



Highly variable abiotic environment induced changes in taxonomic and functional composition of headwater chironomid assemblages within a small mountain range

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With 2 figures, 5 tables and 1 appendix

Abstract: The spatial variability of Chironomidae larvae assemblages was investigated at 6 near-pristine, temperate headwaters in Hungary. Sites were located within a relatively small mountain range but belong to two different catchment areas characterized by highly variable abiotic conditions. We hypothesised there would be differences in taxonomic composition but not in functional composition between different catchment areas and aimed to assess the primary influencing spatial factors structuring the taxonomic and functional compositions of chironomid assemblages. The spatial distribution of chironomid assemblages was examined 4 times during a 1 year period at microhabitat to catchment scales. At each site, streambed morphology, physicochemical attribute, riparian vegetation, microclimate and hydrology data were collected. Three main traits (saprobic preference, stream zonation preference, functional feeding groups) were used to characterize the functional composition of chironomid assemblages. Sharp differences were detected in taxonomic composition between the two sides of the mountain range within a relatively small spatial distance and moderate, but statistically significant differences in functional composition between catchments. The observed spatial changes in taxonomic and functional composition of midges accompanied changes in physicochemical characteristics, riparian vegetation, microclimate and altitude. Internal microhabitat heterogeneity also played a major role in structuring the taxonomic and the functional patterns of chironomid assemblages.

Key words: headwater Chironomidae, small mountain range, habitat heterogeneity, spatial variation, taxonomic and functional composition, multivariate approaches.

Introduction

According to the River Continuum Concept (RCC), longitudinal shifts of macroinvertebrate assemblages are influenced by changing environmental conditions

from spring to mouth (Vannote et al. 1980). At a finer scale, community shifts are subtle within the same reach in permanent streams (Feminella 1996, Progar & Moldenke 2002) due to the relatively slighter environmental gradient. Within a small geographi-

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cal range, relatively small differences are assumed between assemblages of permanent stream sections that are at the same longitudinal position than along the longitudinal continuum (Lindegaard & Brodersen 1995, Puntí et al. 2009, Raposeiro et al. 2011). On the other hand, the Habitat Templet Theory emphasises the important role of abiotic habitat features and their spatial and temporal variability in structuring communities and in the selection of traits that maximize species fitness (Southwood 1977, Townsend & Hildrew 1994, Poff 1997). In headwater streams, the community composition is influenced by both broad scale constraints (e.g. geology and climate) and local scale drivers (e.g. physicochemical characteristics, streambed morphology) (Poff & Ward 1990), which could be highly variable within a small geographical range. Additionally, high internal physical heterogeneity exists within headwater reaches compared to downstream sections (Gooderham et al. 2007). This kind of abiotic heterogeneity could have fundamental importance in shaping headwater communities through providing refuges against temporal disturbances like floods and droughts (Townsend 1989). Gooderham et al. (2007) also pointed out that small headwaters are directly influenced by atmospheric, bedrock, soil and riparian features.

The non-biting midges (Diptera: Chironomidae) are the most widely distributed, most diverse, and often the most abundant family of the whole macroinvertebrate spectrum in lotic ecosystems (Giller & Malmqvist 1998), and they occupy a wide variety of habitats (Pinder 1995). Chironomids are indicators of anthropogenic impact as well as natural environmental gradients, since most genera include species with different ecological traits (Calle-Martínez & Casas 2006, Marziali et al. 2010, Lencioni et al. 2012, Milošević et al. 2012, Móra & Szivák 2012). Thus, the analysis of their larval species composition alone can be used to differentiate sites with varying environmental conditions in streams and rivers (Armitage & Blackburn 1985, Cranston 1995, Orendt 2000, Móra et al. 2008).

Several studies have aimed to identify the driving forces that structure the chironomid assemblages in headwaters at different spatial scales (e.g. Heino 2005, Raunio et al. 2011, Rosa et al. 2011). However, these works mainly focus on the effects of extreme environmental conditions such as droughts (Calle-Martínez & Casas 2006, Puntí et al. 2007), high altitude (Lencioni & Rossaro 2005), location in oceanic islands (Raposeiro et al. 2011) or the effect of large environmental gradients (Heino & Mykrä 2008, Puntí et al. 2009,

Roque et al. 2010, Siqueira et al. 2009). At broader spatial scales, the distribution and diversity of lotic chironomid larval assemblages are constrained mainly by the geographic position of reaches, stream size, land use, geology, thermal regime and slope (Calle-Martínez & Casas 2006, Puntí et al. 2007, 2009, Raposeiro et al. 2011). At the reach scale, the particle size of substrata, water depth and current velocity have the most important role in structuring chironomid assemblages (Lencioni & Rossaro 2005, Rosa et al. 2011). Based on the metacommunity patterns of Chironomidae larvae in boreal calcareous streams within the same drainage system, structures of assemblages show weak relationship with any local scale environmental variables (Heino 2005).

How chironomid assemblages respond to highly variable abiotic environmental conditions (i.e. bedrock geology) within small geographical distances, for example within the same mountain range or catchment, remains unknown. However, it is well known that invertebrates respond quickly to disturbances and environmental heterogeneity at small spatial scales (Townsend 1989). Chironomids are a very diverse group regarding functional traits, which make the species successful colonizers of all types of habitats. Even so, little information is available about the role of abiotic environmental factors in structuring the functional composition of chironomid assemblages in streams. However, analysing the functional composition of assemblages provides precious information about the ecological condition of, and processes in, streams. A trait-based approach could link the biological patterns and processes, and it is independent of the geographical distance between assemblages (Verberk et al. 2008). Patterns in species traits are significantly related to differences in the environmental conditions where the species occur, thus habitats act as a template for species traits (e.g. Statzner et al. 1994, Southwood 1977, Townsend et al. 1997).

Consequently, our study focuses on the variability of taxonomic and functional composition of chironomid assemblages in a small mountain range. We assumed highly variable abiotic condition of habitats in second-order headwater streams located within one mountain range, but consisting of two different catchment areas characterized by different bedrock types. We hypothesised differences between the sites in taxonomic composition but not in functional composition. Our aim was to assess the factors influencing the hierarchical nested spatial scale structuring the taxonomic and functional compositions of chironomid assemblages.

