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Influence of environmental factors on the distribution of caddisfly (Trichoptera) communities in medium-sized lowland streams in Latvia

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Abstract. The understanding of community structuring factors is a fundamental issue in community ecology. The objectives of the study were (1) to identify the distribution of the caddisfly community along the stream continuum; (2) to ascertain hydrochemical, hydrological, substrate, and catchment factors responsible for the distribution of communities; and (3) to summarize the key variance types determining the variance in caddisfly communities. Standard methods were used to investigate hydrological and hydrochemical parameters of nine medium-sized streams in 2003. Sampling and processing of samples of macroinvertebrates followed AQEM methods. A total of 28 taxonomic units of caddisflies were analysed. The upper reaches of streams revealed a relatively low abundance of caddisflies while the middle reaches had high abundances. The abundance in the lower reaches varied in a wide range. TWINSPAN separated the caddisfly species into two distinct groups. One group represented lithal habitat and rheophilous species. The other represented stream reaches with fine mineral sediments rich in organic matter of different size. Hydrochemical and physical variables explained the majority of variance in the preferences of caddisflies to bottom type and other environmental parameters, while all studied variables together explained up to 58% of the data variance. Thus, caddisflies could be used to study the influence of local and regional factors on stream ecosystems. The results of the present study could be also applied in practice to solve problems related to the evaluation of the ecological quality of running waters using benthic macroinvertebrates.

Key words: Trichoptera, microhabitats, environmental factors, spatial scale, medium-sized lowland streams, Latvia.

INTRODUCTION

Caddisflies (Trichoptera) are among the most diverse primary aquatic insects worldwide, exceeded in the number of species only by aquatic Diptera (Mackay & Wiggins, 1979). There are about 1000 more caddisfly species than the other primary aquatic orders combined (Grimaldi & Engel, 2005). Ecological opportunities of caddisflies are explainable by their ability to build portable cases, nets, and shelters

from mineral or organic particles using silk secretion (Mackay & Wiggins, 1979). Caddisfly larvae inhabit a wide range of aquatic microhabitats and virtually occupy all functional feeding groups from filtering collectors to carnivores (Wallace & Merritt, 1980).

Trichoptera larvae are important and beneficial components of the trophic dynamics and energy flow in streams they inhabit (Resh & Rosenberg, 1984). They are one of the best indicator groups of macroinvertebrates, because caddisfly larvae have essential advantages; for example, they have a limited mobility and a relatively long life span, which allow for an easy integration on spatial and temporal scales; they present reasonably cosmopolitan distributions, which enables comparative studies at least at a regional scale; their numerical predominance allows easy sampling and conclusions regarding quantitative distribution patterns (Dohet, 2002).

Streams are heterogeneous and hierarchically organized ecosystems (Frissell et al., 1986; Allan, 1995). All caddisfly families are represented in running waters, but many genera and the majority of species have restricted distribution along the stream continuum (Mackay & Wiggins, 1979). The River Continuum Concept (RCC) (Vannote et al., 1980) proposes that from headwaters to lower reaches, the physical variables within a stream system present a continuous gradient of physical conditions. The longitudinal variability in ecological conditions in streams is due to stream size (headwaters, medium-sized streams, and large rivers), as is the attendant variability in the structural and functional attributes of lotic insect communities (Vannote et al., 1980; Ward, 1992).

Spatial pattern is a fundamental theme in aquatic ecology (Levin, 1992), and multiscale spatial studies of macroinvertebrates have been common since the 1980s (e.g. Boyero, 2003; Sandin & Johnson, 2004). Poff (1997) suggested that species could be described in terms of their functional relationships to various habitat features, which can be defined at different spatial scales and organized hierarchically. Scaled habitat features perform like filters that influence the probability that individual species with specific functional characteristics are able to persist in a local community. Spatial distribution patterns of lotic caddisfly larvae have been well established (e.g. Urbanič et al., 2005; Galbraith et al., 2008). Most studies have focused on species-specific aggregation patterns (Schmera, 2004). The scale at which the lotic ecosystem is observed is important when determining which factors influence its structure (Sandin & Johnson, 2004) and function. It is not easy to categorize substrates on a linear scale as physical variables (Allan, 1995). Streambed substratum also affects the distribution and abundance of lotic invertebrates (Gurtz & Wallace, 1986). It is generally assumed that the scale at which communities exhibit the greatest variation is the scale over which important physical/chemical gradients or biotic interactions control assemblage composition (Li et al., 2001).

Seasonal, local (e.g. reach), and stream-order (e.g. between streams by size) differences in inputs, production, and storage of food resources provide spatially and temporally variable systems from which macroinvertebrates derive their

nutrition (Cummins & Klug, 1979). Macroinvertebrate faunal richness tends to be higher in a spatially heterogeneous environment composed of numerous substrates with elevated patchiness, thus offering a great number of niches for invertebrates and also a greater number of refugia from disturbance and predation (Beisel et al., 2000; Brown, 2003).

Historically, larvae of caddisflies have been well studied in Latvia in comparison with other aquatic insect groups. Until now attention was paid mainly to problems related to their faunistic composition, distribution, and occurrence in lakes and large streams (Spuris, 1967; Kachalova, 1972). However, the ecology of caddisfly larvae in medium-sized and small streams, brooks, and springs has been studied incompletely till now. Considering the ecological importance and specific characteristics of caddisfly larvae, and to reduce the data variability, we analysed from all macroinvertebrate data only the abundance of caddisfly larvae.

The objectives of the study were (1) to characterize the distribution of the caddisfly community along the stream continuum; (2) to ascertain hydrochemical, hydrological, substrate, and catchment factors responsible for the distribution of communities; and (3) to summarize the key variance types that determine the variance in caddisfly communities.

