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LIFE-STRATEGY BASED STRUCTURAL FEATURES OF THE LARVAL MOSQUITO METACOMMUNITIES IN HUNGARY

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Abstract

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The main hypotheses of this present study are: (i) the organization of mosquito metacommunities is based on spectral, spatial and temporal patterns of species-groups with similar life-strategy; (ii) species composition of these metacommunities shows regional differences, but the functional groups are conservative.
Our hypotheses were tested on a database of 8,979 samples collected in Hungary. The following relationships were analysed: (i) concurrent mosquito species (Pearson correlation with Bonferroni and Benjamini-Liu corrections); (ii) seasonality of the communities (cluster-analysis, PCA, PCoA, MDS); (iii) relationships between community structure and water-coverage types (Pearson correlation, cluster-analyses, CCO) and (iiii) species groups with similar life-strategy.
Results showed that (i) the supra-individual organization of mosquitoes composes metacommunities which are characterized by typical seasonality; (ii) species composition of the mosquito metacommunities is heterogeneous but the frequency of different species functional groups is constant.
Our results originated from a temperate zone country with moderately rich Culicidae fauna because this was an ideal starting point for an extensive chain of analysis. Testing of our results herein is justified because of the outstanding relevance of mosquitoes to both public health and tourism.

Key words: mosquitoes, Culicidae, life-strategy, species groups, metacommunities

Introduction

Water ecosystems are generally isolated by discrete borders, so that related ecological researches have focused for a long time on their inner factors such as productivity, diversity and their community-structure. The “mesoscale” analysis of metapopulation systems (Bohonak, Jenkins,

2003) occurring in water habitats are commenced after the analysis of the inner factors (Holt, 1993). These metapopulation systems are maintained by both passive and active dispersion (Bilton et al., 2001; Okamura, Freeland, 2002). In metacommunities which display significant spatial and temporal heterogeneity (Bohonak, Jenkins, 2003) the mobility of the focal taxon exceeds the relatively typical distance between water habitats (Wilson, 1992).

The larval development of mosquitoes (Culicidae) has adapted completely to micro-habitats with fluctuating abiotic factors (Becker, 1989). Factors which play important roles in the organization of mosquito larval communities include the following: the species-interactions, which depend on the size of the larval habitat, pH, water-cover periodicity, size, temperature, vegetation in the larval habitat and the level of insolation (Mohrig, 1969; Livdahl, Willey, 1991; Edgerly, Livdahl, 1992; Paradise, 2000; Becker et al., 2003; Schäfer, 2004; Alfonzo et al., 2005). Community structure is also determined by the phaenological characteristics of the species, including alterations in the seasonal time of development (Russel, 1986), the development span and the number of generations. The inclination of mosquito eggs to hibernate for years also has a serious influence on community organization (Cáceres, Hairston, 1998).

Because of the density and the fast development typical in the majority of species, mosquitoes are suitable for testing general ecological models (Armbruster et al., 1999; Bradshaw et al., 2003, 2004; Mathias et al., 2005; Juliano, Lounibos, 2005; Beketov, Matthias, 2007). The list of the ecological analyses of Culicidae is significant (Horsfall, 1963; Mohrig, 1969; Gutsevich et al., 1974; Tempelis, 1975; Cassani, Bland, 1978; Wood et al., 1979; Sharkey et al., 1988; Lehane, 1991; Ward, Blaustein, 1994; Nilsson, Svensson, 1995; Wekesa et al., 1996; Schneider, Frost, 1996; Blaustein et al., 1999; Schaffner et al., 2001; Becker et al., 2003; Fischer, Schweigmann, 2004). The analyses, however, refer mainly to the ecological requirements and not to the description of the structural features of larval communities (Ferreira et al., 2001; Yanoviak, 2001; Schäfer, 2004; Silberbush et al., 2005).

Significant differences exist in the species' mobility (Mohring, 1969; Becker et al., 2003). The typical distance between mosquito habitats, however, is so far that the dispersal ability of the least mobile species is quite sufficient to maintain metapopulations (Hawley, 1988). Although mosquito-assemblages are characterized by consistent structural parameters in natural, semi-natural and anthropogenic habitats as reported by Becker (1989) to link mosquito species to "*sensu stricto*" habitat-types is difficult or even impossible because of the complex metapopulation structure (Sattler et al., 2005). Therefore the examination of mosquitoes from a community ecological view-point entails complete research of their entire metacommunity system (Wilson, 1992). Although mosquito species' food webs have been intensively investigated (Bradshaw, Holzapfel, 1983; Teng, Apperson, 2000; Griswold, Lounibos, 2005), relevant examinations today still focus on mosquito communities inhabiting water-filled tree-holes. Results of Ellis et al.'s (2006) study on tree-hole mosquito species failed to confirm the four main metacommunity perspectives of patch dynamics, species sorting, mass effect and neutrality (Leibold et al., 2004). Instead, these highlighted features of multiple metacommunity models**.** Defects detected in mosquito-research centre on the lack of studies related to mosquito metacommunities occurring in natural and semi-natural grasslands and other typical breeding habitats.

According to our hypothesis, the organization of mosquito metacommunities is based on spectral, spatial and temporal pattern of species-groups with similar life-strategies in oviposition, generation number, host-seeking and life cycle progression. Although these metacommunities can be described by characteristic features at the species' level, their uniqueness is manifested rather by the presence/absence and density of species-groups with different functional life-strategy features. Our hypothesis stresses that although the species composition of metacommunities shows regional differences, the contribution of different

