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Effects of grazing, vegetation structure and landscape complexity on grassland leafhoppers (Hemiptera: Auchenorrhyncha) and true bugs (Hemiptera: Heteroptera) in Hungary

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Abstract. 1. Agricultural intensification is a major cause of biodiversity loss in European farmlands. Grasslands are particularly important habitats for the conservation of rich insect assemblages of Central and Eastern Europe. Although regular grazing or mowing of these grasslands is required to maintain diversity, there is no information about how such management and other factors influence Hemiptera assemblages.

2. We studied leafhopper and true bug assemblages in semi-natural grasslands in three regions of the Great Hungarian Plain. We investigated how local vegetation factors and landscape complexity influence assemblages and whether they interact with management effects.

3. Seven pairs of intensively (> 1 cow/ha) versus extensively (∼0.5 cow/ha) grazed pastures were sampled in each region by sweep-netting.

4. Sward height was the most important explanatory factor for leafhoppers (84 species, 27264 individuals), as it increased both species number and abundance, and influenced assemblage composition. The extent of grassland surrounding the sample sites negatively affected leafhoppers, whereas extensive grazing decreased abundance and influenced composition. True bug assemblages (140 species, 6656 individuals) were positively affected only by mean sward height, whereas regional differences determined the community composition of both taxa.

5. We conclude that vegetation structure is the primary factor shaping Hemiptera communities and that the various types of grasslands studied are all important habitats for the taxon. Therefore, cattle grazing in its current form is beneficial for the rich Hemiptera fauna in lowland pastures of Hungary. However, in some cases, local and landscape factors and great regional differences may confound the effects of grazing, and this must be considered in conservation planning in the future.

Key words. Abundance, cattle pastures, community composition, grazing intensity, landscape structure, semi-natural grassland, species richness, sward height.

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Introduction

Modern agriculture, characterised by highly intensive land-use, reduction, and fragmentation of natural and semi-natural habitats and increased use of chemicals, is considered as a major cause of biodiversity loss in European farmlands (de Heer *et al.*, 2005; Tscharntke *et al.*, 2005). High biodiversity, however, is still conserved in remnants of low-intensity farming systems; of these semi-natural grasslands are probably the most important due to their extent and unique species assemblages. These grasslands have largely disappeared from lowlands of Western Europe, but still cover considerable areas in Central and Eastern Europe (CEE). Therein, they harbour a diverse and unique biodiversity (e.g. Varga, 1997; Stoate *et al.*, 2009). Batáry *et al.* (2010), for example, found thirty times more species of bees in semi-natural Hungarian compared with improved Dutch grasslands.

The maintenance of semi-natural grasslands largely depends on regular management, which only includes grazing and/or mowing. The intensity of management, however, may greatly influence species richness and composition of arthropod assemblages. For example, Morris (1973) proved that increased grazing or cutting led to the disappearance of many true bug species, Brown *et al.* (1992) and Gibson *et al.* (1992) revealed that species richness and abundance of leafhoppers and true bugs decreased with increased grazing by sheep in calcicolous grasslands in England, whereas Dennis *et al.* (1998) found similar results in upland grasslands in Scotland. In Germany, Kruess and Tscharntke (2002) demonstrated that insect diversity (including leafhoppers and true bugs) is negatively affected by intensive cattle grazing, whereas Nickel and Hildebrandt (2003) showed that number and abundance of leafhopper species (mainly that of specialists) is higher in less-intensively grazed cattle pastures. However, we lack any information concerning lowland semi-natural grasslands in CEE.

Although grazing is a key factor in the management of semi-natural grasslands, its effect can be confounded by local, landscape-scale and regional factors, which may enhance or mitigate the effects of management (e.g. Tscharntke *et al.*, 2005; Hendrickx *et al.*, 2007; Schaffers *et al.*, 2008). Therefore, the understanding of management effects on semi-natural grasslands needs the evaluation of interactions at multiple spatial scales. Herein, we aimed to test the effects of grazing intensity by cattle on the species richness, composition and abundance of Hemiptera assemblages in semi-natural grasslands in three different regions of the Great Hungarian Plain. We attempted to reveal how management effects are confounded by local (vegetation structure) and landscape-scale (grassland cover) factors, and by regional differences.

