



## Impact of rainfall variability and grazing pressure on plant diversity in Mongolian grasslands

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### ABSTRACT

Climate and grazing are the main drivers of plant community composition and species richness in arid environments. This study aimed to examine the vegetation response to a spatial precipitation gradient, interannual rainfall variability, and grazing pressure in Mongolia. To examine the effect of a spatial precipitation gradient, we compared species richness among six sites. To investigate the effects of interannual rainfall variability and grazing pressure, we compared species richness for 2 years at two sites, in desert-steppe and steppe areas. The regional gradient in annual precipitation showed positive and negative relationships with grass richness and shrub richness, respectively, although total species richness did not vary significantly. The proportions of the different functional groups were affected by grazing pressure and rainfall variability in both zones. In the desert-steppe zone, species richness was lower in the drier year but did not vary with grazing pressure. In the steppe zone, species richness varied significantly with grazing pressure but did not vary between years. Precipitation would be more important than grazing pressure on vegetation changes in drier areas with high rainfall variability.

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### 1. Introduction

In arid and semi-arid environments, plant species richness is positively associated with water availability to vegetation (Adler and Levine, 2007; Kutiel et al., 2000; Shmida and Wilson, 1985; Ward and Olsvig-Whittaker, 1993). The water availability generally signifies total precipitation available to support plant growth, and its temporal distribution may determine the dominant plant species from year to year (Adler and Levine, 2007). The alteration of precipitation regimes under climate change is also likely to influence species richness within a local area, especially in arid and semi-arid plant communities, where water is the primary limiting resource (Sala et al., 1988). Therefore, understanding how precipitation influences species richness at both spatial and temporal scales will be critical for predicting the impacts of altered precipitation on vegetation patterns.

Disturbance caused by the grazing of large herbivores is another important determinant of plant community structure in arid and semi-arid regions (Milchunas et al., 1989). The impact of grazing on plant diversity varies across environmental gradients of precipitation and soil fertility (Milchunas et al., 1988). In water- and

nutrient-limited environments, increased grazing is expected to increase plant mortality and ultimately decrease species richness (Huston, 1994; Proulx and Mazumder, 1998). However, recent studies of specific arid ecosystems have demonstrated that the grazing impact in arid rangelands may be exaggerated and confounded by the effects of climatic variability (e.g., Sullivan and Rohde, 2002). Whether vegetation responds to grazing pressure in a predictable and directional way becomes questionable in the context of climatic variability.

The debate between equilibrium and nonequilibrium models of rangeland dynamics has not been adequately resolved (Díaz et al., 1999; Simberloff et al., 1999). The equilibrium models suggest tight coupling of plant–herbivore systems and predict that grassland degradation is due to livestock overgrazing. The nonequilibrium models suggest that vegetation dynamics are susceptible to a high level of climatic variability such that frequent droughts cause crashes in the herbivore populations (Sullivan and Rohde, 2002). Many ecologists have accepted the dualistic approach of considering both equilibrium and nonequilibrium dynamics as the most appropriate means to evaluate vegetation dynamics effectively in grasslands (Briske et al., 2003; Chesson and Case, 1986; Illius and O'Connor, 1999; Lockwood and Lockwood, 1993; Oba et al., 2000, 2003; Walker and Wilson, 2002; Wu and Loucks, 1995). A record of long-term herbaceous vegetation change reported by Fuhlendorf et al. (2001) indicated that semi-arid grasslands (average annual

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precipitation ca. 600 mm) respond to both climatic variability and grazing pressure. Differences in moisture regimes between arid and semi-arid environments may mirror a continuum between nonequilibrium and equilibrium dynamics, as suggested by Wiens (1984), such that drier environments are affected by unpredictable abiotically driven dynamics to a greater extent than are wetter environments. Therefore, in environments characterized by little, erratic rainfall, the effects of climate and grazing on vegetation would be rather complex.

The Mongolian steppe is one of the largest natural grasslands in the world (Fernandez-Gimenez and Allen-Diaz, 2001; Hilbig, 1995). Much of southern Mongolia has mean annual precipitation of less than 250 mm and is classified into two major ecological zones: the desert-steppe and steppe. These two zones are ideal systems for examining responses of plants to rainfall variation and grazing pressure. Ellis and Chuluun (1993) and Ellis (1995) suggested that nonequilibrium dynamics in Mongolia are likely to occur where the coefficient of variation of annual precipitation is greater than 33% and mean annual precipitation is less than 250 mm. However, previous studies in Mongolia have focused on the impact of grazing on vegetation productivity or species composition (Fernandez-Gimenez and Allen-Diaz, 2001; Hoshino et al., 2009; Sasaki et al., 2005, 2008; Van Staalduinen et al., 2007).

