

1 This is the final pre-publication version of:  
2 Pilotto F., Harvey G.L., Wharton G. and Pusch M.T. (2016) Simple large wood structures  
3 promote hydromorphological heterogeneity and benthic macroinvertebrate diversity in low-  
4 gradient rivers. *Aquatic Sciences*.

5

6 **Simple large wood structures promote hydromorphological**  
7 **heterogeneity and benthic macroinvertebrate diversity in**  
8 **low-gradient rivers**

9

10 Francesca Pilotto<sup>1,2,3</sup>, Gemma L. Harvey<sup>3</sup>, Geraldene Wharton<sup>3</sup>, Martin T. Pusch<sup>1</sup>

11 <sup>1</sup>Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany

12 <sup>2</sup> Institute of Biology, Freie Universität Berlin, Berlin, Germany

13 <sup>3</sup> School of Geography, Queen Mary University of London, London, U.K.

14 **Corresponding author:** Francesca Pilotto, Current address: Department of Ecology and  
15 Environmental Science, Umeå University, Tvistevägen 48, 90187 Umeå Sweden. E-mail:  
16 francesca.pilotto@umu.se

17

18 **Abstract**

19 The presence of large wood (LW) in river channels adds an important habitat feature for benthic  
20 macroinvertebrates. However, there has been a lack of studies focusing on the effects of simple  
21 wood structures on hydromorphology and macroinvertebrate diversity in surrounding channel  
22 areas. This study explores whether consistent patterns in LW-related benthic habitat complexity  
23 and macroinvertebrate diversity can be identified across a set of low-gradient streams  
24 dominated by fine sediments. While the presence of LW did not change the average values of  
25 standard hydromorphological variables (flow velocity, turbulence, median sediment grain size  
26 and sorting index), the coefficients of variation of such variables for wood rich sites were  
27 consistently higher than those for wood poor sites (velocity: 85% higher, turbulence: 89%, grain  
28 size: 126%, sorting index: 67% higher). In parallel, beta diversity was on average 31% higher in  
29 the wood rich sites, and positively correlated with the amount of LW at the site. The hotspots of  
30 local (alpha) diversity were located in the river-bed areas surrounding the LW, where taxonomic  
31 richness was 83% higher and Shannon-Wiener diversity 39% higher compared to the sites with  
32 less wood. These results demonstrate that the presence of LW in sandy lowland rivers induces  
33 consistent patterns of increased spatial variability of benthic habitats in the surrounding channel  
34 areas and this significantly enhances alpha and beta diversity of macroinvertebrate  
35 communities. Therefore, LW should be conserved in river channels wherever possible, and its  
36 potential for introduction into degraded systems should be explored further because even  
37 simple pieces of LW introduced to lowland streams can deliver benefits.

38 **Keywords:** Alpha diversity / beta diversity / benthic macroinvertebrates / habitat heterogeneity /  
39 lowland rivers.

40

## 41 **Introduction**

42 In freshwater ecosystems, spatial heterogeneity of physical conditions is usually accompanied  
43 by a higher diversity of biotic communities. This includes alpha diversity (Beisel et al. 2000;  
44 Pilotto et al. 2014), the taxonomic richness (Miller et al. 2010) and diversity at a particular site  
45 (Whittaker 1972), and beta diversity (Passy and Blanchet 2007), the compositional  
46 heterogeneity of biotic assemblages among sites or along environmental gradients (Loreau et  
47 al. 2003; Whittaker 1972). Spatial heterogeneity can also result in changes in ecosystem  
48 functions, such as primary production, retention of drifting particles and respiration of benthic  
49 biofilms (Cardinale et al. 2002; Wanner and Pusch 2001), and in the provision of refugia during  
50 disturbances (Townsend and Hildrew 1994), thus increasing the temporal stability of aquatic  
51 communities (Brown 2003). In streams and rivers, the presence of large wood (LW) induces  
52 complex flow patterns (Gippel et al. 1996) which often lead to changes in channel morphology  
53 and to more heterogeneous distributions and sorting of sediments (Gurnell and Linstead 1998;  
54 Montgomery et al. 2003; Wohl 2013) and particulate organic matter (Daniels 2006). In low-  
55 gradient rivers with fine bed material, LW can contribute substantially to hydraulic roughness,  
56 which is only paralleled by the seasonal appearance of submerged macrophytes (Hilderbrand et  
57 al. 1997; Mutz 2000).

58 Most previous studies on the effects of LW on macroinvertebrates have been conducted in  
59 mountain streams in North America, while comparatively few studies have dealt with European  
60 rivers or lowland reaches (Gerhard and Reich 2000; Hoffmann and Hering 2000; Vaz et al.  
61 2014). Although the surface of submerged wood is widely recognized as a hotspot of  
62 macroinvertebrate abundance, biomass and diversity (Benke and Wallace 2003; Hoffmann and  
63 Hering 2000; O'Connor 1991), less is known about the effects of LW on the communities  
64 colonizing river habitats in the surrounding channel areas. Coe et al. (2009) found that the  
65 positive effects of introduced LW logs for macroinvertebrate densities did not extend to the

66 surrounding substrates in two low-gradient cobble-gravel streams. In contrast, a shift in  
67 macroinvertebrate community composition in response to the addition of LW logs has been  
68 recorded in a high-gradient stream, associated with the formation of depositional areas (Wallace  
69 et al. 1995), and in a low-gradient stream, related to the formation of pools (Hilderbrand et al.  
70 1997). These studies, however, do not report any significant effect of LW on macroinvertebrate  
71 abundance or diversity, which constitute important metrics for river management. There is also  
72 recent evidence that LW may trigger the formation of new mesohabitats, such as patches with  
73 abundant organic material, known to host diverse communities, but so far this has only been  
74 shown for one high-gradient stream (Gerhard and Reich 2000) and one low-gradient river  
75 (Pilotto et al. 2014). Moreover, previous studies do not demonstrate direct linkages between  
76 LW-induced macroinvertebrate diversity and habitat heterogeneity (Miller et al. 2010), nor the  
77 effect of LW on the compositional heterogeneity of the macroinvertebrate assemblages (beta  
78 diversity).

79 Hence, this study examines the relationship between LW, channel hydromorphology and  
80 macroinvertebrate diversity across a set of lowland river reaches. In particular, this study  
81 investigated (i) whether LW increases the variability of hydromorphological habitat conditions in  
82 the surrounding channel areas, (ii) whether the variability of hydromorphological conditions  
83 results in consistent changes in the taxonomic and functional composition and local (alpha)  
84 diversity of the macroinvertebrate assemblages, and (iii) whether the compositional  
85 heterogeneity of the macroinvertebrate assemblages (beta diversity) increases consistently with  
86 increasing frequency of LW in the river channel.

## 87 **Methods**

### 88 *Study area*

89 This study was carried out in three near-natural rivers in Western Poland, the Płociczna,  
90 Korytnica and Pliszka Rivers (Fig. 1). All three are low gradient, sand-dominated lowland rivers  
91 with largely forested floodplains. The Płociczna (length: 51 km) and Korytnica (length: 37 km)  
92 Rivers are tributaries of the Drawa River, while the Pliszka River is a 56-km long tributary of the  
93 Oder River.

94

#### 95 *Study design*

96 For our study, we selected one reach of the Korytnica (KOR) and Pliszka rivers (PLI), and three  
97 distinct reaches (i.e., separated by lakes) in the Płociczna River (PLO1, PLO2 and PLO3, Fig.  
98 1). These reaches allowed a paired-site research design: within the same river reach, a 100-m-  
99 long site naturally rich in in-channel LW ('wood rich'; WR site) was compared in terms of  
100 hydromorphology and stream macroinvertebrate assemblages to a nearby (0.4 - 1.8 km) 100-m-  
101 long site with a lower amount of LW ('wood poor', WP site). The use of the terms "wood rich"  
102 and "wood poor" is to be intended in a relative sense to differentiate between the study sites,  
103 rather than tied to an absolute abundance. In this study, we adopted the conventional definition  
104 of LW as wood material larger than 0.1 m in diameter and 1 m in length (Gippel et al. 1996).  
105 Due to the low gradients of the studied reaches, LW pieces falling into the channel are unlikely  
106 to be transported downstream or re-oriented and thus remain in place mainly as single logs.  
107 Only a few accumulations of LW (jams; Table 1) were recorded within the studied reaches, they  
108 spanned the whole channel width and were composed of smaller wood pieces, such as twigs  
109 (<0.1 m in diameter, < 1 m in length), trapped by larger key elements (i.e., LW). All selected  
110 study sites were relatively straight (to avoid the confounding effect of meanders on channel  
111 geomorphology), with forested banks (mainly alder [*Alnus glutinosa*]) and similar bankfull width,  
112 discharge, and bed substrate (sand-sized sediments) (Table 1).

