



## Responses of macroinvertebrate communities to land use specific sediment food and habitat characteristics in lowland streams



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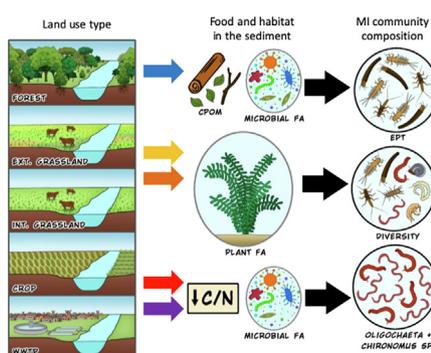
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### HIGHLIGHTS

- Lowland stream sediment food and habitat characteristics were land use specific.
- Macroinvertebrate community composition was also land use specific.
- EPT richness was positively related to the presence of woody debris.
- Shannon-Wiener diversity was well explained by fatty acids origin.
- Oligochaeta and *Chironomus* sp. abundances were explained by a low sediment C/N ratio.

### GRAPHICAL ABSTRACT



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### ABSTRACT

The input of land use specific organic matter into lowland streams may impact sediment characteristics in terms of food resources and habitat structure, resulting in differences in macroinvertebrate community composition. Therefore, we investigated to what extent land use specific sediment food and habitat characteristics structure macroinvertebrate communities. To this purpose linear multiple regression models were constructed, in which macroinvertebrate biotic indices were considered as response variables and sediment characteristics as predictor variables, analysed in 20 stream stretches running through five different land use types. Sediment characteristics and macroinvertebrate community composition were land use specific. The carbon/nitrogen (C/N) ratio, woody debris substrate cover and the origin of fatty acids influenced macroinvertebrate community composition. Shannon-Wiener diversity was better explained by fatty acids origin, such as in grassland streams, where a higher relative content of plant derived fatty acids related to a higher macroinvertebrate diversity. In cropland and wastewater treatment plant (WWTP) streams with a low C/N ratio and dominated by microbial derived fatty acids, higher abundances of Oligochaeta and *Chironomus* sp. were observed. Ephemeroptera, Plecoptera, and Trichoptera (EPT) richness was positively related to woody debris substrate cover, which only occurred in forest streams. Hence, macroinvertebrate community composition was influenced by the origin of the organic material, being either allochthonous or autochthonous and when autochthonous being either autotrophic or heterotrophic. It is therefore concluded that sediment food and habitat characteristics are key ecological filters.

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## 1. Introduction

Catchment land use strongly defines the structure and functioning of stream ecosystems, urging for a better understanding of the connection between terrestrial and aquatic ecosystems (Sponseller and Benfield, 2001; Palmer et al., 2014; de Vries et al., 2019; Krynak et al., 2019). Impacts from different land use types on benthic ecosystems and macroinvertebrate community structure have been reported (Lu et al., 2014; Dalu et al., 2017; Miltner and McLaughlin, 2019; Wang et al., 2019), but the key environmental variables driving land use specific benthic community composition remain unclear. The input of terrestrial fine sediment may influence the sediment characteristics in streams (Burcher and Benfield, 2006; Kominoski and Pringle, 2009; Gieswein et al., 2019), particularly in deposition zones, where allochthonous materials, woody debris, and nutrients accumulate (Golladay et al., 1987; Pusch et al., 1998). Since the composition of allochthonous material differs between land use types (e.g. Matthaei et al., 2010), impacts on stream sediment food and habitat characteristics are expected to be land use specific as well (de Haas et al., 2002; Lu et al., 2014; dos Reis Oliveira et al., 2018), differently affecting local macroinvertebrate communities (Wood and Armitage, 1999; Callisto and Graça, 2013) and aquatic food webs (Cummins and Klug, 1979; Tank et al., 2010). Laboratory studies have indeed shown that macroinvertebrate species respond to differences in sediment characteristics, each preferring a specific sediment food quality (de Haas et al., 2002; Chung and Suberkropp, 2009; Vonk et al., 2016; dos Reis Oliveira et al., 2018). Yet, the role of sediment characteristics in terms of food resources and habitat structure as key ecological filters driving macroinvertebrate community composition remains poorly understood. Therefore, the aim of this study was to determine if lowland stream sediment food and habitat characteristics are land use specific and if they do structure macroinvertebrate communities. To this purpose linear multiple regression models were constructed, in which macroinvertebrate biotic indices were considered as response variables and sediment characteristics as predictor variables. To this end four replicate streams running through five different land use types were sampled, where substrate cover, sediment organic matter composition and the origin of fatty acids were analysed. We hypothesized that the land use specific input of fine sediment and organic matter in lowland stream impact sediment food and habitat characteristics, consequently affecting macroinvertebrate community composition.

