



## Original article

Effects of large herbivore exclusion on southern Mongolian desert steppes<sup>☆</sup>Karsten Wesche<sup>a,\*</sup>, Katrin Ronnenberg<sup>b</sup>, Vroni Retzer<sup>c</sup>, Georg Miede<sup>c</sup><sup>a</sup>Senckenberg Museum of Natural History Görlitz, PO Box 300 154, 02806 Görlitz, Germany<sup>b</sup>Institute of Biology, Department of Geobotany and Botanical Garden, Martin-Luther-University Halle-Wittenberg, 06099 Halle, Germany<sup>c</sup>Faculty of Geography, University of Marburg, 35032 Marburg, Germany

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## ABSTRACT

Large areas of Mongolia have been subject to semi-nomadic pastoralism for centuries, but recently increasing livestock numbers have raised concerns about possible degradation effects. We assessed the impact of grazing in southern Mongolian desert steppes (mean precipitation < 150 mm) over eight years in order to capture the high interannual variation, as well as possible medium-term trends in the management regime. We assessed whether the impact of varying precipitation levels (coefficient of variation > 30%) exceeds the effects of grazing on vegetation composition, species richness, plant flowering activity, biomass production, and soil nutrient content. The data presented here originate from a set of nine fenced exclosures established in 1999.

Plant community composition and species richness showed interannual changes over years of varying precipitation levels: mean species numbers on ungrazed plots ranged between 8 and 19 per 100 m<sup>2</sup>. Grazing effects were apparent but light, as grazed plots had, on average, 1–2 species fewer than ungrazed plots. There was also no evidence of directed succession under grazing exclusion. Mean numbers of flowering species on ungrazed plots ranged between 2 and 14 over the years while numbers on grazed plots were slightly lower (range 1–12). In one moist year, mean biomass production in previously ungrazed plots was higher than in previously grazed plots (ca. 800 kg/ha vs. 250 kg/ha), but differences in a subsequent drier year were negligible. This was paralleled by soil phosphorus content, which tended to be higher inside the exclosures.

The overriding effects of precipitation variability are in line with the non-equilibrium theory of rangeland science and imply that the risk of direct degradation is low in southern Mongolian drylands. However, small but statistically significant differences between grazed and ungrazed sites suggest that herbivore impact is apparent and can alter plant reproduction and, ultimately, soil conditions and productivity.

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## 1. Introduction

Rangeland degradation is a central aspect of the global desertification problem. Much attention has focussed on degradation of subtropical grasslands, but degradation occurs also in the vast areas of semi-arid vegetation in the northern hemisphere. China and (outer) Mongolia have about 3.9 and 1.3 Mio km<sup>2</sup> of steppe vegetation (White et al., 2000) respectively, most of which is intensively grazed by domestic livestock. In China, between 0.9 and 1.6 Mio km<sup>2</sup> of rangelands are threatened with desertification (estimates depend on assessment method, Yang et al., 2005) with overgrazing being the main problem. Not surprisingly, restoration ecology of China's rangelands has become a rapidly growing field of research

(e.g. Li et al., 2005a; Zhang et al., 2005; Zhao et al., 2005). Rangelands in (outer) Mongolia are still comparatively intact (Sneath, 1998), and the interstate boundary is clearly demarcated by denser vegetation cover, even in satellite imagery (von Wehrden and Wesche, 2007). Nonetheless, overgrazing is often reported from the moister northern parts of Mongolia (Ojima and Chuluun, 2002; Batkhisig and Lehmkuhl, 2003; Opp and Hilbig, 2003; Bayarjargal and Karnieli, 2004; Ykhanbai et al., 2004), while studies from the semi-arid south yield conflicting results. A number of transect studies describe limited effects of grazing in the semi-arid parts of Mongolia (Fernandez-Gimenez and Allen-Diaz, 2001; Knopf et al., 2005; Stumpp et al., 2005; Göpfert, 2008) and point to the overwhelming importance of the precipitation regime. In contrast, Sasaki et al. (2005, 2007a, 2008) found relatively pronounced changes of vegetation patterns with increasing livestock activity. Finally, whether degradation is present or not may depend on the spatial scale analysed as well as on the indicator system used (Zemrich, 2007; Zemrich et al., 2007).

<sup>☆</sup> Nomenclatural reference: Scientific names of plants follow Grubov (2001).

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The Mongolian debate forms part of the ongoing controversy about human impact on dry rangelands, which has largely centred around two basic lines of debate (Illius and Connor, 1999; Sullivan and Rohde, 2002). The “equilibrium” model emphasises biotic interactions between herbivores and vegetation: livestock exerts a heavy influence on vegetation, potentially leading to severe anthropogenic degradation. The “non-equilibrium theory of rangeland science” (henceforth “NEQT”) concentrates on abiotic controls, while biotic interactions – including grazing – are regarded as relatively unimportant for the vegetation. The NEQT (we somewhat simplistically include state-and-transition models and true disequilibrium models here; but see Gillson and Hoffman, 2007) is based on the assumption that moisture availability is the overwhelmingly dominant factor in dry regions (Wiens, 1984; Ellis and Swift, 1988). Precipitation levels are low and usually very variable, with droughts being common in such systems, leading to sporadic collapses in herbivore populations. Therefore, the system has no stable state, and livestock is regarded as a driven, rather than a driving, factor in non-equilibrium systems. Animals are thus expected to produce limited effects in dry regions – an assumption which is of obvious relevance for policy development and land management.

