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Structure, zonation, and species diversity of the mayfly communities of the Belá River basin, Slovakia

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Abstract

Four mayfly taxocoena which correspond to zones in the river continuum concept of Vannote *et al.* (1980) and to the zonation concept of Illies & Botoşaneanu (1963), were distinguished by cluster analysis in the Belá River basin, Slovakia.

By principal components analysis, taxocoena were shown to be separated along a complex gradient dominated by altitude and slope.

An increase of species diversity was observed downstreams. The species-diversity data can be fitted to a geometric series, and interpreted by the niche preemption hypothesis. Equitability and the ratio of Baetidae to Heptagenidae are supposed to indicate ecological conditions.

Introduction

The mayflies of the Western Carpathians include several endemic species (Sowa, 1975), form a considerable part of the macrozoobenthos of the area, and are important for a successful determination of river zonation (Illies & Botoşaneanu, 1963; Vannote *et al.,* 1980). Several papers deal with macrozoobenthic zonation in the Western Carpathian streams, in particular the Polish part of the Tatry Mts (Kownacka, 1970; Kownacki, 1971; Kawecka *et al.,* 1971; Sowa, 1975). Krno (1978, 1982) studied mayfly taxocoena in the Nízke Tatry Mts.

The aim of the present paper is to describe the mayfly taxocoena in the river basin of the Belá River, Západné Tatry Mts, Slovakia, and to define their relation with known zonation concepts and species-diversity patterns.

The nomenclature of mayfly species follows Putz (1981).

Field work and material

The field work was done in the basin of the Belá River, situated on the contact of the Západné Tatry and Vysoké Tatry Mts, northern Slovakia. Most of the study area is characterized by glacial relief. A small part is of submountain character, rich in smooth shapes composed of Upper Liptov flysch and other sedimentary rocks. The Západné Tatry Mts are granitic; only a small part (the Červené Vrchy Mts) are dolomitic. Altitude ranges between 600 to 2200 m above sea level.

The river basin is largely deforested, which cause large water level fluctuations in certain stretches of the river. Remnants of spruce woods are found at lower altitude, and spruce bogs occur in some sites as well. The krummholz formation and subalpine and alpine grasslands dominate the area above the timberline. There are some willow (*Salix* spp.) and *Myricaria germanica* L. along the river and its tributaries.

The Belá River is formed where the Tichý Potok and Kôprový Potok Brooks join at an altitude of 975 m (Fig. 1). It flows across Holocene gravels until it joins the Váh River at 630 m above sea level. Right-hand tributaries join the river only in its upper reaches. The flow regime is unbalanced, and ac-

