Effects of habitat and landscape features on grassland Orthoptera on floodplains in the lower reaches of the Tisza River Basin

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Abstract. The Tisza River Basin is an important area as it is a green corridor in which there are highly endangered habitats and a high level of biodiversity. The patterns in the species richness of invertebrates and the environmental conditions affecting these patterns are poorly studied in the grassy habitats in the lower reaches of the Tisza River Basin. The present study focuses on the effects of flooding, habitat and landscape features on the species richness of orthopterans at 24 grassland sites in two different landscapes. The relations between the explanatory variables and the pattern of diversity of orthopterans with different life-history traits were studied, using ordination and Generalized Linear Mixed Models. Although the influential factors for the different trait groups differed, we suggest that landscape features are the most important in shaping orthopteran assemblages, whereas habitat characteristics and flooding have comparatively little effect. Habitat characteristics affected only the non-xerophilous and Ensifera species and only the species richness of non-xerophilous orthopterans in flooded and non-flooded sites differed. We emphasize that even in countries where there are still considerable areas of high value natural grasslands, such as Hungary, non-protected meadows, linear grassy habitats (dikes, ditch banks, road verges, etc.) need more attention and should be given higher priority in the conservation of invertebrates.

INTRODUCTION

In their natural state, riverine landscapes are characterized by mosaics of various habitat patches. Due to their high heterogeneity and connectivity (Naiman et al., 2005), they can support a diverse flora and fauna (Gregory et al., 1991; Zwick, 1992; Ward et al., 1999). However, many European rivers are restricted to narrow riverbeds bordered by dikes and the majority of floodplain habitats have been transformed into agricultural land (Tockner et al., 2009), causing a severe decline in biodiversity (Godreau et al., 1999).

The River Tisza is the largest tributary of the Danube and its catchment includes most of the Carpathian Mountains covering approximately 157,000 km² (Sommerwerk et al., 2009). The regulation of the Tisza in the 19th century caused profound changes; a considerable amount of the former floodplain has since never been flooded. However, on this non-flooded part of the former floodplain (so-called "historical floodplain") there were several high value habitats, i.e. pastures, woody pastures and hay-meadows, in this extensively used mosaic landscape until the 1950s (Deák, 2007; Sendzimir et al., 2008). During the socialist era, intensification of agriculture resulted in a decrease in the area of these grasslands (Deák, 2007). Nowadays,

the remaining grasslands are surrounded by a highly modified landscape consisting of arable fields and forest plantations, often of non-native trees. Despite these changes, the Tisza River Basin (TRB) still includes highly endangered habitats, which are important ecological areas and green corridors (L. Gallé et al., 1995; Rádai, 1995) with a high level of biodiversity (Sommerwerk et al., 2009). The invertebrate fauna in the TRB is well-documented (see e.g. L. Gallé, 2005, 2008), but there are only a few studies on some taxa, e.g. spiders (Araneae) (R. Gallé et al., 2011) and true bugs (Heteroptera) (Torma & Császár, 2013), which indicate the environmental conditions that are likely to influence the species richness of grassland arthropods in this human-modified riverine landscape. To the best of our knowledge, patterns in the diversity of assemblages of Orthoptera in relation to their life-history traits and environmental conditions have not been studied in this region.

Orthopteran assemblages are known to depend on different and often interrelated environmental factors. Vegetation has a great influence on many invertebrates, including orthopterans (Batáry et al., 2007; Poniatowski & Fartmann 2008, 2010). Vegetation is related to soil and microclimate conditions, which are also important for orthopterans (Willott & Hassall, 1998; Gardiner & Dover, 2008). In ripar-

ian landscapes, flooding and land use pressure have a pronounced influence in shaping assemblages of Orthoptera (Dziock et al., 2011). The majority of species of Orthoptera are associated with open grassy habitats; therefore, for these species the amount of grassland in a landscape is important (Marini et al., 2008; Badenhausser & Cordeau, 2012). The "habitat amount hypothesis" (Fahrig, 2013) postulates that patch size and patch isolation effects are both due mainly to the sample area effect, thus patch size and isolation can be replaced with a single variable, the amount of habitat.

In order to determine the main factors affecting orthopterans, we tested the effects of (1) habitat characteristics (soil moisture and vegetation structure and diversity), (2) landscape features (amount of grassland habitat, landscape structure) and (3) flooding (flooded vs. non-flooded sites) on the species composition and richness of assemblages of Orthoptera. The effect of landscape composition on assemblages of Orthoptera is often scale-dependent (e.g. Marini et al., 2009a), thus we also aimed to determine the appropriate spatial scale for assessing the amount of grassland habitat. As species with different life history traits often need different environmental conditions, the effects on species richness of various life-history traits were tested separately.

