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# Long-term grazing changed the spatial distributions of dominant species in typical steppe of Inner Mongolia

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## Abstract

Dominant species occupy a pivotal role in plant community, influencing the structure and function of the ecosystem. The spatial distributions of dominant species can react to the effect of different grazing intensities, thereby reflecting their tolerance and adaptive strategies toward grazing. In this study, geostatistical methods were mainly used to study the spatial distribution characteristics of *Stipa krylovii* Roshev. and *Leymus chinensis* (Trin.) Tzvel. species at two interval scales (quadrat size 5 m × 5 m, 10 m × 10 m) and two treatments (free grazing, FG, 1.66 sheep·ha<sup>-1</sup>·a<sup>-1</sup>; control, CK, 0 sheep·ha<sup>-1</sup>·a<sup>-1</sup>) in typical steppe of Inner Mongolia. A systematic sampling method was used in each 100 m × 100 m representative sample plots to obtain the height, coverage, and density of all species in the community. The results showed that grazing altered the concentrated distribution of *S. krylovii* and the spatial mosaic distribution pattern of *S. krylovii* and *L. chinensis* while having no effect on the spatial clumped distribution of *L. chinensis*. It also found that the spatial distributions of dominant species are primarily affected by structural factors, and random factors such as long-term grazing led to a transition of *S. krylovii* from a concentrated distribution to a small patchy random pattern should not be overlooked. Our findings suggest that long-term grazing alters the spatial distribution pattern of dominant species and that adaptive strategies may be the key for maintaining the dominant role of structural factors.

**Keywords** Dominant species, Grazing disturbance, Spatial distribution, Typical steppe

## Background

The spatial distributions of plant species refer to the composition or configuration of individuals within a specific area [1]. The study of spatial distribution is generally performed by quantifying measures of heterogeneity. Spatial heterogeneity includes the inhomogeneity and complexity of spatial variables [2], a factor that is primarily determined by structural and random factors, and the concentration or patchiness of the distribution of species is an additional factor [3, 4]. Spatial heterogeneity depends extremely on scale (quadrat size), and that changes in scale will lead to changes in spatial heterogeneity [5]. Studying the spatial heterogeneity of plant species not only reveals the spatial distribution of species

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within the community but also provides insights into the processes influencing plant adaptive strategies under perturbed conditions.

Dominant species, occupying a key position within the plant community [6], hold a significant role in shaping and stabilizing the community structure and environmental conditions [7]. Therefore, the spatial distributions of dominant species can determine the spatial patterns of whole vegetation communities. Dominant species can also be used to predict the dynamics and development directions of plant communities under disturbances [8]. Previous studies have found that one or several dominant species are usually resilient to disturbances [9], as they can resist the decline of ecosystem function in the short term which are more stable than secondary species [10]. Accordingly, studying dominant species has become crucial for understanding the spatial distribution of grassland plant communities.

Grazing is a major factor influencing plant growth in grassland ecosystem [11]. Herbivores' grazing, including wandering and trampling, foraging consumption, and deposition of excreta, can alter the spatial patterns of soil nutrients [12], subsequently affecting the distribution of aboveground plants [13]. Meanwhile, long-term grazing can affect the life history and adaptive strategies of plant populations, resulting in varied spatial distribution patterns [14]. Studies have found that plants adopt certain adaptive strategies, such as adjusting their external morphology and physiological characteristics, to avoid or tolerate grazing interference [15]. Lv et al. (2019) concluded that grazing causes spatial aggregation in dominant species such as *Stipa breviflora* Griseb., and this spatial clustering pattern enhances the ability of *S. breviflora* to tolerate grazing so that smaller isolated clusters are able to survive under heavy grazing [16]. Wu et al. (2023) found that the spatial distribution of *Leymus chinensis* (Trin.) Tzvel. is not by its ecological stoichiometry but is mainly dominated by high-probability subsets under different grazing intensities [17]. Given this, the response characteristics and the variation in the spatial distribution of dominant populations under grazing conditions reflect the tolerance of those species to grazing and indicate the stability and dynamics of plant communities.

The typical steppe in northern China where *Stipa krylovii* Roshev. and *L. chinensis* are the main dominant species, hold significant reference value for the conservation and utilization of grassland ecosystems worldwide [18]. Grazing is the main utilization method in this region [19]. The literature indicates that researchers have used various analysis methods and models to reveal the quantitative characteristics and spatial distribution of single species [4, 17, 20], but there is a lack of studies on the changes of spatial heterogeneity of plant populations from the perspective of multiple dominant species. In

the present study, we used a systematic sampling method and geostatistical analysis to investigate the spatial distribution of the dominant plant species *S. krylovii* and *L. chinensis* under long-term grazing (grazing was initiated in 1980) in Xilingol League, Inner Mongolia, China. The study intended to address the following questions: (1) Do the spatial distributions of dominant species change with grazing? (2) Are the dominant factors influencing the spatial distributions of dominant species consistent? (3) What are the response characteristics and patterns of dominant species to grazing? The answers to these questions will provide practical guidance for long-term grazing in the *S. krylovii* steppe as well as a theoretical basis for understanding the evolution of the spatial distribution of plant species and the development trends of grasslands.

