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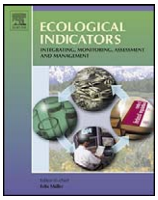

Is fine sediment deposition a main driver for the composition of benthic macroinvertebrate assemblages?

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ABSTRACT

Intensive agriculture causes increased fine sediment and nutrient runoff into running waters. Despite various approaches to quantify the entry of fine sediment into streams, its biological impact is not well understood. In particular, it is unclear whether the potential effects on the biota can be explained by fine sediment loads alone or in combination with other physicochemical and/or hydrological impacts. In this study, we investigated the impact of fine sediment deposition relative to other impacts on the benthic macroinvertebrates in small headwaters in Luxembourg, a region that is sparsely populated and characterised by agricultural land use on the hills and wooded stream valleys. The surficial-deposited fine sediment, content of inorganic sediment, proportions of organic matter, and carbon to nitrogen (C/N) ratio were recorded 1 year. The stream macroinvertebrate assemblages were recorded in the spring and autumn using multi-habitat sampling. A partial canonical correspondence analysis (pCCA) was applied to quantify and verify the impact of individual sediment components and other environmental variables on the community composition, whereas redundancy analysis (RDA) was used to examine the impact of environmental variables on the macroinvertebrate diversity and functional metrics. Oxygen content, C/N ratio as well as fine gravel explained best both the taxa composition and macroinvertebrate metrics, whereas large-scale variables such as land use were less important. The biological response to oxygen deficits and the C/N ratio of the deposited fine sediment indicate the potential effects of fine sediment deposition through oxygen consumption.

Our results show that the chemical composition of the deposited sediment is more important than the amount of sediment, as the C/N ratio alone explained a substantial amount of variance in species composition. Thus, we suggest that future studies on the impact of fine sediment on the macroinvertebrate community should focus on small-scale factors, including the chemical composition of the deposited fine sediment in combination with the physicochemical and hydromorphological stream parameters.

1. Introduction

High amounts of fine sediment are delivered into aquatic systems, mainly through intensive agriculture (Walling and Fang, 2003; Collins and Anthony, 2008; Collins et al., 2011). Although the problem is widely recognised, little is known about the response of biota to fine sediment deposition (Rowe et al., 2003; Bryce et al., 2008; Collins et al., 2011).

Most of the research on the entry of fine sediment and its effects focused on suspended sediment, which can be determined relatively easily (Rowe et al., 2003; Collins et al., 2011). Several studies have addressed bedded subsurface fine particles, which were recorded as substrate composition during freeze-core analyses (Carling, 1981; Ricking and Schulze, 2003). The measurement of suspended fine sediment from interstitial spaces was conducted by Soulsby et al. (2001) and Larsen et al. (2009); sediment-disturbing methods, such as shower sampling (e.g., Kaller and Hartman, 2004) or the imbedding of sediment traps into the streambed (e.g., Fox, 2011), have also been performed. Few studies investigated surficial sediment deposition, which is mostly estimated visually as the substrata bed-cover percentage (e.g., Zweig and Rabeni, 2001; Rowe et al., 2003; Bryce et al., 2008) or identified by proxies, such as flow patterns (partially by Extence et al., 2011). However, the amount of deposited fine sediment is difficult to quantify as no standard method yet exists. Moreover, sediment loads exhibit high spatial and temporal variability (Acornley and Sear, 1999; Collins et al., 2011) exacerbating the quantification of the sediment deposition.

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Elevated fine sediment levels in the suspended solids or the streambed sediments are known to have a wide range of effects on the aquatic biota. Sediment transport and movement of particles affect the feeding and attachment mechanisms of benthic macroinvertebrate such as the clogging of filter-feeding molluscs or blackflies, and the destruction of nets of feeding caddisfly larvae (Kurtak, 1978; Gaugler and Molloy, 1980; Armitage and Blackburn, 2001; Jones et al., 2011). The siltation of streambeds can change the behaviour of organisms by hindering their motility and increasing the drift rate (Culp et al., 1986; Molinos and Donohue, 2009; Larsen and Ormerod, 2010; Jones et al., 2011), and can affect the availability of habitats through a lack of substrate diversity, sediment aggregation and clogging of the interstitial spaces between stones with fine sediment (Burton and Johnston, 2010). This situation can affect the availability of food sources, including the supply of organic matter, and a shift of the periphyton quality (Schofield et al., 2004), thereby influencing the community composition with regard to the richness and abundance of certain invertebrate groups (reviewed by Jones et al., 2011). Indirectly, the entry of fine sediment and organic matter can influence the physical and chemical conditions in streams due to the filling of the interstitial spaces with fine particles, resulting in an increase in decomposition. As a result, the oxygen availability can decline, which is lethal for salmonids spawning in gravels beds and young freshwater pearl mussels (Soulsby et al., 2001; Österling et al., 2010).

Both the sediment load in running waters and aquatic biota are a result of the catchment land use, surrounding vegetation, and in-stream conditions characterised by the geomorphology, hydrology, and topography (Allan, 2004). The non-point input of terrestrial sediments due to soil erosion from tillage or livestock tramping is frequently combined with a runoff of fertilisers, and pesticides and thus is correlated to other stressors (Lenat, 1984; Cooper, 1993; Jones et al., 2001; Allan, 2004). The organic pollution directly or indirectly caused by fertilisers can reduce the abundance of sensitive species (Lenat, 1984; Friberg et al., 2010). Conversely, the surrounding riparian vegetation, such as deep-rooted grasses or trees, stabilises stream banks (Lyons et al., 2000; Allan, 2004; Søvik and Syversen, 2008) and traps sediment and nutrients, thereby reducing the input into aquatic systems (Tomer et al., 2008).

Upland streams are characterised by riffle-pool sequences, a high heterogeneity of substrates, and habitats with different hydrological conditions (Montgomery and MacDonald, 2002). The effect of fine sediment deposition might be expected in riffles due to a high supply of sediment or the accumulation of mud on stones and periphyton, whereas pools may act as natural sinks. The deposited inorganic fine sediment is accompanied to a varying degree by particulate nutrients and organic matter (Parkyn, 2004), and the proportion of mineral particles to organic matter is crucial for decomposition processes and for the quality and availability of food for aquatic macroinvertebrates.

In this study, we measured the fine sediment deposition in 29 riffles and 29 pools of headwater streams 1 year; all of the sites were also subject to standardised macroinvertebrate sampling and the recording of additional environmental variables. With this data, we addressed the following research questions: (1) Do benthic macroinvertebrate assemblages on the reach scale respond to the increased amount of fine sediment deposition? If so, which part of the variability in the community composition is explained by fine sediment deposition in comparison to riparian and catchment variables and physicochemical conditions? (2) Which biotic indices best reflect the biotic response to fine sediment deposition? (3) Is there a quantifiable relationship between the deposition components (amount of fine sediment, organic matter or C/N ratio)? Which component of deposited fine sediments affects the aquatic macroinvertebrate community the most?