Material and methods

Study area

The survey area is located in the Mecsek Mountains, which is one of the most southern mountain ranges in the Carpathian Basin (Fig. 1). It is considerably isolated from other mountain regions and surrounded by plains and low hilly territories. This relatively small (350 km²), geologically and climatically heterogeneous area is located in a biogeographic transition zone (Praeillyricum) between the Pannonian and the Mediterranean (Dinaric, Illyrian, Moesian) ecoregions (Borhidi 2003, Borhidi 2006). The major part of the area is covered by Jurassic and Cretaceous-aged bedrocks of limestone and different volcanic

sediments, whereas red and grey sandstones are dominant in the western region (Gebhardt 1967).

Data collection

Chironomidae larvae samples were taken from second-order streams running in deep, cool and shaded valleys. We chose 3 near-pristine streams from the south-western region and 3 from the north-eastern region that could be characterized by different geological features and belong to two different catchment areas (Fig. 1).

Each site was sampled three times in 2009 (May, July and October) and once in 2010 (March). Samples were quantitatively collected according to the Integrated Assessment System

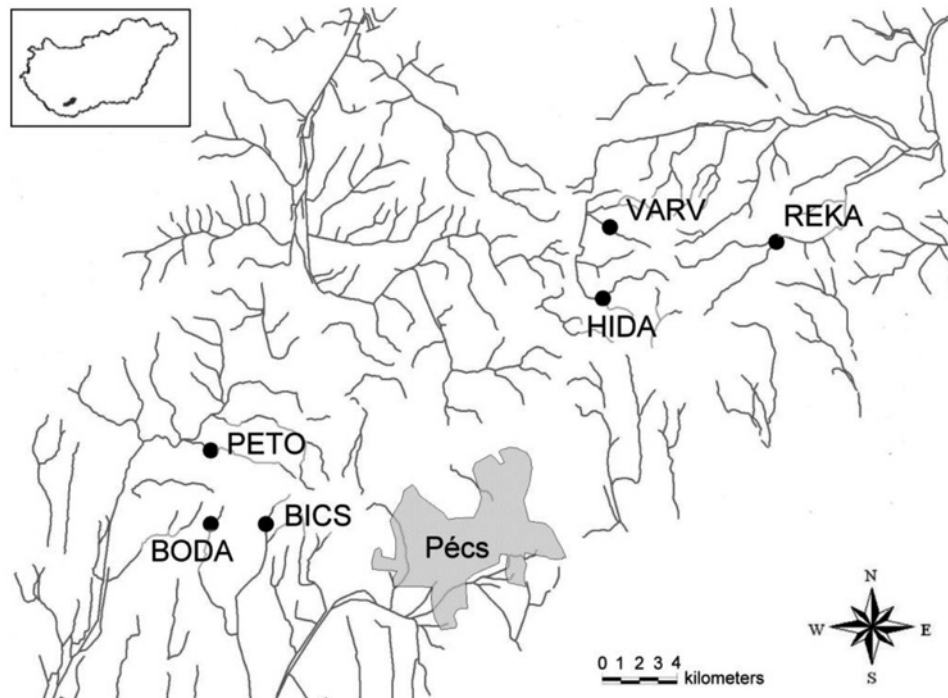


Fig. 1. Schematic outline of the water system and study sites in the Mecsek Mountains. Sites characterized by sandstone bedrock: BICS – Bicsérdi stream (Bakonya; N46° 05' 13.5", E18° 05' 28.9"), BODA – Bodai stream (Boda; N46° 05' 12.1", E18° 03' 13.9"), PETO – Petőczy stream (Bakonya; N46° 07' 16.6", E18° 03' 42.2"); sites characterized by limestone bedrock: HIDA – Hidasi valley (Komló; N46° 11' 39.1", E18° 19' 03.8"), REKA – Réka valley (Mecseknádasd; N46° 13' 17.1", E18° 26' 05.2"), VARV – Vár valley at Máré spring (Magyaregregy; N46° 13' 40.0"; E18° 19' 19.4").

Table 1. List of microhabitat types based on the AQEM protocol (AQEM Consortium 2002) and the cumulative microhabitat groups.

Groups	Type	Definition
Sand, silt	Argyllal	Silt, loam, clay; diameter < 6 µm
	Psammal	Sand; diameter 6 µm–2 mm
Akal	Akal	Fine to medium-sized gravel; diameter 2 mm–2 cm
Lithal	Microlithal	Coarse gravel with medium to fine gravel; diameter 2–6 cm
	Mesolithal	Cobbles with a variable percentage of gravel and sand; diameter 6–20 cm
	Macrolithal	Coarse cobbles, gravel and sand; diameter 20–40 cm
Biotic	Xylal	Tree trunks, dead wood, branches, roots
	CPOM	Deposits of coarse particulate organic matter
	FPOM	Deposits of fine particulate organic matter

Table 2. Mean (standard deviation) values of local environmental variables and their type of transformation for ADONIS. *p*-values indicate statistical significance based on independent *t*-test: *** *p* < 0.001; ** *p* < 0.01; * *p* < 0.05, ns = non-significant (*p* > 0.05); na = no results, because of the zero variance.

