Original Article

Difference in determinants and changing patterns of plant community composition with and without grazing across semi-arid and arid regions in Mongolian steppe

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Highlights

- Determinants and changing patterns in plant community composition of Mongolian steppe along aridity gradients in semi-arid and arid regions were investigated with the consideration of the effects of aridity and edaphic variables for communities with the absence/presence of livestock grazing, respectively.
- Although aridity had significant impacts on community composition regardless of the regions and the absence/presence of grazing, the difference in response patterns was observed between the regions, which did not depend on grazing.
- Regardless of the aridity levels, the effects of soil pH on community composition were eliminated by grazing.

Abstract

Aridity, edaphic variables related to aridity, and livestock grazing are major drivers of plant community composition across dryland grasslands. With accounting these factors, little is known about differences in determinants and changing patterns along aridity gradients with

different average of aridity. Thus, the comparative investigations of communities without and with grazing in semi-arid and arid regions are suitable to clarify the difference in compositional responses along aridity gradients between potential vegetations and degraded ones with grazing. We investigated compositional changes of communities without/with grazing in semi-arid (north) /arid (south) regions across Mongolia. The compositional changes based on Bray-Curtis dissimilarity were investigated by generalized dissimilarity modeling, including geographic distance, aridity, soil pH, and sand and clay contents as independent variables. The determinants and changing patterns of community composition were compared among the four groups.

Aridity had significant impacts on community composition regardless of the regions and the absence/presence of grazing. However, without the dependency on grazing, the difference in response patterns was observed between the regions. The compositional change was steeper especially at the upper edge of aridity rather than the lower edge in the arid region. This indicates the vulnerability of plant communities to aridity shifts due to future climate change in desert steppe of Mongolia. In addition, regardless of the regions, the effects of soil pH on community composition were eliminated by grazing. Because soil pH indirectly affected by aridity shifts can have impacts on community composition of potential vegetations without grazing, the long-term monitoring of vegetation dynamics needs observations of both of communities without and with grazing.

Keywords

dryland, Eurasia steppe, generalized dissimilarity modeling, grassland, soil pH.

Introduction

Plant community composition is a central factor determining the impacts of climate change and anthropogenic disturbances on ecosystem structures and functioning (Chapin et al., 2000). Across dryland ecosystems, aridity and livestock grazing are the most influential factors on these facets via the changes in plant community composition (Maestre et al., 2016).

Berdugo et al. (2020) reported abrupt shifts in the ecosystem structures (e.g. plant cover and species richness) along a broad gradient of aridity. Additionally, aridity affects not only water availability but also edaphic variables through long-term feedback from vegetations (Berdugo et al., 2020; Delgado-Baquerizo et al., 2013; Moreno-Jiménez et al., 2019) Because edaphic variables can have impacts on the patterns of community composition across dryland grasslands (Sasaki et al., 2008b; Zemmrich et al., 2010), the consideration of both of aridity and edaphic variables associated with aridity is required to clarify community assembly in drylands. However, little is known about the consistency in patterns of changes in community composition among different aridity gradients with this consideration. Understanding consistency or inconsistency in compositional changes across different gradients of aridity can provide implications for the impacts of aridity shifts under climate change on plant communities and their functioning in dryland ecosystems.

Grassland vegetations are widely used for livestock grazing to support secondary

production in drylands. Numerous studies have revealed the impact of grazing on community composition mediated by selective herbivory (Díaz et al., 2007; Li et al., 2022; Sasaki et al., 2008a). The grazing impacts on community composition can differ according to differences in water availability. Previous studies have demonstrated that the relative magnitude of grazing impacts on vegetation is relatively low in more arid regions (Herrero-Jáuregui and Oesterheld, 2018; Price et al., 2022). However, regardless of aridity levels, community composition can be drastically altered and homogenized by high intensity of grazing, namely overgrazing (Ahlborn et al., 2020; Sasaki et al., 2009b, 2008a; Wang et al., 2017). Thus, the patterns of changes in community composition along aridity gradients in grazed grasslands can be confounded depending on grazing. To infer how the changes of community composition along different aridity gradients will be driven by climate change, the comparisons of compositional changes are essential with the consideration of the interaction between aridity levels and grazing. Notably, these comparisons have not been conducted.

Here, we investigated the patterns of changes in plant community composition along aridity gradients with different levels of average aridity (semi-arid and arid regions) in the Mongolian steppe depending on the absence/presence of grazing (without/with the long-term exclosure of livestock). Mongolia covers a vast area of the eastern part of the Eurasian Steppe. In Mongolia, the climate is spatially characterized by broad variations in aridity associated with

temperature and precipitation (Vandandorj et al., 2017). Suzuki et al. (2022) demonstrated that aridity was the important driver of plant community composition across the whole range of Mongolia. Thus, we tested the research questions below mentioned to provide implications into the vulnerability of the Mongolian steppe communities and the long-term monitoring of vegetation dynamics to climate change: 1) whether and how the effects of aridity and edaphic variables on community composition differ between semi-arid and arid grasslands, and 2) does grazing alter these effects.