2. Materials and methods

2.1. Study streams

The study area is situated in the Ardennes mountain range in northern Luxembourg (Europe) at elevations ranging from 286 to 530 m above sea level (Fig. 1). The region is characterised by rock and clay or silt layers, which tend to experience soil erosion due to the dominant agricultural land use of the upper slopes (Colling et al., 1994).

A total of twenty-nine stream reaches, with catchment sizes ranging from 0.4 to 6.4 km^2 and 1st or 2nd stream orders, were selected in a way that the total study sites covered riparian zones dominated by non-native coniferous forests (mainly *Picea abies*) and deciduous forests (*Fagus sylvatica*, *Carpinus betulus*, and *Quercus petraea*/*robur*). The stream reaches were 3–7 m wide, with a wetted zone of 0.5–4 m and substrata dominated by boulders and gravel. The stream waters were well-oxygenated with average nitrate concentrations of 10.77 $mg\ NO_3^-\ l^{-1}$, average pH values of 7.4, and conductivities ranging between 126 and 253 $\mu S\ cm^{-1}$. The macroinvertebrate communities were diverse and characterised by spring brook species dominated by Ephemeroptera, Plecoptera and Trichoptera.

2.2. Environmental parameters

We recorded 28 environmental variables characterising the catchment, riparian zone, and in-stream features specifying the deposition parameters, cover of bottom substrates, cover of deposited fine sediment, morphometry, and physicochemical parameters.

Data for the catchment area (km^2), land use type and their cover were deduced partly from the project Interreg Projekt NATOUR and Occupation Biophysique du Sol (OBS, 1999) and completed for the sampling sites using ArcGIS version 9.2 (Environmental Systems Research Institute, ESRI) (Table 1). The land-use categories were based on Corine Land Cover, third level (Commission of the European Communities (CEC), 1993). The forest area was subdivided into deciduous, mixed and coniferous forests.

The riparian vegetation type (deciduous forest, coniferous forest, and grassland; mean ± standard deviation and range % of the total area) and amount of shadowing (mean ± standard deviation % of the total area) were recorded as a proportion of the total cover for a stretch of 25 m up- and downstream and a width of 5 m from the banks of the sampling sites (Table 1).

The deposited fine sediment (<2 mm in diameter) was collected upstream of the macroinvertebrate sampling sites to avoid the entry of additional sediment through macroinvertebrate sampling from September 2008 to September 2009 at two sections (one riffle and one pool) at each tested reach. Artificial turf mats (10 cm × 15 cm) were used for the sampling. The mats were anchored with cable ties and iron sticks to the streambed; at three-week intervals, the mats were carefully removed and placed into zip-lock plastic bags to avoid the loss of sediment and transferred to the laboratory. After the collection, new mats were placed at the same locations to enable consecutive sediment sampling. In the laboratory, the upside-down mats and associated water were transferred to aluminium dishes. The residue in the zip-lock bags was suspended with as little tap water as possible and washed into the corresponding aluminium dish. Following these preparations, the mats were left to suspend of sediment for a couple of hours. The mats were subsequently washed with additional tap water, and the remaining water from the aluminium dish was rinsed through a sieve (mesh width = 2 mm) to remove coarse inorganic and organic matter. As a result of this procedure, all of the collected sediment from one site was concentrated in one aluminium dish. Next, the

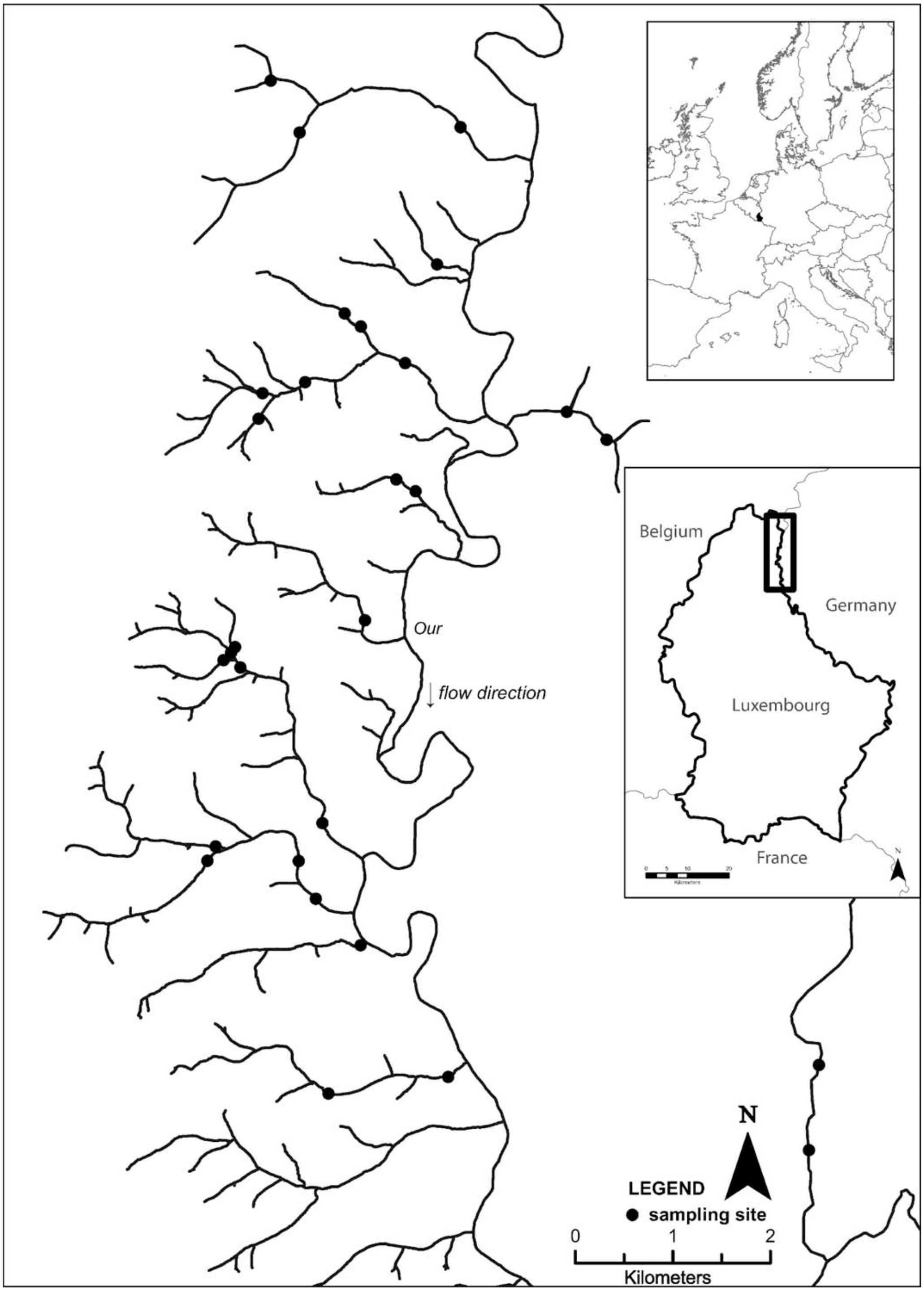

Fig. 1. Sampling sites and streams in the Our catchment (Luxembourg/Germany).

