The influence of habitat heterogeneity on the fine-scale pattern of an Heteroptera assemblage in a sand grassland

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Abstract: The influence of elevation and vegetation characteristics on the spatial pattern of an epigean true bug assemblage was investigated along a transect in a sandy grassland of Kiskunság. A 55 m long transect through wind grooves and dune tops, perpendicular to the vegetation borders was established. Both the moving split window technique and the ordination method revealed that dune top habitat has a distinct Heteroptera assemblage. This sand dune habitat was characterized by the most abundant Heteroptera species. We did not observe a distinct true bug assemblage in the wind groove habitat. Canonical correspondence analysis and multiple linear regressions showed that the relative altitude had a greater effect on the distribution of true bugs than vegetation cover and plant species richness.

Nomenclature follows: Kondorossy (1999).

Abbreviations: CCA—Canonical Correspondence Analysis, MSW—Moving Split Window.

Introduction

Habitat heterogeneity of grasslands derives from changes of several environmental factors (microrelief, exposure, soil moisture, soil organic carbon content). Human land use practices (grazing, moving, fertilising, burning) also influence the heterogeneity of grasslands (for review, see Denton et al. 2003). Heterogeneous habitats consist of more or less distinct habitat patches that are separated by boundaries. If a boundary is sharp, then a well-defined zone between the patches can be considered as ecotone with an abrupt change in the community structure (van der Maarel 1990). The transition between the stands, however, may be gradual without sharp boundary in accordance with the gradual change of background factors. In this case, it is difficult to determine the type and characteristics of such a transition, but it would be necessary to consider the structural properties and behaviour of the boundaries at a fine scale (Zalatnai et al. 2004, 2008).

In general, the spatial pattern of vegetation is the basis of distinguishing habitat patches. It has often been assumed that the arthropod assemblages are influenced by vegetation (Dennis et al. 1998). Several studies reveal the relationship between the characteristics of arthropod assemblages and vegetation properties: mainly the richness and composition of plant species and vegetation phystognomy are important in this respect (e.g. Murdock et al. 1972, Dennis et al. 1998). Other studies emphasize the impact of other background factors, e.g. soil conditions or management practices (Rush et al. 1991, Sanderson et al. 1995). Recently, several papers have been published about arthropod communities related to edge effect or grassland managements (e.g. Magura and Tóthmérész 1997, 1998, Magura 2002, Horváth et al. 2002, Madlif and De Keer 1990, Martin and Major 2001, Guido and Giannell 2001, Bieringer and Zula 2003), which help to understand the properties of transitions and patterns in accordance with the environmental variables.

This study was carried out in the Kiskunság region which is situated in the middle part of the Hungarian Great Plain. The mosaic-like landscape structure of the region consists mainly of agricultural fields and forest plantations, but some patches of the original natural habitats also occur. One of the latter is Böcsa-Bugac sand dune area (10920 ha) belonging to the Kiskunság National Park. The Böcsa-Bugac region is a typical mosaic-like complex with wind grooves and dunes shaped by the wind. These habitats differ in microclimate conditions, vegetation and invertebrate communities (Körmöczi et al. 1981, Győrfy and Pollák 1983, Harmat 1984, Gálle et al. 1987, 1988).

The Heteroptera fauna of Kiskunság is relatively well-known, numerous rare and unique species occur here due to the sericand unique habitats (Bakonyi and Vásárhelyi 1987). True bugs are an ecologically very diverse group, including saprophagous, zoophagous and mainly phytophagous species (Dolling 1991). The richness of the Heteroptera fauna correlates strongly with total insect diversity (Duelli and Obrist 1998). True bugs have an important role in grassland ecosystems mainly as a primary consumer (Knowlton 1967) and they are suitable ecological objects to study the effect of grassland patchiness.

The aims of this study were a) to reveal the fine-scale pattern of epigean Heteroptera assemblages; b) to detect if there are any boundaries indicated by true bugs; c) to seek...
correspondence between vegetation and Heteroptera assemb-
blage patterns in a heterogeneous sandy grassland habitat.