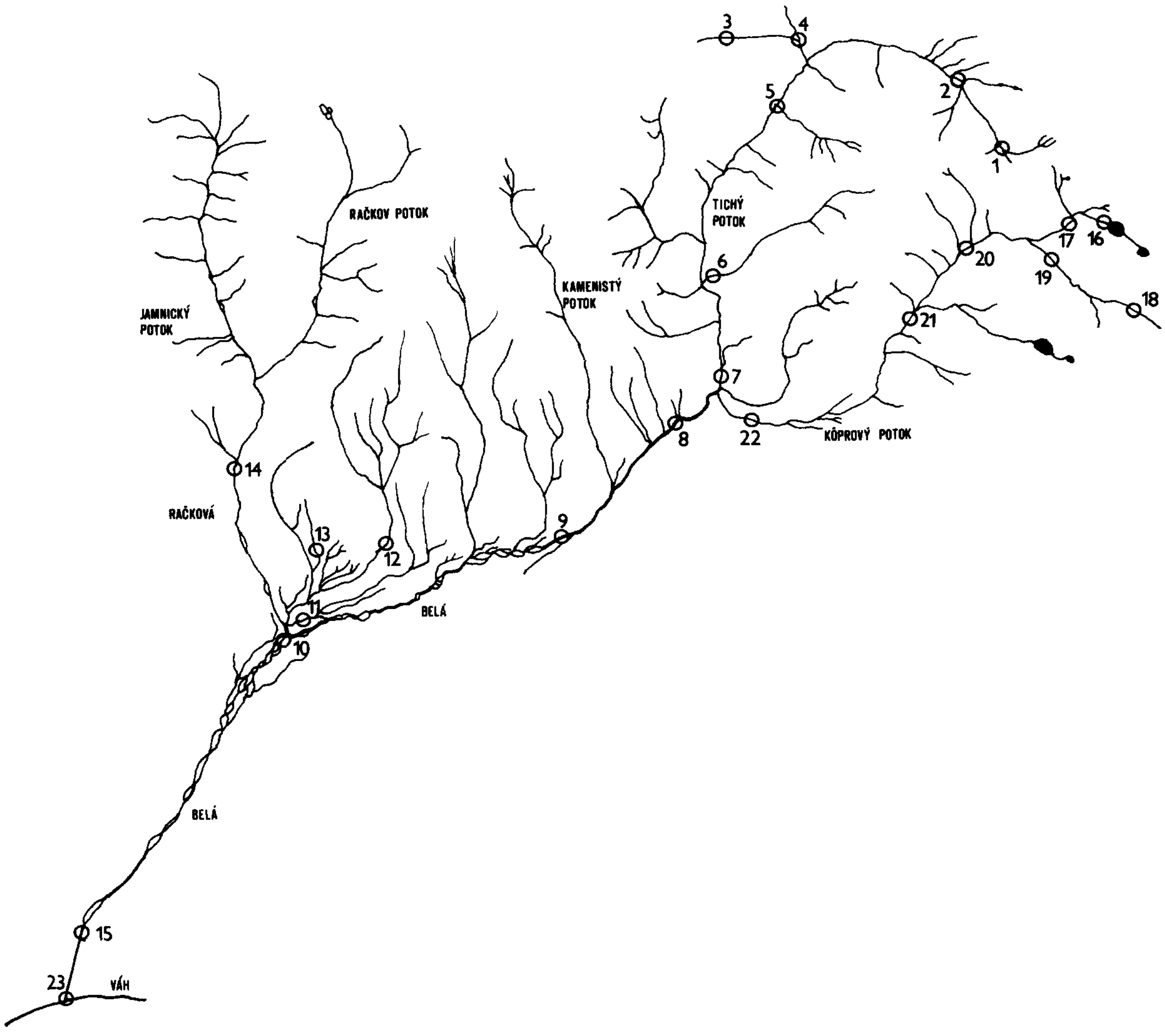

Fig. 1. Map of the river basin of Belá. The sampling stations are numbered from higher towards lower altitudes.

companied by frequent overflows. Discharge is lowest from November to May, but increases considerably after snow melt.

Important tributaries are the Račková, Kamenistý Potok Brook, Hlinná and Javorový Žl'ab Brooks (the only one draining the dolomitic area).

Samples were taken in July and October 1977, and in May, August and September 1978 by Landa's (1964) method. A circular sieve (28 cm ∅) was dragged across the river so close to the river bottom that benthos attached to gravel, stones and underwater plants was stirred up and drawn into the sieve by the current. Stations were located every 100 m of altitude. Additional samples taken with Hraběs sampler (Peňáz, 1966) from 4 localities were also used (collected during May, July and September 1974 to 1976).

At every site, current velocity (according to Kamler, 1967), depth, and temperature were recorded. Average slope for a locality was computed from a curve (Fig. 2) constructed on the basis of topographical maps. The values of the slope were averaged for a range reaching 50 m above and 50 m below the considered locality.

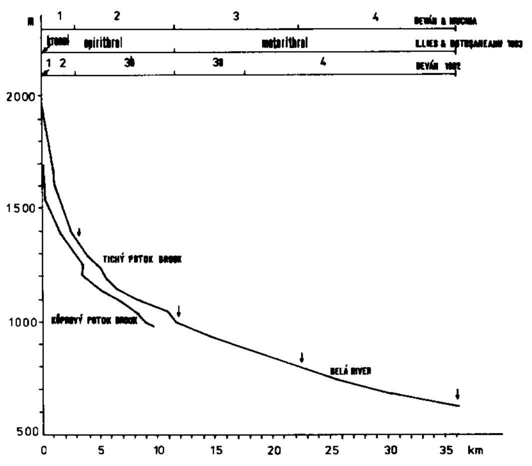

Fig. 2. Profile of the Belá River and the Kôprový Potok Brook, its most important tributary. The arrows indicate the positions of limits of the established taxocoena.

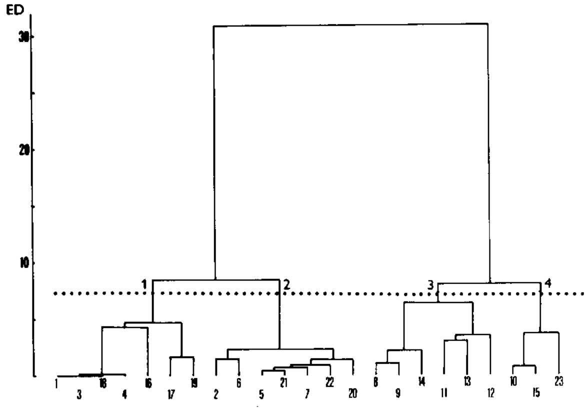

Fig. 3. Sum of squares clustering of sampling stations (the numbering corresponds to that in Table 1).