MATERIAL AND METHODS

Study sites and sampling design

Assemblages of Orthoptera were studied at 24 sites in two different landscapes. The landscapes were located on the same side of the river in Csongrád County, Hungary, and were selected based on intensity of land use and landscape structure. The heterogeneous landscape (HET) was situated near the town of Szeged (approx. 46°17′34″N, E 20°12′45″E) and it consisted of a mosaic of various habitats. The percentage of the area covered by intensively managed arable fields was high (58.3 ± 3.4%, mean ± SE within a radius of 500 m around the sites). Small patches of meadows with trees and abandoned fields were embedded in the matrix of arable fields. Numerous trees and bushes also occurred along road verges, but continuous forest occurred only near the river. The percentage of the area covered by forest habitats, including single trees and bushes, was 18.6 ± 5.6%.

The homogeneous landscape (HOM) was situated approximately 30 km north of Szeged (approx.: 46°27′27″N, 20°9′26″E). The intensity of agricultural activities in this area was moderate (the percentage covered by arable fields was 16.1 ± 1.9%) and the percentage of the area covered with semi-natural grasslands and forests was high. The percentage covered by forest was higher (30.0 ± 3.3%) than in HET due to the oak and poplar forests that bordered and partly divided the relatively continuous grassland area into two parts.

Among the various grassy habitats on the historical floodplain of the Tisza, only those that occurred in both landscapes were selected for this study i.e., sand steppe and alkaline meadows in the non-flooded part of the historical floodplain, dike-slope meadows (strip-like meadows on the slopes of the dikes) and floodplain meadows. Each of these habitats occurred at the three sites sampled, giving a total of 24 sites in the two landscapes. The distance between sites was approximately 500 m, except in the case of floodplain meadows. Orthopterans were collected by sweep netting, which is a widely used technique for sampling these insects (e.g. Bauer & Kenyeres, 2007; Torma et al., 2014). At each site,

sweep netting was carried out along three, 50 m long, fixed transects in 2009. To avoid periods of flooding, sweep netting was carried out in summer. The first samples (30 May–2 June) were collected before mowing and the second samples (22–24 July) when the vegetation started to regrow after mowing. For the data analyses, the sweep netting samples were pooled separately for transects and periods, resulting in a total of 24 statistical samples (one sample per site).

Assessments of explanatory variables

Habitat and landscape features were assessed at each site (Appendix 1). Habitat characteristics included features of the vegetation and soil water content. The vegetation was sampled in three, 1 × 1 m quadrats along each transect. Mean data for the quadrats were used to define variables at the sites sampled. To characterize the structure of vegetation, the average height of the vegetation, the total cover of vegetation at 10 and 40 cm above the ground and cover of litter were recorded. To characterize the richness of vegetation, the total number of species of plants and of only the dicotyledonous plants were recorded in the quadrats. Soil samples were taken from the top 10 centimetres close by the coenological quadrats. The percentage of gravimetric water in soil samples was measured.

To assess the amount of habitat we measured the percentage of the area covered with grassland in a radius of 100, 250, 500 and 750 m around each site using ArcView 3.11 GIS software.

Life-history traits

Dispersal ability, niche breadth and reproductive potential were the traits considered, because they are hypothesized to be key determinants of species persistence (Kotiaho et al., 2005). As a measure of dispersal ability, the mobility index (Reinhardt et al., 2005) was used. However, mobility is not a constant trait for orthopterans; it may differ between and within populations (e.g. Endo, 2006; Poniatowski & Fartmann, 2009). To reduce the effect of this potential variability, broad mobility classes: sedentary, intermediate disperser and mobile species, were identified. Further, intermediate dispersers were excluded from the analyses, as they are often the species whose classification is uncertain (cf. Marini et al., 2009a; 2012). The mean number of ovarioles is a rough measure of the reproductive potential of females (Reinhardt et al., 2005) and is generally coded into three categories: low (<10), intermediate (11–25) and high (>25) (cf. Dziock et al., 2011). However, this trait is proportional to body size and the phylogeny of the species (Dziock et al., 2011), and Ensifera species are usually placed in a higher reproductive category than Caelifera (see also our data in Appendix 1). Further, Ensifera species usually produce larger eggs and lay them individually in plants or under tree bark, behaviour which can increase the chance of hydrochory and thus their passive dispersal ability (Dziock et al., 2011). Therefore, Ensifera and Caelifera were used as examples of the differences in reproductive potential and passive dispersal of the species.

Orthoptera clearly differ in their preference for habitats of different humidity, and this trait is often used to group them in relation to their habitat specialization (cf. Fartmann et al., 2012). As most of the collected species preferred dry habitats and the number of hygrophilous species was rather low, we sorted them into two groups: xerophilous and non-xerophilous (hygrophilous and mezophilous) species.

Data analyses

To evaluate the degree of collinearity, Pearson correlation coefficients were computed between habitat variables (soil water content, vegetation height, the cover of vegetation at 10 and 40 cm above the ground, cover of litter, plant species richness) prior

to analyses (Appendix 2). As the variables were highly inter-cor-
related, a Principal Component Analysis (PCA) was carried out
and the scores on the first axis, which explained 85.2% of the total
variance and correlated significantly with each of the assessed
habitat variables (Appendix 2), were used as a habitat descriptor
(cf. Poniatowski & Fartmann, 2011; Münsch et al., 2013). The
newly created variable represents a gradient from sites with dry
soils and uniform vegetation (low values) to sites with moist soils
and a high architectural complexity and diversity of vegetation
(high values).

