Structure of Orthoptera assemblages in step-like habitat islands and neighbouring grasslands

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Zusammenfassung

Im Südosten Ungarns wurden 1996-98 Orthopteren-Assoziationen (13 Ensifera- und 19 Caelifera-Arten) vergleichend auf 24 steinzeitlichen Grabhügeln (Kurgans) und 21 nahegelegenen Graslandflächen untersucht. Es ging dabei um die Hypothese, nach der sich die Assoziationen auf den inselartigen Steppenhügeln aus Arten des umgebenden Graslandes rekrutieren. Dazu wurden weiterhin 12 Landschafts- und Habitatparameter herangezogen und die Daten mittels Ordinationsanalyse ausgewertet.

Es zeigte sich, dass hinsichtlich der Orthopteren die Kurgans deutlich vom Grasland verschieden waren. Ihre Assoziationen waren vor allem signifikant mit der Vegetationsstruktur gekoppelt. Dagegen spielten der Isolationsgrad der Flächen und das Dispersalvermögen der Arten keine Rolle.

Abstract

Orthoptera associations were studied on 24, presumably one to three thousand years old cemetery hills, "kurgans", covered by steppe vegetation and in 21 grassland areas, which were situated nearby and potentially acting as propagula pools.

Significant differences (p=0.01) were established between the ordination patterns of the observed and randomly generated associations. The Orthoptera associationis affected by the structure of vegetation and the orographic differences between habitats. Regional scale differences between the studied Orthoptera species were revealed, also, however, there was less significant correlation with the rate of isolation and no correlation was found with migration ability. The species composition of kurgan associations were more similar to each other than that of the nearest grasslands, indicating relative autonomy and these associationsare more affected by habitat parameters than metacommunity processes, including the degree of isolation.

Introduction

The tendency that community ecology is becoming popular again is observable in the increasing number of publications on insect communities. In the last decades a lot of studies have been published on development and structuring of insect assemblages. Researchers emphasize the effects of exterior factors (SOUTHWOOD et al. 1979, JERMY 1985, GALLÉ et al. 1991 etc.) on structuring of

insect communities as well as the role of interior regulatory mechanisms, especially the importance of interspecific relations (STRONG et al. 1984, BOSE & DAVIDAR 1990, GALLÉ 1994).

These latter factors are traditionally considered less or not important in herbivorous insects (LAWTON & SCHRÖDER 1978, LAWTON 1983, STINSON & BROWN 1983). As Jermy stated already in 1976, the permanent food supply does not make competition important within herbivorous insect communities. In the last decades, however, the number of observations and experiments on competition between herbivorous insects has increased. Some researchers assume that competition is especially important for suitable vegetation patches and oviposition sites.

We face a similar dilemma if we want to study Orthoptera assemblages consisting of mostly herbivorous populations, but the role of predatory species (first of all grasshoppers) cannot be neglected in these communities either.

Most studies emphasize crucial effects of habitat attributes in structuring Orthoptera assemblages. Vegetation structure, percentage of plant cover, species composition and spatial pattern rank among the most important habitat attributes (KEMP et al. 1992).

There are some studies on the interspecific relations among locust populations (BELOVSKY 1991, BELOVSKY & SLADE 1993, CHASE 1996).

There is, however, fewer information on the effect of external conditions and internal mechanisms on Orthoptera assemblages in fragmented and/or isolated habitats: although these researches give important information for nature conservation, too. The degree of isolation influences the composition of Orthoptera assemblages differently (GALLÉ et. al 1991, KISBENEDEK & BÁLDI 1996, MABELIS & MEKENKAMP 1996).

In Hungary, kurgans are also isolated habitats to a certain extent. They are artificial hill formations usually rising up from monoculture fields in the Great Hungarian Plain, 5-15 meters high, con or hemisphere-shaped, 1000-3000 years old. They are covered by grasslands, as a rule and the grassland area is between 800 and 4000 sq. meters. In the past, they served as human residence and burial sites. They are under protection because of their landscape value, archaeological, faunistical and botanical importance, this latter one especially because of the loess vegetation.

In this paper we focus on the role of those external conditions in structuring Orthoptera assemblages.

