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Small scale ecological zoogeographic methods in explanation of the distribution patterns of grasshoppers

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Abstract

We examined in this study, in a Central-European low mountain range, whether methods of ecological zoogeography can explain better the distribution patterns of grasshopper species and species-groups, than the methods of the historical zoogeography. Our results showed that zoogeographically defined microregions could be specified more precisely by the distribution of species groups of different eco-types than the distribution of species groups of the different faunal-types. We found that the macroclimate elements and landscape features determine the regional distribution patterns of the orthopteran species and species-groups with similar thermal and humidity requirements. Our case study revealed the important role of the ecological zoogeography in zoogeographical analyses of Orthoptera fauna at small geographical scale.

Zusammenfassung

Wir haben untersucht, ob man mit ökologisch-tiergeographischen Methoden die Verteilungsmuster von Heuschrecken in einem mitteleuropäischen Mittelgebirge analysieren kann. Unsere Ergebnisse zeigen, dass die Unterschiede auf dem Niveau der Mikroregion bei den Heuschrecken nicht in den Fauna-Typen, sondern in der Verteilung von Tierarten bzw. Tiergruppen mit unterschiedlichen ökologischen Ansprüchen zu finden sind. Wir können somit die Elemente des Makroklimas und die Merkmale der Landschaft identifizieren, die das lokale Verteilungsmuster von Artengruppen mit ähnlichen ökologischen Ansprüchen, beziehungsweise von bestimmten Tierarten bestimmen.

Introduction

Questions and methodology in the biogeographical searching have been dominated by the conceptions of the historical biogeography for a long time. However, recently search techniques of ecological (MONGE-NÁJERA 2008, POKIVAILOV 2011) and phylogenetic biogeography (HEWITT 2001, SPOONER & RITCHIE 2006) continually gaining ground in the characterisation and definition of areas. It was caused by the fact, that studying the fine-scale distribution patterns of species could be better determined by ecological than historical factors (BONADA et al. 2005).

It has been proved the investigation of distribution patterns of grasshopper species are very useful in description of zoogeographical phenomena and defining of spreading area or borders of regions within the framework of historical biogeography (KIS 1977, 1979, LA GRECA & MESSINA 1982, SERGEEV 1992, RÁCZ 1998a, LOCKWOOD & SERGEEV 2000, VARGA 2002, ÇIPLAK 2004, KENYERES et al. 2009).

The Carpathian Basin is the westernmost area of the Russain-Sibirian Province (SERGEEV 1992, 1993, 1995) belonging to the Skitian Subregion inside the Palearctic Region and that has outstanding high biodiversity in Europe (WILLIAMS et al. 1999). Character species of the above mentioned region can be originated from the widely distributed species of the steppe zone (SERGEEV 1995), but the species spreading from the postglacial East-Mediterranean dispersal centres are also significantly manifested themselves in its fauna supplies (LATTIN 1957, VARGA 1964, 2002). The main zoogeographical features of the Hungarian grasshopper fauna defining by the tools of the historical biogeography, could be described as a manifested matrix of the steppe and ponto-mediterranean species coloured with narrow-distributed fauna elements such as Alpine (e.g. *Miramella alpina*) in western (SZÖVÉNYI & NAGY 1999), Illyrian (e.g. *Odontopodisma schmidtii*) in south-western (NAGY & SZÖVÉNYI 1997), Mediterranean (e.g. *Aiolopus strepens*) in southern (NAGY & NAGY 2000, NAGY 2006), Dacian (e.g. *Leptophyes discoidalis*, *Isophya stysi, Pholidoptera transsylvanica, Odontopodisma rubripes*) in eastern and north-eastern (NAGY & RÁCZ 1996, NAGY et al. 1998, NAGY & SZÖVÉNYI 1999) parts of Hungary.

Former historical biogeography studies were carried out in the Hungarian Middle Mts separated Transdanubian Mts (Pilisicum)(~5,200 km^2, in the western part of the Hungarian Middle Mts) from the Northern Mts (fig. 1) based on the significant presence of Mediterranean fauna-elements (RÁCZ 1998). However, we do not know quantitative analyses even at small scale (e.g. for microregions) neither in Hungarian nor in international literature.

