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SHORT COMMUNICATION

The European ground squirrel increases diversity and structural complexity of grasslands in the Western Carpathians

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Abstract
Disturbances are important natural factors affecting biological diversity, community composition, and ecosystem structure. The European ground squirrel is a semi-fossorial organism, and through disturbances caused by burrowing activities, it can play an important role as an ecosystem engineer of grasslands in central and south-eastern Europe. The aim of this study was to assess the response of grassland vegetation to disturbances by the European ground squirrel. We conducted a pairwise survey within a 1-ha study site with homogenous environmental conditions. We compared the vegetation characteristics of 2 × 2-m plots placed on 30 mounds, with paired control plots situated at a distance of 10 m from each mound. The results showed that plots disturbed by the European ground squirrel achieved a higher species richness and diversity and a distinct species composition compared to the undisturbed control plots. Vertical structure of vegetation was also significantly different with a higher proportion of the high and medium vegetation layers on the mounds. Shifts in the composition of plant life forms and life strategies were reflected by the reduction of graminoids and plant competitors, and support of forbs on the mounds. These findings suggest that the European ground squirrel helps to maintain heterogeneity in grassland ecosystems and creates patches of higher diversity and higher structural complexity in the relatively homogenous grassland vegetation of the Western Carpathians.

Keywords *Spermophilus citellus* · European souslik · Impact on vegetation · Ecosystem engineering · Plant communities

Introduction

Disturbance is an important natural phenomenon in grasslands, occurring worldwide at a wide variety of spatial and temporal scales (Gibson 2009). Disturbances alter the physical environment, disrupt ecosystem development, change resource and substrate availability (White and Pickett 1985), and affect biological diversity, community composition, and ecosystem structure (White 1979; Sousa 1984).

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Small-scale disturbances made by soil-moving animals usually disrupt dominant perennial plant cover and create environmental patchiness that influences patterns of species richness and community structure by increasing habitat heterogeneity and permitting the coexistence of species with different competitive and colonization abilities (Milton et al. 1997). Animal disturbances also vary in size and depth, temporal frequency, spatial distribution, and duration (White and Pickett 1985). Such variation should influence patterns of species richness by providing a variety of regeneration niches for plant species (Grubb 1977). The increase or decrease in plant species richness as a response to animal disturbances depends mainly on the biogeographic region, habitat type, disturbance type, and mammal species as a disturbance agent (Root-Bernstein and Ebensperger 2013).

Especially, burrowing activities by rodents have a significant impact on soil properties (e.g., Carlson and White 1987; Canals et al. 2003; Galiano et al. 2014), plant communities (e.g., Weltzin et al. 1997; Davidson and Lightfoot 2006; Van Staalduinen and Werger 2006), and other groups of organisms (e.g., Bangert and Slobodchikoff 2006; Davidson and Lightfoot 2007; Yoshihara et al. 2010) in grassland ecosystems around the world (Kinlaw 1999; Whitford and Key

1999; Davidson et al. 2012). Therefore, burrowing small mammals are considered important biotic disturbance agents in grassland ecosystems (Gibson 2009), and they can play a role as ecosystem engineers and keystone species (Ceballos et al. 1999; Zhang et al. 2003; Kotliar et al. 2006). Jones et al. (1994) defined ecosystem engineers as organisms that create, maintain, and modify their environment. Species that have large overall effects on community or ecosystem structure or function, and their effect is disproportionately large relative to their abundance, were described by Power et al. (1996) as a keystone species.

The European ground squirrel (*Spermophilus citellus* L.) is a medium-sized ground squirrel living in colonies, endemic to central and south-eastern Europe. *Spermophilus citellus* is classified as a vulnerable species facing a high risk of extinction in the wild (Coroiu et al. 2008). Genetic studies of this species show population fragmentation, isolation, and high risk of local extinction, especially in the peripheral zones of its distribution (Hulová and Sedláček 2008; Říčanová et al. 2011; Slimen et al. 2012).