113 Field work was carried out in April-May 2012 when the water level was 80 – 92% of bankfull. In  
114 each reach, six in-channel pieces of LW were selected at the respective wood rich site. These  
115 were single LW pieces between 12 and 41 cm in diameter and 2.5 – 18.8 m in length, oriented  
116 perpendicular (angles within the range 80° – 100°) to river flow, submersed and partially resting  
117 on the surface of the bed sediment or anchored in the bed sediment. The selected LW pieces  
118 were separated by distances > 5 m in order to avoid overlapping effects.

119 For each selected LW piece, hydromorphological and biotic data were collected from three  
120 substrata: the surface of the LW (W1), the river-bed sediment around the LW (at ca. 10 cm from  
121 the LW; W2), and the river-bed sediment outside the direct hydrological influence of the LW log,  
122 i.e., where scouring or depositional processes were not visible (> 5 m from the LW; W3). We set  
123 one sampling point in the W1 and W3 substrata of each selected LW piece, and three sampling  
124 points in the W2 substratum (upstream, downstream and lateral to the LW). In each wood poor  
125 site we set six sampling points covering the range of water depths present there (WP).

### 126 *Hydromorphological variables*

127 Channel bed elevation was recorded across three to five cross-sections within each site, using a  
128 total station (TCRA 1205+, Leica, Heerbrugg, Switzerland), and water depth was measured at  
129 1-m intervals. Two cross-sections were located at the beginning and end of the site, the others  
130 were set to be equidistant from one another. To avoid one cross-section overlapping a LW  
131 piece, that cross-section was moved downstream so that the measurements of channel bed  
132 elevation were not directly affected by the LW. The locations of the LW pieces were also  
133 surveyed using the total station. Mean channel width, channel area, and orientation angle of  
134 each piece of LW relative to the channel, were calculated using ArcGIS 9.2. The slope of the  
135 riverbed and the slope of the water level were calculated along the thalweg as the difference in  
136 the elevation between the most upstream and downstream cross-sections divided by the reach

137 length (i.e., 100 m). To estimate the volume of LW in each site, we measured the length of each  
138 in-channel LW piece and its diameter at its ends, assuming a cylindrical shape. The blockage  
139 ratio (B) was defined as the partial cross-sectional area occupied by each piece of LW and  
140 computed as  $B = L d/A$ , where A is the channel cross-sectional area, d the diameter of the LW  
141 piece and L the projected length of the LW against the flow (Gippel et al. 1996).

142 Near-bed (5 cm above the sediment) measurements of the streamwise, transverse and vertical  
143 flow velocity components were recorded in each sampling point for 1 minute (Buffin-Bélanger  
144 and Roy 2005) at 1 Hz, using a FlowTracker (SonTek, San Diego, CA, USA) Acoustic Doppler  
145 Velocimeter, to assess the hydraulic conditions experienced by benthic macroinvertebrates  
146 (Jowett 2003). From those measurements, mean flow velocity was computed and the standard  
147 deviation of the streamwise component of the flow velocity was used as a proxy for turbulence  
148 (Enders et al. 2003; Pilotto et al. 2014).

149 A sediment core (diameter: 10 cm, depth: 5 cm) was collected at each benthic sampling point.  
150 Sediment samples were dried at 60 °C for 36 h and then sieved through a 12-level sieving  
151 cascade with a sieve shaker. Based on the dry weight of each fraction, distribution curves were  
152 calculated, and the median grain size (D50) and the 16th and 84th percentiles (D16 and D84)  
153 were computed. Samples were then combusted at 550° for 5 h to determine the organic  
154 content. A sediment sorting index was computed from the 16th and 84th grain size percentiles,  
155 following Liébault and Piégay (2001). It is an index of heterogeneity of the grain sizes with a  
156 values close to 0 representing homogeneous samples and increasing values describing  
157 increasing heterogeneity.

### 158 *Macroinvertebrates*

159 Benthic macroinvertebrates colonizing the river-bed sediments were sampled using a Surber  
160 sampler (frame size: 23x23 cm, mesh size: 500 µm). The material from five Surber samplers

161 was pooled to produce one sample, which thus represented a total area of 0.26 m<sup>2</sup>.  
162 Macroinvertebrates sampled from the LW surface were dislodged by brushing a surface area of  
163 0.26 m<sup>2</sup> and collecting the material in a net. Samples were preserved in 70% ethanol and  
164 processed in the laboratory, where they were sorted and animals counted and identified under a  
165 binocular microscope (10× magnification). Samples were mostly identified to species or genus  
166 level, Gammaridae (with the exception of *Gammarus roeselii*, Gervais 1835) and some  
167 Trichoptera to family, Chironomidae to subfamily, Oligochaeta as class. The taxonomic level  
168 was the same across all the samples. For site PLO2 sample processing was limited to three  
169 replicates of each substratum instead of six.

#### 170 *Data analysis*

171 The coefficient of variation of the hydromorphological variables was used as a measure of their  
172 spatial heterogeneity (Gostner et al. 2013; Minshall and Robinson 1998).

173 Taxa abundances from the three sampling points on the river-bed sediments surrounding the  
174 same LW (upstream, downstream and lateral) were averaged (W2). Thus, in each reach we  
175 obtained six replicate samples from the wood poor site (WP), six replicate samples from the LW  
176 surface (W1), six replicate samples from the riverbed sediments around the LW (W2) and six  
177 replicate samples from the riverbed sediments outside the direct influence of LW within the  
178 wood rich sites (W3). In the reach PLO2 three replicates for each substratum were available  
179 instead of six. We computed the Shannon-Wiener diversity index and the taxonomic richness  
180 after rarefaction per each sample, using the R software package 'Vegan' (Oksanen et al. 2013;  
181 R Core Team 2013). Beta diversity was computed as global multivariate dispersion, which is a  
182 multivariate measure of compositional heterogeneity in groups of samples (Anderson 2006;  
183 Clarke and Warwick 2001). It was calculated for the wood rich and wood poor sites within each  
184 reach as mean distance of the samples from their group centroid, again using the 'Vegan'

185 package (Oksanen et al. 2013), this was based on the  $\log(x+1)$  transformed invertebrate  
186 taxonomic abundances and the binomial distance (Anderson and Millar 2004). Since the  
187 number of samples differed between the two groups (WR and WP) we applied the  $\sqrt{n/(n-1)}$   
188 correction to the estimated distances to centroid within each group (Stier et al. 2013).

189 To account for the nested design and investigate the common patterns among the different  
190 study reaches, we fitted a series of linear mixed effect models (LME), using the R package  
191 “lme4” (Bates et al. 2012). The models included the factor of interest as a fixed factor, and  
192 random intercepts for the reach (random effect). By including the random effect for the reach we  
193 accounted for the lack of independency among sampling sites within the same river reach.  
194 These models were used to test for differences in the hydromorphological characteristics and  
195 the amount of LW between site types (fixed factor, levels: WR and WP), and in the values and  
196 variability of the hydromorphological variables between site types and among substratum types  
197 (fixed factor, levels: WP, W1, W2 and W3). LME models were also used to test for differences in  
198 the values of macroinvertebrate metrics (abundance, taxonomic richness and Shannon-Wiener  
199 diversity) among substratum types and beta diversity between site types (fixed factor, levels:  
200 WR and WP site). All the LME models were tested by likelihood ratio tests against the reduced  
201 model (without the fixed factor), and the residuals were checked for normality using the Wilk-  
202 Shapiro test. Post-hoc multiple comparisons tests were performed by using the function  
203 “testInteractions” of the R package “phia” (Rosario-Martinez 2013). The relationship between  
204 beta diversity and the amount of LW in the sites was analysed using linear regression.

205 LME models were also used to investigate the relationship between the two invertebrate metrics  
206 of alpha diversity (taxonomic richness and Shannon-Wiener diversity index) recorded on benthic  
207 habitats (WP, W2 and W3) and the mean value and variability of the hydromorphological  
208 variables recorded there (mean flow velocity, turbulence, median sediment grain size, organic  
209 matter content of the riverbed sediments and sediment sorting index). If two or more

210 hydromorphological variables were highly correlated with each other (i.e., Pearson's product-  
211 moment correlation  $>0.30$ ; Bremigan et al. 2008; Table 2), only one of those was included in the  
212 models to avoid collinearity. As above, the models included the reach as random factor and  
213 were tested by likelihood ratio tests against the reduced models (without the fixed factors).