Materials and methods

Across Central Mongolia, ranging from semi-arid to arid regions, over 600 km, 12 study sites were selected at the meteorological sites of the Mongolian Information and Research Institute of Meteorology, Hydrology, and Environment (IRIMHE) (Table 1, and Figure S1). We aimed to ensure that the study area covered a range of vegetation types within the rangeland ecosystems of Mongolia. Central Mongolia has the typical climate of Central Asia, which is characterized by hot and short summers with approximately 70 % annual precipitation and cold winters, including extreme climate events such as drought. Based on the climate data between 1978 and 2017 provided by IRIMHE, the mean annual precipitation ranged from 97 mm at Tsogt-Ovoo to 333 mm at Darkhan; the mean annual temperature ranged from -0.8 °C at Ugtaal

to 7.6 ℃ at Khanbogd. Thus, there is a wide gradient of aridity from north to south regions (Figure S1), which supports three main vegetation types: forest steppe, steppe, and desert steppe (Table 1).

We set three 5 × 5 m blocks, which included three 1 × 1 m plots, at inside and outside of meteorological sites (50 × 50 m), to observe the heterogeneity at both block- and site-level scales. All the sites had ungrazed and grazed replicates. Ungrazed ones were exclosed for at least 50 years to avoid livestock grazing. Because the distances between ungrazed and grazed replicates in each site varies among sites, from a minimum of 25 m to a maximum of 3 km, the comparison of community composition between ungrazed and grazed replicates in each site was not performed in this study. In each plot, vegetation was sampled by identifying all species rooting in each plot, and absolute cover (%) of each species was recorded from July to August 2022. Then, the vegetation data were pooled for each block. Simpson diversity index, which reflects the diversity index mainly based on relative abundance of dominant species, was almost saturated when the vegetation data of more than two plots was used for the calculation of Simpson index in each site (Figure S2).

Aridity, which is calculated as [1–precipitation/potential evapotranspiration], based on climatic data for the 1970–2000 period was obtained from the Global Aridity Index and Potential Evapotranspiration Climate Database v3 (Trabucco and Zomer, 2022). The edaphic

variables were investigated based on the measurement of a soil sample in each block: total nitrogen content in cg/kg; soil organic carbon content in dg/kg; soil pH in H_2O; clay, sand, and silt content mass fraction in %. Soil cores with 5 cm in diameter and 10 cm in length in three plots were pooled by each block, and used for the measurement of edaphic variables. Because of the high level of correlations (absolute value of a correlation > 0.6) between aridity, and total nitrogen and soil organic carbon, and between sand and silt content, we used the aridity, soil pH, sand content, and clay content as the environmental variables in the subsequent analysis.

Nonmetric multi-dimensional scaling (NMDS) based on Bray-Curtis dissimilarity was performed for the whole dataset of vegetation using the function 'metaMDS' of the R package 'vegan.' The dimensional reduction to two dimensions was performed because the stress value (0.093) was lower than 0.2 (Kruskal, 1964). In addition, the clustering based on Ward's algorithm was conducted using the Bray-Curtis dissimilarity matrix.

We performed the analysis independently for the following four groups: the groups from the north (semi-arid) and south (arid) regions in Mongolia without/with grazing (north-ungrazed, north-grazed, south-ungrazed, and south-grazed). To assess the difference in community composition among the study sites, Bray-Curtis dissimilarity was calculated for each group. The abundance-based dissimilarity was then partitioned into balanced variation in abundance and abundance gradient using the function 'beta.multi.abund' of the R package

148 ‘betapart’ (Baselga, 2017). This partitioning informs relative contributions of species turnover
149 (balanced variation) and nestedness (abundance gradient) to community composition difference.
150 Moveorver, to identify factors influencing community compositions, we applied generalized
151 dissimilarity modeling (GDM; Ferrier et al. (2007)). GDM is a matrix regression technique that
152 permits non-linear responses of compositional dissimilarity to spatial or environmental
153 gradients. This approach has an additional advantage to depict the rate of compositional shift at
154 any point along the gradient of a variable because GDM fits monotonically increasing flexible
155 *I*-spline functions for each independent variable. When a *I*-spline was plotted, the maximum
156 height depicts the magnitude in an effect of a given variable on compositional dissimilarity
157 (partial dissimilarity) with holding all the other independent variables constant. The first
158 derivatives (slopes) of a spline indicates the rate of compositional shift at any point along the
159 gradient of a variable. Using the function ‘gdm’ of the R package ‘gdm’, we fitted full GDMs
160 with pairwise geographical distance and the selected environmental variables as independent
161 variables for each group. These models were fitted with the three *I*-spline basis functions per
162 variable, and regression coefficient at each point (lower edge, mid-point, and upper edge) along
163 an independent variable was estimated. The uncertainty for each GDM plot (standard deviation)
164 was calculated using the function ‘plotUncertainty’ with 1,000 bootstrap iterations. Additionally,
165 we fitted GDMs with a single independent variable. From these models, the significance of each

166 variable was calculated using Monte Carlo permutation by the function 'gdm.varImp.' We
167 investigated 1) whether and how the effects of aridity and edaphic variables on community
168 composition differ between semi-arid and arid grasslands, based on the comparisons in the
169 results of GDMs between the north and south regions. In addition, the comparisons in the results
170 of GDMs between the ungrazed and grazed communities assessed that 2) does grazing alter
171 these effects. To check correlations between the matrices of distance (geographical distance and
172 differences in the selected environmental variables), the calculation of Mantel's correlation
173 coefficient based on Spearman correlation coefficient and Mantel test for each pair of the
174 variables were performed.
175
176 **Results**
177 The result of NMDS and clustering showed that there were mainly two groups of community
178 composition along the first axis (Figure S3–S5). These two groups corresponded to the
179 communities in the north (forest steppe) and south (steppe and desert steppe) regions in Central
180 Mongolia (Figure S5). The partitioning of Bray-Curtis dissimilarity exhibited the large
181 contribution with more than 90% of balanced variation in abundance (species turnover) rather
182 than abundance gradient (nestedness) (Table S1). GDMs revealed that the significant effects of
183 geographic distance and aridity on the variation of community composition across all the groups

