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Ecological impact of Eurasian beaver (*Castor fiber*) activity on macroinvertebrate communities in Lithuanian trout streams

Research Article

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Abstract: Our study found that beaver activity affects macroinvertebrate assemblages of both beaver ponds and downstream sites. The percentage composition of the invertebrate faunae of beaver ponds was strikingly different from the invertebrate faunae of upstream forested and downstream sites. The number of EPT (ephemeropteran, plecopteran, trichopteran) taxa in the upstream forested sites in all streams was higher than in beaver pond and downstream sites. Statistically significant differences were found in absolute and relative abundances of EPT and Chironomidae between different streams sites. The absolute and relative abundance of pollution-sensitive EPT was significantly higher in forested sites than in beaver pond and downstream sites in all measured streams. Beaver ponds had a significantly higher absolute and relative abundance of Chironomidae compared with upstream forested and downstream sites. We found that Plecoptera and Coleoptera were absent from beaver pond sites. The absolute abundance of Plecoptera was significantly higher in upstream forested sites than in downstream sites in all three streams. Gatherers were the dominant functional feeding group in relative abundance in all three habitat types. The percentage of gatherers was higher in beaver ponds than in forested and downstream sites.

Keywords: *Streams • Beaver • Macroinvertebrates*

1. Introduction

The influence of beaver ponds on stream morphology [1], sediment retention [2], biogeochemical processes [3] and wetland hydropody [4] has been described in detail in the literature. The macroinvertebrate communities in beaver ponds are reported to be considerably different from those in unimpounded sections [5,6]. Beaver dams affect stream habitats by slowing down the current, increasing depth and width, and creating an environment more similar to lentic systems [7].

Beaver dams have also been found to alter the export and retention of nutrients in streams, as well as modifying the hydrology of rivers, by changing stream flow upon flooding the original habitat and decreasing stream velocity [8]. The change in stream dynamics may also have a strong effect on organisms in the ecosystem. Specifically, studies have shown that as beaver dams significantly influence the existing riparian ecosystem, benthic stream invertebrate populations in the beaver-created ponds are also influenced [9].

The most frequently cited benefits of beaver dams and the ponds they create are increased habitat heterogeneity, rearing and overwintering habitat, flow refuge areas, and invertebrate production [10].

Wright *et al.* [11] predicted that the impact of beavers on invertebrate species richness might be less relevant in landscapes where lentic freshwater habitats independent of beaver activity occur. They also predicted that the total species richness would decrease if beaver-modified wetlands dominated the riparian ecosystem, as the number of unengineered patches may not be sufficient to support the entire complement of species.

Naiman *et al.* [12] concluded that beavers can greatly affect the structure (channel morphology, vegetation characteristics), diversity (habitat, species), and function (productivity, connectivity, resistance, and resilience to perturbations) of river corridors. They assumed that streams have relatively low resilience to perturbations, partly because they lack spatial heterogeneity [13]. Beaver dams are important functional elements in river channels, and the resulting beaver ponds function as

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large-mass, slow-turnover components of the corridor buffering the ecosystem from perturbations [13].

Beaver colonization effects on both community and ecosystem parameters occur predominantly *via* increased retention of fine particulate organic matter, which are associated with reduced macroinvertebrate richness and diversity and increased macroinvertebrate biomass and production [14].

Gard reported that the density of macroinvertebrates decreases, but biomass in beaver ponds increases [15].

Beaver impacts on macroinvertebrate communities are typically driven by the trophic guilds, or functional feeding groups (FFG), of macroinvertebrates that can benefit from changes in food resources, particularly collector-gatherers and predators [16].

Although beavers were exterminated in Lithuania, reintroductions in the last century have re-established the species. According to the official census, the number of beavers in Lithuania has dramatically increased over the last 10–15 years due to reduced trapping and continuous colonization of new territories. The number of beavers recorded in 1995 was approximately 19,000, while in 2000 they totaled 36,000. According to the most recent data, the minimum number of beavers in Lithuania is estimated at 85,879, while the maximum estimate is 121,025 individuals [17].

According to Ulevičius (2001), the average relative abundance of beavers in the Merkys River increased within 9–10 years [17]. Ulevičius states that, “A considerable increase in the relative abundance of beavers in the Merkys, as well as great concentration of the signs of beaver activity on practically all banks of the river might be a consequence of the lack of peripheral habitats for beavers”. Ulevičius derived a statistically reliable estimate for the average beaver density in Lithuania of 1.5 individuals/km^2 [17].

Biotopic distribution of beaver-engineered sites is determined by two principal factors – availability and attractiveness of habitats (selectivity). Field canals clearly dominate among beaver habitats (about 34%); however, the number of beaver-engineered sites recorded in such habitats was only about 8%, showing that habitat selectivity of beavers with respect to field canals is rather low. Quite a different situation is found with respect to forest and outskirt canals where proportion of beaver sites is higher than the proportion of these habitats (forest and outskirt canals) in the total number of the beaver preferred habitats. It is obvious that the dominance of beaver activity sites in canals in Lithuania is due to their preference for forest and outskirt canals. Large and small natural rivers are also attractive habitats for beavers; however, few beavers in Lithuania are present in either of these habitats due to their low availablity/rarity in Lithuania. Low negative habitat selectivity of beavers was observed with respect to lakes. Approximately 36% of all beaver activity sites are located in canals of land reclamation, which are the most commonly used habitat by beavers in Lithuania. Approximately 18% of beaver activity sites were recorded in large rivers, 16.5% in lakes, 14.5% in swamps, 11.9% in small rivers, and 7.8% in field canals. Habitat selectivity by beavers varied for different types of bodies of water. Large rivers, small rivers, and forest and outskirt canals were positively selected by beavers, whereas field canals were selected highly negatively [18].

