

Temporal and spatial macroinvertebrate variance compared: crucial role of CPOM in a headwater stream

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Abstract The aim of the present study was to estimate the extent to which macroinvertebrate assemblages in a headwater stream are determined by environmental conditions and temporal dynamics. Six mesohabitats defined by substratum were sampled monthly throughout one year, environmental conditions at each sampling point being precisely described. Environmental variables could be truncated into two main gradients related to (a) the availability of food and space resources (CPOM) and (b) hydraulic conditions. The response of the macroinvertebrate assemblage to the environmental gradients and temporal dynamics were analyzed using GAM and (p)RDA. Twice as high portion of variance in the faunal data was attributed to environmental gradients compared to temporal dynamics. Total abundance, as well as the abundance of almost all feeding groups, was dependent on the availability of food and space resources (CPOM), while their proportions were

determined by the quality of food resources driven by hydraulic conditions. Temporal dynamics was of lower importance. Our results suggest the role of CPOM be crucial in woodland headwater streams, as it greatly enhances habitat quality, serving both as a food source to dominant shredders and a space source to most macroinvertebrates.

Keywords Spatial distribution · Temporal changes · Functional feeding groups · Substratum · Mesohabitat · Streams

Introduction

Benthic macroinvertebrate distribution varies greatly in space and time (Ward, 1989). Macroinvertebrate communities mainly respond to environmental conditions, and specific, hierarchically organized distributional patterns can be observed depending on the spatial scale (Frissell et al., 1986).

Mesohabitat, defined as a “visually distinct unit within the stream, recognizable from the bank and with apparent physical uniformity” (Pardo & Armitage, 1997), was found to be extremely useful since it provides a practical basic unit for studying stream ecosystems. The concept of a mesohabitat-scale basic unit was independently introduced by several researchers who named this basic unit differently: “functional habitat” in Harper et al. (1998) and “channel unit” in Rabeni et al. (2002). However, the general idea of the

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basic unit, to provide an effective tool for ecological research and stream management, was shared by all researchers. This approach is based on the assumption that it is more practical to manage and protect channel units rather than individual species (Storey & Lynas, 2007).

Distinct mesohabitats are inhabited by different macroinvertebrate communities and have been used to assess stream (Harper et al., 2000; Tickner et al., 2000) and lake (White & Irvine, 2003) ecological quality, to evaluate river rehabilitation success (Kemp et al., 1999), and to assess the minimum flow requirements of benthic macroinvertebrates (Brunke et al., 2001). Even though in some cases the visual distinction of mesohabitats fails to reveal biological differences (Pedersen & Friberg, 2007), surveys on a mesohabitat scale provide an important tool for stream management (Harper & Everard, 1998).

The knowledge about spatial and temporal patterns in macroinvertebrate assemblages is fundamental not only to understand stream ecosystem functions (Brown, 2007), but also for planning biomonitoring programs (Álvarez-Cabria et al., 2010) and restoration measures (Lake et al., 2007). The concern of policy makers and environmental managers for the headwater streams, therefore, recently strongly increases (Adams, 2008). However, studies on the spatial distribution of macroinvertebrate assemblages on a mesohabitat scale have mainly been conducted in rivers and lowland streams (e.g., Pardo & Armitage, 1997), whereas comparable studies on small woodland streams are lacking. Headwater streams differ in a number of fundamental ways from larger streams (Richardson & Danehy, 2007) and yet these ecosystems have been largely overlooked by stream ecologists despite their huge importance as sources of water, sediments and biota for downstream reaches (Meyer & Wallace, 2001; Clarke et al., 2008).

In this study, we focused on the spatial and temporal variation in benthic macroinvertebrate assemblages on the mesohabitat scale in a headwater woodland stream. Our aims were: (i) to assess the environmental distinctness of mesohabitats within a stream; (ii) to assess spatial and temporal patterns in total abundance and taxa richness of macroinvertebrate assemblages and proportions of functional feeding groups, and (iii) to partition the variance in macroinvertebrate assemblages due to the environmental distinctness of mesohabitats and temporal dynamics.

Materials and methods

Study site

Field work was carried out within a 100 m long reach of the Hadůvka brook. Hadůvka brook at the site (49°25'N, 16°16'E) is a Strahler's first order stream and flows through the Czech-Moravian Highlands (Czech Republic, Hercynian region, gneiss bedrock). It has a relatively stable flow regime with an average daily discharge of about $0.001 \text{ m}^3 \text{ s}^{-1}$. It flows through deciduous forest with alders (*Alnus* sp.) dominating the riparian vegetation. Width ranges from 0.5 to 1.5 m and depth does not exceed 25 cm and is usually below 10 cm. The natural stream channel is composed of alternating erosive and sedimentary parts with occasional formations of debris dams that consist mostly of accumulated woody debris (branches, twigs, bark fragments) and leaf litter. The stream current was immeasurable most of the year due to very low water depth (often only a few centimetres). During highest discharges (April) the current velocity on the studied mesohabitats ranged from 0 to 0.47 m s^{-1} .

Sampling and data collection

Six mesohabitats (sensu Armitage et al., 1995a), i.e., visually distinct habitat areas identifiable from the river bank, were identified in the Hadůvka brook: fine sediment, pure sandy bottom, sand covered with leaf litter, gravel covered with leaf litter, pure gravel and accumulated woody debris—debris dams. Sand samples were taken from areas where inorganic particles smaller than 2 mm dominated (covered >50% of the bottom surface), whereas gravel samples were taken from areas dominated by particles larger than 10 mm.

Samples were taken monthly from September 2004 to August 2005. On each sampling occasion one sample from each mesohabitat was taken. These samples were supplemented by additional samples according to the share of mesohabitats up to the final number of 9–10 samples. On three occasions (February, March, and August) a lower number of samples (2, 7, and 8, resp.) was taken due to logistic difficulties or bad weather conditions (e.g., the stream was almost completely frozen on February). Similarly, sand covered with leaf litter could not be sampled on three occasions due to its absence at the site (March, July,

August). On each sampling occasion the samples were taken from different points, so that the areas that had been disturbed during the previous sampling campaigns were not sampled again. In total, 104 samples were taken and processed (see Table 1 for the number of samples taken per each combination of mesohabitat and month).

The sampling itself consisted of collecting substratum using Hess sampler (area 0.03 m², 100 µm mesh size) to a depth of 5 cm. Samples were decanted and elutriated (a process in which lighter particles are carried by the current over a raised outflow edge) through three nets with 500, 250, and 100 µm mesh sizes (Omesová & Helešic, 2004). The material from the 100 µm mesh size net was decanted once more to separate inorganic matter from fine particulate organic matter (FPOM, particle size between 100 and 250 µm).

The inorganic sediment that had left after decantation and elutriation was dry-sieved in a shaker through a stack of standard steel sieves. Although it is difficult to express substratum composition by a single value (Young et al., 1991), we have chosen to use median grain size (Q50) as a measure of substratum roughness, as it was shown to reflect major hydrologic forces in small streams (Golden & Springer, 2006).

All of the macroinvertebrates and particles of wood and leaves larger than 1.5 cm were sorted from the 500 µm mesh size fraction, giving samples of macroinvertebrates, woody debris (WD, >1.5 cm), leaf litter (LL, >1.5 cm) and the remaining medium particulate organic matter (MPOM, from 0.5 mm to 1.5 cm). The fractions of organic matter (FPOM, MPOM, WD, and LL) were dried and weighed (see

Table 2 for interquartile range of observed environmental parameters). Macroinvertebrate identifications were based on Freude et al. (1971) (Coleoptera), Waringer & Graf (1997) (Trichoptera), Rozkošný (1980) (other insect groups) and Buchar et al. (1995) (other non-insect groups). The macroinvertebrates were identified to genera or species and counted, except for Nematoda, Hydracarina, Oligochaeta, Chironomidae, part of Limoniidae, Psychodidae, Scatopsidae, and Sciomyssidae which were only counted (for a complete list of taxa see Electronic Supplementary Material 1).

