

BIODIVERSITY PATTERNS IN A SUBALPINE FLOODPLAIN

The role of islands and tributaries as possible hotspots



Christian Hossli (D-BIOL)
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EAWAG:
Swiss Federal Institute of Aquatic Science and Technology
Aquatic Ecology

Supervision:
PD Dr. C. Robinson
Dr. M. Doering

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Abstract

Floodplains are highly heterogeneous ecosystems, containing a mosaic of different aquatic and terrestrial habitat types. In this study I could show that this high heterogeneity positively influences macroinvertebrate diversity. I assessed the biodiversity of five different habitat types (main and side channel, tributary, braided section and island) in a subalpine floodplain (Urbachtal, BE, Switzerland) on two sampling dates (in May/June and August 2012) and identified environmental factors influencing it.

Comparing the different habitat types, there was one which stood out clearly: side channels. Side channel generally showed the highest density and taxon richness and it was the most distinct habitat (highest β -diversity values) in all the five habitat types, on both sampling dates.

The main factors positively influencing biodiversity were organic matter content and water temperature. What also seemed to affect diversity was flow velocity, generally having a negative effect on biodiversity.

I was especially interested in the role of tributaries and islands because they were thought to be biodiversity hotspots within a floodplain. In the case of tributaries this idea could partially be supported. They showed not the highest diverse but a quite unique taxa composition, quite different from the other habitats. As also in other studies mentioned, tributaries may act as refugia for animals which no longer find suitable habitats in the main channel, during dry periods. Islands, on the other side, couldn't meet my predictions and didn't show higher diversities compared to the other habitats.

Additionally I found some positive relations between aquatic and terrestrial samples, indicating the importance of aquatic subsidies for terrestrial animals (e.g. predators) and vice versa.

In conclusion, these findings underline the positive effect of a highly heterogeneous environment on macroinvertebrate diversity. A high connectivity (especially lateral, between the river and surrounding floodplain) increases the taxonomic richness and results in a generally healthier ecosystem. Renaturation efforts should focus on increasing the spatial heterogeneity and reducing homogenizing elements like dams or channelized sections.

1 Introduction

Floodplains are highly diverse and complex ecosystems. They are composed of a variety of different interconnected aquatic and terrestrial habitats and therefore play an important role in linking these two systems (Doering et al., 2011). The different habitats differ widely in structural and physico-chemical properties, such as substrate size, water depth and organic matter content, flow velocity and water conductivity, controlling abiotic and biotic processes (Valett et al., 2005; Doering et al., 2011). However, the major forces governing the spatio-temporal structure of a floodplain are temperature and fluvial dynamics such as flood disturbances (Ward and Stanford, 1995; Junk et al., 2000; Tockner et al., 2000; Doering et al., 2007; Doering et al., 2011). Because of this high spatial and temporal variability, floodplains provide excellent opportunities to examine relationships between environmental factors and organisms (Ward et al., 2002; Naiman et al., 2005; Renofalt et al., 2005; Tockner et al., 2010).

One of these environmental factors is disturbance. Disturbance regulates species diversity by generating heterogeneous habitats, it induces species turnover, and therefore influences community dynamics (Death, 2002; Hughes et al., 2007; Ilg et al., 2008). It is one of the key factors structuring ecological communities and significantly influences the functioning of an ecosystem (Hooper et al., 2005; Diaz et al., 2007). In floodplains, flood disturbance controls both the spatial and temporal distributions of organisms (Diaz et al., 2007), as well as their life-history strategies (Lytle and Poff, 2004). Other studies showed that species abundance generally increases with higher levels of disturbance, although decreasing at the highest level (Gerisch et al., 2011). These findings are in line with the intermediate disturbance hypothesis (IDH) (Connell, 1978) and the stress hypothesis (SH) (Gray, 1989), suggesting the highest species diversity at intermediate levels of disturbance.

Another factor playing an important role in maintaining natural ecological processes and biodiversity in freshwater systems is spatial connectivity (Petts, 1996; Pringle, 2001; Fausch et al., 2002; Nel et al., 2011). Spatial connectivity of a river occurs in three directions: longitudinal (upstream-downstream), lateral (between the river and surrounding floodplain) and vertical (between the river and groundwater). Longitudinal connectivity allows long and short distance migration of riverine organisms and is important for dispersal, reproduction and long-term population dynamics of many fish species, for example. Lateral connectivity ensures the connection and exchange between aquatic and terrestrial floodplain habitats, e.g. the interaction between the river and surrounding riparian vegetation. Drivers influencing the composition, productivity and state of succession of the riparian vegetation, which then affects water temperature, aquatic light conditions and the amount and quality of incoming organic matter (Ward, 1989). Additionally, a functioning lateral connectivity helps maintain

viable populations of water-dependent species that use the main channel as a refuge during the dry season (Welcomme, 1979). Vertical connectivity is crucial for surface ecosystems that depend on groundwater (Stanford and Ward, 1988) and for organisms that spend parts of their life cycles in the hyporheic habitat (Amoros and Bornette, 2002).

Floodplains house a highly diverse flora and fauna, due to their high dynamics and heterogeneity (Robinson et al., 2002; Stanford et al., 2005). The heterogeneity of a floodplain occurs at different scales and at different points: it exists within and between habitat types as there are differences between the different spatial zones of floodplains (e.g. upper and lower floodplain) and there are habitat-specific upwelling and downwelling zones. Additionally, the whole system changes dynamically over time (daily and seasonally), making a floodplain highly complex and highly interesting. In this study, I was interested in these different levels of spatial pattern and how they influence biodiversity. Looking at differences between habitat types, I was especially interested in the role of tributaries and islands because I could imagine them to be biodiversity “hotspots” within a floodplain. In the case of tributaries, there is already evidence for this idea, presenting the confluence zones (the actual mixing zones of water) of tributaries as highly diverse zones in terms of invertebrate diversity (Rice et al., 2001). Reasons for this increase in biodiversity could be increased habitat complexity (Rice et al., 2001; Benda et al., 2004; Kiffney et al., 2006), better food availability due to input or retention of organic matter (Wallis et al., 2009) or as potential refuges for species no longer finding appropriate habitat in the main channel. Of course one must take into account the source of a tributary (snowmelt, glacier, groundwater) and through the kind of catchment (agricultural, urban, natural) it flows, resulting in different nutrient and ionic concentrations (sometimes also containing pesticides or herbicides) (Hynes, 1975; Likens and Bormann, 1977). Islands on the other hand, separate the main channel, changing flow velocities, bringing in additional nutrients (e.g. through falling leaves) and by increasing the overall connectivity between the aquatic and terrestrial system through an increased shoreline length. Because of this, it is easy to conceive that islands also represent kind of “hotspots” in biodiversity in a floodplain.

As for islands in particular, it is quite interesting to study possible linkages between the aquatic and terrestrial system. As others studies showed, rivers can provide important sources of energy for riparian biota (Paetzold et al., 2005). Aquatic insects can make up a dominant part of the diet of riparian arthropod predators (e.g. for some staphylinid beetles). This predation by terrestrial predators, on the other side, also has an influence on taxonomic composition of emerging aquatic insects. The abundance and composition of emerging aquatic insects may change seasonally, depending on the current dominant predator at the time of emergence (Paetzold and Tockner, 2005).

In this study, the invertebrate biodiversity (aquatic and terrestrial) of different habitat types occurring in a subalpine floodplain was measured. The main objectives of the study were to: (i) Quantify the biodiversity of different habitats within a subalpine floodplain; (ii) Identify potential factors influencing invertebrate biodiversity in a floodplain; (iii) Qualify tributaries and islands concerning their potential role as biodiversity hotspots; and (iv) Detect possible relationships between the aquatic and terrestrial systems. My final goal was to get a better understanding of the influence of habitat properties, such as connectivity, on biodiversity in a complex riverine floodplain. In the end, the acquired knowledge may then help possible restorations in this or other floodplains to improve biodiversity and the overall integrity of a floodplain.

2 Material and Methods

2.1 Study area

The study area, the floodplain of the Urbach river, is located in the Bernese Alps, southwest of Innertkirchen, Switzerland (Fig. 1) (46°40' N, 8°12'E). It is 3.4 km long, up to 600 m wide and 800-900 m a.s.l. While the right side opens up into grassland areas, bordered by forested mountain slopes, the left side of the valley is bordered by a ca. 1600 m high steep wall. Geology is mainly characterized by limestone and granite. Temperature is highly seasonal (annual average temperature: 2.8 °C) and precipitation is moderate (1614 mm y⁻¹). Alder (*Alnus incana*) and different willow species (*Salix spp.*) dominate the vegetation. This floodplain contains all the typical habitat types for a natural floodplain, including grassland, riparian forest, islands, exposed gravel bars, tributaries, main and side channels. The discharge regime is near-natural and is driven mostly by glacial melt-water and periodic precipitation events. Additionally, after 1950^s discharge is impacted by the local power supplier KWO (Kraftwerke Oberhasli AG), abstracting approximately 30 % of the water. As measures for flood protection, several levees have been installed (mostly in 1990^s) along the active part of the floodplain.

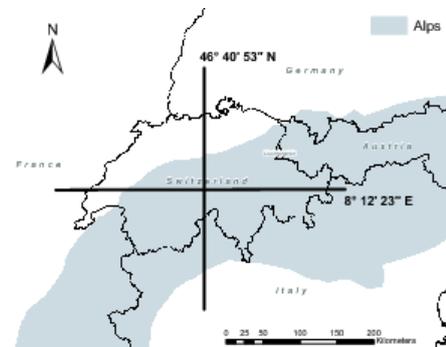


Fig. 1 Location of the Urbach floodplain

2.2 Field sampling

Samples were collected from 5 different habitat types (tributary, braided section, island, main and side channel) (Tab. 1). For each habitat type, 3 sampling sites were chosen, distributed over the entire Urbach floodplain (See App. 8.1). Within each sampling site 3 sub-samples were taken (*a*, *b* and *c*) within a radius of ~10 m. At each sampling spot, an aquatic sample and two kinds of terrestrial samples were collected. For the



Fig. 2 Pitfall trap

aquatic part, in the case of tributaries, sample *a* was taken in the main channel right above the incoming tributary, sample *b* in the tributary itself and sample *c* in the main channel right below the tributary. For islands, I took sample *a* on the upper end of the island (upstream), *b* besides the island and *c* on the lower end (downstream). The samples for the main channel,

for side channels and for braided sections, were taken in a row, from a downstream to *b* and *c*. The terrestrial samples were collected at the corresponding spots on land, parallel to the aquatic sampling points. The aquatic ones were collected with a Hess sampler (sampling time: 30s, mesh size: 250 µm). Pitfall traps (exposed for 24h) and a “loop-technique” were used for the terrestrial samples.