We focused on Hemiptera because both leafhoppers (Auchenorrhyncha) and true bugs (Heteroptera) occur in high number of species and individuals in semi-natural grasslands, and they account for a significant proportion of the biomass and species richness of aboveground insects in temperate grasslands (Curry, 1994; Tscharntke & Greiler, 1995; Nickel, 2003). They play an important role in ecosystems both as herbivores and as prey for higher trophic levels (Waloff, 1980), show diverse life-history strategies and display variation in ecological characteristics (Dolling, 1991; Novotný, 1995; Nickel, 2003). Moreover, their responses to habitat management are immediate (Morris, 1979, 1981; Morris & Plant, 1983; Mortimer *et al.*, 1998), and their species richness is strongly correlated with total arthropod and plant species richness in cultivated landscapes (Denno, 1994; Duelli & Obrist, 1998). Despite being potentially an excellent group of indicators for biodiversity evaluation (Biedermann *et al.*, 2005), they are largely missing from research on farmland management (Stoate *et al.*, 2009). This is especially true for CEE farmlands, where most available studies have concentrated on more popular taxa. In Hungary, these include birds (Báldi *et al.*, 2005), bees (Sárospataki *et al.*, 2009), or plants (Kovács-Hostyánszki *et al.*, 2011). Therefore, this study is important as it may show if agricultural management (i.e. grazing intensity) has similar or different effects on Hemiptera than on more popular taxa. In earlier studies in the same study area, we found only minor effects of grazing intensity and landscape complexity on arthropod diversity, whereas local factors and regional differences proved to be highly influential and the studied taxa showed species-specific responses (Batáry *et al.*, 2007a,b; Batáry *et al.*, 2008). Therefore, in the present study, we hypothesised that (i) effects of management and landscape complexity would be of minor importance affecting Hemiptera assemblages, (ii) species with different life-history strategies will respond differently to the environmental variables, (iii) local factors (such as sward height) will significantly affect the number of species and individuals, and (iv) regional differences will be considerable.

Materials and methods

Study sites

Seven pairs of semi-natural grasslands with high and low grazing pressure were selected in the vicinity of each other in each of three distinct biogeographical regions of the Great Hungarian Plain. The first study region (Region 1) was situated in the Kiskunság National Park (Central Hungary) consisting of habitat patches with secondary Pannonic alkali steppe vegetation on solonchak soils. The vegetation of the second region (Region 2, also in the Kiskunság National Park, 30 km far from Region 1) was a mosaic of swamp meadows, calcareous purple moorgrass meadows, salt steppes and Pannonic sand steppe grasslands. The third region (Region 3) was located in the Heves Landscape Protection Area (Eastern Hungary, ~100 km far from the other two regions) and was dominated by dry and wet alkali grasslands and marshes on solonetz soil. For a detailed description and a map of the study sites, see Báldi *et al.* (2005). In all regions, grasslands were the most abundant land-cover type (> 60%), at least in the studied landscapes. None of the extensively grazed pastures and only 14% of the intensively grazed pastures were fenced. All sites had been grazed by cattle for at least 5 years from early spring to late autumn. Cattle density was about 0.5 cows/ha on extensive, and 1–1.2 cow/ha on intensive fields. The former corresponds with the density set by the Hungarian agri-environment scheme, and the latter corresponds to the usual grazing density values in the region. No fertiliser or herbicides were used on any of the fields.

Sampling method

On each of the 42 pastures, two parallel 95 m long transects were established, one at the field edge and the other one 50 m towards the centre of the grassland. The landscape structure of all pairs of extensively and intensively grazed fields was as similar as possible.

Leafhoppers and true bugs were sampled by sweep-netting along the transects in 2003. On each transect, two sweep-net samplings were carried out consisting of 3 × 20 sweeps with a heavy duty sweep net (38 cm diameter, 7215HS, BioQuip) in May and June. The individuals captured were preserved in alcohol and identified to species in the laboratory (leafhoppers were identified only from June samples because of the large number of specimens).

