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ORIGINAL PAPER

Disturbances by the European ground squirrel enhance diversity and spatial heterogeneity of plant communities in temperate grassland

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Abstract
Fossorial rodents are recognized as diversity drivers in grassland ecosystems and are therefore considered ecosystem engineers and keystone species. However, there is a lack of evidence regarding this function for species in temperate grasslands, especially one of the most threatened, the European ground squirrel. We examined the effect of the European ground squirrel on plant species composition and diversity along the disturbance gradient mediated by their different population density and subsequently different disturbance intensity. We evaluated the effect of ground squirrel disturbance on plant diversity patterns in two plant communities with different species richness to determine whether the same pattern exists in contrasting habitats. In each plant community, we established transect of 25 × 250 m composed of 10 quadrats with different disturbance intensities of the ground squirrels. Vascular plant species were recorded in 320 plots of 1 m^2. The distribution of individual species along the ground squirrel-mediated disturbance gradient was analysed using redundancy analysis. Diversity measures were calculated and modelled as a function of disturbances using generalized additive models. We observed significant compositional changes in plant communities accompanied by a reduction in dominant graminoid cover and a non-decreasing trend in forb cover along the disturbance gradient in both types of communities. We found that increasing disturbance activity leads to an increase in diversity at coarse spatial scale (625 m^2) and spatial heterogeneity in species composition of both species-poor and species-rich plant community. The fine-scale (1 m^2) diversity increased significantly only in species-poor community. Our results demonstrate that the European ground squirrel can be deservedly labelled as an important ecosystem engineer and keystone species promoting the diversity and heterogeneity of European temperate grasslands.

Keywords European ground squirrel · *Spermophilus citellus* · Disturbance · Diversity · Plant communities · Species composition

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Introduction

Disturbance by biological agents is recognized as a driver of plant and animal diversity in grassland ecosystems, affecting habitat heterogeneity and community dynamics across a continuum of spatial scales (Gibson 2009; Root-Bernstein and Ebensperger 2013; Mallen-Cooper et al. 2019). Local, among-site, and regional diversity can all be driven by disturbances (Whittaker 1960; Tuomisto 2010). The response of diversity to disturbance is highly variable depending on biogeographical region, habitat type and disturbance type and intensity (Dumbrell et al. 2008; Root-Bernstein and Ebensperger 2013).

Disturbances are also related to other relevant concepts of conservation theory. For instance, ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to other species by causing physical state changes in biotic or abiotic materials (Jones et al. 1994). Ecosystem engineering as the creation and modification of habitat is an important mechanism generating high species diversity and heterogeneity of biotic communities (Jones et al. 1994, 1997; Wright and Jones 2006). The next concept in conservation biology related to disturbances are keystone species. Keystone species are described as those that have a disproportionately large effect on their environment relative to their abundance (Power et al. 1996). However, the original definition was used to identify keystone species through trophic interactions (Paine 1966); the concept has also been subsequently applied to species with non-trophic effects on other species such as keystone modifiers, providing disturbances in an ecosystem and influencing the number of species (Mills et al. 1993).

Fossorial rodents are frequently recognized as both ecosystem engineers and keystone species in grassland ecosystems (e.g., Brown and Heske 1990; Kotliar et al. 1999; Berke 2010; Ewacha et al. 2016). One of the most threatened fossorial rodent is the European ground squirrel (*Spermophilus citellus*). This species is a medium-sized ground squirrel living in colonies and occurring in central and south-eastern Europe. Although ground squirrels (sensu lato tribe Marmotini, Pocock 1923) are generally recognized as a key functional group of social and burrowing mammals shaping grassland ecosystems (Davidson et al. 2012), the status of ecosystem engineers and keystone species is mostly assigned to the largest members of this group (e.g., Ceballos et al. 1999; Kotliar et al. 1999; Miller et al. 1994, 2007). Consideration of smaller or medium-sized ground squirrels as ecosystem engineers is quite rare (e.g., Ewacha et al. 2016), and their status as keystone species is questionable (Wheeler and Hik 2013).

