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Functional traits of hyporheic and benthic invertebrates reveal importance of wood-driven geomorphological processes in rivers

Chiara Magliozzi[a], Philippe Usseglio-Polatera[b], Albin Meyer[b], Robert C. Grabowski[a*]

[a]*Water Science Institute, School of Water, Energy and Environment, Cranfield University, Cranfield, Bedfordshire, MK43 0AL*

[b]*Laboratoire Interdisciplinaire des Environnements Continentaux (LIEC, CNRS UMR 7360), Université de Lorraine, Metz, F-57070*

[*]Corresponding author

Email address: r.c.grabowski@cranfield.ac.uk (Robert Grabowski)

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Abstract

1. Large wood (LW) is a natural element of river environments and an integral component of many river restoration schemes to promote biodiversity. It is an important habitat in itself, but it also induces a wide range of hydraulic, hydrological, geomorphological, and chemical conditions that influence the ecological community. However, the effects of hydro-geomorphological processes induced by LW on local benthic and hyporheic invertebrates have not been well characterized.
2. A functional approach was applied to invertebrate data collected in a field survey at sites with LW and without LW (control), to investigate the response of hyporheic and benthic invertebrates' trait profiles in response to local LW-induced processes.
3. We hypothesized LW sites to be associated with different trait modalities than control sites in relation to wood-induced processes and conditions (i.e. hyporheic exchange flow, oxygen availability, temporal stability, organic matter, denitrification, hydraulic conductivity). Multivariate analyses and Partial Least Squares (PLS) Path Modelling were used to detect the differences in trait profiles between LW and control sites and to study the variation of traits as a function of hydrological, sedimentological, physical and chemical variables.
4. Biological (i.e. aquatic stages, reproduction), physiological (i.e. dispersal, feeding habits) and behavioural (i.e. substrate preferences) trait utilization by the hyporheic meiofauna differed between LW and control sites. At LW sites, the hyporheic meiofaunal assemblage was significantly associated with aquatic active dispersal, aquatic eggs and hard substrate preferences. This trait category selection was linked to changes in physical-sedimentological processes at LW sites when compared to control sites. Macrofaunal benthic and hyporheic

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functional traits did not differ significantly between wood and control sites, suggesting similar functioning of these assemblages at the surface-subsurface interface.

5. This study found that LW affects invertebrate traits by altering fluvial processes to produce, locally, a mosaic of habitats. Hyporheic meiofauna trait responses to LW-processes have suggested (i) the crucial role of LW in supporting river benthic zone functioning, and thus (ii) a possible benefit to river restoration by enhancing functional interactions among different ecological niches.

Keywords: large wood, river ecology, macrofauna, meiofauna, hyporheic zone, river restoration.

1. Introduction

Rivers are dynamic environments that vary markedly over short distances and timescales. Consequently, organisms living in them are subjected to large differences and fluctuations in physico-chemical conditions, caused by variable water flow velocities, the movement of sediment, availability of food resources, and nutrient input. The adaptations that a species has to this environment appear in functional traits, the ensemble of morphological, physiological, phenological and behavioural attributes that reflect organismal performance, which determines the community fitness (McGill, Enquist, Weiher, & Westoby, 2006).

Trait-based approaches have been advocated as a mechanistic alternative to traditional taxonomic descriptors and applied from the organism-level to global biodiversity patterns to investigate changes and losses of ecosystem function (Gagic et al., 2015; Mondy & Usseglio-Polatera, 2013; Statzner & Bêche, 2010). They have been widely adopted to study benthic invertebrates, i.e. invertebrates living on or near the surface of the riverbed (Usseglio-Polatera, Richoux, Bournaud, & Tachet, 2001), but less commonly for the invertebrate community that lives deeper in the sediment, i.e. the hyporheic community (Descloux, Datry, & Usseglio-Polatera, 2014; Dunscombe, Robertson, Peralta-Maraver, & Shaw, 2018). However, a functional approach could help to investigate the hydrological, sedimentological, chemical and physical processes occurring in the hyporheic zone and their effects on local river invertebrate communities (HZ, Orghidan 1959; Boulton, 2007).

The HZ is an ecotone below and surrounding the river bed, crucial to hydrological and ecological connectivity in rivers (Ward, 1989). It is a dynamic environment with a distinctive fauna

71 (hyporheos) and a subsurface water flow, named hyporheic exchange flow (HEF). Studies
72 coupling taxonomy-based ecological and hydrological data on geomorphic structures (i.e. riffles
73 and large wood) and HEF have provided evidence for the likely mechanisms by which HEF affects
74 river ecology by controlling dissolved oxygen concentration and fine sediment deposition
75 (Mathers, Millett, Robertson, Stubbington, & Wood, 2014), nutrients (Krause, Tecklenburg,
76 Munz, & Naden, 2013), metabolic processes (Krause et al., 2011), and water temperature
77 (Menichino & Hester, 2014). However, like the river at large, the physico-chemical conditions of
78 the HZ vary spatially and temporally over small scales. There are a number of factors (i.e. geology,
79 topography) that drive changes in the hyporheic physical environment in terms of flow, nutrient
80 retention and temperature (Magliozzi, Grabowski, Packman, & Krause, 2018), meaning that
81 organisms are likely to be exposed to spatially variable and temporally varying physical and
82 chemical conditions and would possess functional traits enabling them to cope with selective
83 environmental processes (e.g. denitrification, flow and sediment disturbance).

84 Large wood (LW; length > 1 m; diameter > 10 cm; Wohl et al., 2010), for example, is a natural
85 hydrostatic-driver of HEF (Krause et al., 2014), enhancing HEF by increasing riverbed roughness
86 and creating hydraulic gradients (Lautz, Siegel, & Bauer, 2006; Mutz, Kalbus, & Meinecke, 2007).
87 LW induces multiple hydrological (i.e. flow deflection and scour), geomorphological (i.e.
88 sediment entrainment and transport) and chemical (i.e. organic matter deposition, nutrient
89 retention) processes that are key to river ecology (i.e. habitat for invertebrates) (Table 1) (Benke
90 & Wallace, 2003) and to river restoration (Grabowski et al. 2019; Larson, Booth, & Morley, 2001).
91 Reaches with LW are usually more geomorphologically and hydraulically heterogeneous in space
92 and time than sites without LW (Gurnell, 2013; Gurnell & Grabowski, 2016; Krause et al., 2014).