MATERIAL AND METHODS

Study area

Latvia is located in the north-western part of the East European Platform (Ecoregion No. 15) (Illies, 1978). The surface has a flat topography (57% of Latvia's territory is located below 100 m a.s.l. and only 2.5% of the area reaches a height above 200 m a.s.l.). The geological structure of Latvia consists of two main compartments – the crystalline basement and a cover of sedimentary rocks (Stinkulis, 1999). The surface water quality is most strongly affected by the upper-most sediment layers – Quaternary sediments: Quaternary tills and glaciofluvial and glaciolacustrine deposits (thickness from a few metres to up to 100–160 metres) (Kļaviņš et al., 2002). Three types of river beds determining water chemistry can be distinguished: carbonatic river beds, which consist of Devonian sediments (dolomite, clay, calcite, etc.); silicic river beds, which consist of Quarternary sediments (sand, gravel, clay, marl), and organic river beds (Kļaviņš et al., 2002).

The caddisfly communities were investigated in nine medium-sized lowland streams (<200 m a.s.l.; total catchment area 100–1000 km^2) in the territory of Latvia (Fig. 1, Table 1) in 2003.

Sampling design

A hierarchical sampling design was applied for 27 reaches of nine streams and three river basins: stream reach (upper, middle, and lower reaches), stream, and

river basin (Fig. 1). The samples were collected during the implementation of the STAR project (EC Fifth Framework Programme project 'Standardisation of River Classifications: Framework method for calibrating different biological survey results against ecological quality classifications to be developed for the Water Framework Directive') (Springe et al., 2006). Only caddisfly data were analysed in the current study.

Table 1. Characterization of the investigated stream reaches, streams, and river basins (1, upper reaches; 2, middle reaches; 3, lower reaches)

Stream name	Stream reach	Catchment area, km^2	Slope, %	Distance to source, km	Discharge, L/s
		Daugava River basin			
Pededze	Pededze 1	17.36	1.2	0.62	790
	Pededze 2	108.08	1.6	11.92	1290
	Pededze 3	196.11	0.8	19.47	2320
Arona	Arona 1	46.19	3.0	3.04	120
	Arona 2	111.84	3.2	14.43	290
	Arona 3	197.48	1.6	34.93	656
Mergupe	Mergupe 1	16.28	3.2	3.37	440
	Mergupe 2	29.8	7.4	7.41	130
	Mergupe 3	196.81	0.8	32.40	3300
		Gauja River basin			
Rauza	Rauza 1	49.91	3.6	6.82	50
	Rauza 2	59.87	2.8	14.47	80
	Rauza 3	175.26	0.8	34.88	370
Raunis	Raunis 1	49.19	1.2	11.36	150
	Raunis 2	62.56	13.0	16.92	180
	Raunis 3	78.57	8.2	23.41	300
Strīķupe	Strīķupe 1	74.31	0.6	8.39	580
	Strīķupe 2	81.03	2.0	12.63	620
	Strīķupe 3	85.94	3.0	15.54	1040
		Venta River basin			
Amula	Amula 1	53.9	0.8	11.04	120
	Amula 2	97.0	1.6	17.67	350
	Amula 3	207.8	4.4	44.91	480
Riežupe	Riežupe 1	148.6	0.2	30.61	490
	Riežupe 2	155.6	1.4	34.27	570
	Riežupe 3	241.9	1.8	40.08	850
Koja	Koja 1	14.8	1.6	4.54	70
	Koja 2	26.4	4.2	8.82	270
	Koja 3	73.4	1.8	23.74	680

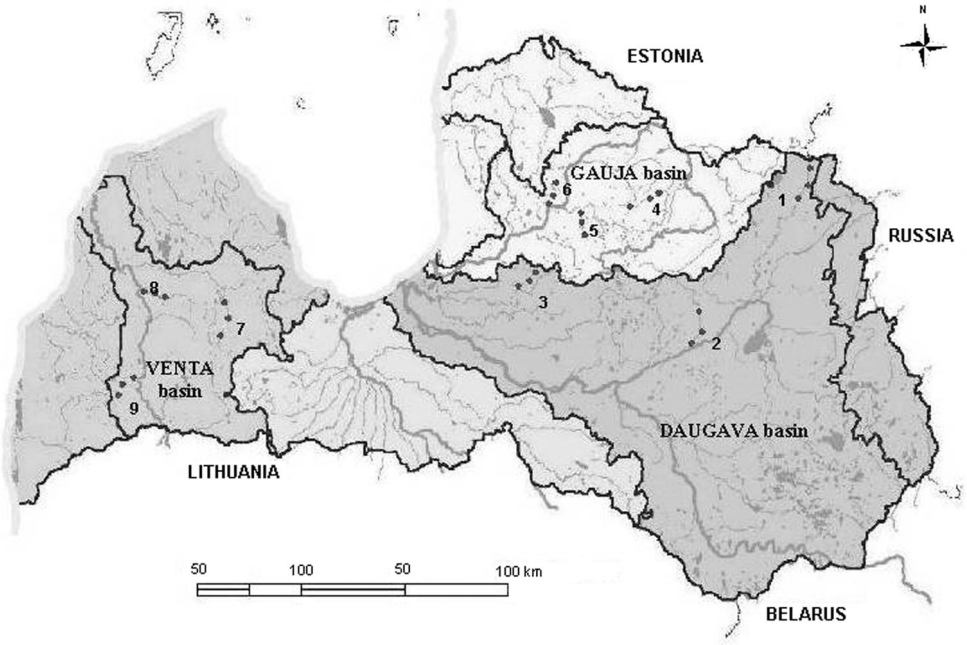

Fig. 1. Location of the sampling sites in Latvia. Daugava River basin: 1 – Pededze Stream, 2 – Arona Stream, 3 – Mergupe Stream; Gauja River basin: 4 – Rauza Stream, 5 – Raunis Stream, 6 – Strīķupe Stream; Venta River basin: 7 – Amula Stream, 8 – Riežupe Stream, 9 – Koja Stream (after Briede et al., 2006).