This disappearing species plays an important natural role in the steppic grassland ecosystem because it represents one of the main prey for several top predators (Ramos-Lara et al. 2014) and provides the opportunity of existence for some rare invertebrates, such as coprophagous scarab beetles from the genera *Onthophagus* and *Aphodius* (Zunino and Halffter 2008; Carpaneto et al. 2011). Nevertheless, many aspects of the European ground squirrel's role in European grasslands are still unclear. Ground squirrels are generally considered a key functional group of social, burrowing, herbivorous mammals, which partially shape grassland ecosystems (Davidson et al. 2012); however, there is currently no evidence evaluating the European ground squirrel as a keystone species or ecosystem engineer in European grasslands (Janák et al. 2013).

The function of the European ground squirrel as a potential ecosystem engineer, keystone species, or disturbance agent is largely overlooked, and to our knowledge there is no published information regarding the effect of European ground squirrels on grassland plant communities and their diversity, composition, and structure. Therefore, the aim of this paper is to examine the response of grassland vegetation to disturbances by the European ground squirrel. We expect that burrowing activities of the European ground squirrel significantly alter grassland plant communities. We hypothesize that (i) there is higher plant species richness and diversity on the mounds, (ii) these patches are occupied by different plant species assemblages compared to the surrounding vegetation, and (iii) there is a modification of the vertical structure of vegetation and a distinct composition of life forms and life strategies of plants on the mounds compared to adjacent vegetation.

Methods

Study area

In northeastern Slovakia (the Spiš region), one of the last complexes of the European ground squirrel colonies in the Western Carpathians persists. A colony in the Kozie chrbty Mountains was selected for this research. The climate of the area is continental, cool, and moderately humid. The mean annual air temperature reaches 6–7 °C. The mean annual precipitation ranges between 550 and 600 mm. The soils of the study area are classified as Cambisols on sandstone and/or claystone bedrock (Miklós 2002). Permanent grassland has been managed only by cattle grazing for several decades. A rectangular study site of the size 50 × 200 m (coordinates of the center of the study site: 49° 00′ 26.2" N 20° 25′ 49.8″ E) with homogenous environmental conditions was established during the vegetation season of 2011. The study site was located at the base of a hillslope, south of peak Hradisko. The whole study site was represented by moderate slopes with 5–10° with a south-west aspect and altitudes between 585 and 600 m a.s.l. The vegetation of the study site represented intensively grazed pasture vegetation classified as *Lolietum perennis* Gams 1927 association.

Sampling methods

Within the study site, 30 mounds inhabited by European ground squirrels were haphazardly selected. A 2 × 2 m on-mound plot was then placed on these selected mounds. We selected only active older mounds with developed vegetation for our study. Newly created mounds that consisted of fresh excavated bare soil with no settlement of vascular plants were excluded from our study, because they lacked vegetation. The on-mound plots were characterized by burrow entrances and disturbed soil in the surroundings. For each on-mound plot, we systematically placed an off-mound control plot in a pairwise manner at a fixed distance of 10 m from the study mound in the direction, where no other mounds or burrow entrances occurred. The off-mound plots represented undisturbed pasture vegetation without any burrow entrances. Pairs of plots with and without burrows were treated as matched pairs. All on-mound and off-mound plots were sampled following the Zürich-Montpellier approach (Braun-Blanquet 1964), where all vascular plant species were recorded and their abundance-cover values were estimated using the adapted Braun-Blanquet's scale (Barkmann et al. 1964).

Vegetation characteristics

For each sampling plot, species richness (total number of species), Shannon indices (Shannon and Weaver 1949), and evenness indices (Pielou 1975) were calculated in the JUICE program (Tichý 2002). Three vertical layers of vascular plants were registered as follows: high (> 40 cm), medium (20–40 cm), and low (< 20 cm). Vertical structure was assessed as a proportion of each layer from total plant cover. Life forms (Raunkiaer 1934) and plant strategies (Grime 2006) were recognized using plant species data from the BIOLFLOR database (Klotz et al. 2002). Classifications are listed in Table 2. For the analysis, we used the sum of covers of relevant species from each category of the life forms and plant strategies per plot.

