



Species asynchrony as the key driver of reduced temporal stability in typical grassland community productivity

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Abstract

Livestock grazing is a key factor influencing structure, functioning and stability of grassland ecosystems. However, the effects of grazing intensity on the temporal stability of plant community aboveground net primary productivity (ANPP) and the driving mechanisms remain poorly understood in typical steppe ecosystems. In a 6-year experimental study, we investigated how varying grazing intensities (light, moderate, heavy, and no grazing) affect the temporal stability of ANPP in plant communities and functional groups. Our findings revealed that both plant community ANPP and species richness increased significantly under all grazing intensities. Moderate and heavy grazing also led to a significant reduction in the temporal stability of ANPP of community and dominant species. Structural equation modelling further identified species asynchrony as the primary driver of community productivity stability across different grazing intensities in semi-arid grasslands.

Introduction

Grasslands, covering 40% of Earth's terrestrial surface, are critical for biodiversity and livestock production (Wen *et al.* 2011). However, they have suffered significant biodiversity loss, ecosystem degradation, and reduced stability, largely due to livestock grazing (White *et al.* 2000; Shan *et al.* 2011). Grazing alters plant community structure, diversity, and productivity, thereby impacting ecosystem stability (Filazzola *et al.* 2020; Li *et al.* 2022; Sun *et al.* 2023). Maintaining grassland stability is crucial for sustaining ecosystem services, necessitating a better understanding of how grazing influences these systems.

Temporal stability, defined as the consistency of aboveground biomass over time, is vital for sustaining multiple ecosystem functions (Tilman and Clark 2014; White *et al.* 2021). It is influenced by species diversity (Hautier *et al.* 2015), species asynchrony (Hautier *et al.* 2014), and the stability of dominant species (Hillebrand *et al.* 2008). Species diversity enhances stability by promoting species asynchrony, where different species respond differently to environmental variability, buffering productivity fluctuations (Wang and Loreau 2016; Xu *et al.* 2021). Grazing, a widespread land-use practice, impacts grassland stability by altering species richness and asynchrony (Blüthgen *et al.* 2016). Moderate grazing may enhance stability, whereas heavy grazing often reduces it by decreasing species richness (Li *et al.* 2018; Ren *et al.* 2018).

The temperate grasslands of Inner Mongolia, including meadow steppe, typical steppe, and desert steppe, have historically supported traditional grazing due to their unique ecological characteristics (Zhu *et al.* 2023). However, these grasslands have degraded in recent decades due to overgrazing, human activities, and climate change (Bai *et al.* 2015). Overgrazing has led to severe ecosystem degradation in the semi-arid steppe. Understanding how grazing intensity affects productivity stability is critical for developing sustainable grazing management strategies in these regions. In this study, we conducted a six-year field experiment in the Inner Mongolian grasslands to examine how grazing intensity influences productivity stability. Specifically, we addressed two key questions: (1) How do different grazing intensities affect the temporal stability of aboveground net primary productivity (ANPP)? (2) What are the key drivers of temporal stability under different grazing intensities? Our findings aim to clarify the mechanisms regulating productivity stability in semi-arid grasslands and provide a scientific basis for sustainable grazing management in temperate steppes.

Methods

Study site and experimental design

The study was conducted at the Grassland Ecosystem Research Station of Inner Mongolia University, 60 km northeast of Xilinhot city, Inner Mongolia, China (116°31'18" - 116°32'28"E, 44°15'24" - 44°15'41"N, 1146 m a.s.l.). In 2016, a grazing experiment was initiated in a level grassland area, with 16 experimental paddocks (0.25 hm² each). Four grazing treatments—nil grazing (NG), light grazing (LG), moderate grazing (MG), and heavy grazing (HG)—were randomly assigned, each replicated in four blocks. Grazing intensities were achieved by introducing 0, 3, 6, or 9 sheep to the respective paddocks, using a rotational grazing system. Sheep were introduced in June, July, and August, and after each grazing event, they were removed, leaving a residual grass height of about 6 cm in MG paddocks (approximately 60 g dry matter/m²). The experiment ran from 2017 to 2022 to assess the long-term effects of grazing intensity on grassland ecosystem structure and function.

Sampling and measurements

Three moving cages of 1.2 m in length, 1.2 m in width, and 1.0 m height were randomly placed in each paddock to protect the grassland from grazing before each animal grazing rotation in June, July, or August. Plant aboveground biomass (AGB) was determined by harvesting (clipping) plant materials species by species from the ground surface at the end of each grazing rotation, both inside and outside each moving cage, using the quadrat of 1 m × 1 m, and then these cages were moved to other places for excluding animal grazing in next rotation. The harvested plant biomass was oven-dried at 65°C for 48 h and weighed.

