Research Articles

Abrupt shifts in the plant species richness and community composition along an aridity gradient in the Mongolian grasslands

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Highlights

- Patterns in plant species richness and composition in Mongolian steppe were studied
- Shifts in species richness and community composition were nonlinear along an aridity gradient abrupt at high aridity
- Nonlinear shift indicates the vulnerability of plant communities to changes in highly arid regions

Abstract

Aridification is a major facet of climate changes in drylands. However, little is known about the shifts in the plant community composition to aridity. Dryland grasslands are widely used for livestock grazing. Although grazing impacts can be relatively small in arid regions, overgrazing has great impacts on vegetation, regardless of aridity. Thus, investigations under long-term grazing exclusion are suitable to clarify the response of composition to aridity without confounding effect of grazing. We investigated the shifting patterns in species richness and composition with grazing exclosure along a broad range of aridity (0.6–0.95) in Mongolia. The shifts in the species richness and composition (the axis of NMDS) were investigated by model

selection for GLMs, including the linear and quadratic terms of aridity, and soil environments. The best models included both the linear and quadratic terms of aridity, which showed nonlinear and unimodal responses to aridity. Particularly, their shifts were relatively abrupt at high aridity, which might be attributed to environmental filtering by aridity and competitive exclusion by aridity specialists. Our study firstly demonstrated the nonlinear shift of plant community composition to aridity, indicating the vulnerability of plant communities to press changes of aridity, especially in highly arid regions.

Keywords

Aridity, community composition, dissimilarity, Mongolia, species richness, steppe.

1. Introduction

Shifts in community composition along climatic gradients can help predict the impacts of climate change on an ecosystem's structure and functioning (Chapin et al., 2000). Changes in species richness and community composition caused by environmental changes also have substantial effects (Sasaki et al., 2022; Spaak et al., 2017; Wang and Ali, 2021). Aridification, which increases aridity (calculated as [1 – precipitation/potential evapotranspiration]), is one of the major facets of ongoing climate change in terrestrial ecosystems (Huang et al., 2016). Drylands are particularly vulnerable to aridification (Huang et al., 2016), resulting in shifts in multiple structural and functional attributes in the communities and ecosystems (Berdugo et al., 2022, 2020; Maestre et al., 2016). (Berdugo et al., 2020) reported abrupt changes in vegetation cover and plant species richness along aridity gradients (Berdugo et al., 2020). However, little is known about the shift patterns in the plant community composition along an aridity gradient. Previous studies have suggested that shifts in the composition of soil bacterial and nematode communities in China exhibit nonlinear responses to changing aridity gradients (Pan et al., 2022; Xiong et al., 2020). Understanding whether the shifting pattern in the plant community composition along an aridity gradient is consistent with that in other taxa can provide implications for the impacts of aridity shifts under future climate change conditions on an ecosystem's functioning and inter-trophic interactions.

Grassland vegetation is widely used for livestock grazing to support secondary production in drylands. Numerous studies have revealed the impact of livestock grazing on plant community composition mediated by selective herbivory, depending on the livestock species (Díaz et al., 2007; Li et al., 2022; Sasaki et al., 2008a). The grazing impacts on plant species richness and community composition differed according to changes in water availability among the sites. Previous studies have demonstrated that the relative magnitude of grazing impacts on the vegetation is relatively low in high-aridity regions (Herrero-Jáuregui and Oesterheld, 2018; Price et al., 2022). However, species richness and composition of plant communities can drastically be altered and homogenized by overgrazing, regardless of aridity (Ahlborn et al., 2020; Sasaki et al., 2008a, 2009; Wang et al., 2017). Thus, the spatial patterns of the plant community composition in grazed grasslands can be confounded by grazing impacts across a broad range of aridity levels. To infer how future changes in the plant community composition will be driven by aridity, investigations of plant communities under long-term grazing exclusion are essential. Notably, shifts in the plant community composition along a wide range of aridity gradients remain poorly understood in the Eurasian steppe.