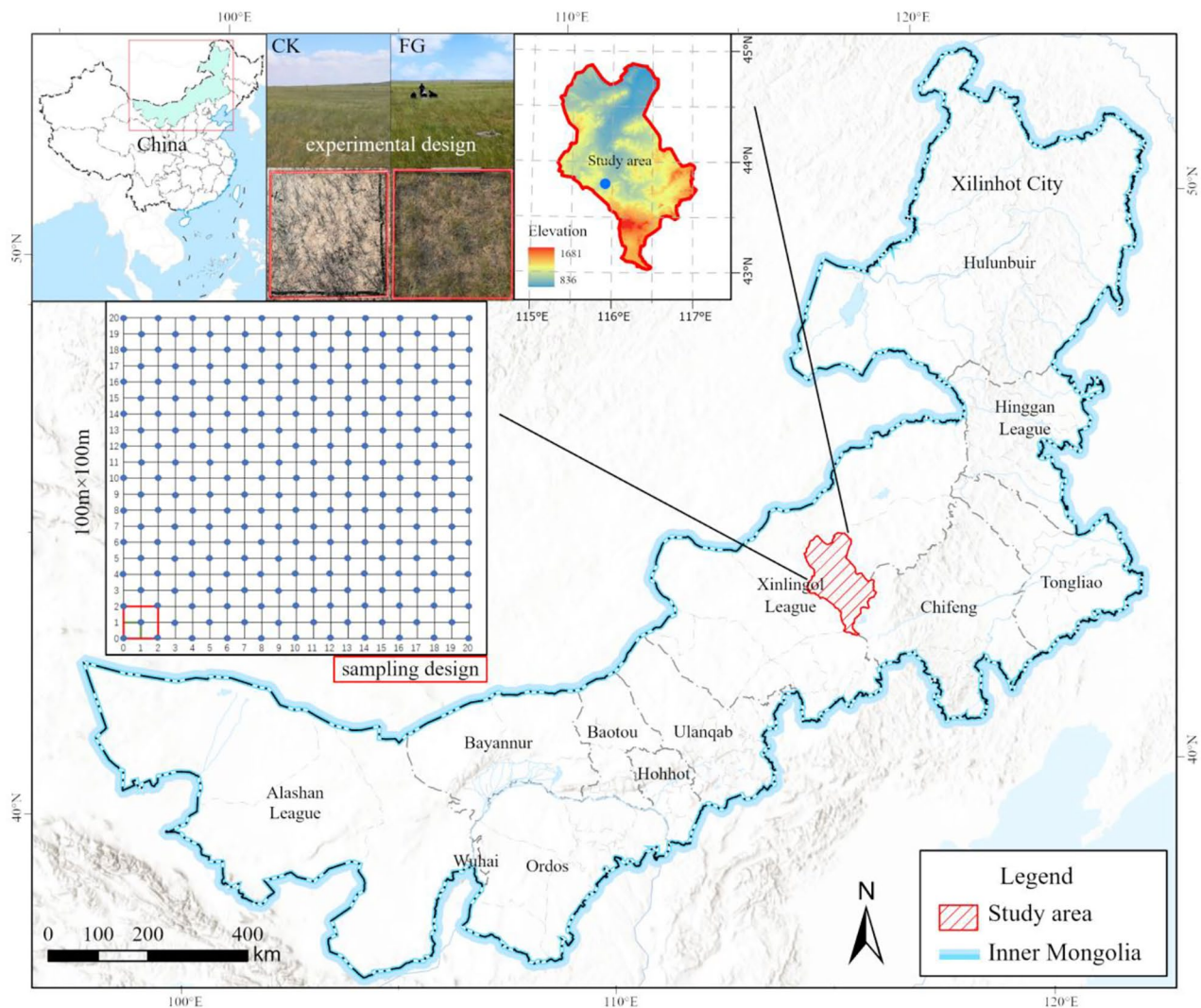
## Materials and methods

### Study area

The study site (43°44'54.80" N, 115°48'14.24" E; elevation 1080 m) was located in the central part of Xilingol Pasture, a typical grassland in the central region of Inner Mongolia, northern China (Fig. 1). The region features a medium-temperate arid continental climate. Summers are short and hot, while winters are long and cold, with an average annual temperature of 4.4 °C and mean annual precipitation of 170–370 mm, with about 60–80% of precipitation falling in the growing season (May to August) [21]. The total sunshine ranges from 2853 to 3107 h, and the frost-free period lasts from 98 to 130 days [22]. The vegetation zone type is a *S. krylovii* meadow, with a grass height of 10–30 cm and 20–35% coverage. The dominant species include *S. krylovii* and *L. chinensis*, while the companion species include *Cleistogenes squarrosa* (Trin.) Keng, *Caragana stenophylla* Pojark., *Heteropappus altaicus* (Willd.) Novopokr., *Medicago ruthenica* (L.) Trautv., and *Convolvulus ammannii* Desr. The main soil type is light chestnut soil (Chinese classification) or calcic Kastanozems (FAO soil classification). The soil texture is sandy loam with 44–51% sand, 32–38% silt, and 16–18% clay [23].

