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1                                   **The scales of variability of stream fish assemblages**  
2                                   **at tributary confluences**

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49                                   19                                   **Running head:** organization of stream fishes at tributary confluences

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21 **Abstract**

22 Tributary confluences play an important role in the dispersal of organisms, and consequently,  
23 in shaping regional scale diversity in stream networks. Despite their importance in dispersal  
24 processes, little is known about how ecological assemblages are organized in these habitats.  
25 We studied the scales of variability of stream fish assemblages over three seasons using a  
26 hierarchical sampling design, which incorporated three tributaries, three sites at the mouth of  
27 each tributary and using four sampling units at each site. We found strong scale dependent  
28 variability in species richness, composition and relative abundance. Most of the variation was  
29 accounted for by the interactive effect of season, between stream and between site effects,  
30 while habitat structure of the sampling units had a relatively minor role. Species richness  
31 showed a continuous decrease from the mainstem river in most cases, while species  
32 composition and relative abundance changed less consistently along the longitudinal profile.  
33 Consequently, we found that not only the junctions presented a strong filter on the species  
34 pool, but some species were filtered out if they passed this critical habitat bottleneck. Overall,  
35 our results suggest high variability in fish assemblages across multiple scales at tributary  
36 confluences. Environmental management should take a more critical care on the filtering role  
37 of tributary confluences in species dispersal, for better understanding patterns and processes  
38 in the branches of dendritic stream networks.

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40 **Keywords:** stream networks; tributaries; ecotones; habitat bottlenecks; environmental  
41 filtering; dispersal

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## 44 Introduction

1  
2 45 A central task of community ecology is to disentangle how environmental filtering processes  
3 46 and biotic interactions select the assembly of local communities from the regional species  
4 47 pool (Vellend 2010). The act of environmental filtering tends to be the most prominent at the  
5 48 interface of those habitat patches which largely differ in their environmental conditions  
6 49 (ecotones). Characterizing how species disperse through these habitat bottlenecks and  
7 50 distribute themselves among patches is important, among others, for a more regional scale  
8 51 understanding of the organization of ecological communities (Risser 1995).

12 52 In dendritic stream networks tributary confluences (or junctions) provide one of the most  
13 53 characteristic examples of within stream ecotones (Ward and Wiens 2001). Here, abrupt  
14 54 changes often happen in width, depth, sediment characteristics and water quality along the  
15 55 longitudinal profile of the stream (Rice et al. 2008). Tributary confluences can also increase  
16 56 physical heterogeneity (e.g. in water and sediment characteristics) in the recipient river which  
17 57 have important consequences in channel and floodplain morphology (Benda et al. 2004; Rice  
18 58 et al. 2006). Confluences thus serve as key habitat structures, which may influence dispersal  
19 59 processes for stream organisms in both directions (i.e. from the tributary to the main channel  
20 60 and *vica versa*). However, despite their importance relative to their small spatial extent,  
21 61 ecological studies in stream networks concentrated mainly on understanding patterns and  
22 62 processes in the branches and not in the junctions (sensu Grant et al. 2007).

29 63 Studies which would specifically focus on the role of confluences considered mainly changes  
30 64 in the composition of the main river assemblages below tributary mouth sections (see e.g.  
31 65 Rice et al. 2001; Kiffney et al. 2006; Milesi and Melo 2014). Studies, which would have  
32 66 specifically considered the upstream filtering role of tributary mouths are especially rare (but  
33 67 see e.g. Grenouillet et al. 2004; Hitt and Angermeier 2008), and in most cases used only  
34 68 indirect evidence for the permeability vs. resistance function of the tributary-mainstem  
35 69 ecotone. For stream macroinvertebrates Beckmann et al. (2005) highlighted that not only  
36 70 tributaries influence the composition and assemblage structure of the main river, but that  
37 71 mainstem assemblages can intensively use the tributary mouth for habitat. For stream fish  
38 72 assemblages Thornbrugh and Guido (2010) showed an abrupt change in assemblage  
39 73 composition between mainstem river sites and tributary sample sites above confluences,  
40 74 followed by a gradual taxonomic change with increasing upstream distance. Overall, these  
41 75 studies suggest that confluences play a strong filter on the species pool of mainstem rivers and  
42 76 has an overarching role on assemblage organization of tributary streams.

49 77 Stream systems show extreme heterogeneity at a hierarchy of spatial scales from microhabitat  
50 78 to the catchment (Hildrew and Giller 1994; Poff 1997). Determining the scales at which  
51 79 stream organisms varies the most is essential for understanding the predictability of  
52 80 assemblages and providing implications for management (Heino et al. 2004, Erős and  
53 81 Schmera 2010; Ligeiro et al. 2010). Variability of stream assemblages can be especially high  
54 82 at tributary confluences due to the importance of these habitats (i.e. crossroad function) in the  
55 83 dispersal of organism in the dendritic network. Quantifying the importance of scale related  
56 84 variability at tributary confluences is thus important for understanding the variability of

85 assemblages upstream in the branches. For example, if one finds large between stream  
1 86 variability already at the tributary mouth section, this could (partly) explain the differences in  
2 87 the composition of assemblages among the branches, at least for those stream organisms,  
3 88 which dispersal is restricted exclusively to within stream movement. However, the relative  
4 89 role of different scales (e.g. between vs within stream effects, mesohabitat level heterogeneity  
5 90 within sites) is largely unknown on the assembly of stream organisms at tributary  
6 91 confluences.  
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10 92 In this study, we examine the filtering role of confluences on stream fish assemblages. Our  
11 93 goal was to determine the major scales of assemblage variation at tributary mouth sections.  
12 94 Specifically, we used a hierarchical (i.e. nested) sampling design to assess the role of season,  
13 95 stream identity (i.e. between stream differences), spatial position at the tributary mouth  
14 96 section (between reach differences), and habitat structure (between sampling unit or  
15 97 mesohabitat level differences) on the structure of fish assemblages using survey data from  
16 98 three tributary mouth sections of a lowland medium size river. Such studies have importance  
17 99 for a more complete understanding of the role of the junctions in the organization of  
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22 100 assemblages in stream networks.  
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## 26 102 Materials and Methods

### 28 103 Study area

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31 104 Our study streams were the 33.3 km long Hajagos (catchment area: 236.9 km<sup>2</sup>), the 57.1 km  
32 105 long Gerence (310.3 km<sup>2</sup>) and the 45.4 km long Sokoroi (349 km<sup>2</sup>) streams. These streams are  
33 106 the right side tributaries of the Marcal River, a 100.5 km long lowland river, which is situated  
34 107 in North-Western Hungary. At the middle and downstream part of the Marcal, the average  
35 108 wet width is 10–15 m and the mean annual discharge is 6.8 m<sup>3</sup> s<sup>-1</sup>. The tributary mouths of the  
36 109 three studied streams are on average 20.3 km from each other along the Marcal. In their  
37 110 middle and downstream sections, the streams run on an agricultural landscape. They have of  
38 111 lowland character, with low flow, fine substrate (predominantly sand, silty sand, and fine and  
39 112 coarse gravel) and with no clear riffle-pool structure. At the most downstream (i.e. tributary  
40 113 mouth) section the mean channel width, velocity and depth varied between 2.89 and 5.19 m,  
41 114 6.1 and 13.4 cm s<sup>-1</sup>, 43.5 and 88.1 cm, respectively (see Table 1 for details). Emergent (e.g.  
42 115 reed *Phragmites australis*, broadleaf and narrowleaf cattail *Typha latifolia* and *Typha*  
43 116 *angustifolia*, sweet-grass *Glyceria sp.*) and floating (yellow water-lily *Nuphar lutea*,  
44 117 duckweeds *Lemna sp.*) macrophytes can be abundant at some sites.  
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### 51 118 Fish and habitat sampling