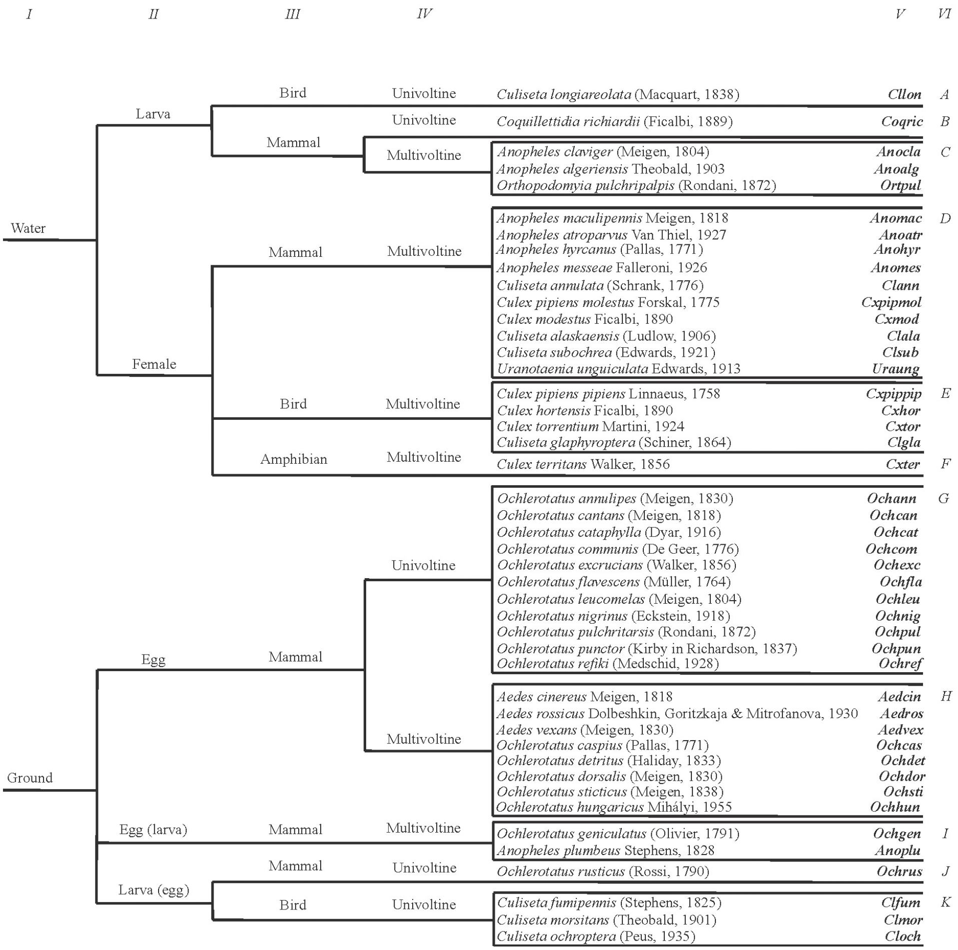

Fig. 1. Functional groups of the Hungarian mosquito species [completed and corrected after Schäfer (2004), some species (*Ochloretatus pullatus* (Coquillett, 1904), *Culex mimeticus* Noé, 1899, *Culex theileri* Theobald, 1903, *Culex martinii* Medschid, 1930) are unsuitable for classification, because they are recognized in only a few localities]. Legends: I – oviposition site; II – hibernation state; III – biting orientation of females; IV – number of generations within a year; V – code of the species; VI – code of the functional group (A–H).

functional groups are conservative. Metacommunities are organized from assemblages connected to patches with discrete habitat borders, and although the species composition of the assemblages is heterogeneous, different degrees of overlap exist.

Our hypothesis was tested on a database of 8,979 samples collected in Hungary with 194,966 larvae from 47 mosquito species (abbreviations are in Fig. 1). We revealed concurrent species and determined the typical seasonality of metacommunities and species-groups whose unique life-strategy increase unique structure.

Material and methods

The analyzed database contains 8,979 samples, partly from the 1,239 samples collected for this study and partly from the 7,740 samples processed as published data in Hungary (Tóth, 2004, 2006). These 1,239 new samples were collected in the studied area of 11.3 km^2 around lake Tisza, and the 10.3 km^2 area studied near lake Balaton. 7,740 samples proceed from the published data covered the entire Hungarian area of 93,000 km^2 which is rich in mosquito breeding sites.

Some of the sampling sites were sampled repeatedly, but many were sampled just once. Merging samples taken in the same place at different times was considered to be unreasonable, because ecological factors in the usually temporary breeding sites can be assigned to the time of the given sampling. The 194,966 collected larvae belong to 47 Culicidae species. This covers the number of mosquito species collected in larval stages in Hungary. Here, it is noteworthy that Tóth (2004) reported that *Ochlerotatus detritus* has only been collected in the imago stage in Hungary. These analyzed samples represent all the important Culicidae breeding habitat types (Dévai, 1997). The number of samples from the given water-coverage type is almost directly proportional to the portion shown in the habitat structure highlighted in Appendix I.

A 10 m^2 quadrate was studied in each sampling site. The following factors were recorded in the sample areas (1–3 in all of them, 4–9 in the newly sampled 1,239 habitats): (1) the mosquito species' densities in 1 litre water; (2) the altitude; (3) plant association(s) in the habitat; (4) the most typical plant species in the water and water-banks; (5) the pH of habitats in marsh and marshy-meadow areas; (6) the habitat temperature, depth and character, where "0" was assigned to temporary habitats and "1" to permanent ones; (7) the water-surface cover in a scale of 1–5, where 1 = 0%, 2 = 1–20%, 3 = 21–40%, 4 = 41–60%, 5 = 61–100%; (8) clarity in a scale of 1–5 and (9) degree of shade in a 1–5 scale, where: 1 = a lack of screening; 2 = screening by grass length < 20 cm, 3 = screening by tall grass > 20 cm, or recessing in canals, 4=open forest and forest ecotone, and 5 = closed forest. Sampling of the mosquito larval assemblages was accomplished in a 20 cm-circlular straining net. This net texture was able to collect even younger larvae (L_1 stage). Larvae collected in 2–3 dips were defined as being one sample. The examination of 1 litre of breeding water was considered in this same way in each site, so that collected data was suitable for statistical comparisons. Adult male specimens were collected by net and biting females by aspirator.

Only data occurring in at least 1% of the species samples were considered, in order to eliminate statistical artificial products and to simplify database handling.

Hungarian mosquito fauna species' functional groups were determined on the basis of the most important life-strategy features covering oviposition site, hibernation period, female biting orientation and number of generations produced within a year; according to Schäfer (2004) (Fig. 1).

The following relationships were analyzed:

1. concurrent mosquito species (Pearson correlation with Bonferroni and Benjamini-Liu corrections);
2. seasonality (using both density and relative frequency values; cluster-analysis by Euclidean distances and Ward methodology; PCoA; MDS);
3. the relationship between community structure and water-coverage breeding sites (using both density and relative frequency values; Pearson correlation; cluster-analysis; CCO);
4. species-groups with similar life-strategy.

1. Correlation analysis treats the matrix with a binary character for the occurrences of rare species, which although considered random, also identifies a significant relationship. The evaluation of correlations which qualified as being significant were performed as follows: (1) calculation the number of positive (presence) samples per

species; (2) determination of the number of common occurrences of the concurrent species-pairs which exhibited a significant relationship; (3) determination of the percentage rate of all occurrences and common occurrences of species pairs; (4) the significant correlations were considered to be typically related when both species occurred in at least 1% of the samples and the above-mentioned proportion exceeded 15% for both species. Establishing this limit of 15% was justified by the statistical distribution of the cases.

2. The analysis of mosquito communities' seasonality was instituted to maintain objectivity. Since the majority of Culicidae breeding sites occur in temporarily flooded areas, comparison of samples at different times would not have revealed communities based on actual simultaneous occurrences, but only describe rather abstract phenomena. Samples were divided into four time-intervals based on sampling dates and analysis was performed within these interval limits. Based on phaenological phenomena, application of meteorological season boundaries was considered as the most appropriate approach. Here, spring covers March, April and May; summer occupies June, July and August; autumn includes September, October and November, while winter spans December, January and February.

3. Water-body types of Dévai (1997) were recorded during our field work, and these were constantly mentioned in the used literary data on habitat.

4. The most important species life characteristics were evaluated for each sample: oviposition site with water surface designated by 1, and dry surfaces on ground, plant, and artificial surfaces designated by 2, biting orientation of females (mammal-1/other vertebrata-2), number of generations within a year (one-1/several-2) and hibernation state (egg-1/larva-2/female-3). Species-groups' characteristic life-strategy features were also examined statistically (Fig. 1). The deviations and medians of the average values of the above mentioned variables were examined per water-body type by PCoA. Recorded values were compared to generated data lists characterized by the induced maximum diversity in Box Plots.

The values were ranked according to values of the oviposition place. The theoretical frequencies of the different variants determined by the 8,979 samples were collaterally represented. In accordance with our hypothesis, we also examined the following three most related life-style features in a ternary-diagram: oviposition site, the female biting orientation and the number of generations within a year.

Nomenclature of mosquito species here follows Becker et al (2003), and statistical analysis was performed with Statistica 6.0 (Statsoft, 1995), SYN-TAX 2000 (Podani, 2001) and PAST (Hammer et al., 2001) programmes.