Environmental parameters

Hydrochemical analyses were made in the laboratory according to *Standard Methods for the Examination of Water and Wastewater* (APHA et al., 1992). The investigated stream reaches were characterized according to the STAR site protocol (STAR site protocol, 2010). Three groups of environmental variables were used in Canonical Correspondence Analyses: (1) local chemical variables: pH value, conductivity (µS/cm), alkalinity (CO_3^{2-}) (mmol/L), Cl^- (mg/L), NH_4^+ (mg/L), NO_2^- (mg/L), NO_3^- (mg/L), PO_4^{3-} (µg/L), N_{tot} (mg/L), P_{tot} (µg/L), Si (mg/L), total hardness (mgekv/L), BOD_5 (mg/L), temperature (°C), dissolved oxygen content (mg/L); (2) local physical variables: average stream width (m), mean depth (m), mean current velocity (m/s), bottom substrate types – psammal (sand) (<2 mm) (%), akal (gravel) (>2 mm–2 cm) (%), microlithal (>2 cm–6 cm) (%), mesolithal (>6 cm–20 cm) (%), macrolithal (>20 cm–40 cm) (%), FPOM (%), CPOM (%), xylal (%), submerged macrophytes (%), macroalgae (%); and (3) regional variables: land use in the catchment area – forests (%), agricultural land (%), bog area (%), others (%), catchment area (km^2), distance to source (km), altitude (m a.s.l.), discharge (L/s), and slope (%).

Sampling

The AQEM (EU 5th Framework Programme project 'The Development and Testing of an Integrated Assessment System for the Ecological Quality of Streams and Rivers Throughout Europe Using Benthic Macroinvertebrates') multi-habitat sampling technique (Hering et al., 2004) was used. The major habitats were sampled according to their proportional distribution within a sampling stream reach. A total of 20 replicates were taken from all major habitat types in each reach by using a Surber sampler (frame size 0.25 m × 0.25 m, mesh size 0.5 mm). Consequently, the multi-habitat sample was taken from a 1.25 m^2 area (AQEM Consortium, 2002). Samples were preserved in 4% (final concentration) formaldehyde solution.

Laboratory analysis of samples

Macroinvertebrate samples were processed according to AQEM guidelines. Samples were carefully rinsed on a 0.5 mm sieve to remove the preservative and fine sediment particles. For the majority of samples, only 1/6 from the whole sample was sorted (AQEM Consortium, 2002) on a white photo. The animals were identified to the best achievable taxonomic level (units) using keys (Lepneva, 1964, 1966; Waringer & Graf, 1997; Wallace et al., 2003; Edington & Hildrew, 2005).

Data analysis

To avoid overlapping of taxa, taxonomic adjustment of data was used in three ways: aggregating species to a higher taxonomic level (e.g., in case the frequency of occurrence of a genus was more than 20% of the frequencies of occurrence of the underlying species together, all species were aggregated to the genus level); omitting a higher taxonomic level (e.g., when a genus was generally identified to the species level, with the exception of only a few specimens, the genus level was omitted and specimens identified as '*Genus* sp.' were distributed among the species kept) and distributing individuals that were only determined to the genus level according to the relative share of individuals determined to the species level (e.g., 100 individuals determined as *Hydropsyche* spp. could be divided among *Hydropsyche instabilis* (60 individuals determined) and *Hydropsyche pellucidula* (140 individuals determined) according to their relative occurrence 30 : 70) (AQEM Consortium, 2002).

Analysis of Variance (ANOVA) and multiple range test (Fisher's least significant difference (LSD) procedure) at the 95% confidence limit were applied using STATGRAPHICS Plus 4.1. software to test whether there were significant differences in the abundance and number of taxa of caddisflies at upstream, middle, and downstream reaches of streams.

The two-way indicator species analysis (TWINSPAN) classification method (Lepš & Šmilauer, 2003) was used to characterize the structure of caddisfly

communities. TWINSPAN analysis was done using WinTWINS software (Hill & Šmilauer, 2005). Five cut levels (0, 0.02, 0.05, 0.1, and 0.2) were used.

Canoco for Windows 4.5 was used for multivariate data analyses (Lepš & Šmilauer, 2003). Before the ordination analyses, caddisfly taxa abundances were log-transformed and rare taxa were downweighted using the Canoco for Windows 4.5 standard procedure (Ter Braak & Šmilauer, 2002).

Detrended Correspondence Analysis (DCA) was used to determine the length of the gradient for the caddisfly community data (beta diversity). As the gradient was long (3.82 standard deviations, called 'grey zone'), Correspondence Analysis (CA) was chosen for the further ordination analyses (Lepš & Šmilauer, 2003).

To measure the amount of variation in the caddisfly community, the abundance data were used in Canonical Correspondence Analysis (CCA) with three predictor matrices – local chemical, local physical, and regional variables (Borcard et al., 1992; Sandin & Johnson, 2004; Galbraith et al., 2008). Three separate CCA were performed for each response matrix (caddisfly taxa abundance) and each predictor matrix. To test the significance of the environmental variables, automatic forward selection was used with the Monte Carlo permutation test (999 permutations). The CCA analyses were repeated only with statistically significant environmental variables ($p \leq 0.05$). Explained percentages were calculated by dividing the explained variance (sum of all canonical eigenvalues) by total inertia and multiplying by 100. When covariables were used, the sum of all eigenvalues was subtracted from the total inertia, multiplied by 100, and divided by the total inertia (Lepš & Šmilauer, 2003).

For variation partitioning nine partial CCA (pCCA) analyses were performed using statistically significant variables in three explanatory data sets individually as covariables and after that removing the combined effects of the two matrices (Galbraith et al., 2008).

The Generalized Linear Model (GLM) (quadratic degree, binomial distribution) was used from the CanoDraw package (species response curve) to test the significance ($p < 0.05$) of the relation between the caddisfly taxa (response variables) and significant environmental variables (predictor variables) from CCA.

RESULTS

We identified 73 caddisfly taxonomic units belonging to different taxonomic levels (e.g., family, genus, and species). After taxonomic adjustments, only 28 units, belonging to 14 families, were left (Appendix 1).