dishes were left undisturbed for at least 2 h to allow the sediment to settle. When the overlaying water was clear, it was removed by suction, leaving only the moist sediment in the dish. The moist sediment was dried in a compartment drier (Memmert, Modell UFE-600) at 100 °C for approximately 5 h. With this procedure, we ensured that the inorganic fraction <2 mm was obtained. All of the samples were weighed using a balance (FAUST FA 1500-2, maximum weight 1.500 g and an accuracy of 0.01 g). The following fine sediment components were obtained. The total carbon (TC) and total nitrogen (TN) were recorded using an Elemental Analyser (EuroEA, HEKAtech GmbH). The presence of $CaCO_3$ was evaluated using HCl and was not found in the sediment; hence, the TC equals the organic carbon (OC). The percentage of organic matter was calculated as a multiplication of the OC by 1.724, assuming the soil material contains 58% carbon (Ad-hoc-Arbeitsgruppe Boden, 2005; Rowell, 1994). The C/N ratio was calculated by dividing the organic carbon (OC = OT) by the total nitrogen (TN). The sediment variables were calculated as the arithmetic means for each sampled reach per year. For linking the sediment deposition patterns to the biota, we calculated all of the sediment variables

Table 1
Mean ± standard deviation (SD) values and range of environmental variables recorded for the 29 sampling sites. CPOM, coarse particulate organic matter. For further explanation, see text.

Variable	Unit	Mean ± SD	Range
Catchment variables			
Catchment area	km^2	2.0 ± 1.6	0.3–6.4
Deciduous forest	%	13.5 ± 9.3	0–30.3
Coniferous forest	%	19.9 ± 9.7	5.2–45.3
Mixed forest		1.1 ± 3.2	0–15.4
Cropland	%	26.6 ± 11.8	4.8–57.1
Pasture	%	30.8 ± 8.8	14.6–47.2
Urban development	%	3.8 ± 3.3	0–10.8
Riparian zone (*R*) land use (5 m)			
Coniferous forest	%	46.6 ± 40.4	0–100
Deciduous forest	%	19.1 ± 32.7	0–100
Grassland	%	7.4 ± 17.6	0–50
Shading	%	68.4 ± 29.1	0–100
Sediment variables			
Fine sediment (deposited)	kg m^{-2}	2.8 ± 1.2	0.9–6.1
Organic matter	%	11.8 ± 3.0	7.7–18.3
C/N ratio		13.1 ± 1.7	10.8–17.3
In-stream variables			
Fine gravel (0.2–2 cm)	%	6.7 ± 8.7	0–30
Microlithal (2–6 cm)	%	21.9 ± 12.1	0–50
Macrolithal (20–40 cm)	%	8.3 ± 12.0	0–40
CPOM	%	7.8 ± 5.1	0–20
Dead wood	%	6.2 ± 8.7	0–40
Cover of deposited fine sediment (<2 mm) (visual estimated)	%	54 ± 24.6	10–95
Pool	%	12.4 ± 10.3	2–35
Max. bank height (R/L)	m	1.07 ± 0.99	0.2–3.5
Physico-chemical parameters (for oxygen mean of two measurements)			
Oxygen (dissolved)		10.2 ± 0.5	9.4–11.6
Oxygen (saturation)	mg l^{-1}	93.4 ± 4.6	85.5–101.2
Conductivity	μS cm^{-1}	239.5 ± 48.7	146.5–329
NH$_4^+$	mg l^{-1}	0.21 ± 0.10	0.05–0.44
NO$_3^-$	mg l^{-1}	9.13 ± 1.68	4.76–12.60
NO$_2^-$	mg l^{-1}	0.05 ± 0.02	0.01–0.12

per season and site (Table 2). The seasons were defined as follows: winter (December–February), spring (March–May), summer (June–August), and autumn (September–November).

The in-stream parameters of substrate cover, percentage of fine sediments (<2 mm), and morphometry were collected prior to and after each sediment sampling period, the estimates based on a length of 25 m up- and downstream of the sampling site. The percentages of the substrates were estimated prior to the macroinvertebrate sampling; the percentage of fine sediment and the proportion of pool habitats were visually estimated. The maximum value of the bank height was obtained from the right and left bank. The following physicochemical parameters were collected: the pH value; the dissolved oxygen (mg l^{-1}), available oxygen (% of saturation), and conductivity (μS cm^{-1}) were measured using the Multi350i (Wissenschaftlich-Technische Werkstätten GmbH, WTW); and the nitrogen components (NO$_3^-$, NO$_2^-$, and NH$_4^+$) were obtained using a photometric analysis using the 109713 Nitrate Test (Merc Spectroquant® Tests). The conductivity was measured at all of the sediment samplings, and the maximum value per site was used for further analyses. The remaining parameters were measured once per macroinvertebrate sampling season, except for the nitrogen fractions, which were measured in spring of 2009 only.

Table 2
Mean ± SD values and range of fine sediment deposition, organic matter content and C/N ratios for 29 headwater streams sampled in 2008–2009 in the Our catchment Luxembourg (Europe). The organic matter and C/N ratios are proportion of the fine sediment content measured.