Results

Concurrent mosquito species

Although original analysis of connected occurrences of the detected mosquito species revealed several significant correlations, only a small number formed the evaluation detailed in the methodology chapter (Fig. 2). Parallel occurrences of Culicidae species confirmed by the Pearson-correlation are presented in Table 1, with the most typical relationships between (1) *Culiseta annulata, Anopheles claviger, A. maculipennis, Culex modestus, Cx. pipiens*; (2) *Ochlerotatus cantans, O. cataphylla, O. rusticus, Culiseta morsitans*; (3) *Ochlerotatus sticticus* and *Aedes vexans.*

Mosquito metacommunities

Cluster-analysis, PCA (cumulative percentage variance of species data/axes$_{\text{spring}}$: 1: 53.6; 2: 64.4; 3: 72.2; 4: 78.1 – cpv/axes$_{\text{summer}}$: 1: 79.3; 2: 86.1; 3: 91.2; 4: 94.0 – cpv/axes$_{\text{autumn}}$: 1: 58.3; 2: 78.4; 3: 87.9; 4: 92.4 – cpv/axes$_{\text{winter}}$: 1: 74.0; 2: 84.9; 3: 90.7; 4: 95.4), PCoA and MDS gave the same results in this investigation. Figs. 3–4 show the results of the non-metric multi-dimensional scaling by marking the minimum span periods of spring and

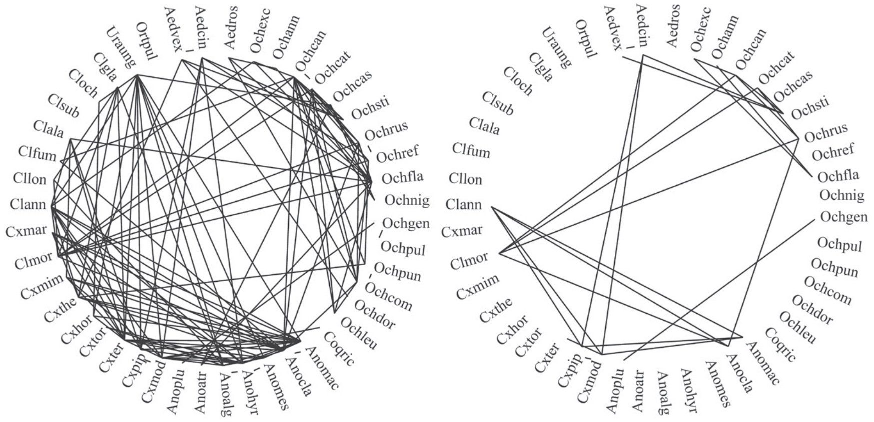

Fig. 2. All established significant correlations between the presence of the mosquito species (left) and typical significant correlations confirmed by valuation (right).

winter (Bray-Curtis similarities see in Tables 2–5). Analysis of relative frequency and density showed similar results, but the latter was represented more prominently than relative frequency.

Both the spatial and temporal conservative structures of mosquito communities are apparent in the analysis of monthly handled data, but metacommunities were sharply differentiated when species representation was examined on the seasonal level.

Our results recorded the following mosquito metacommunities in Hungary on the seasonal level, and the continuous line below represents species closely related to the community and broken lines designate species less closely community-related.

Spring (March–May) (Fig. 3): (a) *Anocla–Clmor–Ochrus–Ochref–Ochcan–Ochcat;* (b) *Clann----Cxpip–Anomac–Cxmod----Coqric;* (c) *Anomes–Cxter–Clann----Ochexc;* (d) *Aedcin----Ochann----Ochfla–Ochcas–Ochsti----Aedvex;* (e) *Ochgen–Anoplu*.

Summer (June–August): (a) *Cxter–Clann–Anomac–Cxmod----Coqric;* (b) *Ochcat–Ochfla;* (c) *Ochsti–Aedvex–Ochann*; (d) *Ochgen–Anoplu.*

Autumn (September–November): (a) *Uraung----Cxpip–Anomes–Anomac–Cxmod----Coqric;* (b) *Cxter–Anocla----Clmor*; (c) *Ochgen–Anoplu.* Autumn the unique occurrence of several diagnostic species from the earlier period appears, and samples with low species number which frequently have one mono-dominant species are especially typical.

Winter (December–February) (Fig. 4): (a) *Clann–Anocla;* (b) *Clmor–Ochcat–Ochexc–Ochrus;* (c) *Ochfla–Ochann–Ochcan.* The three cold-tolerant communities are typical in winter, and are quite compact without relationships or overlaps. In this winter period, both species hibernating in the larval stage and the larvae of species hatching after snow-melt and hatching in early spring are found equally in the larval habitats. This observation concerning Culicidae communities in this period represents their generalized chronological ranking in winter.

T a b l e 1. Significant (bold) relations (Pearson-correlation) between Culicidae species (based on 8,979 samples) (* = confirmed by Bonnferroni and Benjamini-Liu corrections).

	Aedes cinereus	*Ochlerotatus sticticus*	*Culex modestus*	*Culex pipiens*	*Ochlerotatus cataphylla*	*Ochlerotatus flavescens*	*Ochlerotatus rusticus*	*Culiseta morsitans*	*Anopheles plumbeus*	*Culiseta annulata*	*Culex territans*
Aedes cinereus		**r = 0.026 p = 0.011**	**r = 0.022 p = 0.034**	**r = 0.032 p = 0.002**	r = -0.005 p = 0.619	r = 0.001 p = 0.918	r = -0.011 p = 0.294	r = -0.001 p = 0.858	r = -0.010 p = 0.333	**r = 0.053 p < 0.001***	r = 0.007 p = 0.474
Aedes vexans	**r = 0.079 p < 0.001***	**r = 0.537 p < 0.001***	r = -0.006 p = 0.565	r = -0.002 p = 0.821	r = -0.014 p = 0.178	**r = 0.094 p < 0.001**	r = -0.015 p = 0.137	r = -0.012 p = 0.228	r = -0.015 p = 0.135	r = -0.014 p = 0.177	r = -0.014 p = 0.174
Anopheles claviger	**r = 0.002 p = 0.839**	r = -0.012 p = 0.240	r = -0.017 p = 0.097	**r = -0.033 p = 0.002**	r = 0.021 p = 0.047	r = 0.001 p = 0.994	**r = 0.033 p = 0.002**	**r = 0.121 p < 0.001***	r = -0.023 p = 0.030	**r = 0.056 p < 0.001***	**r = 0.190 p = 0.001**
Anopheles maculipennis	r = 0.020 p = 0.051	r = -0.015 p = 0.148	**r = 0.168 p < 0.001***	**r = 0.149 p < 0.001**	**r = -0.042 p < 0.001**	**r = -0.034 p = 0.001**	**r = -0.048 p < 0.001**	**r = -0.031 p = 0.003**	**r = -0.033 p = 0.001**	**r = 0.132 p < 0.001***	**r = 0.206 p = 0.001**
Culex modestus	**r = 0.022 p = 0.034**	r = -0.009 p = 0.373		**r = 0.125 p < 0.001**	**r = -0.022 p = 0.035**	**r = -0.021 p = 0.044**	**r = -0.027 p = 0.010**	r = -0.019 p = 0.064	r = -0.016 p = 0.126	**r = 0.068 p < 0.0001***	**r = 0.041 p = 0.001**
Culex pipiens	**r = 0.032 p = 0.002**	r = -0.012 p = 0.250	r = 0.125 p = 0.051		**r = -0.032 p = 0.002**	**r = -0.030 p = 0.004**	**r = -0.039 p = 0.001**	**r = -0.028 p = 0.007**	r = -0.016 p = 0.122	**r = 0.130 p < 0.001***	r = 0.006 p = 0.545
Ochlerotatus annulipes	r = 0.007 p = 0.454	r = 0.002 p = 0.809	**r = -0.025 p = 0.017**	**r = -0.033 p = 0.002**	r = 0.010 p = 0.341	**r = 0.146 p < 0.001**	r = 0.011 p = 0.281	r = 0.001 p = 0.884	r = -0.013 p = 0.215	r = -0.015 p = 0.139	r = -0.017 p = 0.091
Ochlerotatus cantans	r = -0.004 p = 0.660	**r = 0.027 p = 0.009**	r = -0.029 p = 0.006	**r = -0.041 p < 0.001**	**r = 0.349 p < 0.001***	r = 0.020 p = 0.058	**r = 0.108 p < 0.001***	**r = 0.085 p < 0.001***	r = -0.015 p = 0.155	**r = -0.031 p = 0.003**	r = -0.017 p = 0.096
Ochlerotatus cataphylla	r = -0.005 p = 0.619	**r = 0.029 p = 0.006**	**r = -0.022 p = 0.035**	**r = -0.032 p = 0.002**		r = 0.018 p = 0.073	**r = 0.109 p < 0.001***	**r = 0.046 p < 0.001**	r = -0.011 p = 0.282	**r = -0.026 p = 0.014**	r = -0.013 p = 0.219
Ochlerotatus excrucians	r = -0.004 p = 0.666	r = -0.002 p = 0.822	r = -0.010 p = 0.340	r = -0.009 p = 0.371	**r = 0.023 p = 0.029**	**r = 0.041 p < 0.001**	r = 0.014 p = 0.180	r = 0.020 p = 0.056	r = -0.005 p = 0.619	**r = 0.023 p = 0.025**	r = -0.006 p = 0.518
Ochlerotatus geniculatus	r = -0.011 p = 0.288	r = -0.010 p = 0.328	r = -0.019 p = 0.062	**r = -0.021 p = 0.039**	r = -0.013 p = 0.205	r = -0.013 p = 0.198	r = -0.016 p = 0.119	r = -0.012 p = 0.246	**r = 0.257 p < 0.001***	**r = -0.025 p = 0.014**	r = -0.014 p = 0.175
Ochlerotatus rusticus	r = -0.011 p = 0.294	r = 0.005 p = 0.582	**r = -0.027 p = 0.010**	**r = -0.039 p < 0.001**	**r = 0.109 p < 0.001**	**r = 0.022 p = 0.032**		**r = 0.059 p < 0.001***	r = -0.014 p = 0.171	**r = -0.031 p = 0.003**	r = -0.014 p = 0.186

