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Biological zonation of the last unbound big river in the West Carpathians: reference scheme based on caddisfly communities

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ABSTRACT

Key-words: *Trichoptera, classification, Hron River, longitudinal profile, Carpathians*

A thorough understanding of biotic communities distribution in predisturbance state is essential for predictions of their future changes related to human activities. In this regard, pre-damming data on spatial distribution of benthic communities are highly valuable. Caddisflies were sampled at 14 sites of the Hron River and analysed in order to establish longitudinal zonation of the river and to determine environmental factors affecting assemblages' distribution in the longitudinal profile. A total of 2600 individuals of caddisflies belonging to 40 taxa of 12 families were recorded. Diversity of caddisflies was found to be higher in the upper (rhithral) part of the river. Major change, with shift to much more uniform caddisfly assemblages, occurred in the middle part of the river. Four zones (subzones) were distinguished using caddisfly communities: epirhithral, metarhithral, hyporhithral and epipotamal. Canonical correspondence analysis demonstrated the determining influence of altitude and conductivity on the caddisflies. Pre-damming zonation patterns presented here could serve as basic information for management of the Hron River as well as a reference scheme for other, previously dammed big rivers in the West Carpathian region.

RÉSUMÉ

Zonation biologique de la dernière grande rivière non endiguée des Carpates occidentales : système de référence basé sur les communautés de trichoptères

Mots-clés : *Trichoptères, classification, rivière Hron, profil longitudinal, Carpates*

Une compréhension approfondie de la distribution des communautés biotiques en état avant perturbation est essentielle pour la prévision de leurs futurs changements liés aux activités humaines. À cet égard, les données pré-endiguement sur la répartition spatiale des communautés benthiques sont très précieuses. Les trichoptères ont été échantillonnés dans 14 sites de la rivière Hron et analysés afin d'établir un zonage longitudinal de la rivière et de déterminer les facteurs environnementaux qui influent sur la distribution des assemblages dans le profil longitudinal. Un total de 2600 trichoptères appartenant à 40 taxons de 12 familles a été enregistré. La diversité des trichoptères a été trouvée la plus élevée dans la partie supérieure (rhithral) de la rivière. Le changement majeur, avec décalage vers

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des assemblages de trichoptères beaucoup plus uniformes, s'est produit dans la partie médiane de la rivière. Quatre zones (sous-zones) ont été distinguées en utilisant les communautés de trichoptères : épirhithral, métarhithral, hyporhithral et épipotamal. L'analyse canonique des correspondances a démontré l'influence déterminante de l'altitude et de la conductivité sur les trichoptères. Les modèles de zonage pré-endiguement présentés ici pourraient servir d'information de base pour la gestion de la rivière Hron ainsi que d'un système de référence pour d'autres, les grandes rivières endiguées auparavant dans la région de l'Ouest des Carpates.

INTRODUCTION

In aquatic sciences, classifications provide a very effective tool for monitoring, conservation and management of aquatic biotopes (Gerritsen *et al*., 2000). However, classification of aquatic ecosystems is complicated due to the physical and biological heterogeneity of these systems in space and time (Hynes, 1970; Minshall *et al*., 1983; Palmer and Poff, 1997). In classification of running waters, each water flow should be considered as a unique entity with individual conditions (Hynes, 1975). Moreover, in the effort to classify running waters, one encounters a problem with grouping of continual processes. The continual nature of changes in river ecosystems is established in most widely used theory, which explains the functioning of the flowing waters – the River Continuum Concept (RCC; Vannote *et al*., 1980; Bruns *et al*., 1984; Bruns and Minshall, 1985; Minshall *et al*., 1985). RCC critics pointed out that tributaries, changes of geological substrate, morphologic and hydraulic properties of running water make up natural discontinuities (Statzner and Higler, 1985; Perry and Schaeffer, 1987; Brussock and Brown, 1991; Bretschko, 1995; Ward *et al*., 2002) that could result in distinct zonation of flowing waters. Besides natural discontinuities, human activities introduce artificial discontinuities into river ecosystems (*e.g.* Ward and Stanford, 1983a). Damming, regulations and pollution of rivers are the main causes of these discontinuities that overlap natural variability of conditions in space and time.

Biological classifications are based on the structural changes of aquatic communities. In running waters, aquatic invertebrates are traditionally used (Macan, 1961; Illies and Botosaneanu, 1963; Cummins, 1974; Wright *et al*., 1984) as they excellently reflect conditions of the aquatic environment (Wallace and Webster, 1996; Huryn and Wallace, 2000).

Caddisflies represent an important part of riverine benthic communities. Due to relatively well known taxonomy, good knowledge of ecological requirements and a diverse range of ecological and biological traits, Trichoptera are considered suitable indicators of water quality, river biotic integrity and human impact on river ecosystems (Rosenberg and Resh, 1993; Statzner *et al*., 2001; Dohet, 2002; Solà and Prat, 2006). Also, they are frequently used to investigate the effect of various variables on longitudinal distribution of aquatic macroinvertebrates (*e.g.* Wiberg-Larsen *et al*., 2000; Gombeer *et al*., 2011).

The Hron River (Slovakia, Central Europe) was strongly polluted by urban sewage and industrial wastewaters in the middle of the 20th century and still suffers from some, albeit low, degree of pollution (Krno, 2007). However, the river was not seriously affected by the construction of dams. After considerable improvement of water quality in the 1990s (Bitušík *et al*., 2006), the Hron River was considered a near ideal reference system with an original river channel and well preserved ecosystem of big West Carpathian rivers. Recently, rising interest in construction of small hydropower stations (SHPS) in Slovakia represents a serious threat to the ecosystem of the Hron River. More than 30 SHPS dammings are intended and about 14 have already been realised along the whole longitudinal profile of the river. These interventions are expected to cause fragmentation of the stream and seriously affect the entire river ecosystem (Ward and Stanford, 1987).