Data analysis

Data of edge and interior transects of the May and June samples were pooled for each sampling site, therefore we had 42 samples. Species richness and log-transformed abundance were analysed by generalised linear mixed models with the following set of explanatory variables: (i) percentage cover of grassland within a radius of 500 m around the sample sites, which in former studies of the same study area (Batáry *et al*., 2007a,b) proved to be a landscape parameter representing the landscape complexity well (had sufficiently high variance, and was similar in the three study regions; see also Purtauf *et al*., 2005), (ii) management (extensive or intensive grazing), (iii) mean sward height (measured in ten 5 × 10 m plots along each transect): used as a local parameter because it is thought to be an important structural index of the vegetation, which strongly affects the occurence of herbivores, such as of leafhoppers and true bugs (e.g. Morris, 1973; Gibson *et al*., 1992; Kruess & Tscharntke, 2002; Littlewood *et al*., 2006; Zurbrügg & Frank, 2006). A manual backward stepwise selection of models was used based on *P*-values and likelihood ratio tests. The full models included the interaction terms between management and sward height and between management and grassland cover. According to the sampling design, hierarchical random effects were applied (7 pairs nested in each of 3 regions). Instead of being a random factor, region could have been used as a fixed effect to test for its significance, but the study regions were randomly selected from a wider set of regions in the Great Hungarian Plain, and our aim was to reveal something about the variance among the regions in general (see Faraway, 2006). When diagnostic plots suggested the violation of model assumptions, a Poisson error distribution was used. The packages 'nlme' (Pinheiro *et al*., 2011) and 'MASS' (Venables & Ripley, 2002) of the R 2.9.0 statistical software (R Development Core Team 2009) were applied.

Leafhopper species were categorised as generalists or specialists according to their habitat and host plant preferences (Schiemenz *et al*., 1996; Nickel & Hildebrandt, 2003; expert knowledge (AO)) and data for the two groups were analysed separately. For true bugs, we applied three dichotomous categorisations: phytophagous vs. carnivorous species, plant-dwelling vs. ground-dwelling species and species hibernating as larvae vs. adults (expert knowledge (DR)). For each group, the same procedure of model selection was performed.

Finally, a conditional redundancy analysis (RDA) was carried out for the two taxa to reveal how species composition was influenced by management, local and landscape variables and region. Two types of models were tested. Firstly, management, mean sward height and percentage cover of grassland were the constrained variables and region was the conditional variable. In the second type, we tested the effects of region as a constrained variable and all other variables were conditional to filter out their effects. Significance of each term was separately tested by permutation tests (using 1000 permutations). Hellinger transformation was performed for each species matrix allowing the use of ordination methods such as RDA, which are Euclidean-based, with community composition data containing many zeros (Legendre & Gallagher, 2001). The analyses were performed using the 'vegan' package (version 1.17 Oksanen *et al*., 2010) of R 2.9.0 statistical software.

Results

Leafhoppers

A total of 27264 specimens, comprising 84 species, were identified (Appendix S1 in Supporting Information). Thirty species were represented with a very low abundance (< 10 individuals), whereas > 1000 individuals were collected for each of eight species. Twenty species were categorised as generalists and 64 were categorised as specialists. The species recorded in this study represent a significant part of the Hungarian leafhopper fauna (~16% (Györffy *et al*., 2009)).

Species richness was negatively influenced by percentage cover of grassland within 500 m, and increased sward height had a positive effect. Regarding the random effects, 52% of the total variance was explained by the region, whereas the effect of pairs was negligible. The number of generalist species was positively affected by increased sward height only, whereas species richness of specialist leafhoppers responded negatively to grassland cover (Table 1). Figure 1 shows a tendency that (mainly specialist) leafhopper species benefited from extensive grazing in Regions 1 and 2, but in Region 3 species richness was lower in the extensive pastures. Extensive grazing also had contrasting effects on generalist species in the different regions: in Region 2 it increased and in Region 3 it decreased the number of species, whereas in Region 1 it seemed to have no effect (Fig. 1b). Herein, the region random effect accounted for 12% of the total variance. In specialist species, the random effects were negligible.

Leafhoppers abundance was negatively affected by extensive grazing and by percentage cover of grassland within 500 m, whereas increased sward height had a positive effect (Table 2). The interaction between management and grassland cover was also significant, indicating that grassland cover had a negative effect in the intensively grazed pastures only (Fig. 2b). Region explained 46% of the total variance, which is due to extensive grazing having a negative effect on abundance in Region 1 only, whereas it had no effect in Regions 2 and 3 (Fig. 3a). For generalist species, extensive grazing had a significant negative effect on abundance. We

Table 1. Results of the best models for species richness. Only groups, where significant variables were found, are shown.

