

CRANFIELD UNIVERSITY

Chiara Magliozzi

**Hydroecological investigations on the hyporheic
zone to support river management from reaches to
catchments**

School of Water, Energy and Environment

PhD

Academic Year: 2015–2018

Supervisors: Dr. Robert Grabowski and Mr. Martin Janes
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Submitted in partial fulfilment of the requirements of the degree of
Doctor of Philosophy

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Abstract

The hyporheic zone (HZ) is an area of interaction between surface and ground waters in riverbeds. It is characterized by a diverse fauna and by a bidirectional flow (hyporheic exchange flow - HEF). HZ plays a significant role in river ecosystems as location of major physical, biogeochemical and ecological processes. Yet, predicting HEF in rivers and assessing its ecological effects is challenging due to physical and biological process- interactions in time and space.

This thesis investigates HEF from a hierarchical scaling perspective and it has two components: (i) physical, and (ii) biological. The first component includes discriminating and integrating the drivers of HEF across spatial scales and developing a multiscale statistical method for river restoration planning. The second component consists of testing the interaction between physical and biological processes on in-channel large wood (LW), by quantifying, in the field, the effects on hyporheic and benthic invertebrates assemblages taxonomic structure and functional traits.

The multiscale approach shows that suitable areas for HEF-focused restoration embed a summary of environmental information across the domains of hydrology, geomorphology, and ecology. Field results about invertebrates' taxonomic and functional metrics, demonstrate that the increased spatial and temporal variability of abiotic conditions at LW sites drives changes in abundance, biomass, diversity and functional traits of hyporheic meiofaunal assemblages. In contrast, benthic macrofaunal assemblages were less wood-impacted.

To support restoration targeting the HZ, this research emphasizes the need to (i) recognize different spatial scales of HEF to identify the underlying processes; (ii) coordinate approaches to pool hyporheic data and create long-term datasets to quantitatively assess model predictions; and (iii) establish further knowledge on how LW effects HZ in different valleys and river types.

Keywords: hyporheic zone, multiscale, functional traits, large wood, invertebrates, taxonomy

This research project was funded by the European Union and part of the HypoTRAIN project: Marie Skłodowska-Curie Innovative Training Network (ITN). Grant Agreement number: 641939.

Acknowledgements

“Takes two to tango”- thank you!

To Bob, for stimulating my intellectual independence, self-reflection and, critical thinking, but especially for your guidance and support in the past three years. To Martin, for your valuable advices and for reminding me about research “on the ground”. To Gianpaolo and Fernando, for encouraging my learning and developing skills. To Aaron, Anne, Philippe, Stefan, and the rest of the HypoTRAIN advisory team for providing research, guidance, logistical and funding support. To Ian, for your helpful comments and for chairing the advisory committee.

To the RRC, for your care and laughs which were a great distraction from daily work. To my officemates and all HypoTRAIN ESRs, for your enthusiasm and passion for science, the chats, the trips and lunches, the perfect support to go through PhD-life.

Loving thanks to my family and my friends back in Italy, for your confidence in me, the support, and the energy. And to Marco, for your manifest love, your practical and emotional support over the course of this research.

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Chapter 1

Introduction

Rivers are an essential element of Earth's ecosystems and the health and survival of billions of people. They are also intensively impacted systems by human activities: urbanization, soil erosion, forest degradation, peatland and wetland drainage, have impaired natural hydrological regimes and caused a widespread decline in river habitats across Europe and an estimated worldwide ecosystem damage of US\$ 6.3 trillion a year (Ding et al., 2017).

The cumulative impact of all these changes suggests that there has never been a more pressing moment to restore degraded rivers and their landscapes (Ding et al., 2017; McDonald et al., 2016). This is the ambition of river ecological restoration, which is “ the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed ” (Society for Ecological Restoration International Science & Policy Working Group, 2004).

Currently, best practice ecological restoration is underpinned by the principles of “effectiveness”, “efficiency” and “engagement” (McDonald et al., 2016; Keenleyside et al., 2012) that are adopted throughout the stages of planning, implementing, monitoring and evaluating restoration projects (McDonald et al., 2016). Key steps include the choice of priority sites and of restoration measures (The River Restoration Centre, 2013) both at catchment or at reach scale. Accurate selection of priority sites enables identifying the most effective set of variables to achieve restoration objectives and reduce the uncertainty when implementing the scheme, while the selection of appropriate restoration measures maximizes restoration outputs (i.e. biodiversity).

However, restoration interventions in rivers are impaired by rapid environmental, cultural, innovative and investment changes, and have often resulted in little improvement of river hydro-ecological conditions (Palmer et al., 2010; Wohl et al., 2005). Part of this failure stems from i) the lack of crafted goals derived by little interdisciplinary un-

derstanding of the relationship between physical and biological factors (Schirmer et al., 2014) and ii) the difficulty of defining prioritization and approaches from catchment assessments as consequence of paucity of interdisciplinary supporting tool (Mendoza-Lera and Datry, 2017; Hester et al., 2016; Hester and Gooseff, 2011, 2010; Palmer et al., 2010). Hence, holistic approaches and cross-border cooperation to manage river ecosystems have been advocated to keep river restoration open and flexible to the challenges of restoring natural functioning of rivers in current times of changes (Higgs et al., 2018; Wohl et al., 2015). In this direction, river restoration has been encouraged to adopt more interdisciplinary approaches at the interface of hydrology, geomorphology and ecology by including, for example, the hyporheic zone (HZ) in their planning (Hester and Gooseff, 2010).

1.1 What is the hyporheic zone?

The term “hyporheic zone” (Orghidan, 1959) refers to “. . . saturated subsurface including flow paths that originate from and return to surface water where interactions occur within a temporal scale relevant to the process of interest, and processes of interest occur continuously from the stream - subsurface interface to the hyporheic - groundwater continuum” (Ward, 2016) (Figure 1.1). The HZ is therefore the region where surface and ground waters mix together, characterized by a diverse fauna (hyporheos) (Brunke and Gonser, 1997) and a bidirectional flow of water known as hyporheic exchange flow (HEF) (Tonina, 2012; Gooseff, 2010; Storey et al., 2003; Harvey et al., 1996). Being at the interface of surface and subsurface waters, it is an active region of interlinked physical, chemical, and biological processes, and of key ecosystem functions (Ward, 2016; Boulton et al., 1998).

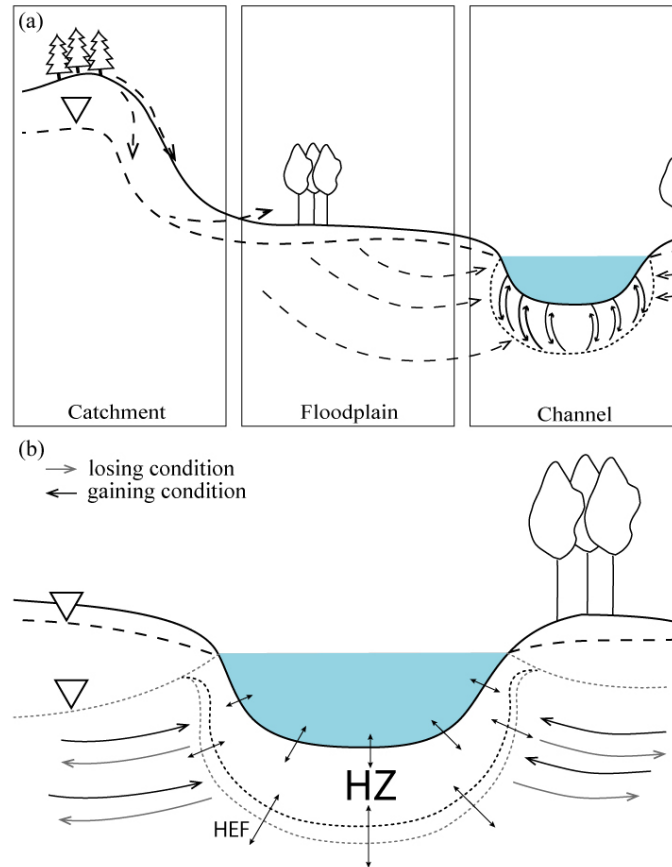


Figure 1.1: (a) Cross section of HZ across catchment, valley and reach. From origin and partitioning of water between surface and subsurface flow at catchment scale, to flow through valleys and river channels. (b) River cross-section representing the hyporheic zone and hyporheic exchange flow. Arrows of different colours represent two possible stream conditions: losing and gaining stream.

The HZ underpins fundamental river ecosystem functions, “river liver” (Fischer et al., 2005), due to the interaction between the hyporheic physical and biological systems (Ward, 2016; Krause et al., 2011b; Brunke and Gonser, 1997; Findlay, 1995).

The physical system refers to the environment where the hyporheic mixing occurs and to the exchange of water and solutes itself (Ward, 2016)(Figure 1.1). This hyporheic flow is defined by the interaction between surface and groundwater, and regulated by gradients (i.e. potential and kinetic energy) at the streambed interface that force surface water to enter the hyporheic zone and to upwell in more gently slopes areas of the river

(Boano et al., 2014; Cardenas et al., 2004; Elliott and Brooks, 1997; Packman and Brooks, 2001).

As the HEF is driven by potential and kinetic energy gradients, several factors at the river surface and subsurface influence the hyporheic physical system (Figure 1.2), and therefore the occurrence of HEF, by changing the distributions of hydraulic head (Boano et al., 2014). In fact, hyporheic exchange exhibits scale-dependency where HEF at reach and sub-reach scales is influenced significantly by larger-scale hydrogeological patterns and processes (Wörman et al., 2007). This fractal dimension to HEF means that the higher the number of factors (i.e. hydrological, topographical, geological), the higher HEF spatial variation and the more difficult it is to decipher the underlying processes and drivers of HEF and to transfer findings on HEF from fieldwork to other river types and at larger scales (>1 km).

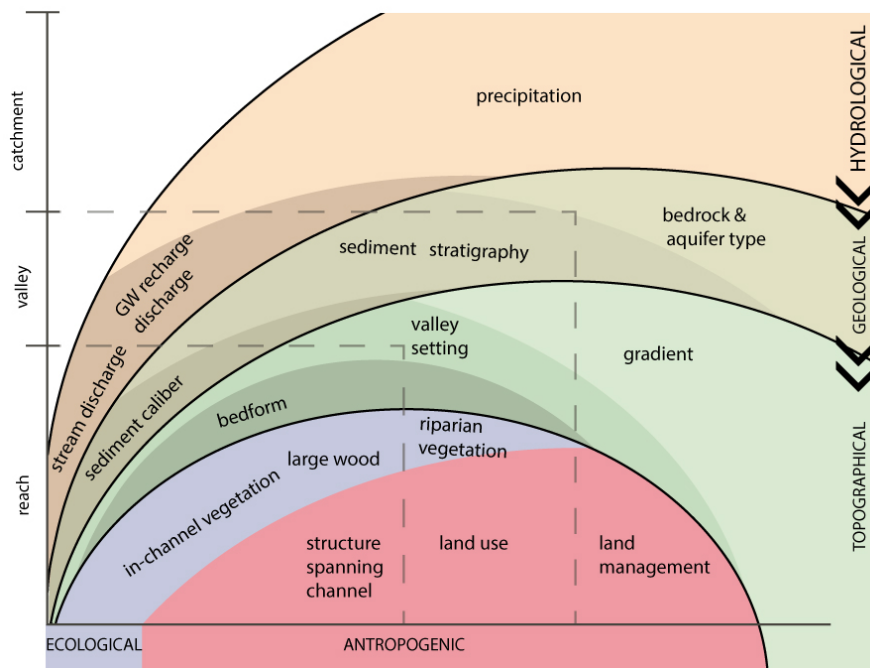


Figure 1.2: On the y axis the spatial scales, on the x and secondary y axis the main factors spatially related to the HEF. This diagram can be read from both directions: right to left (top down approach) or left to right (bottom up approach). Black arrows indicate that processes have mixed drivers (i.e. topography is the combination of geology and hydrology).

The spatial and temporal variation of HEF in turn controls the types and rates of physical (e.g. thermal regimes), chemical (i.e. nutrient attenuation, cycling of oxygen, mineral dissolution and precipitation), geomorphological (i.e. sediment distribution and transport) and ecological processes (i.e. secondary production) (Ward, 2016; Merrill and Tonjes, 2014; Krause et al., 2011b; Boulton, 2000; Brunke and Gonser, 1997). Many of the hyporheic flow functions are indeed mediated by hyporheic communities that constitute the biological system. The hyporheic zone hosts assemblages of invertebrates that represent 58 - 81% of the total number of species in rivers (Robertson, 2000), are important prey for fish (Schmid-Araya and Schmid, 2000), and grazers of algae and bacteria (Borchardt and Bott, 1995; Perlmutter and Meyer, 1991). Perhaps, the best-known examples of the interaction between physical and biological systems concern bacterial respiration and organic carbon turnover (Stegen et al., 2016), the supply of oxygen into the sediment (Corson-Rikert et al., 2016; Gibbins et al., 2016), bioturbation (Boulton, 2007), and the microbial-mediated biogeochemical transformation (i.e. denitrification and nitrification) (Mendoza-Lera and Datry, 2017; Heppell et al., 2014; Nogaro et al., 2010; Wood and Armitage, 1999). As the HEF is highly variable, mosaics of different ecological responses to HEF arise from site-specific interactions. A scientific understanding of HEF driving factors is therefore needed to predict how these flows generate and support river functioning.

Finally, river restoration aims to address physical habitat degradation to improve biodiversity (i.e. species and ecosystem diversity), and, as hyporheic functioning underpins stream health, targeting the HZ in restoration plans would be a logical direction for a holistic approach to river functioning (Hester and Gooseff, 2011). Many restoration measures can induce or enhance HEF through the generation of hydraulic gradients, creation of geomorphological heterogeneity (i.e. bedforms) and decrease of fine sediment load (Hester and Doyle, 2008; Schirmer et al., 2014; Gordon et al., 2013; Tuttle et al., 2014), thus, they could be used at different scales to promote HEF. At present, there are collaborative scientific initiatives for river restoration, embedding working at a river catchment scale (Department for Environment and Affairs, 2013) and based on the “naturalness criteria” (physical, hydrological, chemical and biological) for selecting priority habitats (Mainstone et al., 2014), but there is no framework representing

the complexity of multiple inter-related and cross-scale processes affecting HEF, taking account of typical data availability for river restoration and planning. Therefore, it is important to understand the drivers of HEF to determine potential benefits and develop restoration strategies.

1.2 Knowledge gap and research needs

Prediction of HEF and quantification of biological responses to hyporheic flow is the first step to assess the potential impact of HEF in rivers and for the development of appropriate management strategies. However, to predict and quantify biological responses to HEF, we need comprehensive knowledge of the main factors and interactions driving hyporheic dynamics and their role in determining HEF spatial and temporal variations (Figure 1.2). Therefore this research takes an inclusive view of the HZ and identified two key research needs about its physical and biological components to support river restoration.

First, there is a need for studies that identify and synthesise driving factors and underlying processes for HEF across multiple spatial scales (Hester et al., 2017; Ward, 2016) (Figure 1.2). To date, the mechanisms driving this mixing of surface and groundwater in the beds and banks of rivers are well understood from a theoretical perspective and supported by empirical work at the reach scale (Harvey and Gooseff, 2015; Boano et al., 2014). However, this research is limited by the number of sites, scale and the diversity of river types within which HEF has been quantified, making prediction difficult based on direct measurements of HEF (Ward, 2016).

Second, to test the hypothesis about hyporheic flow and its ecosystem functions, we also need more detailed information on how HEF affects the distribution, taxonomic-based descriptors and functional traits of living biota (i.e. invertebrate). To date, most studies have focused on HEF and hyporheic biota in single or multiple riffles (Mathers et al., 2017; Descloux et al., 2014; Davy-Bowker et al., 2006) that have been confirmed to drive HEF. Other in-channel geomorphological structures such as large wood (LW) promote HEF (Sawyer et al., 2011) and lately have received particular attention in river restoration because they are low-cost, time efficient and having more than a flow

attenuation effect in rivers (Harvey and Gooseff, 2015). Research has demonstrated LW increasing nutrient attenuation (Klaar et al., 2016), river respiration (Blaen et al., 2018), species richness and biomass of macroinvertebrates assemblages (Pilotto et al., 2016, 2014) but research has not investigated how LW influences taxonomic descriptors and functional traits of HZ communities. The lack of hyporheic biotic data associated with LW complicates our ability to identify the processes controlling HEF in wood sites, the ecological functioning of the HZ, and emphasizes the need for further research to generate an evidence base for river restoration plans.

1.3 Aim and objectives

This thesis aims to investigate the multi-scale drivers for spatial and temporal variation of HEF, and the effects of structure-induced HEF on hyporheic and benthic biodiversity for river restoration planning. These findings provide a comprehensive hydro-ecological knowledge of aquatic ecosystems across scales (Figure 1.3) and support river restoration prioritizing sites and approaches to target the HZ.

Objective 1: to discriminate and integrate the multi-scale factors driving the spatial and temporal variation of HEF and propose a methodology to predict HEF for river restoration planning (Chapter 2 and Chapter 3).

Objective 2: to quantify hyporheic and benthic biodiversity (community structure descriptors and functional traits) in response to large wood (structure-induced HEF) for river restoration planning (Chapter 4 and Chapter 5).

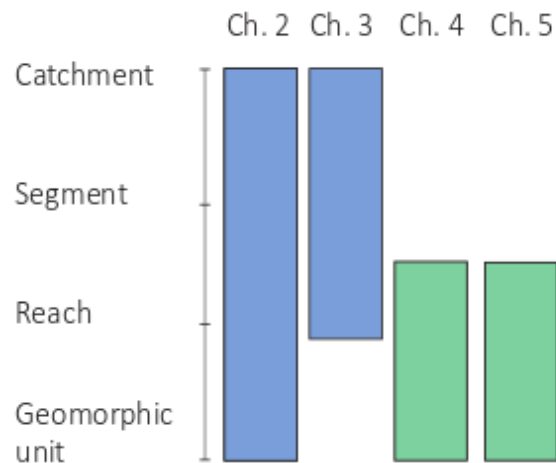


Figure 1.3: Spatial scales comprised by this thesis in each chapter.

