Patch and matrix characteristics determine the outcome of ecosystem engineering: a case study on the vegetation of mole rat mounds

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Abstract

Background. Burrowing mammals are important ecosystem engineers, especially in open ecosystems in the arid and semi-arid regions, where they create patches that differ from the surrounding matrix in their structure or ecosystem functions.
Methods. We evaluated the fine-scale effects of a subterranean ecosystem engineer, the western blind mole rat mounds on the vegetation composition of sandy dry grasslands in Hungary. In this model system we tested whether the characteristics of the patch (mound size) and the matrix (total vegetation cover in the undisturbed grassland) influence the structural and functional contrasts between the mounds and the undisturbed grasslands. We sampled the vegetation of 80 mounds and 80 undisturbed grassland plots, where we recorded the total vegetation cover, and the list and cover of each vascular plant species. We used two proxies to characterise the patches (mounds) and the matrix (undisturbed grassland): the perimeter of the mounds and the total vegetation cover of the undisturbed grasslands. First, we compared the vegetation characteristics of the mounds and the surrounding grasslands with general linear models. Second, we characterised the contrasts between the patches (mounds) and the matrix (undisturbed grassland) by relative response indices (RRIs) of the vegetation characteristics studied in the first step.
Results. Species composition of the vegetation of the mounds and undisturbed grasslands was well separated in ~~case of~~ three out of the four study sites. Mounds were characterised by smaller vegetation cover, smaller cover of perennial graminoids, and higher diversity, and evenness compared to undisturbed grasslands. The contrast in vegetation cover between patches and the

matrix increased with decreasing patch size. Increasing vegetation cover in the matrix grasslands increased the contrasts between the patches and the matrix in terms of total cover, diversity, and evenness. Our results suggest that mole rat mounds provide improved establishment conditions for subordinate species, because they are larger than other types of natural gaps and are characterised by less intense belowground competition. The ecosystem engineering effect, i.e., the contrast between the patches and the matrix was the largest in the more closed grasslands.

Introduction

Ecosystem engineer organisms create patches that differ from the surrounding matrix in their structure or ecosystem functions (Jones, Lawton & Shachak, 1994). This way they alter the resource distribution in the landscape (Mallen-Cooper, Nakagawa & Eldridge, 2018; Neilly, Cale & Eldridge, 2022; Valkó et al., 2022). Previous syntheses on ecosystem engineers found that there are several factors determining the characteristics of the engineered patches, including the traits of the engineer, the habitat, climate and soil type (Mallen-Cooper, Nakagawa & Eldridge, 2018; Root-Bernstein and Ebensperger, 2013). Burrowing mammals are important ecosystem engineers, especially in the arid and semi-arid regions (Davidson, Detling & Brown, 2012, Valkó et al., 2021; Whitford and Kay, 1998). Through their mound-building and burrowing activities, they move large amounts of soil and create sparsely vegetated patches that often have different vegetation compared to the surrounding habitat matrix (Coggan, Hayward & Gibb, 2018; Mallen-Cooper, Nakagawa & Eldridge, 2018).

Mole rats inhabit arid and semi-arid regions in Africa (mole rats, Bathyergidae family, Visser, Bennett & van Vuuren, 2019) and Eurasia (blind mole rats, Spalacidae family, Németh et al., 2020a). They are highly specialised to subterranean lifestyle and most of the mole rat species spend majority of the time below ground. Therefore, their ecosystem engineering effect is different from ~~those~~ burrowing mammals that feed and graze aboveground, like marmots (Valkó et al., 2021) or prairie dogs (Winter, Cully Jr. & Pontius, 2002). Mole rats can alter vegetation composition by two mechanisms: 1) they generally feed on belowground plant organs, such as roots and bulbs which can decrease the abundance of certain plant species, 2) they create mounds with open soil surface that can play a role in vegetation dynamics as establishment gaps (Reichman and Jarvis, 1998).