Data representing the past community structure and their longitudinal organisation in the near-natural state would be of high relevance in monitoring and assessment of the damages

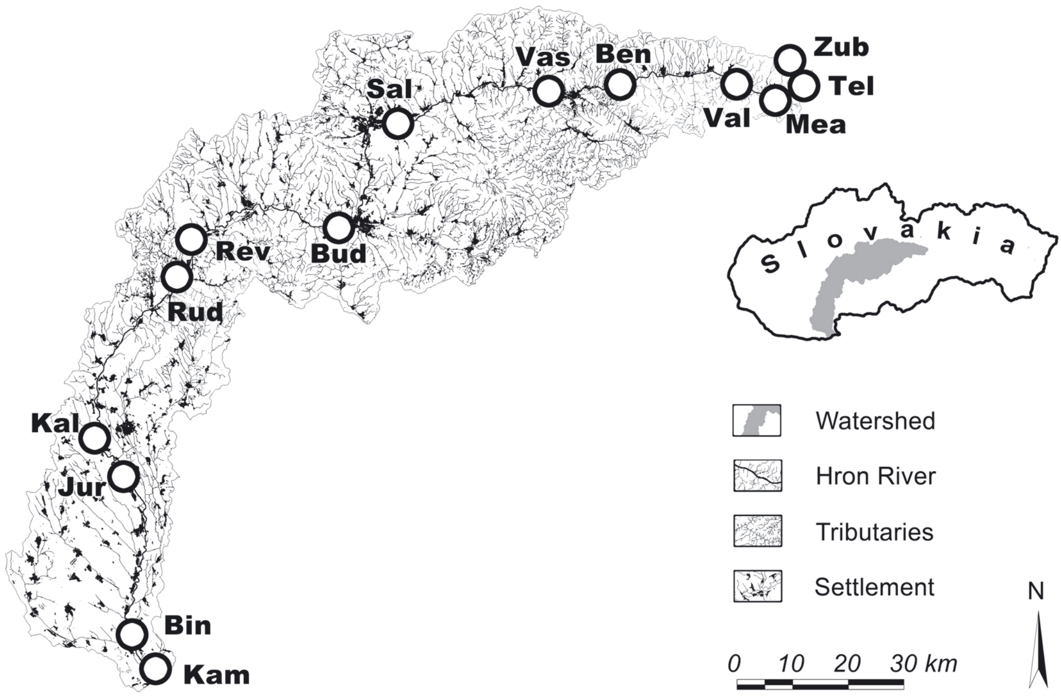

Figure 1
Map of the Hron River watershed showing the sampling sites. Abbreviations of the site names: Zub – Zubrovica, Tel – Telgárt, Mea – NPR Meandre Hrona, Val – Val'kovňa, Ben – Beňuš, Vas – Valaská, Sal – Šálková, Bud – Budča, Rev – Revištské Podzámčie, Rud – Rudno n. Hronom, Kal – Kalná n. Hronom, Jur – Jur n. Hronom, Bin – Bíňa, Kam – Kamenica n. Hronom. Note that the sampling site Zub is situated on the tributary, not on the main watercourse.

caused by excessive building of SHPS. During 2004, we sampled caddisfly communities of the entire longitudinal profile of the Hron River. Here, we present the longitudinal zonation scheme of the Hron River based on the caddisfly communities sampled several years before the construction of the first SPHS. The zonation can serve as a reference scheme for the monitoring of human impact on the West Carpathian rivers.

The specific aims of this study were: (i) to classify caddisfly communities and to identify indicator species for each biotic zone, and (ii) to examine the relationship between caddisfly community composition and environmental characteristics in a longitudinal profile of the Hron River.

MATERIAL AND METHODS

> *STUDY AREA AND SAMPLING SITES*

The Hron River is a 278 km long left-hand tributary of the Danube River. It arises at the elevation of 934 m a.s.l. and empties into the Danube River at the elevation of 103 m a.s.l. near Štúrovo. The total elevation range is 831 m, which makes the average slope 2.9‰. The catchment area is 5465 km^2; 40% of it is covered by forests (Bitušík *et al*., 2006).

In the early 1990s, a strong decline in effluent discharges from the largest industrial companies was followed by considerable improvement of water quality in the Hron River (Bitušík *et al*., 2006). For this study, 14 sampling sites were chosen along the river with respect to main changes in physical habitat (Figure 1). Basic characteristics of the sampling sites are shown in Table I. Physicochemical characteristics were measured in the field using a Multi 3401i water parameter meter (WTW) with SenTix 41-3 and TetraCon® 325 probes (WTW, Weilheim, Germany).

Table I

Basic characteristics of the study sites. Average values of physicochemical variables based on measurements taken on 4 sampling dates are presented. Mean annual discharges were taken from the nearest hydrological stations of the Slovak Hydrometeorological Institute. Habitat quality characteristics come from Bulánková (2006) and were obtained using the River Habitat Survey method (Raven et al., 1997). For abbreviations of site names see Figure 1.

