

FINE SCALE PATTERN OF TRUE BUG ASSEMBLAGES (HETEROPTERA) ACROSS TWO NATURAL EDGES

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The spatial pattern of epigeic true bug assemblages was studied across natural edges at a forest steppe region in Hungary. Two edges were investigated: a poplar forest – open sand grassland (site one) and a juniper forest – open sand grassland (site two). The abundance and variety of true bugs was sampled by pitfall traps. Altogether 1396 adult individuals belonging to 49 species were collected. Some species occurred exclusively at forest habitats and significant indicator species were found in both forest and grassland habitats. However, distinct Heteroptera assemblages were found only at grasslands. The response of the grassland Heteroptera assemblages to the proximity of the edge differed between the two sites. At site one, an approximately seven-meter wide transition zone could be observed from the grassland into the forest, which was characterized by the dissolution of the grassland true bug assemblage. The species richness decreased significantly toward the edge. At site two, an abrupt change in the structure of the Heteroptera assemblage denoted a sharp boundary near to the edge in the juniper forest. The species richness did not change toward the juniper edge. We found that the cover of dicotyledonous plants, mosses and lichens, bare soil surface and leaf litter had a significant joint effect on true bug assemblages. The characteristic species of the grasslands responded differently to the edges. Specialist herbivorous bugs seemed to be affected more strongly and negatively by edges than generalist herbivorous and predaceous species.

Key words: juniper, poplar, open sand grassland, epigeic

INTRODUCTION

The term edge effect was introduced to describe the increase in the abundance and species diversity in the transition zone between two habitats (LEOPOLD 1933, ODUM 1971). At present, the changes in both biotic and abiotic conditions, taking place at the transition zones between adjacent habitats, are referred to as edge effects (MURCIA 1995). The edges may influence the distribution and abundance of populations (MOLNÁR *et al.* 2001), the interactions between populations (FERGUSON 2004) and the structure of communities (BURGESS *et al.* 2001). The edge may have positive (MÁTHÉ 2006), negative (BIERINGER & ZULKA 2003) and neutral (DURĀES *et al.* 2005) effects on organisms.

A number of studies contributed to the knowledge about patterns of various arthropod taxa across natural edges (e.g. MAGURA & TÓTHMÉRÉSZ 1997, 1998, KOTZE & SAMWAYS 2001, HORVÁTH *et al.* 2002, TABOADA *et al.* 2004, DURĀES

et al. 2005, YU *et al.* 2006, WERMELINGER *et al.* 2007, HOCHKIRCH *et al.* 2008, GALLÉ & TORMA 2009), however, only a few papers focused on true bugs (e.g. CAPPUCINO & ROOT 1992, MÜLLER *et al.* 2007), especially on epigeic true bugs. Collecting true bugs from the ground-level generally needs great effort and has trifling result compared with collecting from the vegetation (RÉDEI *et al.* 2003). However, epigeic true bugs are characteristic of, and rather abundant in dry, sandy habitats. SPUNGIS (2005) found a higher species richness of epigeic true bugs than plant dwelling true bugs at a coastal dune area. Numerous studies (e.g. GALLÉ *et al.* 1988, HARMAT 1984, KERÉNYI, 1997, TORMA & KÖRMÖCZI 2009; GALLÉ *et al.* 2010) recommended epigeic true bugs for community studies at dry sand grasslands.

The aims of this study were a) to reveal how the species richness and composition of epigeic true bug assemblages changes across two natural sharp edges b) to find correspondence between the distance from the edge of the habitat properties of grasslands and Heteroptera assemblage patterns c) to detect indicator species in the different habitats and d) to reveal the influence of the edges on the abundance of characteristic species.

MATERIALS AND METHODS

Study site and sampling

Present study was carried out near Bugac village in the central part of the Danube–Tisza interfluvium, which is situated at a higher elevation than the rest of the lowland, as a result, of a large Quaternary alluvial fan of the Danube, composed of sand, sandy loess and loess in restricted areas (TÖRÖK *et al.* 2003). The area lies in the warm temperate zone with an annual mean temperature between 10.2 and 10.8 °C; the mean annual precipitation is approximately 550 mm with two precipitation peaks (spring and autumn) and a drought in summer, therefore the climate is strongly semiarid (TÖRÖK *et al.* 2003).

The remnants of the natural vegetation consisting of open grasslands (*Potentillo–Festucetum vaginatae*) and juniper-poplar forests (*Junipero–Populetum albae*) are embedded in agricultural fields. The composition of juniper-poplar forests varies widely: some patches consist almost exclusively of juniper, composing a dense scrubland whereas in other patches junipers are absent (VIDÉKI 2004).

Two sharp vegetational edges were studied: poplar forest – open sand grassland (site 1: N 46°43.48', E 19°39.35') and juniper forest – open sand grassland (site 2: N 46°43.49', E 19°40.26'). The distance between the sites was approximately two kilometers. At site one, the forest was characterised by high poplar trees and accordingly by the presence of thick deciduous leaf litter. Junipers occurred sparsely. At site two, the approximately 2–3 meter high juniper bushes formed a closed canopy layer, and the ground level was covered with Juniper leaf litter. The dominant monocotyledonous plant species of the grasslands were *Festuca vaginata*, *Stipa borysthénica* at site one and *Stipa borysthénica*, *Poa bulbosa* and *Koeleria glauca* at site two. The most dominant dicotyledonous plants of both grasslands were *Arenaria serpyllifolia*, *Euphorbia cyparissias* and *Alkanna tinctoria*. The high coverage of mosses and lichens (*Tortula ruralis*, *Cladonia magyárica*, *C. rangiferina*) was typical at both sites.

Although, sweep netting or suction sampling are generally used to sample true bug assemblages in grasslands (STANDEN 2000, COSCARON *et al.* 2009), but we used pitfall traps (65 mm in diameter, filled with ethylene glycol as killing-preservative solution) for several reasons. Sweep netting is not a suitable sampling method in the case of such a fine scale. Suction sampling collects arthropods from both the vegetation and ground surface (SAMU & SÁROSPATAKI 1995), but it is difficult to use in the case of loose sand soil, because of the great amount of sand sucked during the collecting.

At both two sites, 20 groups of traps arranged in rows were placed parallel to the edge (Fig. 1). Each group of traps contained 5 pitfall traps the same distance from the edge. The intertrap distance within the groups of traps was two meters. The distance between the groups of traps was one meter to obtain a fine resolution. To maximize the inter trap distance, every second group of traps was shifted by one meter parallel to the edge. The pitfall traps were open for two-week periods in April, May, July and September, in the years of 2004 and 2005. The majority of individuals (82%) were collected in the summer, thus, we did not analyze the data of the sampling periods separately. Only adult individuals were identified to species level. The nomenclature of true bugs followed the work of KONDOROSY (1999).