184 (Table 2). On the other hand, only in the ungrazed communities of the both regions, the impacts
185 of soil pH on community composition were significant. We observed the similar response
186 patterns of community composition (partial Bray-Curtis dissimilarity) to geographic distance
187 and soil pH in the both regions (Table 2, and Figure 1). However, the different response patterns
188 to aridity were visually observed between the north and south regions: the steeper slope in the
189 lower edge of aridity and saturated response in the upper edge in the north region, and the
190 steeper response in the mid-point and upper edge in the south region. This pattern was not
191 depended on the absence/presence of grazing. Mantel correlation coefficients between
192 geographic distance and aridity difference in the north and south regions were similarly high,
193 0.748 and 0.790, respectively (Table S2).
194

195 **Discussions**

196 Although aridity had significant impacts on community compositions in both of the semi-arid
197 and arid regions of Mongolia (Table 2), we firstly demonstrated the difference in response
198 patterns along the aridity gradients between these regions regardless of grazing (Figure 1). Thus,
199 grazing did not confound the aridity impacts on community composition. The changes in
200 community composition in the south and arid region was abrupt especially at the upper edge of
201 aridity (Figure 1). This pattern might be mainly attributed to the relatively high level of

environmental filtering and species turnover because of abiotic and biotic factors by high level of aridity. Because of the physiological limitations associated with aridity, the dominance of stress-tolerant species and exclusion of non-tolerant species can often be observed in dryland ecosystems (Berdugo et al., 2019; Grime, 1977; Le Bagousse-Pinguet et al., 2017). Previous studies have also demonstrated that high aridity contributes to the severe limitations of not only water availability but also soil nutrient availability, such as nitrogen, carbon, and micronutrients, via long-term feedback from vegetations (Berdugo et al., 2020; Delgado-Baquerizo et al., 2013; Moreno-Jiménez et al., 2019), resulting in severe environmental filtering by the abiotic factors associated with aridity. As a biotic factor, species turnover via competitive exclusion by highly adapted species in severely arid environments (Berdugo et al., 2019; Grime, 1977; Macarthur and Levins, 1967; Michalet et al., 2014) might attribute to the observed response patterns of community composition in this study. Increasing aridity can lead to the dominance of aridity specialists and an increase in the relative importance of competitive exclusion by the superior specialists, rather than facilitation (Berdugo et al., 2019). Some of previous studies have indicated that negative effects on water availability by aridity specialists (e.g. shrub species) can cause competitive exclusion in dryland ecosystems (Butterfield et al., 2016; O'Brien et al., 2017). In this study, one or two shrub species were dominant or predominant in the sites with the highest aridity (e.g., *Zygophyllum kaschgaricum*, *Potaninia mongolica*, *Anabasis brevifolia*,

220 and *Salsola passerina*; Table 1) In addition, the relative abundance of these shrub species was
221 positively correlated with aridity (Table S3), which might support the competitive exclusions
222 by shrub species.

223 Our study also emphasized that the elimination of the effects of soil pH on grassland
224 community composition across the semi-arid and arid regions by grazing (Table 2, and Figure
225 1). Although the relationships between species richness and soil pH, which is related to nutrient
226 availability, were negative or absent in semi-arid and arid regions (Palpurina et al., 2017), the
227 community composition including relative abundance of component species only without
228 grazing was significantly affected by soil pH in both of the semi-arid and arid regions. This
229 indicated that the grazed communities lost some variations of community composition
230 associated with spatial heterogeneity of soil pH. In a coastal dune community, grazing removed
231 the impact of soil pH on community composition (Tahmasebi Kohyani et al., 2008). In addition,
232 grazing drastically decreased the number of species of which abundance were strongly affected
233 by soil pH in a limestone plant community (Amezaga et al., 2004). Selective herbivory by
234 livestock can lead to communities with biased life history and functional traits (e.g. annual and
235 small-height plants) (Díaz et al., 2007), resulting in community composition less sensitive to
236 soil pH via the reduction in diversity of responses to nutrient heterogeneity among species.

237 Our study indicated the vulnerability of plant communities to aridity shifts due to future

climate change, especially in the upper edge of aridity range of Mongolia, namely desert steppes. Because accurate threshold detections for community composition along the aridity gradients (Berdugo et al., 2020) could not be performed in this study, future studies should use continuous and intensive vegetation sampling across the whole range of the Eurasian steppe and other regions. As a limitation in this study, there is no observation of temporal variability of vegetation and aridity. For example, Sasaki et al. (2009a) observed the inter-annual variations of plant community composition in the Mongolian steppe. Then, we propose the temporal observations of the relationships between community composition, aridity, and edaphic variables along multiple aridity gradients as a next step for understanding community assembly related to aridity, and its spatial and temporal variability. As another important aspect of this study, we raised the elimination of the impacts of soil pH, which is positively correlated with aridity globally (Moreno-Jiménez et al., 2019), on community composition by grazing. Because soil pH can have impacts on community composition of potential vegetations via indirect effects of aridity shifts, our study empathized the importance of not only grazed communities but also ungrazed ones for the long-term monitoring regarding vegetation dynamics exposed to climate change.

Ethics approval

Not applicable.

Consent to participate

All the authors approved participation in this study.

Consent for publication

All the authors approved the publication of this study.

