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ORIGINAL PAPER

Relationship of different feeding groups of true bugs (Hemiptera: Heteroptera) with habitat and landscape features in Pannonic salt grasslands

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Abstract Eastern European grasslands are still inhabited by a rich arthropod fauna, but the drivers and mechanisms influencing their communities have to be understood to ensure their future survival. Heteroptera communities were studied in 20 plot-pairs in Pannonic salt steppe–salt marsh mosaics in Hungary. The effects of vegetation characteristics, landscape diversity and the proportion of surrounding grasslands on the composition, species richness and abundance of different feeding groups of true bugs (carnivores, specialist and generalist herbivores) were examined using ordinations and mixed-effect models. We found distinct herbivorous assemblages corresponding to microtopography-driven differences in water regime and vegetation between steppe and marsh plots, but this pattern was less pronounced in carnivorous assemblages. A higher species richness of true bugs was found in the more diverse steppe vegetation than in the salt marsh vegetation, while the abundance pattern of true bugs was opposite. Landscape diversity had a positive effect on the species richness and abundance of generalist herbivores and carnivores. Our results suggested that generalist herbivores and carnivores appear to drive diversity patterns in the local landscape due to their high dispersal abilities and the broader range of resources they can utilize. Specialist herbivores strongly influence the local insect biomass in relation to the distribution and density of their host plants. The present study highlights the importance of both habitat and landscape diversity for local insect diversity in Pannonic salt grasslands and suggests that the main threats for arthropod diversity are those processes and activities that homogenize these areas.

Keywords Abundance · Carnivores · Composition · Generalists · Herbivores · Diversity · Specialists

Introduction

Arthropods are an important component of grassland ecosystems, contributing significantly to biodiversity and ecosystem structure and function (Tscharntke and Greiler 1995). Understanding patterns of their diversity, however, is a great challenge for science (Joern and Laws 2013), and the number of studies scrutinizing the diversity and conservation of grassland arthropods is still very low in Central and Eastern Europe compared with Western Europe (Stoate et al. 2009). As a result, we still have very little knowledge on how central and eastern European grasslands should be managed to maintain natural arthropod diversity (Báldi et al. 2013). Thus, there is a growing need to understand the drivers and mechanisms influencing eastern European grassland arthropod communities in order to establish proper conservation measures. Such measures would be particularly valuable, as the remaining natural and semi-natural grasslands host large populations of invertebrates that are declining or have gone extinct in the rest of Europe (e.g., Holusa et al. 2012; Szentirmai et al. 2014).

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Hungarian grasslands have a special position in Europe due to their geographical location and continental character and because they still harbour the unique biota of the Pannonian biogeographic region, which covers all Hungary and some smaller areas from neighbouring countries. Among the various grassy habitats of the region, Pannonic salt steppes and salt marshes occur mainly in the Pannonian biogeographical region and are listed among the priority habitats of Annex 1 of the Habitats Directive of the European Union (Council of European Communities 1992). Due to the restricted geographical distribution, Pannonic salt steppes and salt marshes belong to the most threatened habitats of Europe (Šefferová Stanová et al. 2008). As a result of the diverse microtopography and salt and water content of the soil, these grasslands form mosaics of compositionally distinct vegetation patches and support a rich fauna and flora, with numerous endemic species (Šefferová Stanová et al. 2008; Török et al. 2011). As the poor soil quality and fluctuating water regime render salt grasslands unsuitable for intensive agriculture and forestry, they are traditionally used as extensive pastures, and thus are one of the best preserved grasslands in Europe, providing important feeding and breeding habitats for many endangered bird species e.g., *Chlidonias leucopterus, Charadrius alexandrinus, Glareola pratincola, Otis tarda* (Török et al. 2011). As the preservation and conservation of these habitats are important issues, their vegetation is well studied regarding the effects of grazing, mowing (Török et al. 2011), burning (Valkó et al. 2016) water regime and soil salinity (Ladányi et al. 2016). Besides birds and plants, salt grasslands also harbour unique invertebrate assemblages, but very few studies (Zulka et al. 1997; Kőrösi et al. 2012; Torma et al. 2014; Valkó et al. 2016) have contributed to our knowledge about the community patterns of arthropods inhabiting these grasslands, and the majority of these studies did not focus exclusively on salt habitats (but see Zulka et al. 1997).

In contrast to Pannonic salt grasslands, the literature of coastal salt grasslands, a somewhat similar habitat, is fairly abundant. Coastal salt grasslands are of interest to ecologists because they are fairly simple communities, display striking community patterns across strong gradients in physical stress, and are relatively easy to manipulate. As a result, they are good model systems to study how physical and biological factors interact to create pattern in natural communities (Pennings and Bertness 2001). However to extrapolate findings in coastal salt marshes to inland salt marshes cannot be done directly because of the differences in both biotic and abiotic factors such as salt and water regime or vegetation composition and production.

