Patch and matrix characteristics determine the outcome of ecosystem engineering by mole rats in dry grasslands

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Abstract

Background. Burrowing mammals are important ecosystem engineers, especially in open ecosystems 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 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 in four sites, where we recorded the total vegetation cover, and the occurrence and cover of each vascular plant species. We used two proxies to characterise the patches (mounds) and the matrix (undisturbed grassland): we measured the perimeter of the mounds and estimated 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 mounds and the 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 three out of the four study sites. Mounds were characterised by lower vegetation cover, lower cover of perennial graminoids, and higher diversity, and evenness compared to undisturbed grasslands. The contrast in vegetation cover between mounds and undisturbed grasslands increased

40 with decreasing patch size. Increasing vegetation cover in the matrix grasslands increased the
41 contrasts between the mounds and undisturbed grasslands in terms of total cover, perennial
42 graminoid cover, diversity, and evenness. Our results suggest that mole rat mounds provide
43 improved establishment conditions for subordinate species, because they are larger than other
44 types of natural gaps and are characterised by less intense belowground competition. The
45 ecosystem engineering effect, i.e., the contrast between the patches and the matrix was the largest
46 in the more closed grasslands.
47
48 **Introduction**
49
50 Ecosystem engineer organisms create patches that differ from the surrounding matrix in their
51 structure or ecosystem functions (Jones, Lawton & Shachak, 1994). In this way they alter the
52 resource distribution in the landscape (Mallen-Cooper, Nakagawa & Eldridge, 2018; Neilly, Cale
53 & Eldridge, 2022; Valkó et al., 2022). Previous syntheses on ecosystem engineers found that there
54 are several factors determining the characteristics of the engineered patches, including the traits of
55 the engineer, the habitat, climate and soil type (Mallen-Cooper, Nakagawa & Eldridge, 2018;
56 Root-Bernstein and Ebensperger, 2013). Burrowing mammals are important ecosystem engineers,
57 especially in open habitats (Davidson, Detling & Brown, 2012; Reichman and Seabloom, 2012;
58 Valkó et al., 2021; Whitford and Kay, 1998). Many of these animals are endangered due to land
59 use changes and various human activities, therefore it is crucial to understand the ecological
60 functions they provide to support their more effective protection (Davidson et al., 2012). Through
61 their mound-building and burrowing activities, they move large amounts of soil and create sparsely
62 vegetated patches that often have different vegetation compared to the surrounding habitat matrix
63 (Coggan, Hayward & Gibb, 2018; Mallen-Cooper, Nakagawa & Eldridge, 2018).
64
65 Subterranean rodents inhabit open landscapes, including open woodland savanna in Africa (e.g.,
66 African mole-rats or blesmols, Bathyergidae family, Nevo, 1999; Visser, Bennett & van Vuuren,
67 2019) and Mediterranean and continental steppes of Eurasia (e.g., blind mole rats, Spalacidae
68 family, Németh et al., 2020a, Nevo, 1999; and zokors, Myotalpinae family Zhang, Zhang & Liu,
69 2003). They are highly specialised to a subterranean lifestyle and most of these species spend the
70 majority of their time below ground. Therefore, their ecosystem engineering effect is different
71 from burrowing mammals that feed and graze aboveground, like marmots (Valkó et al., 2021) or
72 prairie dogs (Winter, Cully Jr. & Pontius, 2002). Subterranean rodents can alter vegetation
73 composition by several mechanisms: 1) they generally feed on belowground plant organs, such as
74 roots and bulbs which can decrease the abundance of certain plant species (Šklíba et al., 2017); 2)
75 they create mounds with open soil surface that can play a role in vegetation dynamics as
76 establishment gaps (Reichman and Jarvis, 1998); 3) their underground activity affects soil structure
77 and several soil parameters, therefore vegetation as well (Platt et al., 2016; Reichman and
78 Seabloom, 2012; Zhang et al., 2003). Blind mole rats make food storages by hoarding bulbs,

79   rhizomes and tubers and sometimes they do not eat all the stored plant organs so these can sprout
80   later (Szabó and Zimmermann, 2012).