	Parameters of the best model			Variances for the random effects	
Taxon	Explanatory variables	Parameter estimation (±SE)	*P*	Region	Pair
Leafhoppers	Grassland cover	−0.122 (0.053)	0.029	32 (52%)	0
	Mean sward height	0.264 (0.113)	0.025		
Generalists	Mean sward height	0.025 (0.001)	0.014	0.16 (12%)	0
Specialists	Grassland cover	−0.009 (0.002)	< 0.001	0	0
True bugs	Mean sward height	0.657 (0.161)	< 0.001	15.35 (18%)	13.76 (16%)
Phytophagous	Mean sward height	0.623 (0.141)	< 0.001	10.36 (16%)	10.25 (16%)
Plant-dwelling	Mean sward height	0.642 (0.137)	< 0.001	12.26 (19%)	12.47 (19%)
Adult hibernates	Mean sward height	0.389 (0.109)	< 0.01	0	0
Larva hibernates	Mean sward height	0.274 (0.063)	< 0.001	7.96 (37%)	5.99 (28%)

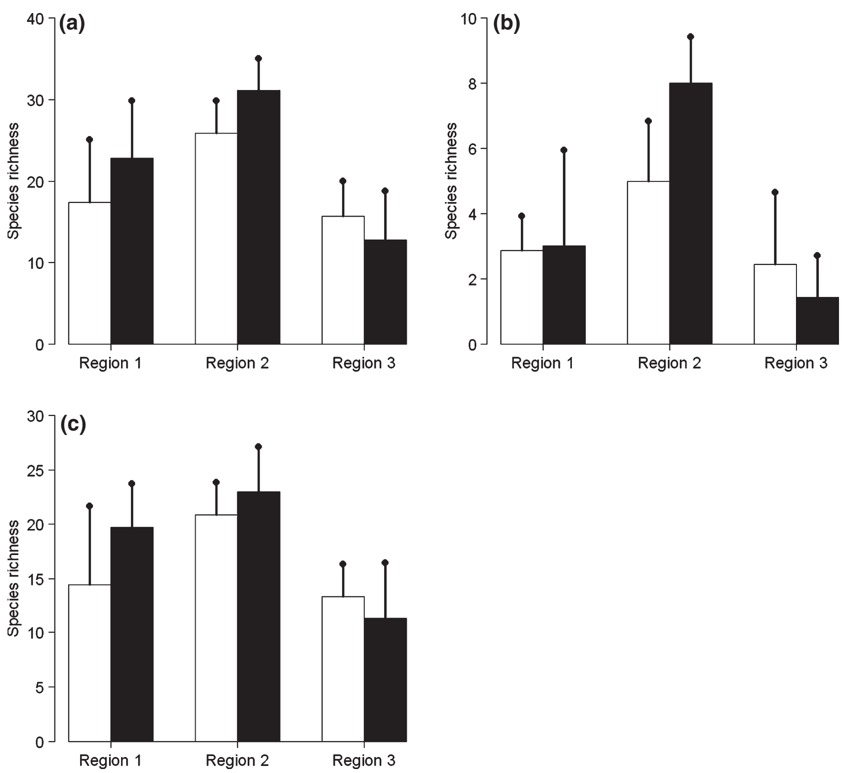

Fig. 1. Effects of grazing intensity on mean species richness of leafhoppers in the different study regions. (a) all species, (b) generalist species, (c) specialist species. Open bars: intensive grazing; solid bars: extensive grazing. Whiskers indicate SD.

found no significant explanatory variables in the model for the abundance of specialist species. Extensive grazing slightly decreased the abundance of specialist species in Region 1, but it had no effect in Regions 2 and 3 (Fig. 3c).

The first RDA model showed that management was a significant factor affecting leafhopper assemblages ($F = 1.79$, $P = 0.021$), whereas mean sward height had a near significant effect ($F = 1.45$, $P = 0.089$). However, these constrained variables explained only 6.1% of the total variance, whereas region as a conditional variable explained 24%. Both grazing intensity and mean sward height were correlated with both axes. In the second type of RDA model, region was a highly significant variable ($F = 4.99$, $P < 0.001$) explaining 18.8% of total variance, whereas the conditional variables explained 13.4% (Appendix S2, S5 in Supporting Information).

True bugs

A total of 6656 specimens of 140 species were collected (Appendix S3 in Supporting Information). Most of the species (89) were represented by < 10 individuals and > 100 specimens were collected for each of 21 species, all of which were phytophagous. For 8 of the 10 zoophagous species, < 10 individuals were sampled. Thirty-seven and 103 species were categorised as ground-dwelling and plant-dwelling, respectively. Ninety-four species hibernate as an adult and 46 hibernate in an immature stage. The species recorded represent ~17% of the Hungarian true bug fauna (Kondorosy, 1999).

