




# Functional Assemblages of Macroinvertebrates in Pools and Ditches in Drained Forest Landscape

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## Abstract

Artificially drained commercial forests are hydrologically novel ecosystems, where the array of aquatic habitats consists of ditches and remnant pools. In general the network of ditches has been found to have longer hydroperiod, the knowledge, however, about aquatic invertebrates in this system is scarce. We examined which environmental factors are impacting the biomass and abundance of functional feeding groups. Scrapers and shredders were aggregated to ditches and gatherers to pools. Filterers' distribution pattern suggested that the function of filtering is carried out by different taxa in pools and ditches. Ditches were rather more suitable for feeding groups that rely on autochthonous resources. Acidity was a major driver of functional community composition, for example, one of the causes for higher scraper frequency in ditches. Predators exhibited greater quantities in extensive macrophyte cover regardless of water body type. Our results suggest that the trophic organization in ditches and pools is different because habitat factors select the feeding groups directly through food resources, but also because of the environmental filter on the other biological traits of the organisms. To support complex ecosystems with several trophic levels also in commercial forests, we suggest to avoid destroying macrophyte rich pools and ditches during silvicultural management.

**Keywords** Functional feeding groups · forestry drainage · temporary water bodies · drainage ditches

## Introduction

Forestry drainage has been regionally widespread practice for at least 40 years, transforming large areas of (semi)open wetlands and swamps into productive forests (Paavilainen and Päivänen 1995). Forestry drainage is accomplished by excavation of open ditches that lead away excess surface water, lower the ground water table and as a result, improve conditions for tree growth (Laine et al. 1995). Such practices have long-term and largely irreversible repercussions, such as changes in hydrological and disturbance regime,

homogenization of landscape elements, disappearance of wetland-dependent species, reduction of peat soils, and alteration of stand structure and composition (Lõhmus et al. 2015; Paavilainen and Päivänen, 1995). Such novel landscapes are presently encompassing 20–25% of all the forest areas in top-drained regions: Finland, the Baltic States, and parts of Sweden (Paavilainen and Päivänen 1995); in Canada and the US State of North Carolina (Skaggs et al. 2016). Even more, the effects of modified hydrology extend beyond the drained sites to the ecosystems that receive the runoff water (Vuori et al. 1998).

Although forestry drainage does not unambiguously decrease the habitat availability for aquatic organisms, it shortens the hydroperiod of natural pools (Remm et al. 2015; Suislepp et al. 2011) and partly replaces natural water bodies with linear ditch networks (Remm et al. 2015). Ditches have relatively longer hydroperiod (Remm et al. 2015) and connectivity adds the possibility to escape from local drying. In the context of seminatural forestry, the taxonomic composition of macroinvertebrates is similar in ditches and in water bodies in undrained forests; but the gamma diversity is much lower in pools that remain in drained forests (Vaikre et al. 2015). Apart from this, the knowledge about aquatic

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invertebrates in artificially drained forests is scarce and studies on functional communities non-existent (Löhmus et al. 2015).

Functional traits (biological traits) of organisms – well-defined, measurable characteristics that influence species performance in given environment, reflect the response of biota to the environment or its effects to ecosystem processes (McGill et al. 2006; Nock et al. 2016) and could be a useful tool aiding conservation and restoration activities (Diaz and Cabido 2001; Nock et al. 2016). Hydroperiod length may determine the distribution of functional feeding groups that rely on autochthonous resources and thus the differences in functional communities between ditches and pools in a drained forest ecosystem. The abundance and species richness of periphytic algae may increase with shorter hydroperiod, but the abundance of diatoms – critical nutritional component of periphyton (Anderson and Cummins 1979) – is higher in water bodies with longer hydroperiod (Gottlieb et al. 2006; Rober et al. 2013) as is the amount of phytoplankton (Boven et al. 2008).

However, certain environmental factors may be more important than hydroperiod in shaping functional communities. For example, in sun exposed ponds and ditches macrophyte beds favor shredders and scrapers, providing food such as plant litter or algae growing on vascular plants, whereas gathering-collectors predominate in sediments (Bazzanti 2015; Bazzanti et al. 2009; Leslie and Lamp 2017; Sychra et al. 2010). In forest streams, shredders' habitat is mainly formed in concurrence of tree cover with boulders and logs, the latter increasing retentiveness (Haapala et al. 2003; Houghton et al. 2011; Masese et al. 2014), whereas increases in sediment loads, originating from ditching in catchment area, may shift the community to dominance of collector-filterers (Vuori and Joensuu 1996).

