

Grazing-Mediated State Transition in Grassland Plant Communities: A Mean-Field Analysis

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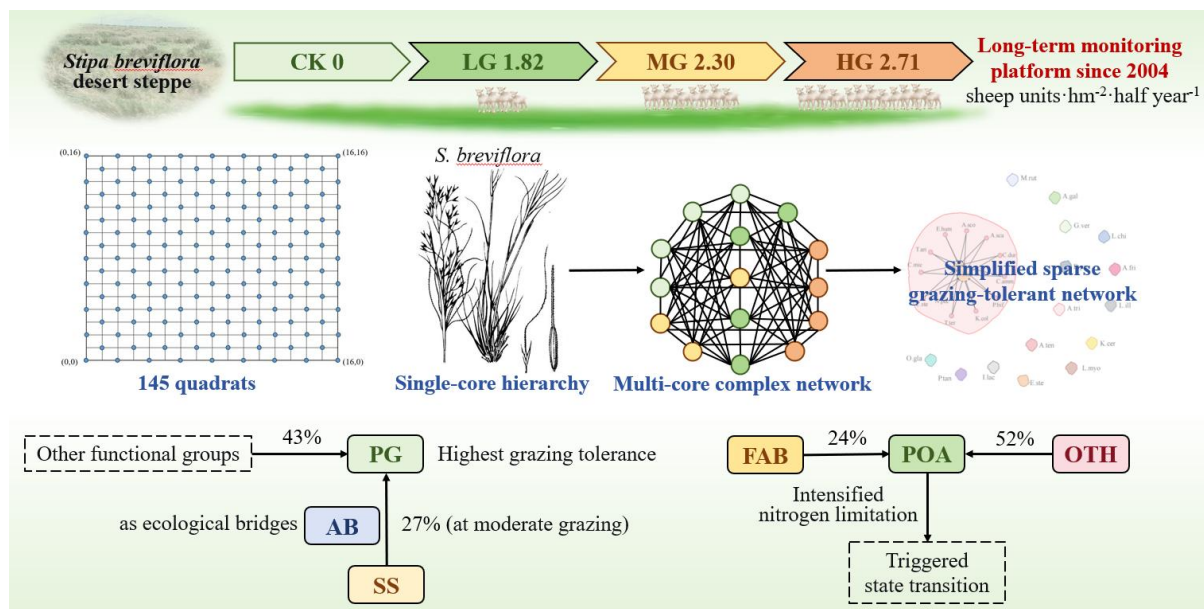
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Graphical Abstract



Abstract

Grazing-induced state transitions in desert steppe remain poorly understood, particularly regarding changes in interspecific interactions and network dynamics. Using a long-term grazing platform established in 2004 in a *Stipa breviflora* desert steppe of Inner Mongolia, we examined four stocking rates (0, 1.82, 2.30, and 2.71 sheep units·hm⁻²·half year⁻¹) across 145 quadrats. Mean occurrence probability and transition probability models quantified species-, functional group-, and family-level transitions. Increasing stocking rate shifted the species network from a single-core structure dominated by *S. breviflora* to a multi-core network, followed by simplification into a sparse network dominated by grazing-tolerant species. Perennial grasses showed the highest grazing tolerance, receiving up to 43% of transitions from other functional groups. Shrubs and semi-shrubs supported system stability by transferring 27% of transition probability to perennial grasses under moderate grazing, while annual-biennials acted as ecological bridges. Poaceae increasingly received transitions from other families (up to 52%), whereas Fabaceae-to-Poaceae transfer (24%) intensified nitrogen limitation and promoted state transition. Stocking rates ≤ 1.82 sheep units·hm⁻²·half year⁻¹ maintained multistability.

Transition-probability-based monitoring effectively detects grazing-induced state shifts and supports adaptive desert-steppe management.

Key words: Desert steppe; stocking rate; state transition; plant functional group

1.Introduction

Ecosystem restoration in semi-arid regions is often hampered by difficulties in identifying threshold levels at which vegetation undergoes abrupt transitions and in devising measures to preserve resilience (Scheffer et al., 2003; Suding and Hobbs, 2009). Within this context, the desert steppe across Eurasia serves as a valuable case study, given its long-standing recognition for both ecological fragility and inherent stability (Li et al., 2018; Hilker et al., 2014). Grazing pressure, intensified by concurrent global warming and human activities, is widely viewed as a predominant force driving the directional change of herbaceous communities (Milchunas et al., 1988; Eldridge et al., 2016). Nevertheless, important uncertainties persist concerning the response of *Stipa breviflora* desert steppe—a representative temperate grassland type—to differential grazing intensities (Wang et al., 2020; Wang et al., 2025). Although earlier work has shown that excessive grazing weakens the prominence of keystone taxa and restructures functional assemblages (Huang et al., 2018), the mechanistic basis for reconfigurations of interspecific interaction networks along grazing-intensity gradients remains poorly understood (Bestelmeyer et al., 2011; Tylianakis et al., 2008; Pilosof et al., 2017).