To characterize the properties of habitats, the number of plant species, the percentage cover of leaf litter and vegetation (mosses and lichens, monocotyledonous plants, dicotyledonous plants, separately) was recorded in 1×1 meter quadrats close to the pitfall-traps. The mean of data of the quadrats the same distance from the edge was used for analyses.

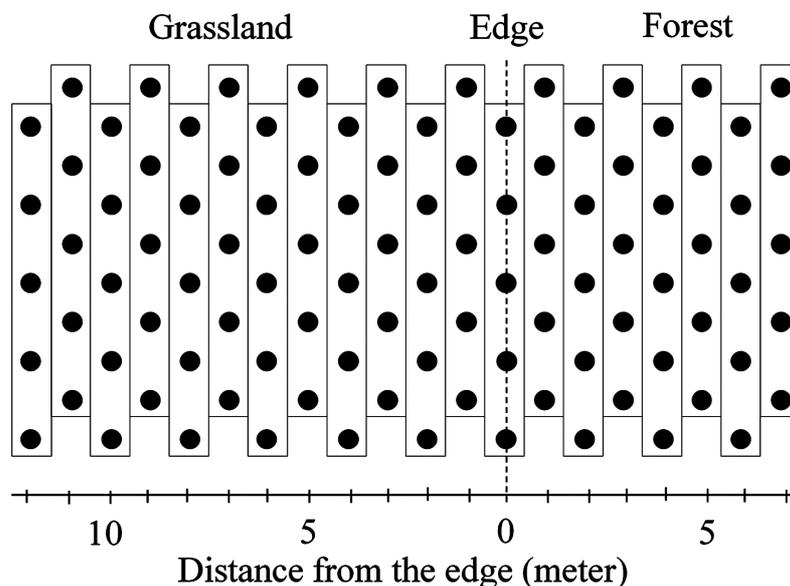


Fig. 1. The scheme of the sampling design. The black circles symbolise the pitfall traps. The groups of traps are surrounded by boxes. Twenty groups of traps containing 5 pitfall traps were placed parallel to the edge. The distance between the traps was two meters; the distance between the groups of traps was one meter. Every second group of traps was shifted by one meter. The data belonging to a group of traps was pooled, and used as a sample unit

Data analysis

The data of pitfall traps at the same distance from the edge were pooled for the analyses. Thus we gained 20 samples (equal to the number of the groups of traps) perpendicular to the edge with a distance of one meter between the subsequent samples.

To detect the changes in the structure of the true bug assemblages, the Chao's Jaccard-type and the Morisita-Horn indices were calculated between the adjacent samples using EstimateS 8.0 software (COLWELL 2004). The Chao's Jaccard-type index was used, as this index is less biased than the classic Jaccard index (CHAO *et al.* 2005). The Morisita-Horn index was applied as a widely used abundance-based index (MAGURRAN 2004).

To show the natural grouping of samples Non-metric Multidimensional Scaling (NMDS) with Bray-Curtis dissimilarity was used. NMDS is recommended by LEGENDRE and LEGENDRE (1998) and OKSANEN (2011), because in the case of NMDS various dissimilarities and distances can be applied and it uses rank information and maps the ranks non-linearly onto ordination space. To determine the main habitat variables which influenced the distribution patterns of true bugs constrained ordination (RDA – Redundancy Analysis) was used (LEPŠ & ŠMILAUER 2003). The marginal and partial effects of the variables were calculated. Marginal effects denoted the variability explained by a variable without considering other variables, and partial effects denoted the variability explained by a given variable after removing the confounding effect of one or more other variables (SCHWEIGER *et al.* 2005). Marginal and partial effects were tested for significance by Monte Carlo procedure with 1000 permutations. To visualise the effects of the significant variables, they were fitted to the scatterplot of NMDS. For the fitting the envfit function was used (OKSANEN 2011). The direction of the arrow shows the direction of the gradient, and the length of the arrow is proportional to the correlation between the variable and the ordination (OKSANEN 2011). We used the Vegan R package (OKSANEN *et al.* 2006) for the ordination methods.

To detect species related to the different habitats, we used indicator value approach (DUFRENE & LEGENDRE 1997). The habitats were identified primarily as grassland and forest according to the vegetation. Indicator values were calculated using the labdsv package (ROBERTS 2010) of R statistic. To test the statistical significance of indicator values we used the Monte Carlo procedure with 1000 permutations.

According to several studies (e.g. MURCIA 1995, BIERINGER & ZULKA 2003), edge effects do not necessarily lead to linear response patterns. Therefore we used Sperman's coefficient of rank correlation to analyse correlations between the species richness of true bugs, the measured habitat variables and the distance from the edge. We restricted the correlation analyses to the grassland samples to avoid spurious trends because of great differences between the habitat properties of forests and grasslands. Since we performed a number of tests on the same data set, a Bonferroni type error adjustment was used (SOKAL & ROHLF 1995). The correlations were calculated in R statistic (R DEVELOPMENT CORE TEAM 2007).

To reveal the species influenced by the edges, simple linear regressions were applied on the abundance of true bugs against the distance from the edge. Due to the indicator values, only the relevant grassland indicator species and additionally the frequent species were analysed. The abundance of the species per samples were log (abundance+1) transformed.

RESULTS

Altogether 1396 adult individuals belonging to 49 species were collected (Table 1). At site one, a continuous change of the assemblage structure was observed which started approximately 7 m far from the edge in the grassland (Fig. 2a). At site two, changes in the assemblage structure (Fig. 2b) were observed in the forest and the assemblage structure changed abruptly, contrary to site one.