The “loop-technique” means that we randomly threw a loop of a fixed diameter (0.42 m), examined the area enclosed by the loop for about 5 minutes, and collected every animal we found within the loop area.

Sampling was conducted twice, the first took place in May/June 2012 (25.05, 19./20., 27./28.06.12), the second in August (06.-08.08.2012).

In total, 180 samples were collected (5 habitats*3 replicates*3 samples/site*2 systems*2 times). All samples were stored in PVC bags, conserved with ethanol, cooled in cooling boxes, and taken to the laboratory where they were stored at 4 °C.

Table 1 Characteristics with foto examples (taken in the Urbach floodplain) of the 5 habitat types sampled in this study. Adapted from (Doering et al., 2012).

Habitat type	Characteristics
<i>Main channel</i>	Permanent aquatic habitat type, composed of coarse permeable gravel sediments, fringed by gravel bars.
<i>Side channel</i>	Permanent aquatic habitat type with coarse permeable gravel sediments, flowing typically more or less parallel to the main channel. Channel width and depth smaller than in the main channel, typically with lower flow velocity. They can fall dry rarely.
<i>Tributary</i>	Smaller streams originating from other rivers, snowmelt or groundwater entering the main channel. In some cases (e.g. snowmelt streams), they exist only temporarily and they fall dry from time to time.
<i>Braided section</i>	A section of the main channel where the river bed is widened around gravel bars, splitting up the river. Typically lower water depths and slower flow velocities than in normal main channel habitats.
<i>Island</i>	Predominantly terrestrial habitat type characterized by sandy substrata and partially developed soil (Eutrocheptu fluvisol), mainly colonized by different willow (<i>Salix sp.</i>) species and <i>Alnus incana</i> . These habitats are surrounded by channel water or exposed gravel (Gurnell et al., 2001).

<i>Main channel</i>	<i>Side channel</i>	<i>Tributary</i>	<i>Braided section</i>	<i>Island</i>
				

2.3 Habitat measurements

At each sampling site, a series of habitat measurements were conducted, including water temperature, conductivity, velocity (near-bed and at 60% water depth), water depth and substrate size (by measuring 3 stones typical for the site).

2.4 Laboratory analyses and species identification

To assess the organic matter content (BOM) at a site, the non-faunal parts of the Hess samples were taken. They were dried (at 60 °C for 48 h), weighted, ashed at 500°C for 3 h and weighted again (differences in g = $AFDM_{Hess}$, eq. 1). To measure periphyton biomass, representative stones were collected at each site. In the lab, the stones were cleaned from the periphyton by a steel brush. From the algal suspension, a small amount (5-10 ml) was taken and filtered by a vacuum pump. The filters (Whatman™ GF/F) with the periphyton were dried (at 60 °C for 48 h), weighted, ashed at 500 °C for 3 h and weighted again (differences in g = $AFDM_{pp}$, eq. 2).

The organic matter content of the Hess samples was expressed as grams per square meter ($AFDM_{Hess}$ g/m²):

$$AFDM_{Hess} \text{ (g/m}^2\text{)} = (m_{60C} - m_{500C}) * \left(\frac{1}{A_{Hess}}\right) \quad (1)$$

where m_{60C} is the mass (g) of a dried sample at 60 °C and m_{500C} is the mass (g) of an ashed sample at 500 °C. A_{Hess} (m²) stands for the area of the Hess sampler.

Periphyton biomass was calculated as grams per stone surface ($AFDM_{pp}$ g/m²):

$$AFDM_{pp} \text{ (g/m}^2\text{)} = \frac{(m_{60C} - m_{500C})}{S_{Stone}} * 10000 \quad (2)$$

where S_{Stone} is the surface (cm²) of a stone. It was calculated using the following equation:

$$S_{Stone} \text{ (cm}^2\text{)} = (L_S * W_S) * (3.14/4) \quad (3)$$

where L_S is the length (cm) and W_S (cm) the width of a stone.



Fig. 3 Identification of a terrestrial sample

For the identification of the different invertebrates, a stereo zoom microscope (Olympus SZH) was used. For identification, keys of Tachet (“Invertébrés d’eau douce”) for the aquatic part and the keys of Stresemann (“Exkursionsfauna von Deutschland – Wirbellose: Insekten”) and of Bährman (“Bestimmung wirbelloser Tiere”) for the terrestrial part were used.

2.5 Biodiversity measures

From the data obtained by identifying and counting all the animals found in the samples, the different biodiversity measures for the different sampling methods were calculated:

Species density:

$$\text{Hess samples: Species density (Individuals/m}^2\text{)} = \sum \text{Individuals} * \left(\frac{1}{A_{\text{Hess}}}\right) \quad (4)$$

$$\text{Loop samples: Species density (Individuals/m}^2\text{)} = \sum \text{Individuals} * \left(\frac{1}{A_{\text{Loop}}}\right) \quad (5)$$

$$\text{Pitfall traps: Species density (Individuals/m}^2\text{)} = \sum \text{Individuals} \quad (6)$$

Species richness (also referred as α -diversity) (for all three sampling methods the same):

$$\text{Species richness (Taxa)} = \sum \text{diff. taxonomic groups} \quad (7)$$

Additionally, for Hess samples, the other two diversity levels (β -, and γ -diversity) were calculated:

$$\beta - \text{Diversity} = \frac{a+b+c}{(2a+b+c)/2} \quad (\text{Whittaker, 1960}) \quad (8)$$

$$\gamma - \text{Diversity} = \sum \text{diff. taxonomic groups (whole floodplain)} \quad (9)$$

where a is the total number of species occurring in both habitats, b and c standing for the number of species occurring just in the one but not in the other habitat.

2.6 Statistical analysis

To analyze variation in species density and taxon richness between habitats and to look for a possible date effect, a two-way Analysis of Variance (ANOVA) with an *a posteriori* test (Tukey *post hoc*) was used. ANOVA was calculated using the Statistical Package for Social Sciences (SPSS) version 20.0 for windows (SPSS Inc., Chicago, IL, U.S.A.). To compare the structural properties of the different habitat types, a principal component analyses (PCA) was conducted. PCA was based on a correlation matrix, where data on habitat properties was standardized and centered. To explore similarities or dissimilarities in the taxon richness between the different habitats, a non-metric multidimensional scaling (NMDS) was conducted. NDMS was based on a similarity-matrix, where data on taxon richness was standardized and centered.

PCA and NDMS were done using STATISTICA version 11.0 for windows (STATISTICA, Statsoft, Tulsa, OK, U.S.A). Density and taxon richness values of the different sampling methods were tested for significant correlations with habitat properties using Pearson correlation, followed by a pairwise t-test.

3 Results

3.1 Habitat-specific water properties

The 5 different habitat types differed greatly in physico-chemical water properties (Table 2). Average temperature ranged from 9.1 ± 2.2 °C at tributaries to 12.1 ± 1.9 °C at islands. Water conductivity was highest at side channels (173.7 ± 14.1 $\mu\text{S}/\text{cm}$) and lowest in braided sections (66.4 ± 25.9 $\mu\text{S}/\text{cm}$). Flow velocities were the highest in the main channel (0.8 ± 0.5 m/s near bed, 1.0 ± 0.5 m/s at 60% water depth) and the lowest in side channels (0.3 ± 0.1 m/s, 0.5 ± 0.2 m/s). Average depth was quite uniform, ranging from 0.2 ± 0.1 m in side channels and tributaries to 0.3 ± 0.1 m in the main channel, braided sections and islands. Substrate size ranged from 21.3 ± 10.3 cm to 33.1 ± 10.1 cm. Organic matter content (AFDM, ash-free dry mass) of the Hess samples was highest in side channels (1.7 ± 2.6 g/m^2) followed by islands (0.8 ± 1.1 g/m^2). Periphyton biomass was quite similar across the habitats ($0.4\text{-}0.5 \pm 0.1\text{-}0.4$ g/m^2) except for side channels at 1.5 ± 1.7 g/m^2 .

Table 2 Physico-chemical properties with corresponding F-values of the different habitats from the sampled floodplain. Numbers present averages (combined of both dates) and standard deviations.

Habitat property	Main channel <i>n</i> = 18	Side channel <i>n</i> = 17	Tributary <i>n</i> = 15	Braided <i>n</i> = 18	Island <i>n</i> = 18	F
Temperature [°C]	9.8 ± 2.0	11.0 ± 1.6	9.1 ± 2.2	9.7 ± 2.7	12.2 ± 1.9	11.0*
Conductivity [$\mu\text{S}/\text{cm}$]	57.1 ± 7.4	173.7 ± 14.1	73.2 ± 25.7	66.4 ± 25.9	102.3 ± 43.5	49.5*
Flow velocity						
near bed [m/s]	0.8 ± 0.5	0.3 ± 0.1	0.4 ± 0.3	0.6 ± 0.3	0.6 ± 0.4	6.3*
60% depth [m/s]	1.0 ± 0.5	0.5 ± 0.2	0.6 ± 0.4	0.9 ± 0.4	1.0 ± 0.5	7.2*
Depth [m]	0.3 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	4.5*
Substrate size [cm]	33.1 ± 10.1	21.3 ± 10.3	23.1 ± 9.8	26.2 ± 12.3	29.1 ± 16.0	2.7*
AFDM _{Hess} [g/m^2]	0.5 ± 0.5	1.7 ± 2.6	0.3 ± 0.3	0.7 ± 1.5	0.8 ± 1.1	2.2
AFDM _{PP} [g/m^2]	0.4 ± 0.1	1.5 ± 1.7	0.4 ± 0.1	0.4 ± 0.1	0.5 ± 0.4	13.8*

AFDM, ash-free dry mass; PP, periphyton; *n*, number of samples in each habitat ; *, the mean difference is significant at the .05 level (*p*).

