



UvA-DARE (Digital Academic Repository)

The landscape drives the stream

Unraveling ecological mechanisms to improve restoration

dos Reis Oliveira, P.C.

Publication date

2019

Document Version

Other version

License

Other

[Link to publication](#)

Citation for published version (APA):

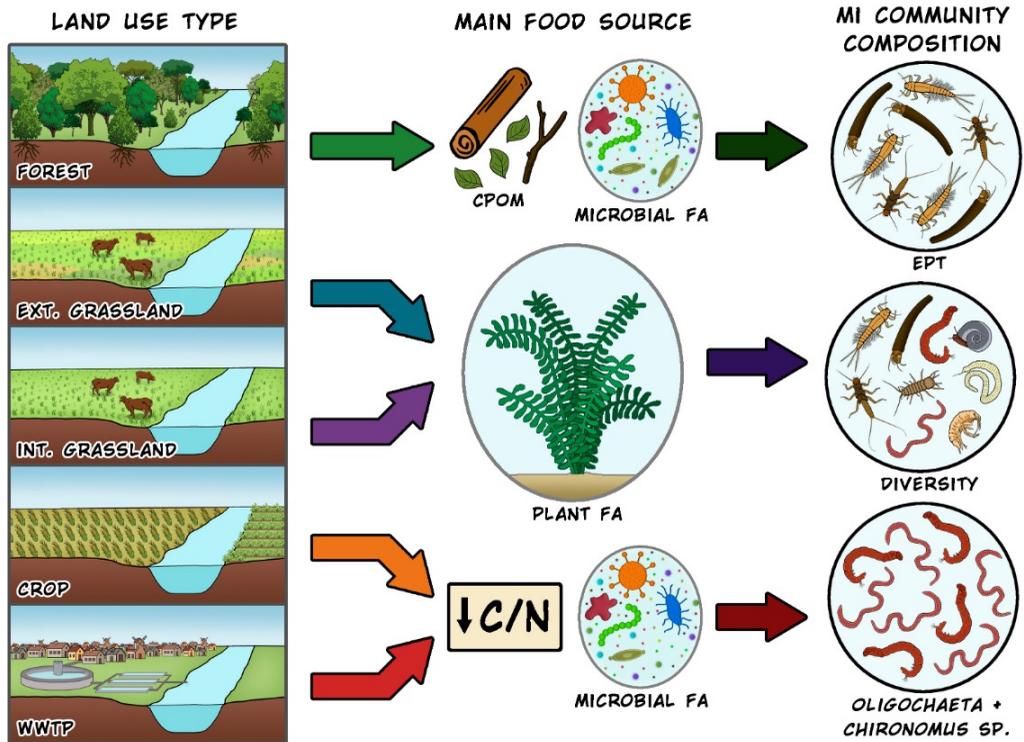
dos Reis Oliveira, P. C. (2019). *The landscape drives the stream: Unraveling ecological mechanisms to improve restoration*.

General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <https://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.



Chapter 5

Responses of macroinvertebrate communities to land use specific sediment characteristics in lowland streams

Paula C. dos Reis Oliveira

Michiel H. S. Kraak

Michelle Pena-Ortiz

Harm G. van der Geest

Piet F. M. Verdonschot

Science of the Total Environment, under review

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.

Highlights

- Lowland stream sediment 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 best explained by fatty acids origin, and
- Oligochaeta and *Chironomus* sp. by low sediment C/N ratio.

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 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. 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 WWTP streams with a low C/N ratio and dominated by microbial derived fatty acids, higher abundances of Oligochaeta and *Chironomus* sp. were observed. 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. Yet, in spite of the observed relation between sediment characteristics and macroinvertebrate community composition, this is obviously not the only driver of community composition. But, if the minimum requirements of the other ecological parameters such as oxygen, habitat heterogeneity and stream velocity are fulfilled, sediment characteristics can certainly be considered as a key ecological filter.