According to Bluzma [19], the number of active beaver-engineered sites in a hilly landscape in eastern Lithuania increased from 8 sites in 1983 to 46 sites, or 1.9 site/km^2 in 2001. The number of active beaver-engineered sites in swamps and small, shallow rivulets and ditches, with a lodge being the most common type of main shelter, increased respectively (up to 74%) [19].

The relative abundance of beavers in bodies of water of different types is very similar, fluctuating from 0.81 beaver ponds/km in natural streams with discharge exceeding 0.5m^3/s to 1.1 beaver ponds/km in canals [17,18,20].

While much is known about the re-introduced beaver population in Lithuania, the impact of beaver activity on the macoinvertebrate fauna has not been studied. Our hypothesis is that beaver dam-building activity on streams will create ponds, which will influence the macroinvertebrate diversity and density compared to open water sections of the streams because of slower current, which will increase sedimentation and change the substrate for macroinvertebrate fauna.

The aim of our work was to investigate how beavers, as ecosystem engineers, altered the structure of a benthic macroinvertebrate community.

2. Experimental Procedures

Our study was conducted in July 2008 in three streams in Lithuania (Figure 1). Each stream had three sampling locations: an upstream forested reach not impacted by beavers (forested site), an active beaver pond (beaver pond), and a site downstream of the beaver pond (downstream site). The downstream sites were about 10 m from the beaver ponds.

All three study streams – Derežna, Saria and Dūkšta – are trout-type streams in different regions and different river basins. The Saria and Derežna streams flow through pinewoods, whereas the Dūkšta stream flows through a mixed landscape. The Derežna stream

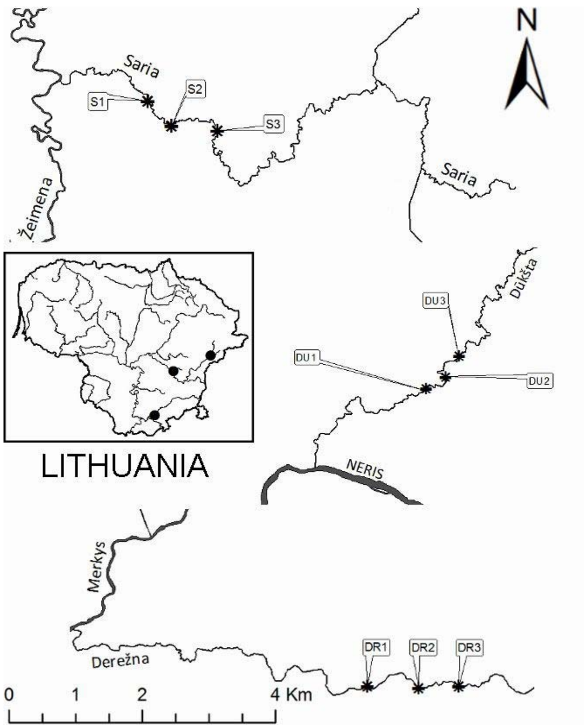

Figure 1. Maps of the Derežna, Saria, and Dūkšta streams and distribution of study sites in 2008. Site abbreviations defined in Table 1.

(length 13.4 km, basin area 32.9 km^2) is part of the Merkys basin (southern Lithuania). The Saria stream (length 27.9 km, basin area 78.7 km^2) is part of the Žeimena River basin (southeast Lithuania). The Dūkšta stream (length 29.2 km, basin area 137.3 km^2) is part of the Neris River basin (southeast Lithuania) [21].

The age of ponds in the Derežna and Dūkšta streams is 3–5 years, whereas those of the Saria are about 10 years old. Beaver activity sites in the Derežna and Dūkšta rivers are permanent. The Saria beaver sites are not permanently used for shortage of food (where food is left by beavers and returned for later).

Macroinvertebrate samples were dredged from three 0.1 m^2 areas at each site using a kick-sampling method [22] (500 μm mesh net). Additional samples of macroinvertebrates (two samples per site) were taken from plants, stones or stumps to determine the Danish Stream Fauna Index (DSFI). A total of 45 samples were collected, sieved using a 500 μm mesh, transferred into plastic flasks, and stored in a 4% formaldehyde solution. In the laboratory, all animals were separated, counted, and identified to the species or genus level (except for Oligochaeta) under a binocular dissecting microscope.

We calculated the total macroinvertebrate taxa number (SR), the ephemeropteran, plecopteran, and trichopteran taxa number (EPT), and the total abundance (ind.m^{-2} = individuals per m^2) and relative abundance (%) of indicatory taxonomic groups (Ephemeroptera, Plecoptera, Trichoptera, EPT, Coleoptera, Chironomidae, Oligochaeta, and Amphipoda).

The DSFI [23] and Hilsenhoff Biotic Index (HBI) [24] were calculated to assess the ecological status of investigated river sites. HBI tolerance values were taken from Mandaville [25].

Five functional feeding groups of macroinvertebrates (gatherers, shredders, filters, scrapers, and predators) were used to classify the recorded taxa according to Cummins and Klug [26], Merritt and Cummins [27], Moog [28], and Wright *et al*. [29].