Variables	Sandstone	Limestone	Transf.	<i>p</i>
Streambed morphology				
% proportion of microhabitat types:				
% Macrolithal	0.27 (0.52)	0.98 (1.53)	$\arcsin(x/100)^{0.5}$	ns
% Mesolithal	18.63 (15.13)	45.46 (15.07)	$\arcsin(x/100)^{0.5}$	***
% Microlithal	18.87 (13.24)	13.056 (9.54)	$\arcsin(x/100)^{0.5}$	ns
% Akal	17.51 (14.6)	13.35 (11.16)	$\arcsin(x/100)^{0.5}$	ns
% Psammal	28.25 (15.87)	15.25 (12.05)	$\arcsin(x/100)^{0.5}$	ns
% Argyllal	14.14 (14.97)	8.55 (6.21)	$\arcsin(x/100)^{0.5}$	ns
% Xylal	4.21 (4.15)	4.63 (3.96)	$\arcsin(x/100)^{0.5}$	ns
% CPOM	9.18 (9.75)	12.14 (10.45)	$\arcsin(x/100)^{0.5}$	ns
% FPOM	1.8 (3.72)	0 (0)	$\arcsin(x/100)^{0.5}$	na
% frequency of detritus (FPOM, CPOM) in 100 m	28.15 (14.53)	31.08 (11.96)	$\arcsin(x/100)^{0.5}$	ns
% frequency of washaway in 100 m	19.84 (13.25)	15.45 (6.86)	$\arcsin(x/100)^{0.5}$	ns
Number of riffles in 100 m	4.67 (3.65)	5 (1.76)	$\ln(x+1)$	ns
Number of pools in 100 m	2.92 (2.43)	4.33 (1.92)	$\ln(x+1)$	ns
Number of woods in 100 m	6.58 (3.15)	12.5 (5.55)	$\ln(x+1)$	ns
Number of bends in 100 m	4.17 (2.25)	3.67 (1.15)	$\ln(x+1)$	ns
Average channel width (m)	1.42 (0.56)	2.56 (0.59)	$\ln(x+1)$	***
Average water depth (m)	0.09 (0.09)	0.08 (0.03)	$\ln(x+1)$	ns
Physicochemical features				
Water temperature (°C)	13.28 (3.32)	12.4 (4.38)	$\ln(x+1)$	ns
pH	8.34 (0.25)	8.31 (0.31)	$\exp(x/100)$	ns
Conductivity (µS/cm)	856.25 (162.68)	537.13 (24.27)	$\exp(x)/100$	***
dissolved O ₂ (mg l ⁻¹)	7.52 (2.21)	7.98 (1.66)	$\ln(x+1)$	ns
SO ₄ ²⁻ (mg l ⁻¹)	98.57 (128.62)	32.12 (21.67)	$\ln(x+1)$	ns
Ca ²⁺ (mg l ⁻¹)	117.03 (36.47)	93.12 (10.64)	$\ln(x+1)$	ns
Mg ²⁺ (mg l ⁻¹)	62.55 (44.41)	16.33 (6.39)	$\ln(x+1)$	**
Cl ⁻	10.76 (4.43)	3.03 (0.54)	$\ln(x+1)$	***
HCO ₃ ⁻	428.03 (103.7)	304.28 (62.86)	$\ln(x+1)$	**
m alkalinity	7.19 (1.41)	5.28 (0.82)	$\ln(x+1)$	***
Riparian vegetation				
% Tree (0–1 m)	12.16 (8.66)	16.56 (8.03)	$\arcsin(x/100)^{0.5}$	ns
% shrubs (0–1 m)	11.93 (7.67)	6.58 (5.8)	$\arcsin(x/100)^{0.5}$	*
% herbaceous (0–1 m)	61.87 (18.44)	46.66 (14.42)	$\arcsin(x/100)^{0.5}$	*
META naturalness index at the valley floor	3.53 (0.15)	3.87 (0.15)	$\ln(x+1)$	***
% Forest coverage at the valley floor	93.33 (9.85)	98.33 (2.46)	$\arcsin(x/100)^{0.5}$	ns
% of natural habitats of vegetation at valley floor	50 (0)	66.7(0)	$\arcsin(x/100)^{0.5}$	na
META naturalness index at the nearest slopes	3.5 (0.43)	3.82 (0.3)	$\ln(x+1)$	*
% Forest coverage at the nearest slopes	83.33 (17.75)	100 (0)	$\arcsin(x/100)^{0.5}$	**
% of natural habitats of vegetation at slope	44.4 (43.4)	100 (0)	$\arcsin(x/100)^{0.5}$	na
Climate				
Annual mean temperature (°C)	10.7 (0.26)	9.97 (0.06)	$\ln(x+1)$	**
Mean diurnal range	9.17 (0.06)	8.97 (0.06)	$\ln(x+1)$	*
Temperature seasonality	773.27 (5.54)	768.3 (1.57)	$\ln(x+1)$	ns
Max temperature of warmest month (°C)	26.8 (0.35)	25.87 (0.06)	$\ln(x+1)$	*
Min temperature of coldest month (°C)	-4.27 (0.15)	-4.67 (0.06)	$\ln(x+1)$	*
Temperature annual range	31.07 (0.21)	30.53 (0.06)	$\ln(x+1)$	*
Mean temp. of wettest quarter (°C)	18.57 (0.29)	17.87 (0.06)	$\ln(x+1)$	*
Mean temperature of driest quarter (°C)	1.93 (0.15)	1.2 (0)	$\ln(x+1)$	na
Mean temperature of warmest quarter (°C)	20.07 (0.29)	19.37 (0.06)	$\ln(x+1)$	*
Mean temperature of coldest quarter (°C)	0.13 (0.15)	-0.43 (0.06)	$\ln(x+1)$	*
Annual precipitation (mm)	669.67 (10.12)	664.33 (8.02)	$\ln(x+1)$	ns
Precipitation of wettest month (mm)	89.67 (2.31)	90.67 (1.53)	$\ln(x+1)$	ns

Table 2. Continued.

Variables	Sandstone	Limestone	Transf.	<i>p</i>
Precipitation of driest month (mm)	37.67 (0.58)	35.33 (0.58)	ln(x + 1)	**
Precipitation seasonality	26.67 (0.58)	26.67 (0.58)	ln(x + 1)	ns
Precipitation of wettest quarter (mm)	224 (5.2)	223.67 (3.51)	ln(x + 1)	ns
Precipitation of driest quarter (mm)	117 (1.73)	120.33 (1.53)	ln(x + 1)	ns
Precipitation of warmest quarter (mm)	221.33 (4.62)	220 (3.61)	ln(x + 1)	ns
Precipitation of coldest quarter (mm)	131 (1.73)	133.33 (1.53)	ln(x + 1)	ns
Hydrology				
Distance from source (km)	2.8 (1.17)	3.93 (0.79)	ln(x + 1)	ns
Altitude (m)	213.67 (37.61)	331.33 (14.5)	ln(x + 1)	*
Aspect	215.74 (92.87)	131.79 (59.77)	ln(x + 1)	ns
Slope (%)	6 (1)	5.3 (1.5)	ln(x + 1)	ns

for the Ecological Quality of Streams and Rivers throughout Europe using Benthic Macroinvertebrates (AQEM) (AQEM Consortium 2002), which focuses on a multihabitat scheme designed for sampling major habitats in proportion to their presence within 100 m long sampling reaches. Nine microhabitat types were determined (Table 1) based on the original AQEM microhabitats. After collection, each sampling unit was fully and accurately sorted into sampling bottles in the field keeping the samples separate from each other. For appropriate identification, the specimens were slide-mounted in Euparal. The chironomid larvae were identified using keys and descriptions of Cranston (1982), Wiederholm (1983), Janacek (1998), Sæther et al. (2000) and Vallenduuk & Møller Pillot (2007). The nomenclature follows Sæther & Spies (2011).

