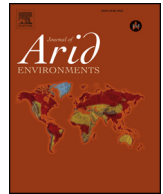




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Steppe Marmot (*Marmota bobak*) as ecosystem engineer in arid steppes

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ABSTRACT

Burrow-dwelling rodents are often considered ecosystem engineer species in arid environments. They create distinct habitat patches by building burrows: they move large amounts of soil, mix soil layers and change soil properties locally. Our aim was to explore the role of Steppe Marmot as an ecosystem engineer in shaping the plant species composition and diversity of steppes. First, we made a literature search to gather information on the ecosystem engineering effect of the species. Second, in a case study, we compared the vegetation of marmot burrows with the surrounding intact steppes in North-Kazakhstan to identify differences in species composition and plant functional groups. Vegetation of the burrows was structurally and compositionally different from the intact steppe vegetation. Burrows were characterised by lower total vegetation cover, higher cover of annuals and lower cover of perennial grasses compared to the intact steppe. We found an increased cover of ruderal species on the burrows, but also several specialist species, such as *Agropyron cristatum*, *Anabasis salsa*, *Kochia prostrata* and *Petrosimonia* spp. were confined to the burrow vegetation. Our results suggest that marmot burrows increase the landscape-scale heterogeneity of the steppe vegetation and could act as stepping stones for the dispersal of several steppe-specialist species.

1. Introduction

Plants and animals living in harsh environments developed several morphological, phenological, physiological and behavioural adaptations to tackle extreme temperature, aridity or nutrient-deficiency (Kinlaw, 1999; Díaz et al., 2004). However, there are a few ecosystem engineer species which not only tolerate harsh conditions, but can also transform their micro-environment to bring it closer to their optimum. Ecosystem engineers have the ability to directly or indirectly modulate the availability of resources to other species (Jones et al., 1994). They have always been in the focus of scientific interest, and there are many studies about their effects on local environmental conditions and landscape-scale diversity (e.g. Davidson et al., 2012; Wesche et al., 2007; Yoshihara et al., 2010a).

Burrow-dwelling rodents, such as marmots (*Marmota* spp.), prairie dogs (*Cynomys* spp.) and ground squirrels (*Spermophilus* spp.) are

among the ecosystem engineers studied in greatest detail (Davidson et al., 2012; Zimmermann et al., 2014). Most of them inhabit dry grasslands. They modify ecosystem attributes affecting the distribution of other species, and this effect usually lasts longer than the lifespan of the engineer specimens (Hastings et al., 2007). Burrow-dwelling rodents are social animals living in colonies, which use distinct habitat patches for feeding and nesting (Yoshihara et al., 2010a). They build burrows of different size and complexity, and move large amounts of soil during the construction (Davidson et al., 2012); they alter soil properties by mixing soil layers and change soil compactness, nutrient and moisture content (Aho et al., 1998). The focal area of all their activities is concentrated on their burrows (Yoshihara et al., 2010a), usually experiencing increased level of trampling, grazing, defecation and urination (Van Staaldin and Werger, 2007; Wesche et al., 2007).

Besides building burrows, these rodents also play an important role

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in grassland ecosystems as herbivores. They consume plant biomass, disperse seeds and create establishment microsites for plant species during their activities (Wesche et al., 2007). Studying the effects of herbivores on the vegetation has always been a central issue in plant ecology (Milchunas et al., 1988), and it is still an urgent task, considering the serious changes in the diversity and productivity of present day's grassland ecosystems, which are strongly connected with the activity and patterns of herbivory (Bakker et al., 2006; Wesche et al., 2016). Even though the effects of wild ungulates and domestic livestock on diversity and species composition of grasslands have been well studied in various ecosystems, effects of small herbivores are less explored (Bakker et al., 2006).

The vegetation of steppes has always been shaped by herbivores, which are among the major drivers of the habitat structure and plant species composition of these open landscapes (Wesche et al., 2016). Due to recent changes in the abundance and distribution of herbivores, steppes experience severe changes in their ecosystem functioning. In many parts of the Eurasian steppe zone livestock grazing schemes changed considerably due to sedentarization and urbanisation. As a result, large areas of steppe have become ungrazed by livestock in Kazakhstan, and grazing is now mainly confined to the vicinity of settlements. Intensive poaching and diseases of wild grazers, such as the Saiga Antelope (*Saiga tatarica*), have further increased the area of ungrazed steppes (Kamp et al., 2016), leading to the disappearance of formerly typical domestic and wild megaherbivores from many habitats (see also Bakker et al., 2006). In these large areas, burrow-dwelling mammals, such as Steppe Marmot (*Marmota bobak*), Steppe Pika (*Ochotona pusilla*), Susliks (*Spermophilus* spp.) and other rodents are the most important herbivores (Kamp et al., 2016). Steppe Marmot (*Marmota bobak*) is a typical and formerly widespread species of Eurasian steppes. In the first half of the 20th century hunting and habitat loss caused by the conversion of steppe to arable land significantly reduced its populations and distribution range; thus, the species is now listed on the IUCN Red List. Currently the majority of its range is restricted to the Urals and North-Kazakhstan, but it sporadically occurs in the Russian lowlands and in Ukraine as well (Tsytsulina et al., 2016).

Our aim was to explore the role of Steppe Marmot as an ecosystem engineer species in shaping the plant species composition and diversity of steppes. The major novelty of our study is that by combining a literature review with a vegetation ecological field study, we aim to reveal possible mechanisms and feedbacks between the ecology and behaviour of a rodent species and the vegetation developed on its burrows. Marmots in general, and also the Steppe Marmot are important model organisms for ecologists because of their well-developed social behaviour (Armitage, 2014; Nikol'skii & Savchenko 2009), vocal communication (Blumstein, 2007), and since they are key prey items for raptors (Katzner et al. 2006). There are several studies about habitat and forage preferences of marmots (Ronkin et al., 2009; Savchenko and Ronkin, 2018), the characteristics of their burrow system (Nikol'skii 2009, Nikol'skii & Savchenko 2009) and their effects on soil parameters (Rumiantsev, 1992), or about the detection of marmot burrows using remote sensing tools (Koshkina et al., 2020). However, despite the large knowledge accumulated about marmots, up to our knowledge, there were no studies evaluating the links between the activities of the Steppe Marmots and the species composition, diversity and conservation value of the burrow vegetation.

To fill these knowledge gaps, first we reviewed the available studies on the ecology, life cycle and habitat use of Steppe Marmot from the perspective of ecological engineering. We asked the following questions: (i) What are the functions of burrows for Steppe Marmot? (ii) How do they build their burrows? (iii) How do they modify local environmental conditions during the construction and use of their burrows?

Second, in a case study, we compared the vegetation of actively used marmot burrows with that of surrounding intact steppes to identify differences in species composition and plant functional groups. We

studied two burrow types, i.e. flat and mounded burrows that represent two types of microhabitats created by the rodents. We tested the following hypotheses: (i) Marmot burrows are characterised by a vegetation distinct from the surrounding steppe matrix. (ii) Annual and ruderal species are more abundant, while perennial and steppe specialist species are less abundant on burrows than in the adjacent intact steppe. (iii) Vegetation of flat and mounded burrows is different due to the differences of soil moisture content caused by different topography.