Heteroptera is an ideal group to study insect diversity patterns in grassland ecosystems, even though their ecology is still understudied. They are the most diverse group of hemimetabolous insects. Their diversity has been shown to be a good indicator of the total insect diversity (Duelli and Obrist 1998), and is sensitive to grassland characteristics and disturbances (Di Giulio et al. 2001; Frank and Künzle 2006; Zurbrügg and Frank 2006). True bugs are also shown to be an important component of insect communities in salt marsh ecosystems (Ford et al. 2013; Pennings et al. 2014). Similarly to other taxa, the sensitivity of Heteroptera species to environmental conditions is a function of their ecological and life history traits. In the present study we focused only on the feeding behaviour of species. This trait has a prominent role in shaping the assemblages of Heteroptera (Torma and Császár 2013; Torma et al. 2014) and of arthropods in general (Schweiger et al. 2005; Albrecht et al. 2010), as it highly influences the response of particular species with different environmental conditions. Vegetation has a pronounced influence on arthropods and it is generally assumed that highly structured and diverse vegetation maintains the diversity and abundance of arthropods by providing a greater potential surface for colonization, oviposition, resting, hiding and overwintering (Price et al. 1980; Lawton 1983; Obermaier et al. 2008). Numerous studies (e.g., Zurbrügg and Frank 2006; Entling et al. 2007; Woodcock et al. 2007; Lambeets et al. 2008; Gallé and Torma 2009) emphasized that it is not the species diversity but the structural complexity of the vegetation that influences the diversity of predaceous arthropods. However, for herbivores, a species rich vegetation patch has several advantages. More plant species allow more species of specialized herbivores to colonize an area (Brändle et al. 2001). Because of the differences in nutrient content between different plant species, more available plant species are beneficial for less specialized herbivores too, since this allows them to switch between plant species. Furthermore, some species are dependent on a variety of host plants for their larval development and survival (Di Giulio and Edwards 2003). The surrounding landscape also has a great impact on local arthropod communities, influencing their migration and colonization patterns (Joern and Laws 2013). Surrounding habitats in the local landscape can offer complementary or supplementary resources for some species. Cross-habitat foraging may couple the dynamics of different habitats or landscape elements; however, this is highly dependent on the feeding behaviour of species. Generalist feeding species are more likely than specialists to find sufficient resources and to utilize corridors within a fragmented landscape (Collinge 2000; Joern and Laws 2013).

To clarify the possible relationships of different feeding groups of true bugs with habitat and landscape features in salt marsh-steppe mosaics, Heteroptera assemblages were studied in 20 pairs of salt steppe–salt marsh plots situated in the same local landscape. More specifically, we addressed the following questions:

i. How do differences in habitat quality, i.e., vegetation characteristics and temporary water cover, affect the abundance, species richness and composition of true bugs?
ii. How do differences in local landscape characteristics, i.e., the proportion of semi-natural grasslands and the diversity of the local landscape, affect the abundance, species richness and composition of true bugs?
iii. Do the compositional and diversity patterns vary according to the trophic level and host specialization of true bugs?

Materials and methods

Study sites and sampling

The study was carried out in the southern part of the Danube–Tisza Interfluve, Csongrád County, Hungary (Fig. 1). The area lies in the warm temperate zone with an annual mean temperature of 10.5 °C. The annual precipitation ranges from 550 to 600 mm (Kröel-Dulay and Kovács-Láng 2008). The soil of the area is composed of mainly sand. The studied grasslands are ancient, primary salt grasslands on naturally developed alkali soils, which are present in the region since the Pleistocene (Török et al. 2011). In accordance with the diverse microtopography, grassland remnants are made up of mosaics of different vegetation types. The water table is close to the surface of low-lying depressions all year round and the salt concentration is also rather high; therefore, these areas are dominated by salt-tolerant grasses, sedges and rushes, like *Puccinellia*