Both views have been challenged as being rather extreme, because real systems often behave in an intermediate manner (Briske et al., 2003; Vetter, 2005). Steppes in Mongolia show gradual, rather than abrupt, transitions between moister equilibrium and drier non-equilibrium systems (Fernandez-Gimenez and Allen-Diaz, 1999). In dry parts of China, the type of land-use (i.e. sedentary vs. semi-nomadic) appears to be as important to rangeland conditions as the climate (Ho, 2001). Moreover, there may be other indirect effects which are not considered in the aforementioned theories. Semi-nomadic animal husbandry causes translocations of soil nutrients in dry Central Asian steppes (Knopf et al., 2005; Stump et al., 2005; Sasaki et al., 2007a), and there is evidence that lack of nutrients may reduce biomass production even under the dry conditions of southern Mongolia (Slemnev et al., 2004; Wesche and Ronnenberg, 2009). Herbivores may also detrimentally affect flowering, seed set, and seedling establishment (Lavrenko and Karamyshva, 1993), and thus cause changes in vegetation composition in the long run.

Several other conceptual models try to include such effects by emphasizing the importance of site-specific factors such as the evolutionary history of grazing at a given site (Cingolani et al., 2005). Thus, data from a wide range of sites are needed. Since the benchmark review by Milchunas & Lauenroth (1993), a large number of experiments have been published, but data from Central Asia are still relatively limited. Exclosure experiments represent the most straightforward approach, but unfortunately, very few publications from Mongolia are based on direct manipulation of grazing. Where this has been achieved, study duration was usually only one to a few years, or the number of replicates was limited (Fernandez-Gimenez and Allen-Diaz, 1999; Sasaki et al., 2007b).

Central Asia differs from the mid-latitude drylands of North and South America as the highly continental conditions result in rains being strongly concentrated in the short growing season. As a consequence, continuous vegetation can be observed, even under relatively dry conditions. In Mongolia, pastures suitable for grazing are found in desert steppes of the Gobi region, with <150 mm mean annual precipitation and a coefficient of variation >30%. Such desert steppes represent some 40% of the grasslands in the country. Non-equilibrium conditions are expected to prevail under such a precipitation regime (Fernandez-Gimenez and Allen-Diaz, 1999, 2001).

Here we present the results of eight years of continued experimental grazing exclusion on grazed desert steppes, and concentrate on the following questions:

- 1) Does the cessation of grazing result in changes in plant species diversity and vegetation composition?
- 2) How great is the impact of variable precipitation levels on the vegetation compared to that of grazing impact?
- 3) Are there any effects of grazing and precipitation variability on plant flowering activity?
- 4) Does plant biomass increase by grazing exclusion?
- 5) Does grazing exclusion lead to improved soil nutrient conditions?

## 2. Study area

Data were collected in the Gobi Gurvan Saykhan National Park in southern Mongolia. The reserve was designated in the 1990s, but in spite of its protection status, virtually all suitable sites are grazed by domestic livestock, with sheep, goats and horses being the main species (Retzer et al., 2006). Semi-nomadic animal husbandry is the major form of land-use in the Gobi and palynological evidence from the study region implies that grazing has persisted for millennia (Miehe et al., 2007). Wild ungulates occur but are relatively unimportant in terms of biomass consumption (Retzer et al., 2006). Locally, small mammals (mainly pikas, *Ochotona pallasi*, Lagomorpha) may consume much of the available biomass, but they are largely restricted to sites above 2200 m asl. (Nadrowski, 2006). Outside the few oases, the most productive pastures are found in and around the mountain ranges. Their steep slopes range between 2300 and 2900 m asl; lower altitudes are covered by extensive, gently sloping piedmont regions.

The climate is (semi-)arid continental with cold and dry winters and warm and relatively moist summers. Mean annual precipitation is between 100 and 150 mm on the piedmont regions and up to 200 mm in the summit regions, more than 75% of which falls in summer. The interannual variability of precipitation is high, and coefficients of variation for permanent weather stations are all well above 30% (National Meteorological Service Mongolia), which is also true for the mountain regions (own measurements). Precipitation is spatially heterogeneous, and herders move freely with their livestock in response to rains and associated local fodder availability. This makes it impossible to give reliable figures on livestock densities for a given site. During the study period, all piedmont regions were, however, used as pastures. Herders left the study region only in late summer/autumn 2001, when a severe drought affected southern Mongolia (Retzer et al., 2006).

This study was performed in montane desert steppes, which form the most important pastures and cover some 20% of the area (von Wehrden et al., 2006). Most of the dominant species are grasses such as *Agropyron cristatum*, *Stipa gobica* and *Stipa glareosa*; other dominants include the onion *Allium polyrrhizum* and the dwarf shrub *Artemisia frigida* (Wesche et al., 2005a). Shrubs (*Artemisia santolinifolia*, *Caragana leucophloea*) are restricted to disturbed sites or erosion gullies where they escape competition from the hemi-cryptophytes. Trees are restricted to water surplus sites; annual species occur on heavily disturbed sites but are unimportant in terms of overall cover and biomass production.