### Experimental design

This experiment was conducted in a natural grassland of a pastoral holding. The existing natural grassland area of the pasture was 334 ha and was divided into a free grazing area where livestock freely grazed and roamed without management measures during the growing season (330 ha, grazing since 1980) and an enclosed control area (4 ha, enclosed since 1980). The pasture supported 400 sheep and 30 cattle, equivalent to 550 sheep units, and the stocking rate was 1.66 sheep·ha<sup>-1</sup>·a<sup>-1</sup>, which was moderate grazing based on grassland productivity and consumption rate. In the two treatment areas of



**Fig. 1** Study area and distribution of sampling points in fixed sites

free grazing (FG) and enclosed (CK), representative plots measuring  $100\text{ m} \times 100\text{ m}$  were selected for sampling.

### Sampling design

In August 2022,  $100\text{ m} \times 100\text{ m}$  representative plots (similar in plant species composition and topography) were selected in the FG and the CK treatments using a systematic sampling method (Fig. 1). The southwest corner intersection served as the origin  $(x_0, y_0)$ , and the coordinates of the point farthest from the origin were  $(x_{20}, y_{20})$ . The x-axis was set from west to east, and the y-axis was set from south to north. Eleven quadrats were taken from even rows and ten from odd rows for sampling, with the interval of each point being 10 m. As shown in Fig. 1, where each blue dot represents the center of a  $0.5\text{ m} \times 0.5\text{ m}$  quadrat, there were 221 quadrats in each site. Plant species within each quadrat were measured for height,

coverage, and density, and the relative positions of each quadrat  $(x_i, y_i)$  were recorded.

The interval scale was divided according to the distribution of sample points. The first small plot at the  $5\text{ m} \times 5\text{ m}$  scale contained  $(x_0, y_0)$  and  $(x_1, y_1)$  (light blue area in Fig. 1), while the first small plot at the  $10\text{ m} \times 10\text{ m}$  scale consisted of  $(x_0, y_0)$ ,  $(x_0, y_2)$ ,  $(x_1, y_1)$ ,  $(x_2, y_0)$ , and  $(x_2, y_2)$  (red area in Fig. 1). The plots were divided into  $5\text{ m} \times 5\text{ m}$  and  $10\text{ m} \times 10\text{ m}$  plots by analogy, and the average height (cm), coverage (%), and density ( $\text{clusters} \cdot \text{m}^{-2}$ ) of the corresponding quadrats were calculated. The sizes of the corresponding samples were 400 and 100 at scales of  $5\text{ m} \times 5\text{ m}$  and  $10\text{ m} \times 10\text{ m}$ , respectively. The experimental design thus comprised a two-factor nonrepetitive design.

## Data analysis

### Calculation of importance values (IV)

According to the small plots divided by scale, the importance values of *S. krylovii* and *L. chinensis* were calculated for small plots in different scales. The calculation formula was as follows.

$$IV = \frac{H + C + D}{3} \times 100\%$$

where IV is the importance value, H is the relative height, C is the relative coverage and D is the relative density. The average value of the three indices was multiplied by 100% to obtain the IV of plant populations in each coordinate.

### Analysis of comparison and sample variability

SAS 9.4 software was used to analyse the IVs of *S. krylovii* and *L. chinensis* using a U test ( $P < 0.05$ ). The coefficient of variation (CV) was calculated, and the formula for the CV was the standard deviation of the IV divided by the mean value. The results of the statistical analysis and the extreme values (maximum and minimum) of the sample data are summarized in tables.

### Regression analysis

Scatter plots of the IVs of *S. krylovii* and *L. chinensis* at different scales and treatments were drawn, and linear fitting was performed (where the IV of *S. krylovii* was used as the x variable, the IV of *L. chinensis* was used as the y variable, and the fitted model was  $y = ax + b + \epsilon$ ). The 95% confidence limits of the regression model were drawn. The fitting process and graph plotting were performed in R (version R-4.2.2; <https://www.r-project.org>) using the `quantreg` and `ggplot2` packages.

### Analysis of spatial distributions

Semivariance analysis [24] was carried out to explore the spatial distributions of *S. krylovii* and *L. chinensis*. The formula for the semivariance function was as follows.

$$r(h) = \frac{1}{2N(h)} \sum_{i=1}^n (Z(x_i) - Z(x_{i+h}))^2 \quad i = 1, 2, 3, \dots, N(h)$$

where  $r(h)$  is the semivariance function and  $h$  is the step size.  $Z(x_i)$  and  $Z(x_{i+h})$  are the measured values (the IVs of *S. krylovii* and *L. chinensis*) of the regional random variable  $Z(x)$  at spatial positions  $x_i$  and  $x_{i+h}$ , respectively;  $N(h)$  refers to the number of samples with interval  $h$ .

The spatial data structure and autocorrelation were evaluated by the optimal estimation of semivariance model parameters [25]. In this model, Nugget Variance ( $C_0$ ), Sill ( $C_0 + C$ ), Structure ratio ( $C / (C_0 + C)$ ), and Range parameter ( $A_0$ ) are important parameters (Table 1). When  $C / (C_0 + C)$  is less than 25%, this represents weak spatial autocorrelation, while values in the range of 25–75% represent moderate spatial autocorrelation, and values greater than 75% represent strong spatial autocorrelation [26]. We used the residual sum of squares (RSS) from the least squares method to select linear, spherical, exponential, and Gaussian models. These models have different spatial autocorrelation ranges: linear, exponential, spherical, and Gaussian models have ranges of  $A_0$ ,  $3A_0$ ,  $A_0$ , and  $\sqrt{3}A_0$ , respectively. The kriging method was used for spatial interpolation, and the spatial distribution maps of *S. krylovii* and *L. chinensis* were drawn according to the semivariance function. Geostatistical analysis was performed in GS+ software (Version 9, Gamma Design software, 2014).