Interior structuring mechanisms, especially intraspecific competition will be discussed in a separate paper. Detailed data analyses were concentrated on four questions:

(1) Do the patterns of kurgan Orthoptera assemblages differ from those of randomly generated assemblages?
(2) Which habitat attributes affect the composition of Orthoptera assemblages?
(3) Does isolation have any importance in structuring these assemblages?
(4) Besides external factors, is there any modification influence of the differential migration ability of Orthoptera species?

Study sites and methods

Field sampling

Field studies were carried out in the Great Hungarian Plain on twenty-four cemetery hills (so called "kurgans"), usually surrounded by agricultural fields, and twenty-one neighbouring grasslands, potentially acting as species pools for kurgan assemblages (Fig. 1.). Samples were collected on each sampled site, three times in each year from 1996 to 1998. We sampled Orthoptera populations with sweep nets, using 400-500 sweeps in each plot proportional to the size of habitat. In the second and third year, in order to prevent an excessive decrease of the number of individuals we identified the collected specimens in the field and released them, only some difficultly determineted species were collected. The larvaes were determined to genus.
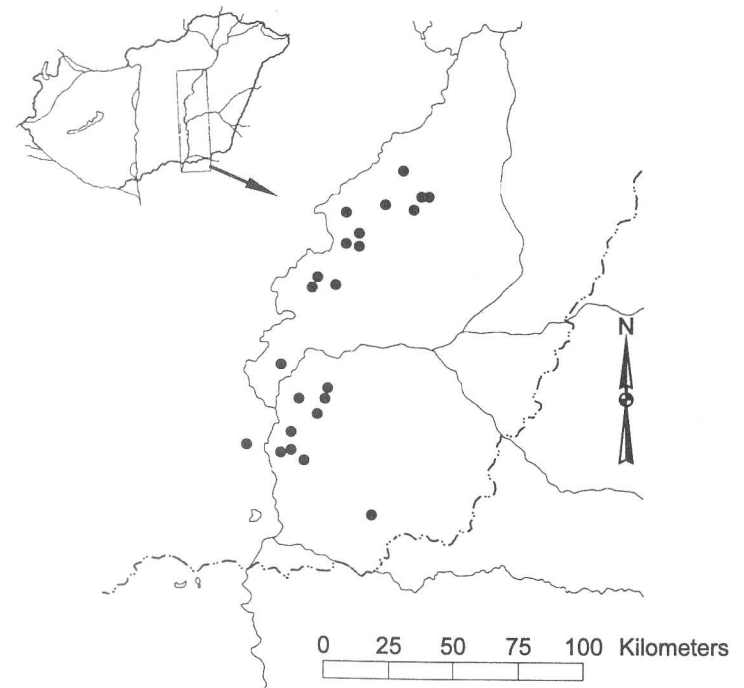

Fig.1.: Distribution of kurgans in the Great Hungarian Plain. (One point in the map identifies two kurgans very cloose to each other)

Habitats were characterized by the following attributes: (1) size (area) in sq. m.; (2) regional position (one = kurgans on the Southern Great Hungarian Plain, two = kurgans on Northern Great Hungarian Plain); (3) relative height (in the case of kurgans only); (4) species diversity of the vegetation (Shannon-Wiener diversity index, based overgrounness of plant species during May 1997 and 1998); (5)

degree of degradation (according to the degradation scale employed); (6) average vegetation height (short, medium. tall grasses and tall grasses lain down by wind); (7) total vegetation cover; (8) coverage of monocot species; (9) degree of isolation (distance from the nearest grassland: minimum 0 m -maximum 1000m); (10)permeability of the surrounding areas (e.g. grassland, medic, cereals, maize, sunflower, mixed culture or asphalt road) for Orthoptera species; (11) age of isolation (before 1782, between 1782 and 1872, after 1872, not isolated yet); (12) presence of an assumed connecting corridor (strip-like habitat between kurgans and the nearest grasslands, presumably promoting Orthoptera migration).