## 3. Methods

### 3.1. Data collection

The experiment was laid out in blocks comprising an exclosure and a fully grazed control. Exclosures were built in 1999 and have been maintained by a nature conservation project led by the national park administration. Exclosures are between 500 and 5000 m<sup>2</sup> in size and efficiently exclude all large ungulates (mainly domestic livestock), but they allow access to small mammals. The 9 fenced-in sites were originally chosen to represent a spatially comprehensive

sample of the montane desert steppes (Table 1). They partly represent different communities, but this phytosociological classification is based on the presence or absence of certain character species. The overall species set was still relatively similar, spanning a floristic gradient of not even one full species turnover (see below). The enclosures were monitored once a year from 2000 to 2007 and samples were taken at optimum vegetation development (late July to early August). Species composition and estimated species cover was recorded on permanently marked plots 100 m<sup>2</sup> in size inside the enclosures and on adjacent control plots outside the enclosures. From 2003 onwards, we also recorded whether at least one individual of a given species was flowering on a plot or not.

In 2004 and 2005, maximum standing crop was recorded as a proxy for productivity. We randomly placed two sets of three cages (approx. 0.3 m<sup>2</sup>) inside and outside each of the enclosures. The cages also excluded small mammals. Locations of cages were not changed during the course of the study. Above-ground biomass was harvested once at peak standing crop (late July–early August), all plant material was cut 3 mm above the surface and weighed after drying at 105 °C. For subsequent analysis, figures from the three cages were pooled. Monitoring by park staff ceased due to a lack of funding in the winter of 2005/2006; as a consequence most small cages and even 3 of the large enclosures were destroyed.

In 2004, we also took samples of top soil (–5 to –10 cm). At least five subsamples spread over 4 m<sup>2</sup> were mixed together. Lab analysis included pH and conductivity (20 g dry fine soil, 50 ml H<sub>2</sub>O) measured with a standard probe (SenTix 21, WTW, Germany). Total carbon and nitrogen was determined with a CN-Analyser (Vario EL, ELEMENTAR, Germany). Soil cations were extracted by slow percolation with BaCl<sub>2</sub> solution (0.1 mol/l); Ca and Mg were analysed by means of Atomic Absorption Spectrometry and K and Na with flame spectrometry (Flame AAS Vario EL, Analytik Jena, Germany). Available phosphate was extracted with Ca-Lactate at pH 3.6 and measured with a photometer (NANODROP, USA). Carbonate content was measured by way of a Scheibler instrument using HCl (10%). Total carbon figures were corrected for carbonate-borne C. All data refer to dry (105 °C), fine soil (<2 mm).

### 3.2. Data analysis

We allowed some time for the effects of exclusion to become apparent and omitted the data from 2000 from the statistical tests. Data for the three destroyed fences were absent from 2006 onwards, so all statistical tests were restricted to the period 2001–2005. However, results were not qualitatively different when calculated for the reduced data set with  $n = 6$  for the whole period until 2007. Results were also not different if subsets with similar vegetation types were analysed. Descriptive diagrams were drawn for the full data set. Cover values were highly variable over time but showed no clear trends (Table 2); we refrained from performing statistical tests because of the lack of any normal distribution. Further data analysis was based on species' presence/absence as the most straightforward

**Table 2**

Median (and interquartile ranges) for visually estimated cover of field and litter layer (in %; figures for 2006 and 2007 based on the reduced data set).

	Field		Litter	
	In	Out	In	Out
2000	40 (40–60)	35 (35–45)	3 (1–12)	1 (0–1)
2001	35 (30–40)	20 (15–40)	5 (1–8)	2 (0–8)
2002	9 (7–13)	7 (4–10)	8 (1–12)	0 (0–1)
2003	26 (14–29)	15 (15–18)	3 (1–6)	0 (0–0)
2004	14 (11–20)	15 (8–18)	14 (6–19)	7 (4–10)
2005	12 (8–16)	8 (5–14)	5 (3–10)	4 (3–4)
2006	1 (1–3)	1 (0–2)	11 (8–25)	10 (9–14)
2007	20 (16–24)	14 (12–18)	5 (2–6)	5 (2–6)

measure of diversity. Vegetation composition was analysed by comparing pairs of plots inside and outside the enclosure in an ordination; species with less than 2 occurrences were omitted. We used DCA because it provides a meaningful scaling of the ordination space (multivariate standard deviations, Jongman et al., 1995), and subjected all repeated samples from all paired plots to one joint analysis. Samples from 2006 and 2007 were fitted as passive samples in the ordination plot (i.e. they were fitted to the ordination space after the DCA was performed). The relative importance of the three factors block (pairs of sites), interannual variability (year) and grazing exclusion were assessed by means of variance partitioning based on a CCA (ter Braak and Šmilauer, 2002), because the DCA suggested moderately long floristic gradients. An initial CCA was constrained by the full set of three factors, subsequent CCAs were based on a given main factor using the other factor(s) as covariates. The significances of the various partial ordinations were tested with permutation tests (999 runs); the permutation scheme was adjusted to the repeated measures design following methods described in Lepš and Šmilauer (2003). There was no evidence for continuous temporal trends, so years were coded as separate dummy variables.