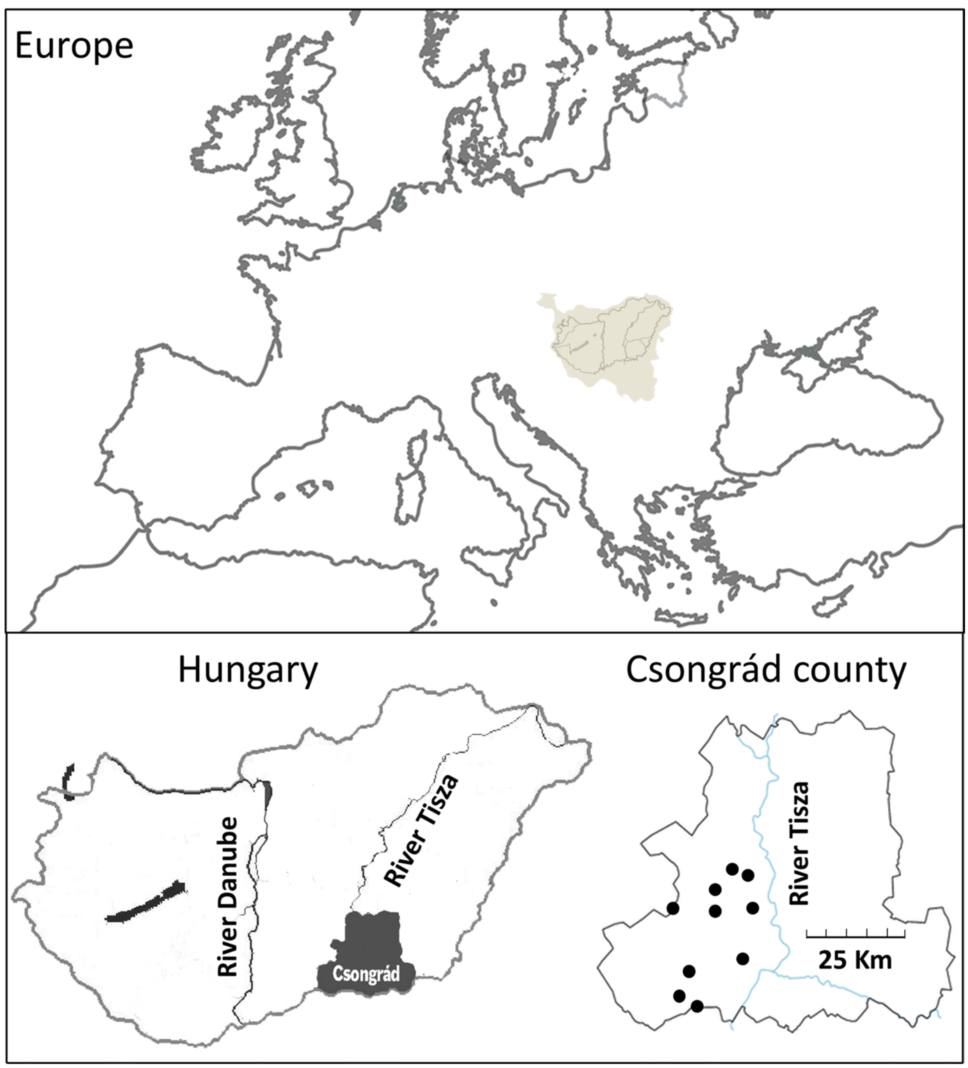

Fig. 1 The position of the Pannon Biogeographical Region and Hungary in Europe (*above*) and the postion of studied grasslands in Hungary (*below*). The area of the Pannon Biogeographical Region is coloured in grey. Black circles mark the position of sampled Pannonic salt steppe–salt marsh habitats in Csongrád County, Hungary

limosa, Agrostis stolonifera, Bolboschoenus maritimus, Juncus gerardi, etc. The resulting vegetation (henceforth salt marshes) is dense and tall but comparatively species poor. Salt marshes are surrounded or interrupted by never-inundated terraces, which are covered by dry grasslands dominated by *Festuca pseudovina* (henceforth salt steppes). Though the difference in elevation is only a few decimetres, the salt content is lower, enabling more plant species to inhabit this vegetation type. The most common forb species include *Achillea* spp., *Euphorbia cyparissias, Gallium verum, Centaurea scabiosa* ssp. *sadleriana*, etc. The slopes between the terraces of salt steppes and the depressions of salt marshes are usually steep; therefore, the share of intermediate vegetation zones is low at the landscape level.

We sampled the Heteroptera assemblages of ten primary salt grasslands. In each grassland, two sampling sites were established at least 500 m apart. Within each site, plot pairs were selected; one plot was on a higher elevation with salt steppe vegetation and next to it another one on a lower elevation with salt marsh vegetation. The distance between the members of plot pairs was approximately 50 m.

To cover the seasonal activity of the majority of species, true bugs were collected three times (15–16 May, 15–16 June and 27–28 September) in 2010, using sweep netting. Although a later sampling in the summer would be also useful, it is difficult, because of the agricultural activities e.g., mechanical mowing in this period. At each sampling plot 3×50 sweeps was carried out along three 30 m long transects. To avoid pseudoreplication, the data of transects at each plot were pooled. Since our focus was not on the seasonal dynamics of the assemblages, data of different periods were also pooled, making a total of 40 statistical samples.

Assessment of habitat and landscape variables

To characterize the vegetation, the number of plant species, the average height of the vegetation and the percentage cover of the vegetation at 10 and 40 cm above ground were recorded in two 1×1 m quadrats along each transect. A principal component analysis (PCA) was performed on the assessed structural parameters of the vegetation and the values of the first axis were used as a structural measure of vegetation (hereafter vegetation structure).

To characterise landscape composition, the proportion of grasslands in the local landscape and the diversity of the local landscape were used. Based on Google satellite images, the area covered with the main surrounding landscape elements (grasslands, reeds, forests, arable fields and inhabited areas) were assessed in a radius of 500 m around each sampling site using QGIS software. The proportion of grasslands in the local landscape (hereafter proportion of grasslands) was calculated as the percentage of area covered with grassland. The diversity of local landscape (hereafter landscape diversity) was calculated using the Shannon-Wiener formula based on the area of the main surrounding landscape elements excluding grasslands. Although the area of surrounding grasslands is a main component of landscape diversity in our study sites, it was omitted from the calculation of landscape diversity to avoid the obvious correlation ($r = -0.68$, $p < 0.001$) between the proportion of grasslands and landscape diversity calculated from all landscape elements including grasslands. In this way, we could also assess the effect of landscape elements other than grasslands separately. Numerous true bug species, which generally inhabit grasslands, are known to utilize other habitat types e.g., for overwintering (Wheeler and Stimmel 1988).

Statistical analyses

The vegetation can be assumed to depend on the astatic water regime, thus we tested whether assessed vegetation characteristics were different between salt marsh and salt steppe plots using Mann–Whitney tests.

We analysed the composition, abundance and species richness of all true bugs together and also separately according to feeding behaviour. Following Torma et al. (2014), we used three main feeding groups: carnivores (predaceous and zoophytophagous species), generalist herbivores (polyphagous and grass-feeder species) and specialist herbivores (mono- and oligophagous species).

The relationship between the composition of true bug assemblages and the explanatory variables (vegetation type of sampled plots i.e., steppe vs. marsh, vegetation structure, proportion of grasslands and landscape diversity) was analysed with canonical correspondence analyses (CCA) with Bray–Curtis dissimilarity. The effects of the explanatory variables were tested for significance using Monte Carlo procedure with 1000 permutations. For visualizing the groupings of the sampled plots according to the distribution of true bugs, we used non-metric multidimensional scaling (NMDS) with Bray–Curtis dissimilarity, because NMDS scatter plots are more reliable in revealing natural groupings of samples than CCA scatter plots.

