Functional Ecology, Volume 33, Issue 9, September 2019, pp. 1758-1770
DOI: 10.1111/1365-2435.13381

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)

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

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

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

They are usually characterized by steep head gradients and result in pronounced upwelling and downwelling zones upstream and downstream LW, exhibit enhanced oxygen availability, deeper hyporheic flows and longer residence times than sites without LW (Krause et al., 2014; Sawyer, Cardenas, & Buttles, 2011) (Table 1). LW and the geomorphological changes it induces in the channel, facilitate the deposition of organic material (i.e. litter) and sediment material (fine sand and coarse gravel) and promotes nutrient processes (i.e. nitrate accumulation or denitrification) (Blaen et al., 2018; Shelley, Klaar, Krause, & Trimmer, 2017). To this end, ecological research has shown that LW itself and the surrounding LW habitat have an effect on the benthic macroinvertebrate taxonomic structure, in terms of greater abundance, diversity and biomass than in absence of wood (Benke & Wallace, 2003; Thompson et al., 2018). However, very little information is available to investigate the existing connections between LW-induced processes and benthic and hyporheic functional traits (i.e. exception of feeding groups, Flores et al., 2017; Pilotto, Harvey, Wharton, & Pusch, 2016) for understanding the action of processes in the HZ. LW-induced hydro-geomorphological and chemical processes could favor the occurrence of specific behavioral, biological, morphological and physiological functional traits in river invertebrates (Table 2, Section S1).

The aim of this study is to investigate hyporheic and benthic invertebrates' functional traits in response to local LW-induced processes (Table 1). Functional trait expression is expected to differ in LW and control sites, taking into account LW-conditions and driving processes: i.e. increasing vertical hyporheic exchange, sediment hydraulic conductivity, oxygen and organic matter availability, and lower temporal stability (i.e. lower variability of environmental parameters in control than LW) and denitrification (Table 1). Specifically, we hypothesized that: (i) the trait profiles of both macrofaunal and meiofaunal assemblages would differ between LW and control sites; (ii) specific behavioural, biological, morphological and physiological trait-modalities would differ in LW and control sites, as summarized in Table 2 (see also Section S1 in Supporting Information), for both macrofaunal and meiofaunal assemblages; and (iii) trait variation in LW and control sites could be explained by hydrological, physical, sedimentological and chemical 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) upstream, downstream and laterally to the LW between areas of maximum fine deposition and the pool to avoid erosional and sedimentation zones and ii) in control sites (Fig. 1). Hyporheic samples were collected using colonization pots (Crossman, Bradley, Milner, & Pinay, 2013) placed between 5 cm and 25 cm deep in the sediment, while benthic samples were taken using a Surber sampler (0.05 m^2, mesh size = 500 µm) from the sediment surface. Pots were left *in-situ* for six weeks to allow sufficient time for invertebrate colonization (Coleman & Hynes, 1970). Hyporheic and benthic samples were collected on the same day. Immediately after collection the samples were stored in plastic jars with 90 % ethanol and returned to the laboratory, where they were rinsed with water and filtered over a set of sieves. For the colonization samples, a 500 µm sieve was used to retain hyporheic macrofaunal individuals; the rest of the sample was filtered through a 45 µm sieve for meiofauna, preserved in 100% ethanol, and stained with Rose Bengal. These meiofaunal samples were sorted within five days of collection (Stead et al., 2003).

The Surber samples were sieved with a 500 µm sieve and benthic meiofauna was not sampled given the coarser mesh size of the Surber net. All macrofaunal samples were preserved in 80% ethanol. Preserved samples were sorted and identified to the lowest taxonomic level possible, genus or species, under a stereomicroscope or an Olympus Bx50 (Olympus Optical) microscope. Some taxa (i.e. Plecoptera, Trichoptera) were damaged in collection, processing, or storage, possibly due to the high amount of fine sediment in the samples or physical abrasion during the sieving process, and thus identified only to family level. Meiofaunal taxa such as Nematoda, Oligochaeta, Cyclopoida, Acari, Anomopoda, Cladocera, Ctenopoda, Ostracoda were identified to order or class level (Dobson, Pawley, Fletcher, & Powell, 2012; Tachet, Richoux, Bournaud, & Usseglio-Polatera, 2010).

2.3 Environmental data

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

2.5 Data analysis

2.5.1 Biological data

Hyporheic macrofauna, hyporheic meiofauna, and benthic macrofauna were analysed separately because a preliminary correspondence analysis conducted on faunal abundances showed that there were significant differences between sampling methods (colonisation pots *vs* Surbers) and between ecological zones (benthic *vs* hyporheic). Abundances of all identified taxa were merged by reach, treatment (wood *vs* control) and sampling campaign (period). The mean trait profile of sample assemblages was obtained by weighting the individual trait profiles of corresponding taxa by their log-transformed (x+1) abundances in the sample. Rare taxa (< 5 individuals over the whole sampling design) were removed to avoid extremes in the analysis (Cao, Larsen, & Thorne, 2001; Gauch, 1982). Then, within reach x campaign analysis (Within Class Analysis, WCA) (*wca* function of the R package ade4; Dray, Dufour, & Thioulouse, 2017) was performed to assess whether trait composition in i) hyporheic meiofauna and macrofauna and ii) benthic assemblages was identical in wood and control sites. The WCA performs a particular case of principal component analysis (PCA) with respect to the variable of interest (i.e. wood vs control in this study) (Benzécri, 1983). It is an effective method to eliminate the effects of confounding variables (i.e. reach and campaign date in this study) in the analysed dataset (Castella, Richardot-Coulet, Roux, & Richoux, 1991; Dolédec & Chessel, 1989; Dole-Olivier, , Marmonier, & Beffy, 1997; Van Looy, Floury, Ferréol, Prieto-Montes, & Souchon, 2016). Subsequently, the conditional inference tree approach (CIT) (*ctree* function R package party; Hothorn, Hornik, Strobl, & Zeileis, 2017) was applied to distinguish groups of sites with significantly different combinations of trait profiles, based on their coordinates along the successive factorial axes in WCA. CIT is a recursive, non-parametric, partitioning method that allows estimating regression relationships between variables (Hothorn, Hornik, & Zeileis, 2006; Section 5 in Supporting Information). In our study, CIT was tested using Bonferroni permutation test (9999 permutations, $\alpha = 0.01$). Finally, taxon trait-profiles among wood and control sites ($n = 48$) were compared using the non-parametric Wilcoxon signed-rank test. Bonferroni corrections (p-value < 0.001) were applied for selecting trait modalities with significant differences between LW vs control sites.