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54 119 We chose three sampling sites per stream. Their downstream end point situated at 0 m, 500 m  
55 120 and 1000 m from the tributary mouth (Fig. 1). Each site was 200 m long and were further  
56 121 divided into four 50 m long sampling units, to examine the effect of habitat structure on fish  
57 122 assemblage characteristics at a finer scale. We sampled fishes and characterized the habitat  
58 123 during three sampling periods in 2013: (1) spring (end of April, early May), (2) summer (early  
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124 July), and (3) autumn (early October). This sampling effort yielded a total of 108 samples (3  
125 seasons  $\times$  3 streams  $\times$  3 sites per stream  $\times$  4 habitat units per site).

126 We surveyed the 200 m long sites by wading, single pass electrofishing using a backpack  
127 electrofishing gear (IG200/2B, PDC, 50-100 Hz, 350-650 V, max. 10 kW; Hans Grassl  
128 GmbH, Germany). The 50 m long sampling units were block netted before electrofishing,  
129 with nets of 2 mm mesh size anchored with chain to the bottom. Pulsating direct current with  
130 a frequency of 75–100 Hz and a voltage of 200–300 V was used. The 2 m long catcher rod  
131 had a ring shaped anode with a diameter of 40 cm equipped with a net (mesh size 6 mm). The  
132 sampling crew consisted of 3–4 people: the electrofisher operator who effectively caught the  
133 fish and handled the machine, a netter who helped to catch escaping or unseen fish and one or  
134 two helpers who carried the buckets on the bank, took care of the fish and measured their  
135 standard length. The team electrofished the whole stream width while moving slowly  
136 upstream and trying to catch all fish in the study area. All fish were placed in large containers  
137 filled with water and released back to the stream after identification and length measurement.

138 Transect based measurements of habitat data were taken at each 50 m long unit after fish  
139 sampling. At each unit, four transects were placed perpendicular to the main axis of the  
140 stream at equal distances from each other. We measured wet width of the channel with a tape  
141 measure, depth and current velocity with a meter stick and a water velocity meter (FP101  
142 Global Flow Probe, Global Water Instrumentation Inc., Gold River, CA, USA), respectively,  
143 at five equally spaced points along each transect. We also recorded aquatic vegetation type  
144 and substrate type (see Table 1) at every transect point. We calculated the mean values of the  
145 aforementioned environmental variables and the percentage occurrence of the categorical  
146 variables (i.e., substrate type and aquatic vegetation type) to characterise habitat features at  
147 the sample unit scale.

148 We also used fish monitoring data from the Marcal River for comparing similarities and  
149 differences in fish assemblages between the mainstem Marcal and the tributary fish  
150 assemblages. The river was sampled from a boat using the same electrofishing device and its  
151 accessories as was used for the tributary streams. To allow effective maneuvering in this  
152 shallow and vegetated river, a small rubber boat (Yamaha 300S) was used. The crew  
153 comprised two persons: one for catching the fish with the hand-held anode (2.5 m long pole  
154 with a net of 40 cm diameter, mesh size 6 mm) and one for driving the boat. Two 400 m long  
155 reaches (altogether 800 m long sections) were electrofished in the vicinity (i.e. within 5 km)  
156 of each tributary at our standard monitoring sites in this river. Continuous electrofishing was  
157 carried out, by dipping the anode into the water at approximately 2 m long intervals and  
158 pulling the anode toward the boat, while moving slowly downstream with the flow and  
159 controlling the boat by an oar if it was necessary. As for the tributary streams fish were  
160 released back to the river after identification and length measurement.

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163 Statistical analysis

164 We used linear models in a nested design to assess the effect of (1) seasons, (2) tributary  
165 streams within seasons, (3) sites within tributary streams and seasons, and (4) habitat data  
166 nested within seasons and tributary streams on (1) species richness and (2) ecological  
167 dissimilarity of the assemblages compared to the main river. For dissimilarity index the  
168 Jaccard and the Bray-Curtis indices were used for species composition and relative abundance  
169 data (see Legendre and Legendre 1998), respectively.

170 We used principal component analysis on the variance-covariance matrix of the recorded  
171 habitat data (PCA) to characterize the physical structure of the habitat units, and used the first  
172 three component scores (hereafter habitat PC scores) to quantify habitat data in the nested  
173 model. The advantage of this procedure is that it reduces the number of the original habitat  
174 variables which usually are correlated with each other. The correlation between the habitat  
175 variables could be a nuisance factor in linear models, which phenomenon is known as  
176 multicollinearity (Graham 2003; Dormann et al. 2013). Here, the first three principal  
177 components of the PCA explained 24.4%, x% and Y% of the variance, which justify their  
178 inclusion in the models. In PC1, habitat units with the strongest negative loadings were  
179 relatively deep and wide with relatively high velocity, silty-sand substrate and relatively dense  
180 submerged macrophyte vegetation. Units with strong positive loadings were relatively  
181 shallow with low velocity and relatively dense emergent vegetation (Table 5). In PC2 the  
182 habitat gradient was mainly characterized by differences in substrate composition, and  
183 especially sandy silt (negative loadings) and fine gravel (positive loadings). Although  
184 biologically less interpretable, abiotic differences between habitat units along PC3 were  
185 further refined by substrate composition and differences in vegetation structure (Table 6).

186 For a more complete understanding of confluence effects, we examined changes in species  
187 richness, and dissimilarity in species composition (Jaccard index) and relative abundance  
188 (Bray-Curtis index) from the mainstem Marcal River for each stream and in each season.  
189 Spearman correlation tests were used to test whether the values of these assemblage level  
190 variables showed significant decay with rank distance upstream from the mainstem at the  
191 level of habitat units (n=12 in each test).

192 Then, focusing exclusively on the tributaries, we used principal coordinate analysis (PCoA) to  
193 reveal patterns in species composition and relative abundance between seasons, streams and  
194 sites. Here, data from individual habitat units were pooled for the ease of visualization. The  
195 Jaccard and the Bray-Curtis indices were used for species composition and relative  
196 abundance, respectively. Finally, we used nested permutational analysis of variance  
197 (PERMANOVA) to identify the scales at which species composition and relative abundance  
198 of the tributary fish assemblages varied the most. As with the PCoA, the Jaccard and the  
199 Bray-Curtis indices were used for species composition and relative abundance, respectively.