Univariate data were analysed with analysis of variance. Residuals were graphically assessed for normality, and values were log-transformed. We used Repeated Measures ANOVA with year as the within-subject factor, and fencing and block (site) as between-subject factors. Soil data were analysed with a non-parametric Wilcoxon test. Statistics were calculated with SPSS 12.0 (SPSSInc., 2003) and Canoco 4.5 (ter Braak and Šmilauer, 2002).

## 4. Results

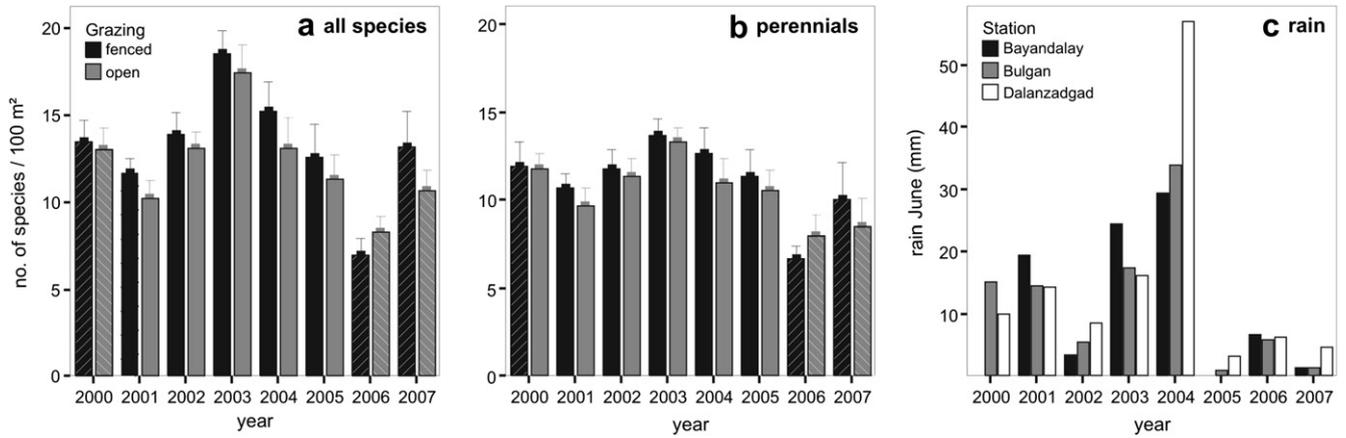
### 4.1. Species richness

Cover estimates for the vegetation and the litter layer were highly variable over time but tended to be higher inside enclosures (Table 2). Differences in species richness between sites were moderate (standard errors of mean richness ranged between 0.8 and 1.9 over the study years), but diversity differed among years ranging between 5 and 25 species (Fig. 1a). The highest diversity

**Table 1**

Site names, approximate size, position, and plant communities (according to Wesche et al., 2005a) of the enclosures. Those that were destroyed in 2006 in italics.

Site	No.	Size (m <sup>2</sup> )	Coordinates (WGS 84)	Plant community
Gegetiyn Am (west)	1	900	43°47.8'N/103°12.1'E	<i>Stipa gobica</i> community
(east)	2	900		<i>Stipa gobica</i> community
Khalgan (valley)	3	500	43°45.4'N/103°30.7'E	<i>Artemisia santolinifolia</i> community
(slope)	4	500		<i>Stipa gobica</i> community
Bulgan Sum South	5	5000	44°00.7'N/103°33.5'E	<i>Allio polyrrhizi</i> - <i>Stipetum glareosae</i>
Barun Saykhan North	6	5000	43°52.9'N/103°34.6'E	<i>Stipa gobica</i> community
<i>Pass Dund/Zuun Saykhan (steppe)</i>	7	1000	43°34.2'N/104°02.0'E	<i>Stipa gobica</i> community
(scrub)	8	1000		<i>Artemisio xerophyticae</i> - <i>Caraganetum leucophloae</i>
<i>Dalanzadgad</i>	9	900	43°36.3'N/104°07.5'E	<i>Allio polyrrhizi</i> - <i>Stipetum glareosae</i>



**Fig. 1.** Vascular plant species richness inside ('fenced') and outside ('open') enclosures for the years 2000–2005. a) Data for all growth forms; b) perennials only (bars indicate mean plus 1 standard error, hatching indicates data not used for statistical tests). c) June precipitation at Bayandalay and Dalanzadgad for the same period.

was recorded in 2003 and 2004. This was mainly an effect of additional annual species, as the temporal difference largely disappeared when only the perennial species were taken into account (Fig. 1b). Compared to the large interannual variability, differences between grazed and ungrazed plots were relatively small. Annual differences in total species richness were statistically significant (Table 3a). For perennial species alone, differences among years were apparent as well, and the effect of grazing was again smaller, though statistically significant (Table 3b). The interannual variability was apparently related to precipitation levels as the years with higher diversity tended to be relatively moist, although records differed among weather stations (Fig. 1c, correlations not formally tested as climatic data came from different locations). The spatial heterogeneity in rain patterns over time is also indicated by the significant year x block interactions (Table 3). Effects of grazing were relatively small though significant.

