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The effects of micro-habitats and grazing intensity on the vegetation of burial mounds in the Kazakh steppes

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Background: Burial mounds (kurgans) of Eurasian steppes are man-made habitat islands that have the potential to harbour rich plant diversity due to micro-habitats associated with their topography.

Aims: We assessed whether kurgan micro-habitats harboured different species pools and functional groups from those found on the surrounding steppes. In addition, we asked if these mounds were affected by different grazing intensities from those on the surrounding vegetation.

Methods: We surveyed kurgan micro-habitats (northern and southern slopes, surrounding ditch) and adjacent steppe plains in non-grazed, moderately grazed and heavily grazed sites in northern Kazakhstan. We analysed differences in species composition of four habitats under three grazing regimes using Generalised Linear Mixed Models, PCA ordination and indicator species analysis.

Results: Kurgan micro-habitats had diverse vegetation and supported the co-existence of plant species with different environmental needs. We identified 16 steppe specialists confined to kurgan micro-habitats. Steppe vegetation was well-adapted to extensive grazing, although heavy grazing supported ruderals and a decline in steppe specialists. There was a significant interaction between grazing intensity and habitat type: heavy grazing supported ruderals and suppressed steppe specialists especially on the slopes.

Conclusions: We highlighted that kurgans play an important role as maintaining high plant diversity locally in extensive steppe plains in Central-Asia by increasing environmental heterogeneity and supporting specialist species confined to these micro-habitats.

Keywords: degradation; kurgan; livestock; microsite; plant diversity; slope

Introduction

Arching through the continental parts of Eurasia, the steppe biome makes up a considerable proportion of the world's temperate grasslands (Wesche et al. 2016). Due to continent-wide changes in land use, the area of steppes has been dramatically reduced over the past centuries, which especially affected the western part of the biome (Löki et al. 2015; Deák et al. 2016a; Molnár et al. 2017). Despite these dramatic losses, Central-Asian steppes located mainly in China, Kazakhstan and Mongolia still harbour a substantial proportion of the world's remaining near-natural temperate grasslands. Kazakh steppes provide habitat for a rich wildlife with many endangered species restricted to the biome, including the critically endangered Saiga Antelope (Saiga tatarica), the Black Lark (Melanocorypha yeltoniensis) and several plant species such as Adonis volgensis, Anemone flavescens, Tulipa biebersteiniana, T. suaveolens, and T. patens (Rachkovskaya and Bragina 2012; Demina and Bragina 2014; Kamp et al. 2016). In addition, extensive steppes have a high cultural value by preserving the original open landscape, together with the ancient traditions and the

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archaeological monuments of Eurasian nomadic cultures (Lisetskii et al. 2014).

Burial mounds - the so-called 'kurgans' - are among the most characteristic and widespread cultural monuments of the Eurasian steppes from Hungary to Mongolia (Deák et al. 2016a). They were built for burial purposes by nomadic tribes such as the Yamnaja culture, Schytians, Sarmatians, and Cumans from the Late Copper Age-Early Bronze Age (3600-2800 BC) to the medieval period (Bede 2012). Analogous burial mounds can also be found in the Atlantic and boreal regions of Eurasia (e.g. in the Czech Republic -Hejcman et al. 2013; Germany - Dreibrodt et al. 2009; England – Andrews and Fernandez-Jalvo 2012). Kurgans were raised by using the topsoil layer of the adjacent areas. Most of them are few meters high, but larger ones can be up to 10–15 m and range in area from few hundreds of m^{-2} to even ca 1 ha (Dembicz et al. 2016). To create the mounds, the soil around was excavated in concentric ditches, which are still visible in undisturbed steppes (Sudnik-Wójcikowska and Moysiyenko 2008; Tóth et al. 2014). Based on the review of Deák et al. (2016a) the present number of kurgans

is estimated between 400,000 and 600,000, with the majority located in the Asian steppes.