1.3.1 Thesis outline

The thesis has been written in a paper format therefore the main chapters are written as individual scientific articles (Chapter 2 to 5). Chapter 2 and 3 were under review at Hydrology and Earth System Sciences (HESS) and Environmental Modelling & Software respectively at the time of writing. Chapter 4 and 5 were submitted to Freshwater Biology and to Functional Ecology respectively at the time of completion of this thesis. Please note that due to the format of the thesis, repetition in data description occurs in Chapter 4 and 5. All original work was carried out by the author of this thesis, and the contributions of the co-authors are stated in Table 1.1.

Chapter 2 presents an up-to-date critical review of the main factors controlling spatial and temporal variability of HEF in rivers. It provides new theoretical knowledge regarding HEF by drawing together published literature from different disciplines (catchment hydrology, fluvial geomorphology and ecology) and summarising for the first time how factors across a range of spatial and temporal scales influence its expression in rivers (Obj. 1).

Chapter 3 describes a novel and transferable multiscale method for identifying areas with potentially significant hyporheic exchange combining environmental information at reach, segment, and catchment scales, for use in restoration priority planning (Obj. 1). The method uses a deductive approach and avoids the reliance on detailed site-specific data of HEF which is spatially limited. The chapter is a base for a holistic process-based approach to use in river restoration.

Chapter 4 reports on a field study investigating the effect of in-channel large wood on invertebrate taxonomic-based structural descriptors and the ecological responses to wood-driven processes (Obj. 2). This chapter outlines the effects of LW, as geomorphological feature driving HEF on benthic and hyporheic invertebrate abundance, biomass and taxonomic diversity and provides initial insights on the potential effects on wood-based restoration design in the hyporheic zone.

Chapter 5 presents a field study investigating the link between wood-driven processes and the variation of invertebrates functional traits (Obj. 2). The chapter highlights the close relationships between species traits and local LW environmental conditions, providing further understanding on the functional role of LW in rivers.

Chapter 6 discusses how the results presented in the previous chapters contribute to identifying the underlying factors and process interactions controlling HEF variation towards improving prediction and quantification of biological responses to HEF and supporting the development of hyporheic-targeted river restoration strategies. The chapter outlines recommendations for further research and river restoration recommendations based on the findings and limitation of this research.

Finally, Appendices are included at the end of the document following References and provide more detail on data, methodologies and statistical approaches used in each Chapter.

Table 1.1: Authors' contributions to Chapter 2, 3, 4 and 5 already submitted for publication in peer-reviewed academic journals. Both R. Grabowski and Mr. Martin Janes provided guidance and advice on Chapter 1 and Chapter 6.

	Chapter 2	Chapter 3	Chapter 4	Chapter 5
C. Magliozzi	Literature review, synthesis, layout, writing	Data collection, analysis, methodology development, discussion, layout and writing	Data collection, analysis, methodology development, discussion, layout and writing	Data collection, analysis, methodology development, discussion, layout and writing
R. Grabowski (supervisor)	Guidance on structure, advice, editing	Guidance on structure, editing	Guidance on structure, editing	Guidance on structure, editing
A.I. Packman (advisor HypoTRAIN)	Guidance on structure, advice, editing	Guidance on structure, editing	/	/
S. Krause (advisor HypoTRAIN)	Conceptual advice	Conceptual advice	/	/
G. Coro (external collaborator)	/	Supervision on statistical approach, guidance on structure, editing	/	/
A. Robertson (advisor HypoTRAIN)	/	/	Guidance on structure, advice, editing	/
P. Usseglio Polatera (advisor HypoTRAIN)	/	/	advice, editing	Supervision on statistical approach, guidance on structure, editing
A.Mayer (external collaborator)	/	/	advice, editing	assisted in the analysis, editing

Chapter 2

Toward a conceptual framework of hyporheic exchange across spatial scales

1

Abstract

Rivers are not isolated systems but continuously interact with the subsurface from headwaters to large river valleys. In the last few decades, research on the hyporheic zone (HZ) from multiple perspectives has increased appreciation of the hydrological importance and ecological significance of connected river and groundwater systems. While recent reviews, modelling and field studies have explored hydrological, biogeochemical and ecohydrological processes in the HZ from bedform to reach scales, a comprehensive understanding of the interactions driving hyporheic exchange flows (HEF) at larger scales is still missing. In particular, there is only fragmentary information on how hydrological, topographical, hydrogeological, ecological and anthropogenic drivers interact to drive hyporheic exchange flows at larger scales. Therefore, this review aims to conceptualize the factors at catchment, valley and reach scales that interact and control spatial and temporal variations in hyporheic exchange flows. The implications of these drivers are discussed for each scale, and co-occurrences across scale are highlighted in a case study. By using a multi-scale perspective, this review connects field observations and modelling studies to identify process driving patterns and dynamics of HEF. Finally, the case study illustrates how understanding of local hydrogeological and geomorphological context can help to explain patterns in bedform-driven HEF. This conceptual framework will aid the development of approaches to interpret hyporheic

¹An early version of this Chapter in paper format, is available as HESS-discussion paper here

exchange across scales, infer scaling relationships, and inform catchment management decisions.

Keywords: hyporheic zone, multi-scale, catchment, valley, reach, conceptual framework

2.1 Introduction

Hyporheic zones (HZ) are unique components of river systems that underpin fundamental stream ecosystem functions (Ward, 2016; Harvey and Gooseff, 2015; Boano et al., 2014; Merrill and Tonjes, 2014; Krause et al., 2011b; Boulton et al., 1998; Brunke and Gonser, 1997; Orghidan, 1959). At the interface between rivers and aquifers, hyporheic zones are the expression of vertical and lateral connection of rivers with floodplains and the underlying aquifers, and are defined by the interchange of surface and ground waters through hyporheic exchange flows (HEF) (Lautz et al., 2010; Cardenas and Wilson, 2007; Gooseff et al., 2007; Boano et al., 2006; Wondzell, 2006; Wörman et al., 2006; Malard et al., 2002; Elliott and Brooks, 1997). HEF plays a significant role in biogeochemical cycling (e.g., carbon and nutrient availability and transformation), ecological food webs, and habitat for diverse organisms (Ward, 2016; Merrill and Tonjes, 2014; Krause et al., 2011b; Boulton et al., 1998; Brunke and Gonser, 1997).

HEF is driven by potential and kinetic energy gradients near the streambed that change hydraulic head and force surface water to flow into, through and out of the bed (Boano et al., 2014; Cardenas et al., 2004; Elliott and Brooks, 1997). Both hydrostatic, i.e. sum of elevation head, and hydrodynamic forces, i.e. sum of velocity head, of the hydraulic head contribute to HEF variations within rivers and floodplains (Boano et al., 2014; Cardenas et al., 2004; Packman and Brooks, 2001; Elliott and Brooks, 1997). Turbulence and (i.e. gravel bed substrate) and biological processes (i.e. bioturbation) also can drive HEF but less studied in streams and rivers (Boano et al., 2014).

The hierarchical and heterogeneous nature of river and floodplain systems creates complex spatial and temporal patterns of exchange flows (Cardenas, 2008; Wörman et al., 2007). There are strong gradients of structure and flow conditions formed by the drainage network that result from: (i) the temporal and spatial scales of the stream system from upstream to downstream, vertically and laterally (i.e. flood spates, overbank

flows-(Minshall et al., 1985; Newbold et al., 1982, 1981), and (ii) complex geomorphological structures (armorings, bedforms, bars and other lateral variability within channels, braiding, meanders and floodplain deposits). Therefore, understanding and predicting HEF dynamics requires a consideration of the hydrological, topographical, hydrogeological, anthropogenic and ecological processes operating across a spectrum of spatial and temporal scales (Ward, 2016).

Previous work has identified multi-scale HEF processes, but has focused primarily on individual processes and controls within river corridors (Ward, 2016; Harvey and Gooseff, 2015; Boano et al., 2014). Existing information has not been synthesized to assess the multiple factors and characteristics that control HEF at catchment scales across geographic regions (Tables 1,2,3 to download from public link ²). Similarly, earlier reviews have furthered our understanding of the ecological and functional significance of HZ (Krause et al., 2011b; Boulton et al., 1998; Brunke and Gonser, 1997), the range of mechanisms and biogeochemical implications that influence HEF (Boano et al., 2014; Merrill and Tonjes, 2014; Dent et al., 2001), and the challenges and perspectives to support interdisciplinary river research (Datry et al., 2017; Ward, 2016; Harvey and Gooseff, 2015). Despite this intensive investigation of HEF processes, there has been little investigation of hyporheic processes at catchment scale rather than at individual geomorphic units (Ward, 2016; Harvey and Gooseff, 2015; Krause et al., 2011b). Recently, Ward (2016) recognized that hyporheic science is still facing the challenge of enabling cross-site comparisons of findings. One of the reasons is the absence of conceptual frameworks to translate patterns of hyporheic flows across scales, enable multi-scale assessment of process controls, and enable identification of common variables.

Therefore, this paper reviews the state of knowledge of HEF with respect to two primary topics. With respect to the drivers of HEF, Sections 2.3-2.7 discuss five main drivers, hydrological, topographical, hydrogeological, ecological and anthropogenic, and how spatial and temporal variability in these drivers controls HEF. In the context of multiscale interactions, Section 2.8 discusses how these drivers interact to create spatial and temporal heterogeneity in HEF direction and magnitude. Both sections highlight knowledge gaps that are important in terms of fundamental understanding and man-

²<https://goo.gl/QVNFcE>

agement of hyporheic zones. The review follows a hierarchical spatial approach, from reaches to catchment, and provides a structure upon which to explore the individual and interaction effects of factors on HEF and to upscale and downscale across spatially and temporally variable hyporheic processes (Figure 2.1, 2.2).



Figure 2.1: Illustration of catchment complexity: scales and features that influence hyporheic exchange flows. Spatial changes in surface topography, land use and vegetation, drive geomorphological and hydrological changes at valley and reach scale. At catchment scale, variations in surface topography shapes valleys and channel types. Feature 1 refers to confined valleys characterized by straight channels, meandered and braided, and the following floodplain features: scour holes and gravel splays (a). The straight channel presents in-channel cascades (b) geomorphic features. Feature 2 refers to braided channel morphology with multi-thread channel, an undulating floodplain of bars and islands. In-channel geomorphic units are several types of bars (e), such as mid and lateral bars, and vegetated islands (f). Feature 3 represents a sinuous-meandering floodplain with occasional oxbow lakes and backwater swamps (m, n, k) and in channel: longitudinal bar (c), transverse bar (d), counterpoint bar (h), pond-riffle (i), point bar (l), chute channel (j). Feature 4 indicates an anabranching valley with multi-thread channels including abandoned channels (o) and backwater swamps (p). The channel can be quite deep and include islands covered with vegetation. The symbol * refers to irrigation system of the adjacent agricultural fields.

2.2 Concepts and terminology

The term “hyporheic zone” has been defined variously in the literature, and some confusion still exists within the wider research community about the extent and nature of the HZ. To help facilitate the integration and presentation of results from a large number of studies spanning a range of disciplines in this review, we will use a simplified and standardized terminology for the HZ and hyporheic exchange flows (HEF).

Herein, we follow the “flexible” definition of HZ, as reported by Ward (2016): “saturated subsurface including flow paths that originate from and return to surface water where interactions occur within a temporal scale relevant to the process of interest, and processes of interest occur continuously from the stream–subsurface interface to the hyporheic–groundwater continuum”. In terms of hyporheic exchange, we recognize that a continuum of hyporheic flow paths is associated with different hydrologic residence times (Boano et al., 2014; Cardenas, 2008; Wörman et al., 2007).

In the context of multi-scale exchange, HEF is related to large-scale groundwater surface-water exchange (GSE), but the terms are not synonymous (Ward, 2016). HEF is an interchange between surface and subsurface waters occurring in short time scales (i.e. minutes to weeks), whereas GSE flows occur at a much larger scale and may take long times to return to the stream (i.e. months to millennia) (Toth, 1980). At the scale of HEF, GSE can be considered as unidirectional exchange (i.e. losing, river recharges the aquifer, and gaining flow conditions, the river is fed by the aquifer). HEF and GSE can act in opposite directions (Stonedahl et al., 2012; Sawyer et al., 2009; Cardenas and Wilson, 2006). For example, a reach under losing condition due to groundwater (GW) recharge can have superimposed HEF occurring simultaneously (Fox et al., 2014; Stonedahl et al., 2012). Consequently, this review considers large-scale GSE in addition to HEF. We also refer to hyporheic “extent” when the HZ expands or contracts in the horizontal (“lateral extent”) or vertical (“vertical extent”) directions, respectively. Finally, we use the term bank storage exchange for the case where lateral HEF between the river and floodplain is induced by the rise and fall of river water levels (Cranswick and Cook, 2015; Pinder and Sauer, 1971). Vegetation (i.e. vegetation density, riparian and in-channel vegetation) is considered in this review as the main ecological factor that

influences HEF (Heppell et al., 2009; Corenblit et al., 2007). Although not reported in this paper, we acknowledge that other ecological factors such as hyporheic freshwater invertebrates and biofilm have a major role in interacting with HEF (Peralta-Maraver et al., 2018).

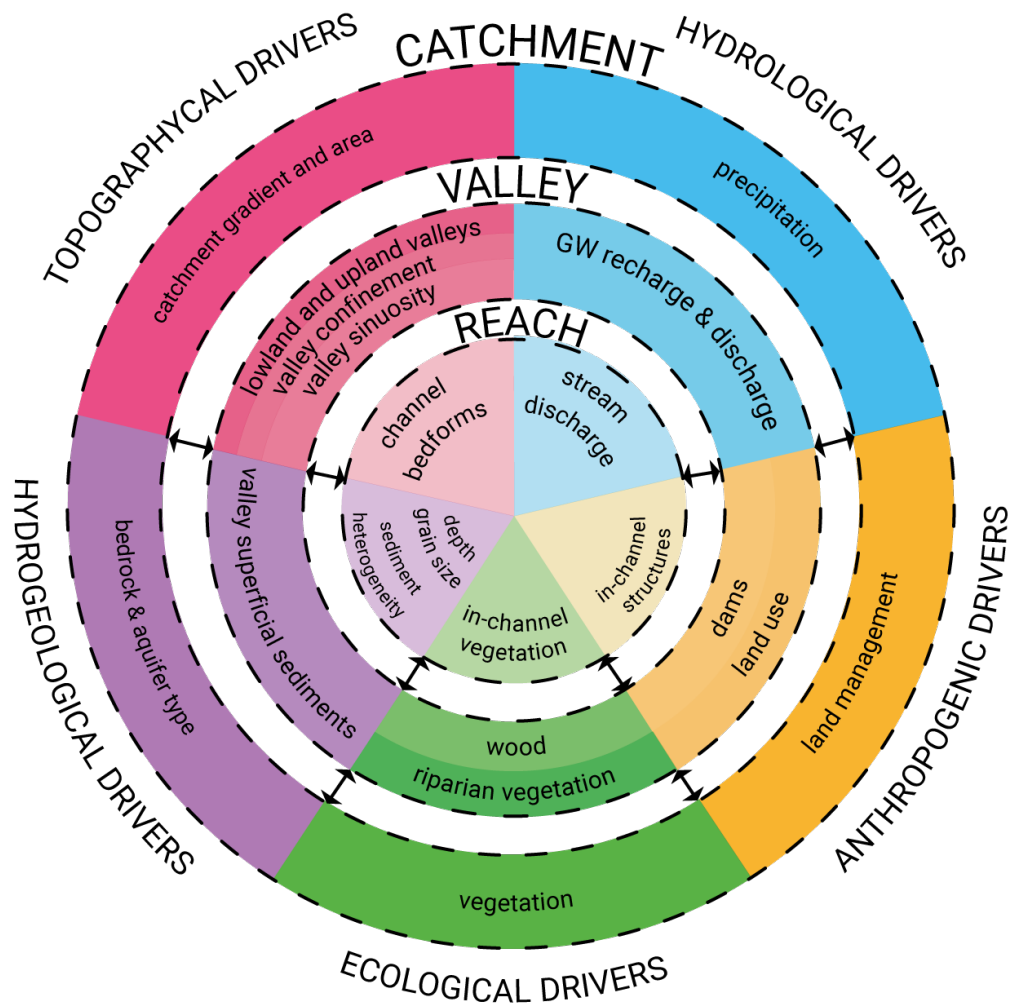


Figure 2.2: Conceptual diagram of the key drivers of the hyporheic exchange across scales. This diagram can be read from the centre to the outer part and viceversa as indicated by the black arrows. Dashed lines represent hidden boundauries between scales. Colour gradient, from light to dark, follows the hierarchical approach of this review from channel-scale to reach-scale to catchment-scale.

2.3 Hydrological drivers

Hydrological drivers influence HEF by changing surface- and ground-water flow regimes and distributions of hydraulic head. In this section, we provide a summary of how groundwater and river level fluctuations control the spatial and temporal distribution of hydraulic heads to affect HZ and HEF paths at reach (Section 2.3.1), valley and catchment scale (Section 2.3.2).

2.3.1 Groundwater and stream discharge at reach scale

HEF responds systematically to changes in hydrological conditions at the reach scale. Together, river flow regime and event based fluctuations of groundwater levels control reach-scale hyporheic exchange by changing the distributions of hydraulic head (Boano et al., 2014).

