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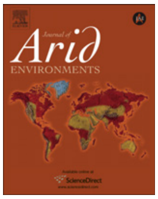

Driving environmental factors and the role of grazing in grassland communities: A comparative study along an altitudinal gradient in Western Mongolia

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ABSTRACT

In order to address questions relating to the driving factors in grassland vegetation, the potential role of grazing, and how the importance of these factors may vary along an altitudinal gradient of decreasing aridity, we studied grassland communities of desert steppe, mountain steppe, and alpine vegetation in Western Mongolia. Based on vegetation, soil parameters, and additional environmental data collected along grazing gradients, the variables of highest explanatory power for variation in vegetation were identified and ranked using a complementary approach of unconstrained and constrained ordination techniques. In desert steppe soil moisture deficiency is the main driving factor. While grazing is of minor importance in desert steppe, in mountain steppe it leads to substantial floristic and edaphic changes. In the alpine belt, a complex suite of driving factors involves thermal supply, water saturation, energy cycling, and grazing. Our study demonstrates how the role of vegetation as a site-affecting factor rises with increasing precipitation and productivity. It furthermore reveals how ecosystems may change from primarily abiotically driven to both abiotically and biotically driven systems. Finally, the study provides empirical evidence that the severity of grazing impact is coupled with the magnitude of importance of vegetation as a site-affecting factor; an aspect that has until now not been incorporated into the non-equilibrium paradigm of rangeland dynamics.

1. Introduction

The vegetation of Central Asian grasslands has been an important venue for studies in grazing, climate change, and desertification (Christensen et al., 2004; Sneath, 1998). To assess human-caused changes to grasslands, it is necessary to understand vegetation responses to a wide range of environmental gradients. These gradients remain insufficiently studied (Briske et al., 2006; Fernandez-Gimenez and Allen-Diaz, 2001). Thus, the role of abiotic factors in relation to the impact of grazing on grasslands is not fully understood (Christensen et al., 2004; Richardson et al., 2005). The assessment of the relative importance of abiotic and biotic factors as well as their mutual interdependencies in grassland development and restoration is an ongoing scientific challenge worldwide (US National Research Council, 1992).

The non-equilibrium paradigm (NEP) of rangeland dynamics refers to grazing-resilient ecosystems that are driven primarily by stochastic abiotic factors rather than by grazing (Behnke and Scoones, 1993; Vetter, 2005). This paradigm relates the highly variable biomass productivity in (semi)arid grasslands to highly variable rainfall patterns. Thus, it emphasizes the role of precipitation as the main driving factor for primary production (Ellis, 1994; Ludwig, 1987) and challenges the general importance of grazing as a dominant factor in grassland vegetation dynamics (Vetter, 2005). The adoption of NEP allowed the development of state-and-transition models as a conceptual framework for rangeland ecology (Westoby et al., 1989). These models were proposed as an alternative procedure for rangeland assessment to address the limitations of traditional succession-based models, and to consider the entire spectrum of possible vegetation states within rangeland sites (Walker, 1993). Grazing impact is thought to depend both on average rainfall and associated interannual variability in precipitation (Cingolani et al., 2005; Milchunas and Lauenroth, 1993) and effects of grazing may vary from the decline of vegetation cover, often associated with increasing soil erosion, to a complete absence of changes to vegetation (Fernandez-Gimenez and Allen-Diaz, 1999; Skarpe, 1991).

Although very large areas of Central Asian grasslands have been devastated or converted to cropland, Mongolia still harbors vast grasslands that represent rare reference ecosystems in near-natural

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condition (Nan, 2005; Sneath, 1998). Starting in the early 1970s, numerous international scientific expeditions have been conducted (Pavlov et al., 2005), collecting extensive data on Mongolia's steppe ecosystems (Hilbig, 1991). The nationwide vegetation classification of Hilbig (1995, 2000) and further local classifications (Wallis de Vries et al., 1996; Wesche et al., 2005) comprise qualitative descriptions of habitat conditions. Until recently, few quantitative analyses have considered vegetation-environment relationships (Fernandez-Gimenez and Allen-Diaz, 2001; Strauss and Schickhoff, 2006). In dry steppes, current vegetation studies revealed a high importance of interannual rainfall variation and a low importance of grazing intensity on vegetation characteristics, which is consistent with the NEP (Fernandez-Gimenez and Allen-Diaz, 2001). However, even studies with one-time sampling have demonstrated negligible grazing impacts on vegetation composition in dry steppes (Stumpp et al., 2005; Zemmrich, 2006). Therefore, we hypothesize that additional factors, currently not included in the NEP, also account for variation in grazing susceptibility across different ecosystems (Vetter, 2005).

Here, we present an analysis of vegetation-site relationships in the three altitudinal belts, desert steppe, mountain steppe and alpine belt in Western Mongolia that also represent a gradient of decreasing aridity. Our research objectives are: (1) to separately detect driving environmental variables and related factors controlling species composition within each altitudinal belt, (2) to describe grazing-induced floristic and edaphic changes within plant communities, and (3) to investigate the relative importance of driving environmental factors along the aridity gradient with special regard to grazing. We hypothesize that site susceptibility to grazing damage depends on the capability of local vegetation to influence site conditions through, for example, soil organic matter, which in term, increases with decreasing aridity.