Values of the main physiochemical variables present at the investigated sites (measured at the end of July) were obtained from the Environmental Protection Agency of Lithuania.

Similarities of macroinvertebrate taxonomic abundance between samples were assessed using the Bray-Curtis similarity index [30] in the CLUSTER program of the PRIMER 5.2.3 package.

The General Linear Model ANOVA and the Fisher LSD test were used to determine differences in macroinvertebrate metrices and morphological characteristics among groups of stream sites. All species data were log (1+x) transformed prior to analysis. Calculations were done with Statistica for Windows, Version 6.0 (STATISTICA 2001).

3. Results

The substrates of beaver ponds differed from the substrates of forested and downstream sites (except for the Saria stream) (Table 1). In the Derežna and Dūkšta streams, beaver ponds had sand-silt substrates, and forested and downstream sites had pebble substrates. The beaver pond and the downstream site in the Saria stream had the same substrates (gravel).

Relief structure, hydrological regime, and other parameters differ between regions across Lithuania, and water temperature variations between the studied streams were great, ranging from 11.9°C to 18°C (Table 1). The highest water temperature was recorded in the Dūkšta stream. Water temperature was higher in beaver ponds than in forested and downstream sites in the Saria and Derežna streams. Dissolved oxygen (oxygen saturation), pH, and conductivity varied greatly between streams. The highest values of the above-mentioned parameters were recorded in the Dūkšta stream, and the lowest in the Derežna stream. Table 1 illustrates that water temperature, dissolved oxygen, oxygen saturation, pH, and conductivity in beaver-impounded sites in the same stream did not differ from

Streams	Site number	Site location	Water temperature (°C)	Dissolved oxygen (mg/L)	Oxygen saturation (%)	pH	Conductivity (µS/m)	Width of study site (m)	Average depth of the study site (cm)	Current rate (m/s)	Substrate
Derežna forested	DR1	54°11´76´´ N, 24°58´02´´ E	11.9	7.58	71.2	7.27	256	5	50	0.7	pebbles
Derežna beaver pond	DR2	54°11´79´´N, 24°29´82´´ E	12.1	7.38	70	6.97	259	9	100	0.02	sand-silt
Derežna downstream	DR3	54°11´82´´N, 24°29´52´´ E	11.9	7.58	71.2	7.27	256	5	50	0.7	pebbles
Dūkšta forested	DU1	54°49´86´´N, 24°58´02´´E	18.0	9.4	100.5	8.2	581	4.5	35	0.4	pebbles
Dūkšta beaver pond	DU2	54°49´74´´N, 24°58´28´´ E	18.0	9.42	107	8.14	583	6	80	0.02	sand-silt
Dūkšta downstream	DU3	54°49´68´´N, 24°57´90´´ E	18.0	9.4	100.5	8.2	581	4.5	35	0.4	pebbles
Saria forested	S1	55°02´82´´N, 25°53´88´´ E	14.7	8.43	83.9	7.83	406	4.0	60	0.1	pebbles
Saria beaver pond	S2	55°02´85´´N, 25°54´13´´ E	15.2	8.58	86.7	7.77	406	3.5	70	0.1	gravel
Saria downstream	S3	55°02´87´´N, 25°54´24´´ E	14.7	8.43	83.9	7.83	406	4	60	0.1	gravel

Table 1. Characteristics and water parameters of sites in the investigated streams (Nemunas basin, Lithuania).

respective parameters in free-flowing sites. Water depth was considerably lower in forested and downstream sites than in beaver ponds (Table 1). The current rate was the same in all sections of the Saria stream, and the current rate in beaver pond sites in the Saria stream was greater than in beaver pond sites in Derežna and Dūkšta streams.

The measured values of the main chemical variables in the investigated streams are presented in Table 2. The total elevated phosphate and total phosphorus concentrations only exceeded the maximum permissible concentration approved by the Ministry of Environment of Lithuania [31] in the Dūkšta stream, which receives wastewater from Dūkštos. Polluted and insufficiently treated waters could extend into the middle reaches of the stream from the wastewater of the town of Dūkštos and treatment facilities of UAB Biovela. Therefore, total elevated phosphate and total phosphorus concentrations are affected by wastewater from the town of Dūkštos and the meat processing plant as well as the beaver activity site.

We identified a total of 72 macroinvertebrate taxa and one Oligochaeta class in the three investigated streams (including 61 identified species) (see Appendix). The greatest species richness was recorded for Trichoptera (15 species/1 higher taxon) and Chironomidae (14 species/1 higher taxon). They were followed by Ephemeroptera (10 species/1 higher taxon) and Mollusca (8 species/1 higher taxon). The mayfly *Ephemera danica*, the chironomid *Cricotopus algarum*, and oligochaetes were detected in all sites of the investigated streams. There are two macroinvertebrate species in the Saria system (the mayfly *Brachycercus harrisella* and the chironomid *Orthocladius rubinundus*), four species in the Derežna system (the caddisfly *Limnephilus stigma*, the megalopteran *Sialis lutaria*, and the chironomids *Clinotanypus nervosus* and *Procladius ferrugineus*), and 5 species in the Dūkšta system (the molluscs *Pisidium supinum* and *Sphaerium rivicola*, the mayfly *Siphlonurus alternatus*, and the chironomids *Glyptotendipes cauliginellus* and *Demicryptochironomus vulneratus*) that are only found in the beaver ponds.