Community distribution along the stream continuum

The abundance of caddisflies varied along the stream continuum (longitudinal gradient). Despite the typological differences of stream reaches (e.g. in the composition of main bottom substrate types), obvious tendencies were established. The abundance

was low in the upper reaches, high in the middle reaches, and varied within a wide range in the lower reaches (Fig. 2).

ANOVA revealed a statistically significant difference between the abundances of individuals at different reaches ($F_{0.05} = 4.66$; $p = 0.02 < 0.05$). Fisher's LSD procedure showed that there was a significant difference between the abundances at the upper and lower reaches, but not between the abundances of the middle and lower reaches. However, there was no statistically significant difference between the number of taxonomic units at the upper, middle, and lower reaches ($F_{0.05} = 0.57$; $p = 0.58 > 0.05$) (Fig. 3).

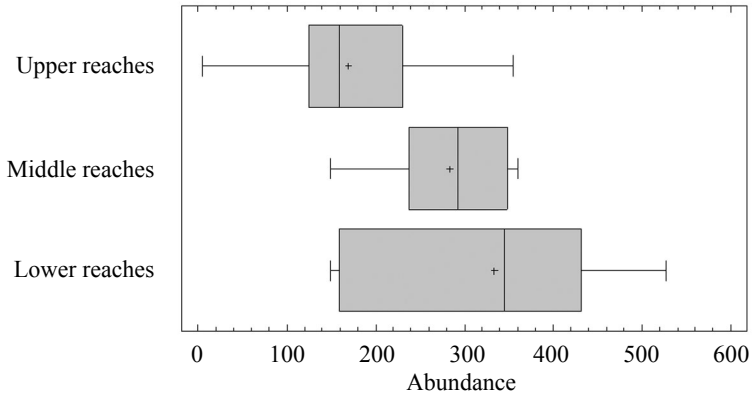

Fig. 2. Box-and-Whisker plot of the abundance of caddisfly individuals (1 m^{-2}) in the upper ($n = 9$), middle ($n = 8$), and lower ($n = 9$) reaches of the investigated streams in spring 2003. Range bars show minimum and maximum; boxes are interquartile ranges (25 percentile to 75 percentile); bars in boxes are medians; small crosses, the mean.

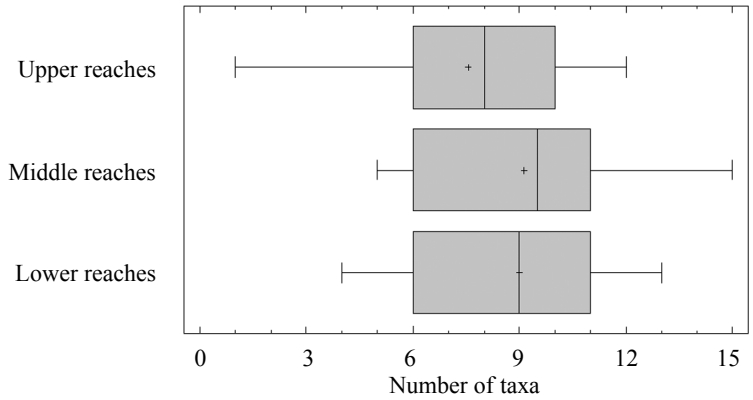

Fig. 3. Box-and-Whisker plot of the number of caddisfly taxa in the upper ($n = 9$), middle ($n = 8$), and lower ($n = 9$) reaches of the investigated streams in spring 2003. Range bars show minimum and maximum; boxes are interquartile ranges (25 percentile to 75 percentile); bars in boxes are medians; small crosses, the mean.

Caddisfly communities and TWINSPAN indicator species

At the first division (I), the locality Amula_1_V was separated from the other data because of poor fauna (only one caddisfly species was found) (Fig. 4). At the second (II) division level, the stream reaches were classified into two large groups with negative (located in the left side of the dendrogram) indicator species *Rhyacophila* sp. and *Silo pallipes* and a positive (located in the right side of the dendrogram) indicator species *Anabolia laevis*. The first group (00) represented lithal habitat (micro-, meso-, and macrolithal) dominance and reophilous species. The second group (01) represented stream reaches with finer mineral sediments, rich in organic matter of various size (psammal, akal, CPOM, and FPOM) (Fig. 4).

As to caddisfly communities, all three reaches were similar only in the Raunis Stream. The three reaches of the other streams were classified into different groups. The river basin had no significant effect on caddisfly communities.

Role of environmental parameters

Axis 1 of CA explained 17.8%, axis 2 16.7%, and axis 3 13.27% of the total inertia (1.779) (eigenvalues 0.316 and 0.298, respectively). Axis 1 potentially showed the gradient of the mineral substrate composition and particle size. For example, at the lower reaches of the Koja and Strikupe streams (Koja3 and Strik3), the bedrock was composed mostly of sand, unlike the Raunis Stream