The relationship between the explanatory variables and the species richness and log-transformed abundance data of true bug assemblages was analysed with generalized linear mixed models (GLMM). Poisson and Gaussian error terms were used for species richness and abundance data, respectively. The effect of vegetation type, vegetation structure, proportion of grasslands and landscape diversity were used as fixed effects and the effect of study sites and grasslands as random effects. Possible interacting effects between habitat and landscape characteristics were also examined in global models. Automated model selection was carried out, and the effects of different explanatory factors and variables were averaged across the best models with delta <2 (Grueber et al. 2011). All statistical analyses were carried out in an R Statistical Environment (R Development Core Team 2013) using Vegan (Oksanen et al. 2010), lme4 (Bates et al. 2013) and MuMIn (Bartoń 2013) packages.

Results

Vegetation characteristics

The first axis of the PCA performed on the assessed structural parameters of the vegetation explained 68% of the total variance. It was positively correlated with the vegetation coverage at a height of 10 cm ($r = 0.62$, $P < 0.001$) and of 40 cm ($r = 0.83$, $P < 0.001$) and with the vegetation height ($r = 0.81$, $P < 0.001$), suggesting that our measure of vegetation structure i.e., the first axis, represents a gradient from sites with relatively sparse and low vegetation (low values) to sites with dense and high vegetation (high values). Mann–Whitney tests indicated significantly more plant species in the salt steppe than in the salt marsh vegetation ($P = 0.002$; for the salt steppe vegetation: $N = 20$, mean rank = 13.08; for the salt marsh vegetation $N = 20$, mean rank = 7.42), but the vegetation structure did not differ significantly ($P = 0.08$; for salt steppe vegetation: $N = 20$, mean rank = 8.63; for salt marsh vegetation $N = 20$, mean rank = 11.88). Because of the strong relationship between vegetation type and plant species richness, plant species richness was omitted from further analyses.

Composition of true bug assemblages

Altogether 16,093 adult individuals of 159 true bug species were collected. In terms of feeding behaviour, we found 24 carnivorous, 76 generalist herbivorous and 58 specialist herbivorous species (870, 8474 and 6748 specimens, respectively) (Electronic Supplementary Material). The most frequent carnivores were *Orius* and *Nabis* species [mainly *Orius niger* (Wolff, 1811) and *Nabis pseudoferus* Remane, 1949], representing 85% of all collected carnivorous individuals. The majority of herbivores were either common grass-feeding species, such as *Acetropis carinata* (Herrich-Schaeffer, 1841) and *Stenodema calcarata* (Fallén, 1807), or species specialized to alkaline habitats, e.g., *Henestaris halophilus* (Burmeister, 1835), *Agramma atricapillum* (Spinola, 1837), *Conostethus hungaricus* (Wagner, 1941) and *Antheminia varicornis* (Jakovlev, 1837). Some phytophagous species such as *Trigonotylus caelestialium* (Kirkaldy, 1802) and *Lygus rugulipennis* Poppius, 1911, which are not exclusively grassland species, were also collected in high numbers.

The NMDS scatter plots (Fig. 2) showed that the herbivores and the total Heteroptera assemblages of the sampled sites grouped according to the corresponding type of vegetation. Carnivore assemblages did not follow this pattern. Although the constrained axes of the CCA had a significant joint effect on the species composition in each case (total assemblages: $\chi^2 = 1.309$ $F_{(4,35)} = 3.318$, $P < 0.001$, residual $\chi^2 = 3.451$; specialists: $\chi^2 = 1.404$, $F_{(4,35)} = 2.135$, $P < 0.001$ residual $\chi^2 = 5.753$; generalists: $\chi^2 = 0.975$, $F_{(4,35)} = 3.623$, $P < 0.001$ residual $\chi^2 = 2.354$; carnivores: $\chi^2 = 0.755$, $F_{(4,35)} = 2.361$, $P = 0.026$ residual $\chi^2 = 2.800$), the implemented permutation tests also showed that species composition patterns of true bugs depended significantly on the vegetation but there was no significant relationship with landscape variables (Table 1). Vegetation structure was the only explanatory variable with a significant effect on the species composition of total Heteroptera assemblages and on each feeding groups, separately; the composition of herbivore-groups and of the total Heteroptera assemblages were also significantly determined by the vegetation type (Table 1).

Species richness of true bug assemblages

The highest weights of the GLMM components of the average best models for the species richness of true bugs were less than 0.9 in each case (Electronic Supplementary Material), showing that model averaging, instead of finding one best model, was supported.

The model selection for the entire assemblages resulted in an average best model that included the effect of all explanatory variables and the interacting effect of vegetation type and landscape diversity, but the species richness of true bugs related significantly only to vegetation type and structure (Table 2). The number of true bug species was lower in salt marshes than in salt steppes (Fig. 3a), and related positively to the vegetation structure (Fig. 4a).

For specialist herbivores, the average best model included the effect of vegetation type, landscape diversity and the proportion of surrounding grasslands (Table 2), but only the effect of the vegetation type was significant, and more specialist herbivorous species were found in steppe than marsh plots (Fig. 3a).

The species richness of generalist herbivores was significantly related to the landscape diversity, vegetation type and vegetation structure; neither of the other variables were included in the average best model (Table 2). Similarly to the above, the species richness was higher in salt steppes (Fig. 3a), and had a positive relationship with the vegetation structure (Fig. 4b). Furthermore, we found a positive relationship between the species richness of generalist herbivores and landscape diversity (Fig. 5a).