Key words: food resource, C:N ratio, substrate cover, fatty acids, macroinvertebrate indices, GLM

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 (Allan, 2004; Bunn et al., 1999; Palmer et al., 2014; Sponseller and Benfield, 2001). Impacts from different land use types on benthic ecosystems and macroinvertebrate community structure have been reported (Lu et al., 2014; Meyer et al., 1998; Niyogi et al., 2007; Niyogi et al., 2004; Quinn et al., 1997), 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), 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 characteristics are expected to be land use specific as well (De Haas et al., 2002; dos Reis Oliveira et al., 2018), differently affecting local macroinvertebrate communities (Callisto and Graça, 2013; Wood and Armitage, 1999) 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 (Chung and Suberkropp, 2009; De Haas et al., 2002; dos Reis Oliveira et al., 2018; Vonk et al., 2016). Yet, it remains poorly known whether sediment characteristics in terms of food resources and habitat structure are key ecological filters driving macroinvertebrate community composition to the same extent as for example oxygen (e.g. Jacobsen, 2008), habitat heterogeneity (Burdon et al., 2013; Whatley et al., 2014) and stream velocity (e.g. White et al., 2017) do. Therefore, the aim of this study was to determine if lowland stream sediment 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, being either microbial or plant derived, were analysed.

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 0.004–0.022 m³/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 streams in the forested areas served as natural reference sites. The selection criteria for the streams in the forest, grasslands and cropland catchments were based on the percentage of surface covered ($> 2/3$) by the selected land use type, as indicated on the national Dutch land use map (LGN5) (Hazeu et al., 2011). WWTP effluent receiving streams were selected based on the presence of a sewage treatment plant outflow (~50.000 people).

2.2 Sediment sampling

In each of the 20 streams deposition zones were identified in a 20 m stretch, defined as deeper instream areas where current velocity was low and where fine particulate organic matter (FPOM) accumulated. A sediment sample was taken from representative deposition zones by sampling the top 2 cm layer using an acrylic core several times until 500 g sample was collected 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). Substrate cover was determined by the relative amount of woody debris, macrophytes, CPOM (coarse particulate organic matter) and FPOM (fine particulate organic matter) on the sediment, estimated according to Hering et al. (2003) in a 20 m stream stretch.

To determine sediment composition, a subsample of ball-milled sediment was taken for organic matter content (OM), total carbon (C), total nitrogen (N) and

chlorophyll-*a* content (Chl*a*) measurements in each stream. 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 hours. 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).

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 the short 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 the 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., 2014). 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

In each stream, four replicate macroinvertebrate samples were taken from deposition zones using a Surber sampler (surface area: 625 cm²; mesh size: 0.5 mm). Within 48 hours, 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. In addition, all individuals were classified according to their functional feeding traits according to the autecological database for freshwater

organisms, version 7.0, accessed on 01.02.2019 (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, log-transformed data of substrate cover of woody debris, macrophytes, CPOM (coarse particulate organic matter) and FPOM (fine particulate organic matter), OM content, C/N ratio, chlorophyll-*a*, and microbial and plant derived fatty acid content and the SB/MP ratio were included in a PCA, performed in CANOCO for Windows version 5.12 (ter Braak and Smilauer, 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 (R-package multcompView). To test the differences between microbial and plant derived fatty acids content per land use type, T-tests were used.

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 and Brockhoff, 2017).

To evaluate how much of the variance in macroinvertebrate community composition was explained by the sediment characteristics, 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 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 combination 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 adjusted R^2 (R^2_{adj}) was determined as a measure to explain the variation of 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 ordination of the sediment characteristics, the total variance explained was 31.9%, of which 73 % was explained by the first two axis together. On axis 1, all forest streams were grouped, positively related to woody debris, CPOM substrate cover, and C/N ratio. All agricultural and WWTP streams were grouped on the opposite side of axis 1, related to macrophyte cover. On axis 2, WWTPs were positively related to microbial derived fatty acids. Most of the agricultural streams were clustered on the opposite side of axis 2, related to plant derived fatty acids and FPOM (Figure 1 and Table S1 in sup. material). Overall, axis 1 separated sites where the organic matter source was either allochthonous or autochthonous, and axis 2 separated sites where the organic matter originated either from autotrophic or from heterotrophic organisms.