Statistical analyses

Two methods were used to test the effect of plot position (on-mound vs. off-mound) on the vegetation characteristics of sampling plots. Paired *t* tests were employed to test for differences in total plant cover, species richness, Shannon indices, and evenness indices. Redundancy analysis (RDA) was used to compare species composition, vertical structure, plant life forms, and life strategies between on-mound and off-mound plots. Probabilities in both methods were calculated from 10,000 randomizations of the original data. To obtain proper probabilities, we accounted for a paired sample design and restricted the randomization scheme to free permutations within pairs of plots (no permutations between pairs were allowed). Analyses were performed in R (R Core team 2015) using the vegan package (Oksanen et al. 2016).

Data availability All data generated or analyzed during this study are included in this published article and its supplementary information file.

Results

The species pool recorded on all plots consisted of 79 vascular plant species. Vegetation in undisturbed off-mound plots consisted of only 43 species. Communities of the on-mound plots were more diverse and supported 76 species, almost twice as many species as the off-mound plots (see the Electronic Supplementary Material). On-mound plots reached significantly higher species richness, Shannon indices, and evenness indices compared to the off-mound plots (Table 1).

Table 1 Comparison of vegetation characteristics in off-mound and on-mound plots using paired *t* test. Mean values ± SD, test statistics (t), and probabilities (*p*) are displayed

Vegetation characteristics	Off-mound	On-mound	*t*	*p*
Plant cover (%)	92.67 ± 3.14	61.33 ± 5.56	26.9	< 0.0001
Species richness	12.97 ± 3.03	22.47 ± 3.81	10.7	< 0.0001
Shannon indices	1.32 ± 0.39	1.90 ± 0.24	7.0	< 0.0001
Evenness	0.52 ± 0.14	0.61 ± 0.08	3.4	0.0004

Overall plant cover was significantly lower in the on-mounds plots than in undisturbed off-mound plots.

Species composition differed significantly among on-mound and off-mound plots (pseudo-$F = 19.11$, $p < 0.0001$). An ordination diagram of RDA results shows the distribution and preferences of frequent plant species in relation to the plot's position (Fig. 1). Species such as *Trifolium repens*, *Lolium perenne*, and *Poa annua* were strongly associated with undisturbed off-mound plots, whereas *Cerastium holosteoides* was weakly more prevalent in the off-mound plots. On the other hand, *Fragaria viridis* was more prevalent in the on-mound plots. Other species, including *Festuca pratensis*, *Galium verum*, *Thymus pannonicus*, *Dactylis glomerata*, *Potentilla argentea*, *Senecio jacobaea*, *Veronica chamaedrys*, *Arenaria serpyllifolia*, and *Ranunculus bulbosus*, were weakly more prevalent in the on-mound plots. Several species, such as *Plantago lanceolata* and *P. media*, appeared relatively unaffected by the burrowing activities of the European ground squirrel.

The vertical structure of vegetation showed significant differences between on-mound and off-mound plots (Table 2). Vegetation in the on-mound plots achieved a higher proportion of vascular plants in the high and medium vegetation layers compared to vegetation in the off-mound plots. Contrary, off-mound plots were absolutely dominated by the low vegetation layer.

Additionally, changes in the cover of plant life forms were considerable. In the on-mound plots, graminoid species had less cover than in the off-mound plots. Conversely, forbs achieved higher cover in the on-mound plots compared to the off-mound plots. Hemicryptophytes dominated both types of communities. The cover of therophytes was highly variable. Changes in therophyte cover were affected especially by *P. annua*, which frequently dominated in the off-mound plots. The cover of chamaephytes was higher in the on-mound plots than in the off-mound plots. Phanerophytes and geophytes were detected only rarely.