Taxa richness was rarefied to 30 individuals according to Heck et al. (1975) and was only calculated for samples with at least 60 individuals (80 samples, Table 1). Only macroinvertebrates identified to the genus level or lower were considered in the taxa richness calculation process. Total macroinvertebrate abundance was determined for all samples and the whole assemblage.

Functional feeding group proportions (further in text as proportions of collectors-gatherers, predators etc.) were calculated based on the abundance of macroinvertebrates. Chironomidae were not considered in the functional feeding groups calculations, because they are too diverse and abundant at the site to be evaluated at the family level. In general, species characteristics listed in the autecological database used in ASTERICS software (AQEM Consortium, 2008) were adopted, while characteristics of a few dipteran taxa listed in Rozkošný & Vaňhara (2004) were used (Electronic supplementary material 1). The abundance of feeding strategies was calculated as the number of all points assigned to the strategies in a

Table 1 Number of samples within each combination of mesohabitat and month/number of samples used for rarefied taxa richness analysis (i.e., number of samples with total abundance >60)

Mesohabitat	Month											
	1	2	3	4	5	6	7	8	9	10	11	12
SED	2/1	0	1	2/1	2/0	2/0	2/0	2/0	1/0	1	1	2/1
SNDP	1/0	0	1/0	1	1	1	2	1/0	1	1	1	1
SNDOM	1	0	0	1	2	1	0	0	1	2	1	1
GRP	2	1/0	2/0	3/0	3/1	3	2	3	1	2	2	2
GROM	2	1	1	1/0	1	1	2	2	2	1	3	2
DD	2	0	2	2	1	2	2	2	2	2	1	1

SED fine sediment, SNDP pure sand, SNDOM sand covered with leaf litter, GRP pure gravel, GROM gravel covered with leaf litter, DD debris dams

Table 2 Interquartile range of environmental parameters

	Q50 (mm)	FPOM (g)	MPOM (g)	LL (g)	WD (g)
SED	0.37–0.81	7.34–16.26	2.36–4.86	0.00–0.02	0.34–1.90
SNDP	0.43–0.90	1.64–4.09	0.56–1.89	0.00–0.02	0.00–0.76
SNDOM	1.04–2.15	0.87–2.67	2.42–3.11	0.15–2.98	8.20–22.09
GRP	10.40–16.88	0.11–0.42	0.27–0.68	0.00–0.05	0.14–0.47
GROM	12.82–21.15	0.14–0.51	0.58–1.88	0.26–1.88	0.90–6.63
DD	0.84–4.00	0.26–0.95	3.54–11.17	0.28–1.61	29.07–68.78

SED fine sediment, *SNDP* pure sand, *SNDOM* sand covered with leaf litter, *GRP* pure gravel, *GROM* gravel covered with leaf litter, *DD* debris dam, *Q50* median grain size, *FPOM* fine particulate organic matter (100–250 μm), *MPOM* medium particulate organic matter (0.5–15 mm), *LL* leaf litter (>15 mm), *WD* woody debris (>15 mm)

sample divided by 10 (multiplying the abundance matrix by the matrix of feeding preferences and dividing by 10, 10 is the number of points per taxon). E.g., the abundance of shredders would be 12 if there were 20 individuals of one species with 6 points for shredding in a sample.

Statistical analysis

Prior to statistical analysis the environmental data were $\log(x + 0.01)$ transformed (0.01 was the lowest measurable value of the weights of the substratum fractions) to achieve an approximately normal data distribution.

Principal component analysis (PCA) on all environmental variables scaled to unit variance was used to find the main gradients in the environmental data and to identify the relationships between the variables. These gradients were interpreted using their correlations with individual environmental variables (Spearman's rho). The first two gradients explained most of the variation in the environmental data (see "Results") and were used as composite environmental gradients (env1, env2) in subsequent analyses.

The temporal changes in the total abundance and taxa richness of benthic macroinvertebrates as well as the abundance and proportion of functional feeding groups throughout the year and their response to the two environmental gradients were modelled using generalized additive models (GAM). These models allow the response variable to change non-linearly with the explanatory variables (as was expected based on data exploration). The environmental gradients (continuous variables) and month (an integer 1–12) were used as explanatory variables. Poisson family with log link function and binomial family with logit

link function, both corrected for overdispersion, were used for count and proportional data, respectively, while Gaussian family was used for rarefied taxa richness (normally distributed). A penalized cubic regression spline was used to smooth the environmental gradients, whereas a penalized cyclic cubic regression spline was used for month, as cyclic changes in the abundance and taxa richness throughout the year were expected. With penalized splines, the bendiness (degrees of freedom) is estimated during the fitting process (Wood, 2006). Hypothesis testing with stepwise backwards selection was used to build the models. The full models were in the form of response variable $\sim s(\text{env1}) + s(\text{env2}) + s(\text{month})$, where the response variable varies as a smooth function of environmental gradients and month. Insignificant terms were removed from the model step by step, until all of the included terms were significant.

We acknowledge that model residuals might be violating the assumption of independence, as they can be expected to be temporally autocorrelated (all the samples were taken repeatedly from the same stream). We tried to model the autocorrelation by including an autocorrelation structure in the models (Autoregressive process of order 1 in Generalized Additive Mixed Models). However, some models had numerical problems, therefore, we decided to keep all the models consistently simpler, i.e., without the correlation structure. Thus, the interpretation of the models, especially of the significance of their temporal components, should be done with care. It should also be noted that Generalized Additive Mixed Models are highly complex and still in the development process.

Because of our intention to quantify variance in the faunal data due to habitat differences and temporal dynamics, the effects of habitat differences and

temporal dynamics needed to be separated. Therefore, the samples were coded according to the month in which they were taken. Graphically, individual months can be displayed in an annual cycle, and since a cycle is a two-dimensional object, months can be coded using two variables. Twelve new variables representing relative seasonality (termed “rJanuary” through “rDecember” to distinguish the values from actual dates or categorical variables) were created and for each of these variables a value was assigned for each sample in each month. These values ranged between 1.0 (assigned to the relative seasonality variable corresponding to the month the sample was taken) and 0.0 (assigned to the relative seasonality opposite to the month the sample was taken), and were scaled by 0.1667 (i.e., 1/6) representing a relative decrease of one month in each direction away from the sample month in the annual cycle. For example, for a sample taken in January, a value of 1.0 was assigned to “rJanuary”, values of 0.8333 were assigned to both “rDecember” and “rFebruary”, 0.6666 to both “rMarch” and “rNovember”, and so on, until a value of 0.0 for “rJuly”. For a particular sample, this yields a unimodal distribution across the relative seasonality variables centered on the month the sample was taken with decreasing values moving in either direction in the annual cycle, reaching a zero value at the opposite month. Obviously, each pair of opposite relative seasonality variables (e.g., “rJanuary” and “rJuly”) is in absolute correlation; therefore, only six relative seasonality variables are actually needed. Nevertheless, PCA was performed on these 12 new variables and sample scores on the first two PCA axes were used as the two variables representing the annual cycle in multivariate analysis used to partition variance in faunal data (see below).

The amount of variance in the faunal data due to habitat differences and temporal dynamics was assessed using a direct ordination technique. Only the counts of invertebrates identified at least to the genus level were used in this analysis. Prior to the multivariate analysis, the faunal data were $\log(x + 1)$ transformed. In order to decide between using linear or unimodal ordination techniques, detrended correspondence analysis (DCA) was applied to the faunal data to identify the length of the main gradient. The gradient length was 2.09 standard deviation units (SDU), indicating that the linear models were more suitable (Ter Braak & Prentice, 1988). Therefore, (partial)

redundancy analysis (p)RDA was applied and the statistical significance of the environmental gradients and temporal dynamics was tested by 999 unrestricted Monte Carlo permutations. Experimentally applied equivalent unimodal ordination techniques provided results much the same as the linear models, therefore only results of the linear models are presented.

All analyses were performed in R, version 2.12.0 (R Development Core Team, 2010) with the use of “vegan” (Oksanen et al., 2010) and “mgcv” (Wood, 2006) packages.