Finally, we linked the effects of burrow building and marmot activity with plant species composition, and identified potential linkages between ecosystem engineering effect (burrow building and use) and burrow vegetation. We also discussed the possible role of marmot burrows in maintaining landscape-scale diversity in steppes.

2. Methods

2.1. Literature search

We searched for scientific papers about Steppe Marmot in Google Scholar, using the search terms 'Marmota bobak' OR 'Marmota bobac' (because there is an ambiguity in its vernacular name). The search retained 755 hits. We screened all hits by title and omitted those which were not concerned with the biology of the species (mainly paleontological or epidemiological papers). All other papers were screened by abstract, and finally we found 37 papers which were available in English (or at least with English summary) focusing on the ecology, behaviour, distribution, or conservation status of Steppe Marmot. We also included relevant findings from studies on other marmot species, in case when no information was available for Steppe Marmot.

2.2. Case study on the vegetation of Steppe Marmot burrows

2.2.1. Study area

The study area was located in the Turgai Plateau, in the Naurzum State National Nature Reserve, Northern Kazakhstan (Fig. 1A). The study area belongs to the UNESCO World Heritage site 'Saryarka – Steppes and Lakes of Northern Kazakhstan' which harbours stands of virgin steppe formed on dark chestnut carbonate heavy loam soil (Bragina, 2016). Feathergrass steppes are dominated by *Stipa lessingiana* and *Festuca valesiaca*; typical forbs include *Artemisia lercheana*, *Galatella tatarica*, *Palimbia salsa*, *Phlomis agraria*, *Silaum silaus* and *Tanacetum achilleifolium* (Lavrenko et al., 1991). The climate of the region is dry continental, with a mean annual temperature of 3.6 °C (−19°C in January and 22°C in July) and mean annual precipitation of 240–260 mm (<https://en.climate-data.org>). There is no grazing livestock in the area and grazing by wild megaherbivores is also negligible; thus, it is an ideal place for detecting the effects of marmots on plant species composition and diversity. The estimated number of Steppe Marmot population in the Naurzum State National Nature Reserve at present time is 900–1000 individuals (Bragina and Bragina, 2017).

2.2.2. Sampling design

We studied the vegetation of marmot burrows and surrounding intact steppes in two feathergrass steppe sites (Site 1 N 51°40'45" E 63°45'12", 250 m a.s.l. and Site 2 N 51°39'36" E 63°43'12", 238 m a.s.l.) in early July 2016. Both sites are flat lowland areas. We had 16 sampling units per site: eight actively used marmot burrows and eight control plots (16 actively used burrows and 16 control plots in total). Burrows in the higher-elevated Site 1 were flat, equal to ground level and without mounds (Fig. 1D). Burrows in the lower-elevated Site 2 were characterised by 0.5–0.8 m high definite mounds (Fig. 1E) which can protect marmots in case of occasional inundation.

Surface area of the marmot burrows was approximated to an ellipsis, and was calculated using equation $A = r_1 \times r_2 \times \pi$; where r_1 and r_2 are the long and short radii of the ellipsis, respectively. Mean surface area of the flat burrows ($72.3 \pm 43.9 \text{ m}^2$ mean \pm SD) in Site

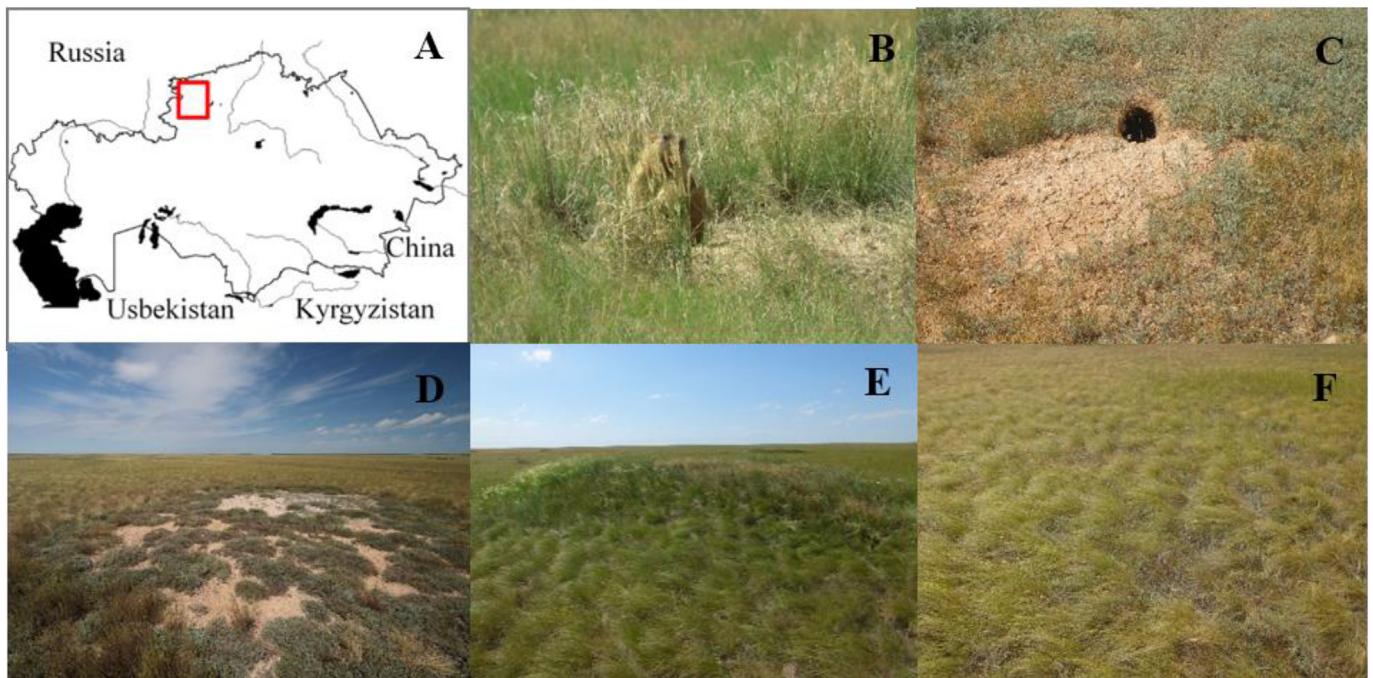


Fig. 1. (A) Map of the study area, (B) Steppe Marmot (*Marmota bobak*), (C) Burrow entrance and surrounding trampled platform, (D) Flat marmot burrow, (E) Mounded marmot burrow and (F) Intact feathergrass steppe. Photos taken by O. Valkó (B, F), A. Kelemen (C), B. Deák (D) and R. Gallé (E).

1, and that of mounded burrows ($102.3 \pm 50.9 \text{ m}^2$ mean \pm SD) in Site 2 were not different (independent sample *t*-test; $t = -1.264$, $p = 0.227$). We designated a ‘control’ plot 30 m from each burrow in the intact steppe. Each control plot had the same size and shape as the corresponding marmot burrow.