The grouping of samples in the ordination space (Fig. 3) confirmed the relevant changes of the assemblage structures. At site one, the samples situated far from the edge in the grassland were grouped whereas other samples which were situated in the forest and near the edge in the grassland were scattered. At site two, the sam-

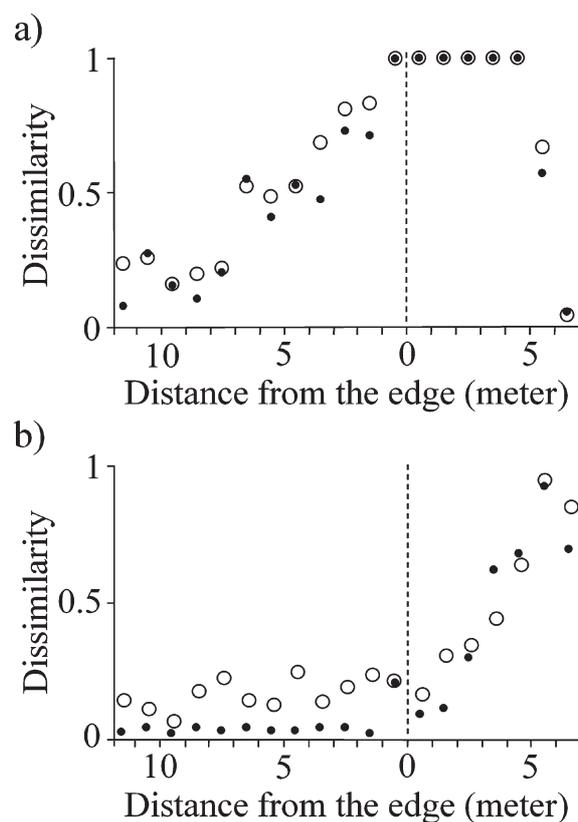


Fig. 2. The figures show the changes in the assemblage structure of true bugs according to the complement of Morisita-Horn (black circles) and the Chao's Jaccard-type (empty circles) indices as dissimilarities between the subsequent samples at site 1 (a) and at site 2 (b). The vertical line marks the edge

Table 1. The abundance and the indicator value of the collected Heteroptera species. G = grassland, F = forest, S = schrubland the number of samples in bracket, No: the number of individuals, InV: the indicator value of species. The significance of indicator values were tested with the Monte-Carlo procedure (1000 iterations). The level of significance: * < 0.05, ** < 0.01, *** < 0.001.

Taxa	Site one				Site two			
	G (13)		F (7)		G (13)		S (7)	
	No	InV	No	InV	No	InV	No	InV
Ceratocombidae								
<i>Ceratocombus coleopratus</i> (ZETTERSTEDT, 1819)			4	0.57**				
Tingidae								
<i>Acalypta gracilis</i> (FIEBER, 1844)	47	0.85**			26	0.74**	2	0.02
<i>Acalypta marginata</i> (WOLFF, 1804)	2	0.15					1	0.14
<i>Agramma minutum</i> HORVÁTH, 1874	1	0.08						
<i>Catoplatus carthusianus</i> (GOEZE, 1778)					1	0.08		
<i>Dictyla echii</i> (SCHRANK, 1781)	1	0.08			1	0.03	1	0.09
<i>Dictyla rotundata</i> (HERRICH-SCHÄFFER, 1835)	6	0.38			1	0.08		
Nabidae								
<i>Alloeorrhynchus flavipes</i> FIEBER, 1836	1	0.08						
<i>Nabis pseudoferus</i> REMANE, 1949	1	0.08			2	0.08	1	0.07
Anthocoridae								
<i>Xylocoris cursitans</i> (FALLÉN, 1807)					1	0.08		
Reduviidae								
<i>Coranus kerzhneri</i> P. PUTSHKOV, 1982	16	0.77**			34	0.66	3	0.06
Piesmatidae								
<i>Piesma maculatum</i> (LAPORTE, 1832)					1	0.08		
Berytidae								
<i>Neides tipularius</i> (LINNAEUS, 1758)	13	0.47	1	0.02	35	0.46	19	0.43
Lygaeidae sensu lato								
<i>Acompus rufipes</i> (WOLFF, 1804)							1	0.14
<i>Aellopus atratus</i> (GOEZE, 1778)	84	0.77**			118	0.93***	5	0.02
<i>Arocatus longiceps</i> STÅL, 1872	1	0.08						
<i>Dimorphopterus doriae</i> (FERRARI, 1874)	16	0.31			1	0.08		
<i>Emblethis ciliatus</i> HORVÁTH, 1875	23	0.69*			511	0.86***	43	0.10
<i>Eremocoris fenestratus</i> (HERRICH-SCHÄFFER, 1839)							1	0.14
<i>Graptopeltus lynceus</i> (FABRICIUS, 1775)	2	0.15						
<i>Lygaeosoma sardeum</i> SPINOLA, 1837	1	0.08			8	0.21	2	0.05
<i>Melanocoryphus tristrami</i> (DOUGLAS et SCOTT, 1868)					2	0.08	1	0.07
<i>Ortholomus punctipennis</i> (HERRICH-SCHÄFFER, 1839)	3	0.23			3	0.15		

Table 1 (continued)

Taxa	Site one				Site two			
	G (13)		F (7)		G (13)		S (7)	
	No	InV	No	InV	No	InV	No	InV
<i>Peritrechus nubilus</i> (FALLÉN, 1807)	1	0.08						
<i>Pionosomus opacellus</i> HORVÁTH, 1895	62	0.77**			105	0.63	26	0.32
<i>Plinthisus longicollis</i> FIEBER, 1861	2	0.15						
<i>Raglius alboacuminatus</i> (GOEZE, 1778)					1	0.08		
<i>Rhyparochromus vulgaris</i> (SCHILLING, 1829)			1	0.14			2	0.29
<i>Stygnocoris rusticus</i> (FALLÉN, 1807)							1	0.14
<i>Stygnocoris sabulosus</i> (SCHILLING, 1829)							3	0.43*
<i>Tropidophlebia costalis</i> (HERRICH-SCHÄFFER, 1850)	2	0.15			5	0.15	4	0.26
<i>Xanthochilus quadratus</i> (FABRICIUS, 1798)	13	0.54*			23	0.56	3	0.08
Coreidae								
<i>Bathysolen nubilus</i> (FALLÉN, 1807)	1	0.08						
<i>Ceraleptus gracilicornis</i> (HERRICH-SCHÄFFER, 1835)							2	0.29
<i>Ceraleptus obtusus</i> (BRULLÉ, 1839)	2	0.15			1	0.08		
<i>Gonocerus juniperi</i> (HERRICH-SCHÄFFER, 1839)							1	0.14
<i>Spathocera obscura</i> (GERMAR, 1842)					1	0.08		
<i>Syromaster rhombeus</i> (LINNAEUS, 1767)	1	0.08			5	0.11	3	0.15
Rhopalidae								
<i>Brachycarenum tigrinus</i> (SCHILLING, 1817)	1	0.08			6	0.16	3	0.14
<i>Chorosoma gracile</i> JOSIFOV, 1968	4	0.31			17	0.69*		
<i>Rhopalus parumpunctatus</i> (SCHILLING, 1817)	4	0.31			5	0.31		
Aradidae								
<i>Aradus depressus</i> (FABRICIUS, 1794)			3	0.29				
Cydnidae								
<i>Cydnus aterrimus</i> (FÖRSTER, 1771)					1	0.08		
Scutellaridae								
<i>Eurygaster maura</i> (LINNAEUS, 1758)	2	0.15			1	0.08		
Pentatomidae								
<i>Aelia acuminata</i> (LINNAEUS, 1758)	1	0.02	1	0.09	3	0.14	1	0.05
<i>Dolycoris baccarum</i> (LINNAEUS, 1758)					1			
<i>Eusarcoris aeneus</i> (SCOPOLI, 1763)	1	0.08						
<i>Menaccarus arenicola</i> (SCHOLTZ, 1846)	12	0.46					8	0.28
<i>Neottiglossa leporina</i> (HERRICH-SCHÄFFER, 1830)					2	0.15		

ples situated near the edge in the Juniper forest were grouped with the samples of the grassland. Both the species richness and the abundance were very low in the forest habitats and the occurrence of species in the samples were sporadic, hence a consistent species composition was not found, distinct assemblages existed only in grassland habitats. The constrained axes of RDA explained 73.52% of the total variance. The implemented permutation test indicated the significant joint effect of