(1) Aboveground Net Primary Productivity (ANPP): ANPP was determined as the total aboveground biomass produced by plants during the growing season, which included both livestock feed intake during the grazing rotations and the residual plant biomass remaining at the end of the final grazing rotation. The total ANPP for each paddock was measured at the end of each grazing season.

(2) The daily forage intake of grazing sheep (DI): in each grazing rotation was determined as the difference between plant AGB inside (AGB_i) and outside (AGB_g) of the moving cages after each grazing rotation:

$$DI = (AGB_i - AGB_g) \times 2500 \text{ m}^2 / N_L / D_g$$

Where DI was in g·head⁻¹·d⁻¹; AGB_i and AGB_g were in g·m⁻²; N_L is the number of sheep in grazing, and D_g is the number of grazing days.

(3) Species richness in each paddock was defined as the total number of species detected in the three quadrats.

(4) The temporal stability of ANPP was defined for each paddock as μ/σ (i.e., the inverse of CV), where μ is the temporal mean of community-level ANPP from the paddock over 6 years period and σ is the temporal standard deviation over the same period. Temporal stability is unitless.

(5) The species asynchrony was quantified using the community-wide asynchrony index by species biomass (Loreau and de Mazancourt 2013a).

$$1-\phi=1-\frac{\sigma^2}{\left(\sum_{i=1}^S\sigma_i\right)^2}$$

Where ϕ is species synchrony, and σ^2 is the temporal variance of community aboveground biomass of species i in a community with S species.

Statistical analysis

In this study, we used the Shapiro-Wilk normality test for the normality of variance for each data set. Repeated-measures ANOVAs were performed to test the effects of grazing treatments on ANPP, species richness, stability and asynchrony. One-way ANOVAs with Duncan’s multiple range tests were used to determine the significance of difference among the grazing treatments. Structure equation modeling (SEM) was used to estimate the strength of direct and indirect relationships between grazing treatments, species asynchrony, species richness, functional groups stability and community temporal stability.

Results

Effect of grazing on plant community ANPP

Compared to the ANPP of total and function groups in the ungrazed grassland, the total ANPP and the ANPP of subordinate species significantly increased under increasing grazing intensity ($P < 0.05$, Fig. 1a, c). The ANPP of dominant species significantly increased under LG and MG, but not under HG ($P < 0.05$, Fig. 1b).

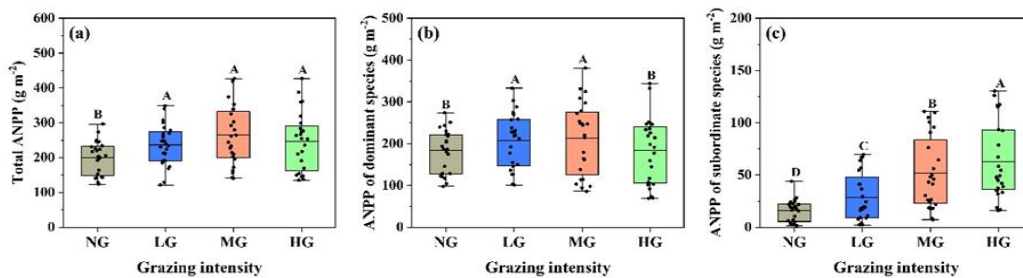


Fig. 1 Effects of different grazing intensity on ANPP of total (a) and function groups (b, c) in a typical steppe grassland. Different uppercase letters indicate significant differences between grazing treatments ($P < 0.05$).

Effects of grazing on temporal stability of ANPP and species asynchrony

Compared with no grazing, the stability of ANPP of community and dominant species significantly decreased under the MG and HG ($P < 0.05$, Fig. 2a, b), and the stability of ANPP of subordinate species significantly increased under moderate grazing ($P < 0.05$, Fig. 2c). Compared with no grazing, the species asynchrony significantly decreased under HG, but the species richness significantly increased under MG and HG ($P < 0.05$, Fig. 2d, e).