2.2.3. Vegetation and soil sampling

We recorded all vascular plants occurring on each sampling unit (burrows and control plots), and recorded their percentage cover scores by visual estimation. Plant nomenclature follows The Plant List (2017).

We also aimed to test the differences between the soil properties of marmot burrows and intact steppes. We only had the possibility for non-destructive on-site soil measurements, thus we measured volumetric moisture content in the upper 20 cm at five random points on each burrow and steppe plot with a Field Scout TDR 300 soil moisture meter (resolution: 0.1 V/V% of water).

2.3. Data processing

Plant species were categorised according to their life form (perennial grasses, perennial forbs, dwarf shrubs and annuals) and habitat indication (steppe specialists and ruderals) based on Brinkert et al. (2016), Deák et al. (2017) and Komarov (1968–2002). We categorised species as ‘salt-tolerant’ if they were listed as a species of saline, solonetz or solonchak soils in Komarov (1968–2002). We calculated Shannon diversity for each plot, and the Sørensen similarity of the vegetation on the burrows and intact steppes.

To visualise the plant species composition on the marmot burrows and control plots in the two sites, a DCA ordination was calculated in CANOCO 5.0 (Ter Braak and Šmilauer, 2012). We passively projected ‘Shannon diversity’, ‘Soil moisture’ and ‘Total cover’ scores on the DCA ordination as an overlay in order to visualise the correlation of above variables on species composition (Fig. 2). Characteristic species of the burrows and control plots were identified by the IndVal procedure (Dufrêne and Legendre, 1997) using the ‘labdsv’ package in R.

We tested the effects of ‘Burrow’ (burrow/control plot, fixed factor), ‘Site’ (Site 1 with flat burrows/Site 2 with mounded burrows, fixed factor) and interaction of ‘Burrow \times Site’ (fixed factor) on the

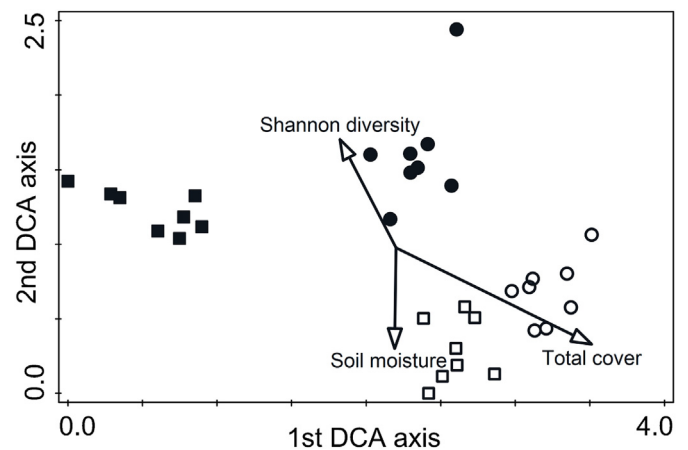


Fig. 2. DCA ordination based on the species composition of Steppe Marmot burrows and steppes in the two study sites. Eigenvalues are 0.61 and 0.26 for the first two axes. Cumulative explained variation of the first two axes is 24.8% and 35.5%. Notations: ■ - Site 1, flat burrows; ● - Site 2, mounded burrows; □ - Site 1, intact steppe; ○ - Site 2, intact steppe. ‘Shannon diversity’, ‘Soil moisture’ and ‘Total cover’ were included as overlay.

dependent variables with Generalised Linear Models. Dependent variables were soil moisture content, total vegetation cover, Shannon diversity and the species richness and cover of functional groups (perennial grasses, perennial forbs, dwarf shrubs, annuals, steppe specialists, ruderals and salt-tolerants). Species richness of functional species groups followed Poisson distribution and we used a log link function. Soil moisture content, Shannon diversity as well as the cover of perennial forbs and steppe specialists followed normal distribution, while cover of other functional groups were log ($x+1$) transformed to approximate them to normal distribution, and we used identity link for these variables in the GLMs. GLMs were calculated in SPSS 20.0. We also fitted fixed factors used in the GLMMs (burrow, site) onto DCA ordination to test burrow and site effects on the estimated DCA axes, using the ‘envfit’ function of the ‘vegan’ R-package.

3. Results

3.1. Literature review

3.1.1. Functions of Steppe Marmot burrows

Burrow building in general is a unique adaptation to harsh environments. Formosov (1966) pointed out that out of the 90 mammal species of the Eurasian steppe, 72 are closely associated with burrows. The reviewed studies showed that burrows are of crucial importance for marmot's life. Mating occurs in the burrow (Armitage, 2014) and cubs remain in the burrow until they are able to walk, which is around one month of age (Tsytulina et al., 2016). The reviewed papers mentioned various shelter functions of burrows, i.e. ameliorating microclimate and providing refuge from predators. Based on the literature, burrow-building has the following functions:

Place for hibernation. The primary function of burrows is the protection of the hibernating family (Nikolskii, 2009). The more continental the climate the colder the winter is; thus, deeper burrows are needed for maintaining proper temperature. It was found that the depth of the burrows increases from Ukraine (mean of 150 cm) to Kazakhshtan (up to 450 cm) in line with the increasing continentality of the climate (Nikolskii, 2009).

Protection against extreme weather. Steppe vegetation is characterised by narrow-leaved grasses and forbs, which do not provide enough shade against extreme solar radiation and heat (Formosov, 1966). Steppe Marmots usually spend the hottest hours in the burrow and they often return there to cool down their body (Andreychev and Zhalilov, 2017). Burrow temperature varies between 15 and 20 °C with only minor fluctuations during the hot summer days (Nikolskii, 2009). In occasional wet years, inundation might occur also in arid steppe. In these years, the burrow hill provides important refuge against flood (Formosov, 1966).

Shelter from predators. Steppe Marmots are preferred prey items of eagles (Katzner et al., 2006). The only way to escape is hiding in the burrow. Andreychev and Zhalilov (2017) found that Steppe Marmots spend the last 1.5 h before sunset in the burrow, because this is the peak activity period of birds of prey. All their aboveground activities are concentrated near the burrow in order to be able to quickly hide from predators. Reproductive females are usually foraging in the close vicinity of the burrow, males have larger foraging areas, but they rarely go further than 100–300 m from the burrow either (Andreychev and Zhalilov, 2017; Nikolskii and Savchneko, 1999).

3.1.2. Burrow structure and the seasonality of burrow use

Steppe Marmot burrows have complex tunnel systems, which may be up to 4–5 m in depth. There are summer and winter burrows, both usually with pronounced mounds, which can be up to 1 m high, and 10–15 m in diameter (Zimina and Gerasimov, 1973). On the ground near the residential hole there is a trampled platform, from which the marmots can inspect the surroundings. Permanent burrows can have a very complex underground architecture, with tunnels and differently sized brood chambers. Steppe Marmots do not stock up for winter; instead they hibernate for at least six months a year, between September/October and March/April (Tsytulina et al., 2016). Formosov (1966) reported that marmots renew the lining of their nests every summer. They bring out old nest material (Nikolskii, 2009) and possibly also the cadavers of individuals died during hibernation (observed in *M. camtschatica bungei*, Semenov et al., 2001). Tunnel systems that have been inhabited for a long time always have a number of empty passages and tunnels, wherein a marmot pursued by a predator can hide or, if necessary, can dig deeper (Formosov, 1966).