Several studies report that seasonal (i.e., spring-summer and summer-fall transition) and event-based changes in the gradient between river water and groundwater levels cause HZ to expand or contract (Malzone et al., 2016, 2015). In both losing and gaining flow conditions, the volume of the hyporheic zone contracts under a relatively small flux, while hyporheic residence times decrease moderately (Fox et al., 2016). In particular, during gaining conditions, steep stream-ward hydrologic gradients limit the extent of the HZ (Fox et al., 2014; Wondzell and Gooseff, 2013; Cardenas, 2009a; Cardenas and Wilson, 2007; Malcolm et al., 2005; Storey et al., 2003; Wroblicky et al., 1998; Harvey and Bencala, 1993). Conversely, the extent of the HZ and the hyporheic residence time increase during floods (Drummond et al., 2017; Zimmer and Lautz, 2014; Swanson and Cardenas, 2010; Wondzell et al., 2010; Poole et al., 2006). This enlargement is caused by the increases in stream stage and velocity, that in turn increase the exchange rate during the flood and drive water farther from the channel (Bhaskar et al., 2012; Malcolm et al., 2004). Conversely, inconsistent patterns of HZ have been observed in response to changes to stream discharge (Ward et al., 2013; Wondzell, 2006). In mountainous streams, the HZ has been found to expand in small streams at lower base flow discharge ($Q < 0.01 \text{ m}^3 \text{ s}^{-1}$) compared to higher-discharge streams (Wondzell,

2011). This behaviour has been interpreted to result from increasing hydrostatic head gradients associated with flow around channel morphological elements at low flow, such as development of lateral channels and flow around bars (Wondzell, 2006).

Consistently with the above findings, HEF paths do not respond uniformly to stream discharge and groundwater flow at reach scale. Groundwater discharge reduces HEF flux and flow path residence time and length, while stream discharge alone does not significantly affect HEF length and residence time (Schmadel et al., 2017; Gomez-Velez et al., 2015; Boano et al., 2008; Cardenas and Wilson, 2007). In spatially heterogeneous reach morphology, these responses are exacerbated by the presence of reach morphological features ((Dudley-Southern and Binley, 2015; Zimmer and Lautz, 2014); Figure 4 in (Schmadel et al., 2017)). Schmadel et al. (2017) observed that flow paths generated by large hydraulic gradients (i.e. bedforms) are less sensitive to changes in hydrological conditions than those generated by the larger context of the valley gradient (Schmadel et al., 2017).

Such complex interactions between groundwater and river regimes generally makes it difficult to identify the dominant drivers of HEF without considering multiple spatial scales. To develop frameworks with improved spatio-temporal resolution of HEF, comprehensive understanding of the valley hydrological condition is required.

2.3.2 Groundwater and stream discharge at large spatial scales

Interactions at the reach scale between the factors described in Section 2.3.1 often results in heterogeneous responses of HEF that require the consideration of processes at a larger scale.

HEF and residence time in river reaches are affected by the relationship between hillslope structure and hillslope water table (Hoagland et al., 2017; Torres et al., 2015; Godsey, 2014; Jencso et al., 2010). To date, model simulations have showed that diel fluctuations of hillslope water tables affect both the length and the residence time of HEF. These fluctuations, which occur due to the temporal lag between stream and aquifer responses, produce a wide range of hydraulic gradients (Wondzell et al., 2010, 2007) and affect HEF by several orders of magnitude. Longer hyporheic flow paths

result in locations with larger hydraulic conductivity, large stream amplitude and large hillslope amplitude with respect to the stream (Schmadel et al., 2017, 2016).

Given the diverse geomorphology of river valleys and the seasonal responses of hillslope water table fluctuations to large scale controls (e.g., precipitation), the relationship between dynamic hydrological valley conditions and HEF remains an area of active research (Schmadel et al., 2017; Bergstrom et al., 2016; Schmadel et al., 2016; Nippgen et al., 2015; Wondzell and Gooseff, 2013; Jencso et al., 2009).

Recent studies have started to consider precipitation inputs to the catchment to enable cross-catchment comparisons of HEF (Hoagland et al., 2017; Jasechko et al., 2016). The drivers discussed in Section 2.3.1 and 2.3.2 vary within and among catchments depending on catchment topography, geology and finally geography (Hoagland et al., 2017; Jasechko et al., 2016). For example, steep, headwater catchments respond rapidly to rainfall because of their small storage capacity (Penna et al., 2016; Gomi et al., 2002; Woods et al., 1995). Rainfall is strongly correlated with seasonal groundwater fluctuations in catchments dominated by transmissive soils (Bachmair and Weiler, 2012). Conversely, in headwater catchment with low permeability soils, rainfall is only a secondary control, after topography, on the response time of groundwater levels (Rinderer et al., 2016). On the other hand, lowland catchments usually have slower response to rainfall (days to weeks), although heavy precipitation events can cause local flooding (Monincx, 2006).

Finally, the relationship between groundwater, stream discharge and HEF is dynamic in nature, depending on the cross-scale interaction of hydrological gradients. Thus, HEF findings at reach scale may not be representative when major changes, e.g., seasonal variations, occur in valley- or catchment-scale characteristics.

2.4 Topographical drivers

Topography is one of the primary drivers of spatial HEF variability. From bedforms to catchments, topographic gradients cause nested hyporheic flow paths (Cardenas, 2008; Wörman et al., 2007). In order to understand how HEF varies spatially within the catchment and how these variations in turn affect temporal variations, we will discuss

HEF at scales within channel topography (individual bedforms and bedforms sequences: Sections 2.4.1.1 and 2.4.1.2), within a valley hydrological (bedforms in valley context: Section 2.4.2) and geomorphological context (valley confinement: Section 2.4.3) and then within the catchment (Section 2.4.5).

2.4.1 In-channel bedforms

Over the last decades, a range of studies have demonstrated that hydrodynamic and hydrostatic forces generated by in channel bedforms have large effects on the variability of HEF from cm to m scale. In this section, we provide a concise summary of the main effects on HEF by single bedforms (i.e. steps, riffles and bars) and bedforms sequences (i.e. step-pool, pool-riffle). We considered bedforms that induce hydrodynamically-driven HEF, i.e. ripples and dunes (Section 2.4.1.1), and larger topographic features, i.e. steps, riffles and bars, that contribute to hydrostatically-driven HEF (Section 2.4.1.2) (Boano et al., 2014).

2.4.1.1 HEF generation by an in-channel bedforms

Head pressure gradients created by the channel bedforms drive advective pore water flow into, through, and out of the bed (Elliott and Brooks, 1997).

Most of the current knowledge of hyporheic fluxes and their spatio-temporal variability in submerged bedforms has been obtained from simulations and laboratory experiments, owing to the difficulties in making high-resolution subsurface measurements within stream channels (Boano et al., 2014; Fox et al., 2014; Irvine et al., 2014; Trauth et al., 2014; Stonedahl et al., 2013; Janssen et al., 2012; Cardenas and Wilson, 2007; Tonina and Buffington, 2007; Glaser et al., 2004; Elliott and Brooks, 1997).

Bedforms develop characteristic shapes due to the interplay of stream flow and bed sediment transport. Dunes and ripples are characterized by a smooth water surface profile (Packman et al., 2004) implying that the spatial variation of water surface topography is minimized and the pressure profile strongly depends on dynamic pressures (Marion et al., 2002; Elliott and Brooks, 1997).

In the case of hydrostatical-driven HEF, the flow is a function of the head gradient, the size and the hydraulic conductivity around the bedform (Hester and Doyle, 2008; Gooseff et al., 2006). High channel slope will normally result in deeper HEF and higher HZ depth (Hester and Doyle, 2008; Gooseff et al., 2006). Riffle-scale exchange, for example, is possible only when high permeability materials surround the stream channel. Hyporheic flow structure is controlled by the spatial relationship of bedforms to high- and low-permeability regions of the streambed (Stonedahl et al., 2018; Pryshlak et al., 2015; Sawyer and Cardenas, 2009; Packman et al., 2004; Salehin et al., 2004). Water upwells where permeability or depth of gravel decreases in the direction of streamflow and where the longitudinal bed profile is concave (Buffington and Tonina, 2009; Elliott and Brooks, 1997; Harvey and Bencala, 1993). Water downwells where permeability or depth of gravel increases, in the direction of streamflow, or where the longitudinal bed profile is convex (Buffington and Tonina, 2009; Elliott and Brooks, 1997; Harvey and Bencala, 1993). Modelling studies have showed that flow paths and exchange rate vary in the alluvium around riffles across seasons and with the extent of groundwater discharge (Stonedahl et al., 2018, 2012; Storey et al., 2003). Gravel bars are also functionally equivalent to riffle bedforms for HEF; the hydrologic retention in gravel bars is strongly influenced by bar structure and stream water levels (Trauth et al., 2015; Tonina and Buffington, 2007; Marzadri et al., 2010; Boulton et al., 1998). Unlike fully submerged features, recent findings by Trauth et al. (2015) suggest that HEF in partially submerged gravel bars decreases with increasing stream discharge as the hydraulic head gradients across the bedform decrease, leading to long residence times under low flow conditions.

In conclusion, an in-channel bedform can have significant effects on its own on HEF and on its residence time distributions. More complex interactions are expected to occur across the spectrum of topographic features (Stonedahl et al., 2010).

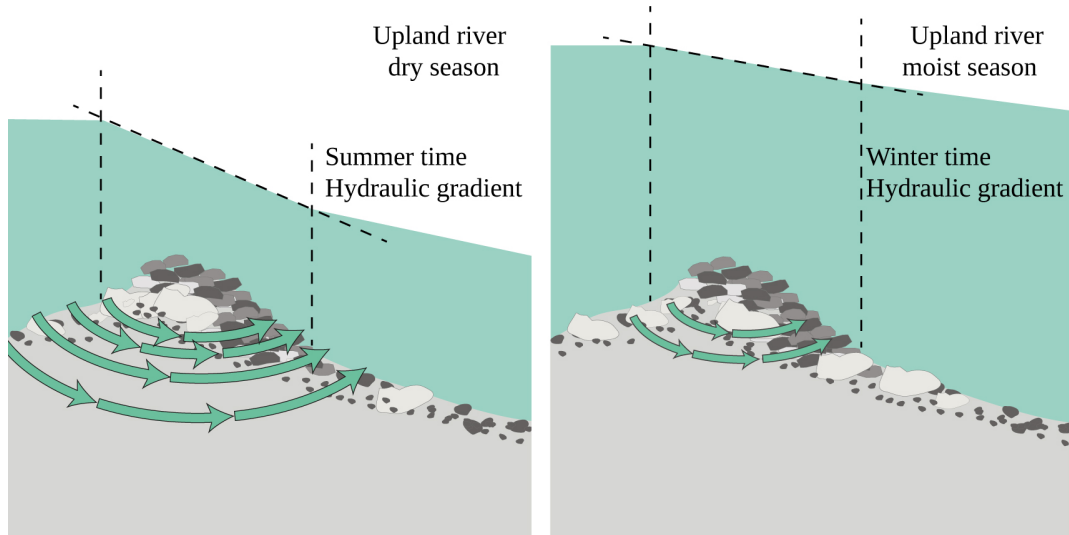


Figure 2.3: Conceptual representation of seasonal variation of hydraulic gradient with water stages in a upland environment. Development of hyporheic exchange in a riffle considering extension and contraction of hyporheic sediment.

2.4.1.2 In-channel bedform sequences

The complexity of nested hyporheic flows will increase with the number and diversity of bedforms in the channel. Local-scale variation of bedforms size will drive longitudinal patterns of upwelling and downwelling, along with multiscale distributions of HEF at reach scale (Stonedahl et al., 2015, 2013, 2010; Gooseff et al., 2006).

Step-pool morphology behaves differently than pool-riffle and dune-like bedforms (Hassan et al., 2015; Marzadri et al., 2010; Tonina and Buffington, 2007; Storey et al., 2003). HEF will develop around a pool-riffle sequence only where hydraulic gradients toward the stream from the sides and beneath are less than or near than the longitudinal hydraulic gradient between the upstream and downstream ends of the riffle (Storey et al., 2003). In gravel bed pool-riffle sequences, significant hydrostatic forces across the channel, high permeability of sediment and low submergence time generate substantial large-scale hyporheic flow (Tonina and Buffington, 2011, 2007; Buffington and Tonina, 2009; Wondzell and Swanson, 1996).

A detailed case study on a upland, gravel-bed river with a riffle-pool bedform sequence showed that, although the expected pattern of downwelling and upwelling conditions were generally observed along the bedform sequence, seasonal variations in hyporheic fluxes occurred because of asynchronous local ground water recharge relative to flow regime (Gariglio et al., 2013). At the riffle-pool scale, this is consistent with previous studies reporting seasonal variations in hyporheic temperature dynamics, with stream topography, sediment stratification, and groundwater interaction all affecting local upwelling and downwelling in riffle-pool systems (Krause et al., 2013; Hannah et al., 2009).

Dune-ripple complexes are less influenced by hydrostatic forces than riffle-pool sequences (Tonina and Buffington, 2011); gradients are much lower than for riffle/pool and step/pool sequences and little affected by spatial and temporal changes in water surface elevation. Simulations have also shown that dunes contribute more than meanders and bars to reach-scale HEF (Stonedahl et al., 2013). Further, the volume of water exchanged and the hyporheic residence time across bedforms is not linearly additive (Stonedahl et al., 2013). Instead, hyporheic exchange is maximized when one topographic feature dominates (Stonedahl et al., 2013). In lowland rivers, the lower slope, finer sediments and more constant flows favour the development of dune-ripple sequences (Elliott and Brooks, 1997; Marion et al., 2002) characterized by high relative submergence and smooth water surface profiles (Packman et al., 2004). Under these conditions, the spatial variation of water surface topography is minimized and HEF is induced primarily by dynamic pressure variations.

These findings suggest that in-channel bedforms often control HEF, although these local exchange flows are still strongly modulated by stream and groundwater dynamics at reach and valley scale.

2.4.2 Alteration of in-channel bedform induced HEF by valley hydrology

The patterns of HEF generated by individual bedforms and bedform sequences are altered by the hydrodynamic conditions of the valley. Longitudinal valley gradients

create hydrostatic head gradients that influence water moving cross and down valley and thus HEF (Harvey and Bencala, 1993).

Schmadel et al. (2016) suggested that valley slope primarily controls the timing of HEF while cross-valley slope and down-valley slope determine net gaining or losing conditions. When bedforms are analyzed with respect to channel gradient, it can be seen that gentle slopes of lowland rivers generate slower currents with deeper flows, lower relative roughness, and less valley confinement, resulting in less bedform-induced exchange (Tonina and Buffington, 2007) (Figures 2.4). For example, dune-ripple streams that occur in lowland rivers, typically exhibit less spatial and temporal variability in water surface elevation than riffle-pool streams (Tonina and Buffington, 2011). In higher-gradient valleys, the flow is predominantly down-valley and spatial variations of hydraulic gradients are paired with changes in cross-sectional areas of the valley and with the hydrodynamic head gradients generated by in-channel bedforms to induce water downwelling into the HZ (Wondzell, 2012; Cardenas et al., 2004). In this setting, hydrogeological properties can have a major role in controlling valley hydrologic exchange: Ward et al. (2012) and Anderson et al. (2005) observed that in steep and constrained sections of his study area, the HEF in step-pool sequences is limited by the underlying bedrock rather than by hydraulic gradients.

In conclusion, both positive and negative relationships between hyporheic zone extent and down- and cross- valley gradients have been reported in literature, suggesting that detailed resolution of hydraulic gradients and knowledge about the valley setting are necessary to understand controls on HEF (Ward et al., 2012).

2.4.3 Valley confinement

The extent of valley confinement indicates different process domains and determines the capacity of the river to adjust in planform (Table 2.1).

Several studies have linked HEF to valley confinement, and showed that HZ depth is restricted, HEF is reduced, and hyporheic residence time is decreased in highly confined valleys (Buffington and Tonina, 2009; Wright et al., 2005; D'angelo et al., 1993; Stanford and Ward, 1993)(Table 2.1). While GSE and HEF are both limited in confined

valleys, bedrock fractures and fissures may allow some hyporheic exchange, depending on their degree of connectivity with the aquifer (i.e. bedrock and colluvial channels in straight and sinuous planforms) (Gurnell et al., 2016; Graham et al., 2010; Freer et al., 2002; McDonnell et al., 1997, 1996). Certainly, the coupling of small changes in water table elevation and bedrock topography can have a large impact on the hyporheic flows (Oxtobee and Novakowski, 2002). For example, HEF transport is expected to be more uniform when the water table is continuous on the bedrock than when the water table falls and interacts directly with bedrock topography (Ward et al., 2012). Bedrock outcrops at valley margins can have opposing impacts on HEF. On one hand, they can limit the infiltration of the stream water into the subsurface and restrict the hyporheic zone (Kasahara and Wondzell, 2003). Indeed, bedrock outcrops can constrain valleys where steep positive vertical hydraulic gradients results from discontinuities of superficial deposits permeability and shallow bedrock (Ibrahim et al., 2010). In this case the HEF can be limited to superficial layers of the riverbed. On the other hand, the irregularities of bedrock projections favour changes in the alluvium volume (Buffington and Tonina, 2009), thus driving stronger hyporheic exchange from the subsurface to the stream and preventing deeper GSE. In fact, the interchange between bedrock and alluvial valleys favours HEF, because of increased downwelling and upwelling where a thin layer of alluvial deposits overlies shallow bedrock (Ward et al., 2012; Wondzell, 2012).

Conversely, in unconfined valleys, floodplain sediments typically represent a mosaic of coarse and fine sediments that originate from hillslopes, bed material (i.e. bedload) and suspended sediment deposited during overbank flooding, within the context of channel adjustment over time (e.g., migration and avulsion) (Nanson and Croke, 1992)(Table 2.1). Tonina and Buffington (2009) classified channel types by examining how bedforms generate hydrodynamic pressure variations and drive hyporheic exchange (Figures 2.4). Generally, unconfined channels have smaller vertical hydraulic gradients and discharges than confined channels, caused by the lower channel gradients and by the heterogeneity of sedimentary deposits (Ibrahim et al., 2010). We synthesize available information on underlying geology, in-channel sediment, valley confinement at valley and reach scales in Table 2.1, where for different channel planforms, geomorphic units

and floodplain characteristics potential HEF response is indicated.

In conclusion, empirical and modelling studies not only suggest the dominance of hydrologic exchange flows by small geomorphic features but also that lateral exchanges of water affect movement of material and energy between rivers and floodplains.