In current study, we explore functional feeding groups of macroinvertebrates inhabiting ditches and pools in artificially drained commercial forests, where the whole ecosystem, including the pools, are hydrologically altered. Specifically we aim to:

1) Compare functional feeding communities between ditches and pools. We hypothesize that feeding groups that benefit from autochthonously produced resources (scrapers and filterers) are mostly aggregated to ditches.

2) Measure the responses of functional feeding groups to environmental gradients and find out which contemporary and local habitat factors could explain the possible differences in functional communities between ditches and pools.

## Material and Methods

### Study Area and Design

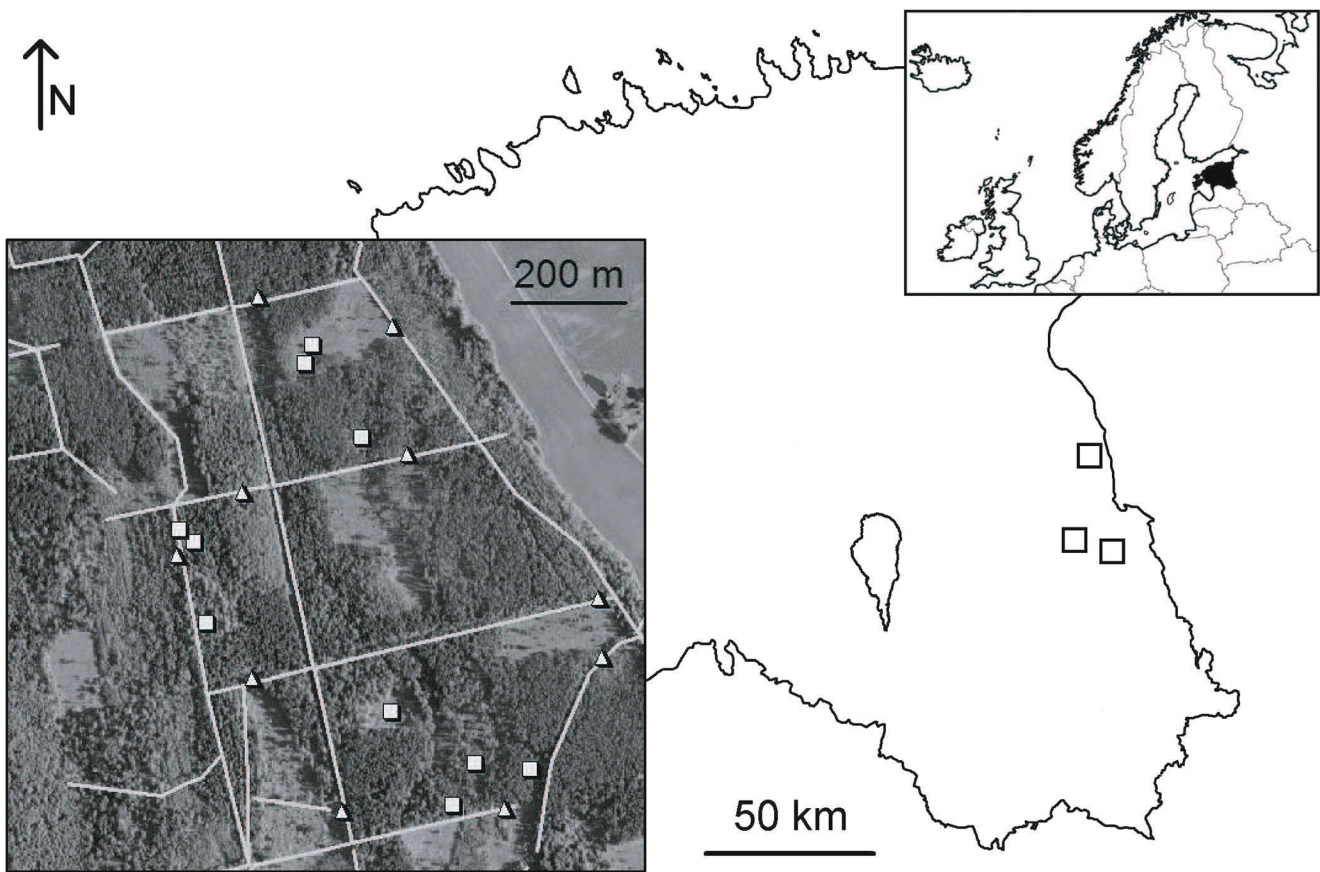
Our study was conducted in Estonia, where large-scale systematized drainage was carried out in the 1950–1980s and resulted in approximately 25% of forests impacted by