## Result

### Variation and comparison of the IV between *S. Krylovii* and *L. Chinensis*

Regarding Table 2, the IV of *S. krylovii* at the 5 m × 5 m scale was significantly higher than at the 10 m × 10 m scale in the CK treatment ( $P < 0.05$ , the same below), while there was no significant difference in the IV of *L. chinensis* between the 5 m × 5 m and 10 m × 10 m scales ( $P \geq 0.05$ , the same below). There was no significant difference between *S. krylovii* and *L. chinensis* in the FG treatment at any other scale. The IV of *S. krylovii* showed an increasing trend under grazing but did not reach a significant level (both the 5 m × 5 m and 10 m × 10 m scales were consistent). In contrast, the IV of *L. chinensis* decreased significantly, performing equally at both the 5 m × 5 m and 10 m × 10 m scales.

The mean variation in *S. krylovii* and *L. chinensis* was 64.56% and 36.33% in the CK treatment and 32.14% and

**Table 1** Semivariogram parameters

Parameters	Abbreviation	Interpreting
Nugget variance	$C_0$	Spatial variation caused by random factors.
Sagitta	C	Spatial variation caused by structural factors (e.g., soil, topography, physiognomy, etc.).
Sill	$C_0 + C$	The model asymptote.
Structural ratio	$C / (C_0 + C)$	The proportion of structural spatial distribution factors in the maximum spatial variation.
Range parameter	$A_0$	The model's parameter is used to calculate the effective range.
Determination coefficient	$R^2$	Testing the optimal fitting model; the larger, the better
Residual sum of squares	RSS	Testing the optimal fitting model; the smaller, the better

**Table 2** Descriptive statistics of important values of *S. Krylovii* and *L. Chinensis* under different experimental treatments and scales

Treatment	Species	Scale	Mean value	Standard deviation	Minimum	Maximum	Coefficient of variation	Mean variation
CK	<i>S. krylovii</i>	5 m × 5 m	0.1994aA	0.1096	0.0225	0.4451	54.95	64.56
		10 m × 10 m	0.1485bA	0.1102	0.0160	0.3954	74.18	
	<i>L. chinensis</i>	5 m × 5 m	0.3360aA	0.1343	0.0464	0.6824	39.97	36.33
		10 m × 10 m	0.3305aA	0.1080	0.0848	0.5762	32.69	
FG	<i>S. krylovii</i>	5 m × 5 m	0.2581aA	0.0953	0.0519	0.6126	36.95	32.14
		10 m × 10 m	0.2598aA	0.0710	0.1295	0.5183	27.34	
	<i>L. chinensis</i>	5 m × 5 m	0.2255aB	0.1044	0.0205	0.4912	46.31	42.61
		10 m × 10 m	0.2193aB	0.0853	0.0292	0.3976	38.90	

Note: The same lowercase letter indicated no significant difference between the IV of different scales under the same grazing treatment ( $P > 0.05$ ); The same uppercase letter showed no significant difference in IV between grazing treatments at the same scale ( $P > 0.05$ )

42.61% in the FG treatment, respectively. Comparing the mean variation and the CV at different scales, the CV of the IV of *S. krylovii* at the 10 m × 10 m scale is greater than that at the 5 m × 5 m scale and also greater than the mean variation. The CV at the 5 m × 5 m scale is higher than that at the 10 m × 10 m scale in the FG area. For *L. chinensis*, the CV at the 5 m × 5 m scale is greater than that at the 10 m × 10 m scale and greater than the average variability across all treatments. Overall, grazing increased the IV of *S. krylovii* and decreased the variation in the unit mean value, while the results of *L. chinensis* were on the contrary.

#### Regression analysis of the spatial distributions of *S. Krylovii* and *L. Chinensis*

In both treatments, a significant correlation was observed between the IVs of *S. krylovii* and *L. chinensis* ( $P < 0.01$ , Fig. 2). Specifically, the IV of *S. krylovii* increased as the IV of *L. chinensis* decreased, indicating a negative correlation. The absolute value of the regression coefficient for *S. krylovii* and *L. chinensis* increased with the spatial scale, from 0.468 at the 5 m × 5 m scale to 0.539 at the 10 m × 10 m scale in the CK treatment and ranged from 0.557 at the 5 m × 5 m scale to 0.676 at the 10 m × 10 m scale in the FG treatment. This suggested that the correlation between *S. krylovii* and *L. chinensis* at the 10 m × 10 m scale was higher than that at the 5 m × 5 m scale. Since the absolute value of the regression coefficient represented the correlation intensity of *S. krylovii* and *L. chinensis*, and the regression coefficient was negative. The interspecific relationship between *S. krylovii* and *L. chinensis* should be competitive, with lower competition intensity at the smaller scale (5 m × 5 m).