200 All data analyses were performed in the R statistical environment (R Core Team 2013).  
201 PERMANOVA was conducted with ‘adonis’ function of the R package named vegan  
202 (Oksanen et al. 2013).

204 Results

205 Most species that occurred in the mainstem river appeared also in the tributaries (Table 2). In  
206 fact, only large bodied and/or strongly riverine species did not appear in the tributaries such as  
207 asp (*Aspius aspius*), barbel (*Barbus barbus*), European catfish (*Silurus glanis*), zingel (*Zingel*  
208 *zingel*). However, these species were rather rare in the mainstem river as well.

209 Species richness varied significantly at a variety of sampling scales in the tributaries (Table  
210 3). Most of the variation was related to stream (36.4%;  $P < 0.001$ ) and site level variability  
211 (19.3%;  $P < 0.001$ ), although seasonal differences also proved to be significant (7.5%;  
212  $P < 0.001$ ). Species richness distributed relatively evenly among streams and sites in spring  
213 (Fig. 2), while it tended to decrease upstream in both summer and autumn. Species richness  
214 also varied among streams according to their upstream-downstream position in the mainstem  
215 in both summer and autumn. The most downstream Sokoroi stream had the highest species  
216 richness, while the most upstream Hajagos had the lowest. Interestingly, habitat structure (i.e.  
217 PC1-3) did not significantly influence species richness, although the overall contribution of  
218 the biologically interpretable most significant environmental gradients (i.e. PC1-3) were in  
219 fact higher than the effect of season (14.7%).

220 Jaccard dissimilarity of species composition from the mainstem showed similar influence of  
221 sampling scales to species richness (Table 3). Most of the variation was related to stream  
222 (39.0%;  $P < 0.001$ ) and site level variability (23.6%;  $P < 0.001$ ), although seasonal differences  
223 (3.2%;  $P < 0.05$ ) and the effect of habitat structure (i.e. PC2 6.7%;  $P = 0.026$ ) also proved to be  
224 significant. Dissimilarity from the mainstem was more even among streams and sites in spring  
225 (Fig. 3), while it tended to increase upstream among sites in the tributaries and among streams  
226 along their upstream-downstream position in the mainstem, both summer and autumn. For  
227 Bray-Curtis dissimilarity of relative abundance data seasonal changes proved to be the most  
228 influential (54.3%;  $P < 0.001$ ). Clearly, dissimilarity from the mainstem increased from spring  
229 to autumn (Fig. 3), while the effect of hierarchical spatial levels proved to be low, albeit  
230 significant at the stream (6.4%;  $P = 0.003$ ) and site (12.4%;  $P < 0.001$ ) levels.

231 Species richness showed a continuous decrease from the mainstem river in most seasons and  
232 streams (Fig. 4; Table 4). However, species composition and relative abundance changed less  
233 consistently along the longitudinal profile. Dissimilarity in species composition generally  
234 increased from the mainstem in both summer and autumn, with the exception of the Sokoroi  
235 stream. On the contrary, dissimilarity in relative abundance showed a variety of patterns. For  
236 example, it decreased in the Gerence stream in both spring and summer, while it increased in  
237 the Sokoroi stream in autumn.

238 Species composition of the streams and sites within streams was determined by several  
239 species (Fig. 5). However, no clear pattern in assemblage composition was found regarding  
240 seasonal, between stream or between site differences. PERMANOVA analysis (Table 5)  
241 confirmed these findings and showed that relatively equal amount of variation of species  
242 composition was related to seasonal (14.6%;  $P < 0.001$ ) and to between stream (22.4%;  
243  $P < 0.001$ ) and between site (13.7%;  $P < 0.001$ ) effects. Habitat structure also significantly  
244 influenced species richness (i.e. PC2 6.5%;  $P = 0.018$ ), and the overall contribution of the



245 biologically interpretable most significant environmental gradients (i.e. PC1-3) was in fact  
246 higher (15.8%) than the effect of season. Relative abundance data were mostly influenced by  
247 three dominant species (i.e. roach *Rutilus rutilus*, bitterling *Rhodeus sericeus*, pike *Esox*  
248 *lucius*; Fig. 5). Here, the greatest amount of variation in fish abundance data was related to the  
249 site scale (20.7%;  $P < 0.001$ ), although seasonal (12.6%;  $P < 0.001$ ) and stream level (17.8%;  
250  $P < 0.001$ ) effects, and the effect of individual environmental gradients (PC1 7.1%;  $P = 0.007$ ;  
251 PC2 6.4%;  $P = 0.022$ ; PC3 6.4%;  $P = 0.021$ ) also proved to be significant (Table 5).

## 253 Discussion

254 In this study we examined the scales of variation of stream fishes at tributary confluences and  
255 found that the majority of assemblage variation could be explained by the joint effect of  
256 different hierarchical (spatial and temporal) scales. In general, seasonal, between stream and  
257 site level effects proved to be the most important in explaining assemblage structure, whereas  
258 physical attributes of the sample units (50 m long each) had a relatively minor role. These  
259 results on the importance of season, spatial positioning in the stream network (between stream  
260 effects) and positioning within a stream (between site effects) may suggest that dispersal  
261 processes had critical importance for fish assemblage organization at tributary confluences,  
262 and will be discussed below in more detail.

263 Most of the studies that considered the role of spatial processes (e.g. dispersal limitation,  
264 neutral effects) in stream networks used a metacommunity perspective and examined the  
265 relative role of environmental factors and spatial positioning of the sampling sites at large  
266 spatial extents (i.e. within and among different subcatchments) (e.g. Mykrä et al. 2007; Erős  
267 et al. 2012). The logical consensus of these studies is that the role of spatial effects decreases  
268 at smaller spatial extents (Heino et al. 2012; Muneeppeerakul et al. 2008). However, it has been  
269 also shown that spatial processes like dispersal limitation can be very important at smaller  
270 extents too, for example within and between branches of the dendritic network (Fagan 2002;  
271 Erős and Schmera 2010). Our field study shows that between stream effects can be significant  
272 even among streams with relatively similar environmental and topographic characteristic and  
273 spatial positioning along the mainstem river, which, to our knowledge, has not been addressed  
274 in other studies.

275 Between stream effects were high for species richness and dissimilarity of species  
276 composition from the mainstem river (Table 3). Specifically, we found a reverse pattern  
277 between species richness and dissimilarity in species composition from the mainstem. Species  
278 richness was the highest in the Sokoroi and lowest in the Hajagos stream, while dissimilarity  
279 in species composition from the mainstem was the lowest in the Sokoroi and highest in the  
280 Hajagos, at least in summer and autumn. Lower species richness and higher dissimilarity from  
281 the mainstem in species composition suggest lower colonization potential of the Hajagos from  
282 the Marcal River. Confluences thus served as natural habitat bottlenecks for stream fishes in a  
283 stream specific manner. The results may suggest the role of stochastic effects in the  
284 colonization of tributary mouths by different species from the mainstem and/or suggest the

285 role of tributary spatial position in the mainstem river (see Osborne and Wiley 1992), even if  
286 the tributaries were relatively close to each other.