214 The effects of the reach (KOR, PLI, PLO1, PLO2 and PLO3) and substratum (WP, W1, W2 and  
215 W3) in shaping the macroinvertebrate taxonomic composition were tested by a permutational  
216 multivariate ANOVA, perMANOVA (Anderson 2001), using  $\log(x+1)$  transformed  
217 macroinvertebrate taxonomic abundances and binomial distance (Anderson and Millar 2004).  
218 This involved 999 permutations which were constrained within each river reach in order to  
219 account for the nested design (i.e., substrata nested in reaches). Macroinvertebrate taxonomic  
220 composition in the study reaches and on the various substrata was then plotted using non-  
221 metric multidimensional scaling (nMDS). PerMANOVA and nMDS analyses were run in the R  
222 package "Vegan" (Oksanen et al. 2013). Indicator value analysis was performed to identify the  
223 functional traits which were significantly associated with each substratum, using the function  
224 "multipatt" in the R package "indicspecies" (Cáceres and Legendre 2009). This analysis was run  
225 on the functional rather than on the taxonomic structure of the assemblages as it is less  
226 sensitive to bio-geographical constraints (Feld and Hering 2007). Therefore, indicator value  
227 analysis was performed on the percent abundance of functional feeding groups (i.e., grazers  
228 and scrapers, miners, xylophages, shredders, gatherer collectors, active and passive filterers,  
229 predators and parasites) and current velocity preferences (i.e., percent abundance of  
230 limnobiont, limnophil, limno- rheophil, rheo-limnophil, rheophil and rheobiont taxa; these classes  
231 indicate preferences for current velocities ranging progressively from standing water to high  
232 flow) as obtained from the ASTERICS software (Aqem Consortium 2008).

233

## 234 **Results**

### 235 *Hydromorphological variables*

236 Wood rich and wood poor sites within each reach were not statistically different for most  
237 hydromorphological variables (LME:  $P > 0.05$ ; Table 1), except for the number of wood pieces  
238 (LME:  $P < 0.05$ ; Table 1), the LW volume:bankfull channel area ratio (LME:  $P < 0.05$ ; Table 1)  
239 and the water level slope ( $P = 0.05$ ). Wood rich sites exhibited a higher water surface gradient,  
240 while the longitudinal gradient of the channel bed did not differ significantly between wood rich  
241 and wood poor sites (LME:  $P > 0.05$ ; Table 1). The wood rich sites exhibited on average 11.4  
242 logs with a blockage ratio higher than 0.10, compared to only 4.4 in wood poor sites sites (Table  
243 1).

244 Flow velocity, turbulence, percentage of sediment organic matter, median sediment grain size  
245 and sorting index showed no consistent mean differences between wood rich and wood poor  
246 sites (LME analysis, likelihood ratio test:  $P > 0.05$ ; Fig. 2a, c, e, g and i). However, their  
247 variability (i.e., their coefficient of variation) was on average 85%, 89%, 57%, 126%, and 67%  
248 larger in the wood rich sites than in the wood poor sites, respectively. LME analysis confirmed  
249 significant differences in the coefficients of variation for mean flow velocity, turbulence, median  
250 grain size and sorting index (likelihood ratio test:  $P < 0.05$ ; Fig. 2b, d, h and j).

251 The higher physical variability in the wood rich sites was due to the high variability recorded in  
252 the measurement points near the wood logs (W2) within all the studied reaches. The  
253 coefficients of variation for mean flow velocity, turbulence, sediment organic matter, median  
254 grain size and sorting index were significantly higher there than in all the other substrata (WP,  
255 W1 and W3; LME analysis, likelihood ratio test:  $P < 0.05$ ; Fig. 3), in particular they were 101%,  
256 89%, 148%, 57% and 221% higher there than in the measurement points in the wood poor site  
257 (WP).

258

259 *Macroinvertebrates*

260 In total we collected ca. 137,000 macroinvertebrates, belonging to 138 taxa, the most abundant  
261 orders were Diptera (65%), Trichoptera (9%) and Ephemeroptera (9%). Macroinvertebrate  
262 communities showed a consistent pattern of differences between wood rich and wood poor sites  
263 in terms of taxonomic composition and diversity.

264 Within each reach, different communities colonized the sediments in the wood poor sites and  
265 the sediments around the wood logs (W2, Fig. 4). The community inhabiting the wood logs (W1)  
266 differed from the others in all the reaches, except at PLO3 where it was similar to that inhabiting  
267 the sediments around the logs. W3 showed overlaps with W2 (KOR) and WP samples (KOR,  
268 PLI) and generally was located in between those two substrata in the ordination plots (Fig. 4).  
269 The taxonomic composition of the macroinvertebrate community was significantly influenced by  
270 both reach and substratum with the reach explaining 39% (perMANOVA,  $F(4) = 22.27$ ,  $P < 0.01$ )  
271 of the taxonomic variance, and the substratum accounting for 17% (perMANOVA,  $F(4) = 12.48$ ,  
272  $P < 0.01$ ). Active filterers were significantly associated with wood poor sites (indicator value:  
273 0.60,  $p < 0.05$ ), while shredders were associated with W3 (indicator value: 0.63,  $p < 0.01$ ) and  
274 xylophages with W1 (indicator value: 0.68,  $p < 0.01$ ). Taxa showing preferences for lower flow  
275 velocities (rheo-limophil taxa; indicator value: 0.62,  $p < 0.01$ ) were more abundant on W1, while  
276 both rheobiont (preferences for high flow velocities; indicator value: 0.63,  $p < 0.01$ ) and limno-  
277 rheophil (preferences for standing water or low flow velocities; indicator value: 0.53,  $p < 0.05$ )  
278 taxa were more abundant on W2.

279 Beta diversity was on average 31% higher (range: 12 – 38%) in the wood rich sites than in the  
280 wood poor sites; this difference was significant and consistent across the studied reaches (LME  
281 analysis, likelihood ratio test:  $P < 0.01$ ; Fig. 5A). Moreover, beta diversity was positively

282 correlated with the number of LW logs in the site, although with some scatter (regression  
283 analysis: Beta diversity = 0.07 Number of LW + 5.4,  $R^2 = 0.43$ ,  $F(1,8) = 5.97$ ,  $P = 0.04$ ; Fig. 5B).

284 The highest values of taxonomic richness and Shannon-Wiener diversity were consistently  
285 recorded on the sediment around the wood logs (W2), where on average values 83% and 39%  
286 higher were recorded in comparison to the wood poor sites (LME analysis, likelihood ratio test:  
287  $P < 0.01$ ; Fig. 6). The highest macroinvertebrate abundances were recorded on the surface of  
288 the wood (LME analysis, likelihood ratio test:  $P < 0.01$ ; Fig. 6).

289 The metrics of alpha diversity, taxonomic richness and Shannon-Wiener diversity, were  
290 positively correlated with the variability of the hydromorphological variables. In particular, they  
291 significantly increased with increasing coefficient of variation of the median grain size of the  
292 riverbed sediments (Table 3; LME,  $P < 0.01$ ).

## 293 **Discussion**

294 Our results show that wood rich sites had greater hydromorphological variability (CV of flow  
295 velocity, turbulence, sediment grain size and sorting) and that locations closest to the wood  
296 pieces showed the greatest variability in these parameters. Macroinvertebrate community  
297 structures were consistently distinct between samples at wood poor sites and those immediately  
298 adjacent to wood. The wood surface was associated with the highest abundance of  
299 macroinvertebrates while the highest taxonomic richness and diversity was found immediately  
300 adjacent to the wood. Macroinvertebrate beta diversity was higher in wood rich sites than in  
301 wood poor sites, and it increased with the amount of wood present.