Comparing the life strategies of plants, we found that competitive stress-tolerant ruderals dominated in the on-mound plots, and they reached higher average cover than in the off-mound plots. Competitors dominated in the off-mound plots, and achieved higher average plant cover than in the on-mound plots. The cover of ruderal strategists in the on-mound plots was lower than in surrounding vegetation; this was caused by *P. annua*, which frequently dominates in the off-mound plots. Other plant strategies were observed only rarely.

Discussion

Our results demonstrate that the disturbance caused by burrowing activities of the European ground squirrel affects

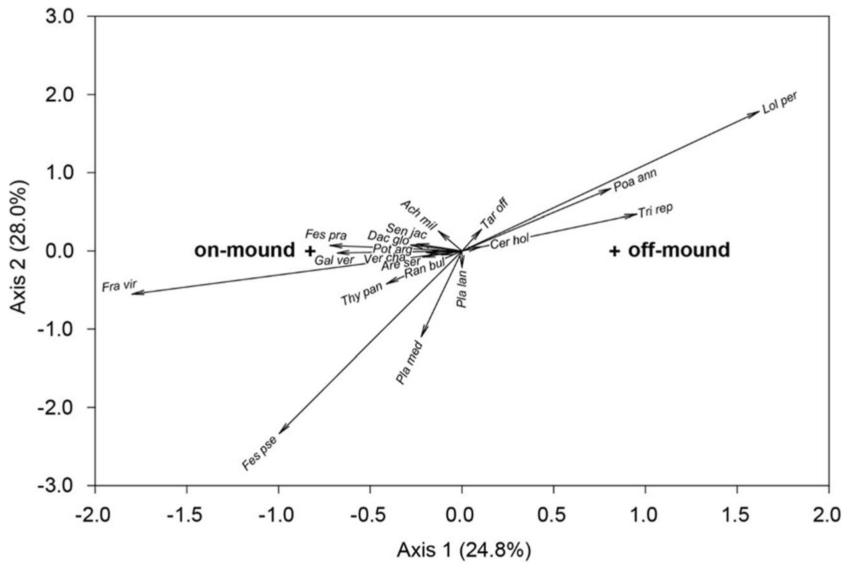

Fig. 1 Ordination plot of redundancy analysis testing the effect of plot position (on-mound vs. off-mound) on the plant species composition. The variance explained by the ordination axes is given in parentheses. The scaling of the ordination is focused on species correlations. For brevity, only species with a frequency ≥ 0.25 are displayed. The abbreviations of species names include the first three letters of the genus and species scientific names: *Ach mil*, *Achillea millefolium*; *Are ser*, *Arenaria serpyllifolia*; *Cer hol*, *Cerastium holosteoides*; *Dac glo*, *Dactylis glomerata*; *Fes pra*, *Festuca pratensis*; *Fes pse*, *Festuca pseudovina*; *Fra vir*, *Fragaria viridis*; *Gal ver*, *Galium verum*; *Lol per*, *Lolium perenne*; *Pla lan*, *Plantago lanceolata*; *Pla med*, *Plantago media*; *Poa ann*, *Poa annua*; *Pot arg*, *Potentilla argentea*; *Ran bul*, *Ranunculus bulbosus*; *Sen jac*, *Senecio jacobaea*; *Tar off*, *Taraxacum officinale*; *Thy pan*, *Thymus pannonicus*; *Tri rep*, *Trifolium repens*; and *Ver cha*, *Veronica chamaedrys*

plant communities. We determined the increase in plant species richness and diversity in the on-mound plots comparing to the off-mound plots. The response of plant communities to disturbances was reflected by distinct plant species assemblages that occupied the on-mound plots in comparison to the off-mound plots. We also detected a modification of the vertical structure and a shift in the composition of life forms and life strategies of vascular plants.