Data analysis

Relations between the Orthoptera assemblages of the single habitats were analysed with PCoA ordination using Czekanowski's similarity coefficients (PODANI 1988). Employing this techniques, we computed both the similarity pattern of real assemblages, and their departure from randomness. For this latter, a nullmodel was established by randomisation of the values of the original matrix with fixed marginal sums of the rows and the columns, representing species and kurgans, respectively. Deviation from the null model was tested with the distance to the nearest neighbour, analysis of aggregation of points representing each kurgan's assemblages in the ordination space. The averages of the smallest distances belonging to each object (kurgans) in the dissimilarity matrix was computed from real field data and 99 random reference data, respectively. The smaller calculated average value: the more aggregated point distribution in ordination space.

We studied the external correlates that presumably affect the structure of Orthoptera assemblages with principal coordinate analysis based on Czekanowski's similarity coefficient (PODANI 1988). The tests were made as follows (GALLÉ et al.1991). The sampling sites (kurgans and other grasslands) were ordinated by PCoA on the basis of the composition of their Orthoptera assemblages. Then the relative position of the points in the factor space was expressed by multidimensional Euclidean distances. Spearman's rank correlation was computed between these distances and differences in vegetation structure, real spatial distances, distances to nearest grassland, isolation indices and relief differences.
In the study we took the different migration ability of each population into consideration. Following NAGY's (1992) classification, we divided the Orthoptera species into three categories according to their migration ability and wing length: (1) short winged species (with no wings or only with wing stumps); (2) mobile species with moderate short wings; (3) very mobile, long winged species.

Results

Structure compared to random

We found altogether 32 Orthoptera species on the studied kurgan habitats (Table 1). The species number varied from 6 to 18 in the individual kurgans and did not increase significantly with habitat size (Fig. 2.). Orthoptera assemblages of kurgans show an aggregation pattern in PCoA factor space (Fig. 3.). The average of nearest neighbour's distances was 0.32 in the real field data, whereas it changed

from 0.45 to 0.62 in random references. Since all values of the random data exceeded the field data, it can be stated that ordination pattern of kurgan Orthoptera assemblages differs significantly from randomness (p=0.01).

Table 1.: List of species collected on kurgans. Frequency (number of kurgans settled) and migration ability (according to Nagy 1991) also represented .

List of species	Frequency	Migration ability
Tettigonidae		
Phaneroptera nana Fieber, 1853	4	3
Phaneroptera falcata (Poda, 1761)	4	3
Leptophyes albovittata (Kollar, 1833)	7	1
Conocephalus discolor Thunberg, 1815	4	3
Ruspolia nitidula (Scopoli, 1786)	4	3
Tettigonia viridissima (L., 1758)	2	3
Platycleis albopunctata (Fabricius, 1781)	5	3
Platycleis affinis (Fieber, 1853)	11	3
Tesselana vittata (Charpentier, 1825)	21	2
Metrioptera bicolor (Philippi, 1830)	3	2
Metrioptera roeselii (Zeuner, 1941)	1	2
Gampsocleis glabra (Herbst, 1786)	1	3
Gryllidae		
Oecanthus pellucens (Scopoli, 1763)	16	3
Acrididae		
Tetrix tenuicornis Sahlberg, 1893	1	1
Pezotettix giornae (Rossi, 1794)	19	1
Calliptamus barbarus (Costa, 1836)	1	2
Calliptamus italicus (L., 1758)	12	3
Oedipoda caerulescens (L., 1758)	1	3
Aiolopus thalassinus (Fabricius, 1781)	4	3
Dociostaurus brevicollis (Eversmann, 1848)	7	2
Omocestus petraeus (Brisout, 1856)	3	3
Omocestus haemorrhoidalis (Charpentier, 1825)	4	2
Omocestus rufipes (Zetterstedt, 1821)	10	2
Stenobothrus crassipes (Charpentier, 1825)	3	1
Chorthippus brunneus (Thunberg, 1815)	12	3
Chorthippus mollis (Charpentier, 1825)	8	3
Chorthippus biguttulus (L., 1758)	7	3
Chorthippus dichrous (Eversmann, 1859)	9	3
Chorthippus dorsatus (Zetterstedt, 1821)	12	3
Chorthippus parallelus (Zetterstedt, 1821)	7	1
Chorthippus albomarginatus (DeGeer, 1773)	14	3
Euchorthippus declivus (Brisout, 1849)	21	2

