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Structure and spatial variability of mayfly (Ephemeroptera) communities in the upper Hron River basin

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Abstract: Mayflies were sampled from eleven sites in six tributaries of the upper Hron River. Mayfly communities were ordinated and related to environmental factors using multiple regression and principal component analysis. Communities of headwater sites were dominated by *Rhithrogena iridina* which was gradually replaced by *Baetis alpinus*, at the lower reaches. Total mayfly species richness was inversely related to stream slope and overall abundance was inversely related to altitude. The prominent factor influencing mayfly communities was a complex longitudinal gradient as proposed by the river continuum concept. There were no significant differences in community composition and structure between the left- and right-hand tributaries of the Hron River.

Key words: Benthos, mayflies, Ephemeroptera, communities, longitudinal gradient, Carpathians, Slovakia.

Introduction

Mayfly fauna of the upper Hron River has attracted little attention from biologists. Some faunistic information on the mayfly assemblages of the study area can be found in LANDA (1969) and LANDA & SOLDÁN (1989). They recorded 21 mayfly species mainly from the Hron River. There is no information about the composition and structure of mayfly communities of this area.

It is well established that the longitudinal gradient of environmental factors proposed by the River Continuum Concept (RCC; VANNOTE et al., 1980) leads to natural responses in macroinvertebrate communities (e.g., ORMEROD et al., 1994; KRNO et al., 1996). The geological substrate is a physical template that can have a number of effects on headwater streams (GRIFFITH et al., 1994). Variables such as pH and water hardness may play a key role in the distribution of stream macroinvertebrates (TOWNSEND et al., 1983; ORMEROD & EDWARDS, 1987; PETCHEY et al., 2004). Since there is a hypothesised link between variables such as water chemistry and substrate, and distribution of the fauna, the chemical/physical variables and faunal community should change abruptly when there are abrupt changes in physiography (PERRY & SCHAFFER, 1987).

Basins of the left-hand tributaries are partially built from limestone in contrast to the granite basins of the right-hand tributaries. Consequently, differences between the mayfly fauna of the southern slope of the Nízke Tatry Mts and the northern slope of the Muránska Planina Mts are predicted.

The aims of this study were (i) to describe the composition and structure of mayfly communities of the study area, and (ii) to assess the relationships between environmental factors and spatial variability of mayfly communities.