Results

Environmental gradients

Two main gradients (principal components) in the environmental data were identified using PCA. The first principal component (env1) explained 42.37% of the variance in the data and correlated best with all of the variables representing the amount of coarse particulate organic matter—CPOM (MPOM, WD, and LL) (Table 3). The second principal component (env2) (36.37%) correlated negatively with fine particulate organic matter (FPOM) and positively with median substratum grain size (Q50) (Table 3). The remaining components explained noticeably lower portions of variance and no environmental variable correlated with any of them better (i.e., with a higher rho value) than with one of the first two components. Therefore, the first two principal components (environmental gradients), together accounting for 78.7% of the variance in the environmental

Table 3 Spearman’s rank correlations between the two environmental gradients (principal components obtained by PCA on the environmental data) and environmental variables

Variable	env1	env2
Q50	−0.367	0.846
FPOM	0.306	−0.854
MPOM	0.852	−0.309
LL	0.622	0.571
WD	0.824	0.280

Q50 median substratum grain size, FPOM fine particulate organic matter, MPOM medium particulate organic matter, LL leaf litter, WD woody debris. All of the correlations are significant, with $P < 0.01$

data, were considered as gradients that sufficiently represented the main variance in the environmental data and entered further statistical analysis. Although these gradients were perpendicular to each other (as the result of PCA), individual environmental variables represented by these gradients should not be regarded as being independent (at the same time, all of the environmental variables correlated strongly with one of the two principal components and weakly with the other). Three mesohabitats—fine sediment, pure gravel, and debris dams—can be regarded as being environmentally “extreme,” whereas the others are transitional between them (Fig. 1a).

Total abundance of macroinvertebrates and rarefied taxa richness

In total, 40,347 individuals of benthic macroinvertebrates belonging to 81 taxa were collected (Electronic supplementary material 1). The final model for total abundance included smooth functions of env1 and month and explained 68.3% of deviance in the total abundance. According to the model, total abundance strongly increased along the first environmental gradient ($F = 36.9$, $P < 0.001$) (Fig. 2a), while the effect of seasonal dynamics was weaker ($F = 10.6$, $P < 0.001$) with total abundance having two noticeable peaks during the year: the first (lower) in late winter (February), and the second (higher) in late summer

(August) (Fig. 2b). The effect of the second environmental gradient was not significant.

The final model for rarefied taxa richness included smooth functions of env1 and env2 and explained only 22.6% of the deviance in the data. According to the model, taxa richness did not change significantly during the year; however, it changed along the environmental gradients (Fig. 3a, b). The effect of gradient env1 was stronger ($F = 7.8$, $P = 0.005$) and taxa richness decreased almost linearly along it. The effect of gradient env2 was weaker ($F = 4.5$, $P = 0.011$) with taxa richness first increasing relatively steeply along it and then remaining almost constant from about the middle of the gradient.

Functional feeding groups

The assemblage of the studied site was dominated by shredders followed by collectors/gatherers, grazers/scrapers, and predators (Fig. 4). Xylophags, parasites, and passive and active filter feeders had the lowest proportion. Xylophags and parasites were not considered in the analysis due to their scarcity.

Despite our expectation, the abundance of all functional feeding groups except for passive filter feeders, increased along the first environmental gradient env1 following the overall increase in total abundance (Fig. 5). However, shredders were the only feeding group which proportion increased along this

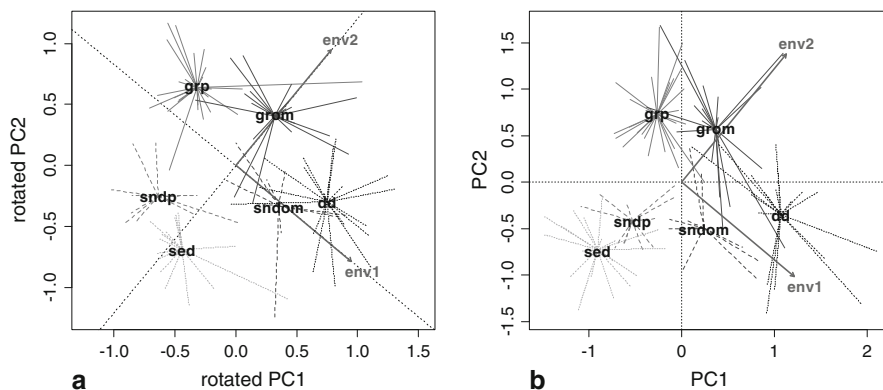


Fig. 1 The mutual resemblance of the configurations of samples resulting from the PCA ordinations according to (a) environmental and (b) faunal data (79 and 41% of variance explained, respectively). The configuration of points in the environmental ordination was rotated to maximum similarity with the faunal ordination to aid visual interpretation. Faunal PCA conditioned by temporal dynamics to highlight the effects

of environmental conditions. Principal components of the environmental PCA (a) correspond to the environmental gradients, which were used in the statistical analyses and fitted into the faunal ordination (the fit statistics: env1— $R^2 = 0.529$, $P < 0.0001$, env2— $R^2 = 0.672$, $P < 0.0001$). dd debris dams, grom gravel covered with leaf litter, grp pure gravel, sed fine sediment, sndom sand covered with leaf litter, sndp pure sand

Fig. 2 GAM smoothing curves fitted to the partial effects of explanatory variables on macroinvertebrate total abundance. Total abundance is represented as a function of environmental gradients env1 (a) and month (b). Grey bands represent 95% confidence intervals

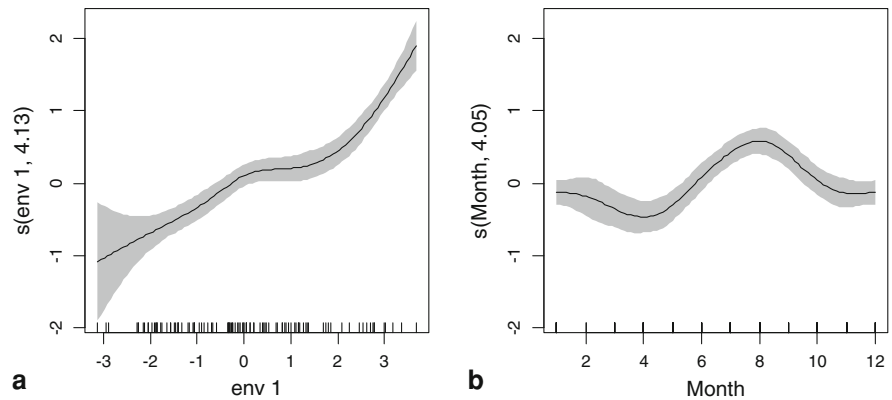


Fig. 3 GAM smoothing curves fitted to the partial effects of explanatory variables on rarefied macroinvertebrate taxa richness. Taxa richness is represented as a function of environmental gradients env1 (a) and env2 (b). Grey bands represent 95% confidence intervals

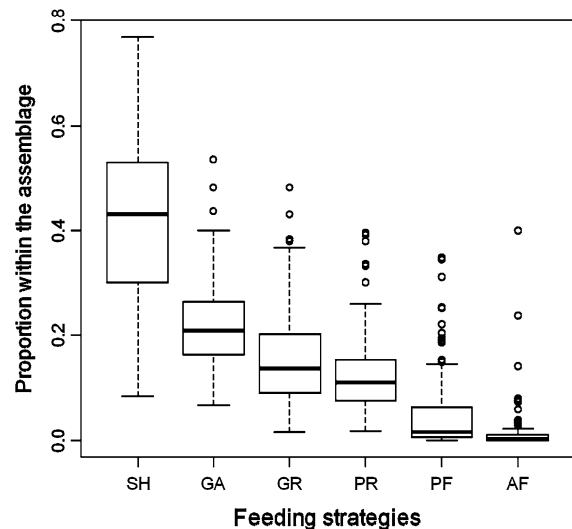
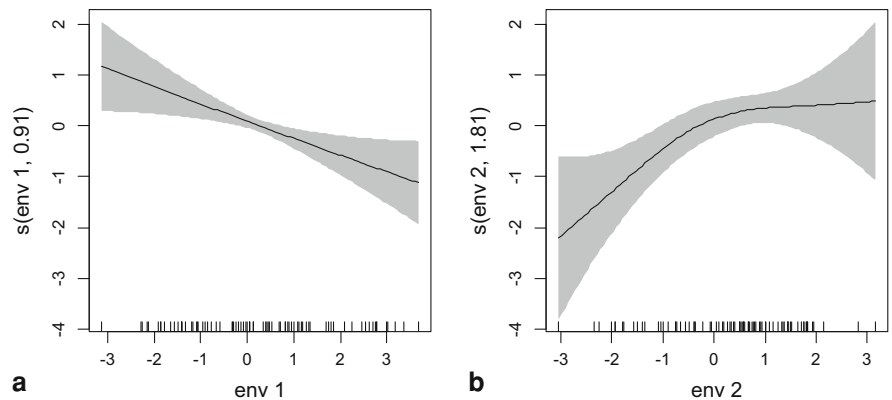