Variable/Sampling site	Zub	Tel	Mea	Val	Ben	Vas	Sal	Bud	Rev	Rud	Kal	Jur	Bin	Kam
North Latitude	48°51′50″	48°51′10″	48°49′59″	48°50′15″	48°49′52″	48°48′39″	48°44′24″	48°33′41″	48°31′16″	48°25′42″	48°12′04″	48°07′47″	47°55′15″	47°49′38″
East Longitude	20°11′34″	20°12′09″	20°10′35″	20°02′44″	19°46′39″	19°35′53″	19°13′17″	19°01′41″	18°43′38″	18°40′27″	18°31′23″	18°36′41″	18°38′45″	18°43′11″
Morphological variables														
Altitude [m]	987	893	832	704	543	480	355	267	220	188	157	142	117	107
Slope [‰]	95.8	24.3	10.7	6.6	3.5	2.7	2.5	1.5	1.2	0.8	0.7	1.0	0.7	0.5
Mean ann. discharge [$m^{-3}.s^{-1}$]	–	0.3	0.5	0.9	3.3	6	6.8	23.9	29.1	30.3	31.5	31.8	32.2	32.4
Stream width [m]	1.1	1.5	4.3	7.3	19	27	45	47	54	54	46	34	20	55
Stream depth [m]	0.08	0.14	0.16	0.23	0.5	0.4	0.2	0.3	1	0.5	0.4	0.2	0.3	0.3
Stream order	II	II	III	IV	VI	VI	VII	VII	VII	VII	VII	VII	VII	VII
Physicochemical variables														
Temperature [° C]	6.2	6.7	7.7	7.4	6.2	7.9	10.0	10.7	11.7	11.9	12.4	13.4	14.4	14
pH	7.3	7.6	7.5	7.8	7.7	8.0	8.0	7.6	7.6	7.7	7.6	7.7	7.9	7.8
Conductivity [$\mu S.cm^{-1}$]	33.8	179.6	210.5	235.8	163.1	175.5	203	277.1	294.3	320.8	329.2	354	401.5	369.5
Habitat variables														
Habitat diversity score	44	35	41	42	39	31	32	34	37	26	33	32	34	24
Human influence score	1	7	9	2	6	3	10	11	5	3	20	20	9	12

> SAMPLE COLLECTION AND LABORATORY

Semiquantitative samples of caddisfly larvae were taken at 14 sampling sites in February, April, August and October 2004. Samples of benthic invertebrates were collected using the kicking technique (Frost *et al*., 1971) during 5 minutes with sampling effort divided proportionally to the coverage of substrate types (Lenat, 1988). A benthic hand net with square frame (30 × 30 cm, mesh size 0.5 mm) was used for the sampling. Samples were fixed with 4% formaldehyde in the field and taken to the laboratory for further processing. Caddisflies were hand sorted and identified to the lowest possible taxonomic level using taxonomic keys Rozkošný (1980), Pitsch (1993) and Waringer and Graf (2011). Systematic review was based on Zat'ovičová and Novikmec (2003).

> DATA ANALYSIS

Data from each sampling date were pooled and average data on species/taxa abundances were used for analysis. Non-hierarchical cluster analysis K-means partitioning was used to create groups of sites with the lowest variability within the groups and the highest variability between the groups (K-means 2; Legendre, 2001). Bray-Curtis index was used as a dissimilarity measure. Due to the non-metric character of the index, analysis was performed on the principal coordinates derived by program the PrCoord 1.0 (ter Braak and Šmilauer, 2002). Species characteristic for each group of sites were obtained using the analysis of indicator species in the program IndVal 2 (Dufrêne and Legendre, 1997). Indicative weight of species was tested by Monte Carlo permutation test (9999 permutations). Optimal number of site groups was determined on the basis of the number of statistically significant indicator species (McCune and Grace, 2002).

Effect of environmental variables on caddisfly communities was identified using direct ordination analysis in CANOCO (ter Braak and Šmilauer, 2002). Due to the fact that dominant gradient of species turnover assessed by detrended correspondence analysis was longer than 5 SD, canonical correspondence analysis (CCA) with Monte Carlo permutation test (999 permutations; $p < 0.05$) was chosen as an appropriate ordination technique (Lepš and Šmilauer, 2003). Potentially important factors controlling caddisfly communities were selected from 3 groups of environmental variables (morphological, physicochemical and habitat) (Table I) in 2 steps by: (1) sequential deleting of collinear variables with high variance inflation factor (VIF) until all of the remaining variables had VIF < 10, and (2) forward selection associated with Monte Carlo permutation tests (999 permutations; $p < 0.05$). Probability level in the forward selection was adjusted using sequential Bonferroni correction (Holm, 1979). Rare species were down-weighted to reduce their influence in the analysis (ter Braak and Šmilauer, 2002). Variation partitioning procedure (Borcard *et al*., 1992) was applied to distinguish independence and relative importance of selected environmental variables to caddisfly assemblages. The variation partitioning was done by means of series of partial CCAs.

RESULTS

A total of 2600 individuals of caddisflies belonging to 40 taxa of 12 families were recorded on 14 sampling sites in 2004. An overview of recorded taxa is given in Table II.

The highest taxa richness and abundance was recorded at the Ben sampling site. Overall, the upstream sampling sites (Zub-Sal) were taxonomically richer with 8–17 taxa per site compared to 6−10 taxa per site in the downstream section of the river.

> RIVER ZONATION

Non-hierarchical cluster analysis divided sampling sites into 6 groups (Figure 2). Indicator values of particular species are presented in Table III.

Table II
List of caddisfly taxa recorded at sampling sites of the Hron River. Numbers indicate total abundances from 4 sampling dates. For abbreviations of site names see Figure 1.