Species richness was positively influenced by mean sward height only. Region and pair as random factors explained 18% and 16% of the total variance, respectively. Figure 4a indicates

Table 2. Results of the best models for abundance (log-transformed). Only groups, where significant variables were found, are shown.

	Parameters of the best model			Variances for the random effects	
Taxon	Explanatory variables	Parameter estimation (±SE)	*P*	Region	Pair
Leafhoppers	Grassland cover	−0.024 (0.012)	0.055	0.42 (46%)	0
	Management	−2.906 (1.004)	0.0065		
	Management × grassland cover	0.036 (0.015)	0.018		
	Mean sward height	0.038 (0.017)	0.033		
Generalists	Management	−0.770 (0.299)	0.018	2.42 (56%)	0.97 (22%)
True bugs	Mean sward height	0.052 (0.018)	0.01	0	0.69 (51%)
Phytophagous	Grassland cover	−0.0196 (0.011)	0.079	0	0.599 (47%)
	Mean sward height	0.054 (0.019)	< 0.01		
Plant-dwelling	Grassland cover	−0.0196 (0.011)	0.081	0	0.51 (40%)
	Mean sward height	0.053 (0.019)	0.013		
Adult hibernates	Grassland cover	−0.022 (0.011)	0.059	0	0.11 (8.5%)
	Mean sward height	0.054 (0.022)	0.023		
Larva hibernates	Mean sward height	0.066 (0.023)	0.01	0.4 (20%)	0.52 (26%)

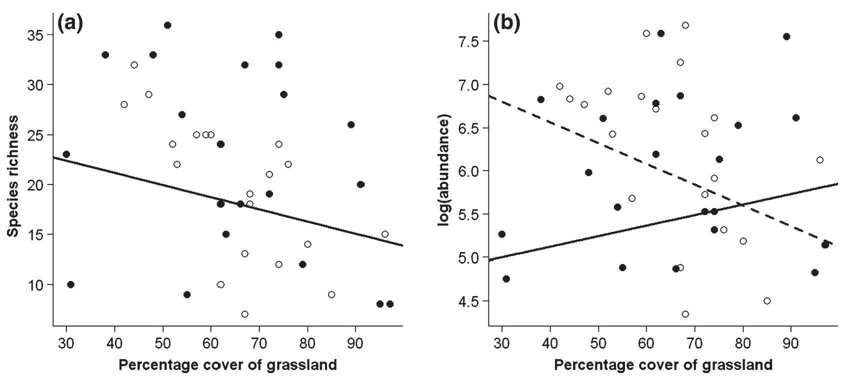

Fig. 2. Relationship between grassland cover and species richness (a) and abundance (b) of leafhoppers. Open circles: intensively grazed pastures; solid circles: extensively grazed pastures. (a) solid line represents the regression line from the GLMM (Table 1.) (b) dashed line represents the regression line for intensive pastures, solid line for the extensive pastures from the GLMM (Table 2).

that species richness was not significantly higher in extensive pastures than in intensive pastures in any region. As the majority of the species was phytophagous (130), their species richness was also influenced by mean sward height only. Carnivorous species were represented by very low numbers of species (10) and individuals (160), and therefore we analysed their presence/absence by a binomial model, but none of the explanatory variables was significant. The number of plant-dwelling species was also affected positively by mean sward height, whereas no significant predictor was found for ground-dwelling species. Species richness of true bugs hibernating as either adults or immatures was positively affected by mean sward height (Table 1).

Mean sward height had a positive effect on true bug abundance as well, but in this model the variance between pairs accounted for 51% of the total variance, whereas the effect of region was negligible. Mean abundance was higher in extensively grazed pastures in all three regions, but the difference was not significant (Table 2, Fig. 4b). Abundance of phytophagous bugs was positively affected by mean sward height, whereas the percentage cover of grassland within 500 m had a near significant negative effect. In this model regional differences were negligible. The same results were found for plant-dwelling species and for species hibernating as adults. For species hibernating in immature stages, sward height was the only significant predictor. In this latter case, the region explained a higher proportion of the total variance than in other groups of true bugs.