#### Semivariance function for *S. Krylovii* and *L. Chinensis*

In the CK treatment, the best-fitting models of the semivariogram of *S. krylovii* were spherical and Gaussian models at the 5 m × 5 m and 10 m × 10 m scales (Table 3). The structure ratios of *S. krylovii* at the two scales were 0.858 and 0.869, respectively, indicating that the spatial distribution was more affected by structural factors as

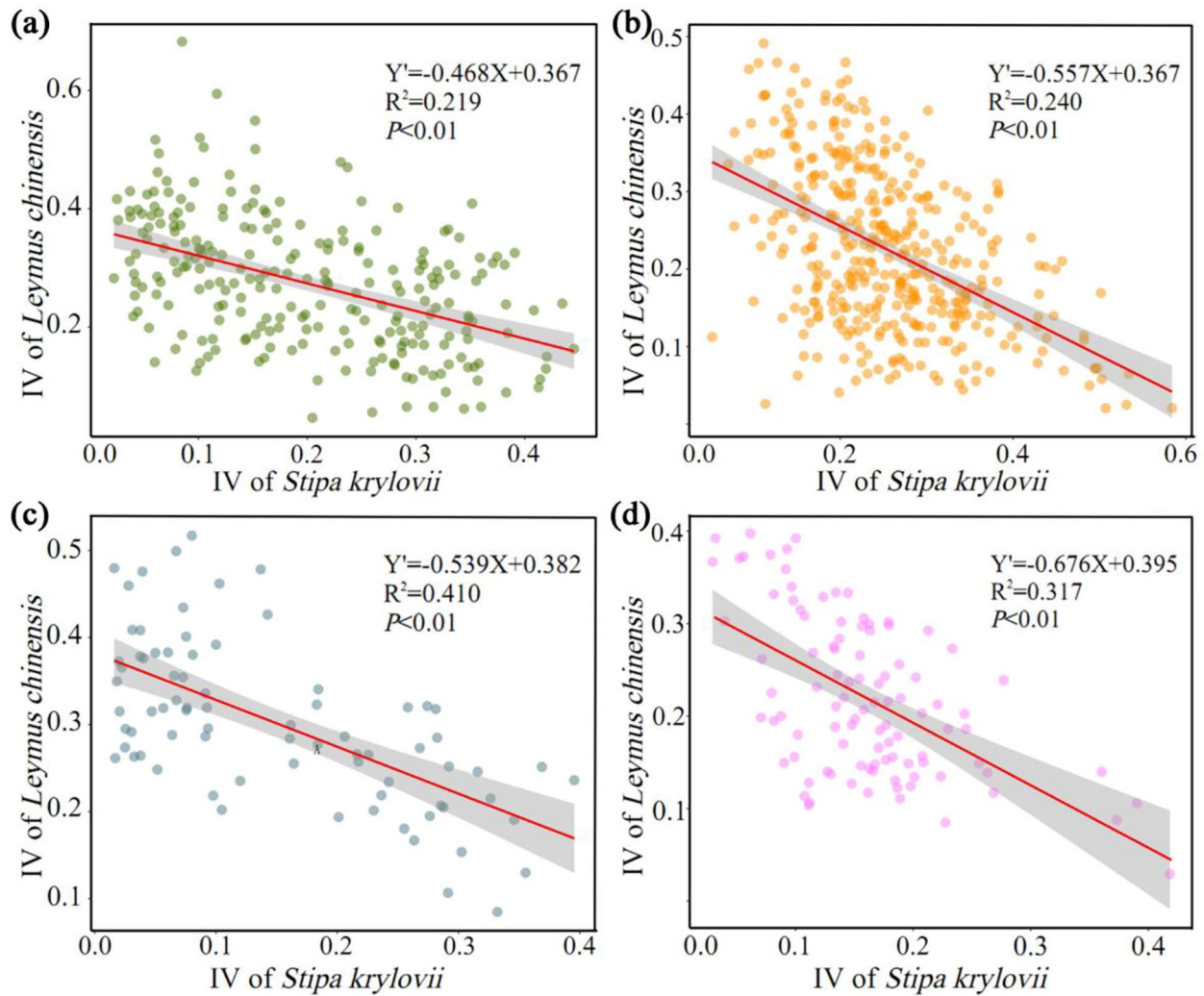
the spatial scale increased. The values of the spatial autocorrelation function were 85.90 and 40.00 m at 5 m × 5 m and 10 m × 10 m scales, respectively ( $A_0$  is multiplied by the scale in the table; the same applies below), indicating that the stronger the spatial heterogeneity, the larger the scale of autocorrelation. For *L. chinensis*, exponential and Gaussian models were best fitted at 5 m × 5 m and 10 m × 10 m scales (Table 3), with structure ratios of 0.913 and 0.834, respectively. The spatial autocorrelation values were 17.20 and 21.10 m at the 5 m × 5 m and 10 m × 10 m scales, respectively.

In the FG treatment, exponential and Gaussian models were fitted for *S. krylovii* at the 5 m × 5 m and 10 m × 10 m scales, respectively (Table 3). The structure ratios of *S. krylovii* were 0.967 and 0.997, and the ranges of spatial autocorrelation were 8.75 and 13.90 m, indicating that the spatial distribution of *S. krylovii* was controlled by structural factors. The optimal functions for the semivariogram of *L. chinensis* at the 5 m × 5 m and 10 m × 10 m scales were spherical and Gaussian models (Table 3), with structure ratios of 0.887 and 0.838 and spatial autocorrelation scales of 43.85 and 24.50 m, respectively.