	Sampling site													
Taxa	**Zub**	**Tel**	**Mea**	**Val**	**Ben**	**Vas**	**Sal**	**Bud**	**Rev**	**Rud**	**Kal**	**Jur**	**Bin**	**Kam**
***Rhyacophila cf. dorsalis* (Curtis, 1834)**			1											
***Rhyacophila* cf. *obliterata* McLachlan, 1863**			1											
***Rhyacophila philopotamoides* McLachlan, 1880**	1													
***Rhyacophila pubescens* Pictet, 1834**	2			1										
***Rhyacophila tristis* Pictet, 1835**	21	14		50		1								
***Rhyacophila* s.str.**	12	22	31	80	78	57	11	7	3	4				
***Glossosoma boltoni* Curtis, 1834**					2									
***Glossosoma conformis* Neboiss, 1963**		1		1										
***Glossosoma* sp. juv.**	1					1								
***Philopotamus ludificatus* McLachlan, 1878**	5													
***Philopotamus montanus* (Donovan, 1813)**					2									
***Philopotamus* sp.**	7													
***Hydropsyche bulbifera* McLachlan, 1878**								3				1		
***Hydropsyche contubernalis* McLachlan, 1865**								13	11	18	19	2	30	138
***Hydropsyche exocellata* Dufour, 1841**											2	39	11	5
***Hydropsyche cf. incognita* Pitsch, 1993**					44	14	43	39	113	19	6	2	5	1
***Hydropsyche modesta* Navás, 1925**							5				16		1	6
***Hydropsyche* spp. juv.**			1	1	93	22	12	111	198	57	18	63	80	18
***Polycentropus flavomaculatus* (Pictet, 1834)**					4		8			1				1
***Psychomyia pusilla* (Fabricius, 1781)**					2	2		1	2	6	2	1	32	9
***Tinodes* sp.**														6
***Brachycentrus subnubilus* Curtis, 1834**						7			2	1	2			1
***Micrasema minimum* McLachlan, 1876**				70										

Table II
Continued.

	Sampling site													
Taxa	Zub	Tel	Mea	Val	Ben	Vas	Sal	Bud	Rev	Rud	Kal	Jur	Bin	Kam
Drusus discolor **(Rambur, 1842)**	5													
Ecclisopteryx dalecarlica **Kolenati, 1848**			2	7	27	2	1							
Ecclisopteryx madida **(McLachlan, 1867)**	14	16	7	2										
Annitella obscurata **(Mclachlan, 1876)**	1				1									
Chaetopteryx **sp.**			1		2	5	1	1						
Allogamus auricollis **(Pictet, 1834)**					3									
Allogamus uncatus **(Brauer, 1857)**	4													
Halesus rubricollis **(Pictet, 1834)**	3													
Potamophylax latipennis/luctuosus		3			1									
Potamophylax **sp.**			3		1									
Limnephilinae indet. juv.	4	25	39	32	18	1								
Silo pallipes **(Fabricius, 1781)**		1		1	1									
Goeridae indet.			1											
Athripsodes cinereus **(Curtis, 1834)**														1
Leptoceridae indet. juv.											1		1	
Sericostoma **sp.**	1	2		12	110	30	3		2					
Odontocerum albicorne **(Scopoli, 1763)**				4	1									

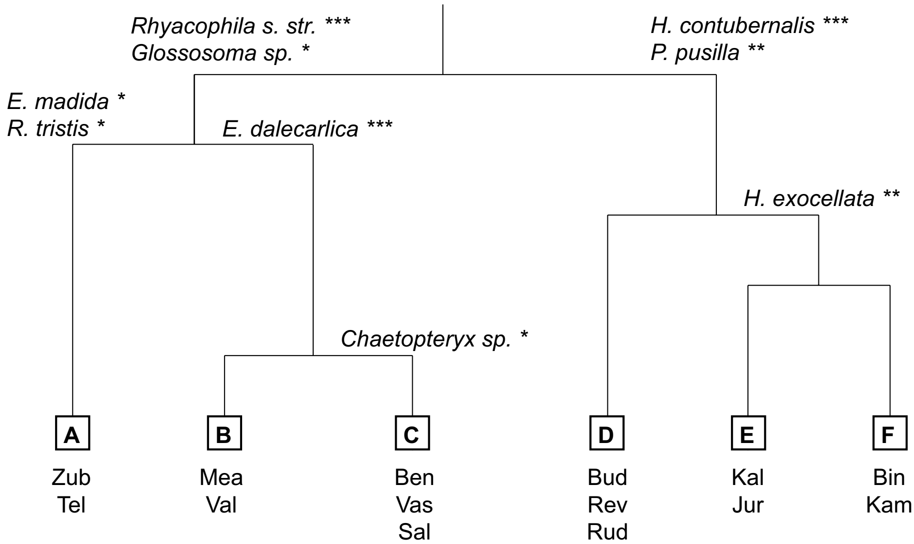

Figure 2
Dendrogram based on the K-means partitioning dividing sampling sites into 6 groups (A-F). Species with statistically significant IndVal are shown. Asterisks represent statistical significance at $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***) based on permutation tests (9999 permutations). For abbreviations of site names see Figure 1.

Groups of sites A, B, and C represent the rhithral zone while groups D, E and F the epipotamal zone. Within the rhithral zone, epirhithral (group A, sites Zub and Tel), metarhithral (group B, sites Mea and Val) and hyporhithral (group C, sites Ben-Sal) subzones were distinguished (see discussion).

> *INFLUENCE OF ENVIRONMENTAL VARIABLES*

Overall the CCA model consisting of nine environmental explanatory variables was simplified to three variables following forward selection. The final model involved altitude, conductivity and human influence score of the River Habitat Survey (pseudo-F = 2.35; $p < 0.001$). Plotted ordination axes (Figure 3) explained 22.7% ($\lambda_1 = 0.814$) and 12.6% ($\lambda_2 = 0.453$) of the total inertia. The altitude, conductivity and human influence score accounted for 41.3% of the total variation in the dataset. Altitude alone explained 14.3% (pseudo-F = 2.43; $p < 0.01$) and conductivity 10.8% (pseudo-F = 1.85; $p < 0.05$) of the variation in caddisfly data (Figure 4). The effect of both factors was relatively independent (only 2.2% of shared influence). The effect of habitat degradation (represented by human influence score) is shared to a large extent with the mentioned variables. Pure effect of habitat degradation accounted for 7.2% of the total inertia (pseudo-F = 1.22; $p = 0.245$). Low negative values of shared explained variability are the result of the subtraction of the larger fractions (Legendre and Legendre, 1998).