Table 2.1: Expected hyporheic exchange flows in different floodplain types (FT) and channel planform types (CT). Confined, steep/narrow valley (type I); Braided confined, partly confined, unconfined (type II); Sinuous meandering (type III); Anabranching (type IV). Geomorphic unit refers exclusively to in-channel features. Sources: Gurnell et al. (2016); Wondzell and Gooseff (2013); Buffington and Tonina (2009); Nanson and Croke (1992).

FT	Characteristics floodplain	Floodplain geomorphic units	Expected HEF floodplain scale	Channel planform type	Channel geomorphic units	Expected HEF channel
I	High energy, coarse sediment from poorly sorted, boulders and gravel with sand and soils to basal gravels with sand and silt.	Large boulder, levee, deep black channels, scour holes	Confined HEF which is driven by in-channel geomorphic units. Short residence times.	Colluvial: single-threat or straight sinuous.	Rock-steps, cascades, rapids.	Colluvial, channels are usually strongly confined and stable. Very coarse and supply-sediment limited. Cascade and rock steps would likely allow head variations and near-bed turbulence which enhance HEF.
II	Medium energy. Abundant sediment load from gravel to sand and silt	Abandoned channels, bars, islands.	Lateral HEF enhanced by alluvium and head variations (hydraulic conductivity). High residence time	Alluvial: single - threat or straight sinuous.	Small pools, step-pools, bars.	Alluvial channels are relatively stable for long (very coarse to coarse material). Broken, fast-flowing turbulent flow. Where step-pool units occur the HEF is enhanced.
III	Medium energy. Mostly sand with silt and gravel	Smooth to undulating, floodplain surface often with areas of vertically accreted fine sediments, ponds backswards, ponds	Lateral HEF enhanced by alluvium and head variations (hydraulic conductivity) or limited by fine deposited areas. High residence time.	Alluvial channels. Multi-thread	Pools, riffles, riffle-pools, laterals bars, mid-channel bars, islands.	Highly instable vertically and laterally. Sediment supply high. Expected head variations, alluvial volume variations and hydraulic conductivity variations that likely enhance HEF.
IV	Low energy. Fine sediments from silts and clays to sands	Flat, floodplains, extensive islands, peat and lakes swamps, splayes, side-levee	Vertical HEF enhanced or limited by alluvium and head variations.	Single, thread-sinuous or meandering	Pools, riffles, point bars, dunes.	Relatively unstable and subjected to progressive migration. The instability reflects the geomorphologic units that likely promote HEF.
				Multi-thread anabranching	Islands, ripples and dunes, abandoned channels.	Predominantly, stable. Channel variation in sediment alluvium would likely drive some vertical HEF.

2.4.4 Channel planform

As with valley confinement (Section 2.4.3), channel planform is an indicator of lateral HEF interactions with floodplains. Sinuosity is often used as a measure of channel complexity and has been found to be directly correlated with lateral hyporheic exchange in meander bends, and in the parafluvial zone beneath the streambanks (Kiel and Bayani Cardenas, 2014; Cardenas, 2008; Boano et al., 2006; Wroblicky et al., 1998; Holmes et al., 1996). Sinuosity establishes pressure gradients across meanders that induce HEF (Boano et al., 2008, 2006) and influences the amount of water exchanged within a river segment (Han and Endreny, 2013; Gomez et al., 2012; Cardenas, 2009a; Brunke and Gonser, 1997).

High sinuosity rivers (e.g., multi-thread or single/sinuuous meandering) are less prone to a reduction of the hyporheic volume with depth, and maintain the HZ under both losing and gaining conditions (Cardenas, 2009a) (Table 2.1). Meander planimetry drives hyporheic flows and influences hyporheic residence times by creating differences in the elevation head of surface water around a meander bend, with spatial and temporal variations as meanders evolve (Stonedahl et al., 2013; Boano et al., 2008; Revelli et al., 2008; Boano et al., 2006). Naturally forced by the longitudinal head gradient, the hyporheic exchange flows through the meander neck as river water infiltrates into the hyporheic zone at the upstream half of the meander and returns to the river along its downstream half (Kiel and Bayani Cardenas, 2014; Boano et al., 2006; Cardenas et al., 2004). This pattern becomes more complex with the inclusion of floodplain sediment and channel geomorphic features. Lateral hyporheic residence time is short in areas with coarse floodplain sediments and high sediment hydraulic conductivity, and increases in meanders with fine-textured sediments (Boano et al., 2006). In multi-thread planforms, simulations have identified the importance of hyporheic flow paths beyond the active channels toward secondary channels and across the floodplain (Kasahara and Wondzell, 2003) (Table 2.1). Along laterally unconfined valleys, meander creation, extension and cutoff allow significant river adjustment and river-floodplain interactions, causing both in-stream and off-channel geomorphic features to drive lateral hyporheic exchange (Boano et al., 2006).

In conclusion, studies of valley setting, confinement and sinuosity suggest that valley topography provides important clues about disconnection within catchments and can be potentially used as a quantitative and quantitative predictor of HEF. As demonstrated by the above studies, the source of spatial complexity of HEF is not only the result of single geomorphic structures but of the topographical structure of the valley and of the whole catchment.

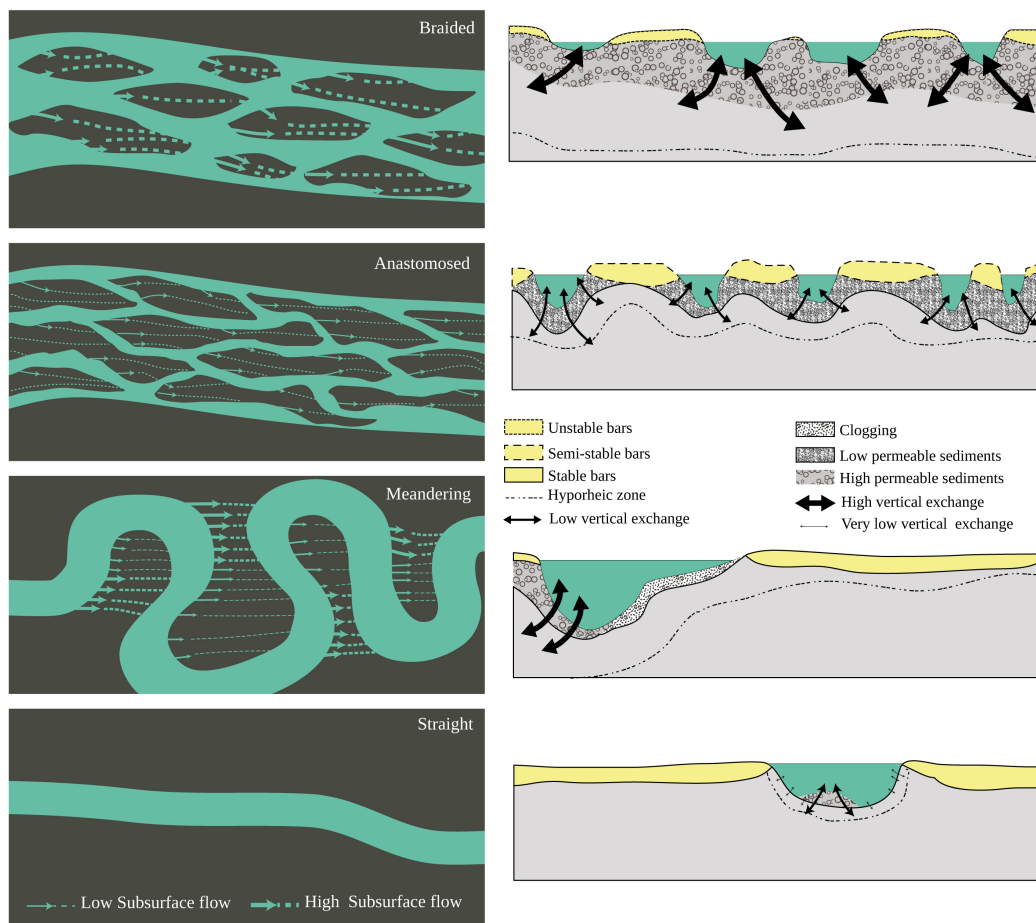


Figure 2.4: Representation of channel planforms. Sinuosity influences water exchange within a river segment. Hyporheic exchange increases with sinuosity due to hydraulic gradients in the meander neck (Section 2.4.4).

2.4.5 HEF in the catchment topography context

Studies have suggested that catchments with larger surface areas have greater hyporheic exchange fluxes (Bergstrom et al., 2016; Laenen and Bencala, 2001; Harvey and Wagner, 2000). Greater variation in water stage correlates on average to greater hyporheic fluxes, but few direct observations are available to support or refute this assumption. The catchment topographic slope defines the direction of flow by creating discontinuities and localized groundwater flow paths (Jencso and McGlynn, 2011; Jencso et al., 2009; Wörman et al., 2006; Winter, 1998).

Emerging upscaling models have started incorporating the information of the catchment area, channel network structure, and head variations of surface topography. These models include i) the first order control of water inputs and groundwater head distribution (Caruso et al., 2016; Jencso and McGlynn, 2011; Laudon et al., 2007), (ii) indications of subsurface flow (Caruso et al., 2016; Jencso and McGlynn, 2011; Jencso et al., 2009; Wörman et al., 2006); and (iii) discretizing the catchment into sub-catchments and identifying topographically contributing recharge and discharge areas (Wörman et al., 2007, 2006). These studies indicate that linking topographic complexity to HEF is likely to be an important priority area of research. Patterns of upwelling and downwelling within reaches were observed to occur where the stream profile is concave and convex, respectively and used to predict patterns of HEF in high-gradient headwater mountain streams (Anderson et al., 2005). While upwelling zones do not show a significant trend with increasing catchment area, the length of downwelling zones increases with stream size, spacing of channel slope and decrease of water surface concavity (Anderson et al., 2005).

These findings encourage interdisciplinary efforts to provide supporting evidence that link HEF across the continuum of headwater, mid-order and lowland streams as a result of systematic changes in hydrogeomorphological characteristics along the stream network.

2.5 Hydrogeological drivers

Geology affects both the distribution of groundwater in aquifers and HEF flows. In this section hydrogeological effects on HEF are summarized into: i) channel sediment impacts on bedform-induced HEF (Section 2.5.1), ii) floodplain sediment impacts on GSE between the valley aquifer and the channel (Section 2.5.2), and iii) bedrock and aquifer type impacts on valley geomorphology (Section 2.5.3).

2.5.1 Channel sediment and bedform-induced HEF

Sedimentological properties strongly control HEF at reach scale. Water flowing through the river bed is affected by sediment grain size, sediment heterogeneity, and depth, promoting spatially diverse hyporheic exchange (Packman et al., 2004).

Given the direct coupling of stream and pore water flow, exchange is generally greatly enhanced in coarser sediments (Packman et al., 2004). As mentioned in Section 1, high velocity gradients and turbulence generated at the surface of coarse sediment beds can also increase diffusion processes which can produce considerable exchange even when the bed surface is flat and no flows are induced by bed topography (Marion et al., 2008; Packman et al., 2004). The presence of high hydraulic conductivity layers in the streambed increases dispersive mixing between hyporheic water and groundwater (Hester et al., 2013) and creates preferential HEF, either short or long paths, by controlling the ability of the sediment to support advective pumping (Pryshlak et al., 2015; Cardenas, 2009a, 2008; Salehin et al., 2004).

Dye injections have shown that hyporheic flow patterns are controlled by the spatial relationship of high and low permeability regions of the streambed, resulting in faster near-surface transport and shallower penetration and a shorter mean residence time (Salehin et al., 2004). Further, longer hyporheic flow paths are generated in streams having greater connectivity of sediment strata (Pryshlak et al., 2015) despite that in coarser bed material, fine sediments accumulate and clog pores (Hartwig and Borchardt, 2015; Bardini et al., 2012; Brunke and Gonser, 1997).

To date, few studies have addressed the effect of sediment heterogeneity on HEF

variability at scales larger than the bedform, although recent works have showed strong impact of sand and gravel deposits on HEF at the reach scale (Zhou et al., 2014) and identified sediment heterogeneity as one of the main drivers of lateral connectivity as well (Pryshlak et al., 2015). In river segments dominated by gravel beds, such as in confined high-energy braided rivers, the hydraulic conductivity is generally high but also highly variable because it depends on the sorting of sediments in the floodplain and on the amount of silt and clay present (Table 2.1 and Figures 2.4). Highly permeable riverbed sediments allow surface water to penetrate easily into the HZ, causing vertical hydraulic gradients (VHG) to change strongly with local sediment permeability (Packman and MacKay, 2003; Wroblicky et al., 1998; Vaux, 1968).

2.5.2 Hydrogeology in river and floodplain type

Channel planforms respond not only to changes in regional physiography and hydrology (Section 2.4.4) but also to sediment loads (Table 2.1) (Gurnell et al., 2016; Nanson and Croke, 1992). Differences in particle sizes in river planforms result in fact, from longitudinal, lateral, spatio-temporal variation of river flows and sediment supply (Bridge, 2009; Baldwin and Mitchell, 2000).

Sediment permeability allows varying hyporheic residence time responses accordingly to finer or coarser deposits (Hester et al., 2016; Pryshlak et al., 2015; Azinheira et al., 2014; Brunke and Gonser, 1997) (Figure 2.4). Braided channels (Section 2.4.4) can occur across a range of valley slopes depending on the grain size of the bed material in transport, and present either a pool-riffle morphology or a bar-riffle morphology (Gurnell et al., 2016). HEF tends to be very dynamic and spatially varying; steep head gradients between channels create cross-valley head gradients that control the location and direction of flow paths through the HZ (Figure 2.4, Section 2.4.4) (Malard et al., 2002; Ward and Stanford, 1995). This transverse exchange evolves with migration and river sediment transports processes (Stonedahl et al., 2010; Boano et al., 2006; Kasahara and Wondzell, 2003). In sinuous, medium energy meandering floodplains, HEF is also usually driven by variations in head gradients (advection processes), which are greater than diffusive transport by two or more orders of magnitude (Elliott and Brooks, 1997;

Larkin and Sharp, 1992). This type of floodplain typically presents vertically accreted fine sediments (silt and clay). These local low-permeability units and thick sequences of unconsolidated deposits become more compact and less permeable with depth (Winter, 1998) thus they are characterized by localized groundwater flows and restricted HEF (Angermann et al., 2012; Krause et al., 2012; Stonedahl et al., 2012).

In lowland settings with abundant fine sediment load, reduction of groundwater up-welling due to low sediment conductivity layers causes surface water to downwell and induces horizontal hyporheic flow into shallow streambed sediments above low conductivity strata (Angermann et al., 2012; Stonedahl et al., 2012). Spatial variations in the thickness of fluvial-alluvial deposits increased local gradients around clay lenses, therefore creating locally confined conditions (Ellis et al., 2007).

All of these studies indicate that the thickness of superficial deposits controls the extent and rate of hyporheic exchange (Tonina and Buffington, 2011; Buffington and Tonina, 2009; Anderson et al., 2005).

2.5.3 Hydrogeology in the catchment: bedrock and aquifer type

From reach to regional scale, geology affects the distribution of groundwater in aquifers and the spatial variability of GSE and HEF via the aquifer geometry and hydrogeological properties. Lithologic types and structure, weathering history of bedrock and types of aquifers, impact HEF by altering the distribution of hydraulic conductivities (Fox et al., 2014; Gomez-Velez and Harvey, 2014; Angermann et al., 2012; Krause et al., 2011a; Hiscock, 2007; Woessner, 2000; Morrice et al., 1997; Winter, 1998).

Bedrock exerts vertical and lateral constraints on river forms and processes, by controlling the interaction of GSE and HEF subsurface flows and defining valley confinement (Section 2.4.3). Different relationships appear depending on whether the structure is consolidated or semi-consolidated, and on the primary and secondary porosity of rock deposits including limestone, dolomite, shale, siltstone, sandstone, and conglomerate (e.g., pores and fractures) (Binet et al., 2017; Hoagland et al., 2017; Jencso et al., 2010; Sear et al., 1999). For example, hyporheic studies in chalk catchments have shown

the importance of groundwater in supporting surface-subsurface exchange at catchment (Lapworth et al., 2009; Grapes et al., 2005), valley and reaches scales (Griffiths et al., 2006; Grapes et al., 2005), although vertical hyporheic exchange in these systems is often restricted by local low-conductivity superficial deposits (Allen et al., 2010; Pretty et al., 2006) (Section 2.5.1).

In addition to the characteristics of the bedrock, the degree of confinement of the aquifer due to impermeable layers would prevent or limit GSE and HEF to local interactions (Gurnell et al., 2016). In confined aquifers, which are separated from the surface by aquitards with low hydraulic conductivities, GSE would likely be prevented (Winter, 1998). If the confinement is due to the presence of near-surface bedrock, HEF would also be prevented by the lack of highly porous alluvium and the low permeability of the bedrock (Buffington and Tonina, 2009; Kasahara and Wondzell, 2003). In confined bedrock, colluvial channels, and confined alluvial channels, GSE and HEF are limited by the local structure of the local sediment (e.g., coarse or fine particles) and the rock structure (e.g., continuous or discontinuous confinement) (Table 7.5 in Gurnell et al. (2016)).

In unconfined aquifers, generally groundwater is easily conveyed in all directions leading to high opportunity for both vertical and lateral HEF exchange (Winter, 1998). However, in unconfined alluvial channels, GSE and HEF can be prevented or limited to local interactions depending on local sediment (e.g., coarse or fine particle size) (Table 7.5 in Gurnell et al. (2016)).

In conclusion, HEF from reach to catchment scales is highly related to bedrock lithology and superficial sediment. The complexity of geological properties at the catchment scale results in spatio-temporal variations in HEF, in the channel and throughout the river network. A point upstream in the catchment may exhibit HEF dynamics driven by entirely hydrogeological processes compared to the catchment outlet. These differences are especially heightened in catchment with mixed land use and anthropogenic pressures (e.g., dams) for which comprehensive understanding is required of the timescales of water and solute flux with different geologies.