It is important to understand the main drivers of plant community composition and species richness in arid and semi-arid areas. Except for one study that tested the nonequilibrium model in central Mongolia (Fernandez-Gimenez and Allen-Diaz, 1999), few observational studies have been conducted to determine the effects of grazing pressure and rainfall variability on vegetation in Mongolia. Therefore, the aims of this study were to examine the vegetation response to a spatial precipitation gradient, interannual rainfall variability, and grazing pressure. To examine the effect of a spatial precipitation gradient, we compared species richness among six Mongolian grassland sites. To investigate the effects of interannual rainfall variability and grazing pressure in different vegetation zones, we compared species richness for 2 years at two sites, in desert-steppe and steppe areas.

## 2. Methods

### 2.1. Study area and data collection

To compare species richness across a regional gradient of mean annual precipitation, we assembled census data for six widely scattered sites in the central and southern grasslands of Mongolia (Table 1). Mean annual precipitation at these sites ranges between 94 mm in the bush desert-steppe at Hanbogd and 158 mm in the short-grass steppe at Bayan Unjuul. Vegetation surveys in the six sites were conducted during periods of peak vegetation cover (early September) in 2008, according to the phytosociological method of

Braun-Blanquet (1964). Plots for relevés had a size of 10 × 10 m, which is larger than the plot size usually recommended for phytosociological relevés in grasslands (Chytrý and Otypkova, 2003; Dierschke, 1994; Dulamsuren et al., 2005), but a standard plot size was preferred for both bushlands and grasslands to ensure complete comparability in the statistical analyses. The species composition of each plot was recorded, based on Braun-Blanquet's cover-abundance scale, and plant communities were classified on the basis of their differential species (Braun-Blanquet, 1964; Mueller-Dombois and Ellenberg, 1974). At each plot, the altitude, direction and inclination of the slope, maximum plant height, and the extent of vegetation cover were recorded. A total of 86 vascular plant species were observed at the six study sites. Our vegetation nomenclature follows Grubov (1982). Livestock density (i.e., grazing pressure) is usually highest close to water sources or settlements and decreases with distance away from such localities. Many ecological studies have sampled vegetation and soils along grazing gradients from water sources or settlements to determine the effects of grazing pressure on rangeland structure and function (Andrew and Lange, 1986; Fernandez-Gimenez and Allen-Diaz, 1999, 2001; Landsberg et al., 2003; McClaran and Anable, 1992; Sasaki et al., 2008; Todd, 2006; Tolsma et al., 1987). The Bulgan and Bayan Unjuul sites were selected as representatives of desert-steppe and steppe zones, respectively. At these two sites, we conducted vegetation surveys in early September 2008 and 2009 to analyze the effects of interannual rainfall variability and grazing pressure. A transect sampling design along the grazing gradient was chosen to establish a grazing gradient with increasing distance from a settlement, with four or five replicates (transects) at each site. The farthest plots were set at the same distance from a water source or shelter. The site surrounding each settlement was stratified into three concentric levels at the Bulgan site and four concentric levels at the Bayan Unjuul site at intervals of 5 km from a settlement. The concentric levels represented the following: 0 km from a settlement as heavy grazing, 5 km as medium grazing, and 10 km as light grazing. In addition, for the Bayan Unjuul site 35 km from a settlement represented no grazing; this was a winter grazing area that is not used in summer.