Fig. 4 Overall proportions of functional feeding groups within the macroinvertebrate assemblages. Median (middle line), interquartile range (box) and min–max range (whiskers) are displayed. SH shredders, GA gatherers/collectors, GR grazers/scrapers, PR predators, PF passive filter-feeders, AF active filter-feeders

gradient, while other groups decreased or did not show any response (Fig. 6; Table 4).

Most of the feeding groups showed similar patterns along the second environmental gradient env2. The optimal conditions were found about near the middle of the gradient env2 and the abundance weakly lowered at both ends (Fig. 5). Only the abundance of active and passive filter feeders obviously decreased and increased, respectively, along this gradient (Fig. 5). Proportionally, however, grazers increased and predators decreased along the second gradient, while the proportions of both active and passive filter feeders followed their abundance patterns (Fig. 6).

Regarding seasonal dynamics, the abundance of three dominant feeding groups (shredders, gatherers, and grazers) showed a response to month, all of them peaking in late summer (Fig. 5). However, only the proportion of dominant shredders followed a pattern similar to their abundance, while the patterns of the other feeding groups were almost opposite; shredders peaked in late summer and autumn while gatherers and grazers peaked in early summer and the predators and passive filter feeders in spring (Fig. 6).

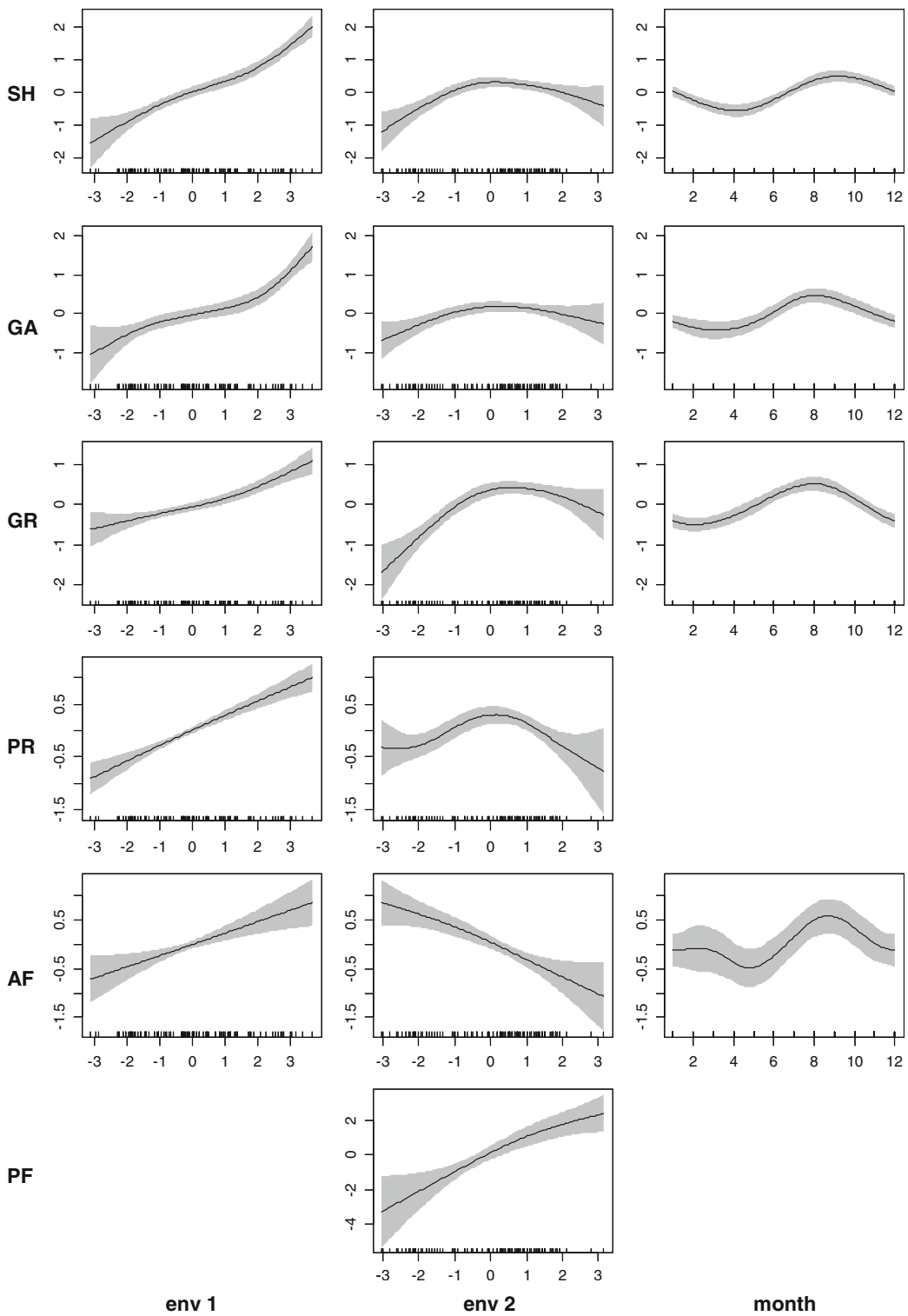


Fig. 5 The abundance of functional feeding groups as a function of environmental gradients and month. Gray bands represent 95% confidence intervals. For the models' statistics

see Table 4. Only significant smoothers are displayed. *SH* shredders, *GA* gatherers/collectors, *GR* grazers/scrapers, *PR* predators, *AF* active filter-feeders, *PF* passive filter-feeders