## 2. Material and methods

### 2.1. Study area

This study was conducted in October and November 2017, in 20 lowland streams in the Netherlands representing five common land use types. For each land use type, four replicate streams with similar morphological characteristics were selected (mean depth 0.13–0.35 m; width 2.0–2.9 m; current velocity 0.02–0.19 m/s; discharge 0.003–0.022 m<sup>3</sup>/s). The land use types included forest, serving as natural reference sites (hereafter referred to as forest) and streams in areas with non-fertilized pasture (extensive grassland (EG)), fertilized pasture (intensive grassland (IG)), arable field (cropland) and waste water treatment plants (WWTP). The selection criterion for the streams of the land use types forest, grasslands and cropland was the percentage of surface covered in the catchment (>2/3) by the selected land use type (Table S1), as indicated on the national Dutch land use map (LGN5) (Hazeu et al., 2011). The WWTP effluent receiving streams were selected based

on the presence of a sewage treatment plant outflow (~50,000 people).

The stream oxygen conditions differed between the land use types, where dissolved oxygen saturation (DO) in the water column was the lowest in cropland streams and the sediment oxygen demand (SOD) was the highest in WWTP streams (Table 1) (dos Reis Oliveira et al., submitted for publication).

### 2.2. Sediment sampling

In the middle reach of each of the 20 streams deposition zones were identified as a 20 m stretch, defined as deeper instream areas where current velocity was low, measured with an electromagnetic current meter Valeport model 802 and where fine particulate organic matter (FPOM) accumulated. A composite sediment sample was taken per stream from representative deposition zones by sampling the top 2 cm layer using an acrylic core several times until 500 g sediment was collected, allowing to perform all analyses. The samples were freeze-dried (CoolSafe 55-9 Pro) directly after sampling and subsequently analysed for sediment characteristics.

### 2.3. Sediment characteristics

In the present study, sediment characteristics included substrate cover, sediment composition and the origin of fatty acids. Substrate cover and sediment composition data were obtained from a parallel study in the same streams (dos Reis Oliveira et al., submitted for publication). Substrate cover, used as a proxy for habitat structure, was determined by the relative amount of woody debris, macrophytes, coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) on the sediment of a 20 m stream stretch. Substrate cover was estimated according to Hering et al. (2003), quantifying the cover percentage of all mineral substrates and biotic microhabitats.

To determine the sediment composition, a subsample of ball-milled sediment was taken per stream for organic matter content (OM), total carbon (TC), total nitrogen (TN) and chlorophyll-*a* content (Chl<sub>a</sub>) measurements. The TC and TN were measured using an elemental analyzer (Elementar Vario EL, Hanau, Germany) and OM by loss of weight-on ignition of oven dried (105 °C) material at 550 °C for 16 h. Sediment chlorophyll-*a* concentrations were quantified according to Porra et al. (1989) and Brito et al. (2009), and the respective concentrations were calculated using Lorenzen's equation (Lorenzen, 1967), modified for sediment samples.

$$\text{Chl } a \text{ (mg/g)} = \frac{A \times K \times (665b - 665a) \times V}{g \times l}$$

in which: A is the absorption coefficient of chlorophyll *a* = 11.63, K is the factor to equate the reduction in absorbancy to initial chlorophyll concentration 2.43, 665<sub>b</sub> is the absorbance before acidification, 665<sub>a</sub> is the absorbance after acidification, V is the volume of acetone used for the extraction (ml), g is the grams of sediment sample, l is the path length of cuvette (cm)

Fatty acids origin was determined by first weighing 2 sets of 1 g sediment, extracted by accelerated solvent extraction (ASE) and analysed by gas chromatography-mass spectrometry (GC/MS), performed on a ThermoQuest Trace GC 2000 gas chromatograph connected to a Finnigan Trace MS quadrupole mass spectrometer, according to Jansen et al. (2006). Peak areas for individual fatty acids were identified and quantified using the Xcalibur program (version 1.0.0.1). The origin of fatty acids from various organisms can be identified by the carbon chain length and by the level of unsaturation. Firstly, fatty acids from microbial origin (FA micro) were categorized as the sum of saturated and unsaturated short

**Table 1**

Mean ( $n = 4$ ,  $\pm$  sd) 48 h dissolved oxygen saturation (mean DO sat.), minimum dissolved oxygen saturation during 48 h in the water column and sediment oxygen demand over 24 h (dos Reis Oliveira et al., submitted for publication).

	Forest	EG	IG	Cropland	WWTP
Mean DO sat. (%)	63.6 (13.5)	36.9 (20.8)	66.3 (3.9)	35.9 (45.4)	72.6 (7.5)
Minimum DO sat. (%)	52.9 (15.9)	21.6 (19.8)	53.0 (7.2)	16.9 (23.0)	53.2 (10.7)
SOD (gO <sub>2</sub> m <sup>-2</sup> day <sup>-1</sup> )	0.32 (0.10)	0.33 (0.03)	0.34 (0.08)	0.40 (0.17)	0.68 (0.18)

carbon chain fatty acids (C14 to C18) (Napolitano, 1999; Bianchi and Canuel, 2011), while plant derived fatty acids (FA plant) were considered to be the sum of saturated and unsaturated long carbon chains (C22 to C32) (Meyers and Ishiwatari, 1993; Bianchi and Canuel, 2011). Secondly, the autotrophic or heterotrophic nature of the microbial fatty acids was determined (Whatley et al., 2014a). Here, heterotrophic microbial fatty acids were identified by summing the saturated and branched fatty acids, while fatty acids originating from autotrophic microbes were categorized as the sum of monounsaturated and polyunsaturated fatty acids. Subsequently, the ratio between heterotrophic/autotrophic microbial fatty acids (SB/MP) was calculated per stream.