Mole rats are ideal organisms for the study of patches created by burrowing rodents as they create clearly visible mounds with sharp boundaries that are distinct patches in the grassland matrix. Mole rats are considered as ecosystem engineers in fynbos ecosystems, where their mounds are characterised by lower vegetation cover and higher species richness compared to the surrounding matrix (Davies et al., 1986; Hagenah and Bennett, 2012; Reichman and Jarvis, 1998). Their engineer effect was tested in temperate dry grasslands in Europe, in a study comparing twelve burrows with undisturbed grasslands (Zimmermann et al., 2014). No difference was found between the vegetation characteristics and species richness of the burrows and the surrounding grasslands, but some differences in the species composition were found. This weak engineering effect detected in European compared to African grasslands might be due to generally more accentuated effects of ecosystem engineers at lower latitudes (Romero et al., 2015). However, given the similar ecological function of African and Eurasian mole rats, we believe that a more detailed analysis on their potential engineer effect in temperate Eurasia is necessary.

The aim of our study was to evaluate the fine-scale effect of western blind mole rat mounds on the vegetation composition of dry grasslands in Hungary. In this model system we tested whether the characteristics of the patch (mound size) and the matrix (total vegetation cover in the neighbouring undisturbed grassland) influence the structural and functional contrasts between the mounds and the undisturbed grasslands. We tested the following hypotheses: i) Mounds have different vegetation structure, species composition and diversity patterns compared to the undisturbed grasslands. ii) Larger mounds are less affected by the edge effect so the structural and functional contrasts between the mounds and the undisturbed grasslands increases with increasing mound size. iii) The structural and functional contrasts between the mounds and the undisturbed grasslands increases with increasing canopy cover in the grassland matrix. As mole rats create a large number of mounds locally in an ecosystem type where gap dynamics are crucial driver of the vegetation composition, the study system is ideal for testing these hypotheses.

Materials & Methods

Study system

The western blind mole rat (*Nannospalax* [superspecies *leucodon*]) superspecies complex includes several morphologically very similar but genetically isolated species (Németh et al., 2020a). Besides genetic differences within the superspecies complex, involved taxa have the same ecological function and lifestyle, hence here we did not distinguish between them. These subterranean mammals are strictly protected and critically endangered in Central Europe. They inhabit dry grasslands, old-fields, and sometimes also urban areas (Németh, Moldován & Szél, 2020b). We sampled four study sites that all hold large populations of the mole rats. The study sites represent the largest known localities of the species in Hungary and are characterised by pristine sandy grassland vegetation in a good conservation status (Németh Moldován & Szél, 2020b). The study sites are located in the Hortobágy National Park (Bagamér site – N 47.47028, E 21.95873, and Hajdúbagos site – N 47.41340, E 21.67606) and in the Kiskunság National Park (Ásotthalom site – N 46.22235, E 19.67164, and Baja site –N 46.19643, E 18.99083). he Trans-Tisza Environmental, Nature Protection and Water Inspectorate approved this study (6646/08/2014). The characteristic vegetation of the study sites is dry sandy grassland, the dominant grass species are *Festuca pseudovina*, *F. rupicola*, *F. vaginata* and *Koeleria glauca.* The sites provide habitat to several protected grassland plant species, such as *Astragalus varius*, *Colchicum arenarium*, and the strictly protected *Pulsatilla flavescens* (Borhidi et al., 2012).

Sampling design

In each study site in April 2020, we selected 20 mounds built by mole rats. We selected mounds that were built one year before the survey. Instead of using a fix-sized sampling quadrat, we considered one mound as one sampling unit as in this case we could capture the potential within-mound variety in the vegetation. We adjusted a measuring tape along the mound edge and used the same measuring tape for delineating a control plot with the same size and shape as the mound. Control plots were designated in the undisturbed sandy grassland one meter from each mound. We recorded the perimeter of each mound.

We sampled the vegetation of 80 mounds and 80 undisturbed grassland plots: we recorded the total vegetation cover, and the list and cover of each vascular plant species. Plant nomenclature follows the work of Király (2009).