Ground squirrels exhibit different levels of sociality which range from solitary individuals to grouping individuals into the large colonies (Matějů et al. 2016), and thus, the overall effect on biotic communities can be highly dependent on their densities in a landscape. Therefore, the first aim of this study is to analyse the effect on composition and diversity of plant communities along the disturbance gradient mediated by different population density of ground squirrels and subsequently different disturbance intensity. Although many studies refer to the effect of disturbances by fossorial rodents on species diversity at mound scale, studies evaluating the effect of fossorial rodents at multiple spatial scales are less frequent (e.g., Bangert and Slobodchikoff 2006; Questad and Foster 2007; Case et al. 2013). Therefore, the second aim of this study is to examine whether the European ground squirrel also facilitates species diversity at multiple spatial scales. Finally, the effect of small mammal disturbances can be also context dependent. In other words, they can have positive, negative or no effects on diversity across habitats (Power et al. 1996), and their effect can be determined by different community types with different species pools (Root-Bernstein and Ebensperger 2013). Therefore, the third aim of this paper is to evaluate the effect of the European ground squirrel on diversity patterns in two typical communities of temperate grasslands with different species richness to identify if the same pattern exists in contrasting habitats.

Methods

Study sites

The research was performed at two study sites situated in the north-eastern part of Slovakia. The first site was located in the Kozie chrbty Mountains, in the area surrounding the peak Hradisko (N 49° 00′ 46.4″; E 20° 25′ 41.7″), at an altitude of 630 m a.s.l. The second study site was located in the Hornád Basin, in the area surrounding the peak Pieskovec (N 48° 55′ 41.1″; E 20° 33′ 13.1″), at an altitude of 495 m a.s.l. The climate of both sites 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 (Miklós 2002). The soil of the first site (Hradisko) consists of cambisols on variegated shales and volcanic bedrock with an average pH of 5.0. The soil of the second site (Pieskovec) consists of rendzina on calcareous conglomerates and breccias bedrock with a pH of 7.2. Both study sites represent mesic pastures with intensively grazed vegetation consisting of the *Cynosurion cristati* Tüxen 1947 alliance. The study site Hradisko is under cattle grazing for several decades. The land-use history of the study site Pieskovec combined cattle and sheep grazing with occasional mowing in last decades. We detected a total of 81 plant species along the studied transects at both study sites. The plant community at study site Hradisko contained, on average, 10 vascular plant species per m^2. The plant community at study site Pieskovec contained, on average, 19 species per m^2.

Sampling design and measurements

At each study site, we established a transect of 25 × 250 m consisting of 10 quadrats of 25 × 25 m. Transects were placed throughout homogeneous environmental conditions across ground squirrel colonies spanning a wide range of their densities. Mound density ranged between 2 and 16 mounds per quadrat at Hradisko study site and 2–14 mounds per quadrat at Pieskovec study site. Each quadrat consisted of 16 plots with a size of 1 m^2 systematically placed in the 7 × 7 m matrix (Fig. 1). Study scales were determined by following factors. The size of plot level was 1 m^2 because this is the average size of mounds created by ground squirrels. The distance between mounds ranges from 5 m in high-dense colonies to more than 20 m in very low-dense colonies, and therefore, quadrat size of 25 × 25 m represents a minimal area where we can obtain some ground squirrels density data and subsequently disturbance intensity data. Finally, the transect length of 250 m was limited by the size of ground squirrel colonies. All vascular plant species were recorded in each 1 m^2 plot, and their covers were estimated as percentages. Plant communities were sampled from May to July during the year 2017. Within 1 m^2 plots, the percent cover of disturbances by the European ground squirrel was estimated. As a ground squirrel disturbance we considered mounds, burrows and pathways created by the ground squirrels. For each quadrat, we measured fine-scale diversity, coarse-scale diversity, heterogeneity of plant communities and disturbance intensity. Fine-scale diversity was measured as the mean number of plant species per 1 m^2 plot in a quadrat.