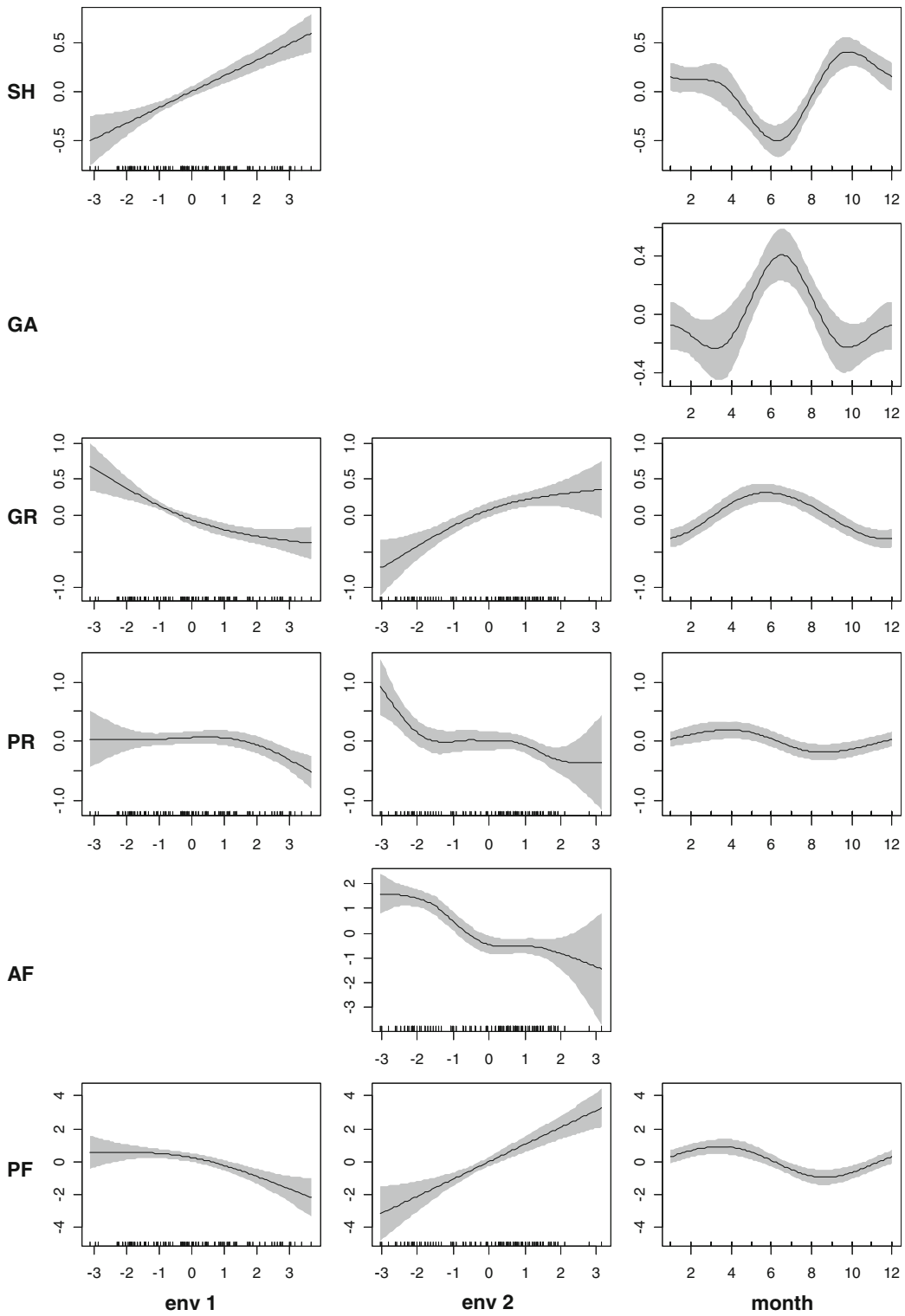


Fig. 6 Proportions of functional feeding groups as a function of environmental gradients and month. *Gray bands* represent 95% confidence intervals. For the models' statistics see Table 4.

Only significant smoothers are displayed. *SH* shredders, *GA* gatherers/collectors, *GR* grazers/scrapers, *PR* predators, *AF* active filter-feeders, *PF* passive filter-feeders

Table 4 Summary of GAMs in which abundance and proportion of each macroinvertebrate functional feeding group is modelled as a function of environmental gradients and month

	Explained deviance (%)	env1			env2			Month		
		edf	<i>F</i>	<i>P</i> value	edf	<i>F</i>	<i>P</i> value	edf	<i>F</i>	<i>P</i> value
Grazers										
Abundance	64.2	2.0	19.7	<0.001	2.7	12.7	<0.001	1.9	18.5	<0.001
Proportion	48.9	1.7	19.4	<0.001	1.7	9.9	<0.001	1.8	13.5	<0.001
Gatherers										
Abundance	65.2	3.3	29.3	<0.001	2.2	4.5	0.006	2.6	8.8	<0.001
Proportion	18.4			n.i.			n.i.	2.8	7.9	<0.001
Active filter-feeders										
Abundance	35.4	1.0	9.9	0.001	1.3	14.1	<0.001	3.2	3.2	0.015
Proportion	42.9			n.i.	3.8	16.5	<0.001			n.i.
Passive filter-feeders										
Abundance	31.5			n.i.	1.7	12.7	<0.001			n.i.
Proportion	49.7	1.8	8.4	<0.001	1.2	27.3	<0.001	1.8	9.6	<0.001
Predators										
Abundance	52.3	1.2	37	<0.001	3.2	4.7	0.002			n.i.
Proportion	37.9	2.3	5.3	0.002	4.1	4	0.002	2.0	3.8	0.017
Shredders										
Abundance	77.3	2.9	59.9	<0.001	2.7	7.2	<0.001	1.9	17.4	<0.001
Proportion	51.9	1.3	16.8	<0.001			n.i.	2.8	16.3	<0.001

F *F* statistics, *edf* effective degrees of freedom of the smoothers, *P* *value* significance of the smoothers, *n.i.* insignificant terms that were not included in the model

The variance explained by environmental gradients and temporal dynamics

According to RDA, the first and second environmental gradients explained about 11.5 and 11.4% of the variance in the faunal data, respectively. As there was no shared variance between them (they resulted from PCA), both together explained 22.8% of the variance in the faunal data. Both of these gradients could be linearly fitted into a PCA ordination diagram conditioned by temporal dynamics, suggesting they were related to the main gradients in the faunal data after the temporal dynamics were left aside (Fig. 1b).

Temporal dynamics (the annual cycle) were responsible for 12.0% of the variance in the faunal data. The variance attributable to temporal dynamics lowered to 11.6% in the ordination conditioned by the two environmental gradients (i.e., after accounting for the variance explained by the environmental gradients), suggesting that the variance shared by temporal dynamics and the captured environmental distinctness was about 0.4%.

In summary, the environmental distinctness alone, the temporal dynamics alone and both together accounted for 22.4, 11.6, and 34.4% of the variance in the faunal data, respectively. All of the presented (p)RDA models were highly significant ($P < 0.001$), as well as all of their components.

Discussion

Environmental gradients

The environmental conditions in the mesohabitats could be characterized by two main independent gradients—the gradient of the amount of CPOM (env1) and the gradient of the amount of FPOM (env2), the latter of which was conversely related to the substratum median grain size (Q50).

In headwater streams, accumulations of CPOM occur typically in the surroundings of large, stable structural obstructions (e.g., large stones and branches) (Gooderham et al., 2007). Such structures can be more

influential on the distribution of CPOM than local hydraulic conditions (Hoover et al., 2006). Therefore, the first environmental gradient (env1) can be considered more or less independent of hydraulic conditions and interpreted in terms of the amount of available food and space resources (see Functional feeding groups discussion).

On the other hand, mineral substratum grain size is determined by present and past flows with FPOM sedimentation in areas with low shear stress (Jowett, 2003). As larger substrata are less susceptible to disturbance than finer-grained substrata, larger substrata are likely to occur in riffles. The second environmental gradient (env2) was, therefore, interpreted as a gradient of interconnected hydraulic conditions and substratum roughness.

Total abundance patterns

Total macroinvertebrate abundance clearly increased with the amount of CPOM (gradient env1) and varied within the year with two peaks in August and February (Fig. 2).

CPOM provides macroinvertebrates with space (Schneider & Winemiller, 2008) and (primarily) food resources (Richardson, 1992) and is known to limit their abundance (Richardson, 1991; Dobson & Hildrew, 1992; Wallace et al., 1999). Therefore, the strong effect of CPOM on the total abundance observed in this study is not surprising and is in agreement with many other studies (e.g., Egglisshaw, 1964; Drake, 1984; Flecker, 1984; González & Graça, 2005; Eedy & Giberson, 2007).

Although seasonal patterns in the abundance (or biomass) of some macroinvertebrate taxa are well documented (e.g., Towns, 1983; Lindegaard & Mortensen, 1988; Phillips & Kilambi, 1994; Huryň & Wallace, 2000; López-Rodríguez et al., 2008), it is hard or even impossible to make generalizations about total macroinvertebrate abundance because it is influenced by a number of factors, including temperature (Sweeney, 1993; Haidekker & Hering, 2008), photoperiod (Schierwater & Hauenschild, 1990), biotic interactions (Lieske & Zwick, 2008), and disturbances (Lytle, 2002; Stubbington et al., 2009). For example, the peak in total abundance was observed in winter by Giberson & Hall (1988) and in spring by Boulton et al. (1992). Robinson et al. (1993) observed a spring peak in one stream, while they found no temporal pattern in

another. Similarly, Hutchens et al. (1998) observed different temporal patterns in one stream over five different years.