Material and methods

Study site

Investigations were carried out in a sand dune area of the
Kiskunság National Park nearby Bugacpusztaháza village.
The study site was an approximately 2.4 ha area and it was
earthera sandy pasture. The site was fenced in the 1970-sand
no management (grazing or cutting) has been applied since
then.

The relief is characterized by sand dunes and wind
grooves with an average elevation difference of approxi-
mately 2 m. The elevation difference between the highest
and lowest points of the study area is 2.8 m. The soil is loose sand
on the dunes and humous sand in the grooves. Plant associa-
tions of the higher sand hills are calciphilous Sesame steppe
(Festucetum vaginatae) and Pannonian sand pusztas (Poten-
tillo-Festucetum pseudovinaceum), and bronze sward (Brontum
tectorum) in the very dry patches. The 1.5-2 m deep wind
grooves are covered with purple moorgrass meadow
(Molino-Salicetum rosmarinifolii, Körömisczi 1983). By
now, the Molinia series are in a transitional state toward the
dry grasslands due to the drop of the water table (Kör-
ömöczi et al. 2000).

Sampling methods

To investigate the habitat heterogeneity, we established
a 55 m × 55 m, SW-NE running transect through wind grooves
and dune-tops perpendicular to the supposed vegetation borders.
We recorded the relative elevation along the transect.

Percentage cover of plant species was recorded in 0.25/0.25
m² continuously placed quadrats (N = 220) along the transect
in May 2003. We used pitfall traps (55 mm in diameter) with
ethylene glycol as a killing-preserve solution for sampling
epigeic true bugs. 110 pitfall traps were applied in two parallel
transects. Distance between the traps was 1 m and they
worked for two weeks three times in the year 2003 (May 20
–June 3, July 29 – August 8, and September 4–18). Although
a combined sweep net and D-vac sample is an adequate tech-
nique to collect true bugs according to Standen (2000), we
used pitfall traps for several reasons.

Sweep netting is not a suitable sampling method in the
case of such a fine scale and it samples only the plant-dwell-
ning arthropods. However, in the sand dune area of the
Kiskunság, epigeic true bugs are more abundant (Harmat
1984, Kerényi 1997); moreover, Spungsis (2005) found
a higher species richness of epigeic true bugs then plant-dwell-
ing true bugs at a coastal dune area. Suction sampling collects
animals from both the vegetation and ground surface (Samu
and Sámúspatik 1995), but it needs a great effort to sort the
material collected from open sandy grassland because of the
great amount of sand picked up during the sampling process.
Finally, both Harmat (1984) and Kerényi (1997) found that

pitfall trapping was a suitable method for ecological investiga-
tions in open sand grasslands. Only the adult individuals
were identified at the species level.

Data analysis

The parallel transects of pitfall traps were pooled for the
analyses. We used the moving split window technique
(MSW) with squared Euclidean distance and the com-
plement of R forkon Simon index as dissimilarity function
to detect the discontinuities in Heteroptera assemblages and
vegetation along the transect. This is a powerful method for
detecting boundaries in the case of both vegetation (Whitt-
taker 1956, van der Maarel 1976, Körömisczi 2005) and
animal assemblages (Magura 2002, Gallé et al. 2007). Both
quantitative and presence/absence data were applied in the
boundary detection.

The significance of the peaks was tested with the Z-score
transformation of the squared Euclidean distance values

Random forest was made with the Monte Carlo method: the population patterns were randomly shifted com-
pared to each other (Horváth 1998), and 1000 randomiza-
tions were performed. The differential profiles were drawn
from Z-scores averaged over 1 to 20 half-window sizes for
the vegetation and over 1 to 5 half-window sizes for the true
bugs. For further analysis, the vegetation samples were
pooled in 0.5 m² quadrats (N = 55) for comparison with Het-
eroptera samples.

The Mantel test with Bray-Curtis similarity was applied to
reveal the correlation between the plant and Heteroptera
assemblages (Leps et al. 2001). We calculated the percentage
cover of plant species and plant species richness per quad-
art as well as the relative elevation to use them as explanatory
variables. We used the same explanatory variables for further
analyses.