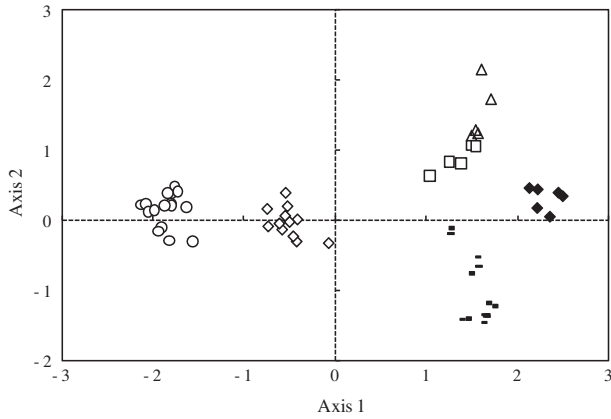
### 2.2. Data analysis

Detrended correspondence analysis (DCA; Hill, 1979) was used to visualize the general relationships between community composition and structure. Prior to ordination, species with frequency less than the median frequency were down-weighted in proportion to their frequency (Eilertsen et al., 1990). Ordination diagrams were plotted for the first and second axes; in all cases, these had considerably higher eigenvalues than the lower-order axes. Plant cover data for each species in each plot were used in these analyses.

**Table 1**  
Summary of the environmental data for the study sites.

Site name	Latitude	Longitude	Altitude (m)	Precipitation (mm) <sup>a</sup>	Temperature (°C) <sup>a</sup>		Vegetation	Dominant plant species
				mean annual	Min. (January)	Max. (July)		
Bayan Unjuul	47° 03' N	105° 57' E	1159–1269	158	−22.8	20.7	steppe	<i>Stipa krylovii</i> ; <i>Kochia prostrata</i>
Erdenedalay	46° 00' N	104° 56' E	1406–1461	138	−19.0	21.0	steppe	<i>Caragana pygmaea</i> ; <i>Cleistogenes soongorica</i>
Saikhan Ovoo	45° 28' N	103° 54' E	1308–1319	118	−19.1	20.2	desert-steppe	<i>Stipa glareosa</i> ; <i>Salsola collina</i>
Bulgan	44° 06' N	103° 32' E	1285–1376	123	−13.6	22.7	desert-steppe	<i>Caragana korshinskii</i> ; <i>Stipa gobica</i>
Dalanzadgad	43° 35' N	104° 25' E	1463–1466	131	−14.5	21.6	desert-steppe	<i>Allium polyrrhizum</i> ; <i>Salsola collina</i>
Hanbogd	43° 12' N	107° 12' E	1102–1149	94	−11.1	25.0	desert-steppe	<i>Eurotia ceratoides</i> ; <i>Zygophyllum xanthoxylon</i>

<sup>a</sup> The data are from the Institute of Meteorology and Hydrology, Mongolia. Means are based on 14 years of data from Bayan Unjuul, 14 years from Erdenedalay, 20 years from Saikhan Ovoo, 48 years from Bulgan, 44 years from Dalanzadgad, and 29 years from Hanbogd.



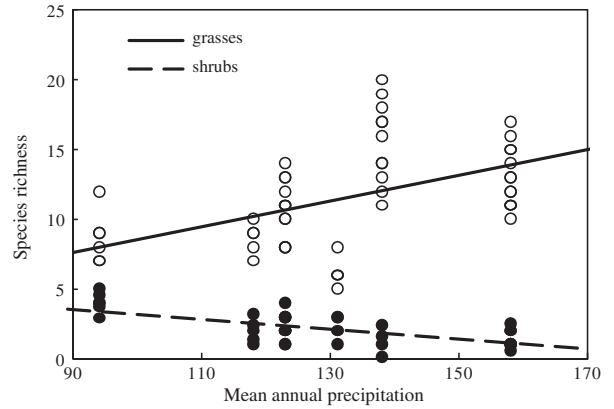
**Fig. 1.** Detrended correspondence analysis based on frequency of ground-cover plants at the sites along the study gradients. (See Table 1 for gradient definition and descriptions.) ○: Bayan Unjuul ◇: Erdenedalay □: Saikhan Ovoo - Bulgan △: Dalanzadgad ◆: Hanbogd.

To investigate whether mean annual precipitation causes a regional trend in species richness despite within-site variability, we quantified the relationship between mean annual precipitation (recorded at the nearest meteorological station) and species richness by means of linear regression based on all data points.

Repeated-measures ANOVA was used to compare the effect of distance from settlement (a proxy for grazing pressure at three levels in Bulgan site and four levels in Bayan Unjuul site) and year (two levels: 2008 and 2009) on standing species richness and proportion of life forms (annual grasses and others, including perennial grasses and shrubs). When the distance-by-year interaction was statistically significant, the repeated-measures ANOVA was followed by post hoc contrast tests (*t*-tests with Bonferroni's correction) for the between-year comparisons. All statistical analyses were performed with SPSS (version 13.0; SPSS Inc., Chicago, IL, USA) and R software (version 2.8.0, R Development Core Team., 2008).