Variable	Season	Unit	Mean ± SD	Range
Fine sediment	Winter	kg m^{-2}	6.1 ± 2.4	2.0–10.9
Fine sediment	Spring	kg m^{-2}	2.0 ± 1.2	0.3–4.8
Fine sediment	Summer	kg m^{-2}	1.3 ± 1.6	0.2–6.6
Fine sediment	Autumn	kg m^{-2}	1.1 ± 1.1	0.2–5.4
Organic matter	Winter	%/site	6.6 ± 2.4	3.6–11.6
Organic matter	Spring	%/site	10.2 ± 3.4	4.9–16.0
Organic matter	Summer	%/site	15.6 ± 3.8	8.8–24.8
Organic matter	Autumn	%/site	16.1 ± 4.7	7.4–26.3
C/N	Winter	Ratio/site	11.7 ± 1.8	9.61–11.2
C/N	Spring	Ratio/site	13.3 ± 2.2	10.41–18.5
C/N	Summer	Ratio/site	13.8 ± 2.0	9.6–18.0
C/N	Autumn	Ratio/site	13.6 ± 2.1	10.5–18.8

2.3. Macroinvertebrate sampling

Macroinvertebrate samples were collected using a 25 cm × 25 cm frame shovel sampler (500 μm mesh width) in two seasons: 29 samples in the early autumn of 2008 (September/October) and 29 in the spring of 2009 (March/April). The substrate composition was estimated prior to the multi-habitat sampling procedure (Barbour et al., 1999; Hering et al., 2004). Ten samples reflecting the substrate composition were collected in the riffles and pools within a 25 m stretch, preserved (96% ethanol), and transferred to the laboratory for sorting, identification, and counting. When possible, the organisms were identified to the species level with the exception of Oligochaeta (family level) and Diptera (mostly family or tribus level). For further analysis, taxalists resulting from both of the sampling seasons were tallied and used for the calculation of the taxa composition and density for each reach. With the resulting composite taxalists, we calculated the biotic indices and species traits that potentially reflected the influence of fine sediment deposition, such as the diversity and functional metrics (Table 3).

2.4. Biological indices

Twelve biotic indices and species traits were assumed to reflect the impact of sediment on the benthic macroinvertebrates and

Table 3
Mean ± SD of biological metrics calculated for the 29 sampling sites.

Biotic indices	Unit	Mean ± SD	Range
Shannon-Wiener-Index		3.02 ± 0.36	1.86–3.48
Evenness		0.74 ± 0.08	0.47–0.85
Pelal	%	9.54 ± 6.44	2.59–37.10
Agryllal	%	0.35 ± 0.51	0.00–1.92
Gatherer/collector	%	33.20 ± 7.33	17.44–52.62
Grazer	%	25.71 ± 6.39	10.40–36.04
Active filter	%	3.87 ± 2.77	0.88–12.49
Passive filter	%	5.87 ± 6.50	0.76–33.87
Predators	%	8.00 ± 2.87	2.03–13.75
Burrowing/boring	%	18.00 ± 8.02	5.72–39.44
EPT richness	%	57.22 ± 15.38	24.54–79.55
LIFE (Lotic-Invertebrate Index for Flow Evaluation)		7.85 ± 0.22	7.31–8.21

were calculated using Asterics 3.3 (ASTERICS, 2008) (Table 3). We utilised a metric of the invertebrate richness/diversity using Shannon-Wiener-Index (Shannon and Weaver, 1949) and Evenness. The composition/abundance was addressed by the proportion of Ephemeroptera, Plecoptera, and Trichoptera (EPT). The functional measures, such as the microhabitat preference, feeding types, and locomotion types (Schmidt-Kloiber and Hering, 2012), potentially provide additional information on the response to sediment deposition. We selected a proportion of the species preferring habitats of pelal (mud) and agryllal (clay) because the occurrence of these groups may be increased by a high accumulation of mud and clay. The enhanced load of inorganic and organic particles affects both the food source quality and availability; the effect is assumed to be positive for gatherer/collector and passive filter feeders (excess of food) and negative for grazers (reduction of periphyton composition; Schofield et al., 2004), active filter feeders (clogging of filters), and predators (high turbidity decreasing the visual range). Furthermore, metrics indicating the locomotion type of the invertebrates were chosen, such as the proportion of burrowing/boring organisms, to test whether a disturbance in the streambed due to clogging and the embeddedness of interstitial spaces may affect the biota. Lastly, we selected the Lotic-Invertebrate Index for Flow Evaluation (LIFE, Extence et al., 1999), which provides information on flow preferences of different invertebrate species and is highly correlated to the Index of Proportion of Sediment-Sensitive Invertebrates (PSI; Extence et al., 2011).

2.5. Statistical analysis

Different ordination methods were used to assess and quantify the impact of the 28 environmental variables and deposited sediment components on the macroinvertebrate community composition and biotic indices. First, a detrended correspondence analysis (DCA) was used to determine the gradient lengths of the response variable data sets (i.e., the community composition and diversity and functional indices). As the gradient length of the community composition data was >1.5 standard deviation units, a canonical corresponded analysis (CCA) as a unimodal method was used to analyse the response of the community composition to environmental variables. Forward selection with Bonferroni correction was used (499 Monte Carlo unrestricted permutations) to identity the single environmental variables explaining the variation in the community composition and metrics. Because the catchment area proved to be dominant within the data set, this parameter was run as a co-variable in the CCA to partial out its influence on the explanatory power of the remaining variables. Furthermore, a partial CCA (pCCA; Borcard et al., 1992) was used to separate and quantify the effect of the sediment components (fine sediment, organic matter and C/N ratio) on the community composition.

In pCCA, the variation in the macroinvertebrate community composition was partitioned and the effect of the sediment components was quantified. In the first run, a CCA with all three sediment components was performed to quantify the total variance (explained and unexplained). Then, several partial CCAs (pCCAs) were performed with two sediment components as main explanators and the third component as co-variables and vice versa. For instance, a run consisted of fine sediment and organic matter as two main explanators and the C/N ratio as co-variable. This step was repeated several times with different combinations of all sediment components, resulting in a total of 13 runs. With three sediment components, the total variation of the macroinvertebrate community composition was then partitioned into seven components including covariance terms. The variation explained by these components is then subtracted from the total variation to obtain the unexplained variation. This procedure was repeated for each season (autumn 2008 and spring 2009) separately.

The DCA with the metric data revealed a gradient length <1.5 standard deviation units; thus, the metrics were analysed using redundancy analysis (RDA; Ter Braak and Šmilauer, 2002). Forward selection with Bonferroni correction was also used (499 Monte Carlo unrestricted permutations) to determine the significant variables explaining the variation within the biological metrics.

Linear regression was used to evaluate the relationship between the amount of fine sediment (kg m^{-2}) and percentage of organic matter and C/N ratio and between the percentage of organic matter and the C/N ratio of the sediments (arithmetic means per annum and site).

Prior to the statistical analyses, all of the environmental variables, catchment area, morphometric data, chemistry data, and content of fine sediment were log-transformed ($x + 1$). The land-use/vegetation cover and substrate variables and shading and percentage of organic matter were square-root-transformed. The community composition data, biological metrics, and C/N ratio were processed untransformed. All of the ordination methods (CCA, RDA and pCCA) were performed using CANOCO Version 4.5 (Ter Braak and Šmilauer, 2002), and the linear regressions were performed using Statistica 10.0 (Statsoft Inc., 2009).