### 302 *Effects of LW on river channel hydromorphology*

303 The hydromorphology of the river channel areas surrounding the LW was consistently  
304 characterized by much more diverse abiotic conditions than channel areas lacking LW, as

305 shown by the coefficients of variation of flow velocity and sediment grain size which were 85%  
306 and 126% times higher, respectively, than in the wood poor sites. This variation was produced  
307 by the complexity of flow patterns generated by the LW in its surroundings, with reduced levels  
308 of flow velocity within its roughness projection area, and increased velocities where flow was  
309 concentrated in the remaining part of the channel cross-section (Gurnell and Linstead 1998;  
310 Montgomery et al. 2003; Mutz 2000; Wallace et al. 1995). In mountain streams, LW induces  
311 changes in hydraulic patterns, which causes a shift from erosional to depositional processes  
312 where flow is reduced by the LW, with subsequent deposition of silt and sand (Buffington and  
313 Montgomery 1999; Wallace et al. 1995). In sand-dominated lowland rivers lacking coarser river-  
314 bed materials (cobbles and boulders) LW has been shown to trigger both depositional and  
315 erosional processes with the formation of depositional patches of fine sediments and scouring  
316 patches resulting in coarser sediments in the areas of flow constriction (Mutz 2000; Pilotto et al.  
317 2014). This likely creates the variability in hydromorphological conditions that was consistently  
318 recorded in this study.

319 The hydraulic roughness induced by LW additionally changes river hydromorphology at a larger  
320 spatial scale, as it causes an upstream increase in the water level (water afflux; Gippel et al.  
321 1996). The extent of this impounding effect mainly depends on the proportion of the channel  
322 cross-section area blocked by the LW, as pieces with a blockage ratio higher than 0.10 have  
323 been shown to be responsible for significant water afflux (Gippel et al. 1996; Gurnell and  
324 Linstead 1998). Accordingly, within each of the reaches studied here, the water surface slope  
325 was considerably steeper ( $1.0 \pm 0.2 \cdot 10^{-3}$  m) in the sites rich in wood, which coincided with  
326 higher loadings of LW with blockage ratio  $>0.10$ , compared to the wood poor sites ( $0.4 \pm 0.2 \cdot 10^{-3}$   
327 m), although the channel bed slope was similar across paired sites ( $2.1 \pm 1.7 \cdot 10^{-3}$  and  
328  $2.4 \pm 2.2 \cdot 10^{-3}$  m). This higher water surface gradient is a further indication of the role of LW in  
329 controlling the hydraulics of the sites.

330 *Effects of LW on macroinvertebrate abundance and diversity*

331 Previous studies have demonstrated that taxonomic richness, abundance and biomass of  
332 aquatic macroinvertebrates are higher on wood than on other benthic habitats (Benke and  
333 Wallace 2003; Hoffmann and Hering 2000; Smock et al. 1989). This study also found the  
334 highest macroinvertebrate abundances on the LW surfaces compared to the river-bed  
335 sediments. In contrast, however, taxonomic richness and diversity were significantly higher on  
336 the river-bed sediments around the LW, even compared to the LW surfaces.

337 The communities colonizing the sediment around the LW consistently showed the highest  
338 values of alpha diversity in the study reaches. Taxonomic richness and Shannon-Wiener  
339 diversity were on average 30% and 45% higher there than in the wood poor sites. This result is  
340 also reflected in the significant correlation of both metrics with the variability of  
341 hydromorphological conditions, in particular with the variability of median grain size. According  
342 to general niche theory (Hutchinson 1961), heterogeneous environments can sustain larger  
343 macroinvertebrate alpha diversity by enabling a larger number of niches for macroinvertebrate  
344 species, as shown by the occurrence of taxa with distinct flow requirements in the proximity of  
345 the LW, and by supporting short-distance dispersal of biota among neighbouring habitats  
346 compared to homogeneous environments (Beisel et al. 2000).

347 The positive effect of LW on alpha diversity was paralleled by a similar effect on beta diversity,  
348 which was on average 31% higher in the sites rich in wood than in the sites with lower amounts  
349 of wood, and positively correlated to the amount of LW in the site. Thus, LW-induced habitat  
350 heterogeneity offers longer environmental gradients even at larger (reach) spatial scales. Those  
351 gradients increase proportionally to the amount of LW and support higher compositional  
352 heterogeneity of biotic assemblages at the local and reach scales, too. This finding also

353 confirms that beta diversity constitutes a suitable measure for the evaluation of restoration  
354 programmes (Passy and Blanchet 2007).

355 *Effects of LW on the taxonomic and functional composition of macroinvertebrate communities*

356 It is well known that macroinvertebrate community composition is driven by factors acting at  
357 different spatial scales (Brosse et al. 2003; Frissell et al. 1986; Townsend et al. 2003). Our  
358 perMANOVA results showed that a large part (39%) of the taxonomic variance of the  
359 macroinvertebrate assemblages was explained by the factor 'reach', which represents the large-  
360 scale variations among reaches (e.g. biogeographic context, river connectivity, geology).  
361 Though, the factor 'substratum', which represents the substratum-specific variations at the local  
362 scale (e.g. sediment composition, hydraulics, trophic resources), constituted an additional  
363 significant driving factor shaping macroinvertebrate assemblages (explained variance: 17%).

364 Consistent and significant differences between the communities colonizing the sediments in  
365 proximity to the LW and those colonizing the sediments in the sites without LW were recorded  
366 throughout the five studied reaches. Moreover, the communities inhabiting the sediments  
367 outside the direct influence of LW in the wood rich sites were generally located in between those  
368 two communities in the ordination plots. This suggests that LW acted in our study as the main  
369 driver of macroinvertebrate community composition even in channel areas outside its direct  
370 influence. This may be due to short-distance dispersals from nearby LW-related assemblages  
371 (Beisel et al. 2000), which act as sources for colonization for other channel areas.

372 As the studied substrata were shaped by local hydraulics, which was influenced by the location  
373 relative to the next LW, the results of this study demonstrate that the taxonomic and functional  
374 composition of the macroinvertebrate assemblages was significantly influenced by the changes  
375 in local hydromorphological conditions induced by LW. Resulting patterns of macroinvertebrate  
376 taxonomic and functional composition and diversity were recorded throughout the five studied

377 reaches, despite the fact that those reaches hosted different macroinvertebrate communities (as  
378 shown by perMANOVA and nMDS analyses). This suggests that the observed  
379 macroinvertebrate distribution patterns around large wood represents a general feature of near-  
380 natural sandy lowland rivers.

### 381 *LW addition for river restoration*

382 Freshwater ecosystems worldwide are subjected to an overarching trend of biotic  
383 homogenization, which has been associated with several human-induced alterations resulting in  
384 reduction of flow (Brunke et al. 2002; Graeber et al. 2013), loss of habitat heterogeneity (Passy  
385 and Blanchet 2007), introduction of invasive species (Olden et al. 2006), nutrient enrichment  
386 (Donohue et al. 2009), and excessive inputs of fine sediments (Heppell et al. 2009). During the  
387 last few decades, numerous attempts have been undertaken to restore hydromorphological  
388 heterogeneity in degraded aquatic systems, with the ultimate aim of increasing biodiversity  
389 (Acuña et al. 2013; Kail et al. 2007; Miller et al. 2010; Pretty et al. 2003). However, restoration  
390 projects have often failed to generate intended improvements in terms of fish and  
391 macroinvertebrate abundance and diversity (Brooks et al. 2002; Lepori et al. 2005; Pretty et al.  
392 2003). This study demonstrates that in near-natural lowland rivers the presence of even simple  
393 LW structures (single logs without many branches or roots) consistently increased the  
394 hydromorphological heterogeneity in the adjacent within-channel areas, which resulted in  
395 elevated levels of both alpha and beta diversity of macroinvertebrates. This finding is particularly  
396 encouraging given the concerns over flood risk and access constraints that can limit the quantity  
397 and complexity of LW introduced through restoration projects. As there is now even stronger  
398 evidence for the crucial role of LW for aquatic biodiversity in lowland rivers, LW should be left in  
399 river channels wherever possible. Although machinery work necessary for installing wood logs  
400 into river channels may have negative short to medium-term consequences on in-stream and  
401 floodplain ecosystems (Laasonen et al. 1998; Muotka and Laasonen 2002), in degraded rivers,

402 active introduction of LW for restoration purposes may offer an effective measure to increase  
403 the heterogeneity of the in-stream habitat and the diversity of macroinvertebrate communities  
404 (Miller et al. 2010; Piégay and Landon 1997) in the long term, where water quality and  
405 availability of sources for biotic colonization are suitable.

#### 406 **Acknowledgements**

407 This work has been carried out within the SMART Joint Doctorate Programme 'Science for the  
408 MAnagement of Rivers and their Tidal systems' funded by the Erasmus Mundus programme of  
409 the European Union. The authors thank Jürgen Schreiber, Marlen Mährlein and Magdalena  
410 Czarnecka for field and lab assistance, and Drawiński National Park for allowing field work in  
411 the Płociczna and Korytnica Rivers, and for helpful support of field work.