Our data show that the total number of macroinvertebrate taxa (SR) and the number of EPT taxa in beaver ponds were smaller in comparison to forested and downstream sites, but for the Saria system the EPT values between beaver pond and downstream were very similar (Table 3).

The results of the Bray-Curtis similarity analysis of individual macroinvertebrate taxa classified benthic invertebrate samplings into five groups (showing the pattern of species distribution) (Figure 2).

Group I includes macroinvertebrate samples collected from the forested sites of the Derežna and Dūkšta streams. The macroinvertebrates of this group were dominated by pollution-sensitive plecopterans (*Leuctra* sp.) and ephemeropterans (*Serratella ignita*).

Stream	NH_4-N, mg l^{-1}	$N0_3$-N, mg l^{-1}	N total, mg l^{-1}	$P0_4$-P, mg l^{-1}	P total, mg l^{-1}
Maximum permissible concentration (MPC)	(0.10)	(2.3)	(2.5)	(0.065)	(0.10)
Derežna	0.09	0.24	1.10	0.037	0.081
Dūkšta	**0.33**	0.08	1.03	**0.088**	**0.198**
Saria	0.07	0.14	0.73	0.036	0.047

Table 2. Values of chemical variables in the investigated streams (Nemunas basin, Lithuania). Data from the Environmental Protection Agency of Lithuania.

Bold indicates where values exceed the maximum permissible concentrations approved by the Ministry of the Environment of Lithuania [31].

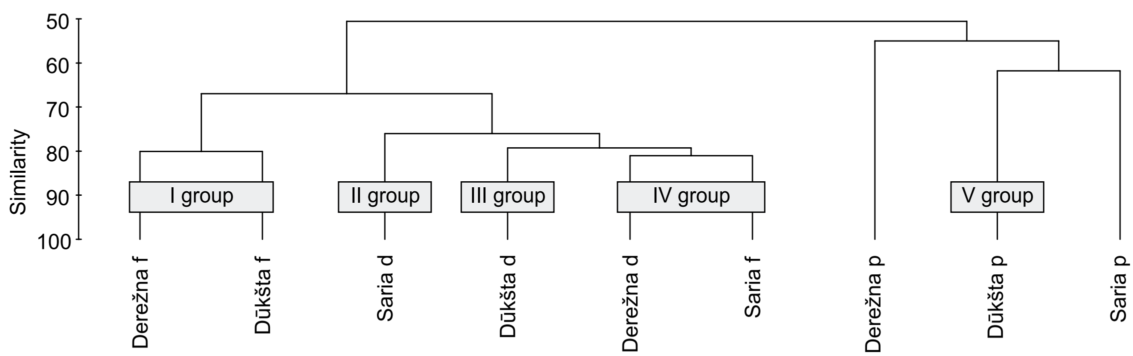

Figure 2. Bray-Curtis index cluster analysis dendrogram showing similarity between macroinvertebrate taxonomic abundances at sampling sites of investigated streams (f = forested, p = beaver pond, d = downstream sites)

Metrics	Derežna			Dūkšta			Saria		
	f	p	d	f	p	d	f	p	d
Richness measures									
SR	39	13	34	33	20	21	34	13	21
Number of EPT taxa	15	2	10	19	5	10	10	4	5
Number of individuals (ind.m^{-2} ±SE)									
Total abundance	2500±92*	800±23	1170±40	1253±34*	883±22	703±20	950±23*	323±35	423±9
Ephemeroptera	493±18*	70±6*	167±9*	250±29	13±3*	213±9	373±28*	77±9*	137±20*
Plecoptera	407±40*	0	190±15*	390±32*	0	83±12*	123±18*	0	57±3*
Trichoptera	333±38*	13±3*	43±9*	220±35*	7±2*	60±6*	83±9*	6±1*	17±3*
EPT	1233±54*	83±7*	400±21*	860±40*	20±4*	356±18*	579±6*	83±9*	211±21*
Coleoptera	210±21*	0	90±21*	113±12*	0	43±12*	140±11*	0	7±1*
Amphipoda	153±23*	80±15	63±9	0	0	0	80±11*	43±9*	60±6*
Chironomidae	33±7	573±18*	67±7	47±3	377±12*	83±9	17±3	113±23*	27±3
Oligochaeta	153±9	17±3*	157±12	30±6	450±29*	57±3	13±3	23±5	27±3
Others	718	47	393	203	36	164	121	61	91
Percentage of functional feeding group (%)									
Gatherer	61.5	99.3	50.9	33.5	92.1	31.0	68.2	97.0	74.0
Predator	8.8	0.3	9.5	14.2	6.0	8.3	2.9	2.3	7.0
Shredder	25.1	0	20.1	18.7	0.3	44.9	9.9	0.7	15.7
Scraper	2.6	0.1	16.0	14.6	0.7	10.1	12.0	0	1.1
Filterer	2.0	0	0	19.0	0	0	7.0	0	0
Others	0	0.3	3.5	0.2	0.9	5.7	0	0	2.2
Biotic index scores									
DSFI value	7	4	6	7	4	6	7	4	6
DSFI status	VG	M	VG	VG	M	VG	VG	M	VG
HBI value	1.63	5.97	4.42	1.92	7.14	3.05	3.64	5.48	4.72
HBI status	E	FP	G	E	P	E	E	F	G

Table 3. Values of macroinvertebrate metrics in the investigated streams (Nemunas basin, Lithuania).