The principal component analysis (PCA) based on physico-chemical water properties of the different habitats explained 38% of the variability in the data on the first axis (F1) and 21% variability on the second axis (F2) (Fig. 4). The first axis was best explained by the flow velocity, water depth and substrate size, while the second axis was correlated with water temperature and conductivity. The different habitats were clearly separated, especially side channels and islands. Side channels typically were characterized by slow flow velocities, shallow water depths and substrate sizes and high conductivities, which is the opposite of main channels with high flow velocities, greater water depths and substrate sizes, and low conductivities. Braided sections were plotted intermediate to other habitat types.

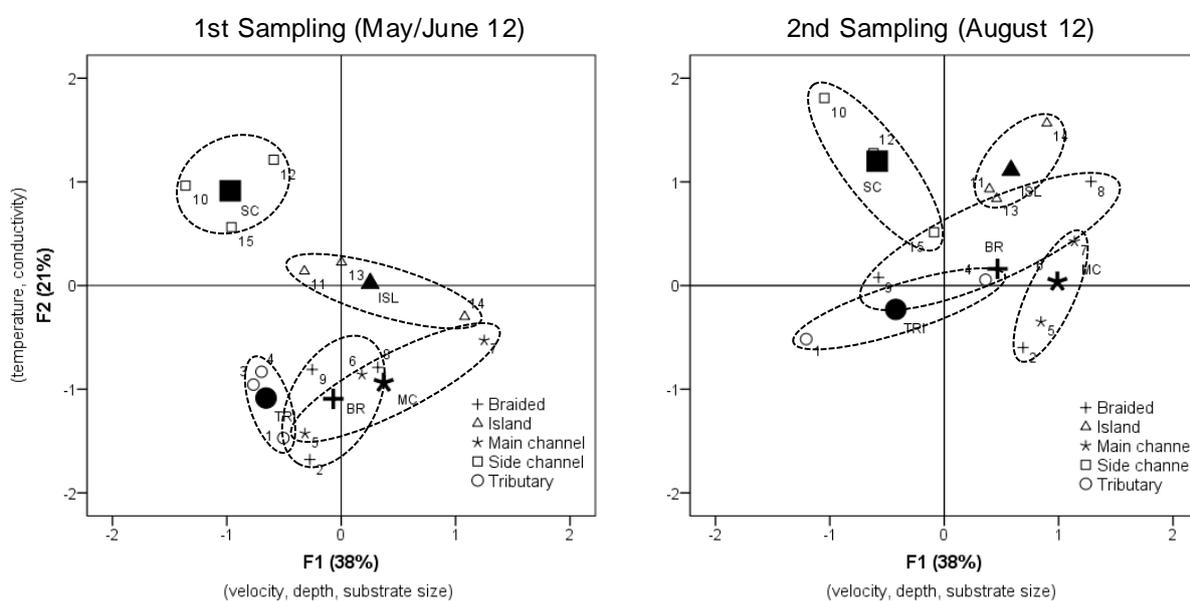


Fig. 4 PCA ordination diagrams of the two sampling dates showing the differentiation of the measured habitats based on measured physico-chemical characteristics. Each small symbol stands for a habitat sample, the large bold symbols represent the average for each habitat. The dashed ellipses group the different habitat samples of each habitat type.

3.2 Density and taxon richness

Aquatic

Average density and taxon richness differed significantly between the 5 different habitat types ($F=3.89$ resp. $F=5.56$, $p\leq 0.05$) (Fig. 5). A *post hoc* Tukey test showed that species density and taxon richness were significantly higher in the main channel and side channels compared to tributaries ($p\leq 0.05$) (Table 3).

For both density and taxon richness, no date effects were detected between the first and second sampling ($p\geq 0.05$) and there were no interaction effects ($p\geq 0.05$).

Terrestrial

In pitfall traps, no significant differences between habitats could be detected, either in density or taxon richness ($F=1.33$, $p=0.266$ resp. $F=1.36$, $p=0.253$). There was a date effect for taxon richness ($F=19.35$, $p\leq 0.05$), showing a significantly higher taxon richness on the first sampling date compared to the second ($T=4.38$, $p\leq 0.001$). There were no interactions between site and date for density or taxon richness ($p\geq 0.05$).

In the loop samples, density and taxon richness differed significantly between habitats ($F=3.89$ $F=5.56$, $p\leq 0.05$, resp.). A *post hoc* Tukey test showed that density was significantly higher in side channels and islands compared to tributaries ($p\leq 0.05$). Taxon richness was significantly higher in side channels compared to tributaries and the main channel ($p\leq 0.05$). There was also a date effect in the loop samples, showing a significantly higher taxon richness on the first sampling date ($T=4.912$, $p\leq 0.001$). There were no interactions between site and date for density or taxon richness ($p\geq 0.05$).

HESS SAMPLES

LOOP SAMPLES

PITFALL TRAPS

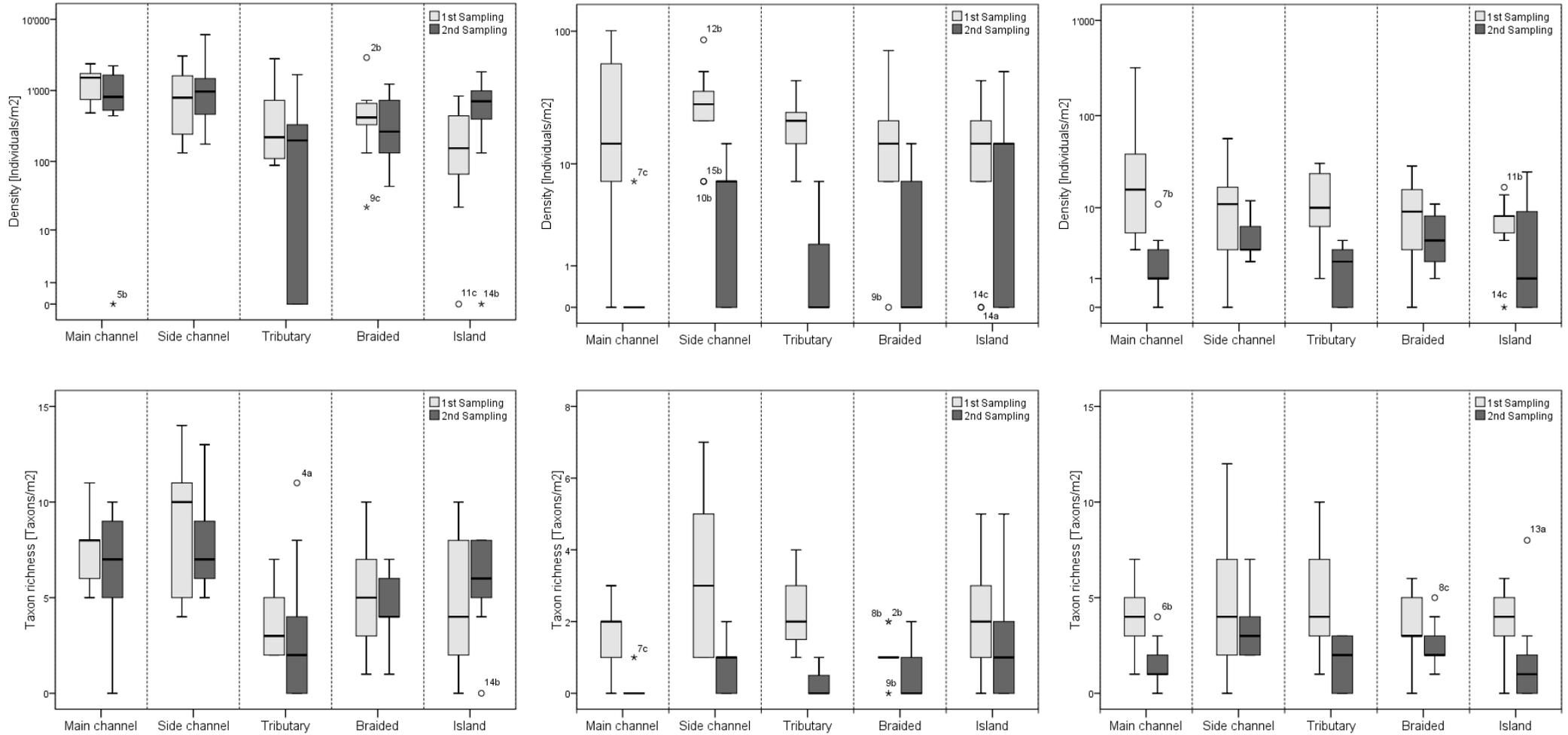


Fig. 5 Density and taxon richness in the different habitat types and different types of samples.

Table 3 *Post hoc* Tukey test table with mean differences in density and taxon richness between the different habitat types. Significant differences are highlighted bold and colored in green if positive or red if negative.