Table 2 Comparison of vegetation and plant characteristics in off-mound and on-mound plots using RDA. Mean values ± SD, test statistics (pseudo-*F*) and probabilities (*p*) are displayed

Vegetation and plant characteristics	Off-mound	On-mound	pseudo-F	*p*
Vertical structure (%)			18.7	0.0004
High layer > 40 cm	1.00 ± 3.32	9.33 ± 11.26		
Medium layer 20–40 cm	19.17 ± 23.78	37.83 ± 16.22		
Low layer < 20 cm	79.83 ± 24.55	52.83 ± 16.49		
Plant life forms (% cover)			7.3	0.0008
Graminoids	49.77 ± 18.59	34.43 ± 17.50		
Forbs	20.81 ± 9.04	37.57 ± 17.62		
Hemicryptophytes	61.43 ± 17.46	66.37 ± 29.19		
Therophytes	7.90 ± 10.24	1.93 ± 1.43		
Chamaephytes	1.26 ± 2.82	3.63 ± 4.98		
Phanerophytes	0.00 ± 0.00	1.39 ± 6.84		
Geophytes	0.00 ± 0.02	0.06 ± 0.14		
Life strategies (% cover)			11.1	< 0.0001
C – competitors	36.30 ± 19.04	21.26 ± 16.23		
S – stress tolerators	0.00 ± 0.02	0.00 ± 0.02		
R – ruderals	7.88 ± 10.26	1.53 ± 1.34		
CSR – competitive stress-tolerant ruderals	25.06 ± 14.87	45.30 ± 29.75		
CS – competitive stress tolerators	0.13 ± 0.17	4.39 ± 6.13		
CR – competitive ruderals	1.20 ± 2.82	0.74 ± 0.65		
SR – stress-tolerant ruderals	0.00 ± 0.02	0.16 ± 0.55		

There are several studies supporting the same patterns of increasing species richness and diversity on sites disturbed by small mammals (e.g., Archer et al. 1987; Guo 1996; Bagchi et al. 2006). In contrast, some studies documented the depletion of species richness in disturbed areas (e.g., Del Moral 1984; Semenov et al. 2001; Van Staalduinen and Werger 2006). The response of vegetation depends mainly on the biogeographical region, habitat type, disturbance type, and mammal species, as was demonstrate by Root-Bernstein and Ebensperger (2013).

The main effect of small mammals on grassland vegetation was mainly through constructing and maintenance of burrow systems. This activity leads to soil excavation from deeper layers and transports the material to aboveground disposal sites, a process that alters soil properties (Kinlaw 1999; Whitford and Key 1999; Canals et al. 2003; Galiano et al. 2014). Such disturbances lead to the creation of barren substrate, which initiates vegetation succession (Walker and Del Moral 2003). Further maintenance and widening of the burrow system periodically refresh the mound of excavated soil. This process leads to the formation of regeneration niches for plant species (Grubb 1977), slows down the colonization of the patches, and creates suitable conditions for ruderal plant species (Grime 2006). However, our results showed that the mean cover of ruderals was higher in the off-mound plots than in the on-mound plots. This can be explained by the fact that the whole study area was heavily grazed by cattle, which also supports the settlement of ruderals (Olff and Ritchie 1998; Tow and Lazenby 2001); in particular, the annual ruderal grass *P. annua* was dominant in this study.

The accumulation of excavated soil and mound building can modify microrelief and lead to the development of specific landforms (Butler 1995; Naylor 2005), which can result in differences in microclimates. In contrast to undisturbed surface covered with vegetation, there can be an increase in soil temperature and a decrease in soil moisture on the mounds (Simkin et al. 2004). On the other hand, there is a burrow entrance, which can play a role of the drainage system and provide air from deeper soil layers (Gibson 2009). These facts could contribute to contrasting floristic composition in the on-mound plots in comparison to the off-mound plots.