2.6 Ecological drivers

Vegetation has long been known to exert a strong control on land surface hydrology by moderating streamflow and groundwater recharge (Section 2.3.2). By altering hydrological processes on channel banks, floodplains and the wider catchment, vegetation-induced feedback on the temporal variability of HEF and likely increase the spatial heterogeneity of this ecological- hydrological relationship. This section describes in-channel (Section 2.6.1), bank and floodplain vegetation by focusing on two key ecological functions: riparian vegetation (Section 2.6.3) and large in-channel wood (Section 2.6.2).

2.6.1 In-channel vegetation

In-channel vegetation controls HEF directly through channel-scale flow resistance and indirectly through sediment and streambed permeability (Jones et al., 2008). A variety of herbs, shrubs and trees grow in stream channels, increase bed roughness and alter flow velocities. They produce a mosaic of hydrodynamic conditions with low flows in vegetation patches and high flows between patches (Corenblit et al., 2007).

Vegetation also alters stage-discharge relationships that affect hyporheic flow, where higher water levels and faster in-channel flows are maintained in mid-summer (Heppell et al., 2009; Harvey et al., 2003). Jones et al. (2008) demonstrated that in-channel vegetation restructures hyporheic flow patterns by creating temporally dynamic deviations of hydraulic gradients. In-channel vegetation increases the friction factor (Harvey et al., 2003) and create low flow areas that increase water residence time (Kjellin et al., 2007; Ensign and Doyle, 2005; Wörman and Kronnäs, 2005; Salehin et al., 2003). This aspect has been observed especially in streams with extensive vegetation where flow can decrease to nearly zero within dense vegetation stands (Ensign and Doyle, 2005; Salehin et al., 2003). Further, the reduction of flow velocity within plant stands leads to increased sediment deposition and the development of plant-mediated sediments that are typically finer-grained than the bed material with more organic material and lower permeabilities (Corenblit et al., 2007), which also reduces HEF.

In conclusion, both field and laboratory studies have suggested that vegetation shapes transient storage in streams channels, even though there are still difficulties in understanding the feedback of mixing due to vegetation and to induced HEF at reach scale. The role of vegetation on patterns of HEF at larger spatial scales is still unexplored. In particular, bank vegetation needs to be considered in terms of hydrological connection between riparian vegetation and the stream (Duke et al., 2007) (Section 2.6.3).

2.6.2 In-channel wood

Within stream channels and valleys, wood deposits drive physical complexity of the river network by altering flow resistance, channel-floodplain connectivity, vertical and lateral accretion of floodplain (Davidson and Eaton, 2013; Wohl, 2013; Phillips, 2012; Jeffries et al., 2003; Mutz, 2000; Sear et al., 1999; Piégay and Gurnell, 1997). Wood affects channel hydraulics and induces deeper HEF by increasing the variability in vertical head and imposing greater hydraulic resistance (Lautz and Fanelli, 2008; Mutz et al., 2007; Mutz, 2000). Wood generally has a comparable effect to other in-channel structures (Section 2.7.1) and channel roughness elements (Section 2.4.1.2) by driving water into the subsurface, where it travels along short hyporheic flow paths (Boano et al., 2006; Lautz et al., 2006). The impact of wood on HEF varies with valley topographic gradient (lowland and upland), groundwater dynamics (gaining and losing) and sediment transport (Gregory et al., 2003; Jeffries et al., 2003).

In lowland rivers, where flow velocity is slow and gradient low, wood induces less HEF and also has less effect on spatial patterns of HEF (Krause et al., 2014). Temporally, Wondzell (2006) observed that, although lowland streams are sensitive to changes in wood delivery, and wood decreases HEF at short time-scales, large-scale channel adjustments reverse the effect of natural wood removal over longer time-scales, causing higher HEF fluxes. Over the long term, wood removal results in longer mean hyporheic residence times, which impacts many hyporheic functions including temperature, nutrient retention, and oxygen concentrations (Sawyer and Cardenas, 2012; Stofleth et al., 2008).

In upland rivers, wood typically creates steeper head gradients that drive hyporheic flow paths (Krause et al., 2014). Interactions between flow and wood also produce spatial heterogeneity in deposits of sediments and organic matter (Osei et al., 2015b,a; Sear et al., 2010; Latterell et al., 2006; Gregory et al., 2003; Naiman et al., 2000). Fines and organic-rich sediments are retained, eventually driving higher spatial heterogeneity in HEF (Section 2.5.2 and 2.7). However, Kasahara and Hill (2006) observed little impact of a large wood-constructed step on oxygen concentrations within the hyporheic zone, presumably due to siltation (Parker et al., 2017; Wohl et al., 2016; Menichino and Hester, 2014).

At the valley scale, wood delivery depends on short- and long-term patterns of land use and geomorphology, often establishing floodplain geomorphology as the dominant control on wood storage in river systems (Benda and Bigelow, 2014). Indeed, one of the variables influencing wood transport and storage is valley geometry. Several studies have documented the importance of woody debris in shaping channel patterns and floodplain evolution in a variety of environments (Collins et al., 2012; Millington and Sear, 2007; Abbe and Montgomery, 2003; Jeffries et al., 2003; Collins et al., 2002; Piégay and Marston, 1998; Sear et al., 2010). However, relatively few studies have examined patterns of wood distribution relative to valley geometry or HEF responses to morphological changes induced by large wood at valley scale (Wohl and Cadol, 2011).

2.6.3 Riparian vegetation

At valley scale, riparian vegetation is well known to shape patterns of GSE by affecting riverbank filtration and altering water-table elevations via transpiration (Jones et al., 2008; Chen, 2007). Vertical and lateral hyporheic flow patterns are characterized by non-linear spatial variations with both vegetation composition (i.e., species) and water consumption (i.e., ET, (Larsen et al., 2014; Wondzell et al., 2010; Martinet et al., 2009).

The ET from riparian vegetation can increase hyporheic fluxes by 1-2 orders of magnitude at time scales of weeks to months (Larsen et al., 2014). The effect of ET on HEF is especially significant in low-energy environments, where ET drives mixing

comparable to that of molecular diffusion and that varies at different times of the year (Bergstrom et al., 2016; Larsen et al., 2014; Iturbe and Porporato, 2004; Porporato et al., 2004). Conversely, in high-energy environments where turbulent mixing and bedform-induced pumping are very rapid (Section 2.4.2 and Figure 2.4), the effect of ET will be lower. On the daily time scale, evapotranspiration changes groundwater gradients with riparian zone vegetation creating the lowest water table in the afternoon, promoting surface water infiltration and hyporheic exchange (Wondzell et al., 2010; Loheide and Lundquist, 2009). Duke et al. (2007) observed a seasonal correlation between transpiration and stream flow with hyporheic gradients. During winter, the correlation is very strong and high water tables and hillslope vegetation lead to negative hyporheic gradients and to high hydraulic head at the bank surface. Conversely, in summer the stream channel has less surface flow and less active exchange within the HZ, and deep flow paths are very important in this period (Duke et al., 2007).

At valley scale, the effect of riparian vegetation has been observed to greatly influence energy inputs to the stream by controlling channel complexity, resulting in increased retention by increasing residence time and contact between stream water and hyporheic zone. This hydrological interaction has been studied in arid catchments (i.e. Sycamore Creek, a Sonoran Desert stream (Schade et al., 2005, 2002)) where soils are often highly impermeable and the presence of riparian vegetation is dependent on stream flows and shallow groundwater tables (Schade et al., 2005, 2002; Stromberg et al., 1996).

Most of these studies have been performed in arid environments, and information on the effects of ET on HEF in humid environments is lacking.

In conclusion, the direct and indirect effects of riparian vegetation on HEF at floodplain/catchment level are poorly studied relative to effects of morphology and groundwater recharge/discharge, although the studies mentioned above provide a foundation for evaluation of groundwater-dependent riparian vegetation on the HZ.

2.7 Anthropogenic drivers

Humans have extensively modified many river systems, and these changes impact the natural factors and processes that control HEF. Alterations to catchments, valleys, and river channels affect the hydrology (e.g., river stage fluctuations), hydraulics (e.g., altering vertical hydraulic gradients) and physiographic setting (e.g., geology, morphology). Effects of three main anthropogenic factors on HEF will be discussed: (i) river stage fluctuations due to in-channel structures and (ii) valley-spanning dams, and (iii) changes in sediment delivery and channel complexity due to land use and land management.

2.7.1 In-channel structures

Channel structures (e.g. weirs, log dams) that control change flow conditions by obstructing the flow and dissipating energy have positive and negative impacts on HEF (Daniluk et al., 2013; Hester and Doyle, 2008; Lautz et al., 2006).

Upstream of the control structure, a decrease in channel velocities and bedform size, combined with an increase in water depth and channel cross-sectional area are usually observed and associated with a reduction of turbulent hyporheic exchange in coarser sediments (Blois et al., 2014; Boano et al., 2010; Jin et al., 2009) and advective HEF by ripples, dunes, and bars (D'angelo et al., 1993).

Downstream of control structures, a decrease in sediment loads, scour, and turbulent fluxes in coarser sediment are usually observed (Hester et al., 2009). Weirs induce HEF upstream of the obstruction, flow beneath it, and upwelling on the downstream side (Jin et al., 2009; Hester and Doyle, 2008). The effect of these structures is complicated and may vary under different flow conditions. Conservative tracer experiments at reach scale have showed that the cumulative effect of multiple weirs increased the cross-sectional area of the surface stream and of the transient storage zones behind weirs, while HEF decreased (Rana et al., 2017). As a consequence, multiple weirs reduce short and fast HEF while inducing long and slow-moving hydrostatically-driven hyporheic flow paths (Rana et al., 2017). Hence, the evaluation of potential effects of channel-spanning

structure on HEF requires rigorous analysis with respect to channel flow variation.

The various effects of these measures are complicated and include disruption of downstream flux of sediment with critical consequences for the alluvial structure and on HEF at streambed or meander scale (Poole and Berman, 2001).

2.7.2 Dams

Large valley-spanning obstructions such as dams can affect HEF by ponding water, disrupting sediment transport, altering vertical hydraulic gradients and varying flow dynamics (Schmadel et al., 2016; Gerecht et al., 2011; Fritz and Arntzen, 2007; Arntzen et al., 2006). The daily stage fluctuation from hydroelectric dams for example, regulate the size of the hyporheic zone and the magnitude and frequency of HEF (Sawyer et al., 2012; Gooseff et al., 2006; Lautz et al., 2006; Harvey and Bencala, 1993). In case of dam-induced water levels changes, a temporal lag occurs between stream stage and aquifer water; HEF is transient and penetrates several meters into the riparian aquifer with residence times of hours (Sawyer et al., 2009). Schmadel et al. (2016) predicted HEF and residence times from the timing and magnitude of diel fluctuations and valley slope, and found that minimal exchange occurs when the magnitude of stream level fluctuations coincide with the hillslope water table, while maximum exchange occurs when stream stage is out of phase with the hillslope and therefore larger amplitude in stream and hillslope occur.

Studies using thermal sensors have reported differences of HEF within the subsurface upstream and downstream of dams, attributed to the overall hydraulic behaviour around the dam and to the changes in topography induced by the dam (Hester et al., 2009; Fanelli and Lautz, 2008). Upstream and downstream pools created by ponding and channel degradation, respectively, have the potential to drive bedform-scale exchange flow. Temperature results suggest that highest hyporheic exchange rates occur downstream of dams, while HEF is limited in upstream pools where fine sediment deposits yield low hydraulic conductivities (Fanelli and Lautz, 2008).

2.7.3 Land management and use: impacts on sediment delivery, channel complexity and hydrological regime

Land cover and management impacts on HEF through several pathways, as it impacts on the quality (i.e. sediment delivery and channel complexity) and quantity (i.e. discharge, infiltration, evapotranspiration (ET)) of groundwater and surface water (Santos et al., 2015; Carrillo-Rivera et al., 2008).

The relationship between land use, sediment delivery and HEF remains an area of active research, but in general both urbanization and agriculture significantly modify channel morphology, streambed sediment size, and hydraulic conductivity by competing effects from increasing fine sediment inputs (which decrease streambed hydraulic conductivity) and stream discharge (which increases advective HEF) (Emanuel et al., 2014; Ryan et al., 2010; Kasahara and Wondzell, 2003; Morrice et al., 1997; D'angelo et al., 1993).

First, decreased porosity and permeability of streambed sediments, e.g., due to increased sediment loads from agriculture, is usually connected to decrease of in channel storage and hyporheic exchange flows (Packman and MacKay, 2003; Brunke and Gonser, 1997).

Secondly, water abstraction often include both pumping stream surface and groundwater, which can increase groundwater levels and thereby increase groundwater discharge to streams and/or decrease stream water flow to groundwater (Winter, 1998). Lower water tables generally reduce the vertical extent of the HZ by increasing water losses from the stream and reducing the hydraulic gradients that drive HEF (Hancock, 2002). Not only the magnitude but also the length of the hyporheic exchange flows are affected: tracer experiments conducted on several reaches within a single land use type showed a reduction of transient storage as a function of the surrounding land use due to lower geomorphological complexity in agricultural streams, promoting the formation of low-flow zones but reducing HEF (Gooseff et al., 2007). However, little research has been carried out on HEF in urban rivers where low morphological complexity and anthropogenic factors have impacted streams substrates and planforms (Drummond et al., 2017; Gooseff et al., 2007; Grimm et al., 2005; Groffman et al., 2005; Walsh

et al., 2005).

2.8 Case study: the River Tern

While previous sections described how individual factors influence HEF, these factors interact across spatial scales to produce a high degree of spatial and temporal heterogeneity in HEF. To illustrate the challenges in resolving hyporheic exchange across scales, we use the River Tern (UK) as a case study. We first review previously published research on HEF in this stream, and then discuss the multi-scale factors that influence HEF based on the review presented previously in Sections 2.3 to 2.7.

HEF has been studied in great detail at the sub-reach scale in the River Tern (Krause et al., 2013; Angermann et al., 2012; Krause et al., 2011a; Hannah et al., 2009). Results indicate that that spatial variations in surficial geology of the floodplain and temporal variations in groundwater levels control local river-aquifer interactions, and dictate the rates and patterns of HEF. Strong correlations between rainfall and groundwater levels indicate that the river acted as a recharge boundary, and pumping tests suggest that hydraulic continuity of bedrock with the River Tern is greater at high flows than at low flows (Streetly and Shepley, 2005). At more local scales, Hannah et al. (2009) and Angermann et al. (2012) found that spatial heterogeneity in HEF is controlled by both topography and streambed strata. Heat tracer studies identified inhibition of hyporheic flow in peat and clay lenses below the stream (Angermann et al., 2012). Given this structure, hyporheic flow paths in riffles did not coincide with the patterns expected from topography-induced head distributions, and instead seem to be driven by locations of confining peat and clay strata Angermann et al. (2012). Temperature data indicated that advected surface water or groundwater control heat transport within the hyporheic zone (Hannah et al., 2009). Hannah et al. (2009) and Anibas et al. (2012) showed that the local hydrogeological and geomorphological context explains the observed seasonal thermal differences between riffles: increased downwelling at riffle tails during winter results from greater groundwater influence and high water stage (Figure 2.3).

These results highlight the need to integrate interpretations of observed rates and patterns of hyporheic exchange with hydrogeological and geomorphological context. As

a starting point, valley type can be used to predict the development and extent of lateral hyporheic exchange. We illustrate the generic nature of valley confinement for the River Tern considering the headwater valley of the Tern at Norton-in-Hales and including the 150 m reach considered in previous studies (Hannah et al., 2009).

The catchment is low-lying, with average elevations between 50 and 120 m, and the area is predominantly agricultural, with croplands and pastures accounting for the majority of the land area (Fuller et al., 2002). The valley section has an elevation ranging from 91 to 114 m, a low channel gradient between 0 and 0.2% and is laterally unconfined. The River Tern and its tributaries are underlain by Permo-Triassic sedimentary rocks (sandstone and conglomerate interbedded), which dominate river-aquifer interactions at regional scale (Allen et al., 1997). This permeable geology supports unconfined highly, moderately-productive aquifers characterized by intergranular flows. However, most of the surficial geology of the catchment is from the Pleistocene age, ranging from sand and gravel to diamicton, peat and clay. The thickness varies spatially across the catchment, with thicker areas in the western part of the catchment comprising up to 30 m of till (Streetly and Shepley, 2005). Throughout the length of the selected section, the river is fringed by wet woodland, predominantly *Alnus glutinosa*. The bedrock is mainly sandstone and mudstone, whereas the superficial geology is sand and gravel with some silt, clay and diamicton. The valley was divided into reach sections of 850 m and analyzed the confinement according to the framework of Fryirs et al. (2016). Some reaches are laterally constrained by anthropogenic structures (roads, houses) in one or both sides (Table 2.2, Figure 2.5). The anthropogenic confinement is most prominent in proximity to the town, where the active floodplain is artificially disconnected by engineered structures. Given that the channel planform is mostly meandering, and is not constrained by bedrock (Section 2.4.3), lateral hyporheic flows will likely occur predominately in unconfined areas, where the planform can adjust to its sinuous-meandering shape (i.e. reaches 1, 4, 5, 6, 7, 8, 9, 10 in Table 2.2). According to the hydrogeology of the area (Section 2.5.1), hydraulic conductivities are expected to be highly variable as consequence of the sediment sorting and HEF will likely vary within reaches when arenaceous and rudaceous lithologies dominate on argillic and peat sediments (i.e. reaches 2, 4, 5, 6, 8, 9 in Table 2.2). Finally, differences along the general gradient of

the network (Sections 2.4.4 and 2.4.5) are expected where the conjunction of increase of riverbed slope, meander bends, and bedforms (Section 2.4.1.2) will likely increase hydraulic head gradients and induce HEF (i.e. reaches 4, 5, 7, 8 in Table 2.2).