4.2. Species composition

Patterns in plant community composition showed similar trends. The DCA revealed that differences among sites (blocks) comprised less than one species turnover (Fig. 2, length of gradient axis 1: 3.8 s.d.). Temporal trends on any given plot did not follow clear successional trends in the ordination space (see vectors in Fig. 2); overall differences between samples on any plot were 1 s.d. at most. Trends were not directional but often cyclical, and no stand developed into another phytosociological community. Compared to these interannual changes, differences among grazed and ungrazed sites were minor; vector directions and length did not differ among pairs of grazed and ungrazed plots; and their centroids, representing the mean of all repeated samples on a given plot, were clustered in the ordination space (Fig. 2).

Variance partitioning confirmed these inferences. Overall, the three factors block, year, and grazing exclusion accounted for 57% of the total variance (Table 4). The independent contributions of block, year, and grazing together accounted for some 55%, rendering shared effects among factors unimportant. Interactions between grazing and year were also small and were thus not explicitly tested. Site had the strongest influence (49.5%); years alone contributed some 4.9%, while the independent effect of grazing exclusion was less than 1%. The latter CCA was not stable ( $p > 0.5$ ) – indicating that the effect of grazing can be neglected even where differences between blocks are accounted for.

4.3. Flowering activity

The numbers of flowering species showed similar trends to those of species richness; numbers generally decreased between 2003 and 2007 (Fig. 3a). In the relatively moist summer of 2003, a mean of 14 species flowered per 100 m<sup>2</sup> ungrazed vegetation while in the subsequent years figures were, at most, half as high. Grazed sites generally had lower numbers, but the differences were small – usually only one or two species. The effect of grazing was nonetheless significant according to the ANOVA (years 2003–2005), although not as large as the effect of the interannual changes (Table 5a). More than 70% of all species present on a given plot flowered in the moist year of 2003, but this figure dropped to 50% or less in the subsequent drier years (Fig. 3b).

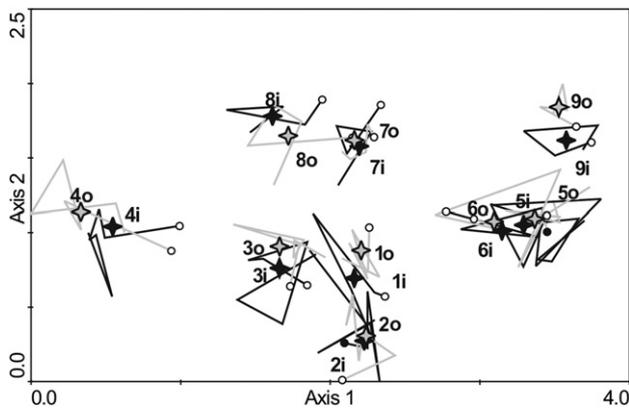
4.4. Productivity

As a proxy for productivity, standing crop was harvested over two years with differing total precipitation (Fig. 3c), e.g. the Bulgan station, which received 115 mm in 2004 and 101 mm in 2005. Annual differences were even more pronounced for summer precipitation

**Table 3**

Effects of interannual variability and grazing exclusion on species richness of vascular plants in southern Mongolian desert steppes: a) all growth forms; b) only perennial species. Analyses were calculated for the complete data set (2001–2005) only (repeated measures ANOVA, site as block factor, data log-transformed).

Factor	a) All species				b) Perennials			
	df	Mean sum of squares	F	P	df	Mean sum of squares	F	P
<i>Within subjects</i>								
Year	4	0.135	54.814	<0.001	4	0.048	26.884	<0.001
<i>Between subjects</i>								
Grazing	1	49.878	13.655	0.006	1	0.027	6.004	0.040
Block (site)	8	130.753	35.795	<0.001	8	0.176	39.279	<0.001
<i>Interactions</i>								
Year x Grazing	4	0.002	0.931	0.458	4	0.030	1.535	0.216
Year x Block	32	0.014	5.783	<0.001	32	0.090	5.257	<0.001



**Fig. 2.** DCA of repeated samples of the vegetation composition at the enclosures for the years 2001–2005. Samples for 2006 and 2007 were added to the graph after calculation of the ordination (i.e. the last segments of vectors). Vectors indicate developments within a given plot, centroids indicate its mean position (dark symbols inside, grey symbols outside enclosures, open circles indicate starting points). Numbers refer to site numbers according to Table 1 ('i' = inside, 'o' = outside). Data were presence/absence-transformed, species with less than two occurrences were excluded (1. axis "length of gradient" 3.79/eigenvalue 0.47; 2. axis 2.00/0.18; 3. axis 1.89/0.14).

(Fig. 1c). In 2004, early summer was relatively moist allowing for reasonable plant growth in June and July, while precipitation started later in 2005. Species were able to flower in both years, but overall productivity was lower in 2005 compared to 2004. Dry mass of standing crop extrapolated from the harvest data (means of three cages each inside/outside) ranged between 200 and 1300 kg ha<sup>-1</sup> (mean ca. 770 kg ha<sup>-1</sup>, Fig. 3c) in 2004, and 200–500 kg ha<sup>-1</sup> in 2005. In 2004, the ungrazed sites inside the enclosures yielded a much higher crop level than the controls outside. Trends were heterogeneous in 2005, when some blocks showed grazing effects on biomass and some did not. The effect of year was non-significant (Table 5b), and interaction terms were also non-significant. In contrast, the grazing effect was highly significant in this ANOVA.