287 Temporal variability also had some legacy on between stream differences in richness and  
288 dissimilarity of species composition from the mainstem. These differences were relatively  
289 minor in spring and showed consistent pattern in summer and autumn. Higher water levels in  
290 spring could diminish between stream differences in habitat availability of the junctions for  
291 mainstem fishes, since alluvium bars (i.e. sand and gravel bars) at the mouth may hinder  
292 upstream migration at low water periods. Higher movement activity of fish during spring  
293 (spawning migrations) may also dampened differences among the tributaries. Dissimilarity  
294 from the mainstem in relative abundance data supports this argument on seasonality.  
295 Dissimilarity values were the lowest in spring and the highest in autumn. In fact, dissimilarity  
296 from the mainstem was most related to variation among seasons for relative abundance data  
297 (Table 3), reflecting seasonal differences in habitat availability and/or in movement activity for  
298 the dominant species (Gorman 1986; Roberts and Hitt 2010).

299 At a lower hierarchical level, all assemblage attributes varied significantly between sites,  
300 which further indicates the importance of spatial processes for stream fishes at very small  
301 spatial extents (here within a 1 km long section). Species richness generally decreased  
302 upstream at least in summer and autumn (Fig. 2), while dissimilarity in species composition  
303 increased from the mainstem. To our knowledge no study examined differences in fish  
304 assemblages from the mainstem at such a small spatial extent, but these data and studies at  
305 larger spatial extents (Hitt and Angermeier 2008; Thornbrugh and Gido 2010) indicate that  
306 not only the junctions present a strong filter on the species pool, but that some species are  
307 filtered out even if they passed through this most critical habitat bottleneck. Dissimilarity in  
308 relative abundance from the mainstem was less related to variation between sites, which,  
309 compared with results on composition, indicates the effect of some dominant species on these  
310 results. Some habitat generalist species, like roach, bitterling and bleak (*Alburnus alburnus*),  
311 which are dominant both in the mainstem river and in the tributaries were abundant at all sites  
312 and could increase assemblage similarity at the site level, similarly to their effect at the stream  
313 level. Patterns in distance decay from the mainstem (Fig. 4) confirmed site level changes, and  
314 indicated the most consistent pattern between seasons and streams for species richness (i.e.  
315 decrease in richness upstream) and the least consistent patterns for relative abundance data.

316 Analyses which did not consider similarities and differences from the mainstem, but focused  
317 on assemblage variability in the tributaries exclusively (i.e. PCoA and PERMANOVA),  
318 showed that relatively equal amount of variation was related to season, and between stream  
319 and between site variation for both compositional and relative abundance data. These results  
320 suggest strong context dependency in fish assemblage organization at tributary confluences,  
321 which may harden generalizations across sites, streams and seasons (see Heino et al., 2012 for  
322 a larger scale study). The relatively high amount of variation explained (66.4–71.0%) suggest  
323 that the joint consideration of seasonal effects and between and within stream positioning of  
324 the sampling sites is critically important for better understanding assemblage organization,  
325 beside the consideration of habitat structure.

326 For the lowest hierarchical level (i.e. sampling unit scale), we found that habitat structure had  
327 low importance relative to seasonal, between stream, and between site variation. Habitat  
328 structure is clearly the most important factor (group) for the organization of stream fishes  
329 (Matthews 1998; Jackson et al. 2001). It seems however that larger scale factors (e.g.  
330 permeability of the junctions, dispersal ability of species) can also significantly influence the  
331 species pool of lower hierarchical levels (i.e. species composition and relative abundance of  
332 fishes at the meso-habitat level) and in case of relatively homogenous habitat units, they can  
333 override the effect of habitat structure (see Grönroos and Heino 2012 for a study on stream  
334 macroinvertebrates). In this lowland system, the units had relatively similar physical  
335 characteristics regarding width, flow, depth and substrate, although the type and coverage of  
336 macrovegetation provided some heterogeneity, which could influence the distribution of fish  
337 to some extent.

338 In conclusion, we found strong scale dependent variability in species richness, composition  
339 and relative abundance of stream fish assemblages at tributary confluences. Most of the  
340 variation was accounted for by the interactive effect of season, between stream and between  
341 site effects, while habitat structure of the sampling units (i.e. mesohabitat level structure) had  
342 a lower role. The results suggest that dispersal processes (e.g. permeability, dispersal  
343 limitation and movement activity of fishes) have critical importance on the assembly of  
344 stream fishes at very small spatial extents, which may strongly determine fish assemblages  
345 more upstream in the branches of the dendritic network. From an applied perspective  
346 revitalization projects often focus on enhancing instream habitat quality for the biota of  
347 streams (Lepori et al. 2005; Palmer et al. 2010). We suggest that environmental management  
348 of stream networks should take a more critical care on the filtering role of tributary  
349 confluences in species dispersal, for better understanding patterns and processes in the  
350 branches of dendritic stream networks.

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Table 1. The average habitat characteristics of the 200 m long sample sites in the Hajagos (H), Gerence (G) and Sokoroi (S) streams. Each mean value is based on the pooled mean data of seasonal (i.e. spring, summer, autumn) transect based surveys (see methods for details).

	Hajagos stream			Gerence stream			Sokorói stream		
	H1	H2	H3	G1	G2	G3	S1	S2	S3
Width (m)	4.90 (1.35)	4.00 (0.17)	3.98 (0.38)	5.19 (1.14)	3.56 (0.62)	2.89 (0.79)	4.98 (0.76)	3.90 (0.21)	3.66 (0.47)
Depth (cm)	72.7 (25.9)	50.7 (10.3)	43.5 (7.8)	76.0 (22.4)	44.8 (18.0)	47.3 (19.8)	88.1 (10.1)	71.9 (10.1)	54.6 (17.0)
Velocity (cm s <sup>-1</sup> )	8.1 (4.9)	7.7 (7.7)	10.4 (8.8)	6.1 (4.9)	13.4 (12.6)	9.7 (6.2)	6.6 (4.4)	9.8 (4.6)	7.5 (6.1)
Silty sand (%)	49.1 (23.5)	38.7 (23.4)	28.1 (7.0)	46.3 (18.4)	47.6 (28.2)	81.9 (13.4)	81.3 (23.5)	77.1 (28.0)	56.3 (16.4)
Sand (%)	0.4 (1.4)	-	-	-	1.1 (1.7)	3.2 (9.6)	2.1 (4.5)	4.6 (5.4)	8.3 (12.3)
Fine gravel (%)	30.1 (16.7)	16.1 (10.8)	25.2 (13.2)	35.6 (15.5)	25.9 (16.3)	12.4 (11.9)	8.3 (12.3)	18.3 (23.0)	30.8 (21.7)
Coarse gravel (%)	8.9 (10.3)	45.2 (15.8)	46.7 (10.9)	11.4 (17.9)	25.4 (25.2)	2.5 (3.2)	8.3 (12.3)	-	4.6 (7.8)
Stone (%)	9.6 (12.9)	-	-	5.4 (14.4)	-	-	-	-	-
Rock (%)	1.9 (5.8)	-	-	1.3 (3.1)	-	-	-	-	-
Emergent plant (%)	52.3 (40.1)	61.9 (40.8)	67.7 (35.8)	23.7 (21.6)	27.5 (26.5)	53.1 (22.2)	15.6 (9.2)	26.6 (10.9)	69.2 (24.0)
Submerged plant (%)	24.9 (31.0)	22.9 (34.1)	17.1 (26.7)	2.1 (5.8)	15.2 (18.2)	9.8 (14.8)	14.0 (6.8)	16.7 (11.2)	6.5 (7.5)
Floating leaved plant (%)	4.4 (6.0)	8.5 (15.9)	4.3 (8.2)	20.6 (35.6)	0.1 (0.3)	-	17.1 (27.8)	3.1 (6.1)	-
Filamentous algae (%)	-	-	-	-	0.2 (0.4)	-	4.6 (6.9)	13.3 (20.6)	2.2 (3.6)