Environmental variables

At each site, 36 local scale environmental variables were taken in all seasons related to streambed morphology (17), physicochemical attribute (10) and riparian vegetation (9) (Table 2). Water samples for physicochemical analyses were taken prior to the biological sampling. We calculated indices of naturalness of riparian vegetation and vegetation of the nearest slopes based on the Landscape Ecological Vegetation Database and Map of Hungary (Molnár et al. 2007, Molnár & Horváth 2008).

Furthermore, we obtained the microclimatic condition of sampling sites from the WorldClim–Global Climate Data website (www.worldclim.org, Hijmans et al. 2005). At first, layers of the latest 30 years' mean climatic parameters related to the temperature and the precipitation were downloaded, and then projected the locality coordinates to these layers. Finally, we gained the values of 18 selected climatic parameters for each site (Table 2). Hydrological parameters (slope, aspect, altitude) were also determined from WorldClim–Global Climate Data website. For these procedures we used software R ver. 2.14.0 (R Development Core team 2011) using the packages 'rgdal' and 'dismo'. The longitudinal position of sites was obtained by measuring the streamline distance of the sites from source using Geographical Information System (GIS).

Due to sampling procedures, the local scale environmental parameters were measured seasonally. While seasonal information about the microclimate and hydrological parameters was not available, these were derived from the monthly data (Hijmans et al. 2005). Despite weaker comparability, we kept the seasonal data of local scale environmental variables to increase the reliability of statistical analysis.

Species traits

We considered three main traits to characterize the functional composition of chironomid assemblages: (1) saprobic preference, (2) stream zonation preference, and (3) functional feeding groups (Table 4). These traits are highly influential for functional organisation of freshwater macroinvertebrate assemblages (Moog 2002). The categories of traits and the basic autecological information of species were provided according to Moog (2002), Schmedtje & Colling (1996), and the information collected by AQEM consortium (Brabec et al. 2007). We calculated the percentage proportion of trait categories at each sample using Asterics ver. 3.3.1 software (AQEM Consortium 2002). For all analyses, the three main traits were handled separately, since each one characterizes different ecological attributes of streams (Moog 2002).

Data analysis

Prior to all analysis, we removed the extremely rare taxa (<0.2 % relative abundance) from the dataset to reduce their disproportionate effect in the multivariate analysis (Legendre & Legendre 1998). The assemblage dataset was log₁₀(x+1) transformed.

To evaluate the differences in the abiotic habitat conditions between two catchments and four sampling times, we conducted permutational multivariate analyses of variance using distance matrices (ADONIS; 9999 runs, Euclidean distance measure) (Oksanen 2011). We used sampling occasions (6 sites × 4 times) as objects, environmental parameters as response variables, and catchment (2 levels) and sampling time (4 levels) as grouping variables within one model. We excluded the interaction of two grouping variables from our models. We handled the five environmental variable groups (streambed morphology, physicochemical attributes, riparian vegetation, microclimate and hydrology) separately. Before the analyses, the environmental variables were transformed depending on their scale of measurement to reach their normality and reduce heteroscedasticity (see Table 2). We also used independent t-tests to determine the significantly different ($\alpha=0.05$) environmental variables between catchments having distinct bedrock type. Finally, we tested the significantly different abiotic variables for autocorrelation using Spearman rank-correlation.

We examined the differences of taxonomic and functional composition between sites and catchments using Discriminant Analysis of Principal Components (DAPC). This method was

originally developed to identify and describe genetic clusters, although it can be applied to any quantitative data (Jombart et al. 2010). This multivariate approach gains the principal components of raw data using Principal Component Analysis (PCA) as a prior step to Discriminant Analysis (DA). Then during DA, linear combinations of the retained principal components called discriminant functions are constructed, which provide the best separation between the groups. The coefficients of the original variables used in DA quantify their relative contributions to the discriminant functions. The value of relative contribution could vary between 0 and 1, where 1 means the summarized contribution of the original variables to the distinct discriminant function. Moreover, being based on the DA, the cross-validation procedure within DAPC provides membership probabilities of each object for the different groups based on the retained discriminant functions. The advantage of this method over other indirect ordination methods (e.g. PCA, CA, DA) is that it ensures that variables submitted to DA are perfectly uncorrelated and their number is less than the number of the analysed objects. Other ordination methods (e.g. PCA, CA, DA) are sensitive for these latter settings (further details in Jombart et al. 2010). Without implying a necessary loss of information, this transformation allows DA to be applied to any ecological dataset, which suffer from large amounts of highly correlated variables, but low numbers of objects. In our case, less variables existed than objects (e.g. saprobic categories, feeding categories), but these were highly correlated. Furthermore, in contrast to other non-linear ordination or clustering techniques (e.g. NMDS) the DAPC provides information not only about the differences or similarities between the objects but also those variables that cause the separation of objects. We used four input matrixes in our settings. Abundance data of species and the relative frequencies of traits were used as variables, and the sampling occasions (sampling site \times sampling time) were used as objects. We applied six *a priori* groups according to sampling sites. Centroids of these groups, as a mean of x and y coordinates of objects (sampling occasions) belonging to the same group (sampling site), were calculated and marked on our ordination plots. To clarify the meanings of discriminant functions within DAPC, Pearson correlations were calculated between the discriminant axes and the original variables.

ADONIS was also used to test for differences in chironomid assemblages in a nested hierarchical design accounting for 1) microhabitats 2) within streams 3) within catchments and separate sampling times (see also Garcia-Rogers et al. 2011). A total of 9999 runs were performed on Bray-Curtis distance matrix for the taxonomic dataset and Gower distance matrix for the functional datasets. For these analyses, we contracted the nine microhabitat types into four wider habitat groups (Table 1). We separated Akal from other lithal microhabitat types. Presumably, it has different chironomid assemblages because the small grain sized Akal microhabitat could not provide shelters against water-current for bigger chironomid species. We cumulated the abundance of each species and standardized them to 1 m², because different numbers of sampling units of single microhabitat types were available in each sampling site.