2.5.2 Environment-trait relationships

The relationship between environmental data and taxon traits was investigated by applying the Partial Least Squares (PLS) Path Modelling (Wold, 1982) using the *plspm* function of the R package plspm (Sanchez, Trinchera, & Russolillo, 2017). PLS was applied to link hydrological, physical, sedimentological and chemical variables to the variations of invertebrate trait modalities (Fig. S1). PLS is a statistical method that quantifies the relationships between observed manifest (indicators or items) and latent variables (indirectly measured - LVs) in a system of multiple linear regressions (Vinzi, Trinchera, & Amato, 2010). In the last few years, this approach has been increasingly applied to a wide range of disciplines including econometrics, social sciences and ecology (Bizzi, Surridge, & Lerner, 2013; Villeneuve, Piffady, Valette, Souchon, & Usseglio-Polatera, et al., 2018). First, the PLS approach includes the estimation of the latent variables as linear combinations of their respective blocks of manifest variables (Tenenhaus, Vinzi, Chatelin, & Lauro, 2005). This first step is an iterative process in which the latent variables are calculated as the weighed sum of their manifest variables till convergence of the weights is reached

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

3. Results

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

35%. Sedimentological and physical LVs had the greatest effects on trait modalities (25%-44% and 22%-43%, respectively) despite the response patterns differing between sites (Fig. 5a). Trait modalities at wood sites were affected mostly by physical variables (43%) with important effects for sedimentological and hydrological LVs (respectively 25% and 20%; Fig. 5a). In control sites, the direct effects of sedimentological and chemical LVs explained most of the trait variation (44 % and 31%), whereas hydrological variables had only a minor effect (3%). When looking at the total effects, the contribution of LVs to trait variation changed, due to indirect effects (Fig. 5a). A higher effect of hydrology (+16% to +29%) and a decrease in the effect of sedimentological variables (-7% to -18%) were shown in both control and wood sites (Fig. 5a). Finally, sedimentological and physical LVs exhibited higher impact (50-80%) on substrate preferences (i.e. sand and twigs/roots) and aquatic stages (i.e. egg, nymph) variation, in control sites (Fig. 5b). In wood sites, the relative contribution of the LVs to the trait variation was more similar among modalities (Fig. 5b).

4. Discussion

This study investigated multiple functional traits of meiofaunal and macrofaunal invertebrates to study their response to LW-induced processes in rivers. Wood and control site hyporheic assemblages exhibited different profiles of traits, with general patterns emerging in terms of responses to wood and wood-induced processes. In this section we discuss wood-related traits in the hyporheic and benthic zones (Section 4.1) and the major environmental predictors of trait modality variation (Section 4.2).

4.1 Wood-related traits of the meiofauna and macrofauna in LW habitats

Our study found that meiofaunal functional trait profiles differed in wood and control sites, suggesting functional relationships between traits and environmental forces in the HZ, and upholding our first hypothesis that LW would affect the trait profiles of the hyporheic meiofauna. Significant differences between LW and control sites were recorded for individual biological, physiological and behavioural meiofaunal trait modalities, reflecting organismal adaptations in the HZ. These specific trait modalities partly support our second hypothesis that multiple functional traits and trait-modalities would be affected by LW.

Significant trait modalities in LW included aquatic active dispersal, aquatic eggs and hard substrate preferences (Fig. 3). These trait modalities relate strongly to temporal instability, flow disturbance and sediment hydraulic conductivity (Bilton, Freeland, & Okamura, 2001; Descloux, Datry, & Marmonier, 2014; Larsen, Pace, & Ormerod, 2011). Active aquatic dispersal was recorded as significant behavioural feature, counter to our expectations (Table 2), for meiofaunal assemblages in LW, suggesting that hyporheic hydrology might not play a strong role in determining where meiofaunal species occur both spatially and temporally (see also Section 4.2). Active aquatic dispersal entails self-generating organism movements often associated with flightless aquatic invertebrates that display an active behaviour triggered by changing and unstable environmental conditions (Stubbington et al., 2017; Tonkin et al., 2017). However as the cues that trigger aquatic 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

- to erosional and deposition areas or flow paths. This might be another reason why functional differences in macroinvertebrate assemblages between LW and control sites were not detected in the results.

4.2 Environmental drivers of hyporheic meiofauna trait variation

Trait variation in LW and control sites was mainly explained by sedimentological and physical variables, although their relative contributions differed between sites. In this study, wood-related physical LVs, described by pH, conductivity, dissolved oxygen and, temperature, were the most important in explaining the overall variation of taxon traits (Fig. 4), implying that these traits exhibit strong relationships to local LW environmental conditions when viewed at local scale. The relative contribution of LVs to wood-trait variation is similar among modalities, underscoring a similar importance of all studied environmental drivers at LW sites