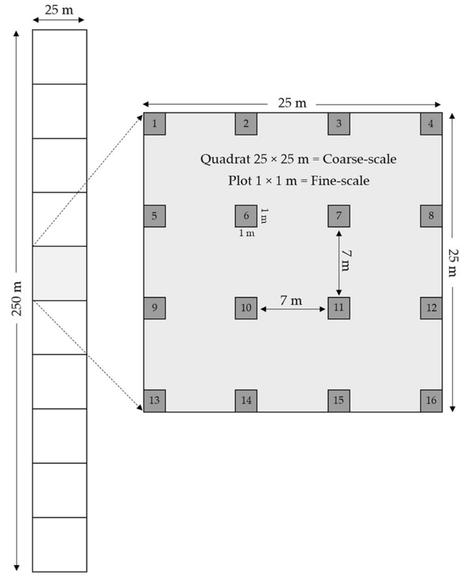

Fig. 1 Sampling design of the study. Two 250 m-long linear transects (left) were placed across ground squirrel colonies in two sites. Ten 25 × 25 m quadrats (light gray) were sampled in each transect with sixteen 1 × 1 m plots (dark gray) within each quadrat

Coarse-scale diversity was measured as the total number of plant species recorded in all 16 plots of a quadrat. Spatial heterogeneity in species composition of plant community (further referred as heterogeneity) was calculated for each quadrat according to Whittaker's beta diversity as follows: $\beta = \gamma/\alpha - 1$ (Whittaker 1960), where α represented fine-scale diversity and γ coarse-scale diversity. As a measurement of disturbance intensity in a quadrat, we used the mean percent cover of ground squirrel disturbance in all 16 plots of a quadrat.

Statistical analysis

The influence of ground squirrel disturbances on the diversity of plant communities was assessed using generalized additive models (GAMs), a flexible approach that allows for non-linear responses and non-normal error distributions (Hastie and Tibshirani 1990). Each response variable (fine-scale diversity, coarse-scale diversity and heterogeneity) was fitted using a series of four GAMs with decreasing complexity: (1) an interaction model that assumes different relationships between the cover of disturbed area and diversity in each plant community (species-poor versus species-rich), (2) a parallel model expecting the same disturbance-diversity relationship in each plant community but different diversity values between communities, (3) a general model assuming no effect of plant community on the disturbance-diversity relationship, and (4) a null model of no relationship between diversity measures and the cover of areas disturbed by ground squirrels. GAMs with a Gaussian distribution and identity link function were used to model fine-scale diversity and heterogeneity, while a Poisson model with a log link function was used to fit coarse-scale diversity. Since the dispersion parameters of the Poisson GAMs deviated from one, the standard errors in these models were computed by a quasi-likelihood procedure. To prevent biologically improbable models (e.g., multimodal responses), we constrained the level of smoothness by setting the upper limit on the degrees of freedom to three and fitted GAMs as tensor product smooths constructed from penalized cubic regression splines

(Wood 2017). GAMs with the same settings were also used to assess relationships between ground squirrel disturbances and the cover of vegetation, forbs and graminoids respectively. Generalized likelihood ratio tests were employed to select among the four competing models. In addition, we calculated small-sample corrected (quasi) Akaike information criterions (AICc/qAICc) (Burnham and Anderson 2003) to measure the likelihood that a given model would be the best-supported among the set of models fitted. In the final models, the significance of parametric and smooth terms was assessed using Wald-type t and F tests, respectively (Wood 2013).

Since all data were sampled from a regular grid of plots along two transects, residuals of the final models were checked for spatial autocorrelation using spline correlograms (Bjornstad and Falck 2001); no significant autocorrelation patterns were found.