During early summer marmots deposit their faeces in a special small cavity located at one of the burrow entrances. Later they use one of the blind passages in the depth of the burrow as a latrine (Nikolskii, 2009). Before entering hibernation in early autumn, marmots bury secondary entrances with soil from outside. They close the main entrance of the

burrow from inside with a dense plug made of soil mixed with faeces from the latrine, and plant particles used as cementing material (Formosov, 1966). The plug is several meters thick (1.5–3 m) and almost completely prevents heat exchange between the air within and outside the burrow (Nikolskii, 2009). When the burrow is plugged, the inside temperature depends on the temperature of the surrounding soil (Nikolskii, 2009).

The causes of the abandonment of a burrow are not reported in detail. According to Formosov (1928) year by year these burrows are extended and renewed; the old ones are abandoned and new ones are dug. Formosov (1966) reported that if ectoparasites (e.g. fleas and ticks) greatly annoy the marmots, they plug the entrance of the old nest chamber with a compact earth plug and use a new nest. Reasons for burrow abandonment are the death of the family members or the successional development of burrow vegetation. Young marmots reach sexual maturity and disperse to establish a new burrow usually at the age of three years (Armitage, 2014; Tsytulina et al., 2016).

3.1.3. Effects of burrows on local environmental conditions

Burrows alter local micro-environment by altering soil properties, such as aeration, water runoff, nutrient content and salinity. Yoshihara et al. (2010a) reported that the burrows of the Siberian Marmot (*M. sibirica*) represent soil patches with coarse particles and associated large macropores. Several studies found increased soil nutrient content on the mounds, because of the concentrated defecation and urination of marmots. For Black-capped Marmot (*M. camtschatica*), Semenov et al. (2001) found that concentrated defecation, urination, as well as the transport of nest litter and carcasses of individuals died during hibernation likely result in increased nutrient content; thus, more rapid plant growth and increased phytomass production. On the burrows of Woodchucks (*M. monax*) 1.7 times higher nitrogen content was measured compared with the adjacent grasslands (Merriam and Merriam, 1965). Mounds of the Siberian Marmot (*M. sibirica*) are characterised by an increased level of soil nitrogen and phosphorus content (Van Staaldnuinen and Werger, 2007).

Several studies found that marmot burrows alter local salinization patterns, create salt concentrations and rise carbonate content (Rumiantsev, 1992). The excavated soil thrown out of the burrows is much richer in mineral salts, and poorer in organic substances than the surrounding, superficial soil layers (Formosov, 1928). Another source for local salt accumulation might be the sediments left after the evaporation of urine in the topsoil (Yoshihara et al., 2010a). In solonetz steppes the thrown up soil has high lime content; thus, in these patches, sodium is replaced by calcium (Formosov, 1928). Thus, in solonetz steppes, marmots act as soil ameliorators. Formosov (1928) estimated that in a few centuries, chlorides and sulphates can be entirely leached, and humus accumulation can be observed, making soil parameters of abandoned burrows similar to intact steppe.

To the best of our knowledge, our case study is the first to compare the vegetation of Steppe Marmot burrows and surrounding intact steppe in a quantitative way. However, non-quantitative descriptions of vegetation differences between Steppe Marmot burrows and surrounding steppes are provided in Formosov (1928), Ronkin and Savchenko (2004) and Ronkin et al. (2009). Formosov (1928) was the first, who highlighted the spectacular effects of marmots on steppe vegetation and mentioned the distinct vegetation patches of the burrows as 'marmot gardens'. He reported that vegetation on the burrows is dominated by ruderal plants, and due to the digging activity of marmots, the progress of secondary succession is hampered, the vegetation remains at a pioneer stage. He also proposed that this way marmots assist the maintenance of vegetation, 'to which they became adapted'.

3.2. Case study on the vegetation of burrows

3.2.1. Plant species composition of burrows and intact steppes

We recorded a total of 77 vascular plant species in the 32 study

Table 1

Characteristic species of marmot burrows and intact steppe on Site 1 and Site 2, identified by indicator species analysis. Salt-tolerant species are marked with an asterisk. Notations: Habitat ind. – Habitat indication; FB – flat burrow; MB – mounded burrow; IS- intact steppe; Freq. – Frequency.

Species	Habitat ind.	Site	Burrow/ Steppe	IndVal	<i>p</i>	Freq.
<i>Anabasis salsa</i> *	S	1	FB	0.50	0.010	4
<i>Artemisia pauciflora</i> *	S	1	FB	0.87	0.001	9
<i>Climacoptera brachiata</i> *	R	1	FB	0.62	0.003	6
<i>Iris humilis</i>	S	1	FB	0.52	0.025	9
<i>Petrosimonia glaucescens</i> *	S	1	FB	1.00	0.001	8
<i>Petrosimonia triandra</i> *	S	1	FB	0.65	0.003	8
<i>Achillea nobilis</i> *	S	1	IS	0.60	0.005	8
<i>Stipa lessingiana</i>	S	1	IS	0.43	0.011	30
<i>Agropyron cristatum</i>	S	2	MB	0.61	0.002	26
<i>Atriplex nitens</i>	R	2	MB	0.49	0.005	5
<i>Bassia sedoides</i> *	S	2	MB	0.49	0.015	13
<i>Chenopodium album</i>	R	2	MB	0.50	0.018	5
<i>Descurainia sophia</i>	R	2	MB	0.48	0.014	9
<i>Kochia prostrata</i> *	S	2	MB	0.60	0.004	7
<i>Lactuca serriola</i>	R	2	MB	0.38	0.040	3
<i>Polygonum patulum</i> *	R	2	MB	0.75	0.002	6
<i>Stipa capillata</i>	S	2	MB	0.86	0.001	13
<i>Artemisia lercheana</i> *	S	2	IS	0.42	0.048	24
<i>Artemisia schrenkiana</i> *	S	2	IS	0.38	0.045	3
<i>Astragalus testiculatus</i>	S	2	IS	0.44	0.036	5
<i>Eryngium planum</i>	S	2	IS	0.75	0.001	6
<i>Galatella tatarica</i> *	S	2	IS	0.85	0.001	14
<i>Jurinea multiflora</i> *	S	2	IS	0.44	0.048	13
<i>Nepeta ucrainica</i>	S	2	IS	0.44	0.020	8
<i>Palimbia salsa</i> *	S	2	IS	0.76	0.002	20
<i>Phlomis agraria</i>	S	2	IS	0.55	0.009	13
<i>Potentilla humifusa</i>	S	2	IS	0.74	0.002	7
<i>Scorzonera stricta</i> *	S	2	IS	0.49	0.026	5
<i>Silaum silaum</i> *	S	2	IS	0.48	0.015	6
<i>Tragopogon capitatus</i>	S	2	IS	0.47	0.017	5
<i>Veronica prostrata</i>	S	2	IS	0.38	0.045	3
<i>Veronica spicata</i>	S	2	IS	0.38	0.040	3

plots, from which 27 species were found on flat burrows (Site 1), 47 on mounded burrows (Site 2) and 38 and 45 species in the intact steppe plots in Site 1 and Site 2, respectively. In Site 1, Sørensen similarity of the vegetation composition of flat burrows and steppes ranged between 0.25 and 0.52. In Site 2 with mounded burrows, the same scores ranged between 0.26 and 0.51.