#### 2.4. Macroinvertebrate community composition

To characterize the effects of fine sediment input in stream ecosystems on macroinvertebrates, in each stream four replicate macroinvertebrate samples were taken from the deposition zones using a Surber sampler (surface area: 625 cm<sup>2</sup>; mesh size: 0.5 mm). Within 48 h, the collected organisms were sorted and identified to the genus level. Species richness (number of taxa), Shannon–Wiener diversity index, relative abundance of Ephemeroptera, Plecoptera and Trichoptera (EPT) individuals, EPT richness, the relative abundance of Oligochaeta individuals (O), the sum of the relative abundance of Oligochaeta and Chironomidae individuals (O + Ch) and the total number of *Chironomus* sp. individuals divided by the total number of Chironomidae (C/Ch) were calculated. To assess the quality of the stream in terms of macroinvertebrate community composition, EPT and EPT richness were used to indicate good quality, as these taxa are considered to be sensitive to stream degradation (e.g. Lenat and Resh, 2001), while O + Ch and C/Ch were indicative of poor environmental quality, as many Oligochaeta and Chironomidae taxa, especially *Chironomus* sp. can tolerate high levels of organic pollution (e.g. Kerans and Karr, 1994; Czerniawska-Kusza, 2005). In addition, all individuals were classified according to their functional feeding traits derived from the autecological database for freshwater organisms, version 7.0, accessed on 01 February 2019 ([www.freshwaterecology.info](http://www.freshwaterecology.info)), and subsequently the relative abundances of the different functional feeding groups (Moog, 1995) were calculated.

#### 2.5. Data analyses

To evaluate whether sediment characteristics were land use specific, a principal component analysis (PCA) was performed on log-transformed data of substrate cover of woody debris, macrophytes, CPOM and FPOM, OM content, C/N ratio, chlorophyll-a, and microbial and plant derived fatty acid content and the SB/MP ratio. As the sediment characteristics (response data) were compositional and had a 0.9 SD units long gradient, a linear method was recommended (Ter Braak and Šmilauer, 2002). The PCA was therefore performed in CANOCO for Windows version 5.12 (Ter Braak and Šmilauer, 2002).

Differences in fatty acid origin between land use types were tested separately using one-way analysis of variance (ANOVA), followed by a Tukey post hoc test (R-package stats). In the cases where the conditions of data normality (Shapiro–Wilk test) and

homogeneity of variances (Levene's test) were violated, differences between means were evaluated using the non-parametric Kruskal–Wallis test, followed by a Mann–Whitney pairwise comparison test (Bonferroni corrected: 0.05/4,  $\alpha = 0.0125$ ) to compare the streams from the five different land use types (R-package multcompView). To test the differences between microbial and plant derived fatty acids content per land use type, T-tests were used.

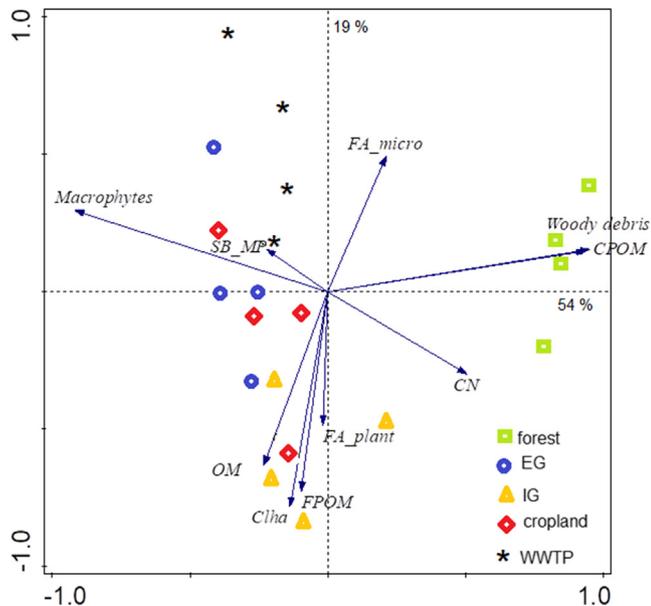
In order to consider the multiple streams and the surber replicates per stream in the statistical analyses, differences in macroinvertebrate community indexes and functional feeding groups between land use types were tested using a linear mixed effect model with land use type and within stream location as fixed effects and stream surber replicates as random effect (R-packages lmerTest and emmeans) (Kuznetsova et al., 2017).