In conclusion, the structure ratios of the spatial distributions of *S. krylovii* and *L. chinensis* were all greater than 0.75, indicating that the dominant factors influencing the spatial distributions of both species were structural. Structural factors refer to changes caused by soil parent material, topography, climate, and utilization methods [4]. The dominance of structural factors in the spatial distribution of *S. krylovii* increased with the spatial scale, and the spatial heterogeneity of *L. chinensis* increased. Compared with the CK treatment, grazing reduced the spatial heterogeneity of *S. krylovii*, while that of *L. chinensis* decreased at the 10 m × 10 m scale. Therefore, grazing reduced the spatial heterogeneity of both *S. krylovii* and *L. chinensis*.

#### Analysis of spatial variation for *S. Krylovii* and *L. Chinensis*

In the CK treatment, *S. krylovii* exhibited a concentrated distribution with large patches in the southeast at the 5 m × 5 m scale, gradually decreasing toward the northwest



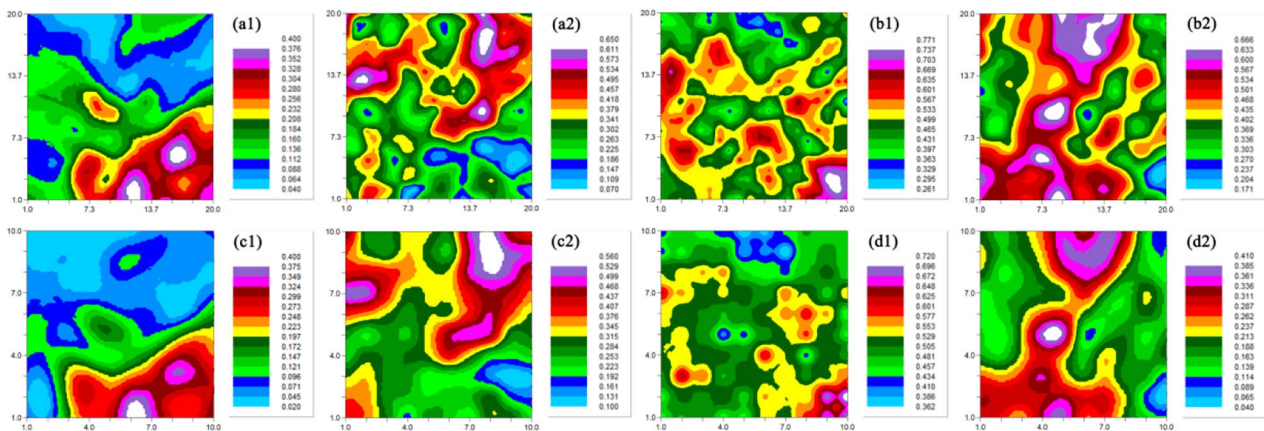
**Fig. 2** Linear regression diagrams of *S. krylovii* and *L. chinensis* at different spatial scales under different grazing treatments. (a) 5 m × 5 m scale in the CK treatment; (b) 5 m × 5 m scale in the FG treatment; (c) 10 m × 10 m scale in the CK treatment; (d) 10 m × 10 m scale in the FG treatment. The shaded areas represent 95% confidence intervals

**Table 3** Semi-variance functions of *S. Krylovii* and *L. Chinensis* at different scales under different experimental treatments and spatial scales

Treatment	Species	Scale	Model	C <sub>0</sub>	C <sub>0</sub> +C	C / (C <sub>0</sub> +C)	A <sub>0</sub>	R <sup>2</sup>	RSS
CK	<i>S. krylovii</i>	5 m × 5 m	Spherical	0.00230	0.01620	0.858	17.18	0.990	1.560 × 10 <sup>-6</sup>
		10 m × 10 m	Gaussian	0.00191	0.01462	0.869	4.00	0.995	2.934 × 10 <sup>-7</sup>
	<i>L. chinensis</i>	5 m × 5 m	Exponential	0.00168	0.01926	0.913	3.44	0.969	4.955 × 10 <sup>-6</sup>
		10 m × 10 m	Gaussian	0.00194	0.01168	0.834	2.11	0.980	6.959 × 10 <sup>-7</sup>
FG	<i>S. krylovii</i>	5 m × 5 m	Exponential	0.00027	0.00826	0.967	1.75	0.935	1.195 × 10 <sup>-6</sup>
		10 m × 10 m	Gaussian	0.00001	0.00386	0.997	1.39	0.963	1.013 × 10 <sup>-7</sup>
	<i>L. chinensis</i>	5 m × 5 m	Spherical	0.00174	0.01538	0.887	8.77	0.992	1.311 × 10 <sup>-6</sup>
		10 m × 10 m	Gaussian	0.00147	0.00910	0.838	2.45	0.997	7.310 × 10 <sup>-8</sup>

and forming a banded distribution (Fig. 3a1). *L. chinensis* was mainly distributed in the north and west, showing an apparent patchy distribution (Fig. 3a2). The areas with high IV for *S. krylovii* corresponded precisely to the areas with a low distribution of *L. chinensis*, resulting in a

mosaic distribution. *S. krylovii* formed dense patches in the southeast at the 10 m × 10 m scale then spread and decreased to the northwest (Fig. 3c1), similar to its distribution pattern at the 5 m × 5 m scale. *L. chinensis* was densely distributed in the north and west (Fig. 3c2), with



**Fig. 3** Two-dimensional spatial pattern maps of *S. krylovii* and *L. chinensis* under different grazing treatments and spatial scales. (a) 5 m × 5 m scale in the CK treatment; (b) 5 m × 5 m scale in the FG treatment; (c) 10 m × 10 m scale in the CK treatment; (d) 10 m × 10 m scale in the FG treatment; 1 *S. krylovii*; 2 *L. chinensis*. The colors of the figure from blue to white indicate the values from small to large. The first half is the north, the second half is the south, the left half is the west, and the right half is the east

fewer patches in the south and only one dense patch in the southwest corner at the 10 m × 10 m scale.