Here, we investigated the shifts in species richness and composition of plant communities in the long-term grazing exclosure along an aridity gradient in Mongolian grasslands. Mongolia covers a vast area of the eastern part of the Eurasian Steppe. In Mongolia,

the climate is spatially characterized by broad variations in temperature and precipitation (Vandandorj et al., 2017). In this study, we aimed to determine whether the response patterns of the plant species richness and community composition to aridity are linear or convex to provide insights into the vulnerability of plant communities to future aridification.

2. Materials and methods

2.1. Study sites and survey design

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) (Figure 1). 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 (site 11) to 333 mm at Darkhan (site 05); the mean annual temperature ranged from -0.8 ℃ at Ugtaal (site 06) to 7.6 ℃ at Khanbogd (site 12). Thus, there is a wide gradient of aridity from north to south (Figure 1) that 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 each meteorological site (50 × 50 m), to observe the heterogeneity at both block- and site-level scales. All the sites were enclosed for at least 50 years to avoid livestock grazing. In each plot, vegetation was sampled by identifying all the species present from July to August 2022, and the vegetation data were pooled for each site.

2.2. Environmental variables

Climatic and soil environmental data were collected across the study sites. The aridity, calculated as [1 – precipitation/potential evapotranspiration], was obtained from the Global Aridity Index and Potential Evapotranspiration Climate Database v3 (Trabucco and Zomer, 2022). Since the soil environmental variables can explain the large-scale patterns of the plant community composition across the Mongolian grasslands (Sasaki et al., 2008b), we derived the soil environmental variables based on information from SoilGrids at a resolution of 250 m (Hengl et al., 2017): N, total nitrogen content in cg/kg; SOC, soil organic carbon content in dg/kg; pH, soil pH in H_2O; clay content mass fraction in %; sand, sand content mass fraction in %; silt, silt content mass fraction in %. Because of the high correlations between aridity and N, SOC, and pH, and between the sand and silt content (Figure S1), we used the aridity, clay,

and silt content as the environmental variables in the subsequent analysis. The former correlations, which resulted from the long-term feedback between plant biomass production and edaphic variables, were consistent with the patterns observed in previous studies (Berdugo et al., 2020; Delgado-Baquerizo et al., 2013; Moreno-Jiménez et al., 2019).

2.3. Data analysis

The species richness and community composition were quantified based on a species-by-site matrix. To compare the community composition among the different sites, nonmetric multi-dimensional scaling (NMDS) based on Sorensen dissimilarity was conducted using the function 'metaMDS' of the R package 'vegan.' Sorensen dissimilarity was used to focus on the shift in community composition via species replacement and changes in species richness rather than changes in abundance. In this study, the dimensional reduction to one dimension was performed because the stress value (0.077) was lower than 0.2 (Kruskal, 1964).

To investigate the linear and quadratic relationships between the species richness, community composition (axis of NMDS), and environmental variables (aridity, clay, and silt content), we performed a generalized linear model (GLM) analysis. In the species richness models, a Poisson distribution with a log link was used. A Gaussian GLM was used in the models for community composition. The model selection was based on the Akaike Information

Criterion (AIC) using the function 'dredge' of the R package 'MuMIn.'

3. Results

As a result of the model selection for species richness and community composition (the axis of NMDS), both the best models with the lowest AIC included the linear and quadratic terms of aridity (Table 2 and Table S2); this indicated that aridity induces nonlinear responses in species richness and community composition and relatively abrupt shifts in high aridity levels (Figure 2). In both of the best models, which included edaphic variables, the linear and quadratic terms of aridity were significant (Table 2). The best model for species richness included linear or quadratic terms of clay and silt content, and the coefficients were not significant. In the best models for community composition, the quadratic term of silt content was significant, which showed a unimodal relationship, but a lower effect size than that of aridity. Visual inspection of the reductions in species richness and the axis of NMDS with aridity showed that species richness and composition changed only slightly at low aridity, but abruptly at high aridity (Figure 2).