3. Results

3.1. Relationship between environmental variables and community composition

All of the environmental variables explained 20.8% (cumulative percentage of species data of the first two CCA axes) of the variance in the benthic invertebrate assemblages. The variance in the community composition was best explained by the oxygen saturation, 15% ($F = 2.56$; $p = 0.002$), followed by the percentage of fine gravel on the streambed (13%; $F = 2.38$; $p = 0.002$) and C/N ratio (11%; $F = 2.04$; $p = 0.002$). The catchment variables, such as land-use cover and the amount of deposited fine sediment in the sampling sites are not significant for explaining the community composition (Fig. 2).

Many taxa were correlated with the presence of fine gravel on the streambed, such as *Brachyptera risi* (Morton, 1896), *Nemurella pictetii* Klapalek, 1900, *Nemoura* sp., *Siphonoperla* sp. (Plecoptera), *Simulium* sp., *Tipula* sp. Linnaeus, 1758 (Diptera), and *Gammarus fossarum* Koch in Panzer, 1836 (Crustacea) (Fig. 2). The oxygen saturation is positively related to *Rhithrogena semicolorata*-Gr. (Ephemeroptera) but negatively to *Sialis fuliginosa* Pictet, 1836 (Megaloptera), *Ibisia marginata* (Fabricius, 1781), Psychodidae Gen. sp. (Diptera) and larvae of *Haliplus* sp. A high C/N ratio correlated with *Crunoecia irrorata irrorata* (Curtis, 1834), *Plectrocnemia conspersa* (Curtis, 1834), *Sericostoma personatum* (Kirby and Spencer, 1826), *Wormaldia occipitalis occipitalis* (Pictet, 1834) (Trichoptera)

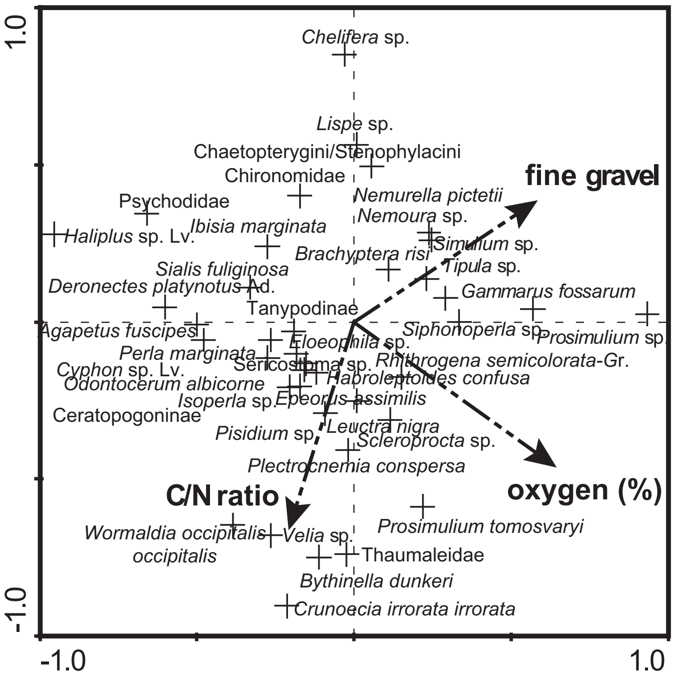

Fig. 2. CCA biplot of significant environmental variables explaining the community composition variation. Taxa with a fit range >10% are also shown. The fit range affords a measure for the variance explained by an individual species (Ter Braak and Šmilauer, 2002). Fine gravel = percentage of fine gravel in the substrate cover; oxygen (%) = oxygen saturation.

Bythinella dunkeri (von Frauenfeld, 1857), *Pisidium* sp. Pfeiffer, 1821 (Bivalvia), *Scleroprocta* sp. Edwards, 1938, Thaumaleidae Gen. sp. (Diptera), *Velia* sp. (Heteroptera), *Leuctra nigra* (Olivier, 1811), *Isoperla* sp. (Plecoptera), *Epeorus sylvicola* (Pictet, 1865), and *Habroleptoides confusa* Sartori and Jacob, 1986 (Ephemeroptera).

3.2. *Relationship between environmental variables and biological metrics*

Two environmental variables explained 33.6% of the variance in the biotic metrics (cumulative percentage of the metric data of the first two RDA axes): the C/N ratio in the deposited fine sediment explained 18% ($F = 6.83$; $p = 0.004$) and dissolved oxygen 16% ($F = 5.42$; $p = 0.016$) of the variance in the biotic metrics. The content of dissolved oxygen was linked to the abundance of passive filter feeders, such as caddisfly larvae (e.g., *Philopotamus ludificatus* and *Hydropsyche instabilis*), but it was negatively correlated to the gatherers and sediment collectors (e.g., worms and certain Ephemeroptera, respectively; Fig. 3). The C/N ratio was connected with taxa richness, such as the evenness, Shannon-Wiener-Index and EPT richness, burrowing/boring biota and LIFE metric, and correlated negatively to the number of active filter feeders (e.g., molluscs) and taxa preferring the pelal. The remaining metrics showed no obvious relationships.

3.3. *Relationship between components of the deposited fine sediment to each other and to the taxa composition with regard to the season*

The amount of deposited fine sediment was negatively correlated to the organic matter content with high significance ($R^2 = 0.51$, $p < 0.0001$) and the C/N ratio ($R^2 = 0.46$), $p < 0.0001$; Fig. 4A and B). In contrast, the correlation between the organic matter and the C/N ratio is positive but weak ($R^2 = 0.32$, $p < 0.05$; Fig. 4C).

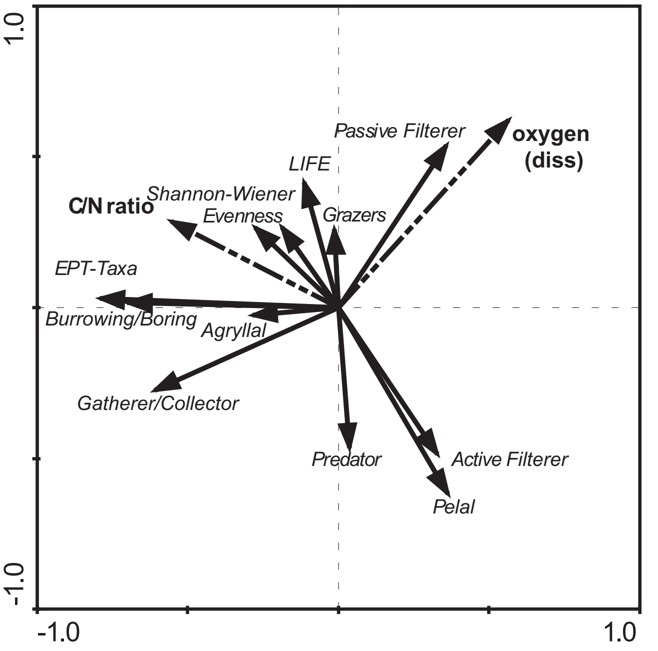

Fig. 3. RDA biplot of the environmental variables in relation to the selected biotic metrics. Only significant variables are shown. LIFE, Lotic-Invertebrate Index for Flow Evaluation; EPT-Taxa, proportion of Ephemeroptera, Plecoptera, and Trichoptera; oxygen (diss), dissolved oxygen.