*Site abbreviations defined in Table 1. (f - forested, p - beaver pond, d - downstream sites) Biotic index status abbreviations: E = excellent, VG = very good, G = good, M = moderate, P = poor, F = fair, FP = fairly poor. *Indicates statistically significant difference from all other study reaches (non-parametric Kruskal-Wallis ANOVA, P < 0.05; Fisher's LSD test, P < 0.05).*

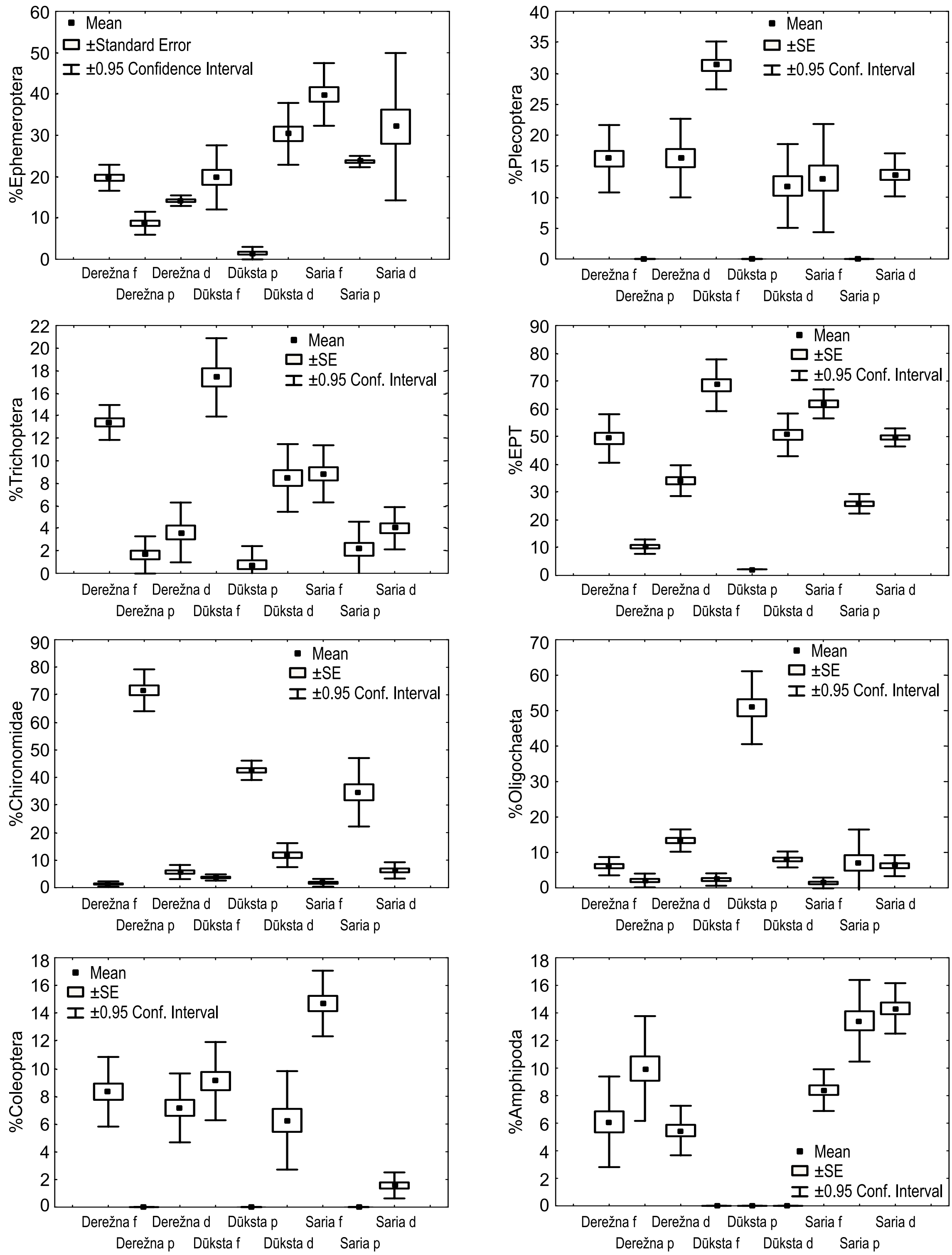

Figure 3. Relative abundances of different macroinvertebrate groups in the investigated streams (f = forested, p = beaver pond, d = downstream sites).

The absolute abundance of Plecoptera was statistically significantly higher in group I than in groups II–IV. Plecopterans were absent from group V. Group II included macroinvertebrate samples collected from the Saria downstream site, and group III included macroinvertebrates collected from the Dūkšta downstream site. Amphipods were not recorded at any sites within the Dūkšta system.

Group IV was comprised of samples of benthic macroinvertebrates collected from the Derežna downstream site and the Saria forested site. At both sites, the streams flowed through pinewoods and had pebbly substrates. The total number of macroinvertebrate taxa (SR) and the number of EPT taxa were the same in both study sites.

Macroinvertebrate samples collected from beaver ponds form group V. Group V differs from other groups in statistically significantly higher rates of absolute and relative abundance of Chironomidae, and in the smallest absolute and relative abundance of Trichoptera (Fisher LSD test, $P<0.05$). Plecoptera and Coleoptera were absent from this group. The benthic communities of beaver pond sites (group V) were dominated by Chironomidae (*Rheotanytarsus* spp., *Chironomus plumosus*, *Prodiamesa olivacea*). *Chironomus plumosus* was found only in this group.