To gain insight into the distribution of individual species along the ground squirrel-mediated disturbance gradient, the species mean abundance matrix (means for 20 quadrats from 320 one-square-metre plots) was converted to Bray–Curtis dissimilarities and analysed using partial distance-based redundancy analysis (partial db-RDA; Legendre and Anderson 1999). In the analysis, the effect of community type was partialled out, and the influence of the disturbance gradient was assessed using a randomization test (10,000 permutations of residuals). The results of partial db-RDA were displayed in an ordination plot with the cover of disturbed area fitted into the ordination space as a GAM-based response surface (Oksanen et al. 2017).

Analyses were performed in R (R Core Team 2017) using the libraries mgcv (Wood 2017), ncf (Bjornstad 2016) and vegan (Oksanen et al. 2017).

Results

Species composition

The effect of ground squirrel disturbances was apparent as a significant shift in community composition along the disturbance gradient (pseudo-$F = 4.22$, $p < 0.0001$). While *Trifolium repens* and *Trisetum flavescens* were typical of low disturbance intensity, *Agrostis stolonifera*, *Cirsium vulgare*, *Dactylis glomerata* and *Descurainia sophia* predominantly occurred under a higher disturbance intensity (Fig. 2).

Total vegetation cover was significantly influenced by ground squirrel disturbances regardless of the plant community type—general model (Table 1). The vegetation cover initially steeply decreased with increasing disturbance intensity and reached an asymptote at approximately 25% disturbed area (equivalent degrees of freedom ($edf = 2.66$, $F = 42.73$, $p < 0.0001$) (Fig. 3). Species-poor and species-rich communities differed in forb cover ($t = -7.27$, $p < 0.0001$), with no effect of disturbances ($edf = 1$, $F = 0.18$, $p = 0.673$). In contrast, the graminoid cover of both communities decreased with increasing disturbance in a similar way as the total vegetation cover ($edf = 2.55$, $F = 7.27$, $p = 0.002$).

Plant community diversity and heterogeneity

The fine-scale diversity, coarse-scale diversity and heterogeneity of the studied communities were significantly related to ground squirrel-mediated disturbances, but the effect was dependent on the community type (Table 2). The fine-scale diversity of the species-poor community was positively influenced by the disturbances (edf = 1, F = 27.69, p < 0.0001), while the species-rich community was unaffected (edf = 1, F = 1.46, p = 0.244), which corresponded to the interaction model (Fig. 4). While the species richness at fine spatial scale of the species-poor community increased rapidly from 10 species per m^2 in the least disturbed quadrat to 15 species per m^2 in the most disturbed quadrat, it exhibited a non-significant trend in the species-rich community (18.5 species per m^2 in the least disturbed quadrat and 18.3 species per m^2 in the most disturbed quadrat). The coarse-scale diversity of the species-rich community increased with disturbance at significantly lower rates (edf = 1, F = 9.16, p = 0.0078) than did the coarse-scale diversity of the species-poor community (edf = 1, F = 55.47, p < 0.0001), which eventually reached the same number of species under a high disturbance intensity (cover of disturbed areas > 20%). Finally, the pattern of heterogeneity was best described by a parallel model in which the heterogeneity of both communities increased with disturbance at the same rate (edf = 1.27, F = 22.81, p < 0.0001), but the absolute heterogeneity values were higher in the species-poor community than in the species-rich community (t = 6.49, p < 0.0001).