drainage (Torim and Sults 2005). Data originate from three artificially drained commercial forest plots (total area 239 ha) (Fig. 1) located on Gleysols and to a smaller extent on shallow peat soils. The tree stand consists of native species: birch (dominant on 39% of the area), pine (32%) and spruce (17%). Prevalent forest site types (Löhmus 1984) were *Vaccinium*, *Oxalis*, *Aegopodium*, *Filipendula*, mesotrophic bog, and stagnant water swamp. Clear cuts with stands younger than five years covered 2.6% of the area and stands older than 60 years 31%. Forestry drainage ditches comprised 98% of the network of lotic water bodies (76 m/ha) and have not been cleaned or reconstructed since the digging. Ditches were mostly overgrown with Sphagnum mosses and macrophytes and in respect of minor flow velocity resembled pools rather than streams. Only three ditches from our study plots were visibly flowing. For this reason we assumed that hydroperiod would be the main factor causing differences in functional communities between ditches and pools.

Macroinvertebrates were sampled in May 2013 and 2014, 26 days after the mean air temperature rose over +5 °C, i.e., the beginning of growing season. From each study plot we selected 10 ditches and 10 pools (natural floodings, wheel rut pools etc.; with depth > 15 cm), from different forest site types according to the relative area of the site type. We dip-netted an area of 4 m<sup>2</sup> for 20 s with 0.5 mm mesh D-frame net (17 × 19 cm) in each water body. Samples were preserved on-site in 96% ethanol. We recorded 12 environmental variables from each water body that could influence the arrangement of macroinvertebrates' functional communities (see Table 1). We used 57 of the sampled water bodies from both year for analyses.

Invertebrates were sorted from the detritus, counted, and identified in laboratory. We estimated the abundance of very numerous taxa (> 100 or > 10 specimens in a 1/25 subsample) using 3/25 or 5/25 of the sample respectively. Individuals were identified to lowest possible taxonomic level, mostly to species or genus, except for Psychodidae, which were identified to family level. We assigned each taxon to functional feeding group (Appendix) following Merritt et al. (1996), Heino (2000), Paunović et al. (2006), Zilli et al. (2008) and Bazzanti et al. (2009). In case the adults and larvae of the same taxon exhibiting different feeding modalities, we assigned them to different functional groups. As species of Chironomidae represent many different feeding strategies and we were not able to determine them further than to family level, we excluded this group from the analyses.

To describe the quantity of functional feeding groups in community level, we used abundance (the number of individuals) and biomass per sample. Abundance has been the most applied metrics in functional group analyses and is believed to reflect the interspecific patterns of resource division (Magurran 1988). However, in case of species with wide variety of body masses, the



**Fig. 1** Locations of study plots in Estonia. Left panel shows the sampling locations (triangles for ditches and squares for pools) in one of the study plots

relationship between abundance and functional impact may be over- or underestimated. Also, energy flow through trophic levels are more strongly connected to the total biomass than the abundance (Brown et al. 2004; Saint-Germain et al. 2007). Moreover, abundance and biomass have shown to have different responses to environmental conditions (Laux and Torgan 2015).

The total biomass of each taxon in a water body was calculated from individual lengths or head widths using equations, preferably from similar and geographically close habitats (Baumgärtner and Rothhaupt 2003; Benke et al. 1999; Edwards et al. 2009; Haas et al. 2007; Mährlein et al. 2016; Méthot et al. 2012). Dry mass of the individuals of a species in a water body was estimated using all the collected specimens (if  $N < 20$ ) or 20 specimens and extrapolated to others. Dry mass of molluscs was considered without the shell. For Oligochaeta we estimated the dry mass using cylindrical volume of pieces or whole individuals according to Schworbel (1994) and Haas et al. (2007). In case the individuals were accidentally discarded after determination (23%), we used constant species specific weights or constant lengths with equation (according to Timm (1999) or consulting with Tarmo Timm).