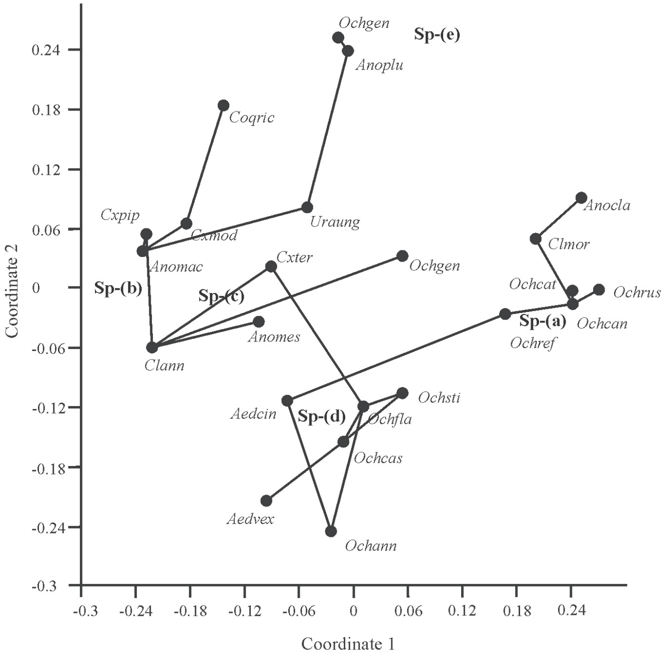

Fig. 3. MDS of samples collected in spring (March–May) (with min. span tree).

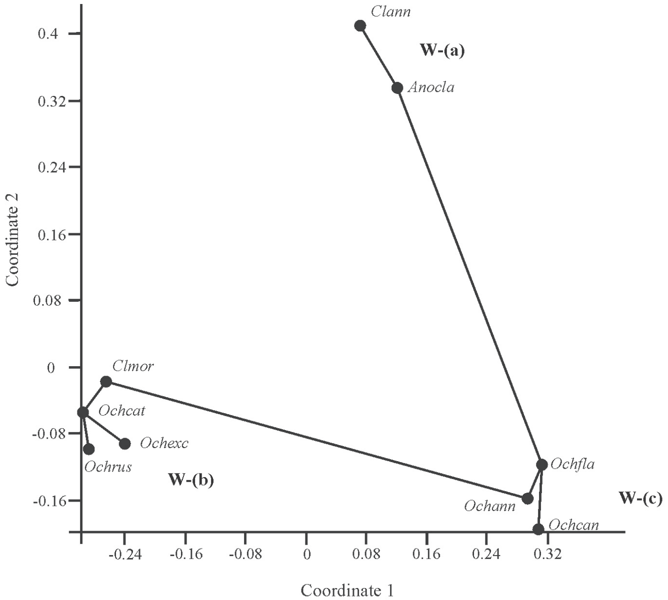

Fig. 4. MDS of samples collected in winter (December–February) (with min. span tree).

T a b l e 2. Established mosquito metacommunities occurring in spring in Hungary (Bray-Curtis similarities of MDS).