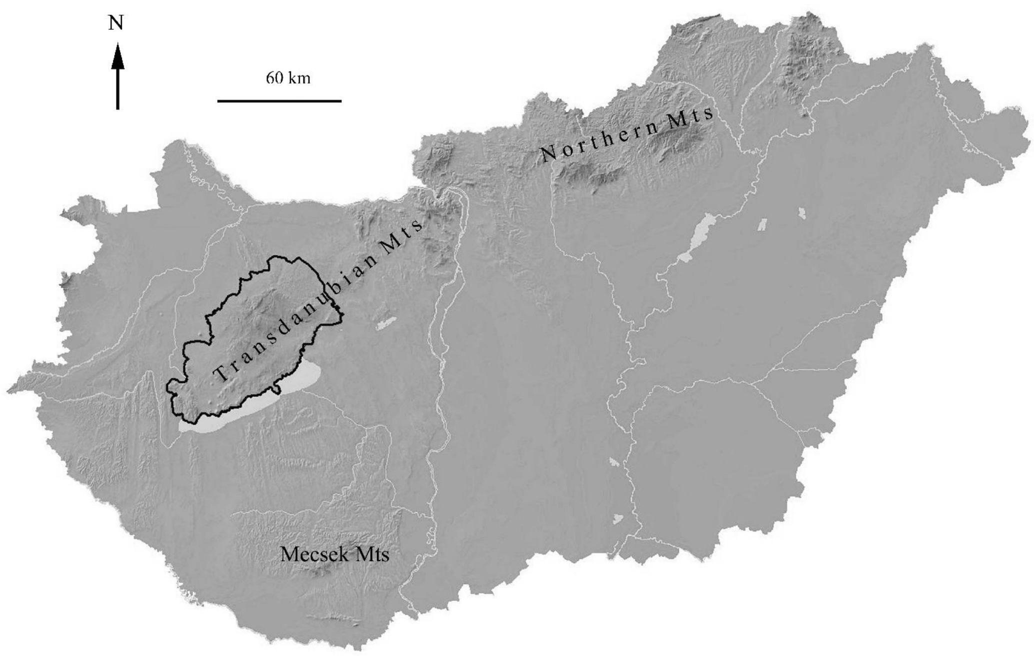

Fig. 1: Study area on the relief of Hungary.

Bakony Region (~3,700 km^2), covering up a large part of the Transdanubian Mts, is a very interesting and sufficient site for small scale ecological biogeographic analyses, because of its geomorphological (FUTÓ 2009), climatic (MERSICH et al. 2002) and biogeograhical diversity (PAPP 1968). The studied area could be divided into five microregions based on general zoological data (PAPP 1968), but RÁCZ (1973, 1979) described a more added sixth microregion using the distribution pattern of Orthoptera species.

Aims of our analyses were: (1) to describe the local distribution patterns of grasshopper species or species-groups with the help of the habitat requirements; (2) to define of the zoogeographical borders of microregions; (3) to reveal the potential indicator variables which influencing the zoogeographical features of the local Orthoptera fauna.

Area and methods

The study area was located on an individual part of the Transdanubian Mts, Bakony Region (W-Hungary) (MAROSI & SOMOGYI 1990) (fig. 1). The estimated cover of the natural habitats including broad-leaved forests, coniferous forests, mixed forests, pastures, natural grasslands, transitional woodland-shrubs and inland marches was found about 60% on the Corine LC GIS-based map. More potential habitats for grasshopper (e.g. natural grasslands, pastures and shrubby ecotones) can be 17.5% of the study area.

The heterogeneous climate of the Bakony Region makes it a really good field for case studies of ecological biogeography (DÖVÉNYI 2010) (fig. 2). Differences in annual mean temperature is over 2 °C (8.5–10.7 °C), annual insolation is between 1,950 and 2,030 hours, annual rainfall in high altitude is > 900 mm, in western part of the region characterized by heavy rainfalls is > 700 mm, and in the eastern and southern part of the region is 550–590 mm. Number of the snow cover days changes between 27 and 70.