Table 2. The fish species, species codes and the relative abundance of species collected in the mainstem Marcal River (M) and the Sokoroi (S), Gerence (G) and Hajagos (H) tributary streams.

Species name	Species code	Relab (M) (%)	Relab (S) (%)	Relab (G) (%)	Relab (H) (%)
<i>Abramis brama</i> (Linnaeus, 1758)	abrbra	0.094	0.247	-	0.191
<i>Alburnus alburnus</i> (Linnaeus, 1758)	albalb	40.508	5.890	2.476	4.498
<i>Ameiurus melas</i> (Rafinesque, 1820)	amemel	0.399	0.038	-	0.383
<i>Aspius aspius</i> (Linnaeus, 1758)	aspasp	0.141	-	-	-
<i>Ballerus ballerus</i> (Linnaeus, 1758)	balbal	0.047	1.102	0.667	-
<i>Barbatula barbatula</i> (Linnaeus, 1758)	ortbar	0.023	-	0.334	-
<i>Barbus barbus</i> (Linnaeus, 1758)	barbar	0.141	-	-	-
<i>Blicca bjoerkna</i> (Linnaeus, 1758)	blibjo	1.739	2.451	7.322	12.344
<i>Carassius gibelio</i> (Bloch, 1782)	cargib	0.352	0.418	-	2.967
<i>Chondrostoma nasus</i> (Linnaeus, 1758)	chonas	0.094	-	0.018	-
<i>Cobitis elongatoides</i> (Băcescu & Maier, 1969)	cobelo	0.235	1.045	0.474	0.287
<i>Cyprinus carpio</i> (Linnaeus, 1758)	cypcar	0.023	0.019	-	-
<i>Esox lucius</i> (Linnaeus, 1758)	esoluc	2.867	4.275	1.247	7.464
<i>Gobio obtusirostris</i> (Valenciennes, 1842)	gobgob	-	-	0.246	-
<i>Gymnocephalus cernuus</i> (Linnaeus, 1758)	gymcer	-	-	0.018	-
<i>Lepomis gibbosus</i> (Linnaeus, 1758)	lepgib	0.258	0.038	1.826	0.096
<i>Leuciscus idus</i> (Linnaeus, 1758)	leuidu	1.386	3.040	0.158	1.627
<i>Leuciscus leuciscus</i> (Linnaeus, 1758)	leuleu	0.752	0.817	1.212	0.670
<i>Misgurnus fossilis</i> (Linnaeus, 1758)	misfos	-	0.247	0.228	2.584
<i>Neogobius fluviatilis</i> (Pallas, 1814)	neoflu	0.728	0.171	1.159	0.957
<i>Neogobius melanostomus</i> (Pallas, 1814)	neomel	1.269	0.095	1.054	1.053
<i>Perca fluviatilis</i> (Linnaeus, 1758)	perflu	1.621	3.648	1.018	0.191
<i>Phoxinus phoxinus</i> (Linnaeus, 1758)	phopho	-	-	0.035	-
<i>Proterorhinus semilunaris</i> (Pallas, 1814)	prosem	1.692	2.812	0.544	3.923
<i>Pseudorasbora parva</i> (Temminck & Schlegel, 1842)	psepar	-	0.399	0.105	2.105
<i>Rhodeus sericeus</i> (Pallas, 1776)	rhoser	11.302	46.114	58.472	25.359
<i>Rutilus rutilus</i> (Linnaeus, 1758)	rutrut	31.790	23.580	18.262	28.134
<i>Scardinius erythrophthalmus</i> (Linnaeus, 1758)	scaery	0.705	0.836	0.070	0.957
<i>Silurus glanis</i> (Linnaeus, 1758)	silgla	0.211	-	-	-
<i>Squalius cephalus</i> (Linnaeus, 1758)	squcep	1.081	2.641	3.020	4.115
<i>Tinca tinca</i> (Linnaeus, 1758)	tintin	0.023	0.038	-	0.096
<i>Vimba vimba</i> (Linnaeus, 1758)	vimvim	0.470	0.038	0.035	-
<i>Zingel zingel</i> (Linnaeus, 1758)	zinzin	0.047	-	-	-



Table 3. Summary results of the linear models (nested design) for species richness, and dissimilarity of species composition and relative abundance of fishes from the mainstem Marcal River.

Source of variation	d.f.	MS	<i>F</i>	<i>P</i>	% variance
<b>Species richness</b>					
Season	2	42.19	10.62	<0.001	7.5
Stream (within season)	6	68.30	17.19	<0.001	36.4
Site (within season and stream)	9	24.19	6.09	<0.001	19.3
Habitat PC1 (within season and stream)	9	6.85	1.72	0.102	5.5
Habitat PC2 (within season and stream)	9	7.13	1.79	0.087	5.7
Habitat PC3 (within season and stream)	9	4.33	1.09	0.384	3.5
Residuals	63	3.97			22.2
<b>Dissimilarity in species composition</b>					
Season	2	0.03	5.00	0.010	3.2
Stream (within season)	6	0.12	20.26	<0.001	39.0
Site (within season and stream)	9	0.05	8.19	<0.001	23.6
Habitat PC1 (within season and stream)	9	0.01	1.95	0.061	5.6
Habitat PC2 (within season and stream)	9	0.01	2.31	0.026	6.7
Habitat PC3 (within season and stream)	9	0.00	0.60	0.792	1.7
Residuals	63	0.01			20.2
<b>Dissimilarity in relative abundance</b>					
Season	2	1.36	95.77	<0.001	54.3
Stream (within season)	6	0.05	3.76	0.003	6.4
Site (within season and stream)	9	0.07	4.88	<0.001	12.4
Habitat PC1 (within season and stream)	9	0.02	1.56	0.147	4.0
Habitat PC2 (within season and stream)	9	0.01	0.65	0.750	1.7
Habitat PC3 (within season and stream)	9	0.02	1.30	0.253	3.3
Residuals	63	0.01			17.9

Table 4. Spearman correlation tests between species richness and rank distance from the junction, dissimilarity in species composition (Jaccard index) and rank distance from the junction, and relative abundance (Bray-Curtis index) and rank distance from the junction for each stream and season (n=12 in each test).