	Acla	Cmor	Orus	Oref	Ocan	Ocat	Cx-pip	Amac	Cx-mod	Cric	Ames	Cx-ter	Clann	Oexc	Acin	Oann	Ofla	Ocas	Osti	Avex	Aplu	Ogen
Anopheles claviger Acla		0.22	0.14	0.03	0.11	0.10	0.02	0.06	**	0.03	0.01	0.03	0.05	0.12	0.05	0.07	0.06	0.03	0.06	0.02	**	**
Culiseta morsitans Cmor	0.22		0.13	0.05	0.11	0.09	**	0.02	**	0.01	0.01	0.03	0.02	0.13	0.06	0.03	0.07	0.01	0.04	0.01	**	**
Ochlerotatus rusticus Orus	0.14	0.13		0.07	0.18	0.18	0.01	0.02	**	0.01	**	0.01	0.03	0.09	0.04	0.06	0.05	0.01	0.08	0.02	**	**
Ochlerotatus refiki Oref	0.03	0.05	0.07		0.10	0.09	**	0.01	**	**	**	**	**	0.03	0.08	0.02	0.03	0.01	0.05	0.01	**	**
Ochlerotatus cantans Ocan	0.11	0.11	0.18	0.10		0.28	0.01	0.01	**	0.01	0.01	0.01	0.03	0.08	0.05	0.05	0.04	0.01	0.11	0.02	**	**
Ochlerotatus cataphylla Ocat	0.10	0.09	0.18	0.09	0.28		0.01	0.02	**	0.01	**	0.01	0.02	0.06	0.04	0.05	0.05	0.01	0.12	0.02	**	**
Culex pipiens Cxpip	0.02	**	0.01	**	0.01	0.01		0.12	0.01	0.01	0.01	0.02	0.22	0.03	0.06	0.04	0.01	0.01	0.04	0.06	**	**
Anopheles maculipennis Amac	0.06	0.02	0.02	0.01	0.01	0.02	0.12		0.06	0.03	0.02	0.07	0.12	0.03	0.11	0.03	0.04	0.04	0.05	0.04	**	**
Culex modestus Cxmod	**	**	**	**	**	**	0.01	0.06		0.02	0.06	0.02	0.01	**	0.02	**	**	**	**	**	**	**
Coquillettidia richiardii Cric	0.03	0.01	0.01	**	0.01	0.01	0.01	0.03	0.02		0.01	**	0.03	0.03	0.01	0.02	0.02	0.01	0.01	0.01	**	**
Anopheles messeae Ames	0.01	0.01	**	**	0.01	**	0.01	0.02	0.06	0.01		0.04	0.03	0.01	0.03	0.01	0.01	0.02	0.01	**	**	**
Culex territans Cxter	0.03	0.03	0.01	**	0.01	0.01	0.02	0.07	0.02	**	0.04		0.06	0.01	0.03	**	0.02	**	0.01	**	**	**
Culiseta annulata Clann	0.05	0.02	0.03	**	0.03	0.02	0.22	0.12	0.01	0.03	0.03	0.06		0.07	0.07	0.06	0.05	0.03	0.06	0.05	**	**
Ochlerotatus excrucians Oexc	0.12	0.13	0.09	0.03	0.08	0.06	0.03	0.03	**	0.03	0.01	0.01	0.07		0.04	0.04	0.10	0.02	0.03	0.02	**	**
Aedes cinereus Acin	0.05	0.06	0.04	0.08	0.05	0.04	0.06	0.11	0.02	0.01	0.03	0.03	0.07	0.04		0.10	0.08	0.05	0.10	0.07	**	**
Ochlerotatus annulipes Oann	0.07	0.03	0.06	0.02	0.05	0.05	0.04	0.03	**	0.02	0.01	**	0.06	0.04	0.10		0.12	0.05	0.07	0.11	**	**
Ochlerotatus flavescens Ofla	0.06	0.07	0.05	0.03	0.04	0.05	0.01	0.04	**	0.02	0.01	0.02	0.05	0.10	0.08	0.12		0.08	0.07	0.05	**	**
Ochlerotatus caspius Ocas	0.03	0.01	0.01	0.01	0.01	0.01	0.01	0.04	**	0.01	0.02	**	0.03	0.02	0.05	0.05	0.08		0.07	0.06	**	**
Ochlerotatus sticticus Osti	0.06	0.04	0.08	0.05	0.11	0.12	0.04	0.05	**	0.01	0.01	0.01	0.06	0.03	0.10	0.07	0.07	0.07		0.28	**	**
Aedes vexans Avex	0.02	0.01	0.02	0.01	0.02	0.02	0.06	0.04	**	0.01	**	**	0.05	0.02	0.07	0.11	0.05	0.06	0.28		**	**
Anopheles plumbeus Aplu	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**		0.06
Ochlerotatus geniculatus Ogen	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	0.06	

T a b l e 3. Established mosquito metacommunities occurring in summer in Hungary (Bray-Curtis similarities of MDS).

	Cxter	Clann	Amac	Cxmod	Cric	Ocat	Ofla	Osti	Avex	Oann	Ogen	Aplu
Culex territans Cxter		0.10	0.15	0.08	**	**	**	0.03	0.03	**	**	**
Culiseta annulata Clann	0.10		0.19	0.12	**	**	**	0.05	0.09	**	**	**
Anopheles maculipennis Amac	0.15	0.19		0.24	0.01	**	**	0.09	0.13	**	**	**
Culex modestus Cxmod	0.08	0.12	0.24		0.02	**	**	0.06	0.10	**	**	**
Coquillettidia richiardii Cric	**	**	0.01	0.02		**	0.01	**	**	**	**	**
Ochlerotatus cataphylla Ocat	**	**	**	**	**		0.20	0.01	**	**	**	**
Ochlerotatus flavescens Ofla	**	**	**	**	0.01	0.20		0.01	0.01	**	**	**
Ochlerotatus sticticus Osti	0.03	0.05	0.09	0.06	**	0.01	0.01		0.15	0.01	**	**
Aedes vexans Avex	0.03	0.09	0.13	0.10	**	**	0.01	0.15		0.01	**	**
Ochlerotatus annulipes Oann	**	**	**	**	**	**	**	0.01	0.01		**	**
Ochlerotatus geniculatus Ogen	**	**	**	**	**	**	**	**	**	**		0.23
Anopheles plumbeus Aplu	**	**	**	**	**	**	**	**	**	**	0.23	

T a b l e 4. Established mosquito metacommunities occurring in autumn in Hungary (Bray-Curtis similarities of MDS).

	Uung	Cxpip	Ames	Amac	Cxmod	Cric	Cxter	Acla	Clmor	Ogen	Aplu
Uranotaenia unguiculata Uung		0.03	0.04	0.05	0.06	0.03	0.06	0.01	0.02	**	**
Culex pipiens Cxpip	0.03		0.01	0.17	0.13	0.01	0.04	0.07	**	**	**
Anopheles messeae Ames	0.04	0.01		0.05	0.06	0.01	0.08	0.03	0.02	**	**
Anopheles maculipennis Amac	0.05	0.17	0.05		0.31	0.03	0.18	0.16	0.02	**	**
Culex modestus Cxmod	0.06	0.13	0.06	0.31		0.05	0.11	0.11	0.01	**	**
Coquillettidia richiardii Cric	0.03	0.01	0.01	0.03	0.05		0.01	0.02	0.01	**	**
Culex territans Cxter	0.06	0.04	0.08	0.18	0.11	0.01		0.22	0.05	**	0.01
Anopheles claviger Acla	0.01	0.07	0.03	0.16	0.11	0.02	0.22		0.09	**	**
Culiseta morsitans Cmor	0.02	**	0.02	0.02	0.01	0.01	0.05	0.09		**	0.01
Ochlerotatus geniculatus Ogen	**	**	**	**	**	**	**	**	**		0.22
Anopheles plumbeus Aplu	**	**	**	**	**	**	0.01	**	0.01	0.22	

Table 5. Established mosquito metacommunities occurring in autumn in Hungary (Bray-Curtis similarities of MDS).

	Clann	Acla	Clmor	Ocat	Oexc	Orus	Ofla	Oann	Ocan
Culiseta annulata Clann		0.03	0.03	**	**	**	**	**	**
Anopheles claviger Acla	0.03		0.15	0.16	0.04	0.17	0.07	0.10	0.21
Culiseta morsitans Cmor	0.03	0.15		0.28	0.03	0.17	**	0.05	0.06
Ochlerotatus cataphylla Ocat	**	0.16	0.28		0.15	0.33	**	0.02	0.04
Ochlerotatus excrucians Oexc	**	0.04	0.03	0.15		0.05	**	0.05	0.01
Ochlerotatus rusticus Orus	**	0.17	0.17	0.33	0.05		0.01	0.01	0.17
Ochlerotatus flavescens Ofla	**	0.07	**	**	**	0.01		0.12	0.07
Ochlerotatus annulipes Oann	**	0.10	0.05	0.02	0.05	0.01	0.12		0.14
Ochlerotatus cantans Ocan	**	0.21	0.06	0.04	0.01	0.17	0.07	0.14	

Correlations between mosquito metacommunities and water-body types

Table 6 shows that similar mosquito species composition (with the dominance of *Anomac, Anocla, Cxmod, Cxter, Cxpip* and *Coqric* species) related to habitat types are characterized by constant water coverage with more significant water depth and pond-weed vegetation. This water-body type includes the littoro-profundal shallow lakes (1110), small lake-like natural ponds (1310), small lake-like dead channels (1320), small lake-like water pools (1330), small lake-like fishponds (1340), other small lake-like artificial ponds (1350) and slough-like natural ponds (1410).