### 3. Results

The majority of the variation along DCA axis 1 in Fig. 1 (eigenvalue = 0.746) was explained as differences between sites, which clearly showed a geographical gradient. Plots from the steppe zone were positioned near the low-score end of the axis, whereas plots from the desert-steppe zone appeared at the high-score end. The regression analysis indicated that variation in species composition at each site, which was expressed on axis 1 (Fig. 1), had a significant negative correlation with annual precipitation ( $r^2 = 0.92, P < 0.001$ ). Moving from bush desert-steppe (the dry region) to short-grass steppe (the relatively wet region), grass (perennial and annual) species richness increased from 5 to 19 species, whereas shrub species richness decreases from 5 to



**Fig. 2.** The relationship between species richness at the 100 m<sup>2</sup> scale and mean annual precipitation in the study areas. Grass species richness:  $r^2 = 0.14$ ; Shrub species richness:  $r^2 = 0.50$ . The slopes of the two regression lines are significant ( $P = 0.048$ ;  $P < 0.001$ ).

0 species (Fig. 2). The regional gradient in annual precipitation thus showed positive and negative relationships with grass richness ( $r^2 = 0.14, P = 0.048$ ) and shrub richness ( $r^2 = 0.50, P < 0.001$ ), respectively, although total species richness was not significantly correlated with annual precipitation.

Monthly rainfall during the growing season (April–September) is shown in Table 2. At the Bulgan site, in 2008 the growing season rainfall was approximately the same as that of the 1995–2009 average, but in 2009 it was considerably lower than the average. At the Bayan Unjuul site, however, in both 2008 and 2009 growing season rainfall was above the average. The gradient in species composition along DCA axis 1 in Fig. 3 generally followed the grazing gradient, with decreasing grazing pressure with increasing DCA scores at both the Bulgan (desert-steppe) and Bayan Unjuul (steppe) sites. The gradient along DCA axis 2 generally reflected the interannual variability in precipitation between 2008 and 2009. Plots measured in the year with relatively more rainfall were positioned near the lower scores, and those measured in the year with less rainfall had the higher scores on the DCA axis 2 (Table 2, Fig. 3).

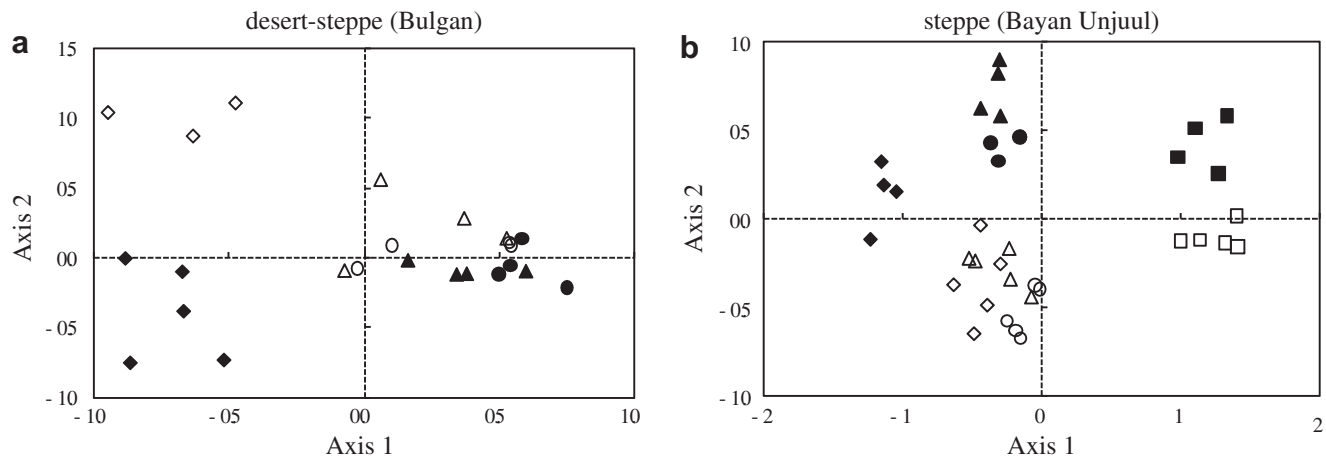
Species composition, presented as the ratio of annual species to others (perennial grasses and shrubs) was affected significantly by grazing pressure and rainfall variability at both the sites (Table 3). However, the patterns of species richness along grazing gradients differed substantially between the two ecological zones (Fig. 4). In the desert-steppe zone, species richness was significantly lower in 2009 than in 2008 but did not vary with distance from a settlement; hence, no significant distance-by-year interaction was found (Fig. 4, Table 3). The change of species richness was related to the disappearance of the considerable numbers of annual species in 2009 due to a drought during the growing season (Table 2). In the steppe zone, species richness changed significantly with grazing pressure but did not vary between years (Table 3). There was