To evaluate how much of the variance in macroinvertebrate community composition was explained by the sediment food and habitat characteristics, generalized linear models (GLM) were applied. To this purpose linear models (multiple regression, assuming Gaussian errors) were formulated, fitted and validated according to Burnham and Anderson (2002), using data from the 20 studied streams. The macroinvertebrate biotic indices and functional feeding group classes means per stream were considered as response variables, and sediment characteristics as predictor variables. Predictor variables were categorized as substrate cover (macrophyte, woody debris, CPOM, FPOM), sediment composition (OM content, C/N ratio, chlorophyll-a concentration) and sediment fatty acid origin (microbial, plant and SB/MP). For each group of predictor variables, models were constructed with all possible combinations of parameters. The Akaike Information Criterion (AIC) was used to select the best statistical models. Models were considered adequate and retained when differing less than 2 AIC from the model with the lowest (best) AIC value. In the resulting model ensemble, the mean of the adjusted R<sup>2</sup> (R<sup>2</sup><sub>adj</sub>) was determined as a measure to explain the variation in macroinvertebrate community composition according to sediment characteristics. Within each group of sediment characteristics, the importance of the contributing parameters was determined by calculating their relative frequency of occurrence in the model ensembles. All analyses were performed in R (R Core Team 2015), using functions from the packages plyr, reshape, rpart (Wickham, 2007; Wickham, 2009; Wickham, 2011; Therneau and Atkinson 2018).

### 3. Results

#### 3.1. Sediment characteristics

In the PCA, the first two axes together explained 73% of the ordination of the sediment characteristics. On axis 1, all forest streams were grouped, positively related to woody debris (factor score = 0.94), CPOM substrate cover (factor score = 0.95), and C/N ratio (factor score = 0.50). All agricultural and WWTP streams were grouped on the opposite side of axis 1, related to macrophyte cover (factor score = -0.50). On axis 2, WWTP streams were positively related to microbial derived fatty acids (factor score = 0.50). Most of the agricultural streams were clustered on the opposite side of axis 2, related to plant derived fatty acids (factor score = -0.50),



**Fig. 1.** Principle Component Analysis biplot for ordination of sediment characteristics in 4 replicate streams per land use type (forest, EG – extensive grassland, IG – intensive grassland, Crop – cropland and WWTP – Wastewater Treatment Plant). The arrows represent the environmental variables C/N ratio (CN), chlorophyll-a (Chla) and organic matter percentage (OM) in the sediment; wood debris, coarse particulate organic matter (CPOM), fine particulate organic matter (FPOM) and macrophytes substrate cover; plant derived fatty acids (FA\_plant), microbial derived fatty acids (FA\_micro) and the ratio between heterotrophic/autotrophic microbial fatty acids (SB/MP).

Chlorophyll-a (Chla) (factor score =  $-0.78$ ), OM (factor score =  $-0.63$ ) and FPOM (factor score =  $-0.73$ ) (Fig. 1 and Table S2). Overall, axis 1 separated sites where the organic matter source was either allochthonous or autochthonous, while axis 2 separated sites where the organic matter originated either from autotrophic (FA\_plant and Chla) or from heterotrophic (SB\_MP) organisms.

### 3.2. Sediment fatty acid origin

Microbial derived fatty acids content (C14 to C18) was significantly ( $p < 0.05$ ) higher in WWTP streams than in EG and IG streams (Fig. 2A). In contrast, in EG and IG streams, plant derived fatty acids content (C22 to C32) was significantly ( $p < 0.05$ ) higher than in WWTP streams (Fig. 2B).

Microbial derived fatty acids content was significantly ( $p < 0.05$ ) higher than plant derived fatty acids content in forest and WWTP streams, while plant derived fatty acids content was significantly ( $p < 0.05$ ) higher than microbial fatty acid contents in EG streams (Fig. 2C). The ratio heterotrophic/autotrophic microbial fatty acids (SB/MP) was higher in WWTP and cropland streams than in forest, EG and IG streams, but these differences were not significant (Fig. 2D).

### 3.3. Macroinvertebrate community composition

#### 3.3.1. Abundances and indices

The WWTP streams were characterized by significant ( $p < 0.05$ ) higher total macroinvertebrate abundances compared to the streams of the other land use types, except for forest. In IG streams, the Shannon-wiener diversity was significantly ( $p < 0.05$ ) higher than in cropland and WWTP streams. Forest streams showed the highest EPT scores, significantly ( $p < 0.05$ ) higher than in the IG and WWTP streams, while also EPT richness was highest in forest

streams, significantly ( $p < 0.05$ ) higher than in all other streams. WWTP streams were characterized by significantly ( $p < 0.05$ ) higher abundances of Oligochaeta. Cropland and WWTP streams contained significantly ( $p < 0.05$ ) higher numbers of *Chironomus* sp. (C/Ch) (Table 2 and S3).

#### 3.3.2. Functional feeding groups

The macroinvertebrate functional feeding groups composition differed between land use types. The relative abundance of grazers was significantly ( $p < 0.05$ ) higher in cropland than in forest and WWTP streams. Shredder numbers were significantly ( $p < 0.05$ ) higher in EG streams than in cropland streams. Gatherers showed significantly ( $p < 0.05$ ) lower relative abundances in EG streams. Relative abundances of active filter feeders (AFF) were significantly ( $p < 0.05$ ) higher in EG streams than in all other streams, except for cropland streams. Passive filter feeder relative abundances (PFF) were significantly ( $p < 0.05$ ) lower in forest streams than in EG and WWTP streams (Table 3).