Data availability

Data are available from the corresponding author upon reasonable request.

Code availability

Codes are available from the corresponding author upon reasonable request.

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 study.

Author Contributions

N.I.I., G.B., G.T., M.K., and T.S. designed the study. All the authors contributed to the field surveys. N.I.I. performed the analyses and wrote the first draft of the manuscript. All the authors have contributed to the revisions.

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Tables and figures

Table 1. Locations, aridity, vegetation type, and dominant species of the 12 study sites. Aridity is calculated as 1 – (precipitation/potential evapotranspiration).

Region	Site	ID	Latitude	Longitude	Aridity	Vegetation	Dominant species
North (semi-arid) region	Erdenet	ERD	49°02'07.08"N	106°56'20.74"E	0.62	Forest steppe	*Elymus chinensis, Koeleria macrantha, Medicago ruthenica*
	Hutag	HUT	49°23'37.32"N	106°50'50.38"E	0.64	Forest steppe	*Artemisia frigida, Stipa krylovii, Medicago ruthenica*
	Bulgan	BUL	48°49'05.52"N	106°54'04.54"E	0.64	Forest steppe	*Agropyron cristatum, Stipa krylovii, Cleistogenes squarrosa*
	Tarialan	TAR	49°36'33.12"N	106°47'56.30"E	0.65	Forest steppe	*Artemisia frigida, Cleistogenes squarrosa, Heteropapus hispidus*
	Darkhan	DAR	49°29'25.44"N	107°03'45.58"E	0.69	Steppe	*Carex pediformis, Artemisia scoparia, Heteropapus hispidus*
	Ugtaal	UGT	48°15'29.16"N	107°01'37.27"E	0.72	Steppe	*Potentilla acaulis, Elymus chinensis, Stipa krylovii*
	Zuunmod	ZUU	47°42'47.52"N	107°07'48.46"E	0.72	Steppe	*Artemisia frigida, Stipa krylovii, Arenaria capillaris*

	Mandalgobi	MAN	45°44'35.52"N	107°05'03.43"E	0.87	Desert steppe	*Carex stenophylloides, Stipa glareosa, Allium polyrrhizm*
South (arid) region	Dalanzadgad	DAL	43°34'37.92"N	106°57'40.39"E	0.92	Desert steppe	*Stipa gobica, Artemisia pectinata, Convolvulus amanii*
	Saikhan	SAI	44°05'42.00"N	106°54'09.12"E	0.92	Desert steppe	*Convolvulus amanii, Stipa gobica, Cleistogenes songorica*
	Tsogt-Ovoo	TSO	44°25'23.52"N	107°01'16.39"E	0.93	Desert steppe	*Allium polyrrhizm, Anabasis brevifolia, Salsola passerina*
	Khanbogd	KHA	43°11'44.52"N	107°08'46.46"E	0.94	Desert steppe	*Zygophyllum kaschgaricum, Cleistogenes songorica, Potaninia mongolica*

402

403 **Table 2.** Regression coefficients and their significance of geographic distance, aridity, and soil pH based on generalized dissimilarity

404 modeling (GDM) in ungrazed and grazed communities of the north and south regions. Regression coefficients on a spline (in Figure 1) at the

405 lower edge, mid-point, and upper edge of each independent variable in each group (north-ungrazed, north-grazed, south-ungrazed, and south-

406 grazed) are shown. Bold characters denote statistically significant variables.

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Region	Ungrazed/grazed community	Proportion of variation explained (%)	Independent variable	Regression coefficient		*P* value
North (semi-arid) region	Ungrazed community	66.3	**Geographic distance**	lower edge	0.705	<0.001
				mid-point	0.000	
				upper edge	0.000	
			Aridity	lower edge	0.626	0.003
				mid-point	0.000	
				upper edge	0.000	
			pH	lower edge	0.141	0.010
				mid-point	0.000	
				upper edge	0.909	
			Sand	lower edge	0.000	0.231
				mid-point	0.000	
				upper edge	0.012	

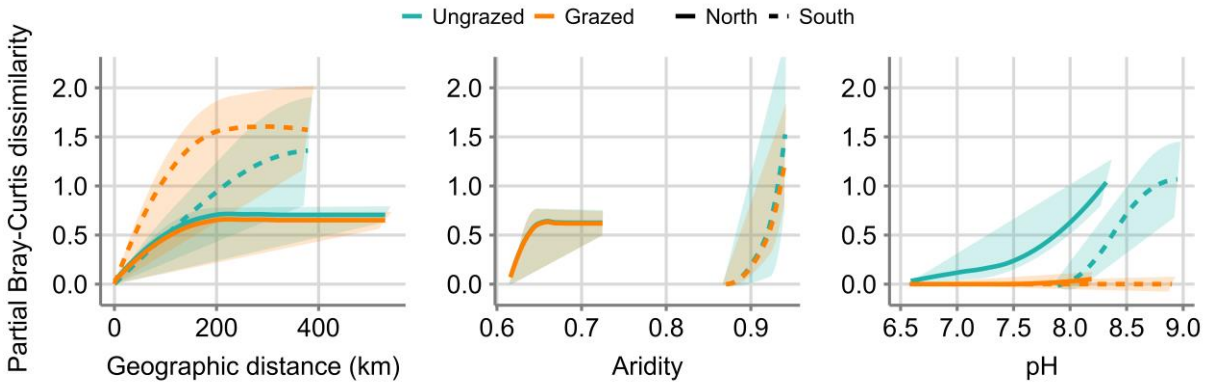
			Clay	lower edge	0.000	
				mid-point	0.000	0.633
				upper edge	0.000	
	Grazed community	55.9	**Geographic distance**	lower edge	0.651	
				mid-point	0.000	<0.001
				upper edge	0.000	
			Aridity	lower edge	0.618	
				mid-point	0.000	0.004
				upper edge	0.000	
			pH	lower edge	0.000	
				mid-point	0.000	0.337
				upper edge	0.053	
			Sand	lower edge	0.000	
				mid-point	0.000	1.000
				upper edge	0.000	
			Clay	lower edge	0.137	
				mid-point	0.000	0.328
				upper edge	0.000	
South (arid) region	Ungrazed community	77.6	**Geographic distance**	lower edge	0.588	
				mid-point	0.765	0.008
				upper edge	0.000	
			Aridity	lower edge	0.000	
				mid-point	0.828	0.001
				upper edge	0.841	