The DCA ordination showed a clear distinction of the species composition between burrows and steppes. The two steppe sites had very similar and homogeneous species composition. Vegetation of steppes and burrows were separated along the first axis, vegetation of the flat and mounded burrows were separated along the second axis (Fig. 2).

The indicator species analysis showed that several salt-tolerant steppe specialist species, such as *Anabasis salsa*, *Artemisia pauciflora*, *Petrosimonia glaucescens* and *P. triandra* were characteristic of flat burrows (Table 1). Mounded burrows were mainly characterised by ruderal species, such as *Atriplex nitens*, *Chenopodium album*, *Descurainia sophia* and *Lactuca serriola*. A few steppe specialists were also characteristic of the mounded burrows, such as *Agropyron cristatum*, *Bassia sedoides* and *Kochia prostrata*. Most of the steppe specialists were character species of intact steppes (Table 1).

3.2.2. Vegetation characteristics and functional groups

Both the presence of burrows, and interaction between 'Burrow' and 'Site' affected soil moisture content. We detected the lowest soil moisture content on mounded burrows in Site 2 (Fig. 3A, Table 2). Total vegetation cover was affected by all studied factors, and was the lowest on the flat burrows (Fig. 3B, Table 2). Higher Shannon diversity was recorded on burrows compared to intact steppe (Fig. 3C, Table 2).

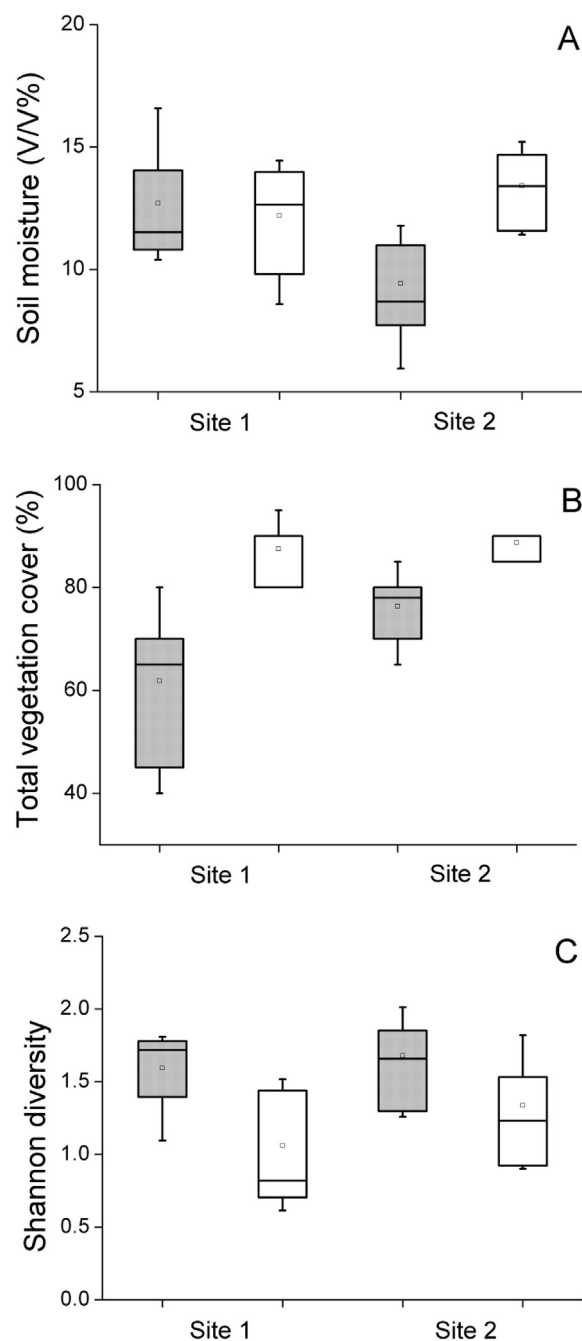


Fig. 3. (A) Soil moisture content, (B) Total vegetation cover and (C) Shannon diversity of the marmot burrows (grey boxes) and intact steppe (white boxes) in the two study sites.

Species richness and cover of annuals were higher on marmot burrows than in the intact steppe. Cover of annuals was also affected by 'Site' and by the interaction between 'Burrow' and 'Site'; we recorded the highest scores on flat burrows of Site 1 (Fig. 4A–B, Table 2). The cover of perennial grasses was affected by all studied factors, and was the highest in the steppe plots of Site 1; their species richness remained unaffected (Fig. 4C–D, Table 2). Species richness of perennial forbs was affected by 'Burrow' and 'Site'; their cover was affected by the interaction between 'Burrow' and 'Site' (Fig. 4E–F, Table 2). Dwarf shrubs were unaffected by the studied factors (Fig. 4G–H, Table 2). The cover and species richness of steppe specialists were the highest in the intact steppe, while cover of ruderal species was the highest on marmot burrows (Fig. 5A–D, Table 2). Species richness of salt-tolerants was

Table 2

Effect of 'Burrow' (marmot burrow/intact steppe), 'Site' (Site 1/Site 2) and 'Burrow × Site' on soil moisture content and vegetation characteristics, displayed by Generalised Linear Models. Significant effects ($p < 0.05$) are marked with boldface.

	Burrow		Site		Burrow × Site	
	F	p	F	p	F	p
Soil moisture content	8.31	0.007	1.67	0.206	13.79	0.001
Shannon diversity	19.91	0.000	2.07	0.162	0.95	0.339
Species richness						
Annual	30.38	0.000	1.55	0.224	0.11	0.740
Perennial grass	0.02	0.894	0.88	0.356	2.83	0.104
Perennial forb	24.88	0.000	13.39	0.001	0.01	0.919
Dwarf shrub	0.08	0.779	0.29	0.596	0.08	0.779
Steppe specialist	6.49	0.017	8.63	0.007	0.04	0.838
Ruderal	5.91	0.022	6.03	0.021	1.83	0.187
Salt-tolerant	0.17	0.688	0.43	0.518	0.17	0.687
Percentage cover						
Total	46.20	0.000	5.09	0.032	7.92	0.009
Annual	316.26	0.000	15.59	0.000	17.33	0.000
Perennial grass	75.73	0.000	59.30	0.000	69.23	0.000
Perennial forb	0.74	0.398	0.13	0.720	6.28	0.018
Dwarf shrub	0.37	0.547	0.97	0.333	3.27	0.081
Steppe specialist	8.73	0.030	0.87	0.358	0.73	0.400
Ruderal	31.97	0.000	0.02	0.890	3.20	0.084
Salt-tolerant	6.56	0.016	12.29	0.002	21.18	0.000

unaffected, but their cover was significantly influenced by all studied factors. Cover of salt-tolerant species was the highest on the flat burrows (Site 1) (Fig. 5E–F, Table 2). Fitting the fixed factors of the GLMM onto DCA ordination showed that both site ($P = 0.005$, $R^2 = 0.178$) and burrow ($P = 0.001$, $R^2 = 0.309$) effects were significant on the estimated DCA axes.