81

82   Subterranean rodents are ideal organisms for the study of ecosystem engineering, as they often
83   create clearly visible mounds with sharp boundaries that are distinct patches in the grassland matrix
84   (Boldog, 2010). African mole-rats are considered as ecosystem engineers in fynbos ecosystems,
85   where their mounds are characterised by lower vegetation cover and higher species richness
86   compared to the surrounding matrix (Davies et al., 1986; Hagenah and Bennett, 2012; Reichman
87   and Jarvis, 1998). The engineer effect of European blind mole rats was tested in one study
88   conducted in temperate dry grasslands, where the vegetation of twelve mounds was compared with
89   undisturbed grasslands (Zimmermann et al., 2014). No difference was found between the
90   vegetation characteristics and species richness of the mounds and the surrounding grasslands, but
91   some differences in the species composition were found. This weak engineering effect detected in
92   European blind mole rats compared to African mole-rats might be due to the generally more
93   accentuated effects of ecosystem engineers at lower latitudes (Romero et al., 2015). However,
94   given the similarities in some ecological functions of African and Eurasian subterranean rodents,
95   we believe that a more detailed analysis on the potential engineer effect of mole rats in temperate
96   Eurasia is necessary.

97

98   The aim of our study was to evaluate the fine-scale effect of Lesser blind mole rat (*Nannospalax*
99   [superspecies *leucodon*]) mounds on the vegetation composition of dry grasslands in Hungary. In
100   this model system we tested whether the characteristics of the patch (mound size) and the matrix
101   (total vegetation cover in the neighbouring undisturbed grassland) influence the structural and
102   functional contrasts between the mounds and the undisturbed grasslands. We tested the following
103   hypotheses: i) Mounds have a more open vegetation structure, and different species composition
104   and diversity patterns compared to the undisturbed grasslands. ii) Vegetation of larger mounds are
105   less affected by the edge effect so the structural and functional contrasts between the mounds and
106   the undisturbed grasslands decrease with increasing mound size. iii) The structural and functional
107   contrasts between the vegetation of mounds and the undisturbed grasslands increases with
108   increasing vegetation cover in the grassland matrix. As mole rats create a large number of mounds
109   locally in an ecosystem type where gap dynamics are crucial driver of the vegetation composition,
110   the study system is ideal for testing these hypotheses.

111

Materials & Methods

112

113

114   *Study system*

115

116   The western blind mole rat (*Nannospalax* [superspecies *leucodon*]) superspecies complex includes
117   several morphologically very similar but genetically isolated species (Csorba et al., 2015; Németh
118   et al., 2020a). Besides genetic differences within the superspecies complex, involved taxa have the

119   same ecological function and lifestyle, hence here we did not distinguish between them. These
120   subterranean mammals are strictly protected and critically endangered in Central Europe (Csorba
121   et al., 2015). They inhabit dry grasslands, old-fields, and sometimes also urban areas (Németh,
122   Moldován & Szél, 2020b). We sampled four study sites that all hold large populations of the mole
123   rats. In Bagamér and Hajdúbagos sites the *Nannospalax* (*leucodon*) *transsylvanicus* taxon, while
124   in Ásotthalom and Baja sites the *Nannospalax* (*leucodon*) *hungaricus* taxon occurs according to
125   Csorba et al., 2015. The study sites include many of the largest known populations of the species
126   in Hungary and are characterised by pristine sandy grassland vegetation in a good conservation
127   status (Csorba et al., 2015; Németh Moldován & Szél, 2020b). The study sites are located in the
128   operation area of the Hortobágy National Park (Bagamér site – N 47.47028, E 21.95873, and
129   Hajdúbagos site – N 47.41340, E 21.67606) and the Kiskunság National Park (Ásotthalom site –
130   N 46.22235, E 19.67164, and Baja site –N 46.19643, E 18.99083). The Trans-Tisza
131   Environmental, Nature Protection and Water Inspectorate approved this study (6646/08/2014).
132   The characteristic vegetation of the study sites is dry sandy grassland, the dominant grass species
133   are *Festuca pseudovina*, *F. rupicola*, *F. vaginata* and *Koeleria glauca*. The sites provide habitat to
134   several protected grassland plant species, such as *Astragalus varius*, *Colchicum arenarium*, and
135   the strictly protected *Pulsatilla flavescens* (Borhidi et al., 2012).