DISCUSSION

At least 226 species of Trichoptera are known from Slovakia (Lukáš and Chvojka, 2011), and approximately half of these show preferences for lotic habitats. Thus, the recorded taxa represent about 40% of the species pool, which would be expected in running waters of Slovakia. Some species recorded recently in the lower part of the Hron River (*e.g. Ceraclea dissimilis* (Stephens, 1836), *Mystacides azurea* (Linnaeus, 1761), *Oecetis furva* (Rambur, 1842)) (Krno, 2006) were absent in our dataset as well as some rare species reported in the past (*e.g. Ithytrichia lamellaris* Eaton, 1873, *Triaenodes bicolor* (Curtis, 1834)) (Dudich, 1958). However, most of those missing species are inhabitants of the slow flowing near-bank zone of rivers and could have been omitted from our standardized kick-net samples.

Table III
List of indicator taxa for each group of sites derived by cluster analysis (Figure 2). Indicator values (IndVal) and abundance/number of sites within the group are given for each species. Groups for which the species is an indicator are in bold. Asterisks represent statistically significant results of permutation tests (9999 permutations) at $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***).

Taxa	IndVal (%)	Group					
		A	B	C	D	E	F
all habitats							
Hydropsyche cf. *incognita*	71			**101/3**	**171/3**	**8/2**	**6/2**
Brachycentrus subnubilus	36			**7/1**	**3/2**	**2/1**	**1/1**
rhithral (A + B + C)							
Rhyacophila s. str.	97***	**34/2**	**113/2**	**246/3**	14/3		
Glossosoma sp.	71*	**2/2**	**1/1**	**3/2**			
Potamophylax sp.	43	**3/1**	**3/1**	**2/1**			
Silo pallipes	43	**1/1**	**1/1**	**1/1**			
epirhithral (A)							
Ecclisopteryx madida	89*	**30/2**	9/2				
Rhyacophila tristis	89*	**166/2**	50/1	1/1			
Rhyacophila philopotamoides	50	**1/1**					
Philopotamus ludificatus	50	**5/1**					
Drusus discolor	50	**5/1**					
Allogamus uncatus	50	**4/1**					
Halesus rubricollis	50	**3/1**					
Rhyacophila pubescens	42	**2/1**	1/1				
Annitella obscurata	36	**1/1**		1/1			
metarhithral + hyporhithral (B + C)							
Ecclisopteryx dalecarlica	100***		**9/2**	**30/3**			
metarhithral (B)							
Micrasema minimum	50		**70/1**				
Odontocerum albicorne	43		**4/1**	1/1			
hyporhithral (C)							
Sericostoma sp.	85	3/2	12/1	**143/3**	2/1		
Chaetopteryx sp.	76*		1/1	**8/3**	1/1		
Polycentropus flavomaculatus	55			**12/2**	1/1		1/1
Philopotamus montanus	33			**2/1**			
Allogamus auricollis	33			**3/1**			
epipotamal (D + E + F)							
Hydropsyche conturbernalis	100***				**42/3**	**21/2**	**168/2**
Psychomyia pusilla	93**			4/2	**9/3**	**3/2**	**41/2**
Hydropsyche bulbifera	29				**3/1**	**1/1**	
epipotamal (D)							
no indicator species							
epipotamal (E + F)							
Hydropsyche exocellata	100**					**41/2**	**16/2**
Hydropsyche modesta	61			5/1	1/1	**16/1**	**7/2**
epipotamal (E)							
no indicator species							
epipotamal (F)							
Tinodes sp.	50						**6/1**
Athripsodes cinereus	50						**1/1**