## Data Analysis

Differences in functional group composition were evaluated using two-way factorial permutation-based nonparametric MANOVA (PerMANOVA) analysis with Sørensen dissimilarity and ‘water body type’ (fixed) and ‘plot’ as factors. Biomass and richness data from both years were summed up. Community matrices were then relativized dividing the quantity of a certain feeding group in a sample with the total quantity of the feeding group in all water bodies. Whereas PerMANOVA requires balanced design, we randomly selected some water bodies to be deleted and ran the analysis 50 times using batch command with sample size of 54.

To find out whether the abundance and biomass of feeding groups differ between water body types and which habitat factors influence given group, we used general linear models (GLM). Abundance and biomass data were log-transformed to fit the normality assumption. Models were built according to the following procedure: (1) test for the significance (GLM:  $p < 0.15$ ) of each habitat factor and water body type; (2) search for correlating habitat factors (Spearman correlation:  $p < 0.05$ ); (3) multifactorial GLM with significant and non-correlating factors. The best model was defined as the

**Table 1** Mean values with standard deviations of habitat factors

Habitat factor	Ditch		Pool	
	2013	2014	2013	2014
Electrical conductivity (mS $\text{cm}^{-1}$ )	0.25 ± 0.14	0.33 ± 0.28	0.19 ± 0.11	0.36 ± 0.43
pH	6.01 ± 1.01	6.07 ± 0.88	5.42 ± 1.17	5.67 ± 0.93
Depth of water (cm)	24 ± 8	24 ± 11	25 ± 9	23 ± 12
Thickness of sediments (cm)	5 ± 4	5 ± 4	5 ± 4	4 ± 3
Shading (%)	46 ± 21	30 ± 18	43 ± 21	38 ± 22
Bottom cover (%)				
tree leaf litter	31 ± 32	29 ± 26	31 ± 25	34 ± 27
woody debris	5 ± 6	14 ± 19	6 ± 8	9 ± 11
<i>Sphagnum</i> mosses	18 ± 30	17 ± 29	19 ± 31	12 ± 26
mud	15 ± 25	15 ± 24	17 ± 29	16 ± 28
graminoid litter	18 ± 21	16 ± 21	23 ± 27	25 ± 28
Macrophyte cover (%)	16 ± 20	11 ± 19	18 ± 17	19 ± 22
Clear-cuts in 100 m vicinity (%)	17 ± 19	20 ± 19	22 ± 28	26 ± 30

There were no statistically significant differences between ditches and pools (for all factors in both years;  $p > 0.058$ )

one with lowest Akaike's information criterion value and all the habitat factors significant ( $p < 0.05$ ) in multifactorial GLM. Finally, water body type, when significant in first step, was added to the best model to see whether it loses its significance, i.e. habitat factors explain the difference between ditches and pools. Year and plot were included in all models as independent factors, but to find the correlating factors (step 2) all the observations were merged. Scrapers were absent in a large part of samples, therefore we built models for two subsets: for the samples containing scrapers ( $N = 70$ ) and, by logistic regression with occurrence data for the whole dataset ( $N = 114$ ). Statistical analyses were carried out using PC-ord 6.07 (McCune and Mefford 2011) and Statistica 7.