**Table 2**  
Monthly rainfall (mm) during the growing season (April–September) at the Bulgan and Bayan Unjuul sites.

		Apr	May	June	July	Aug.	Sept.	Apr.–Sept.	Anomalies <sup>a</sup>
Bulgan (desert-steppe)	1995–2009 average	5	15	14	29	30	10	103	
	2008	5	0	40	4	54	1	104	0.01
	2009	5	13	6	3	10	0	37	-0.64
Bayan Unjuul (steppe)	1995–2009 average	5	18	27	35	44	12	141	
	2008	3	7	71	46	23	4	154	0.09
	2009	6	14	29	56	72	7	184	0.30

Data were provided by Institute of Meteorology and Hydrology of Mongolia.

<sup>a</sup> Rainfall anomalies = (growing season rainfall of study year - average) / average.



**Fig. 3.** Detrended correspondence analysis based on frequency of ground-cover plants at the two sites along the grazing gradients.  $\diamond$ : HG-2008  $\blacklozenge$ : HG-2009  $\triangle$ : MG-2008  $\blacktriangle$ : MG-2009  $\circ$ : LG-2008  $\bullet$ : LG-2009  $\square$ : NG-2008  $\blacksquare$ : NG-2009 HG: Heavy grazing; MG: Medium grazing; LG: Light grazing; NG: No grazing.

a significant distance-by-year interaction affecting species richness in the steppe zone. Species richness increased significantly only at the heavy grazing level, but there was no difference among the other three grazing pressure levels in 2009 (Fig. 4).

#### 4. Discussion

The DCA identified a clear separation of species composition between regions, and the regions separated along DCA axis 1 could be explained by the water availability, which was related to precipitation (Fig. 1). Moreover, clear relationships between mean annual precipitation and species richness was revealed by functional group analysis (Fig. 2), with positive and negative effects of precipitation on grass richness and shrub richness, respectively. This finding agrees with previous reports showing that this relationship is common in North America (Paruelo and Lauenroth, 1996), as well as in northeastern China and southeastern Mongolia (Ni, 2003). Adler and Levine (2007) also demonstrated that species richness had a positive relationship with mean annual precipitation. However, our result did not support the conclusion that total species richness responded significantly to precipitation at the regional spatial scale (Fig. 2). One possible explanation for the result is that the mean annual precipitation range among the six sites in our study (94–158 mm) may be not large enough to elicit a response of total species richness to precipitation. Instead, we found that the species richness of each plant functional type was affected by precipitation. Much of southern Mongolia receives less

than 200 mm of precipitation annually, and species richness for all study sites is low (fewer than 21 species in each plot). Here, water is the key limiting resource and a slight change in rainfall will greatly affect the species composition at the regional spatial scale. Therefore, to predict the impacts of altered precipitation on vegetation patterns it seems more important to understand the influence of rainfall on the species richness of each plant functional type rather than on total species richness at the regional spatial scale.

Species composition (the ratio of annual to other species types) was affected by rainfall variability and grazing pressure in both desert-steppe and steppe (Fig. 3, Table 3). A distinct separation between habitat types was noted in the DCA, corresponding to species composition (Fig. 3). In addition, the habitats of different plots were separated according to distance from a settlement (i.e., grazing pressure) and years; DCA axis 1 corresponded to grazing pressure, and DCA axis 2 corresponded to habitat attributes based on the interannual rainfall variability. In both the desert-steppe and steppe zones, the plots near a settlement with high grazing pressure were separated more than those far from a settlement with low grazing pressure along DCA axis 2, indicating that increasing livestock grazing leads to species composition being more susceptible to rainfall variability.