Control sites exhibited higher homogeneity in sedimentological variables, suggesting an increase in temporal stability partly due to the absence of wood-induced physical processes (Table 1). Sedimentological variables explained more than the 25% of hyporheic meiofaunal trait variation for all significant modalities (Fig. 5b). They explained much more of the variation of traits in control sites than LW sites, although significant trait modalities did not reflect a strong sedimentological impact (Fig. 5b). This finding is supported by other studies that have observed weaker effects of sediment size on hyporheic than epibenthic trait profiles (Descloux, Datry, & Marmonier, 2013; Descloux, Datry, & Usseglio-Polatera, 2014). Chemical and physical LVs explained 50% of the hyporheic meiofaunal trait variation for aquatic stages, dispersal and substrate preferences (Fig. 5b). Chemical LVs explained much more of the variation of traits for hyporheic meiofaunal assemblages in control than wood sites (Fig. 4). This result is consistent with a recently published study on the , sandy section of the Hammer stream that shows LW sites were characterized by short hyporheic flow-paths inhibiting local nitrate reduction (Shelley, Klaar, Krause, & Trimmer, 2017). The responses of benthic invertebrate assemblages to nutrients are well documented, but those of the hyporheic meiofaunal assemblages are far less known (Marmonier et al., 2012). Certain groups of invertebrates have proved to be good indicators of moderately eutrophic rivers. Many caddisflies belonging to the Glossosomatidae, Psychomyiidae and Hydropsychidae families for example, have been found intolerant or withstanding only a low-moderate range of nitrate concentrations (Nijboer, 2004; Pacioglu, Moldovan, Shaw, & Robertson, 2016). In our study, Psychomyiidae and *Hydropsyche* spp. instars were observed in hyporheic samples of control sites exhibiting higher concentrations of ammonium and phosphates than LW sites, thus supporting previous finding by providing a global indication of the chemical conditions in the HZ. Besides, other taxonomic groups (e.g. Chironomidae, Oligochaeta, Nematoda and Amphipoda), widespread among wood and control sites, have demonstrated high tolerance to nutrients in previous studies (Pacioglu, Moldovan, Shaw, & Robertson, 2016).

Finally, our findings confirmed the mechanistic impact of LW on hyporheic meiofauna trait-selection as the result of a combination of LW-driving processes. The effects are more pronounced on meiofaunal than macrofaunal assemblages highlighting the importance of LW in triggering physical and sedimentological impacts on faunal communities of lowland systems. LW impacts on hyporheic meiofauna are potentially important given that many benthic invertebrate species rely closely on the HZ in their life cycle (Robertson & Wood, 2010). Our findings provide further evidence of the mechanisms responsible for local invertebrate assemblage structure in LW, reflecting adaptations to dominant regional and local environmental stresses.

5. Conclusions

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

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

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

Acknowledgements

This work was supported by the Marie Sklodowska-Curie Action, Horizon 2020 within the project HypoTRAIN (Grant agreement number 641939). Thanks to the Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB) for performing the pore water chemical analysis.

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.

References

Benke, A. C., & Wallace, J. B. (2003). Influence of wood on invertebrate communities in streams and rivers. American Fisheries Society Symposium, 37, 149–177.

Benzécri, J. P. (1983). Analyse de l'inertie intra-classe par l'analyse d'un tableau de correspondances. Les Cahiers de l'Analyse des données, 8 (3), 351-358.

Bilton, D. T., Freeland, J. R., & Okamura, B. (2001). Dispersal in freshwater invertebrates. Annual Review of Ecology and Systematics, 32, 159–181. doi.org/10.1146/annurev.ecolsys.32.081501.114016.

Bizzi, S., Surridge, B. W., & Lerner, D. N. (2013). Structural equation modelling: a novel statistical framework for exploring the spatial distribution of benthic macroinvertebrates in riverine ecosystems. River Research and Applications, 29, 743–759. doi.org/10.1002/rra.2563.

Blaen, P. J., Kurz, M. J., Drummond, J. D., Knapp, J. L., Mendoza-Lera, C., Schmadel, N. M., Klaar, M. J., ... & Ward, A. S. (2018). Woody debris is related to reach-scale hotspots of lowland stream ecosystem respiration under baseflow conditions. Ecohydrology, e1952. https://doi.org/10.1002/eco.1952

Blott, S. J., & Pye, K. (2001). Gradistat: a grain size distribution and statistics package for the analysis of unconsolidated sediments. Earth Surface Processes and Landforms, 26, 1237–1248. doi.org/10.1002/esp.261

Boulton, A. J. (2007). Hyporheic rehabilitation in rivers: restoring vertical connectivity. Freshwater Biology, 52, 632–650. doi.org/10.1111/j.1365-2427.2006.01710.x

Brock, M., Nielsen, D. L., Shiel, R. J., Green, J. D., & Langley, J. D. (2003). Drought and aquatic community resilience: the role of eggs and seeds in sediments of temporary wetlands. Freshwater Biology, 48, 1207–1218. doi.org/10.1046/j.1365-2427.2003.01083.x

Cao, Y., Larsen, D. P. & Thorne R. ST - J. (2001). Rare species in multivariate analysis for bioassessment: some considerations. Journal of the North American Benthological Society, 20: 144–153. https://doi.org/10.2307/1468195

Castella, E., Richardot-Coulet, M., Roux, C. & Richoux, P. (1991). Aquatic macroinvertebrate assemblages of two contrasting floodplains: The Rhône and Ain rivers, France. Regulated Rivers: Research & Management, 6, 289-300. https://doi.org/10.1002/rrr.3450060407

Chevenet, F., Dolédec, S., & Chessel, D. (1994). A fuzzy coding approach for the analysis of long-term ecological data. Freshwater Biology, 31, 295–309. doi.org/10.1111/j.1365-2427.1994.tb01742.x

Coleman, M. J., & Hynes, H. (1970). The vertical distribution of the invertebrate fauna in the bed of a stream. Limnology and Oceanography, 15, 31–40. doi.org/10.4319/lo.1970.15.1.0031

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. Science, 199, 1302–1310. DOI: 10.1126/science.199.4335.1302

Crossman, J., Bradley, C., Milner, A., & Pinay, G. (2013). Influence of environmental instability of groundwater-fed streams on hyporheic fauna, on a glacial floodplain, Denali National Park, Alaska. River Research and Applications, 29, 548–559. doi.org/10.1002/rra.1619

Croutsche, J. J. (2002). Étude des relations de causalité: Utilisation des modèles d'équations structurelles (approche méthodologique). La Revue des Sciences de Gestion: Direction et Gestion, p. 81.