4. Discussion

In this study, we first demonstrated nonlinear shifts in species richness and community

composition of exclosed plant communities along the aridity gradient across the Mongolian steppes. Notably, the decline in species richness and the shift in community composition along the broad spatial gradient of aridity were more abrupt at high aridity levels (aridity > 0.8) (Figure 2). Previous research has shown that aridity is a critical determinant of community composition throughout the entire area of grazed rangelands in Mongolia (Suzuki et al., 2022). Our study is novel because we demonstrated a nonlinear response in plant community composition to spatial changes in aridity, by eliminating the confounding effects of grazing.

The nonlinear shift in the plant community composition along the aridity gradient was mainly attributed to the relatively high level of environmental filtering as a result of abiotic and biotic factors in the high-aridity regions. In addition to the ungrazed plant communities investigated in our study, a larger variation in plant species composition was observed in the desert steppe and the transition zone between the desert steppe and steppe compared to the steppe and forest steppe across the grazed rangelands in Mongolia (Ahlborn et al., 2020). The relatively high level of variation in community composition of both the ungrazed and grazed communities, under high aridity, might be a result of an intensifying reduction in species richness and species turnover.

Because of environmental filtering by aridity, the dominance of stress-tolerant species and exclusion of non-tolerant species can often be observed in arid and semi-arid ecosystems

with high aridity (Berdugo et al., 2019; Grime, 1977; Le Bagousse-Pinguet et al., 2017). A global meta-analysis demonstrated the nonlinear and threshold responses of plant species richness to aridity, and the relatively steep decrease at aridity > 0.78 (Berdugo et al., 2020), which was roughly consistent with the extreme decline in species richness at aridity > 0.8 in this study (Figure 2a). This result repeatedly indicates that aridity is an important determinant of community composition in high-aridity regions. In addition, previous studies have demonstrated that high aridity contributes to the severe limitations of not only water unavailability but also nutrient unavailability via long-term feedback from the vegetation (e.g., nitrogen, carbon, micronutrients, and soil pH) (Berdugo et al., 2020; Delgado-Baquerizo et al., 2013; Moreno-Jiménez et al., 2019), resulting in severe environmental filtering by abiotic factors indirectly associated with aridity.

The relatively abrupt shift in community composition under high aridity conditions may also be attributed to species turnover via competitive exclusion by highly adapted species in arid environments (Berdugo et al., 2019; Grime, 1977; Macarthur and Levins, 1967). Contrary to the stress gradient hypothesis (Bertness and Callaway, 1994), 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). Previous studies have also 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). The decrease in niche breadth due to aridity might cause ecological divergence (limiting similarity) in functional strategies to minimize fitness differences and mediate interspecific competition at local scales (Macarthur and Levins, 1967), although ecological convergence is pronounced with an increase in aridity at regional scales (Le Bagousse-Pinguet et al., 2017).

Across the study sites with high aridity (sites 09–12) in this study, one or two shrub species were dominant or predominant in each site (e.g., *Zygophyllum kaschgaricum*, *Potaninia mongolica*, *Anabasis brevifolia*, and *Salsola passerina*; Table 1), and the turnover of these shrub species among the sites was relatively large. Additionally, the spatial distributions of grass and forb species were allopatric to the shrub species in each plot across the sites (N.I. Ishii, personal observation). Although we could not empirically evaluate the impact of competition and facilitation on the community composition, the limiting similarity among the shrub species and the absence of facilitative effects by the same on composition were partially explained in the context of the previous paragraph.

The present study demonstrated the relatively abrupt response of the plant species richness and community composition in the high aridity levels across Mongolia, indicating the vulnerability of the plant communities to changes in aridity due to future climate change,

especially in a desert steppe. Although accurate threshold detection for species richness and community composition along the aridity gradient (Berdugo et al., 2020) could not be performed in this study because of the small sample size of the study sites, future studies should use continuous and intensive vegetation sampling across the whole area of the Eurasian steppe. Although space-for-time substitution is a promising method for predicting community responses to climate change from snapshots of spatial patterns (Blois et al., 2013; Fukami and Wardle, 2005), the spatial and temporal shifts of community and functional compositions to environmental changes do not necessarily coincide (Sandel et al., 2010). Therefore, long-term monitoring of the plant community composition across large environmental gradients is crucial to validate the results based on spatial data such as ours.