All statistical analyses were performed with software R ver. 2.14.0 (R Development Core team 2011) using the packages ‘vegan’ for ADONIS and ‘ade4’ for DAPC.

Results

Abiotic habitat characterization

Using ADONIS, three out of five environmental variable groups showed significant differences ($\alpha = 0.05$) between two groups of sites having distinct bedrock type and belong to two different catchments (Table 3). The influence of catchments was more effective in differentiation of samples regarding their riparian vegetation (39 % significantly explained variance), microclimate (87 % explained variance) and hydrology (33 % explained variance) than in differentiation of samples regarding their physicochemical features (15 % significantly explained variance) and streambed morphology (11 % significantly explained variance). The seasonal effect was statistically significant only in the case of physicochemical characteristics (74 % explained variance). Analysing the environmental variables separately using independent t-tests, two variables within streambed morphology, five within physicochemical feature of water, five within riparian vegetation, nine within microclimate and one within hydrology were significantly different between catchments having distinct bedrock types (Table 2). Among the significantly different physicochemical variables, 5 pairs (conductivity – Mg²⁺, Cl⁻, HCO₃⁻, m alkalinity; HCO₃⁻ m alkalinity) highly correlated (Spearman

Table 3. Results of ADONIS assessing the effect of spatial and temporal variability on abiotic habitat conditions. The different types of environmental variables were analysed separately.

Source of variation	df	F	R ²	p
Streambed morphology				
Catchment	1	2.818	0.11	0.038
Season	3	0.899	0.11	0.529
Residuals	19		0.77	
Physicochemical feature				
Catchment	1	24.847	0.15	0.000
Season	3	41.563	0.74	0.000
Residuals	19		0.11	
Riparian vegetation				
Catchment	1	12.499	0.39	0.000
Season	3	0.118	0.01	0.997
Residuals	19		0.59	
Microclimatic condition				
Catchment	1	25.923	0.87	0.101
Residuals	4		0.13	
Hydrology				
Catchment	1	1.935	0.33	0.192
Residuals	4		0.67	

$r > 0.7$) with each other. Among the significantly different climate parameters, only 1 pair (annual range of temperature – precipitation of driest month) did not show high correlation (Spearman $r > 0.7$) with each other. We did not find strongly correlated variable pairs among significantly different streambed and riparian vegetation characteristics.

Variability of taxonomic and functional composition

A total of 715 specimens belonging to 36 taxa (24 genera and 5 subfamilies) were found at 6 sites during our

one-year investigation. Five taxa were specific in sites situated in limestone bedrock, 23 in sandstone and only 6 were common on both bedrock types (Appendix 1). Eleven taxa were extremely rare ($< 0.2\%$ relative abundance), thus we omitted these from further analyses. We did not find any chironomid individuals in Réka valley during autumn.

DAPC revealed that four sampling sites (BICS, BODA, PETO, REKA) form separate groups along the first two discriminant functions (Fig. 2A). Slight separation and frequent overlapping can be seen between our *a priori* groups (sampling sites) on the ordination diagrams of functional compositions (Fig. 2B,