Descloux, S., Datry, T., & Marmonier, P. (2013). Benthic and hyporheic invertebrate assemblages along a gradient of increasing streambed colmation by fine sediment. Aquatic Sciences, 75, 493–507. doi.org/10.1007/s00027-013-0295-6

Descloux, S., Datry, T., & Usseglio-Polatera, P. (2014). Trait-based structure of invertebrates along a gradient of sediment colmation: Benthos versus hyporheos responses. Science of the Total Environment, 466, 265–276. doi.org/10.1016/j.scitotenv.2013.06.082

Dole-Olivier, M. - J., Marmonier, P. & Beffy J. - L. (1997). Response of invertebrates to lotic disturbance: is the hyporheic zone a patchy refugium?. Freshwater Biology, 37, 257-276. https://doi.org/10.1046/j.1365-2427.1997.00140.x

Dolédec, S., & Chessel, D. (1989). Seasonal successions and spatial variables in freshwater environments. II. Distinction between seasonal and environmental effects within faunistic data (in French). Acta Oecologica, 10, 207–232.

Dray, S., Dufour, A. B., & Thioulouse, J. (2017). ade4: Analysis of Ecological Data: Exploratory and Euclidean Methods in Environmental Sciences. R package version, 1.7-10.

Dunscombe, M., Robertson, A., Peralta-Maraver, I., & Shaw, P. (2018). Community structure and functioning below the streambed across contrasting geologies. Science of the Total Environment, 630, 1028–1035. doi.org/10.1016/j.scitotenv.2018.02.274

Flores, L., Giorgi, A., González, J. M., Larrañaga, A., Díez, J. R., & Elosegi, A. (2017). Effects of wood addition on stream benthic invertebrates differed among seasons at both habitat and reach scales. Ecological Engineering, 106, 116–123. doi.org/10.1016/j.ecoleng.2017.05.036

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E. M., … Bommarco, R. (2015). Functional identity and diversity of animals predict ecosystem functioning better than species- based indices. Proceedings of the Royal Society of London B: Biological Sciences, 282, 20142620. DOI:10.1098/rspb.2014.2620

Gauch, H.G. (1982). Multivariate analysis in community ecology. Cambridge University Press, Cambridge, UK.

Gippel, C. J., O'Neill, I. C., Finlayson, B. L., & Schnatz, I. (1996). Hydraulic guidelines for the re-introduction and management of large woody debris in lowland rivers. Regulated Rivers Research & Management, 12, 223–236.

Götz, O., Liehr-Gobbers, K., & Krafft, M. (2010). Evaluation of structural equation models using the partial least squares (pls) approach. Handbook of Partial Least Squares, pp. 691–711, Springer.

Grabowski, R. C., Gurnell, A. M., Burgess-Gamble, L., England, J., Holland, D., Klaar, M. J., ... Wharton, G. (2019). The current state of the use of large wood in river restoration and management. Water and Environment Journal. doi: 10.1111/wej.12465.

Grabowski, R. & Magliozzi, C. (2019). Effects of large wood on invertebrate assemblages in the bed of a lowland river using a functional trait approach (Version 1). figshare. https://doi.org/10.17862/cranfield.rd.7539305.v1

Grime, J. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of Ecology, 86, 902–910. doi.org/10.1046/j.1365-2745.1998.00306.x.

Gurnell, A. M., & Grabowski, R. C (2016). Vegetation-hydrogeomorphology interactions in a low-energy, human-impacted river. River Research and Applications, 3, 202–215. doi: 10.1002/rra.2922.

Gurnell, A. M. (2013). Wood in fluvial systems. In Shroder Jr., J. and Wohl, E. (eds) *Treatise on Geomorphology (pp. 163–188).* San Diego, CA, USA: Academic Press.

Heiri, O., Lotter, A. F., & Lemcke, G. (2001). Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. Journal of Paleolimnology, 25, 101–110. doi.org/10.1023/A:10081196

Hothorn, T., Hornik, K., Strobl, C., & Zeileis, A. (2017). party: A Laboratory for Recursive Partytioning. R package version, 1.2-4.

Hothorn, T., Hornik, K., & Zeileis, A. (2006). Unbiased recursive partitioning: A conditional inference framework. Journal of Computational and Graphical Statistics, 15, 651–674.

Kaller, M. D. and Kelso, W. E. (2007). Association of macroinvertebrate assemblages with dissolved oxygen concentration and wood surface area in selected subtropical streams of the southeastern USA. Aquatic Ecology, 41, 95–110.

Kondolf, G., Boulton, A., O'Daniel, S., Poole, G., Rahel, F., Stanley, E., Wohl, E., … Nakamura, K. (2006). Process-based ecological river restoration: visualizing three-dimensional connectivity and dynamic vectors to recover lost linkages. Ecology and Society, 11, 5.

Krause, S., Klaar, M. J., Hannah, D. M., Mant, J., Bridgeman, J., Trimmer, M., & Manning Jones, S. (2014). The potential of large woody debris to alter biogeochemical processes and ecosystem services in lowland rivers. Wiley Interdisciplinary Reviews: Water, 1, 263-275. https://doi.org/10.1002/wat2.1019

Krause, S., Tecklenburg, C., Munz, M., & Naden, E. (2013). Streambed nitrogen cycling beyond the hyporheic zone: Flow controls on horizontal patterns and depth distribution of nitrate and dissolved oxygen in the upwelling groundwater of a lowland river. Journal of Geophysical Research: Biogeosciences, 118, 54–67. doi.org/10.1029/2012JG002122

Larsen, S., Pace, G., & Ormerod, S. (2011). Experimental effects of sediment deposition on the structure and function of macroinvertebrate assemblages in temperate streams. River Research and Applications, 27, 257–267. doi.org/10.1002/rra.1361

Larson, M. G., Booth, D. B., & Morley, S. A. (2001). Effectiveness of large woody debris in stream rehabilitation projects in urban basins. Ecological Engineering, 18, 211–226. doi.org/10.1016/S0925-8574(01)00079-9

Lautz, L. K., Siegel, D. I., & Bauer, R. L. (2006). Impact of debris dams on hyporheic interaction along a semi-arid stream. Hydrological Processes, 20, 183–196. doi.org/10.1002/hyp.5910

Lewandowski, J., Putschew, A., Schwesig, D., Neumann, C., & Radke, M. (2011). Fate of organic micropollutants in the hyporheic zone of a eutrophic lowland stream: Results of a preliminary field study. Science of the Total Environment, 409, 1824–1835. doi.org/10.1016/j.scitotenv.2011.01.028

Magliozzi, C., Grabowski, R., Packman, A. I., & Krause, S. (2018). Toward a conceptual framework of hyporheic exchange across spatial scales. Hydrology and Earth System Sciences, 22, 6163-6185. https://doi.org/10.5194/hess-22-6163-2018, 2018.