136

137   *Sampling design*

138

139   The study was performed in April 2020 and in each study site, we selected 20 mounds built by
140   mole rats. We selected mounds that were built at least one year before the survey. We did not
141   survey freshly built mounds with no vegetation and also, we did not consider mounds where the
142   mound structure had been disintegrated. Instead of using a fix-sized sampling quadrat, we
143   considered one mound as one sampling unit as in this case we could capture the potential within-
144   mound variety in the vegetation. We adjusted a measuring tape along the mound edge and used
145   the same measuring tape for delineating a control plot with the same size and shape as the mound.
146   Control plots were designated in the undisturbed sandy grassland in one meter distance from each
147   mound. We recorded the perimeter of each mound.

148

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

152

153   *Data analysis*

154

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

158

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

164

165 Second, we characterised the contrasts between the mounds and the undisturbed grassland by
166 relative response indices (RRIs, Armas, Ordiales & Pugnaire, 2004; Perkins and Hatfield, 2014)
167 of the vegetation characteristics studied in the first step. RRIs were calculated based on the
168 following equation: $RRI = (X_M − X_G) / (X_M + X_G)$; where X_M is the value of a dependent variable
169 (e.g., Shannon diversity) in a mound and X_G is the value of the same dependent variable in the
170 undisturbed grassland plot paired with the adjacent mound plot. Value of RRI ranges between −1
171 and +1. The closer is |RRI| to 1, the higher the contrast between the mounds and the undisturbed
172 grasslands. With generalized linear mixed models (GLMMs), we tested the effects of patch size
173 (fixed factor) and total vegetation cover in matrix grassland (fixed factor) on the contrasts between
174 the mounds and the undisturbed grasslands (i.e., |RRI|s of the studied vegetation characteristics).
175 Study site was used as random factor. GLMs and GLMMs were calculated using SPSS 17.0.

176

177 We applied non-metric multidimensional scaling (NMDS) using Bray-Curtis index of dissimilarity
178 to test differences in the species composition of the mounds and undisturbed grasslands in
179 CANOCO 5.0 program (ter Braak and Šmilauer, 2012). We made the calculations for each site
180 separately.

181

182 **Results**

183

184 We recorded in total 112 vascular plant species, out of which 102 species occurred on mounds and
185 93 in undisturbed grassland plots. Nineteen species occurred exclusively on mounds and ten
186 exclusively in the grassland plots. Sixty-four species were more frequent on mounds than in the
187 undisturbed grasslands, 18 occurred with the same frequency, and 30 species were more frequent
188 in the undisturbed grasslands. Out of the six protected plant species recorded at the study sites, one
189 occurred only on mounds (*Pulsatilla flavescens*), four occurred both on mounds and grassland
190 plots (*Colchicum arenarium*, *Dianthus serotinus*, *Onosma arenaria*, *Stipa borysthenica*) and one
191 only in undisturbed grassland plots (*Astragalus varius*). For the complete list of the recorded
192 species, please see Appendix 1.

193

194 Species composition of the vegetation of the mounds and undisturbed grasslands was well
195 separated in three of the study sites (Hajdúbagos, Bagamér and Ásotthalom), whilst it showed
196 considerable similarity in the case of the Baja site (**Figure 1**). The dominant grass species (*Festuca*
197 spp.) and some typical perennial (such as *Thymus glabrescens*, *Potentilla arenaria*, *Euphorbia*
198 *cyparissias*) species of the studied dry grasslands characterised the undisturbed grasslands.