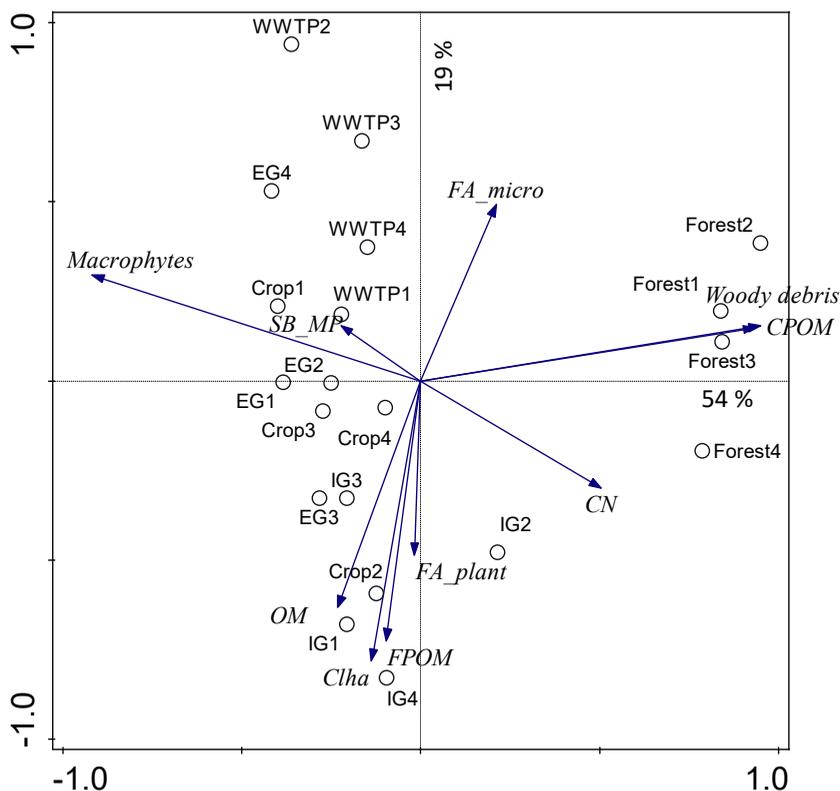


Figure 1: PCA biplot for ordination of sediment characteristics in 4 replicate streams per land use type (forest, EG - extensive grassland, IG - intensive grassland, Crop - cropland and WWTP).

3.2 Sediment fatty acid origin

Microbial derived fatty acids content was significantly ($p < 0.05$) higher in WWTP streams than in EG and IG streams (Figure 2A). Oppositely, in EG and IG streams, plant derived fatty acids content was significantly ($p < 0.05$) higher than in WWTP streams (Figure 2B).