Prior to agricultural intensification, most kurgans were covered by steppe vegetation (Lisetskii et al. 2016). Today, in the western part of the steppe biome (Ukraine, Hungary, Bulgaria and a considerable part of European Russia) the original vegetation of many kurgans has been destroyed by arable agriculture, mineral extraction, improper management, afforestation and urbanisation (Deák et al. 2016a). However, in spite of the large changes in land use, many of these kurgans still harbour steppe vegetation and have a considerable conservation role (Sudnik-Wójcikowska and Moysiyenko 2008; Deák et al. 2016a; Valkó et al. 2018). Studies focusing on large, iconic kurgans (>3 m tall) in the western part of the steppe biome found that environmental heterogeneity (e.g. slopes with a different exposure) supports the co-existence of different plant assemblages and thus a high plant diversity within a relatively small area (Sudnik-Wójcikowska and Moysiyenko 2008; Deák et al. 2016a). The micro-habitats formed on the different slopes differ in soil moisture, humus content and the amount of insolation, which accordingly filter different sets of plant species (Sudnik-Wójcikowska and Moysiyenko 2008; Lisetskii et al. 2016). Special abiotic conditions provided by the kurgan micro-habitats usually result in a difference between the vegetation of the kurgan and the adjacent steppes (Deák et al. 2016a). Unlike the western steppe biome, the importance of kurgans in preserving steppe vegetation seems to be subordinate in the eastern part of Eurasia because of the availability of large intact steppe areas. As a consequence, studies focusing on the vegetation of Central-Asian kurgans are scarce (but see Kuksova 2011), and are mostly in available in Russian.

Originally, extensive steppe habitats were grazed by large wild herbivores, such as the Saiga antelope, and the constantly moving livestock of the nomadic tribes (Wesche et al. 2016). Due to intense poaching, conversion of steppe habitats to arable land and sedentarisation of pastoral communities during the Soviet era, populations of wild and domestic megaherbivores declined considerably (Kamp et al. 2016). Even though there was an increase in the number of grazing animals over the past two decades, grazing patterns have changed fundamentally and become imbalanced (Brinkert et al. 2016). Grazing animals are mostly concentrated in the close vicinity of settlements, resulting in a sharp contrast between the vegetation of the lightly grazed steppes distant from the settlements, and the heavily grazed vegetation surrounding the settlements (Kamp et al. 2012). Different grazing regimes are expected to have considerable effects on the vegetation of the kurgans by altering both the abiotic conditions and biotic interactions (Olff and Ritchie 1998). In steppes, abandonment or undergrazing can lead to a gradual loss of overall diversity due to litter accumulation, increased levels of competition, lack of proper microsites for plant establishment and reduced plant dispersal (i.e. the lack of animal dispersal vectors) (Metera et al. 2010; Kelemen et al. 2013). Even though steppe

species are well adapted to grazing, long-term heavy grazing results in a considerable loss of plant diversity, homogenisation of vegetation structure, and the encroachment of ruderal species caused by the increased level of biomass removal, trampling and nutrient input (Peco et al. 2006; Koyama et al. 2015), characteristic of overgrazing.

In our study we aimed to reveal the role of averagesized kurgans in sustaining the plant diversity of steppes in their main distributional range (Asian steppes). We also aimed to study the role of micro-habitat heterogeneity and the effects of grazing on the plant diversity of kurgans. We addressed the following questions: (i) Do kurgan micro-habitats (i.e. northern and southern slopes and adjacent ditch) harbour different species pools and plant functional groups than the surrounding flatland steppe? (ii) What are the effects of different grazing intensities on the vegetation of kurgan micro-habitats? (iii) Do differently grazed kurgans embedded in steppe landscape concentrate local plant diversity of steppe specialist species?

Materials and methods

Study sites

Our study sites were located in Kostanay Oblast, North Kazakhstan (196,001 km²; N 52° 50' E 63° 34'). The region has a continental climate. The mean annual temperature is between 2.4-3.1°C; minimum temperature is between -24.2 and -22.1°C in January, and maximum temperature is between 25.9 and 27.6°C in July (Supplemental Appendix S1). Mean annual precipitation is 228-328 mm (Fick and Hijmans 2017). The area is characterised by southern chernozem and dark-chestnut soils (Supplemental Appendix S1). Even though a high proportion of the steppes has been transformed into arable land in the past, a considerable amount of steppe habitat still persists in the area (Rachkovskaya and Bragina 2012; Bátori et al. 2017a). The most severe habitat losses took place during the Virgin Lands Campaign (1954-1960), when almost 25 M ha of steppe habitats were converted to agricultural land (mostly cereals and fodder crops) in Kazakhstan (Kamp et al. 2016).

Kurgans are characteristic features of the study region, typically occurring in small groups. The documented number of kurgan groups is 82 in the area; with each kurgan group consisting of 1–14 kurgans (Database of the Ministry of Justice, 2016). We selected nine kurgans, which were embedded in a steppe matrix and had average spatial characteristics regarding height, diameter and ditch size (Figure 1; Supplemental Appendix S1). These parameters were measured with theodolyte along a north to south transect traversing the top of the kurgans. The mean height and diameter of the kurgans was 1.2 and 7.8 m, respectively. We chose kurgans with nearly circular base. The depth of the ditches was around 20 cm and their width ranged between 1.5 and 2.0 m. The studied kurgans were constructed in the Early Iron Age (from VIII BC to III



Figure 1. Map of the study area. a - non-grazed, b - moderately grazed and c - heavily grazed kurgan.