Grazing disturbance drives the trajectory of community succession by altering resource allocation patterns (Adler et al., 2001; Liu et al., 2022). Classical theory posits that the divergence of plant functional traits is a key strategy for communities to adapt to grazing pressure (Díaz et al., 2007)—exemplified by the clonal growth capacity of grasses (Ma et al. 2020) and the nitrogen-fixing compensatory effect of legumes (Cech et al., 2010). However, whether the state transition pathways at the functional group level are predictable remains debated (Lavorel et al., 2015; Suding et al., 2008). Recent studies suggest that functional redundancy among shrubs and sub-shrubs may buffer the negative impacts of moderate grazing (Wu et al., 2020; Le Bagousse-Pinguet et al., 2012), yet this hypothesis lacks validation through long-term controlled experiments. More notably, the role of annual and biennial plants as "ecological bridges" along disturbance gradients (Pakeman et al., 2011; Ning et al., 2022), as well as the mechanisms balancing their resource competition with perennial species, remain poorly understood (Yang et al., 2019).

Traditional measures of biodiversity frequently fail to capture the temporal dynamics that underpin species interactions (Ibanez et al., 2018). In contrast, transition probability models based on Markov chains have emerged as a promising tool for elucidating community assembly pathways (Hill et al., 2020). Although these approaches have proven useful in tracking species turnover during forest succession (Chisholm et al., 2014), their adoption in grazing-affected ecosystems remains largely tentative (Fagan et al., 2021; Nelis and Wootton, 2010). A central unresolved issue in theoretical ecology is whether universal rules govern the hierarchical integration of state-transition matrices when these are examined across multiple taxonomic levels—i.e., species, functional groups, and families (Gotelli et al., 2022). Addressing this question, alongside the quantitative characterisation of vegetation state shifts, calls for substantial methodological innovation (Suding et al., 2004).

While stocking rate regulation has been widely adopted in grassland management (Bai et al., 2004; Jablonski et al., 2024), its ecological implications require deeper exploration: First, whether the “hub” function of core species in network restructuring undergoes qualitative shifts with increasing grazing intensity remains unclear (Saiz et al., 2021); second, it is uncertain if the stability of functional groups serves as a systemic “firewall” against grazing disturbance (Soliveres et al., 2016; Hooper et al., 2005); lastly, how spatiotemporal heterogeneity in species occurrence probability influences state transition thresholds demands further

investigation (Kefi et al., 2016). Addressing these questions will advance the paradigm of sustainable management in desert steppes from experience-based practices to mechanism-driven strategies (Osterheld et al., 2021). Through long-term field experiments, this study aims to provide empirical evidence for these unresolved scientific puzzles.

2. Materials and methods

2.1 Study site

The field experiment was carried out at the comprehensive demonstration base of the Inner Mongolia Academy of Agriculture and Animal Husbandry Sciences, which lies in Siziwang Banner (at 41°46'43.6" N, 111°53'41.7" E, with an elevation of 1450 m; Fig. 1). The area falls within the mid-temperate continental monsoon climatic belt. Over the course of the study, the long-term annual mean temperature stood at 3.7°C, with January recording the lowest values and July the highest. The yearly accumulated temperature above 10°C ranged between 2200 and 2500°C, while mean annual precipitation was roughly 240 mm, the bulk of which occurs from June to September (Zhang et al., 2023). In terms of vegetation, the site is representative of *Stipa breviflora* desert steppe, where *S. breviflora* serves as the foundational species and *Artemisia frigida* together with *Cleistogenes songorica* are the dominant accompanying taxa. The soils are classified as Kastanozems Luvic (commonly termed light chestnut soil) under the FAO system.

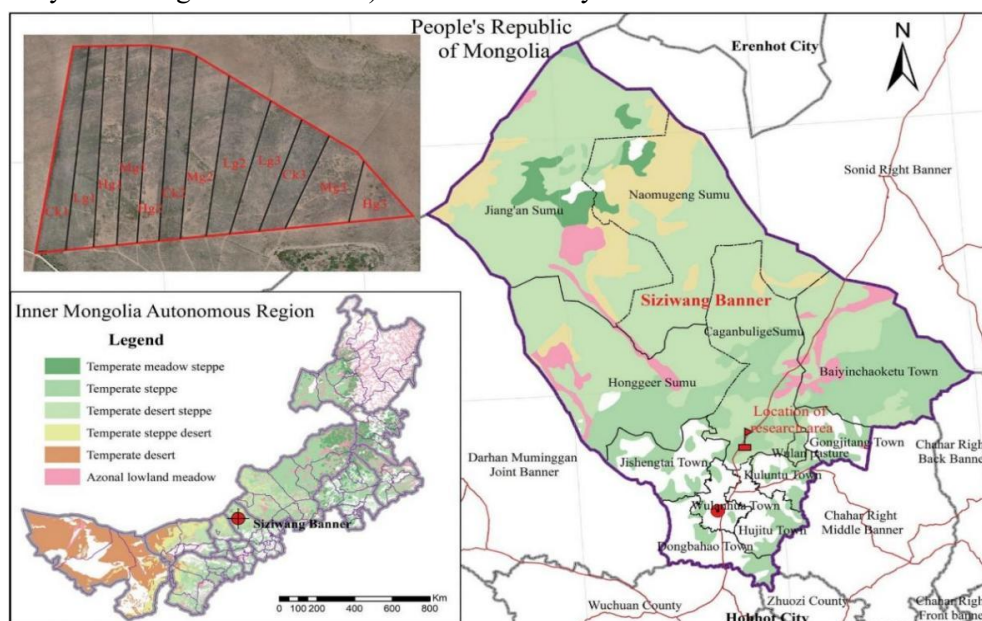


Fig. 1. Location of the study area in Inner Mongolia, China and layout of the experiment plots.