Marmonier, P., Archambaud, G., Belaidi, N., Bougon, N., Breil, P., Chauvet, E., … Vervier, P. (2012). The role of organisms in hyporheic processes: gaps in current knowledge, needs for future research and applications. Annales de Limnologie-International Journal of Limnology, 48, 253–266. doi.org/10.1051/limn/2012009

Marmonier, P., Delettre, Y., Lefebvre, S., Guyon, J., & Boulton, A. (2004). A simple technique using wooden stakes to estimate vertical patterns of interstitial oxygenation in the beds of rivers. Archiv für Hydrobiologie, 160, 133–143. doi.org/10.1127/0003-9136/2004/0160-0133

Mathers, K. L., Millett, J., Robertson, A. L., Stubbington, R., & Wood, P. J. (2014). Faunal response to benthic and hyporheic sedimentation varies with direction of vertical hydrological exchange. Freshwater Biology, 59, 2278–2289. doi.org/10.1111/fwb.12430

Matthaei, C., Peacock, K. A., & Townsend, C. R. (1999). Scour and fill patterns in a New Zealand stream and potential implications for invertebrate refugia. Freshwater Biology, 42, 41–57. doi.org/10.1046/j.1365-2427.1999.00456.x

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. Trends in Ecology & Evolution, 21, 178–185. doi.org/10.1016/j.tree.2006.02.002

Menichino, G. T., & Hester, E. T. (2014). Hydraulic and thermal effects of in-stream structure-induced hyporheic exchange across a range of hydraulic conductivities. Water Resources Research, 50, 4643–4661. doi.org/10.1002/2013WR014758

Mondy, C. P., & Usseglio-Polatera, P. (2013). Using conditional tree forests and life history traits to assess specific risks of stream degradation under multiple pressure scenario. Science of the Total Environment, 461, 750– 760. doi.org/10.1016/j.scitotenv.2013.05.072

Mutz, M., Kalbus, E., & Meinecke, S. (2007). Effect of instream wood on vertical water flux in low-energy sand bed flume experiments. Water Resources Research, 43, 1–10. doi.org/10.1029/2006WR005676

Nijboer, R. (2004). The ecological requirements of *Agapetus fuscipes* CURTIS (Glossosomatidae), a characteristic species in unimpacted streams. Limnologica-Ecology and Management of Inland Waters, 34, 213–223. doi.org/10.1016/S0075-9511(04)80046-X

Orghidan, T. (1959). Ein neuer Lebensraum des unterirdischen Wassers: der hyporheische Biotop. Archiv für Hydrobiologie, 55, 392–414.

Pacioglu, O., Moldovan, O. T., Shaw, P., & Robertson, A. (2016). Response of invertebrates from the hyporheic zone of Chalk rivers to eutrophication and land use. Environmental Science and Pollution Research, 23, 4729–4740. doi.org/10.1007/s11356-015-5703-0

Pilotto, F., Bertoncin, A., Harvey, G. L., Wharton, G., & Pusch, M. T. (2014). Diversification of stream invertebrate communities by large wood. Freshwater Biology, 59, 2571–2583. doi.org/10.1111/fwb.12454

Pilotto, F., Harvey, G. L., Wharton, G., & Pusch, M. T. (2016). Simple large wood structures promote hydromorphological heterogeneity and benthic macroinvertebrate diversity in low-gradient rivers. Aquatic Sciences, 78, 755–766. doi.org/10.1007/s00027-016-0467-2

Robertson, A., & Wood, P. (2010). Ecology of the hyporheic zone: origins, current knowledge and future directions. Fundamental and Applied Limnology/Archiv für Hydrobiologie, 176, 279–289. doi.org/10.1127/1863-9135/2010/0176-0279

Sanchez, G. (2013). Pls path modeling with r. Berkeley: Trowchez Editions.

Sanchez, G., Trinchera, L., & Russolillo, G. (2017). plspm: Tools for Partial Least Squares Path Modeling (PLS-PM). R package version, 0.4.9.

Sawyer, A. H., Cardenas, B. M., & Buttles, J. (2011). Hyporheic exchange due to channel-spanning logs. Water Resources Research, 47, W08502. doi:10.1029/2011WR010484

Shelley, F., Klaar, M., Krause, S., & Trimmer, M. (2017). Enhanced hyporheic exchange flow around woody debris does not increase nitrate reduction in a sandy streambed. Biogeochemistry, 136, 353–372. doi.org/10.1007/s10533-017-0401-2

Statzner, B., & Bêche, L.A. (2010). Can biological invertebrate traits resolve effects of multiple stressors on running water ecosystems? Freshwater Biology, 55, 80–119. doi.org/10.1111/j.1365-2427.2009.02369.x

Stead, T. K., Schmid-Araya, J. M., & Hildrew, A. G. (2003). All creatures great and small: patterns in the stream benthos across a wide range of metazoan body size. Freshwater Biology, 48, 532–547. doi.org/10.1046/j.1365-2427.2003.01025.x

Stubbington, R., Bogan, M. T., Bonada, N., Boulton, A. J., Datry, T., Leigh, C., & Vander Vorste, R. (2017). The biota of intermittent rivers and ephemeral streams: aquatic invertebrates.

Intermittent Rivers and Ephemeral Streams, pp. 217–243, Elsevier. doi.org/10.1016/B978-0-12-803835-2.00007-3

Tachet, H., Richoux, P., Bournaud, M., & Usseglio-Polatera, P. (2010). Invertébrés d’eau douce. Systématique, biologie, écologie. (2nd edition). CNRS éditions, Paris.

Tenenhaus, M., Vinzi, V. E., Chatelin, Y. M., & Lauro, C. (2005). Pls path modeling. Computational Statistics & Data Analysis, 48, 159–205.