2. Methods

2.1. Study area

Our study area is located in western Mongolia, extending from the Great Lake Basin to the Mongolian Altai (48°00′N, 91°05′E and 48°23′N, 93°10′E) and covers an altitudinal gradient from 1150 to 3050 m asl (Fig. 1). Within a distance of 150 km it cuts across the vegetation belts of desert steppe, mountain steppe, and alpine vegetation. Situated in a sheltered position of surrounding mountains (Tannu Ola Mts. north, Khangay Mts. east, Gobi Altai south, Mongolian Altai west), the area is characterized by an extremely continental climate with long, cold, and dry winters, short and warm summers, and strong daily and seasonal temperature fluctuations. About 70–90% of annual precipitation occurs in summer, even though quantities may vary considerably over the years. Winter precipitation is low, failing to create an isolating snow cover (Gunin et al., 1999). The altitudinal gradient reflects an aridity gradient, gradually shifting from arid conditions in the lowlands of the desert steppe via semi-arid conditions in the mountain steppe belt up to humid conditions in the alpine belt. It is accompanied by a decreasing length of growing season from the desert steppe to the alpine belt expressed by the sum of hours with mean temperature above 10 °C (Table 2). Along the gradient, vegetation gradually changes from bunch grass and subshrub-dominated desert steppe and shrub desert steppe via grass-dominated mountain steppe to alpine steppe, cryophyte steppe, and alpine-belt sedge mat. These

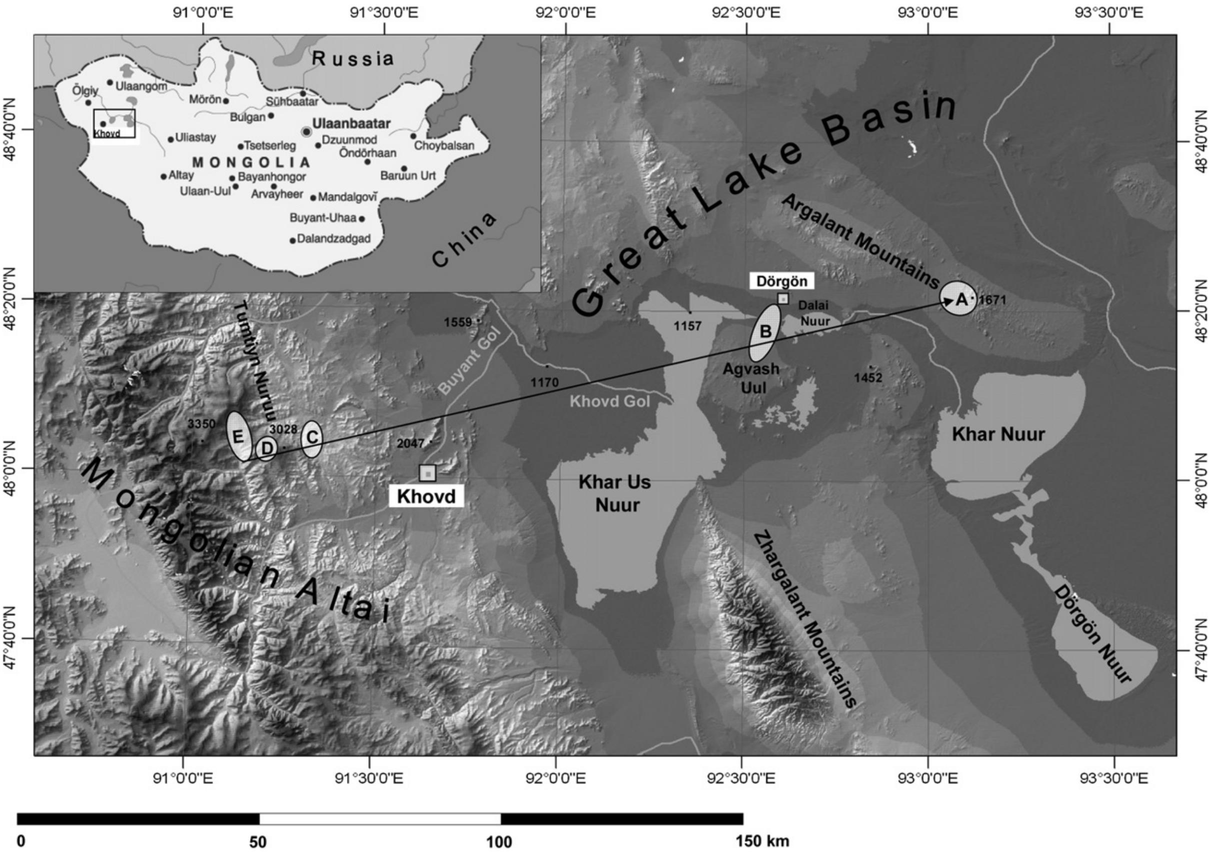

Fig. 1. Study sites along the altitudinal gradient from the Great Lake Basin to the Mongolian Altai. Characters indicating a study site conform to characters in Table 2 (modified after Kretschmer, 2008).

spatially varying climatic conditions induce a gradient in site characteristics. For example, low biomass productivity and faster rates of decomposition and mineralization occur in the lower elevation of desert steppe where lengthy periods of summer rainfall conditions promote prolonged microbial activity, this in contrast to high biomass productivity and slower decomposition in the alpine belt (Haase, 1983).

The study area is traditionally used on a seasonal basis for mobile livestock herding, with an average of four household and livestock movements per year. Spring pastures are situated in the desert steppe belt in the plains. Autumn and further spring pastures are located in the transition from upper desert steppe to mountain steppe around Khovd city and in the wetlands around the lakes (Fig. 1). Summer pasturing occurs in the alpine belt. Extensive winter pastures are spread over the mountain steppe at approximately 2000 m asl. This higher elevation for pasturing is due to temperature inversions during winter that involve warm air layers at medium elevations in mountainous areas perched above a cold air mass in the valley bottom. In all altitudinal belts, livestock herds consist mainly of sheep and goats, supplemented by cattle, camels, and horses. Only camels graze below the alpine belt during summer, sometimes far from herder camps. Daily movement of livestock can vary between 3 and 10 km, depending on animal species and the season. Each livestock species grazes separately, except sheep and goats graze in mixed herds. Lactating females and young animals graze close to herder camps within 1 km distance. As protection against low temperatures and wolves, sheep and goats are fenced and stay overnight in livestock corrals next to herder camps. This concentration of livestock into corrals generates long-term grazing hotspots (Zemmrich et al., 2007).

