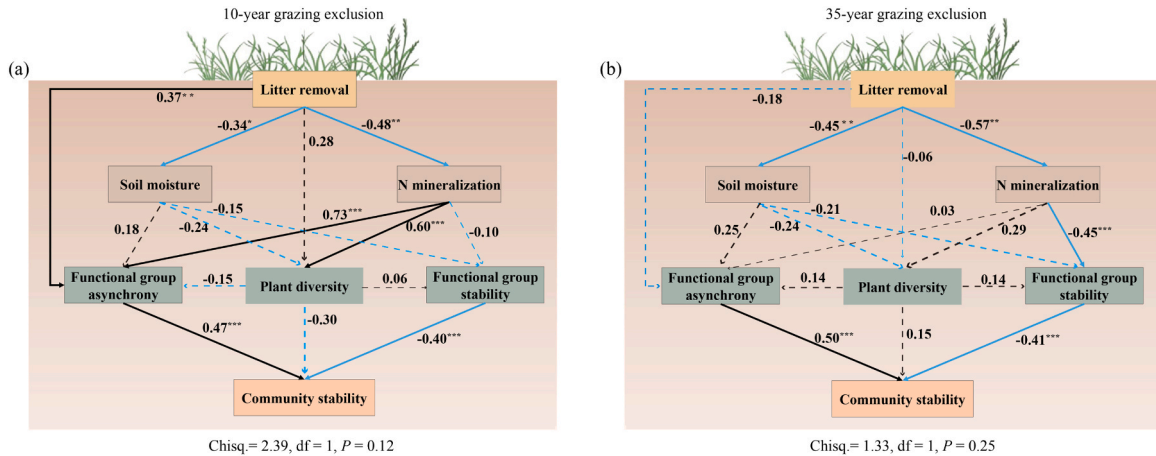
**Table 2**  
ANOVA results (*P* values) for the effect of litter removal (LR), slope aspect (SA), slope position (SP) and their interactions on the temporal stability of the biomass of the community and five functional groups (grass, forb, legume, sedge, and subshrub), functional group asynchrony (FGA) and stability (FGS) in the 10-year and 35-year grazing exclusion grasslands, respectively.

	Community stability	FGA	FGS	Grass stability	Forb stability	Legume stability	Sedge stability	Subshrub stability
<b>10-year grazing exclusion</b>								
LR	0.9995	0.9944	0.5547	0.4312	0.5976	<b>0.0799</b>	0.2293	0.5151
SA	0.8422	0.6710	0.7526	0.8935	0.8250	<b>0.0010</b>	<b>0.0013</b>	<b>0.0017</b>
SP	0.2977	0.2738	0.6207	0.7908	0.9113	0.6015	0.2558	<b>0.0028</b>
LR×SA	0.5116	0.4883	0.2678	0.6141	0.9703	0.4432	0.2929	0.5949
LR×SP	0.4817	0.2367	0.4421	0.4907	0.2455	0.1731	<b>0.0826</b>	0.1814
SA×SP	0.5489	<b>0.0933</b>	<b>0.0627</b>	0.1567	0.9158	0.8978	0.5069	<b>0.0129</b>
LR×SA×SP	0.2931	0.4877	0.6932	0.9901	0.4812	<b>0.0887</b>	0.5645	<b>0.0797</b>
<b>35-year grazing exclusion</b>								
LR	<b>0.0097</b>	<b>0.0922</b>	0.5991	0.5315	<b>0.0654</b>	0.4401	<b>0.0764</b>	0.9938
SA	0.1101	<b>0.0634</b>	0.9656	0.5766	0.8476	0.2165	0.3898	0.0445
SP	<b>0.0798</b>	0.1163	0.6447	0.9084	0.3473	0.2165	0.1070	0.6601
LR×SA	0.8245	0.4467	0.6683	0.9658	0.6432	0.2165	0.9037	0.4196
LR×SP	0.9049	0.5818	0.3157	0.7738	0.8782	0.2165	0.6076	0.5699
SA×SP	0.1658	<b>0.0637</b>	<b>0.0248</b>	0.2288	<b>0.0024</b>	<b>0.0039</b>	0.4145	0.2018
LR×SA×SP	0.7359	0.1299	0.3642	0.6974	<b>0.0411</b>	0.4401	0.9591	0.7144

Bold values indicate statistical significance. All the models used log<sub>10</sub> values for the response variables.