Thompson, M. S., Brooks, S. J., Sayer, C. D., Woodward, G., Axmacher, J. C., Perkins, D. M., & Gray, C. (2018). Large woody debris rewilding rapidly restores biodiversity in riverine food webs. Journal of Applied Ecology, 55, 895–904. doi.org/10.1111/1365-2664.13013

Tonkin, J. D., Shah, T., Devi, R., Shah, D. N., Hoppeler, F., Jähnig, S. C., & Pauls, S. U. (2017). Metacommunity structuring in Himalayan streams over large elevational gradients: the role of dispersal routes and niche characteristics. Journal of Biogeography, 44, 62–74. doi.org/10.1111/jbi.12895

Townsend, C. R., & Hildrew, A. G. (1994). Species traits in relation to a habitat templet for river systems. Freshwater Biology, 31, 265–275. doi.org/10.1111/j.1365-2427.1994.tb01740.x

Usseglio-Polatera, P., Richoux, P., Bournaud, M., & Tachet, H. (2001). A functional classification of benthic macroinvertebrates based on biological and ecological traits: application to river condition assessment and stream management. Archiv für Hydrobiologie. Supplement band. Monographische Beiträge, 139, 53–83.

Van Looy, K., Floury, M., Ferréol, M., Prieto-Montes, M. & Souchon, Y. (2016). Long-term changes in temperate stream invertebrate communities reveal a synchronous trophic amplification at the turn of the millennium. Science of the Total Environment, 565, 481-488. https://doi.org/10.1016/j.scitotenv.2016.04.193

Villéger, S., Mason, N. W., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology, 89, 2290–2301. doi.org/10.1890/07-1206.1.

Villeneuve, B., Piffady, J., Valette, L., Souchon, Y., & Usseglio-Polatera, P. (2018). Direct and indirect effects of multiple stressors on stream invertebrates across watershed, reach and site scales: A structural equation modelling better informing on hydromorphological impacts. Science of the Total Environment, 612, 660–671. doi.org/10.1016/j.scitotenv.2017.08.197

Vinzi, V. E., Trinchera, L., & Amato, S. (2010). Pls path modeling: from foundations to recent developments and open issues for model assessment and improvement. Handbook of partial least squares, pp. 47–82, Springer.

Wagenhoff, A., & Olsen, D. (2014). Does large woody debris affect the hyporheic ecology of a small New Zealand pasture stream? New Zealand Journal of Marine and Freshwater Research, 48, 547–559. doi.org/10.1080/00288330.2014.924539

Ward, J. (1989). The four-dimensional nature of lotic ecosystems. Journal of the North American Benthological Society, 8, 2–8. doi.org/10.2307/1467397

Wohl, E., Lane, S. N., & Wilcox, A. C. (2015). The science and practice of river restoration. Water Resources Research, 51, 5974-5997. doi:10.1002/2014WR016874.

Wohl, E., Cenderelli, D. A., Dwire, K. A., Ryan-Burkett, S. E., Young, M. K., & Fausch, K. D. (2010). Large in-stream wood studies: a call for common metrics. Earth Surface Processes and Landforms, 35, 618–625. doi.org/10.1002/esp.1966

Wold, H. (1982) Soft modelling: the basic design and some extensions. Systems Under Indirect Observation, Part II pp. 36–37.

Zwick, P. (1996). Variable egg development of *Dinocras* spp. (Plecoptera, Perlidae) and the stonefly seed bank theory. Freshwater Biology, 35, 81–100. doi.org/10.1046/j.1365-2427.1996.00482.x

Tables and Figures

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

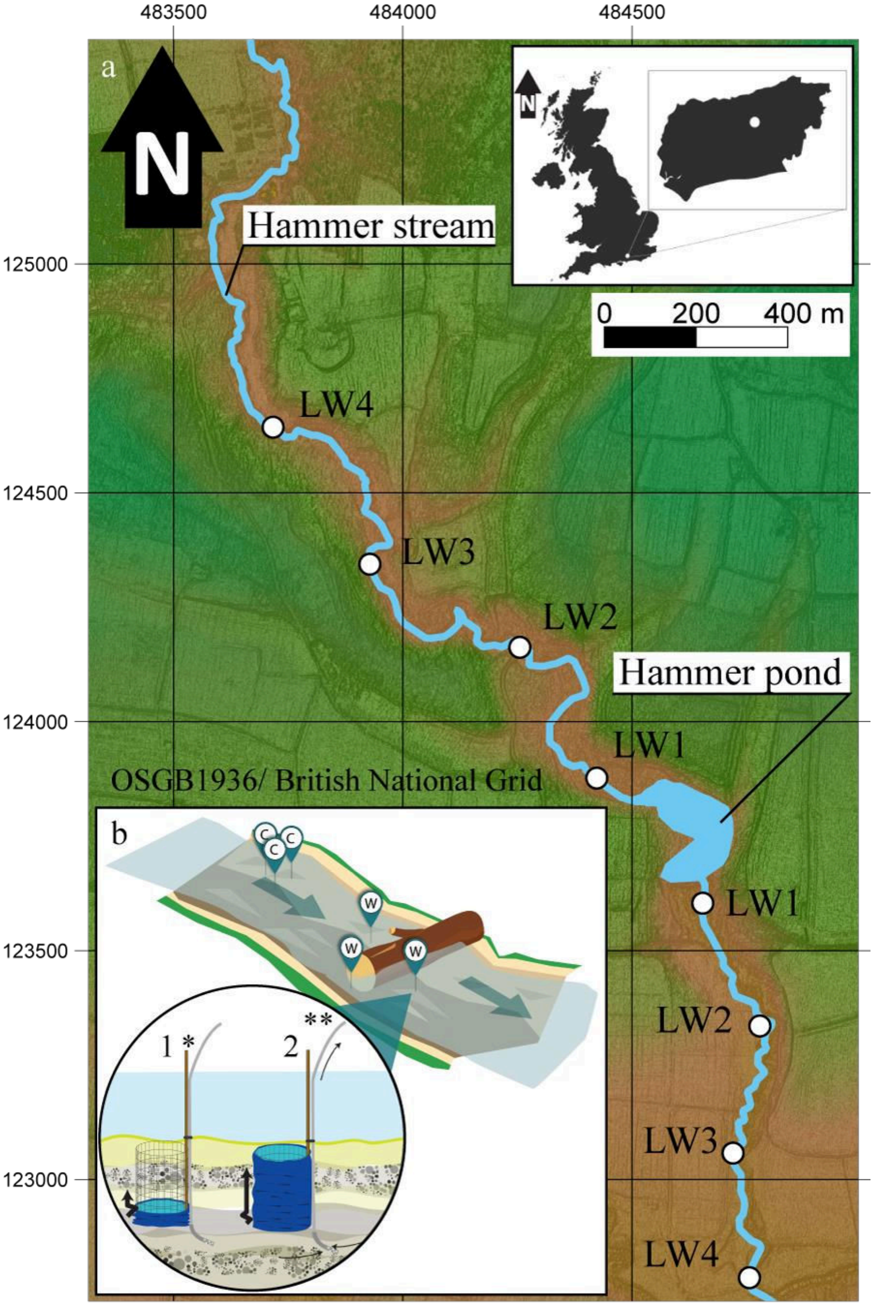
Processes & Conditions	Wood	Control	References
1. Hyporheic exchange flow	+	-	Krause et al., 2014
2. Oxygen availability	+	-	Kaller & Kelso, 2007
3. Temporal stability	-	+	Gurnell, 2013
4. Organic matter	+	-	Blaen et al., 2018
5. Denitrification	-	+	Klaar, Krause, & Trimmer, 2017
6. Hydraulic conductivity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