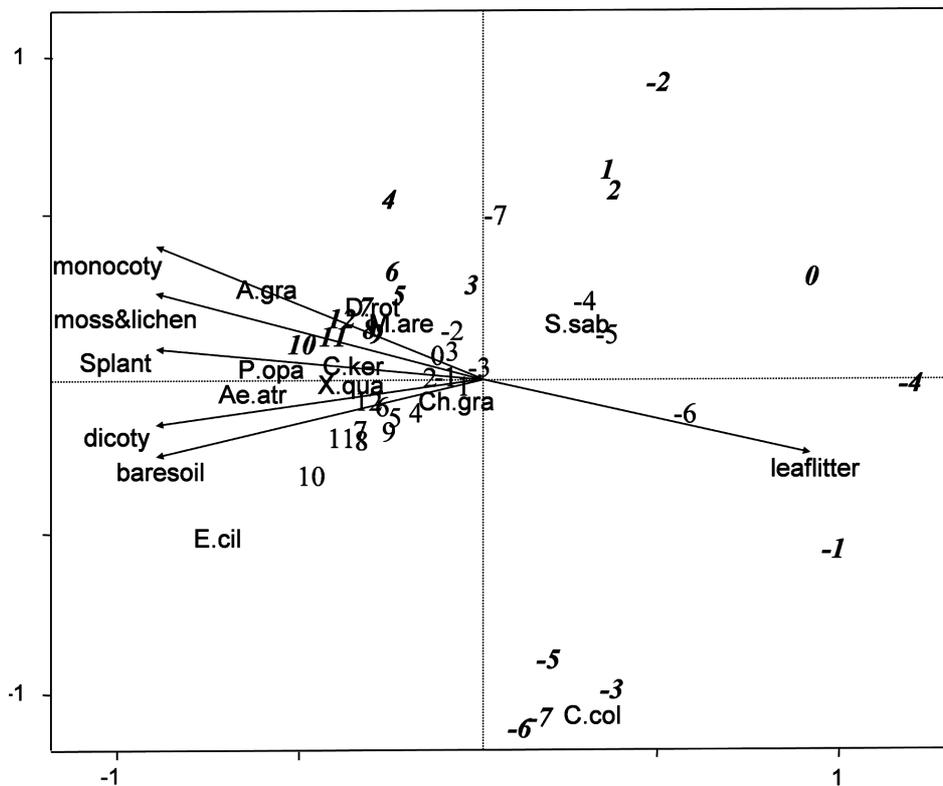


Fig. 3. The scatterplot of NMS based on Bray-Curtis similarity shows the natural grouping of samples and the relevant species. The numbers mark the samples and mean their distance from the edge (in meters). Positive numbers mark the samples of grasslands, negative numbers mark the samples of forests. Numbers in italic mark the samples at site one and numbers in bold mark the samples at site two. The arrows symbolise the effects of the habitat variables (plant species richness, percentage cover of monocotyledonous plants, dicotyledonous plants, mosses and lichens, leaf litter, bare soil surface). The variables were fitted passively onto the ordination diagram to visualise their effects. The abbreviations of the characteristic species: A.gra = *Acalypta gracilis*, Ae.atr = *Aellopus atratus*, C.col = *Ceratocombus coleopratus*, C.ker = *Coranus kerzhneri*, Ch.gra = *Chorosoma gracile*, D.rot = *Diclytla rotundata*, E.cil = *Emblethis ciliatus*, M.are = *Menaccarus arenicola*, P.opa = *Pionosomus opacellus*, S.sab = *Stygnocoris sabulosus*, X.qua = *Xanthochilus quadratus*

Table 2. The table shows the explained variance of the habitat parameters (plant species richness, percentage cover of monocotyledonous plants, dicotyledonous plants, mosses and lichens, leaf litter, bare soil surface) according to RDAs. The marginal and partial effects of the parameters on the true bug assemblages are given in separated columns. Significance of parameters was tested by Monte-Carlo procedure with 1000 permutations.

Habitat parameters	Variance explained (%)	
	Marginal effect	Partial effect
Monocotyledonous plants	20.28 (p = 0.005)	3.00 (p = 0.032.)
Dicotyledonous plants	57.48 (p = 0.005)	3.21 (p = 0.022)
Mosses and lichens	8.20 (p = 0.055)	4.61 (p = 0.013)
Leaf litter	36.55 (p = 0.005)	4.54 (p = 0.015)
Bare soil surface	58.04 (p = 0.005)	3.41 (p = 0.032)
Plant species richness	34.54 (p = 0.005)	1.90 (p = 0.090)

constraints (pseudo-F = 15.27, $p = 0.005$, based on Monte-Carlo procedure with 1000 permutations). According to variance partitioning, most of the measured environmental variables influenced the bug assemblages significantly, however, their effects overlapped highly (Table 2).