**Fig. 5.** Effects of litter removal on the functional group stability (a) and asynchrony (b) at lower and upper positions of north and south slopes in the 10-year (GE10y) and 35-year (GE35y) grazing exclusion grasslands. The values were calculated across 5 experimental years. Error bars are standard errors of the means (*n* = 3). Asterisks indicate statistical significance based on the paired *t*-test (\*, *P* < 0.1; \*\*, *P* < 0.05; \*\*\*, *P* < 0.01).



**Fig. 6.** Structural equation model describing litter removal effects on the temporal stability of community biomass. The structural equation model illustrates the direct and indirect effects of litter removal on the temporal stability of community biomass in 10-year (a, *R*<sup>2</sup>=0.33) and 35-year (b, *R*<sup>2</sup>=0.86) grazing exclusion grasslands. Solid black and blue lines represent significantly positive and negative paths, respectively (\*, *p* < 0.1, \*\*, *p* < 0.05, \*\*\*, *p* < 0.01). Gray dashed lines represent non-significant paths. Numbers along the arrows indicate standardized path coefficients.

removal would enhance plant growth (H2). Additionally, litter removal had a greater effect on plant community stability and species diversity in the 35-year grazing exclusion grasslands than in the 10-year grazing

exclusion grasslands, and these effects varied significantly with topographic conditions, supporting hypotheses of context-dependent effects of litter removal (H3 and H4).



#### 4.1. Effects on soil moisture and N cycling

The results indicated a significant reduction in soil moisture by litter removal in this fenced grassland, which could be ascribed to the enlarged soil evaporation and land surface runoff in this slope. Although these two processes were not measured in this study, previous studies have demonstrated that litter removal in the arid and semiarid grassland ecosystems increased soil evaporation and land surface runoff due to the loss of its buffering effect against environmental changes (Deutsch et al., 2010a,b; Ruprecht et al., 2010). Moreover, the effects of litter removal on these two processes might be exacerbated by the reduction in plant cover in the litter removal plots (Table S5). Therefore, litter removal may intensify soil moisture limitation in this semiarid grassland ecosystems.

Litter removal decreased the rates of net N mineralization in this study might be due to the reduced substrate availability for microbial decomposition and the enhanced soil moisture limitation (Holub et al., 2005; S  neca et al., 2020; Kong et al., 2022). Soil mineralization rates usually increase with increasing availability of substrate and moisture in the semiarid regions (Butcher et al., 2020; Morris et al., 2022). Litter removal not only decreases soil moisture (Ruprecht et al., 2010; Melendez et al., 2019), but also decreases availability of substrate to microorganisms through the reduction of organic matter inputs (Chen and Chen 2018; Zhang et al., 2023), and also decreases extracellular enzyme activities associated with the nitrogen cycle (Zuccarini et al., 2023). Additionally, the reduction in soil moisture also contributes to the lower accessibility of substrates (Patel et al., 2021; V  d  re et al., 2022).

#### 4.2. Effects on net productivity of grassland community

The 5-year litter removal experiment showed a reduction in above-ground net primary productivity by litter removal in both 10-year and 35-year grazing exclusion grasslands, primarily due to the exacerbated soil moisture and N limitation in this semiarid region (Chen et al., 2024a,b). This explanation was supported by our observation that litter removal induced the reduction in soil moisture and N mineralization, and the positive correlations between ANPP and soil moisture (Table S4). The results in this study further demonstrated that such reduction in ANPP was associated with asynchronous responses of different functional groups to litter removal. In this study, litter removal increased legume biomass in the 10-year and sedge and forb biomass in the 35-year grazing exclusion grassland, mainly due to the higher seed germination rates and seedling recruitment induced by greater dispersal and resource-use capacity in the plots without litter (Craine and Dybzinski, 2013; Zhang et al., 2019). Moreover, the increasing seed bank densities associated with these functional groups after litter removal also support the rapid dispersal, germination, and colonization into open ground (Coomes and Grubb, 2003; Quintana-Ascencio et al., 2019; Guittar et al., 2020), and thus indirectly increase biomass of these functional groups. Our study was consistent with a recent study in semiarid grasslands that litter removal shifted plant community composition from grass-dominated to forb-dominated due to inducing species-specific soil environments through drought (Chen et al., 2024a). Additionally, the effects of litter removal on biomass of sedge, legume and subshrub varied with aspects and positions of slope, likely because of the variations in environmental factors, i.e., temperature, moisture, and light resources, which had significant regulation on functional trait plasticity, resource-use strategies and dispersal ability (Roscher et al., 2015), and finally the interspecific competition (He et al., 2023; Wang et al., 2023).