Data analysis

Mayflies were identified according to Landa (1969), Müller-Liebenau (1969), Sowa (1970, 1971, 1973a, b, 1974) and Illies (1967, 1978). The data on species composition were summed over the year for each locality. Abundance values were transformed according to Kownacki (1971), so as to arrive at species dominance scales. The following transformation scale was used: 100 to 10% (dominant: 5), 9.9 to 1% (subdominant: 4), 0.9 to 0.1% (adominant A: 3), 0.09 to 0.01% (adominant B: 2), less than 0.01% (accidental: 1). Species diversity H′ and equitability J were computed according to Shannon-Wiener (see Whittaker, 1975: 95) and Pielou (1966). The index B:H expresses the ratio between the Baetidae and Heptageniidae. This ratio allows evaluation of the character of a water course (Deván, 1980). Baetidae indicate fast-flowing streams, while Heptageniidae are primarily found in flooded gravel banks and shallow riffles.

Sum of squares clustering (Orlóci, 1967, 1978) was used in numerical classification of the sample stations and species as well. This method minimizes variance (heterogeneity) within and maximizes variance between clusters. Distance between two clusters is defined as the increase of heterogeneity after the two clusters merge. Clusters fuse in order of (minimal) increase of heterogeneity defined by sum of squares of deviations from group means.

The programme package of CLUSTAN 1C (Wishart, 1978) was used in numerical classification. Both sampling stations and species were classified to produce clusters interpreted as taxocoena (Fig. 3) and clusters of species, i.e. groups supposed to characterize the taxocoena (Fig. 4). Taxocoena were established on the basis of the combination of the species groups present or absent within the clusters of samples.

Principal components analysis (PCA) was used as an ordination technique, and used for representing a data continuum (termed coenocline) in ordination of community samples. The relevant coenocline is usually interpreted in terms of ecological gradients supposed to be responsible for the coenocline pattern. For further particulars on the interpretation see Nichols (1977), Noy-Meir & Whittaker (1977), Van der Maarel (1980) and Dargie (1983). The programme PCFLOR of Goldstein & Grigal (1972) was used for ordination. The product-moment correlation matrix derived from the dominance data (see above) was adopted.

Results

The following mayfly taxocoena of the river basin of Belá River have been determined by numerical classification (Table 1):