In the FG treatment, *S. krylovii* no longer had large, dense patches at the 5 m × 5 m scale. Instead, the species showed a scattered distribution with small, distinct patches, appearing in a relatively random pattern (Fig. 3b1). However, *L. chinensis* still showed a concentrated distribution, with larger concentrated band-like distributions in the southwest and northeast diagonal regions (Fig. 3b2). At the scale of 10 m × 10 m, the spatial distribution of *S. krylovii* in the FG treatment became more fragmented, with reduced patchiness. There was only a dense patch in the southeast corner and a less concentrated patch in the north (Fig. 3d1). In contrast, *L. chinensis* exhibited a strip-like dense distribution pattern from southwest to northeast, gradually decreasing from the intensive area to the west and east (Fig. 3d2). Grazing apparently caused the disappearance of the spatial mosaic distribution pattern between *S. krylovii* and *L. chinensis*.

Based on the above results, free grazing appeared to transform the spatial distribution of *S. krylovii* from a concentrated distribution to a fragmented pattern with small patches, and the spatial distribution appeared more uniform. In addition, free grazing resulted in the disappearance of the spatial mosaic distribution pattern between *S. krylovii* and *L. chinensis*. However, *L. chinensis* was not altered by free grazing. At the scale of 5 m × 5 m, both *S. krylovii* and *L. chinensis* showed distinct patchy distribution patterns, indicating a high degree of heterogeneity. At the scale of 10 m × 10 m, *S. krylovii* and *L. chinensis* presented stronger concentrations, indicating a higher degree of homogeneity.

## Discussion

### The adaptive dynamics of spatial distributions of plants

Plant species typically employ a range of strategies to maintain a balance between growth and defense in response to environmental challenges [27]. Dominant species play a crucial role in affecting spatial heterogeneity and maintaining the stability of plant communities [28]. Studies have shown that the compensatory growth mechanisms adopted by plants after being grazed is related to grazing intensity, grazing system, grazing time and physiological and ecological adaptability of plants [29, 30]. Our study found that long-term grazing led to a concentrated distribution of *L. chinensis*, while *S. krylovii* showed a fragmented distribution, and the two species no longer displayed a spatial mosaic distribution under enclosure. The reason for this phenomenon may be the diverse adaptive strategies of different dominant species for coping with grazing.

*S. krylovii* is a perennial dense bunch grass [31], and it reproduces both sexually and asexually. Generally, the tillering of *S. krylovii* is centered around the mother plant, with secondary tillering occurring after the initial tillering, forming tiller clusters in an exponential manner. However, under long-term grazing disturbance, the reproductive strategies of *Stipa* may change, with sexual reproduction being somewhat suppressed, i.e., the density of vegetative growth increases, while the density of reproductive growth decreases, resulting in larger clusters of more tolerant tillers [7]. As *S. krylovii* has its growth point above ground, it is sensitive to trampling by livestock which can stimulate the vegetative growth and tillering of the population [32]. Therefore, in this study, the original continuous spatial distribution of *S. krylovii*, which spread from the mother plant to be transformed to a random, patchy distribution, and the tiller clusters may

be fragmented or miniaturized accordingly. The fragmentation of tiller clusters can also affect vegetation biomass and seed yield. Consequently, some researchers consider that the fragmentation of perennial dense bunch grasses is a positive response to grazing, and this could be developed in independent plants in the future [33].

*L. chinensis* is a perennial rhizome grass with high reproductive capacity and nutritional value [34], possessing strong adaptability that allows it to maintain a dominant position in variable environment [35]. Our study revealed that the spatial distribution of *L. chinensis* remained concentrated under both FG and CK treatments, possibly due to its adaptive traits. Some scholars have found that the spatial heterogeneity of *L. chinensis* responds positively to grazing [20]. *L. chinensis* under grazing disturbance balances its response according to the asymmetric response mechanisms of traits [36], a response that is characterized by dwarfing phenomena such as smaller stems, lower plant height, and other adaptive characteristics. These adaptations collectively act as a defense mechanism against herbivores [37]. Moreover, Zheng et al. (2020) found that grazing stimulated the compensatory growth and asexual reproduction of *L. chinensis* to some extent but had minimal effect on the spatial distribution [20]. These findings are consistent with our results in the FG treatment. This may be attributed to the fact that *L. chinensis* is a perennial rhizome grass; the tillering nodes are located underground, and the rhizomes are thicker [38], thus being less affected by destructive behaviors such as livestock foraging and trampling.