Habitat		Hess samples		Pitfall traps		Loop samples	
		D	R	D	R	D	R
Main channel <i>n</i> = 18	B	0.384	0.145	0.223	0.074	-0.211	-0.110
	I	0.600	0.163	0.296	0.002	-0.343	-0.111
	S	-0.040	-0.067	0.023	-0.086	-0.409	-0.239*
	T	0.779⁻	0.296⁻	0.006	-0.081	0.109	0.049
Side channel <i>n</i> = 17	B	0.424	0.212	0.201	0.161	0.198	0.129
	I	0.640	0.231	0.273	0.088	0.067	0.128
	M	0.040	0.067	-0.023	0.086	0.409	0.239⁻
	T	0.819⁻	0.363⁻	-0.017	0.006	0.519⁻	0.288⁻
Tributary <i>n</i> = 15	B	-0.395	-0.151	0.217	0.155	-0.321	-0.159
	I	-0.179	-0.133	0.289	0.082	-0.452*	-0.159
	M	-0.779*	-0.296*	-0.006	0.081	-0.109	-0.049
	S	-0.819*	-0.363*	0.017	-0.006	-0.519*	-0.288*
Braided <i>n</i> = 18	I	0.216	0.018	0.072	-0.073	-0.132	-0.001
	M	-0.384	-0.145	-0.223	-0.074	0.211	0.110
	S	-0.424	-0.212	-0.201	-0.161	-0.198	-0.129
	T	0.395	0.151	-0.217	-0.155	0.321	0.159
Island <i>n</i> = 18	B	-0.216	-0.018	-0.072	0.073	0.132	0.001
	M	-0.600	-0.163	-0.296	-0.002	0.343	0.111
	S	-0.640	-0.231	-0.273	-0.088	-0.067	-0.128
	T	0.179	0.133	-0.289	-0.082	0.452⁻	0.159

D, density; R, taxon richness; *n*, number of samples;

B, braided section; I, island; S, side channel; T, tributary; M, main channel;

*, the mean difference is significant at the .05 level.

Non-metric multidimensional scaling (NMDS) of taxa distributions in the different habitats resulted in a stress value of 0.15 (Fig. 6). For the first sampling dates, the different habitats overlapped to a large extent except for side channels that were again clearly separate. On the second sampling date, all 5 habitats were clearly separated, indicating significant differences in taxa composition.

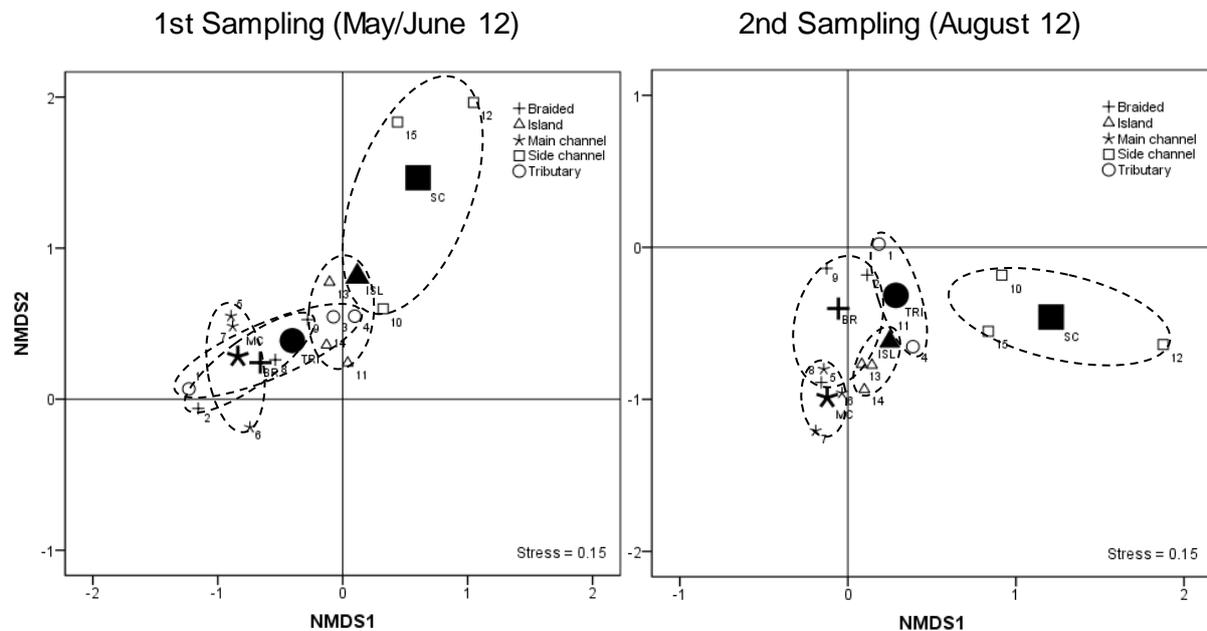


Fig. 6 NMDS plots for the two sampling dates presenting the differentiation between habitats in terms of taxa composition. Each small symbol stands for a habitat sample, the large bold ones represent the average of each habitat. The dashed ellipses group the different habitat samples of each habitat type.

3.3 Biodiversity levels

α -Diversity was, on both sampling dates, highest in side channels (21 taxa on both dates) and lowest in braided sections (12, 11 taxa, resp.)(Fig. 7). There was no general trend detectable from the first to the second sampling. In the main channel, a drastic drop in α -diversity (from 18 to 11 taxa) was detected from the first to the second sampling date, in braided sections it dropped slightly (from 12 to 11 taxa), whereas it remained constant in side channels (21 taxa on both dates) and it even increased slightly in tributaries (from 12 to 15 taxa) and islands (from 13 to 16 taxa).

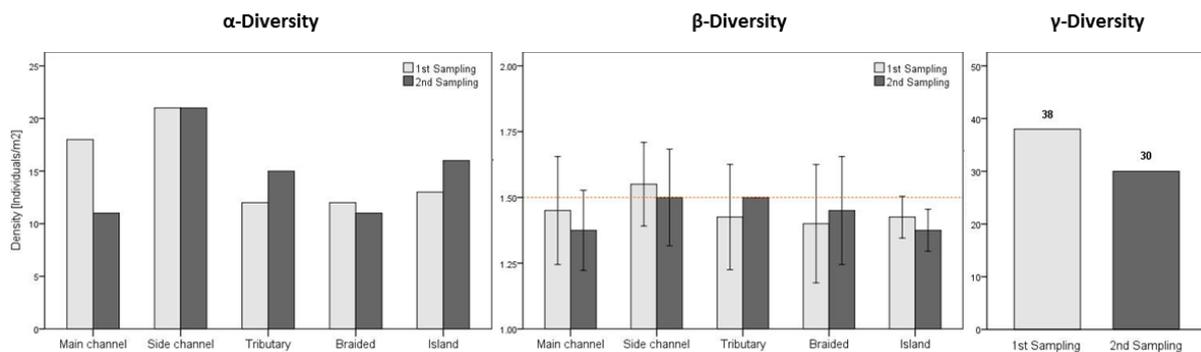


Fig. 7 Plots of the different diversity levels in the study floodplain. α -Diversity, standing for the total number of taxa found in a habitat type; β -Diversity, representing the differences in diversity between habitat types (averages with 95%-CIs; the orange, dotted line stands for the breaking point from similarity [1-1.5] to dissimilarity [1.5-2.0]); γ -Diversity, standing for the total number of taxa found in the whole floodplain.

Average β -diversity ranged from 1.38 ± 0.12 in braided habitats to 1.57 ± 0.09 in side channels for the first sampling date and from 1.35 ± 0.09 in the main channel to 1.49 ± 0.07 in side channels for the second sampling date (Fig. 7).

Looking at individual β -diversity values between two different habitats, in the first sampling the highest values were found between side channels and the main channel (1.64) resp. tributaries (1.64) (Table 4). The most similar taxa distributions (lowest β -diversity) were found between braided sections and tributaries (1.25). On the second sampling date, the highest β -diversity was found between side channels and braided sections (1.56), whereas the lowest existed between islands and the main channel (1.26).

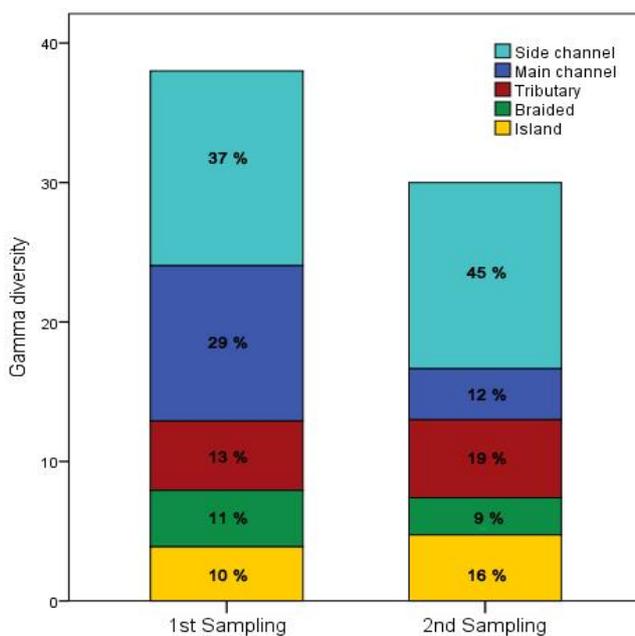
Considering the two different sampling dates, β -diversity generally decreased from the first to the second sampling date, except between braided sections and tributaries and islands, where it increased from 1.25 to 1.46 and from 1.36 to 1.41, respectively.

Table 4 Beta biodiversity values representing the differences in diversity between the different habitat types. Colors indicate the similarity or dissimilarity of a specific comparison (green=similar, red=dissimilar).

	MC	SC	TRI	BRAI	ISL	Average β	SD	
1st Sampling	Main channel	-	1.64	1.40	1.33	1.48	1.46	0.12
	Side channel	1.64	-	1.64	1.58	1.41	1.57	0.09
	Tributary	1.40	1.64	-	1.25	1.44	1.43	0.14
	Braided	1.33	1.58	1.25	-	1.36	1.38	0.12
	Island	1.48	1.41	1.44	1.36	-	1.42	0.04
2nd Sampling	Mainchannel	-	1.44	1.38	1.30	1.26	1.35	0.07
	Sidechannel	1.44	-	1.55	1.56	1.41	1.49	0.07
	Tributary	1.38	1.55	-	1.46	1.42	1.46	0.06
	Braided	1.30	1.56	1.46	-	1.41	1.43	0.09
	Island	1.26	1.41	1.42	1.41	-	1.37	0.07

MC, main channel; SC, side channel; TRI, tributary; BRAI, braided; ISL, island; SD, standard deviation

Gamma diversity (γ) decreased in the floodplain from the first (38 taxa) to the second sampling date (30 taxa) (Fig. 7).