Another explanation of the floristic changes could be the fact that mounds are used as feeding places by the European ground squirrel (Grulich 1960). Therefore, a variety of graminoid and herb seeds can be accumulated at these patches, as was shown in kangaroo rat mounds, which accumulated more seeds and supported different seed compositions than the adjacent grassland (Koontz and Simpson 2010). One interesting fact is that we recorded two phanerophyte species (*Rosa canina* and *Crataegus* sp.) only in the on-mound plots (see the Electronic Supplementary Material). These shrub species are primarily dispersed by birds, and their occurrence on the mounds can be linked to the successful germination on free niches. Nevertheless, the distribution of shrub species into the grassland by the European ground squirrels could also be a plausible explanation. To support the hypothesis of the role of the European ground squirrel as a seed disperser, further research is needed; specifically, seed-bank studies would be useful.

In general, small mammal disturbances increase plant biomass in grassland ecosystems (Root-Bernstein and Ebensperger 2013), which could be an explanation for the vertical structure modification in the on-mound plots. The study site was under intensive cattle grazing, which generally concentrates most of the vegetation canopy in the lowest layer (Sala et al. 1986; Marriott and Carrére 1998). The fact that the vertical distribution of plant material in the on-mound plots was more diverse with higher proportions of medium and high layers leads to the assumption that livestock avoid these mound areas, which creates diverse patches and supports the heterogeneity of pasture vegetation. Structural complexity, the physical arrangement of objects in space, is a fundamental property of all ecological systems (Bell et al. 1991). Increased structural complexity mediates species interactions and can influence predator-prey interactions by decreasing predation risk through the inability to visually detect European ground squirrel individuals (Denno et al. 2005).

Significantly higher vegetation in the on-mound plots may also be discussed from an opposite view and explained by another aspect of the behavioral ecology of the European ground squirrel. Ground squirrels sometimes prefer patches of higher vegetation as a form of shelter, especially during the initial period of burrow construction, which was shown in a field experiment by Gedeon et al. (2012). Similarly, it can be assumed that the higher richness in the on-mound plots is caused by the preference of ground squirrels to construct their burrow systems in species-rich patches of vegetation. However, according to Matějů et al. (2011), the occurrence of the European ground squirrel seems to be unrelated to some specific plant species or vegetation types, and they tend to also occupy homogenous lawns of golf courses with very low species richness and diversity. We hypothesize that ground squirrels are not restricted to species-rich patches; in fact, their burrowing activities promote the development of more diverse vegetation.

Comparing the life strategies of plants, we can see that the European ground squirrel created gaps in vegetation where competitive interactions between plants are more relaxed, as was described by White and Pickett (1985). The European ground squirrel activity creates microhabitats that reduce graminoid species and plant competitors, and support the establishment of forbs. Similarly, Archer et al. (1987) observed vegetation changes associated with prairie dogs in North American mixed-grass prairies. They found that perennial grasses were rapidly displaced from the site of colonization by prairie dogs and were replaced by annual forbs. In the same way, Del Moral (1984) documented effects by the Olympic marmots on subalpine vegetation and noted the decline of graminoid species and the increase of ruderal species that accompanied the increasing marmot impact. Additionally, Fields et al. (1999) studied the burrowing activities of kangaroo rats and detected lower cover of perennial grasses and higher cover of forbs, shrubs, and succulents on the edges of mounds.

While many studies have demonstrated that burrowing mammals play a keystone role in the world's grasslands (Davidson et al. 2012), there is no evidence evaluating the European ground squirrel as a keystone species or an ecosystem engineer in European grasslands (Janák et al. 2013). Our results lead to the conclusion that the European ground squirrel diversifies vascular plant communities by disturbances related to its burrowing activities. It maintains heterogeneity of grassland ecosystems and creates specific patches within relatively homogeneous vegetation. Our results contribute to the discussion about the role and function of the European ground squirrel in European grassland ecosystems. We showed that the potential loss of this vulnerable species may result in a decrease in diversity and changes in species composition of grasslands in the Western Carpathians.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies of human participants or animals performed by any of the authors.

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