412

413 **References**

- 414 Acuña V, Díez JR, Flores L, Meleason M, Elozegi A (2013) Does it make economic sense to  
415 restore rivers for their ecosystem services? *J Appl Ecol* 50:988-997
- 416 Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral*  
417 *ecology* 26:32-46
- 418 Anderson MJ (2006) Distance-Based Tests for Homogeneity of Multivariate Dispersions.  
419 *Biometrics* 62:245-253
- 420 Anderson MJ, Millar RB (2004) Spatial variation and effects of habitat on temperate reef fish  
421 assemblages in northeastern New Zealand. *Journal of Experimental Marine Biology and*  
422 *Ecology* 305:191-221
- 423 Aqem Consortium (2008) ASTERICS: AQEM. STAR Ecological river classification system,  
424 Version 31
- 425 Bates D, Maechler M, Bolker B (2012) lme4: Linear mixed-effects models using S4 classes.  
426 <http://CRANR-project.org/package=lme4>
- 427 Beisel J-N, Usseglio-Polatera P, Moreteau J-C (2000) The spatial heterogeneity of a river  
428 bottom: a key factor determining macroinvertebrate communities. *Hydrobiologia*  
429 422/433:163-171
- 430 Benke A, Wallace JB (2003) Influence of wood on invertebrate communities in streams and  
431 rivers. In: Gregory SV, Boyer KL, Gurnell AM (eds) *The ecology and management of*  
432 *wood in world rivers*. American Fisheries Society, Symposium 37, Bethesda, Maryland,  
433 pp 149-177

- 434 Bremigan MT et al. (2008) Hydrogeomorphic features mediate the effects of land use/cover on  
435 reservoir productivity and food webs. *Limnology and Oceanography* 53:1420
- 436 Brooks SS, Palmer MA, Cardinale BJ, Swan CM, Ribblett S (2002) Assessing stream  
437 ecosystem rehabilitation: limitations of community structure data. *Restoration Ecology*  
438 10:156-168
- 439 Brosse S, Arbuckle CJ, Townsend CR (2003) Habitat scale and biodiversity: influence of  
440 catchment, stream reach and bedform scales on local invertebrate diversity. *Biodiversity  
441 & Conservation* 12:2057-2075
- 442 Brown BL (2003) Spatial heterogeneity reduces temporal variability in stream insect  
443 communities. *Ecology Letters* 6:316-325
- 444 Brunke M, Hoffmann A, Pusch M (2002) Association between invertebrate assemblages and  
445 mesohabitats in a lowland river (Spree, Germany): A chance for predictions? *Archiv für  
446 Hydrobiologie* 154:239-259
- 447 Buffin-Bélanger T, Roy AG (2005) 1 min in the life of a river: selecting the optimal record length  
448 for the measurement of turbulence in fluvial boundary layers. *Geomorphology* 68:77-94
- 449 Buffington JM, Montgomery DR (1999) Effects of hydraulic roughness on surface textures of  
450 gravel-bed rivers. *Water Resources Research* 35:3507-3521
- 451 Cáceres MD, Legendre P (2009) Associations between species and groups of sites: indices and  
452 statistical inference. *Ecology* 90:3566-3574
- 453 Cardinale BJ, Palmer MA, Swan CM, Brooks S, Poff NL (2002) The influence of substrate  
454 heterogeneity on biofilm metabolism in a stream ecosystem. *Ecology* 83:412-422

455 Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical  
456 analysis and interpretation. 2nd Edition edn. PRIMER-E Ltd, Plymouth U.K.

457 Coe HJ, Kiffney PM, Pess GR, Kloehn KK, McHenry ML (2009) Periphyton and invertebrate  
458 response to wood placement in large pacific coastal rivers. River research and  
459 applications 25:1025-1035

460 Daniels MD (2006) Distribution and dynamics of large woody debris and organic matter in a low-  
461 energy meandering stream. Geomorphology 77:286-298  
462 doi:10.1016/j.geomorph.2006.01.011

463 Donohue I, Jackson AL, Pusch MT, Irvine K (2009) Nutrient enrichment homogenizes lake  
464 benthic assemblages at local and regional scales. Ecology 90:3470-3477

465 Enders EC, Boisclair D, Roy AG (2003) The effect of turbulence on the cost of swimming for  
466 juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic  
467 Sciences 60:1149-1160

468 Feld CK, Hering D (2007) Community structure or function: effects of environmental stress on  
469 benthic macroinvertebrates at different spatial scales. Freshwater Biology 52:1380-1399

470 Frissell CA, Liss WJ, Warren CE, Hurley MD (1986) A hierarchical framework for stream habitat  
471 classification: viewing streams in a watershed context. Environmental management  
472 10:199-214

473 Gerhard M, Reich M (2000) Restoration of streams with large wood: Effects of accumulated and  
474 built-in wood on channel morphology, habitat diversity and aquatic fauna. International  
475 Review of Hydrobiology 85:123-137 doi:10.1002/(sici)1522-2632(200003)85:1<123::aid-  
476 iroh123>3.0.co;2-t

477 Gippel CJ, O'Neill IC, Finlayson BL, Schnatz I (1996) Hydraulic guidelines for the re-introduction  
478 and management of large woody debris in lowland rivers. *Regulated Rivers-Research &*  
479 *Management* 12:223-236 doi:10.1002/(SICI)1099-1646(199603)12:2/3<223::AID-  
480 RRR391>3.0.CO;2-#

481 Gostner W, Alp M, Schleiss AJ, Robinson CT (2013) The hydro-morphological index of diversity:  
482 a tool for describing habitat heterogeneity in river engineering projects. *Hydrobiologia*  
483 712:43-60

484 Graeber D, Pusch MT, Lorenz S, Brauns M (2013) Cascading effects of flow reduction on the  
485 benthic invertebrate community in a lowland river. *Hydrobiologia* 717:147-159

486 Gurnell AM, Linstead C (1998) Interactions between large woody debris accumulations,  
487 hydrological processes and channel morphology in British headwater rivers. In: Wheeler  
488 H, Kirby C (eds) *Hydrology in a Changing Environment*, vol 1. Wiley, Chichester, pp 381-  
489 395

490 Heppell C, Wharton G, Cotton J, Bass J, Roberts S (2009) Sediment storage in the shallow  
491 hyporheic of lowland vegetated river reaches. *Hydrological processes* 23:2239-2251

492 Hilderbrand RH, Lemly AD, Dolloff CA, Harpster KL (1997) Effects of large woody debris  
493 placement on stream channels and benthic macroinvertebrates. *Canadian Journal of*  
494 *Fisheries and Aquatic Sciences* 54:931-939

495 Hoffmann A, Hering D (2000) Wood-associated macroinvertebrate fauna in central European  
496 streams. *International Review of Hydrobiology* 85:25-48

497 Hutchinson GE (1961) The paradox of the plankton. *American Naturalist* 95:137-145

498 Jowett I (2003) Hydraulic constraints on habitat suitability for benthic invertebrates in gravel-bed  
499 rivers. *River Research and Applications* 19:495-507

500 Kail J, Hering D, Muhar S, Gerhard M, Preis S (2007) The use of large wood in stream  
501 restoration: experiences from 50 projects in Germany and Austria. *J Appl Ecol* 44:1145-  
502 1155 doi:DOI 10.1111/j.1365-2664.2007.01401.x

503 Laasonen P, Muotka T, Kivijärvi I (1998) Recovery of macroinvertebrate communities from  
504 stream habitat restoration. *Aquatic Conservation: Marine and Freshwater Ecosystems*  
505 8:101-113

506 Lepori F, Palm D, Brännäs E, Malmqvist B (2005) Does restoration of structural heterogeneity in  
507 streams enhance fish and macroinvertebrate diversity? *Ecological Applications* 15:2060-  
508 2071

509 Liébault F, Piégay H (2001) Assessment of channel changes due to long-term bedload supply  
510 decrease, Roubion River, France. *Geomorphology* 36:167-186

511 Loreau M, Mouquet N, Gonzalez A (2003) Biodiversity as spatial insurance in heterogeneous  
512 landscapes. *Proceedings of the National Academy of Sciences* 100:12765-12770