Data analysis

We used two proxies to characterise the patches (mounds) and the matrix (undisturbed grassland): the perimeter of the mounds and the total vegetation cover of the undisturbed grasslands. We calculated the Shannon diversity and the evenness of the vegetation in each sampling unit.

First, we compared the vegetation characteristics of the mounds and the surrounding grasslands with general linear models, where the fix factor was microsite type (mound vs. undisturbed grassland), and site was random factor. In the analysis, the following dependent variables were used: total vegetation cover, cover of perennial graminoids, species richness, Shannon diversity, and evenness.

Second, we characterised the contrasts between the patches (mounds) and the matrix (undisturbed grassland) by relative response indices (RRIs, Armas, Ordiales & Pugnaire, 2004; Perkins and Hatfield, 2014) of the vegetation characteristics studied in the first step. RRIs were calculated based on the following equation: $RRI = (X_M - X_G) / (X_M + X_G)$; where X_M is the value of a dependent variable (e.g. Shannon diversity) in a mound and X_G is the value of the same dependent variable in the undisturbed grassland plot paired with the mound plot. Value of RRI ranges between −1 and +1. The closer is |RRI| to 1, the higher the contrast between the patches and the matrix. With generalized linear mixed models (GLMMs), we tested the effects of patch size (fixed factor) and total vegetation cover in matrix grassland (fixed factor) on the

contrasts between the patches and the matrix (i.e., |RRI|s of the studied vegetation characteristics). Study site was used as random factor. GLMs and GLMMs were calculated in the SPSS 17.0 program.
We applied non-metric multidimensional scaling (NMDS) using Bray-Curtis index of dissimilarity to test differences in the species composition of the mounds and undisturbed grasslands in CANOCO 5.0 program (ter Braak and Šmilauer, 2012). We made the calculations for each site separately.

Results

We recorded in total 112 vascular plant species, out of which 102 species occurred on mounds and 93 in undisturbed grasslands. 19 species occurred exclusively on mounds and 10 exclusively in the matrix. 64 species were more frequent on mounds than in the undisturbed grasslands, 18 occurred with the same frequency, and 30 species were more frequent in the undisturbed grasslands. Out of the six protected plant species recorded at the study sites, one occurred only on mounds (*Pulsatilla flavescens*), four occurred both on mounds and grasslands (*Colchicum arenarium*, *Dianthus serotinus*, *Onosma arenaria*, *Stipa borystenica*) and one only in undisturbed grasslands (*Astragalus varius*).

Species composition of the vegetation of the mounds and undisturbed grasslands was well separated in ~~case of~~ three study sites (Hajdúbagos, Bagamér and Ásotthalom), whilst showed considerable similarity in the case of the Baja site (**Figure 1**). The matrix grass species (*Festuca* spp.) and some typical perennial (such as *Thymus glabrescens*, *Potentilla arenaria*, *Euphorbia cyparissias*) species of the studied dry grasslands characterised the undisturbed grasslands. Vegetation of mounds were characterised by several disturbance-tolerant species (such as *Erophila verna*, *Eryngium campestre*, *Poa bulbosa*, *Rumex acetosella*, *Vicia lathyroides*).

Mounds were characterised by smaller vegetation cover (F = 87.168, $p = 0.003$), smaller cover of perennial graminoids (F = 93.503, $p = 0.002$), higher Shannon diversity (F = 16.422, $p = 0.027$) and evenness (F = 15.780, $p = 0.029$) compared to undisturbed grasslands (**Figure 2**). Species richness on the mounds and in the undisturbed grasslands was not different (F = 6.820, $p = 0.080$).

The average perimeter of the mounds was 2.18 m ± 0.88 SD, and the total vegetation cover in the undisturbed grasslands was 66.94% ± 14.17 SD. There was a high contrast in total vegetation cover between small patches and the matrix, which decreased with increasing patch size (**Table 1**). Increasing vegetation cover in the matrix grasslands increased the contrasts between the patches and the matrix in terms of total cover, Shannon diversity and evenness.