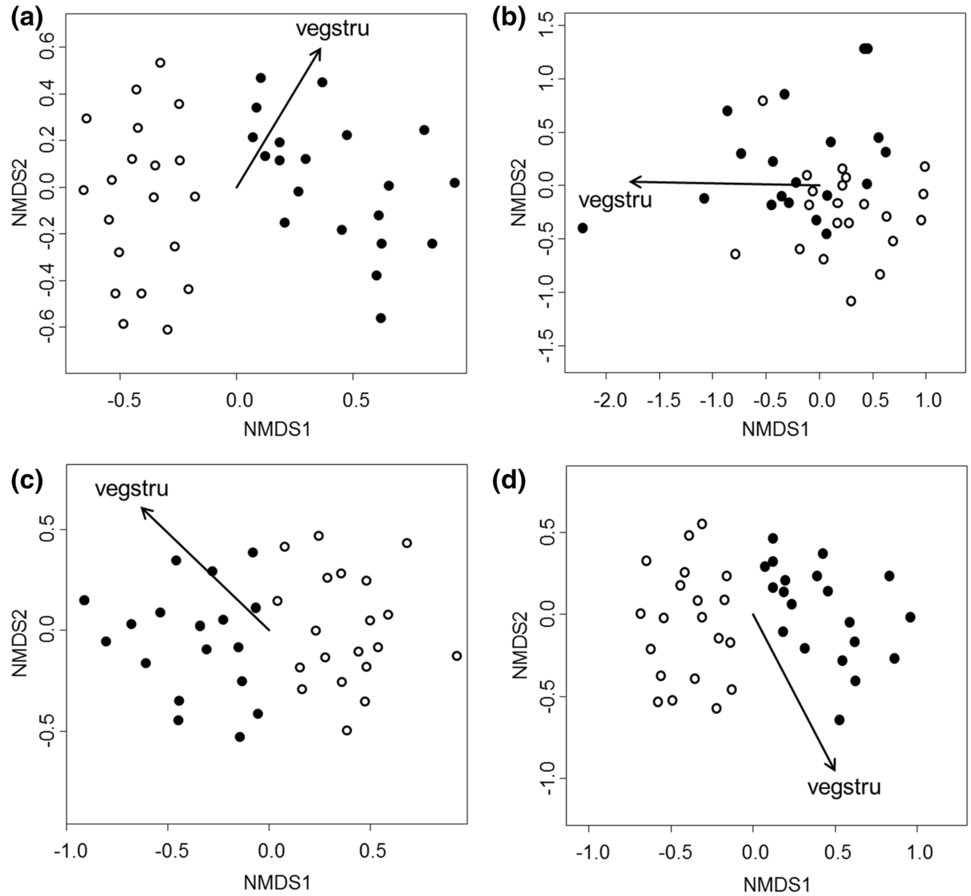

Fig. 2 Scatterplots of NMDS showing the grouping of sampled plots according to the data of all (**a**), carnivorous (**b**), generalist herbivorous (**c**) and specialist herbivorous (**d**) species. The values of stress factors are 0.20, 0.19, 0.21 and 0.18, respectively. Salt marsh and salt steppe plots are marked with *black* and *empty circles*, respectively. The *arrow* indicates the significant effect of vegetation structure on true bug assemblages delineated by the CCA and the implemented permutation tests (Table 1). It was fitted passively onto NMDS scatterplots with the help of the "envfit" function

Table 1 Effects and significance of the variables influencing the composition of true bug assemblages according to CCA and the implemented permutation tests

Heteroptera assemblages	Variables	χ^2	F-ratio (d.f. 1, 35)	P-value
All species	Vegetation type	0.7042	7.1422	**0.001**
	Vegetation structure	0.3174	3.2196	**0.003**
	Landscape diversity	0.1261	1.2789	0.356
	Proportion of grasslands	0.161	1.633	0.138
Generalist herbivores	Vegetation type	0.5669	8.427	**0.001**
	Vegetation structure	0.1928	2.8661	**0.022**
	Landscape diversity	0.1122	1.6682	0.256
	Proportion of grasslands	0.1031	1.5322	0.302
Specialist herbivores	Vegetation type	0.808	4.9151	**0.001**
	Vegetation structure	0.2128	1.2947	**0.025**
	Landscape diversity	0.0881	0.5358	0.398
	Proportion of grasslands	0.1602	0.9745	0.122
Carnivores	Vegetation type	0.1661	2.0765	0.08
	Vegetation structure	0.2708	3.3852	**0.022**
	Landscape diversity	0.1895	0.9697	0.516
	Proportion of grasslands	0.0968	1.2099	0.351

Significant values are marked in bold

Table 2 The effects of variables according to the average best models explaining the species richness of the different feeding groups and total assemblages of true bugs

Variables (relative variable impotance)	Estimated parameters (SE)	t-value	P-value
All true bugs			
Steppe vegetation (1)	0.393 (0.165)	2.371	**0.017**
Landscape diversity (1)	0.295 (0.228)	1.293	0.196
Vegetation structure (1)	0.0475 (0.017)	2.673	**0.007**
Steppe vegetation × landscape diversity (0.53)	0.424 (0.232)	1.824	0.068
Proportion of meadows (0.45)	−0.450 (0.274)	1.644	0.100
Specialist herbivores			
Steppe vegetation (1)	0.797 (0.141)	5.653	**<0.001**
Landscape diversity (0.65)	0.490 (0.248)	1.890	0.058
Proportion of meadows (0.67)	−1.00 (0.525)	1.914	0.056
Generalist herbivores			
Steppe vegetation (1)	0.490 (0.078)	6.212	**<0.001**
Landscape diversity (0.66)	0.052 (0.019)	2.157	**0.031**
Vegetation structure (1)	0.591 (0.299)	2.741	**0.006**
Carnivores			
Landscape diversity (0.71)	0.591 (0.299)	1.975	**0.048**
Vegetation structure (0.30)	0.057 (0.040)	1.433	0.151
Proportion of meadows (0.34)	−0.744 (0.649)	1.146	0.252