2.2. *Data sampling*

Between 2002 and 2003, we sampled 169 vegetation relevés and gathered 35 soil samples in the desert steppe between 1150 and 1460 m asl, 141 relevés and 30 soil samples in the mountain steppe between 1900 and 2200 m asl, and 101 relevés and 24 soil samples in the alpine belt between 2300 and 3050 m asl (Fig. 1, Table 2). To avoid influence of interannual rainfall variability each altitudinal belt was sampled within one year. To include variation in grazing intensity as an environmental variable, sampling sites within each belt were placed along transects crossing established grazing intensity gradients centering on grazing hotspots. These hotspots are identified as areas within livestock corrals (Zemmrich et al., 2007). Within a 50-m radius from livestock corrals, sampling sites were chosen at intervals of 5–10 m, followed by an interval of 50 m. Beyond the 100-m radius, intervals of 100 m were chosen. At each sampling site we sampled one soil sample and 3–5 vegetation relevés with a size of 4–100 m^2, depending on the homogeneity of vegetation and the availability of spatial homogeneity. For each relevé, environmental variables representing potential key factors for vegetation were recorded (Table 1).

Each soil sample consists of three 100 cm^3 cylinder samples. They were taken between 5 and 20 cm below soil surface, where living roots are most abundant (Titlyanova et al., 1999). Bulk density of all cylinder samples was measured and the samples were then mixed for the analysis of soil variables (Table 1). Soil data refer to dry fine soil fraction (105 °C/<2 mm). Scientific names of vascular plants follow Gubanov (1996).

The position of all sample plots and surrounding livestock corrals was recorded with a handheld GPS device to determine the distance to the nearest grazing hot spot by means of Geographical Information System (GIS). In total, 411 vegetation relevés and 89 soil samples were evaluated.

Table 1

Overview of examined environmental and soil variables, methods of analysis and applied instruments.

Environmental/soil variable	Method/instrument
Elevation	GPS readings: eTrex, Garmin Ltd.
Slope aspect	Boden (1994)
Inclination	Boden (1994)
Relief position	Boden (1994)
Microrelief	Boden (1994)
Water regime	Qualitative description
Grazing	In terms of distance from a livestock corral
Natural disturbances (e.g. rodent activities, erosion of sediments)	Qualitative description
pH	In $CaCl_2$/pH 96, WTW, Germany
Total soil carbon	CN-analyser/Vario EL, ELEMENTAR, Germany
Total soil nitrogen (*N*)	
Soil organic carbon (*C*)	Mathematical calculation accord. to $CaCO_3$ content
Corg/Ntotal (*C*/*N*)	
$CaCO_3$	Volumetrically accord. to Scheibler (Boden, 1994)
Electrical conductivity (*EC*)	Soil–water 1:5 saturation extract/Conductivity Meter LF 325, WTW, Germany
Effective cation exchange capacity (*CEC*)	Exchange solution: $BaCl_2$, re-exchange solution: $MgSO_4$/Flame AAS 1100, Perkin–Elmer, Germany
Phosphorus (*P*)	Extraction of plant available phosphate by citric acid and mathematical conversion to pure *P*, photometrically/UV/VIS Spectrometer Lambda 12, Perkin–Elmer, Germany
Soil texture	German DIN methods (Boden, 1994)

2.3. *Data analysis*

To provide a plant community reference, a vegetation classification was generated (Zemmrich, 2006) on the basis of differentiating species groups using phytosociological tabular treatment (Mueller-Dombois and Ellenberg, 1974; data not shown).

To assess the relative importance of environmental variables (henceforth including soil variables) for the variance of species composition, we used a complementary approach of unconstrained and constrained ordination techniques (Økland, 1996). In a first step, we applied Detrended Correspondence Analysis (DCA; Hill and Gauch, 1980) to extract the strongest pattern in species composition and to verify the tabular classification. We then correlated the environmental variables to the first three ordination axes and selected only those variables for the subsequent constrained ordination that exceeded Pearson's correlation coefficient threshold of $R > 0.5$ for one or more DCA axes. In order to explore possible nonlinear vegetation–environment relationships, we correlated both untransformed and square-root transformed variables with the DCA axes and selected the variables with higher absolute correlation coefficient for the subsequent constraint ordination analysis. In a second step, we used the forward selection modus of a Canonical Correspondence Analysis (CCA; Lepš and Šmilauer, 2003) to rank the selected variables according to their importance in the species–environment relationship model of the CCA. Monte-Carlo tests with 1000 unrestricted permutations were performed to test the statistical significance of environmental variables for the variance of species composition. In both analyses species with constancy of less than 2% were excluded and a downweighting of rare species was performed. Environmental variables of highest explanatory power for vegetation variation derived in the DCA were further tested for significant differences by a one-way Analysis of Variance (ANOVA), using community as the single factor. Gabriel's post hoc test was used because communities were sampled using unequal numbers of plots (Brosius, 2004). As species may change their ecological behavior across biomes with different climates, analyses were conducted separately for each altitudinal belt. Statistics were carried out using

Table 2
Overview of main vegetation and climate data along the altitudinal gradient of the study area. Percentage of annuals and perennials refers to total species number per community.