Total abundance values of macroinvertebrates were significantly higher in the forested sites than in beaver ponds and downstream sites in all three streams (Table 3).

The results of our investigation show different macroinvertebrate assemblages on the substrates of beaver ponds compared with the in-stream sites. The major feature of the faunae of beaver ponds was the larger proportion of chironomid larvae (34.6–71.7%) compared with the in-stream sites (Figure 3). For example, the number of chironomid larvae collected from the Derežna stream beaver pond site was 573 ind.m^{-2} (Table 3) compared to 33 and 67 ind.m^{-2} in the forested and downstream sites, respectively.

Statistically significant differences were found in absolute (ind.m^{-2}) and relative (%) ($F=64718.95$, $P=0.000$) abundances of EPT between different stream sites (Table 3, Figure 3). Beaver ponds had a significantly higher absolute and relative abundance of Chironomidae ($F=7530.57$, $P=0.000$), compared to forested and downstream sites. The absolute and relative abundance of Oligochaeta in beaver ponds of the Dūkšta stream ($F=4077.67$, $P=0.000$) significantly differed from those in other sites. The absolute abundance of Plecoptera was significantly higher in forested sites than in downstream sites for all three streams, and the relative abundance of Plecoptera in the forested site ($F=12726.62$, $P=0.000$) significantly differed from that of the downstream site only in the Dūkšta stream (Figure 3, Table 3). Stoneflies were absent from beaver pond sites.

Gatherers were the dominant functional feeding group in terms of relative abundance in all three habitat types (Table 3). The percentage of gatherers was higher in beaver ponds than in forested and downstream sites. The relative abundance of scrapers, shredders, and predators in beaver ponds was small or they were absent. Filterers were found only in forested sites.

The Hilsenhoff Biotic Index (HBI) showed variation between the three habitat types (Table 3). All beaver pond sites had higher HBI values than forested and downstream sites. Based on HBI indices, the status of the macroinvertebrate community was classified as excellent in forested sites, excellent or good in downstream sites, and fair, fairly poor, or poor in beaver ponds. Poor water quality in the investigated beaver pond sites was supported by the prevalence of contamination-tolerant chironomids in macrozoobenthic communities. The relative abundance of chironomids was positively correlated with HBI ($r=0.66$, $P=0.036$).

According to the DSFI, water quality was very good in forested and downstream sites and moderate in beaver ponds (Table 3).

4. Discussion

While a number of recent studies [9,32,33] investigated the impact of beavers on macroinvertebrate communities, no research has previously been conducted in Lithuania. Our data are the first to document the role of beaver dams (and the ponds they create) on the composition of macoinvertebrate faunae on streams in Lithuania. Ecological theory argues that taxonomic richness increases with habitat heterogeneity. This assertion can be supported by studies that examined multiple taxa, scales, and ecosystems [34-36]. Crooks [37] extended this concept to ecosystem engineers, positing that the influence of ecosystem engineering on species richness should be related to whether or not the engineer increases or decreases habitat diversity, which in turn is dependent on the context in relation to the surrounding landscape. Due to increased sedimentation, beaver ponds are usually a less complex environment, with a smaller range of water velocities than more lotic habitats in the same stream. This decrease in water velocity and increase in sedimentation rate may explain the lower taxonomic richness in beaver ponds. The results of our study support this assertion, as beaver engineering activities along streams reduced taxonomic richness of macroinvertebrates as a function of reduced benthic substrate heterogeneity.

Our investigations showed that beaver ponds had lower macroinvertebrate taxonomic richness and diversity compared to the forested and downstream sites of investigated streams. According to Anderson and Rosemond [14], beaver ponds created by introduced beavers in Argentina also had significantly lower macroinvertebrate taxonomic richness and diversity.

The EPT fauna is very sensitive to environmental disturbances [38] and thus is a good indicator of ecosystem dynamics. Our data clearly show that the richness and abundance of EPT taxa was higher in forested sites than in beaver ponds or downstream sites. This is significant since the forested sites represent undisturbed sites that have not been impacted by beaver engineering.

The data show that the beaver pond sites of the investigated streams differed from the forested and downstream sites in the dominance of individual taxa. For example, stoneflies *Leuctra* spp. and mayfly *Serratella ignita* were the dominant taxa in the forested sites. Downstream sites were dominated by the mayfly *Caenis macrura* in the Derežna stream, by the stoneflies *Leuctra* spp. in the Dūkšta, and by the mayfly *Baetis rhodani* in the Saria. The benthic communities in all beaver pond sites were dominated by the chironomids *Rheotanytarsus* spp. and *Prodiamesa olivacea* (except for the Saria stream). The dominance of Chironomidae and Oligochaeta has been reported in other beaver impoundments [9,16] and appears to represent a significant beaver-induced alteration. Our study indicates that during times of low relative abundance of mayflies, the abundance of chironomids is high. Similar findings have also been reported by many other authors [39,40].

Margolis *et al*. [9] found that the major difference in the taxonomic structure between impounded and above-impounded assemblages in two Appalachian streams was the dominance of segmented worms (Oligochaeta) and midges within the impoundments. Similarly, in a recently formed beaver pond in Ontario, Sprules [41] recorded an increase in midges, while obligate lotic species, including mayflies, caddisflies, stoneflies, and some true flies (Diptera) died or migrated. However, while beaver alterations to a German stream resulted in the disappearance of some species, it also accommodated a significantly higher number of species of dragonflies, damselflies, caddisflies, and some snails and mussels [6].