Canonical correspondence analysis (CCA) was used to
explain bug species variations in samples by the variation of
the ecological parameters (Ter Braak 1986). Significance for
explanatory variables was obtained by the permutation test
available in R vegan package (Oksanen et al. 2006). Number
of permutations was 500. Two CCA procedures were carried
out. The first one was carried out with the whole data set,
whereas in the second procedure the species under 0.5% fre-
quency were omitted. In spite of the fact that the explained
inertia was double in the second procedure, the significant
factors and their significance levels were the same. Hence,
we omitted no species from analysis, and present only the
results of the first procedure. Moreover, rare species may be
good indicators for ecological quality of habitat (Lyons et
al. 1995) or species richness (Cuise et al. 2000), therefore
eclusion of these species may result in losing valuable infor-
mation (Cao et al. 2001).

To reveal the relation ship between the bug assemblages
and habitat heteromorphy we used multiple regression analy-
sis. The structure of Heteroptera assemblages was described.
by the species richness and abundance given as the average number of species per trap and the total number of individuals per trap, respectively. About 75% of the total number of individuals belonged to the three most abundant species therefore we computed further regressions to reveal the impact of factors on these species. The number of individuals of these species was transformed by square root transformation, which resulted the best fit of linear regression.

Spearman’s coefficient of rank correlation was used to analyse correlations between the distribution of the monophagous species *Piesma kochiae* and its host plant.

Analyses were carried out with R (R Development Core Team 2007) and SPSS 11.5 for WINDOWS software packages.

**Results**

The vegetation of the transect consisted of 52 species, 19 of which were observed at least twice. The most frequent species were the xerotolerant grasses and cryptogam species on higher relief, but longleaf (*Falcaria vulgaris*), which was the most frequent species in the transect, occurred also in the grooves. Longleaf indicates a certain degraded state of the grassland due to the long dry period. Most of the species showed a strongly aggregated spatial distribution, thus the arrangement of the dominant species marked the characteristic segments of the transect, which are identified as community types of the sandy grassland (Zulatnaï et al. 2008).

Based on the composition of vegetation, four patches were separated by a narrower peak (at 12 m) and two wider transitional zones (at 19-21 m and 42-45 m; see Fig. 1d). This pattern corresponded to the relief profile, since the mesophytic species were situated mainly in the grooves forming recognizable vegetation patches. The boundaries detected along the transect were neither wide transitional zones with the average width of 3 m. Midpoints of the boundaries revealed by the MSW-analyses were at 12 m, 20.5 m and 43.5 m.

A total of 911 adult individuals belonging to 41 Heteroptera species were collected. Eleven species occurred with only one specimen in the traps and about 75% of the individuals belonged to the most abundant species, *Emblethis ciliatus* (49.40%), *Pionosomus opacellus* (17.12%) and *Piesma kochiae* (6.37%).

With the MSW analysis of the quantitative data, we detected two significant peaks (Fig. 1c) that delineated the Heteroptera assemblage of the dune-top habitat. This was the place of the most abundant occurrence of the dominant species. Significant Z-score peaks at 37 m and 40 m using quantitative data emphasize the large abundance of the dominant Heteroptera species. Analysis of binary data, however, showed peaks at 12, 17, 22 and 27 m, the first two of which were significant with Renkonen index (Fig. 1a), and the second two with squared Euclidean distance (Fig. 1b), indicating considerable differences in species composition and species frequency, respectively (Kömöczi 2005). Full coincidence of the Z-score peaks of true bugs and vegetation was observed only at one point (12 m) where both the vegetation and the Heteroptera assemblage showed a sharp change.

The Mantel test showed no significant correlation between the Heteroptera and plant assemblages (r = 0.183; p = 0.0589).