199 Vegetation of mounds were characterised by several disturbance-tolerant species (such as *Erophila*
200 *verna*, *Eryngium campestre*, *Poa bulbosa*, *Rumex acetosella*, *Vicia lathyroides*).
201
202 Mounds were characterised by lower vegetation cover (F = 87.168, *p* = 0.003), lower cover of
203 perennial graminoids (F = 93.503, *p* = 0.002), higher Shannon diversity (F = 16.422, *p* = 0.027)
204 and evenness (F = 15.780, *p* = 0.029) compared to undisturbed grasslands (**Figure 2**). Species
205 richness on the mounds and in the undisturbed grasslands was not different (F = 6.820, *p* = 0.080).
206
207 The average perimeter of the mounds was 2.18 m ± 0.88 SD, and the total vegetation cover in the
208 undisturbed grasslands was 66.94% ± 14.17 SD. There was a high contrast in total vegetation
209 cover between small patches and the matrix, which decreased with increasing patch size (**Table 1**).
210 RRI calculated for total vegetation cover was the lowest in small patches and increased with
211 increasing patch size. The RRIs calculated for perennial graminoid cover, species richness,
212 Shannon diversity and evenness were not affected by patch size (Table 1, Appendix 2).
213
214 Increasing vegetation cover in the matrix grasslands increased the contrasts between the vegetation
215 of the mounds and undisturbed grasslands in terms of total cover, perennial graminoid cover,
216 Shannon diversity and evenness (Table 1, Appendix 3). RRIs calculated for total vegetation cover
217 and perennial graminoid cover were lower in more closed grasslands, indicating larger contrasts
218 between the mounds and the undisturbed grasslands than in more open grasslands. RRIs calculated
219 for Shannon diversity and evenness increased with increasing cover of the matrix grasslands,
220 indicating that mole rat mounds are more diverse than the undisturbed grasslands in the more
221 closed grasslands (Appendix 3).
222
223
224 **Discussion**
225
226 We found that western blind mole rats created patches with different structural attributes (lower
227 vegetation cover, lower cover of perennial graminoids) compared to the surrounding sand
228 grassland. The vegetation of the mounds and undisturbed grasslands was different in terms of total
229 vegetation cover, cover of perennial graminoids as well as Shannon diversity and evenness, which
230 confirmed our first hypothesis. This suggests that the mole rats play an important role in the gap
231 dynamics in the study system. We found a more open vegetation with lower cover of perennial
232 graminoids on the mounds, which is a general pattern observed on mounds of various burrowing
233 mammals (e.g., root-rats: Asefa et al., 2022; prairie dogs: Winter, Cully Jr. & Pontius, 2002; pikas:
234 Wesche, Nadrowski & Retzer, 2007; marmots: Valkó et al., 2021). These are notable effects
235 considering the small size of the mounds. Note that the vegetation of the control plots might also
236 have been influenced by the underground activity of the mole rats (e.g., root consumption), which
237 is a potential limitation of our study. However, this potential bias is consistent in all the 80 pairs

238   of mounds and control plots, as these paired treatments were always situated at the same distance
239   (1 m) from each other.

240

241   In the studied sandy grassland ecosystems, the vegetation is open, but there is an intense
242   belowground competition between the perennial graminoids and other subordinate plant species
243   (Borhidi, Kevey & Lendvai, 2012). It is possible that the gaps created by mole rats can provide
244   improved establishment conditions for subordinate species, because the mounds are larger than
245   other types of natural gaps. Also, as mole rats feed on roots and other belowground organs (Corbet,
246   1984), they can locally decrease the belowground competition which gives an establishment
247   advantage to subordinate species over perennial graminoids. Similar results were obtained in a
248   study about the effect of plateau zokor (*Myospalax fontanierii*) mounds on the vegetation of alpine
249   meadows in the Tibetean Plateau (Zhang et al., 2003). A study on the root-rat (*Tachyoryctes*
250   *macrocephalus*) mounds in Ethiopian grasslands found that the mounds were characterised by
251   lower cover of the dominant species and higher cover of subordinate plants (Šklíba et al., 2017),
252   which is also in line with our findings. The differences between the vegetation of the mole rat
253   mounds and the undisturbed grasslands is interesting also because of the subterranean lifestyle of
254   the mole rats. In most burrowing mammals, mounds are not only biogeomorphological features
255   but the mammals' activities on the mound surface also shape vegetation composition, e.g., by
256   trampling and manuring (e.g., foxes, Godó et al., 2018; marmots, Valkó et al., 2021; pikas,
257   Yoshihara et al., 2010), but this is not the case in mole rats that spend most of their life
258   underground.