The correlation analysis separated three characteristically different water-body-type groups on the basis of mosquito species' relationships: (1) the marshy type, (2) plashy type and (3) "tömpöly" type (tömpöly represents a small annual water body which dries only during extreme drought years). The marshy type natural ponds (1610) and marshy type artificial ponds (1620) belonging to group (1) above are rich in species and also suitable for species related to continuous water coverage (diagnostic species: *Aedvex, Aedcin, Ochcan, Ochexc, Ochann, Ochcasp, Ochfla, Clmor, Clann, Uraung Anomac, Anocla* and *Cxmod*). The relationship of multivoltine species (*Aedvex, Ochcas, Ochsti, Cxpip*) to the plashy habitat type (2) is typically found in pools of flood-waters (1721) and also in pits of meteoric water (1722). Due to the phaenology of the *Ochcan, Ochcat, Ochrus* and *Ochref* species, these are related to the natural small waters of the "tömpöly" type, and therefore ranked in group 3. This separation can be explained on the basis of the species composition during the spring period. The tree-holes (1752) contain the two dendrotelm specialist species of *Ochge* and *Anoplu*, and these are listed as a separate category in each analysis. Only the few species of *Anomac, Anocla, Cxpi,* and *Cxter* are related to the peculiar circumstances provided by artificial containers, and only *Anomac, Anocla, Anomes* and *Cxter* are also related to the water-body group of slightly streaming waters, more accurately, to middle sized rivers (2220), brooklets (2330), artificial small streams (2340) and shelter springs (3400).

Table 6. Significant positive correlations between water-bodies and mosquito species (see legends in Appendix).

1110 – *Cxmod* (r = 0.0822; P = 0.0001).
1310 – *Cxmod* (r = 0.0622; P = 0.0001). *Anomac* (r = 0.0432; P = 0.0001).
1320 – *Anomac* (r = 0.0284; P = 0.007).
1330 – *Anomac* (r = 0.0643; P = 0.0001). *Anocla* (r = 0.0227; P = 0.032). *Cxmod* (r = 0.0583; P = 0.0001). *Cxter* (r = 0.0348; P = 0.001).
1340 – *Anomac* (r = 0.043; P = 0.0002). *Cxmod* (r = 0.0231; P = 0.029). *Cxter* (r = 0.0226; P = 0.033).
1350 – *Anomac* (r = 0.055; P = 0.0001). *Cxter* (r = 0.03; P = 0.005).
1410 – *Cxmod* (r = 0.0464; P = 0.001). *Coqric* (r = 0.2179; P = 0.001). *Cxpip* (r = 0.0395; P = 0.0001).
1610 – *Aedvex* (r = 0.0327; P = 0.002). *Aedcin* (r = 0.0553; P = 0.0001). *Ochexc* (r = 0.0406; P = 0.0001). *Ochann* (r = 0.0876; P = 0.0001). *Ochcan* (r = 0.0254; P = 0.016). *Ochcasp* (r = 0.0222; P = 0.035). *Ochfla* (r = 0.1; P = 0.0001). *Clmor* (r = 0.0309; P = 0.003). *Clann* (r = 0.0514; P = 0.0001). *Uraung* (r = 0.0262; P = 0.013).
1620 – *Ochcas* (r = 0.0757; P = 0.0001). *Anomac* (r = 0.0588; P = 0.0001). *Anocla* (r = 0.0308; P = 0.004). *Cxmod* (r = 0.04; P = 0.0001).
1711 – *Ochcan* (r = 0.072; P = 0.0001). *Ochcat* (r = 0.0615; P = 0.0001). *Ochrus* (r = 0.0963; P = 0.0001). *Ochref* (r = 0.0318; P = 0.003).
1721 – *Aedvex* (r = 0.0588; P = 0.0001). *Ochann* (r = 0.0241; P = 0.022). *Ochcas* (r = 0.0286; P = 0.007).
1722 – *Aedvex* (r = 0.066; P = 0.0001). *Ochsti* (r = 0.0238; P = 0.024). *Ochfla* (r = 0.0286; P = 0.007). *Cxpip* (r = 0.0483; P = 0.0001).
1730 – *Ochcan* (r = 0.0284; P = 0.007). *Ochsti* (r = 0.0241; P = 0.022).
1752 – *Ochgen* (r = 0.5105; P = 0.0001). *Anoplu* (r = 0.4552; P = 0.0001).
1755 – *Anomac* (r = 0.0155; P = 0.0001). *Anocla* (r = 0.0411; P = 0.0001). *Cxpip* (r = 0.1202; P = 0.0001). *Cxter* (r = 0.0434; P = 0.0001).
2220 – *Anomac* (r = 0.0216; P = 0.041). *Anocla* (r = 0.0215; P = 0.042). *Cxmod* (r = 0.0443; P = 0.0001). *Cxter* (r = 0.0207; P = 0.050).
2330 – *Anomac* (r = 0.1; P = 0.0001). *Anocla* (r = 0.0449; P = 0.0001). *Anomes* (r = 0.0241; P = 0.0001). *Cxter* (r = 0.0752; P = 0.0001).
2340 – *Anomac* (r = 0.0683; P = 0.0001). *Cxmod* (r = 0.0239; P = 0.024). *Uraung* (r = 0.0748; P = 0.0001).
3400 – *Anocla* (r = 0.1152; P = 0.0001). *Cxter* (r = 0.0279; P = 0.008).
2320 – *Ochcan* (r = 0.0471; P = 0.0001). *Ochcat* (r = 0.0245; P = 0.02). *Ochrus* (r = 0.0252; P = 0.017). *Ochref* (r = 0.0445; P = 0.0001). *Anocla* (r = 0.0655; P = 0.0001).

The correlations between mosquito species and water body types separated the following 7 unique water-body-type groups: (1) permanent waters; (2) transient habitats with marshy vegetation; (3) pools; (4) fresh floodwaters; (5) tree-holes; (6) artificial containers and (7) flowing waters.

The results of the correlation analyses were confirmed by MDS. Based on this analysis (Figs. 3–4), and considering seasonality, the following Culicidae communities display separation in the spring period; the number (2) transient habitats with marshy vegetation, the (3) pools and the (4) fresh floodwaters. Although this separation is also apparent in the summer period, only the (2) transient habitats with marshy vegetation demonstrate individuality for the autumn period. The distance of pools (3) and fresh floodwaters (4) from the remainder decreases to a minimum during this interval. The MDS shows that the structural separation of the (5) tree-holes and the (6) artificial containers does not approach the separation of the previously mentioned types during spring. The difference in structure of the two mentioned types from the remainder increases in summer and it decreases again by autumn. The MDS did not verify the structural deviation of the (1) permanent waters and the (7) flowing waters expected from correlation analysis. Based on the MDS, the breeding habitats characterized by continuous water coverage do not reveal significant structural differences in any season on the basis of their Culicidae larval communities. Only smaller, transitional structural differences can be observed in certain types, such as in the littoro-profundal shallow lakes during summer and autumn. In winter, the heterogeneous group of transient habitats with marshy vegetation (2), pools (3) and fresh floodwaters (4), as well as other breeding habitat-types can be separated by MDS. The separation of the artificial containers (6) can be distinguished in this heterogeneous group.