The aim of the correspondence analysis was to reveal the variation in Heteroptera samples induced by vegetation cover, plant richness and relative altitude. The ordination re-

![Figure 1](image-url). Profile diagram of Z-score values for the Heteroptera assemblage (Renkonen index (a) and binary (b) and quantitative data (c) analysed with squared Euclidean distance) averaged over 1-5 half-window width and for the vegetation averaged over 1-20 half window width (d). Horizontal broken lines indicate 5% significance levels for the separate analyses. Vertical solid lines mark peaks significant on the profile diagrams (a), (b) and (c). Profile diagrams are shifted compared to each other with their own significance levels, therefore the vertical scale is not relevant. The profile of relative elevation is marked with a thick broken line.
Table 1. Partial CCA revealing the impact of plant species richness, total cover of vegetation and relative elevation on true bug assemblage. Significance of parameters was tested by a Monte-Carlo procedure with 500 permutations.

<table>
<thead>
<tr>
<th>Environmental variables</th>
<th>Inertia explained (%)</th>
<th>F-ratio</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>relative altitude</td>
<td>6.07</td>
<td>2.4704</td>
<td>&lt;0.005</td>
</tr>
<tr>
<td>cover of vegetation</td>
<td>0.98</td>
<td>0.3071</td>
<td>0.885</td>
</tr>
<tr>
<td>plant species</td>
<td>2.48</td>
<td>1.0101</td>
<td>0.01</td>
</tr>
<tr>
<td>richness</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Multiple linear regression analysis revealing the relation between species richness and the abundance of true bugs and habitat properties, as well as between the abundance of dominant species and habitat properties. (Abbreviations: cov: total cover of vegetation; plants: plant species richness; rel: relative elevation)

<table>
<thead>
<tr>
<th>Species</th>
<th>Model</th>
<th>cov</th>
<th>plants</th>
<th>rel</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average number of bug species per trap</td>
<td>$R^2 = 0.450$</td>
<td>$b = 0.250$</td>
<td>$b = 0.061$</td>
<td>$b = 0.742$</td>
</tr>
<tr>
<td></td>
<td>$F = 15.490$</td>
<td>$p = 0.797$</td>
<td>$p = 0.004$</td>
<td>$p = 0.001$</td>
</tr>
<tr>
<td>Total number of bug species per trap</td>
<td>$R^2 = 0.476$</td>
<td>$b = 0.072$</td>
<td>$b = 0.079$</td>
<td>$b = 0.617$</td>
</tr>
<tr>
<td></td>
<td>$F = 17.050$</td>
<td>$p = 0.704$</td>
<td>$p = 0.005$</td>
<td>$p = 0.001$</td>
</tr>
<tr>
<td>Embachius citatus</td>
<td>$R^2 = 0.434$</td>
<td>$b = 0.333$</td>
<td>$b = 0.155$</td>
<td>$b = 0.005$</td>
</tr>
<tr>
<td></td>
<td>$F = 14.811$</td>
<td>$p = 0.267$</td>
<td>$p = 1.378$</td>
<td>$p = 0.001$</td>
</tr>
<tr>
<td>P. kochiae</td>
<td>$R^2 = 0.585$</td>
<td>$b = 0.136$</td>
<td>$b = 0.267$</td>
<td>$b = 0.651$</td>
</tr>
<tr>
<td></td>
<td>$F = 28.262$</td>
<td>$p = 0.208$</td>
<td>$p = 0.025$</td>
<td>$p = 0.001$</td>
</tr>
<tr>
<td>P. kochiae</td>
<td>$R^2 = 0.512$</td>
<td>$b = 0.090$</td>
<td>$b = 0.154$</td>
<td>$b = 0.656$</td>
</tr>
<tr>
<td></td>
<td>$F = 19.590$</td>
<td>$p = 0.521$</td>
<td>$p = 1.256$</td>
<td>$p = 4.769$</td>
</tr>
</tbody>
</table>

Results showed that the samples that were located at dune top handled together, while the samples of lower relief were scattered and overlapped each other (Fig. 2). The three constrained axes represented 9.11% of the total inertia. The first axis corresponds to elevation ($r = -0.9446$), and the second axis corresponds to plant species richness ($r = -0.8042$). Of the three explanatory variables, relative elevation and plant species richness contributed significantly to the distribution of true bugs (Table 1). The constrained axes of CCA explained a low amount of the total inertia, however Okanen (2008) suggested to concentrate on the whole result instead of the proportions of inertia, because the total inertia does not have a clear meaning in CCA and most of the total inertia may be random noise.