#### 4.3. Effects on diversity of grassland community

In this study, litter removal significantly increased plant diversity (species richness and Shannon-Wiener index) in the 35-year grazing

exclusion, which could be ascribed to the elimination of the negative effects of litter accumulation in terms of chemical toxicity and mechanical barriers (Foster and Gross, 1998; Letts et al., 2015; Mazzoleni et al., 2015; Wainwright et al., 2017). The accumulation of litter usually increases toxicological substances (e.g., Phenolic compounds, Terpenoids, and Quinones) in soils and the chance of seed predation and physical interference, and decreases light availability and water-heat exchange, inhibiting seed germination and seedling establishment (Loydi et al., 2013; Warren et al., 2013; Letts et al., 2015; Eskelinen et al., 2022). The removal of litter thus promotes the emergence of new species and helps to increase the species evenness by eliminating the negative effects of litter accumulation. However, plant diversity was not affected by litter removal in the 10-year grazing exclusion grassland, possibly due to the relatively lower litter amount and depth compared with the 35-year grazing exclusion (Eckstein and Donath, 2005; Loydi et al., 2013). For example, an early meta-analysis reported the neutral to positive effects of litter presence on grassland community structure and composition when the litter amount and depth were smaller than 250 g m<sup>-2</sup> and 1.5 cm, respectively, but negative effects when the litter amount was greater than 500 g m<sup>-2</sup> (Loydi et al., 2013).

#### 4.4. Effects on stability of grassland community

The results showed that the temporal stability of plant community biomass was decreased by litter removal in the 35-year grazing exclusion, probably due to the increased variability of plant community productivity with environmental fluctuations in the litter removal plots (Parker et al., 2019; Thakur et al., 2021; Chen et al., 2024a). Plant litter can act as a long-term stable buffering material for grassland ecosystems to reduce the direct effects of environmental pulses on community productivity (or composition) (Sayer, 2006; Letts et al., 2015). Additionally, increased species richness might also have increased interspecific competition for resources (Douda et al., 2018), reducing communities' stability. The biodiversity-productivity/stability theory suggests a significant and positive relationship between community productivity stability and species diversity (Lambers et al., 2004; Mori et al., 2021). However, our results did not provide such a positive relationship. The possible explanation is that the gained species after litter removal were mainly annual forbs, which are rare species and account for only a small fraction of community biomass in this experimental site, and thus their contribution to biomass stability was relatively little (Parker et al., 2019; Su et al., 2022; Dee et al., 2023), making species diversity a non-significant predictor of stability. Additionally, litter removal induced a reduction in functional group asynchrony and grass stability could also reduce community biomass stability as predicted by the positive relationship among them. These results suggest that litter removal in the long-term grazing exclusion grassland helps to increase species diversity, but is detrimental to the maintenance of productivity and stability of dominant functional group.

#### 4.5. The importance of grazer exclusion times and slope aspects and positions in regulating effects of litter removal

The results further revealed that the effects of litter removal on soil and plant ecological processes varied with time of grazer exclusion. For the grazer excluded grasslands, the amount and depth of litter accumulation increase with the time of grazer exclusion, and can be a direct determinant of litter removal effects (Xiong and Nilsson, 1999; Eckstein and Donath, 2005; Loydi et al., 2013; Jessen et al., 2023). In this study, the average amount and depth of litter accumulation in the 35-year grazing exclusion grassland were 543 g m<sup>-2</sup> and 5.4 cm, which were significantly higher than those in the 10-year grazing exclusion grassland (160 g m<sup>-2</sup> and 1.9 cm) (Table S6). Whereas, the dense litter layer could become a hazardous medium for plant community structure and function when the amount and depth of litter accumulation exceed threshold value (ranging from 250 to 500 g m<sup>-2</sup> and 1.5–4 cm for the