While the relative magnitude of grazing impacts on vegetation is lower in highly arid regions (Herrero-Jáuregui and Oesterheld, 2018; Price et al., 2022), species richness and composition of plant communities can be drastically altered and homogenized by overgrazing regardless of the climatic context (Ahlborn et al., 2020; Sasaki et al., 2009, 2008a; Wang et al., 2017). Recently, livestock numbers have rapidly increased across the Eurasian steppe (Kakinuma et al., 2019), leading to the expansion of overgrazing impacts on vegetation. Therefore, comparisons of species richness and community composition between grazed and ungrazed communities will become increasingly important to clarify the pure effects of aridity

and the interactive effects of aridity and grazing on vegetation. Assessing the differentiation of grazed communities from communities with grazing exclosures as a ‘reference community’ will be a powerful tool for predicting the response of not only community composition, but also ecosystem functioning and services in drylands, to the interaction of aridification and grazing (Maestre et al., 2022).

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).

Table 1.

Site	ID	Latitude	Longitude	Aridity	Vegetation	Dominant species
Erdenet	01	49°02'07.08"N	106°56'20.74"E	0.62	Forest steppe	*Elymus chinensis, Koeleria macrantha, Medicago ruthenica*
Hutag	02	49°23'37.32"N	106°50'50.38"E	0.64	Forest steppe	*Artemisia frigida, Stipa krylovii, Medicago ruthenica*
Bulgan	03	48°49'05.52"N	106°54'04.54"E	0.64	Forest steppe	*Agropyron cristatum, Stipa krylovii, Cleistogenes squarrosa*
Tarialan	04	49°36'33.12"N	106°47'56.30"E	0.65	Forest steppe	*Artemisia frigida, Cleistogenes squarrosa, Heteropapus hispidus*
Darkhan	05	49°29'25.44"N	107°03'45.58"E	0.69	Steppe	*Carex pediformis, Artemisia scoparia, Heteropapus hispidus*
Ugtaal	06	48°15'29.16"N	107°01'37.27"E	0.72	Steppe	*Potentilla acaulis, Elymus chinensis, Stipa krylovii*
Zuunmod	07	47°42'47.52"N	107°07'48.46"E	0.72	Steppe	*Artemisia frigida, Stipa krylovii, Arenaria capillaris*
Mandalgobi	08	45°44'35.52"N	107°05'03.43"E	0.87	Desert steppe	*Carex stenophylloides, Stipa glareosa, Allium polyrrhizm*
Dalanzadgad	09	43°34'37.92"N	106°57'40.39"E	0.92	Desert steppe	*Stipa gobica, Artemisia pectinata, Convolvulus amanii*

Saikhan	10	44°05'42.00"N	106°54'09.12"E	0.92	Desert steppe	*Convolvulus amanii, Stipa gobica, Cleistogenes songorica*
Tsogt-Ovoo	11	44°25'23.52"N	107°01'16.39"E	0.93	Desert steppe	*Allium polyrrhizm, Anabasis brevifolia, Salsola passerina*
Khanbogd	12	43°11'44.52"N	107°08'46.46"E	0.94	Desert steppe	*Zygophyllum kaschgaricum, Cleistogenes songorica, Potaninia mongolica*

Table 2. Results of the generalized linear models (GLM) for the environmental variables on species richness and community composition (the axis of nonmetric multi-dimensional scaling, NMDS). The full models included the linear and quadratic terms of aridity (shown as aridity and aridity^2, respectively) and the clay and silt content as the independent variables. The standardized regression coefficients and the standard error of the best model, based on AIC, (Figure S2) were shown.