The total regression models were significant in each case (Table 2). According to the partial correlation coefficients, elevation had a significant effect on the structure of Heteroptera assemblages and on the abundance of dominant species along the transect and the plant species richness had negative effect on the abundance of $P.$ opacillus (Table 2). A significant correlation ($r = 0.411; p = 0.002$) was found between the distribution of $P.$ kochiae and its host plant Kochia laniflora.

Discussion

Multivariate data on Heteroptera assemblage were collected in a transect parallel with vegetation sampling to reveal their spatial pattern and the patchiness of habitats. The results suggest that MSW analysis is a successful method to detect boundaries on such a fine scale and shows similar results to ordination. Both methods reveal that the dune top habitat has a distinct Heteroptera assemblage. Beyond the top, at the southern slope, there is a transition zone characterized by the dissolving of the dune top assemblage. MSW analysis, however, showed significant changes of species composition also at the margins of wind grove, but we did not find a distinct Heteroptera assemblage in the wind grove habitat, contrary to Harmat (1984). We did not find a consistent species composition of the samples situated at the wind grove: the samples varied strongly. Moreover, the abundance and species richness were rather low in these samples. According to Harmat (1984), five abundant species were associated with wind grove habitats from which, Rhyparochromus pini and Xanthochilus quadratus also occurred in our sample, but their abundance was rather low. We did not observe Dimorphopterus spinolai, which was the dominant species in wind groves, according to both Harmat (1984) and Kerényi (1997). Thus, the wind grove was not characterized by a distinct bug assemblage associated with this habitat type. Most bug species, particularly the dominant ones, were observed in the dune top habitat where the species composition was similar to what was ascertained by Harmat (1984).

We hypothesized that at the point where a vegetation boundary was detected, a similar boundary should be expected in phytophagous insect assemblages, too. Despite the fact that the order Heteroptera includes mainly herbivorous
species which are associated with the vegetation (Zurbrügg and Frank 2006) and several studies reported the relation between epigeic bugs and vegetation properties, e.g. vegetation height and density (Bröring and Wiegleb 2005), or coenological structure (Gallé et al. 2007), we did not find clear accordance in vegetation and Heteroptera boundaries. Moreover, the Mantel test showed no correlation between the species composition of the vegetation and Heteroptera assemblages.

Di Giulio et al. (2001) found that the bug fauna is affected more strongly by the texture and the microclimatic conditions of the grasslands than by plant species richness. They suggested that in the case of zoophagous and polyphagous herbivore species the plant species richness might play a less important role than the textural diversity of the habitat.

In spite of the low amount of the explained inertia in CCA, we found that elevation, which primarily determines the microclimate, had a greater effect than vegetation variables (plant species richness or the cover of vegetation) on true bugs. The regression analysis confirmed the result of CCA, indicating a strong relationship between species richness and abundance of true bugs and elevation as well as between the abundance of dominant species and elevation. In the case of P. opacellus and E. ciliatus, this relationship may be explained by their habitat choice. Both species prefer the dune top, therefore their distribution related to elevation strongly. According to the observations of Harmat (1984), P. kochiae was not associated with dune top habitat and it was not an abundant species. The relationship between elevation and the abundance of this monophagous species may be explained by the distribution of its host plant. P. kochiae correlated strongly with its host plant, Kochia laniflora which was observed with high density at the top and the southern slope of the dune.

It seems that elevation and microrelief determine the Heteroptera assemblage structure in a sand dune ecosystem. This relation would be more convincing if there was a distinct assemblage in the wind groove, however numerous species were represented by few individuals or occurred in few traps and they increased the noise of data (Voigt et al. 2003). The lack of a distinct bug assemblage is presumably due to the relatively small size of wind grooves as already suggested by Gallé et al. (1987). However, Kerényi (1997) found, that the bug assemblage in wind grooves depended more strongly on climatic conditions than the bug assemblage at dune tops. A dry period could cause a decline in species richness and abundance in wind grooves. The long-term dry period observed in the Kiskunság may cause intrinsic changes in assemblage structure of true bugs in this manner, but further studies are needed to reveal the real impact of the dry period.

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References