Vegetation Belt	Desert Steppe				Mountain Steppe					Alpine Vegetation				
Minima – Maxima: long-term value of annual precipitation in mm acc. to Climate Station Khovd	30–182:62				250–300:275					300–375: 350				
Long-term January, July yearly average, temperature in °C acc. to Climate Station Khovd	−22.2, 21.7, 3.2				Not available					Not available				
Growing season in hours acc. to Climate Station Khovd	1500–2000				700–1000					500–1000				
Study site (Fig. 1)	A	A	B	A	C	C	C	C	D	D	E	E	E	E
Running number		1	2	3	4	5	6	7	8	9	10	11	12	13
Plant community	Annual facies of comm. 1	*Anabasis brevifolia – Allium mongolicum*	*Artemisia xerophytica*	*Krascheninnikovia ceratoides – Caragana leucophloea*	Grazing-mediated *Leymus secalinus*	*Artemisia dolosa – Stipa krylovii*	*Rhinactinidia eremophila – Stipa krylovii*	Grazingmediated *Leymus chinensis*	*Aster alpinus – Koeleria cristata*	Grazingmediated *Potentilla bifurca – Koeleria cristata*	Grazingmediated *Artemisia frigida – Festuca lenensis*	*Saussurea leucophylla – Festuca lenensis*	*Poa altaica – Kobresia myosuroides*	Grazingmediated *Koeleria cristata – Kobresia myosuroides*
Number of relevés	19	58	55	37	12	58	61	10	9	12	15	45	10	10
Number of soil samples	4	11	13	7	3	11	14	2	3	3	3	9	3	3
Distance to grazing hot spot (m)	0–100	200–1900	0–2500	0–1800	0–30	100–2300	50–2700	0–40	800–1300	100–200	0–100	200–2500	800–1500	50–800
Average species number for all relevés	12	9	8	17	3	17	23	12	23	12	13	18	17	17
Average total cover of vegetation for all relevés	29	7	13	30	61	24	23	54	56	18	46	55	68	75
% of Annuals in community composition	57	42	63	43	63	14	16	32	0	5	7	3	3	6
% of Perennials in community composition	43	58	38	57	38	86	84	68	100	95	93	97	98	94

PC-Ord 5.0 for DCA, CANOCO 4.5 for CCA, and SPSS 11.5 for descriptive statistics and ANOVA.

3. Results

3.1. Unconstrained ordination and grazing impact on soil and vegetation

In the desert steppe, variation in species composition was best correlated to elevation, soil texture variables including fine soil/gravel, and the soil chemistry variables *N*, *C*, and *CEC* (Table 3). While community 1 is found at upper pediments of mountain forelands on clayey and silty soils, community 2 is distributed in the lowest part of the Great Lake Basin on flat plains having sandy soils. Community 3 occurs in dry valleys where periodic floods deposit gravel, wash away fine soil, and temporarily recharge groundwater (Fig. 2).

Within community 1 an additional occurrence of annual species within a distance of 100 m from livestock corrals contributes to species diversity (Table 2). Since abundances of dominant perennial desert-steppe species show no trend, this addition of annuals constitutes a phytosociological subunit with higher species richness and enhanced vegetation cover (Table 2). Soil variables are nearly constant except for an increase (not significant) of *C* and *N* (Fig. 2). All other communities show no difference in vegetation or soil variables along grazing gradients (Zemmrich, 2006).

In the mountain steppe vegetation patterns were mainly related to variables of salinity (electric conductivity), soil organic matter (SOM) *C*, *N*, *C/N*, grazing including *P*, *CEC*, *pH*, and $CaCO_3$ (Table 3). According to soil texture, the pair of corresponding communities, 4 and 5, occurs in valley bottom positions, and both have soils with high fine soil fractions. By contrast, corresponding communities 6 and 7 occupy slopes with gravelly soils (Fig. 3). These communities form a pair, as do communities 4 and 5, and the communities of both of these pairs are divided based only on distance from grazing hotspots. Within 0–40m of livestock corrals in communities 4 and 7, an obvious change of soil characteristics is apparent in grazing susceptible variables such as *C*, *N*, *C/N*, *P*, and further variables such as $CaCO_3$, *pH*, *EC*, *CEC* (Fig. 3). Floristically they differ from their less grazing-impacted corresponding community by a considerable species loss and an apparently enhanced vegetation cover of dominant annual weeds and grazing-tolerant rhizomatous grasses such as *Leymus secalinus* and *Leymus chinensis* (Table 2).

In the alpine belt, elevation, soil chemistry variables *C/N*, *P*, *C*, and *N*, and the soil texture variables sand and silt had the highest correlation with the first DCA axes (Table 3). Among them, elevation significantly separates the communities of alpine steppe 8 and 9 between 2350 and 2600 m asl from all other communities of the upper alpine belt above 2700 m asl (Fig. 4). While community 8 occurs on slopes within 800–1300 m distance from livestock corrals, community 9 is found in valley bottom positions, where herders set up their camps within 100–200 m of livestock corrals. Community 9 represents a grazing-impacted vegetation type that is characterized by lower species richness, lower vegetation cover, higher *P* concentrations (350–2000 vs. 300 ppm, Fig. 4, Table 2), and the occurrence of grazing indicators such as *Potentilla bifurca* and *Carex duriuscula*. Grazing impact is further suggested by the presence of species typical for lower elevations like *Stipa krylovii*, *Oxytropis myriophylla*, and *Ephedra monosperma* (data not shown).

Within the upper alpine belt, cryophyte steppe communities 10 and 11 are distributed along well-drained slopes and mountain passes, while sedge mat communities 12 and 13 are restricted to valley floors influenced by inflow of water and fine soil from adjacent slopes (Fig. 4). Both groups comprise corresponding communities that are separated by variation in grazing intensity. Grazing-impacted communities 10 and 12 are characterized by ruderal species like *Axyris prostrata*, *Artemisia frigida*, *Sibbaldianthe adpressa*, and an enhanced frequency of characteristic mountain steppe species like *Koeleria cristata*, *Dontostemon integrifolius*, and *Senecio integrifolius* (data not shown).

While soil texture variables combine the communities 8 and 9, 10 and 11 as well as 12 and 13 into corresponding pairs, differences in the variables sensitive to grazing such as *P*, *C*, *N*, and *C/N* allow a differentiation within the groups (Fig. 4).

3.2. Constrained ordination

In the desert steppe data the sum of all canonical axes explains 37% of the variance in the community matrix (Table 3). Elevation, clay, and *C* indicate highest explanatory power and together account for 73% of total variance explained by all environmental variables. The variables silt, *N*, *CEC*, sand, and fine soil account for the remaining 27%.

In the mountain steppe data 42% of species variance is explained. The variables *C*, fine soil, and $CaCO_3$ account for 77% of total explained variance and the remaining variables grazing distance, *P*, *CEC*, *pH*, *EC*, *C/N*, and *N* explain 23% (Table 3).