93 They are usually characterized by steep head gradients and result in pronounced upwelling and
94 downwelling zones upstream and downstream LW, exhibit enhanced oxygen availability, deeper
95 hyporheic flows and longer residence times than sites without LW (Krause et al., 2014; Sawyer,
96 Cardenas, & Buttles, 2011) (Table 1). LW and the geomorphological changes it induces in the
97 channel, facilitate the deposition of organic material (i.e. litter) and sediment material (fine sand
98 and coarse gravel) and promotes nutrient processes (i.e. nitrate accumulation or denitrification)
99 (Blaen et al., 2018; Shelley, Klaar, Krause, & Trimmer, 2017). To this end, ecological research
100 has shown that LW itself and the surrounding LW habitat have an effect on the benthic
101 macroinvertebrate taxonomic structure, in terms of greater abundance, diversity and biomass than
102 in absence of wood (Benke & Wallace, 2003; Thompson et al., 2018). However, very little
103 information is available to investigate the existing connections between LW-induced processes
104 and benthic and hyporheic functional traits (i.e. exception of feeding groups, Flores et al., 2017;
105 Pilotto, Harvey, Wharton, & Pusch, 2016) for understanding the action of processes in the HZ.
106 LW-induced hydro-geomorphological and chemical processes could favor the occurrence of
107 specific behavioral, biological, morphological and physiological functional traits in river
108 invertebrates (Table 2, Section S1).
109 The aim of this study is to investigate hyporheic and benthic invertebrates' functional traits in
110 response to local LW-induced processes (Table 1). Functional trait expression is expected to differ
111 in LW and control sites, taking into account LW-conditions and driving processes: i.e. increasing
112 vertical hyporheic exchange, sediment hydraulic conductivity, oxygen and organic matter
113 availability, and lower temporal stability (i.e. lower variability of environmental parameters in
114 control than LW) and denitrification (Table 1). Specifically, we hypothesized that: (i) the trait

115 profiles of both macrofaunal and meiofaunal assemblages would differ between LW and control
116 sites; (ii) specific behavioural, biological, morphological and physiological trait-modalities would
117 differ in LW and control sites, as summarized in Table 2 (see also Section S1 in Supporting
118 Information), for both macrofaunal and meiofaunal assemblages; and (iii) trait variation in LW
119 and control sites could be explained by hydrological, physical, sedimentological and chemical
120 environmental variables responding to LW-driven processes (Table 1).

2 Material and Methods

2.1 Study area and design

The study was conducted in the Hammer stream, West Sussex, UK (catchment area 24.6 km^2, Shelley, Klaar, Krause, & Trimmer, 2017). It is a woodland stream where LW occurs naturally and drives local hyporheic exchange flows (Shelley, Klaar, Krause, & Trimmer, 2017; section S2). Following geomorphological surveys, four reaches with a single in-channel LW were identified in both gravel and sand sections. The studied LWs were natural, active or complete jams, with a significant water afflux (Gippel, O'Neill, Finlayson, & Schnatz, 1996), and were stable during the study period. LW sites were located in different reaches, separated by a distance of >150 m (>20 times the channel width) apart to avoid spatial dependencies in the studied local LW effects (Fig. 1). Control sites were chosen in each reach upstream of the LW, in the gravel and sand sections. Sites were i) bare areas of the riverbed without woody material (wood > 3 cm in diameter or accumulation of woody fragments of smaller dimensions), and ii) located upstream of the LW by a distance of *ca.* 10 times the channel width. At this distance upstream, control sites were not affected by LW-induced hydrological and geomorphological processes (afflux caused by blockage) as confirmed by cross-sections, total station, and velocity measurements. Both LW and control sites were selected on relatively straight areas of the channel to avoid confounding effects of channel geomorphology on potential HEF.

2.2 Sampling protocol

Each sampling site was sampled in three occasions, in November 2016, May 2017 and August 2017. Three replicates of hyporheic and benthic samples were taken within 1 m distance: i)

142 upstream, downstream and laterally to the LW between areas of maximum fine deposition and the
143 pool to avoid erosional and sedimentation zones and ii) in control sites (Fig. 1). Hyporheic samples
144 were collected using colonization pots (Crossman, Bradley, Milner, & Pinay, 2013) placed
145 between 5 cm and 25 cm deep in the sediment, while benthic samples were taken using a Surber
146 sampler (0.05 m^2, mesh size = 500 µm) from the sediment surface. Pots were left *in-situ* for six
147 weeks to allow sufficient time for invertebrate colonization (Coleman & Hynes, 1970). Hyporheic
148 and benthic samples were collected on the same day. Immediately after collection the samples
149 were stored in plastic jars with 90 % ethanol and returned to the laboratory, where they were rinsed
150 with water and filtered over a set of sieves. For the colonization samples, a 500 µm sieve was used
151 to retain hyporheic macrofaunal individuals; the rest of the sample was filtered through a 45 µm
152 sieve for meiofauna, preserved in 100% ethanol, and stained with Rose Bengal. These meiofaunal
153 samples were sorted within five days of collection (Stead et al., 2003).
154 The Surber samples were sieved with a 500 µm sieve and benthic meiofauna was not sampled
155 given the coarser mesh size of the Surber net. All macrofaunal samples were preserved in 80%
156 ethanol. Preserved samples were sorted and identified to the lowest taxonomic level possible,
157 genus or species, under a stereomicroscope or an Olympus Bx50 (Olympus Optical) microscope.
158 Some taxa (i.e. Plecoptera, Trichoptera) were damaged in collection, processing, or storage,
159 possibly due to the high amount of fine sediment in the samples or physical abrasion during the
160 sieving process, and thus identified only to family level. Meiofaunal taxa such as Nematoda,
161 Oligochaeta, Cyclopoida, Acari, Anomopoda, Cladocera, Ctenopoda, Ostracoda were identified to
162 order or class level (Dobson, Pawley, Fletcher, & Powell, 2012; Tachet, Richoux, Bournaud, &
163 Usseglio-Polatera, 2010).

164

165 **2.3 Environmental data**

166 Environmental variables were measured in triplicate at each sampling site on every sampling
167 occasion (Table 3). Temperature (T; °C), pH, dissolved oxygen (DO; %), electric conductivity
168 (EC; µS cm^{-1}) were measured with a multiparameter probe (Hannah HI98196). Velocity
169 measurements were taken using a Flow Tracker Acoustic Doppler Velocimeter (SonTek) upstream
170 and downstream LW and used with the channel width and water depth to calculate discharge
171 (velocity-area method). A total station (TS06 Leica) and georeferential GPS (GS08plus, Leica
172 Viva) were used to survey the location of LW pieces. The bankfull width, wetted width, and the
173 orientation angle of each LW relative to the channel, alongside the length and diameter of each
174 large wood were calculated using ArcGIS 10.1 (Table S5). Sediment cores (diameter 5 cm, depth
175 25 cm) were collected for sediment grain size analysis (Blott & Pye, 2001) and organic content
176 estimation by loss of ignition (incinerated at 550°C for 5 h) (Heiri, Lotter, & Lemcke, 2001).
177 Median grain size, sorting coefficient, skewness and cumulative percentile values (i.e. D_{10}, D_{90})
178 were calculated from the dry weight of the different sediment fractions using the geometric Falk
179 and Ward (1957) method (GRADISTAT program; Blott & Pye, 2011). Wooden stakes of untreated
180 *Pinus pinaster* were inserted into the sediment with colonization pots and used to estimate vertical
181 patterns of interstitial oxygenation (Marmonier et al., 2004). Finally, sediment pore water at 25 cm
182 depth was collected using minipiezometers (Lewandowski, Putschew, Schwesig, Neumann, &
183 Radke, 2011) for measurements of nitrate, nitrite, ammonium and phosphate, discarding 1.5 to 2
184 times the inner volume of the minipiezometer tube before filtering the sample. The samples were
185 filtered into 5 mL sample vials using syringe filters (28 mm, 0.2 µm); a new filter was used for

each sample. After filtration, the samples were acidified (2 M HCl, pH *ca.* 2). Filtration and acidification were conducted within 30 minutes after the sample collection (Lewandowski, Putschew, Schwesig, Neumann, & Radke, 2011).