		pH	lower edge	0.000	0.007
			mid-point	1.066	
			upper edge	0.000	
		Sand	lower edge	0.000	0.423
			mid-point	0.000	
			upper edge	0.000	
		Clay	lower edge	0.000	1.000
			mid-point	0.000	
			upper edge	0.032	
Grazed community	78.0	**Geographic distance**	lower edge	1.572	<0.001
			mid-point	0.019	
			upper edge	0.000	
		Aridity	lower edge	0.000	<0.001
			mid-point	0.753	
			upper edge	0.599	
		pH	lower edge	0.000	1.000
			mid-point	0.000	
			upper edge	0.000	
		Sand	lower edge	0.000	0.317
			mid-point	0.000	
			upper edge	0.447	
		Clay	lower edge	0.000	0.741
			mid-point	0.000	

	upper edge	0.051

408

Figure 1. Relationships between partial Bray-Curtis dissimilarity and geographic distance, aridity, and soil pH based on generalized dissimilarity modeling (GDM). The estimated splines and their confidence intervals are denoted.



Supplementary information

Table S1. Partitioning of Bray-Curtis dissimilarity to balanced variation in abundance (species turnover) and abundance gradient (nestedness).

Region	Ungrazed/grazed community	Balanced variation in abundance (%)	Abundance gradient (%)
North (semi-arid) region	Ungrazed community	97.6	2.4
	Grazed community	97.2	2.8
South (arid) region	Ungrazed community	95.4	4.6
	Grazed community	91.4	8.6

Table S2. Mantel correlation coefficients based on Spearman's ρ between variables in ungrazed and grazed communities of the north and south regions. Bold characters denote statistically significant correlations.

Variable	Variable	North_Ungrazed	North_Grazed	South_Ungrazed	South_Grazed
Geographic distance	Aridity	**0.748**	**0.748**	**0.790**	**0.790**
Geographic distance	pH	0.128	**0.236**	0.117	**0.327**
Geographic distance	Sand	**0.188**	**0.275**	0.137	**0.460**
Geographic distance	Clay	0.072	-0.036	-0.010	-0.074
Aridity	pH	0.079	**0.174**	0.008	**0.472**
Aridity	Sand	**0.336**	**0.237**	0.171	**0.255**
Aridity	Clay	-0.050	0.050	0.089	-0.088
pH	Sand	0.037	**0.176**	-0.009	-0.030
pH	Clay	**0.289**	-0.006	-0.019	0.024
Sand	Clay	**0.261**	0.069	**0.423**	0.132

Table S3. Spearman's ρ between aridity and relative abundance of shrub species in ungrazed and grazed communities of the north and south regions. Bold characters denote statistically significant correlations.

Region	Fence	ρ
North (semi-arid) region	Ungrazed community	0.295
	Grazed community	0.106
South (arid) region	Ungrazed community	**0.622**
	Grazed community	**0.644**

Figure S1. Spatial distribution of the 12 study sites and aridity in Mongolia. Aridity is calculated as 1 – (precipitation/potential evapotranspiration).