Previous research suggests that the mosaics of hyporheic exchange in the River Tern are induced by spatial variations in streambed topography and sediment permeability and temporal variations in groundwater recharge. Through the discussion of this case study, we illustrated that assessment of the geological and morphological context for the river channel can help to explained observed patterns in bedform-driven HEF. This work outlines the opportunity to build HEF scaling relationships from basic patterns of channel morphology, valley confinement, and hydrogeological properties.

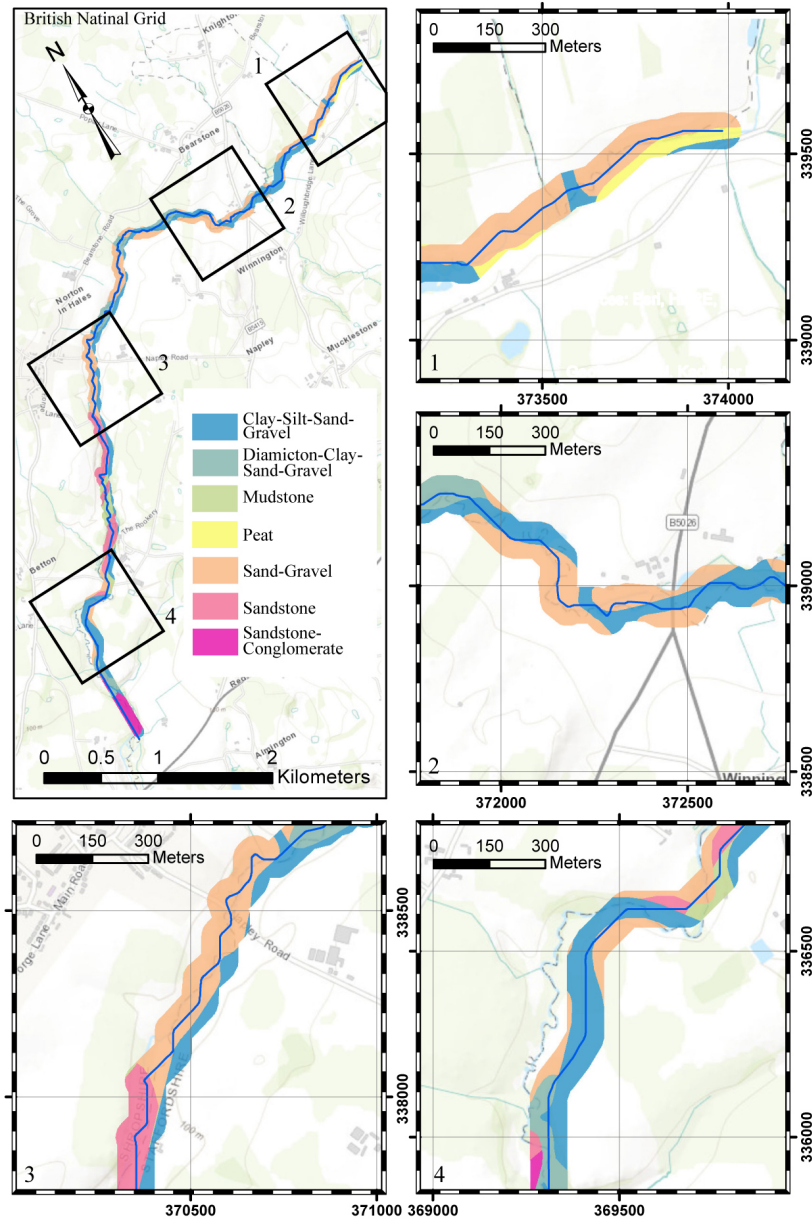


Figure 2.5: Examples of reaches of the River Tern analysed for HEF (Table 2.2). The river is subdivided into reaches based on their planform morphology (sinuosity units: when the overall direction of the planimetric course changes) and classified in Table 2.2. The figure represents for each reach, the main river, surficial and bedrock geology in a buffer area of 50 m from the main channel. Surficial and bedrock geology are represented as greater the connectivity within sediment strata and higher the HEF. Vertical HEF will be restricted by low permeability units and unconsolidated deposits and lateral HEF by grain size material, river sinuosity and cross-valley head gradients.

Table 2.2: Case study about the river Tern, UK (Section 2.8). The table describes the 10 reaches sections (RS) obtained by dividing the river channel into sinuosity (S) units based on changes in the axis of the overall planimetric course. The units that differed in sinuosity by more than 10% were considered separate reaches. Surface geology and valley type are evaluated with respect to the extent of lateral hyporheic exchange. The sections are enumerated and described from upstream to downstream. Information of geology extracted from the British Geological Survey website.

RS	Underlying geology	In-channel sediment	Description	Channel Gradient (%)	S
1	Sandstone-conglomerate bedrock of Triassic period. Superficial geology, sedimentary substrate of quaternary period. Alluvial, fluvial and glacial sediments	Min grain is clay. Max grain is gravel. Mixed argillic and arenaceous grains.	Unconfined valley on both banks. The river is meandering and the riparian vegetation is abundant	0.001	1.089
2	Mudstone and sandstone bedrock of Triassic period. Superficial geology, sedimentary substrate of quaternary period. Alluvial and glacio-fluvial sediments.	Predominant min grain is sand and max grain is gravel. Dominant grain is sand. Arenaceous -rudaceous grains.	Partially confined valley due to industrial plants and homes on the right bank of the river. The river is sinuous with the presence of a big meander and abundant riparian vegetation	0	0.487
3	Bedrock: mudstone and sandstone interspersed. Sedimentary geology of Triassic period. Dominance of fluvial sediments.	Min grain mud and clay and max grain is gravel. Dominant grain sand and mud. Argillic -rudaceous grains.	Partially confined valley due to homes on the right bank of the river. The river is overall sinuous with the presence of small meander and very abundant riparian vegetation	0.052	0.537
4	Bedrock: sandstone. Superficial geology, sedimentary substrate of Triassic period. Dominance of fluvial deposits.	Min grain is mud, max grain is gravel. Dominant grain is sand. Arenaceous rudaceous grains.	Mostly unconfined valley, presence of homes on the right bank of the river. The river is meandering and abundant riparian vegetation	0.261	1.962
5	Superficial geology of quaternary period. Dominance of glacio-fluvial deposit.	Min grain is clay, max grain is gravel. Dominant grain is sand. Arenaceous -rudaceous grains.	Mostly unconfined valley, presence of homes on the left bank of the river. The river is forming small meanders and abundant riparian vegetation	0.030	0.718

Continued on next page

Table 2.2 – *Continued from previous page*

RS	Underlying geology	In-channel sediment	Description	Channel Gradient (%)	S
6	Superficial geology of quaternary period. Dominance of glaciofluvial and glacial deposit.	Min grain is clay, max grain is gravel. Dominant grain is sand. Arenaceous -rudaceous grains.	Unconfined valley on both banks. The river is meandering and riparian vegetation is present throughout its length but mostly on the left bank.	0.011	0.600
7	Superficial geology of quaternary period. Dominance of glaciofluvial and glacial deposit.	Min grain is clay, max grain is gravel. Dominance of clay with gravel. Mixed argillic and rudaceous grains.	Unconfined valley on both banks presence of a small bridge. The river is meandering and riparian vegetation is present. Throughout its length although more scarce with comparison to previous sections.	0.06	1.870
8	Superficial geology of quaternary period. Dominance of glaciofluvial and alluvial deposits.	Min is clay and max is gravel. Mixed arenaceous and argillic grain.	Mostly unconfined valley, presence of industrial plant on the left bank of the river. On the left bank there are two ponds. The river is forming small meanders, riparian vegetation is present.	0.05	1.060
9	Superficial geology of quaternary period. Dominance of glaciofluvial and alluvial deposit.	Min is clay and max is gravel. Predominance of sand grains.	Unconfined valley on both banks. The river is meandering and riparian vegetation is present and abundant on the left bank. Presence of pond.	0.003	0.943
10	Superficial geology of quaternary period. Dominance of glaciofluvial and fluvial deposits.	Min grain is clay and max grain is gravel with presence of silt. Mix of arenaceous and rudaceous grains with peat and argillic.	Unconfined valley on both banks. The river is mostly sinuous and riparian vegetation is abundant on both banks.	0.012	0.826

2.9 Conclusion

Information on the underlying drivers of HEF across space and time, and unravelling the process interactions between them, is essential to predicting HEF patterns

in catchments. However, we are currently unable to fully capture the extent of the interaction between factors that drive HEF.

This review highlighted the factors operating over multiple spatial and temporal scales that govern HEF, and summarise how they interact to determine HEF. Predictive relationships are needed to enable upscaling to catchment scales or downscaling to sub-reach-scales, as well as the response of HEF to changing hydrological, topographical, geological, ecological and anthropogenic conditions. The ability to understand the temporal and spatial dynamics of HEF depends on the holistic perspective suggested here, which considers co-variations between flow, slope, valley confinement, catchment area, sediment size, and river planform and bedforms morphology. Direct data on HEF at larger scale than reaches are severely limited.

By summarizing the factors responsible for rates and patterns of HEF in river systems this review provides a comprehensive understanding and evaluate the characteristics of hyporheic flows in conjunction with and embedded within catchment and valley characteristics.

Acknowledgements

This work was supported by the Marie Skłodowska-Curie Action, Horizon2020 within the project HypoTRAIN. Grant agreement no: 641939.

Chapter 3

A multiscale statistical method to identify potential areas of hyporheic exchange for river restoration planning

Abstract

The hyporheic zone (HZ) is an area of interaction between surface and ground waters present in and around river beds. Bidirectional mixing within the HZ, termed hyporheic exchange flow (HEF), plays significant roles in nutrient transport, organic matter and biogeochemical processing in rivers. The functional importance of the HZ in river ecology and hydrology suggests that river managers should consider the HZ in their planning to help compromised systems recover. However, to date available river restoration planning tools fail to take the HZ into account. This paper describes a novel multiscale transferable method for identifying areas with potentially significant HEF, combining environmental information at different scales, for use in restoration priority planning. It uses a deductive approach that is suited for data-poor cases, given the very limited data on the spatial occurrence of areas of hyporheic exchange. Results on nine contrasting European rivers, demonstrate its potential to inform river management.

Keywords: multiscale, hyporheic zone, geostatistics, clustering analysis, river management

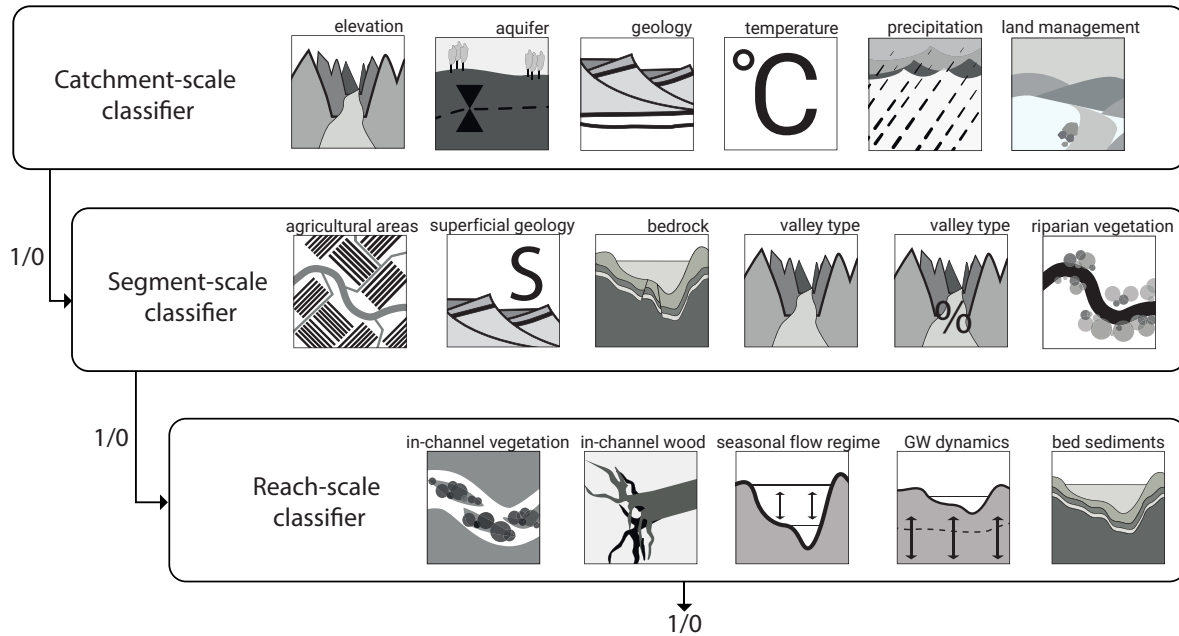


Figure 3.1: Conceptual model of the hyporheic classifiers, i.e. “1” or “0” in every spatial scale and the related environmental hyporheic drivers. The classifier of one scale informs on the classifier on the first smaller scale.

3.1 Introduction

The hyporheic zone (HZ, Orghidan (1959)) is a region where surface and ground waters mix together within the bed and banks of a river. It is characterized by a diverse fauna and by a bidirectional flow of water known as hyporheic exchange flow (HEF, Robertson and Wood (2010)). A large body of scientific literature has shown that both the physical and the biological components of the HZ play a major role in river functioning (Krause et al., 2011b; Brunke and Gonser, 1997; Findlay, 1995). HEF is important for nutrient transport and cycling (Battin et al., 2008; Triska et al., 1993), stream water temperature variation (Dugdale et al., 2018), contaminant deposition and breakdown (Palumbo-Roe et al., 2017; Fuller and Harvey, 2000), organic matter processing (Danczak et al., 2016; Drummond et al., 2014; Zarnetske et al., 2011; Sobczak and Findlay, 2002) and the distribution and abundance of ecological communities (Battin et al.,

2016; Dole-Olivier et al., 2014; Boulton, 2007). Perhaps, the best-known examples of the importance of HEF on driving ecological processes concern the supply of oxygen into the sediment (Corson-Rikert et al., 2016; Gibbins et al., 2016) and the modulation of biogeochemical transformation (i.e. denitrification and nitrification processes) (Mendoza-Lera and Datry, 2017; Heppell et al., 2014; Nogaro et al., 2010; Wood and Armitage, 1999). As result of the scientific evidence for HEF supporting ecosystem level processes in river systems, restoration practitioners have started to incorporate measures that promote HEF to mitigate water quality impacts, support biodiversity and increase ecological resilience (Mendoza-Lera and Datry, 2017; Hester and Gooseff, 2011).

Restoration measures can induce or enhance HEF through the generation of hydraulic gradients, creation of geomorphological heterogeneity (i.e. bedforms, sediment sorting) and decrease of sediment load (Tuttle et al., 2014; Gordon et al., 2013; Schirmer et al., 2014; Hester and Doyle, 2008). However, at present there is little guidance on appropriate siting of restoration measures to locations where HEF has the greatest potential to be enhanced, and most of the hyporheic-restoration work has focused on in-channel factors. As HEF is defined by the interaction between surface and groundwater, both surface and subsurface conditions influence the occurrence of HEF at multiple spatial scales (Boano et al., 2014). In fact, hyporheic exchange exhibits scale-dependency where HEF at reach and sub-reach scale is influenced significantly by larger-scale hydrogeological patterns and processes (Aubeneau et al., 2015; Stonedahl et al., 2010; Cardenas, 2008, 2007; Wörman et al., 2007; Boano et al., 2006).

This fractal dimension to HEF means that the occurrence, rates, spatial patterns and temporal variability of HEF are determined by the interaction of physical, chemical and biological processes in the river valley and catchment (Ward, 2016; Boano et al., 2014). There are a large number of factors that influence these processes, which can be divided into three broad and overlapping categories: (1) hydrological, (2) hydrogeological, (3) topographic, (4) anthropogenic and (5) ecological (Table A.1, Table 3.1, Table 3.2).

Currently no framework exists to represent the complexity of multiple inter-related and cross-scale processes affecting the importance of HEF, taking account of typical

data availability (Ward, 2016), in river restoration prioritization and planning. Therefore restoration measures could be used at different scales to promote HEF but the difficulty of prioritizing restoration sites and selecting approaches (i.e. measures) from catchment assessments is caused by the lack of supporting tools for explicitly targeting the HZ and monitoring its physical and ecological responses (Mendoza-Lera and Datry, 2017; Hester et al., 2016; Hester and Gooseff, 2011; Palmer et al., 2010). A critical step forward would be the development of methods to assist practitioners (Hester and Gooseff, 2011).

In this paper we propose a novel and transferable method to identify potential areas of HEF in river networks by combining and evaluating environmental data at reach, segment, and catchment scales. The multiscale method combines statistical analyses with a priori knowledge on the processes controlling the HEF and their relationships to provide an assessment of HEF across broad spatial scales and where the availability of measured or modelled hyporheic data is scarce or absent. This deductive approach, using high-quality hydrologically-relevant environmental datasets that relate to the processes that enhance or limit HEF, avoids the reliance on detailed site-specific information of HEF, which is rarely available for most rivers, to inform restoration prioritisation and planning.

3.2 Material and Methods

In this research, we developed and applied a multiscale statistical method to identify potential *suitable* areas for HEF-focused restoration (Figure 3.2). The term *suitable* refers to conditions where factors indicate that HEF has the potential to exist.

The method is used in hierarchy and consists of a supervised system that classifies HEF at three spatial scales (catchment, segment and reach). It is based on environmental factors that hydrological theory suggests be related with hyporheic flow (Table 3.1, 3.2 and Table A.1) but which association to diagnose HEF in river systems has not been studied. The multiscale method represents a deductive approach to HEF classification that is geographically independent and depicted by a mosaic of factors across the catchment. It uses readily available spatially comprehensive datasets rather than

extensive hyporheic data as inputs, cause those are often not available at scales of analysis greater than sub-reach and reach scale (>100 m), and finally expert knowledge. In this paper we present the application of the method to three scales, but the formulae and the rationale explained are applicable to a finer resolution of scales.