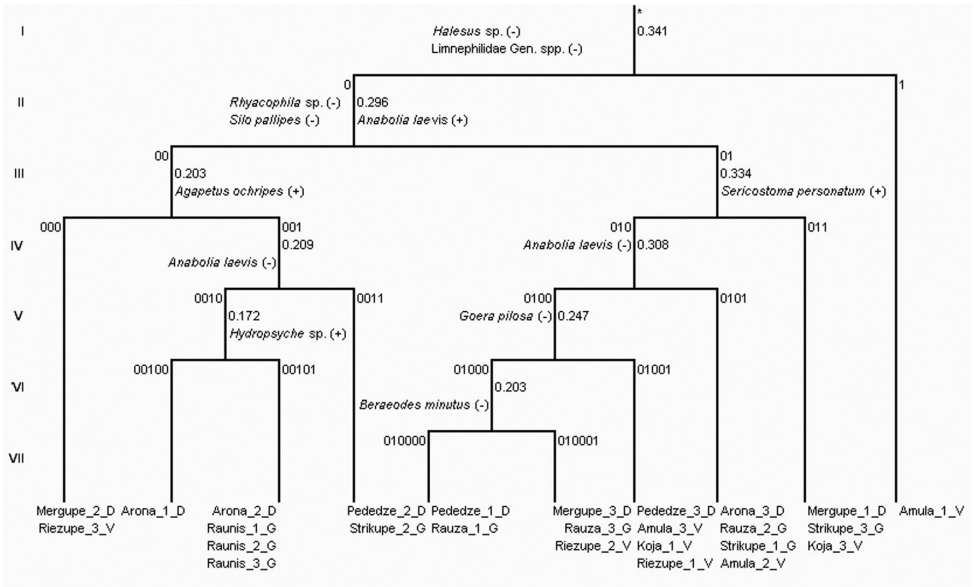

Fig. 4. TWINSPAN classification cluster for the investigated stream reaches. For each division level eigenvalues and indicator species are shown. In the stream names the number 1 indicates the upper reaches, 2 middle reaches, and 3 lower reaches; D designates Daugava River basin, G Gauja River basin, and V Venta River basin.

where the bottom was covered with micro-, meso-, and macrolithal substrates (Fig. 5). Axis 2 cannot be properly explained (Fig. 5).

Axis 1 (eigenvalue 0.239, $F_{0.05} = 2.793$, $p = 0.005$) and all canonical axes (trace = 0.792, $F_{0.05} = 2.06$, $p = 0.001$) of CCA were significant. Also pH, alkalinity, and NH^{+}_{4} content were statistically significant ($p \leq 0.05$) and explained an essential part of the species data variance. Of local physical variables mean depth (m), psammal (%), and xylal (%) substrates and of regional variables catchment area (km^2) were statistically significant variables (Table 2). Local chemical, local physical, and regional (catchment area) explained 57.56% of the variance of total abundance of caddisfly taxa.

The caddisfly taxa that prefer depositional microhabitats related significantly to psammal substrate (for *Agraylea* sp. $F_{0.05} = 11.17$, $p = 0.00004$; *Molanna*

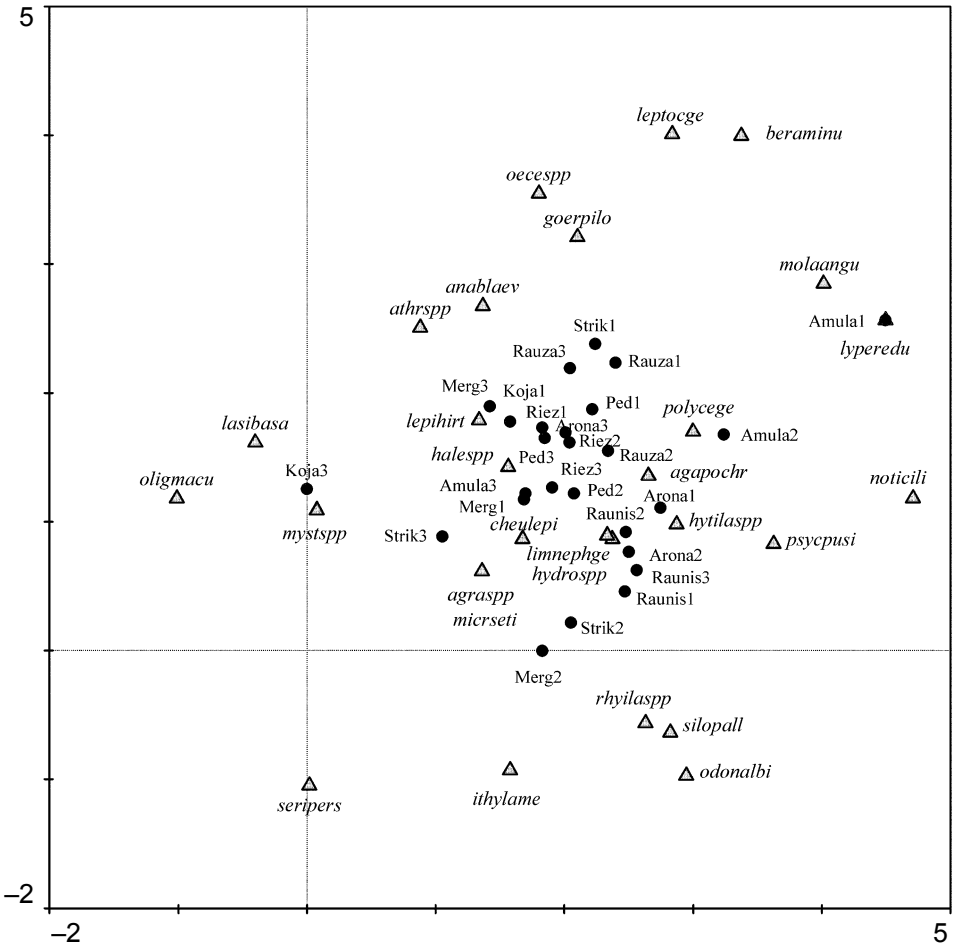

Fig. 5. Correspondence Analysis (CA) ordination biplot displaying stream reaches and abundance of caddisfly taxa. In the stream names 1 indicates the upper reaches, 2 the middle reaches, and 3 the lower reaches. Abbreviations of the species see in Appendix 1.