BC). The vegetation of the study sites was characterised by fescue-feather grass steppe, dominated by *Festuca valesiaca*, *Stipa pennata*, *S. capillata* and *Artemisia* species.

Three kurgans were not grazed, three were moderately grazed (ca. 0.3 animal unit/ha) and three were heavily grazed (>1.8 animal unit/ha). Kurgans and adjacent steppes were grazed by mixed herds of cattle and horses in a community herding scheme. Cattle grazing was typical from April to October, whilst horses grazed year-round. No other management type was applied in the study sites (e.g. mowing), but grazing by small mammals (Steppe Marmot – *Marmota bobak*, ground squirrels – *Spermophilus* spp. and Steppe Pica – *Ocotona pusilla*) is typical in the region.

Heavily grazed sites were situated in the northern part, non-grazed sites in the central part and the moderately grazed sites in the southern part of the study region (Supplemental Appendix S1). Because of the spatial distribution of kurgans with similar attributes (height, size, age, and steppe matrix) and also to spatially split of the grazing treatments (see also Brinkert et al. 2016) we had our sites 145.0 ± 30.1 km (mean \pm SE) far from each other. The slight climatic differences between the study sites (Supplemental Appendix S1) fell well within the climatic range of the steppe biome (mean annual temperature between -1° C and $+7^{\circ}$ C; mean annual precipitation between 230 and 450 mm; Wesche et al. 2016); thus, the geographical position of the kurgans was unlikely to confound the effects of management on the vegetation. Furthermore, we used several functional group-based analyses in order to minimise any potential effect of climatedriven differences on species composition.

Data collection and analysis

We surveyed the vegetation of three predefined kurgan micro-habitats (i.e. the northern and southern slopes and the adjacent ditch) and the surrounding steppe, using five, randomly placed plots, each measuring 1 m × 1 m in size, per habitat type in each site. Thus, there were 20 plots per site and 60 plots per management type, making a total of 180 plots. The absolute per cent cover of each vascular plant species was recorded in each plot in July 2016. Thus, the sum of species covers can exceed 100%, because of the overlapping parts of individuals. Plant nomenclature follows The Plant List (2017). To minimise the potential effect of climate-driven differences in species pools, we classified plant species into functional groups according to their habitat indicator value (steppe specialists and ruderals) and life form (perennial grasses, perennial forbs, dwarf shrubs and annuals). For the classification, we used the categories of Brinkert et al. (2016) and Komarov (1968-2002) (see Supplemental Appendix S2 for the classification and mean per cent cover data of species).

To assess the differences in vegetation composition of the four studied habitats under the three grazing regimes we used PCA ordinations, as preliminary calculations using DCA resulted in gradient lengths shorter than 3 SD units (CANOCO 5; Ter Braak and Šmilauer 2012). We used the log-transformed per cent cover values of the species as the main matrix, the per cent cover of steppe specialists, ruderal species, and total vegetation cover were scaled on the ordination as an overlay to visualise their proportions in the different habitat types under different grazing regimes.

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To test the effects of different grazing intensities on the vegetation of the studied habitats, we used generalised linear mixed models (GLMM, Zuur et a1 2009).'Management' (no grazing, moderate grazing and heavy grazing) and 'habitat type' (northern-, southern slope, ditch, and steppe) were included as explanatory variables. 'Site' nested in 'management' was included as random factor. We used the total vegetation cover, Shannon diversity, the per cent cover of species and the species richness of steppe specialists, ruderals and life form categories as response variables. The species richness of steppe specialists, ruderals, perennial grasses, perennial forbs, dwarf shrubs, and annuals were analysed using a Poisson distribution with a log link function. Per cent cover scores of steppe specialists, ruderals, perennial grasses, perennial forbs, dwarf shrubs, and annuals were log-transformed to approximate them to normal distribution and were analysed using an identity link. Post hoc pair-wise comparisons were calculated using Fisher's Least Significant Difference (LSD) method. To calculate GLMMs, we used the SPSS v. 22 (IBM Corp 2013). We carried out an indicator species analysis to detect species that indicated different habitats under the three studied grazing regimes (Dufrêne and Legendre 1997). For the analyses, we used the 'labdsv' package in an R environment.