Similar to previous studies (e.g. Steffan-Dewenter et al., 2002;
Cozzi et al., 2008), as landscape variables quantified at nested
spatial scales were obviously highly correlated, we determined
the scale which best explained the variation for orthopterans. To
evaluate the spatial scale, we used a Generalized Linear Model
(GLM, Poisson errors) to describe the relationships between the
response and landscape variables (percentage of surrounding
area that is grassland) for each radius separately (cf. Marini et
al., 2009b).

To analyse the species composition of assemblages of Ortho-
ptera and its relationship with environmental variables, Non-met-
ric Multidimensional Scaling (NMDS, Bray-Curtis dissimilarity)
was used and environmental vectors were fitted onto the ordina-
tion space. Generalized Linear Mixed Models (GLMM, Poisson
errors, maximum likelihood fit) were used to test the effects of
explanatory variables and factors on the species richness of the
Orthoptera. In the GLMM, the effect of habitats sampled was
used as a random effect and the selected explanatory variables
(habitat descriptor, amount of grassland) as fixed effects. To test
for significances, the effect of landscape (HOM vs. HET) and of
flooding (flooded vs. non-flooded sites) were also subjected to
GLMM as fixed effects. 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). GLMM was
performed using the glmer function in lme4 package (Bates et
al., 2013); automated model selection was carried out with the
dredge function in MuMIn package (Bartoń, 2013). Ordinations
were performed in the Vegan package (Oksanen et al., 2013); en-
vironmental vectors and factors were fitted onto ordination space
using the envfit function.

RESULTS

Orthopteran assemblages

Altogether 1529 adult individuals of 16 species of
Caelifera and 11 of Ensifera were collected (Appendix 1).
In terms of mobility 15 were categorized as mobile, 5 as
intermediate dispersers and 7 as sedentary and in terms of
habitat preference 16 and 11 of these species were cate-
gorized xerophilous and non-xerophilous, respectively.
The most abundant species was *Euchorthippus declivus*
(Brisout de Barneville, 1849), which made up 31.92% of
the total number collected. Other abundant species were
Chotrhippus dichrous (Eversmann, 1859) (12.10%), *Ch.
dorsatus* (Zetterstedt, 1821) (11.05%) and *Pezotettix gior-
nae* (Rossi, 1794) (10.92%).

Numerous endangered, critically endangered or pro-
tected species such as *Gampsocleis glabra* (Herbst, 1786),
Ruspolia nitidula (Scopoli, 1786), *Platycleis vittata* (Char-
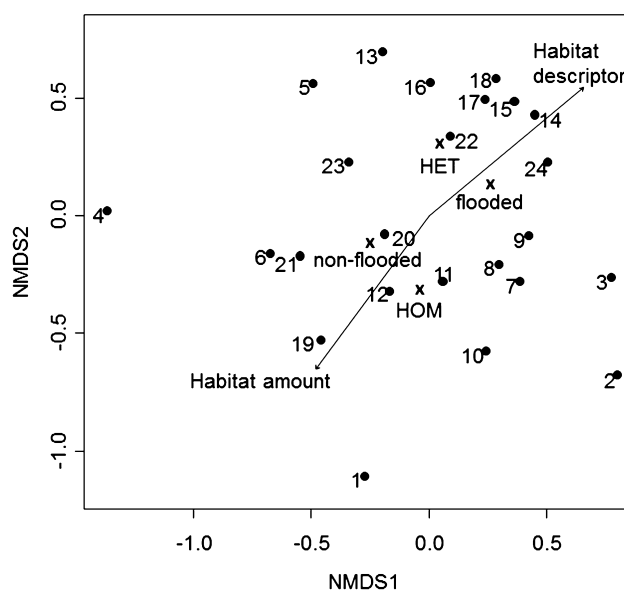pentier, 1825), *Acrida hungarica* Herbst, 1786 and *Epac-

Fig. 1. NMDS ordination (stress: 19.97) showing the natural group-
ing of sites based on the species composition of Orthoptera. Black
circles and numbers indicate the sites sampled in sand steppe
meadows (1–3, 22–24), alkaline meadows (4–6, 19–21), floodplain
meadows (7–9, 13–15) and dike-slope meadows (10–12, 16–18)
in homogeneous (1–12) and heterogeneous (13–24) landscapes,
respectively. The environmental variables (habitat descriptor and
amount of surrounding grassland) and factors (flooded vs. non-
flooded sites, homogenous vs. heterogeneous landscape) were
passively fitted onto the ordination diagram. For significances of
their effects see Table 1.

romius coerulipes (Ivanov, 1888) were also collected.
Although these species need different environmental con-
ditions, e.g. *R. nitidula* is a rare inhabitant of wetlands, *P.
vittata* and *G. glabra* prefer xeric, tall grassy vegetation,
they were almost all collected in the dike slope habitat.
Specimens of *E. coerulipes* were collected only at alkaline
sites in the HET landscape.