Chironomidae were the most abundant group in our study, which makes them largely responsible for the patterns observed in the total abundance of macroinvertebrates. Most chironomid species are bivoltine in temperate regions (Armitage et al., 1995b) and the two observed abundance peaks were at least partly caused by the hatching of Chironomid larvae from eggs. The second (late summer) peak was probably supported by the hatching of other species that mated in spring (mainly stoneflies). Moreover, in August, the water level was low, which might have caused concentration of macroinvertebrates in wet areas (Hutchens et al., 1998; Řezníčková et al., 2007). Similarly, numerous leaf accumulations in the stream in autumn might have led to a more even distribution of macroinvertebrates on a larger area of the stream bottom, which might also have contributed to the decrease of abundance (which is related to the sampled area) in autumn, while high abundance of macroinvertebrates in summer might have been supported by their accumulation in relatively scarce leaf patches (Fenoglio et al., 2005).

Temporal patterns, however, were examined only during one year with no replication and might be expected to vary between years depending on disturbances (discharge fluctuations), weather conditions (temperature) or other factors (Hutchens et al., 1998).

Taxa richness patterns

Macroinvertebrate taxa richness (rarefied) decreased with the increasing amount of CPOM (gradient env1), but increased with the median substratum grain size (gradient env2) until the middle of the gradient, from where it remained almost constant.

Previous studies from small streams identified a strong positive relationship between the amount of food resources (organic matter) and number of taxa (Flecker, 1984; Fenoglio et al., 2005). Increasing number of taxa with the amount of CPOM (gradient env1) was also observed in this study (linear regression model, adjusted $R^2 = 0.18$, $P < 0.001$) and was associated with the highest number of taxa collected from spatially complex, organically rich substrata (debris dams). However, the number of taxa increased linearly with the logarithm of total abundance and in these habitats, only a few taxa dominated, leading to a

decrease in the rarefied taxa richness with the increasing amount of CPOM.

Higher taxa richness in rougher substrata (gradient env2) was probably caused by their higher habitat complexity and stability (Robson & Chester, 1999). Moreover, concentration of dissolved oxygen might be lower at places of low current (with fine organic sediment) (Wood & Armitage, 1997), leading to the exclusion of some taxa (Madsen, 1968; Ward, 1992; Genkai-Kato et al., 2005).

It should be noted that a considerable portion of variation remained unexplained (the model explained about 23%), suggesting that some other factors played an important role in the determination of macroinvertebrate taxa richness. These factors might be related to habitat stability and colonization history (Death, 1996; Beisel et al., 1998), which play an important role in headwater streams (Schlosser & Ebel, 1989; Whiles & Wallace, 1995). Moreover, since rarefied taxa richness takes into account assemblage dominance, it may be related to factors controlling dominance as well (e.g., heterogeneity of available resources, Beisel et al., 2000). However, collecting material in stable substrata poor in CPOM would probably yield a higher number of taxa per unit of sample-processing effort (sorting and identification of individuals).

Functional feeding groups

The dominance of shredders at the study site and their increasing abundance with the amount of organic matter is a logical consequence of their dietary requirements, since allochthonous organic matter represents the main food source in small woodland streams (Hawkins & Sedell, 1981).

However, the abundance of almost all of the other feeding groups increased with the amount of CPOM following the pattern of total abundance, and indicating that CPOM served as a space resource as well, providing structurally complex microhabitats (O'Connor, 1991) and refugia (Everett & Ruiz, 1993).

Despite the increasing abundance of almost all taxonomic groups, only the proportion of shredders increased with the amount of CPOM. This suggests that although the quantity of available resources increased along this gradient allowing more individuals to inhabit the area of a sampling point, the quality of the resources favoured shredders by providing them with a high amount of food in the form of CPOM.

The responses of the proportions of most of the other feeding groups to environmental gradients were in correspondence with a general knowledge that grazers and passive filter-feeders prefer faster currents, while active filter-feeders prefer slow currents (Angradi, 1996; Rempel et al., 2000; Syrovátka & Brabec, 2010). The preference of predators for slow current was shaped by the domination of *Dugesia gonocephala* and dipterans (*Bezzia* sp., *Limnophila* sp.) among predators and corresponds with the results of Syrovátka et al. (2009), who analyzed chironomid assemblages. This is, however, contradictory to findings of Rempel et al. (2000) and Syrovátka & Brabec (2010), who reported higher proportion of predators in fast currents and a unimodal response to hydraulic conditions, respectively. The preference of predators for particular environmental conditions, therefore, seems to depend largely on the predator's mode of reaching its prey.

The same temporal pattern followed by almost all feeding groups indicates that they might have been driven by the same temporal processes, possibly changes in discharge and the availability of food and space resources. However, their proportions were probably shaped by the proportion of dominant shredders, who were able to exploit the resources more effectively; only the proportion of shredders followed temporal patterns similar to their abundance, in contrast to the other feeding strategies, proportions of which followed patterns almost opposite to their abundance.

Assemblage structure patterns

The environmental distinctness of the mesohabitats proved to be more important to the macroinvertebrate taxonomic structure as it explained about 23% of variance in the faunal data, compared to about 12% explained by temporal dynamics. This supports results of Armitage et al. (1995a), who found spatial variation to be the most important feature influencing faunal composition in Mill Stream, while seasonal dynamics were of secondary importance. Macroinvertebrate assemblages of distinct mesohabitats have been found to differ also in many other studies (Pardo & Armitage, 1997; Buffagni et al., 2000; Costa & Melo, 2008; Gualdoni et al., 2009; Zilli & Marchese, 2011). In the present study, only the assemblages of the "extreme" mesohabitats located at the ends of the environmental gradients—fine sediment, pure gravel,

and debris dams—largely differed from each other (Fig. 1b). The assemblages of the other mesohabitats were transitional between the three “extremes”.

The most probable driving force behind the shift in the assemblage taxonomic structure were dietary requirements of the taxa, as demonstrated by changes in the proportions of functional feeding groups along the environmental gradients. On the other hand, the temporal shifts in the assemblage structure were most probably due to the life histories of individual taxa (Hynes, 1970). Despite the ability of benthic macroinvertebrates' life histories to be adjusted according to the predictable availability of food resources (Huryn & Wallace, 2000), macroinvertebrate taxa were separated in space (along the environmental gradients) rather than in time in the present study.

Conclusions

Even though the research of headwater streams is currently focused mainly on the understanding of processes in whole headwater networks and their downstream linkages (Gomi et al., 2002), understanding of small scale dynamics is still fundamentally important. This study demonstrated that local habitat heterogeneity is fundamental for high biological diversity with spatial variability playing a crucial role being more important than seasonal dynamics. Moreover, our results indicated that coarse organic matter played a crucial role in woodland headwater streams providing macroinvertebrates of all feeding groups with food and space resources, which were, however, best exploited by shredders. However, to draw a general conclusion about spatial and temporal patterns in the macroinvertebrate assemblage structure, further long-term research is needed at a more detailed taxonomic level.