Results

We recorded a total of 101 vascular plant species in the study sites (Supplemental Appendix S2). Total species numbers were 48 (10.15 \pm 0.32 mean \pm SE) in the non-grazed, 56 (10.47 \pm 0.29 mean \pm SE) in the moderately grazed and 53 (8.1 \pm 0.30 mean \pm SE) in the heavily grazed sites. Habitat type and the interaction of habitat type and grazing intensity were significantly related with total vegetation cover (Table 1). At the non-grazed and moderately

grazed sites, total vegetation cover was smallest on the southern slopes (Figure 2). We detected no differences in the total vegetation cover of the four habitats at the heavily grazed sites. Shannon diversity was related to both grazing intensity and habitat type and to their interaction. Increasing grazing intensity decreased Shannon diversity (Table 1, Figure 3). We detected the highest Shannon diversity on the southern slopes of non-grazed kurgans and in the ditches of moderately grazed mounds. In heavily grazed sites, the ditch and the steppe were characterised by the highest diversity.

Functional species groups

Grazing intensity and the interaction of grazing and habitat type were significantly related to the species richness of steppe specialists. The cover of steppe specialists was related to habitat type and the interaction of grazing and habitat (Table 1). Whilst there were only slight differences between the richness and cover of steppe specialists in non-grazed and moderately grazed sites, we observed their marked decrease in heavily grazed sites (Figures 2–3). In non-grazed and moderately grazed sites, the cover of steppe specialists was the lowest on the southern slope. In overgrazed sites, the cover of specialists was higher in the ditch and in the steppe compared with the slopes (Figure 2).

The species richness and cover of ruderals increased with increasing grazing intensity (Table 1). Increasing grazing intensity resulted in increased species richness of ruderals (Figure 3). We detected no effect of the habitat type on the cover of ruderal species in non-grazed sites. In moderately grazed sites, the cover of ruderals was higher on the southern slope and in the ditch than on the northern slope and in the steppe. In heavily grazed sites, the cover of ruderals was higher on the northern and southern slopes of the kurgan than either in the ditch or in the surrounding

Table 1. Effects of grazing, and micro-habitat type and their interaction on vegetation attributes (Generalised Linear Mixed Models).

	Grazing		Micro-habitat		Grazing× micro-habitat	
	F	Р	F	Р	F	Р
Total vegetation cover	2.20	n.s.	17.59	***	4.59	***
Shannon diversity	13.03	***	16.83	***	17.44	***
Species richness						
Steppe specialists	37.44	***	1.67	n.s.	2.19	*
Ruderals	8.38	***	0.82	n.s.	1.03	n.s.
Perennial grasses	3.68	*	2.94	*	1.04	n.s.
Perennial forbs	17.23	***	2.06	n.s.	5.46	***
Dwarf shrubs	13.94	***	1.19	n.s.	0.90	n.s.
Annuals	5.67	**	1.30	n.s.	1.18	n.s.
Cover						
Steppe specialists	2.83	n.s.	8.79	***	4.50	***
Ruderals	7.95	***	1.35	n.s.	2.057	n.s.
Perennial grasses	18.07	***	30.10	***	17.14	***
Perennial forbs	4.79	*	7.30	***	5.15	***
Dwarf shrubs	24.34	***	16.04	***	5.56	***
Annuals	9.35	***	5.77	***	2.93	***

Note: ***P < 0.001; **P < 0.01; *P < 0.05; n.s.: non-significant.



Figure 2. Mean scores and standard errors of the cover of steppe specialists, ruderals, perennial grasses, perennial forbs, dwarf shrubs, annuals and the total vegetation cover (%). For pair-wise comparisons we used Fisher's LSD test. Superscript capital letters indicate significant differences due to grazing intensity; superscript lower-case letters indicate differences between micro-habitats. Different grazing intensities are denoted using differently coloured columns (non-grazed – light grey; moderately grazed – grey; heavily grazed – dark grey).

steppe. Heavy grazing resulted in a significant increase in the cover of ruderal species (Figure 2).

Life forms

Both species richness and cover of perennial grasses were affected by grazing intensity and habitat type. Cover of perennial grasses was also affected by the interaction of grazing and habitat type (Table 1). The richness of perennial grasses was the lowest on the southern slopes of heavily grazed sites (Figure 3). In non-grazed sites, the cover of perennial grasses was highest in the steppe. The cover of perennial grasses was similar in the four habitats at moderately grazed sites. In heavily grazed sites, the ditch and the steppe hosted the highest cover of perennial grasses (Figure 2).



Figure 3. Mean scores and standard errors of the species richness of steppe specialists, ruderals, perennial grasses, perennial forbs, dwarf shrubs, annuals and Shannon diversity. For pair-wise comparisons we used Fisher's LSD tests. Superscript capital letters indicate significant differences due to grazing intensity; superscript lower-case letters indicate differences between micro-habitats. Different grazing intensities are denoted using differently coloured columns (non-grazed – light grey; moderately grazed – grey; overgrazed – dark grey).