#### The dominant factors influencing the spatial distributions of plants

Geostatistics considers that structural and random factors cause variations in spatial variables [39]. Therefore, the spatial distributions of dominant species are jointly controlled by structural and random factors. Structural factors primarily refer to those that do not change over a short period of time, such as soil parent material, topography, climate and utilization modes. Random factors include the variation caused by grazing behaviors such as selective trampling, wandering, and foraging of domestic animals, resulting in sexual reproduction in plant populations. The structural ratio  $C / (C_0 + C)$ , is an important measure and represents the weight of variation distribution given by the semivariance function [3]. It reflects the proportion of spatial heterogeneity caused by structural factors within the total spatial heterogeneity. Our study found that the structural ratios for both treatments are greater than 0.75. Based on previous research results, it can be inferred that in the CK treatment, *S. krylovii* and *L. chinensis* were primarily affected by structural factors, showing a mosaic distribution with a relatively simple

spatial pattern. In contrast, despite structural factors remaining the primary causes of the spatial distribution, the influence of random factors introduced by herbivores resulted in a relatively complex spatial pattern [40].

The behaviors of herbivores such as foraging, trampling, and excreta deposition are the main external factors that control and affect the spatial distributions of plants [41]. These factors lead to small-scale spatial heterogeneity in grassland vegetation [42]. Herbivores have a preference for specific foods and can use spatial memory to select and repeatedly feed on eclipsed patches [43]. Different herbivores have varying feeding preferences. For example, cattle primarily prefer to graze on dominant grass species like *L. chinensis*, while sheep tend to favor weeds and legumes [44]. This behavior will reduce the uniformity of plant distributions and form unique spatial distribution patterns. In our study, *S. krylovii* presented a concentrated pattern in the CK treatment and a randomly distributed pattern in the FG treatment. Liu et al. (2016) found that the deposition of livestock excreta would form nutrient-rich patches [45], affecting the chemical composition of plants in a small area and resulting in changes in the spatial distribution of plant communities. The trampling of herbivores persists throughout the grazing period and has a long-lasting and direct impact on grassland components [46]. This trampling will cause mechanical damage to sessile plants and lead to the reduction of grass species that are not resistant to trampling. Lv et al. (2020) found that grazing caused the fragmentation of bunchy grasses [7], which may be the main reason for the spatially random distribution of *S. krylovii* under FG treatment.

The random factors of different herbivores can influence the characteristics of dominant species in response to grazing. Lin et al. [47] found that at a spatial scale of less than 2 m, increased grazing intensity by sheep can fragment large patches into smaller ones. Research by Augustine and Frank [25] suggests that grazing by cattle alone can enhance plant diversity on a small scale, while in natural grasslands, mixed grazing by multiple herbivore species leads to distinct changes in the spatial distribution of plants. In our study, conducted in an area with mixed cattle and sheep grazing, both *S. krylovii* and *L. chinensis* showed strong spatial autocorrelation under grazing conditions, with structure ratios greater than 0.75. This indicates that long-term grazing had not altered the dominant position of structural factors in determining the spatial distributions of plants in this grassland, consistent with the findings of Yin et al. (2017) in a moderately grazed desert steppe [48]. These results also indicate that the grassland ecosystem has a strong tolerance to random external disturbances. Under heavy grazing intensity, increased trampling by livestock causes large clumps of *Stipa* to break up into smaller clumps,



reducing the complexity of its spatial distribution, leading to a more uniform distribution and diminishing its dominance [16]. This fragmentation negatively impacts the stability and productivity of the grassland ecosystem. The spatial distribution of rhizomatous grasses like *L. chinensis* showed a clustered distribution in both treatments. Apart from its inherent tolerance, this clustering pattern is closely related to its self-regulation adaptations such as plant miniaturization [37] and tiller node changes [49]. While grazing induces changes in the spatial distributions of dominant species, the adaptive ability and self-regulatory mechanisms of these plants help maintain their dominance, thereby making the grassland ecosystem tolerant to external disturbances.

## Conclusion

The spatial distributions of *S. krylovii* and *L. chinensis* showed a mosaic pattern under enclosed conditions. In the free grazing area, the clustered distribution of *S. krylovii* disappeared, transforming into a patchy random distribution, while the concentration of *L. chinensis* remained largely unaffected. The spatial distributions of both *S. krylovii* and *L. chinensis* were dominated by structural factors. Grazing, a random factor, can lead to changes in the spatial distributions of dominant species. Additionally, long-term moderate grazing intensity benefits the growth of grazing-resistant grasses such as *S. krylovii*, maintains the spatial heterogeneity of grasslands, and promotes the healthy development of grassland ecosystems. Therefore, it is crucial to continue monitoring plant species changes and soil health in the future, providing essential data support for effective grazing management in typical grasslands.

## Abbreviations

CK	Enclosed control
CV	Coefficient of variation
FG	Free grazing
IV	Importance values
RSS	Residual sum of squares

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## Author contributions

SJL conceived and designed the study. MZL, JRW, JYY collected and analyzed the data. MZL drafted the manuscript, and JLZ, BX, LZ critically revised it for important intellectual content. XJY and SJL supervised the project. All authors read and approved the final manuscript.

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## Data availability

The data used to support the findings of this study are available from the corresponding author upon request.

## Declarations

### Ethics approval and consent to participate

The plant sample of *Stipa krylovii* and *Leymus chinensis* collected by us is not an endangered species, and has been approved by herdsmen. This sample collection complies with relevant institutional, national, and international guidelines and legislation. All steps in the study were performed in accordance with the relevant guidelines and regulations.

### Consent for publication

Not applicable.

### Competing interests

The authors declare no competing interests.

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