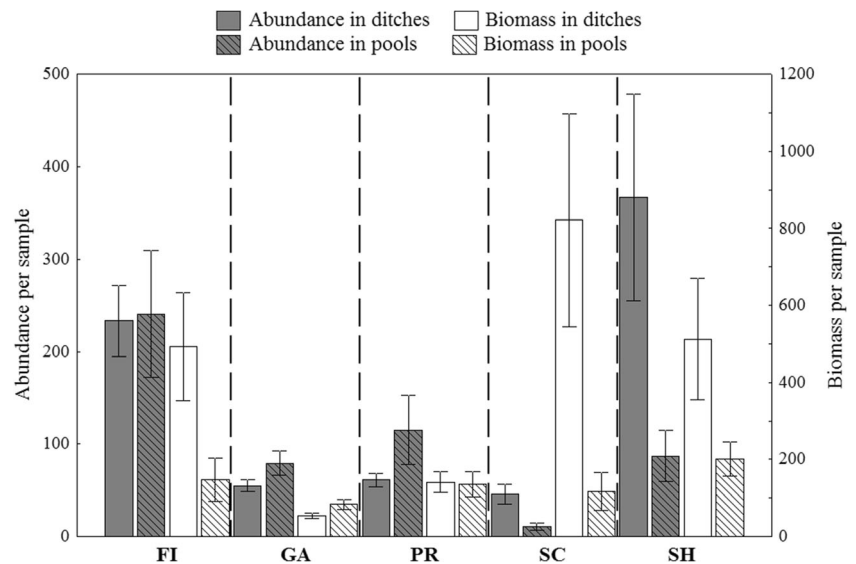
## Results

The biomass, abundance and taxa richness varied among feeding groups (Fig. 2; Appendix). We observed two distribution patterns resulting in large total biomass of a feeding group: (i) very large individuals abundant only in a few and absent from majority of water bodies; (ii) individuals with medium biomass numerous in majority of the water bodies. First distribution pattern was typical to scrapers in ditches, e.g., gastropods *Planorbis planorbis*, *Aplexa hypnorum* and *Lymnaea stagnalis*, whereas the overall taxa richness of scrapers was small. Second pattern characterizes shredders in ditches, including generalistic species such as waterlouse *Asellus aquaticus*, stonefly *Nemoura cinerea* and caddisflies

*Limnephilus stigma* and *Trichostegia minor*. Similarly abundant and ubiquitous were filterers, though they had high biomass only in ditches. There 70% of the filterer individuals were bivalves (mostly *Pisidium* spp.), but in pools 66% of individuals belonged to *Nematocera* (e.g., *Aedes*, *Culex*, *Culiseta* and *Dixella* sp). Feeding groups with lowest total biomass — predators and gatherers — had highest taxa richness and were moderately abundant.

Functional group composition differed between water body types and plots in regards of biomass (PerMANOVA:  $F = 7.8$ – $2.5$ ;  $p < 0.006$ ) and abundance ( $F = 7.6$ – $2.6$ ;  $p < 0.004$ ). Scrapers occurrence (GLZ first step:  $\chi^2 = 4.3$ ;  $p = 0.037$ ), abundance (GLM first step:  $F = 14.9$ ;  $p < 0.001$ ), and biomass ( $F = 23.7$ ;  $p < 0.001$ ) was significantly higher in ditches. Ditches had also higher mean abundance ( $F = 20.3$ ;  $p < 0.001$ ) and biomass ( $F = 8.0$ ;  $p = 0.005$ ) of shredders and biomass of filterers ( $F = 7.1$ ;  $p = 0.008$ ), while pools had higher biomass ( $F = 5.9$ ;  $p = 0.016$ ) of gatherers. Neither abundance nor biomass of predators differed between water body types (Table 2, Fig. 2). Ditches and pools did not differ conspicuously in respect of habitat factors (Table 1). Better than water body type, water depth and graminoid litter explained the biomass of gatherers; and pH and shade explained the frequency of scrapers. In other cases, water body type remained significant in multifactorial model (Table 2). In case of scraper abundance, pH lost its significance (in first step  $p = 0.001$ ) if together with water body type in the model, which suggests that it is probably one of the reasons for greater abundance of scrapers in ditches. This also occurred

**Fig. 2** Mean abundance (number of individuals) and biomass with standard errors of functional feeding groups per sample collected during 20 s from 4 m<sup>2</sup> in each water body. For abbreviations see Table 2



with water depth in case of gatherers abundance (in first step  $p = 0.045$ ).

## Discussion

Our study shows that the variability of macroinvertebrate functional communities and thus functioning of aquatic ecosystems, including the difference between the networks of ditches and isolated pools, is remarkable in artificially drained forests. Ditches and pools had distinctly different feeding group composition – scrapers, filterers (and less contrastingly shredders) were aggregated to ditches and gatherers to pools. This supports our hypothesis that the longer hydroperiod of ditches (Remm et al. 2015; Suislepp et al. 2011) favors feeding groups that rely on autochthonously produced resources. Surprisingly, water depth did not explain this difference, and thus is not a good proxy for the length of hydroperiod in such small water bodies.