Species richness of perennial forbs was related to grazing intensity and the interaction of grazing and habitat type. The cover of perennial forbs was affected both by grazing and habitat type and also by their interaction (Table 1). Species richness of perennial forbs was the highest on the northern slope in the non-grazed sites. In the moderately grazed and heavily grazed sites, it was higher in the ditch and the steppe than on the slopes (Figure 3). We found the highest cover of perennial forbs on the southern slopes of the non-grazed sites. In the moderately grazed sites, the cover of perennial forbs was higher in the ditch and on the southern slope than in the northern slope and in the surrounding steppe. In the heavily grazed sites, the cover of perennial forbs was

higher in the ditch and the steppe than on the slopes of the kurgan. With increasing grazing intensity, the cover of perennial forbs decreased on the slopes and in the ditch (Figure 2).

Only grazing intensity was significantly related to the species richness of dwarf shrubs, and all studied factors and their interaction affected their cover (Table 1). In non-grazed sites, we detected the highest number of dwarf shrub species on the northern slope (Figure 3); the cover of dwarf shrubs was the highest on the northern slope and in the ditch. In moderately grazed sites, northern slopes harboured the highest cover of dwarf shrubs. In heavily grazed sites, the cover of dwarf shrubs was higher on the slopes than in the ditch or in the steppe. The cover of dwarf shrubs increased with grazing intensity on the slopes and in the steppe (Figure 2).

Grazing intensity affected the species richness of annuals. The cover of annuals was affected by grazing intensity, habitat type and their interaction (Table 1). In non-grazed sites, the cover of annuals was low and there was no difference among the habitats. In moderately grazed sites, the richness of annuals was the highest on the southern slopes. In heavily grazed sites, a higher richness of annuals was recorded on the northern and southern slopes than in the ditch and in the steppe (Figure 3). Increase in grazing intensity increased both the species richness and cover of annuals (Figure 2).

Species composition

In non-grazed sites, the vegetation of the northern slope and the ditch showed a considerable similarity; the vegetation of the southern slopes plotted separately on the PCA (Figure 4A). Plots from the steppe were scattered in an intermediate position. Several steppe specialists (such as *Allium pallasii, Dianthus borbasii, Gypsophila paniculata, Stipa pennata* and *Veronica spuria*) and dwarf shrubs indicating steppe vegetation (*Artemisia pontica, Spiraea*) *hypericifolia* and *Thymus pulegioides*) were typical of the northern slope and the ditch (Table 2). Total vegetation cover was higher in these two positions. The southern slopes also harboured several steppe indicator species such as *Carex stenophylla, Ferula caspica* and *Iris pumila*. The only indicator species of the non-grazed steppe was *Festuca valesiaca*.

In moderately grazed sites, the northern slope and the ditch showed some similarity, however their plots were scattered across a large area in the ordination space and overlapped with the plots of the other two microhabitat types (Figure 4B). Northern slopes and the ditch were characterised by a high total cover, and a high cover of steppe specialists. Indicator steppe specialist species of these micro-habitat types were Centaurea scabiosa subsp. adpressa, Galium verum and Stipa capillata (Table 2). The indicator species analysis showed that the typical dwarf shrub species of the northern slopes was Spiraea hypericifolia. Indicator species of the southern slopes was Polygonum aviculare, an annual ruderal species. The vegetation of the steppe showed a homogenous pattern and was characterised by Artemisia schrenkiana, Koeleria glauca, and Potentilla humifusa.

In the heavily grazed sites, northern and southern slopes had similar vegetation and were separated from the vegetation of the ditch and the steppe (Figure 4C). Indicator species of kurgan micro-habitats were mostly ruderal species, such as Amaranthus spp., Capsella bursa-pastoris and Lolium perenne. However, indicator species analysis showed that the steppe specialist Artemisia austriaca was an indicator species of the overgrazed southern slopes. The vegetation of the steppe and the ditch was heterogeneous and harboured a high cover of steppe species (even though they were not indicator species), mainly perennial grasses such as Agropyron cristatum, Festuca valesiaca and Stipa capillata. In the steppe and the ditch, the most abundant indicator species were Artemisia dracunculus, Elymus repens and Leonurus cardiaca (Table 2).



Figure 4. PCA ordination plots on the species composition of non-grazed (a), moderately grazed (b) and overgrazed (c) sites. Total percentage vegetation cover and the percentage cover of steppe specialists and ruderals were included as overlays. Eigenvalues for the first and second axis were 0.201 and 0.153 in non-grazed, 0.242 and 0.161 in moderately grazed and 0.355, and 0.114 in overgrazed plots. Cumulative percentage variance of species data was 20.1 and 35.4 in non-grazed, 24.2 and 40.3 in moderately grazed and 35.5 and 46.9 in overgrazed sites. Notations: Δ – northern slope, \Box – southern slope, \circ – ditch, \diamond – steppe.