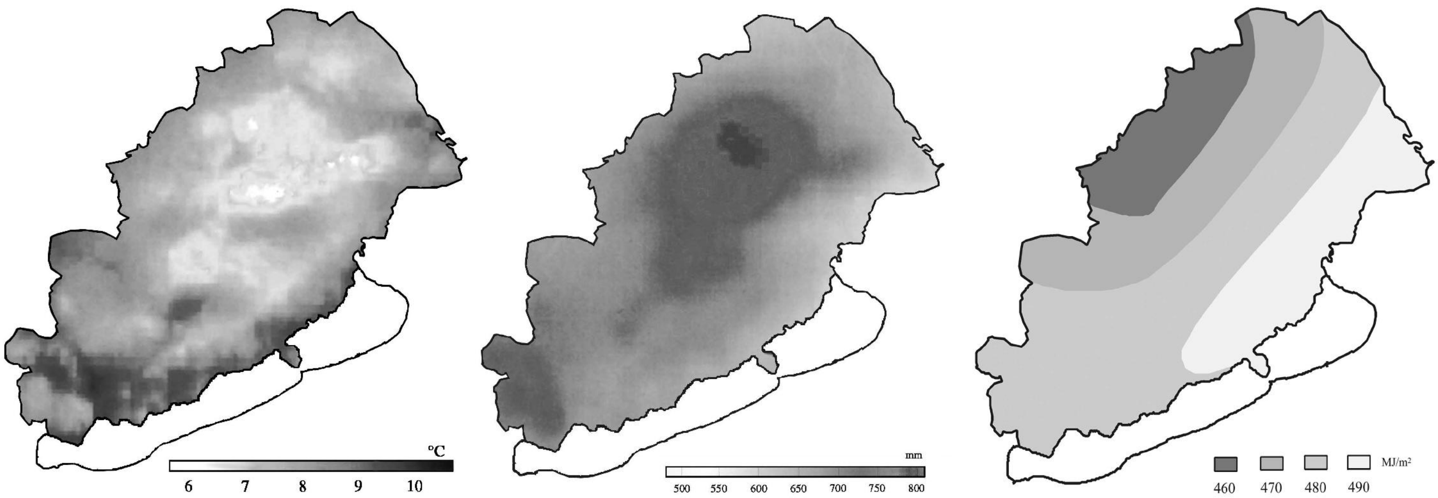

Fig. 2: Annual mean temperature, rainfall and insolation (April) in the studied area (after MERSICH et al. 2000).

The analyses were carried out based on digitally mapped presence-absence data of 84 grasshopper species (40 Ensifera and 44 Caelifera) (KENYERES 2010) at the scale of 2.5 × 2.5 UTM-grid. The presence-absence data of the grasshopper species per UTM quadrates, were gained from the available publications and collections of Natural History Museum of Bakony Mountains and Hungarian Natural History Museum, and were completed that with our own data from our former studies in the Region. Assessing the research-intensity on our study sites (KENYERES 2010), we could ascertain that distribution of the grasshopper species is quite well revealed, except of two microregions, which proved poor in natural habitats.

For the determination of species distribution and fauna element we used the results of VARGA (1997), INGRISCH & KÖHLER (1998) and RÁCZ (1998). Life-forms and ecological requirements of the grasshopper species were determined by definitions of INGRISCH & KÖHLER (1998), except the pseudo-psammophilous life-formed species, which were handled after determination of KRIŠTÍN et al. (2009). Life-form types of INGRISCH & KÖHLER (1998) were more suitable for zoogeographical analyses than the categories of Rácz (1998), because of the fine division of thamnobiont grasshopper species and appearance of grassland/forest preferences in the categorization. Rácz' thamnobiont category is divided arboricol, arbusticol and pratinicol types by the system of INGRISCH & KÖHLER (1998). Furthermore graminicol species are distinguished from silvicol species occurring also in grass-level.

The following abiotic background variables were connected to the UTM-quadrates: altitude; annual mean temperature; annual rainfall; insolation in April and July. Altitude was defined based on M 1:100,000 topographical maps, where the altitude in the centre of the quadrate to the 20 metres place was applied. Climatic data were based on the survey of MERSICH et al. (2000). The landscape characterisation and habitat-structure variables of the area were defined by database of Corine Land Cover and MÉTA (Landscape Ecological Vegetation Database & Map of Hungary) programs (HORVÁTH & POLGÁR 2008, HORVÁTH et al. 2008). So the characterisation variables such as surface cover and relative frequency of agrarian habitats, scrubs, broad leaved forests, grasslands, anthropogenic and wetland habitats descending from CLC; while variables number of the habitat-patches, habitat-diversity, cover of the relevant in Hungarian so called Á-NÉR, that is General National Habitat-classification System, categories and merged categories of them as Humid grasslands and marshes, Mountainous grasslands, Open dry grasslands, Closed dry and semi-dry grasslands, Shrub forests, scrubs and ecotones, diversity (*DQ*), overall cover and patch-numbers of the Á-NÉR categories came from MÉTA program.

