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

9

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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 m².
162 Macroinvertebrates sampled from the LW surface were dislodged by brushing a surface area of
163 0.26 m² 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.

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412

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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	WR	WP	WR	WP	WR	WP	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 ³ s ⁻¹)	2.0	2.1	1.6	1.8	1.4	1.5	2.0	3.2	3.4	2.9
Water level slope (x10 ⁻³) *	1.3	0.2	0.5	0.1	0.5	0.4	1.4	0.2	1.4	1.1
River-bed slope (x10 ⁻³)	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 ³ ha ⁻¹) *	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 ≥ 0.30 and ≤ -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
Mean flow velocity	mean	-0.31								
Turbulence	CV	0.54	-0.22							
	mean	0.07	0.83	0.05						
Organic matter	CV	0.78	-0.21	0.47	0.07					
	mean	0.21	0.22	0.49	0.25	0.36				
Median grain size	CV	0.39	0.07	0.55	0.42	0.32	0.09			
	mean	-0.20	0.83	-0.24	0.85	-0.22	-0.04	0.24		
Sorting index	CV	0.24	-0.44	0.63	-0.14	0.30	0.12	0.57	-0.44	
	mean	-0.36	0.75	-0.33	0.64	-0.41	0.01	0.02	0.84	-0.46

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.

	Taxonomic richness	Shannon-Wiener diversity
Model estimates		
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**
Likelihood ratio test		
chi ²	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

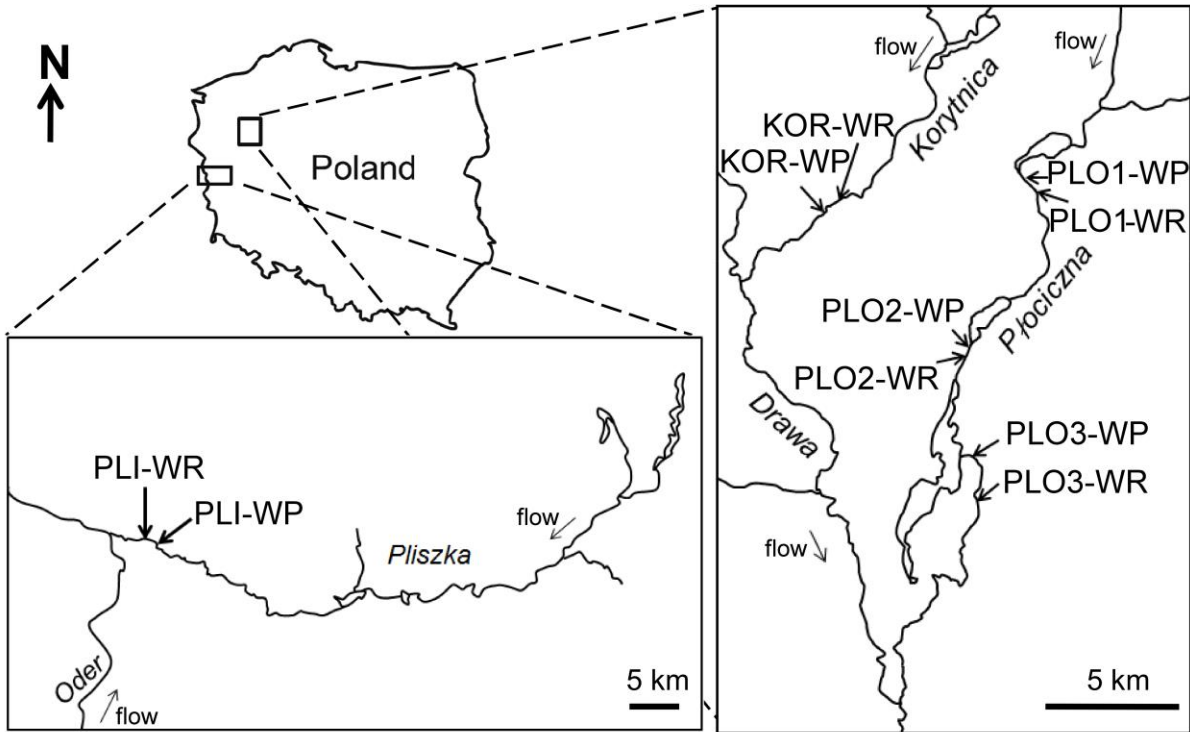
599 **Fig. 5** Beta diversity of the macroinvertebrate communities (a) in the wood poor and wood rich
600 sites (WP, WR; mean \pm SE; likelihood ratio test: $P < 0.01$) and (b) its correlation with the number