#### 3.4. The relationship between sediment characteristics and macroinvertebrate community composition

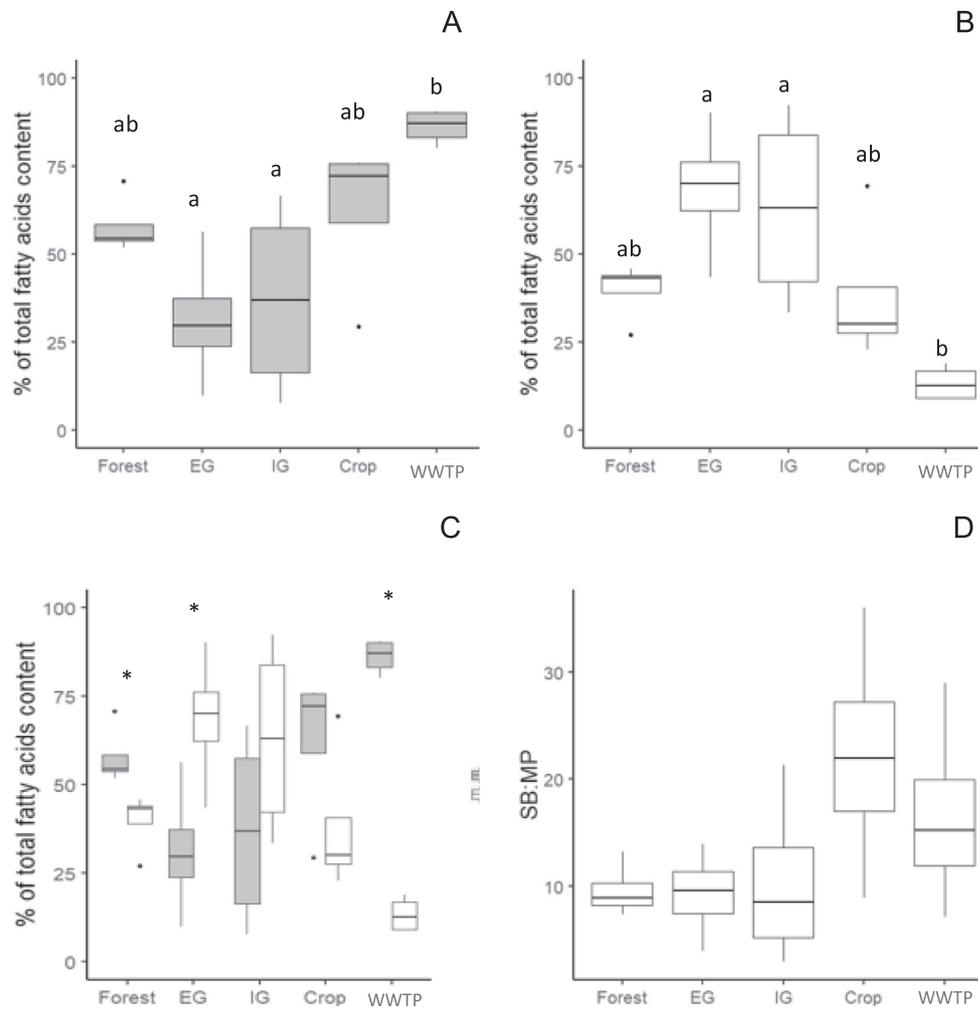
To evaluate the relationship between macroinvertebrate community composition and the sediment characteristics in terms of food resources and habitat structure, GLM analyses were performed. Fatty acids origin was the response variable that better explained macroinvertebrate community indexes: 32 ( $\pm 3$ ) % of the Shannon-Wiener diversity, 21 ( $\pm 1$ ) % of the Oligochaeta abundances, 15 ( $\pm 1$ ) % of the C/Ch ratio and 16 ( $\pm 1$ ) % of the total richness (Fig. 3A). Sediment composition best explained worm abundances ( $24 \pm 1\%$ ) and the C/Ch ratio ( $18 \pm 3\%$ ), where in both cases the C/N ratio occurred in all models (Table S4). Sediment cover better explained EPT richness ( $20 \pm 2\%$ ) and total richness ( $18 \pm 6\%$ ), where for EPT richness the woody debris substrate cover occurred in all models, while for total richness the FPOM cover occurred in all models (Table S4).

When functional feeding groups were used as response variable, sediment characteristics explained no more than 15% of miners and passive and active filter feeders variation (Fig. 3B). The highest  $R^2_{adj}$  was related to the occurrence of active filter feeding individuals in relation to fatty acid origin of the sediment. Concerning the most abundant functional feeding groups (gatherers, grazers and shredders, Table 3), only 2% of the occurrence of gatherers was explained by FA. For grazers, sediment composition explained 10%, where C/N ratio was present in all models (Table S4). For shredders, sediment cover explained 7%, where C/N ratio was present in all models (Table S4, Fig. 3B).