In the first RDA analysis of Heteroptera, mean sward height was the only significant variable ($F = 2.76, P < 0.001$) explaining 6% of the total variance. The conditional term explained 14%, whereas 80% of the total variance remained unexplained by the model. Sward height was correlated with RDA1 axis, but it rarely separated the bug species. In the second model, region as a constrained term was highly significant ($F = 2.87$, $P < 0.001$) and explained 12% of total variance, whereas the

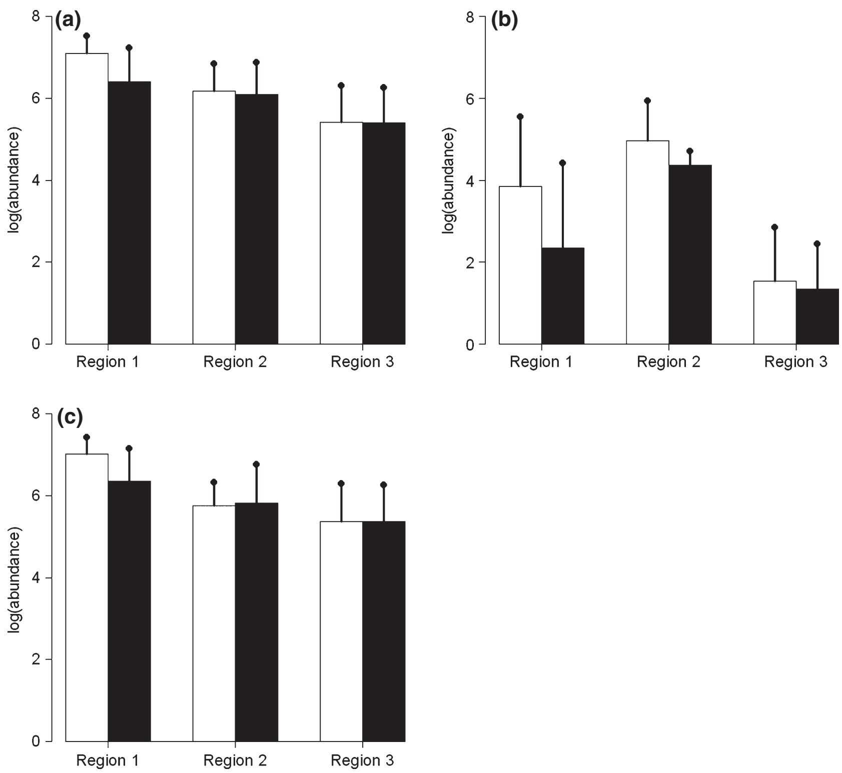

Fig. 3. Effects of grazing intensity on mean abundance of leafhoppers in the different study regions. (a) all species, (b) generalist species, and (c) specialist species. Open bars: intensive grazing; solid bars: extensive grazing. Whiskers indicate SD.

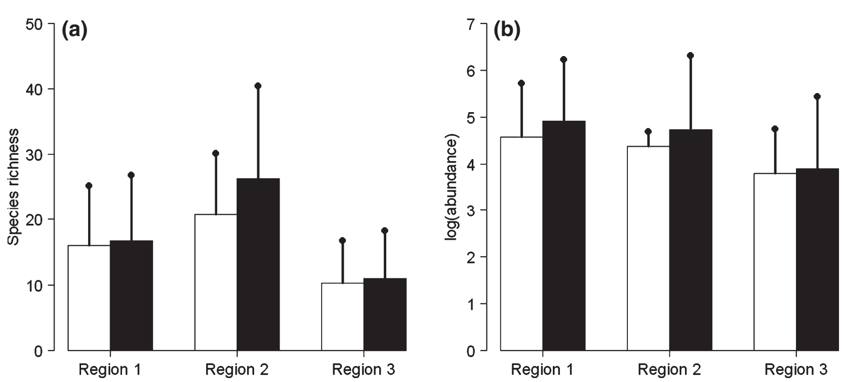

Fig. 4. Effects of grazing intensity on mean species richness (a) and mean abundance (b) of true bugs in the different study regions. Open bars: intensive grazing; solid bars: extensive grazing. Whiskers indicate SD.

conditional terms explained 11% (Appendix S4, S5 in Supporting Information).

Discussion

In this study, we revealed that both intensively and extensively grazed semi-natural lowland pastures in the Great Hungarian Plain harbour a rich leafhopper and true bug fauna. This diversity is partly a consequence of large differences between regions, and partly due to local and landscape factors. According to our expectations, we found that grazing intensity had only a minor effect on leafhopper and true bug assemblages. Local and landscape scale factors (vegetation structure and grassland cover, respectively) affected the two taxa similarly, but the contribution of the random effects (region and pair) to the total variance was different.