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

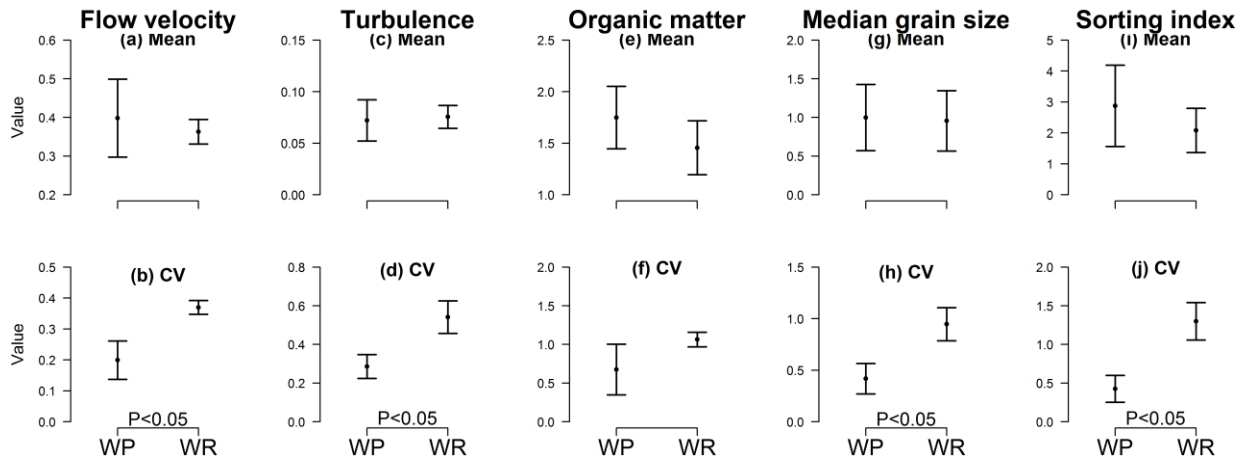
610 Figure 1



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613 Figure 2

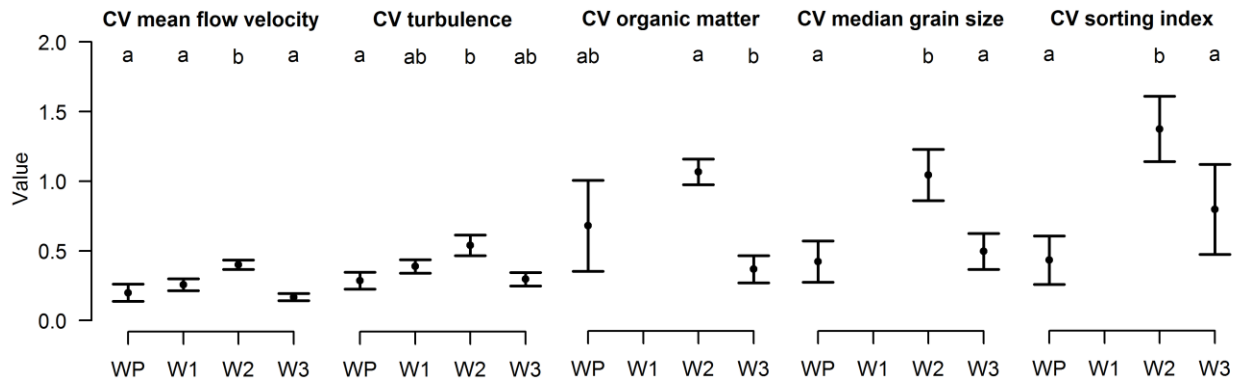


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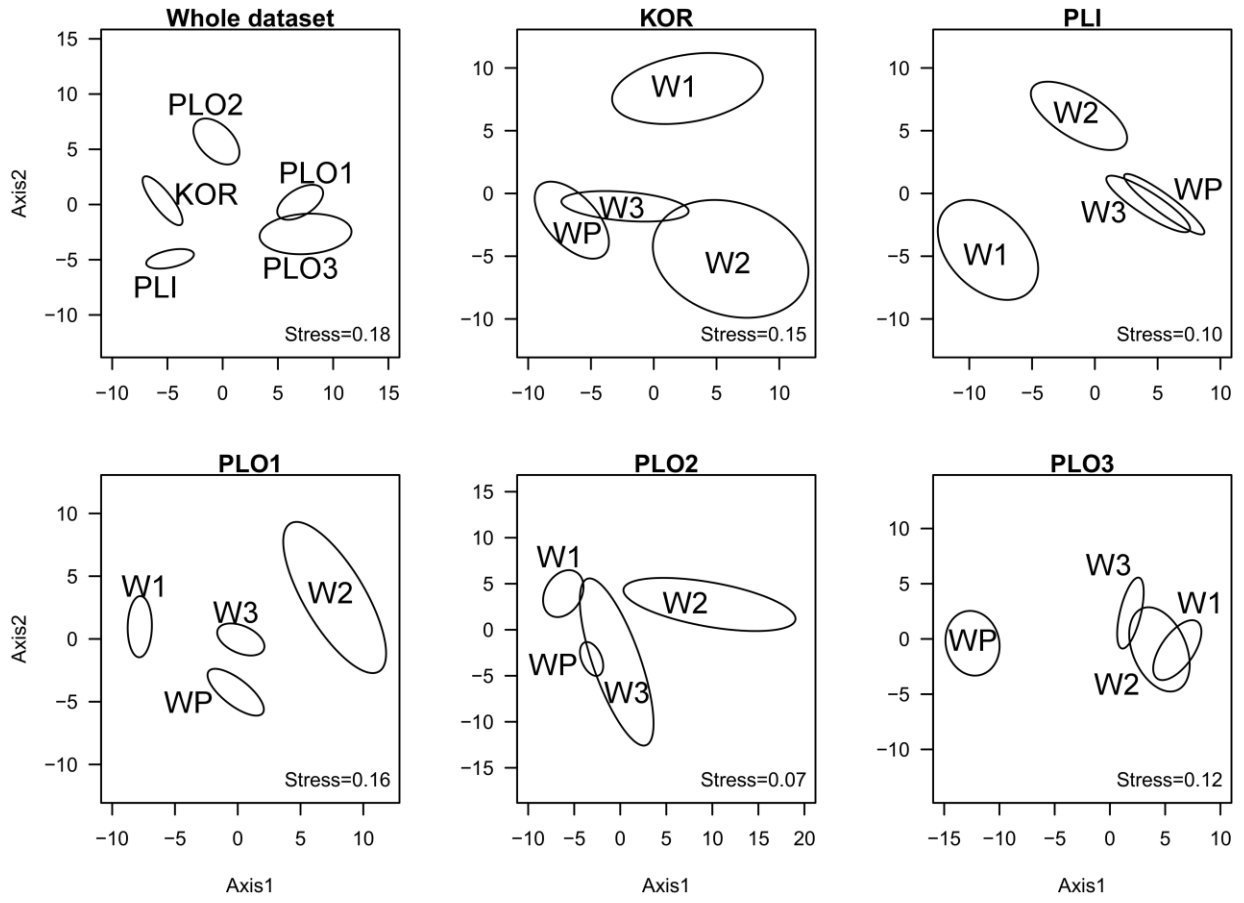
617 Figure 3