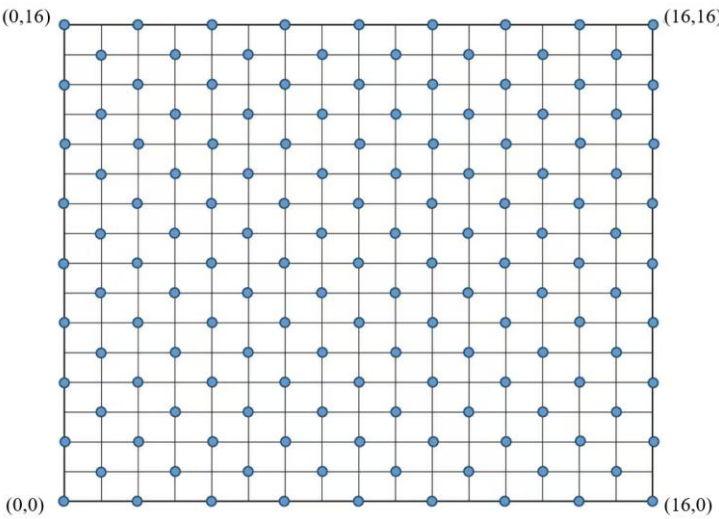
2.2 Experimental design

The grazing experiment followed a completely randomized block design. Within the study area, separate paddocks were fenced off to represent individual treatment units, and these were grouped into three replicate blocks. The experiment has been running since 2004, with each block subjected to four distinct grazing regimes: ungrazed control (CK), light (LG), moderate (MG), and heavy (HG) stocking. Between May and October each year, the corresponding plots received 0, 4, 8, and 12 two-year-old castrated Mongolian rams, respectively. In terms of stocking density, these treatments translated to 0, 1.82, 2.30, and 2.71 sheep units per hectare per half-year. The chosen intensities were grounded in the recommended carrying capacities for *Stipa breviflora* desert steppe established by Wei and colleagues (2000, 2006). On each grazing day, the animals were moved

100 into the designated plots at 6:00 a.m. and brought back to holding pens at 6:00 p.m., with no access to the plots
101 outside this daily window.

102
103 **2.3 Sampling design**

104 For the sampling campaign, a single representative plot measuring 40 m × 40 m was chosen from among the
105 three replicate blocks of each grazing treatment (CK, LG, MG, and HG), with all selected plots sharing
106 comparable topographic features and species composition. The plot's south-western corner served as the spatial
107 reference origin (0 m, 0 m), and the opposite extreme was set at (40 m, 40 m). Along the south–north axis, 17
108 parallel transects were laid out, consecutively numbered from 0 through 16. On those transects bearing even
109 numbers (including 0), the first sampling position was placed at the longitudinal coordinate of 0 m; on
110 odd-numbered transects, by contrast, the starting point was offset to 2.5 m. This arrangement generated a total
111 of 145 sampling locations across the plot (Fig. 2). At every location, we deployed a 0.5 m × 0.5 m quadrat to
112 record three population attributes: plant height (in cm), percentage cover, and individual density (expressed as
113 number per 0.25 m²). The resulting occurrence data for each species, along with their assigned functional groups
114 and familial affiliations under the various stocking regimes, are compiled in Table 1.



115
116 **Fig. 2.** Distribution of mechanical sampling points in the representative repeating treatment.

117
118 **Table 1** Occurrence and classification of plant populations in each treatment area

Species	Abbreviation	Functional groups	Families	CK	LG	MG	HG
<i>Stipa breviflora</i>	S. bre	PG	POA	395	431	435	435
<i>Cleistogenes songorica</i>	C. son	PG	POA	395	356	405	409
<i>Artemisia frigida</i>	A. fri	SS	AST	33	10	—	—
<i>Neopallasia pectinata</i>	N. pec	AB	AST	4	7	2	—
<i>Convolvulus ammannii</i>	C. amm	PF	OTH	173	179	142	165
<i>Allium tenuissimum</i>	A. ten	PF	OTH	4	1	—	—
<i>Artemisia scoparia</i>	A. sco	AB	AST	—	—	1	—
<i>Kali collinum</i>	K. col	AB	CHE	105	19	2	47
<i>Bassia prostrata</i>	B. pro	SS	CHE	68	12	—	—
<i>Caragana stenophylla</i>	C. ste	SS	FAB	71	12	29	21
<i>Oxybasis glauca</i>	O. gla	AB	CHE	55	112	—	—
<i>Teloxys aristata</i>	T. ari	AB	CHE	194	360	407	233