Our data show that the abundance of pollution-tolerant Oligochaeta was significantly higher in beaver ponds than in forested and downstream sites in the Dūkšta stream. However, the abundance of oligochaetes was significantly lower in the beaver ponds of the Derežna and not significantly different in the Saria. The Dūkšta is subject to human-produced pollution, and our data suggest that the beaver pond site on this stream accumulates these pollutants (as indicated by the greater abundance of oligochaetes).

It is well known that individuals of order Plecoptera are considered highly sensitive to environmental degradation [42,43]. Our study found that they were absent from beaver ponds and their numbers in downstream sites were lower than in forested sites. The most “polluted” stream, the Dūkšta, had more plecopterans in its forested site than in that of the Saria stream, which could be attributed to a higher water temperature in the forested site of the Dūkšta stream (18°C) than the Saria stream (14.7°C).

Our results indicate that the absolute and relative abundance of ephemeropteran taxa was lower in beaver pond sites than in downstream and forested sites. Members of Order Ephemeroptera are considered to be sensitive to environmental stress [44]. By burying the streambed under a layer of organic matter, beavers reduced the complexity of benthic habitats in the ponds, in contrast with unimpacted or downstream sites, where a variety of substrates and microhabitats were present [14].

This study confirms that beaver ponds have a higher proportion of gatherers, such as chironomids, compared with forested and downstream sites. The relative abundance of scrapers, shredders and predators in beaver ponds was low or they were absent. The relative abundance of shredders was found to be smaller in beaver ponds compared to forested and downstream sites. However, according Margolis *et al*. [9], in beaver-impounded sections of streams, the relative abundance of shredders decreases, even though large quantities of coarse particulate organic matter are available. McDowell and Naiman [16] suggested this decrease may be due to inadequate velocity and substrate types for the shredders. Beaver activities were found to influence community structure, through replacement of lotic taxa by lentic forms, and community functions, by increasing the absolute abundance of collectors and predators while decreasing the relative importance of shredders and scrapers in impounded sites [16]. Stress is normally seen to reduce diversity [38,45], but physical disturbances are considered important factors regulating the structure of lotic communities [46,47].

In Lithuania beavers were reintroduced in 1947–1959, and after the World War Two began to naturally spread from Belarus [48]. They are currently very abundant and widespread in Lithuania [20,49]. Our study supports the assertion that beaver activities in pond habitats reduced taxonomic richness as a result of reduced benthic substrate heterogeneity relative to unimpacted or downstream sites. Our data document the influence of beaver ponds on macroinvertebrates in Lithuania. Beaver ponds had significantly higher absolute and relative abundances of chironomids in comparison to the forested and downstream sites. The absolute abundance of plecopterans was significantly higher in the forested sites than in downstream sites. Stoneflies were absent from beaver pond sites.

With the number of beaver-engineered sites increasing, the usual community of benthic invertebrates can change markedly through the gradient of the stream. Invertebrate communities influenced by beaver activity do not reflect the normal, undisturbed situation. The impact is dependent on the number of beaver activity sites, where due to beaver-induced hydromorphological changes, typical stream communities will be transformed into standing-water communities. With the number of beaver-engineered sites increasing, considerable distances in streams will become unsuitable for invertebrates dwelling in fast-moving water.

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Appendix

Macroinvertebrate taxonomic composition in the investigated streams (f = forested, p = beaver pond, d = downstream sites).

Order, class, family, taxon	Dūkšta			Saria			Derežna		
	f	p	d	f	p	d	f	p	d
Cl. Leptolida, O. Capitata									
F. Hydridae									
Hydra vulgaris Pallas, 1766									+
Cl. Gordioida, O. Gordea									
F. Gordiidae									
Gordius aquaticus Linnaeus, 1758							+		+
O. Seriata									
F. Planariidae									
Planaria sp.							+		+
Cl. Oligochaeta	+	+	+	+	+	+	+	+	+
Cl. Hirudinea									
O. Arhynchobdellida									
F. Erpobdellidae									
Erpobdella octoculata (Linnaeus, 1758)			+	+		+	+		+
O. Rhynchobdellida									
F. Glossiphoniidae									
Glosiphonia complanata (Linnaeus, 1758)			+		+	+	+	+	+
Cl. Arachnida, O. Prostigmata									
F. Hydrachnidae									
Hydrachna sp.							+		+
Mollusca									
Cl. Bivalvia									
O. Veneroidea									
F. Sphaeriidae									
Pisidium supinum Schmidt, 1851		+							
Sphaerium corneum (Linnaeus, 1758)	+	+		+			+	+	+
Sphaerium rivicola (Lamarck, 1818)		+							
Cl. Gastropoda									
O. Neotaenioglossa									
F. Bithynidae									
Bithynia tentaculata (Linnaeus, 1758)	+						+	+	+
O. Pulmonata									
F. Planorbidae									
Ancylus fluviatilis Müller, 1774	+			+			+		+
Planorbarius corneus (Linnaeus, 1758)									+
Gyraulus albus (Müller, 1774)		+		+			+		+
F. Lymnaeidae									
Radix pereger Müller, 1774			+	+	+	+	+		+
Cl. Malacostraca									
O. Amphipoda									
F. Gammaridae									
Gammarus pulex (Linnaeus, 1758)				+	+	+	+	+	+
O. Isopoda									
F. Asellidae									
Asellus aquaticus (Linnaeus, 1758)				+			+	+	+
Cl. Insecta									
O. Odonata									
F. Calopterygidae									