The following variables of the grasshopper fauna were connected to UTM-quadrates: species number; relative frequency of the species; relative frequency of arboricol, arbusticol, silvicol, pratinicol, graminicol, geophilous and pseudo-psammophilous life-forms; relative frequency of thermophilous, moderate-thermophilous, mesophilous, moderate-hygrophilous and hygrophilous species; diversity (*DQ*) of life-forms and eco-types.

Data of 2.5 × 2.5 UTM-grid were merged for the hierarchical classification, merging of the ranked quadrates was carried out in a way established case numbers equal to each other. The 61 merged samples were analysed by cluster and principal component analysis. Diagnostic species of the cluster analysis was identified by Indval 2.0 programme (relative frequency values, 999 random permutation, $p<0.05$). Correlation-, canonical correspondence- and regression-analyses were used for revealing determinant background variables of the species distribution. ArcView 3.3, SYN-TAX 2000, Statistica 6.0 and PAST 1.95 programmes were used for the statistical analyses.

Results and discussion

Cluster analysis, Ward method and Euclidean distance, of the merged zoogeographical samples (n=61) showed individuality of five microregions of the studied area. The above mentioned segregation between the sites was confirmed by the indicator species analysis (Indval) and relative frequency of life-forms and eco-types (fig. 3).

Comparison the changes of the distribution of grasshopper species and the climatic features we could notice a definite phenomena. As it can be seen on fig. 2 and 3 the spatially changes of the macroclimate parameters were followed by the changes of frequency of species-groups with different ecological requirements.