<i>Caragana microphylla</i>	C. mic	SS	FAB	12	5	9	2
<i>Carex duriuscula</i>	C. dur	PF	OTH	15	11	4	—
<i>Astragalus galactites</i>	A. gal	PF	FAB	1	—	—	—
<i>Lagochilus ilicifolius</i>	L. ili	PF	OTH	5	2	—	—
<i>Leymus chinensis</i>	L. chi	PG	POA	2	34	—	—
<i>Krascheninnikovia ceratoides</i>	K. cer	SS	CHE	25	4	—	—
<i>Asparagus trichophyllus</i>	A. tri	PF	OTH	—	—	—	1
<i>Potentilla tanacetifolia</i>	P. tan	PF	OTH	5	7	—	—
<i>Potentilla bifurca</i>	P. bif	PF	OTH	4	67	1	3
<i>Euphorbia humifusa</i>	E. hum	AB	OTH	2	21	100	84
<i>Lappula myosotis</i>	L. myo	AB	OTH	1	1	—	—
<i>Astragalus scaberrimus</i>	A. sca	PF	FAB	—	5	1	—
<i>Erodium stephanianum</i>	E. ste	AB	OTH	1	3	—	—
<i>Iris lactea</i>	I. lac	PF	OTH	—	6	—	—
<i>Tribulus terrestris</i>	T. ter	AB	OTH	3	8	1	2
<i>Gueldenstaedtia verna</i>	G. ver	PF	FAB	—	—	—	1
<i>Medicago ruthenica</i>	M. rut	PF	FAB	—	1	—	—

Note: In the table, PG, PF, SS and AB respectively represent perennial grasses, perennial hybrid grasses, shrubs and semi-shrubs, and annual and biennial plant functional groups, while POA, AST, CHE, FAB and OTH respectively represent Poaceae, Asteraceae, Chenopodiaceae, Fabaceae and other families. The numbers in the table represent the number of sample squares that appear.

2.4 Data analysis

2.4.1 Calculation of standing crop of spatial sampling quadrats

From the field measurements of height (cm), cover (%), and density (individuals per 0.25 m²) obtained within each quadrat, we first derived the relative values for each of these three variables. The Importance Value (IV) for any given plant population was then computed by taking the sum of these three relative figures, dividing that total by three, and finally multiplying the quotient by 100%, following the formula presented below:

$$IV = \left(\frac{H_i}{\sum_{i=1}^n H_i} + \frac{C_i}{\sum_{i=1}^n C_i} + \frac{D_i}{\sum_{i=1}^n D_i} \right) / 3 \times 100\%$$

where, for each plant population i within a quadrat, its height (H_i), coverage (C_i), and density (D_i) were recorded; the corresponding totals across all populations in that quadrat—namely, total height ($\sum_{i=1}^n H_i$), total

coverage ($\sum_{i=1}^n C_i$), and total density ($\sum_{i=1}^n D_i$)-served as the reference denominators. Based on these values,

importance indices were derived for every population. Subsequently, these indices were aggregated separately by plant functional type and by taxonomic family, yielding composite importance scores for each group and each family. All data processing and calculations were carried out with Microsoft Excel (version 2024).

2.4.2 Mean species occurrence probability per treatment

The mean species occurrence probability per treatment is calculated as follows:

$$P_{d,s} = \frac{\sum_{k \in K_{d,s}} x_{d,s,k}}{|K_{d,s}|}$$

where, for each species-treatment combination (s, d) , let $K_{d,s}$ be the set of samples that contain valid (non-missing) observations. For any sample k -th within this set, $x_{d,s,k}$ is a binary indicator of whether species s is present in that sample. The average probability of occurrence for that species under treatment d is then denoted by $P_{d,s}$.

2.4.3 Calculation of the state transition probability matrix

The value of each element $T_{i,j}$ in the state transition probability matrix is given by the following formula:

$$T_{i,j} = \begin{cases} \frac{t_j}{\sum_{k=1}^n t_k}, & \text{if } f_i > 0, \sum_{k=1}^n t_k > 0 \\ \frac{1}{n}, & \text{other situations} \end{cases}$$

The transition probability matrix is constructed to have row sums equal to unity. For each species i in the donor treatment, let f_i denote its occurrence probability; for species j in the recipient treatment, let t_j represent the corresponding value, and let n be the total number of species. In cases where $f_i \leq 0$ for a given source species, or where the summed occurrence likelihood across all species in the recipient treatment is zero, the transition probabilities are instead set to a uniform distribution over all target taxa.

2.4.4 Data computing and visualization

All computations—including the derivation of current treatment-area states and their associated transition matrices—were carried out in R (version 4.5.0) with the aid of the packages “tidyverse” (v2.0.0), “dplyr” (v1.1.4), and “tidyr” (v1.3.1). For graphical outputs, we generated a transition heatmap across treatment areas and a species-level transition network using “ggplot2” (v3.5.2), “reshape2” (v1.4.4), “patchwork” (v1.3.0), and “igraph” (v2.1.4) for data reshaping, layout composition, and network rendering.