The multiscale statistical approach involves a series of steps applied sequentially to the harmonized data at catchment, segment and reach scales (Figure 3.2):

1. Step 1: Variable subsetting- the definition of several subsets of variables from factors that are identified as linked to HEF (Section 3.2.2). The outcome of Step 1 is a set of testable datasets.
2. Step 2: Variable selection - uses exploratory data mining techniques (PCA and X-Means cluster analysis) to reduce the dimensionality of the input space from Step 1 and to identify factors that are the most related to potential HEF. The outcome of Step 2 is several clusters from each of the tested subsets from Step 1 (Section 3.2.3).
3. Step 3: Hyporheic classifier - the semantic characterization of clusters and the assignment of a classifier 1 (i.e., *suitable*) and 0 (i.e., *unsuitable*) for every cluster in each tested subsets by an expert (Section 3.2.4).
4. Step 4: Classifier merger - uses a mathematical combination function to merge the classifier produced for each cluster and each subset by Step 3 (Section 3.2.5). The output of Step 4 is a single dataset of the merged cluster classifiers across subsets.
5. Step 5: Large scale information merger - the final step involves the application of a mathematical combination function to join the output of Step 4 from one scale with the next larger scale (Section 3.2.6). The output of Step 5 is a single dataset of the merged cluster classifiers across scales.

The end result of the classification is a binary classification of *suitable* and *unsuitable* areas of HEF for clusters of unique variable combinations at each spatial scale (Figure 3.2). The algorithm was developed using the R scripting language (R Core Team, 2015)

and relies on the implementations of X-Means ¹ running on the D4Science ² services (Coro et al., 2013, 2015)(Figure 3.2).

¹<https://i-marine.d4science.org/group/biodiversitylab/data-miner?OperatorId=org.gcube.dataanalysis.wps.statisticalmanager.synchserver.mappedclasses.clusterers.XMEANS>

²<https://i-marine.d4science.org/group/biodiversitylab/data-miner>

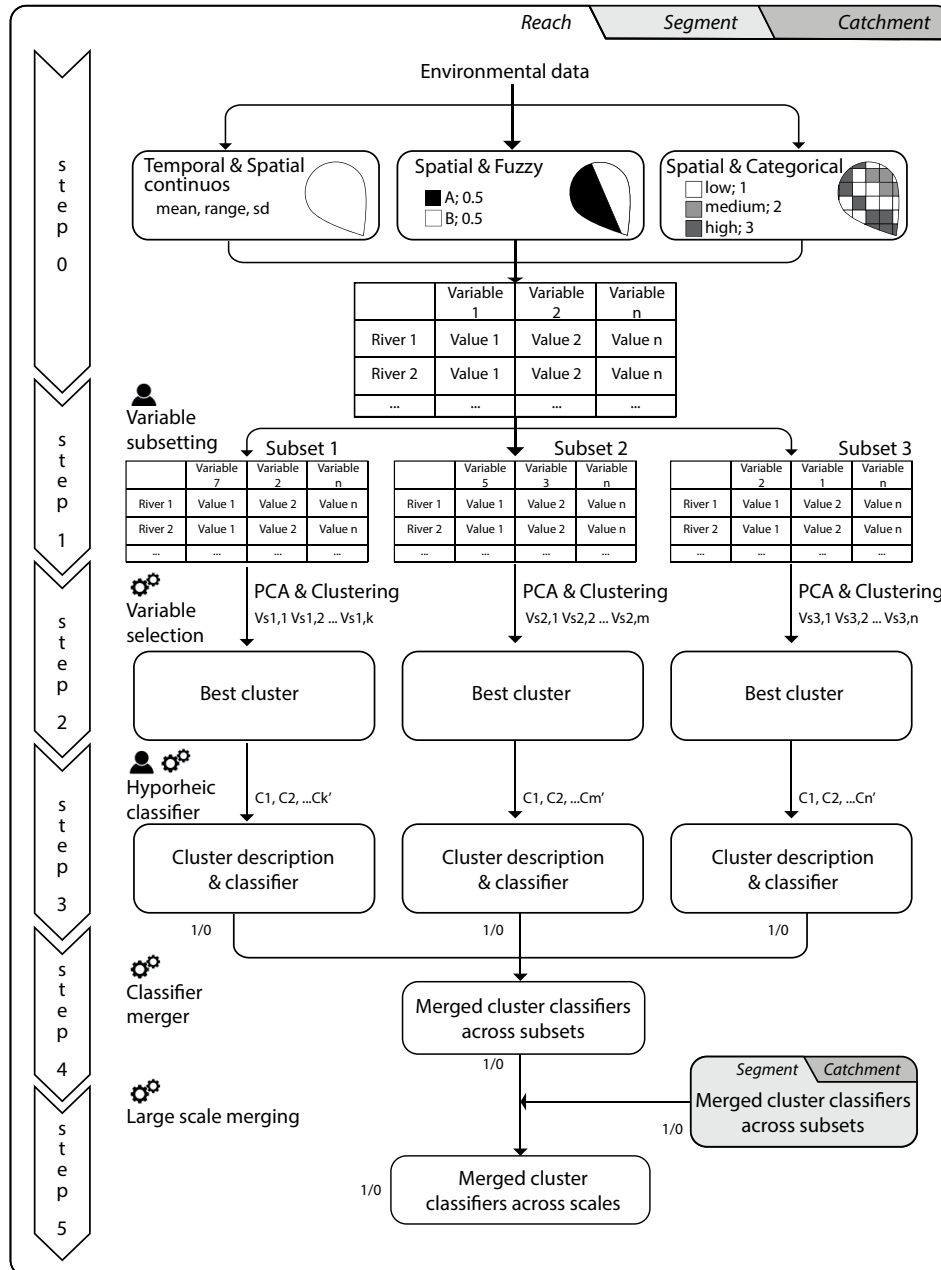


Figure 3.2: Main steps of the method including Step 1 “Variables subsetting” (Section 3.2.2), Step 2 “Variables selection” (Section 3.2.3), Step 3 “Hyporheic classifiers” (Section 3.2.4), Step 4 “Classifier merger” (Section 3.2.5), Step 5 “Large scale information merging” (Section 3.2.6). Cog wheels refer to automatized steps while the person symbol to expert supervised steps.

3.2.1 Environmental Data

3.2.1.1 Selection of environmental data

The environmental data used to develop our method consisted of factors identified in the literature as potential influencing HEF within detailed studies. The association of these factors to diagnose hyporheic conditions in river system has not been studied before. Data were retrieved from remotely sensed and national datasets and consisted of hydrological, hydrogeological, topographic, anthropogenic and ecological factors (Table 3.1, Table 3.2). Hydrological factors related to the quantity of water entering and flowing through the catchment, and expression of surface and groundwater flows, includes river and groundwater discharge (Voltz et al., 2013; Ward et al., 2012; Dragoni and Sukhija, 2008). Hydrogeology encompasses factors that affect the distribution of groundwater in aquifers and subsurface flows: geologic properties (porosity, grain size, hydraulic conductivity), heterogeneity of rocks, type of aquifers and soils (Hartwig and Borchardt, 2015; Kasahara et al., 2013; Bardini et al., 2012; Jones et al., 2008; Packman et al., 2006; Kasahara and Wondzell, 2003; Brunke and Gonser, 1997). Topographic factors were included because topography produces discontinuities in the direction of groundwater flows, thus determining areas of groundwater discharge and recharge, and of stream gradient and channel sinuosity (Caruso et al., 2016; Wörman et al., 2007; Boano et al., 2006; Wörman et al., 2006; Anderson et al., 2005). Similar to topography and hydrogeology, anthropogenic factors influence HEF at multiple spatial and temporal scales. For instance, land cover and use (e.g. agricultural practices) were included as a factor because directly impacting on evapotranspiration, surface runoff, soil compaction, and erosion at valley scale, all of which significantly impact on river hydrology and might represent a sediment source to reduce HEF (Didoné et al., 2014; Ryan et al., 2010).

Finally, ecological factors related to the river-valley lateral and vertical hydrological connectivity include riparian, in-channel vegetation, and in-channel wood. Vegetation dynamics can potentially feedback on the temporal variability of HEF and likely increase the spatial heterogeneity of this ecological- hydrological relationship.

Table 3.1: Environmental data for the UK case studies.

Variables	Dataset	Format	Resolution	Source
Elevation	DTM, LIDAR	ASCII GRID	5 m 1 m	Digimap
Bedrock; Superficial Geology	Bedrock Superficial Geology	Shapefile	1:50,000 1:625,000	BGS50 BGS625
Soils; Aquifers	European Soil Database; Groundwater Resources maps of Europe	Shapefile	1:1,000,000 1:500,000	ESDAC JRC
Vegetation	Land Cover 2007 River Habitat Survey	GeoTIFF raw data	25 m	CEH EA
Precipitation	Gridded monthly 1981-2010	ASCII GRID	5 km	MetOffice
Air Temperature	Gridded daily 1981-2010	ASCII GRID	5 km	MetOffice
River Flows	Mean daily	Discharge	Point data	EA, CEH
Bank; in-channel geology	River Habitat Survey	Raw data, miscellaneous	SPoint data	EA
Land Cover and Use	Land Cover 2007 River Habitat Survey	GeoTIFF	25 m	CEH EA

Table 3.2: Environmental data for the Polish case study.

Variables	Dataset	Format	Resolution	Source
Elevation	DTM	ASCII GRID	25 m, 10 cm	EEA BNP
Bedrock; Superficial Geology	Bedrock & Superficial Geology Polish Geological	Shapefile	1:250,000	GeoLog BNP
Hydrogeology; Aquifers	Institute; National Research Institute	Shapefile	1:50,000	PSH BNP
Precipitation	Gridded daily 1951-2013	GeoTIFF	5 km	BNP (Berezowski et al., 2016)
Air Temperature	Gridded daily 1951-2013	GeoTIFF	5 km	(Berezowski et al., 2016)
River Flows	Discharge	Row data	Point data	(Byczkowski and Fal, 2004)
Groundwater flows	Groundwater levels	Row data	Point data	BNP
Soils; peat depth	Soil type, peat depth	Shapefile		BNP
Land Cover	CORINE	GeoTIFF	25 m	EEA

3.2.1.2 Spatial discretization and data transformation

Data pre-processing included spatial delineation of catchments segments and reaches for our case of study. At first, catchment boundaries were delineated using the Hydrology toolset of the Spatial Analyst Toolbox of ArcGIS 10.2. Secondly, segment units, as sections of river that experience similar valley-scale influences and energy conditions, were delineated based on discontinuities in the gradient along the longitudinal profile of the river network and in sub-catchment areas. The number of segments in a catchment

was related to the increase in catchment area due to tributary confluences. The confluence was deemed significant when the sub-catchment area drained by the tributary, was greater than 20% of the main stem catchment area immediately upstream of the junction (Gurnell et al., 2014). River reaches were delineated based primarily on their channel planform. The river channel was divided into sinuosity units based on changes in the axis of the overall planimetric course. The units that differed in sinuosity by more than 10% were considered separate reaches.

Continuous temporal and spatial variables (i.e. temperature and elevation) were summarized by summary statistics (mean, standard deviation, minimum and maximum) (Figure 3.2, Table A.2 and Table A.3). For spatial fuzzy variables (i.e. bedrock geology) the relative contribution of each bedrock class (i.e. chalk geology) was expressed as percentage of occupied surface area with respect to the variable overall area and then scale in the range 0 and 1 (Figure 3.2, Table A.2 and Table A.3). Spatial categorical variables such as permeability classes, were numerically ranked according to the number of classes (i.e. very high=4, high=3, low=2, very low=1)(Figure 3.2, Table A.2 and Table A.3).

3.2.2 Step 1- Variables subsetting

The full set of data containing the environmental variables for all case of study, is manually subset into groups of variables. This is a necessary preliminary step to statistical discriminant analysis, otherwise not directly applicable given the large set of information reporting dependent variables, noise or missing data. Furthermore, there are usually more variables than rivers that cause difficulties in identify similarity between variables of each group of rivers and minimize the similarity between groups using statistical discriminant analysis. These subsets can contain overlapping variables (e.g. sharing one variable) and can be semantically driven (e.g. subset of aquifer type or temperature ranges) (Figure 3.2). The subsets will be analysed independently. At the end, the independent analysis of multiple variable subsets will provide information about discarded variables that are not correlated with HEF in either Step 2 or Step 4.

3.2.3 Step 2- Variables selection

In Step 2, the variable subsets are analysed independently using principal component analysis (PCA) to explore patterns in data variability among rivers and then complemented by cluster analysis to identify combinations of variables possibly indicating hyporheic responses in a given river area. First, a PCA is performed to reduce the dimensionality of the input space (Jolliffe, 2002). By selecting only the principal components associated with the largest eigenvalues, new vectors are obtained in the transformed-space that have smaller dimensions. These vectors are associated to the largest variance directions of the principal components and hence selected for the cluster analysis (variables selection) (Figure 3.3). Discarded variables can still be included and analysed in other variable subsets or scale, if the presence of those variables is known to be important for HEF.

At this stage, the reduced dimensional space is optimized with respect to the information (variance) contained in the data, thus facilitating the application of cluster analysis to the PCA output (Ding and He, 2004). Our method uses the distance-based X-Means algorithm (Pelleg et al., 2000) a variant of the most common K-Means (MacQueen, 1967). The X-Means algorithm was chosen after testing the DBScan density-based clustering algorithm (Ester et al., 1996), which did not produce meaningful grouping of the case studies, i.e. in most of the cases vectors were all classified as outliers. In contrast to K-Means, XMeans requires indicating a minimum and a maximum number of clusters (Kmin and Kmax). The algorithm applies KMeans to the data for all the possible K values in the indicated range. KMeans finds the best assignment of the vectors to the K clusters and produces a score for this assignment, based on the average squared distance of the points to their clusters centroids (distortion measure). XMeans reports the output of the KMeans execution that produced the best score. The associated K is the best number of clusters. XMeans is also more efficient with respect to KMeans, because it uses kd-trees (Bentley, 1975) and *blacklisting* as support to the processing.

The X-Means algorithm (Pelleg et al., 2000) is applied to the PCA-transformed vectors, generating optimal grouping (clusters) of vectors according to their distances.

Clustering the dimensionally-reduced, PCA-transformed vectors helps to find the best grouping in this space, since the vectors belonging to the same cluster are close in the PCA-transformed space (Ding and He, 2004). Each cluster produced by XMeans is characterized by a centroid, which is a representative vector of the cluster. In our method, the centroid is interpreted as a summary of the characteristics of the cluster in the PCA-transformed space. Re-projecting the clusters centroids to the original space allows obtaining the coordinates of the centroids expressed in terms of the original variables. Re-projection is mathematically possible although the PCA transformed space has reduced dimensionality with respect to the original space. However, during this step, some information is lost, hence our method analyses the distribution of the variables onto the re-projected centroids. Specifically, we calculate the distances between the variable value and the coordinates of the re-projected centroids for each variable. The number of times a centroid coordinate is closest to a real-data value is also recorded. A tolerance threshold of 25% is applied, before the final clustering, on the features having the most uniform distributions over the centroids. This step allows the selection of variables that are equally distributed over the centroids, and accounts for the loss of information during re-projection.

The following example illustrates the criteria used to retain or discard the variables. Suppose 2 data clusters are identified for 8 rivers, defined by vectors of elevation, channel gradient and temperature. If 4 elevation values are determined to be closest to cluster A and the other 4 to cluster B, the elevation variable would be retained, because the 25% tolerance threshold is exceeded (i.e. >2 rivers assigned to a cluster). If 2 channel gradient values were assigned to cluster A and 6 to cluster B, the channel gradient variable would be discarded because the threshold (>2) is not exceeded. And, if 5 temperature values were assigned to cluster A and 3 to cluster B, temperature would be retained in the analysis. In conclusion, by construction of the PCA algorithm, if the variables are independent and carry high variance, then the PCA-transformed space would correspond to the original space. Thus, the centroids would take all of the variables into account, resulting in equal distributions of the vectors coordinates on the centroids coordinates (Ding and He, 2004). A variable that is not assigned to a cluster does not indicate a missing value for that cluster, but it has been discarded during the

clustering analysis.

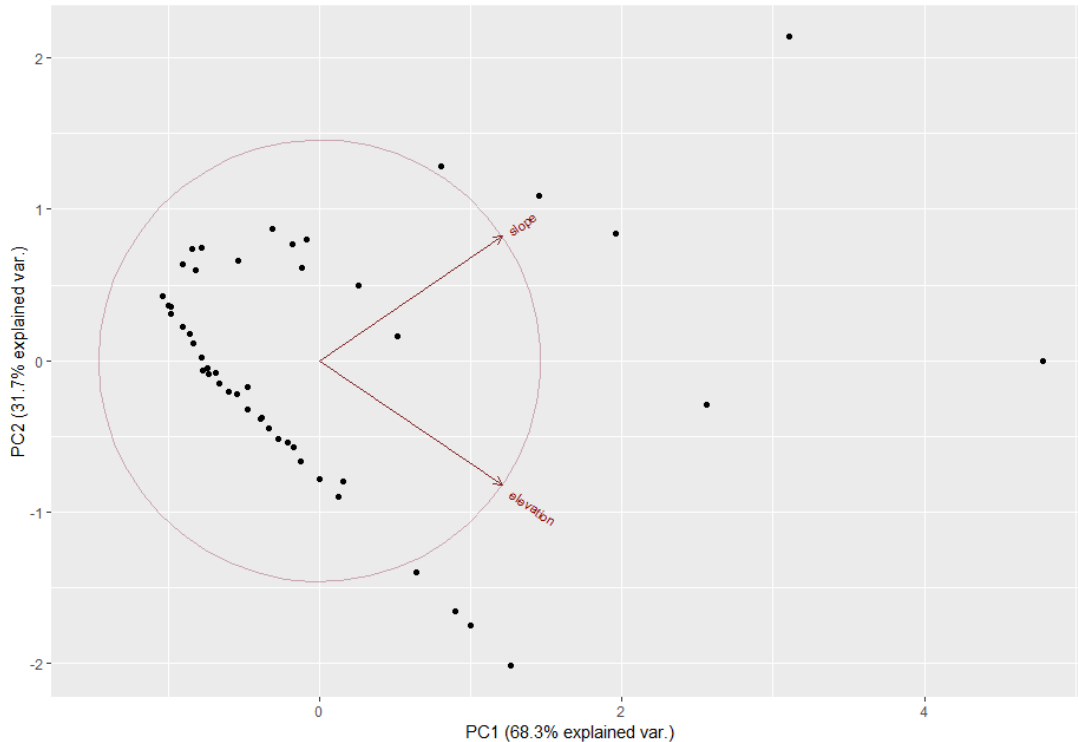


Figure 3.3: The distribution of the vectors of two variables, average elevation and slope of UK rivers and their related PCAs. The new axes identify the largest variance directions (explained var.); the red circle represents highly correlated points that mostly contribute to the correlation matrix. The values are scaled as requested by the PCA.