259

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

266

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

274

275   Most of the species recorded in the study (74%) occurred both on the mounds and in the intact
276   grasslands. This implies that mounds are not unique establishment microsites for the majority of
277   plant species; however, mounds can provide improved establishment opportunities for subordinate

278   species, due to the low level of competition by perennial graminoids. There was no difference
279   between the species richness of the mounds and the undisturbed grasslands, but vegetation patches
280   on the mounds were more diverse and the species were more evenly distributed compared to the
281   undisturbed grassland matrix.

282

283   Our second hypothesis, i.e., that the contrasts between the mounds and the undisturbed grasslands
284   decrease with increasing mound size, was partly supported: in case of total vegetation cover,
285   smaller mounds were more different from the undisturbed grasslands than larger ones. This
286   suggests that the height of the mounds (approximately 20 cm) and their steep slopes provide a
287   sharp vegetation boundary which prevents the clonal growth of the surrounding vegetation on the
288   mound. The colonization of the mounds by plants is probably driven by random dispersal processes
289   (i.e., seed rain), and a higher number of incoming diaspores can be expected on the larger surface
290   of larger patches. Also, besides total vegetation cover, we found that mound size did not affect the
291   other studied variables. Even there was variation in mound size they were rather small so the effect
292   of patch size might be relevant in other scales.

293

294   We confirmed our third hypothesis as the contrasts between the vegetation of mounds and
295   undisturbed grasslands were higher in the more closed grasslands. This suggests that the
296   importance of the ecosystem engineering effect is the highest in the more closed grasslands, where
297   the engineer organisms increase more the structural and functional heterogeneity of the ecosystem.
298   For the conservation of the plant species associated to dry grasslands, creating proper
299   establishment microsites is crucial (Klaus et al., 2018). Our results suggest that mounds of mole
300   rats can provide suitable establishment microsites for approximately 91% of the species pool of
301   the studied sandy dry grasslands. Thus, they might be potentially feasible as establishment gaps in
302   restoration projects or when introducing particular rare species (Kiss et al., 2021; Limb et al.,
303   2010). The spatio-temporal dynamics of the creation and the re-vegetation of the mounds can be
304   an important driver of establishment of subordinate species in the studied grassland ecosystems.
305   These results highlight that the protection of these endangered subterranean rodents is crucial also
306   for maintaining the vegetation dynamics and ecosystem functioning of their habitats. Further
307   studies are needed for testing the effectiveness of natural gaps created by blind mole rats in
308   increasing species richness during restoration.

309

310

Conclusions

312

313   We found that the subterranean mole rats create patches in temperate sandy grasslands that differ
314   from the undisturbed grasslands in species composition and vegetation characteristics. The
315   contrast between the vegetation of the mounds and undisturbed grasslands were the sharpest in
316   grasslands with more closed vegetation cover. We suggest that the contrasts between the patches
317   and the matrix which was proposed in this study as a proxy for the strength of the engineering

318 effect, can be a useful variable also in other studies. The effects of patch and matrix
319 characteristics on the contrasts should be studied in other ecosystems and other organisms for a
320 deeper understanding of the mechanisms beyond ecosystem engineering.
321
322