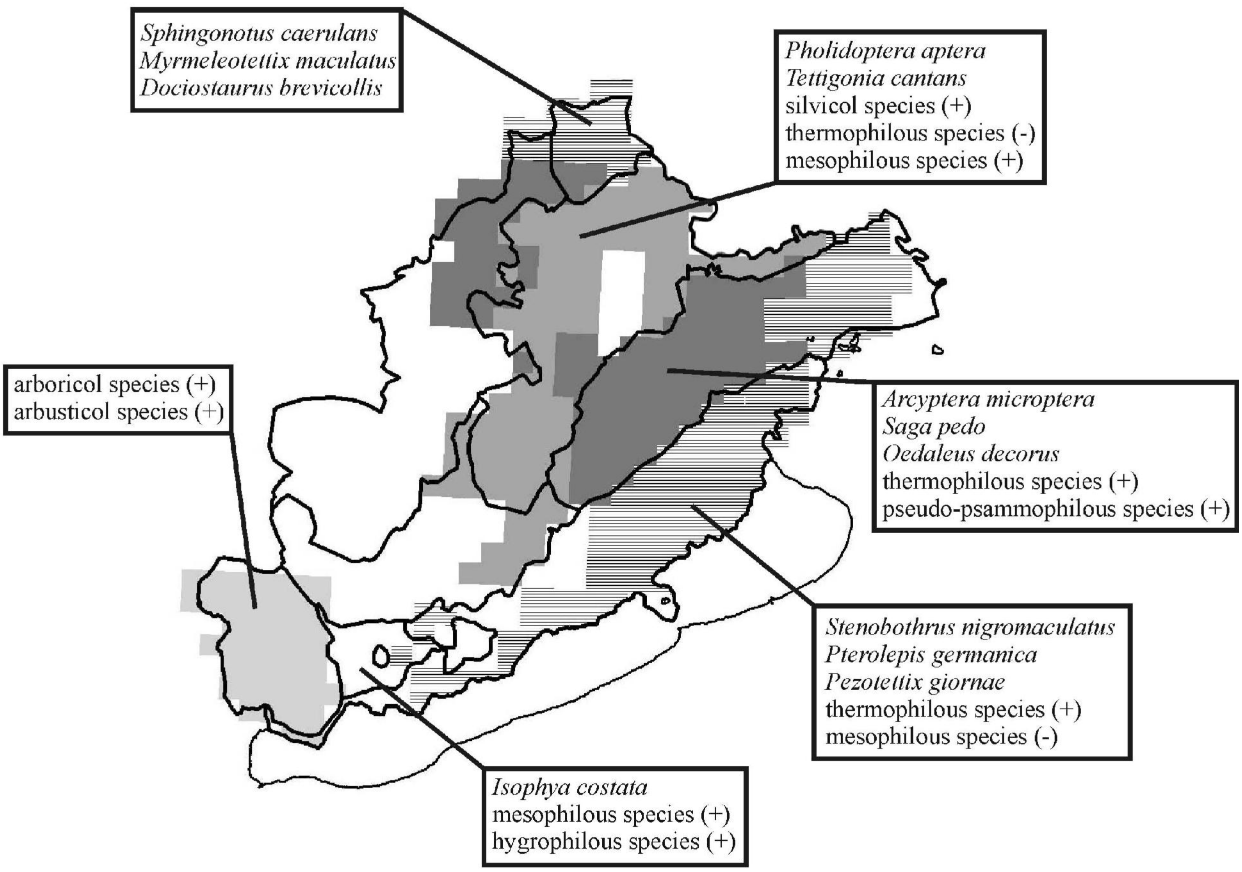

Fig. 3: Revealed zoogeographical borders, indicator species and related life-forms and eco-types (+ = significant positive relationship, – = significant negative relationship).

The correlation analyses (p>0.05; data of 2.5 × 2.5 km UTM-grid, n=673) showed significant relationships among grasshopper species distribution and background variables such as geographical, climatic and habitat-structural. Based on these results the below listed species showed strict habitat dependency: *Ephippiger ephippiger, Ruspolia nitidula, Isophya costata, Isophya modestior, Leptophyes boscii, Pholidoptera aptera, Pholidoptera fallax, Pholidoptera griseoaptera, Platycleis montana, Platycleis albopunctata, Pterolepis germanica, Tettigonia cantans, Calliptamus italicus, Pezotettix giornae, Arcyptera microptera, Chorthippus dorsatus, Gomphocerippus rufus, Omocestus rufipes, Stenobothrus eurasius, Stenobothrus nigromaculatus, Celes variabilis, Oedipoda caerulescens*.

Canonical correspondence analysis showed that the distribution of *Tettigonia cantans, Leptophyes boscii, Pholidoptera aptera, Pholidoptera fallax, Pholidoptera griseoaptera*, *Gomphocerippus rufus, Chorthippus dorsatus* and *Omocestus rufipes* species had significant positive correlation with annual rainfall, altitude and overall cover of the broad leaved forests (fig. 4). Dependency of the above mentioned grasshopper species, except *Chorthippus dorsatus* and *Omocestus rufipes*, from the forest cover was similar to the results of INGRISCH & KÖHLER (1998). Presence of *Chorthippus dorsatus* and *Omocestus rufipes* in the group of silvicol species was presumably caused by their several local detections in small forest clearings, which habitats usually belong to forests in the landscape structure of CLC. It is known that the altitude effects the distribution of orthopterans (CLARIDGE & SINGHRAO 1978) because of the temperature and humidity requirements of the species (DREUX 1962). Our examinations confirmed it in a Central-European low mountain range. Linear regression-analyses revealed that altitude determined the annual mean temperature (r=-0.745, p<0.001), the annual rainfall (r=0.623, p<0.001) and the insolation in July (r=-0.126, p<0.001) at our study scale, too.

Canonical correspondence analysis showed that presence of *Celes variabilis, Platycleis montana, Stenobothrus eurasius* and *Arcyptera microptera* was in significant positive correlation with insolation in April and the relative frequency of the natural grasslands in the landscape structure (fig. 4). Our results confirmed thermophilous character (INGRISCH & KÖHLER 1998) of the above mentioned species and supported that large natural grasslands of the Eastern-Bakony were adaptable for colonization of the Angara Fauna (UVAROV 1927, RÁCZ 1973) spreading from east.

Beside the importance of insolation in April, we revealed strong effects of insolation in July, too. Presence of *Pezotettix giornae* and *Pterolepis germanica* showed significant positive correlations with high degree of insolation in July (fig. 4). These two ponto-mediterranean species were character species of the southern, most dry and warm subregion of the studied area, by the results of the indicator species analyses (fig. 3). These were concordant with those results which stated that *Pterolepis germanica* are typical in shrubby, dry and warm ecotones (HOLUŠA & KOČÁREK 2008, BRAUD 2008) and the *Pezotettix giornae* is a characteristic thermophilous species of the southern part of Central-Europe (KOČÁREK 1999).