Dependent variable	Independent variable	Estimate	SE	z value	P value
Species richness	Aridity	**-0.422**	0.087	-4.827	<0.001
	Aridity^2	**-0.384**	0.140	-2.751	0.006
	Clay^2	-0.150	0.080	-1.866	0.062
	Silt	-0.230	0.127	-1.807	0.071
	Silt^2	-0.164	0.086	-1.907	0.057
MDS	Aridity	**-0.796**	0.039	-20.168	<0.001
	Aridity^2	**-0.361**	0.043	-8.320	<0.001
	Silt^2	**-0.119**	0.040	-2.988	0.017

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

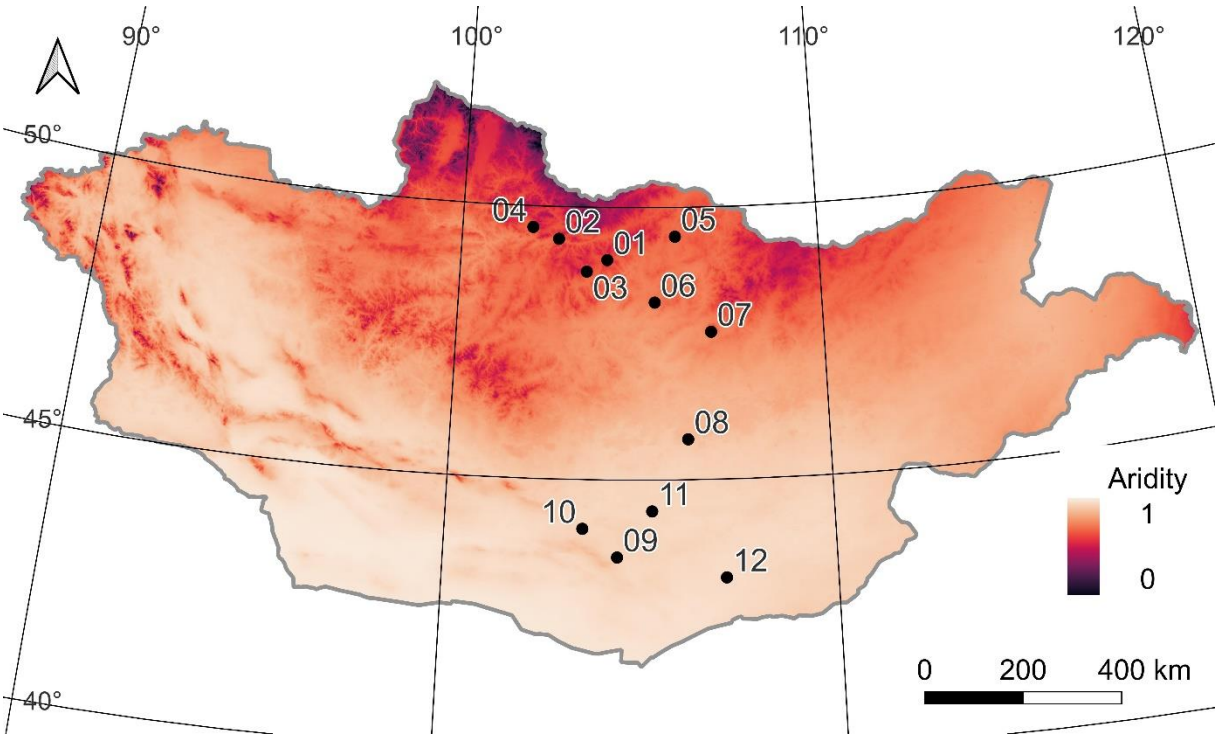
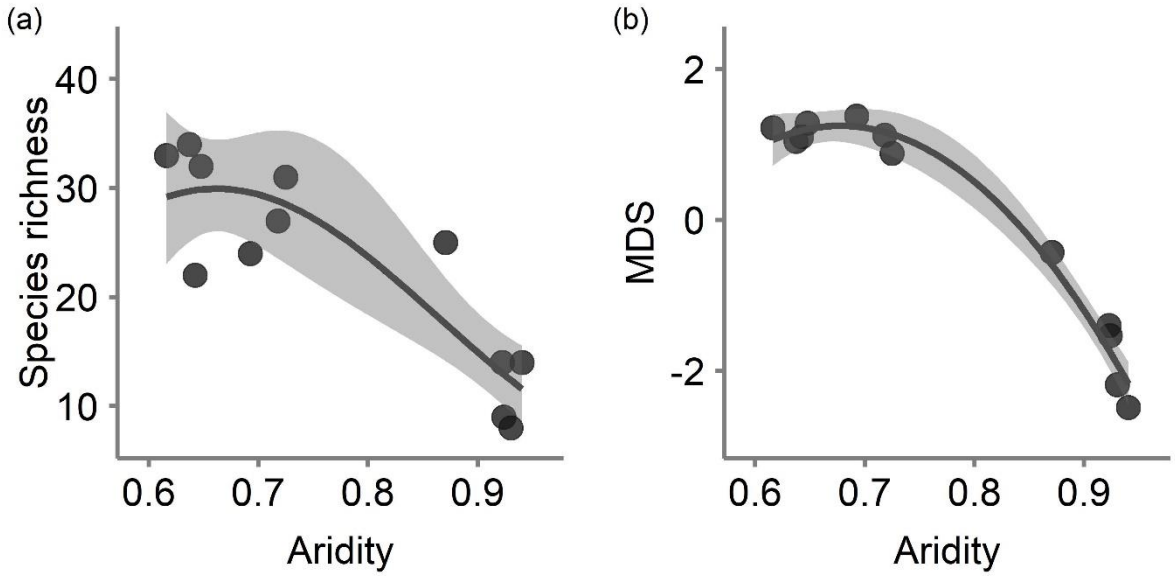