Correlation: r = 0.10982

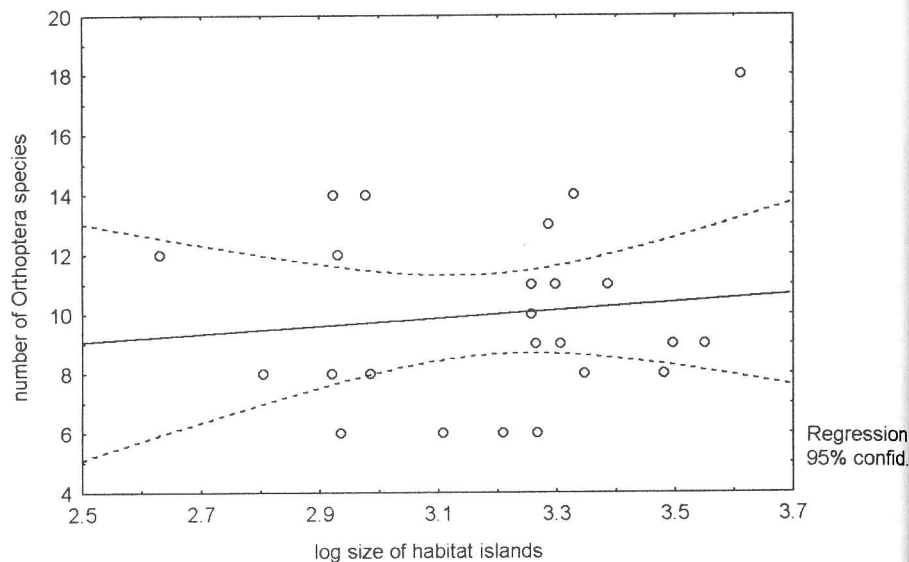p=0.6o9

Fig. 2.: Regression analysis between logarithm of habitat island size (m²) and species number of Orthoptera assemblages.
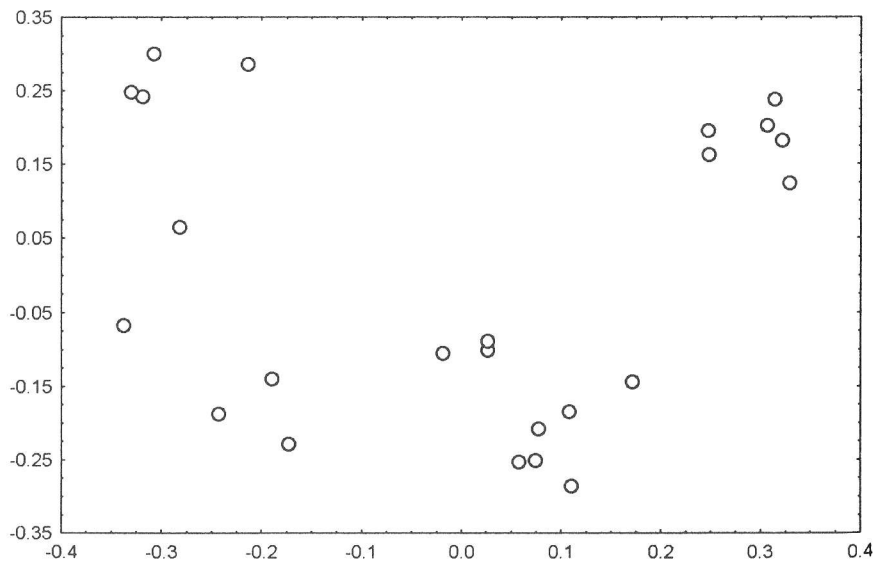

Fig. 3.: PCoA ordination of kurgans on the basis of their Orthoptera assemblages (Czekanowski's similarity coefficient was used).