Management was found to significantly affect the abundance and species composition of leafhoppers, whereas it had no effect on true bugs. The abundance of leafhoppers was significantly lower in extensively grazed pastures, especially for generalist species, though in Regions 1 and 2 only (Fig. 3b). Although mean sward height was also reduced by intensive grazing in these two regions, in Region 3 there was no difference in the sward height between extensively and intensively grazed pastures (Fig. 5). Therefore, we suppose that the effects of management, sward height and region were confounded in this case. Brown *et al.* (1992) found that several species (mainly generalists) increased in abundance with decreasing vegetation height, and in our study the lower abundance of generalist species in extensively

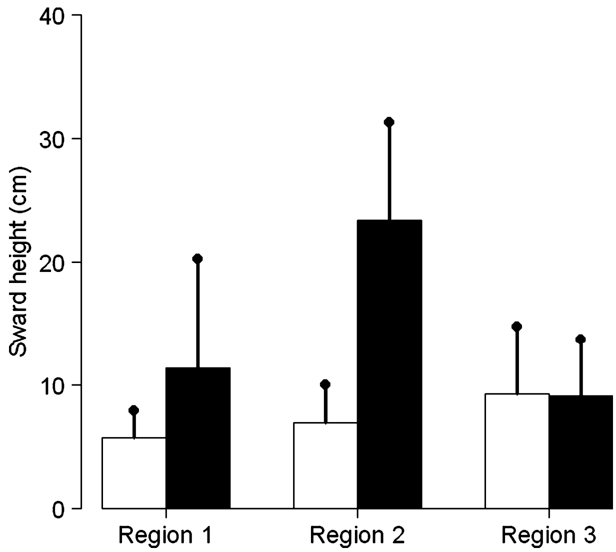

Fig. 5. Effects of grazing intensity on mean sward height in the different study regions. Open bars: intensive grazing; solid bars: extensive grazing. Whiskers indicate SD.

grazed pastures may simply be due to the taller vegetation. Species composition of leafhoppers was significantly affected by management, but it could explain only a small proportion of the total variance and hardly separated the species in the RDA analysis. Several studies revealed that extensive grazing (or cessation of grazing) is beneficial for the diversity and abundance of both leafhoppers and true bugs, whereas highly intensive grazing may detrimentally reduce them (Morris, 1973, 1979, 1981; Gibson *et al*., 1992; Curry, 1994; Dennis *et al*., 1998; Kruess & Tscharntke, 2002; Fisher Barham & Stewart, 2005). Nevertheless, apart from the above mentioned and probably confounded effects, we found no influence of management on true bug assemblages. Our explanation for this result is twofold. First, the difference in grazing pressure in extensive vs. intensive pastures was relatively small in our study compared with some Western European studies (e.g. Kruess & Tscharntke, 2002; Nickel & Hildebrandt, 2003). Our earlier studies on the same study sites also failed to find a strong management effect in other groups of arthropods (Batáry *et al*., 2007a,b; Sárospataki *et al*., 2009). The present results support the hypothesis of Tscharntke *et al.* (2005) that in a landscape where biodiversity is high (in this sense in all of our regions), the effects of management intensity are low. Secondly, the high variance between regions (especially for leafhoppers) may have hindered the finding of significant management effects. For example, for leafhoppers, there was a clear tendency towards higher species richness in extensively grazed pastures in Regions 1 and 2, but the opposite was found in Region 3 (Fig. 1). These outcomes show that even the intensively grazed pastures can harbour a relatively diverse Hemiptera fauna in Hungary, but also highlight that the responses of some taxa to management may depend on regional factors (Báldi *et al*., 2005; Nickel & Achtziger, 2005; Batáry *et al*., 2007b).

Vegetation structure (mean sward height) proved to be the most important factor affecting Hemiptera assemblages (both leafhoppers and true bugs), positively influencing species richness and abundance, and was an important factor affecting species composition. Mean sward height can be used as a simple proxy for the architectural complexity of the vegetation in semi-natural grasslands. There are numerous examples in the literature that both diversity and abundance of leafhoppers and true bugs benefit from the greater structural complexity of vegetation (Morris, 1973; Southwood *et al*., 1979; Brown *et al*., 1992; Gibson *et al*., 1992; Di Giulio *et al*., 2001; Kruess & Tscharntke, 2002; Zurbrügg & Frank, 2006; Woodcock *et al*., 2007). This is because highly structured vegetation can provide a larger potential surface for colonisation and more resources, such as feeding, oviposition, resting and overwintering sites (Price *et al*., 1980; Lawton, 1983; Dennis *et al*., 2003). Moreover, many herbivorous species need particular plant structures for feeding or shelter (Andrzejewska, 1965; Wetton & Gibson, 1982).