2.4 Trait description

The functional traits of both benthic invertebrate macrofauna (individuals retained by 500 µm sieve) in the benthic zone, and hyporheic invertebrate macrofauna (retained by 500 µm) and meiofauna (retained by 45 µm) in the hyporheic zone were investigated using a multivariate approach (Section 2.5.1). The traits used in this study consisted of behavioural, biological, morphological and physiological features identified in the literature as reflecting organismal performance and adaptations to environmental pressures (Table S1) (McGill, Enquist, Weiher, & Westoby, 2006). Each trait was described by 2 to 9 modalities (Table S1). The taxa of the benthic (71 taxa) and hyporheic (72 macrofaunal and 59 meiofaunal taxa) zones were coded, at genus or family level, according to their affinity to each category of a trait using a fuzzy coding approach (Chevenet, Dolédec, & Chessel, 1994). Trait tables from Tachet, Richoux, Bournaud, & Usseglio-Polatera (2010) and Descloux, Datry, & Usseglio-Polatera (2014) were used for coding macrofauna and meiofauna functional traits. Taxa such as Nematoda, Oligochaeta, Cyclopoida, Acari, Anomopoda, Copepoda, Ctenopoda and Ostracoda (52.72% overall abundance in hyporheic meiofauna samples, Table S4) were described as mean trait profiles of their potential families in the corresponding biogeographic area (Descloux, Datry, & Usseglio-Polatera 2014). The affinities of taxa for the modalities of a trait were converted into relative abundance distributions so that the sum of the trait modality affinity scores for an individual trait and a given taxon equals one.

208

209 ## 2.5 Data analysis

210 ### 2.5.1 Biological data

211 Hyporheic macrofauna, hyporheic meiofauna, and benthic macrofauna were analysed separately
212 because a preliminary correspondence analysis conducted on faunal abundances showed that there
213 were significant differences between sampling methods (colonisation pots *vs* Surbers) and between
214 ecological zones (benthic *vs* hyporheic). Abundances of all identified taxa were merged by reach,
215 treatment (wood *vs* control) and sampling campaign (period). The mean trait profile of sample
216 assemblages was obtained by weighting the individual trait profiles of corresponding taxa by their
217 log-transformed (x+1) abundances in the sample. Rare taxa (< 5 individuals over the whole
218 sampling design) were removed to avoid extremes in the analysis (Cao, Larsen, & Thorne, 2001;
219 Gauch, 1982). Then, within reach x campaign analysis (Within Class Analysis, WCA) (*wca*
220 function of the R package ade4; Dray, Dufour, & Thioulouse, 2017) was performed to assess
221 whether trait composition in i) hyporheic meiofauna and macrofauna and ii) benthic assemblages
222 was identical in wood and control sites. The WCA performs a particular case of principal
223 component analysis (PCA) with respect to the variable of interest (i.e. wood vs control in this
224 study) (Benzécri, 1983). It is an effective method to eliminate the effects of confounding variables
225 (i.e. reach and campaign date in this study) in the analysed dataset (Castella, Richardot-Coulet,
226 Roux, & Richoux, 1991; Dolédec & Chessel, 1989; Dole-Olivier, , Marmonier, & Beffy, 1997;
227 Van Looy, Floury, Ferréol, Prieto-Montes, & Souchon, 2016). Subsequently, the conditional
228 inference tree approach (CIT) (*ctree* function R package party; Hothorn, Hornik, Strobl, & Zeileis,
229 2017) was applied to distinguish groups of sites with significantly different combinations of trait

230 profiles, based on their coordinates along the successive factorial axes in WCA. CIT is a recursive,
231 non-parametric, partitioning method that allows estimating regression relationships between
232 variables (Hothorn, Hornik, & Zeileis, 2006; Section 5 in Supporting Information). In our study,
233 CIT was tested using Bonferroni permutation test (9999 permutations, $\alpha = 0.01$). Finally, taxon
234 trait-profiles among wood and control sites ($n = 48$) were compared using the non-parametric
235 Wilcoxon signed-rank test. Bonferroni corrections (p-value < 0.001) were applied for selecting
236 trait modalities with significant differences between LW vs control sites.
237
238 **2.5.2 Environment-trait relationships**
239 The relationship between environmental data and taxon traits was investigated by applying the
240 Partial Least Squares (PLS) Path Modelling (Wold, 1982) using the *plspm* function of the R
241 package plspm (Sanchez, Trinchera, & Russolillo, 2017). PLS was applied to link hydrological,
242 physical, sedimentological and chemical variables to the variations of invertebrate trait modalities
243 (Fig. S1). PLS is a statistical method that quantifies the relationships between observed manifest
244 (indicators or items) and latent variables (indirectly measured - LVs) in a system of multiple linear
245 regressions (Vinzi, Trinchera, & Amato, 2010). In the last few years, this approach has been
246 increasingly applied to a wide range of disciplines including econometrics, social sciences and
247 ecology (Bizzi, Surridge, & Lerner, 2013; Villeneuve, Piffady, Valette, Souchon, & Usseglio-
248 Polatera, et al., 2018). First, the PLS approach includes the estimation of the latent variables as
249 linear combinations of their respective blocks of manifest variables (Tenenhaus, Vinzi, Chatelin,
250 & Lauro, 2005). This first step is an iterative process in which the latent variables are calculated
251 as the weighed sum of their manifest variables till convergence of the weights is reached

252 (Tenenhaus, Vinzi, Chatelin, & Lauro, 2005). The calculations are performed on the outer model,
253 which links the manifest variables to the corresponding latent variables (Vinzi, Trinchera, &
254 Amato, 2010). At the end of the first step, the method calculates the path coefficients between
255 latent variables by ordinary least square regressions on the inner model, which accounts for the
256 relationships between latent variables (Tenenhaus, Vinzi, Chatelin, & Lauro, 2005). The last step
257 of the PLS analysis involves the computation of the loadings by simple correlations in the outer
258 model. In this study, the LVs (hydrological, physical, chemical and sedimentological variables)
259 were standardized and expressed as formative indicators (manifest variables that form the latent
260 variables) while the latent trait-based variables (i.e. "trait modalities") were measured in a
261 reflective way (manifest variables are considered as being caused by the latent variables) (Fig. S1)
262 (Tenenhaus, Vinzi, Chatelin, & Lauro, 2005). PLS analysis was executed on a sub-set of
263 significant trait modalities (Section 2.5.1). The quality of the model was assessed using R^2
264 determination coefficients (Croutsche, 2002) and bootstrap validation (number of resamples:
265 1000) was used to validate the parameter estimates. All the coefficients presented in this work
266 were significant at 95% confidence interval (Götz, Liehr-Gobbers, & Krafft, 2010). Finally, the
267 latent variables were evaluated with respect to trait modalities by looking at the effects (direct and
268 total) of each construct on the trait variation (Sanchez, 2013). The contributions in percentage of
269 direct and total (direct + indirect) effects were calculated in wood and control conditions, for each
270 significant trait modality.
271