Table 2. Local chemical, local physical, and regional variables characterized at each sampling site in spring (May–June) 2003

Variable type	Environmental variable	Mean	Minimum	Maximum	Significance, $p \leq 0.05^*$
Local chemical	pH	7.97	7.58	8.39	0.02*
Local chemical	Conductivity, µS/cm	394.92	171	591	0.788
Local chemical	Alkalinity (CO_3^{2-}), mmol/L	3.93	1.80	6.40	0.022*
Local chemical	Cl^-, mg/L	6.32	2.62	11.01	0.662
Local chemical	NH_4^+, mg/L	0.29	0.14	0.52	0.016*
Local chemical	NO_2^-, mg/L	0.01	0.007	0.02	0.356
Local chemical	NO_3^-, mg/L	1.69	0.27	2.4	0.554
Local chemical	PO_4^{3-}, µg/L	32.23	13	76	0.584
Local chemical	N_{tot}, mg/L	5.00	3.24	8.14	0.23
Local chemical	P_{tot}, µg/L	216.38	141	286	0.892
Local chemical	Si, mg/L	2.22	0.64	3.56	0.944
Local chemical	Total hardness, mgekv/L	4.29	1.87	6.67	0.736
Local chemical	BOD_5, mg/L	2.16	0.64	7.04	0.332
Local chemical	Temperature, °C	14.18	8.6	18.8	0.474
Local chemical	Dissolved oxygen content, mg/L	9.15	4.8	14.7	0.426
Local physical	Average width, m	6.65	2.5	12	0.254
Local physical	Mean depth, m	0.33	0.15	0.70	0.01*
Local physical	Mean current velocity, m/s	0.43	0.14	0.87	0.416
Local physical	Psammal (<sand), %	51.15	0	100	0.014*
Local physical	Akal (gravel) (>2 mm–2 cm), %	13.46	0	40	0.212
Local physical	Microlithal (>2–6 cm), %	6.92	0	20	0.24
Local physical	Mesolithal (>6–20 cm), %	12.12	0	45	0.81
Local physical	Macrolithal (>20–40 cm), %	14.81	0	45	0.536
Local physical	FPOM, %	17.88	0	40	0.216
Local physical	CPOM, %	12.88	5	40	0.202
Local physical	Xylal, %	6.35	0	15	0.016*
Local physical	Submarged macrophytes, %	9.62	0	35	0.88
Local physical	Macroalgae, %	2.06	0	15	0.198
Regional	Forests, %	56.18	31.5	80.67	0.2
Regional	Agricultural land, %	41.71	18.53	64	0.984
Regional	Bog area, %	0.94	0	4.4	0.63
Regional	Others, %	1.18	0	4.5	0.724
Regional	Catchment area, km^2	101.14	14.8	241.91	0.008*
Regional	Distance to source, km	18.42	0.62	44.91	0.728
Regional	Altitude, m a.s.l.	97.88	10	189	0.452
Regional	Discharge, L/s	627.54	50	3300	0.356
Regional	Slope, %	2.75	0.2	13	0.23

* Significance level ($p \leq 0.05$) established using the Forward Selection (999 Monte Carlo permutations) procedure.

angustata $F_{0.05} = 4.05$, $p = 0.03$; *Notidobia ciliaris* $F_{0.05} = 5.95$, $p = 0.008$; and *Psychomyia pusilla* $F_{0.05} = 0.036$, $p = 0.035$), and mean depth (*Agraylea* sp. $F_{0.05} = 6.42$, $p = 0.006$; *Ithytrichia lamellaris* $F_{0.05} = 3.38$, $p = 0.052$; *Lasiocephala basalis* $F_{0.05} = 6.47$, $p = 0.006$; *Lype reducta* $F_{0.05} = 0.05$, $p = 0.049$). However, a close relationship to xylal substrate of *Lype reducta* ($F_{0.05} = 6.9$, $p = 0.0045$), *Agraylea* sp. ($F_{0.05} = 6.42$, $p = 0.0061$), and *Notidobia ciliaris* ($F_{0.05} = 3.59$, $p = 0.044$) was established. *Cheumatopsyche lepida* ($F_{0.05} = 5.58$, $p = 0.011$), *Goera*

pilosa ($F_{0.05} = 4.45$, $p = 0.023$), *Hydroptila* sp. ($F_{0.05} = 4.43$, $p = 0.024$), *Lasiocephala basalis* ($F_{0.05} = 3.69$, $p = 0.041$), *Notidobia ciliaris* ($F_{0.05} = 21.7$, $p = 0.0001$), *Psychomyia pusilla* ($F_{0.05} = 3.36$, $p = 0.053$), and *Sericostoma personatum* ($F_{0.05} = 8.53$, $p = 0.0017$) significantly related to pH and *Hydroptila* sp. ($F_{0.05} = 4.26$, $p = 0.027$), while *Notidobia ciliaris* showed a significant relationship ($F_{0.05} = 21.81$, $p = 0.0001$) to alkalinity. *Agraylea* sp. ($F_{0.05} = 22.74$, $p = 0.0001$) and *Notidobia ciliaris* ($F_{0.05} = 21.81$, $p = 0.0001$) significantly related to ammonia content whereas *Athripsodes* sp. ($F_{0.05} = 18.67$, $p = 0.0001$) and *Lepidostoma hirtum* ($F_{0.05} = 17.37$, $p = 0.0001$) related to catchment area. Alkalinity and pH negatively correlated with psammal substrate and mean depth (Fig. 6).