amount and depth), and thus, resulted in increasing variations in these ecosystems in responding to the effects of litter removal (Ruprecht and Szabó, 2012; Loydi et al., 2013). Additionally, the productivity of plant community increased with the time of grazer exclusion, but its composition and function would be simplified and synchronized due to increasing the effect of plant dominance and the physical barrier of litter accumulation (Oba et al., 2001; Fernández-Lugo et al., 2013; Jing et al., 2014). These processes could intensify the rapid response of plant community to environmental change and human disturbance. (Klimkowska et al., 2009; Schultz et al., 2011; Zelikova et al., 2014). For example, Komatsu et al. (2019) reported that higher productivity ecosystems seem to be more sensitive to global changes, possibly due to greater resource availability and ecological niche space. Thus, litter removal might increase the chances of seed germination and seedling establishment and survival of rare species by improving access to resources. Besides these two explanations, soil nutrient and moisture contents incessantly increased with increasing grazer exclusion time (Qiu et al., 2013), which provided the basis for the early growth and spread of plant after litter removal (Zhang et al., 2022). The litter removal could also increase the need of light and temperature in the bottomland plants, helping to further improve seed germination and survival. Therefore, the effects of litter removal could be greatly pronounced in the 35-year grazing exclusion grassland, but not in the 10-year grazing exclusion grassland.

Topographic factors (mainly slope aspects and positions) could also drive the effects of litter removal on soils and plants by regulating soil and land surface processes. Topography directly determines the intensity of solar radiation and surface evaporation and indirectly regulates soil microclimate changes such as moisture and temperature, thereby, leading to changes in vegetation traits (such as biomass, richness, and cover) (Frank et al., 2011; Sanaei et al., 2019). Generally, lower evaporation and higher moisture conditions in the north-facing slope were profitable for resource-acquisitive species, while opposite environmental conditions in the south-facing slope could support resource-conservative species (Henneron et al., 2020). These trade-offs between plant economic strategies were also observed in different slope aspects and positions in our study. Importantly, plant community structure and composition (including species richness and abundance, plant dominance and litter accumulation), shaped by the availability of resources between topographic factors, could exhibit different response scales under anthropogenic disturbance (Osem et al., 2002; Cheesman et al., 2018). Broderick et al. (2022) indicated that differences in soil moisture, nutrients and texture had a greater effect on plant biomass, community composition and soil respiration in the lowlands than that in the uplands. Our study also showed that the effect of litter removal on soil and plant ecological processes significantly varied with slope aspects and positions, consistent with the results from previous investigations conducted in similar areas as the present study (Liu et al., 2018; Liu et al., 2023). Therefore, topographic factors should be fully considered in litter management practices of grazing exclusion grassland, especially in semi-arid grassland ecosystems with variable topography.

## 5. Conclusion

In this study, we examined how the effects of litter removal on soils and plants community vary with duration of grazing exclusion and topographic conditions in semiarid grazing exclusion grassland ecosystems. We provide direct experimental evidence that, in semiarid grazing exclusion grasslands, litter removal increases species diversity but may be detrimental to the maintenance of the community productivity and stability. These ecological processes are significantly dependent on topographic conditions. We also find that N mineralization can act as a key mediator to regulate the effects of litter removal on community stability by altering the ecological effects of functional groups. Given the important regulatory role of litter management on the restored grasslands and their variations in time and space, such interactions should be

fully considered when predicting the future effects of climate change and human activities on grassland ecosystems, and that the N turnover should also be incorporated when predicting these ecological processes.

In this study, we focused on the effects of litter removal on soils and plant communities. Given that such effects are closely related to changes in habitat environments, soil microbial community composition and nutrient use efficiency, allelopathic substances, linking such changes with our results would provide a comprehensive understanding regarding the effects of litter removal, and thus should be further examined.

## CRediT authorship contribution statement

**Wei Li:** Writing – review & editing, Methodology, Formal analysis. **Mingan Shao:** Writing – review & editing, Methodology, Conceptualization. **Xiang Wang:** Writing – review & editing, Methodology, Formal analysis. **Weibo Kong:** Writing – review & editing, Visualization, Investigation, Funding acquisition. **Xinpeng Tong:** Visualization, Investigation, Data curation. **Xiaorong Wei:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Lingcao Hou:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Jian Liu:** Writing – review & editing, Investigation, Data curation, Conceptualization.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109806.

## Data availability

Data will be made available on request.

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