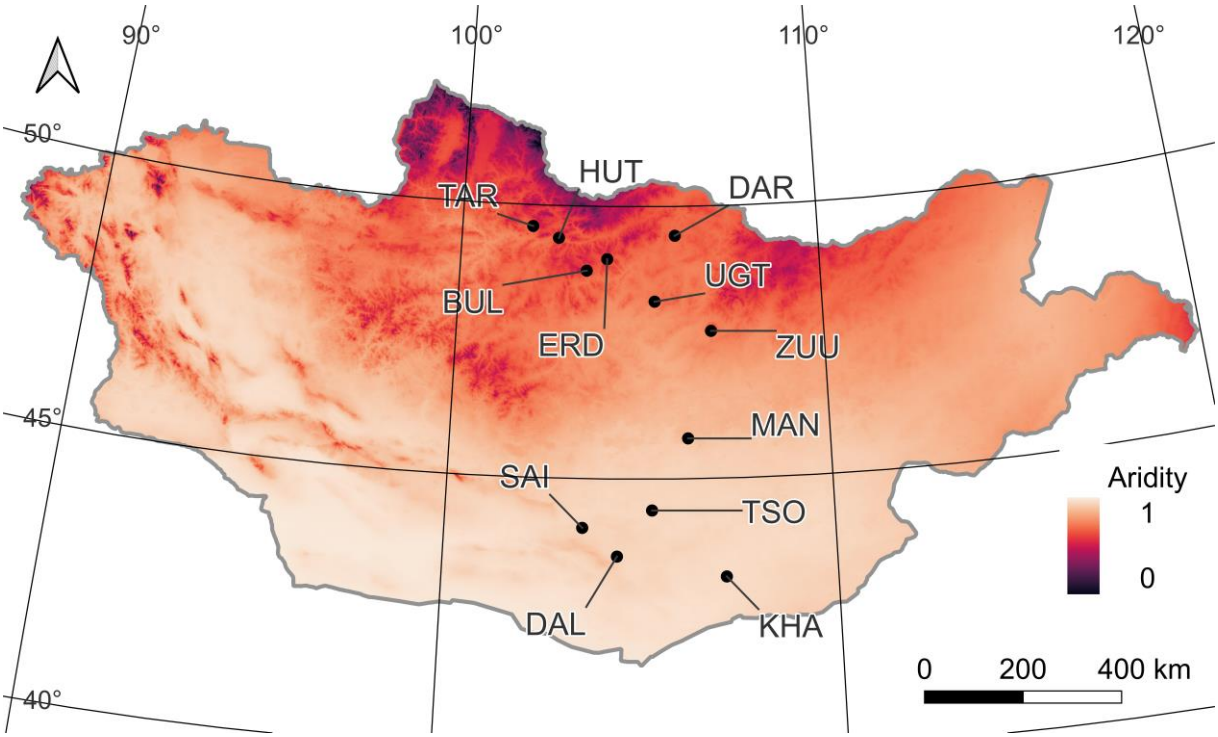


Figure S2. Relationships between number of plots and Simpson diversity index of ungrazed and grazed communities in each site.

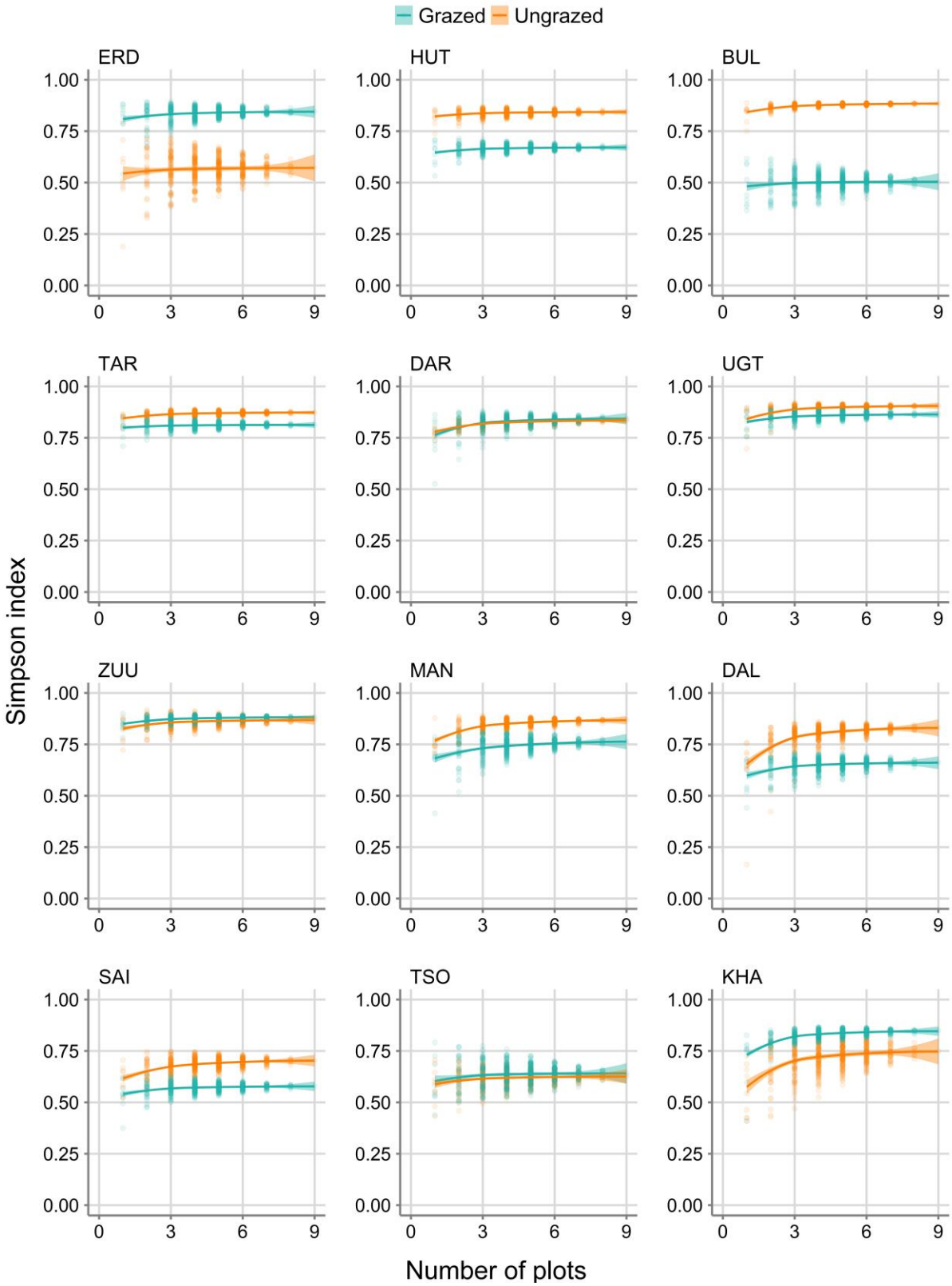


Figure S3. Result of nonmetric multi-dimensional scaling (NMDS) based on Bray-Curtis dissimilarity of ungrazed/grazed communities in the north and south regions.