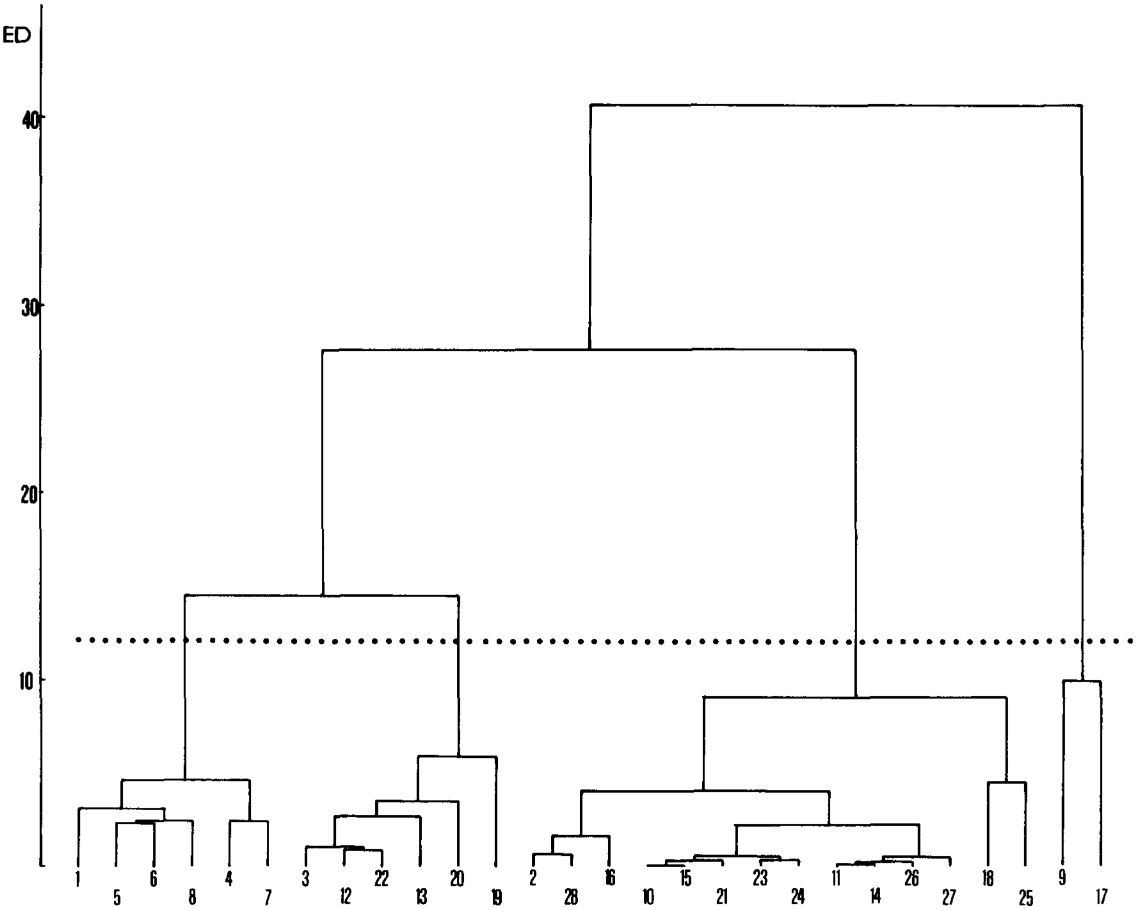

Fig. 4. Sum of squares clustering of species (the numbering corresponds to that in Table 1).

1. Beatis alpinus-Rhitrogena loyolaea

This unit is characterized by the dominance of the aponymous species. *Baetis melanonyx* and *Rhitrogena hercynia* occur accidentally. This taxocoenon occurs above 1 400 m above sea level in locations with a high slope (Fig. 2) and a substrate formed by coarse gravel and boulders. Within the taxocoenon, sampling stations 17 and 19 are separable into a subunit characteristic of the sites with abruptly lowered slope due to glacial relief. At such sites fine-grained material and detritus accumulates and some low-altitude species are found here, including *Baetis muticus, B. rhodani, Rhitrogena iridina* and *Ecdyonurus forcipula,* along with the submountainous *Habroleptoides modesta* (sampling station 17). Station 16 is situated at the outlet of a glacial lake at a site with hardly any slope. Ninety % of its bottom is covered with mosses, and only one mayfly species, *Ameletus inopinatus,* was found in the site.

2. Baetis melanonyx-Ameletus inopinatus

This taxocoenon is special because of the occurrence of many species of Heptageniidae. *Baetis melanonyx* occurs here during summer period and fills a gap between imagos and new nymphs of the high-mountain species *Baetis alpinus.* The occurrence of other *Baetis* species is sporadic. *Ameletus inopinatus* is abundant in this taxocoenon due to the presence of marginal pools with low current, but still of alpine character. The taxocoenon is limited to altitudes of 1 000 to 1 400 m. The sub-

Table 1. The mayfly taxocoena of the Belá River Basin.

	locality	1	3	18	4	16	17	19	2	6	5	21	7	22	20	8	9	14	11	13	12	10	15	23
	taxocoenon	1							2							3						4		
4	Rhitrogena hercynia Landa, 1970	.	.	.	1	.	.	.	2	.	3	2	1	3	.	3	4	3	.	.	.	5	5	4
7	Rhytrogena semicolorata (Curtis,1834)	.	.	.	.	.	.	.	.	.	2	.	2	2	.	3	3	4	.	.	3	3	3	.
1	Ecdyonurus forcipula (Pictet,1843-1845)	.	.	.	.	.	4	.	.	.	2	2	3	.	3	3	4	4	4	.	4	4	4	4
5	Rhitrogena hybrida Eaton, 1885 [x]	.	.	.	.	.	.	.	.	4	4	4	3	4	3	4	4	3	3	.	.	3	3	4
6	Rhitrogena ferruginea Navás, 1905	.	.	.	.	.	2	.	.	2	3	2	2	3	.	.	4	3	4	3	4	4	4	3
8	Rhitrogena irridina (Kolenati, 1860)	.	.	.	.	.	.	4	2	4	4	3	4	5	2	4	4	3	3	3	2	3	3	.
3	Epeorus sylvicola (Pictet,1843-1845)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	4	.	3	3	3	3
12	Ephemerella ignita (Poda, 1761)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	3	3	2	3	3	5
22	Baetis scambus Eaton, 1885	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	1	.	4	.	3	3	3	4
20	Baetis rhodani (Pictet,1843-1845)	.	.	.	.	.	3	.	3	.	.	.	.	.	.	1	2	4	5	5	5	4	4	5
13	Ephemerella mucronata (Bengtsson, 1909)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	4	4	4	1	.	.
19	Baetis muticus (Linnaeus, 1758)	.	.	.	.	.	4	5	.	'.	.	.	.	.	.	2	.	4	.	5	4	4	3	.
2	Caenis beskidensis Sowa, 1973	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	4
28	Habrophlebia lauta Eaton, 1884	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	4
16	Baetis sinaicus (Bogoescu, 1931)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	4	4	5
10	Ephemera vulgata Linnaeus, 1758	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.
15	Ephemerella notata (Eaton, 1887)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.
21	Baetis niger (Linnaeus, 1761)	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	2	1	.
23	Baetis vernus Curtis, 1834	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	2	2	.
24	Baetis lutheri Müller-Liebenau, 1967	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.
11	Ephemera danica Müller, 1764	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	1	.
14	Ephemerella major (Klapálek, 1905)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1	2	.
26	Paraleptophlebia submarginata (Stephens, 1835)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.
27	Habroleptoides modesta (Hagen, 1864)	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	3	2	1	.
18	Baetis melanonyx (Pictet, 1843)	.	.	.	1	.	.	.	2	.	4	4	4	3	4	4	2	.	.	.	.	.	.	.
25	Ameletus inopinatus Eaton, 1887	.	.	.	.	5	3	.	3	3	3	2	2	.	.	.	.	.	.	.	.	.	2	.
9	Rhitrogena loyolaea Navás, 1922	5	5	5	5	.	5	4	5	4	3	5	4	3	5	.	.	.	.	.	.	.	.	.
17	Baetis alpinus (Pictet, 1843-1845)	5	5	5	5	.	5	5	5	5	5	5	5	5	5	5	5	5	5	4	5	5	5	5