Total constrained inertia explains 32% of species variance in the alpine vegetation. Elevation followed by *C/N*, *P*, *C*, and sand show highest explanation power and together account for 89% of total

Table 3
Environmental variables of three altitudinal belts, ranked by their importance for the explanation of vegetation-environment relationships in the CCA. Only those variables were included in the CCA analyses that exceed an absolute correlation coefficient *R* of 0.5 to any of the three first DCA axes of the respective indirect ordination. The "single" columns lists the additional variance each variable explains at the time it was included in the model during a forward selection procedure for the respective dataset. All variables have significant correlations with species composition ($p < 0.001$). Square-root transformed variables are marked with an asterisk. See Table 1 for explanation of variable abbreviations.

Desert Steppe ($N = 196$)			Mountain Steppe ($N = 141$)			Alpine Vegetation ($N = 101$)		
Explained variance of selected variables								
	Single	Cumulative		Single	Cumulative		Single	Cumulative
Elevation *	**0.331**	0.331	**C***	**0.507**	0.507	**Elevation***	**0.444**	0.444
Clay*	**0.232**	0.563	**Fine Soil***	**0.160**	0.667	**C/N***	**0.222**	0.666
C*	**0.192**	0.755	**$CaCO_3$***	**0.119**	0.786	**P**	**0.118**	0.783
Silt*	0.067	0.822	Graz. Dist.*	0.046	0.832	**Corg***	**0.110**	0.893
N*	0.064	0.886	P*	0.042	0.874	**Sand**	**0.108**	1.001
CEC	0.060	0.946	CEC	0.037	0.911	N*	0.079	1.080
Sand	0.042	0.988	pH	0.029	0.940	Silt*	0.050	1.130
Fine Soil	0.041	1.029	EC	0.027	0.967			
			C/N	0.025	0.992			
			N	0.022	1.015			
Total inertia	2.791		Total inertia	2.440		Total inertia	3.489	

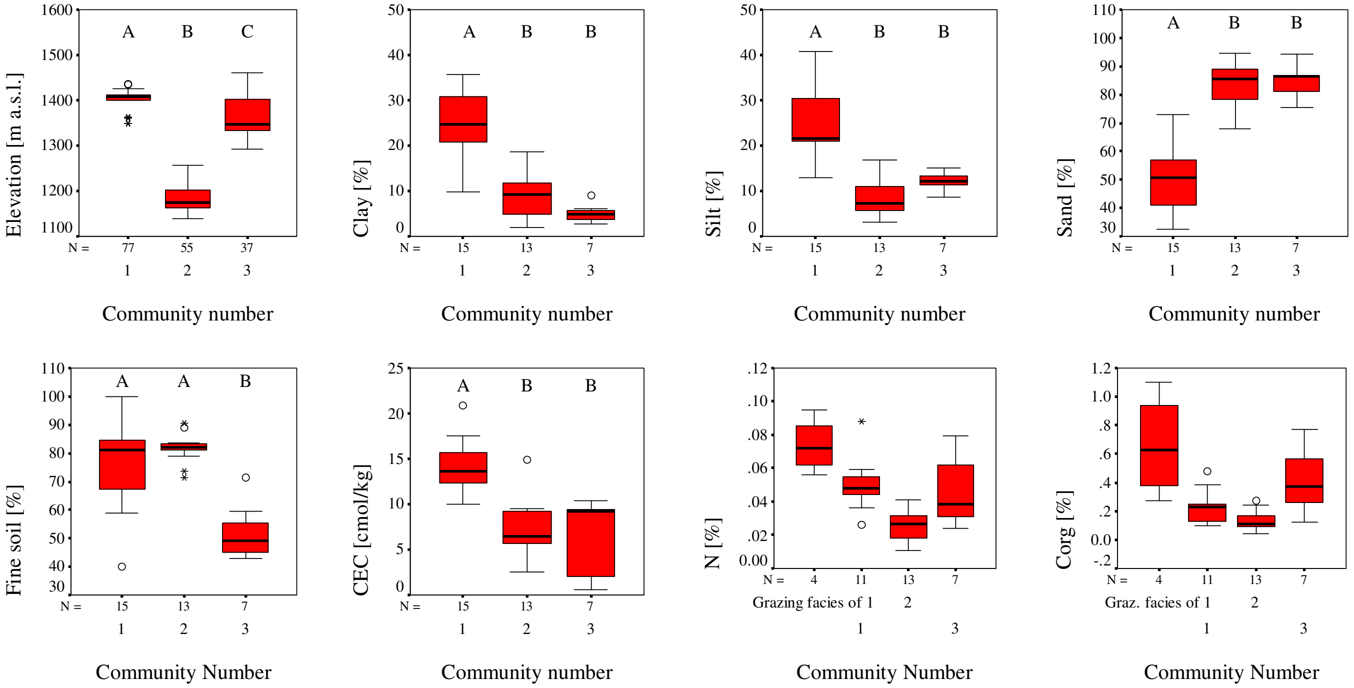

Fig. 2. Box and Whisker Plots of environmental variables of desert steppe communities with $R \geq 0.5$ for extracted DCA axes. Community number 1: *Anabasis brevifolia – Allium mongolicum*, 2: *Artemisia xerophytica*, 3: *Krascheninnikovia ceratoides*. Capitals indicate significantly different subgroups according to Gabriel's post hoc test ($p = 0.01$).

explained variance. Here, *N* and silt explain the remaining 11% (Table 3).

4. Discussion

4.1. Driving environmental factors and the role of grazing

Water availability is the main limiting factor of desert vegetation (Whitford, 2002). Thus, moisture-related variables such as elevation and soil texture are most important for the species composition in **desert steppe** (Fernandez-Gimenez and Allen-Diaz, 2001) and in the present study, significantly differentiate the three communities (Fig. 2). Dense but shallow roots of the dominant grass and subshrub species (Lichtenegger et al., 1997) have no groundwater access. Therefore variation in clay and silt content becomes important in water retention capacity. However, in the mountainous study area clay proportions are low (10–30% vs. 30–70% sand, Fig. 2) and clayey soils with a high fraction of fine pores are spatially negligible. Thus, water-sequestering effects of clay are minimal in soils in the study area. In desert steppe soils poor in organic matter, CEC is mainly controlled by clay content (Scheffer, 2002) and thus determines water retention capacity.