272 **3. Results**

273 **3.1 Hyporheic and benthic trait profiles between wood and control sites**

The functional trait profiles of the hyporheic meiofauna differed between wood and control sites, as confirmed by the WCA (F1 = 12.8%, F2 = 10.0% of explained variance; Fig. 2a) and CIT approach (Fig. 2b). The ordination plots of single trait modalities showed that many trait modalities were differently expressed in wood and control sites (Fig. S2), but these differences were statistically significant (Wilcoxon's test, Bonferroni adjusted p-value < 0.001) for only six of them: i) aquatic active dispersal, ii) aquatic eggs, iii) aquatic nymphs, and preferences for iv) twigs and roots, v) sand and vi) hard substrates (i.e. flags, boulders, cobbles and pebbles; Fbcp in Fig. 3 and Table S2). Control sites were characterized by trait specific substrate preferences (i.e. twigs and roots and sand) and some aquatic stages (i.e. nymph) (Fig. 3). The functional trait profiles of both hyporheic and benthic macrofauna did not differ between wood and control sites (F1 = 11.0% and 9.1%, F2 = 10.3% and 8.8% of explained variance for hyporheic and benthic macrofauna, respectively; Figs. S3, S4), and no trait modalities exhibited statistically significant differences between control and LW sites (Wilcoxon's test, Bonferroni adjusted p-value <0.001). Macrofaunal assemblages were characterized by trait modalities that were not significantly different (p-value ≥ 0.05, Table S3, Fig. S5) in LW and control sites.

3.2 Environmental-trait relationships

PLS analysis was applied to the six significant meiofaunal traits. The PLS inner model showed moderate prediction capacity of meiofaunal trait modality utilization by LVs (R^2: 47 % in wood and 55 % in control) (Fig. 4). Sedimentological and chemical variables were well explained in both control and wood sites (55% < R^2 values < 61%, 40% < R^2 values < 62%, Fig. 4). Physical variables were weakly to moderately explained by the model with R^2 values varying from 14% to

296 35%. Sedimentological and physical LVs had the greatest effects on trait modalities (25%-44%
297 and 22%-43%, respectively) despite the response patterns differing between sites (Fig. 5a). Trait
298 modalities at wood sites were affected mostly by physical variables (43%) with important effects
299 for sedimentological and hydrological LVs (respectively 25% and 20%; Fig. 5a). In control sites,
300 the direct effects of sedimentological and chemical LVs explained most of the trait variation (44
301 % and 31%), whereas hydrological variables had only a minor effect (3%). When looking at the
302 total effects, the contribution of LVs to trait variation changed, due to indirect effects (Fig. 5a). A
303 higher effect of hydrology (+16% to +29%) and a decrease in the effect of sedimentological
304 variables (-7% to -18%) were shown in both control and wood sites (Fig. 5a). Finally,
305 sedimentological and physical LVs exhibited higher impact (50-80%) on substrate preferences (i.e.
306 sand and twigs/roots) and aquatic stages (i.e. egg, nymph) variation, in control sites (Fig. 5b). In
307 wood sites, the relative contribution of the LVs to the trait variation was more similar among
308 modalities (Fig. 5b).
309
310
311
312 **4. Discussion**
313 This study investigated multiple functional traits of meiofaunal and macrofaunal invertebrates to
314 study their response to LW-induced processes in rivers. Wood and control site hyporheic
315 assemblages exhibited different profiles of traits, with general patterns emerging in terms of
316 responses to wood and wood-induced processes. In this section we discuss wood-related traits in

317 the hyporheic and benthic zones (Section 4.1) and the major environmental predictors of trait
318 modality variation (Section 4.2).
319
320 **4.1 Wood-related traits of the meiofauna and macrofauna in LW habitats**
321 Our study found that meiofaunal functional trait profiles differed in wood and control sites,
322 suggesting functional relationships between traits and environmental forces in the HZ, and
323 upholding our first hypothesis that LW would affect the trait profiles of the hyporheic meiofauna.
324 Significant differences between LW and control sites were recorded for individual biological,
325 physiological and behavioural meiofaunal trait modalities, reflecting organismal adaptations in the
326 HZ. These specific trait modalities partly support our second hypothesis that multiple functional
327 traits and trait-modalities would be affected by LW.
328 Significant trait modalities in LW included aquatic active dispersal, aquatic eggs and hard substrate
329 preferences (Fig. 3). These trait modalities relate strongly to temporal instability, flow disturbance
330 and sediment hydraulic conductivity (Bilton, Freeland, & Okamura, 2001; Descloux, Datry, &
331 Marmonier, 2014; Larsen, Pace, & Ormerod, 2011). Active aquatic dispersal was recorded as
332 significant behavioural feature, counter to our expectations (Table 2), for meiofaunal assemblages
333 in LW, suggesting that hyporheic hydrology might not play a strong role in determining where
334 meiofaunal species occur both spatially and temporally (see also Section 4.2). Active aquatic
335 dispersal entails self-generating organism movements often associated with flightless aquatic
336 invertebrates that display an active behaviour triggered by changing and unstable environmental
337 conditions (Stubbington et al., 2017; Tonkin et al., 2017). However as the cues that trigger aquatic
338 and hyporheic insects to disperse are still an active area of research (Bilton, Freeland, & Okamura,

2001), active aquatic dispersal in a heterogeneous and temporally varying environment may be advantageous. This is supported by the presence of more meiofaunal organisms with aquatic eggs in LW sites. Previous studies have already observed invertebrates dispersing in variable habitats by differential egg hatching regimes (e.g. differences in temperature leading to rapid hatching or germination when dormancy is broken) (Brock, Nielsen, Shiel, Green, & Langley, 2003; Zwick, 1996). Wood meiofaunal assemblages also showed substrate preferences for cobbles and pebbles (Fbcp in Fig. 3), possibly due to the more heterogeneous habitat conditions and presence of patches of much coarser sediment around LW (Table 3) (Pilotto, Bertoncin, Harvey, Wharton, & Pusch, 2014).