Study area

The Hron River is one of the longest rivers in Slovakia (West Carpathian Mts). Studied tributaries of the upper Hron River (Fig. 1) are rhithral streams up to the fourth order. The geology of the study area is dominated by granodiorites and granites with a substantial presence of Mesozoic limestone in the catchments of the left-hand tributaries. The climax vegetation of the area is beech (*Fagus sylvatica* L.) forest, although much of this has been cleared and replaced by sylvicultures with spruce (*Picea abies*). The area belongs to a moderately cool climatic subregion with mean July air temperatures ranging from 12 to 16 °C. Mean annual precipitation varies from 600 to 1000 mm (SLOVAK ENVIRONMENTAL AGENCY, 2002). Eleven sampling sites along six streams were selected on the basis of altitude, stream size and the bedrock character. The structure of the riparian vegetation of the chosen sampling sites was relatively natural with the canopy cover varying from 100% to 70% in lower situated reaches. All sampling sites had a similar riffle : pool ratio of approx. 9 : 1. The substrate composition was dominated by pebbles and cobbles across all studied sites. Boulders were present at the uppermost sites whereas gravel was more important in the lower reaches. A detailed description of sampling sites is given in Table 1.
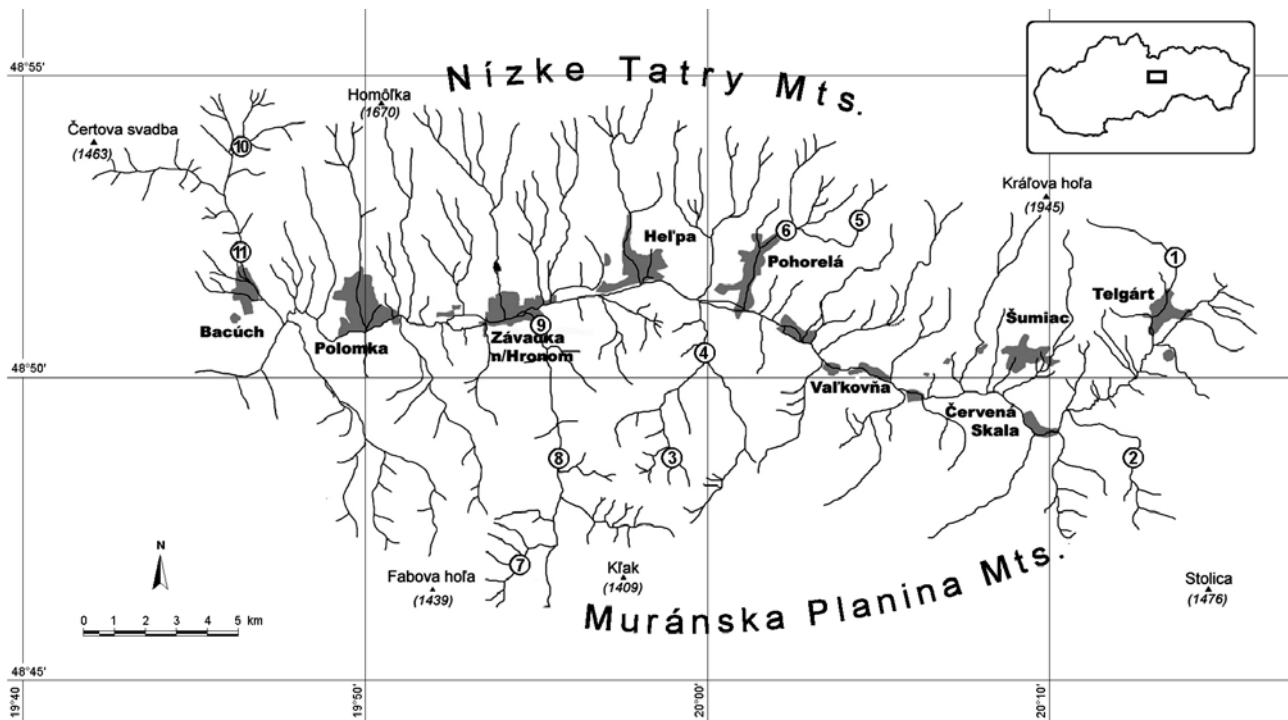
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Fig. 1. Location of sampling sites (numbered circles) in the upper Hron River.

Material and methods

Sampling procedure

Benthic invertebrates were collected over three sampling dates (5.V., 22.VI., 5.X.2004) with the exception of sampling site 10, where only two samples were taken (June and October). Chosen sampling dates were appropriate for compiling an accurate species inventory in the study streams (cf. Bauernfeind & Moog, 2000). Five-minute benthic kick net samples were taken (D-frame net, 500 μm mesh size) proportionally to the substratum composition to achieve comparability of all samples. Samples were preserved in 4% formaldehyde and taken to the laboratory for sorting and identification. Mayflies were identified to the lowest possible taxonomic level using taxonomic keys (Hefti et al., 1989; Haybach, 1999; Soldán & Landa, 1999; Bauernfeind & Humpesch, 2001).

Environmental data were collected simultaneously with the benthos sampling. Discharge was determined from the current velocity measured with a portable current meter. Temperature and pH values were measured electrometrically. Other environmental characteristics were obtained in the field or were determined from a topographic map (Wetzel & Likens, 2000).

Data analysis

Multiple regression analysis (StatSoft Inc., 2001) was used to examine the effect of environmental factors on the overall mayfly community characteristics (species richness, average abundance). Environmental conditions were defined by measured environmental data (Tab. 1). Assumption of normality was tested by the Shapiro-Wilks test. Data were $\log_{10}$ transformed if necessary. Best-subset regression method was used to identify which predictors explained significant variation in mayfly species richness and abundance, respectively. Mallow's Cp was selected as the best-subset criterion.