Figure 2. Relationship between the community composition (the axis of nonmetric multi-dimensional scaling) and environmental variables. The regression line and its confidence interval, based on the regression models shown in Table 2, were denoted.



Supplementary information

Table S1. Pairwise correlation matrix of the environmental variables. Aridity, 1 – (precipitation/potential evapotranspiration); N, total nitrogen content in cg/kg; SOC, soil organic carbon content in dg/kg; pH, soil pH in H_2O; clay content mass fraction in %; sand, sand content mass fraction in %; silt, silt content mass fraction in %.

	Aridity	N	SOC	pH	Clay	Sand	Silt
Aridity	-	-	-	-	-	-	-
N	-0.988	-	-	-	-	-	-
SOC	-0.971	0.956	-	-	-	-	-
pH	0.758	-0.720	-0.762	-	-	-	-
Clay	-0.443	0.480	0.313	-0.150	-	-	-
Sand	0.716	-0.744	-0.738	0.526	-0.352	-	-
Silt	-0.451	0.456	0.557	-0.441	-0.278	-0.801	-

Table S2. Model selection of generalized linear models (GLM) for species richness and community composition (the axis of non-metric multidimensional scaling (NMDS)) using the Akaike Information Criterion (AIC). The models included the linear and quadratic terms of aridity and the clay and silt content as the independent variables. The models were shown to have ΔAIC less than 2.

Dependent variable	Model	Rank	df	AIC	ΔAIC
Species richness	Aridity+Aridity^2+Clay^2+Silt+Silt^{2h}	1	6	74.57	0.00
	Aridity+Aridity^2+Silt^2	2	4	75.70	1.14
	Aridity+Aridity^2	3	3	75.79	1.23
	Aridity+Aridity^2+Clay^2+Silt^2	4	5	75.87	1.31
	Aridity+Aridity^2+Clay^2+Silt	5	5	76.16	1.59
	Aridity+Aridity^2+Silt+Silt^2	6	5	76.21	1.64
	Aridity+Aridity^2+Clay+Clay^2+Silt^2	7	6	76.25	1.69
	Aridity+Aridity^2+Clay+Clay^2+Silt+Silt^2	8	7	76.30	1.73
	Aridity+Clay^2	9	3	76.46	1.89
	Aridity+Aridity^2+Clay^2	10	4	76.47	1.90
	Aridity	11	2	76.55	1.98
MDS	Aridity+Aridity^2+Silt^2	1	5	-12.93	0.00
	Aridity+Aridity^2+Clay+Silt^2	2	6	-12.61	0.32
	Aridity+Aridity^2+Silt+Silt^2	3	6	-11.06	1.87
	Aridity+Aridity^2+Clay^2+Silt^2	4	6	-10.98	1.95