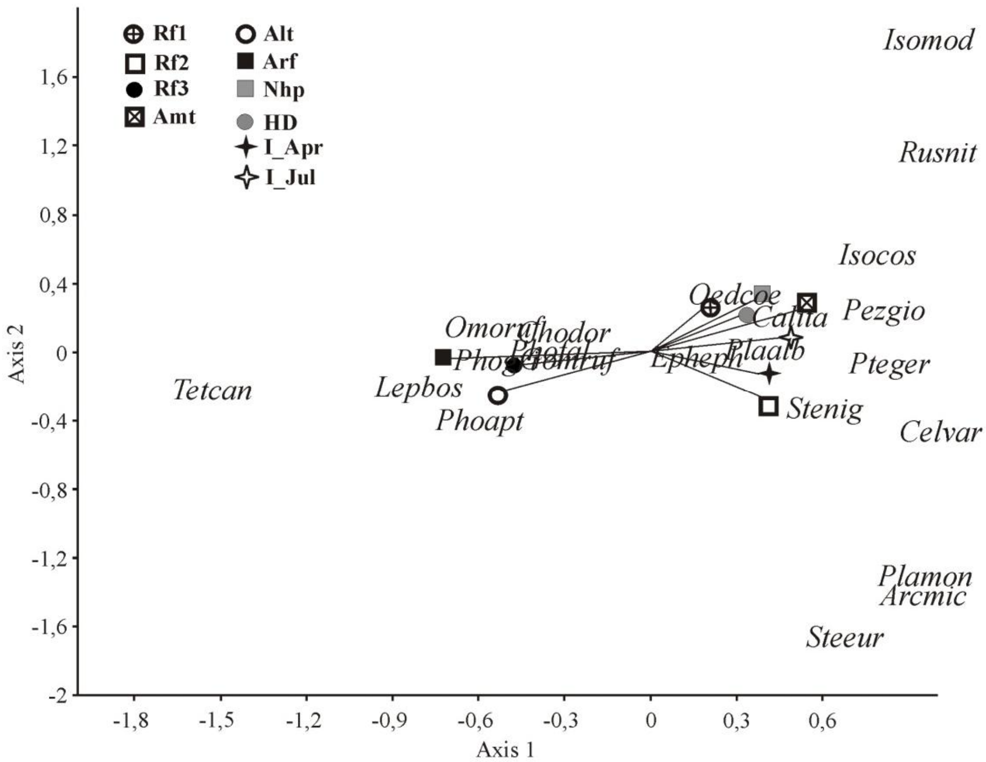

Fig. 4: Result of the canonical correspondence analysis (n=440 of 2.5 × 2.5 km UTM-grid, species with the most significant relation of Pearson-correlation (S=22)) shows that over the relative frequency of forest habitats, the annual rainfall and altitude are also determinant in the distribution of silvicol species (e.g. *Tettigonia cantans, Pholidoptera aptera, Leptophyes boscii*). Relations among macroclimate features (e.g. insolation in April and July) and thermophilous species (e.g. *Pterolepis germanica, Celes variabilis, Stenobothrus nigromaculatus*), and relations among dense vegetation-structure and species with dicotyledonous preference (e.g. *Isophya costata*) were also revealed at small scale. [Abbreviations: relative frequency of agrarian (Rf1), grassland (Rf2) and forest (Rf3) habitats, annual mean temperature (Amt), altitude (Alt), annual rainfall (Arf), number of habitat patches (Nhp), habitat-diversity (HD), insolation in April (I_Apr), insolation in July (I_Jul)]

Canonical correspondence analysis (fig. 4) and more over spectra of life-forms and eco-types managed to show that (1) distribution of silvicol species was positively correlated with the cover of broad leaved forests (CLC); (2) distribution pattern of moderate-hygrophilous and hygrophilous species was related with annual rainfall; (3) distribution of graminicol, pseudo-psammophilous and thermophilous species was affected by insolation in April. According to correlation analyses (table 1): (1) presence of arbusticol and silvicol species depends on the cover of broad leaved forests (CLC); (2) distribution of silvicol species was related to low annual mean temperature, high degree of annual rainfall and homogenous landscape structure; (3) distribution of graminicol species showed positive correlation with extended grasslands of CLC and relative frequency of closed dry and semi-dry grasslands of Á-NÉR (General National Habitat-classification System), with insolation in April and negative correlation with annual rainfall; (4) distribution of thermophilous species was in negative correlation with annual rainfall and in positive correlation with insolation in April; (5) distribution of mesophilous species was in positive correlation with the cover of xerotherm broad leaved forests (CLC) and closed dry and semi-dry grasslands of Á-NÉR; (6) distribution of moderate-hygrophilous and hygrophilous species is in positive correlation with the cover of broad leaved forests (CLC).