According to the NMDS, the variation in the composi-
tion of the samples was caused mainly by the difference
between the two landscapes (Fig. 1, Table 1).

Species richness of orthopteran assemblages

The Poisson regressions indicated that the total species
richness and the richness of species of both Ensifera and
Caelifera were associated in a scale-dependent manner
with the percentage of grassland in the surroundings (Fig.
2). The scale with the largest decrease in residual deviance
was 500 m. For sedentary and non-xerophilous species, the
scale with the largest decrease in residual deviance was

Table 1. The significances of fitted environmental variables and
factors on the NMDS ordination. P values based on 999 permuta-
tions.

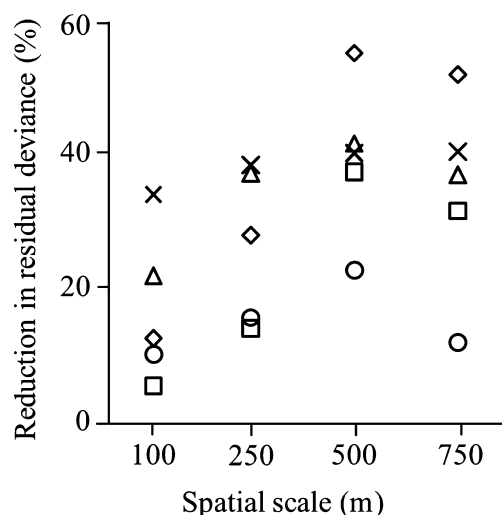| Environmental variables		NMDS1	NMDS2	R^2	P
Habitat descriptor		0.719	0.695	0.23	0.067
Habitat amount		−0.533	−0.846	0.18	0.126
Flooding	Flooded	0.151	0.138	0.09	0.118
	Non-flooded	−0.151	−0.138		
Landscape	Heterogeneous	−0.027	0.253	0.15	0.029*
	Homogeneous	0.027	−0.253		

Fig. 2. Scale-dependent effects of the percentage of grassland in the surroundings on the number of all Orthoptera (diamonds), Ensifera (circles), Caelifera (squares), sedentary (triangles) and non-xerophilous (crosses) species. The Poisson regressions between orthopteran species richness and the percentage of grassland in a radius of 100, 250, 500 and 750 m around the sites sampled indicates a decrease in the residual deviance (percentage). In the case of other trait groups, no significant scale-dependent effect of the percentage of grassland was detected.

also 500 m; however, the differences between the different scales were not large.

For all the species collected, the model selection resulted in an average best model that included the effect of landscape, flooding and amount of habitat (Table 2). The species richness decreased significantly with increase in the percentage of grassland in the surroundings ($z = 2.73$, $P = 0.006$) (Fig. 3a); landscape ($z = 1.33$, $P = 0.184$) and flooding ($z = 1.28$, $P = 0.199$) were not significant.

The average best model for Ensifera (Table 2) included the significant effect of amount of habitat ($z = 2.33$, $P =$

0.020) and the habitat descriptor ($z = 1.92$, $P = 0.049$) (Figs 3b, e).

The average best model explaining the species richness of Caelifera (Table 2) included landscape, flooding, amount of habitat and the habitat descriptor. The effect of landscape was significant ($z = 2.93$, $P = 0.003$) (Fig. 3g), but not the effects of flooding ($z = 1.69$, $P = 0.090$), amount of habitat ($z = 1.79$, $P = 0.073$) and the habitat descriptor ($z = 1.57$, $P = 0.116$).

The best GLMM explaining the species richness of mobile orthopterans included only the effect of landscape (Table 2), which was significant ($z = 2.14$, $P = 0.032$) (Fig. 3e).

For sedentary species, the model selection procedure (Table 2) yielded a best model that only included the significant effect of amount of habitat ($z = 2.90$, $P = 0.004$) (Fig. 3c).

The average best model for xerophilous species included the effects of landscape and the habitat descriptor (Table 2), with the difference associated with landscape significant ($z = 2.10$, $P = 0.036$) (Fig. 3h) but not that associated with the habitat descriptor ($z = 1.42$, $P = 0.156$).

For non-xerophilous orthopterans the model selection (Table 2) resulted in an average best model that included the effects of the amount of habitat, the habitat descriptor, flooding and landscape. Only the effect of the landscape was not significant ($z = 1.26$, $P = 0.206$), but that associated with the percentage of grassland ($z = 2.18$, $P = 0.029$) (Fig. 2d), the habitat descriptor ($z = 2.29$, $P = 0.022$) (Fig. 2f) and flooding ($z = 2.25$, $P = 0.024$) (Fig. 2i) were significant.