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Table 2. Results of indicator species analyses for the species of non-grazed, moderately grazed and overgrazed sites in the four microhabitats.

Species	Grazing intensity	Micro-habitat type	Indicator value	Р	Frequency
Veronica spuria	Non-grazed	North slope	0.61	***	14
Dianthus borbasii	Non-grazed	North slope	0.41	***	10
Gypsophila paniculata	Non-grazed	North slope	0.30	**	31
Thymus pulegioides	Non-grazed	North slope	0.29	***	20
Seseli sp.	Non-grazed	North slope	0.28	***	12
Eremogone procera	Non-grazed	North slope	0.16	**	12
Iris pumila	Non-grazed	South slope	0.41	***	23
Carex stenophylla	Non-grazed	South slope	0.21	**	46
Ferula caspica	Non-grazed	South slope	0.21	**	8
Falcaria vulgaris	Non-grazed	South slope	0.11	*	7
Artemisia pontica	Non-grazed	Ditch	0.31	***	53
Stipa pennata	Non-grazed	Ditch	0.30	***	40
Allium pallasii	Non-grazed	Ditch	0.27	**	22
Sedum telephium	Non-grazed	Ditch	0.17	*	10
Verbascum phoeniceum	Non-grazed	Ditch	0.16	*	5
Festuca valesiaca	Non-grazed	Steppe	0.18	***	142
Spiraea hypericifolia	Moderate	North slope	0.25	***	41
Centaurea scabiosa subsp. adpressa	Moderate	North slope	0.10	*	6
Polygonum aviculare	Moderate	South slope	0.23	**	47
Galium verum	Moderate	Ditch	0.31	***	28
Stipa capillata	Moderate	Ditch	0.22	***	81
Achillea nobilis	Moderate	Ditch	0.21	*	38
Potentilla argentea	Moderate	Ditch	0.19	**	39
Veronica spicata	Moderate	Ditch	0.12	*	7
Silene media	Moderate	Steppe	0.40	***	38
Potentilla humifusa	Moderate	Steppe	0.36	***	19
Artemisia schrenkiana	Moderate	Steppe	0.28	***	53
Koeleria glauca	Moderate	Steppe	0.17	*	52
Eremopyrum orientale	High	North slope	0.37	***	41
Lolium perenne	High	North slope	0.29	***	9
Capsella bursa-pastoris	High	North slope	0.19	**	5
Chenopodium album	High	North slope	0.18	*	23
Taraxacum officinale agg.	High	North slope	0.14	**	7
Alyssum alyssoides	High	North slope	0.12	*	12
Amaranthus sp.	High	South slope	0.39	***	20
Artemisia austriaca	High	South slope	0.34	***	59
Elymus repens	High	Ditch	0.33	***	21
Leonurus cardiaca	High	Ditch	0.20	**	3
Chenopodium sp.	High	Ditch	0.19	**	5
Artemisia dracunculus	High	Steppe	0.77	***	23

Notes: Steppe specialists are denoted by boldface.

***P < 0.001; **P < 0.1; *P < 0.05.

Discussion

Effects of habitat type

Our results showed that micro-habitat type has a considerable role in shaping the vegetation of the kurgans, affecting mostly the cover of the species groups studied (Table 1). The most obvious difference between the vegetation of micro-habitat types was the low total vegetation cover on the southern slopes in non-grazed sites. As shown by Lisetskii et al. (2014) for Ukrainian kurgans, due to the differences in their exposure, southern slopes receive more (+4%) and northern slopes receive less (-9.5%) insolation compared with the adjacent horizontal surfaces. Increased insolation results in an increase in soil temperature and evapotranspiration, both contributing to a decrease in soil moisture. Furthermore, due to the higher level of insolation snowmelt is faster on the southerm slopes, which results in a higher level of water run-off, erosion and nutrient leaching from the topsoil layers (Sudnik-Wójcikowska and Moysiyenko 2008; Lisetskii et al. 2014). In arid and semi-arid regions, water balance has a decisive role in driving plant species composition (Dilts et al. 2015). Variation in water availability due to micro-topographical differences between the kurgan habitats and the surrounding flat steppe seemed to be sufficient to provide ecologically different habitats for plant species. The effect of water deficiency was the most obvious in case of the southern slopes, where low vegetation cover was likely caused by the harsher conditions compared with the other habitats studied, which finally led to an increase in bare ground (Table 1, Figure 2). Due to the harsh environmental conditions, steppe specialists were also represented by a lower cover on the southern slopes.