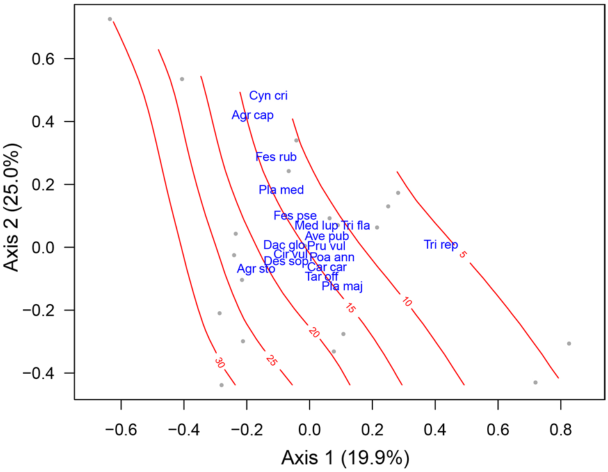

Fig. 2 Ordination plot of partial db-RDA showing preferences of plant species for ground squirrel-mediated disturbances using quadrats of both sites (grey dots). Abundance-based species optima (abbreviations of species names) are overlaid by the GAM (edf = 4.7, F = 9.14, p < 0.0001) of disturbed area cover (contour lines with an indication of disturbed area percentages). Only the species with the best fit to the ordination model (15%) are displayed for brevity. Variation explained by the ordination axes is given in parentheses. The abbreviations of species names include the first three letters of the genus and species scientific names: Agr cap—*Agrostis capillaris*, Agr sto—*Agrostis stolonifera*, Ave pub—*Avenula pubescens*, Car car—*Carum carvi*, Cir vul—*Cirsium vulgare*, Cyn cri—*Cynosurus cristatus*, Dac glo—*Dactylis glomerata*, Des sop—*Descurainia sophia*, Fes pse—*Festuca pseudovina*, Fes rub—*Festuca rubra*, Med lup—*Medicago lupulina*, Pla maj—*Plantago major*, Pla med—*Plantago media*, Poa ann—*Poa annua*, Pru vul—*Prunella vulgaris*, Tar off—*Taraxacum officinale*, Tri fla—*Trisetum flavescens*, Tri rep—*Trifolium repens*

Table 1 Analysis of deviance table sequentially comparing GAM models of decreasing complexity (from the parallel to the null model) that relate cover characteristics of plant communities with ground squirrel-mediated disturbances

	Vegetation cover					Forb cover					Graminoid cover				
Model	AICc	D	ΔD	F	p	AICc	D	ΔD	F	p	AICc	D	ΔD	F	p
Interaction	-83.4	0.00696	-0.00082	2.00	0.1774	-56.4	0.03	-0.01	2.40	0.1408	-72.6	0.012	-0.003	4.75	0.0526
Parallel	-84.9	0.00779	-0.00002	0.05	0.8318	**-57.3**	**0.04**	**-0.12**	**52.89**	**< 0.0001**	**-71.2**	**0.015**	**-0.013**	**13.97**	**0.0019**
General	**-88.6**	**0.00781**	**-0.05449**	**43.91**	**< 0.0001**	-32.2	0.16	-0.02	1.72	0.2064	-62.2	0.028	-0.020	4.22	0.0235
Null	-54.0	0.06230				-33.1	0.18				-59.1	0.048			

The table shows small-sample corrected (quasi) Akaike information criterions (AICc), residual deviances (D), changes in the residual deviance between successive models (ΔD), test statistics (F) and probabilities (p). The best-supported (final) models are highlighted in bold

Table 2 Analysis of deviance table sequentially comparing GAM models of decreasing complexity (from the parallel to the null model) that relate diversity to ground squirrel-mediated disturbances

	Fine -scale diversity					Heterogeneity					Coarse -scale diversity				
Model	AICc	D	ΔD	F	p	AICc	D	ΔD	F	p	qAICc	D	ΔD	F	p
Interaction	**73.9**	**23.11**	**-9.43**	**6.53**	**0.0212**	-6.7	0.41	-0.05	3.49	0.0935	**176.8**	**4.98**	**-3.39**	**10.60**	**0.0050**
Parallel	77.2	32.55	-169.87	88.73	< 0.0001	**-7.2**	**0.46**	**-1.13**	**42.57**	**< 0.0001**	178.0	8.37	-4.44	8.94	0.0082
General	110.5	202.42	-1.39	0.12	0.7289	14.5	1.59	-1.72	12.73	0.0008	181.2	12.82	-14.63	20.84	0.0002
Null	107.9	203.81				25.5	3.31				199.2	27.45			

The table shows small-sample corrected (quasi) Akaike information criterions (AICc/qAICc), residual deviances (D), changes in the residual deviance between successive models (ΔD), test statistics (F) and probabilities (p). The best-supported (final) models are highlighted in bold

Discussion

Our results demonstrate that the species composition and diversity of plant communities are significantly altered by disturbances of the European ground squirrel. We found that increasing disturbance activity of the European ground squirrel led to an increase in coarse-scale diversity and heterogeneity in both types of plant communities, while the fine-scale diversity increased only in the species-poor plant community.