DISCUSSION

Effects of landscape features and spatial scale

Based on the scale-dependent effect of the composition of the landscape recorded in the present study, the percent-

Table 2. The GLMM components included in the average best models explaining the species richness of the different trait groups of Orthoptera. Abbreviations of explanatory variables and factors: homogeneous vs. heterogeneous landscape (Landscape), flooded vs. non-flooded sites (Flooding), percentage of grassland within in a radius of 500 m of the site sampled (Habitat amount), scores of the first PCA axis as habitat descriptor (Habitat).

| Trait groups	Model components	d.f.	logLik	AICc	Delta	Weight
	Habitat amount	3	−49.32	105.84	0	0.48
All species	Landscape + Habitat amount	4	−48.43	106.97	1.12	0.27
	Flooding + Habitat amount	4	−48.52	107.15	1.31	0.25
Ensifera species	Habitat amount	3	−36.91	87.02	0	0.61
	Habitat	3	−40.70	88.59	1.57	0.39
	Habitat amount + Landscape	4	−44.98	100.07	0	0.31
Caelifera species	Landscape	3	−46.64	100.49	0.42	0.25
	Flooding + Landscape	4	−45.20	100.50	0.43	0.25
	Habitat + Landscape	4	−45.41	100.93	0.87	0.20
Mobile species	Landscape	–	–	–	–	–
Sedentary species	Habitat amount	–	–	–	–	–
	Landscape	3	−45.03	97.26	0	0.43
Xerophilous species	Landscape + Habitat	4	−44.10	98.30	1.04	0.19
	Null	2	−46.98	98.53	1.27	0.17
	Habitat amount	3	−36.87	80.94	0	0.29
Non-xerophilous species	Habitat	3	−36.89	80.98	0.04	0.28
	Flooding	3	−36.89	80.99	0.05	0.28
	Flooding + Landscape	4	−36.08	82.27	1.33	0.15
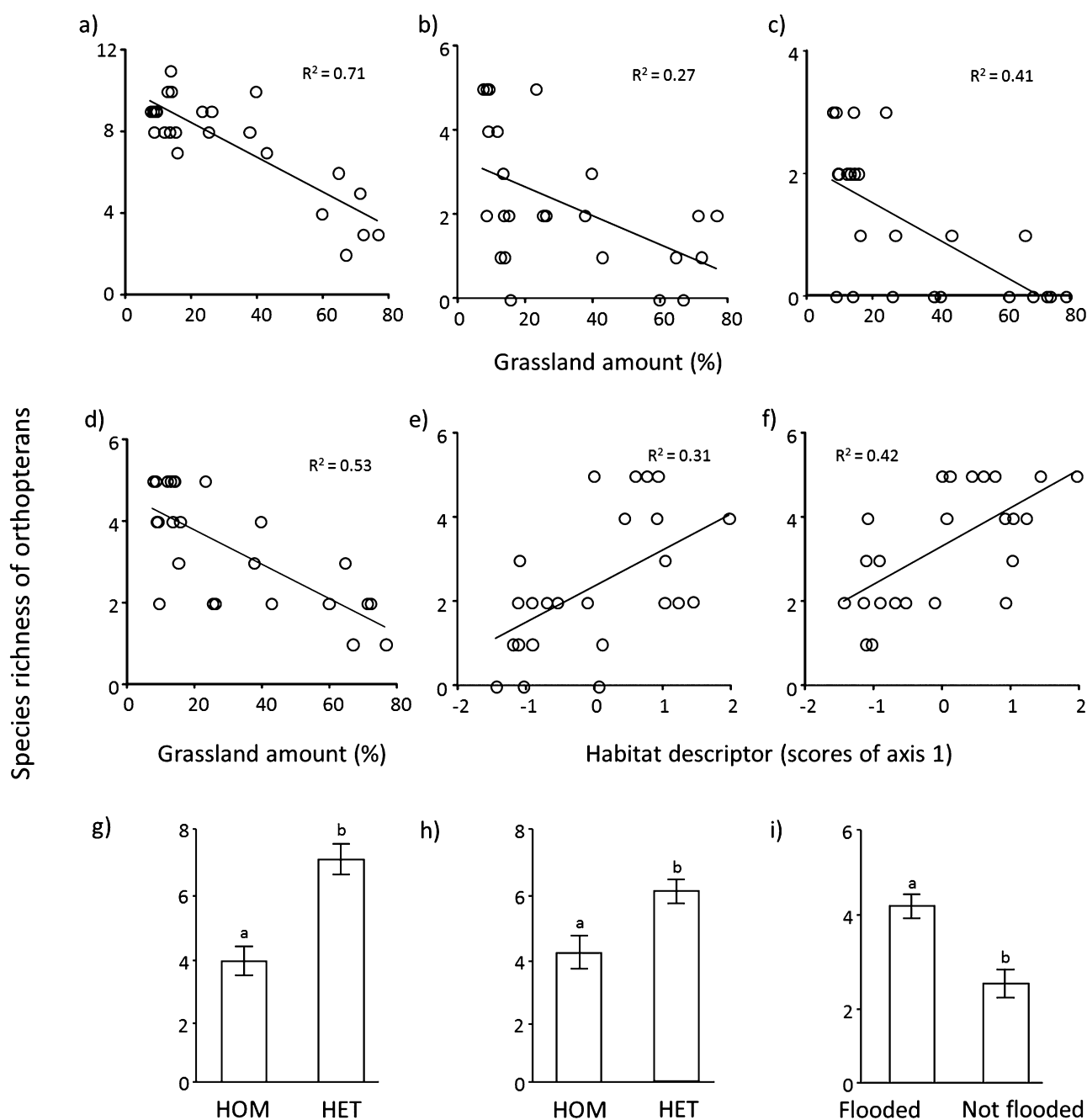
Fig. 3. The significant effects of flooding, habitat characteristics and landscape variables on the species richness of different life-history trait groups of Orthoptera delineated using model selection of GLMM. The effects of the explanatory factors and variables were averaged across the best models with delta < 2. Scatter plots show the relations between the percentage of grassland in the surroundings and the total species richness (a), the species richness of Ensifera (b), sedentary (c) and non-xerophilous (d) orthopterans; the relationship between the habitat descriptor and the species richness of Ensifera (e) and non-xerophilous (f) orthopterans. Bar charts represent the differences in the species richness of Caelifera (g) and mobile orthopterans (h) in the two landscapes; the differences in the species richness of non-xerophilous species (i) at flooded and non-flooded sites. For significances see the results of the model averaging cited in the text.