Functional traits of hyporheic and benthic macrofaunal assemblages did not differ significantly across sites, thereby our first and second hypotheses that trait profiles of macrofaunal and meiofaunal assemblages differ between LW and control sites (Table 2) were not upheld. This result might suggest that the dominant macrofaunal species (hyporheic and benthic) exhibited similar combination of traits (in coherence with the biomass-ratio hypothesis of Grime (1998)) and, at the scale of both benthic and hyporheic zones, were driven by similar functional relationships to environmental processes and forces. Therefore assemblages could have similar functioning and functional divergence (i.e. low niche differentiation, lack or few specialist species), in the study site (Villéger, Mason, & Mouillot, 2008). Results might also suggest a relatively stable taxonomic diversity for macrofaunal assemblages at wood *vs* control scale, and a decrease in functional space with possibly the loss of specialist species with narrow niches between benthic and hyporheic zones (Villéger, Mason, & Mouillot, 2008). Finally, the implemented sampling design did not allow to efficiently depict the variability of functional traits at LW scale, with respect - for example

361 - to erosional and deposition areas or flow paths. This might be another reason why functional
362 differences in macroinvertebrate assemblages between LW and control sites were not detected in
363 the results.
364
365 **4.2 Environmental drivers of hyporheic meiofauna trait variation**
366 Trait variation in LW and control sites was mainly explained by sedimentological and physical
367 variables, although their relative contributions differed between sites. In this study, wood-related
368 physical LVs, described by pH, conductivity, dissolved oxygen and, temperature, were the most
369 important in explaining the overall variation of taxon traits (Fig. 4), implying that these traits
370 exhibit strong relationships to local LW environmental conditions when viewed at local scale. The
371 relative contribution of LVs to wood-trait variation is similar among modalities, underscoring a
372 similar importance of all studied environmental drivers at LW sites
373 Control sites exhibited higher homogeneity in sedimentological variables, suggesting an increase
374 in temporal stability partly due to the absence of wood-induced physical processes (Table 1).
375 Sedimentological variables explained more than the 25% of hyporheic meiofaunal trait variation
376 for all significant modalities (Fig. 5b). They explained much more of the variation of traits in
377 control sites than LW sites, although significant trait modalities did not reflect a strong
378 sedimentological impact (Fig. 5b). This finding is supported by other studies that have observed
379 weaker effects of sediment size on hyporheic than epibenthic trait profiles (Descloux, Datry, &
380 Marmonier, 2013; Descloux, Datry, & Usseglio-Polatera, 2014). Chemical and physical LVs
381 explained 50% of the hyporheic meiofaunal trait variation for aquatic stages, dispersal and
382 substrate preferences (Fig. 5b). Chemical LVs explained much more of the variation of traits for

383 hyporheic meiofaunal assemblages in control than wood sites (Fig. 4). This result is consistent
384 with a recently published study on the , sandy section of the Hammer stream that shows LW sites
385 were characterized by short hyporheic flow-paths inhibiting local nitrate reduction (Shelley,
386 Klaar, Krause, & Trimmer, 2017). The responses of benthic invertebrate assemblages to nutrients
387 are well documented, but those of the hyporheic meiofaunal assemblages are far less known
388 (Marmonier et al., 2012). Certain groups of invertebrates have proved to be good indicators of
389 moderately eutrophic rivers. Many caddisflies belonging to the Glossosomatidae, Psychomyiidae
390 and Hydropsychidae families for example, have been found intolerant or withstanding only a low-
391 moderate range of nitrate concentrations (Nijboer, 2004; Pacioglu, Moldovan, Shaw, & Robertson,
392 2016). In our study, Psychomyiidae and *Hydropsyche* spp. instars were observed in hyporheic
393 samples of control sites exhibiting higher concentrations of ammonium and phosphates than LW
394 sites, thus supporting previous finding by providing a global indication of the chemical conditions
395 in the HZ. Besides, other taxonomic groups (e.g. Chironomidae, Oligochaeta, Nematoda and
396 Amphipoda), widespread among wood and control sites, have demonstrated high tolerance to
397 nutrients in previous studies (Pacioglu, Moldovan, Shaw, & Robertson, 2016).
398 Finally, our findings confirmed the mechanistic impact of LW on hyporheic meiofauna trait-
399 selection as the result of a combination of LW-driving processes. The effects are more pronounced
400 on meiofaunal than macrofaunal assemblages highlighting the importance of LW in triggering
401 physical and sedimentological impacts on faunal communities of lowland systems. LW impacts
402 on hyporheic meiofauna are potentially important given that many benthic invertebrate species
403 rely closely on the HZ in their life cycle (Robertson & Wood, 2010). Our findings provide further

404 evidence of the mechanisms responsible for local invertebrate assemblage structure in LW,
405 reflecting adaptations to dominant regional and local environmental stresses.

406 **5. Conclusions**

407 The functional trait approach offers a mechanistic alternative to traditional taxonomy-based
408 approach for studying functional relationships between invertebrates and wood-habitats. The
409 hyporheic zone and river connectivity are interrelated structural and functional properties of
410 heterogeneous environments (Ward, 1989). Large wood plays a key role in promoting vertical
411 hydrological connectivity (Lautz, Siegel, & Bauer, 2006) and, as evidenced in this study,
412 ecological functions. Both hydrological connectivity and ecological functions are crucial to river
413 functionality (e.g. "biodiversity maintenance"; Liebold & Norberg, 2004) and, as a result, to river
414 management (Kondolf et al., 2006).

415 Our results suggest that a high variability of local abiotic conditions in LW sites promotes species
416 traits related to temporal instability and low refugia availability (Townsend & Hildrew, 1994). As
417 result, LW would likely promote the sustainability of r-strategist species and in turn contribute to
418 maintain the global richness/biodiversity of local invertebrate assemblages by facilitating long-
419 term temporal coexistence between r- and K-strategists at reach scale. r-strategists would exhibit
420 an adaptive advantage for living in more unstable habitats, which function as refugia (following
421 the Intermediate Disturbance Hypothesis (IDH) theory; Connell, 1978). Perhaps, sediment
422 disturbance around the LW, a process not measured in this study, is an important, and possibly
423 under-appreciated, environmental control of hyporheic and benthic invertebrate assemblages and
424 should be considered in the future.

425 Finally, in the context of river restoration, large wood has been gradually integrated into
426 management strategies as a means of improving the biodiversity and conservation value of lowland
427 rivers (Grabowski et al, 2019; Larson, Booth, & Morley, 2001). Yet, such approaches have not
428 always given due attention to the ecological effects of physical processes potentially promoting
429 ecological responses. Our study confirmed the significant effect of large wood on biological,
430 physiological and behavioural traits of the hyporheic meiofauna, suggesting a crucial role in
431 supporting river benthic zone functioning, and thus a possible benefit to river restoration by
432 enhancing functional interactions among different ecological niches. Such data are essential within
433 a process-driven and strategic framework to effective restoration planning (Wohl, Lane, & Wilcox,
434 2015) and has heuristic value for generating further hypotheses about invertebrate functional
435 responses to LW.

Authors' Contributions

C. Magliozzi designed, collected the data, analysed the dataset and wrote the manuscript. P. Usseglio-Polatera coded the species traits, supervised the analysis and contributed to the discussions and editing throughout the manuscript. A. Meyer assisted in the analysis, interpretation and editing of the manuscript. R. Grabowski provided guidance on structure, advice and editing of the manuscript. All authors approved the manuscript and have no competing interests to declare.

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Data Accessibility

The ecological data collected for this project is available on the Cranfield University data repository (Grabowski & Magliozzi, 2019). The data includes (i) abundances of invertebrates and traits and (ii) environmental conditions for the wood and control sites on the River Hammer.

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Tables and Figures

Table 1: Hypothesized effects of wood to promote (+) or inhibit (-) key processes and conditions.