## 4. Discussion

### 4.1. Land use type specific sediment characteristics

Land use type determined the characteristics of the sediments in the deposition zones of the studied lowland streams, in line with other studies (DeLong and Brusven, 1998; Hoffmann, 2005; Rosi-Marshall et al., 2016). In the forest streams, the input of leaves and woody debris from the surrounding terrestrial ecosystem largely determined the sediment characteristics in terms of food resources and habitat structure, composed by microbial derived fatty acids and having a high C/N ratio. Sediment C/N ratio is a reliable indicator of food quality in benthic ecosystems, as higher ratios are associated with streams in catchments with less anthropogenic impacts, as well as a higher food web stability (Rooney and McCann, 2012; Lu et al., 2014; dos Reis Oliveira et al., 2018). In contrast, in the anthropogenically exploited land use types, the



**Fig. 2.** Mean microbial (A) and plant (B) derived fatty acid contents measured in 4 replicate streams per land use type (forest, EG – extensive grassland, IG – intensive grassland, Crop – cropland and WWTP – Wastewater Treatment Plant), the comparison between microbial (Micro) and plant (Plant) derived fatty acid content per land use type (C), and the heterotrophic/autotrophic microbial fatty acids ratio (SB:MP) (D). Different letters indicate a significant difference between the means per land use type ( $p < 0.05$ , analyses of variance followed by multiple comparison test). Asterisks indicate a significant difference between plant and microbial derived fatty acids for each land use type ( $p < 0.05$ ).

**Table 2**

Mean ( $n = 4$ ,  $\pm$ sd) macroinvertebrate community indices per land use type (forest, EG – extensive grassland, IG – intensive grassland, Crop – cropland and WWTP – Wastewater Treatment Plant). EPT is the relative abundance of Ephemeroptera, Plecoptera and Trichoptera individuals; O is the relative abundance of Oligochaeta individuals; O + Ch is the relative abundance of Oligochaeta and Chironomidae; C/Ch is the total number of *Chironomus* sp. individuals divided by the total number of Chironomidae (C/Ch). Different letters indicate a significant difference between the means ( $p < 0.05$ , analyses of variance followed by multiple comparison test).

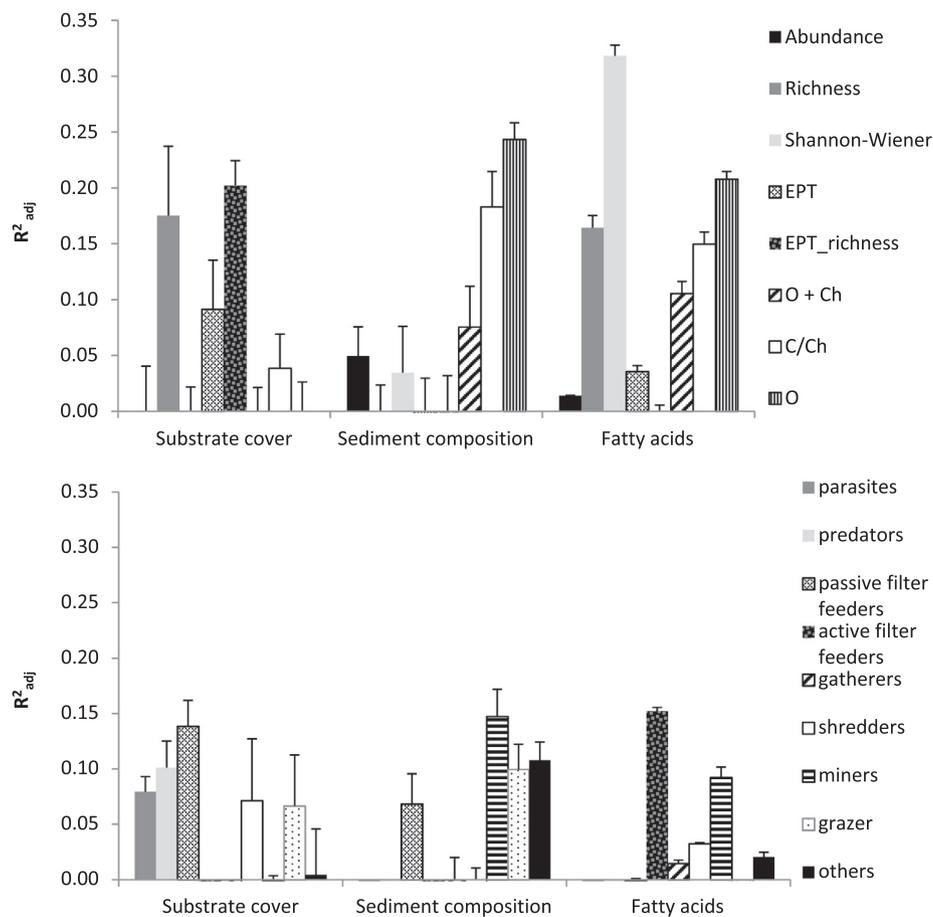
	Forest	EG	IG	Cropland	WWTP
Abundance	400 (581) <sup>ab</sup>	218 (98) <sup>a</sup>	281 (136) <sup>a</sup>	307 (149) <sup>a</sup>	723 (518) <sup>b</sup>
Total number of taxa	19.2 (7.4) <sup>a</sup>	19.4 (5.8) <sup>a</sup>	24.4 (6.5) <sup>a</sup>	19.1 (5.4) <sup>a</sup>	19.3 (10.2) <sup>a</sup>
Shannon-Wiener diversity	1.94 (0.44) <sup>ab</sup>	1.89 (0.68) <sup>ab</sup>	2.33 (0.3) <sup>a</sup>	1.68 (0.44) <sup>bc</sup>	1.17 (0.69) <sup>c</sup>
EPT	0.20 (0.25) <sup>a</sup>	0.15 (0.11) <sup>ab</sup>	0.01 (0.01) <sup>b</sup>	0.11 (0.19) <sup>a</sup>	0.01 (0.01) <sup>b</sup>
EPT richness	6.8 (3.9) <sup>a</sup>	5.3 (2.4) <sup>b</sup>	3.3 (1.7) <sup>b</sup>	1.3 (1.5) <sup>b</sup>	2.8 (2.2) <sup>b</sup>
O	0.12 (0.04) <sup>a</sup>	0.11 (0.05) <sup>a</sup>	0.24 (0.21) <sup>a</sup>	0.35 (0.34) <sup>a</sup>	0.51 (0.32) <sup>b</sup>
O + Ch	0.47 (0.24) <sup>a</sup>	0.20 (0.11) <sup>b</sup>	0.44 (0.26) <sup>a</sup>	0.44 (0.32) <sup>ab</sup>	0.58 (0.35) <sup>a</sup>
C/Ch	0.01 (0.02) <sup>a</sup>	0.12 (0.14) <sup>ab</sup>	0.02 (0.02) <sup>a</sup>	0.34 (0.09) <sup>b</sup>	0.52 (0.44) <sup>c</sup>