age of grassland in the surroundings explained the majority of the variability in orthopteran species richness within a radius of 500 m; this scale has been shown to be relevant in terms of the spatial effects for several arthropod groups (e.g. Schmidt & Tscharntke, 2005; Öberg et al., 2007; Torma & Császár 2013; Torma et al., 2014). With an increase in the percentage of the area covered by grassland, the species richness of orthopterans decreased, which is contrary to the prediction of the habitat amount hypothesis

(Fahrig, 2013). However, Fahrig (2013) emphasized that the amount of habitat can be a good predictor for species richness, but is only part of the effect of the surrounding landscape. The studies (e.g. Marini et al., 2008, 2009a, 2010; Badenhausser & Cordeau, 2012) that report a negative relationship between the proportion of grassland in the surrounding area and Orthopteran species richness emphasize the importance of ecotones. These papers suggest that contrary to the expectation based on the higher mortality of

Orthoptera in large mown grasslands, in a landscape with a relatively low amount of grasslands, the local Orthoptera diversity can benefit from the presence of ecotonal habitats due to what are referred to as rescue effects.

In a previous study, Torma & Császár (2013) show that different landscapes along the lower reaches of TRB host similar assemblages of Heteroptera. Contrary to this, assemblages of Orthoptera in the present study differed in their species composition in the two landscapes, despite sampling similar habitats. Similar to other studies (e.g. Torma et al., 2014) we suggest that different insect groups responded differently to habitat and landscape features, and orthopterans are more affected by landscape features than habitat characteristics in this region. This suggestion is corroborated by the significant positive association between the heterogeneous landscape and species richness of many trait groups recorded in this study. Presumably, in a more heterogeneous landscape, a grassland patch is likely to be colonized by more species from ecotonal habitats as it provides suitable conditions for foraging and reproduction (Marini et al., 2008).

Effect of habitat characteristics

Surprisingly, habitat characteristics affected only the species richness of Ensifera and non-xerophilous species. Non-xerophilous species obviously preferred sites with moist soil and thus more dense vegetation. Species of Ensifera also responded to the habitat characteristics of the sites as they preferred moist sites with more complex vegetation. The importance of humidity for egg and larval development of orthopterans is emphasized in several studies (e.g. Hodek, 2003; Wünsch et al., 2012), and Ensifera generally need more water for egg development than Acrididae (Ingrisch & Köhler, 1998). Differences between Caelifera and Ensifera with regard to vegetation characteristics are also reported by e.g. Marini et al. (2009b), who suggest that Caelifera, unlike Ensifer, prefer regularly mown, less dense vegetation.

Effect of flooding

Flooding is considered to be a major disturbance for invertebrate assemblages in riparian habitats (Foeckler et al., 2006). Although the dispersal ability of species is important for the structuring of invertebrate assemblages in flooded habitats (Rothenbücher& Schaefer, 2006; Lambeets et al., 2009) before and after flooding (Rothenbücher & Schaefer, 2006), we did not find any significant effect of flooding on the different mobility trait groups. Instead of active dispersal, Dziock et al. (2011) emphasize the importance of passive dispersal ability of orthopterans in floodplains. Certain orthopterans lay eggs in plants or under tree bark and their eggs can be transported together with their substrates by water. This potentially enables these species to colonise even remote areas; however a larger number of offspring (eggs) is needed, because a large proportion of them are likely to end up in unfavourable habitats. Compared to Caelifera, Ensifera species are usually more dependent on passive dispersal and have more ovarioles, but

we did not find any significant effect of flooding on Ensifera species richness.

However, our results are hard to generalize as the structure and composition of animal assemblages can change rapidly in riparian areas that are frequently flooded (Lambeets et al., 2009). Presumably, the results of a study following severe flooding would reveal a stronger and more consistent effect of flooding.