Significant values are marked in bold

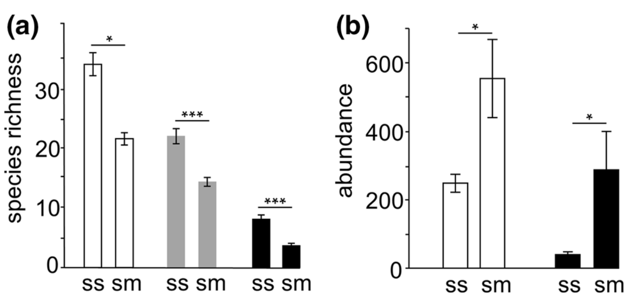

Fig. 3 The differences in the species richness (**a**) and abundance (**b**) of total true bug assemblages (*empty bars*), generalist herbivorous bugs (*grey bars*) and specialist ones (*black bars*) between salt steppes (ss) and salt marshes (sm) as delineated by GLMM (see Tables 2, 3). *Asterisks* mark the level of significance: P < 0.05 (*), 0.01 (**) and 0.001 (***)

The species richness of carnivores also showed a significant positive relationship with landscape diversity (Fig. 5c). Vegetation structure and the proportion of surrounding grasslands were also included in the average best model but their effect was not significant (Table 2).

Abundance of true bug assemblages

In general, only a few model components were included in the average best models explaining the abundance patterns, although the weights of the GLMM components were much lower than 0.9 in all cases (Electronic Supplementary Material).

For all the species collected, the average best model included the effect of vegetation type and landscape diversity, but only the former was significant (Table 3). Contrary to the species richness, the total abundance of true bugs was higher in salt marshes than in salt steppes (Fig. 3b).

Specialist herbivores showed a pattern similar to the total assemblages i.e., their abundance was significantly higher in salt marshes than in salt steppes (Fig. 3b); none of the other variables were included in the average best model (Table 3).

For generalist herbivores, the average best model included only the vegetation structure and landscape diversity, both having a significant effect (Table 3). The abundance of generalists related positively to both vegetation structure (Fig. 4c) and landscape diversity (Fig. 5b).

The average best model explaining the abundance of carnivorous true bugs included the effect of landscape diversity and the proportion of surrounding grasslands (Table 3), but only the positive effect of landscape diversity was significant (Fig. 5d).

Discussion

Different feeding groups of Heteroptera assemblages were studied in Pannonian salt grasslands in relation to habitat and landscape characteristics. Although based on only a one year study period, our results indicate significant relationships of true bugs with habitat and landscape characteristics. Previous studies of Heteroptera in semi-natural

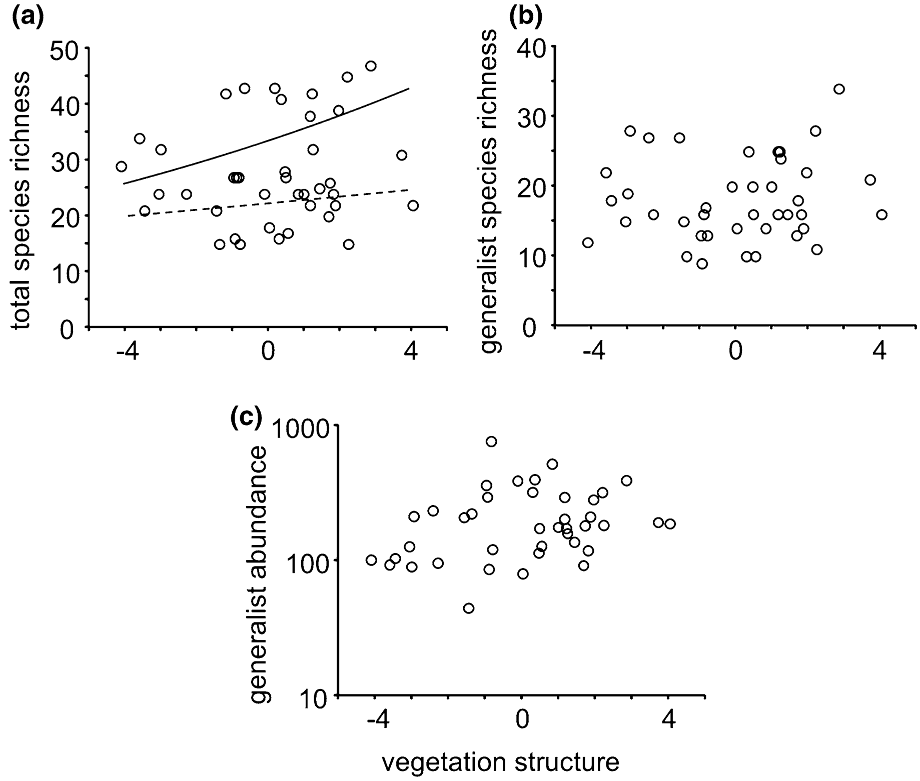

Fig. 4 The relationship between the vegetation structure and the species richness of total true bug assemblages (**a**), and the species richness (**b**) and abundance (**c**) of generalist herbivorous bugs as delineated by GLMM (see Tables 2, 3). In the case of the total assemblages (**a**), *solid* and *dashed curves* show the relationships in salt steppes and salt marshes, respectively. The values of the first axis of a previously performed PCA were used as a measure of vegetation structure, representing a gradient in vegetation height and density. Log-transformed abundance data was used in GLMM, so the number of generalist specimens is shown on a logarithmic scale