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

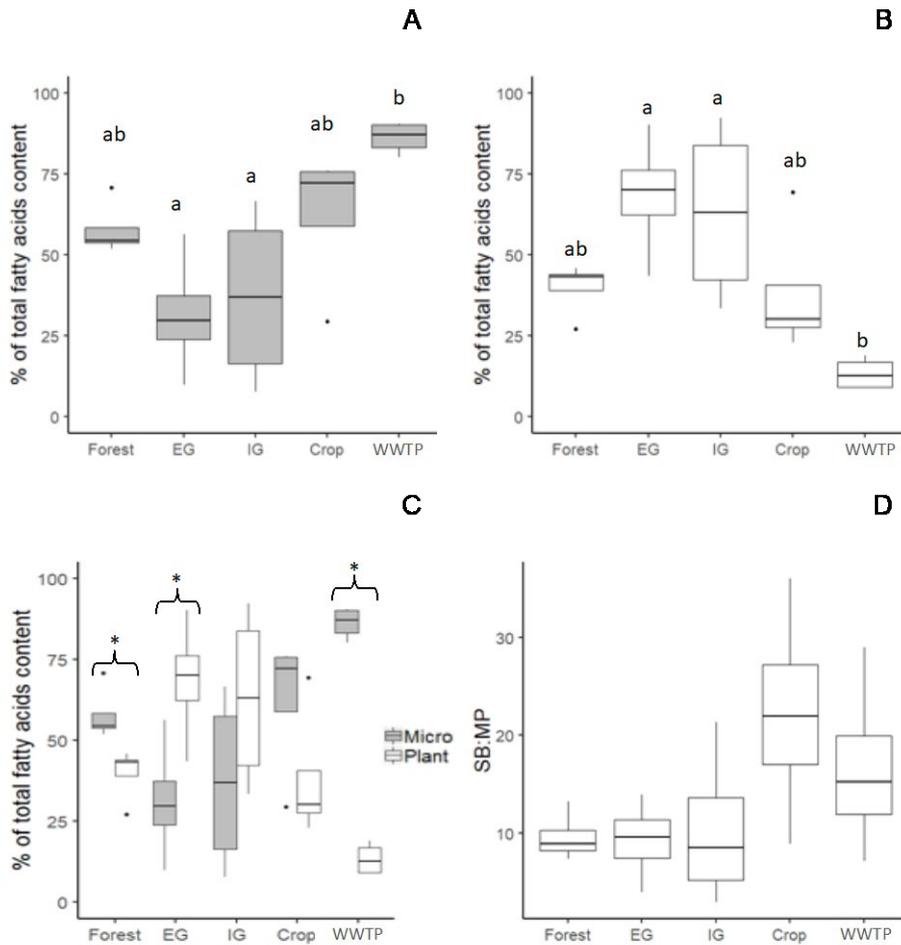


Figure 2: Mean microbial (A) and plant (B) derived fatty acid contents measured in 4 replicate streams per land use type (forest, extensive grassland - EG, intensive grassland - IG, Crop – cropland and WWTP), the comparison between microbial and plant derived fatty acid content per land use type (C), 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 ($p < 0.05$).

3.3 Macroinvertebrate community composition

3.3.1 Abundances and indices

WWTP streams were characterized by a 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 significantly ($p < 0.05$) by higher abundances of Oligochaeta. cropland and WWTP streams contained significantly ($p < 0.05$) higher numbers of *Chironomus* sp. (C/Ch) (Table 1).

Table 1: Mean ($n = 4$, \pm sd) macroinvertebrate community indices per land use type. EPT is the relative abundance of Ephemeroptera, Plecoptera and Trichoptera individuals; O is the relative abundance of Oligochaete 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) ^{ab}	218 (98) ^a	281 (136) ^a	307 (149) ^a	723 (518) ^b
Total number of taxa	19.2 (7.4) ^a	19.4 (5.8) ^a	24.4 (6.5) ^a	19.1 (5.4) ^a	19.3 (10.2) ^a
Shannon-Wiener diversity	1.94 (0.44) ^{ab}	1.89 (0.68) ^{ab}	2.33 (0.3) ^a	1.68 (0.44) ^{bc}	1.17 (0.69) ^c
EPT	0.20 (0.25) ^a	0.15 (0.11) ^{ab}	0.01 (0.01) ^b	0.11 (0.19) ^a	0.01 (0.01) ^b
EPT richness	6.8 (3.9) ^a	5.3 (2.4) ^b	3.3 (1.7) ^b	1.3 (1.5) ^b	2.8 (2.2) ^b
O	0.12 (0.04) ^a	0.11 (0.05) ^a	0.24 (0.21) ^a	0.35 (0.34) ^a	0.51 (0.32) ^b
O + Ch	0.47 (0.24) ^a	0.20 (0.11) ^b	0.44 (0.26) ^a	0.44 (0.32) ^{ab}	0.58 (0.35) ^a
C/Ch	0.01 (0.02) ^a	0.12 (0.14) ^{ab}	0.02 (0.02) ^a	0.34 (0.09) ^b	0.52 (0.44) ^c