Looking at the amount that each habitat contributed to the overall gamma diversity (γ), side channels clearly added the most to it on both sampling dates (37, 45 %, resp.)(Fig. 8). On the first sampling date it was followed by the main channel (29 %) and tributaries (13 %), on the second by tributaries (19 %) and islands (16 %). If we compare these values with the alpha diversities (α) of each habitat (which is maximally 21 in side channels), it is obvious, that the different types of habitats add to the overall floodplain

Fig. 8 Contribution (in %) of each habitat to gamma diversity (γ).

The taxa composition widely differed between the five different habitats (Fig. 9). Although, common to all of them was that Diptera always was the most prominent group with up to 16 different taxa (in main channel, 1st sampling). Within the dipterans the most prominent groups were chironomids (Chironomidae) and black flies (Simuliidae). Caddis- (Trichoptera), may- (Ephemeroptera) and stoneflies (Plecoptera) were also found in every habitat (with the exception of no caddisflies found in tributaries on the first sampling). The most found taxa in these were *Rhitrogena* sp., *Baetis* sp. (both Heptageniidae, Ephemeroptera) and *Rhabdiopteryx* sp. (Taeniopterygidae, Plecoptera). In some habitats I also found some coleopterans (in particular in side channels). In side channels (and also in other habitats) I also found some other animals, not belonging to the insects (“Others”), e.g. earthworms (*Eiseniella* sp.), snails (Pulmonata) or mites (Trombidiformes).

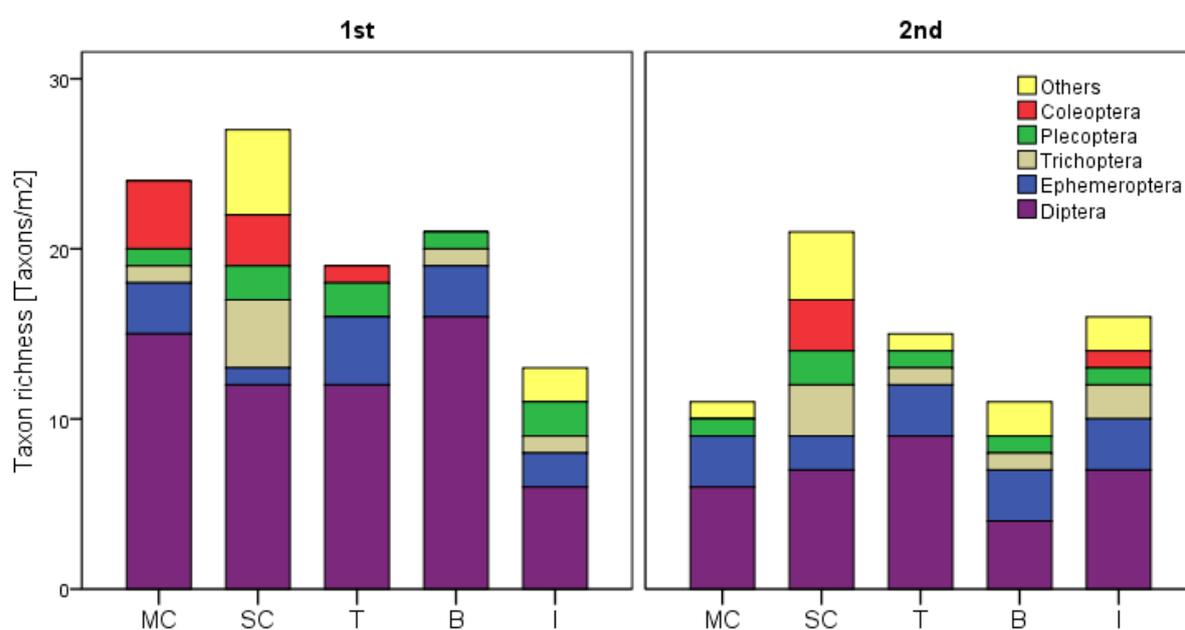


Fig. 9 Taxonomic composition of the different habitats on both sampling dates. MC, main channel; SC, side channel; T, tributary; B, braided; I, island.

3.4 Correlations between aquatic habitat properties and biodiversity

Correlations between physico-chemical habitat properties and biodiversity measures (density and taxon richness) of Hess samples showed one main influencing factor: organic matter content (AFDM_{Hess}, AFDM_{PP}) (Tab. 5). There were significant positive correlations between organic matter (AFDM_{Hess}) and the corresponding density ($R=0.461$, 0.462 resp., $p\leq 0.01$) and taxon richness ($R=0.415$, 0.414 resp., $p\leq 0.01$) in Hess samples for both sampling dates. In the second sampling date, water temperature also was significantly positive correlated with taxon richness. ($R=0.378$, $p\leq 0.05$). All the other habitat properties were not significantly correlated with density or taxon richness ($p\geq 0.05$).

Table 5 Pearson correlation coefficients (R) with significance level (P) (in brackets) of biodiversity measures (density and taxon richness) of Hess samples on physico-chemical habitat properties within each habitat type. Significant correlations are highlighted bold and colored in green if positive or red if negative.

Habitat property	1st Sampling		2nd Sampling	
	Density	Taxon richness	Density	Taxon richness
Temperature [°C]	-0.223 (.141)	-0.011 (.941)	.285 (.071)	.378* (.015)
Conductivity [$\mu\text{S}/\text{cm}$]	-0.142 (.352)	.027 (.859)	.102 (.525)	.226 (.156)
Flow velocity				
ground [m/s]	.087 (.572)	.113 (.461)	.047 (.772)	.017 (.914)
60% depth [m/s]	.138 (.367)	.215 (.157)	.130 (.420)	.089 (.582)
Depth [m]	.062 (.688)	.177 (.246)	.018 (.913)	-0.017 (.914)
Substrate size [m]	.110 (.471)	.200 (.189)	-0.036 (.821)	-0.056 (.729)
AFDM _{Hess} [g/m^2]	.461** (.001)	.415** (.005)	.462** (.002)	.414** (.007)
AFDM _{PP} [g/m^2]	.124 (.416)	.239 (.114)	.119 (.460)	.121 (.450)

AFDM, ash-free dry mass; PP, periphyton;

** Correlation is significant at the 0.01 level (2-tailed),

* Correlation is significant at the 0.05 level (2-tailed)

3.5 Relations between aquatic and terrestrial biodiversity

There were significant correlations found between Hess samples (aquatic) and loop sample (terrestrial) biotic indices (Table 6). On the first sampling date, density of Hess samples correlated positively with taxon richness of loop samples ($R=0.310$, $p\leq 0.05$) and taxon richness of Hess samples correlated positively with density and taxon richness of loop samples ($R=0.400$, 0.413 , resp., $p\leq 0.01$). On the second sampling date, density and taxon richness of Hess samples were both correlated positively with density and taxon richness of loop samples ($p\leq 0.05$).

On both sampling dates, there were no significant correlations in biodiversity measures between Hess samples and pitfall traps ($p\geq 0.05$).

Table 6 Pearson correlation coefficients (R) with significance level (P) (in brackets) between aquatic (Hess samples) and terrestrial (loop samples, pitfall traps) diversity measures (species density and taxon richness). Significant correlations are highlighted bold and colored in green if positive or red if negative.

Hess samples	Loop samples		Pitfall traps	
	Density	Taxon richness	Density	Taxon richness
1st Sampling				
Species density	.276 (.067)	.310* (.038)	.144 (.347)	.039 (.801)
Taxon richness	.400** (.006)	.413** (.005)	.083 (.588)	.041 (.788)
2nd Sampling				
Species density	.347* (.020)	.319* (.033)	-.101 (.510)	-.083 (.590)
Taxon richness	.397** (.007)	.369* (.013)	-.131 (.390)	-.070 (.647)

** Correlation is significant at the 0.01 level (2-tailed),

* Correlation is significant at the 0.05 level (2-tailed)

4 Discussion

Biodiversity is important for several ecosystem processes: it plays an important role in recycling, it helps regulate the climate and it helps regulate the water balance of certain systems (Costanza et al., 1998; Bongaarts, 2007). Above that, it directly meets some human needs by providing pharmaceutical substances, guaranteeing high-quality food and by controlling weeds and pests (Gowdy, 1997; Tilman, 2000). But besides these service roles, biodiversity adds to an amazingly diverse and fascinating ecosystem; this aspect alone should be enough to wake the human interest. Floodplains may act as perfect model-systems to study biodiversity because of their high spatial heterogeneity and distinct temporal dynamics (Ward, 1989; Rice et al., 2001; Paetzold et al., 2005; Valett et al., 2005). However, there is still little knowledge about biodiversity patterns across the different habitat types in a floodplain.

In this study I assessed biodiversity of five different floodplain habitats. I wanted to identify factors influencing biodiversity, estimated the role of islands and tributaries in this habitat mosaic, and looked for linkages between aquatic and terrestrial systems.

4.1 Biodiversity across different floodplain habitats

Comparing the five different habitats studied in this floodplain in terms of biodiversity, there is one habitat that stands out for nearly all biodiversity measures: side channel. Side channels showed the highest density and taxon richness in Hess and loop samples, and it was the most distinct habitat (highest β -diversity values) in all the five habitat types, on both sampling dates. Looking at Hess samples, it was followed by the main channel with the second highest density and taxon richness.

On the other side of the spectrum, tributaries showed the lowest density and taxon richness. This was quite surprising because I expected them to be biodiversity hotspots due to their direct connection between the aquatic and the terrestrial system. I thought that they might create biodiversity nodes where they join the main channel, bringing together different animal communities in a kind of “mixing zone”. On the other hand, I expected the main channel to be quite sparsely populated and less diverse because of harsh environmental conditions with high flow velocities and low organic matter content. Obviously, my predictions were not supported because the main channel showed both a high density and high taxonomic richness, on both dates. However, in the case of tributaries, my hypothesis was partially supported because if we look at β -diversity, we can see that tributaries show quite

high values, especially on the second sampling date. This suggests that tributaries indeed don't harbor a lot of species or a lot of taxa, but they harbor species not present in the other habitats; their taxa composition is quite different.