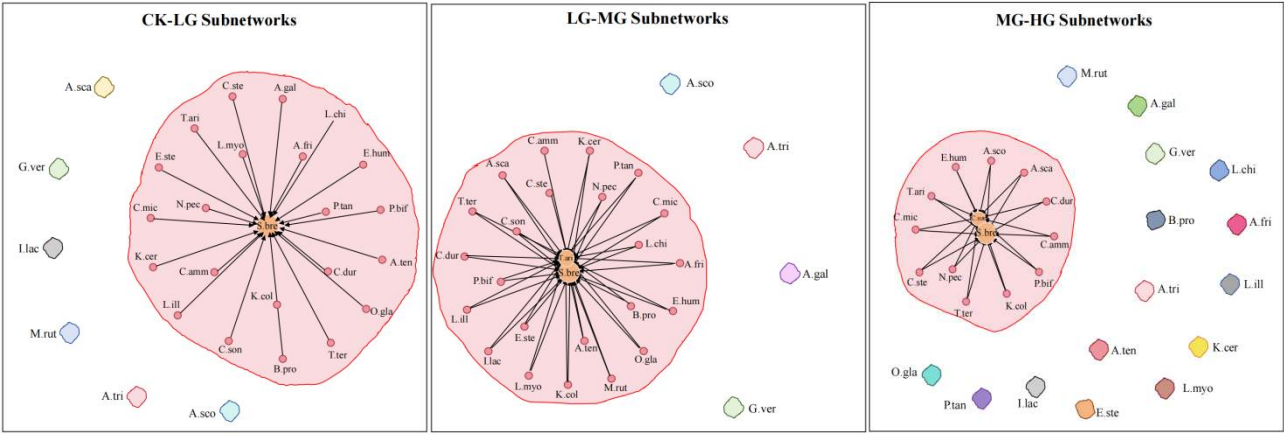
3. Results

3.1 Based on the species-specific grazing state transition process

During the transition from CK to LG (Fig. 3 CK-LG), six out of 29 plant populations were isolated (referred to as isolated species). As shown in Table 1, *Artemisia scoparia* (*A. sco*), *Asparagus trichophyllus* (*A. tri*), and *Gueldenstaedtia verna* (*G. ver*) were absent in both treatment areas, while *Astragalus scaberrimus* (*A. sca*), *Iris lactea* (*I. lac*), and *Medicago ruthenica* (*M. rut*) were absent in the CK treatment but present in the LG treatment. The remaining 23 plant populations clustered within a single zone, forming a species interaction network centered around *Stipa breviflora* (*S. bre*) as the core species. Notably, seven species formed a closely associated network with *Sbreviflora*: *Cleistogenes songorica* (*C. son*), *Artemisia frigida* (*A. fri*), *Carex duriuscula* (*C. dur*), and *Potentilla tanacetifolia* (*P. tan*), all of which are perennial populations, with *C. son* and *A. fri* being dominant species; and *Neopallasia pectinata* (*N. pec*), *Kali collinum* (*K. col*), and *Lappula myosotis* (*L. myo*), which are annual or biennial populations. The remaining 16 plant populations thus constituted the peripheral species in the CK→LG transition. This suggests that under low-disturbance conditions, the plant community forms a

174 complex species interaction network centered around the constructive species *Sbreviflora*, with hierarchical
 175 relationships—closely associated species and peripheral species—organized around this core. The
 176 characteristics of species interaction networks in the LG→MG and MG→HG transitions are detailed in Figure
 177 3.

178 In summary, under low stocking rates, the species interaction network is centered solely around the
 179 constructive species *Stipa breviflora* as the single core. The remaining species can be categorized based on their
 180 association with the core into closely associated species, peripheral species, and isolated species. When the plant
 181 community is subjected to moderate grazing intensity, it maintains relative stability by increasing the number
 182 of core species and forming more complex interactions. Once the stocking rate exceeds the optimal grazing
 183 intensity, the community adapts by converting most peripheral species into isolated species, while transforming
 184 grazing-tolerant dominant species into core species. Species interactions are then maintained through a
 185 simplified network formed by a limited number of species to preserve the basic structure of the community.
 186 Thus, as the stocking rate increases, the characteristics of species responses differ across transition processes.