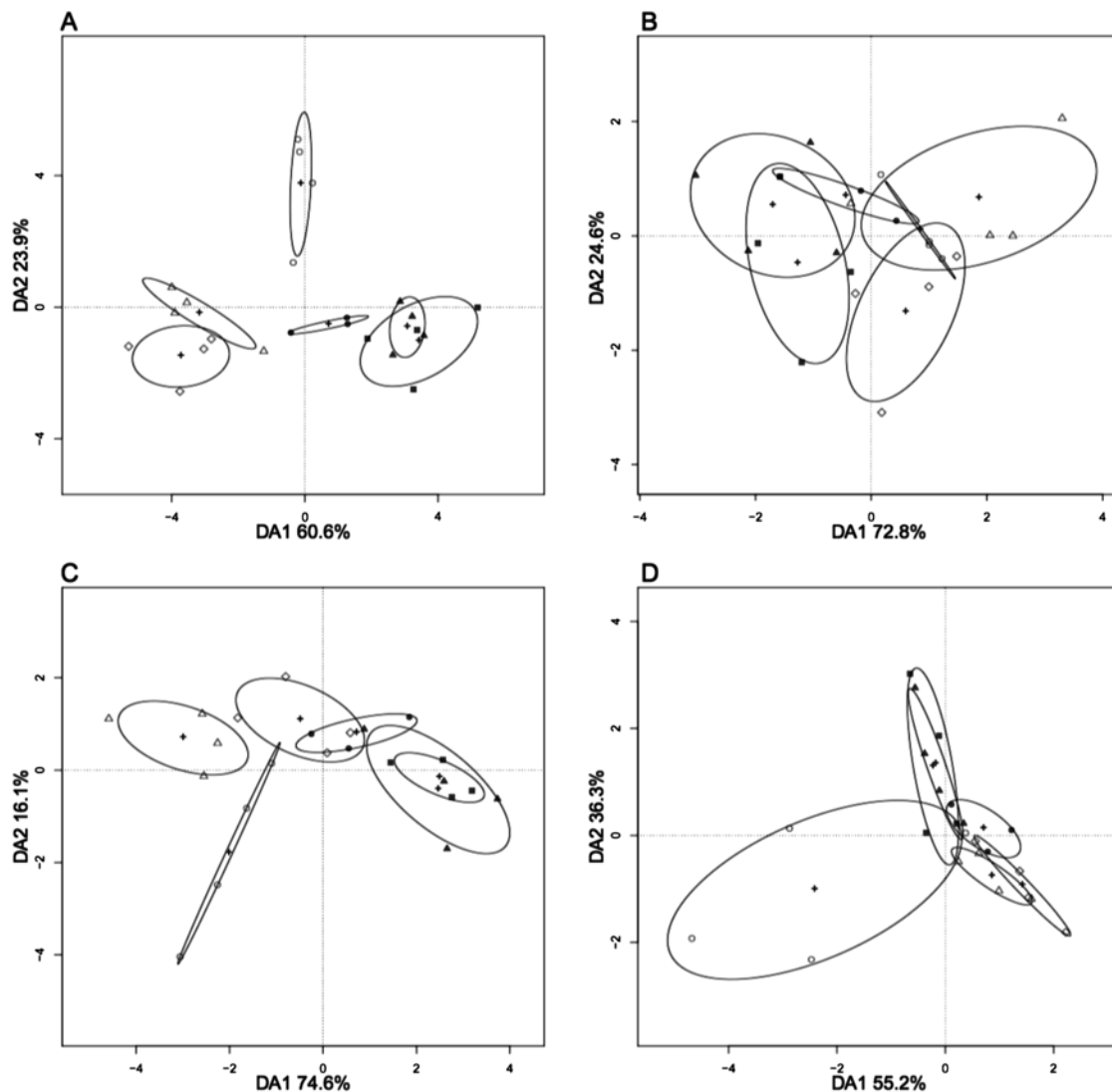


Fig. 2. Using DAPC, differences could be shown in (A) taxonomic and in functional composition: (B) saprobic preference, (C) stream zonation preference, (D) the distribution of functional feeding groups of chironomid assemblages between headwaters belonging to different catchments. Sampling sites were plotted on the ordination diagram. Different symbols mean the sampling occasions at the different sites: \circ – BICS, \triangle – BODA, \diamond – PETO, \blacksquare – HIDA, \bullet – REKA, \blacktriangle – VARV. Sites situated on sandstone bedrock are marked with empty symbols; sites on limestone are marked with fulfilled symbols. The centroids of sites were marked with ‘+’ and 1.5*standard deviation are drawn around the centroids.

Table 4. Relative contribution (rel. contr.) of original variables to the variability of the first two axes of DAPC (DA1, DA2) and Pearson correlation (r) between original variables and the first two discriminant axes. P-values indicate statistical significance based on Pearson correlation: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. The full names of taxa are listed in Appendix 1.

Taxa	rel. contr.		Pearson r		Functional groups	rel. contr.		Pearson r	
	DA1	DA2	DA1	DA2		DA1	DA2	DA1	DA2
A_tri	0.02	0.02	-0.40	0.03	Saprobic preferences				
B_bif	0.01	0.15	-0.11	0.85***	xenosaprob	0.01	0.09	0.67***	0.35
Con_sp	0.01	0.02	-0.43*	0.39	oligosaprob	0.20	0.00	0.31	0.66***
D_cin	0.00	0.01	-0.01	0.58**	β -mesosaprob	0.68	0.01	-0.87***	0.29
E_eph	0.11	0.01	0.36	-0.26	α -mesosaprob	0.00	0.01	-0.68	-0.29
Ma_sp	0.04	0.11	-0.26	0.14	polysaprob	0.11	0.90	0.05	-0.75***
Mi_not	0.02	0.01	-0.53**	0.27	Stream zonation pref.				
Mi_chl	0.03	0.08	0.10	-0.46*	crenal	0.11	0.13	-0.76***	-0.56**
Mi_ped	0.06	0.01	-0.21	-0.31	hcrenal	0.03	0.01	-0.62**	-0.43*
Nat_sp	0.19	0.00	-0.60**	-0.30	epirithral	0.02	0.00	-0.26	0.00
O_ful	0.02	0.00	-0.11	0.36	metarithral	0.04	0.03	0.09	-0.08
Ort_sp	0.01	0.00	-0.17	0.43*	hyporithral	0.14	0.17	0.54**	-0.19
Ort_thi	0.00	0.02	0.10	0.63***	epipotamal	0.01	0.05	0.37	0.12
P_sty	0.02	0.07	-0.12	0.61***	metapotamal	0.40	0.43	0.41	0.17
P_ski	0.01	0.02	0.10	0.26	hypopotamal	0.12	0.11	0.42*	0.10
P_exc	0.01	0.10	-0.01	0.86***	littoral	0.06	0.04	0.49*	-0.02
P_con	0.06	0.14	-0.16	-0.27	profundal	0.07	0.04	0.24	-0.05
P_ped	0.06	0.04	-0.34	-0.28	Functional feeding groups				
P_sca	0.00	0.04	0.06	-0.34	grazers	0.01	0.03	0.04	0.27
Pro_oli	0.00	0.02	-0.28	0.20	shredders	0.69	0.29	-0.83***	-0.48*
Re_fus	0.01	0.02	-0.15	-0.24	collectors	0.07	0.07	0.03	-0.2
Re_atr	0.00	0.01	-0.02	0.55***	active filter feeders	0.06	0.02	0.32	0.10
Rp_sp	0.03	0.01	-0.36	-0.18	passive filter feeders	0.00	0.39	-0.09	0.51*
Rt_sp	0.27	0.06	0.47*	-0.05	predators	0.15	0.18	0.39	-0.61**
Zav_sp	0.01	0.02	-0.36	-0.05	parasites	0.03	0.02	0.00	0.52*

C, D). The first two discriminant functions explained more than 80 % and the first one explained more than 50 % of total variance in each analysis. Assessing the dataset of taxonomic composition globally, 83 % of objects were grouped correctly in multidimensional space based on cross-validation procedure within DAPC, while this value reached only 61 % in the case of saprobic preference, 65 % in the case of stream zonation preference and 57 % in the case of functional feeding groups.

Seven (*Brillia bifida*, *Epoicocladius ephemerae*, *Macropelopia* sp., *Natarsia* sp., *Paratrissocladius excerptus*, *Polypedilum convictum*, *Rheotanytarsus* sp.) out of 25 taxa exceeded 0.1 relative contributions to the first two discriminant functions, which explained the separation of our *a priori* groups (sampling sites) (Table 4). Two groups of sites (located on sandstone and limestone bedrock) separated from each other along the discriminant function 1, defined by low abundance of *Natarsia* sp. and high abundance of *Rheotanytarsus* sp. (Table 4, Figure 2A). On the other hand, *Brillia bifida* and *Paratrissocladius excerptus* positively cor-

related with and highly contributed to the discriminant function 2, which explained the segregation of BICS from the other sites (Table 4, Fig. 2A).