x As imagos were not available, we cannot discard a possibility of the occurrence of R. henschi Klapálek, 1905.

strate is composed of rounded cobbles with admixed boulders and some pebbles. The boulders are covered by diatoms. Detritus is abundant, and thus various *Rhitrogena* species occur. Species diversity is only slightly higher than in taxocoenon 1, because of high water velocity.

3. *Baetis alpinus-Epeorus silvicola*

This taxocoenon is characterized by the occurrence of montane and submontane elements, such as *Epeorus silvicola, Ephemerella ignita, E. mucronata, Baetis fuscatus, B. rhodani* and *B. mu-*

ticus, lack of high-mountain species (*Rhitrogena loyolaea*), but presence of some other *Rhitrogena* species. The taxocoenon is limited to altitudes between 800 to 1000 m. It is heterogeneous, as it comprises localities of the Belá River and of the Račkový Potok Brook found after they leave the narrow valleys (subtaxocoenon 3a, Table 1), but also alluvial localities. The latter are placed within the subtaxocoenon 3b (Table 1). Both subunits have a few submontane species in common, but they are separated by the absence of *Baetis melanonyx* and the dominance of *B. rhodani* and *B. muticus* in the meadow-brook localities. The taxocoenon is limited to habitats of moderate slope (Fig. 2) with cobbles and pebbles accumulated into riffles.

4. Baetis alpinus-Baetis sinaicus

This taxocoenon is characterized by the highest species-diversity values. Most of the species of the above-mentioned unit also occur here. Exceptions are *Rhitrogena loyolaea, Ameletus inopinatus,* and *Baetis melanonyx.* The latter species is replaced by *Baetis sinaicus.* The generally rare *Baetis niger, Caenis beskidensis, Ephemerella major* and *E. notata* are common in this unit. Many species attain their uppermost distribution limit (800 m above sea level) here (e.g. *Baetis lutheri, B. vernus* and *Habrophlebis lauta*). The lower distribution limit of the taxocoenon is situated at 630 m. Current velocity is low, there are no tributaries present. The bottom of the streams is composed mainly of cobbles with admixed boulders; gravel banks are also present.

The sequence of the different taxocoena in relation to altitude represents a zonation influenced by altitude, slope, flow and microrelief. These factors secondarily control the rate of detritus sedimentation, and determine the habitat diversity and species richness (de March, 1976). Boundaries of the taxocoena correspond to abrupt physical changes. The transition between the taxocoena 1 and 2, for example, correspond to an abrupt change of slope; the transition between the taxocoena 2 and 3 is found where the river leaves narrow valleys.

This zonation corresponds to that of Illies & Botoşaneanu (1963): taxocoena 1 and 2 are similar to epirithral, and those 3 and 4 to metarhithral zones.

As indicated by ordination (Fig. 5) the sampling

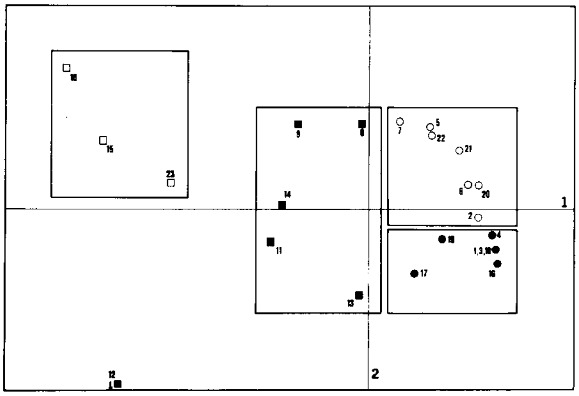

Fig. 5. Ordination of sampling stations. Full circles: taxocoenon 1, empty circles: tax. 2, full squares: tax. 3, empty squares: tax. 4.

stations, associated with taxocoena 1 and 3, are continually distributed along the coenocline detected, in correspondence with the river continuum concept of Vannote *et al.*, 1980 (see also Osborne *et al.,* 1980; Culp & Davies, 1982). The coenocline extends along ordination axis 1 (Fig. 5), which can be interpreted as a complex gradient of elevation and slope (Fig. 6).