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 2: Mean ($n = 4$, \pm sd) relative abundance of functional feeding groups. 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) ^{ac}	17.6 (13.5) ^{abc}	15.1 (4) ^{bc}	24.3 (10.9) ^b	14.8 (4.5) ^c
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) ^{ab}	16.4 (14.9) ^a	12 (7.7) ^{ab}	5.6 (4.5) ^b	12.4 (13.4) ^{ab}
gatherers/ collectors	52.5 (13.5) ^a	29.2 (10.9) ^b	49.7 (12.1) ^a	45.6 (11.1) ^a	54.5 (20.1) ^a
active filter feeders	10.8 (9.2) ^{ac}	20.8 (15.7) ^b	7 (5.3) ^{ac}	12.8 (9.6) ^{ab}	2.6 (3.6) ^c
passive filter feeders	0.6 (0.5) ^a	1.7 (1.1) ^b	0.9 (0.4) ^{ab}	1.3 (0.8) ^{ab}	1.5 (1.2) ^b
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) ^a	1.9 (3.6) ^a	1.4 (1.7) ^a	1.2 (1) ^a	6.7 (8.6) ^b

3.4 The relationship between sediment characteristics and macroinvertebrate community composition

To evaluate the relation between macroinvertebrate community composition and the sediment characteristics in terms of food resources and habitat structure, GLM analyses were performed. One third of the macroinvertebrate community composition expressed by the Shannon-Wiener diversity index was explained by sediment fatty acids origin (Figure 3A). Fatty acids origin was the response variable that better explained macroinvertebrate community indexes: 32 (± 3) % of the Shannon-Wiener diversity, 21 (± 1) % of Oligochaeta abundances, 15 (± 1) % of the C/Ch ratio and 16 (± 1) % of total richness (Figure 3A). Sediment composition explained worm abundances (24 ± 1 %) and the C/Ch ratio (18 ± 3 %), where in both cases the C/N ratio occurred in all models (Table 3). Sediment cover better explained EPT richness (20 ± 2 %) and total richness (18 ± 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 3).

When functional feeding groups were used as response variable, sediment characteristics explained no more than 15% of miners, passive and active filter feeders variation (Figure 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 1),

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 3). For shredders, sediment cover explained 7 %, where C/N ratio was present in all models (Table 3, Figure 3B).