Discussion

We found that western blind mole rats created patches with different structural attributes (smaller vegetation cover, smaller cover of perennial grasses) compared to the surrounding sand grassland matrix. The vegetation of the patches and the matrix were different in terms of total vegetation cover, cover of perennial grasses as well as Shannon diversity and evenness, which confirmed our first hypothesis. This suggests that the mole rats play an important role in the gap dynamics in the study system. We found a more open vegetation with smaller cover of perennial grasses on the mounds, which is a general pattern observed on mounds of various burrowing mammals (e.g., prairie dogs: Winter, Cully Jr. & Pontius, 2002; pikas: Wesche, Nadrowski & Retzer, 2007; marmots: Valkó et al., 2021). These are notable effects considering the small size of the mounds.

In the studied sandy grassland ecosystems, the vegetation is open, but there is an intense belowground competition between the perennial graminoids and other subordinate plant species (Borhidi, Kevey & Lendvai, 2012). It is possible that the gaps created by mole rats can provide improved establishment conditions for subordinate species, because the mounds are larger than the other types of natural gaps. Also, as mole rats feed on roots and other belowground organs (Corbet 1984), they can locally decrease the belowground competition which gives an establishment advantage to subordinate species over perennial graminoids. The differences between the vegetation of the mole rat mounds and the matrix is interesting also because of the subterranean lifestyle of the mole rats. In most burrowing mammals, mounds are not only biogeomorphological features but the mammals' activities on the mound surface also shape vegetation composition, e.g., by trampling and manuring (e.g., foxes, Godó et al., 2018; marmots, Valkó et al., 2021; pikas, Yoshihara et al., 2010), but this is not the case in mole rats that spend most of their life underground.

Compared to the only other published study on the ecosystem engineer effect of mole rat species in temperate Eurasia (Zimmermann et al., 2014), we found more and stronger evidence for the engineer effects. The detected weaker evidence of the engineer effect in the previous study can be either a result of the particular study design (one study site, small sample size, fixed plot size) in the other study or by the slightly different habitat types considered (sandy grasslands in our study and loess steppes in Zimmermann et al., 2014).

The species composition of the mounds and undisturbed grasslands was not different when considering all the sites together; however, looking at the site level we found marked differences in three of the four study sites. This suggests that the effect of mole rats on the vegetation should be considered at the local and not the regional scale. This is in line with another study on the effect of fine-scale environmental heterogeneity on the species composition of grasslands, where the effects of environmental heterogeneity were more pronounced on the local than on the regional scale (Deák et al., 2021).

Most of the species recorded in the study (74%) occurred both on the mounds and in the intact grasslands. This implies that mounds are not unique establishment microsites for the majority of plant species; however, mounds can be considered as temporal biodiversity hotspots, where due to the low level of competition by perennial graminoids, subordinate species can establish. There was no difference between the species richness of the mounds and the undisturbed grasslands, but vegetation patches on the mounds were more diverse and the species were more evenly distributed compared to the undisturbed grassland matrix.

Our second hypothesis was not supported as we found that smaller mounds were structurally more different from the surrounding matrix than larger ones in terms of total vegetation cover. This suggests that the height of the mounds (approximately 10 cm) and their steep slopes provide a sharp vegetation boundary which prevents the clonal growth of the surrounding vegetation on the mound. The colonization of the mounds by plants is probably driven by random dispersal processes (i.e., seed rain), and a higher number of incoming diaspores can be expected on the larger surface of larger patches. Also, besides total vegetation cover, we found that mound size did not affect the other studied variables. Even there was variation in mound size they were rather small so the effect of patch size might be relevant in other scales.

We confirmed our third hypothesis as the contrasts between the matrix and the patch were higher in the case of more closed matrix vegetation. This suggests that the importance of the ecosystem engineering effect is the highest in the more closed grasslands, where the engineer organisms increase more the structural and functional heterogeneity. For the conservation of the plant species associated to dry grasslands, creating proper establishment microsites is crucial (Klaus et al., 2018). Our results suggest that mounds of mole rats can provide suitable establishment microsites for approximately 91% of the species pool of the studied sandy dry grasslands. Thus, they might be potentially feasible as establishment gaps in restoration projects or when introducing particular rare species (Kiss et al., 2021; Limb et al., 2010). The spatio-temporal dynamics of the creation and the re-vegetation of the mounds can be an important driver of establishment of subordinate species in the studied grassland ecosystems. Further studies are needed for testing the effectiveness of such natural gaps in increasing species richness during restoration.