The correlation analyses (Table 3) showed significant correlations between the species richness of true bugs, the distance from the edge and some of the measured habitat variables at site one. The species richness of true bugs correlated positively with the distance from the edge and the coverage of mosses and lichens but

Table 3. Spearman's rho values show correlations between species richness of true bugs (Bugrich), the habitat parameters (plant species richness (Plarich), percentage cover of monocotyledonous plants (Monoc), dicotyledonous plants (Dicot), mosses and lichens (MoLi), leaf litter (Litter), bare soil surface (Soil)) and the distance from the edge (Dist). The triangle above contains the Spearman's rho values at site two. The triangle below contains the Spearman's rho values at site one. The level of p-values (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$) are given after Bonferroni type error adjustments. Significant values before the type error adjustments are marked in bold.

site 1 \ site 2	Monoc	Dicot	MoLi	Litter	Soil	Plarich	Dist	Bugrich
Monoc		-0.07	-0.28	-0.46	-0.41	0.34	0.11	-0.02
Dicot	0.02		-0.25	-0.47	0.37	0.02	0.87**	0.42
MoLi	-0.37	0.59		-0.20	-0.30	-0.43	-0.50	-0.51
Litter	0.14	-0.84**	-0.87**		-0.04	-0.19	-0.46	0.24
Soil	-0.28	0.60	0.42	-0.62		0.28	0.47	0.14
Plarich	-0.23	0.77*	0.34	-0.65	0.59		0.19	0.19
Dist	-0.34	0.62	0.92***	-0.86**	0.43	0.34		0.34
Bugrich	-0.25	0.66	0.91***	-0.90***	0.40	0.43	0.93***	

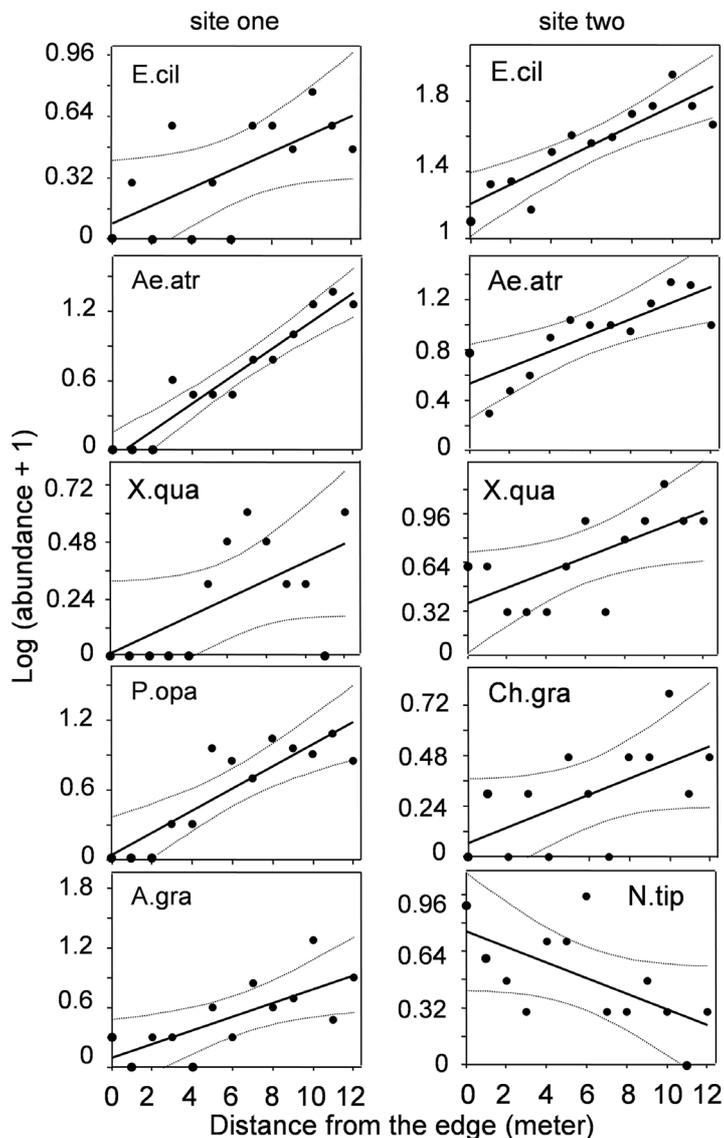


Fig. 4. The significant relations between the abundance of true bug species and the distance from the edge. At site one: E.cil ($r^2 = 0.42$, $F_{1,11} = 8.085$, $p = 0.0159$); Ae.atr ($r^2 = 0.92$, $F_{1,11} = 124.20$, $p < 0.0001$); X.qua ($r^2 = 0.37$, $F_{1,11} = 6.339$, $p = 0.0286$); P.opa ($r^2 = 0.76$, $F_{1,11} = 34.83$, $p = 0.0001$); A.gra ($r^2 = 0.54$, $F_{1,11} = 12.85$, $p = 0.0043$); site two: E.cil ($r^2 = 0.78$, $F_{1,11} = 38.55$, $p < 0.0001$); Ae.atr ($r^2 = 0.66$, $F_{1,11} = 21.06$, $p = 0.0008$); X.qua ($r^2 = 0.37$, $F_{1,11} = 6.339$, $p = 0.0286$); Ch.gra ($r^2 = 0.45$, $F_{1,11} = 9.17$, $p = 0.0114$); N.tip ($r^2 = 0.39$, $F_{1,11} = 6.971$, $p = 0.0229$); The error bands show the 95% confidence for the fitted line. The abbreviations of the species: A.gra = *Acalypta gracilis*, Ae.atr = *Aellopus atratus*, Ch.gra = *Chorosoma gracile*, E.cil = *Emblethis ciliatus*, N.tip = *Neides tipularius*, P.opa = *Pionosomus opacellus*, X.qua = *Xanthochilus quadratus*

negatively with the leaf litter. At site two, the species richness of true bugs did not correlate with any variables. We found significant correlation between the distance from the edge and the cover of dicotyledonous plants, only.

In spite of the fact that several species were observed in the forest habitats, only the indicator values of *Ceratocombus coleoptratus* and *Stygnocoris sabulosus* were significant, according to the indicator species analyses (Table 1). As it was expected, the highest number of species were related to grassland habitats. The most abundant species were *Emblethis ciliatus*; *Aellopus atratus*; *Pionosomus opacellus* and *Acalypta gracilis*, these had high indicator values in the case of both sites. Besides the above species, *Coranus kerzhneri* and *Xanthochilus quadratus* had significant indicator values in the case of site one and *Chorosoma gracile* in the case of site two.

The relations between the abundance of species and the distance from the edge showed that species responded differently to the edge (for the significant relations see Fig. 4). The abundance of *E. ciliatus*, *Ae. atratus* and *X. quadratus* decreased significantly toward the edge at both sites. *P. opacellus* and *A. gracilis* responded negatively to the poplar edge, but they were not affected by the proximity of the juniper edge ($r^2 = 0.11$, $F_{1,11} = 1.352$, $p = 0.2696$ and $r^2 = 0.00$, $F_{1,11} = 0.0435$, $p = 0.8385$, respectively). *Ch. gracile* seemed to respond negatively to edges, however, it was not analysed at site one, because of its low abundance. *Neides tipularius* showed positive relation to the proximity of the edge at site two however, at site one, significant relationship was not found ($r^2 = 0.10$, $F_{1,11} = 1.295$, $p = 0.7293$). *Coranus kerzhneri* was not influenced by the distance from the edges ($r^2 = 0.30$, $F_{1,11} = 4.692$, $p = 0.0531$ and $r^2 = 0.14$, $F_{1,11} = 1.749$, $p = 0.2129$ at site one and site two, respectively).