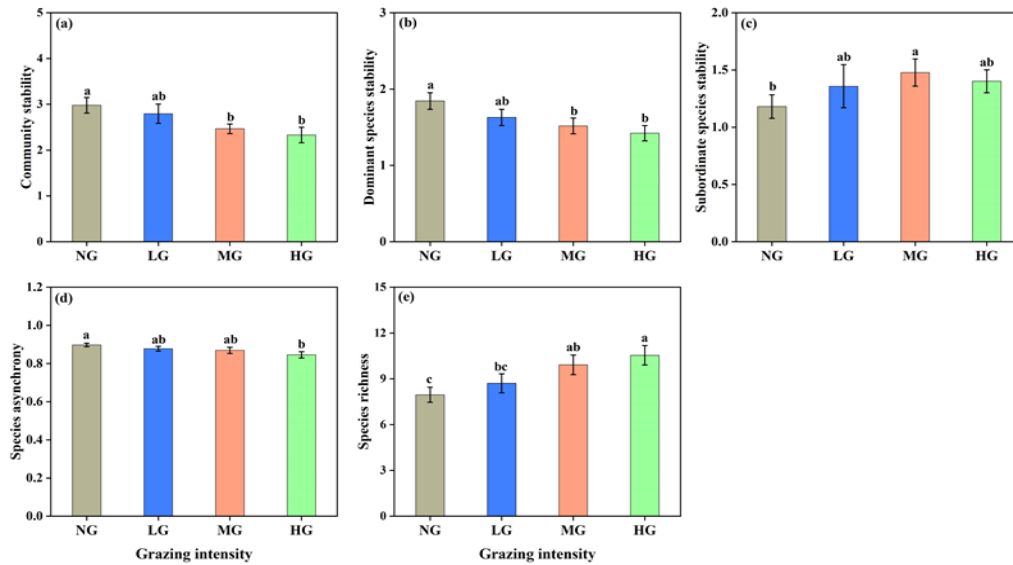


Fig. 2 Effects of different grazing intensity on productivity stability, species asynchrony and species richness in a semi-arid steppe.

Pathways through which grazing intensity influenced community stability

The SEM analysis demonstrated that grazing intensity indirectly reduces temporal stability of community ANPP by reducing dominant species stability and species asynchrony. Additionally, grazing intensity also indirectly reduced community temporal stability through its positive effects on species richness and ANPP. Species asynchrony was the primary factor influencing community temporal stability.

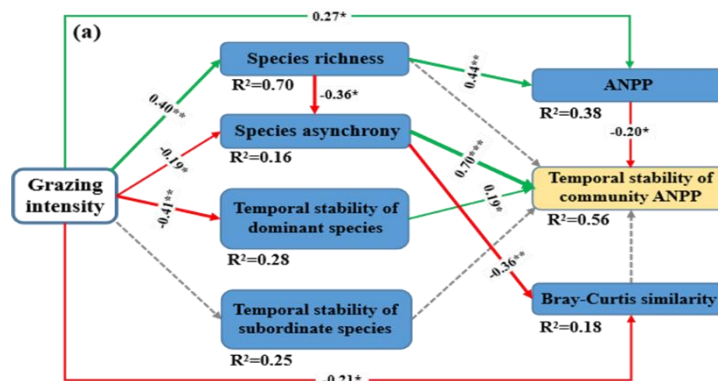


Fig. 3 Structural equation modeling (SEM) depicting the direct and indirect effects of different grazing management on productivity stability in a semi-arid steppe. Red and green arrows indicate negative and positive relationships ($P < 0.05$) respectively, with path coefficients shown on the paths, and dashed gray lines indicating non-significant relationships. Arrow width indicates the strength of the relationship.

Discussion

Our results indicate that grazing intensity increases community ANPP compared to no grazing, primarily due to higher ANPP of subordinate species and, to a lesser extent, dominant species. Previous studies suggest that moderate grazing enhances plant productivity through compensatory growth, while heavy grazing generally reduces productivity (Hilbert *et al.* 1981; Mcnaughton 1983). In our study, however, grassland productivity still increased under heavy grazing, likely for two reasons. First, the grazing intensity may not have been sufficient to

cause significant damage, allowing compensatory growth to persist. Second, increased trampling and grazing pressure reduced biomass of dominant species, potentially altering competitive interactions (Sternberg *et al.* 2000).

In alignment with our expectation that livestock grazing can change productivity stability in temperate grassland, our results show that grazing intensity decreased community and dominant species productivity stability. This is consistent with other studies that have shown that community productivity stability decreases with increasing grazing intensity (Qin *et al.* 2019; Han *et al.* 2023). Summer is a season of vigorous plant growth, and grazing activities can alter the competition for resources (i.e., light and nutrients) among vegetation species (Eskelinen *et al.* 2022), resulting in dynamic changes in the plant community and decreased productivity stability. Grazing reduces the dominant species stability, largely owing to selective feeding by livestock. In general, herbivores prioritize tall and palatable plants (Lv *et al.* 2020), dominant species are highly favored by domestic animals owing to their generally larger size and high proportional abundance (Mariotte *et al.* 2013), whereas compensatory growth after ingestion also induces ANPP instability in the community (Zhu *et al.* 2021).