4. Discussion

4.1. Marmot burrows as micro-habitats

4.1.1. Vegetation composition

Our results suggest that Steppe Marmot burrows are unique micro-habitats in arid steppes. We demonstrated that marmot burrows are characterised by vegetation distinct from the surrounding intact steppe (see Table 1, Fig. 2). Similarly to other rodents, such as Siberian Marmot (Van Staalduin and Werger, 2007; Yoshihara et al., 2010a) or Daurian Pika (*Ochotona daurica*; Wesche et al., 2007), the ecosystem engineering effect of Steppe Marmot is the most apparent on burrows, as most of their activities are focused there (Andreychew and Zhalilov, 2017). Based on the literature review, burrowing, trampling, defecation, urination and grazing create open disturbed soil surfaces, higher soil nutrient content and altered salinization patterns on the burrows. According to our measurements, flat burrows had soil moisture content similar to steppe, while mounded burrows had lower soil moisture content than the surroundings, which can also explain the detected differences in the vegetation composition. Vegetation of the burrows was structurally different from the intact steppe, well reflected by the differences in total vegetation cover, being lower on the burrows, because of frequent and severe disturbance (see also Winter et al., 2002). Another notable structural difference was the higher cover of annuals and lower cover of perennial grasses on the burrows compared to the intact steppe. Similar patterns were found in case of prairie dogs (*Cynomys ludovicianus*; Archer et al., 1987) and Daurian Pika (Wesche et al., 2007). Open soil surface, lower soil moisture content (on mounded burrows) and regular soil disturbance are the likely reasons for increased cover of annuals on the expense of perennial grasses.

4.1.2. Ruderal plants

We found an increased cover of ruderal species on the burrows,

likely because of the intense trampling and nutrient input typical on the open soil surface (see also Ronkin et al., 2009; Ronkin and Savchenko, 2004; Formosov, 1928). However, we did not observe the spread of these ruderal species into the nearby steppe vegetation, thus it does not seem to threaten grassland conservation values. This is likely due to the low competitive ability of ruderal species, which cannot germinate and establish in the closed vegetation (Kelemen et al., 2013).

Rodents in general are considered selective grazers, with a high preference for highly nutritious plants (Bakker et al., 2006; Savchenko and Ronkin, 2018). In an experimental feeding study, Ronkin et al. (2009) found that 80% of the most preferred food items of Steppe Marmot are species typical to early successional vegetation. They found that marmots prefer several ruderal species, such as *Chenopodium album*, *Polygonum* spp., and their 'favourite' was *Lactuca serriola*, when they were able to choose between 200 food species (Ronkin et al., 2009). We found that these preferred ruderal species were present in high frequency and abundance in burrow vegetation, and even the most preferred species *L. serriola* was a significant indicator species on burrows.

4.1.3. Steppe specialist plants

According to our expectations, burrows were characterised by lower species richness and cover of steppe specialist plants compared to the intact steppe, since disturbed patches in an early successional stage generally harbour fewer specialist plants than intact natural vegetation. However, several specialist species of steppes were confined to the flat burrows. Similarly, Black-Capped Marmots were also found to create distinct habitat patches on arctic tundra, which provide important habitats for some rare specialist species (Semenov et al., 2001). We identified several specialist species, such as *Agropyron cristatum*, *Anabasis salsa*, *Kochia prostrata* and *Petrosimonia* spp. that were confined to these small habitat islands. *Agropyron cristatum* is a highly preferred food item of marmots (Ronkin et al., 2009) and was found to be a burrow indicator species also on the mounds of Daurian Pika (Wesche et al., 2007). *A. cristatum* is a typical species of dry steppes, which is in line with the low soil moisture contents we recorded on mounds. We suggest that marmot burrows have a crucial role in maintaining the populations of these plants at the landscape scale by providing small habitat islands in the otherwise homogeneous closed steppe. In this term ancient steppic burial mounds called 'kurgans' play a similar role as marmot burrows, as they also increase landscape-scale microhabitat heterogeneity in steppes (Deák et al., 2016, 2017).

Indicator species of flat burrows included several salt-tolerant ones, such as *Anabasis salsa*, *Artemisia pauciflora*, *Petrosimonia glaucescens* and *P. triandra*. The GLMs also confirmed that the cover of salt-tolerant species was higher on burrows than in intact steppes. By reviewing literature, we found several theories explaining the increase in local salt content on burrows (Formosov, 1928; Rumiantsev, 1992; Yoshihara et al., 2010a). Salt-rich soil layers brought up by the marmots may contain buried seeds of salt-tolerant plants. Salt-tolerant species often have long-term persistent seed banks, which allow them to be dormant for a long period and germinate only in case suitable conditions are present (Valkó et al., 2014a). In our case study, salt-tolerant species were more typical on flat burrows. Halophyte flora growing on flat burrows might be physiologically advantageous for marmots. In the case of North-American marmot species (*M. monax* and *M. flaviventris*), additional salt uptake by licking roads (consuming de-icing NaCl) or mud surface at salt licks was observed by Armitage (2000). Steppe Marmot might consume halophyte species growing on burrows for increasing its salt uptake over the physiological minimum limit; however, this theory needs to be verified by field observations.

4.2. Ecosystem engineering and marmot gardens

In our study we assessed the ways how Steppe Marmots modify their local environment by creating mounds, altering soil nutrient content,