#### 4.5. Soil conditions

Nutrient conditions in the top soil showed mixed responses to grazing exclusion (Table 6). Neither soil carbon and nitrogen contents, nor Mg, Ca, and K cations differed among enclosures and controls. However, there was weak evidence for higher concentration of phosphorus inside the enclosures (Table 6).

## 5. Discussion

### 5.1. Do non-equilibrium conditions govern the study area?

Correlations between responses at the plant level and precipitation are usually not consistent, even in drylands (Fernández,

2007). We nonetheless found strong effects of precipitation variability on plant species diversity, community composition, flower production and biomass productivity. Effects of grazing on plant species' diversity and composition were, in contrast, relatively limited, which supports the main predictions of the NEQT. Vegetation thus showed no evidence of a recovery from a hypothetical degradation stage. Fencing had some effects on flower and biomass productivity and on soil nutrient contents, but there is still only limited evidence for direct degradation through grazing. Abiotic rather than biotic factors seem to control the system. Thus, the NEQT appears to describe conditions in southern dry Mongolia better than the traditional equilibrium model (see also Fernández-Gimenez and Allen-Diaz, 1999; Fernández-Gimenez and Allen-Diaz, 2001; Stump et al., 2005).

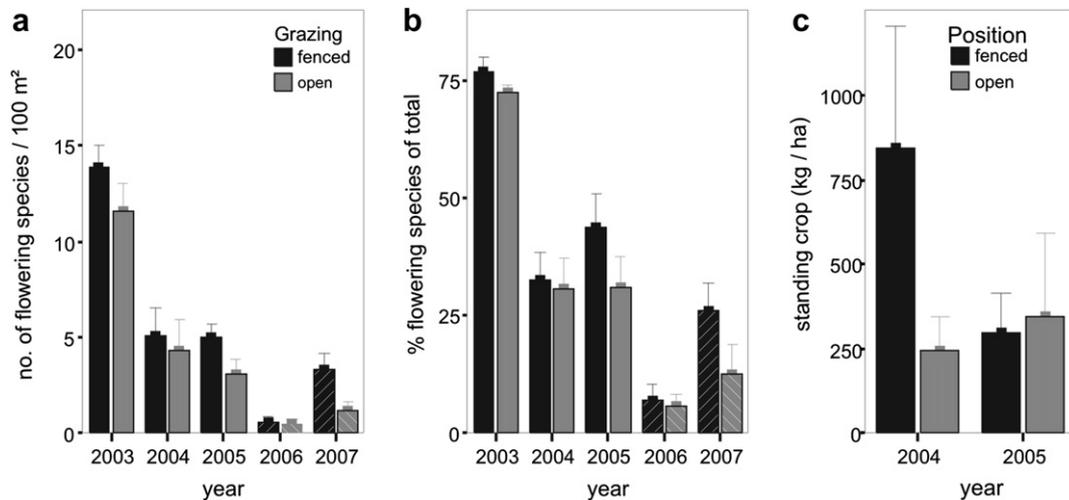
The Mongolian steppes are more heavily dominated by perennials than other dry rangelands with long grazing histories and, as a result, they react slowly to changes, including recovery after grazing exclusion (Milchunas and Lauenroth, 1993; Cingolani et al., 2005). Recruitment events are rare in dry desert steppes and may occur on a scale of several years to decades (Gunin et al., 2003; Ronnenberg et al., 2008), rendering even moderately long observation periods, such as the 8 years reported here, potentially insufficient. However, support for our inferences comes from transect studies along established grazing gradients that find no effect of grazer activities on plant species diversity or plant community composition in Mongolian desert steppes (Fernández-Gimenez and Allen-Diaz, 2001; Knopf et al., 2005; Stump et al., 2005). Our data contradict results obtained by Sasaki et al. (2005) from the desert steppes around Bulgan Sum, north of the study area; but that transect covered several plant communities with presumably different abiotic conditions. In a more extensively replicated approach, Sasaki et al. (2008) found additional evidence for grazing induced changes in southern Mongolian dry steppes. However, their multivariate analyses were apparently based on species cover values (Fernández-Gimenez and Allen-Diaz, 2001; Knopf et al., 2005; Stump et al., 2005, p. 147). Given that grazing generally results in the removal of biomass and thus reduction of cover (even in our case, Table 1), it is difficult to judge to what extent results mirror largely reversible removal of standing crop or potentially lasting changes in species composition. Studies in China reporting often strong effects of grazing on vegetation composition were usually performed under much moister conditions (250–350 mm precipitation, Nakamura et al., 2000; Yiruhan et al., 2001; Xie et al., 2008), where non-equilibrium conditions cannot be expected.

### 5.2. Importance of other resources

Nomadism can be viewed as use of "key resources" (Illius and Connor, 1999), i.e. usage of supplies which are less affected in years of drought. In our study region, herders indeed migrated to Central Mongolia in the drought of 2001. Many animals still died, but losses

**Table 4**  
Variance partitioning for the effects of factors block (site), year, and grazing on vegetation composition, based on multivariate data presented in Fig. 2. Total inertia in the full model was 2.949, the sums of eigenvalues refer to the given partial model (CCA based on presence/absence data, rare species down-weighted, significance based on 999 permutations, customised for block and/or repeated measures design).