Species asynchrony, arising from differential species responses to environmental conditions, is a common feature of communities (Muraina *et al.* 2021). Our results show that heavy grazing reduces species asynchrony. Under heavy grazing, the relative biomass of annuals and biennials increases, while dominant species like *Leymus chinensis* and *Stipa grandis* decrease, leading to less asynchronous population dynamics. Studies have shown that increased species asynchrony enhances community productivity stability (Tilman and Downing 1994; Loreau and de Mazancourt 2013b; Zhou *et al.* 2019). In line with this, our findings suggest that grazing reduces ecosystem stability mainly by decreasing species asynchrony, rather than by affecting species richness. This negative impact on species asynchrony undermines its stabilizing effect, causing a decline in community stability with increasing grazing intensity (Liang *et al.* 2021). Species asynchrony, but not species diversity, are the main driver influencing community productivity stability in semi-arid grassland grazing ecosystems.

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References

- Bai W, Fang Y, Zhou M, Xie T, Li L, Zhang W (2015) Heavily intensified grazing reduces root production in an Inner Mongolia temperate steppe. *Agriculture, Ecosystems & Environment* 200, 143-150.
- Blüthgen N, Simons NK, Jung K, Prati D, Renner SC, Boch S, Fischer M, Hölzel N, Klaus VH, Kleinebecker T, Tschapka M, Weisser WW, Gossner MM (2016) Land use imperils plant and animal community stability through changes in asynchrony rather than diversity. *Nature Communications* 7(1), 10697.
- Eskelinen A, Harpole WS, Jessen M-T, Virtanen R, Hautier Y (2022) Light competition drives herbivore and nutrient effects on plant diversity. *Nature* 611(7935), 301-305.
- Filazzola A, Brown C, Dettlaff MA, Batbaatar A, Grenke J, Bao T, Peetoom Heida I, Cahill Jr JF (2020) The effects of livestock grazing on biodiversity are multi-trophic: a meta-analysis. *Ecology Letters* 23(8), 1298-1309.
- Han Y, Wu Y, Cui J, Li H, Li H, Zhang J, Miao B, Wang L, Li Z, Liang C (2023) Temporal Stability of Grazed Grassland Ecosystems Alters Response to Climate Variability, While Resistance Stability Remains Unchanged. *Agronomy* 13(8), 2030.
- Hautier Y, Seabloom EW, Borer ET, Adler PB, Harpole WS, Hillebrand H, Lind EM, MacDougall AS, Stevens CJ, Bakker JD, Buckley YM, Chu C, Collins SL, Daleo P, Damschen EI, Davies KF, Fay PA, Firn J, Gruner DS, Jin VL, Klein JA, Knops JMH, La Pierre KJ, Li W, McCulley RL, Melbourne BA, Moore JL, O'Halloran LR, Prober SM, Risch AC, Sankaran M, Schuetz M, Hector A (2014) Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature* 508(7497), 521-525.
- Hautier Y, Tilman D, Isbell F, Seabloom E, Borer E, Reich P (2015) Plant ecology. Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science (New York, N.Y.)* 348, 336-340.
- Hilbert DW, Swift DM, Detling JK, Dyer MI (1981) Relative growth rates and the grazing optimization hypothesis. *Oecologia* 51(1), 14-18.