513 Miller SW, Budy P, Schmidt JC (2010) Quantifying Macroinvertebrate Responses to In-Stream  
514 Habitat Restoration: Applications of Meta-Analysis to River Restoration. *Restoration*  
515 *Ecology* 18:8-19

516 Minshall G, Robinson C (1998) Macroinvertebrate community structure in relation to measures  
517 of lotic habitat heterogeneity. *Archiv für Hydrobiologie* 141:129-151

518 Montgomery DR, Collins BD, Buffington JM, Abbe TB (2003) Geomorphic effects of wood in  
519 rivers. *American Fisheries Society Symposium* 37:21-47

520 Muotka T, Laasonen P (2002) Ecosystem recovery in restored headwater streams: the role of  
521 enhanced leaf retention. *J Appl Ecol* 39:145-156

522 Mutz M (2000) Influences of woody debris on flow patterns and channel morphology in a low  
523 energy, sand-bed stream reach. *International Review of Hydrobiology* 85:107-121  
524 doi:10.1002/(sici)1522-2632(200003)85:1<107::aid-iroh107>3.0.co;2-I

525 O'Connor N (1991) The effects of habitat complexity on the macroinvertebrates colonising wood  
526 substrates in a lowland stream. *Oecologia* 85:504-512

527 Oksanen J et al. (2013) vegan: community ecology package. R package version 2.0-7.  
528 <http://CRANR-projectorg/package=vegan>

529 Olden JD, Poff NL, Bestgen KR (2006) Life-history strategies predict fish invasions and  
530 extirpations in the Colorado River Basin. *Ecological Monographs* 76:25-40

531 Passy SI, Blanchet FG (2007) Algal communities in human-impacted stream ecosystems suffer  
532 beta-diversity decline. *Diversity and Distributions* 13:670-679

533 Piégay H, Landon N (1997) Promoting ecological management of riparian forests on the Drôme  
534 River, France. *Aquatic Conservation: Marine and Freshwater Ecosystems* 7:287-304

535 Pilotto F, Bertoncin A, Harvey GL, Wharton G, Pusch MT (2014) Diversification of stream  
536 invertebrate communities by large wood. *Freshwater Biology* 59:2571–2583

537 Pretty J, Harrison S, Shepherd D, Smith C, Hildrew A, Hey R (2003) River rehabilitation and fish  
538 populations: assessing the benefit of instream structures. *J Appl Ecol* 40:251-265

539 R Core Team (2013) R: A language and environment for statistical computing R Foundation for  
540 Statistical Computing, Vienna, Austria <http://wwwR-projectorg/>

541 Rosario-Martinez H (2013) phia: post-hoc interaction analysis. R package version 0.1–3.

542 Smock LA, Metzler GM, Gladden JE (1989) Role of debris dams in the structure and functioning  
543 of low-gradient headwater streams. *Ecology* 70:764-775

544 Stier AC, Geange SW, Hanson KM, Bolker BM (2013) Predator density and timing of arrival  
545 affect reef fish community assembly. *Ecology* 94:1057-1068

546 Townsend CR, Dolédec S, Norris R, Peacock K, Arbuttle C (2003) The influence of scale and  
547 geography on relationships between stream community composition and landscape  
548 variables: description and prediction. *Freshwater Biology* 48:768-785

549 Townsend CR, Hildrew AG (1994) Species traits in relation to a habitat templet for river  
550 systems. *Freshwater Biology* 31:265-275

551 Vaz PG, Dias S, Pinto P, Merten EC, Robinson CT, Warren DR, Rego FC (2014) Effects of burn  
552 status and conditioning on colonization of wood by stream macroinvertebrates.  
553 *Freshwater Science* 33:832-846

554 Wallace JB, Webster JR, Meyer JL (1995) Influence of log additions on physical and biotic  
555 characteristics of a mountain stream. *Canadian Journal of Fisheries and Aquatic  
556 Sciences* 52:2120-2137

557 Wanner SC, Pusch M (2001) Analysis of particulate organic matter retention by benthic  
558 structural elements in a lowland river (River Spree, Germany). *Archiv für Hydrobiologie*  
559 151:475-492

560 Whittaker RH (1972) Evolution and measurement of species diversity. *Taxon*:213-251

561 Wohl E (2013) Floodplains and wood. *Earth-Science Reviews* 123:194-212



563 **Table 1** Geographical position, hydromorphological characteristics and amount of wood at study sites. KOR= Korytnica, PLI=  
 564 Pliszka, PLO1= Płociczna reach 1, PLO2=Płociczna reach 2; PLO3= Płociczna reach 3; WR= wood rich site, WP = wood poor site. \*  
 565 indicates significant difference (P<0.05) between WR and WP sites.

	KOR		PLI		PLO1		PLO2		PLO3	
	WR	WP								
Latitude (North)	53°10'10"	53° 9'58"	52°14'58"	52°14'41"	53°10'29"	53°10'38"	53°07'21"	53°07'28"	53°04'38"	53°05'32"
Longitude (East)	15°55'20"	15°54'59"	14°44'18"	14°45'20"	16°01'14"	16°01'01"	15°59'18"	15°59'25"	15°59'37"	15°59'27"
Bankfull width (m)	15.8	10.9	9.6	7.9	12.1	15.4	16.4	16.6	12.3	14.1
Mean water depth (m)	0.48	0.53	0.58	0.83	0.50	0.56	0.38	0.54	0.70	0.38
Near-bankfull discharge (m <sup>3</sup> s <sup>-1</sup> )	2.0	2.1	1.6	1.8	1.4	1.5	2.0	3.2	3.4	2.9
Water level slope (x10 <sup>-3</sup> ) *	1.3	0.2	0.5	0.1	0.5	0.4	1.4	0.2	1.4	1.1
River-bed slope (x10 <sup>-3</sup> )	4.9	1.6	1.5	6.2	2.1	0.8	1.9	2.0	0.1	1.4
Number of wood logs (log jams)										
in 100m *	22 (0)	1 (0)	19 (0)	3 (0)	20 (5)	7 (2)	27 (3)	15 (1)	31 (2)	8 (0)
Number of wood logs and jams with blockage ratio > 0.10 in 100m *	10	1	9	2	9	5	14	10	15	4
Mean diameter of wood logs (m)	0.26	0.17	0.25	0.22	0.16	0.17	0.20	0.17	0.24	0.24
Mean length of wood logs (m)	6.39	7.76	5.35	6.02	6.47	7.51	7.07	8.80	7.30	5.24
Ratio logs volume/ bankfull channel area (m <sup>3</sup> ha <sup>-1</sup> ) *	65.2	1.7	36.0	5.8	94.4	22.9	53.7	32.7	165.8	9.9

566

567

568 **Table 2** Matrix of correlations among the studied hydromorphological variables (mean values and coefficients of variation, CV). The  
 569 Pearson's product-moment correlations are reported, with values  $\geq 0.30$  and  $\leq -0.30$  indicating strong correlation in bold.

		Mean flow velocity		Turbulence		Organic matter		Median grain size		Sorting index
		CV	mean	CV	mean	CV	mean	CV	mean	CV
<b>Mean flow velocity</b>	mean	<b>-0.31</b>								
<b>Turbulence</b>	CV	<b>0.54</b>	-0.22							
	mean	0.07	<b>0.83</b>	0.05						
<b>Organic matter</b>	CV	<b>0.78</b>	-0.21	<b>0.47</b>	0.07					
	mean	0.21	0.22	<b>0.49</b>	0.25	<b>0.36</b>				
<b>Median grain size</b>	CV	<b>0.39</b>	0.07	<b>0.55</b>	<b>0.42</b>	<b>0.32</b>	0.09			
	mean	-0.20	<b>0.83</b>	-0.24	<b>0.85</b>	-0.22	-0.04	0.24		
<b>Sorting index</b>	CV	0.24	<b>-0.44</b>	<b>0.63</b>	-0.14	<b>0.30</b>	0.12	<b>0.57</b>	-0.44	
	mean	<b>-0.36</b>	<b>0.75</b>	<b>-0.33</b>	<b>0.64</b>	<b>-0.41</b>	0.01	0.02	<b>0.84</b>	<b>-0.46</b>

570 **Table 3** Relationships among the values of the macroinvertebrate metrics and the mean and  
 571 coefficient of variation (CV) of the hydromorphological variables, as resulting from multivariate  
 572 linear mixed effect models (fixed factors: hydromorphological variables, random factor: reach).  
 573 The estimated coefficients and model statistics are reported. Only one hydromorphological  
 574 variable within each group of correlated variables (Table 2) was included in the analysis to avoid  
 575 collinearity. \*= P< 0.05, \*\*= P< 0.01.