The amount of deposited fine sediment, proportion of organic matter, and C/N ratio explained 57.1% of the total variance in the taxa for the autumn samples and 52.9% for the spring samples (Fig. 5A and B). For both seasons, the unique effect of the tested variable on the taxa is explained best by the C/N ratio (20.1% autumn; 18.1% spring) and second-best by the organic matter (14.9% autumn; 15.2% spring) followed by the content of fine sediment (14.5% autumn; 15% spring; Fig. 5A and B). In comparison, the high cumulative effect of the C/N ratio, which was recorded as a total of the combined and unique effect, was higher in the autumn and lower in the spring (Fig. 6A and B). The cumulative effect of the fine sediment on the biota was strong in comparison to the unique value for both seasons (Figs. 5 and 6). The cumulative explanation power was higher for the autumn assemblages that the spring assemblages (Fig. 6A and B).

4. Discussion

4.1. *Relationship between environmental variables and taxa composition*

As a criterion of microbial decomposition, the in-stream variability, characterised by the oxygen saturation, substrate composition and C/N ratio, explained approximately 20.8% of the variance of the macroinvertebrate composition. Certain taxa, mainly occurring in the lentic sections, e.g., larvae of Psychodidae (Diptera) and larvae of alderflies (*S. fuliginosa*), are tolerant to oxygen limitation. Several taxa preferred the sections of fine gravel, including the larvae of Plecoptera (e.g., *N. picteti* and *Nemoura* sp.), which are associated with gravel (Graf et al., 2007), whereas the larvae of the crane fly *Tipula* sp. prefer the wet zone along the shoreline. The strong relationship with the substrate can partly be explained by the preference for certain food sources (Lammert and Allan, 1999; Rempel et al., 2000; Usseglio-Polatera et al., 2000; Piscart et al., 2009). Another impairment reflected by the substrate composition is the clogging of the interstitial spaces between the gravel particles by fine sediments, which may

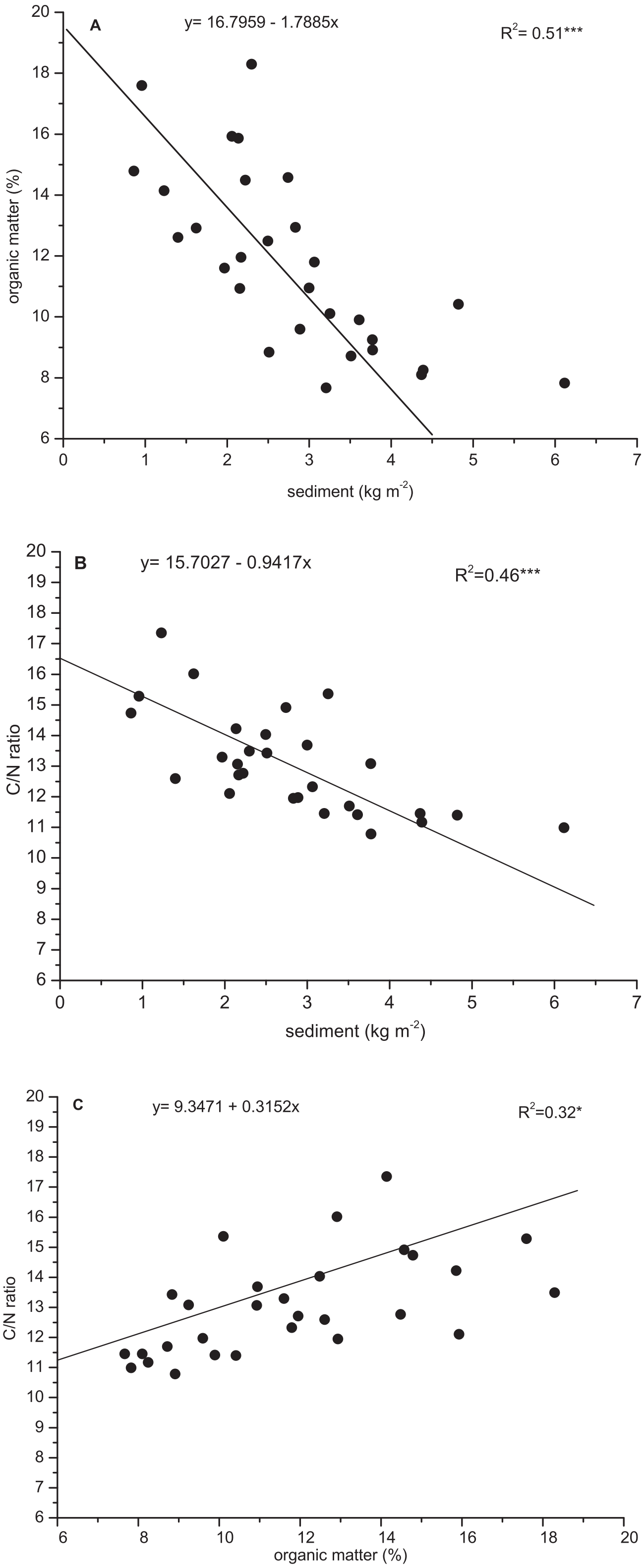

Fig. 4. Linear regression between the components of fine sediment (mean per year at 29 sites showing (A) the amount of fine sediment (kg m^{-2}) and organic matter (%), (B) the amount of fine sediment (kg m^{-2}) and C/N ratio, and (C) the organic matter (%) and C/N ratio. Statistical significance: $^*p < 0.05$; $^{**}p < 0.001$; $^{***}p < 0.0001$.