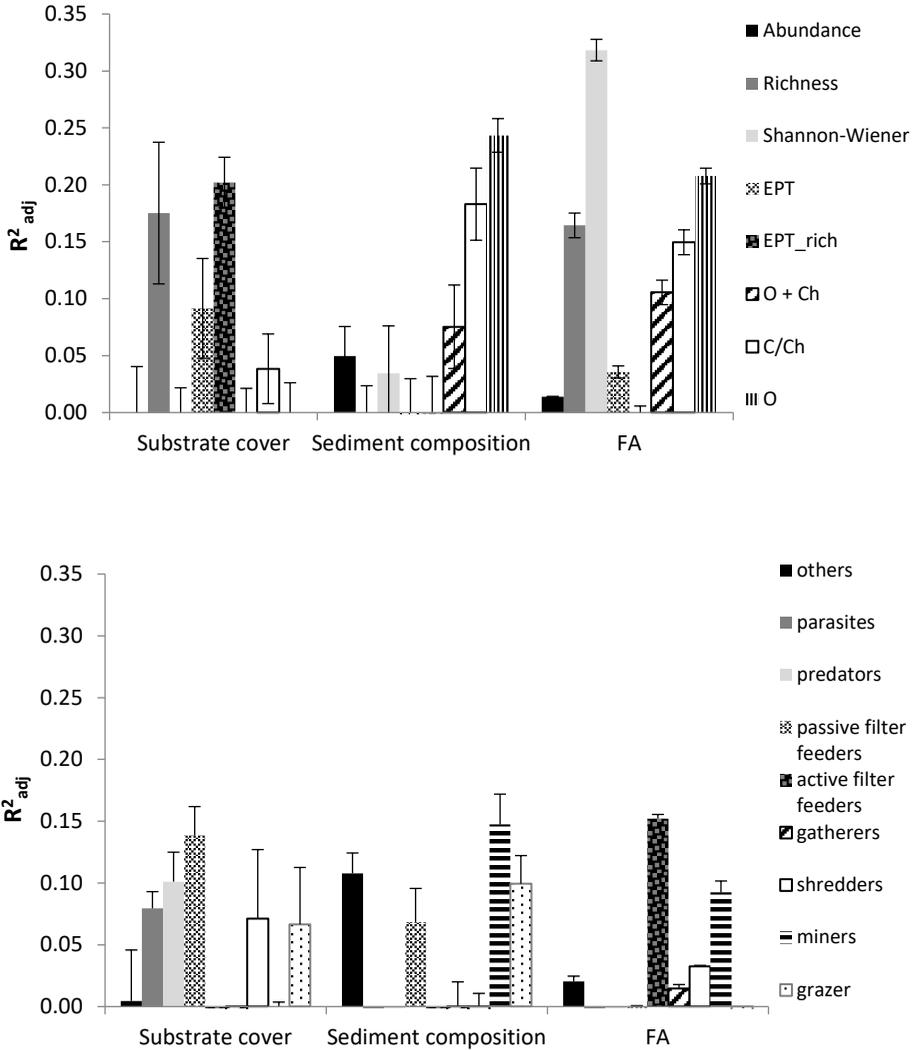


Figure 3: Mean (n = number of models in Table 3, \pm sd) R^2_{adj} of the models ensemble for three food composition response variables: substrate cover, sediment composition and fatty acids origin (FA) explaining the macroinvertebrate community composition indices (a) and functional feeding groups (b) observed in 20 lowland streams.

Table 3: Number of models present in the in ensemble (model) and the fraction of the models in which the variables (FA_{micro}, FA_{plant}; sediment composition: C/N, Chla, OM %; and substrate cover: macrophyte, wood, CPOM and FPOM) were present per variable.

Response variable	Predictor variable												
	Sediment cover					Sediment composition				Fatty acids			
	model	macro- phyte	wood	CPOM	FPOM	model	CN	Chla	OM	model	Micro	Plant	
Macroinvertebrate indices	Abundance	7	0.29	0.29	0.29	0.57	3	1.00	0.30	0.30	3	0.50	0.50
	Richness	3	0.33		0.67	1.00	5	0.40	0.60	0.40	2	0.50	0.50
	Shannon-Wiener	7	0.43	0.43	0.14	0.43	4	0.75	0.50	0.25	2	0.50	0.50
	EPT	3	0.67	1.00		0.33	5	0.40	0.60	0.40	2	0.50	0.50
	EPT _{rich}	3	0.33	1.00		0.33	5	0.40	0.40	0.60	2	0.50	0.50
	O	7	0.29	0.43	0.29	0.43	3	1.00	0.33	0.33	2	0.50	0.50
	O + Ch	7	0.57	0.29	0.29	0.29	4	0.50	0.75	0.25	2	0.50	0.50
	C/Ch	9	0.67	0.44	0.33	0.33	3	1.00	0.33	0.33	2	0.50	0.50
Functional feeding groups	oth	9	0.44	0.33	0.33	0.67	3	1.00	0.33	0.33	2	0.50	0.50
	par	4	0.25	0.75		0.50	5	0.40	0.60	0.40	2	0.50	0.50
	pre	4	1.00	0.25	0.25	0.25	5	0.60	0.40	0.40	2	0.50	0.50
	pff	4	1.00	0.25	0.25	0.25	3	1.00	0.33	0.33	2	0.50	0.50
	aff	7	0.57	0.29	0.29	0.29	5	0.40	0.40	0.60	2	0.50	0.50
	gat	7	0.29	0.29	0.29	0.57	5	0.60	0.40	0.40	2	0.50	0.50
	shr	4	0.50	0.50	0.25	1.00	5	0.60	0.40	0.40	2	0.50	0.50
	min	7	0.29	0.43	0.29	0.43	4	1.00	0.50	0.50	2	0.50	0.50
	gra	5	0.20	0.60	0.20	0.80	3	1.00	0.33	0.33	2	0.50	0.50

4 Discussion

In this study, sediment characteristics in terms of food resources and habitat structure included the categories substrate cover, sediment composition and sediment fatty acid origin. Below, we discuss the differences in sediment characteristics between land use types and evaluate the effects on benthic macroinvertebrate community composition.