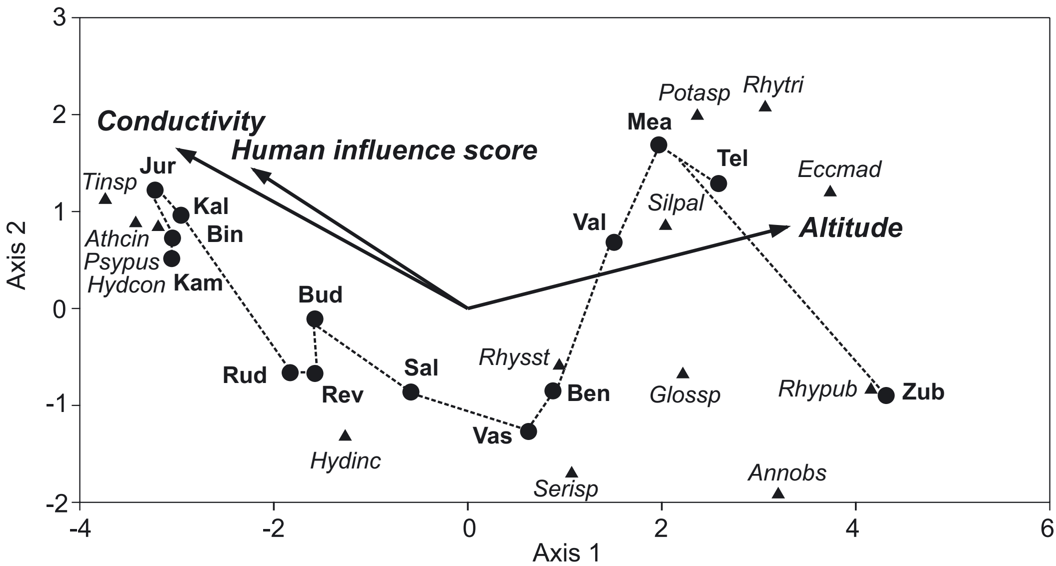

Figure 3
Canonical correspondence analysis (CCA) triplot using Hill's scaling. Triangles indicate centroids of species abundances and circles centroids of sites. A dashed line represents river course. Only species with best fit to the model are displayed (>25% fit). For abbreviations of site names see Figure 1. Abbreviations of species names: Rhypub – Rhyacophila pubescens, Rhytri – Rhyacophila tristis, Rhysst – Rhyacophila s. str., Glossp – Glossosoma sp., Hydcon – Hydropsyche contubernalis, Hydinc – Hydropsyche cf. incognita, Psypus – Psychomyia pusilla, Tinsp – Tinodes sp., Eccmad – Ecclisopteryx madida, Annobs – Annitella obscurata, Potasp – Potamophylax sp., Silpal – Silo pallipes, Athcin – Athripsodes cinereus, Serisp – Sericostoma sp.

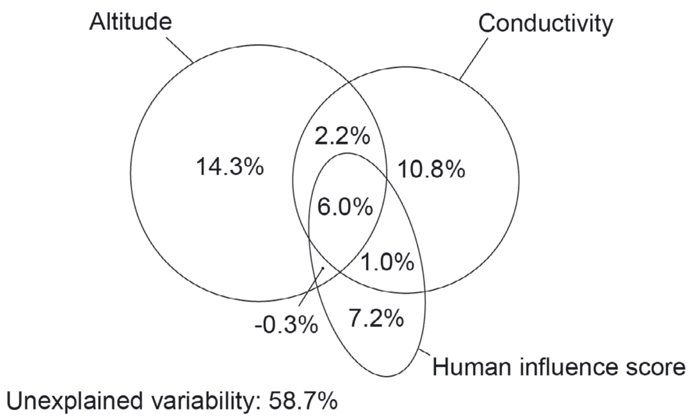

Figure 4
Venn diagram for partitioning the variability in caddisfly species data explained by altitude, conductivity and human influence score.

> RIVER ZONATION

The widely cited general model of RCC (Vannote *et al.*, 1980) predicts continual increase of diversity from source up to the middle (hypothetically 5th order) sections of streams, where diversity reaches the highest values, and afterwards continually decreases downstream. However, it seems that various groups of macroinvertebrates may show different diversity patterns along the same river due to different response to natural longitudinal changes and/or increasing intensity of human impact. In the Hron River, for example, alpha diversity of stoneflies decreased downstream (Krno, 2007).

Several studies demonstrated strong influence of stream size on macroinvertebrate diversity – low species richness in spring areas and its increase in the downstream direction (*e.g.* Wiberg-Larsen *et al*., 2000; Heino *et al*., 2005). The same diversity pattern was observed in mayfly assemblages of upstream tributaries of the Hron River (Svitok, 2006) but not in caddisfly assemblages of the same sites (Novikmec, 2005). A positive relationship between "size-related" factors (*e.g.* stream width, discharge, stream order) and benthic macroinvertebrate species richness seems to be a general pattern in European streams of the first to fifth order (*cf.* Wiberg-Larsen *et al*., 2000). In our study, diversity of caddisflies was higher in the upper part of the Hron River than in the lower stretches. Caddisfly richness increased downstream from the 2nd to 6th order section with the highest value recorded at the Ben site. This might support the hypothesis that larger altitudinal variation increases the heterogeneity of freshwater habitats, which has positive effects on diversity (Heino, 2009 ; Astorga *et al*., 2011). This mechanism should apply at the regional scale (Astorga *et al*., 2011) as well as at the catchment level. Indeed, habitat diversity based on RHS score (Bulánková, 2006) was significantly higher in the upper part of the Hron River (Zub-Sal *vs*. Bud-Kam, $F_{1,12} = 5.78$, $p < 0.05$).

To conclude, our findings on diversity patterns are roughly in accordance with RCC, with the most diverse communities being recorded in the 6th order section though it is not the middle stretch, considering the total length of the river.

In accordance with Basaguren and Orive (1990), we observed that differences between upper and lower parts of the river were chiefly based on the downstream replacement of the genus *Rhyacophila* by the genus *Hydropsyche*. Whereas *Rhyacophila* constituted more than 40% of all individuals recorded in the upper part and species of the genus *Hydropsyche* only 23%, in the lower part, representatives of the genus *Hydropsyche* absolutely predominated (92% of all recorded individuals). Especially *H*. *contubernalis* McLachlan, 1865 and *H*. *exocellata* Dufour, 1841 showed to be significant indicators of the lower courses. The latter one is known as a typical downstream species (Higler and Tolkamp, 1983).

Cluster analysis delineated six groups of sites based on caddisfly species assemblages. Following the zonation concept of Illies and Botosaneanu (1963), we were able to define four zones of the investigated river. Species with preferences to crenal and epirhithral (Zat'ovičová and Novikmec, 2003; Waringer and Graf, 2011) prevailed at the Zub sampling site (Figure 5A). This site, together with the Tel site, can be characterised as an epirhithral zone with indicator species *E. madida* (McLachlan, 1867) and *R. tristis* Pictet, 1835 and characteristic taxa including *R. pubescens* Pictet, 1834, *P. ludificatus* McLachlan, 1878, *D. discolor* (Rambur, 1842) and *A. uncatus* (Brauer, 1857). Similar caddisfly communities were reported from second and third order tributaries of the upper Hron River (Novikmec, 2005).