Acidity was a major driver of functional community composition and also one of the causes for higher scraper frequency in ditches. The variation in pH probably is caused both by mosaic of soil types, and soil disturbance during artificial drainage. Higher pH in ditches compared to small forest pools is common in Estonia (Remm et al. 2015). This was also evident in our study plots (though statistically not significant), where the cover (15%) and depth (< 1 m; according to soil map provided by the Estonian Land Board) of peat layer was small, hence, ditches were easily penetrated down to mineral soil during digging. The positive scraper-pH correlation is probably not derived from the amount of food as increasing water acidity does not necessarily limit periphyton production (Greenwood &

Lowe 2006). Low pH imposes respiratory and osmoregulatory challenges to aquatic invertebrates in general (Harrison 2001). Scrapers were further limited in our study system, because gastropods made up more than 99% of their quantity. Shell formation and reproduction are depending on calcium-rich habitat with high pH (Dillon 2000). In the context of our study plots snails were mostly absent from water bodies with pH lower than 5.

We found more gatherers in shallow water bodies, especially pools, where the bottom was covered with litter from terrestrial or semiaquatic plants: tree leaves and graminoids. Although long hydroperiod supports rich autochthonous food base (Boven et al. 2008), gatherers are not dependent on that and are instead adept to use allochthonous litter (Kraus and Vonesh 2012). Shallow waters could favor this group, as litter from trees and herbaceous plants may decompose faster and have higher protein content when exposed to air (Bärlocher et al. 1978). Additionally, invertebrates from this group (e.g., *Cloeon dipterum*, *Anacaena lutescens*) often exhibited traits that allow them to exploit temporary water bodies.

Filterers attained higher biomass in ditches, while mean abundance was equally distributed, suggesting that the function of filtering is carried out by different taxa in different water bodies or biodiversity based redundancy (Schmera et al. 2017) ensuring the stability of the effect. Indeed, relatively heavy bivalves were mostly aggregated to ditches, and were replaced with *Nematocera* in pools. Mosquitoes often exhibit life history strategies that allow them to utilize temporary water bodies and some taxa even relay on drought for oviposition (Wiggins et al. 1980). Water acidity affected only filterers' biomass, suggesting it controls foremost bivalves that are pH-sensitive

**Table 2** Final general linear models (logistic regression in case of scrapers' occurrence) from model building, relating abundance and biomass of functional feeding groups to habitat factors and water body type (WBT)

Dependent variable <sup>a</sup>	Factors	F	<i>p</i>	R <sup>2</sup> <i>adj</i>
FI abundance	depth (-)	2.6	0.001	0.11
	year	11.4	0.105	
	plot	1.8	<b>0.001</b>	
FI biomass			0.159	0.16
	shading (+)	8.2	< 0.001	
	pH (+)	9.5	<b>0.004</b>	
	WBT (ditch)	4.3	<b>0.002</b>	
	year	0.6	<b>0.039</b>	
GA abundance	year	0.6	0.445	0.05
	plot	2.1	0.120	
	depth (-)	3.9	0.041	
	graminoid litter (+)	8.8	0.051	
	year	0.6	<b>0.003</b>	
GA biomass	plot	0.7	0.437	0.11
	tree leaf litter (+)	4.6	0.496	
	graminoid litter (+)	7.0	0.005	
	WBT	3.9	<b>0.033</b>	
	year	0.0	<b>0.009</b>	
PR abundance	plot	1.7	0.923	0.28
	macrophytes (+)	5.3	0.159	
	WBT	3.1	< 0.001	
	year	2.0	<b>0.022</b>	
	plot	19.7	0.080	
PR biomass			0.158	0.27
	macrophytes (+)	13.0	< 0.001	
	year	1.6	< 0.001	
	plot	16.7	0.213	
	macrophytes (+)	9.8	< 0.001	
SH abundance	pH (+)	9.8	<b>0.002</b>	0.36
	graminoid litter (+)	10.7	<b>0.001</b>	
	WBT (ditch)	18.9	< 0.001	
	year	6.0	<b>0.015</b>	
	plot	1.3	0.264	
SH biomass			< 0.001	0.37
	depth (+)	4.5	<b>0.036</b>	
	macrophytes (+)	39.0	< 0.001	
	clear-cuts (-)	10.6	<b>0.001</b>	
	WBT (ditch)	12.9	< 0.001	
	year	1.1	0.288	
	plot	5.1	<b>0.007</b>	
	macrophytes (+)	4.8	0.001	
SC abundance	pH (+)	2.9	0.089	0.19
	WBT (ditch)	10.8	<b>0.001</b>	
	year	2.4	0.125	
	plot	0.1	0.861	
	sediments (+)	11.1	< 0.001	
SC biomass	pH (+)	12.9	<b>0.001</b>	0.45
	WBT (ditch)	9.9	<b>0.002</b>	
	year	8.1	<b>0.005</b>	
	plot	0.6	0.563	
	shade (+)	4.8	< 0.001	
SC occurrence	pH (+)	36.5 <sup>b</sup>	<b>0.028</b>	0.48 <sup>c</sup>
	WBT	0.8 <sup>b</sup>	< 0.001	
	year	0.1 <sup>b</sup>	0.365	
	plot	7.6 <sup>b</sup>	0.694	
	clear-cuts (-)	10.6	<b>0.001</b>	
	WBT (ditch)	12.9	< 0.001	