The relatively high explanatory power of the SOM related variables *C* and *N* in the desert steppe belt is more likely the result of confounding effects of other covariables and should not be interpreted as a direct driving factor at the community level for the

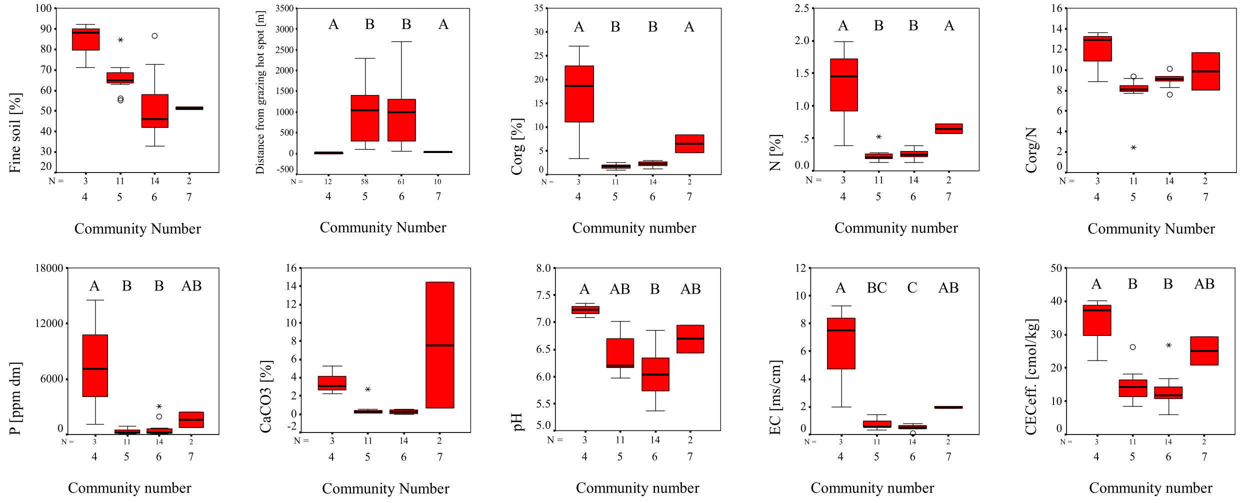

Fig. 3. Box and Whisker Plots of environmental variables of mountain steppe communities with $R \geq 0.5$ for extracted DCA axes. Community number 4: Grazing-mediated *Leymus secalinus*, 5: *Artemisia dolosa – Stipa krylovii*, 6: *Rhinactinidia eremophila – Stipa krylovii*, 7: Grazing-mediated *Leymus chinensis*. Capitals indicate significantly different subgroups according to Gabriel's post hoc test.

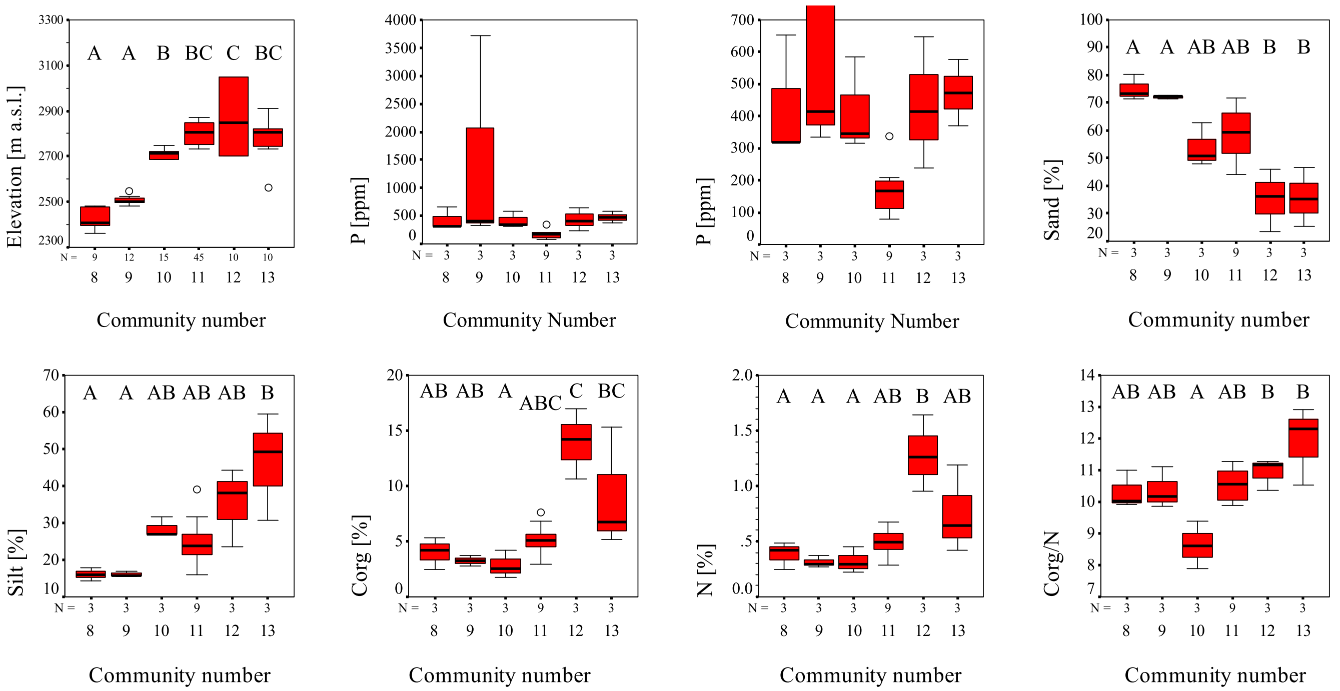

Fig. 4. Box and Whisker Plots of environmental variables of communities of alpine communities with $R \geq 0.5$ for extracted DCA axes. Community number 8: *Aster alpinus – Koeleria cristata* and 9: Grazing-mediated *Potentilla bifurca – Koeleria cristata* (alpine steppe), 10: Grazing-mediated *Festuca lenensis – Artemisia frigida* and 11: *Festuca lenensis – Saussurea leucophylla* (cryophyte steppe), 12: Grazing-mediated *Poa altaica – Kobresia myosuroides* and 13: *Kobresia myosuroides – Koeleria cristata* (sedge mat). Capitals indicate significantly different subgroups according to Gabriel's post hoc test ($p = 0.01$).