Analysing the saprobic preference dataset by DAPC, the sampling sites having different bedrock types form separate groups along the discriminant functions 1 (Fig. 2B), defined by high ratio of xenosaprobic, oligosaprobic preference and low ratio of beta-mesosaprobic preference (Table 4). The beta-mesosaprobic preferences were more frequent on limestone bedrock than on sandstone bedrock, where the high ratios of xenosaprobic and oligosaprobic preferences were typical. Sampling sites were sorted according to longitudinal gradient from eucrenal, hypocrenal to hyporithral and hypopotamal sections based on the analysis of stream zonation preference of chironomid assemblages (Fig. 2C). Sampling sites situated on sandstone bedrock were located at the upper end, whereas sampling sites having limestone bedrock could be found at the lower end of this longitudinal gradient (Fig. 2C). Sites having limestone and sandstone bedrocks showed slight differentiation

Table 5. Summary of the nested ADONIS analyses performed on the taxonomic and functional compositions of chironomid assemblages. The different elements of functional composition were analysed separately.

Source of variation	df	F	R ²	p
Taxonomic composition				
Catchment	1	5.282	0.07	0.00
Stream (catchment)	4	2.081	0.11	0.00
Microhabitat [stream (catchment)]	16	1.218	0.26	0.03
Season	3	2.271	0.09	0.00
Residuals	36		0.47	
Saprobic preferences				
Catchment	1	16.741	0.15	0.00
Stream (catchment)	4	8.114	0.29	0.00
Microhabitat [stream (catchment)]	15	1.763	0.24	0.06
Season	3	3.172	0.09	0.02
Residuals	25		0.23	
Stream zonation preferences				
Catchment	1	7.989	0.10	0.00
Stream (catchment)	4	2.566	0.13	0.02
Microhabitat [stream (catchment)]	15	2.014	0.39	0.01
Season	3	0.998	0.04	0.44
Residuals	26		0.34	
Functional feeding groups				
Catchment	1	5.034	0.08	0.00
Stream (catchment)	4	1.515	0.09	0.13
Microhabitat [stream (catchment)]	16	0.974	0.24	0.52
Season	3	1.927	0.09	0.05
Residuals	33		0.50	

along the discriminant function 2 based on functional feeding groups (Fig. 2D), defined by high ratios of passive filter feeders and low ratios of shredders and predators (Table 4). High temporal variability could be found within several sampling sites (e.g. BICS, VARV, HIDA) caused by varying abundance of shredders and passive filter feeders.

Table 5 shows the summary of the numerous spatially nested (catchment, stream, microhabitat) effects on taxonomic and functional composition analysed by ADONIS. The four models explained 50–77 % of total variance in the datasets of chironomid taxonomic and functional compositions. Taxonomic composition, saprobic preference and stream zonation preference were significantly ($\alpha=0.05$) affected by all of the spatially nested factors, whereas only the catchment level showed significant effects on the frequencies of functional feeding groups. The effects of sampling time were statistically significant ($\alpha=0.05$) except for stream zonation. Microhabitat level (microhabitat within streams within catchment) explained the highest percentage of variance in the datasets of taxonomic

composition (26 %) and stream zonation preference (39 %). The influence of stream level was the most important in structuring the composition of saprobic preference (29 %) and the season (9 %) for functional feeding groups.

Discussion

We showed that spatial changes in taxonomic and functional composition of midges accompanied by changes in habitat features mainly in chemical characteristics related to geology, riparian vegetation, microclimate and altitude. Fine-scale physical structure (i.e. microhabitat scale) played a major role not only in organizing taxonomic composition, but also the functional composition of chironomid assemblages. However, our results should be interpreted with some caution because of the small sample size.

Spatial variability in habitat features

Two habitat types could be distinguished, which were characterized not only by different geological features, but also inorganic chemical characteristics, riparian vegetation, microclimate and altitude (Tables 2 and 3). Sites located at the south-western area of the Mecsek Mts. and having sandstone bedrock could be characterized by higher concentrations of inorganic ions, higher proportions of washaway and herbaceous plants in riparian vegetation, higher annual ranges of temperature, higher air temperatures during the whole year, higher amounts of precipitation in driest month, lower altitudinal positions and smaller channel width than the sites located at the north-eastern part of the mountains having limestone bedrock. These latter sites were surrounded by more natural vegetation than the streams running in sandstone bedrock.

Analysis of abiotic habitat features revealed differences between environmental factors regarding their temporal and spatial variability (Table 3). Slight differences in habitat features were found between the streambed morphology of the two catchment areas. Only 2 out of 16 parameters (proportion of mesolihal microhabitat type, channel width) showed significant differences. From the variables used to describe the longitudinal gradient of streams (e.g. channel width, distance from source, altitude, slope) only two (altitude, channel width) showed statistically significant differences between catchments. Similar hydrological and streambed morphological conditions of sites indicated slight differences between longitudinal posi-

tions of two groups of sites. Only the physicochemical feature of water proved to be significantly different between seasons because of stream flow fluctuations. Due to low numbers of samples (3 samples) within catchments and weak reliability of statistical analysis, our results did not show significant differences between climate conditions of the two catchment areas. However, 9 out of 18 climatic parameters proved to be significantly different. We suspected that microclimatic differences were much more related to the aspect, the direction and the altitude of valley of streams than south-north gradient.

Variability of taxonomic and functional composition

We found differences not only in taxonomic composition but also in functional composition of chironomid assemblages between headwaters belonging to different catchments. Taxonomic composition (6 common out of 36 taxa) differed sharply between the two sides of mountain range within a relatively small spatial distance. This is similar to terrestrial studies on the flora and fauna of Mecsek Mountains and its surroundings. Several studies found strong south-north gradients, which provided evidence for southern colonization processes (e.g. Kevey & Horvát 1986, Meusel & Jager 1989). Despite the observed gradient in taxonomic composition of chironomid assemblages, genera found in the Mecsek Mountains are widely distributed in the Palaearctic (Ashe et al. 1987), and species that occur only in the south-western area of mountains do not have south European origins (Sæther & Spies 2011).

We could not show direct relationships between the variability of chironomid assemblages and local environmental factors, although several previous studies highlighted that the spatial distribution of chironomid larvae is closely related to those abiotic characteristics that were significantly different among two groups of sites in our study (e.g. catchment geology, pH, altitude, local climate) (Calle-Martinez & Casas 2006, Puntí et al. 2009, Raposeiro et al. 2011, Rosa et al. 2011). Puntí et al. (2009) detected the altitude effect on chironomid assemblages in Mediterranean region, due to its considerable influence on local climate and other physical conditions. Raposeiro et al. (2011) emphasised that local scale physicochemical and hydromorphological factors had an important role in determining the distribution patterns of chironomid assemblages after colonization in Azorean streams. Therefore, we believe that species sorting through local adaptation to altering abiotic conditions played an

important role in the separation of chironomid assemblages among catchments compared to geographical and historical effects (e.g. dispersal limitation) within the studied mountain range.