Species diversity increases with decreasing altitude and slope. Taxocoena 2 and 3 form a distinct group with respect to the species diversity. Some anomalies in the species-diversity trend are observed in sampling stations 6 and 7, affected by temporal drainage, while stations 17 and 19, belonging to taxocoenon 1 (Table 1), better fit to taxocoena 2 and 3 according to their species-diversity values.

Despite an increase of species diversity downstream, the dominance-diversity curves (Whittaker, 1965) for particular samples (Fig. 8) can be fitted by a geometric series (see for instance McNaughton & Wolf, 1973; Pielou, 1977) which is functionally interpreted by the niche preemption hypothesis of Whittaker (1965).

The highest values of equitability are found in taxocoenon 1 (stations 3 and 18), in which the presence of both co-dominating species is balanced. The lowest values are found in localities under strong periodical stress, namely those affected by flush-floods. Rather low values also occur in taxocoena 3 and 4, except in sampling station 23.

Unlike diversity, the B:H ratio pattern does not

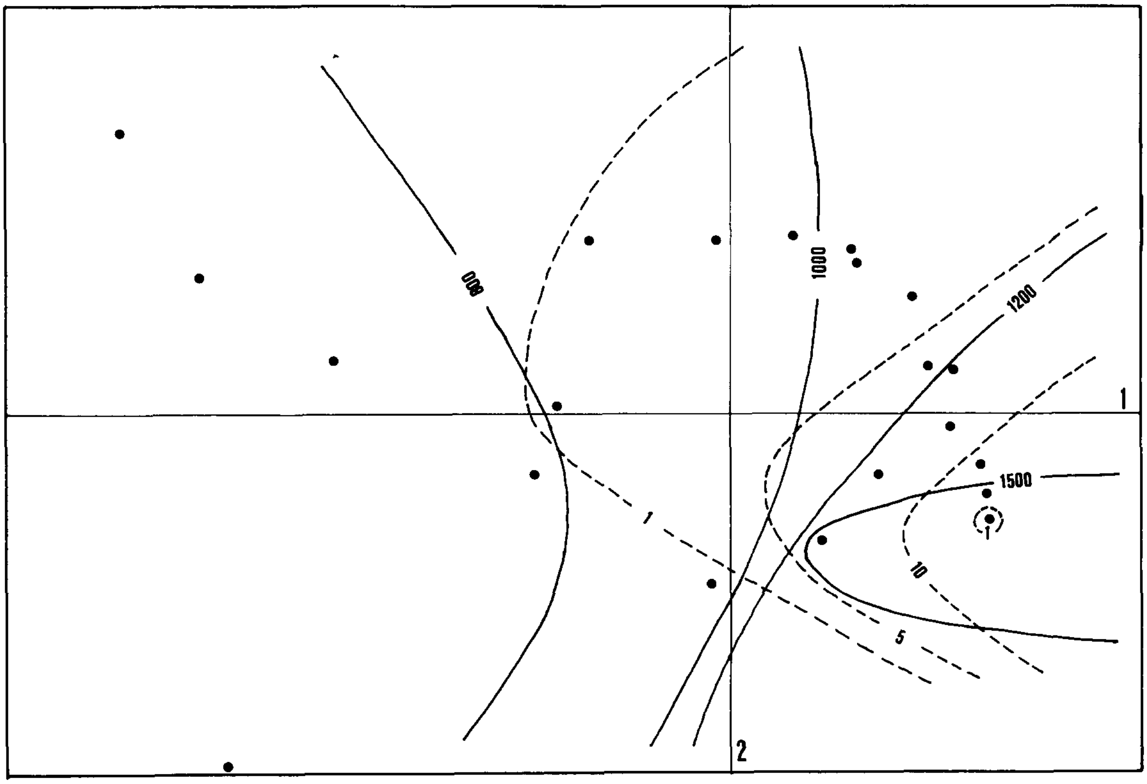

Fig. 6. Elevation and slope in % superimposed onto the ordination plane (see Fig. 5). Full isolines hold for elevation pattern; dashed isolines apply to slope. Fitted by hand.