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; Quinn, 2000; 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 (dos Reis Oliveira et al., 2018; Lu et al., 2014; Rooney and McCann, 2012). In contrast, in the anthropogenically exploited land use types, the composition of the sediments differed, shifting to a prevalence of autochthonous organic matter. In grassland streams, macrophyte-derived food was dominant, as a result of increased nutrient concentrations in the sediment and a high light incidence. Likewise, Finlay (2011) and Mulholland et al. (2008) 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; Vermaat and de Bruyne, 1993), and heterotrophic microbes served as food source instead. In WWTP streams, 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, 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 is also 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 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 (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 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 with 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.

Yet, in spite of the presently observed relation between sediment characteristics and community composition, sediment characteristics are obviously not the only driver of community composition. As a result of the intermingled relationship between oxygen, habitat quality and sediment characteristics, these three key elements probably shape ecosystem structure in concert. In forest streams, heterogeneous allochthonous organic matter, higher 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. Here, sediment fatty acids were mainly plant

derived, no harsh oxygen conditions occurred (dos Reis Oliveira et al. submitted) and a suitable structural habitat for many macroinvertebrate species was provided by the macrophytes (Whatley et al., 2014), jointly sustaining a high biodiversity. Oligochaeta and *Chironomus* sp. were abundantly present in the WWTP and cropland streams, feeding on heterotrophic microbial derived food. Worms and chironomids however, 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 (Stewart and Franklin, 2008), excluding many other species. This way they can take advantage of the excess of food and persist under these conditions (dos Reis Oliveira et al. 2018; de Haas et al. 2005). It is thus argued that oxygen, habitat quality and sediment characteristics shape ecosystem structure in concert. Hence, sediment food quality does not drive macroinvertebrate community composition to the same extent as oxygen (e.g. Jacobsen, 2008), habitat heterogeneity (Burdon et al., 2013; Whatley et al., 2014) and stream velocity (e.g. White et al., 2017) do, but if the minimum requirements of the other ecological parameters are fulfilled, sediment characteristics can certainly be considered as a key ecological filter.

Supplementary material

Table S1: Sediment composition of the deposition zones (organic matter content (OM %), content carbon/nitrogen ratio (C:N), chlorophyll-*a* (chl_a)) and substrate cover (in % estimated according to Hering et al. 2003) are given as means per land use type (n = 4 replicate streams). Standard deviations are given between brackets. Letters indicate a significant difference between land use types (p < 0.05) based on analyses of variance followed by multiple comparison test (dos Reis Oliveira, submitted).

		forest	EG	IG	cropland	WWTP
Substrate cover	Woody debris (%)	6.6 (2.8)	0 (0)	0 (0)	0 (0)	0 (0)
	Macrophytes (%)	0 (0)	52.1 (30.6)	8.7 (8.0)	27.4 (29.0)	34.4 (28.9)
	CPOM (%)	38.8 (23.1)	0 (0)	0 (0)	0 (0)	0 (0)
	FPOM (%)	25.4 (11.9)	46.7 (29.6)	46.7 (19.7)	72.9 (29.6)	27.1 (34.2)
Sediment composition	OM (%)	3.0 (0.6) ^{ab}	7.7 (5.2) ^a	7.9 (6.3) ^a	14.4 (11.5) ^a	1.4 (0.3) ^b
	C/N	20.4 (2.6) ^a	17.8 (1.5) ^{ab}	17.9 (2.8) ^{ab}	16.6 (1.1) ^{bc}	13.9 (1.3) ^c
	Chl _a (mg/g)	6.7 (7.9) ^a	5.6 (2.1) ^a	41.1 (30) ^b	9.2 (9) ^{ab}	5.9 (5.2) ^a

Acknowledgements: We would like to thank the water authorities Hunze en Aa's and Vallei en Veluwe, João Lotufo and Evan for their help in the field. Thijs de Boer for helping with GIS, and Dorine Dekkers for her help in macroinvertebrate identification. We thank laboratory technicians Mariska Beekman and Samira Absalah. PCRO received funding from CNPq Brazil (grant number 200879/2014-6, 2014).