We found moderate but statistically significant separation of functional composition among catchments (Table 4, Fig. 2). In the case of saprobic and stream zonation preference of chironomids, sites were ordered according to an upstream-downstream gradient (Vannote et al. 1980, Moog 2002). Based on the functional preference of midge taxa, sandstone bedrock sites indicated crenal and hypocrenal habitats with low saprobic level, whereas limestone bedrock sites indicated hyporithral and potamal habitats with higher saprobic level. The distribution patterns of functional feeding groups mainly followed the subtle gradient mentioned above corresponding to the predictions of the RCC. However, the observed discrepancies could be explained by stream or catchment specific ecological processes and abiotic characteristics. For example, the ectoparasitic/phoretic (Svensson 1979) *Epoicocladus ephemeræ* was frequent in limestone sites due to the high abundance of its host organism (*Ephemeradanica*) (Szivák et al. 2010, Méhes et al. 2012). At the same sites, the dominance of lithal substrate affected the abundance of grazers and scrapers by providing optimal habitat conditions for periphyton growth (Schneider et al. 2012).

Our results indicated a slight internal shift in functional composition within the second order stream stretches. This gradient seems to be associated with channel width or altitude instead of the distance of the sites from the source. These results are in accordance with Grubbs (2011), who found that subtle downstream functional changes of macroinvertebrate assemblages are typical in forested headwaters.

Spatial variability in taxonomic and functional structure of chironomid assemblages was examined at multiple scales (i.e. from microhabitat to catchment) (Table 4). The most important factor structuring midge assemblages was the microhabitat. Several previous studies (Lencioni & Rossaro 2005, García-Roger et al. 2011, Rosa et al. 2011) pointed out that the microhabitat type has a finer scale effect in structuring macroinvertebrate assemblage, which could explain an important part of the spatial variation. Furthermore, internal microhabitat heterogeneity had an important role in structuring the functional patterns of chironomid assemblages in our streams. Habitats with different particle sizes and features could have very distinct physical conditions (e.g. current velocity, water depth, temperature) and hence, organic nutrient characteris-

tics, which presumably caused the co-occurrence of several species characterized by very diverse zonation and saprobic preference within the same reach of streams. Nevertheless other studies confirmed that spatial distribution of functional feeding groups between habitat patches is a mosaic within reaches (e.g. Winemiller et al. 2010). We did not observe this phenomenon (Table 5). In the case of functional feeding groups, the effects of sampling time and catchments proved to be primarily significant. In conclusion, chironomid larval assemblages were influenced by mountain massif even at relatively small spatial scales. We highlighted that the taxonomic and functional composition of chironomid larvae respond strongly to natural environmental gradients similarly to other macroinvertebrate groups (e.g. Heino et al. 2007).

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Appendix 1. Collected chironomid species, their abbreviation and distribution according to the two areas characterized by different bedrock. Abbrev.: S – area having sandstone bedrock, L – area having limestone bedrock. Taxa marked ‘*’ were omitted from statistical analysis due to their relative abundance less than 0.2%.

Taxon	Codes	Bedrock type
<i>Apsectrotanypus trifascipennis</i> (Zetterstedt, 1838)	A_tri	S
<i>Brillia bifida</i> (Kieffer, 1909)	B_bif	S
<i>Chironomus</i> sp.*	Chi_sp	S
<i>Conchapelopia</i> sp.	Con_sp	S
<i>Corynoneura</i> sp.*	Cor_sp	S
<i>Cricotopus (Isocladius)</i> sp.*	Cri_sp	S
<i>Diamesa cinerella</i> gr. Meigen, 1835	D_cin	S
<i>Diplocladius cultriger</i> Kieffer, 1908*	D_cul	S
<i>Epoicocladius ephemeræ</i> (Kieffer, 1924)	E_eph	L
<i>Macropelopia nebulosa</i> (Meigen, 1804)*	Ma_neb	L
<i>Macropelopia notata</i> (Meigen, 1818)*	Ma_not	S
<i>Macropelopia</i> sp.	Ma_sp	S
<i>Micropsectra notescens</i> (Walker, 1856)	Mi_not	S
<i>Microtendipes chloris</i> (Meigen, 1818)	Mi_chl	L, S
<i>Microtendipes pedellus</i> gr. (De Geer, 1776)	Mi_ped	L, S
<i>Natarsia</i> sp.	Nat_sp	S
<i>Odontomesa fulva</i> (Kieffer, 1919)	O_ful	S
<i>Orthocladius (Orthocladius)</i> sp.*	Ort_O	S
<i>Orthocladius</i> sp.	Ort_sp	S
<i>Orthocladius thienemanni</i> Kieffer, 1906	Ort_thi	L, S
<i>Parametriocnemus stylatus</i> (Spärck, 1923)	P_sty	S
<i>Paratrichocladius skirwithensis</i> (Edwards, 1929)	P_ski	L, S
<i>Paratrisocladius excerptus</i> (Walker, 1856)	P_exc	S
<i>Polypedilum convictum</i> (Walker, 1856)	P_con	L, S
<i>Polypedilum pedestre</i> (Meigen, 1830)	P_ped	S
<i>Polypedilum scalaenum</i> (Schrank, 1803)	P_sca	L, S
<i>Polypedilum</i> sp.*	P_sp	S
<i>Polypedilum uncinatum</i> (Goetghebuer, 1921)*	P_unc	L
<i>Procladius (Holotanypus)</i> sp.*	Pro_sp	L
<i>Prodiamesa olivacea</i> (Meigen, 1818)	Pro_oli	S
<i>Rheocricotopus atripes</i> (Kieffer, 1913)*	Rc_atr	S
<i>Rheocricotopus effusus</i> (Walker, 1856)*	Rc_eff	S
<i>Rheocricotopus fuscipes</i> (Kieffer, 1909)	Rc_fus	L, S
<i>Rheopelopia</i> sp.	Rp_sp	S
<i>Rheotanytarsus</i> sp.	Rt_sp	L
<i>Zavrelimyia</i> sp.	Zav_sp	L, S