Processes & Conditions	Wood	Control	References
1. Hyporheic exchange flow	+	-	Krause et al., 2014
2. Oxygen availability	+	-	Kaller & Kelso, 2007
3. Temporal stability	-	+	Gurnell, 2013
4. Organic matter	+	-	Blaen et al., 2018
5. Denitrification	-	+	Klaar, Krause, & Trimmer, 2017
6. Hydraulic conductivity	+	-	Mutz, Kalbus, & Meinecke, 2007

685 Table 2: Trait modalities predicted to be significantly enhanced by the habitat conditions in
686 the site type (Large wood or Control). Numbers in bold indicate processes (see Table 1 for
687 codes) that are hypothesized to have a strong influence in driving the predicted trait
688 modality.

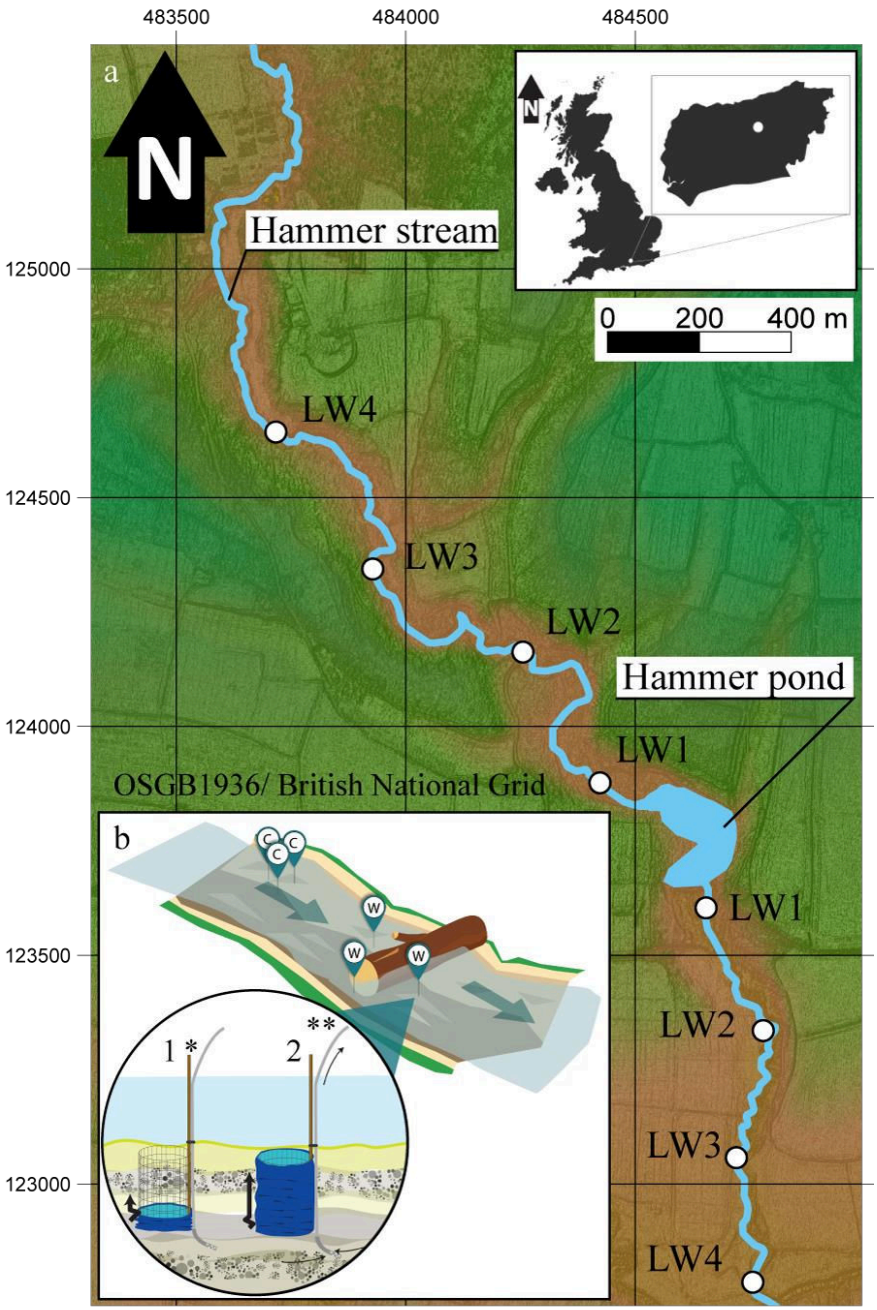
	Traits	Large wood	Control	Processes
Behavioural	Locomotion	attached	interstitial, burrowers, crawlers	**1**, 6
	Substrate preferences	organic detritus, litter, roots	mud, silt	**1**, 4, 6
	Velocity preferences	fast/medium	slow, null	1
	Dispersal	aquatic passive	aquatic active	1
Biological	Aquatic stages	larva, egg	adult, nymph	1, **3**, 2
	Nb cycles/yr	> 1	≤ 1	1, **3**
	Reproduction techniques & resistance forms	high fecundity, resistance stages	low fecundity, none or few resistance stages	3
	Size	small		**3**
Morphological	Body form	flattened, streamlined	cylindrical, spherical	1, **6**
	Body flexibility	low/intermediate	high	1, **6**
Physiological	Feeding habits	filter feeders, shredders	deposit feeders	1, **4**, 5
	Food	microphytes, dead plants (≥ 1 mm)	detritus (< 1 mm) microorganisms	4, 5
	Respiration	spiracle, gills	tegument	2

689

690 Table 3: Mean hydrological, physical, sedimentological and chemical variables (± *sd*) recorded at wood and control sites in the gravel
691 and control reaches of the Hammer stream between October 2016 and August 2017. Mean Water Depth (MW), Discharge (Q),
692 Conductivity (EC), Dissolved Oxygen (DO), Temperature (T), Sediment Grain Size: D10, D50, D90, Sorting Coefficient (SO),
693 Skewness (SK), Sediment Organic Matter (OM), Oxygen Depth (OD), Ammonium NH_4^+ , Nitrate NO_3^- , Nitrite NO_2^-, Phosphate (SRP).
694 Detection limit of 0.1 mg N L^{-1} for Nitrate, 0.01mg N L^{-1} for Nitrite, and 0.03 mg N L^{-1} for Ammonium.