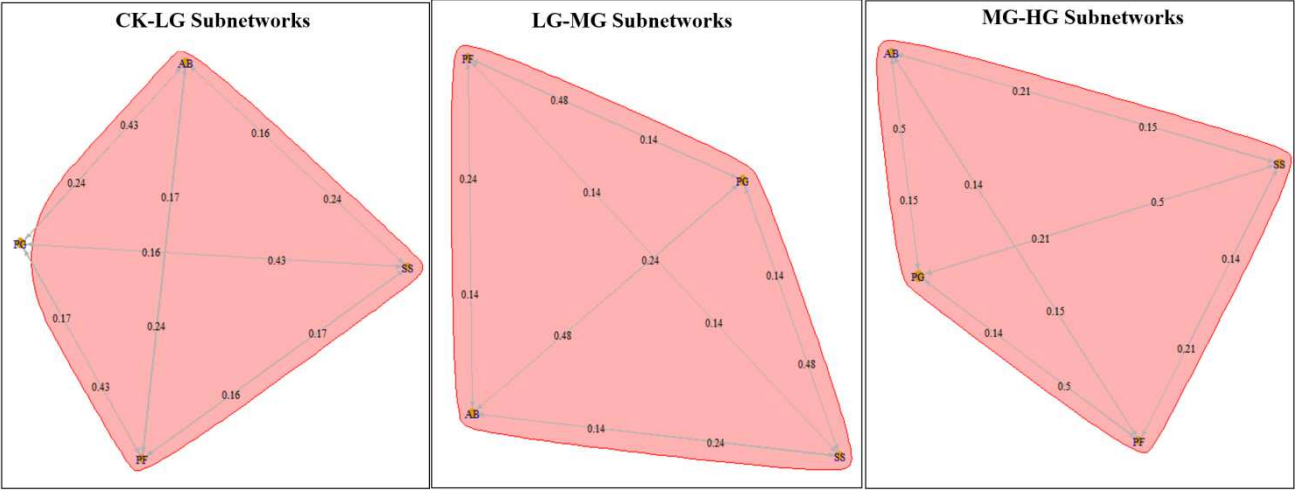
187
 188 **Fig.3.** Changes in species relationships during state transitions across stocking rates.

189
 190 **3.2 Based on the functional groups grazing state transition process**

191 During the transition from CK to LG (Fig.4 CK-LG), the perennial grass functional group (PG) showed a
 192 higher tendency to receive transitions from the perennial forb (PF), shrub-subshrub (SS), and annual-biennial
 193 plant (AB) functional groups, each with a transfer probability of 43% (0.43). The transition probabilities from
 194 PG to PF, SS, and AB were 17%, 16%, and 24%, respectively. Therefore, the probabilities of PG receiving
 195 transitions from PF, SS, and AB were 26%, 27%, and 19%, respectively. Similarly, the transition probabilities
 196 from PF to PG, SS, and AB were 26%, 7%, and -1%, respectively. This indicates that the perennial forb
 197 functional group is more inclined to receive state transitions from the shrub-subshrub functional group. The
 198 transition probabilities from SS to PG, PF, and AB were 27%, 1%, and 8%, respectively, suggesting that the SS
 199 functional group is more likely to transition into other functional groups, reflecting its relatively lower grazing
 200 tolerance. For the AB functional group, the transition probabilities to PG, PF, and SS were 19%, -7%, and -8%,
 201 respectively. The transition processes of each functional group during the LG→MG and MG→HG transitions
 202 are detailed in Figure 4.

203 Overall, as the stocking rate increases, state transitions between adjacent stocking levels exhibit distinct
 204 patterns and regularities among functional groups. Firstly, the transition probabilities from the PF, SS, and AB
 205 functional groups to PG gradually increase, indicating that the perennial grass (PG) functional group is the most
 206 grazing-tolerant. This further demonstrates the strong grazing resistance of *Stipa breviflora* and *Cleistogenes*

207 *songorica*. Secondly, the PF and SS functional groups show a greater tendency to transition toward both PG and AB. Thirdly, under moderate or lower stocking rates, state transitions between PF and SS remain relatively
 208 AB. Thirdly, under moderate or lower stocking rates, state transitions between PF and SS remain relatively
 209 stable, with low mutual transition probabilities. However, under heavy grazing, the transition probability
 210 between PF and SS increases significantly, with PF exhibiting a tendency to transition into SS. Lastly, the
 211 annual-biennial (AB) functional group demonstrates the most complex transition behavior with other functional
 212 groups across the CK→LG, LG→MG, and MG→HG processes, suggesting it may play a unique role in
 213 responding to high stocking rates.



214 **Fig.4.** Reciprocal transitions among plant functional groups during state shifts across stocking rates

215
 216
 217 **3.3 Based on the plant families grazing state transition process**

218 During the transition from CK to LG (Figure 5 CK-LG), regardless of changes in stocking rate, mutual
 219 transitions occurred among the Poaceae (POA), Fabaceae (FAB), Asteraceae (AST), and Chenopodiaceae (CHE)
 220 families during state shifts between adjacent grazing intensities. In contrast, the aggregated other families (OTH)
 221 showed a stronger tendency to transition into POA, AST, CHE, and FAB, with transition probabilities of 37%,
 222 21%, 19%, and 13%, respectively. The Poaceae family acted as the primary recipient group, receiving transitions
 223 from OTH, FAB, CHE, and AST with probabilities of 37%, 24% (i.e., 37% – 13%, same below), 18%, and 16%,
 224 respectively. Beyond receiving transitions from OTH, Fabaceae also tended to transition into POA, AST, and
 225 CHE. These patterns indicate that, excluding the mixed category OTH, Poaceae is the most grazing-tolerant
 226 family, Fabaceae is the most grazing-sensitive, while Asteraceae and Chenopodiaceae exhibit intermediate
 227 grazing tolerance. The transition processes for each plant family during the LG→MG and MG→HG shifts are
 228 detailed in Figure 5.