Species composition changes related to disturbances

Grass competitors (*Lolium perenne*, *Festuca rubra*, *Agrostis capillaris*, *Avenula pubescens* and *Trisetum flavescens*) in association with forbs (*Trifolium repens*, *Trifolium pratense*, *Taraxacum* sp., *Achillea millefolium*, *Crepis biennis* and *Medicago lupulina*) form a relatively uniform community under low disturbance intensity. Within the community, the European ground squirrel activates the niche creation process through disturbances and influences selection pressures on plant species (Odling-Smee et al. 2003; Matthews et al. 2014; Laland et al. 2016), which leads to modification of species composition. The majority of the original grassland species were suppressed under

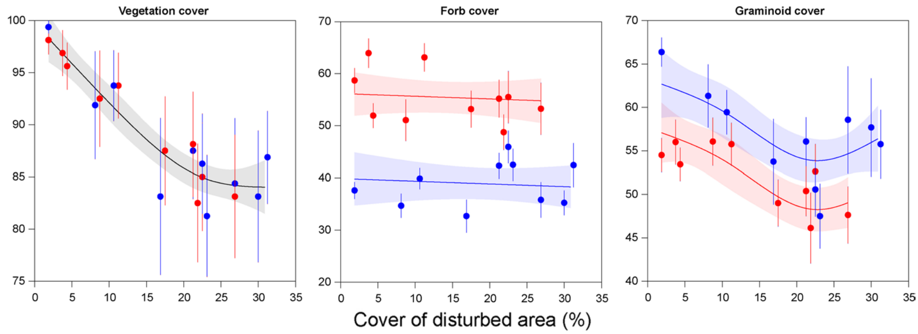

Fig. 3 Significant GAMs showing the effects of ground squirrel disturbances (cover of disturbed area) on total vegetation cover, forb cover and graminoid cover. Mean cover values per quadrat (circles) ± 95% confidence limits (error bars) are displayed along with model estimates (lines) and their 95% confidence intervals (bands). Species-rich and species-poor plant communities are distinguished by red and blue colour, respectively

high disturbance intensities, while other species were favoured. Among these favoured species, the ephemeral field weed *Anagallis arvensis* or annual ruderals such *Cirsium vulgare* represent typical species associated with small-scale animal disturbances in grasslands (Milton et al. 1997). Additionally, the perennial field weed *Cirsium arvense* occurred on bare soil in disturbed patches as an early colonizer, while its proportion in pasture communities is limited by grass competition (Pywell et al. 2010). The perennial grasses *Agrostis stolonifera* and *Elytrigia repens* represented other pioneer species in the disturbed areas in both communities. These ruderal species frequently colonizing spoil habitats (Grime et al. 2014) belong also to weeds of pastures (Hatcher 2017). *Agrostis stolonifera* is a competitive species (Kühn et al. 2004) whose competitive ability increases in overgrazed pastures (Dietl 2013), but it is not frequent in the mesic semi-natural grasslands of Slovakia (Hegedüšová-Vantarová and Škodová 2014). These perennial grass competitors with ruderal dispersal strategies are outcompeting annual ruderals of disturbed patches, but they are gradually suppressed by grassland species after recovery of compact turf. Perennial forbs colonizing disturbed areas (*Agrimonia eupatoria*, *Galium verum*, *Glechoma hederacea*, *Senecio jacobaea*, *Stellaria graminea* or *Thymus pannonicus*) represent species of semi-natural grasslands managed at medium to low intensities. These species are almost missing in the most intensively grazed communities of the *Cynosurion* alliance (Janišová et al. 2014).