Percentage cover of grassland within 500 m around the sampling sites affected the species richness and abundance of leafhoppers negatively (Fig. 2), although the effect was pronounced only in the intensively grazed pastures, and it had a near significant negative effect on true bug abundance. Grassland cover is inversely related to landscape heterogeneity, and thus our results indicate that greater landscape diversity may promote Hemiptera assemblages, especially the species richness of specialist, the abundance of generalist leafhopper species, and marginally the abundance of true bugs. These findings are partly consistent with the results of Jonsen and Fahrig (1997), who revealed that richness and abundance of generalist species increased with increasing landscape diversity, whereas specialists were less affected (see also Batáry *et al*., 2007a). The decreasing species richness of specialist leafhoppers with increasing grassland cover in our case may be because only $\sim$75% of the specialist species were typical grassland specialists. Elsewhere, the positive effect of landscape heterogeneity on the whole species richness of local communities has been recognised in true bugs (Di Giulio *et al*., 2001; Hendrickx *et al*., 2007), in several other groups of arthropods (e.g. Duelli & Obrist, 2003; Schmidt *et al*., 2005; Báldi, 2008; Marini *et al*., 2008) and in general for farmland biodiversity (Benton *et al*., 2003).

Regional differences were great in species richness, abundance and composition of leafhoppers, and in composition of true bug assemblages, which is in line with our expectations and earlier results (Batáry *et al*., 2007b). As Morris (2000) points out, management may interact with several local environmental factors leading to leafhopper assemblages often showing high site-specificity. Clough *et al*. (2005) revealed that large-scale features, interacting with local factors, can confound the effects of management practices on biodiversity at a local scale. Furthermore, Sanderson *et al*. (1995) found some evidence that, besides the species composition of vegetation, soil conditions can significantly affect the species composition of leafhopper assemblages. As both vegetation and soil types varied across our study regions, these may account for the differences in species composition of leafhopper assemblages observed. Finally, we suppose that the different plant species composition in our study regions (Batáry *et al*., 2010) may have significantly affected the species composition of leafhoppers (e.g. Denno, 1994; Tscharntke & Greiler, 1995). In contrast to leafhoppers, high variance occurred among the pairs of extensively and intensively grazed pastures for true bugs. Regional differences were negligible for true bug abundance, whereas for species richness, the two random factors explained similar proportions of total variance. This may be because true bug assemblages were most strongly affected by mean sward height, which is a local factor and varies at the smallest spatial scale among the studied explanatory variables.

We conclude that cattle-grazing in its current form can maintain a relatively high diversity of Hemiptera in semi-natural grasslands of the Great Hungarian Plain. However, sheep-breeding and mowing are also widespread in these regions. Therefore, some comparative studies on the effects of sheep-grazing vs. cattle-grazing vs. mowing on grassland arthropods would be necessary, especially in the light of equivocal results found in other parts of Europe: Dennis *et al.* (2008) revealed that cattle might contribute to the maintenance of higher structural diversity and arthropod abundance in grazed ecosystems due to their lack of selectivity compared with sheep, whereas García *et al.* (2010) found species-specific responses to the flock type of grazers in heathlands. Our present study highlights that insect taxa may respond differently to management intensity and local and landscape factors, and that regional characteristics can influence their responses. This conclusion must be taken into consideration when developing conservation-oriented agri-environmental schemes and a community-based approach to insect conservation (Stewart & New, 2007).

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi:10.1111/j.1752-4598.2011.00153.x

Appendix S1. Species list with total abundances of specialist and generalist leafhoppers. The nomenclature follows Holzinger *et al.* (2003) and Biedermann *et al.* (2005).

Appendix S2. RDA plots for leafhoppers. Grey squares indicate species. Abbreviated names of the most separated species are presented.

Appendix S3. Categorised species list of true bugs with total abundances. The nomenclature follows the catalogue of Aukema & Rieger (1996, 1999, 2001, 2006).

Appendix S4. RDA plots for true bugs. Grey squares indicate species. Abbreviated names of the most separated species are presented.

Appendix S5. Variation partitioning in partial RDA models. In models'1', region was the conditional term, in models'2' it was the only constrained term (see text for more details).

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