Conclusions

We found that the subterranean mole rats create patches in temperate sandy grasslands that differ from the matrix in species composition and vegetation characteristics. The contrast between the patches and the matrix were the sharpest in grasslands with more closed canopy cover. We suggest that the contrasts between the patches and the matrix which was proposed in this study as a proxy for the strength of the engineering effect, can be a useful variable also in other studies. The effects of patch and matrix characteristics on the contrasts should be studied in other ecosystems and other organisms for a deeper understanding of the mechanisms beyond ecosystem engineering.

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Table 1(on next page)

Table1. The effect of patch size and matrix cover (fixed factors) on the contrasts between the vegetation of the mounds and the grassland matrix.

Contrasts were expressed by the absolute values of the relative response indices (|RRI|) calculated between the vegetation characteristics of the mounds and the undisturbed grasslands.

Table 1. The effect of patch size and matrix cover (fixed factors) on the contrasts between the vegetation of the mounds and the grassland matrix. Contrasts were expressed by the absolute values of the relative response indices (|RRI|) calculated between the vegetation characteristics of the mounds and the undisturbed grasslands.

	Patch size			Matrix cover		
	direction	F	p	direction	F	p
Total cover, |RRI|	↓	**6.355**	**0.014**	↑	**31.240**	**0.000**
Species richness, |RRI|		0.715	0.401		0.294	0.589
Perennial grass cover, |RRI|		0.360	0.550	↑	**9.527**	**0.003**
Shannon diversity, |RRI|		0.219	0.641	↑	**4.135**	**0.045**
evenness, |RRI|		0.012	0.912	↑	**9.303**	**0.003**

Figure 1

Figure1. Differences in the species composition of mounds and undisturbed grasslands in the four studied sites (NMDS ordination).

We plotted the 20 most abundant species at each site on the panels. Species names are abbreviated using the first three letters of the genus and species names.