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References

- Adams, P. W., 2008. Policy and management for headwater streams in the Pacific Northwest: synthesis and reflection. *Forest Science* 53: 104–118.
- Álvarez-Cabria, M., J. Barquín & J. A. Juanes, 2010. Spatial and seasonal variability of macroinvertebrate metrics: do macroinvertebrate communities track river health? *Ecological Indicators* 10: 370–379.
- Angradi, T. R., 1996. Inter-habitat variation in benthic community structure, function, and organic matter storage in 3 Appalachian headwater streams. *Journal of the North American Benthological Society* 15: 42–63.
- AQEM Consortium, 2008. ASTERICS: AQEM/STAR Ecological River Classification System, Version 3.1.1 <http://www.fliessgewaesserbewertung.de/download/berechnung/> and <http://www.freshwaterecology.info>.
- Armitage, P. D., I. Pardo & A. Brown, 1995a. Temporal constancy of faunal assemblages in 'mesohabitats'—application to management? *Archiv für Hydrobiologie* 133: 367–387.
- Armitage, P. D., P. S. Cranston & L. C. V. Pinder (eds), 1995b. The Chironomidae. The Biology and Ecology of Non-Biting Midges. Chapman & Hall, Andover.
- Beisel, J.-N., P. Usseglio-Polatera, S. Thomas & J.-C. Moreteau, 1998. Stream community structure in relation to spatial variation: the influence of mesohabitat characteristics. *Hydrobiologia* 398: 73–88.
- Beisel, J.-N., P. Usseglio-Polatera & J.-C. Moreteau, 2000. The spatial heterogeneity of a river bottom: a key factor determining macroinvertebrate communities. *Hydrobiologia* 422(423): 163–171.
- Boulton, A. J., Ch. G. Peterson, N. B. Grimm & S. G. Fisher, 1992. Stability of an aquatic macroinvertebrate community in a multiyear hydrologic disturbance regime. *Ecology* 73: 2192–2207.
- Brown, B. L., 2007. Habitat heterogeneity and disturbance influence patterns of community temporal variability in a small temperate stream. *Hydrobiologia* 586: 93–106.
- Brunke, M., A. Hoffmann & M. Pusch, 2001. Use of mesohabitat specific relationships between flow velocity and river discharge to assess invertebrate minimum flow requirements. *Regulated Rivers: Research & Management* 17: 667–676.
- Buchar, J., V. Ducháč, K. Hůrka & J. Lellák, 1995. Klíč k určování bezobratlých. Scientia, Praha.
- Buffagni, A., G. A. Crosa, D. M. Harper & J. L. Kemp, 2000. Using macroinvertebrate species assemblages to identify river channel habitat units: an application of the functional habitats concept to a large, unpolluted Italian river (River Ticino, northern Italy). *Hydrobiologia* 435: 213–225.
- Clarke, A., R. Mac Nally, N. Bond & P. S. Lake, 2008. Macroinvertebrate diversity in headwater streams: a review. *Freshwater Biology* 53: 1707–1721.
- Costa, S. S. & A. S. Melo, 2008. Beta diversity in stream macroinvertebrate assemblages: among-site and among-microhabitat components. *Hydrobiologia* 598: 131–138.
- Death, R. G., 1996. The effect of patch disturbance on stream invertebrate community structure: the influence of disturbance history. *Oecologia* 108: 567–576.
- Dobson, M. & A. G. Hildrew, 1992. A test of resource limitation among shredding detritivores in low order streams in southern England. *Journal of Animal Ecology* 61: 69–77.
- Drake, J. A., 1984. Species aggregation: the influence of detritus in a benthic invertebrate community. *Hydrobiologia* 112: 109–115.

- Eedy, R. I. & D. J. Giberson, 2007. Macroinvertebrate distribution in a reach of a north temperate eastern Canadian river: relative importance of detritus, substrate and flow. *Fundamental and Applied Limnology* 169: 101–114.
- Egglishaw, H. J., 1964. The distributional relationship between the bottom fauna and plant detritus in streams. *Journal of Animal Ecology* 33: 463–476.
- Everett, R. A. & G. M. Ruiz, 1993. Coarse woody debris as a refuge from predation in aquatic communities. *Oecologia* 93: 475–486.
- Fenoglio, S., T. Bo, P. Agosta & G. Malacarne, 2005. Temporal and spatial patterns of coarse particulate organic matter and macroinvertebrate distribution in a low-order Apennine stream. *Journal of Freshwater Ecology* 20: 539–547.
- Flecker, S. A., 1984. The effects of predation and detritus on the structure of a stream insect community: a field test. *Oecologia* 64: 300–305.
- Freude, H., K. W. Harde & G. A. Lohse, 1971. *Die Käfer Mitteleuropas*. Band 3. Adephaga 2, Palpicornia, Histeroidea, Staphylinioidea 1. Goecke & Evers Verlag, Kresfeld.
- Frissell, Ch A, W. J. Liss, Ch E Warren & M. D. Hurley, 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management* 10: 199–214.
- Genkai-Kato, M., H. Mitsunashi, Y. Kohmatsu, H. Miyasaka, K. Nozaki & M. Nakanishi, 2005. A seasonal change in the distribution of a stream-dwelling stonefly nymph reflects oxygen supply and water flow. *Ecological Research* 20: 223–226.
- Giberson, D. J. & R. J. Hall, 1988. Seasonal variation in faunal distribution within the sediments of a Canadian Shield stream, with emphasis on responses to spring floods. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 1994–2002.
- Golden, L. A. & G. S. Springer, 2006. Channel geometry, median grain size, and stream power in small mountain streams. *Geomorphology* 78: 64–76.
- Gomi, T., R. C. Sidle & J. S. Richardson, 2002. Understanding processes and downstream linkages of headwater systems. *BioScience* 52: 905–916.
- González, M. & M. A. S. Graça, 2005. Influence of detritus on the structure of the invertebrate community in a small Portuguese stream. *International Review of Hydrobiology* 90: 534–545.
- Gooderham, J. P. R., L. A. Barmuta & P. E. Davies, 2007. Upstream heterogenous zones: small stream systems structured by a lack of competence? *Journal of the North American Benthological Society* 26: 365–374.
- Gualdoni, C. M., M. F. Boccolini, A. M. Oberto, R. E. Principe, G. B. Raffaini & M. C. Corigliano, 2009. Potential habitats *versus* functional habitats in a lowland braided river (Córdoba, Argentina). *Annales de Limnologie-International Journal of Limnology* 45: 69–78.
- Haidekker, A. & D. Hering, 2008. Relationship between benthic insects (Ephemeroptera, Plecoptera, Coleoptera, Trichoptera) and temperature in small and medium-sized streams in Germany: a multivariate study. *Aquatic Ecology* 42: 463–481.
- Harper, D. & M. Everard, 1998. Why should the habitat-level approach underpin holistic river survey and management? *Aquatic Conservation-Marine and Freshwater Ecosystems* 8: 395–413.
- Harper, D. M., C. D. Smith, J. L. Kemp & G. A. Crosa, 1998. The use of functional habitats in the conservation, management and rehabilitation of rivers. In Bretschko, G. & J. Helešic (eds), *Advances in River Bottom Ecology*. Backhuys Publishers, Leiden: 315–326.
- Harper, D. M., J. L. Kemp, B. Vogel & M. D. Newson, 2000. Towards the assessment of “ecological integrity in running” waters of the United Kingdom. *Hydrobiologia* 422(423): 133–142.
- Hawkins, Ch. P. & J. R. Sedell, 1981. Longitudinal and seasonal changes in functional organization of macroinvertebrate communities in four Oregon streams. *Ecology* 62: 387–392.
- Heck, K. L., G. van Belle & D. Simberloff, 1975. Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. *Ecology* 56: 1459–1461.
- Hoover, T. M., J. S. Richardson & N. Yonemitsu, 2006. Flow-substrate interactions create and mediate leaf litter resource patches in streams. *Freshwater Biology* 51: 435–447.
- Hurny, A. D. & J. B. Wallace, 2000. Life history and production of stream insects. *Annual Review of Entomology* 45: 83–110.
- Hutchens, J. J., K. Chung & J. B. Wallace, 1998. Temporal variability of stream macroinvertebrate abundance and biomass following pesticide disturbance. *Journal of the North American Benthological Society* 17: 518–534.
- Hynes, H. B. N., 1970. *The Ecology of Running Waters*. Liverpool University Press, Liverpool.
- Jowett, I. G., 2003. Hydraulic constrains on habitat suitability for benthic invertebrates in gravel-bed rivers. *River Research and Applications* 19: 495–507.
- Kemp, J. L., D. M. Harper & G. A. Crosa, 1999. Use of “functional habitats” to link ecology with morphology and hydrology in river rehabilitation. *Aquatic Conservation: Marine and Freshwater Ecosystems* 9: 159–178.
- Lake, P. S., N. Bond & P. Reich, 2007. Linking ecological theory with stream restoration. *Freshwater Biology* 52: 597–615.
- Lieske, R. & P. Zwick, 2008. Effects of intraspecific competition on the life cycle of the stonefly, *Nemurella pictetii* (Plecoptera: Nemouridae). *BMC Ecology* 8: 5.
- Lindegaard, C. & E. Mortensen, 1988. Abundance, life history and production of Chironomidae (Diptera) in a Danish lowland stream. *Archiv für Hydrobiologie, Supplement* 81: 563–587.
- López-Rodríguez, M. J., J. M. Tierno de Figueroa & J. Alba-Tercedor, 2008. Life history and larval feeding of some species of Ephemeroptera and Plecoptera (Insecta) in the Sierra Nevada (Southern Iberian Peninsula). *Hydrobiologia* 610: 277–295.
- Lytle, D. A., 2002. Flash floods and aquatic insect life-history evolution: evaluation of multiple models. *Ecology* 83: 370–385.
- Madsen, B. L., 1968. The distribution of nymphs of *Brachyptera risi* Mort. and *Nemoura flexuosa* Aub. (Plecoptera) in relation to oxygen. *Oikos* 19: 304–310.
- Meyer, J. L. & J. B. Wallace, 2001. Lost linkages and lotic ecology: rediscovering small streams. In Press, M. C., N. J. Huntly & S. Levin (eds), *Ecology: Achievement and Challenge*. Blackwell Science, Oxford: 295–316.