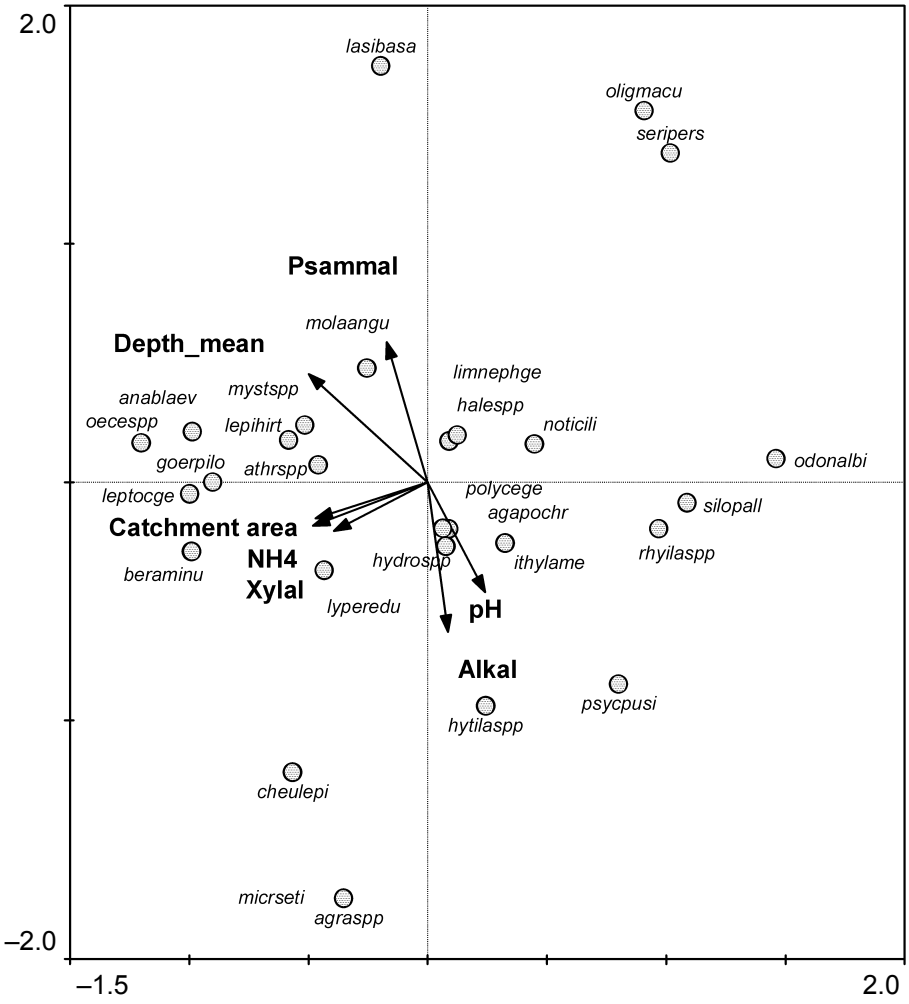

Fig. 6. Canonical Correspondence Analysis (CCA) ordination biplot showing the relationship between the abundance of caddisfly taxa and significant environmental variables ($p \leq 0.05$). Abbreviations of the species see Appendix 1.

Table 3. Results of Partial Canonical Correspondence analyses (pCCA) of the abundance of caddisfly taxa and significant environmental factors ($p \leq 0.05$) with the variance partitioning

Explanatory variables	Explained variance, %	Shared variance, %
Local chemical	16.3	
Local physical	15.68	
Catchments area	4.66	
Local chemical + local physical		3.93
Local chemical + catchment area		1.01
Local physical + catchment area		3.04
Local chemical + local physical + catchment area		12.94
Total variance explained	57.56%	
Residual variance	42.44%	

Hydrochemical and bottom substrate variables explained a large part of the variance of data, while catchment area explained only 4.66% of the variance. Local chemical–local physical, local physical–catchment area, and local chemical–catchment area variables were responsible for similar (relatively small) proportions of the data variance. All three predictor variable matrices together shared a large part of the total caddisfly data variance (Table 3).

DISCUSSION AND CONCLUSIONS

The abundance of caddisflies increased with increasing stream size. Heino et al. (2005) underlined the strong influence of stream size on macroinvertebrate assemblages in Finnish streams. More taxa were added as stream size increased, and no species appeared to be restricted to the headwaters.

TWINSPAN indicator species for two distinct groups differed in substrate preference and functional feeding types. For example, Slack (1936) and Wallace et al. (2003) found that *Agapetus ochripes*, *Goera pilosa*, and *Silo pallipes* are characteristic of stony streams and prefer periphytic algae, whereas *Beraeodes minutus* is associated with submerged roots of emergent vegetation. *Lasiocephala basalis* is particularly associated with submerged wood (Hoffmann, 2000). Net-spinning caddisfly larvae of the family Hydropsychidae are known to prefer microhabitats with large, stable substrate and high flow velocity (Georgian & Thorp, 1992).

Environmental variables strongly relate to communities, but these relationships depend on spatial scale in many cases (Boyero, 2003). Biotic features of streams within the same region and/or longitudinal section tend to be similar, and those characteristics tend to differ when streams belong to more distinct areas (Céréghino et al., 2001). Downes et al. (2000) found that variation among stream sites in the same river is considerably higher than that observed among rivers (Downes et al., 2000). This finding coincides with our results and indicates the

importance of the local environmental variables. As expected, local variables explained the majority of the caddisfly abundance data variance along stream reaches like in other investigations (e.g., Sandin & Johnson, 2004; Costa & Melo 2008; Galbraith et al., 2008). In Swedish streams, local physical factors explain 22% and local chemical variables only 16% of the macroinvertebrate data variance (Sandin & Johnson, 2004).

Similarly to Galbraith et al. (2008), pH and mean depth were significant local variables, which explained a large part of the caddisfly data variance. Species distribution of macroinvertebrates is mostly related to channel width, conductivity, and pH in South Finnish rivers and streams (Soininen & Könönen, 2004). Alkalinity and nitrate ion concentration were the remaining significant local chemical variables. According to Timm et al. (2008), the effect of bedrock on macroinvertebrates usually depends on its alkalinity.

Caddisfly data did not reveal any characteristic river basin pattern (except *Brachycentrus maculatus*, which was found only at streams of the Venta River basin). Regional factors (mainly land use and catchment characteristics) explained a small proportion of the variance due to the specific selection of the sampling sites. The selected streams have a minimal anthropogenic impact and low coverage of agricultural lands in the catchment areas (Springe et al., 2006).

In rivers, habitat is the result of predictable physical processes and so conveniently sits between the forces which structure rivers and the biota, which inhabit them (Harper & Everard, 1998). In many cases, substrate particle size may serve as a common denominator in benthic stream ecology (Cummins & Lauff, 1969). Water depth, roughness, and slope are the principal determinants of hydraulic conditions within river channels. Variation in these parameters results in spatial and temporal heterogeneity in hydraulic conditions (Reid & Thoms, 2008). The microdistribution pattern primarily depends on substrate particle size, food substances, as well as on current velocity and other physical and chemical parameters. Macroinvertebrates probably respond simultaneously to a hierarchical arrangement of such environmental parameters. Thus the degree of discrepancy between tolerance and preference would determine the hierarchical position of an environmental parameter (Cummins & Lauff, 1969). Boyero (2003) found that significant variations of macroinvertebrate communities occur mainly at sample and riffle scales (although different community characteristics may vary at different scales).