This result can also be seen when looking at the contribution of each habitat to the overall floodplain diversity (γ -diversity, See App. 7.4), where tributaries, even with their low densities, add a remarkable amount of different taxa. Also in this aspect, side channels contribute the most. Unfortunately, side channels, in particular, are prone to floodplain modifications. A regulated floodplain often lacks intact lateral connections between the different habitats, e.g. between the main channel and side channels. They may be cut off by levees or channelized to reduce flood risks, resulting in an overall loss of heterogeneity and thus a loss in diversity (Doering et al., 2012).

Another aspect that is very interesting is the fact that biodiversity generally decreased from the first to second sampling date, especially for the terrestrial samples. Both, density and taxon richness in loop samples and pitfall traps decreased significantly from May to August. The reason for this decrease is most probably a strong flood between the two sampling dates, washing away a lot of terrestrial invertebrates. This decrease can also be seen in Hess samples where the overall floodplain diversity (γ -diversity) declined and in a decreasing β -diversity between nearly all habitats (except between tributaries and braided sections and between braided sections and islands where the differences increased).

4.2 Factors influencing invertebrate biodiversity

Comparison of the five different habitat types in terms of physico-chemical properties revealed four clearly separate habitats (side channels, islands, tributaries and main channel) and one which is somehow in between (braided sections). Side channels and tributaries were characterized by slow flow velocities, low water depths and small substrate sizes. What separated them was conductivity, organic matter content and temperature, which were high in side channels and low in tributaries. On the other hand, there were islands and the main channel which had high flow velocities, high water depths and large substrate sizes. They were also separated from other habitats by conductivity, organic matter content and temperature (high in islands, low in main channel).

When we correlated these habitat properties with biodiversity measures, we detected a clearly positive correlation between organic matter content and both density as well as taxon richness. This could be due to an increased respiration, which is affected by organic matter content (Buchmann 2000; Euskirchen, Chen et al. 2003; Tang, Zhou et al. 2006), resulting in generally more productive and more diverse ecosystems. Another factor that

showed a significantly positive effect on biodiversity (although only on taxon richness on the second sampling date) was temperature. Temperature, like organic matter content, also could be due to an increased respiration (Gansert 1994, 1994; Burton, Pregitzer et al. 1998; Buchmann 2000). What also seems to affect biodiversity in these different habitats is flow velocity. The habitat with the highest biodiversity, side channel, is characterized by a low flow velocity. Braided sections and islands with relatively low diversities had quite high flow velocities. This is not that surprising because its quite obvious that fast flowing rivers are challenging for organisms like invertebrates, struggling to not get washed away. What is surprising is the high density of aquatic invertebrates in the main channel where the flow velocity is naturally the highest. This could mean that the organisms have adopted to this harsh environment. In my opinion, this high diversity may rather be the case because the main channel may act as kind of a melting pot where all of the communities from tributaries and side channels come together. Inflowing colonists from other streams and habitats may lead to this high density of macroinvertebrates.

This high diversity in a pretty unstable environment also is in line with the intermediate disturbance hypothesis (IDH) (Connell, 1978) and the stress hypothesis (SH) (Gray, 1989). Both claim moderate disturbance as a factor positively influencing or increasing biodiversity of an ecosystem. Disturbance creates spatially and temporally heterogeneous habitats, influences species turnover and thus community dynamics (Death, 2002; Hughes et al., 2007; Ilg et al., 2008). Besides the constant disturbance of high flow velocities, organisms living in a floodplain have to cope with regularly occurring floods. These floods may wash away a lot of animals, like we've seen it in this study, but it also can create new habitats and it may boost the productivity of certain habitats via an increased microbial activity resulting in a higher respiration (Valett et al., 2005). This is basically what makes a floodplain a floodplain: a naturally dynamically changing habitat mosaic - while some habitats may be fragmented or even destroyed during floods, new habitats emerge.

4.3 The role of islands and tributaries

My hypothesis concerning islands and tributaries was that they might act as biodiversity nodes or biodiversity hotspots in the whole floodplain. I expected them to offer very suitable habitats because of the potential availability of nutrients (Wallis et al., 2009), different (lower) flow velocities, and to their high connectivity with other habitats.

Tributaries also may act as important refuges for aquatic organisms during extreme low flow periods (Doering et al., 2007). Tributaries are extra complex because they differ in their origin (mostly snowmelt and precipitation on the left side of the floodplain, slope and groundwater on the right side) and thus they differ in temperature (left-side tributaries flowed

over an exposed steep rock face, allowing solar warming) and in nutrient concentrations. Additionally, tributaries on the left side were susceptible to drying, whereas right-side tributaries were mostly permanent. This temporary nature normally should result in a lower density and taxon richness of macroinvertebrates inhabiting these habitats (Williams, 1996; Ruegg and Robinson, 2004). However, this was not the case in this study, although one of the sampled left-side tributaries fell dry between the first and second sampling date. The other tributary sampled on the left side showed a similar density and diversity compared to the right-side one. In this particular case, it may be that this left-side tributary is also permanent. Generally, it is interesting that tributaries indeed did not show high densities of organisms or a high taxonomic diversity but they showed a quite different taxa composition, expressed in relatively high β -diversity values. This finding underlines the importance of tributaries, increasing the overall floodplain biodiversity and as possible refugia for some species.

The role of islands as possible hotspots could not be shown in this study. Islands did not show a high density or taxon richness in Hess samples or pitfall traps. Together with braided sections and tributaries, islands seemed to be relatively less populated and less diverse, at least in Hess samples and pitfall traps. However, the loop samples were, density-wise, relatively high and also quite diverse, compared to the other habitats. According to these results, it cannot be claimed that islands are biodiversity hotspots but this aspect should be studied more, if possible with more sampling, especially for the terrestrial part.

A reason for this relatively low diversity on islands could again, like in tributaries, be their temporary nature in a floodplain. It is likely that an island is completely washed away during an intense flooding, thus there may not be enough time to develop a highly diverse fauna. It would be interesting to study islands of different ages, at different successional stages, and to see whether and how diversity develops. I would guess that in older, stable and completely developed islands with intact vegetation, you would find a highly diverse fauna and flora; especially due to the direct exchange between the aquatic and terrestrial system.

4.4 Relations between the aquatic and the terrestrial system

In this study I was not just interested in the aquatic or the terrestrial biodiversity itself but also in potential linkages between these two systems. Other studies (Paetzold et al., 2005) already showed evidence for existing relationships between aquatic insects and terrestrial predators (e.g. spiders). This has also been shown in this study where I found significantly positive correlations between Hess samples, standing for the aquatic component, and loop samples, representing the terrestrial side. It seems that a higher density and diversity in the

aquatic system positively affect density and diversity on shore. This underlines the premise of aquatic energy subsidies for terrestrial predators (Paetzold and Tockner, 2005) or vice versa. However, there was no significant correlation found between Hess samples and pitfall traps. This may be due to the relatively high susceptibility of pitfall traps to environmental factors (like temperature, weather) or their relatively small sample size.

This finding confirms an important aspect of connectivity, generally contributing to a higher degree of diversity within a floodplain (Petts, 1996; Pringle, 2001; Fausch et al., 2002; Nel et al., 2011). In this case, it is the lateral connectivity between the river and surrounding floodplain. An intact lateral connectivity helps maintain viable populations of water-dependent species during dry seasons (Welcomme, 1979). Unfortunately, floodplain regulations (e.g. building levees) often reduce spatial heterogeneity and lateral and vertical connectivity within a floodplain, which mostly results in an overall loss in the diversity of habitats and their flora and fauna (Doering et al., 2012).

4.5 Methodological constraints and future research

The goal of this study was to gain a better knowledge of the biodiversity within a floodplain, detect possible patterns and find influencing factors. Assessing biodiversity is by nature not trivial because there is no technical instrument giving out a simple number as a measure of it. There are multiple ways of sampling, there are multiple methods of analyzing, and there are multiple ways of interpreting it. Doing it for both aquatic and terrestrial systems doesn't make it easier either.

In this study, I used Hess samples to evaluate the aquatic part and pitfall traps together with a loop technique for the terrestrial one. Hess sampling is quite robust and often used in biodiversity studies. It is not that susceptible to environmental factors like weather on the sampling date, for example. On the other hand, the loop technique we used as well as pitfall traps are very susceptible to environmental conditions. The location of a pitfall trap or the spot you randomly threw the loop may heavily influence the sampling content. Insects, for example, are very temperature sensitive. This means that the content of a pitfall trap placed during a warm, sunny weather period may differ widely from a pitfall trap placed during a rainy day. The same holds for loop samples. Other factors that may influence the content of loop samples and pitfall traps are substratum, sun exposition (shady/half-shady/sunny) and time of day. The high susceptibility of these two sampling methods must be taken into account. Ideally, one can take enough samples to cover the whole range of variability and if possible one may find correlations between environmental conditions and the sampling content. Of course, it would have been generally better to have more sampling dates, also for

the Hess samples, but this was unfortunately limited by the fact that it was just a master thesis within a relatively short time frame.

For future research, it would be nice to study this floodplain more deeply and with more time available. For example, it would be interesting to sample more different tributaries, permanent or temporary, from both sides of the river and from different zones of the floodplain (e.g. up- or downwelling). Or, if the floodplain gets renaturated one way or another, it would be interesting to assess the biodiversity again to see if it improved. Generally, I think that there is still a lot of uncharted space concerning natural floodplains and they provide a lot of possibilities to study interactions between organisms and their environment, between different habitat types and even between different systems (aquatic and terrestrial).

5 Conclusions

These results clearly underline the importance of habitat heterogeneity in a floodplain, positively influencing macroinvertebrate biodiversity. They show that homogenizing efforts like in floodplain regulations (e.g. by channelizing side channels or tributaries or by building levees) result in an overall loss of biodiversity within a floodplain. Spatial connectivity between the river and the surrounding floodplain is crucial for a diverse fauna and flora. Thus renaturation efforts should focus on reconnecting cut-off side channels and tributaries. This would lead to a higher spatial heterogeneity, thus to a higher biodiversity, and this would in the end translate into a healthier floodplain in general.