Implication for conservation

As their diversity is currently declining in many temperate regions, assemblages of Orthoptera are the focus of numerous conservation studies. In fact, more than half of the orthopteran species are endangered in Europe (Ingrisch & Köhler, 1998; Reinhardt et al., 2005). The present study was carried out in habitats of low natural value compared to Natura 2000 and other protected areas in Hungary, despite the occurrence of *G. glabra* and *R. nitidula*, which are endangered or critically endangered in surrounding countries (Berg & Zuna-Kratky, 1997; Maas et al., 2002; Krištin et al., 2007; Liana, 2007) and *P. vittata*, which is close to extinction along the edge of the Pannonian Region (Holusa et al., 2012). These facts confirm that the habitats in the TRB can serve to maintain high orthopteran (and presumably other invertebrate) diversity in the Pannonian Region. We agree with Hernández-Manrique et al. (2012), who conclude that existing conservation strategies, which are based mainly on the protection of certain areas, often selected based on the presence there of particular plant and vertebrate species, may be insufficient for ensuring the conservation of invertebrate species. Therefore, we emphasize that even in countries where considerable areas of high natural value grassland still exist, non-protected meadows, strip-like grassy habitats such as dikes, ditch banks, road verges should receive more attention and should be given a major role in the conservation of invertebrate diversity.

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Appendix 1. Collected species of Orthoptera and assessed habitat and landscape features.

Taxa	Moisture preference	Dispersal ability	Reproductive potential	Homogeneous landscape																	Heterogeneous landscape								
				Sand steppe meadow		Alkaline meadow				Floodplain meadow			Dike slope meadow			Floodplain meadow			Dike slope meadow		Alkaline meadow			Sand steppe meadow			
				site 1	site 2	site 3	site 4	site 5	site 6	site 7	site 8	site 9	site 10	site 11	site 12	site 13	site 14	site 15	site 16	site 17	site 18	site 19	site 20	site 21	site 22	site 23	site 24
Ensifera																											
Conocephalus discolor Thunberg, 1815	hygro	mobile	high	0	0	0	0	0	0	1	0	0	2	0	0	0	0	1	1	0	0	0	0	2	0	2	0
Gampsocleis glabra (Herbst, 1786)	xero	sedentary	med	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptophyes albovittata (Kollar, 1833)	xero	sedentary	high	0	0	0	0	0	0	2	2	3	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Leptophyes bosci Fieber, 1853	mezo	sedentary	high	0	0	0	0	0	0	7	6	18	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0
Metrioptera bicolor (Philippi, 1830)	xero	mobile	high	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Metrioptera roeselii (Hagenbach, 1822)	mezo	intermediate	high	0	1	3	0	0	0	3	1	3	1	2	0	3	3	3	2	2	0	6	1	1	0	0	2
Oecanthus pellucens (Scopoli, 1763)	xero	mobile	high	0	0	0	0	0	0	0	1	3	1	0	8	0	0	0	0	3	0	1	0	5	12	9	4
Platycleis affinis Fieber, 1853	xero	intermediate	high	0	1	0	1	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Platycleis albopunctata (Goeze, 1778)	xero	intermediate	high	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Platycleis vittata (Charpentier, 1825)	xero	sedentary	high	0	0	0	0	0	0	0	0	2	2	1	1	1	0	1	2	2	2	0	0	0	1	1	0
Ruspolia nitidula (Scopoli, 1786)	hygro	mobile	high	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0
Caelifera																											
Acrida hungarica Herbst, 1786	xero	mobile		0	0	0	0	0	0	1	0	0	3	2	0	0	0	0	0	0	0	4	4	3	0	1	0
Calliptamus italicus (Linnaeus, 1758)	xero	intermediate	high	0	0	0	0	0	0	0	0	0	0	0	0	5	1	10	15	11	8	0	0	0	16	5	7
Chorthippus oschei Helversen, 1986	mezo	mobile	low	0	0	0	1	0	2	0	0	0	0	10	5	0	0	0	0	0	0	19	19	21	62	0	0
Chorthippus dichrous (Eversmann, 1859)	mezo	mobile	low	0	0	0	0	1	0	0	0	0	0	1	3	17	44	29	28	28	34	0	0	0	0	0	0
Chorthippus dorsatus (Zetterstedt, 1821)	mezo	mobile	low	0	0	17	0	0	0	0	0	0	0	0	0	8	30	35	24	26	46	6	0	0	3	0	2
Chorthippus parallelus (Zetterstedt, 1821)	mezo	mobile	low	2	17	0	0	3	1	0	0	1	0	0	5	3	0	0	5	1	1	1	6	1	3	8	2
Chorthippus brunneus (Thunberg, 1815)	xero	mobile	med	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	2	3	4	1	0	2	2	0	0
Chorthippus mollis (Charpentier, 1825)	xero	mobile	low	0	0	0	0	0	0	0	0	0	6	2	0	0	0	0	0	0	0	8	1	0	1	0	1
Epacromius coerulipes (Ivanov, 1887)	xero	mobile	low	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	1	6	5	0	1
Euchorthippus declivus (Brisout de Barneville, 1849)	xero	mobile	low	41	30	6	0	1	1	45	34	11	39	72	43	2	14	7	39	14	13	36	19	9	6	5	1
Omocestus haemorrhoidalis (Charpentier, 1825)	xero	sedentary	low	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	14	2	2	0	1	0	0	3	0
Omocestus rufipes (Zetterstedt, 1821)	mezo	sedentary	low	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	13	4	9	1	0	0	0	0	0
Mecostethus parapleurus (Hagenbach, 1822)	hygro	intermediate	high	1	0	0	2	2	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Pezotettix giornae (Rossi, 1794)	xero	mobile	low	0	0	0	2	2	1	11	6	21	3	6	4	41	4	18	17	6	6	2	6	9	0	0	0
Stenobothrus stigmaticus (Rambur, 1838)	xero	sedentary	low	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Tetrix subulata (Linnaeus, 1758)	hygro	mobile	med	0	0	0	0	0	0	4	1	5	4	17	9	5	7	4	14	11	8	1	8	0	1	0	0
Acrididae larvae				4	6	5	1	0	3	12	8	7	4	17	9	5	7	4	14	11	9	7	4	5	3	1	1
Conocephalidae larvae				0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0
Gryllidae larvae				0	1	0	0	0	0	2	0	0	0	2	3	0	0	0	2	0	2	1	1	1	2	2	0
Tetrigidae larvae				0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tettigoniidae larvae				0	0	0	0	0	0	2	5	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
Assessed variables																											
Cover of dead vegetation litter				56.67	70	66.67	30	36.67	66.67	30	30	35	20	20	30	33.33	23.33	13.33	26.67	5	10	70	43.33	53.33	41.67	41.67	60
Cover of vegetation at a height of 10 cm				33.33	23.33	30	11.67	11.67	99.4	70	65	80	80	80	70	76.67	60	86.67	43.33	95	90	28.33	16.67	25	51.67	48.33	35
Cover of vegetation at a height of 40 cm				30.02	20.76	13.33	0	0	10.4	10	10	5	5	10	5	18.33	5	30	6.67	46.67	33.33	0	0	6.67	16.67	16.67	3.33
vegetation height				30.02	20.76	13.43	13.03	10.4	42.11	60.12	60.32	61.54	81.56	80	70.01	46.67	50.43	90	66.67	31.01	11.67	21.67	36.67	43.33	41.67		
species richness of dicots				7	9	8	10	8	7	15	13	12	16	13	7	7	13	15	13	11	15	9	11	15	7	10	9
species richness of plants				10	14	12	14	11	8	16	17	17	15	17	17	15	15	18	15	15	23	13	14	19	10	15	11
Soil water content				17.806	15.686	9.447	6.917	6.444	14.245	24.268	23.191	23.385	19.269	17.162	18.567	19.314	16.964	15.041	23.191	24.269	20.528	10.582	12.438	8.289	19.694	18.390	10.262
Proportion of grasslands in a radius of 100 m				93.46	93.44	92.85	95.96	98.2	99.4	41.92	39.65	36.79	42.92	40.65	37.76	50.58	56.58	37.9	56.73	60.39	40.69	87.23	86.59	100	97.21	96.24	100
proportion of grasslands in a radius of 250 m				86.67	88.47	75.95	78.23	89.35	96.97	17.29	15.37	15.19	17.29	15.37	15.19	22.45	23.64	19.16	22.36	22.86	21.3	73.36	78.07	44.97	52.8	83.56	24.97
proportion of grasslands in a radius of 500 m				70.81	76.38	71.83	66.53	64.26	59.42	11.48	8.17	7.33	9.07	8.31	8.71	15.34	14.87	13.16	12.46	13.42	13.7	42.46	39.2	37.35	25.82	22.91	24.97
proportion of grasslands in a radius of 750 m				63.55	59.08	63.31	46.18	43.74	39.32	5.34	5.37	5.37	5.34	5.47	5.37	7.18	7.79	7.44	6.38	6.66	7.5	19.97	23.47	23.83	24.53	26.94	28.82