Psammal as a significant local substrate variable indicated typological differences in the bedrock of the studied streams, because the majority of them had carbonaceous and only a few siliceous river beds. Additionally, psammal substrate cover and mean depth correlated negatively with the pH and alkalinity (CO_3^{2-}) (mmol/L) (Fig. 6). It is well known that psammal substrates are characterized by a low number of individuals and low taxa diversity (e.g. Allan, 1995).

Xylal substrate positively correlated with catchment area and ammonia ion concentrations (Fig. 6). Depending on the ratio of stream size to wood size, the local amount of wood, and its in-channel position, wood affects the hydraulic regime,

sedimentation and retention processes, and the morphology of running waters, thus strongly shaping the physical in-channel environment (Hoffmann, 2000).

Interactions between wood and the associated biota are based either on direct relationships (e.g., surface associations, wood processing) or on indirect relationships acting through influences on the physical environment or through the spatial and temporal dynamics of the organic matter (Hoffmann, 2000). Caddisflies are a diverse component of the wood-associated fauna and Lepidostomatidae are among the taxa most closely associated with wood (Hoffmann, 2000).

According to the results of a complex spatial scale investigation in Latvian streams, the variability of metrics within the different groups of biological quality elements confirms that large-bodied organisms (macrophytes and fish) are less variable than small-bodied organisms (macroinvertebrates and benthic diatoms) at reach, stream, and river basin scales (Springe et al., 2006). Thus, caddisflies could be used for the study of the influence of local and regional factors on stream ecosystems. The obtained results could give new information on the caddisfly community ecology in lowland streams and the results could be also applied in practice to solve problems related to the evaluation of the ecological quality of running waters using benthic macroinvertebrates.

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APPENDIX 1

Caddisfly taxa with abbreviations for CA and CCA analyses and their abundance (ind./m^2)

Taxon	Abbreviation	Range, ind./m^2
BERAEIDAE		
Beraeodes minutus (Linnaeus 1761)	*beraminu*	3–6
BRACHYCENTRIDAE		
Brachycentrus maculatus (Fourcroy 1785)	*oligmacu*	120
Micrasema setiferum (Pictet 1834)	*micrseti*	82

APPENDIX 1. *Continued*

Taxon	Abbreviation	Range, ind./m^2
GLOSSOSOMATIDAE		
Agapetus ochripes Curtis 1834	*agapochr*	3–77
GOERIDAE		
Goera pilosa (Fabricius 1775)	*goerpilo*	2–18
Silo pallipes (Fabricius 1781)	*silopall*	4–67
HYDROPSYCHIDAE		
Cheumatopsyche lepida (Pictet 1834)	*cheulepi*	4–53
Hydropsyche spp.	*hydrospp*	3–70
HYDROPTILIDAE		
Agraylea spp.	*agraspp*	5
Hydroptila spp.	*hytilaspp*	4–86
Ithytrichia lamellaris Eaton 1873	*ithylame*	10–14
LEPIDOSTOMATIDAE		
Lasiocephala basalis (Kolenati 1848)	*lasibasa*	5–19
Lepidostoma hirtum (Fabricius 1775)	*lepihirt*	2–154
LEPTOCERIDAE		
Athripsodes spp.	*athrspp*	5–139
Leptoceridae gen. sp.	*leptocge*	11–77
Mystacides spp.	*mystspp*	5–10
Oecetis spp.	*oecespp*	3–10
LIMNEPHILIDAE		
Anabolia laevis Zetterstedt 1840	*anablaev*	2–65
Halesus spp.	*halespp*	5–82
Limnephilidae gen. spp.	*limnephge*	5–182
Molanna angustata Curtis 1834	*molaangu*	3–14
ODONTOCERIDAE		
Odontocerum albicorne (Scopoli 1763)	*odonalbi*	4–19
POLYCENTROPODIDAE		
Polycentropodidae gen. spp.	*polycege*	5–84
PSYCHOMYIIDAE		
Lype reducta (Hagen 1868)	*lyperedu*	5–24
Psychomyia pusilla (Fabricius 1781)	*psycpusi*	3–125
RHYACOPHILIDAE		
Rhyacophila spp.	*rhyilaspp*	4–120
SERICOSTOMATIDAE		
Notidobia ciliaris (Linnaeus 1761)	*noticili*	19
Sericostoma personatum (Kirby & Spence 1826)	*seripers*	4–82

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Keskkonnatingimuste mõju ehmestiivaliste (Trichoptera) koosluste levikule Läti keskmise suurusega madalikujõgedes

Agnija Skuja ja Voldemārs Spuņģis

Üheksas Läti jões uuriti 2003. aastal, millised hüdrokeemilised, hüdroloogilised, jõepõhja ja valglaga seotud tegurid mõjutavad ehmestiivaliste putukate levikut jõestikus. Loomad koguti ja proovid töödeldi europrojekti AQEM meetodite kohaselt. Analüüsiti 28 erinevat taksonit. Ülemjooksudel oli ehmestiivaliste arvukus väike, keskjooksudel suur ja alamjooksudel varieeruv. Programm TWINSPAN rühmitas liigid kahte suurde gruppi. Esimese moodustasid kivise põhja ja kiire voolu liigid. Teise rühma esindajad asustavad liivase või kruusase põhjaga jõeosi, kus leidub ohtralt lagunemata orgaanilist ainet. Kõik uuritud mõjurid kokku selgitasid ehmestiivaliste koosluste leviku varieeruvusest 58%, sellest kõige suurema osa hüdrokeemilised ja -füüsilised tegurid. Tulemused kinnitasid, et ehmestiivalisi on võimalik kasutada nii kohaliku kui valglapõhise inimmõju hindamiseks Läti vooluvetes.