composition of the sediments differed, shifting to a prevalence of autochthonous organic matter. In grassland streams, the presence of plant derived fatty acids showed that macrophyte-derived food was dominant, as a result of increased nutrient concentrations in the sediment and a high light incidence. Likewise, Mulholland et al. (2008) and Finlay (2011) also showed that streams located in agricultural grasslands were characterized by a higher primary production than forest streams. Despite the high nutrient concentrations in the sediment of the cropland streams, the water turbidity in these streams hampered the development of autotrophic

organisms (Jones et al., 2014) and heterotrophic microbes served as food source instead, as shown by the high prevalence of microbial derived fatty acids. In WWTP streams, having the highest microbial fatty acids content, the food present in the sediment mainly consisted of heterotrophic microbes growing on top of the sediment, as a result of high concentrations of nutrients released from the WWTP (Battin et al., 2016). Our results are in line with Johnson et al. (2009), who also observed that land-use specific organic matter input determined autotrophic and heterotrophic biofilm development on stream bottom substrates. Therefore,

**Table 3**  
Mean ( $n = 4$ ,  $\pm$ sd) relative abundance of functional feeding groups indices per land use type (forest, EG – extensive grassland, IG – intensive grassland, Crop – cropland and WWTP – Wastewater Treatment Plant). Different letters indicate a significant difference between the means per land use type ( $p < 0.05$ , analyses of variance followed by multiple comparison test).

	Forest	EG	IG	Cropland	WWTP
Grazer	9.4 (4.5) <sup>ac</sup>	17.6 (13.5) <sup>abc</sup>	15.1 (4) <sup>bc</sup>	24.3 (10.9) <sup>b</sup>	14.8 (4.5) <sup>c</sup>
Miners	0 (0)	0 (0.1)	0 (0)	0 (0.1)	0 (0)
Xylophagous	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Shredders	14.7 (8.4) <sup>ab</sup>	16.4 (14.9) <sup>a</sup>	12 (7.7) <sup>ab</sup>	5.6 (4.5) <sup>b</sup>	12.4 (13.4) <sup>ab</sup>
Gatherers/collectors	52.5 (13.5) <sup>a</sup>	29.2 (10.9) <sup>b</sup>	49.7 (12.1) <sup>a</sup>	45.6 (11.1) <sup>a</sup>	54.5 (20.1) <sup>a</sup>
Active filter feeders	10.8 (9.2) <sup>ac</sup>	20.8 (15.7) <sup>b</sup>	7 (5.3) <sup>ac</sup>	12.8 (9.6) <sup>ab</sup>	2.6 (3.6) <sup>c</sup>
Passive filter feeders	0.6 (0.5) <sup>a</sup>	1.7 (1.1) <sup>b</sup>	0.9 (0.4) <sup>ab</sup>	1.3 (0.8) <sup>ab</sup>	1.5 (1.2) <sup>b</sup>
Predators	11.4 (6.0)	12.4 (8.0)	13.7 (8)	9.2 (5.1)	7.3 (10.3)
Parasites	0.5 (1.5)	0.0 (0.1)	0 (0)	0 (0.1)	0.1 (0.2)
Other	0.1 (0.2) <sup>a</sup>	1.9 (3.6) <sup>a</sup>	1.4 (1.7) <sup>a</sup>	1.2 (1) <sup>a</sup>	6.7 (8.6) <sup>b</sup>



**Fig. 3.** Mean ( $n =$  number of models in Table 3,  $\pm$ sd)  $R^2_{adj}$  of the models ensemble for three sediment response variables: substrate cover, sediment composition and fatty acids origin (FA), explaining the macroinvertebrate community composition indices (EPT is the relative abundance of Ephemeroptera, Plecoptera and Trichoptera individuals; O + Ch is the relative abundance of Oligochaeta and Chironomidae; C/Ch is the total number of *Chironomus* sp. individuals divided by the total number of Chironomidae (C/Ch); O is the relative abundance of Oligochaete individuals) (a) and functional feeding groups (b) observed in 20 lowland streams.

shifts from allochthonous to autochthonous resources in the diets of macroinvertebrates is not only a river continuum effect (Vannote et al., 1980) or seasonal variation (Hunt et al., 2012), but also seems to be determined by anthropogenic activities in a land use type specific way.