	Control-Gravel	**Wood-Gravel**	**Control-Sand**	**Wood-Sand**
Hydrological variables				
MW (m)	0.20 ± 0.14	0.28 ± 0.09	0.26 ± 0.09	0.31 ± 0.11
Q (m^3s^{-1})	0.07 ± 0.03	0.09 ± 0.05	0.05 ± 0.02	0.06 ± 0.02
Physical variables				
EC (µS cm^{-1})	249.71 ± 19.10	243.29 ±19.26	237.68 ± 19.62	223.58 ± 30.40
DO (%)	89.50 ± 19.96	97.66 ± 34.75	91.40 ± 28.17	91.54 ± 40.09
pH	7.23 ± 0.39	7.02 ± 0.23	6.85 ± 0.60	6.67 ± 0.58
T (°C)	13.07 ± 3.43	12.48 ± 3.11	12.26 ± 2.68	11.78 ± 3.11
Sedimentological variables				
D10 (cm)	0.91 ± 1.11	4.06 ± 5.09	0.04 ± 0.01	0.16 ± 0.02
D90 (cm)	10.68 ± 2.13	31.15 ± 10.16	3.04 ± 8.93	3.14 ± 6.30
D50 (cm)	4.34 ± 2.14	14.09 ± 7.83	0.14 ± 0.15	0.39 ± 0.14
SO (cm)	0.001 ± 0.001	0.003 ± 0.001	0.001 ± 0.000	0.002 ± 0.000
SK (cm)	-0.0001 ± 0.0001	-0.0002 ± 0.0002	-0.0001 ± 0.0001	-0.0001± 0.0001
OM (%)	0.25 ± 0.16	1.10 ± 0.82	2.81 ± 2.89	12.70 ± 7.27
OD (cm)	5.87 ± 4.68	6.25 ± 2.77	4.40 ± 2.71	5.44 ± 3.13
Chemical variables				
$NH4^+$ (mg N L^{-1})	0.13 ± 0.12	0.09 ± 0.06	1.89 ± 1.28	0.54 ± 0.41
$NO3^-$ (mg N L^{-1})	7.04 ± 3.47	7.24 ± 3.10	0.69 ± 0.43	0.67 ± 0.42
$NO2^-$ (mg N L^{-1})	0.02 ± 0.02	0.02 ± 0.01	0.01 ± 0.01	0.01 ± 0.01
SRP (mg PO4 L^{-1})	0.06 ± 0.04	0.05 ± 0.04	0.58 ± 0.42	0.26 ± 0.30

695



696 Figure 1: The study was conducted in the Hammer stream, West Sussex, UK. Invertebrates were sampled
697 at 4 sites in sand (upstream Hammer pond) and gravel (downstream Hammer pond) sections (LW 1-4), with
698 three replicates taken in control and around the LW (b) using colonization pots and Surber net. Inset (left):
699 an illustration of sampling around the LW and of the colonization pot equipped with wood stakes (*) and
700 minipiezometer (**). The pot is cylindrical steel cages (mesh size 1 cm2), a tarpaulin bag with reinforced

701 top and cable which is placed around the base of each pot before inserting the pot in the excavated hole.
702 b1) pot is positioned into the river bed. b2) during the extraction, cable is pulled vertically, driving the wire-
703 reinforced tops to the surface and extending the tarpaulin bags.

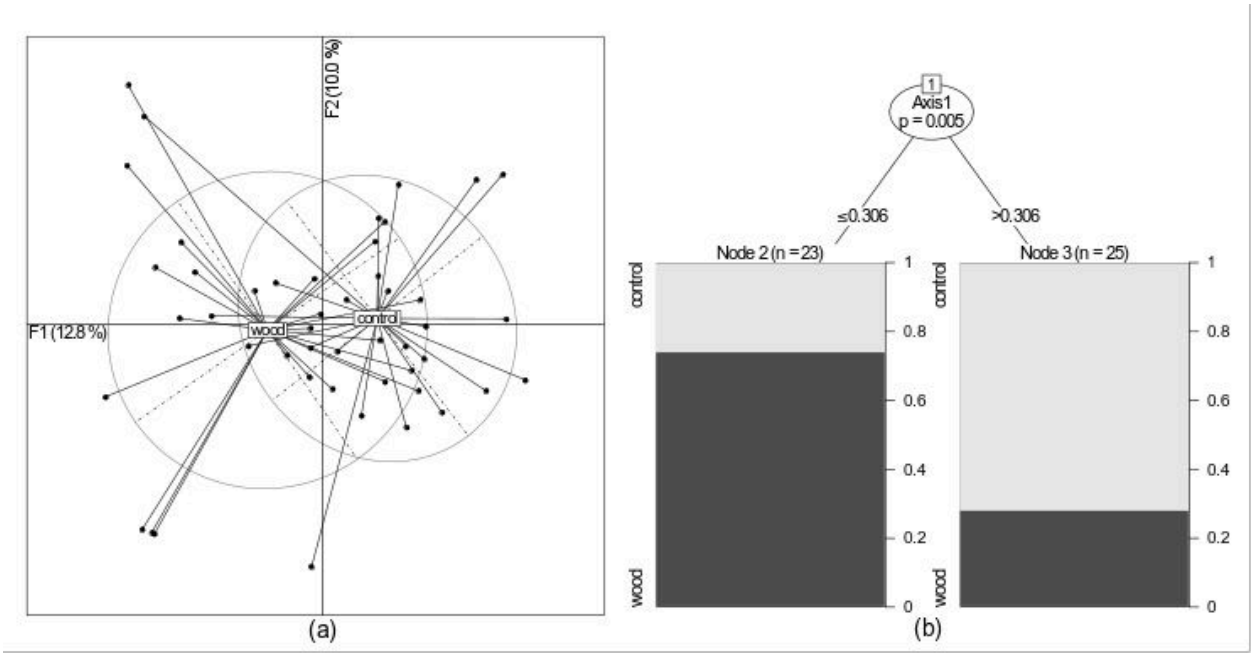


Figure 2: Hyporheic meiofauna trait profiles among wood and control sites. (a) First factorial plane of WCA giving the locations of the 48 samples gathered by wood and control sites. Labels are located at the weighted average (i.e. the centre of the star) of corresponding samples (solid circles). The ellipses of inertia are defined as the 95% confidence interval around the centroids, and the percentage of the total variance explained is indicated for each axis. (b) CIT (9999 Bonferroni permutations; $\alpha = 0.01$) testing the significance of differences in wood and control site locations on the first WCA factorial plane (response variables: coordinates of samples along F1 and F2; n = number of samples).