- Hillebrand H, Bennett DM, Cadotte MW (2008) Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* **89**(6), 1510-1520.
- Stability under climate change and grazing in grasslands: current status and future prospects. *Current Opinion in Environmental Sustainability* **33**, 124-135.
- Li Y, Shi C, Zhang T, Wang H, Yang Z, Tang S, Li FY (2022) Summer grazing by three livestock species at moderate intensity enhances primary productivity and drives community divergence in a semi-arid steppe. *Applied Vegetation Science* **25**(3), e12683.
- Liang M, Liang C, Hautier Y, Wilcox KR, Wang S (2021) Grazing-induced biodiversity loss impairs grassland ecosystem stability at multiple scales. *Ecology Letters* **24**(10), 2054-2064.
- Loreau M, de Mazancourt C (2013a) Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecology Letters* **16**, 106-115.
- Loreau M, de Mazancourt C (2013b) Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecology Letters* **16**(s1), 106-115.
- Lv S, Yan B, Wang Z, Wang Z, Song X, Zhao M, Kang S, Willms W, Han G (2020) Dominant species' dominant role and spatial stability are enhanced with increasing stocking rate. *Science of The Total Environment* **730**, 138900.
- Mariotte P, Meunier C, Johnson D, Thébault A, Spiegelberger T, Buttler A (2013) Arbuscular mycorrhizal fungi reduce the differences in competitiveness between dominant and subordinate plant species. *Mycorrhiza* **23**(4), 267-277.
- Mcnaughton SJ (1983) Compensatory Plant Growth as a Response to Herbivory. *Oikos* **40**(3), 329-336.
- Muraina TO, Xu C, Yu Q, Yang Y, Jing M, Jia X, Jaman MS, Dam Q, Knapp AK, Collins SL, Luo Y, Luo W, Zuo X, Xin X, Han X, Smith MD (2021) Species asynchrony stabilises productivity under extreme drought across Northern China grasslands. *Journal of Ecology* **109**(4), 1665-1675.
- Qin J, Ren H, Han G, Zhang J, Browning D, Willms W, Yang D (2019) Grazing reduces the temporal stability of temperate grasslands in northern China. *Flora* **259**, 151450.
- Ren H, Taube F, Stein C, Zhang Y, Bai Y, Hu S (2018) Grazing weakens temporal stabilizing effects of diversity in the Eurasian steppe. *Ecology and Evolution* **8**(1), 231-241.
- Shan Y, Chen D, Guan X, Zheng S, Chen H, Wang M, Bai Y (2011) Seasonally dependent impacts of grazing on soil nitrogen mineralization and linkages to ecosystem functioning in Inner Mongolia grassland. *Soil Biology and Biochemistry* **43**(9), 1943-1954.
- Sternberg M, Gutman M, Perevolotsky A, Ungar ED, Kigel J (2000) Vegetation response to grazing management in a Mediterranean herbaceous community: a functional group approach. *Journal of Applied Ecology* **37**(2), 224-237.
- Sun S, Zhao S, Liu X, Lv P, Liang M, Li Y, Hu Y, Zuo X (2023) Grazing impairs ecosystem stability through changes in species asynchrony and stability rather than diversity across spatial scales in desert steppe, Northern China. *Agriculture, Ecosystems & Environment* **346**, 108343.
- Tilman D, Clark M (2014) Global diets link environmental sustainability and human health. *Nature* **515**(7528), 518-522.
- Tilman D, Downing JA (1994) Biodiversity and stability in grasslands. *Nature* **367**(6461), 363-365.
- Wang S, Loreau M (2016) Biodiversity and ecosystem stability across scales in metacommunities. *Ecology letters* **19**(5), 510-518.
- Wen L, Liu S, Zhang X, Lassoie J, Yi S, Li X, Li J, Li Y (2011) Vulnerability of Worldwide Pastoralism to Global Changes and Interdisciplinary Strategies for Sustainable Pastoralism. *Ecology and society* **16**.
- White HJ, Caplat P, Emmerson MC, Yearsley JM (2021) Predicting future stability of ecosystem functioning under climate change. *Agriculture, Ecosystems & Environment* **320**, 107600.
- White TA, Campbell BD, Kemp PD, Hunt CL (2000) Sensitivity of three grassland communities to simulated extreme temperature and rainfall events. *Global Change Biology* **6**(6), 671-684.
- Xu Q, Yang X, Yan Y, Wang S, Loreau M, Jiang L (2021) Consistently positive effect of species diversity on ecosystem, but not population, temporal stability. *Ecology Letters* **24**(10), 2256-2266.
- Zhou B, Li S, Li F, Dong S, Ma F, Zhu S, Zhou H, Stufkens P (2019) Plant functional groups asynchrony keep the community biomass stability along with the climate change- a 20-year experimental observation of alpine meadow in eastern Qinghai-Tibet Plateau. *Agriculture, Ecosystems & Environment* **282**(3), 49-57.
- Zhu N, Yan Y, Bai K, Zhang J, Wang C, Wang X, Xu D, Liu J, Xin X, Chen J (2023) Conversion of croplands to shrublands does not improve soil organic carbon and nitrogen but reduces soil phosphorus in a temperate grassland of northern China. *Geoderma* **432**, e116407.
- Zhu Y, Delgado-Baquerizo M, Shan D, Yang X, Eldridge DJ (2021) Grazing impacts on ecosystem functions exceed those from mowing. *Plant and Soil* **464**(1), 579-591.