The assessment of faunal similarity was performed by hierarchical cluster analysis (CAP 3.0; Seaby & Henderson, 2004). The complete linkage method with the Sörensen index as the similarity measure was chosen as an appropriate method to classify patterns of spatial differences in assemblages (Murguía & Villaseñor, 2003).

An ordination analysis was employed in order to summarise the variation and identify major gradients in the mayfly and environmental data sets. Both data sets were averaged in order to get an overall picture of each site. Since the response of the majority of species to the largest environmental gradient was linear rather than curved, as well as with respect to the results of detrended correspondence analysis (gradient length < 2 SD; cf. ter Braak & Šmilauer, 1998), a linear response model was chosen. Principal components analysis (PCA) with standardisation was performed on the environmental data in order to minimise variation caused by different scales of the environmental variables. PCA on species dominance data (semiquantitative data standardised by sample norm) was run to find patterns in community structure. Rare species create a large number of zero values, noise in the data set, which can cause distortion of ordination space. Species with low dominance (< 1% of total numbers) were therefore removed from the analysed data set.

Correlation analysis (Pearson r; StatSoft Inc., 2001) was used to determine which environmental variables and species had significant loadings for their respective ordinations. Correlation analysis was also used to determine if and how eigenvectors from the mayfly and environmental ordinations were related. Significance was determined at $P = 0.05$ by probability adjusted with Holm's sequential Bonferroni

Table 1. Physical and environmental characteristics of sampling sites. Mean values ± SD are based on measurements taken on sampling dates. Values of slope and link number (SHREVE, 1966) are based on a 1 : 50 000 scale topographic map.

| Sampling site code / name	Altitude (m a.s.l.)	Stream slope (%)	Channel width (m)	Stream depth (m)	Link number	Discharge (m^3 s^{-1})	pH	Water temperature (℃)
1 / Zubrovica	970	10.2	1.1	0.08	2	0.065	7.4 ± 0.7	7.2 ± 0.3
2 / Stračaník	859	6.0	0.3	0.20	4	0.084	7.1 ± 0.1	7.7 ± 1.7
3 / Postaľ	870	11.5	1.0	0.15	2	0.025	6.9 ± 0.3	7.2 ± 0.5
4 / Postaľ	748	6.6	4.0	0.30	16	0.170	6.9 ± 0.3	8.7 ± 0.4
5 / Kopanica	922	14.6	1.5	0.15	2	0.110	6.9 ± 0.3	8.6 ± 0.8
6 / Pohorelský potok	850	6.4	2.8	0.30	10	0.190	7.3 ± 0.3	10.6 ± 2.2
7 / Hronec	843	7.3	2.2	0.20	4	0.130	7.6 ± 0.2	8.7 ± 0.5
8 / Hronec	742	3.0	5.0	0.25	22	0.610	7.6 ± 0.3	8.8 ± 0.4
9 / Hronec	646	3.8	5.6	0.30	27	0.770	7.5 ± 0.0	9.8 ± 0.3
10/ Bacúšsky potok	670	17.0	2.1	0.20	7	0.120	7.0 ± 0.2	8.2 ± 1.6
11/ Bacúšsky potok	640	8.5	4.0	0.35	26	0.370	–	–
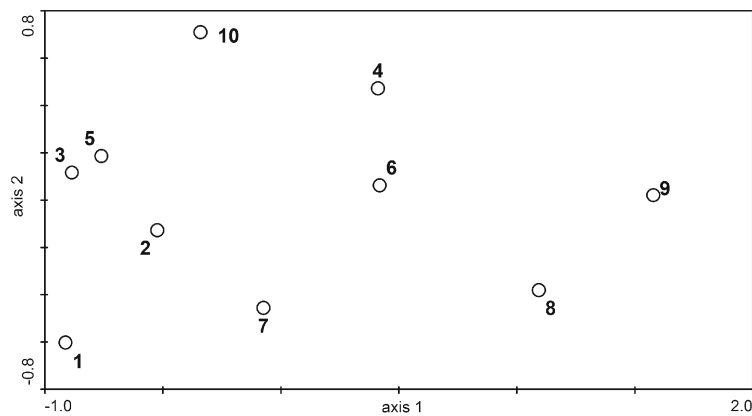
Fig. 2. Ordination plot of the sampling sites based on measured environmental conditions. Numbers represent the sampling sites.