Negative (-) and positive (+) impacts and water body type with higher abundance or biomass are noted. Significant *p* values for habitat factors are marked in bold

<sup>a</sup> FI – filterers; GA – gatherers; PR – predators; SH – shredders; SC – scrapers

<sup>b</sup>  $\chi^2$

<sup>c</sup> Likelihood-ratio based pseudo-R<sup>2</sup>

also in lakes and rivers (Mackie and Flippance 1983; Saunders and Kling 1990).

The quantities of Shredders, which were greater in ditches, correlated positively with pH, water depth, graminoids and macrophyte cover. Surprisingly, the shade or amount of leaf litter had no effect on this group. Experiments in forest stream mesocosms have shown higher abundances of several shredder species following increased leaf litter input, but not necessarily increase in their total abundance (Melody and Richardson 2004; Richardson 1991). It might be supposed that (1) the nutritional quality of leaf litter is more limiting for shredders than the quantity; and (2) periphyton (i.e., essential food resource for shredders; Cummins and Klug 1979) abundance and nutritional quality is enhanced by high water pH (Mulholland et al. 1991) and permanent inundation (Aspbury and Juliano 1998; Inkley et al. 2008; but see (Bärlocher et al. 1978). These correlations may be even stronger because the presence of leaf litter from overstory vegetation can increase acidity by leaching of the humic acids while decomposing (Stoler and Relyea 2011).

The abundance of predators was somewhat higher in pools yet biomass did not differentiate. Such pattern emerged because this group obtained high numbers only in some pools, which functioned as breeding places for *Chaoboridae* — a Family of small-bodied Diptera. Top-down control (predators as a proportion of total of all other functional groups; (Merritt et al. 1996) may be lower in ditches, considering the higher biomass of other feeding groups there. Predators exhibited greater quantities in water bodies with extensive macrophyte cover, which seems to be more important than water body type. Macrophyte beds are preferred by invertebrates that avoid dry phase via migration to permanent water bodies (such as many species of Coleoptera and Hemiptera; (Bazzanti 2015; Bazzanti et al. 2009). Their dispersal ability allows them to benefit from three dimensional structurally complex mesohabitat (Bazzanti et al. 2009). Thus, to support complex ecosystems with several trophic levels also in commercial forests, we suggest to carefully avoid draining, cleaning, and destroying the macrophyte rich pools and ditches.

Our study showed that ditches and pools in commercial forests support various ecosystem function providers. The trophic organization in ditches and pools is different because habitat factors select feeding groups directly through food resources, but also because of the environmental filter on other biological traits of the organisms. The possible results of ditch maintenance: reduction of food amount during ditch cleaning and increase of sun exposure by removing ditch-side vegetation, would probably lead to shifts in functional communities. These, together with the comparison of the functioning of water-bodies in drained forest with natural wetland ecosystems, remain the issues for further studies.

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