	<b>Taxonomic richness</b>	<b>Shannon-Wiener diversity</b>
<b>Model estimates</b>		
Mean flow velocity (correlated with mean flow velocity CV, turbulence, organic matter CV, median grain size, sorting index CV, and sorting index)	-1.27	0.37
Organic matter (correlated with turbulence CV and organic matter CV)	-1.90	-0.08
Median grain size CV (correlated with mean flow velocity CV, turbulence CV, turbulence and sorting index CV)	14.00**	0.84**
<b>Likelihood ratio test</b>		
chi <sup>2</sup>	14.60**	10.85*

576

577

578 **Fig. 1** Map of the study areas

579 **Fig. 2** Mean ( $\pm$  SE; a, c, e, g and i) and coefficient of variation CV (b, d, f, h and j) of the  
580 hydromorphological variables (mean flow velocity, turbulence, sediment organic matter, median  
581 grain size and sediment sorting index) in the wood rich and wood poor sites (WR, WP).  
582 Sediment sorting index increases with increasing heterogeneity of sediment grain size.  $P < 0.05$   
583 indicates significant differences after likelihood ratio test

584 **Fig. 3** Coefficients of variation (mean  $\pm$  SE) of the hydromorphological variables in the sampling  
585 locations (WP, W1, W2 and W3). W1= surface of the wood logs, W2= sediment around the  
586 wood logs, W3= sediment outside the direct influence of wood logs within the wood sites, WP=  
587 sediment in the wood poor site. Sediment characteristics are not available for W1. Different  
588 letters (a and b) indicate significant differences ( $P < 0.05$ ) among substratum types after multiple  
589 comparison test

590 **Fig. 4** Non-metric multidimensional scaling run for the whole dataset, and for the five reach  
591 datasets: KOR= Korytnica, PLI= Pliszka, PLO1= Płociczna reach 1, PLO2= Płociczna reach 2;  
592 PLO3= Płociczna reach 3. W1= macroinvertebrate samples from the surface of the wood logs,  
593 W2= macroinvertebrate samples from the sediments around the wood logs, W3=  
594 macroinvertebrate samples from the sediment outside the direct influence of wood logs within  
595 the wood rich sites, WP= macroinvertebrate samples from the wood poor sites. Ellipses show  
596 the 95% confidence limits for each group of samples. Non-overlapping ellipses indicate  
597 differences in taxonomic composition among reaches (top-left), and sampling locations within  
598 each reach

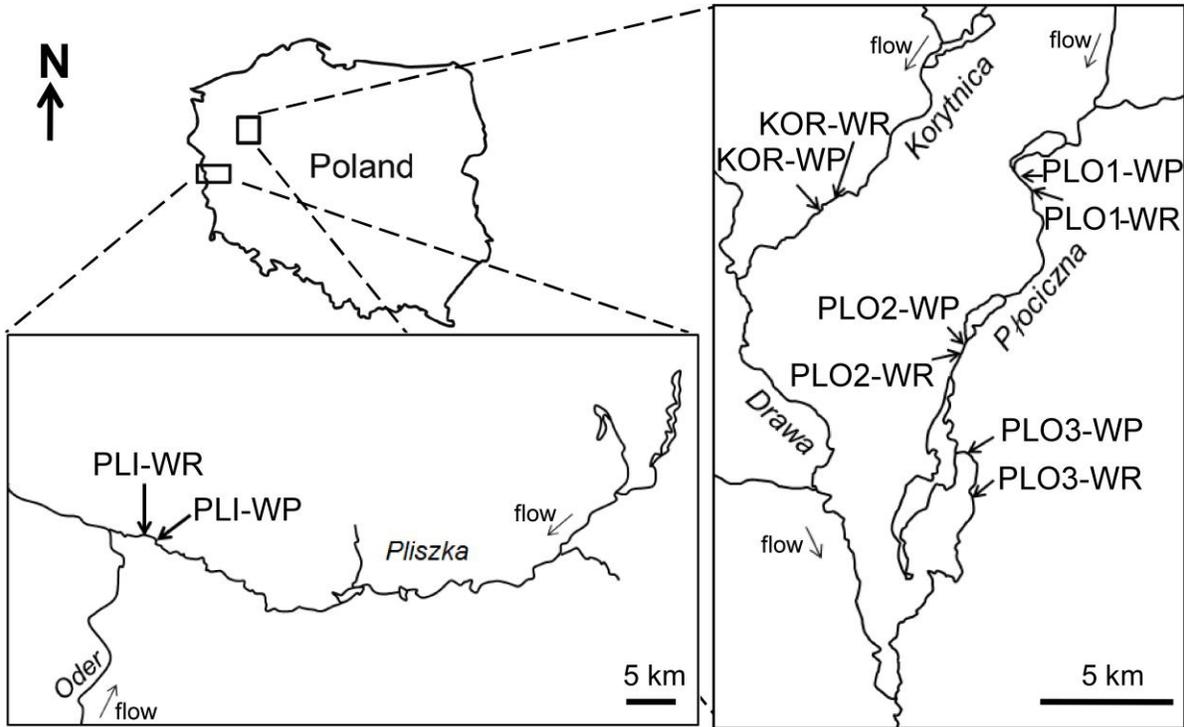
599 **Fig. 5** Beta diversity of the macroinvertebrate communities (a) in the wood poor and wood rich  
600 sites (WP, WR; mean  $\pm$  SE; likelihood ratio test:  $P < 0.01$ ) and (b) its correlation with the number

601 of LW pieces in the 100-m study reaches, regression analysis: Beta diversity = 0.07 Number of  
602 LW + 5.4,  $R^2 = 0.43$ ,  $F(1,8) = 5.97$ ,  $P = 0.04$

603 **Fig. 6** Macroinvertebrate metrics (mean  $\pm$  SE; a: abundance, b: rarefied taxonomic richness, c:  
604 Shannon-Wiener diversity index) in the substratum types (WP, W1, W2 and W3). W1= surface  
605 of the wood logs, W2= sediment around the wood logs, W3= sediment outside the direct  
606 influence of wood logs within the wood rich sites, WP= sediment in the wood poor sites.  
607 Different letters (a, b and c) indicate significant differences ( $P < 0.05$ ) after multiple comparison  
608 test