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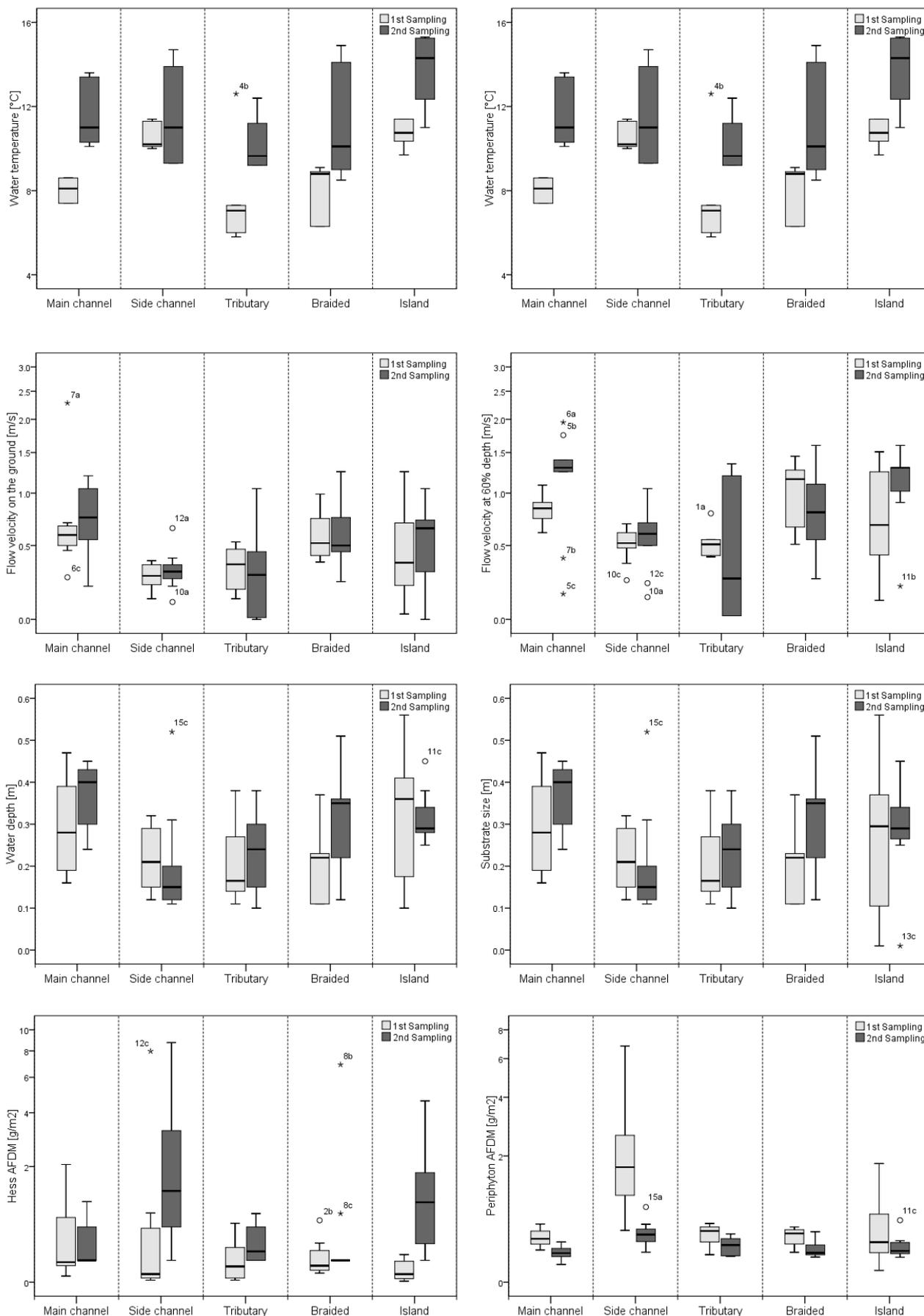
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8 Appendix

8.1 Sampling spots



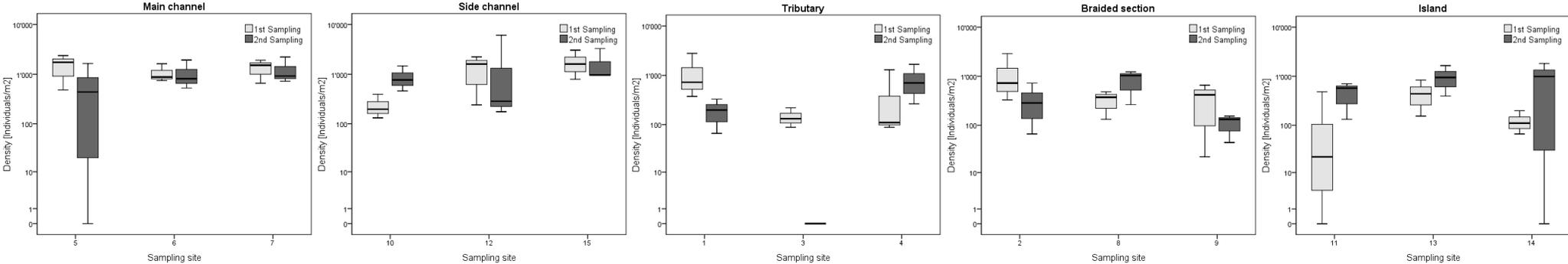
8.2 Habitat properties



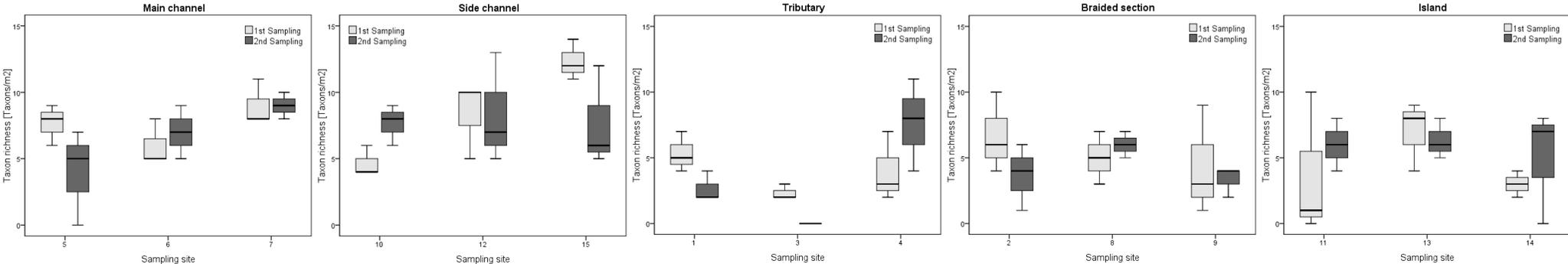
8.3 Density and taxon richness of the different sites