Based on our mound-based study, where we found that mounds exhibited decreased graminoid cover and enhanced forb cover (Lindtner et al. 2018), we expected a similar pattern that could be apparent also at the disturbance gradient mediated by different population densities of ground squirrels. However, in current study, forb cover did not respond to ground squirrel-mediated disturbance gradient. While forb cover was unaffected, graminoid cover decreased along the disturbance gradient, resulting in a grass/forb ratio reduction in intensively disturbed patches. Our findings are consistent with those from other large-scale studies revealing competition release in communities disturbed by fossorial mammals (e.g., Case et al. 2013; Questad and Foster 2007).

Plant community diversity and heterogeneity in disturbed grassland

We expected that diversity would increase with increasing disturbance intensity. However, this relationship was dependent on spatial scale and community type. The fine-scale diversity increased with disturbance intensity only in the species-poor community, but coarse-scale diversity increased in both types of communities. This means that the effect of ground squirrel-mediated disturbances on fine-scale diversity was context dependent. A mixed effect (positive and negative) of small mammal disturbances on local diversity was found across habitats, with the effect depending on the type of disturbance (herbivory, burrows, lawns and mounds), biogeographic region and habitat productivity, species identity and their native or invasive character (Wright and Jones 2004; James et al. 2011; Root-Bernstein and Ebensperger 2013).

We can assume that there is a competition-colonization trade-off in disturbed patches. This trade-off holds that species differ in their ability to disperse and colonize new habitats versus their ability to compete in a habitat (Levins and Culver 1971; Tilman 1994; Yu and Wilson 2001; Kneitel and Chase 2004; Cadotte 2007). In the species-poor community, highly disturbed quadrats contained more species at fine spatial scale than did low disturbed quadrats. There was a relatively high grass/forb ratio in the species-poor community indicating strong competitive interactions among plant species. Highly disturbed quadrats with suppressed grass competitors exhibited a higher number of species at fine spatial scale in comparison to low disturbed quadrats controlled by competitively strong graminoid species. However, the species-rich community showed a lower grass/forb ratio (i.e., a lower proportion of competitors) and, therefore, a high number of species coexisted within quadrats with low disturbance intensity. Increased disturbance intensity by ground squirrels in species-rich community thus promotes species exchange, but without a change in fine-scale diversity.

In contrast to fine-scale diversity, we found similar increasing patterns in the coarse-scale diversity and spatial heterogeneity in species composition along the disturbance gradient in both studied communities. In other words, the impact of the European ground squirrel on the coarse-scale diversity and heterogeneity was not context dependent. High heterogeneity of species composition within a disturbed grassland can be a consequence of increased habitat heterogeneity. The patchiness of disturbance, niche construction and different successional vegetation stages occurring along mound development (Jones et al. 2008; Van Staalduinen and Werger 2007) have a positive effect on diversity on larger spatial scales (Caswell and Cohen 1991; Huston 1994; Rosenzweig 1995; Tamme et al. 2010). Our results indicate that ground squirrels can be valuable for promoting species diversity especially in species-poor communities, where they can enrich the coarse-scale diversity at high disturbance intensities to be comparable with that in species-rich plant communities.

Burrowing activities of fossorial mammals influence heterogeneity not only in plant communities (e.g., Questad and Foster 2007; Galvez-Bravo et al. 2011; Sasaki and Yoshihara 2013) but also in arthropod, reptile, amphibian and small mammal communities (Bangert and Slobodchikoff 2006; Shipley and Reading 2006; Kenney et al. 2016). Therefore, areas disturbed by vertebrate engineers tend to develop into biological hotspots (Mallen-Cooper et al. 2019).