DISCUSSION

The fine scale pattern of Heteroptera assemblages was studied across two natural sharp vegetational edges: poplar forest–open grassland and juniper forest–open grassland. Among the species associated with forest habitats, *C. coleoptratus* lives under dead vegetation, litter and wet mosses at various habitat types (RÉDEI & HUFNAGEL 2002). This species, presumably, found the adequate humidity in deciduous forests at such xeric areas. At site two more species were collected exclusively in the scrubland as several of them e.g. *E. fenestratus*, *G. juniperi* are associated to junipers (WAGNER 1966, PÉRICART 1998). The most collected species were associated to the grassland habitats. These species typically occur in the sandy grasslands of the Kiskunság (BAKONYI & VÁSÁRHELYI 1987).

In spite of the similar species composition, the response of the grassland assemblages to the edge differed between the sites. In general, grassland insect species respond negatively to forest or shrubland edges (BIERINGER & ZULKA 2003, SAMWAYS & MOORE 1991). The decreasing species richness of true bugs toward the edge at site one also suggested a negative edge effect. Moreover, the abundance of the analysed species, except for *C. kerzhneri*, decreased toward the poplar edge. In accordance with these decreasing trends, the change of the assemblage structure denoted an approximately 7 m wide transition zone in the grassland. In the case of site two, however, we found that both the species richness and the assemblage structure of true bugs changed abruptly, close to the edge in the juniper forest. These patterns suggested that the true bug assemblage responded strongly to the change of the habitat quality, but weakly to the proximity of the edge (DURĂES *et al.* 2005).

The different responses of grassland bug assemblages to the edge were probably due to the influence of high trees at site one e.g. on the light regime, leaf litter, vegetation coverage on the nearby part of the grassland. Several authors (e.g. SPARKS & GREATORIX-DAVIES 1992, ENTLING *et al.* 2007, GOSSNER 2009) reported the influence of shading on different arthropods. Moreover, the light level also affected the plant species resulting in linked patterns of light regime, plant and insect species richness at edge zones GREATORIX-DAVIES *et al.* 1994). The impact of various vegetation properties e.g. vegetation species composition (SANDERSON *et al.* 1995, TORMA *et al.* 2010), vegetation structure and flower abundance (ZURBRÜGG & FRANK 2006), plant diversity or plant species richness (FRANK & KÜNZLE 2006) on true bug assemblages is well known. The coverage of mosses and lichens can influence the specialist herbivores feeding on them, e.g. the *Acalypta* species (RÉDEI *et al.* 2004) and it may affect the diversity and population density of epigeic true bugs in general as they may serve as shelters for the species (SPUNGIS 2005). On the other hand, the bare soil surface and leaf litter also had a great impact on the bug assemblages. The movement of true bugs is mainly walking (DOLLING 1991), therefore the complexity of surface is an important factor for their locomotion (YANG 2000). The proportion of bare soil and the type of the leaf litter as a property of the soil surface may be important factors for the ground-dwelling bugs in this sense.

However, various feeder groups (e.g. plant feeders, predators, etc.) presumably are not influenced by the same factors, moreover influential factors may differ between the degrees of feeding specialization, e.g. between specialist and generalist herbivores (JONSEN & FAHRIG 1997). For example, the decreasing patterns of the specialist herbivorous species *E. ciliatus* (feeds on *Euphorbia* spp.) and *Ae. atratus* (feeds on Boraginaceae) may be explained by the decrease in the density of

their host plants. Note, the dominant dicotyledonous plants were *Euphorbia cyparissias* and *Alkanna tinctoria* and the coverage of dicotyledonous plants also decreased toward the edge at both sites. Whereas the abundance of zoophagous (e.g. *C. kerzhneri*) and polyphagous herbivore (e.g. *N. tipularius*) species did not decrease or it decreased only towards the poplar edge (e.g. *P. opacellus*). For zoophagous and polyphagous herbivore species the habitat structure is an important factor (DI GIULIO *et al.* 2001) which changed notably in the case of the poplar edge.

The edge effect is taxon dependent (DANGERFIELD *et al.* 2003) so it was not surprising that different species responded differently to the edges. In spite of this fact, the observed changes of assemblage structure of true bugs seemed to be general patterns at small scale. Both similar sharp boundaries and dissolving zones of epigeic true bug assemblages were observed previously in sand grasslands (TORMA & KÖRMÖCZI 2009, GALLÉ *et al.* 2010). However, a higher species richness in the transition, than adjacent habitats and species turnover in the transition between two habitats were not observed. These patterns seem to be not typical at such small scale. It seems that the general small-scale patterns of true bug assemblages may be driven by the variation in the environmental conditions than by biotic interactions. Sharp changes of environmental conditions cause a sharp boundary while along a gradual change of environmental conditions epigeic true bug assemblages of sand grasslands dissolved.

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REFERENCES

- BAKONYI, G. & VÁSÁRHELYI, T. (1987) The Heteroptera fauna of the Kiskunság National Park. Pp. 85–106. In: MAHUNKA, S. (ed.): *The fauna of the Kiskunság National Park*. Vol. 2. Akadémiai Kiadó, Budapest.
- BIERINGER, G. & ZULKA, K. P. (2003) Shading out species richness: edge effect of a pine plantation on the Orthoptera (Tettigoniidae and Acrididae) assemblage of an adjacent dry grassland. *Biodiversity and Conservation* **12**: 1481–1495.
- BURGESS, V. J., KELLY, D., ROBERTSON, A. W. & LADLEY, J. J. (2001) Positive effects of forest edges on plant reproduction: literature review and a case study of bee visitation to flowers of *Peraxilla tetrapetala* (Loranthaceae). *Plant Ecology* **153**: 347–359.