HESS SAMPLES

Density

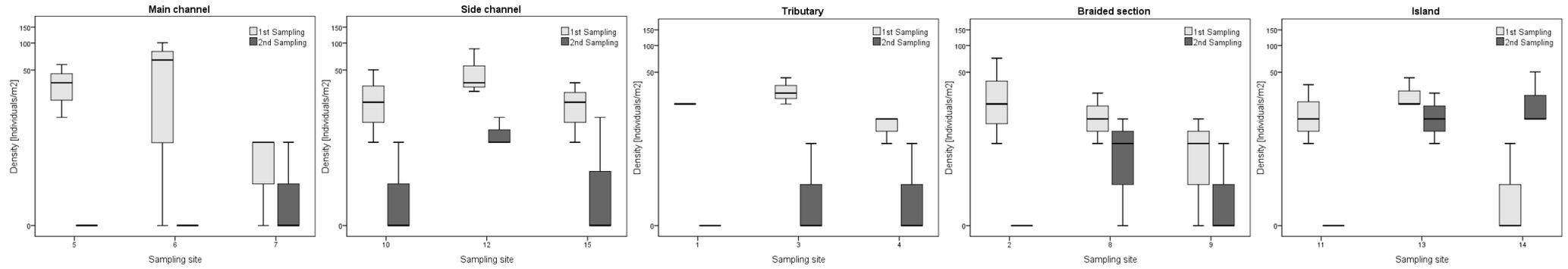


Taxon richness

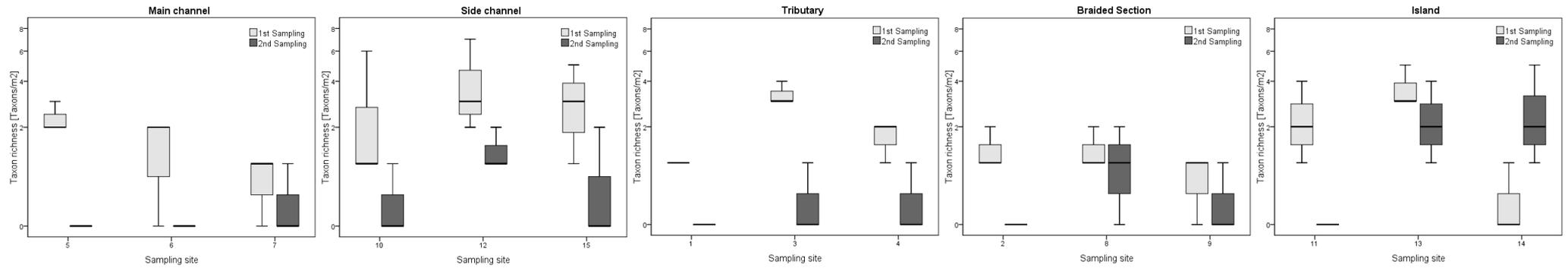


LOOP SAMPLES

Density

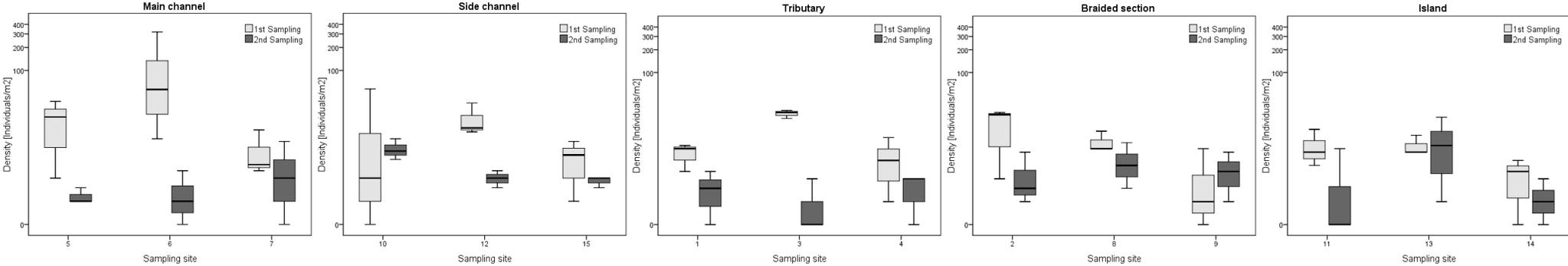


Taxon richness

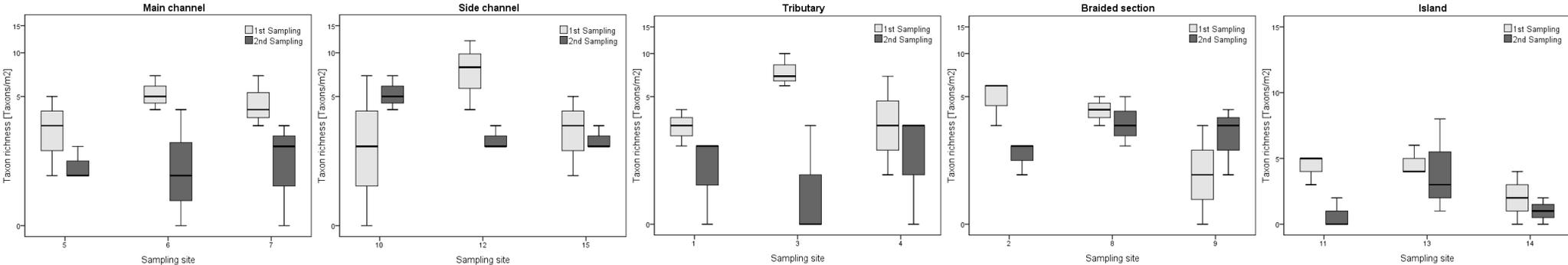


PITFALL TRAPS

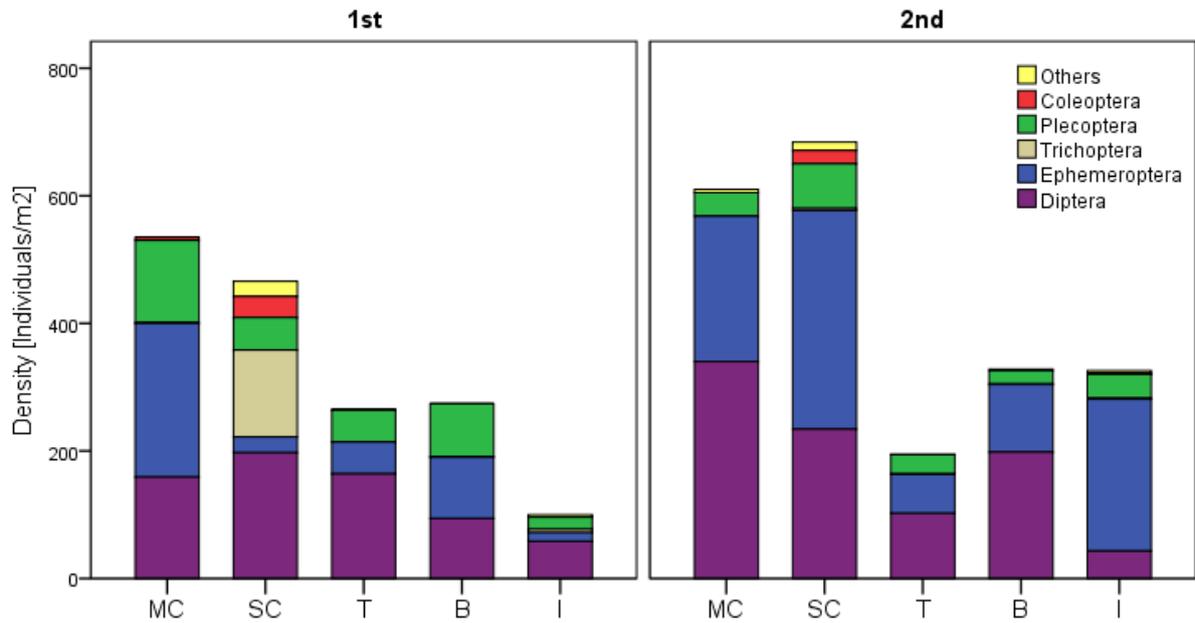
Density



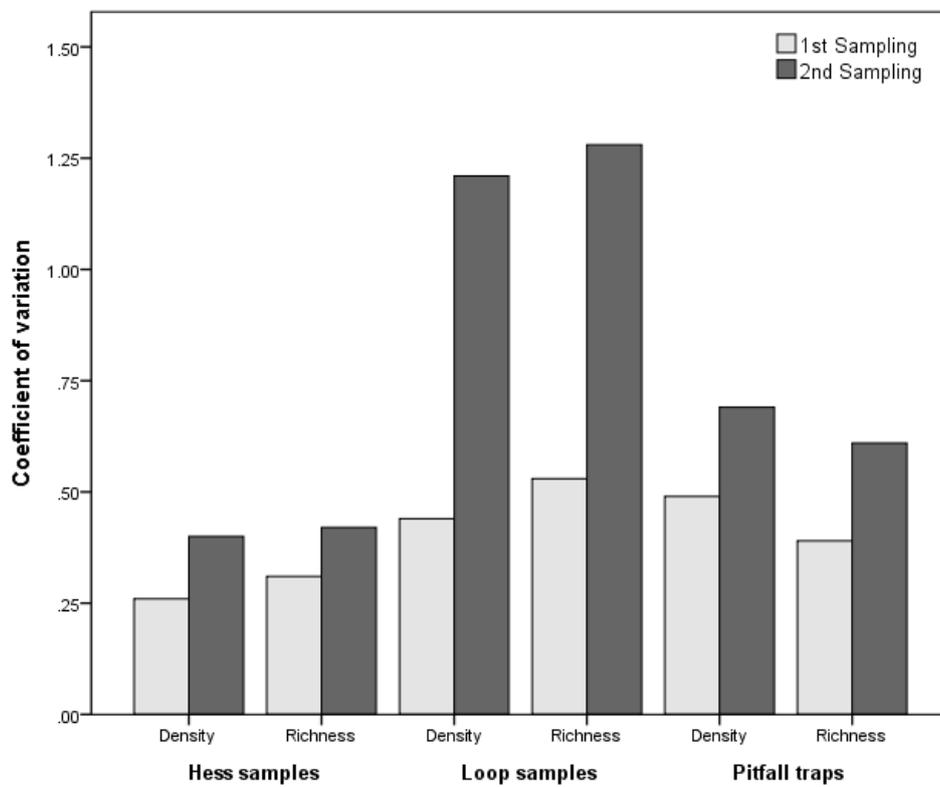
Taxon richness



8.4 Proportions of the different taxonomic groups in each habitat (aquatic)



8.5 Coefficients of variance



8.6 Ranking

1st	Hess D	Hess R	HESS	Loop D	Loop R	LOOP	Pitfall D	Pitfall R	PITFALL	Rank
Main channel	1	2	1.5	2	4	3	1	3	2	2.2
Side channel	2	1	1.5	1	1	1	2	2	2	1.5
Tributary	4	5	4.5	3	2	2.5	3	1	2	3.0
Braided	3	3	3	4	5	4.5	4	5	4.5	4.0
Island	5	4	4.5	5	3	4	5	4	4.5	4.3

2nd	Hess D	Hess R	HESS	Loop D	Loop R	LOOP	Pitfall D	Pitfall R	PITFALL	Rank
Main channel	2	2	2	5	5	5	4	4	4	3.7
Side channel	1	1	1	2	2	2	2	1	1.5	1.5
Tributary	5	5	5	4	4	4	5	5	5	4.7
Braided	4	3	3.5	3	3	3	3	2	2.5	3.0
Island	3	4	3.5	1	1	1	1	3	2	2.2

OVERALL	Hess D	Hess R	HESS	Loop D	Loop R	LOOP	Pitfall D	Pitfall R	PITFALL	Rank
Main channel	2	2	2	2	4	3	1	4	2.5	2.5
Side channel	1	1	1	1	1	1	2	1	1.5	1.1
Tributary	5	5	5	4	3	3.5	4	3	3.5	4.1
Braided	3	4	3.5	5	5	5	3	2	2.5	3.8
Island	4	3	3.5	3	2	2.5	5	5	5	3.5

1st	T	cond	vel_g	vel_60	depth	subst	H_AFDM	P_AFDM
Main channel	middle	low	high	middle	high	high	high	low
Side channel	high	high	low	low	middle	middle	high	high
Tributary	low	middle	low	low	low	low	low	middle
Braided	low	low	high	high	low	low	middle	low
Island	high	high	middle	high	high	high	low	high

2nd	T	cond	vel_g	vel_60	depth	subst	H_AFDM	P_AFDM
Main channel	high	low	high	high	high	high	low	low
Side channel	middle	high	low	low	low	low	high	high
Tributary	low	high						
Braided	low	middle	high	middle	high	high	middle	low
Island	high	high	middle	high	middle	middle	high	middle

OVERALL	T	cond	vel_g	vel_60	depth	subst	H_AFDM	P_AFDM
Main channel	middle	low	high	high	high	high	middle	low
Side channel	middle	high	low	low	low	low	high	high
Tributary	low	low	low	low	low	low	low	middle
Braided	low	low	high	high	low	low	middle	low
Island	high	high	middle	high	high	high	low	middle

8.7 Impressions