229 Overall, as the stocking rate increased, the transition probability from OTH to POA rose, and POA's reception
 230 probabilities from OTH, FAB, AST, and CHE also increased. This further confirms the strong grazing tolerance
 231 of grasses in the desert steppe ecosystem. Additionally, based on transition probabilities, Fabaceae received
 232 transitions from OTH at a relatively high rate during the LG→MG process, while its transition probability
 233 toward POA increased, toward AST decreased sharply under heavy grazing, and toward CHE remained low
 234 during LG→MG.

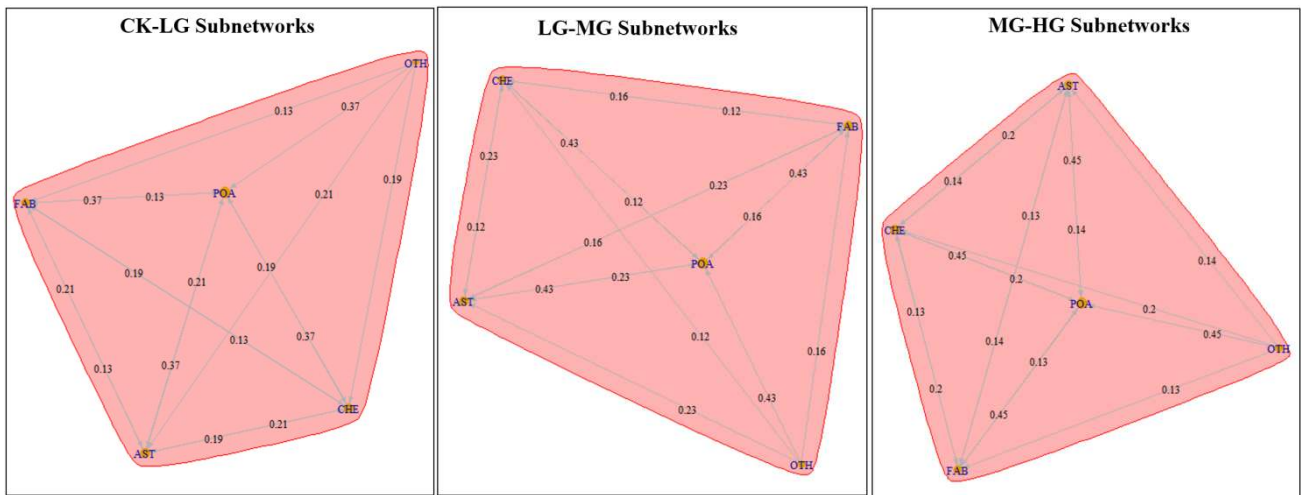


Fig.5. Reciprocal transitions among plant families during state shifts across stocking rates.

4. Discussion

4.1 Reciprocal feedback mechanisms between species network reconfiguration and functional group transitions

We examined how the topological properties of state-transition networks in a desert steppe community varied across grazing intensities. The core-species role of *Stipa breviflora* shifted nonlinearly as stocking rates increased (Fig. 3), which corroborates Saiz et al. (2021) proposition that network architecture underpins ecosystem stability. At low grazing pressure (CK→LG), a single keystone taxon dominated a multi-layered network (23 species total), comprising 7 closely associated and 16 peripheral species, and this configuration preserved community resilience through hierarchical organisation—a pattern aligning with the biodiversity-insurance hypothesis of Soliveres et al. (2016). As grazing intensified to moderate levels (MG), however, network restructuring occurred concurrently with an expansion in the number of dominant species, implying that the plant community bolsters its structural redundancy in response to external stressors (Fillazzola & Laimer, 2020; Pillar et al., 2013; Biggs et al., 2020).

The perennial grass (PG) functional group serves as a “system firewall” (Soliveres et al., 2016), with its probability of receiving transitions from other functional groups increasing under higher stocking rates (reaching 43% during the CK→LG phase). This pattern confirms the disturbance resistance advantage conferred by clonal propagation in grasses (Ma et al., 2020; Wang et al., 2017; Yuan et al., 2020). However, the high transition probability from Fabaceae (FAB) to Poaceae (POA) (24%) reveals the sensitivity of nitrogen-fixing plants to grazing pressure—a finding inconsistent with the global trait-based analysis reported by Díaz et al. (2007) and suggestive of a unique vulnerability among legume species in semiarid regions. Thus, functional group transition pathways further illuminate ecological strategies underpinning ecosystem stability (Table 1, Fig. 4). Notably, under heavy grazing intensity, the annual-biennial (AB) functional group acts as an “ecological bridge” due to its high transition complexity (Fig. 4, MG→HG), potentially delaying systemic collapse through mechanisms of resource competition balance (Yang et al., 2019; Beck et al., 2015; Wang et al., 2025).