Our findings indicate that plant species richness has different responses to grazing pressure and rainfall variability (Table 3). No effect of the distance from a settlement at the desert-steppe site (Table 3) implies that grazing has little influence on species richness. This result supports the nonequilibrium model, which proposes that vegetation in desert-steppe ecosystems varies between years, suggesting that interannual variation in precipitation is an important determinant of species richness in the desert-steppe zone (Ellis and Swift, 1988; Fernandez-Gimenez and Allen-Diaz, 1999; Sullivan and Rohde, 2002).

In the wetter steppe zone of our study area, species richness varied with grazing pressure but not between years (Table 3). In addition, the distance-by-year interaction was also significant (Table 3), and species richness increased significantly only in the area with heavy grazing pressure in 2009 (Fig. 4), suggesting that species richness under heavy grazing pressure is sensitive to interannual changes in rainfall. Although this finding may suggest that grazing pressure plays a more important role in species richness than that of rainfall variability, the lack of interannual variability in species richness was probably a result of sufficient rainfall during the growing season (April–September) both in 2008 and 2009 in this steppe area (Table 2). The differences in the temporal

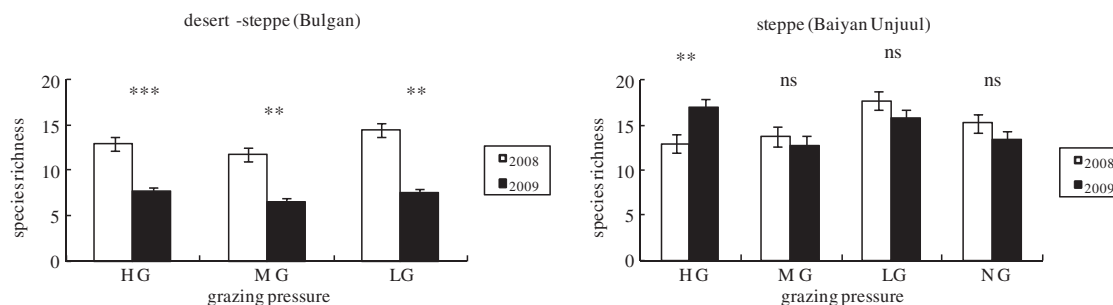
**Table 3**

Results of the repeated-measures ANOVA for the effects of distance from settlement (proxy of grazing pressure) and year on species richness and ratio of annual to other species (2008 and 2009) in the two different vegetation zones.

Variable	Source	desert-steppe (Bulgan)			steppe (Bayan Unjuul)		
		df	F	P	df	F	P
Richness	Distance	2	2.28	ns	3	7.12	**
	Year	1	77.37	***	1	0.67	ns
	Distance x year	2	0.77	ns	3	6.52	**
	Between error	9	-	-	12	-	-
	Within error	9	-	-	12	-	-
Ratio	Distance	2	13.51	**	3	11.28	***
	year	1	64.33	***	1	5.43	*
	Distance x year	2	4.49	*	3	1.95	ns
	Between error	9	-	-	12	-	-
	Within error	9	-	-	12	-	-

ns, not significant; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ .





**Fig. 4.** Changes in species richness with distance from settlement (proxy for grazing pressure) between years (our proxy for annual rainfall) in the steppe and desert-steppe ecological zones. Each bar presents the mean  $\pm$  1 SE of five or four plots. ns, not significant; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ .

rainfall pattern during the growing season between 2008 and 2009 may have driven the vegetation changes at each grazing pressure level. Although these findings improve our understanding of the dynamics of grassland ecosystems in dry regions, this study was limited by the small area examined and 2-year study period.

At the regional spatial scale, the grass species richness increased and shrub species richness decreased as precipitation increased. At a biannual temporal scale, rainfall variability was the more important determinant of species richness, but grazing pressure did not have a significant impact on species richness in the desert-steppe zone. However, species richness changed with grazing pressure in the steppe zone. Our findings indicate that the desert-steppe zone (the dry region) corresponds with the nonequilibrium models of grazing system dynamics, whereas the steppe zone (the relatively wet region) is characterized by equilibrium systems. Precipitation would be more important than grazing pressure as a cause of vegetation changes in dry areas with high variability of rain, although long-term systematic research conducted over a wider area is needed to confirm our general findings.

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