Tab. 1: Results of Pearson-correlation analysis of life-forms, eco-types and habitat-variables (n=440) [significant values: bold italic (p<0.05); significant values confirmed by Bonferroni technique: bold; significant values confirmed by Bonferroni technique and Benjamini-Liu FDR method: bold, underlined]

	Arbu	Sil	Pra	Gra	Geo	Psps	D-Lf	M-ther	Meso	M-hygr	Hygr	D-Et
Alt	r=-0.013	**r=0.160**	r=0.053	**r=-0.204**	r=-0.061	r=-0.076	r=0.008	**r=0.161**	**r=-0.245**	**r=0.161**	**r=0.167**	r=0.037
	p=0.792	**p=0.002**	p=0.313	**p<0.001**	p=0.240	p=0.146	p=0.866	**p=0.002**	**p<0.001**	**p=0.002**	**p=0.001**	p=0.438
Amt	r=0.051	**r=-0.187**	r=0.005	**r=0.144**	r=0.062	=0.060	r=0.093	***r=-0.109***	r=-0.061	r=-0.009	r=0.048	r=0.066
	p=0.267	**p<0.001**	p=0.908	**p=0.002**	p=0.174	p=0.192	p=0.050	***p=0.017***	p=0.184	P=0.839	p=0.295	p=0.168
Arf	r=-0.073	**r=0.216**	r=0.049	**r=-0.304**	r=-0.063	***r=-0.107***	**r=0.123**	r=0.050	**r=0.150**	***r=0.092***	***r=0.119***	r=0.025
	p=0.109	**p<0.001**	p=0.279	**p<0.001**	p=0.166	***p=0.019***	**p=0.010**	p=0.270	**p=0.001**	***p=0.043***	***p=0.009***	p=0.602
I_Apr	r=0.082	r=-0.088	r=0.034	**r=0.293**	r=0.086	r=0.060	**r=0.128**	r=0.079	r=-0.010	***r=-0.096***	**r=-0.136**	r=0.015
	p=0.074	p=0.053	p=0.460	**p<0.001**	p=0.061	p=0.187	**p=0.007**	p=0.083	p=0.824	***p=0.036***	**p=0.003**	p=0.760
I_Jul	r=0.070	r=0.120	r=-0.004	**r=0.115**	r=0.069	r=-0.070	**r=0.133**	r=-0.080	r=-0.040	r=0.032	r=0.018	**r=0.100**
	p=0.127	p=0.009	p=0.926	**p=0.012**	p=0.130	p=0.124	**p=0.005**	p=0.078	p=0.378	p=0.484	p=0.693	**p=0.036**
Agr	**r=-0.240**	**r=-0.297**	**r=-0.150**	**r=-0.124**	**r=-0.142**	**r=-0.159**	**r=-0.218**	**r=-0.218**	**r=-0.171**	r=-0.066	***r=-0.120***	r=-0.074
	p<0.001	**p<0.001**	**p=0.001**	**p=0.007**	**p=0.002**	**p<0.001**	**p<0.001**	**p<0.001**	**p<0.001**	p=0.150	***p=0.008***	p=0.122
Gra	r=0.029	**r=-0,125**	r=0.053	**r=0.194**	r=-0.041	**r=0.144**	r=0.035	r=0.011	r=0.011	r=-0.050	r=-0.015	r=-0.002
	p=0.523	**p=0.006**	p=0.243	**p<0.001**	p=0.366	**p=0.002**	p=0.464	p=0.805	p=0.813	p=0.274	p=0.741	p=0.973
Ff	**r=0.163**	**r=0.401**	***r=0.101***	**r=-0.123**	r=0.086	r=-0.070	r=0.068	**r=0.161**	**r=0.188**	**r=0.150**	**r=0.160**	r=0.082
	p<0.001	**p<0.001**	***p=0.026***	**p=0.007**	p=0.059	p=0.127	p=0.154	**p<0.001**	**p<0.001**	**p=0.001**	**p<0.001**	p=0.086
HD	r=0.006	**r=-0248**	r=0.007	r=0.087	r=0.051	r=0.038	r=0.032	r=-0.021	***r=-0.100***	r=0.003	r=-0.083	r=0.016
	p=0.900	**p<0.001**	p=0.871	p=0.055	p=0.263	p=0.409	p=0.509	p=0.643	***p=0.028***	p=0.944	p=0.069	p=0.731
Nhp	r=0.013	**r=-0.256**	r=0.073	**r=0.121**	r=0.020	r=0.062	r=0.059	r=-0.012	r=-0.049	r=0.075	r=-0.029	r=0.054
	p=0.771	**p<0.001**	p=0.111	**p=0.008**	p=0.659	p=0.172	p=0.220	p=0.797	p=0.287	p=0.101	p=0.530	p=0.260