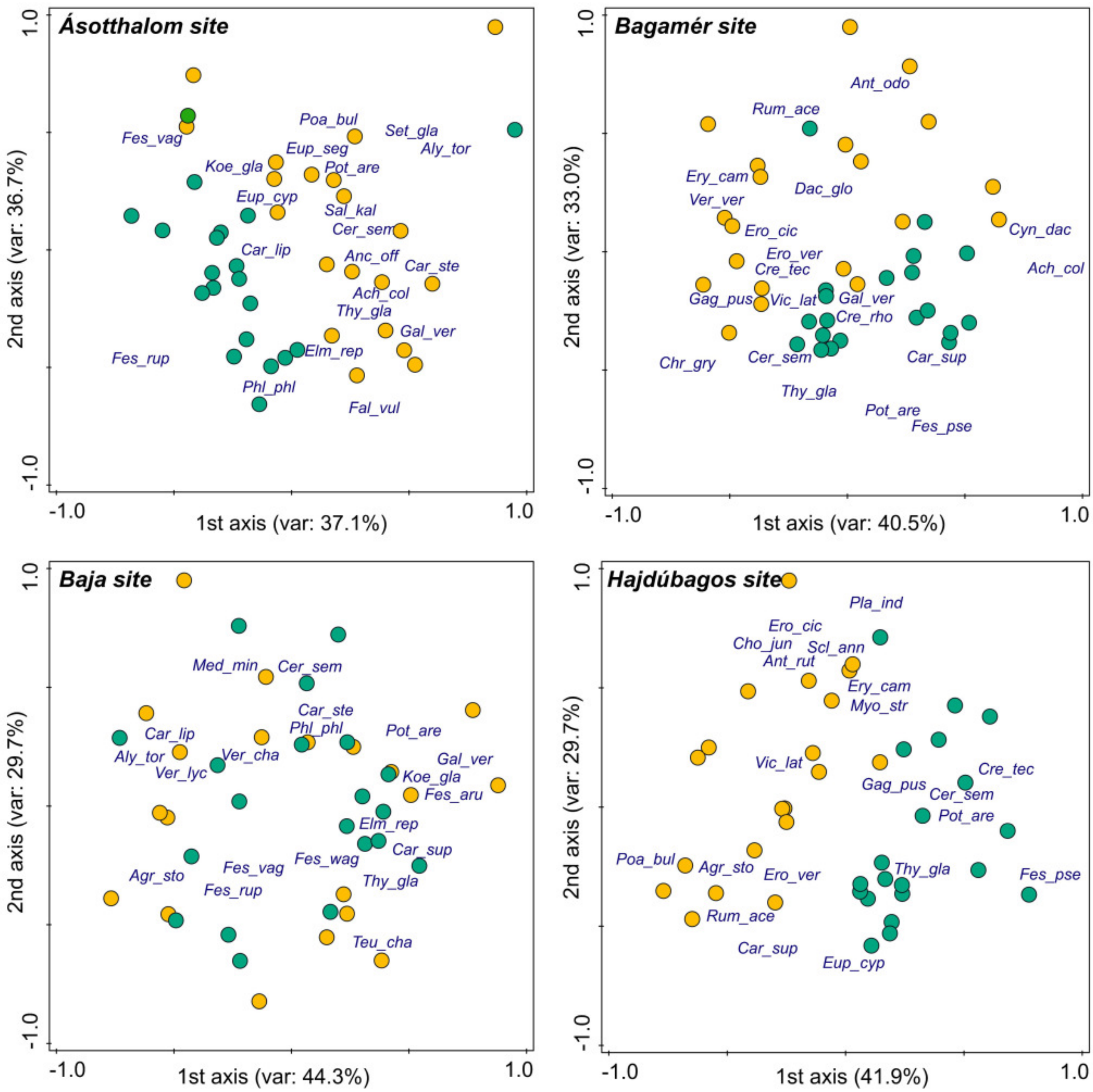
Ásotthalom site
Fes_vag
Poa_bul
Set_gla
Aly_tor
Eup_seg
Koe_gla
Pot_are
Eup_cyp
Sal_kal
Cer_sem
Car_lip
Anc_off
Car_ste
Ach_col
Thy_gla
Gal_ver
Fes_rup
Elm_rep
Phl_phl
Fal_vul
1st axis (var: 37.1%)
2nd axis (var: 36.7%)
Bagamér site
Ant_odo
Rum_ace
Ery_cam
Dac_glo
Ver_ver
Ero_cic
Cyn_dac
Ero_ver
Cre_tec
Ach_col
Gag_pus
Vic_lat
Gal_ver
Cre_rho
Chr_gry
Cer_sem
Car_sup
Thy_gla
Pot_are
Fes_pse
1st axis (var: 40.5%)
2nd axis (var: 33.0%)
Baja site
Med_min
Cer_sem
Car_ste
Phl_phl
Pot_are
Car_lip
Aly_tor
Ver_cha
Ver_lyc
Gal_ver
Koe_gla
Fes_aru
Elm_rep
Car_sup
Fes_wag
Fes_vag
Agr_sto
Fes_rup
Thy_gla
Teu_cha
1st axis (var: 44.3%)
2nd axis (var: 29.7%)
Hajdúbagos site
Pla_ind
Ero_cic
Cho_jun
Scl_ann
Ant_rut
Ery_cam
Myo_str
Vic_lat
Cre_tec
Gag_pus
Cer_sem
Pot_are
Poa_bul
Agr_sto
Ero_ver
Thy_gla
Fes_pse
Rum_ace
Car_sup
Eup_cyp
1st axis (41.9%)
2nd axis (var: 29.7%)
1.0
-1.0

Figure 2

Figure2. Vegetation characteristics on the patches (mole rat mounds) and matrix (undisturbed grasslands).