following reasons: (i) Differences in *C* and *N* within community 1 (Fig. 2) reflect a fertilization effect from dung and urine leading to temporary grazing facies rather than to a separate grazing-mediated community. (ii) Varying SOM across communities may correspond with clayey soils (Parton et al., 1987) that are subjected to reduced decomposition rates (Cepedo-Pizaro and Whitford, 1990). High *C* and *N* in shrub community 3 reflect the nursing effect of shrubs as 'islands of fertility', which provide elevated nutrient supply due to the accumulation of litter (Whitford, 2002). An additional nutrient enrichment effect is produced by the *N*-fixing capability of *Caragana leucophloea* (Fabaceae) (Sanchir, 1974), which is characteristic of community 3. Both of these are biotic feedback effects, driven by vegetation rather than driving factors (Fig. 2). Additionally, with a mean annual precipitation below 150 mm, moisture deficiency should prevent an effect of varying soil nutrients on desert vegetation (Whitford, 2002).

Although not measured directly, effects of natural disturbance can be observed in community 3. Here, high gravel proportions point to sporadic water erosion (Fig. 2), and the erosion-tolerant shrubs *Krascheninnikovia ceratoides* and *C. leucophloea* occur frequently (Baytulin, 1993). Microtopographic heterogeneity, a consequence of sediment erosion that results in stony microsites, causes microclimatic variation. This may support the high species richness of community 3 (Table 2) and can be thought of a moisture-related variable (Whitford, 2002; see Table 4).

Since grazing impacts on floristic composition are restricted to the added occurrence of annual species within community 1 (Table 2), grazing as a driving factor can be ruled out at the community level. The occurrence of these annuals is the result of an exceptionally high rainfall total in 2003 (182 mm vs. mean annual precipitation of 62 mm according to Climate Station Dörgön 1985–2004 near the study area). Particularly in Central Asia, the occurrence of annuals depends strongly on summer precipitation (Lavrenko and Karamysheva, 1993).

In the **mountain steppe** all soil variables of major and minor explanatory value except for fine soil show higher values in the grazing-mediated communities 4 and 7 (Table 3, Fig. 3). This points to grazing as a main factor in this altitudinal belt for the following reasons: High *C*, *N*, and *P* indicate the spatial translocation and concentration of nutrients from the rangeland through dung and urine into livestock corral sites (Fernandez-Gimenez and Allen-Diaz, 2001; Milchunas and Lauenroth, 1993). Since clay content is similar among the soils of all communities (data not shown), *CEC* is enhanced through high SOM (Scheffer, 2002). The increase of $CaCO_3$, *EC*, and *pH* can also be attributed to heavy grazing: The excrement affects total mineral solutes and thus *EC* (Mapfumo et al., 2000). High evaporation rates due to deposition of large quantities of urine during summer create an ascending soil–water stream and the precipitation in the upper soil horizons of soluble salts including carbonates (Haase, 1983). This is indicated by higher *pH* and $CaCO_3$ concentration in the topsoil compared to lower horizons (Zemmrich, 2006). The phenomenon of an increase in soil *pH*, $CaCO_3$ or *EC* under heavy grazing has been reported also from semi-arid rangelands of Mongolia and China (Su et al., 2002; Sasaki et al., 2008; Xiaochuan et al., 1990).

Fine soil, which is also of high explanatory power, is directly related to water retention capacity (i.e. edaphic moisture). Its importance is confirmed by Hilbig (2000), who connects differences in Mongolian mountain steppe communities to variation in soil texture conditions. Slope and aspect, which we expected to influence edaphic moisture, are not important for species composition in any altitudinal belt. This corresponds to results of Beket (2003), who noted a lack of vegetation asymmetry of northern and southern slopes in the central Mongolian Altai. Since sampling in the mountain steppe was limited to the short altitudinal range of 1900–2200 m asl, elevation is not an important factor here, even though it is commonly accepted as having an effect on temperature and length of the growing season (Austin, 2005, Table 4).

Table 4
Summary of main driving factors for vegetation variation and corresponding environmental variables sampled along the altitudinal gradient. Variables with an indirect effect on driving factors are shown in parentheses. Community numbers are given in parentheses.

	Communities	Environmental variables	
Alpine Vegetation	(13) *Koeleria cristata-Kobresia myosuroides* 2703–3050 m asl	Elevation, microrelief	**Temperature (vegetation season)**
	(12) Grazing-mediated *Poa altaica-Kobresia myosuroides* 2564–2909 m asl	Elevation, water saturation; SOM: C, N, C/N, soil texture	**Mineralization – humus accumulation**
	(11) *Saussurea leucophylla-Festuca lenensis* 2732–2872 m asl		
	(10) Grazing-mediated *Artemisia frigida – Festuca lenensis* 2688–2748 m asl	Elevation, topography, water regime	**Water saturation**
	(9) Grazing-mediated *Potentilla bifurca – Koeleria cristata* 2480–2547 m asl	P; SOM: C, N	**Grazing**
	(8) *Aster alpinus – Koeleria cristata* 2363–2480 m asl		
Mountain Steppe	(7) Grazing-mediated *Leymus chinensis* 2029–2167 m asl	Elevation	**Temperature (vegetation season)**
	(6) *Rhinactinidia eremophila – Stipa krylovii* 1911–2202 m asl	Fine soil/gravel	**Edaphic moisture**
	(5) *Artemisia dolosa – Stipa krylovii* 2000–2148 m asl	Distance to livestock corral; SOM: C, N, C/N; (CEC), P, EC, pH, $CaCO_3$	**Grazing**
	(4) Grazing-mediated *Leymus secalinus* 2033–2050 m asl		
Desert Steppe	(3) *Krascheninnikovia ceratoides* 1290–1460 m asl	Elevation, soil texture (CEC), gravel/fine soil, microrelief	**Moisture deficiency**
	(2) *Artemisia xerophytica* 1150–1260 m asl		
	(1) *Anabasis brevifolia – Allium mongolicum* 1350–1440 m asl	Soil texture incl. gravel/fine soil	**Disturbance**