Main factors	Covariates	Sum of canonical eigenvalues	Sum of all eigenvalues	% Variance explained	p (4 axes)
<i>Main effects</i>					
Block (site)	Years, Grazing	1.460	2.728	49.5	≤0.001
Years	Block, Grazing	0.145	1.484	4.9	≤0.001
Grazing, Year × Grazing	Year, Block	0.020	1.339	0.7	>0.500
<i>Joint effects</i>					
Year, Grazing, Block		1.630	2.949	57.0	≤0.001
Not explained		1.343	2.949	43.0	



**Fig. 3.** Reproduction and productivity of vascular plant species inside ('fenced') and outside ('open') grazing exclosures: a) the numbers of flowering plant species for the years from 2003 to 2007; b) percentage of flowering species of the given total; c) productivity measured as maximum standing crop in ungrazed cages for the years 2004 and 2005 (bars indicate mean plus 1 standard error, position refers to inside/outside enclosure).

were not as severe as they probably would have been if herders had stayed within the drought region. With the exception of such rare events, herders usually migrate only within the region (Retzer et al., 2006). Provision of supplementary fodder such as hay has practically ceased since the collapse of the socialist economy, and current herders in the Gobi Gurvan Saykhan region have at most very rare access to key resources that might help to mediate the impact of drought.

A less obvious aspect is the effect of herbivores on soil conditions, which might indirectly influence water availability (Laundre, 1993). We did not test this aspect directly, but fenced-in vegetation tended to accumulate fine material, which may change the hydrological properties of the top soil. More studies are needed here. Effects on soil nutrient levels are equally possible (Fernandez-Gimenez and Allen-Diaz, 2001; Stumpp et al., 2005; Sasaki et al., 2007a). In the relatively moist summer of 2004, plant productivity was higher in the exclosures, whereas differences in the drier summer of 2005 were not clear. This may indicate that improved water availability in the moist year allowed uptake (and investment) of extra nutrients potentially available in the enclosure soils.

We found limited evidence to suggest that fencing improved soil nutrients. Among those tested, only available phosphate tended to be higher inside exclosures. Our sampling scheme did not allow for inferences on the also crucial plant-available nitrogen fractions (nitrate, ammonium), but phosphorus can be a limiting element in drylands (Drenovsky and Richards, 2004). Meta-analyses demonstrate that both nitrogen and phosphorus limit productivity of

grasslands over a huge hygric gradient, including sites with an annual precipitation of ~200 mm (Hooper and Johnson, 1999; Illius and Connor, 1999). This is in line with effects of nitrogen fertilization in desert steppes north of our study area (Slemnev et al., 2004), and is also supported by results of a fertilization experiment conducted by our group in the Dund Saykhan, where productivity almost doubled under NPK-fertilization (Wesche and Ronnenberg, 2009). Land-use is important in this respect, as it triggers large-scale nutrient translocation from the steppes to high impact sites such as wells, winter camps or traditional summer places (Fernandez-Gimenez and Allen-Diaz, 2001; Stumpp et al., 2005). Utilization of dung as the main fuel source further adds to nutrient removal.

A possible explanation for the trends towards higher phosphorus contents within the exclosures is the trapping of fine material. Fine material accumulated over the entire plots, apparently trapped by the denser litter and – to a lesser extent – by the standing vegetation (see Table 2). In some fences, >5 cm of loss had accumulated over time. Such accumulation is possible only if material is blown in from the surrounding sites, and our exclosures can be seen as small traps in huge source areas. Central Asian drylands have been and still are the major source of dust transport in the region (Natsagdorj et al., 2003; Liu et al., 2004). Grazing, and thus the removal of litter cover, has probably facilitated wind erosion. A hypothetical large-scale cessation of grazing and the consequent reduction in size of the source areas would potentially give rise to decreasing accumulation of fine material in sheltered microsites.

Soil properties change even more slowly than vegetation patterns in dry rangelands (Milchunas and Lauenroth, 1993) and, as a result, even longer time frames would be needed to assess the associated dynamics. In any case, evidence is emerging that theories of rangeland dynamics have to take changes in nutrient availability into account (Ho, 2001; Briske et al., 2003; Vetter, 2005).

### 5.3. Flowering activity

Flowering activity in Central Asian steppes is also influenced by nutrient availability (Li et al., 2005b). This may also be the case in our experiment, but the more straightforward explanation for the higher incidence of flowers in ungrazed plots is direct browsing by herbivores. Undoubtedly, herbivores affect flowering, and thus, presumably, seed production. Recruitment is restrained in the dry arid and cold drylands of Central Asia (Lavrenko and Karamysheva,

**Table 5**

Effects of interannual variability and grazing exclusion on a) numbers of flowering plant species (all growth forms) and b) on maximum standing crop as a proxy for productivity (repeated measures ANOVA, site as block factor, data log-transformed).