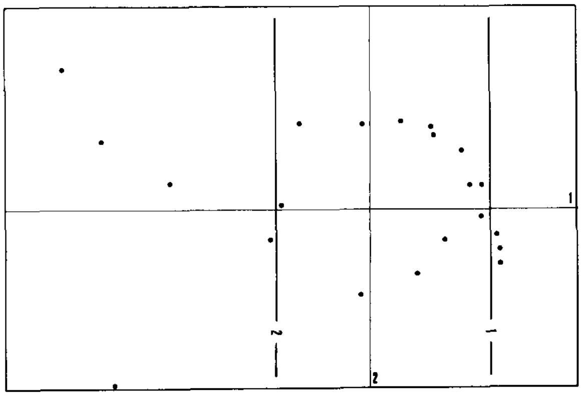

Fig. 7. Species diversity superimposed onto the ordination plane of Fig. 5.

reflect altitude. A high abundance of Baetidae is encountered in most localities with boulders. These offer less shelters for Heptageniidae. These localities have been distinguished as subtaxocoena of the ripal type (Deván, 1980). Taxocoena rich in Baetidae belong to medial type.

Discussion

The sampling methods used yield a representative sample of the mayfly community in a locality. It might seem that a greater chance of being captured is allotted to species living on rather than in the substratum. However, the water current is strong enough to draw all mayflies into drift nets attached to the substratum.

Average water velocity values play only a limited role, since benthic animals are mostly affected by the velocity near the river bottom, which can considerably differ from surface velocity (Kuusela, 1979). The mayfly data from the Belá River basin were subjected to a classification based on species dominance, and diversity and evenness values