Abbreviations: Alt=altitude; Amt=annual mean temperature; Arf=annual rainfall; I_Apr=insolation in April; I_Jul=insolation in July; Agr=relative frequency of agrarian habitats; Gra=relative frequency of grassland habitats; Ff=relative frequency of broad leaved forests; HD=habitat-diversity (Shannon); Nhp=number of habitat patches(CLC); Arbu=arbusticol species; Sil=silvicol species; Pra=pratinicol species; Gra=graminicol species; Geo=geophilous species; Psps=pseudo-psammophilous species; D-Lf=diversity of life-forms; M-ther=moderate-thermophilous species; Meso=mesophilous species; M-hygr=moderate-hygrophilous species; Hygr=hygrophilous species; D-Et=diversity of eco-types

Results of our small scale studies confirmed our knowledge on ecological requirements of grasshoppers (VARGA 1997, INGRISCH & KÖHLER 1998) and revealed the effects of macroclimate (WINGERDEN et al. 1992) and phenology (MESA 1987) of grasshopper species at this scale, too.

We also found significant correlations between diversity of grasshopper life-forms and habitat based landscape structure [related to habitat-diversity (R_{HD}=0.138; p=0.004), number of habitat-categories (R_{NHC}=0.172; p<0.001) and number of the habitat-patches (R_{NHP}=0.190; p=0.004)].

These results join to the previous studies, which stated that over the macroclimate features the small scale habitat-structure is determinant in the forming of the distribution of grasshopper species (KEMP et al. 1990, QUINN et al. 1991, FIELDING & BRUSVEN 1995). Although the mediterranean elements are frequent in the southern part of the studied region, subregional differences inside the studied area were not revealed by the analyses of the distribution of fauna elements. However, we can conclude that in the Bakony Region characterized by dominance of natural habitats the influencing effect of ecological factors (BONADA et al. 2005) to the distribution of grasshoppers is more significant than historical factors.

Conclusions

Quantitative analyses of grasshopper species distribution at small scale have not been published yet. This gap in our knowledge probably is caused by the fact that for small scale analyses local distribution maps of the local fauna is needed, with the scale of min. 2.5 × 2.5 km UTM-grid.

Distribution of grasshopper species-groups, which are characterized by similar life-forms and eco-types, shows significant microregional differences in the studied middle-mountainous area (~3,700 km^2). This result confirmed the relevant role of the ecological zoogeography (WIENS et al. 1986) in the analyses at small geographical scale. Generalization can be made from our results because the revealed zoogeographical borders of the microregion in our study site showed similarity to the local vegetation-based microregional borders (MOLNÁR et al. 2008).

Summarising: (1) quantitative zoogeographical analyses of the Ortoptera species distribution patterns are very usable for the determination of zoogeographical borders at microregional scale; (2) zoogeographical differences of microregions in the Orthoptera fauna are not manifested themselves in the distribution of species groups of different faunal-types, but rather in the distribution of species groups of different eco-types; (3) the identification of the influencing elements of macroclimate and landscape features which determine regional distribution patterns of the Orthopteran species-groups (based on life-form, thermal- and humidity requirements) and species can be possible. These statements revealed importance of ecological zoogeography in zoogeographical analyses of Orthopterans.

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