Table 3 The effects of variables according to the average best models explaining the abundance of the different feeding groups and total assemblages of true bugs

Variables (relative variable impotance)	Estimated parameters (SE)	t-value	P-value
All true bugs			
Steppe vegetation (0.75)	−0.246 (0.089)	2.738	**0.006**
Landscape diversity (0.27)	0.362 (0.204)	1.775	0.076
Specialist herbivores			
Steppe vegetation (0.51)	−0.440 (0.219)	2.011	**0.044**
Generalist herbivores			
Landscape diversity (1)	0.557 (0.130)	4.281	**<0.001**
Vegetation structure (0.42)	0.046 (0.014)	3.089	**0.002**
Carnivores			
Landscape diversity (0.71)	0.674 (0.312)	2.159	**0.031**
Proportion of meadows (0.34)	−0.814 (0.598)	1.361	0.173

Significant values are marked in bold

grasslands in Hungary (Torma et al. 2010; Harmat 1984) found that the composition of true bug assemblages was highly correlated between years.

Influencing factors and mechanisms at the habitat level

In line with the findings of a variety of other studies (Sanderson et al. 1995; Frank and Künzle 2006; Kőrösi et al. 2012; Torma et al. 2014), the ordinations and implemented permutation tests suggested that habitat characteristics have a prominent role in shaping true bug assemblages. NMDS diagrams showed distinct herbivorous assemblages corresponding to microtopography-driven differences in water regime and vegetation between steppe and marsh plots, but this pattern was less pronounced in carnivorous assemblages. Coastal salt marsh studies also emphasized the zonation of various arthropod assemblages e.g., carabids and spiders with elevation, and suggested that decreasing inundation enables more species to inhabit areas on higher elevations (Irmler et al. 2002; Finch et al. 2007). However, drier conditions negatively influenced the costal specialist species both in coastal (e.g., Finch et al. 2007) and inland salt marshes (e.g., Zulka et al. 1997). In true bugs, temporary water cover can also be favourable

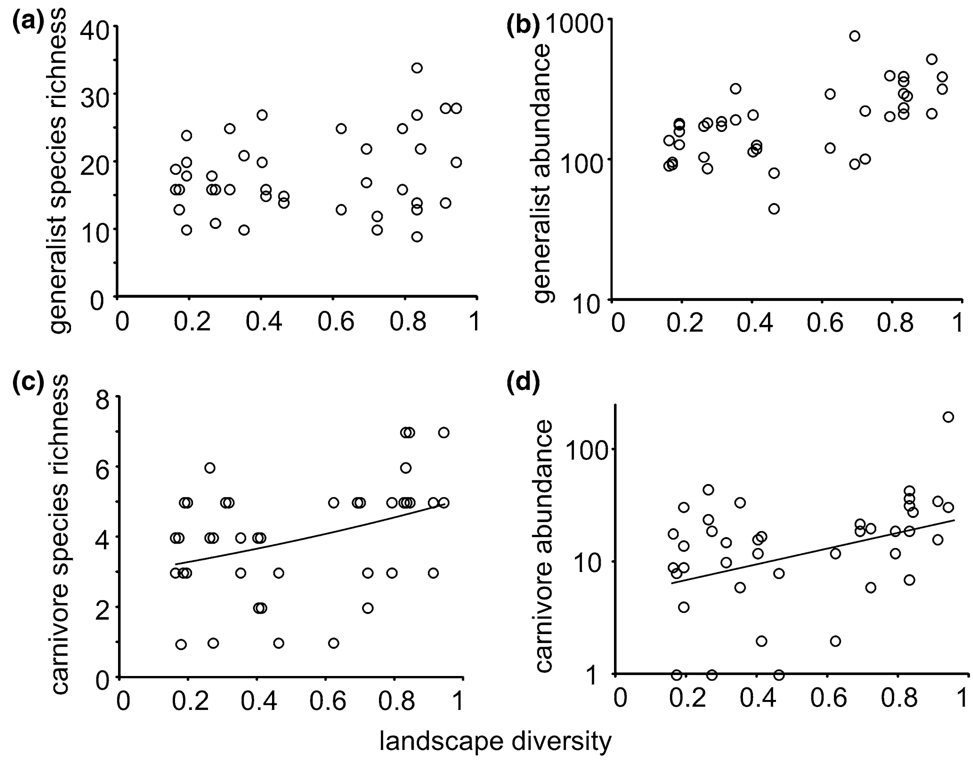

Fig. 5 The relationship between landscape diversity and the species richness (**a**) and abundance (**b**) of generalist herbivorous bugs and the species richness (**c**) and abundance (**d**) of carnivorous bugs as delineated by GLMM (see Tables 2, 3). Log-transformed abundance data was used in GLMM, so the number of specimens is shown on a logarithmic scale

for some semiaquatic species, like shore bugs (*Saldidae*) (Brown 1948). Ford et al. (2013) found that shore bugs were not present in ungrazed salt marshes with drier conditions than grazed salt marshes. Similarly, in the present study shore bugs were not found in dry steppe plots.

Although Sanderson et al. (1995) found that soil parameters influenced true bug assemblages mainly via the vegetation, some true bugs, particularly salt tolerant species presumably respond directly to salt content. However, we cannot assess the direct effect of salinity on true bugs, since we did not measure salt content. The majority of salt tolerant species, e.g., *A. varicornis, H. halophilus* and *C. hungaricus*, which are considered vulnerable, endangered or critically endangered species in neighbouring countries (Rabitsch 2012; Štepanovičová and Bianchi 2001), were associated with lower elevations.