- O'Connor, N. A., 1991. The effects of habitat complexity on the macroinvertebrates colonising wood substrates in a lowland stream. *Oecologia* 85: 504–512.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens & H. Wagner, 2010. *vegan*: Community Ecology Package. R package version 1.17-4. <http://CRAN.R-project.org/package=vegan>.
- Omesová, M. & J. Helešic, 2004. On the processing of freeze-core samples with notes on the impact of sample size. *Scripta Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis* 29: 59–66.
- Pardo, I. & P. D. Armitage, 1997. Species assemblages as descriptors of mesohabitats. *Hydrobiologia* 344: 111–128.
- Pedersen, M. L. & N. Friberg, 2007. Two lowland stream riffles—linkages between physical habitats and macroinvertebrates across multiple spatial scales. *Aquatic Ecology* 41: 475–490.
- Phillips, E. C. & R. V. Kilambi, 1994. Habitat type and seasonal effects on the distribution and density of Plecoptera in Ozark Streams, Arkansas. *Annals of the Entomological Society of America* 87: 321–326.
- R Development Core Team, 2010: R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Rabeni, Ch. F., K. E. Doisy & D. L. Galat, 2002. Testing the biological basis of a stream habitat classification using benthic invertebrates. *Ecological Applications* 12: 782–796.
- Rempel, L. L., J. S. Richardson & M. C. Healey, 2000. Macroinvertebrate community structure along gradients of hydraulic and sedimentary conditions in a large gravel-bed river. *Freshwater Biology* 45: 57–73.
- Řezníčková, P., P. Pařil & S. Zahrádková, 2007. The ecological effect of drought on the macroinvertebrate fauna of a small intermittent stream—an example from the Czech Republic. *International Review of Hydrobiology* 92: 514–526.
- Richardson, J. S., 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. *Ecology* 72: 873–887.
- Richardson, J. S., 1992. Food, microhabitat, or both? Macroinvertebrate use of leaf accumulations in a montane stream. *Freshwater Biology* 27: 169–176.
- Richardson, J. S. & R. J. Danehy, 2007. A synthesis of the ecology of headwater streams and their riparian zones in temperate forests. *Forest Science* 53: 131–147.
- Robinson, Ch. T., G. W. Minshall & L. V. Every, 1993. Seasonal trends and colonization patterns of macroinvertebrate assemblages in two streams with contrasting flow regimes. *The Great Basin Naturalist* 53: 321–331.
- Robson, B. J. & E. T. Chester, 1999. Spatial patterns of invertebrate species richness in a river: the relationship between riffles and microhabitats. *Australian Journal of Ecology* 24: 599–607.
- Rozkošný, R. (ed.), 1980. Klíč vodních larev hmyzu. Academia, Praha.
- Rozkošný, R. & J. Vaňhara, 2004. Diptera (mimo Ceratopogonidae, Chironimidae a Simuliidae). Determinační kurz makrozoobentosu. Manuscript, Brno, <http://www.sci.muni.cz/zoolecol/hydrobio/sbirka/index.php?wh=literatura>.
- Schierwater, B. & C. Hauenschild, 1990. A photoperiod determined life-cycle in an oligochaete worm. *The Biological Bulletin* 178: 111–117.
- Schlosser, I. J. & K. K. Ebel, 1989. Effects of flow regime and cyprinid predation on a headwater stream. *Ecological Monographs* 59: 41–57.
- Schneider, K. N. & K. O. Winemiller, 2008. Structural complexity of woody debris patches influences fish and macroinvertebrate species richness in a temperate floodplain-river system. *Hydrobiologia* 610: 235–244.
- Storey, A. W. & J. Lynas, 2007. Application of the functional habitat concept to the regulated Lower Ord River, Western Australia, Part I, macroinvertebrate assemblages. *Hydrobiologia* 592: 499–512.
- Stubbington, R., A. M. Greenwood, P. J. Wood, P. D. Armitage, J. Gunn & A. L. Robertson, 2009. The response of perennial and temporary headwater stream invertebrate communities to hydrological extremes. *Hydrobiologia* 630: 299–312.
- Sweeney, B. W., 1993. Effect of streamside vegetation on macroinvertebrate communities of White Clay Creek in eastern North America. *Proceedings of the Academy of Natural Sciences of Philadelphia* 144: 291–340.
- Syrovátka, V. & K. Brabec, 2010. The response of chironomid assemblages (Diptera: Chironomidae) to hydraulic conditions: case study in a gravel-bed river. *Fundamental and Applied Limnology* 178: 43–57.
- Syrovátka, V., J. Schenková & K. Brabec, 2009. The distribution of chironomid larvae and oligochaetes within a stony-bottomed river stretch: the role of substrate and hydraulic characteristics. *Fundamental and Applied Limnology* 174: 43–62.
- Ter Braak, C. J. F. & I. C. Prentice, 1988. A theory of gradient analysis. *Advances in Ecological Research* 18: 271–317.
- Tickner, D., P. D. Armitage, M. A. Bickerton & K. A. Hall, 2000. Assessing stream quality using information on mesohabitat distribution and character. *Aquatic Conservation: Marine and Freshwater Ecosystems* 10: 179–196.
- Towns, D. R., 1983. Life history patterns of six sympatric species of *Leptophlebiidae* (Ephemeroptera) in a New Zealand stream and the role of interspecific competition in their evolution. *Hydrobiologia* 99: 37–50.
- Waringer, J. & W. Graf, 1997. Atlas der österreichischen Köcherfliegenlarven unter Einschluss der angrenzenden Gebiete. *Facultas Universitätverlag, Wien*.
- Wallace, J. B., S. L. Eggert, J. L. Meyer & J. R. Webster, 1999. Effect of resource limitation on a detrital-based ecosystem. *Ecological Monographs* 69: 409–442.
- Ward, J. V., 1989. The four-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society* 8: 2–8.
- Ward, J. V., 1992. *Aquatic Insect Ecology*. Wiley, New York.
- Whiles, M. R. & J. B. Wallace, 1995. Macroinvertebrate production in a headwater stream during recovery from anthropogenic disturbance and hydrologic extremes. *Canadian Journal of Fisheries and Aquatic Sciences* 52: 2402–2422.
- White, J. & K. Irvine, 2003. The use of littoral mesohabitats and their macroinvertebrate assemblages in the ecological assessment of lakes. *Aquatic Conservation: Marine and Freshwater Ecosystems* 13: 331–351.

- Wood, S. N., 2006. *Generalized Additive Models: An Introduction* with R. Chapman and Hall/CRC, Boca Raton.
- Wood, P. J. & P. D. Armitage, 1997. Biological effects of fine sediment in the lotic environment. *Environmental Management* 23: 203–217.
- Young, M. K., W. A. Hubert & T. A. Wesche, 1991. Selection of measures of substrate composition to estimate survival to emergence of salmonids and to detect changes in stream substrates. *North American Journal of Fisheries Management* 11: 339–346.
- Zilli, F. L. & M. R. Marchese, 2011. Patterns in macroinvertebrate assemblages at different spatial scales. Implications of hydrological connectivity in a large floodplain river. *Hydrobiologia* 663: 245–257.