Factor	a) No. of flowers				b) Standing crop					
	df	Mean	sum of squares	F	p	df	Mean	sum of squares	F	p
<i>Within subjects</i>										
Year	2	1.281		53.618	<0.001	1	0.399		4.317	0.083
<i>Between subjects</i>										
Grazing	1	0.231		9.581	0.015	1	0.925		24.855	0.002
Block (site)	8	0.148		6.127	0.010	6	0.717		19.273	0.001
<i>Interactions</i>										
Year × Grazing	2	0.025		1.049	0.373	1	0.247		2.665	0.154
Year × Block	16	0.054		2.254	0.057	6	0.073		0.789	0.609

**Table 6**  
Nutrient contents inside and outside the exclosures (top soil, – 5 cm). Significance values according to Wilcoxon-tests for paired samples (values not Bonferroni-corrected).

	pH		Conductivity (ms)		Lime (%)		C (%)		N (%)		Mg (mg/kg)		Ca (mg/g)		K (mg/g)		PO4 (mg/100 g)	
	In	Out	In	Out	In	Out	In	Out	In	Out	In	Out	In	Out	In	Out	In	Out
1	8.17	8.15	118.40	88.00	1.33	0.10	1.07	1.46	0.14	0.19	0.45	0.43	3.21	2.97	0.19	0.25	0.28	<0.1
2	8.15	8.01	99.80	176.60	0.00	0.00	1.34	1.55	0.14	0.21	0.40	0.52	2.64	3.31	0.28	0.36	4.60	1.59
3	7.91	7.29	121.90	87.30	0.61	0.00	1.55	1.48	0.15	0.17	0.25	0.24	3.21	2.49	0.17	0.18	2.65	2.32
4	7.48	7.86	89.00	57.00	0.00	0.00	1.42	1.24	0.15	0.15	0.20	0.19	1.82	2.36	0.39	0.27	3.05	0.23
5	8.14	8.72	150.10	88.60	0.40	3.34	1.35	0.14	0.12	0.05	0.11	0.22	1.71	2.06	0.27	0.28	7.15	6.60
6	8.51	8.59	64.50	88.50	1.01	2.02	0.36	0.56	0.06	0.08	0.11	0.11	1.81	1.75	0.24	0.31	11.45	4.38
7	8.46	8.46	77.10	105.30	1.51	3.63	0.55	0.76	0.11	0.09	0.07	0.11	1.49	2.30	0.24	0.23	5.75	3.21
8	7.88	8.08	121.60	58.00	0.10	0.00	2.25	1.20	0.20	0.14	0.31	0.34	2.80	2.98	0.38	0.34	1.88	0.87
9	8.30	8.18	58.20	77.40	0.10	0.10	0.62	0.85	0.08	0.11	0.22	0.24	2.36	2.43	0.32	0.34	1.74	5.93
<i>p</i>	0.779		0.374		0.612		0.767		0.859		0.139		0.260		0.374		0.086	

1993; Wesche et al., 2005b), which may be one reason why changes in plant community composition inside the exclosures have, as yet, been relatively limited. Seed germination of the crucial *Stipa* spp. is rare in the region and depends on rare climate events such as heavy rains (Ronnenberg et al., 2008). In any case, herbivory adds to the constraints imposed by the harsh climatic conditions, and thus may have important consequences for recruitment in the long run. In Chinese tall grass steppes, heavy grazing has resulted in a loss of genetic diversity due to reduced recruitment (*Stipa* spp., Dan et al., 2006; Zhao et al., 2008). However, as most of the Mongolian landscape has been grazed by livestock for millennia, and certainly even longer by wild large herbivores, reproduction may also have been subject to evolutionary adaptation to grazing (Mack and Thompson, 1982; Adler et al., 2004; Cingolani et al., 2005). Unfortunately, this aspect has, to date, hardly been explored.

## 6. Conclusion: degradation threats in southern Mongolian desert steppes

Overall, our data support most aspects of the NEQT, but confirm the notion that this model may be over-simplistic. Biotic interactions do matter in our experiments and the observed trends towards lower soil nutrient concentrations and fewer flowers outside the exclosures suggest that grazing effects are not negligible. Thus, the connection between NEQT and the lack of degradation may not be as clear-cut as expected by its proponents.

However, neither do our observations support the idea that typical grazing leads to severe degradation. Livestock exclusion has relatively limited effects on rangeland composition and productivity, at least over the time-span studied here. This supports the general notion that direct degradation effects are apparently rare in dry rangelands under non-equilibrium conditions (Sullivan and Rohde, 2002). Circumstances in northern Mongolia are apparently different (Batjargal, 1998; Hilbig and Opp, 2005), but these regions are moister and an equilibrium model may be more appropriate (Fernandez-Gimenez and Allen-Diaz, 2001). Grazing effects in desert steppes appear to be comparatively small, and this also refers to erosion. Wind erosion and gully formation are common phenomena in southern Mongolia, but can be regarded as natural processes in environments with less than 150 mm annual precipitation. Alarming examples of severe erosion in China (Xie and Wittig, 2004; Li et al., 2005a; Zhao et al., 2005) are reported from regions where vegetation cover has been severely reduced by human impact (usually above 200 mm annual precipitation).

With respect to the available data from southern Mongolia however, we have to conclude that consequences of grazing are indeed small compared to the effect exerted by climate. We found that grazing exclusion might result in improved productivity, at least in moist years, while changes in diversity were limited. Thus,

intense grazing should primarily affect fodder production, which forms the basis of the nomadic economy, rather than having any consequences for nature conservation in the traditional sense.

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