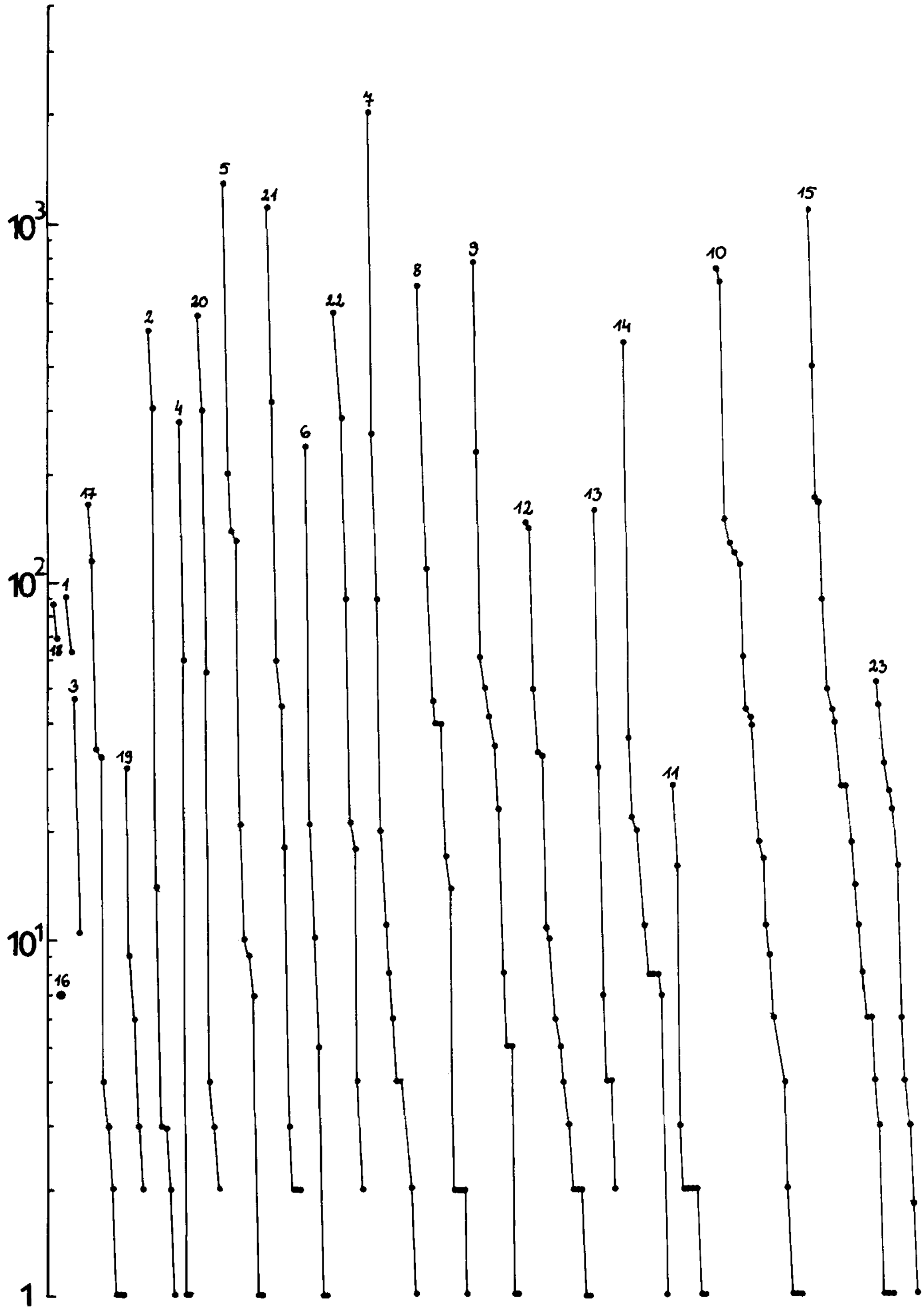

Fig. 8. Diversity-dominance curves of the samples which are sequenced from higher towards lower elevations.

(Deván, 1982, 1984). This classification yielded 4 taxocoena, one of which had 2 subtaxocoena. The krenal, i.e. the region of water springs, contains mayflies only sporadically and was not included in our analysis. The taxocoenon 2 and subtaxocoenon 3b of Deván (*op. cit.*) match our taxocoena 1 and 2, respectively (Fig. 2). The subtaxocoenon 3a of the non-numerical classification corresponds only in part to our taxocoenon 3. The taxocoenon 4 of Deván (*op. cit.*) has a broader distribution, comprising the remainder of our taxocoenon 3 and the entire taxocoenon 4. The discrepancies between non-numerical and numerical classifications are caused by the overweighting of the role of total species composition at the expense of the importance of particular species. The transformation of data according to Kownacki (1971) might affect the classification pattern as well.

There are no sites with an abrupt increase in species richness in the streams studied by Sowa (1975), and the boundaries of the taxocoena he established are not so clear-cut as in our study. This might be due to the characteristics of Sowa's river basin, which was evenly afforested and without traces of glacial activity.

Kuusela (1979) stresses the importance of vegetation, particularly moss-beds, upon the formation of microhabitats. Due to the unbalanced flow pattern of the Belá River, moss cover is limited. In station 16, only *Ameletus inopinatus* survived because of a dense moss cover. Stations 11 and 12 are typical pasture brooks where luxuriant moss mats operate as detritus traps (Kuusela, 1979). This promotes the occurrence of detritus-eating species, such as *Baetis rhodani, B. muticus* and some Heptageniids. Moss mats are found also in the localities of samples 3 and 4, but flow and steep slope cause the moss mats to be drawn away by the current.

Gore (1978) believes that greater species richness occurs on cobble-type substrata. This applies, in the case of the Belá River, to the lower reaches. Mayflies seem to behave in accordance with the zoobenthos as a whole. The differences indicated in the taxocoenon 4 are in accordance with reduced current velocities. Moreover, there are no tributaries joining the river in this reach. Permanent changes in the character of the river bed cause the formation of a variety of microhabitats (Deván, 1980), and hamper penetration of species from lower localities (Sowa, 1975). The conditions, however, are favourable for *Baetis alpinus* which dominates all over the river. Allan (1975) pointed out that the species diversity of benthos increases with the diversity of substrata. This probably also contributes to the special position of taxocoenon 4.

The complex of factors controlling the distribution of the mayfly taxocoena are altitude, temperature, and slope. The character of the river bed is a function of these factors and of geological features. Where the environment is controlled by other factors, such as glacial relief, azonal taxocoena emerge.

Increase of mayfly diversity towards lower altitutes seems to be the rule. Our diversity pattern corresponds with observations of Ward & Berner (1980) who found a selective elimination of mayfly species with altitude in a Rocky Mountain stream. This was also observed by Krno (1978, 1982) in two Slovakian streams, but needs not hold for other macrozoobenthos groups, as shown by Ward (1981) for Trichoptera and by Ward (1982) for Plecoptera. According to Ward & Berner (1980), Heptageniidae are abundant in upstream localities, but Baetidae in lower reaches. This is not our case, where representatives of both families may dominate in any stretch of the river.

A different observation on species diversity was made by King (1981, 1983), who reported a downstream decline in diversity of mayflies in a South African river. This decline was correlated with increasing levels of organic pollution.

Besides temperature, which is a function of altitude, and plays a major role in mayfly distribution (Dodds & Hisaw, 1925; Ide, 1935; Kamler, 1965; Hynes, 1970; Deván, 1980), stream size and associated physical factors are of importance, while Ward & Berner (1980) also cite predation and competition as possible factors responsible for zonation of mayfly taxocoena (see also McAucliffe, 1983; Hart, 1983 and the literature cited therein).

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