#### 4.2. The relationship between sediment characteristics and macroinvertebrate community composition

In line with the differences in sediment characteristics, macroinvertebrate community composition also differed per land use type. Responses of the macroinvertebrate communities to these differences in sediment characteristics were expected,

because consumers react to food composition by changing feeding rates, food selection, production efficiency, biomass and ultimately population growth rate (Bianchi and Canuel, 2002). Indeed, in the present study the sediment characteristics in terms food quality and habitat structure, such as woody debris substrate cover, the C/N ratio and the fatty acid origin all influenced macroinvertebrate community composition. The fatty acids composition better explained the macroinvertebrate Shannon-Wiener diversity, giving valuable insights into the food and energy sources available for aquatic invertebrates (Vonk et al., 2016). In contrast to the community metrics, functional feeding groups were barely related to sediment food composition. In spite of the many attempts to categorize macroinvertebrates into functional feeding groups, in

practice, most macroinvertebrates are omnivores, feeding on different types of food, either fresh or dead organic matter derived from various sources ranging from animals to bacteria (Tierno de Figueroa et al., 2019). Only in cases of excess food availability the species-specific food preferences may be more pronounced. Below, we discuss the relationship between sediment characteristics and macroinvertebrate community composition per land use type.

In forest streams, containing more allochthonous plant derived organic matter characterized by a high C/N ratio, also more EPT taxa were observed. EPT species may take advantage of the presence of the high quality heterogeneous substrates within the wood and CPOM patches, conform Besemer et al. (2009) and Boyero et al. (2011), who argued that heterogeneous substrates support a higher food resource diversity. Moreover, Von Bertrab et al. (2013) reported that a high C/N ratio together with oxygen availability explained the occurrence of EPT taxa. In contrast to the forest areas, in human impacted streams autochthonous organic matter dominated the sediment characteristics. Here, macroinvertebrate community composition varied from a high Shannon-Wiener diversity when the organic matter was plant derived, such as in the grassland streams, to high abundances of *Oligochaeta* and *Chironomus* sp. when the organic matter consisted of heterotrophic microbes, sediment characterized by a low C/N ratio, such as in the WWTP and cropland streams. Hence, macroinvertebrate community composition was influenced by the type of organic matter in the sediment, being either allochthonous or autochthonous and when autochthonous being either autotrophic or heterotrophic.

Sediment characteristics explained approximately one third of the macroinvertebrate community composition ( $GLM R^2_{adj} \leq 32\%$ ), indicating that sediment food quality and habitat structure are obviously not the only drivers of community composition. In forest streams, heterogeneous allochthonous organic matter, high oxygen concentrations and structural habitat availability jointly supported higher numbers of EPT taxa. Yet, the woody debris substrate cover better explained EPT richness, even though no xylophagous species were present. These observations are in strong agreement with Wallace et al. (2015), demonstrating that the addition of physical structures alone in absence of the appropriate detrital food sources did not restore macroinvertebrate communities after anthropogenic disturbance. In the grassland streams, the highest Shannon-Wiener diversity was observed, where autochthonous plant derived food dominated the sediment food sources. Torres-Ruiz et al. (2007) observed that autochthonous organic matter was a richer source of essential fatty acids for most macroinvertebrates than allochthonous matter, which explains partially the higher Shannon-Wiener diversity in grassland streams. Here, sediment fatty acids were mainly plant derived, no harsh oxygen conditions occurred (Table 1) and a suitable structural habitat for many macroinvertebrate species was provided by the macrophytes (Whatley et al., 2014b), jointly sustaining a high biodiversity. *Oligochaeta* and *Chironomus* sp. were abundantly present in the microbial derived fatty acid rich WWTP and cropland streams, feeding on heterotrophic microbial derived food, in line with Fuller et al. (2004). Worms and chironomids which are considered diet generalist (Baumgartner and Robinson, 2017), do not have to feed exclusively on such heterotrophic microbes, but they do survive the low sediment oxygen concentrations caused by the high respiration rate of the microbial activity in the top layer of the sediments (Table 1, Stewart and Franklin, 2008), excluding many other species. This way they can take advantage of the excess of food and persist under these conditions (de Haas et al., 2005; dos Reis Oliveira et al., 2018).

## 5. Conclusions

The present study demonstrated that macroinvertebrate community composition was influenced by the origin of the organic

material, being either allochthonous or autochthonous and when autochthonous being either autotrophic or heterotrophic. It is therefore concluded that sediment food and habitat characteristics are key ecological filters, partially shaping ecosystem structure.

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## Author contributions

PCRO, PFMV, HG and MK designed the experiment. PCRO and MPO conducted the experiment. PCRO and MPO analysed most of the data, and wrote most of the manuscript together with PFMV, HG and MK. PFMV, HG and MK advised on practical issues during the course of the experiment and data processing and contributed to editing and revising draft versions of the manuscript.

## Declaration of Competing Interest

The authors declare no conflict of interests.

## Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2019.135060>.

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