Obvious changes in total species composition from grass to sedge-dominated vegetation along the altitudinal range of 700 m in the **alpine belt** represent a consequence of strong changes in temperature and water supply. The importance of the SOM variables C/N, C, and N in this zone is explained by varying decomposition and mineralization intensities among the communities due to shifting thermal supply and water saturation along the alpine gradient (Scheffer, 2002; Fig. 4). However, dominant species respond mainly to differences in numerous moisture-related variables, including increase in rainfall frequency with elevation, topography-regulated water availability, melting of permafrost layers and involved water regime factors such as infiltration, percolation or in/outflow. These together create habitats with water deficits in the alpine steppe, balanced water supply in the cryophyte steppe, and long-term water saturation in the sedge mat, and each of these habitats is characterized by typical dominant species. Consequently, duration of water saturation in the alpine belt is a further driving factor, related to elevation, topography and water regime (see Table 4).

The six alpine communities can be split up into three communities with low grazing impact and three corresponding grazing-mediated communities (Fig. 4). In contrast to the lower belts (cf. Fig. 4 with Figs. 2 and 3, Table 2), declining C, N, and reduced vegetation cover of strongly grazed communities suggest a defoliation-mediated reduction of below-ground carbon and a possible acceleration of cycling processes of SOM (Bardgett et al., 1998). Additionally, it may indicate a long-term redistribution of organic matter to sites subjected to frequent urine and dung deposition. Both are likely to blur the fertilization effect near grazing hotspots (Milchunas and Lauenroth, 1993). Traditional grazing patterns along the altitudinal gradient reveal the highest concentration of herders and livestock on productive alpine summer pastures (Janzen and Bazargur, 1999). Here, nutritional requirement of livestock is highest during the summer period of reproduction and lactation (Glatzle, 1990). Both result in higher biomass removal by livestock compared to the lower belts. These long established patterns may explain declining C and N under grazing impact in contrast to the lower altitudinal belts. Increased P values and higher P variation in soils of grazing-mediated communities furthermore indicate a typical grazing impact (Bennet et al., 2004; Fig. 4). Additional to soil properties, species composition reflects the grazing impact by the occurrence of ruderal species and common species of lower altitudinal belts. The latter has been recognized as grazing-caused xerophytisation (Gunin et al. 2002) indicating a relatively drier microclimate in grazed vegetation (Skarpe, 1991; Christensen et al., 2004).

5. Conclusion

Along the altitudinal gradient, ecosystems change from water-limited systems to systems limited by temperature and by the length of growing season (Table 4). While moisture deficiency is of highest explanatory value for species composition in the arid desert steppe (Fernandez-Gimenez and Allen-Diaz, 2001), it is replaced by temperature and water saturation in the alpine belt (Table 4). Whereas microtopographic heterogeneity influences moisture supply in desert ecosystems (Whitford, 2002), it is more important as an effect on ground temperature in the alpine belt. With increasing elevation, the role of natural disturbance (i.e. erosion) is reduced due to the increase in vegetative cover. Increasing moisture leads to increasing vegetation cover, ranging from 7–30% in the desert steppe to 55–75% in the alpine belt (Table 2), and vegetation structure shifts from the dominance of subshrubs, shrubs, and annuals towards the dominance of grasses, forbs, and sedges. The coupling of precipitation and productivity (Chase et al., 2000) enhances the role of vegetation as a site-affecting ecosystem component. In desert steppe, low productivity and high mineralization rates prevent the accumulation of SOM (Haase, 1983) resulting in limited influence of vegetation on soil. In the alpine belt, water availability may vary to such an extent that productivity and associated SOM – as biotically induced variables of energy cycling – differ under further influence of relief, soil texture, and grazing among plant communities. Thus, driving factors of vegetation are restricted to abiotic conditions in the desert steppe and extend to biotic factors including energy cycling and grazing in the mountain steppe and alpine belt. While grazing impact has been previously discussed to be mainly controlled by precipitation and precipitation variability in arid and semi-arid ecosystems (Vetter, 2005), our study suggests that the impact of grazing increases parallel to the role of vegetation as site-affecting factor. We offer this empirical hypothesis, based on the ecosystem scale in our study, referring to complex questions of how SOM storage may mitigate or intensify herbivory impacts on decomposition and nutrient mineralization processes and how grazing-related nutrient fluxes interact with soil biota and feedback to community composition (Bardgett et al., 1998). Furthermore, environmental factors become diversified along the altitudinal gradient because increasing moisture supply limits the importance of nutrient variation only at lower elevations (Whitford, 2002) and factors such as water saturation and water regime may interact with nutrient variation. Elevation-dependent factors and the possibility of manifold interactions are likely to give rise to increased ecosystem complexity.

Grime (2002) assumed that ecosystem properties depend on plant resources and their functional characteristics, as well as on primary production and associated energy cycling. In agreement with his findings, the present study demonstrates how the importance of vegetation as a site-affecting factor rises with increased precipitation and coupled biomass productivity, and how ecosystems tend to change from predominantly abiotic-driven systems to systems driven by a complex of abiotic and biotic factors. This case study in near-natural reference ecosystems may provide new insights into processes of vegetation dynamics that depend on environmental characteristics and serve as a basis for rangeland ecology at the landscape scale relevant for management issues (Briske et al., 2006).

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