Appendix 2. Correlation matrix of habitat variables (above: p-values, below: correlation coefficients). Abbreviations: cover of dead vegetation litter (litter), total cover of vegetation at a height of 10 cm (veg.cover10), total cover of vegetation at a height of 40 cm (veg.cover40), average height of the vegetation (veg.height), species richness of all plants (all plants), species richness of only dicotyledonous plants (dicots), soil water content (moisture) and habitat descriptor (axis 1).

	litter	veg.cover10	veg.cover40	veg.height	all plants	dicots	moisture	axis 1
litter		< 0.001	< 0.001	< 0.001	0.001	0.002	0.010	< 0.001
veg.cover10	−0.778		< 0.001	< 0.001	0.001	0.001	< 0.001	< 0.001
veg.cover40	−0.722	0.744		< 0.001	0.012	0.013	0.015	< 0.001
veg.height	−0.711	0.893	0.659		0.003	0.008	< 0.001	< 0.001
all plants	−0.655	0.653	0.502	0.576		< 0.001	0.112	< 0.001
dicots	−0.606	0.619	0.499	0.530	0.803		0.108	0.001
moisture	−0.515	0.733	0.489	0.676	0.333	0.336		< 0.001
axis 1	−0.852	0.977	0.784	0.943	0.667	0.626	0.714	