External correlates

The composition of Orthoptera assemblages of kurgans showed close correlation with the degradation degree of vegetation, percentage of total plant coverage and the average height of the vegetation. It also correlated definitely with the species diversity of vegetation, but no correlation was observed with the isolation attributes (distance of nearest grassland, "permeability" of the fields around the kurgans, existence of a presumable corridor, the age of isolation), and with the habitat size. The composition of assemblages correlated slightly with distances among kurgans, showed significant correlation only with the second axis which possibly referred to regional differences among ranges of studied species. The composition of Orthoptera assemblages of kurgans also correlated with the relative height of the kurgans.
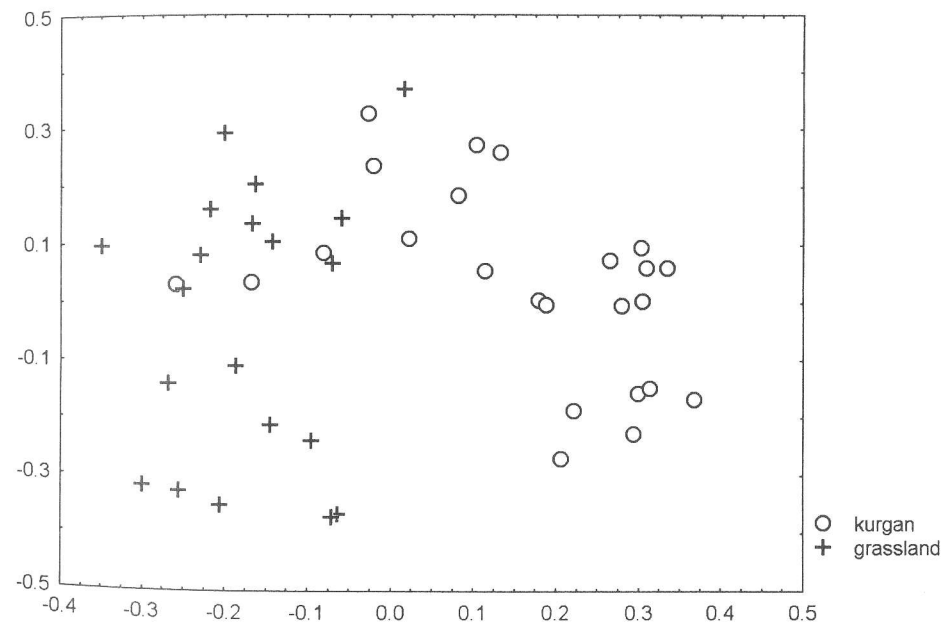

Fig. 4.: Comparing kurgans, as habitat islands and the nearest grasslands on the basis of Orthoptera assemblages, in PCoA ordination space, using Czekanowski's similarity coefficient. o-kurgans, +-grassland

Kurgan assemblages segregated distinctly from those of nearby grasslands (Fig. 4.), and are more similar to each other than to neighbouring grasslands. When correlating distances computed in ordination space with real topographic distances, isolation indices, structural differences of vegetation and differences of

relief, we observe a close correlation between the presence or absence of a presumable corridor and the similarity between kurgans and its nearest grassland neighbour (p=0.05). However, we could not demonstrate, the effect of structural differences of vegetation and the effect of differences deriving from the hill character of kurgans either. In studying annual species composition of Orthoptera assemblages on each kurgans, we can detect hardly any of its changes during this period.

On the basis of these results, a conclusion can be drawn that kurgans have their own Orthoptera assemblages which are less influenced by nearby grasslands, but the quality of kurgans as habitats seems to be important.

Almost half of the kurgan species (13 species) had little (5 species) and moderate (8 species) migration ability according to NAGY (1992). When ordinating the kurgans on the basis of the migration groups of grasshoppers, and computing the relationship of PCoA scores with the studied attributes, we found a significant correlation between each group and vegetation structure and kurgan height.

Table 2.: Spearmann's rank correlation between (1) the Euclidean distances between kurgans and grasslands lying nearest to them, computed on the basis of the composition of Orthoptera assemblages, in PCoA ordination space, using Czekanowski's similarity coefficient, and (2) the differences between habitat attributes of kurgans and their nearby grassland pair. euklbin: three dimensional Euclidean distance computing from binary data, euklquant: three dimensional Euclidean distance computing from quantitative data, isolation: distance to nearest grassland habitat, permeabel: how far the Orthoptera species can cross fields around the habitat islands, corridor: presence or absence of assumed connecting corridor, age: age of isolation, height: relativ height of kurgans, diffdegrad: differences of degradation of the vegetation between kurgans and their nearby grasslands , diffvegheight: height of vegetation, diffvegcover: total coverage of vegetation