Order, class, family, taxon	Dūkšta			Saria			Derežna		
	f	p	d	f	p	d	f	p	d
Calopteryx splendens (Harris, 1782)							+		
F. Gomphidae									
Gomphus vulgatissimus (Linnaeus, 1758)						+			
O. Ephemeroptera									
F. Baetidae									
Baetis rhodani (Pictet, 1843)	+		+	+		+	+		+
Procloeon bifidum (Bengtsson, 1912)	+		+	+					+
F. Caenidae									
Caenis macrura Stephens, 1835		+			+		+		+
Brachycercus harrisella Curtis, 1834					+				
F. Heptageniidae									
Ecdyonurus dispar (Curtis, 1834)	+		+	+			+		
Heptagenia sulphurea (Müller, 1776)	+			+					
F. Ephemeridae									
Ephemera danica Müller, 1764	+	+	+	+	+	+	+	+	+
F. Ephemerellidae									
Serratella ignita (Poda, 1761)	+		+	+		+	+		+
F. Leptophlebiidae									
Habrophlebia fusca (Curtis, 1834)					+		+		
F. Siphlonuridae									
Siphlonurus alternatus (Say, 1824)		+							
O. Plecoptera									
F. Perlodidae									
Isoperla grammatica (Poda, 1761)	+			+			+		+
F. Leuctridae									
Leuctra spp.	+		+	+		+	+		+
O.Hemiptera									
F. Aphelocheiridae									
Aphelocheirus aestivalis (Fabricius, 1794)	+								
O. Coleoptera (larvae)									
F. Elmidae									
Elmis spp.	+		+	+		+	+		+
Limnius volckmari (Panzer, 1793)	+			+			+		+
F. Dytiscidae									
Platambus maculatus (Linnaeus, 1758)									+
O. Coleoptera (imago)									
F. Hydrophilidae									
Hydrochus elongates (Schaller, 1783)	+								+
O. Trichoptera									
F. Hydropsychidae									
Hydropsyche siltalai Dőhler, 1963	+		+						
Hydropsyche angustipennis (Curtis, 1834)	+		+	+			+		
Hydropsyche pellucidula (Curtis, 1834)	+			+			+		+
F. Hydroptilidae									
Hydroptila spp.				+			+		+
Ithytrichia lamellaris Eaton, 1873				+					
F. Sericostomatidae									
Notidobia ciliaris (Linnaeus, 1761)							+		+
F. Goeridae									
Silo pallipes (Fabricius, 1781)				+			+		+
F. Lepidostomatidae									
Lepidostoma hirtum (Fabricius, 1775)	+						+		+
F. Leptoceridae									

Order, class, family, taxon	Dūkšta			Saria			Derežna		
	f	p	d	f	p	d	f	p	d
Athripsodes albifrons (Linnaeus, 1758)	+								
Athripsodes cinereus (Curtis, 1834)	+	+		+			+		
F. Limnephilidae									
Anabolia laevis Zetterstedt, 1840		+	+	+	+	+	+		
Grammotaulius nigropunctatus (Retzius, 1783)	+		+						
Limnephilus stigma Curtis, 1834								+	
F. Psychomyiidae									
Psychomyia pusilla (Fabricius, 1781)	+								
F. Polycentropidae									
Polycentropus flavomaculatus (Pictet, 1834)	+						+	+	
F. Rhyacophilidae									
Rhyacophila nubila Zetterstedt, 1840	+			+			+		+
O.Megaloptera									
F. Sialidae									
Sialis lutaria (Linnaeus, 1758)								+	
O. Diptera									
F. Pediciidae									
Dicranota spp.	+		+	+		+	+		+
F. Athericidae									
Atherix spp.	+			+		+	+		+
F. Tabanidae									
Tabanus spp.		+		+		+			
F. Tipulidae									
Tipula spp.				+					+
F. Simuliidae									
Simulium spp.	+		+	+		+	+		+
F. Chironomidae									
Glyptotendipes cauliginellus (Kieffer, 1913)		+							
Demicryptochironomus vulneratus (Zetterstedt, 1838)		+							
Pentapedilum exsectum (Kieffer, 1916)						+			
Polypedilum scalaenum (Schrank, 1803)	+	+		+			+		+
Polypedilum pedestre (Meigen, 1830)			+						
Chironomus plumosus (Linnaeus, 1758)		+						+	
Rheotanytarsus spp.	+	+	+		+	+		+	+
Cricotopus algarum (Kieffer, 1911)	+	+	+	+	+	+	+	+	+
Eukiefferiella coerulescens (Kieffer, 1926)	+			+		+			
Orthocladius rubicundus (Meigen, 1818)					+				
Monodiamesa bathyphila (Kieffer, 1918)		+	+						
Prodiamesa olivacea (Meigen, 1818)		+	+				+	+	+
Thienemannimyia lentiginosa (Fries, 1823)		+		+	+	+	+	+	+
Clinotanypus nervosus (Meigen, 1818)								+	
Procladius ferrugineus (Kieffer, 1918)								+	