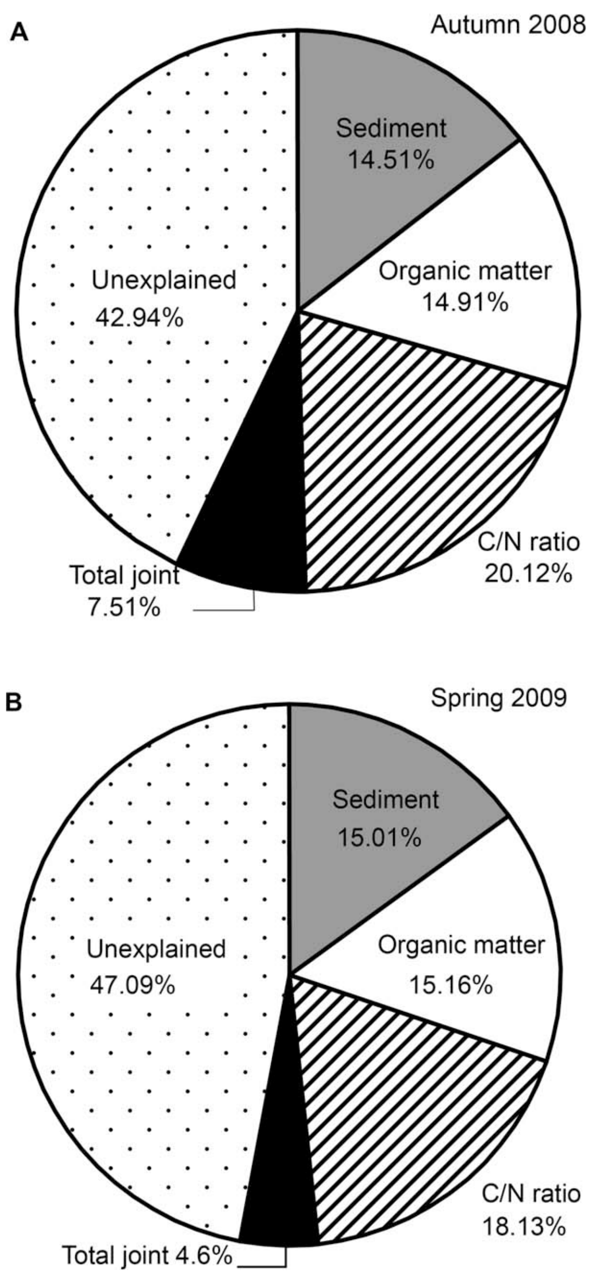

Fig. 5. The sources of variation in the invertebrate composition explained by three components of the fine sediment for autumn 2008 (A) and spring 2009 (B). The percentages of the unique variation for the deposited fine sediment (kg m^{-2}) in grey, percentages of organic matter in white, the C/N ratio (banded), the combined variance of all of the components (in black) and unexplained variance (dotted) of the macroinvertebrate composition are shown.

particularly affect the early larval instars of several taxa living in the hyporheic zone (Minshall, 1984). Several Trichoptera (e.g., *C. irrorata irrorata*, *P. conspersa*, and *W. occipitalis occipitalis*), molluscs (*B. dunkeri* and *Pisidium* sp.), and Plecoptera (*L. nigra* and *Isoperla* sp.) predominantly occurred in the sites with a high C/N ratio. The abundance of these taxa ranged from sporadic (*W. occipitalis occipitalis* and *C. irrorata irrorata*) to highly dense (*Isoperla* sp. and *L. nigra*). Most of these taxa prefer spring brooks and are sensitive to organic pollution; therefore, they prefer unimpaired sites with high C/N ratios. The C/N ratio has a greater effect on the biota than the remaining physicochemical parameters (except for the oxygen saturation). The long-term effect of nutrients in deposited fine sediment might therefore be a key factor for shaping the macroinvertebrate community by impacting the bioavailability of oxygen and dissolved nutrients at the microhabitat level. However, these results could be not validated by other physicochemical variables, such as the biological oxygen demand consumed in

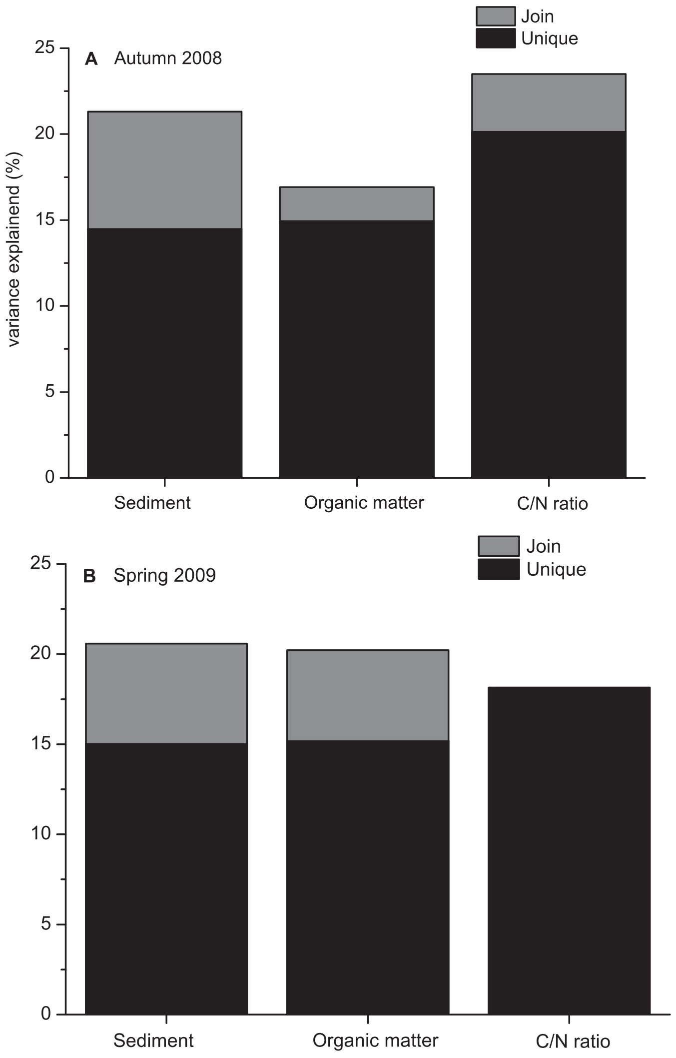

Fig. 6. The cumulative effect of the fine sediment components on the taxa composition in autumn 2008 (A) and spring 2009 (B).