- CAPPUCCINO, N. & ROOT, R. B. (1992) The significance of host patch edges to the colonization and development of *Corythucha marmorata* (Hemiptera: Tingidae). *Ecological Entomology* **17**(2): 109–113.
- CHAO, A., CHAZDON, R. L., COLWELL, R. K. & SHEN, T. J. (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters* **8**: 148–159.
- COLWELL, R. K. (2004) EstimateS, Version 8.0: Statistical Estimation of Species Richness and Shared Species from Samples (Software and User's Guide). Freeware for Windows and Mac OS. <http://viceroy.eeb.uconn.edu/EstimateS>. Accessed at May 12, 2010.
- COSCARON, M. C., MELO, M. C., CODDINGTON, J. & CORRONCA, J. (2009) Estimating biodiversity: a case study on true bugs in Argentinian wetlands. *Biodiversity and Conservation* **18**: 1491–1507.
- DANGERFIELD, J. M., PIK, A. J., BRITTON, D., HOLMES, A., GILLINGS, M., OLIVER, I., BRISCOE, D. & BEATTIE, A. J. (2003) Patterns of invertebrate biodiversity across a natural edge. *Austral Ecology* **28**: 227–236.
- DI GIULIO, M., EDWARDS, P. J. & MEISTER, E. (2001) Enhancing insect diversity in agricultural grasslands: the roles of management and landscape structure. *Journal of Applied Ecology* **38**: 310–319.
- DOLLING, W. R. (1991) *The Hemiptera*. Oxford University Press, Oxford, 273 pp.
- DUFRENE, M. & LEGENDRE, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* **67**(3): 345–366.
- DURÃES, R., MARTINS, W. P. & VAZ-DE-MELLO, F. Z. (2005) Dung Beetle (Coleoptera: Scarabaeidae) assemblages across a natural forest-cerrado ecotone in Minas Gerais, Brazil. *Neotropical Entomology* **34**(5): 721–731.
- ENTLING, W., SCHMIDT, M. H., BACHER, S., BRANDL, R. & NENTWIG, W. (2007) Niche properties of Central European spiders: shading, moisture and the evolution of the habitat niche. *Global Ecology and Biogeography* **16**: 440–448.
- FERGUSON, S. H. (2004) Influence of edge on predator-prey distribution and abundance. *Acta Oecologica* **25**: 111–117.
- FRANK, T. & KÜNZLE, U. (2006) Effect of early succession in wildflower areas on bug assemblages (Insecta: Heteroptera). *European Journal of Entomology* **103**: 61–70.
- GALLÉ, L., GYÖRFFY, GY., HORNUNG, E. & KÖRMÖCZI, L. (1988) Indication of environmental heteromorphy and habitat fragmentation by invertebrate communities in grasslands. Pp. 167–170. In: BOHAC, J. & RUZICKA, V. (eds): *Proc. Vth Int. Conf. Bioindicators Deteriorationis Regionis*. Institute of Landscape Ecology CAS, Czeske Budejovice.
- GALLÉ, R. & FEHÉR, B. (2006) Edge effect on spider assemblages. *Tiscia* **35**: 37–40.
- GALLÉ, R. & TORMA, A. (2009) Epigeic spider (Araneae) assemblages of natural forest edges in the Kiskunság (Hungary). *Community Ecology* **10**(2): 146–151.
- GALLÉ, R., TORMA, A. & KÖRMÖCZI, L. (2010) Small-scale effect of habitat heterogeneity on invertebrate assemblages in sandy grasslands (Hungarian Great Plane). *Polish Journal of Ecology* **58**(2): 333–346.
- GOSSNER, M. M. (2009) Light intensity affects spatial distribution of Heteroptera in deciduous forests. *European Journal of Entomology* **106**: 241–252.
- GREATOREX-DAVIES, J. N., SPARKS, T. H. & HALL, M. L. (1994) The response of Heteroptera and Coleoptera species to shade and aspect in rides of coniferised lowland woods in Southern England. *Biological Conservation* **67**: 255–273.
- HARMAT, B. (1984) *Ecological studies of true bug assemblages in an open sand grassland*. PhD thesis, József Attila University, Szeged, 93 pp. [In Hungarian]

- HOCHKIRCH, A., GÄRTNER, A. C. & BRANDT, T. (2008) Effects of forest-dune ecotone management on the endangered heath grasshopper, *Chorthippus vagans* (Orthoptera: Acrididae). *Bulletin of Entomological Research* **98**: 449–456.
- HORVÁTH, R., MAGURA, T., PÉTER, G. & TÓTHMÉRÉSZ, B. (2002) Edge effect on weevils and spiders. *Web Ecology* **3**: 43–47.
- JONSEN, I. D. & FAHRIG, L. (1997) Response of generalist and specialist insect herbivores to landscape spatial structure. *Landscape Ecology* **12**: 185–197.
- KERÉNYI, Z. (1997) *Changes in the structure of true bug assemblages affected by disturbance in an open sand grassland*. Thesis, József Attila University, Szeged, 39 pp. [In Hungarian]
- KONDOROSY, E. (1999) Checklist of the Hungarian bug fauna (Heteroptera). *Folia Entomologica Hungarica* **60**: 125–152.
- KOTZE, D. J. & SAMWAYS, M. J. (2001) No general edge effect for invertebrates at Afromontane forest/grassland ecotones. *Biodiversity and Conservation* **10**: 443–466.
- LEGENDRE, P. & LEGENDRE, L. (1998) *Numerical ecology* (2nd English edition). Elsevier Science BV, Amsterdam, 853 pp.
- LEPŠ, J. & ŠMILAUER, P. (2003) *Multivariate analysis of ecological data using CANOCO*. Cambridge University Press, Cambridge, UK, 292 pp.
- LEOPOLD, A. (1933) *Game management*. Charles Scribner and Sons, New York, 375 pp.
- MAGURA, T. & TÓTHMÉRÉSZ, B. (1997) Testing edge effect on carabid assemblages in an oak-hornbeam forest. *Acta Zoologica Academiae Scientiarum Hungariae* **43**(4): 303–312.
- MAGURA, T. & TÓTHMÉRÉSZ, B. (1998) Edge effect on carabids in an oak-hornbeam forest at the Aggtelek National Park (Hungary). *Acta Phytopathologica et Entomologica Hungarica* **33**: 379–387.
- MAGURRAN, A. E. (2004) *Measuring biological diversity*. Blackwell Publishing, Oxford, 256 pp.
- MÁTHÉ, I. (2006) Forest edge and carabid diversity on a Carpathian beech forest. *Community Ecology* **7**: 90–97.
- MOLNÁR, T., MAGURA, T., TÓTHMÉRÉSZ, B. & ELEK, Z. (2001) Ground beetles (Carabidae) and edge effect in oak-hornbeam forest and grassland transects. *European Journal of Soil Biology* **37**: 297–300.
- MULLEN, K., FAHY, O. & GORMALLY, M. (2003) Ground flora and associated arthropod communities of forest road edges in Connemara, Ireland. *Biodiversity and Conservation* **12**: 87–101.
- MURCIA, C. (1995) Edge effect in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* **10**: 58–62.
- MÜLLER, J., BUBLER, H., GROBNER, M., GRUPPE, A., JARZABEK-MÜLLER, A., PREIS, M. & RETTELBACH, T. (2007) Forest edges in the mixed-montane zone of the Bavarian Forest National Park – hot spots of biodiversity. *Silva Gabreta* **13**(2): 121–148.
- ODUM, E. P. (1971) *Fundamentals in ecology*. 3rd ed. Philadelphia, Saunders, 574 pp.
- OKSANEN, J., KINDT, R., LEGENDRE, P. & O'HARA, R. B. (2006) *Vegan: Community Ecology Package*. Version 1.8–3.
- OKSANEN, J. (2011) Multivariate analysis of ecological communities in R: vegan tutorial. <http://cran.r-project.org>.
- PÉRICART, J. (1998) Hémiptères Lygaeidae Euro-Méditerranéens, France et régions limitrophes. Vol. 1. In: *Faune de France. Vol. 84a*. Fédération Française des Sociétés de Sciences Naturelles, Paris, 468 pp.
- R DEVELOPMENT CORE TEAM (2007) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3–900051–07–0, <http://www.R-project.org>.
- RÉDEI, D. & HUFNAGEL, L. (2002) Beiträge zur Kenntnis der Dipsocoromorpha-Arten (Insecta: Heteroptera) in Ungarn. *Opuscula Zoologica* **34**: 67–76.