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

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



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

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

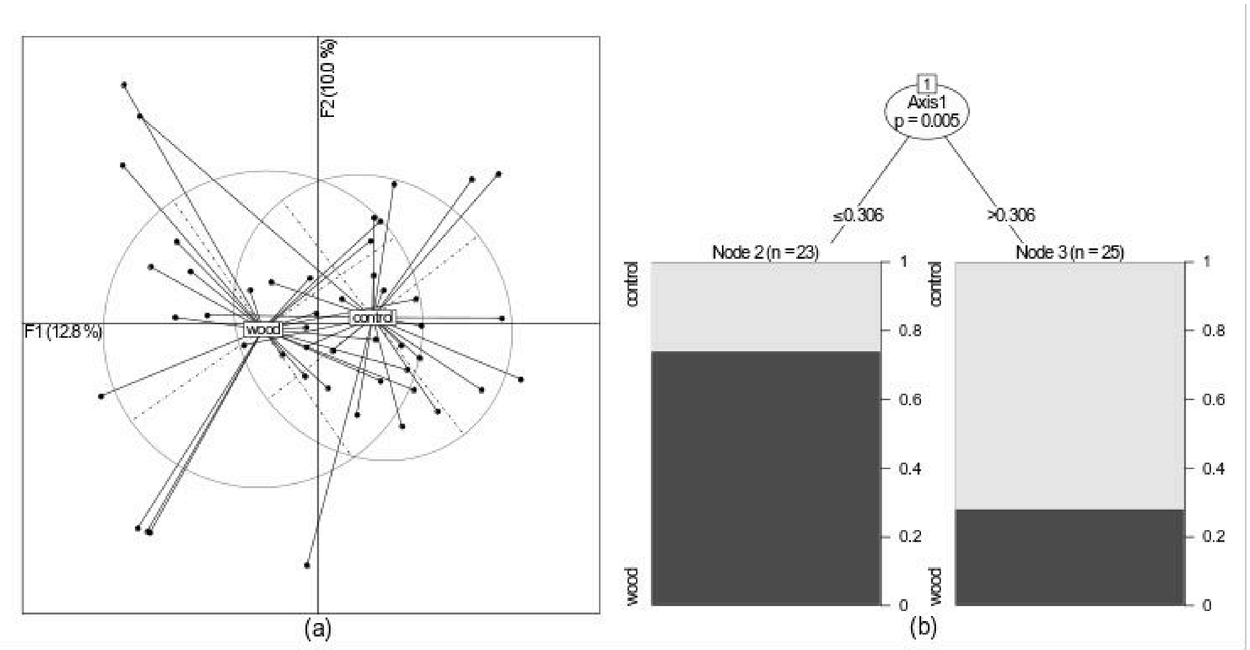


Figure 2: Hyporheic meiofauna trait profiles among wood and control sites. (a) First factorial plane of WCA giving the locations of the 48 samples gathered by wood and control sites. Labels are located at the weighted average (i.e. the centre of the star) of corresponding samples (solid circles). The 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).