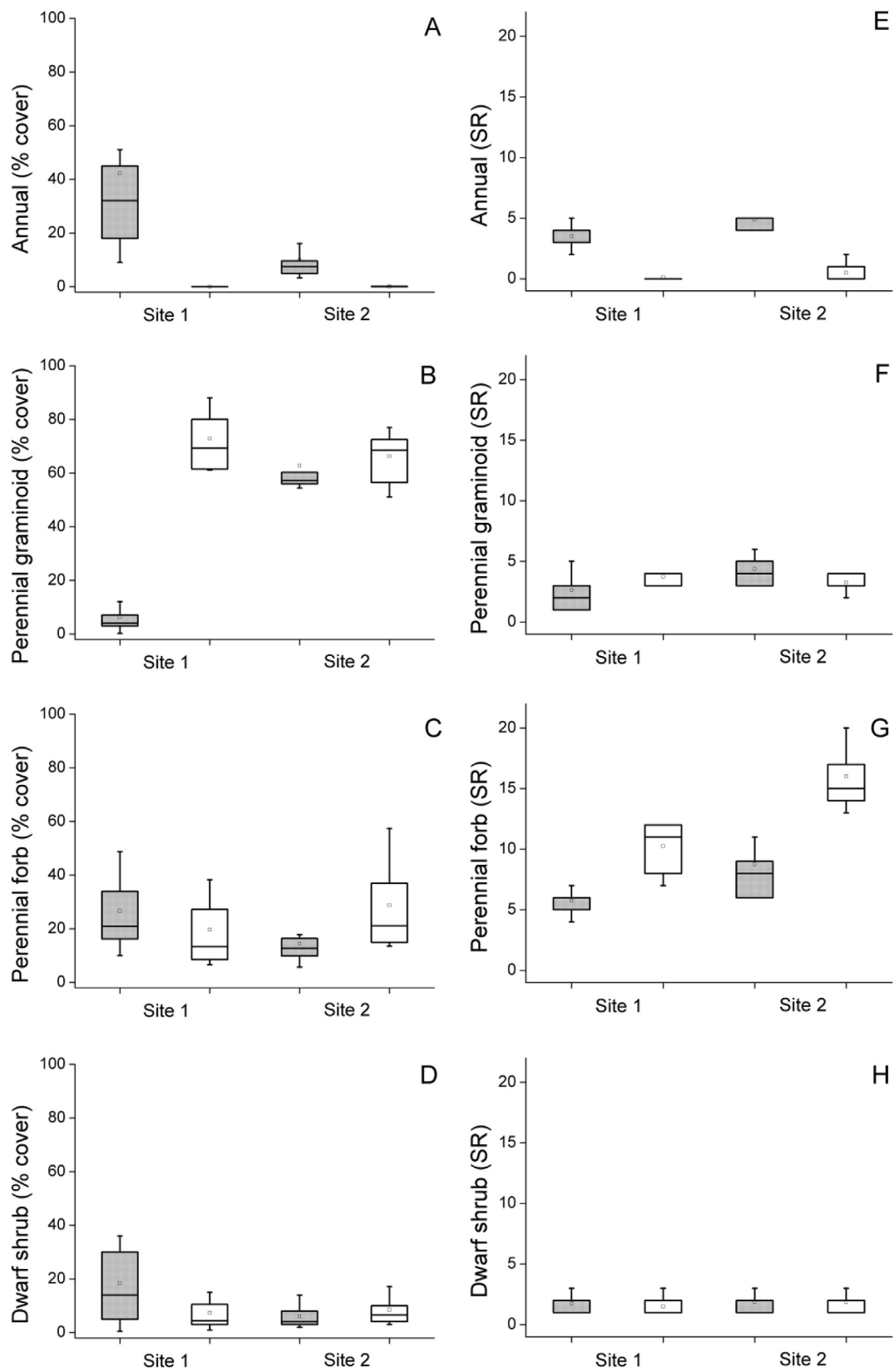


Fig. 4. Vegetation characteristics of the marmot burrows (grey boxes) and intact steppe (white boxes) in the two study sites. (A) Cover of annuals, (B) Cover of perennial graminoids, (C) Cover of perennial forbs, (D) Cover of dwarf shrubs, (E) Species richness of annuals, (F) Species richness of perennial graminoids, (G) Species richness of perennial forbs, (H) Species richness of dwarf shrubs.

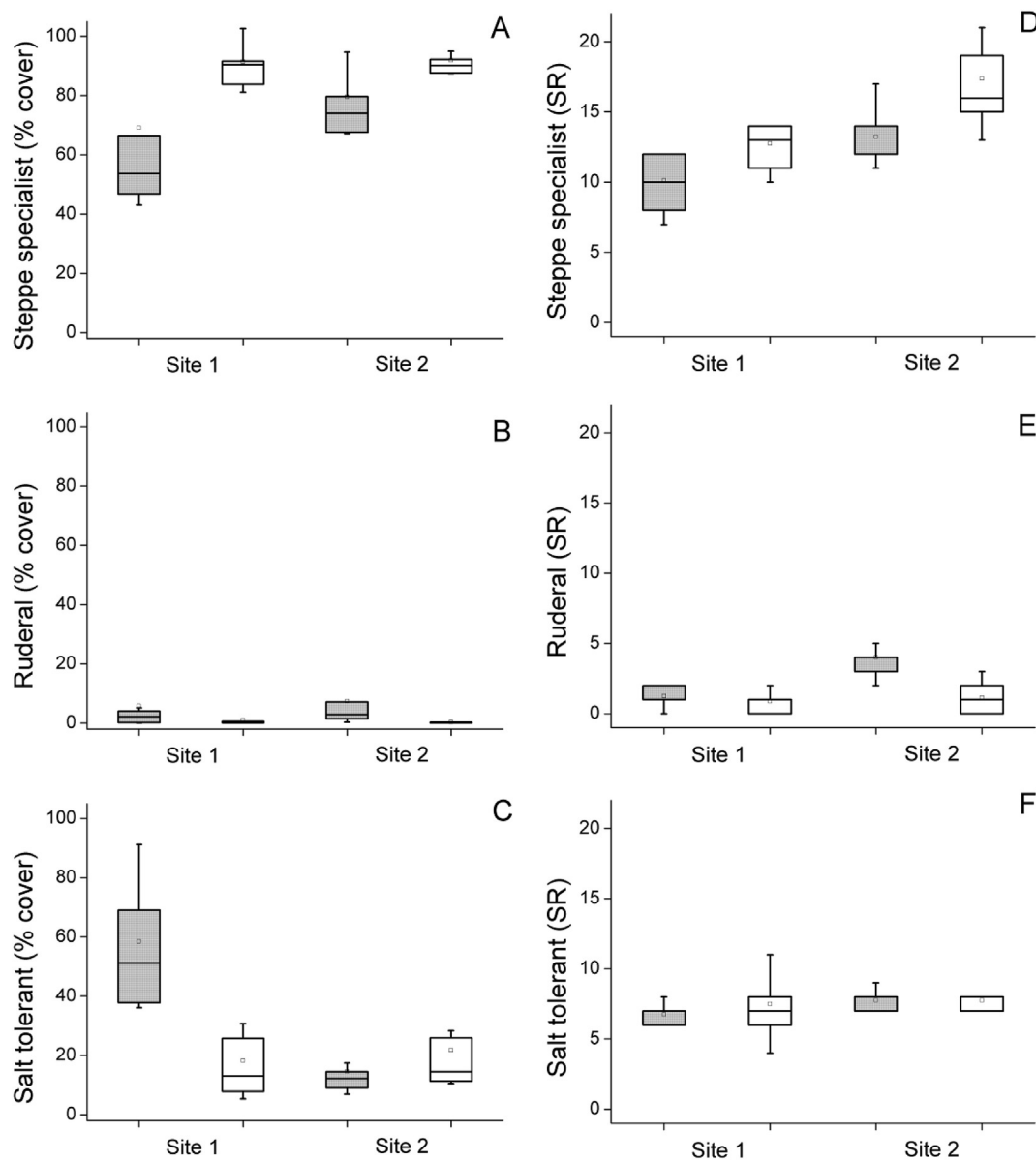


Fig. 5. Vegetation characteristics of the marmot burrows (grey boxes) and intact steppe (white boxes) in the two study sites. (A) Cover of steppe specialists, (B) Cover of ruderals, (C) Cover of salt-tolerants, (D) Species richness of steppe specialists, (E) Species richness of ruderals, (F) Species richness of salt-tolerants.

moisture and salinity. We demonstrated that, as a consequence of ecosystem engineering effects, a unique vegetation develops on marmot burrows. By creating new micro-habitats, marmot burrows might increase landscape-scale plant diversity in arid steppes. Studying Siberian Marmot (*M. sibirica*) in Mongolian mountain steppe, Sasaki and Yoshihara (2013) found that burrows did not increase landscape-scale plant diversity. The reason for this might be that the ecosystem engineering effect of marmots is supposed to be higher in flat lowland regions (Yoshihara et al., 2010c), where even small differences in elevation (i.e. no more than a couple of decimetres) might lead to marked changes in soil moisture content and vegetation patterns (see also Deák et al., 2014).