method (P_c) which reduces over-interpretation of results (cf. QUINN & KEOUGH, 2002).

Partial redundancy analysis (RDA) on qualitative and standardised semiquantitative species data was used to test the hypothesis that there is no difference in community composition and structure between the left- and right-hand tributaries after the effect of link number (complex representative of longitudinal gradient) was partialled out. The Monte Carlo permutation test (999 permutations) on the first axis was employed to assess the statistical significance of the models analysed. Multivariate analyses were performed with CANOCO software (TER BRAAK & ŠMILAUER, 1998).

Due to the incomplete environmental or species data sets, sites 10 and 11 were excluded from some numerical analyses.

Results

Environmental conditions
During the investigation period, seasonally fluctuating environmental variables (pH and temperature) were comparable between the right- and left-hand tributaries (Tab. 1). A major environmental gradient was apparent from the ordination plot where the displayed axes explained 66.3% and 15.1% of the variation in the data set (Fig. 2). Headwater sites occupied the left side of the ordination space and the foothill sites occupied the right side. Log$_{10}$ link number ($r = 0.95$, $P < P_c = 0.006$) and interrelated variables [width ($r = 0.95$, $P < P_c = 0.007$), depth ($r = 0.85$, $P < P_c = 0.01$) and log$_{10}$ discharge ($r = 0.93$, $P < P_c = 0.008$)] were significantly positively correlated with the first component. Values of pH indicated some relation to the second component ($r = -0.75$), although not significantly. The remaining environmental variables did not demonstrate a linear relationship to the displayed axis.

Community composition
Altogether 6,104 mayfly larvae were collected during the sampling period at the 11 sampling sites. A total of 19 species was identified (Appendix 1). Larvae identified here as *Ecdyonurus* cf. *austriacus* differed from the specimens of *E. austriacus* described in HEFTI & TOMKA (1986) and HEFTI et al. (1989) by the shape and arrangement of the tergo-abdominal spines, and the shape of the pronotum expansion. Interestingly, some specimens of *Rhithrogena iridina* from sites 1, 8 and 9 were parasitized with chironomid midge larvae *Symbiocladius rhithrogenae* (Zavřel, 1924). In the sample taken in October at site 1, at least 20% of the host's population were infected.
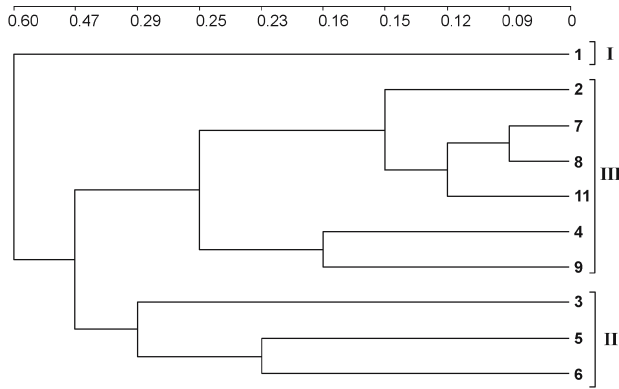
Fig. 3. Complete linkage dendrogram of sampling sites based on the community composition (qualitative data). Axis represents magnitude of dissimilarity (1 − Sörensen index). Discussed groups of sites are depicted.