Analysis of species groups with similar life-strategy

Analysis based on the life characteristics of oviposition site, hibernating stage, host-seeking by the female and number of generations of the species-groups with similar life-strategy of

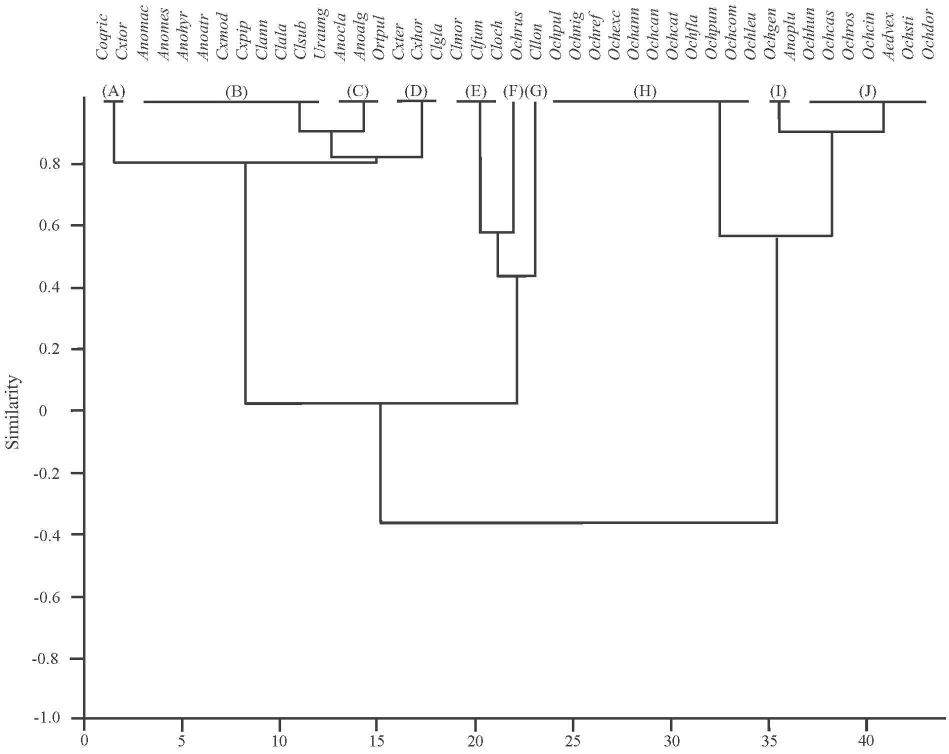

Fig. 5. Functional groups of the mosquito metacommunities (based on the life-strategy features of oviposition site; hibernation state; biting orientation of females and number of generations within a year).

metacommunities highlighted in Fig. 1 separated the following functional species groups: (a) *Coqric, Cxtor*; (b) *Anomac, Anomes, Anohyr, Anoatr, Cxmod, Cxpip, Clann, Clala, Clsub, Uraung*; (c) *Anocla, Anoalg, Orthpul*; (d) *Cxter, Cxhor, Clgla*; (e) *Clmor, Clfum, Cloch*; (f) *Ochrus*; (g) *Cllon*; (h) *Ochpul, Ochnig, Ochref, Ochexc, Ochann, Ochcan, Ochcat, Ochfla, Ochpun, Ochcom, Ochleu*; (i) *Ochgen, Anoplu*; (j) *Ochhun, Ochcas, Aedros, Aedcin, Aedvex, Ochsti, Ochdor*. Although cluster-analysis and MDS delivered the same results, the cluster analysis graphic is more representative (Fig. 5).

Based on the comparison of the theoretical frequency of life-strategies in Fig. 1, a close relationship was established between oviposition site, hibernating state and the number of generations (Fig. 6). This was also confirmed by the ternary-diagram.

The dispersion of the life-strategy indices of the different water-body types based on PCoA and characterized by individual mosquito community-structure is lower in every case than dispersion generated with induced maximum diversity (Fig. 7). This mainly holds true for tree-hole and artificial container habitats. The position of the median of the indices numerically mirrors the differences between the water-body types separated by the PCoA, as also depicted in Fig. 7.

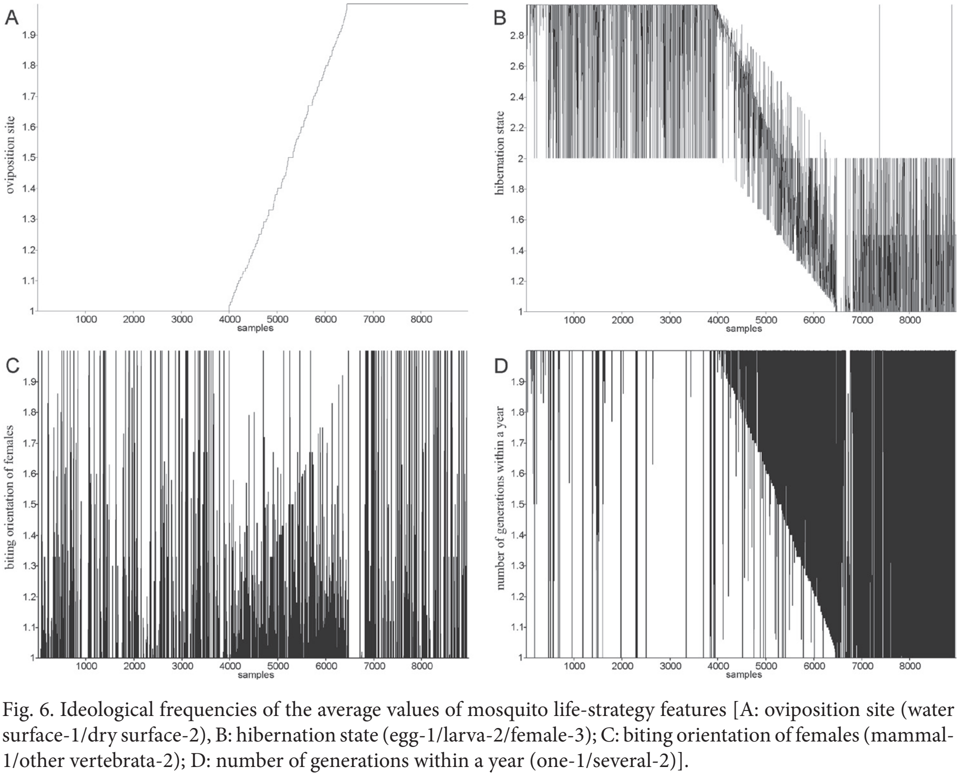

Fig. 6. Ideological frequencies of the average values of mosquito life-strategy features [A: oviposition site (water surface-1/dry surface-2), B: hibernation state (egg-1/larva-2/female-3); C: biting orientation of females (mammal-1/other vertebrata-2); D: number of generations within a year (one-1/several-2)].

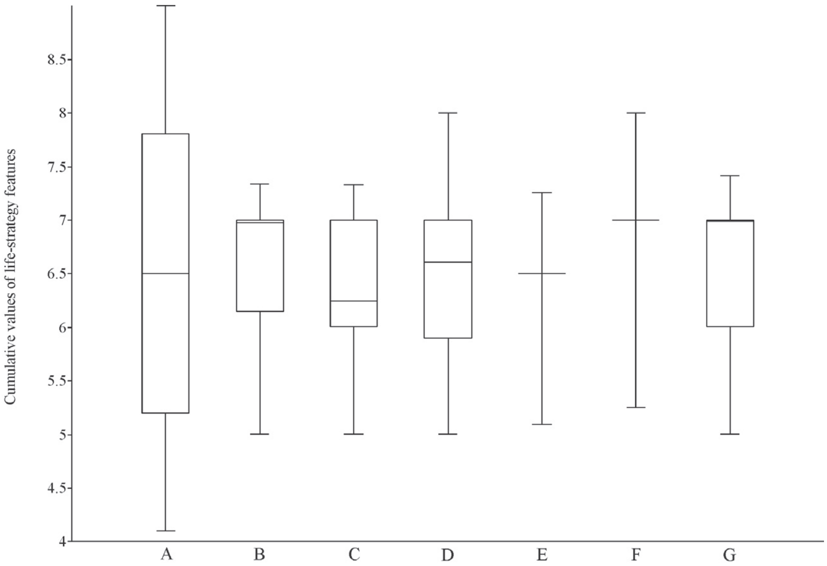

Fig. 7. Cumulative values of life-strategy features. (Legends: A – generated data with maximum diversity, B – (2) transient habitats with marshy vegetation, C – (4) pits, D – (3) „tömpöly" waters, E – (5) treeholes, F – (6) technotelms, G – (1) permanent waters)

Discussion

The mosquito communities and metacommunities of Central Europe which occur in the typical temporary habitats of natural and semi-natural vegetation, such as humid grasslands and reed beds, have not previously been studied from community ecology aspects. Our results show that mosquito breeding sites can characterize the spatial and temporal combinations of species' larval assemblages (Figs 1, 5, Table 7). The species combinations published within this paper mostly equate with the species combinations in Hungary depicted by semi-quantitative methods (Mihályi, Gulyás, 1963).