Species richness						
	Spring		Summer		Autumn	
	R <sup>2</sup>	P	R <sup>2</sup>	P	R <sup>2</sup>	P
Sokoroi	-0.79	0.002	-0.52	0.080	-0.61	0.037
Gerence	-0.69	0.013	-0.79	0.002	-0.76	0.004
Hajagos	-0.12	0.704	-0.54	0.067	-0.89	<0.001
Species composition						
	Spring		Summer		Autumn	
	R <sup>2</sup>	P	R <sup>2</sup>	P	R <sup>2</sup>	P
Sokoroi	-0.45	0.138	0.09	0.770	0.34	0.276
Gerence	0.30	0.338	0.80	0.002	0.83	<0.001
Hajagos	0.29	0.367	0.69	0.013	0.80	0.002
Relative abundance						
	Spring		Summer		Autumn	
	R <sup>2</sup>	P	R <sup>2</sup>	P	R <sup>2</sup>	P
Sokoroi	-0.60	0.039	-0.37	0.236	0.85	<0.001
Gerence	-0.71	0.009	-0.71	0.009	0.04	0.914
Hajagos	-0.04	0.914	0.25	0.430	0.03	0.931

Table 5. Summary results of the PERMANOVA analyses for species composition and relative abundance data.

Source of variation	d.f.	MS	<i>F</i>	<i>P</i>	% variance
Dissimilarity in species composition					
Season	2	1.90	13.70	<0.001	14.6
Stream (within season)	6	0.97	6.99	<0.001	22.4
Site (within season and stream)	9	0.39	2.85	<0.001	13.7
Habitat PC1 (within season and stream)	9	0.16	1.16	0.154	5.6
Habitat PC2 (within season and stream)	9	0.19	1.35	0.018	6.5
Habitat PC3 (within season and stream)	9	0.11	0.78	0.938	3.7
Residuals	63	0.14			33.6
Dissimilarity in relative abundance					
Season	2	1.47	13.75	<0.001	12.6
Stream (within season)	6	0.69	6.44	<0.001	17.8
Site (within season and stream)	9	0.54	5.01	<0.001	20.7
Habitat PC1 (within season and stream)	9	0.18	1.71	0.007	7.1
Habitat PC2 (within season and stream)	9	0.17	1.55	0.022	6.4
Habitat PC3 (within season and stream)	9	0.17	1.55	0.021	6.4
Residuals	63	0.11			29.0

Captions to figures

**Fig. 1** Scheme of the study design using three tributary streams (Sokoroi, Gerence, Hajagos) and three sites in each stream in the Marcal River system, North Western, Hungary. The sites were situated 0, 500 and 1000 m from the tributary mouth. Numbers indicate individual habitat units (50 m long each)

**Fig. 2** Mean species richness ( $\pm$ S.D.) of the sampling units (50 m long each) at three different sites in the Sokoroi, Gerence and Hajagos streams of the Marcal River in spring, summer and autumn

**Fig. 3** Mean dissimilarity ( $\pm$ S.D.) of the sampling units (50 m long each) from the mainstem Marcal River for (a) species composition (Jaccard index) and (b) relative abundance (Bray-Curtis index) data of fishes at three different sites in the Sokoroi, Gerence and Hajagos streams in spring, summer and autumn

**Fig. 4** Changes in (a) species richness, and dissimilarity in (b) species composition (Jaccard index) and (c) relative abundance (Bray-Curtis index) data from the mainstem Marcal River at the level of the sampling units (50 m long each) in the Sokoroi, Gerence and Hajagos streams in spring, summer and autumn

**Fig. 5** Principal Coordinate Analyses (PCoA) summarizing the variation across sites in three tributaries of the Marcal River for (a) species composition and (c) relative abundance data, and their associated species loadings (b and d). For species code abbreviations see Table 2

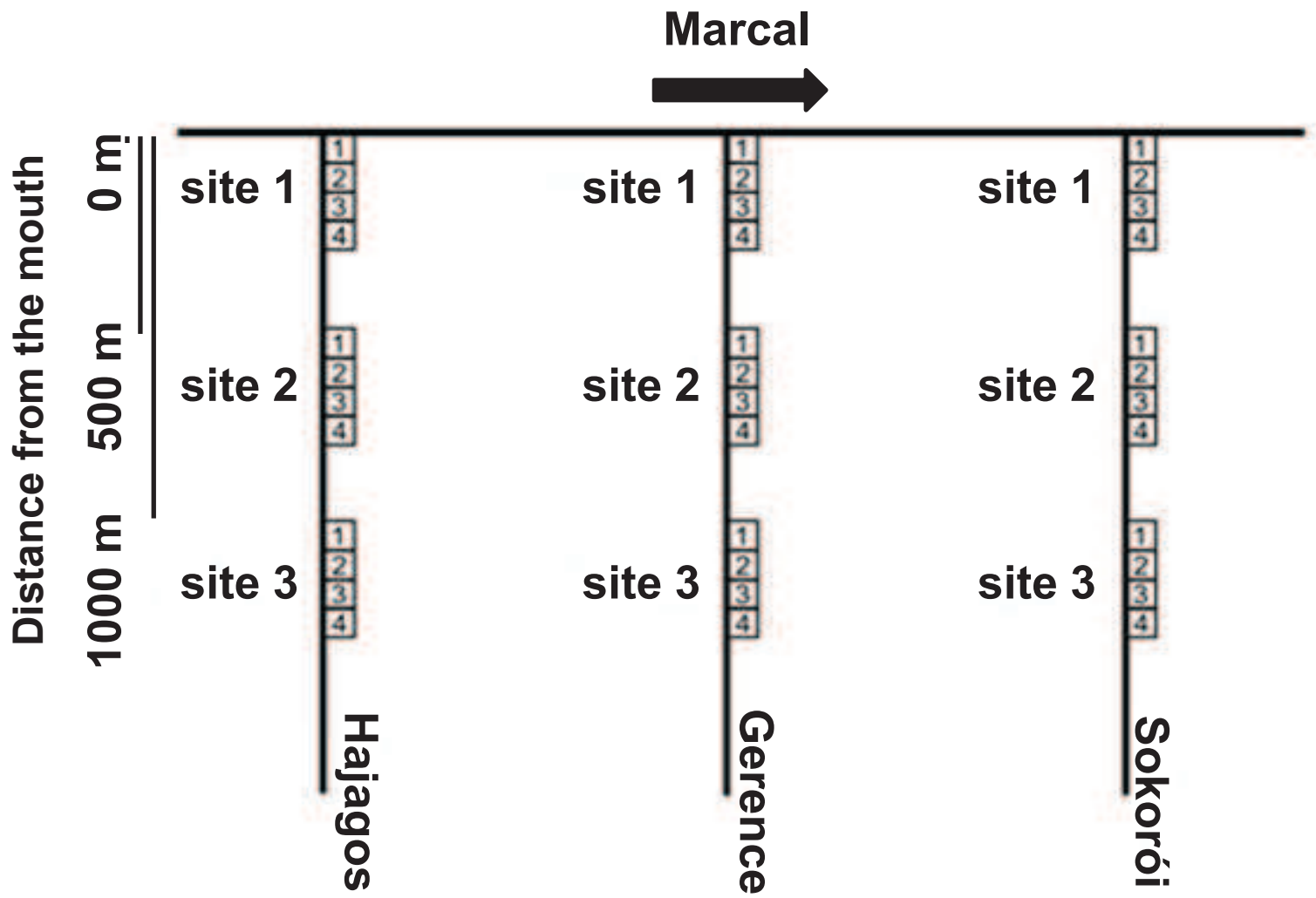
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Appendix