The river section of sampling sites Mea and Val could be classified as metarhithral. In contrast to the uppermost zone, channel slope decreased importantly and stream width increased, accompanied by canopy openness. The metarhithral section of the Hron River was indicated by *M. minimum* McLachlan, 1876, *O. albicorne* (Scopoli, 1763), and widely distributed inhabitant of fast flowing submountain streams, *E. dalecarlica* Kolenati, 1848 (Krno *et al*., 1996).

The proportion of rhithro-potamophilous species continuously increased downstream of the Ben site. On the other hand, a gradual reduction of rhithral species was observed in this river section. Thus, we have classified the rest of the rhithral zone (Ben, Vas and Sal sites) as hyporhithral. Trichoptera communities of this zone were typical for presence of *Sericostoma* sp., *Chaetopteryx* sp., *P. flavomaculatus* (Pictet, 1834), *P. montanus* (Donovan, 1813), *A. auricollis* (Pictet, 1834) and persisting occurrence of *E*. *dalecarlica*. All of these taxa frequently inhabit rhithral zones of West Carpathian rivers (*cf.* Krno, 1983; Krno *et al*., 1996).

Schmitz (1955) suggested and Stoneburner (1977) confirmed that the greatest shifts in assemblage composition should occur in transition zones where physical parameters change abruptly. Or, as likewise defined by Statzner and Higler (1985), zonation of stream benthos is mainly governed by physical characteristics of flow ('stream hydraulics'). A similar pattern may be observed in our study since apparent changes in hydraulic conditions (*e.g.* four-time increase of discharge) occurred in the middle part of the river, between sampling sites Sal and Bud. These were manifested by a shift towards much more uniform caddisfly assemblage with the absolute predominance of filtering caddisflies *Hydropsyche* (Tables II, III, Figure 5B).

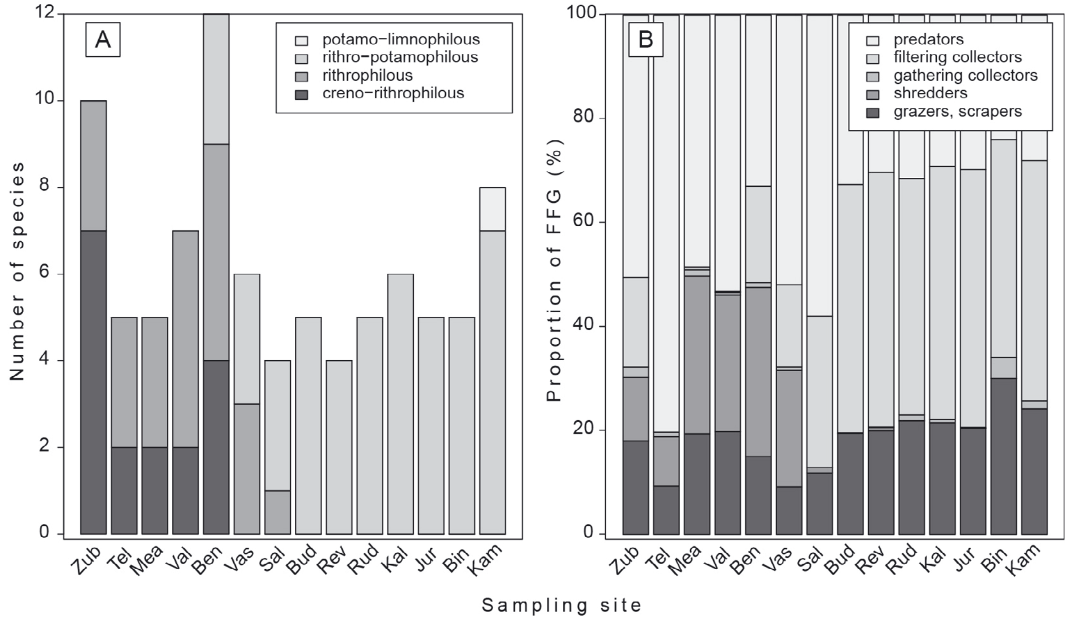

Figure 5
Distribution of creno-rhithrophilous, rhithrophilous, rhithro-potamophilous and potamo-limnophilous species (A) and proportion of functional feeding groups (FFG) (B) of Trichoptera in longitudinal profile of the Hron River. Classification to longitudinal preferences and FFG follows Zat'ovičová and Novikmec (2003). For abbreviations of site names see Figure 1.

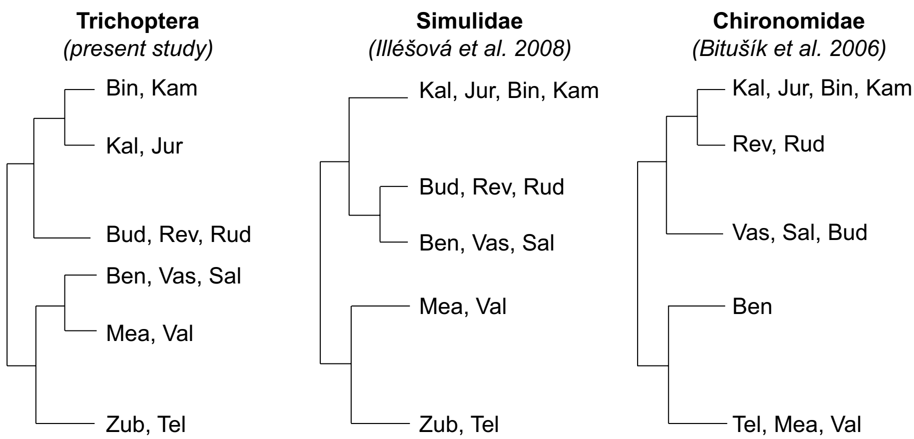

Figure 6
Schematic comparison of the Hron River classifications based on caddisfly, blackfly and chironomid communities. For abbreviations of site names see Figure 1. Note that the Zub sampling site was not included in classification of chironomid assemblages.