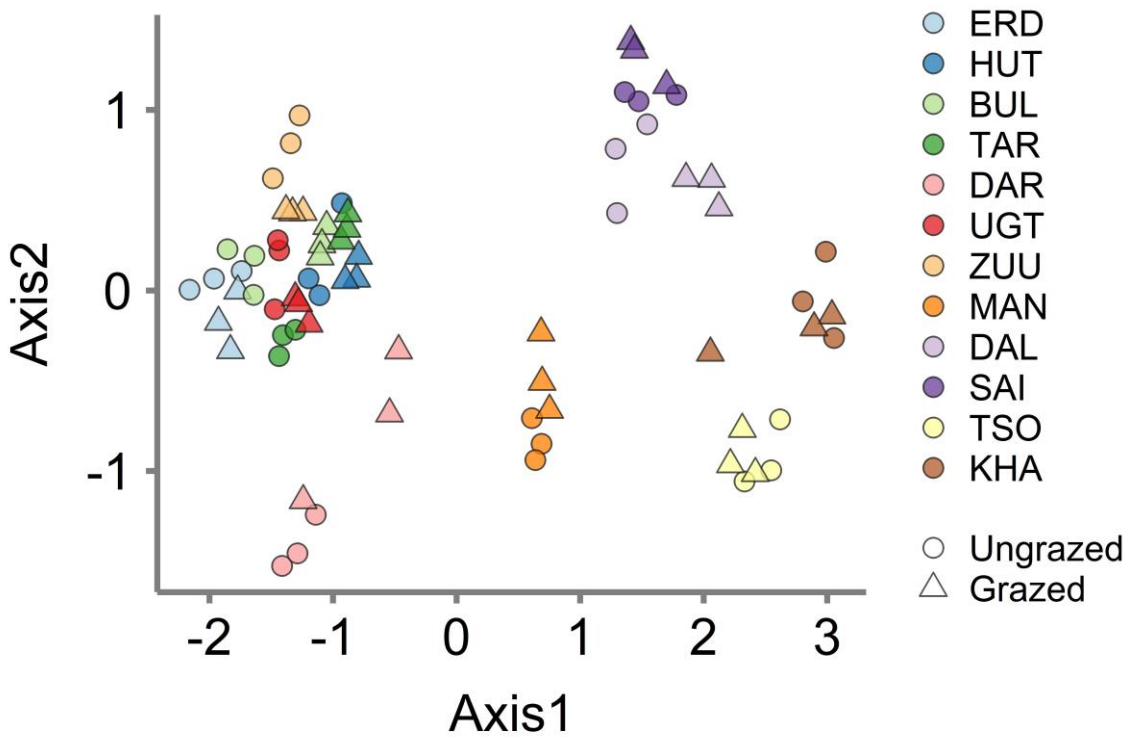


Figure S4. Result of loading values of species in nonmetric multi-dimensional scaling (NMDS) based on Bray-Curtis dissimilarity of ungrazed/grazed communities in the north and south regions.