We conclude that vegetation developed on the burrows is favourable for the marmots. The presence of fresh and green forage, preferred food items and halophyte species suggests that there are positive feedbacks between burrow-building and the appropriateness of the burrow vegetation for the marmots. Thus, even though the primary function of the burrows is the provision of shelter, they have also an important role as 'gardens'. An important function of marmot gardens is

that they provide fresh and green forage in critical periods of the life cycle of marmots. In spring, when marmots are weakened right after the hibernation, ruderal plants on burrows sprouting earlier than steppe vegetation can provide nutrient-rich forage for recovering marmots. In late summer, when marmots need sufficient forage for fattening before hibernation, they can consume the green vegetation of the gardens, even when steppe vegetation is dried out (Zimina and Gerasimov, 1973; Savchenko and Ronkin, 2018). Studying Black-capped Marmot in arctic tundra, Semenov et al. (2001) suggested that burrow vegetation provides plant material for stuffing chambers and green forage at the end of summer.

We also identified mechanisms (trampling, nutrient input, grazing) through which marmots can maintain this preferred vegetation structure for several years. These activities have analogues in human gardening activities: soil disturbance (an analogue of ploughing and harrowing), mediation of seed dispersal processes by bringing up buried seeds and endo- and epizoochorous seed dispersal (analogues of seed sowing), nutrient input (an analogue of manuring or fertilisation) and grazing (an analogue of pruning). Nevertheless, further studies are

needed to reveal more details of these interesting mechanisms. The importance of burrow vegetation in the critical early spring and late summer periods could be tested by directly quantifying the nutrient content of palatable plants growing on burrows and surrounding steppe during the vegetation season. The time spent on grazing burrow vegetation, regarding its daily and seasonal dynamics and differences between males, females and cubs could be quantified by individual-based observation of the grazing behaviour of marmots. The role of marmots in epi- and endozoochorous seed dispersal, especially for their preferred food items could be estimated by germinating the seeds attached to the fur of the marmots or inside their droppings.

Site fidelity of marmots also supports the gardening theory. Families live in the same burrow for years, and groups of families are confined to the same area for many generations (Formosov, 1928). Their burrow systems transform the landscape in a way beneficial for themselves, as they create stepping stones as well as new habitats for their preferred forage plants. This way they can sustain the meta-population structure for these plants for several years or decades. Yoshihara et al. (2010b) found that vegetation on mounds created by Siberian Marmots attracted more pollinators by increased flower numbers and by making flowers more conspicuous by raising them above the surrounding vegetation. This way, burrow systems can support an increased rate of pollination for inhabiting plant species.

4.3. Outlook

Our study showed that Steppe Marmot as a keystone species plays a crucial role in steppe ecosystems. Besides that it is impressive how one organism can modify the local micro-environment, our findings have further implications also at larger spatial and temporal scales. Even though there has been a dramatic decrease in the populations of Steppe Marmot in almost its whole range (Tsytulina et al., 2016), there are still around 6 million individuals in Kazakhstan (Koshkina et al., 2020), implying that there are around 1,200,000 actively used burrows (considering a family containing on average five members, Nikolskii and Savchenko, 1999). Besides the actively used burrows, there are also millions of abandoned burrows of different age. These numbers illustrate well the magnitude and effect of burrow systems in steppe landscapes. From the descriptions of travellers from the 19th century, we can learn that in some steppe landscapes, marmot burrows covered more than 10% of the area, and gave the impression of undulating surface (Formosov, 1928).

It is a very interesting question, how long do burrows exist. There is evidence that burrows can retain their morphology even for several thousands of years (Zimina, 1996). Considering the former larger range of Steppe Marmot (Tsytulina et al., 2016), it is possible that the legacy of former colonies lasted for several centuries in the past and could have an effect on vegetation history. Of course, it is not likely that ancient burrows have distinct vegetation today, especially because the secondary succession on burrows usually ends in steppe vegetation similar to the surroundings (Formosov, 1928). However, it might be possible that burrows acted as stepping stones for the dispersal of plant species in the past and supported the colonisation of new sites or even regions during climatic shifts.

We showed that it is crucial to consider the dramatic decreases of Steppe Marmot populations in the last century not only from the species perspective, but also from the perspective of the steppe ecosystem functioning. Decreased or unstable populations of Steppe Marmot will entail decreasing microhabitat heterogeneity, which will be further aggravated by decreased populations of wild megaherbivores and changes in grazing and wildfire regimes. Distinct vegetation patches on marmot burrows will become increasingly important, if we consider the increasing areas of steppe where no livestock or wild ungulates are present. In those areas, suitable open microsites for steppe specialists are hardly available because of litter accumulation (Kelemen et al., 2013) and grass-dominated, species-poor steppe vegetation can develop

(Brinkert et al., 2016). Wildfires that can create open microsites are common in these areas, however they often have such high frequency, severity and extent that they can hinder the establishment of subordinate steppe specialists and favour a few fire-tolerant species (Brinkert et al., 2016; Valkó et al., 2014b). These findings all highlight the importance of the Steppe Marmot and their burrows in maintaining plant diversity on large spatial and temporal scales, and call for future studies on the complex interactions of burrowing rodents and megaherbivores in arid steppes.

ORCID iD authorship contribution statement

Orsolya Valkó: Conceptualization, Methodology, Investigation, Data curation, Writing - original draft, Writing - review & editing, Supervision. **Csaba Tölgyesi:** Conceptualization, Methodology, Investigation, Writing - review & editing, Project administration. **András Kelemen:** Methodology, Investigation, Writing - review & editing. **Zoltán Bátori:** Methodology, Investigation, Writing - review & editing. **Róbert Gallé:** Methodology, Investigation, Writing - review & editing. **Zoltán Rádai:** Formal analysis, Writing - review & editing. **Tatyana M. Bragina:** Conceptualization, Methodology, Investigation. **Yevgeny A. Bragin:** Conceptualization, Methodology, Investigation. **Balázs Deák:** Conceptualization, Methodology, Investigation, Formal analysis, Writing - review & editing.

Declaration of competing interest

The authors declare no conflict of interest.

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