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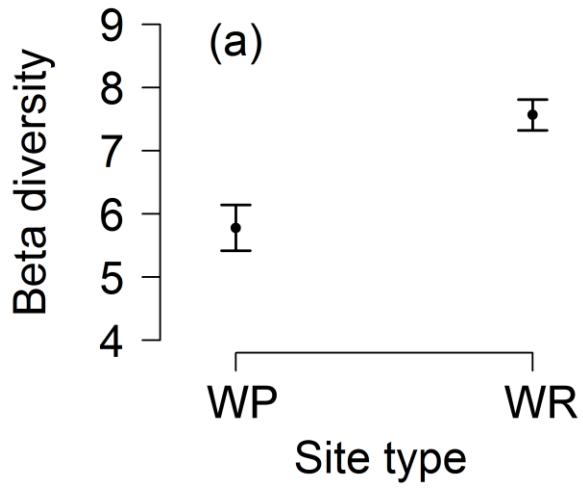
620 Figure 4



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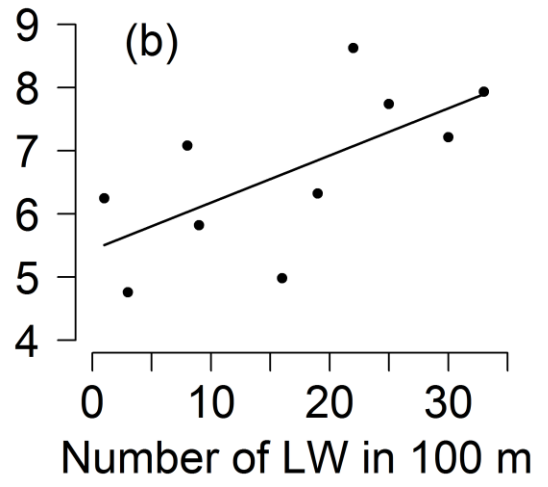
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623 Figure 5

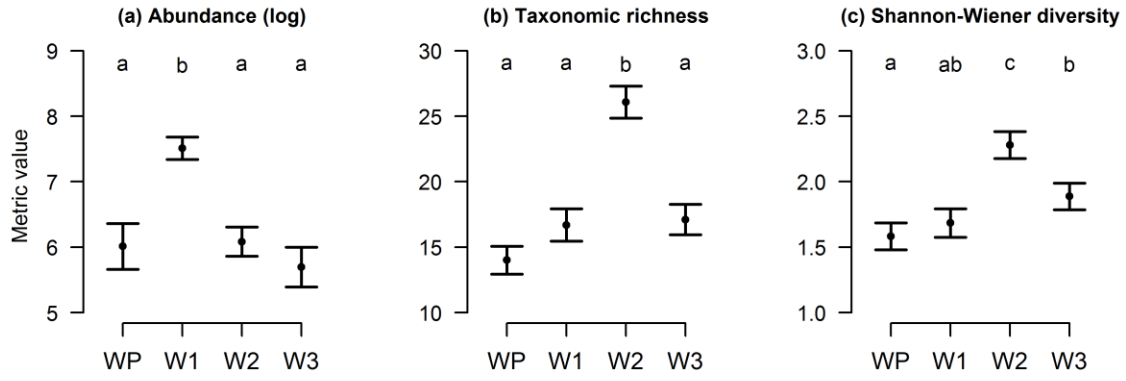


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626 Figure 6



627