The positive relationship found between the species richness of herbivores and the structure and diversity of vegetation are in accordance with numerous studies (Siemann 1998; Siemann et al. 1998; Prendergast et al. 1993; Brändle et al. 2001), supporting the "resource diversity hypothesis" and the "structural complexity hypothesis", which postulate that the plant species or the structural diversity of vegetation, respectively, can enhance the diversity of insects. However, the present study does not confirm the cascading effect of vegetation diversity up to carnivores contrary to other studies on Heteroptera (Brändle et al. 2001; Torma and Császár 2013). The majority of the collected carnivores (e.g., *Nabis* and *Orius* species) are highly mobile generalist predators with good colonizing abilities (Lattin 1989, 1999). They occur in various habitats from natural grasslands and forests to agricultural lands such as orchards, arable fields and vineyards (Fauvel 1999; Gilbert et al. 2015; Franin et al. 2016) and are shown to be affected by the local landscape rather than by the vegetation (Elliott et al. 2002). This is also corroborated by our results, since carnivore abundance and richness were significantly related only to landscape diversity (see below).

A more surprizing finding was the opposite patterns of abundance and species richness. In salt marshes a higher abundance and a lower species richness of true bugs were found compared with salt steppes. This finding contradicts some previous studies in salt grasslands, claiming a parallel change of species richness and abundance (e.g., Wimp et al. 2010; Klink et al. 2013). A possible explanation of this phenomenon can be a negative relationship between plant diversity and insect abundance, as found in numerous works mainly in agroecosystems (Root 1973; Risch 1981; Andow 1990). The 'Resource Concentration Hypothesis' (Root 1973) postulates that herbivores, particularly specialist species, are more likely to be found in pure stands of their host plants. This can explain why some specialist true bugs were abundant in salt marshes with species poor but dense vegetation. On the other hand, Haddad et al. (2001) suggested that as the diversity of the vegetation increases in a sampling site, it is more likely that C4 grasses have a higher share in the plant community, leading to a decrease in total insect abundance. Grasses that photosynthesize via the C4 pathway are known to be of poorer quality for herbivores because of the low nutrition and refractory nature of the lignocellulosic structure of these plants (Boutton et al. 1978). In coastal salt marshes characterized by a high biomass of the C4 *Spartina alterniflora*, it is suggested that invertebrate consumers have to utilize a wide variety of other resources besides cordgrass to balance their nutritional demands (Kreeger and Newell 2002). Pannonic salt marshes, however, are characterised by a high biomass of C3 graminoids, for instance *P. limosa, J. gerardi* and *A. stolonifera*, and thus still can support a high abundance of arthropods.

Influencing factors and mechanisms at the landscape level

In accordance with previous studies on grassland insects (Marini et al. 2008; Badenhausser and Cordeau 2012; Kőrösi et al. 2012), we found that the species richness of true bugs was not related positively to the proportion of semi-natural grasslands in the surroundings. In addition, Marini et al. (2008) and Torma and Bozsó (2016) found that the species richness of orthopterans decreased with the increase of grasslands in the surroundings, suggesting the importance of other habitats or edges for local insect diversity. For example, in mown grasslands, ecotonal habitats serve as suitable refugia, enabling recolonization after mowing (Guido and Gianelle 2001). The positive relationship between landscape diversity and species richness of true bugs suggested the importance of the surrounding habitats for local Heteroptera diversity, similarly to various arthropod groups (e.g., Krauss et al. 2003; Schindler et al. 2013; Querner et al. 2013; Slancarova et al. 2014). The majority of true bugs are highly mobile species with a high dispersal potential (Southwood 1960, 1962; Bröring and Wiegleb 2005). Organisms like these can also utilize complementary or supplementary resources in the surrounding habitats (Debinski 2006). However, similarly to Jonsen and Fahrig (1997) and Krauss et al. (2003), we suggest that generalist herbivores and carnivores are affected by landscape diversity more than specialists. Presumably, specialist true bugs benefit less from alternative resources in the surrounding habitats due to their strong dependence on host plants. Besides feeding on these host plants, bugs frequently rest, hide and overwinter in/under them and females usually lay their eggs directly onto them (Panizzi et al. 2002; Martínez et al. 2013).

Although we found a weak relationship of carnivorous bugs to landscape diversity, the majority of our results and that of some other studies (Brändle et al. 2001; Kőrösi et al. 2012), suggested that carnivorous true bugs seem to develop less consistent assemblages and show no or only a weak relationship with environmental conditions that are significant for herbivorous true bugs. Presumably, competitive relationships may be more important in limiting carnivore diversity (Brändle et al. 2001). However, this aspect is much understudied in true bugs.

Conclusion

Identifying the determinants and revealing the mechanisms of grassland arthropod diversity is an important issue of nature conservation. The majority of our findings coincide with generally detected patterns of arthropod assemblages in relation to vegetation and landscape characteristics, although these relationships were influenced by the feeding behaviour of the species. We highlight, however, the opposite patterns of species richness and abundance and the weak relationships between carnivorous assemblages and environmental variables.

The present study suggests that the main driver of arthropod diversity in Pannonic salt steppe and salt marsh mosaics is the heterogeneity of the vegetation, caused by microtopography-driven differences in water regime. Therefore, the main threats for arthropod diversity are those processes and activities that homogenize these grasslands. Such unfavourable factors include drying (a combination of climate change and active draining), overgrazing and the abandonment of traditional management.

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