As an indicator of faunal similarity, Sörensen index ranged from 0.4 (few common species) to 0.9 (almost identical species composition) (Fig. 3). The clustering procedure arranged sampling sites into three major groups. Group I (sampling site 1) was composed of species-poor assemblage (6 spp.) of the highest situated site (970 m a.s.l.) and defined by the occurrence of *Ecdyonurus subalpinus* and *E.* cf. *austriacus*. Group II (sampling site 3, 5 and 6) comprised high gradient

sites (mean slope > 10%) with a mean altitude of 880 m a.s.l. Their assemblages were poor (5–8 spp.) with missing *Ecdyonurus* species. Group III (remaining sampling sites) included relatively rich assemblages (> 10 spp.) of lower altitudes (mean altitude < 730 m a.s.l.) and lower gradient (mean slope < 8%). Assemblages of this group were distinguished from the others by the presence of *Ecdyonurus venosus*.

Community structure

Community structure of the surveyed streams was characterised by a dominance of *Baetis alpinus* and *Rhithrogena iridina*. Both species occurred at all sites and made up, respectively, 52% (*B. alpinus*) and 20% (*R. iridina*) of total mayfly abundance. The first two axes for the PCA carried out on mean species dominance explained, respectively, 86.7% and 5.6% of the variation in the data set (Fig. 4). The relative proportion of *R. iridina* ($r = 0.99$, $P < P_c = 0.005$) was significantly correlated with the first component. The proportion of *Baetis rhodani* was significantly correlated with the second component ($r = -0.83$, $P < P_c = 0.005$). However, none of the measured environmental variables or environmental eigenvectors was clearly related to the displayed axes. The right part of the ordination space is occupied by shallow headwater sites of low link numbers – group A. Their respective communities were dominated by *R. iridina*.
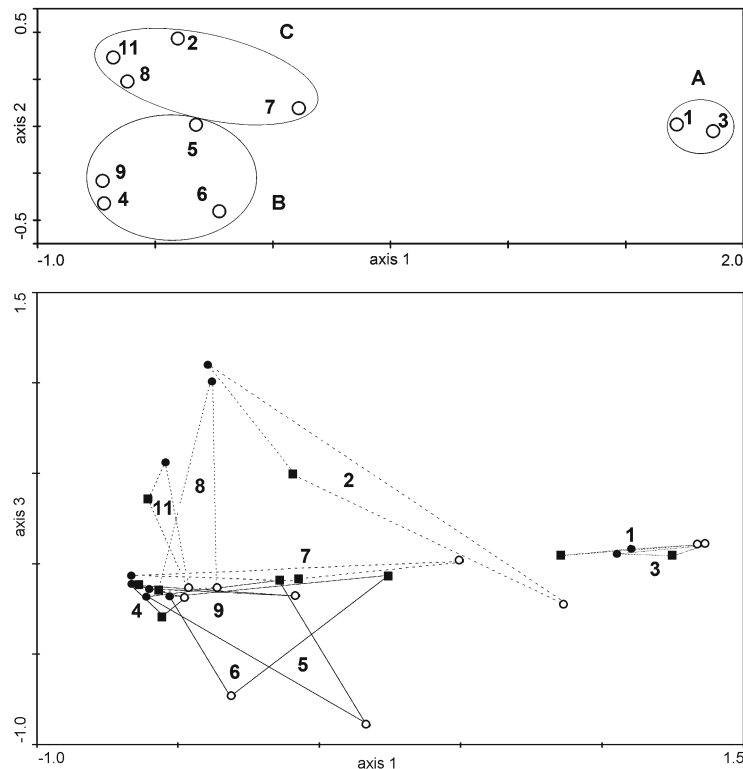

Fig. 4. Ordination plot of the averaged (upper plot) and seasonal samples (lower plot) for each site based on mayfly dominance data, 1% censorship level. Membership to A, B and C group is depicted by dotted, solid and dashed line, respectively. Empty circles, full circles and square centroids (lower plot) represent June, May and October samples, repectively.