- RÉDEI, D., GAÁL, M. & HUFNAGEL, L. (2003) Spatial and temporal patterns of true bug assemblages extracted with Berlese funnels (Data to the knowledge on the ground-living Heteroptera of Hungary, No. 2). *Applied Ecology and Environmental Research* **1**: 115–142.
- RÉDEI, D., HARMAT, B. & HUFNAGEL, L. (2004) Ecology of the Acalypta species occurring in Hungary (Insecta: Heteroptera: Tingidae) (Data to the knowledge on the ground-living Heteroptera of Hungary, No. 3). *Applied Ecology and Environmental Research* **2**: 73–90.
- ROBERTS, D. W. (2010) labdsv: Ordination and Multivariate analysis for ecology. <http://ecology.msu.montana.edu/labdsv/R>
- SAMU, F. & SÁROSPATAKI, M. (1995) Design and use of a hand-held suction sampler, and its comparison with sweep net and pitfall trap sampling. *Folia Entomologica Hungarica* **56**: 195–203.
- SAMWAYS, M. J. & MOORE, S. D. (1991) Influence of exotic conifer patches on grasshopper (Orthoptera) assemblages in a grassland matrix at a recreational resort, Natal, South Africa. *Biological Conservation* **57**: 117–137.
- SANDERSON, R. A., RUSHTON, S. P., CHERILL, A. J. & BYRNE, J. P. (1995) Soil, vegetation and space: an analysis of their effects on the invertebrate communities of a moorland in north-east England. *Journal of Applied Ecology* **32**: 506–518.
- SCHWEIGER, O., MAELFAIT, J. P., VAN WINGERDEN, W., HENDRICKX, F., BILLETER, R., SPEELMANS, M., AUGENSTEIN, I., AUKEMA, B., AVIRON, S., BAILEY, D., BUKACEK, R., BUREL, F., DIEKOTTER, T., DIRKSEN, J., FRENZEL, M., HERZOG, F., LIIRA, J., ROUBALOVA, M. & BUGTER, R. (2005) Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. *Journal of Applied Ecology* **42**: 1129–1139.
- SOKAL, R. R. & ROHLF, F. J. (1995) *Biometry. The principles and practice of statistics in biological research*. 3rd ed. Freeman, New York, 887 pp.
- SPARKS, T. H. & GRETOREX-DAVIES, J. N. (1992) The effects of shade in plantation woodland on invertebrate abundance and diversity. *Aspects of Applied Biology* **29**: 89–96.
- SPUNGIS, V. (2005) Fauna and ecology of bugs (Hemiptera, Heteroptera) in the coastal grey dunes in Latvia. *Latvijas Entomologs* **42**: 95–105.
- STANDEN, V. (2000) The adequacy of collecting techniques for estimating species richness of grassland invertebrates. *Journal of Applied Ecology* **37**: 884–893.
- TABOADA, A., KOTZE, D. J. & SALGADO, J. M. (2004) Carabid beetle occurrence at the edges of oak and beech forests in NW Spain. *European Journal of Entomology* **101**: 555–563.
- TORMA, A. & KÖRMÖCZI, L. (2009) The influence of habitat heterogeneity on the fine-scale pattern of a Heteroptera assemblage in a sand grassland. *Community Ecology* **10**: 75–80.
- TORMA, A., VARGA, CS. & VARGA, M. (2010) Spatial pattern of true bugs (Heteroptera) in a heterogeneous grassland – preliminary results. *Acta Phytopathologica et Entomologica Hungarica* **45**(1): 81–87.
- TÖRÖK, K., HALASSY, M. & SZABÓ, R. (2003) Restoration strategy for endemic grasslands in a low productive region of Hungary. Pp. 1132–1138. In: ALLSOPP, N., PALMER, A. R., MILTON, S. J., KIRKMAN, K. P., KERLEY, G. I. H., HURT, C. R. & BROWN, C. J. (eds): *Proceedings of the VIIth International Rangelands Congress*. Durban, South Africa.
- VIDÉKI, R. (2004) Vegetation of sand dune areas in Kiskunság. Pp. 135–142. In: MOLNÁR, ZS. (ed.): *Dry sand vegetation of the Kiskunság*. Természetbúvár Kiadó, Budapest.
- WAGNER, E. (1966) Wanzen oder Heteropteren I. Pentatomorpha. In: DAHL, F. (ed.): *Die Tierwelt Deutschlands*. Vol. 55. VEB Gustav Fisher Verlag, Jena, 234 pp.
- WERMELINGER, B., FLÜCKIGER, P. F., OBRIST, M. K. & DUELLI, P. (2007) Horizontal and vertical distribution of saproxylic beetles (Col., Buprestidae, Cerambycidae, Scolytinae) across sections of forest edges. *Journal of Applied Entomology* **131**(2): 104–114.

- YANG, L. H. (2000) Effects of body size and plant structure on the movement ability of a predaceous stinkbug, *Podisus maculiventris* (Heteroptera: Pentatomidae). *Oecologia* **125**: 85–90.
- YU, X. D., LUO, T. H., YANG, J. & ZHOU, H. Z. (2006) Distribution of ground-dwelling beetles (Coleoptera) across a forest – clearcut ecotone in Wolong Natural Reserve, southwestern China. *Insect Science* **13**: 127–135.
- ZURBRÜGG, C. & FRANK, T. (2006) Factors influencing bug diversity (Insecta: Heteroptera) in semi-natural habitats. *Biodiversity and Conservation* **15**: 275–294.

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