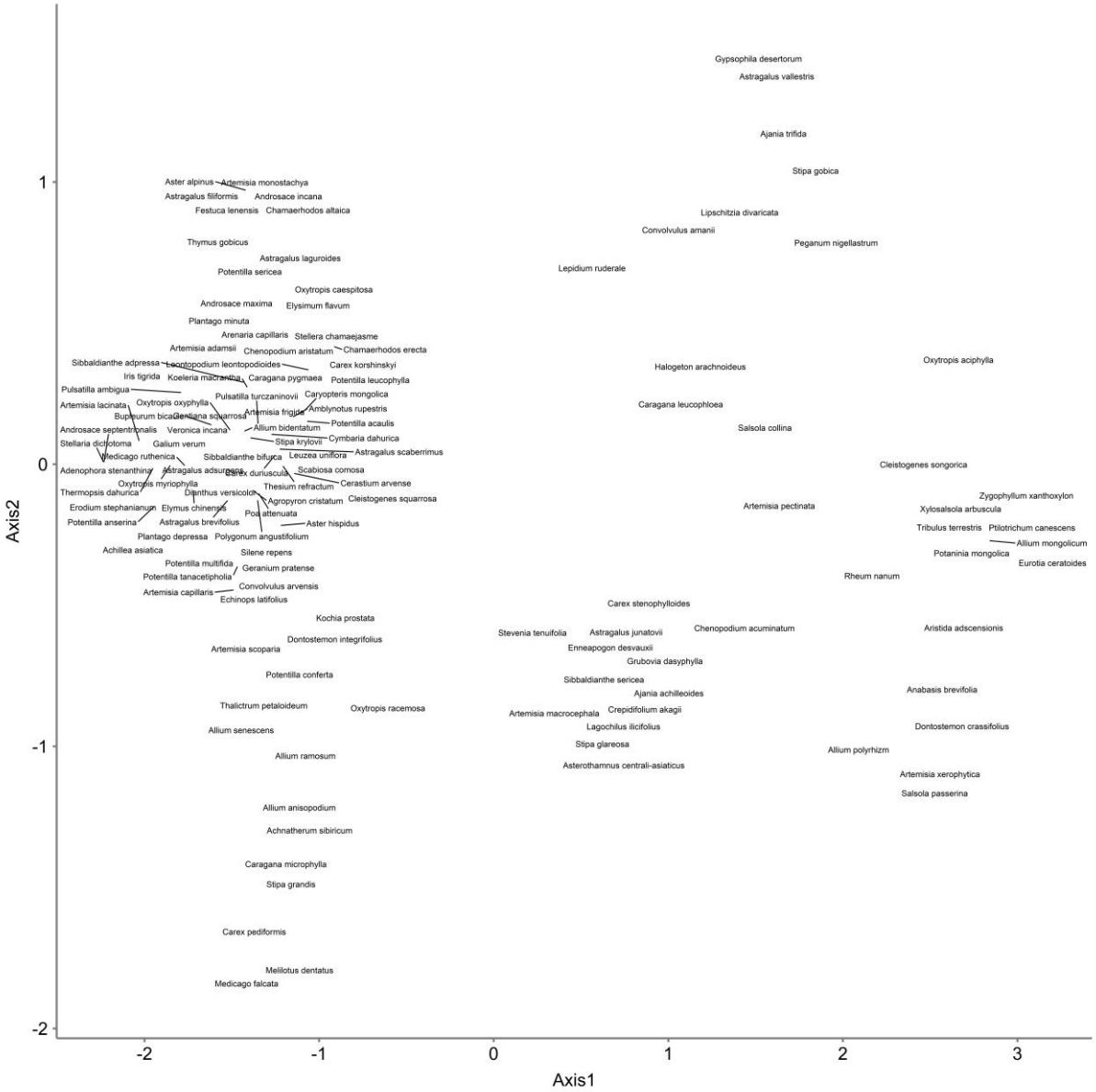
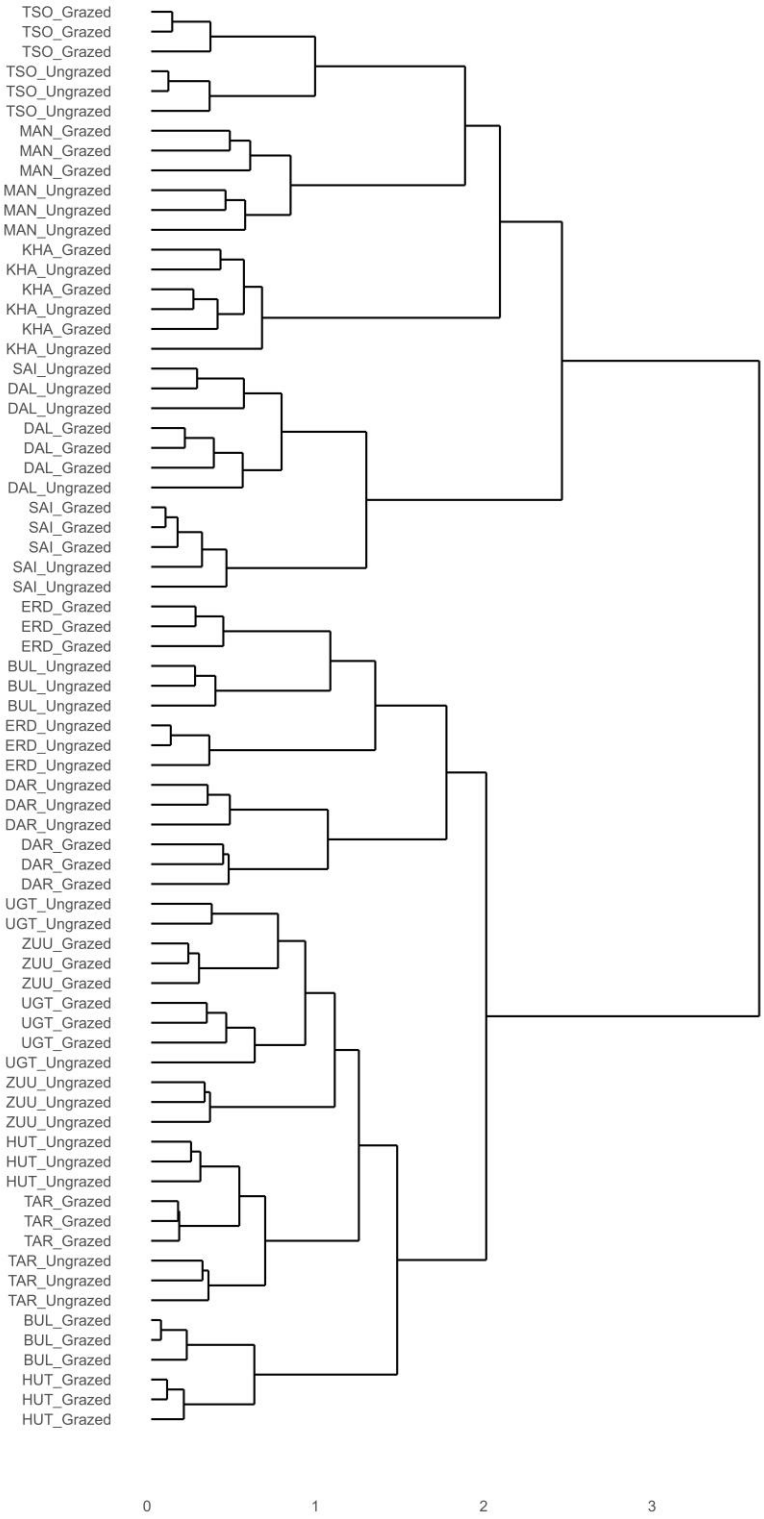



Figure S5. Result of clustering based on Ward's algorithm of ungrazed/grazed communities in the north and south regions. Bray-Curtis dissimilarity matrix was used as a distance matrix.