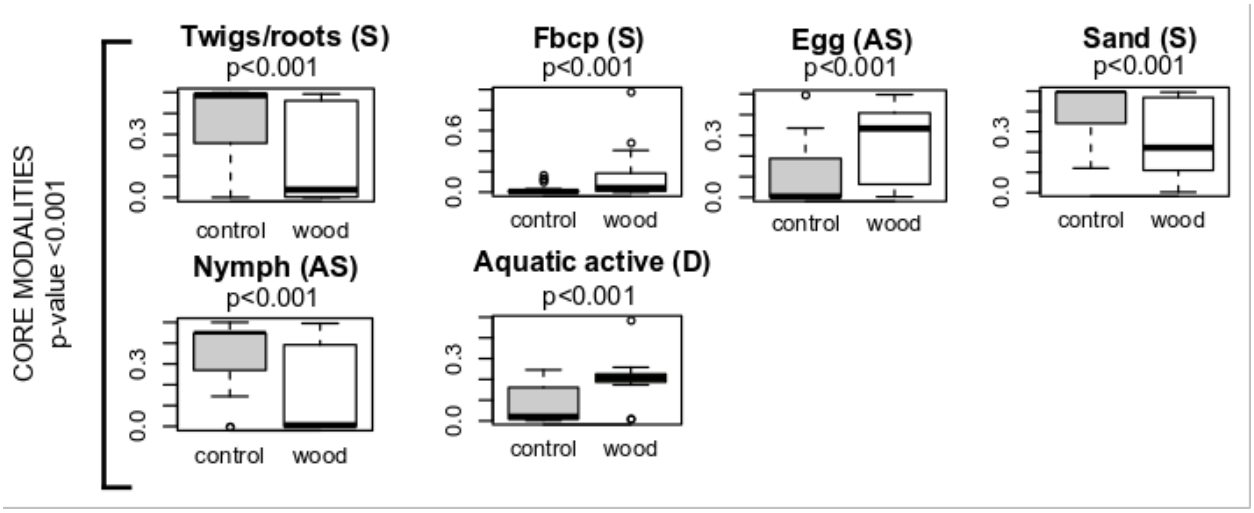
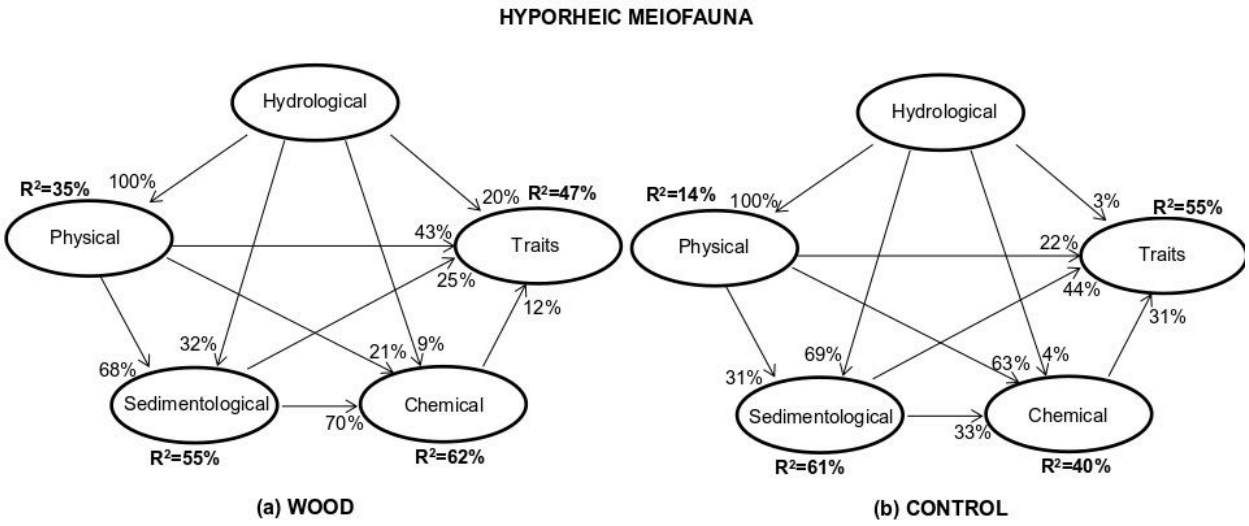


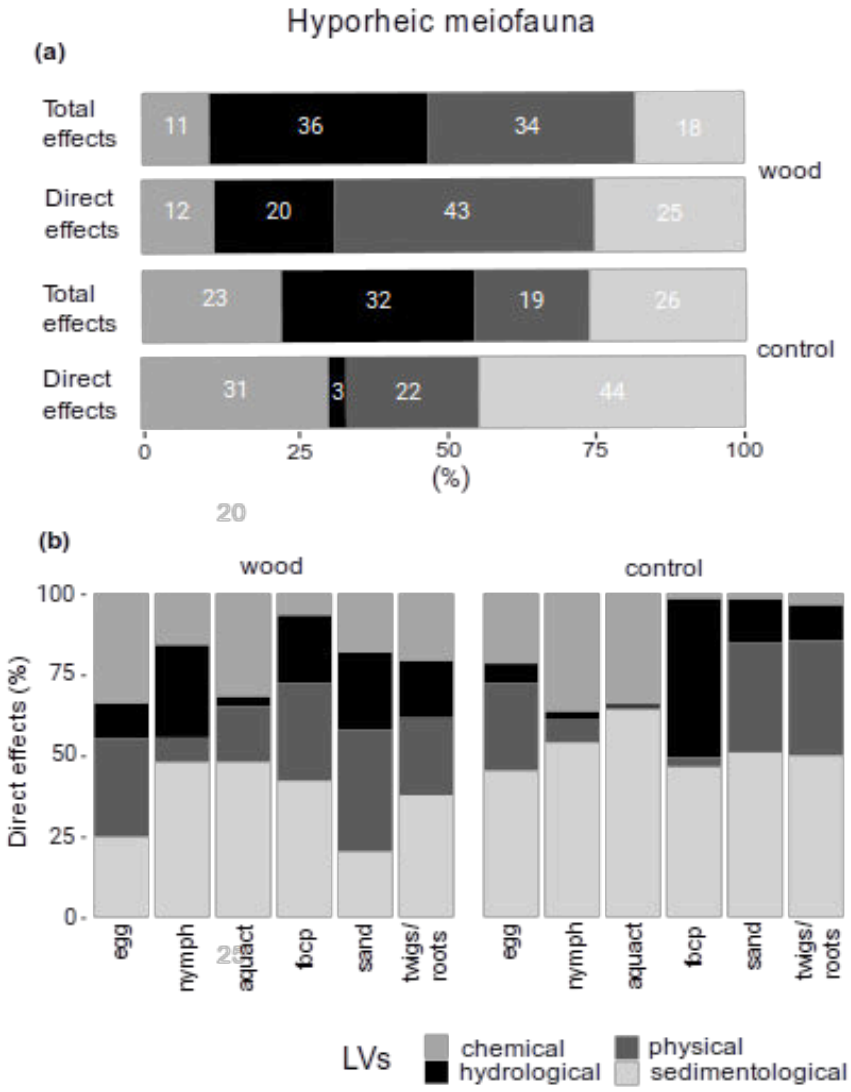
Figure 3: Relative frequency of trait modalities (see Table S1 for abbreviations) for hyporheic meiofauna in control *vs* LW sites. Only trait modalities exhibiting significant differences (Wilcoxon test, adjusted p-values < 0.001) between control and LW sites are presented. Traits are indicated in bracket: AS = Aquatic stages, D = Dispersal, S = Substrate preferences.



721

722 Figure 4: PLS path models for the hyporheic meiofauna in (a) wood and (b) control sites, showing
723 latent variables connected by direct effects. R^2 is reported for each internal model and for the
724 contributions of latent variables to the variation in trait modalities (in bold).

725



726 Figure 5: (a) Relative contribution (%) of latent variables (LVs) to the variation of the trait
727 modalities of hyporheic meiofauna significantly differing between wood and control sites
728 (Wilcoxon test, adjusted p-value < 0.001), based on direct and total (= direct + indirect) effects.
729 (b) Direct effects of LVs on the trait modalities of hyporheic meiofauna significantly differing
730 between wood and control sites (Wilcoxon test, adjusted p-value < 0.001).



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Functional traits of hyporheic and benthic invertebrates reveal importance of wood-driven geomorphological processes to rivers

Magliozzi, Chiara; Usseglio-Polatera, Philippe; Meyer, Albin; Grabowski, Robert C.

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