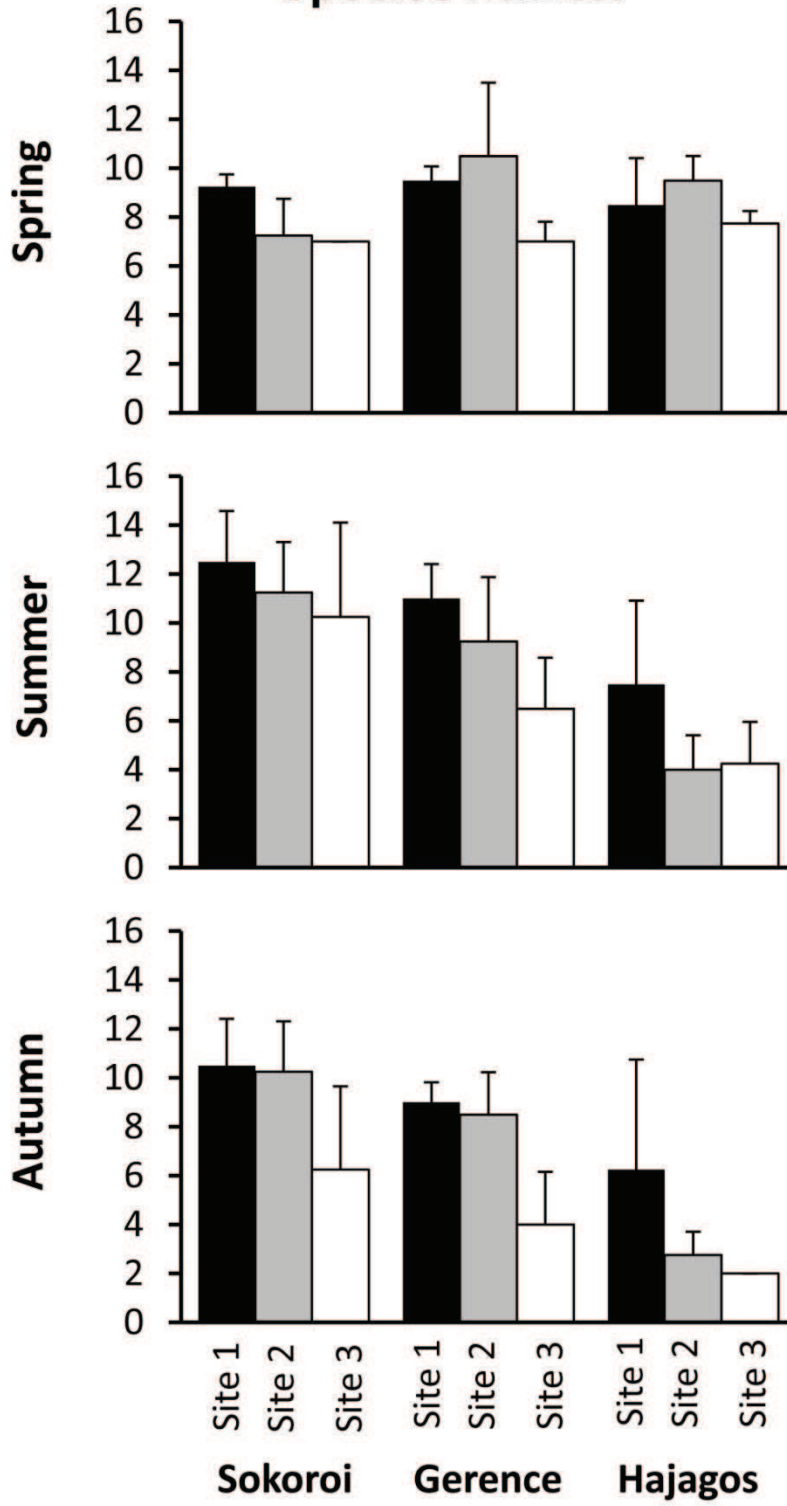
Table 6. Pearson correlation matrix of the abiotic variables and the first three principal component axes (PC1, PC2, PC3). Lower and upper diagonals show correlations and their significance values, respectively.