Towards the left, the proportion of *R. iridina* decreased with a simultaneously increased proportion of *B. alpinus*. Sites situated in the left part of the ordination plot are completely dominated by *B. alpinus*. Two groups of sites were clustered to the left and arranged along the second axis. Communities of group B were defined and separated by a substantially higher proportion of *B. rhodani*. Low numbers of *Rhithrogena circumtatrica* or its complete absence and overall low species richness (with the exception of site 9) are characteristic for this group. In contrast, communities of group C have an altered ratio in favour of *R. circumtatrica* and seemed to be rich in species.

In terms of seasonal fluctuations, axes 1 and 3 (46.5% and 15.6% of explained variance) had the same biological sense as the axes from the previous ordination (Fig. 4). The first component of respective ordination was strongly correlated with the first component extracted from the environmental data set ($r = -0.66$, $P < P_c = 0.006$). Differentiation of season-sites triangles along the first axis is therefore attributable to the longitudinal environmental gradient. Proportions of *B. alpinus* ($r = -0.68$, $P < P_c = 0.005$), *Epeorus assimilis* ($r = -0.55$, $P < P_c = 0.006$) and *R. iridina* ($r = 0.95$, $P < P_c = 0.005$) were significantly related to the first axis. *R. circumtatrica* ($r = 0.82$, $P < P_c = 0.005$) and *Ephemerella mucronata* ($r = -0.57$, $P < P_c = 0.005$) had significant loadings along the second axis. Again, headwater sites of group A were clustered together. Site 7 showed similar seasonal change to group A. It pulsed along the first axis in concordance with the ratio of *B. alpinus* to *R. iridina*. The seasonal pattern of group C was predominantly governed by the life history of *R. circumtatrica*. Larvae of the winter generation were sampled in May, absent in June samples and re-appeared in October as a subsequent generation. Patterns of seasonal variation in group B were not uniform. In the same valley, communities of site 5 and 6 widely fluctuated among sampling dates. In contrast, sites 4 and 9 exhibited relatively little seasonal change.

Spatial differences
The total mayfly species richness ranged from 5 to 14 among sites. The lowest richness was recorded at headwater sites 5, 1 and 3, and the highest at sites 9 and 11. The best regression model describing the relationship between environmental conditions and mayfly species richness included stream slope as a single predictor ($F_{1,7} = 19.80$, $r^2 = 0.74$, $P < 0.01$). Species richness significantly increased from headwater sites with a high slope towards the reaches with a lower slope (species richness = 15.20 − 0.75 × slope). Altitude seems to be the best predictor of overall average abundance which decreased with increased altitude ($F_{1,7} = 10.13$, $r^2 = 0.59$, $P < 0.05$, average abundance = 738.78 − 0.65 × altitude).

Results of partial RDA on the qualitative data set

($F = 2.118$, $P = 0.125$) and averaged dominance data set ($F = 0.222$, $P = 0.92$) suggest that there were no statistically significant differences in community composition and structure between the left- and right-hand tributaries.

Discussion

Following the ranking methodology for describing zonation patterns of mayfly species (DERKA, 2003) based on ILLIES & BOTOSANEANU (1963), we can conclude that the assemblages studied consist of predominantly epirhithral species. The proportion of hypocrenal species was higher at site 1, and the proportion of meta- and hyporhithral elements increased towards the lower reaches. The classification pattern based on Sörensen's index reflects natural changes along the longitudinal gradient of streams and the species turnover along the gradient is comparable with other studies carried out on mayfly communities (e.g., KRNO et al., 1996; DERKA, 2000).

Unidentified larvae of the *Ecdyonurus helveticus*-group close to *E. austriacus* may belong to a new species. According to the great intraspecific morphological variability of the species belonging to the *E. helveticus*-group, we may have reasonably expected the presence of more species and/or subspecies in the area (cf. SOLDÁN, 2003; GODUNKO & KLONOWSKA-OLEJNIK, 2004; GODUNKO et al., 2004). In the case of the validity of DINODAL biome distribution (MALICKY, 1983) for *E. helveticus*-groups, this inter-group variability may be a consequence of glacial refugial isolation (cf. HAYBACH, 2003).