Non-hierarchical cluster analysis confirmed our findings by splitting the longitudinal profile into two parts just between the sites Sal and Bud (Figure 2). In the lower part of the river, only rhithro-potamophilous and potamophilous species were recorded. All of the lower section of the river can be classified as epipotamal.

Previous efforts to distinguish discrete zones of the Hron River based on chironomids (Bitušík *et al*., 2006) and blackflies (Illéšová *et al*., 2008) revealed slightly different schemes (Figure 6). The most apparent change in caddisfly communities was observed at the river section where filtering caddisflies become dominant, probably mirroring changes in food supply. In contrast to caddisflies, blackflies and chironomids showed upstream shifts in the position of major division of assemblage types. Blackflies, all being filtering gatherers, had naturally shown different organisation of assemblages along the river than caddisflies. Chironomids are sometimes questioned as a group suitable for recognition of water types (Verdonschot *et al*., 1992). In the use for river classification, they are still limited by vagueness in importance of environmental factors responsible for chironomid species distribution (Bitušík *et al*., 2006). When individual groups of benthic invertebrates with different ecological requirements are used to classify river zones, we may not expect identical results. We do not claim that caddisflies are a better group for determination of river zones than the other groups. However, Trichoptera are generally thought to be reliable environmental indicators and a valuable group to study patterns in longitudinal distribution of species (*cf.* Dohet, 2002; Gombeer *et al*., 2011). Rather we suggest that this inconsistency in classifications of the Hron River underlines the need for detailed knowledge of the whole benthic communities in an effort to provide comprehensive river typology.

> *INFLUENCE OF ENVIRONMENTAL VARIABLES*

The multivariate analysis revealed significant relationships between altitude, conductivity, human influence score and caddisfly community structure. Those variables represent morphological, physicochemical and habitat changes of the river. Altitude is a complex environmental gradient controlling lotic communities (Krno, 1987). It influences many aspects of macroinvertebrates' life history due to its covariance with climatic variables such as temperature (*e.g.* Sweeny, 1984) and also other abiotic factors changing with altitude (Ward, 1980).

Indeed, altitude appeared to be the major driving force behind the longitudinal patterns of caddisfly communities but its effect changes along the river. Altitude-induced changes are more obvious in the upper section of the river (sampling sites Zub-Sal with elevation range 632 m) than in the lower course with elevation range 160 m. In Slovakia, Krno (1992) documented that discharge and stream size influence patterns in distribution of Trichoptera and Plecoptera communities, and found clear less dependence on hypsometric position of sites in watershed of narrow altitudinal range. Relatively high explanatory power of conductivity (10.8% of variance in community composition) indirectly suggests the influence of pollution on caddisfly communities. Conductivity increased along the river, which can be related to increasing intensity of pollution either from urban agglomerations (*cf.* Krno, 2007) or character of landscape cover. In the lower section, the Hron River flows through open agricultural landscape with low forest coverage. Such attributes of a river basin are often accompanied by pollution (*cf.* Gombeer *et al*., 2011; Ruiz-García *et al*., 2012).

Based on River Habitat Survey, Buláneková (2006) showed that human impact was moderately high with the highest scores reached in lowland part of the Hron River. The caddisfly assemblages composition usually changes in response to human impact on physical habitats (*e.g.* Basaguren and Orive, 1990; Ruiz-García *et al*., 2012). Savić *et al*. (2013) indicated that the positions of the sites along the course of the river as well as anthropogenic impact are the main factors that affect the differentiation of the caddisfly assemblages. Similar patterns were found in chironomid and stonefly communities (Bitušík *et al*., 2006; Krno 2007).

> *RIVER ZONATION AS A REFERENCE SCHEME*

A sound understanding of the past (near-natural) longitudinal patterns in benthic communities is an essential tool for effective assessment of expected impacts on river ecosystem related to planned and ongoing human activities at the Hron River. Biological classifications, if meaningfully used, provide valuable information on longitudinal structural changes of aquatic communities. Even individual (but certainly serial) damming of the river fundamentally transforms whole river ecosystems by fragmenting channels and altering river flows (Andersson *et al*., 2000; Renöfält *et al*., 2010). A serious problem in attempts to assess or to mitigate negative impacts caused by river regulation is the lack of pre-damming data (Malmquist and Rundle, 2002). For these reasons, we tried to delineate distinct biotic zones of the Hron River and used caddisfly species as indicators of those zones. Along with the results provided elsewhere (Bitušík *et al*., 2006; Krno, 2007; Illéšová *et al*., 2008) we obtained important information on predisturbance longitudinal patterns in benthic assemblages of the Hron River.

Dams affect the sediment dynamics and distribution, dispersal, and abundance of benthic macroinvertebrates and other aquatic organisms (Stanford *et al*., 1996; Kiraly *et al*., 2014). Multiple damming of a river may result in longitudinal modifications towards upstream or (more likely) downstream abiotic and biotic conditions (Ward and Stanford, 1983b) and subsequently in alternation of spatial organisation of the whole river ecosystem. In an upper part of the Hron River (rhithral zone), damming would probably cause a shift towards more uniform benthic communities with lower proportion of rhithrophilous species. As a consequence of serial damming of the lower course of the Hron River (where the majority of SHPS are planned and some already constructed), most of the river's length in this section will probably be made up of impoundments with slow flow and artificial organisation of riverine communities.

We are convinced that pre-damming zonation patterns are of very high value for both the decision makers responsible for management of the Hron River and any subjects involved in monitoring the consequences of planned or already realised human activities. River zonation provided here could serve as a reference scheme for the other big rivers in the West Carpathian region that were dammed a long time ago (*e.g.* the Váh River).

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