	logsize	size	distance	plantdiv	vegdegrad	vegheight	vegcover	gramincov	height	isolation	permeabil	age	corridor
koor1	n.s.	n.s.	n.s.	p=0.0019	p=0.0059	p=0.0003	p=0.0016	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
koor2	n.s.	n.s.	p=0.036	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
mig1	n.s.	n.s.	n.s.		n.s.	p=0.025	p=0.079	n.s.	p=0.096	n.s.	n.s.	n.s.	p=0.086
mig2	n.s.	n.s.	n.s.	p=0.0035	p=0.0004	p=0.0018	n.s.	p=0.098	n.s.	n.s.	n.s.	n.s.
mig3	n.s.	n.s.	n.s.	p=0.059	p=0.026	p=0.098	n.s.	p=0.098	n.s.	n.s.	n.s.	n.s.

Discussion

Non random structure

Revealing the difference from random is the first step in every pattern study. For the statistical evaluation of the results, traditional tests could not be employed in the multivariate cases, therefore we applied null models in this study by randomisation of real field abundance values. The pattern of kurgan Orthoptera assemblages differs significantly from random structures, namely it shows more aggregated distribution in ordination space than the random ones. It means that assemblages of each kurgans are more similar to each other than expected from random data. From these results we can also conclude the existence of assembly rules of kurgan Orthopterans.

Are kurgans islands?

From our results the question arises whether kurgans can be regarded as habitat islands for Orthoptera assemblages. We found that the traditional principles of island biogeography can not be proved for kurgan assemblages though they can be verified also in the case of some terrestrial habitat islands. Our result agrees with studies by GALLÉ et al. (1992) carried out in 56 isolated habitats (out of which 9 were kurgans), in the Southern Great Hungarian Plain. They also found that neither species number nor Shannon diversity of Cicadinea and Orthoptera communities increase with size of isolated habitats and they demonstrated even a slight negative correlation between species number or diversity and habitat size in the case of Cicadinea group. According to their interpretation the reason of these observations may be the lower resistance of small habitat islands against species invasion from neighbouring areas, which may result in increasing species number in spite of the small habitat size. On the other hand, special circumstances of phytophagous insects (STRONG et al. 1984) also must be considered, namely the distribution and architectural complexity of host plants may effect species number, as well. The small size (800-4000 m^2) of the kurgans may also be the cause why species number does not increase with island area. The results of KISBENEDEK & BÁLDI (1996), BÁLDI & KISBENEDEK (1999) also support the latter. In these studies, size effect was demonstrated in the case of Orthoptera assemblages living in isolated but larger grassland patches. DAVIES & MARGULES (1998) examined Carabid assemblages and did not prove that the species number increased with the size of forest patches though there were larger size differences among the studied habitat islands.

The correlation between the distances of habitats presumed to be isolated and similarities between some phytophagous insect assemblages (KRAUSZ et al. 1995) can be demonstrated but only, very slightly in this study because of the larger distances.

Relative height of kurgans effects the structure of Orthoptera assemblages indirectly, presumably through a changing microclimate, the importance of which was proved in several studies (QUINN & WALGENBACH 1990, KEMP 1992, KOHLMANN 1996).

The composition and structure of vegetation seem to be important environmental factors, their effects on Orthoptera assemblages were demonstrated in most studied habitats also (ANDERSON 1964, JOERN & LAWLOR 1981).

The distance to the nearest grassland, which was expected to have the strongest effect on species' composition of isolated assemblages due to its possible species' pool function, did not influence the composition of Orthoptera assemblages living on the studied kurgans, even when each was studied separately each Orthoptera group of different migration ability. These results contrasted with several studies in which negative correlation was found between an increasing degree of isolation and existence of some species (or the decrease of a species diversity was pointed out when studying more isolated habitats BAZ & GARCIA-

BOYERO 1995). We could not demonstrate any correlation of the species composition of Orthoptera assemblages with either the permeability of the surrounding cultivated lands, or the age of the isolation. From among isolated attributes, only the existence of presumable habitat corridors seemed to be the affecting factor in structuring kurgan assemblages, however, we did not study the actual role of these corridors in distributing Orthoptera species, so the importance of their connecting role is not known (GALLÉ et al. 1995).

Our main conclusion is that kurgans have their own Orthoptera assemblages and the structure of which is influenced more by habitat parameters than by the degree of isolation.

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