Both northern slopes and the ditch can be considered less exposed micro-habitats compared with southern slopes (Sudnik-Wójcikowska and Moysiyenko 2008; Lisetskii et al. 2016). We also confirmed this pattern in terms of higher species richness of steppe specialists on the northern slopes in non-grazed sites (Figure 3). Even though in non-grazed sites species richness of steppe specialists was lower in the ditch compared with the slopes, some specialists (such as Allium pallasii, Artemisia pontica, and Stipa pennata) could gain dominance there. Due to its topographical position, we can assume that the soil of the ditch has higher moisture content than adjacent areas and accumulates nutrients that might be leached from the slopes during occasional water runoff (Lisetskii et al. 2016). The ditch had an especially important role in preserving steppe specialists in the moderately grazed sites, which were situated in a slightly more continental climate compared to the non-grazed and heavily grazed sites (see Supplemental Appendix S1). This moist microhabitat could support the increased covers of perennial forbs and specialists under a slightly more arid climate.

We found that the special and diverse environmental conditions have led to a high plant diversity in kurgan micro-habitats, and ungrazed kurgans harboured several steppe specialists, mostly perennial forbs (such as Adonis volgensis, Allium paniculatum, Dianthus borbasii, Ephedra distachya, Ferula caspica and Veronica spuria) which were absent from the adjacent steppe plots, thus resulting in a considerably increased beta-diversity of the steppe landscape (Table 2). Recent studies have also suggested that microsites with diverse environmental conditions (e.g. microclimate, nutrient content and soil moisture) may act as local species-rich enclaves by enhancing the co-existence of species with different environmental requirements (Opedal et al. 2015; Deák et al. 2016b; Bátori et al. 2017b). The positive effect of microtopographical heterogeneity on species composition was also shown in terms of functional groups. While the nongrazed steppe sites were mostly dominated by perennial grasses, kurgan micro-habitats were characterised by a mixture of perennial grasses, perennial forbs and dwarf shrubs. In the non-grazed and moderately grazed sites, the cover of dwarf shrubs was the highest on the northern slope and in the ditch, which were likely the moistest habitats (Lisetskii et al. 2016). The preference of dwarf shrubs for moist habitat conditions was also shown by the fact that they were typical in the hollows dug by grave robbers (authors' personal observation).

Effects of grazing intensity and the interaction of grazing and micro-habitats

We found that there was a significant interaction between habitat type and grazing for most of the response variables studied, including total vegetation cover, Shannon diversity and the cover of most functional groups. This might be due to the fact that at heavily grazed sites vegetation composition is much affected by heavy trampling and biomass. Heavy grazing apparently cancelled the differentiating effects of abiotic site conditions probably resulted in no differences in total plant cover among habitats. There were several ruderal (Artemisia dracunculus, Elymus repens and Lolium perenne) and some steppe specialist species (such as Artemisia austriaca and Eremopyrum orientale) that appeared to be tolerant of grazing, and they had their highest cover, irrespective of habitat, at the heavily grazed sites. Interestingly, whilst we found a significant decrease in Shannon diversity of northern and southern slopes with increasing grazing intensity, grazing intensity had no effect on the Shannon diversity of the steppe where micro-topography and associated exposure were negligible and thus did not play result in species sorting. Our results are partly in line with the findings of Török et al. (2016), who has found that grazing intensity did not influence the species richness and species pool of Pannonian alkali steppes, affecting only the abundance patterns of species present. In our case, the proportion of the functional groups was considerably changed by grazing, but the diversity of the steppes remained unaffected. The reason for the different vegetation response might be the presence of different stress factors. In Pannonian alkali steppes, the main driver of the vegetation composition is the salt stress, whilst in the studied Kazakh steppes vegetation is rather influenced by the drought stress provided by the continental climate (Rachkovskaya and Bragina 2012; Godó et al. 2017). Given the high salt content of the soil, only a certain sort of species are able to exist in the alkali steppes, thus even in case of a heavy disturbance there is a limited chance for the establishment of new species (Godó et al. 2017). In contrast in arid environments without salt stress due to biomass removal and trampling a wide set of drought- and disturbance-tolerant species can establish in the vegetation (Peco et al. 2006). Our findings suggest that compared to the adjacent steppes, on kurgans heavy grazing causes a marked decrease in plant diversity, and therefore kurgans would need careful management so that they would continue enriching locally the steppes.