The high incidence of infection of *R. iridina* by *S. rhithrogenae* was not exceptional in the surveyed area. LANDA (1969) recorded even higher infection of *Ecdyonurus dispar* (Curtis, 1834) by *S. rhithrogenae* in a right-hand tributary Hlboká near Bravächovo.

Ordination based on both averaged and seasonal dominance data sets clearly separated site group A from the other sites. The separation along the first component is attributable to differences in the proportions of the dominant species; *R. iridina* and *B. alpinus*. Both species are typical members of epirhithral communities whereas *B. alpinus* is characterised by a higher tolerance to altitudinal zonation than *R. iridina* (SOLDÁN et al., 1998; DERKA, 2003). The results given in this paper indicate that the most numerous species, *B. alpinus*, appeared to lose its dominant status in conditions of higher altitudes and low stream link numbers such as sites group A, which are dominated by *R. iridina*. Although low link number and high altitude sites 2 and 7 were not clustered in group A, they showed, in the seasonal analysis, a certain degree of similarity to this group to which they physiographically belong (cf. Fig. 4). It was not possible, on the basis of these results, to determine causality of distinction between groups B and C or potential

Table 2. Spearman rank correlation matrix between all environmental variables measured at the upper Hron River tributaries.

	Altitude	Slope	Width	Depth	Link no.	Discharge	pH
Slope	0.78*						
Width	−0.83**	−0.57					
Depth	−0.85**	−0.70*	0.75*				
Link number	−0.95***	−0.88**	0.85**	0.90***			
Discharge	−0.87**	−0.73*	0.93***	0.85**	0.92***		
pH	−0.48	−0.57	0.45	0.18	0.46	0.50	
Temperature	−0.76*	−0.64	0.83**	0.87**	0.82**	0.94***	0.43

Key: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

subgroups. Factors such as substrate composition, flow regime and impact of land use which were not considered here may play an important part in the separation of these groups. The first eigenvector from the analysis of environmental conditions was a dominant correlate with the ordination and classification patterns produced in this paper as predicted from RCC (Vannote et al., 1980). In other words, stream link magnitude and related factors were more prominent than pH.

Among the measured environmental variables, stream slope showed strongest correlation with mayfly species richness, in which the slope alone explained 74% of the variation in species richness. Mayfly abundance was most strongly related to altitude, which explained 59% of variation in the overall average abundance. However, the environmental variables showed high collinearity (Tab. 2) and therefore it was impossible to strictly specify the main factor influencing the mayfly communities. Among them, altitude represents a complex environmental gradient controlling lotic communities. Due to its covariance with climatic variables such as temperature, altitude influences many aspects of macroinvertebrates life history (Sweeny, 1984). Magnitude of channel slope affects sediment quality which, in turn, influences the benthic macroinvertebrate community (Minshall, 1984). A negative relationship between mayfly species richness and slope was found by Breitenmoser-Würsten & Sartori (1995) when they analysed communities in prealpine streams.

Mayfly species richness has been also related to river zonation. Bauernfeind & Moog (2000) illustrated an increase in mayfly species richness from the springs to the potamal using an example of pristine to moderately disturbed streams in Austria. Several other studies have demonstrated low mayfly species richness in spring areas (Erman, 2002) and its increase in a downstream fashion from headwater streams to the lower reaches (e.g., Landa & Soldán, 1989; Deván, 1993). Allan (1995) concluded that, in general, more species are found in large rivers than small streams, apparently because the spatial area and habitat diversity are greater in larger systems.

Higher species diversity may be linked with a wider range of food resources. The communities studied consist mainly of representatives of the scraper guild, which found considerably more food in the middle reaches with an open canopy cover rather than in heavily shaded headwater sites (Vannote et al., 1980; Bruns et al., 1987).