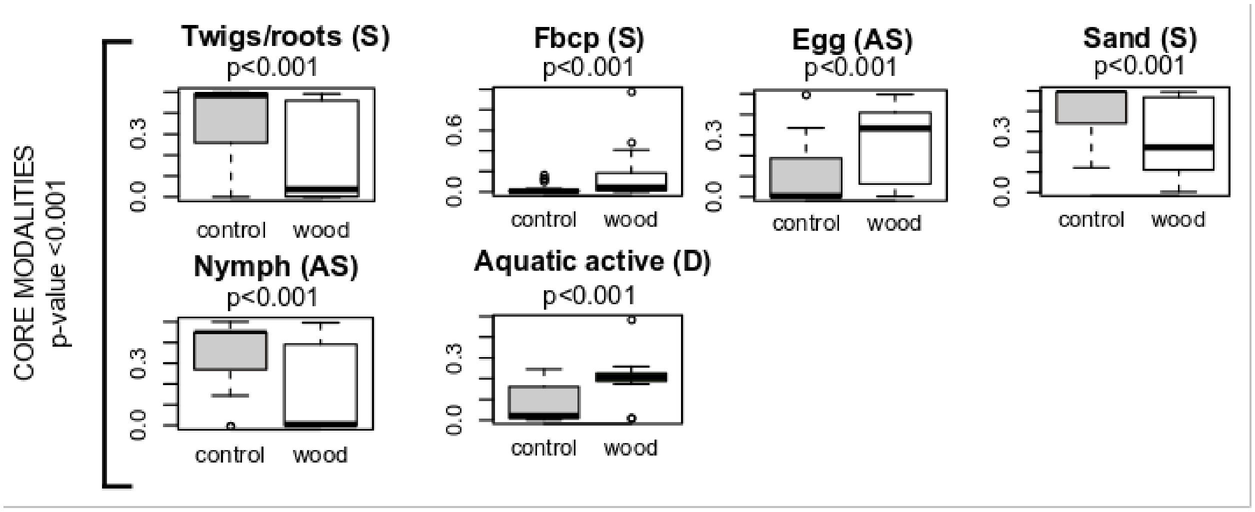
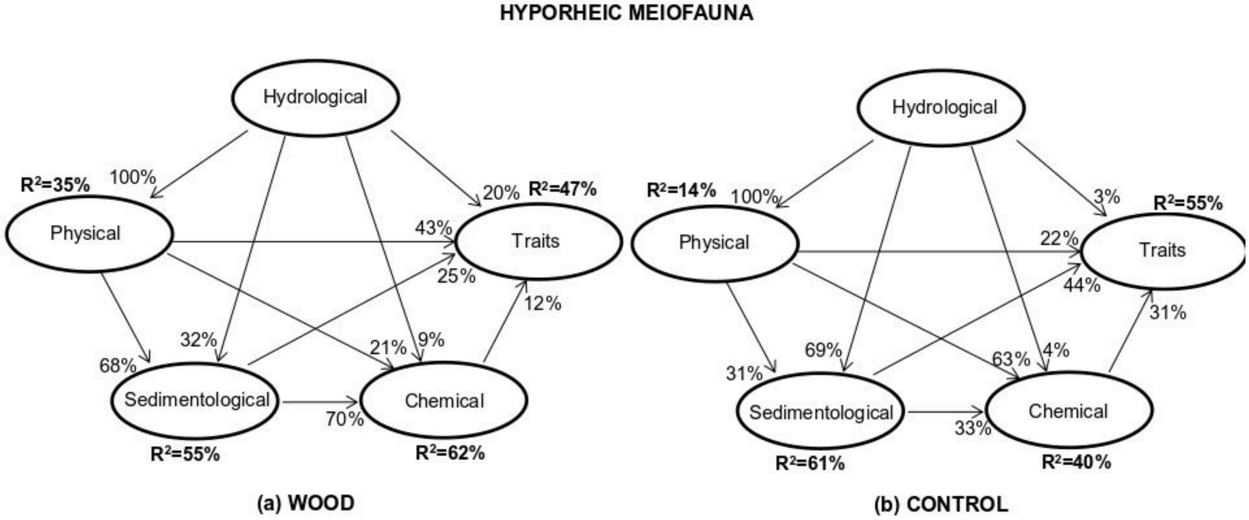


Figure 3: Relative frequency of trait modalities (see Table S1 for abbreviations) for hyporheic meiofauna in control *vs* LW sites. Only trait modalities exhibiting significant differences (Wilcoxon test, adjusted p-values < 0.001) between control and LW sites are presented. Traits are indicated in bracket: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



(a) WOOD (b) CONTROL

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

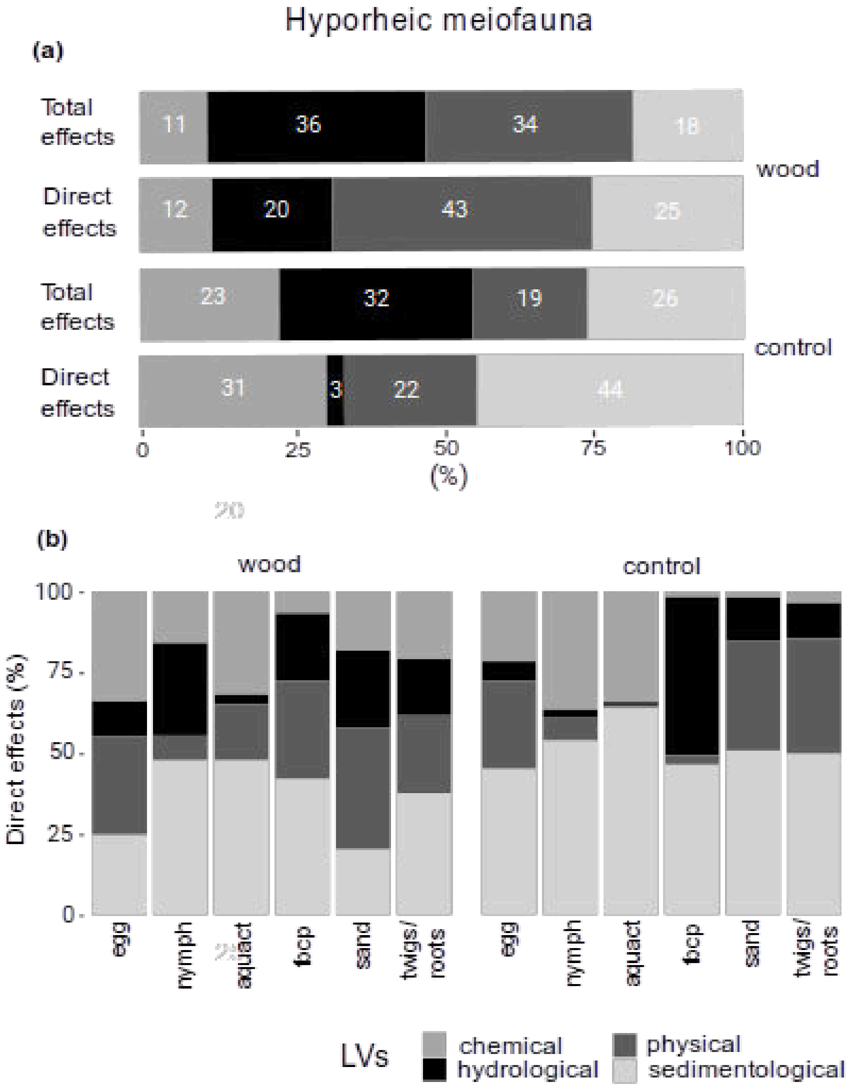


Figure 5: (a) Relative contribution (%) of latent variables (LVs) to the variation of the trait modalities of hyporheic meiofauna significantly differing between wood and control sites (Wilcoxon test, adjusted p-value < 0.001), based on direct and total (= direct + indirect) effects. (b) Direct effects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