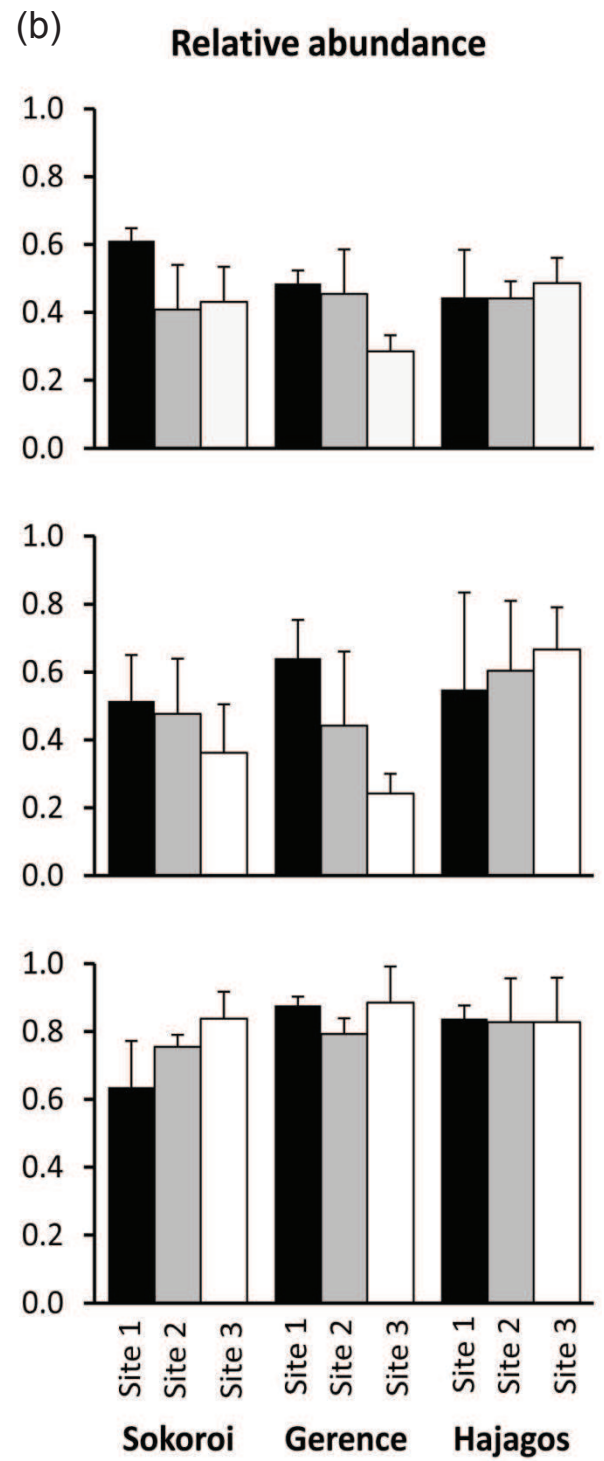
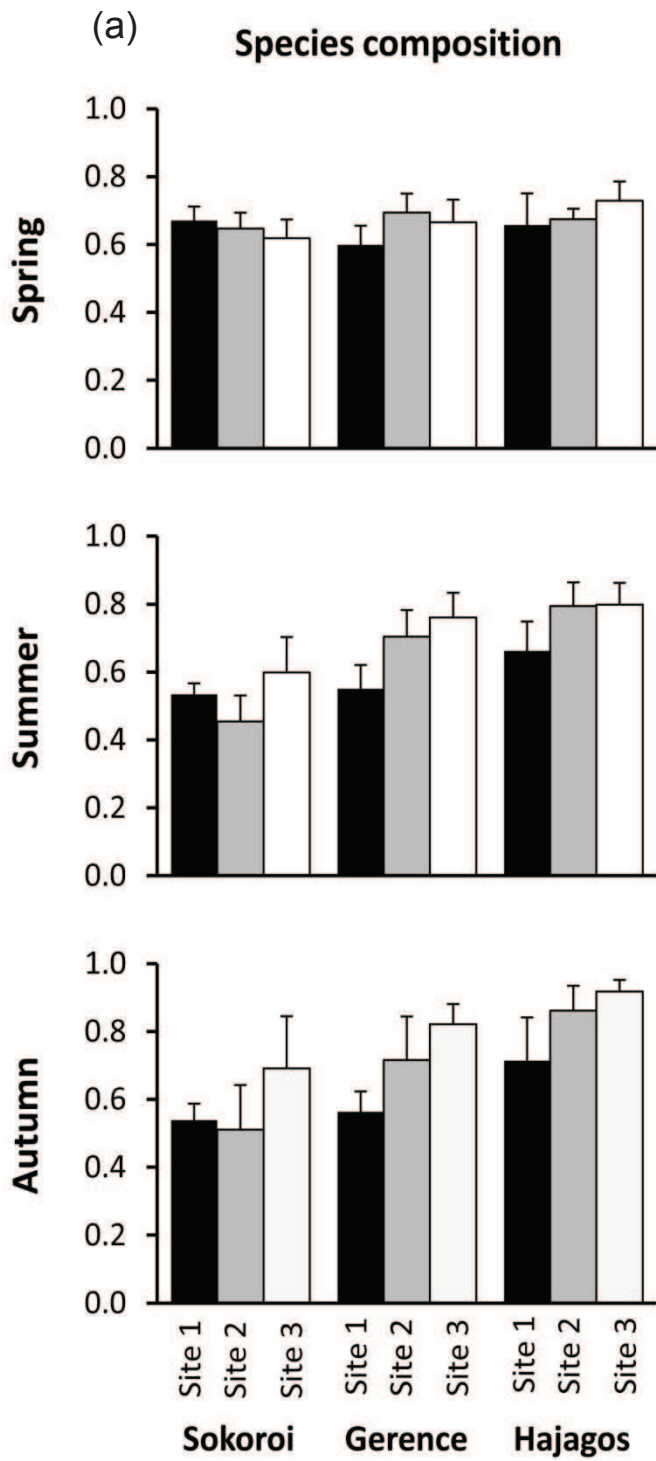
	PC1	PC2	PC3	Width (m)	Depth (cm)	Velocity (cm s <sup>-1</sup> )	Silty sand (%)	Sand (%)	Fine gravel (%)	Coarse gravel (%)	Stone and rock (%)	Emergent plant (%)	Submerged plant (%)	Floating leaved plant (%)	Filamentous algae (%)
PC1	-	1.000	1.000	<0.001	<0.001	<0.001	<0.001	0.001	0.151	<0.001	0.054	<0.001	<0.001	0.137	0.424
PC2	<0.001	-	1.000	<0.001	0.002	0.091	<0.001	0.027	<0.001	0.001	<0.001	0.447	0.483	<0.001	0.006
PC3	<0.001	<0.001	-	0.331	<0.001	<0.001	<0.001	<0.001	0.194	<0.001	0.827	0.59	<0.001	0.007	<0.001
Width (m)	-0.603	0.55	0.095	-	<0.001	0.281	0.342	0.003	0.011	0.279	0.002	<0.001	0.038	0.541	0.627
Depth (cm)	-0.794	0.297	0.334	0.732	-	0.085	0.016	0.05	0.789	<0.001	0.002	<0.001	0.001	0.661	0.162
Velocity (cm s <sup>-1</sup> )	-0.614	-0.164	-0.489	0.105	0.167	-	0.238	0.014	0.646	0.807	0.586	<0.001	<0.001	0.003	0.054
Silty sand (%)	-0.4	-0.76	0.404	-0.092	0.231	0.115	-	0.709	<0.001	<0.001	0.013	0.02	0.509	0.035	0.177
Sand (%)	0.306	-0.213	0.394	-0.282	-0.189	-0.236	-0.036	-	0.284	0.168	0.558	0.317	0.264	0.33	<0.001
Fine gravel (%)	0.139	0.731	0.126	0.243	0.026	-0.045	-0.587	-0.104	-	0.579	0.913	0.548	0.059	0.005	0.007
Coarse gravel (%)	0.375	0.305	-0.73	-0.105	-0.367	-0.024	-0.703	-0.134	-0.054	-	0.725	0.03	0.389	0.362	0.208
Stone and rock (%)	-0.186	0.355	-0.021	0.293	0.297	-0.053	-0.237	-0.057	0.011	-0.034	-	0.966	0.617	0.514	0.44
Emergent plant (%)	0.792	-0.074	-0.052	-0.347	-0.567	-0.501	-0.223	0.097	0.058	0.209	0.004	-	<0.001	0.145	0.209
Submerged plant (%)	-0.67	-0.068	-0.417	0.2	0.316	0.609	0.064	-0.108	-0.182	0.084	0.049	-0.568	-	0.038	0.72
Floating leaved plant (%)	0.144	0.484	0.258	0.06	0.043	-0.288	-0.203	-0.095	0.266	0.089	-0.063	-0.141	-0.2	-	0.072
Filamentous algae (%)	0.078	0.263	0.535	-0.047	0.135	-0.186	-0.131	0.346	0.26	-0.122	-0.075	-0.122	-0.035	0.174	-

Figure  
[Click here to download Figure: confluenceFigs.ppt](#)



### Species richness







### Species richness

### Species composition

### Relative abundance