Our results showed the positive linear relationship between the ground squirrel disturbances and the diversity and heterogeneity of plant communities. The disturbance heterogeneity model suggests that disturbance increases community heterogeneity

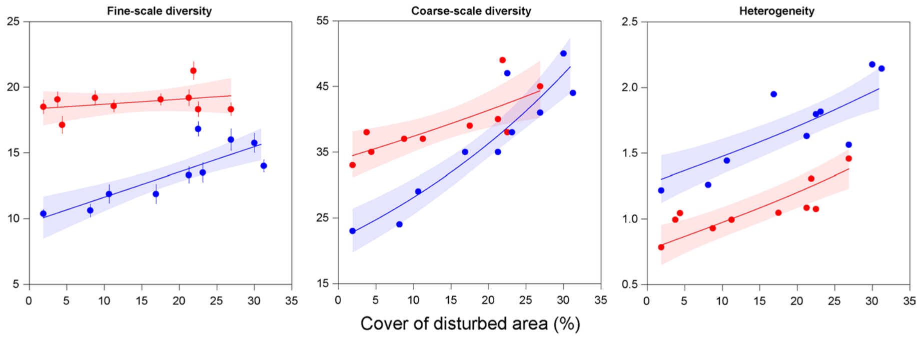

Fig. 4 Significant GAMs showing the effects of ground squirrel disturbances (cover of disturbed area) on the fine-scale diversity, coarse-scale diversity and spatial heterogeneity in species composition of plant communities. Model estimates (lines) and their 95% confidence intervals (bands) are displayed along with diversity values recorded in quadrats (circles). For fine-scale diversity, mean species richness ± 95% confidence limits (error bars) are shown. Species-rich and species-poor communities are distinguished by red and blue colour, respectively

between patches so long as the disturbance is small relative to the size of the community (Kolasa and Rollo 1991). Small-scale disturbances are thus a mechanism for generating and maintaining spatial heterogeneity in communities, in contrast to large-scale disturbances such as intensive grazing or fire which were shown to decrease diversity and heterogeneity (Gibson 2009). Ground squirrels and also other colonial and fossorial rodents create patchy disturbances in a pattern determined by spatial relationships between individuals (Michener 1979; Boellstorff and Owings 1995). In natural conditions, cover of disturbances by fossorial rodents such as prairie dogs, pocket gophers and plateau zokors ranges usually between 1 and 20% of the ground surface (Zhang et al., 2003; Lauenroth and Burke 2008). The spectrum of our disturbance gradient ranged from 2 to 30% of the cover of disturbed area at both studied sites. Almost linearly increasing diversity along this gradient in our case seems to be in contradiction of the classic intermediate disturbance hypothesis (Connell 1978) that predicts a hump-back pattern. However, hypothetical higher disturbance rates in case of potentially overpopulated colonies would lead to decreasing plant species diversity expected by the hypothesis.

By finding a linear relationship between the ground squirrel disturbances and diversity and heterogeneity of plant communities, the relevant question is about the causality. One can assume that ground squirrels prefer the species rich patches in vegetation to construct their burrow systems. But, our previous study showed that plant species enhancing grassland diversity were found directly on the mounds as a result of ground squirrel activities (Lindtner et al. 2018). Moreover, the European ground squirrel seems to be not related to some specific plant species or vegetation types, and they use to occupy also homogenous lawn of golf courses with very low species richness and diversity (Matějů et al. 2011). Therefore, we suppose that ground squirrels are not restricted to species rich patches, contrariwise, their burrowing activities promote development of high diverse vegetation.

Conclusion

Our results indicate that the European ground squirrel influences a wide spectrum of ecological processes in temperate grassland grazed by cattle resulting in species composition changes, species heterogeneity increase and species diversity increase at multiple spatial scales. Positive effect on species diversity is more pronounced in species poor community. The European ground squirrel modifies, maintains and creates habitat patches, and therefore, can be deservedly labelled as an important ecosystem engineer in European grasslands. Our results further reveal the diversity dependency on the activities of the European ground squirrel indicating the keystone function of this endemic species in grassland ecosystems. Given the keystone function of the European ground squirrel, we may conclude that continued loss of this endangered animal species can lead to simplification of European grassland ecosystems.

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Compliance with ethical standards

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

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

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