5 days by bacteria (BOD$_5$) or hardness, because these variables were not recorded. In contrast to the C/N ratio, the amount of fine sediment and the proportion of organic matter have no significant effect on the composition of taxa. The C/N ratio affects the physiological conditions directly, whereas the ecological impact of increased amounts of fine particles on the biota is wide-ranging and more complex. The critical effect of fine particle release might be dependent on the physicochemical and hydrological streams conditions. The response of aquatic insects to the sediment load might also be influenced by their actual life stage, i.e., emergence or juvenile. For instance, Hanquet et al. (2004) found that the larvae of *Ephemera danica* prefer different sections of the substrate, depending on larval stage. The young larvae occur in the sections with a higher frequency of coarse substrates and in medium depth, whereas larger nymphs prefer shallow and sandy sections. Many studies suggested that the land-use cover in the catchment and riparian land can predict the biota diversity (e.g., Lenat, 1984; Fritzpatrick et al., 2001), and this linkage is based on the terrestrial provision of nutrients and the alternation of structures in the surrounding area (Lammert and Allan, 1999; Vondracek et al., 2005; Yates et al., 2007). The relationship between the catchment land cover and riparian vegetation to the biota could not be demonstrated directly by our results. Allan (2004) suggested that the impact of land-use variables on the biota is the highest when the land-use status in the catchment area ranges from nearly natural to degraded. This co-variation of the anthropogenic and natural gradient in our study is marginal because of the typical topography of low mountain ranges. This rural region is sparsely populated and dominated by agricultural use in the upper hills and wooded downstream areas. However, the impact of the land-use cover was indirectly connected through the physicochemistry in our study.

In conclusion, our results lend support to the conjecture that chemical composition of the deposited substrates plays a major role and small-scale in-stream factors are crucial for the macroinvertebrate community composition of small streams, which is in contrast to what has been described for streams of a higher stream order (Vondracek et al., 2005; Feld and Hering, 2007; Walsh et al., 2007; Wasson et al., 2010). Hence the land use cover such as in particular the proportion of urbanisation or riparian zone is also a strong significant for the taxonomic composition.

4.2. *Relationship between environmental variables and biological metrics*

Only two in-stream variables, the C/N ratio and oxygen solubility, were related to the metrics; the remaining variables, including the amount of fine sediment in the deposition, were not significantly linked. In several studies regarding the increase of the fine sediment load, a decline of taxa richness (e.g., Cline et al., 1982; Quinn et al., 1992; Jones et al., 2011) and proportion of EPT taxa (Kaller et al., 2001; Matthaei et al., 2006; Pollard and Yuan, 2009) was observed. Those changes in the biota were caused by the modification of the substrate and food sources and by behavioural changes. The C/N ratio is associated with the processes of decomposition and nitrification, which impact the food quality and particularly affect the oxygen concentration. The patches of deposited fine sediment are probably characterised by a reduced oxygen uptake, which alters the diversity of certain sensitive species.

The linkage of the taxa preferring muddy habitats to the physicochemical conditions was obvious, as these taxa tolerate the limitation of oxygen to a greater extent. However, the occurrence of active filterers was negatively correlated to the C/N ratio, and these taxa were generally rare in the spring brooks. In our study, this group was dominated by the mayfly *E. danica* and the mollusc *Pisidium* sp., which occupy muddy substrates that are characterised by a high level of oxygen consumption due to the deposition of fine particles. Passive filterers (for example larvae of the black fly Simuliidae) occurred mainly at the sites with high oxygen saturation, being feeding groups that usually benefit from the supply of particles and an enhanced oxygen availability. This is also shown by the correlation of the LIFE metric for the flow response of the invertebrates and increase of the C/N ratio and amount of oxygen.

4.3. *Relationship between components of the deposited fine sediment to each other and to the taxon composition with regard to the season*

The amount of deposited material per annum is variable, and the ratio between the inorganic sediment and organic matter within this deposited fine material is also variable: the more total material is deposited, the more the proportion of organic material decreases. Although the entry of sediment is a consequence to episodic runoff events, which translates into a short-term increase of the inorganic content, the terrestrial supply of organic matter is more consistent and strongly linked to the surrounding vegetation, such as the dropping of leaves or branches (e.g., Webster et al., 1990; Nietch et al., 2005). The shift between the proportion of a low and high total deposition is caused by the runoff from the surrounding land

and hydrological events throughout the hydrological year, such as discharge peaks (e.g., Delmas et al., 2011).

The weak relationship between the organic matter and C/N ratio suggests that the nutrient content is not solely derived from the organic matter and decomposition processes but is also enhanced through the runoff of fertiliser or animal faeces (e.g., Jarvie et al., 2010). These fractions ultimately accumulate in streambeds.

The results of the pCCA emphasise the high importance of the C/N ratio in comparison to the organic matter and the amount of fine sediment for the benthic macroinvertebrate community and confirm the results of the CCA and RDA with various environmental variables. Aquatic insects represent a wide variety of life history patterns, such as emergence, which has a temporal pattern (Corbet, 1964). Due to this variety, we expected a seasonal difference in the impact of the chemical composition on the taxa composition. The impairment of fine sediment on the biota is equal for both assemblages. In contrast to the organic matter, the cumulative effect of the C/N ratio was stronger in the autumn compared to the spring. These differences might be due to the increase of the algal biomass and the beginning of decomposition processes in the spring, thereby supplying fresh organic matter during this period.

5. Conclusions

The impact of fine sediment on the macroinvertebrate community in running waters has been discussed intensively. In this study, we mainly addressed the question of whether the fine sediment load has a separate effect on the biota or whether the impairment by sediment entry might be intensified as a result of the synergy with variables, such as the flow pattern, solids or nutrient supply (Lemly, 1982; Matthaei et al., 2010; Ormerod et al., 2010). Furthermore, we were interested in the spatial scale to which communities respond, such as the reach scale or patch/microhabitat scale (cf. Larsen et al., 2009). Our results suggest that the chemical composition of fine sediment is mainly responsible for the alternation of the macroinvertebrate community composition in small headwater streams; whereas the overall amount of fine sediment offered no significant explanation for community composition. Both the C/N ratio of the deposited fine sediment and variables representing the oxygen availability were significantly explanatory for the taxa composition. The oxygen demand probably becomes stronger in patches with deposited fine sediment due to silty fractions with lower proportions of fine sand, which is characteristic of fine sediment grains in this region. These cohesive sediments have an affinity for the absorption of organic or toxic components (e.g., Droppo et al., 1997). Agricultural and forested areas dominated in our study; thus, portions of the sediment contain high amounts of nutrients, which can advance the decomposition processes. The significance of fine gravel stretches for the biota reveals the importance of the local stream conditions, which may have a greater effect on the relative abundance of the benthic communities compared to the catchment land-use variables. According to our results, the proportion of EPT Taxa, diversity (Shannon-Wiener-Index and Evenness) and functional metrics such as the LIFE metric are suitable parameters for assessing responses to fine sediment. Although the chemical composition of the sediment load is more important than the actual amount entering the stream, certain mitigation measurements such as having a natural riparian zone, the maintaining of the patchy structure of the stream bed as well the river course help reducing the sediment load into the stream as well as provide more qualitative food such as leaves, and thus reduce the decomposition and the lack of oxygen. However, further experimental studies are needed to measure the impact of sediment load, nutrient supply and oxygen demand of the different fine sediment fractions as well as the impact on aquatic biota.

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