Our study revealed that the supra-individual organization of mosquitoes composes metacommunities characterized by typical seasonality and interactions between local assemblages of separated water-bodies. This finding corroborates Wilson's conclusion in 1992 that metacommunities have spatial heterogeneity and their fragments form a mosaic of patches. These fragments of mosquito metacommunities' organization are determined by the system of different water habitats separated by discrete boundaries. The distance between the elements of the habitat-structure is traversable for Culicidae species with the least mobility (Hawley, 1988). Furthermore, the species display only a small difference in their colonizing ability (Wilson, 1992) and in deterministic habitat requirements (Mohrig, 1969; Becker et al., 2003; Schäfer, 2004; Alfonzo et al., 2005).

Table 7. The sum of results shows that species groups characterized by similar life-strategy are characterized by similar species composition (see legends in Appendix I., * = in Hungary, the species was collected only in imago stage, cursive = belonging to the species group which was not confirmed by other statistical analyses).

Code of Fig. 1	Spec. groups	Code of Fig. 5	Spec. groups	Code of MDS (*-see Figs. 3-4)	Spec. groups	Water-body type groups
A	Cllon	(G)	*Cllon*			
B	Coqric	(A)	Coqric (*Cxtor*)			
C	Anocla Anoalg Ortpul	(C)	Anocla Anoalg Orthpul	W-(a)*	Anocla *(Clann)*	
D	Anomac Anoatr Anohyr Anomes Clann Cxpip Cxmod Clala Clsub Uraung	(B)	Anomac Anomes Anohyr Anoatr Cxmod Cxpip Clann Clala Clsub Uraung	A-(a)	Uraung Cxpip Anomes Anomac Cxmod	(2) transient habitats with marshy vegetation
				Sp-(b)*	Cxpip Clann Anomac Cxmod	(1) permanent waters (1) permanent waters
				Sp-(c)*	Anomes *(Cxter)* Clann	(2) transient habitats with marshy vegetation
				Su-(a)	*(Cxter)* Clann Anomac Cxmod	
E	Cxpip Cxhor (*Cxtor*) Clgla	(D)	(*Cxter*) Cxhor Clgla			(6) technotelms
F	Cxter			A-(b)	Cxter *(Anocla)*	
G	Ochann Ochcan Ochcat Ochcom Ochexc Ochfla Ochleu Ochnig Ochpul Ochpun Ochref	(H)	Ochpul Ochnig Ochref Ochexc Ochann Ochcan Ochcat Ochfla Ochpun Ochcom Ochleu	W-(c)*	Ochfla Ochann Ochcan	(2) transient habitats with marshy vegetation
				Su-(b)	Ochcat Ochfla	(3) „tömpöly”
				Sp-(a)*	*(Anocla)* *(Clmor)* *(Ochrus)* Ochref Ochcan Ochcat	(3) „tömpöly”
				W-(b)*	*(Clmor)* Ochcat Ochexc *(Ochrus)*	(3) „tömpöly”

Table 7. (Continued)

Code of Fig. 1	Spec. groups	Code of Fig. 5	Spec. groups	Code of MDS (*-see Figs. 3-4)	Spec. groups	Water-body type groups
H	Aedcin Aedros Aedvex Ochcas Ochdet* Ochdor Ochsti Ochhun	(J)	Ochhun Ochcas Aedros Aedcin Aedvex Ochsti Ochdor	Su-(c) Sp-(d)*	Ochsti Aedvex *(Ochann)* Aedcin *(Ochfla)* Ochcas Ochsti Aedvex	(4) pits
I	Ochgen Anoplu	(I)	Ochgen Anoplu	Sp-(e)* Su-(d) A-(c)	Ochgen Anoplu	(5) treeholes
J	Ochrus	(F)	Ochrus			
K	Clfum Clmor Cloch	(E)	Clmor Clfum Cloch			

Structure of the mosquito metacommunities in local assemblages of separated water-bodies can be defined by the spectra of the functional groups of the mosquito species. Although species composition of the mosquito metacommunities is heterogeneous, the participation of different functional species groups is consequent. Species of the different species-groups are characterized by similar life-strategy. Arising from this, the structure of Culicidae metacommunities can mainly be appropriately described by the functional species groups characterized by their similar life-strategy, and not by species combination. The particular species combination within the functional units is formed by historic, bio-geographical and random determinants. The importance of functional species groups in community organization is apparent when our results are compared with examinations carried out in Sweden (Schäfer, 2004) or Venezuela (Alfonzo et al., 2005). Differences in species lists are not followed by differences in species functional groups, because they are related to habitat types characterized globally by similar basic circumstances. The functional diversity of the mosquito metacommunities is most likely small, and it depends mainly on the oviposition site which is usually closely related to the state during hibernation, and related to the female biting orientation.

The aggregation of species into functional groups has been acknowledged for a long time within community ecology (Schröder, 2006). Although groups of several European mosquito species with similar life-strategy have been defined by Schäfer (2004), these groups have not yet been examined as metacommunity functional groups. Our results originated from a temperate zone country with moderately rich Culicidae fauna, and they provide an appropriate basis for future extensive research. Further validation of our results is extremely important due to the outstanding relevance of mosquitoes in public health and tourism.

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Appendix

Water body type and code	N samples	N larvae
Large, shallow, humic lake (1110)	1,139	15,601
Shallow storage-lake (1130)	17	157
Small lake-like natural pond (1310)	74	1,263
Small lake-like dead channel (1320)	12	86
Small lake-like water pool (1330)	106	2,182
Small lake-like fishpond (1340)	65	1,254
Small lake-like other artificial pond (1350)	94	1,530
Slough-like natural pond (1410)	173	5,062
Morass (1520)	7	156
Marshy type natural pond (1610)	2,396	61,065
Marshy type artificial pond (1620)	279	6,780
“Tömpöly” type natural small water body (1711)	1,897	37,534
“Tömpöly” type artificial small water body (1712)	283	7,982
Pits of flood-water (1721)	83	2,129
Pits of meteoric water (1722)	723	22,278
Pits of ground-water (1723)	4	32
Wallowing-place (1730)	145	2,093
Phytotelm (1751)	3	17
Treehole (1752)	369	3,622
Malacotelm (1753)	2	5
Lithotelm (1754)	6	204
Artificial container (~technotelm)(1755)	154	6,244
Middle sized river (2220)	11	205
Small river-type artificial stream (2250)	10	162
Rivulet (2310)	26	263
Streamlet (2320)	101	1,684
Brooklet (2330)	491	9,753
Artificial small stream (2340)	220	4,536
Limnokren spring (3200)	6	142
Helokren spring (3300)	36	402
Shelter spring (3400)	47	543