A downstream increase in mayfly abundance may also be related to increasing food availability. This longitudinal pattern in mayfly abundance has also been found by other authors (e.g., Ward, 1986; Miserendino & Pizzolón, 2001; but see Krno et al., 1996).

Despite the differences in geological character of the basins of the left- and right-hand tributaries, neither compositional nor structural changes between respective mayfly communities were found. These results fully correspond to those of Novikmec (2005), who compared caddis flies assemblages of the same tributaries.

Allan (1995) pointed out that the number of species commonly increases with water hardness. In a large-scale study, Ormerod & Edwards (1987) found that macroinvertebrates in the Wye River basin do not follow a simple gradient proposed by RCC but multiple gradients separated by pH or hardness. Krueger & Waters (1983) compared macroinvertebrate communities of headwater streams that differed in watershed geologic origin and in total alkalinity. They found substantial differences in the structure of communities and a positive association between macroinvertebrate annual production and stream alkalinity. Griffith et al. (1994) obtained similar results when comparing communities of streams with different alkalinity. However, the biological importance of variation in chemical composition is evident only at the extremes (Allan, 1995). In our case, values of pH were comparable among streams flowing from the basins with different bedrock (cf. Tab. 1; Fig. 2) and therefore the high community similarity of both parts of upper Hron River basin is adequate. More precise data would be necessary to discover if a stronger and closer spatial pattern of the mayfly fauna referable to changes in bedrock character exists.

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Appendix 1. Average abundance of mayfly taxa recorded at studied sites.

Taxon	Sampling site										
	1	2	3	4	5	6	7	8	9	10	11
Habroleptoides confusa Sartori et Jacob, 1986	0	0	0	3	0	0	0	0	0	0	1
Ephemerella mucronata (Bengtsson, 1909)	0	5	1	14	3	11	3	12	8	1	3
Ameletus inopinatus Eaton, 1887	0	1	0	0	0	0	0	0	0	0	0
Baetis spp. juv.	1	5	34	64	56	18	22	30	41	11	24
Baetis alpinus (Pictet, 1843)	8	15	12	73	62	49	68	190	119	24	64
Baetis lutheri Müller-Liebenau, 1967	0	0	0	0	0	0	0	0	2	0	0
Baetis melanonyx (Pictet, 1843)	1	0	0	1	2	1	1	2	2	1	2
Baetis rhodani (Pictet, 1843)	2	2	3	12	7	12	3	14	24	0	1
Baetis vernus Curtis, 1834	0	0	0	0	0	0	0	0	2	0	1
Baetis muticus (L., 1758)	0	3	1	6	0	1	1	3	1	0	2
Ecdyonurus spp juv.	3	16	1	5	1	0	2	2	2	0	2
Ecdyonurus cf. *austriacus* Kimmins, 1958	4	0	0	0	0	0	0	0	0	0	0
Ecdyonurus starmachi Sowa, 1971	0	0	0	0	0	0	1	0	0	0	1
Ecdyonurus subalpinus (Klapálek, 1907)	7	0	0	0	0	0	0	0	0	0	0
Ecdyonurus venosus (F., 1775)	0	6	0	3	0	0	1	2	4	0	1
Epeorus assimilis Eaton, 1885	0	4	0	15	0	5	2	6	17	0	6
Rhithrogena spp. juv.	37	11	64	15	7	8	69	43	15	40	17
Rhithrogena carpatoalpina Klonowska et al., 1987	0	3	3	5	0	0	2	8	5	2	1
Rhithrogena circumtatrica Sowa et Soldán, 1986	0	11	0	0	0	0	1	29	1	11	13
Rhithrogena gr. *hercynia*	0	0	0	1	0	0	0	0	1	1	0
Rhithrogena iridina (Kolenati, 1859)	19	12	38	5	16	16	33	22	7	15	6
Rhithrogena semicolorata (Curtis, 1834)	0	0	0	7	0	2	0	4	18	1	12