While the “hub” role of core species has been confirmed, it remains unclear whether this function is regulated by interspecific interactions—such as competition between *Stipa breviflora* and *Artemisia frigida*. Similarly, although the “bridge” role of the annual-biennial (AB) functional group has been demonstrated, further controlled experiments are needed to determine whether this bridging effect depends on specific species—such as the high persistence of *Euphorbia humifusa* during the MG/HG stages (Lavorel et al. 2015; Du et al., 2024).

4.2 A three-dimensional driving framework for the maintenance of multistability

Under light to moderate stocking rates, *Stipa breviflora* maintains microhabitat stability through its root network (Wu et al., 2021). With a presence probability exceeding 95% (Table 1), it serves as a structural anchor for the community, corroborating the hypothesis proposed by Kefi et al. (2016) regarding keystone species regulating transition thresholds. However, when stocking rates reach heavy grazing (HG) intensity, grazing-tolerant species such as *Teloxys aristata* displace the constructive species and become the new core, indicating that the system can achieve state transition through “core species replacement”. (Scheffer et al. 2001; Westoby et al., 1989; Briske et al., 2005).

A key buffering mechanism against grazing-induced state shifts lies in the functional-group compensation effect (Bai et al., 2004; Yachi and Loreau, 1999; Elmqvist et al., 2003), whereby subordinate groups offset losses incurred by dominant ones. This is exemplified during moderate grazing (MG): the transition probability from the shrub-subshrub (SS) group to perennial grasses (PG) reached 27%, markedly exceeding the reverse direction (16%), suggesting that SS species sustain overall community function at the expense of their own abundance (Wu et al., 2021). The exceptional grazing resilience of the PG group itself is attributable to two complementary traits: the C₄ photosynthetic pathway operating in *Cleistogenes songorica* leaves (Zhang et al., 2023; Wang, 2007; Osborne and Freckleton, 2009), and the intrinsic reserve-allocation strategy of the dominant perennial taxa (Huang et al., 2018). Together, these features constitute a multi-layered defensive framework that helps the community resist transition to alternative states.

The plant family transition network reveals pathways of resource reallocation (Fig. 5). The transition probability from OTH (other families) to POA (Poaceae) increased with stocking rate (rising from 37% to 52% from LG to HG), indicating a shift of limited resources toward more grazing-tolerant taxa. Meanwhile, the directional flow of resources from Fabaceae (FAB) to Poaceae (POA) (24%) may exacerbate nitrogen limitation and trigger a positive feedback loop (Osterheld et al., 2021; Soussana and Tallec, 2010), explaining the sharp decline of legume species during the MG→HG transition (Table 1).

The family-level transition network illustrates how resources are redistributed under increasing grazing pressure (Fig. 5). Notably, the dramatic reduction in legume abundance observed from moderate to heavy grazing (MG→HG, Table 1) can be attributed to the asymmetric resource flow from Fabaceae to Poaceae (24%), which is likely to intensify nitrogen deficiency and establish a self-reinforcing cycle (Osterheld et al., 2021; Soussana and Tallec, 2010). Concurrently, the probability of transition from other families (OTH) to Poaceae rose markedly with stocking rate, climbing from 37% under light grazing to 52% under heavy grazing, suggesting that limiting resources are progressively channelled towards taxa that are more capable of enduring high defoliation pressure.

In summary, maintaining multistability in the desert steppe requires controlling the stocking rate below 1.82 sheep units·ha⁻²·6 months⁻¹ (MG). Within this range, the complexity of the core species network (with >20 species associations) can buffer disturbances (Bestelmeyer et al., 2011). The probability of the PG functional group receiving transitions and the OTH→POA transition probability help maintain resource allocation flexibility while preventing functional imbalance.

5. Conclusion

(1) As the stocking rate increases, the plant community shifts from a hierarchical network centered around a single core species (*Stipa breviflora*) to a complex multi-core species network, eventually transitioning to a simplified structure maintained by grazing-tolerant species to preserve the basic state of the community.

(2) Perennial grasses (PG) exhibit the highest grazing tolerance. Annual-biennial plants (AB) act as ecological bridges under heavy grazing due to their high transition complexity, while shrubs and subshrubs (SS)

contribute to maintaining systemic functionality through self-sacrifice.

(3) The Poaceae family (POA) sustains its dominant role by continuously receiving resources from other plant families—particularly under moderate to heavy grazing pressure. Meanwhile, the directional transfer of resources from Fabaceae (FAB) to POA intensifies nitrogen limitation in the grassland, thereby triggering a state transition in the grazed grassland ecosystem.

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Authors' contributions Conceptualization: H.L.; data curation: H.L. and S.L.; investigation and validation: H.L.; formal analysis: H.L., H.Z. and F.Z.; methodology: H.L., B.Z., Z.W., G.H., H.Z. and F.Z.; software: B.Z.; supervision and project administration: S.L.; funding acquisition: S.L.; resources: S.L.; writing—original draft preparation: H.L. and B.Z.; writing—review and editing: S.L., Z.L., H.R. and Z.Q.; grammar correction: Z.W. and G.H. H.L. and B.Z. contributed equally to this work and share first authorship. S.L. is the corresponding author.

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Data availability statement

The data that supports the findings of this study are available in the supplementary material of this article.

Declaration of competing interest

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

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