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324

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327

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329

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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 relative response indices (RRIs) calculated between the vegetation characteristics of the mounds and the undisturbed grasslands.
1 **Table 1.** The effect of patch size and matrix cover (fixed factors) on the contrasts between the
2 vegetation of the mounds and the grassland matrix. Contrasts were expressed by the relative
3 response indices (RRIs) calculated between the vegetation characteristics of the mounds and the
4 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 graminoid 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. Yellow circles denote mole rat mounds, green circles denote undisturbed grasslands.
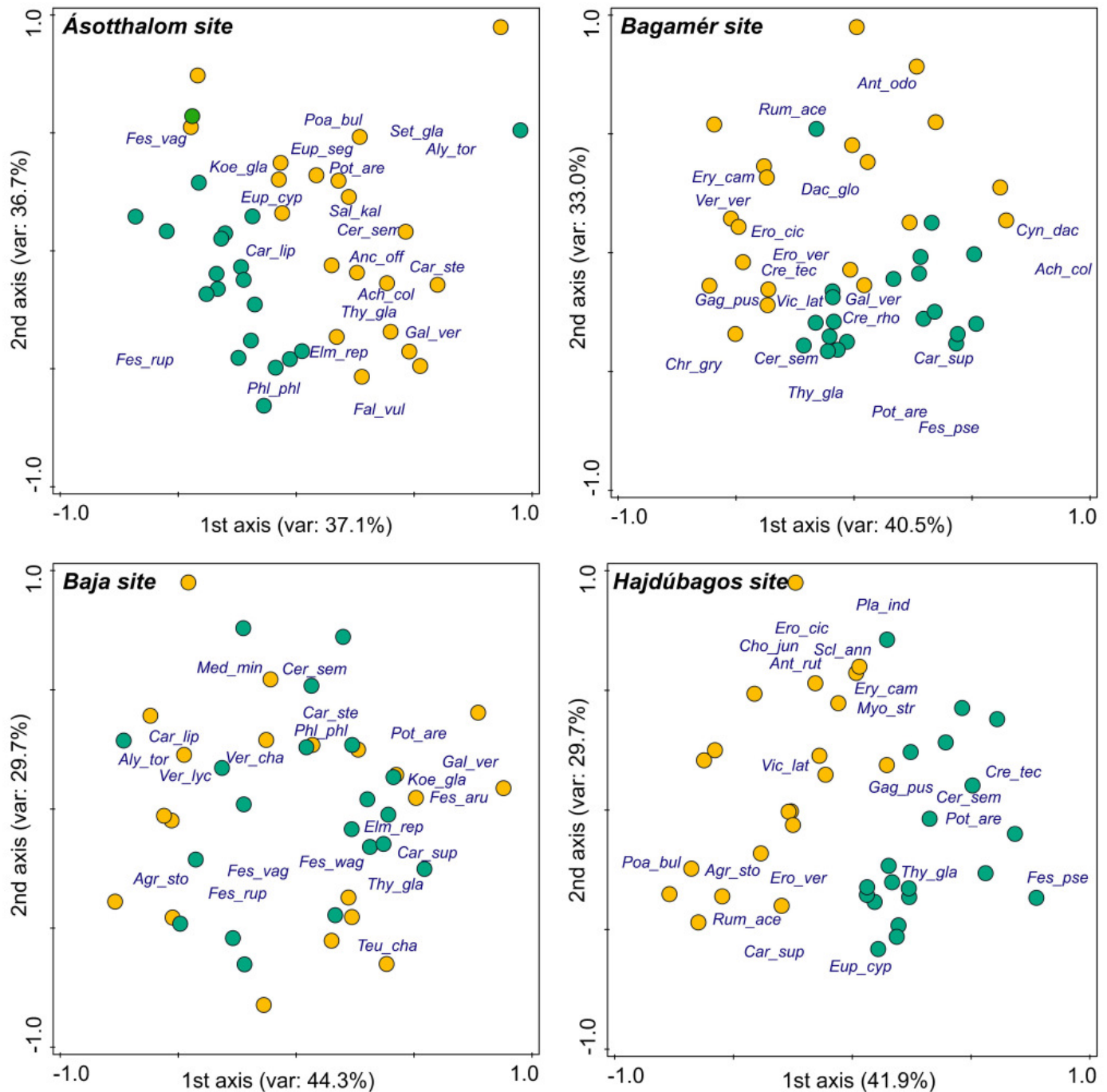
Figure 2

Figure 2. Vegetation characteristics on the patches (mole rat mounds) and matrix (undisturbed grasslands).

Yellow boxes denote mole rat mounds, green boxes denote undisturbed grasslands.