We found that heavy grazing decreased the species richness of steppe specialists. Given their historical coevolution with grazing megaherbivores, steppe specialists are highly resistant to moderate grazing (Milchunas and Lauenroth 1993). However, under high grazing pressure several steppe specialists were affected negatively, especially those growing on the slopes of the kurgans. The grazing behaviour of animals can further increase the effect of grazing on the kurgans. According to our personal observations, on hot days animals prefer to stay on the kurgans that stand out from the flatlands, as a slightly stronger wind there can cool the animals and can alleviate nuisance caused by insects. Changes in the cover of steppe specialists were not as obvious as in the case of their species richness. There was a significant interaction between habitat type and grazing intensity, as the cover of specialists on the northern slopes did not change with grazing intensity, while it sometimes increased on the

southern slopes. The main reason for this pattern was the considerable increase in the cover of *Artemisia austriaca*, which is a grazing-tolerant dwarf shrub, typical of heavily grazed steppes (Brinkert et al. 2016).

Heavy trampling and biomass removal under heavy grazing intensity decreased the cover of perennial grasses and forbs in all habitats. This is in contrast with the findings of Tóth et al. (2016) who found that grazing intensity did not affect the cover of perennial grasses in alkali steppes. We found that due to heavy grazing, the proportion of *Festuca valesiaca* and *Stipa* species with a dense and shallow root system decreased considerably and the trampling-tolerant *Elymus repens* and *Lolium perenne* with deep and stoloniferous below-ground organs gained dominance (Kutschera et al. 1982). These changes were most expressed on the southern slopes, where the effects of overgrazing were likely magnified by the arid environment.

Grazing considerably decreased the species richness of dwarf shrubs on the slopes and in the ditch, but not in the surrounding steppe. The reason for this pattern is the elimination of grazing-sensitive shrubs (such as *Ephedra distachya* and *Spiraea hypericifolia*) which are typical for kurgan micro-habitats in non-grazed and moderately grazed sites. In parallel, in the heavily grazed habitats, we detected a considerable increase in the cover of dwarf shrubs which can cope with the increased trampling and are resistant to grazing (such as *Artemisia austriaca* and *A. dracunculus*) because they are unpalatable for grazers (Brinkert et al. 2016; Gaitán et al. 2017).

Both species richness and the cover of ruderals and annuals were low in non-grazed and moderately grazed sites and were significantly increased by intensive grazing (Brinkert et al. 2016), which was the most pronounced on the arid slopes. Generally, these species (such as *Carduus nutans*, and *Polygonum aviculare*) are characterised by a high trampling- and grazing tolerance. In our study, the likely reason for the increased the cover of annual and ruderal species with increasing grazing intensity is the potential of grazing to reduce competition by eliminating dominant competitor species (such as perennial grasses). Biomass removal and trampling associated with high grazing intensity as well as increased nutrient input by the droppings of animals create open micro-sites with a disturbed soil surface for species establishment (Peco et al. 2006; Török et al. 2016).

Conclusions

Previous studies, mostly from the western part of the steppe biome, have emphasised the role of kurgans in providing refuges for remnants of the steppe vegetation and sustaining landscape-scale diversity in intensively used landscapes (Deák et al. 2016a, 2016b; Sudnik-Wójcikowska and Moysiyenko 2014). The importance of kurgans in preserving the steppe vegetation of central Asia has been underappreciated because of the continued presence of large intact steppe areas. Our results show that kurgans have a considerable role in enhancing overall local plant diversity in the vast expanses of central Asian steppes. We also found that micro-habitats with distinct vegetation are present even on average-sized kurgans (of ca. 1.5 m in height) likely due to the differences in insolation, soil moisture and nutrient content. We also pointed out that besides the slopes, the ditch also has a considerable role in preserving biodiversity and has the potential to harbour unique vegetation.

Even though kurgans are valued as sacred places, historical monuments and iconic landscape elements of the steppe region, their nature conservation values are rarely acknowledged. As a consequence, in Russia and Kazakhstan legal protection of the kurgans covers their archaeological value, without considering their importance for natural heritage. Despite their being local species-rich enclaves in the steppes, without protection, urbanisation, land use intensification and change threaten the wildlife of kurgans (Deák et al. 2016a). Such impacts are less in nature reserves; however, there is no legal protection for the large number of kurgans outside protected areas. Thus, we suggest that decision makers should extend kurgan protection in an integrative way, focusing both on the conservation of both cultural and natural heritage for a more effective protection of these iconic sites. In addition to the above factors, the intensity of land use can also considerably influence the vegetation of kurgans. In line with previous studies (Brinkert et al. 2016), we conclude that a moderate level of grazing would be the most beneficial for maximising over the long-term steppe plant diversity. This goal would require the revitalisation of nomadic herding systems (a socially contentious issue) and by supporting the populations of wild mega-herbivores.

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