609

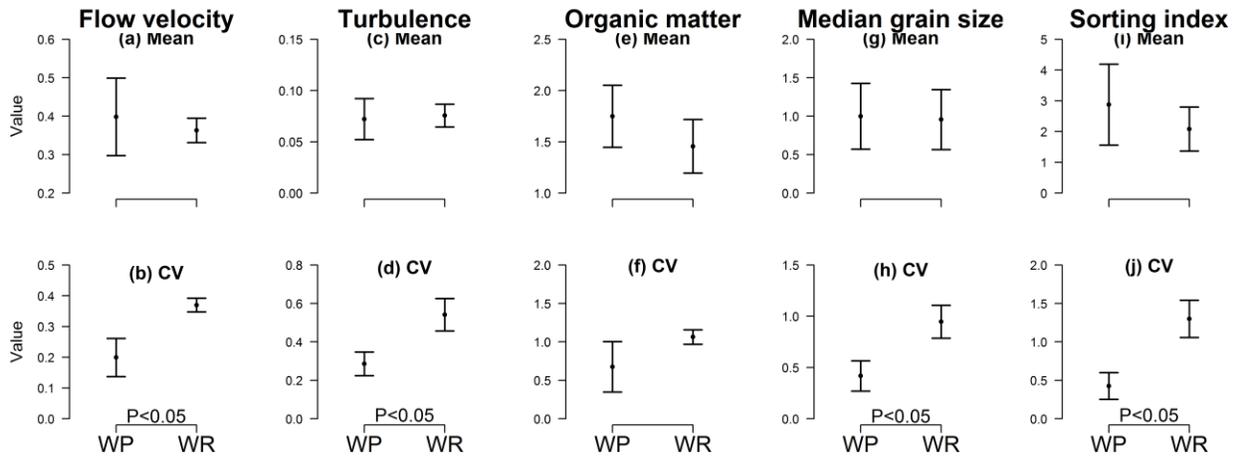
610 Figure 1



611

612

613 Figure 2

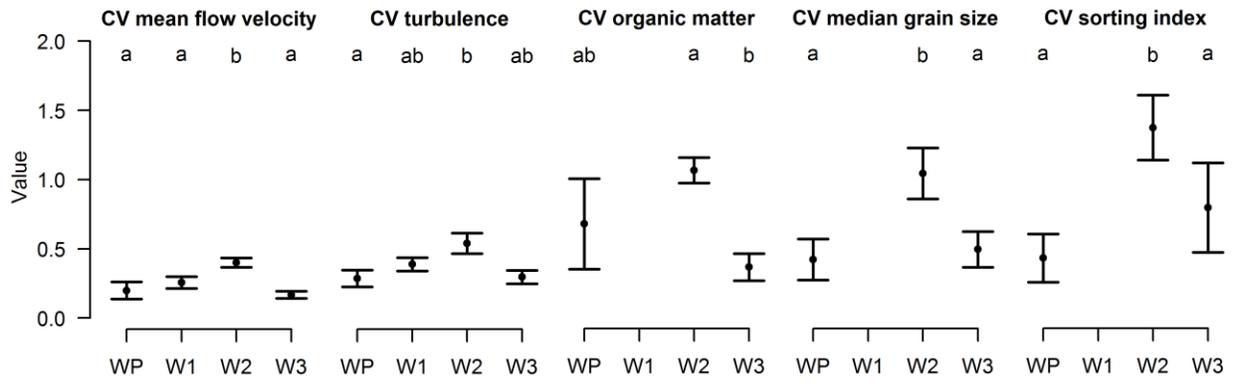


614

615

616

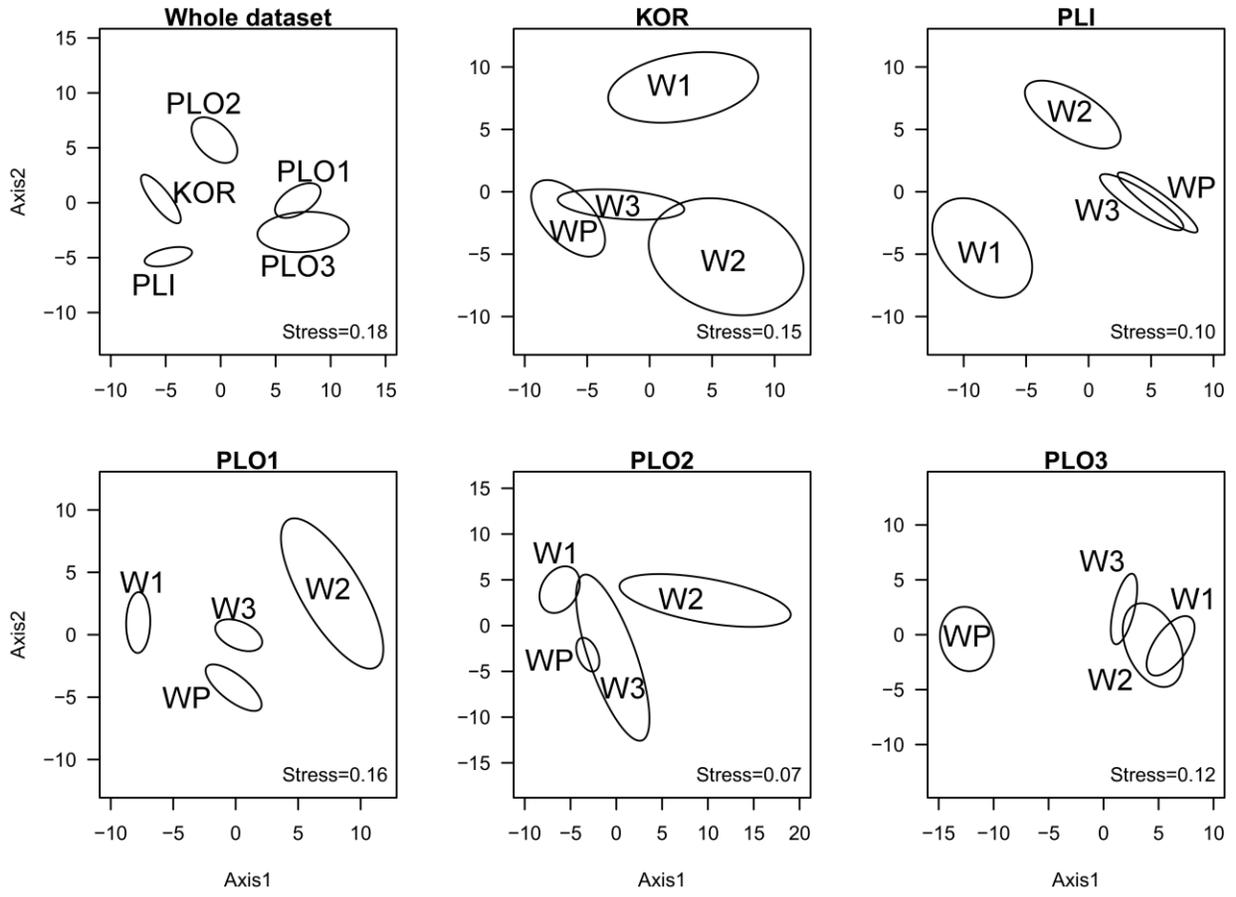
617 Figure 3



618

619

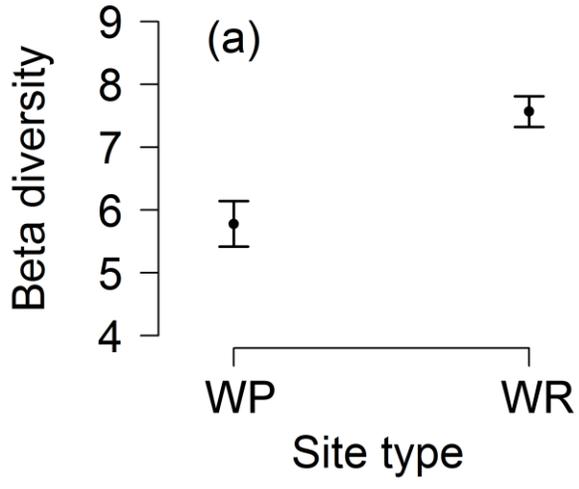
620 Figure 4



621

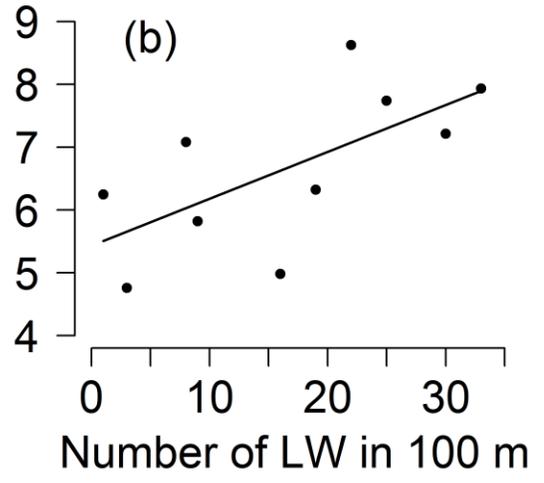
622

623 Figure 5

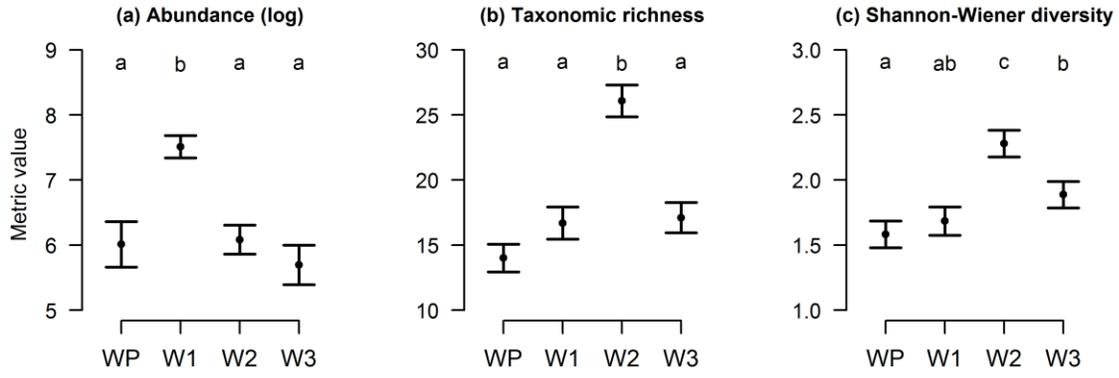


624

625



626 Figure 6



627