3.2.4 Step 3- Hyporheic classifiers

The unique combinations of variables that are generated by the cluster analysis (Step 2), and their centroids are used to assess *suitable* and *unsuitable* areas for HEF-restoration for a river area using human expertise. The expert provides a semantic description to each cluster in each subset using the centroid of the cluster and then assigns an hyporheic classifier, 1 (*suitable*) or 0 (*unsuitable*), which indicates if the environmental conditions depicted by the clusters lead (i.e. 1) or not (i.e. 0) to HEF. The use of expert knowledge is required because empirical data on HEF is not available

for all of these unique combinations. The expert bases this assignment on the variable types, the distribution of the variables in each cluster and on the knowledge of the hydrological, hydrogeologic, topographic, anthropogenic and ecological factors that yield HEF following the relationships summarized in Table A.1. At the end of the Step 3, the initial set of variables has been factored into clusters, semantically described and labelled. The next section explains how these clusters are combined, which corrects errors in the cluster label assignment and cluster analysis.

3.2.5 Step 4- Classifier merger

Classifiers for each cluster and subset are merged together using a mathematical combination function. The criterion used for the mathematical combination function is to indicate that areas of HEF are *suitable* only if over half of the hyporheic classifiers indicate that it is *suitable*. The mathematical combination function allows us to account for errors in the hyporheic classifiers due to mis-labelling of the clusters. The combination function is the normalized sum of all the sub-classification for each case study:

$$Cs(r) = \frac{\sum_{i=1}^N C_{s_i}(r)}{N}$$

$$C(r) = \begin{cases} 1, & Cs(r) > 50\% \\ 0, & otherwise \end{cases}$$

where r is the complete set of variables associated to a river area; s_i is the i -th (of N) variable subset; $C_{s_i}(r)$ is the i -th binary hyporheic classification over the s_i variable subset; $Cs(r)$ is the normalised sum of all the sub-classifications for the river area r and $C(r)$ is the final classification function. If $Cs(r)$ is higher than 50%, the river area r is classified as *suitable*, otherwise the classifier assesses *unsuitable*. This threshold was set after heuristic evaluation of a small (20%) subset of our data.

3.2.6 Step 5- Large scale merging

To increase the accuracy of predictions as the spatial scale becomes finer, the last step of the method is to combine the binary classifiers from different scales using a downscaling approach. The rationale behind the combination function is the following: if the system predicts that HEF areas are *suitable* in a river at a large spatial scale, then it is more likely to present *suitable* areas at smaller spatial scales nestled within the larger area. For example, a positive (binary “1”) classification at catchment scale suggests that *suitable* environmental conditions exist for HEF in the catchment area. At this scale of analysis, the accuracy of the classification is generally higher because it is not required to precisely identify the specific location of hyporheic exchange. Hence, a smaller-scale classifier can use the information from a larger-scale classifier because it represents the presence of factors that drive HEF. Our method embeds this approach using a “bonus function” (20% weighting in the equation) that combines the output of a classifier with the output of the next-largest-scale classifier. The classification is recalculated for finer scales as follows:

$$Clarge(r) = Cs(r) + 20\% Clargescale(r)$$

$$C(r) = \begin{cases} 1, & Clarge(r) > 50\% \\ 0, & otherwise \end{cases}$$

Where $Cs(r)$ is the normalized sum of all the sub-classifications for river area r , and $Clargescale(r)$ is the dichotomic score of the first larger scale. Also in this case, the threshold (50%) has been set after heuristic analysis on a small (20%) subset of our data.

3.3 Results

This section reports the results of the application of the multiscale statistical method to the nine test catchments. The cluster results were compared to expert opinion (Section 3.3.1) and discussed at each spatial scale (Section 3.3.2).

Table 3.3: Selected Rivers in Europe. Coordinates (WGS84) refer to the downstream-most point in the case studied rivers, which was used for catchment delineation.

River catchment	Latitude Longitude	Catchment Area (km ²)	Bedrock Geology
Dove	53.207; -1.928	212.154	Carboniferous Limestone
Wye	53.327; -1.851	270.776	Carboniferous Limestone
Exe	51.160; -3.830	103.162	Permo-Triassic Sandstone
Tone	51.088; -3.380	461.857	Permo-Triassic Sandstone
Frome	50.835; -2.652	467.610	Cretaceous Chalk
Piddle	50.835; -2.431	202.471	Cretaceous Chalk
Tern	52.945; -2.336	852	Permo-Triassic Sandstone
Rother	51.087; -0.926	379.795	Greensand Sandstone
Biebrza	54.188; 22.625	7062.618	Marl Sands

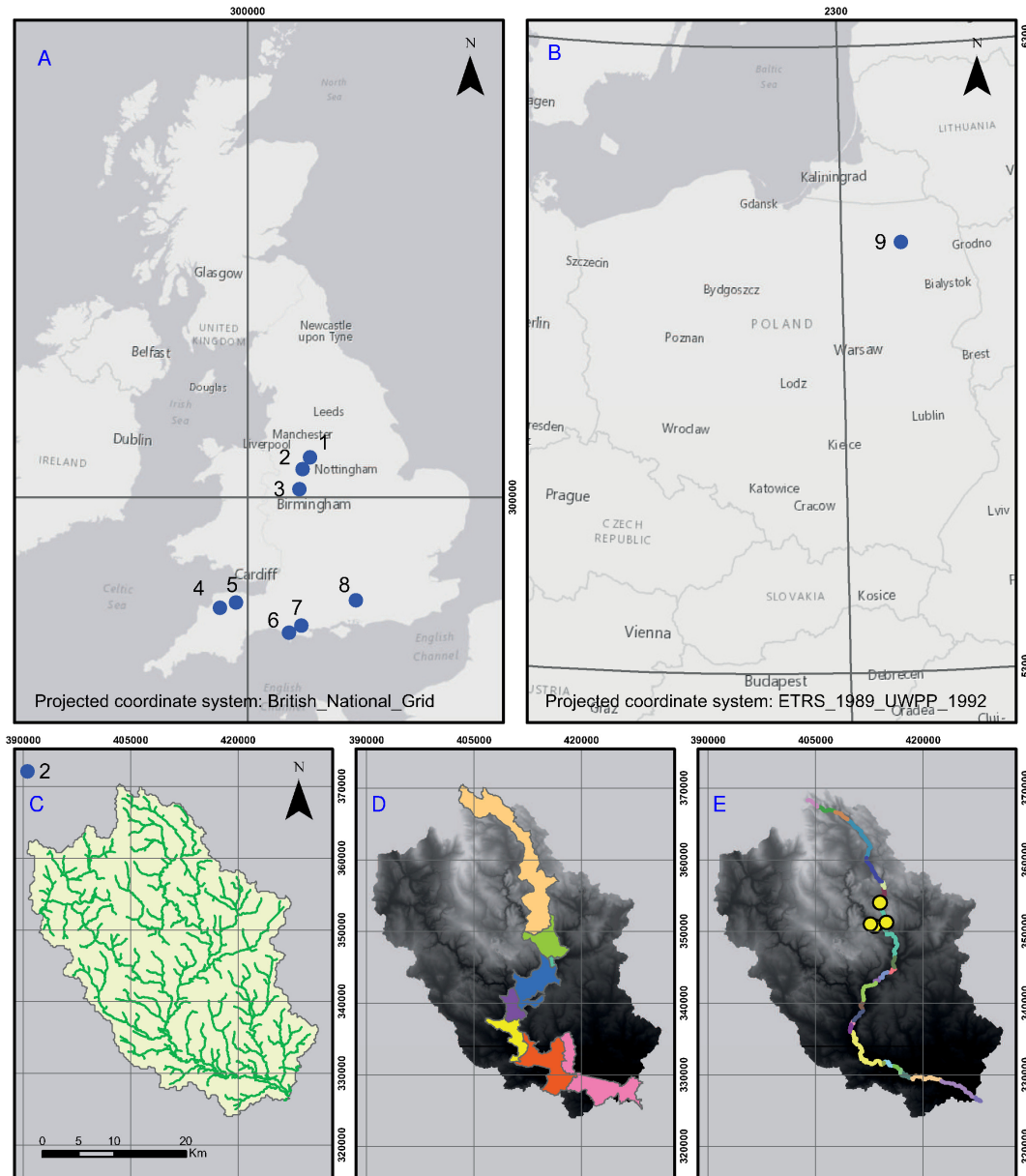


Figure 3.4: Panels A and B represent the locations of the two cases of study UK (A) and Poland (B). Panels C,D,E represent the River Dove in UK and the examined spatial scales: catchment (C), segments (D), reaches (E). In panel A the numbers refer to: (1) the River Wye,(2) the River Dove, (3) the River Tern, (4) the River Exe, (5) the River Tone, (6) the River Frome, (7) the River Piddle, (8) the River Rother, (9) the River Biebrza. The yellow points in panel E refer to literature studies carried out on that particular reach of the catchment by Dunscombe (2011).

3.3.1 Validation and reliability of the classification results

The X-Means algorithm identified three optimal clusters in all the three spatial scales considered in the study. To evaluate whether the developed multiscale statistical approach could identify *suitable* and *unsuitable* areas for hyporheic exchange to occur, the reliability of the identified clusters was evaluated by examining the representativeness of the variables among the clusters against human expertise by the authors. In the assessment, the lead author manually assigned one of the interpretations of the XMeans clusters (i.e. 1 or 0) to each river catchment (i.e. 8 catchments and 118 variables for the UK case of study; 86 variables for the Polish case study), segment (51 segments and 48 variables for the UK case of study; 10 segments and 35 variables for the Polish case study) and reach (135 reaches and 59 variables for the UK case of study; 11 reaches and 74 variables for the Polish case study). At this stage, the expert evaluation differs from the expert information within the model (Step 4) because it is performed on the original environmental data (Section 3.2.1) and not on the clusters. A confusion matrix was used to assess the agreement between the expert assignment (binary “1” and “0”) and X-means clusters as the percentage of matching assignments (absolute percentage of agreement). Furthermore, the Cohen’s Kappa (Cohen, 1960) was calculated to estimate the agreement between the expert and the model compared to purely random assignments. The X-Means results agreed generally with expert opinion indicating reliable semantic interpretations of the categories identified in the clusters variations. At the catchment scale the absolute percentage of agreement is 88% and 75%, at segment 75% and 78% and at reach 74% and 82% for the UK and Polish case studies respectively (Table 3.4, Table 3.5).

Table 3.4: UK case study: confusion matrix for classification at the catchment, segment and reach scale.

Clustering Catchment scale			
Expert	Classifier 1	Classifier 0	Total
Classifier 1	4	1	5
Classifier 0	0	3	3
Total	4	4	8
Agreement	4	3	7
By Chance	2.51	1.50	4.01
Kappa		0.75	Fleiss <i>Good</i> Landis-Koch <i>Substantial</i>
Absolute % of agreement		88%	
Clustering Segment Scale			
Expert	Classifier 1	Classifiers 0	Total
Classifier 1	16	7	23
Classifiers 0	6	22	28
Total	22	29	51
Agreement	16	22	38
By Chance	9.92	15.92	25.84
Kappa		0.48	Fleiss <i>Good</i> Landis-Koch <i>Moderate</i>
Absolute % of agreement		75%	
Clustering Reach scale			
Expert	Classifier 1	Classifier 0	Total
Classifier 1	25	7	32
Classifier 0	27	70	97
Total	52	77	129
Agreement	25	70	95
By Chance	12.90	57.90	70.80
Kappa		0.42	Fleiss <i>Good</i> Landis-Koch <i>Moderate</i>
Absolute % of agreement		74%	

Table 3.5: Polish case study: confusion matrix for classification at the catchment, segment and reach scale.

Clustering Catchment scale			
Expert	Classifier 1	Classifier 0	Total
Classifier 1	1	1	2
Classifier 0	0	2	2
Total	1	3	4
Agreement	1	2	3
By Chance	0.52	1.53	2.31
		Fleiss	Landis-Koch
Kappa	0.5	<i>Good</i>	<i>Moderate</i>
Absolute % of agreement	75%		
Clustering Segment scale			
Expert	Classifier 1	Classifiers 0	Total
Classifier 1	24	9	33
Classifiers 0	7	7	7
Total	24	16	40
Agreement	24	7	31
By Chance	19.81	2.82	22.61
		Fleiss	Landis-Koch
Kappa	0.48	<i>Good</i>	<i>Moderate</i>
Absolute % of agreement	78%		
Clustering Reach scale			
Expert	Classifier 1	Classifier 0	Total
Classifier 1	3	0	3
Classifier 0	2	6	8
Total	5	6	11
Agreement	3	6	9
By Chance	1.36	4.36	5.72
		Fleiss	Landis-Koch
Kappa	0.62	<i>Good</i>	<i>Substantial</i>
Absolute % of agreement	82%		

As the binary classifiers for each scale in Step 5 take account of the information from the next-largest scale (i.e. catchment classifiers influencing segment classifiers) to represent the scale dependence in HEF, the model performance is expected to increase

within decreasing scale. In the UK case of study, the catchment scale effectively added information to the segment scale (Step 5) because the agreement increases of 1 percentage point (Table 3.6). However, in the Biebrza application, no performance increase was detected (Table A.4).

Table 3.6: UK case study Step 5: confusion matrix segment agreement with enrichment of 20% using the information of the catchment.

Clustering Segment-Catchment			
Expert	Classifier 1	Classifier 0	Total
Classifier 1	22	1	23
Classifier 0	11	17	28
Total	33	18	51
Agreement	22	17	39
By Chance	14.88	9.88	24.76
		Fleiss	Landis-Koch
Kappa	0.54	<i>Good</i>	<i>Moderate</i>
Absolute % of agreement	76%		

3.3.2 Prediction of HEF at different spatial scales

HEF *suitable* and *unsuitable* areas were predicted at all three spatial scales for the examined rivers (Figure 3.5, Table 3.3). At catchment scale, *unsuitable* conditions for HEF are predicted for the Rivers Dove, Exe, Tone and Wye (Figure 3.5). These rivers are predominantly characterized by confined or semiconfined aquifers, poorly sorted superficial deposits, from coarse sand to silt and clay (>50% cover over the catchment). In contrast, for the Rivers Frome, Piddle, Tern and Rother, the semi-automatic classification method predicts *suitable* areas for HEF to occur. The clusters for these rivers depict predominantly complex aquifers with flows through fractures and discontinuities, terrigenous deposits with sorted sand and gravel (30 to 45%), silt and clay deposits less than 20% of cover on the catchment.

At the segment scale, HEF was found to be characterized by *suitable* areas for all

the identified segments in the Rivers Piddle, Tern, Wye and the Biebrza River (Figure 3.5, Table 3.3). Conversely, HEF is predicted to be low for all the segments in the Rivers Dove, Rother and Tone. The Rivers Exe and Frome are predicted to have a mixture of *suitable* and *unsuitable* HEF areas in different segments. Where *suitable* HEF condition is predicted, the clusters are mainly characterized by sandstone geology, a low fraction fine sediments (between 10 and 30% cover over the segments), large fraction of sorted gravel and sand deposits (between 20 and 50% cover over the segments), channel sinuosity of ≥ 1.2 and low channel gradient (0.002). In segments with *unsuitable* conditions for HEF, the clusters describe mudstone and sandstone geology, low channel gradients, high percentage of clay and fines ($>55\%$ cover) and high percentage of arable and grassland ($>70\%$ cover) within 150 m of the river channel. For the Biebrza River, the segments which are predicted to have *suitable* HEF conditions are characterized by sinuosity ≥ 1.3 , high percentage of gravel and sand deposits ($>40\%$), high percentage of productive aquifer, and low percentage of pasture lands ($<10\%$) within 150 m of the main river channel.

Table 3.7: Frequency of the categories, *suitable* “1”, *unsuitable* “0” HEF in the catchments, segments, reaches.

River	Catchment		Segment		Reach	
	1	0	1	0	1	0
Biebrza	1	-	10	-	5	6
Dove	-	1	-	8	-	19
Exe	-	1	3	4	-	16
Frome	1	-	5	1	37	1
Piddle	1	-	4	-	15	6
Rother	1	-	-	10	-	11
Tern	1	-	4	-	-	9
Tone	-	1	-	6	-	10
Wye	-	1	6	-	-	11

Finally, at reach scale, the multiscale statistical method predicted *suitable* HEF areas for 3 rivers of the 9 evaluated: the Frome, Piddle and Biebrza (Figure 3.5, Ta-

ble 3.3). Generally, the clusters indicating *suitable* conditions for HEF exhibit a low percentage of in-channel vegetation (2-10% of the reach), gravel substrates (>10%), very low percentage of silt and clay deposits (<1%), presence of pools and riffles (5-10%), and a low percentage of poached or overgrazed river banks (<5%). Cluster indicating *unsuitable* HEF areas are mainly described by poached river banks, presence of in-channel emergent vegetation and reeds, low percentage of gravel substrates, low number of pools and riffles, and low mean flow velocity. In the Biebrza River, clusters indicating suitability relate to superficial geology dominated by peat (80% cover on the entire reach) and mud (10%), while those indicating unsuitability were dominated by mud (60%) and peat (<10%) deposits, low percentage of sand and gravels, and high percentage of unsorted till deposit (>50%) and pasture lands.

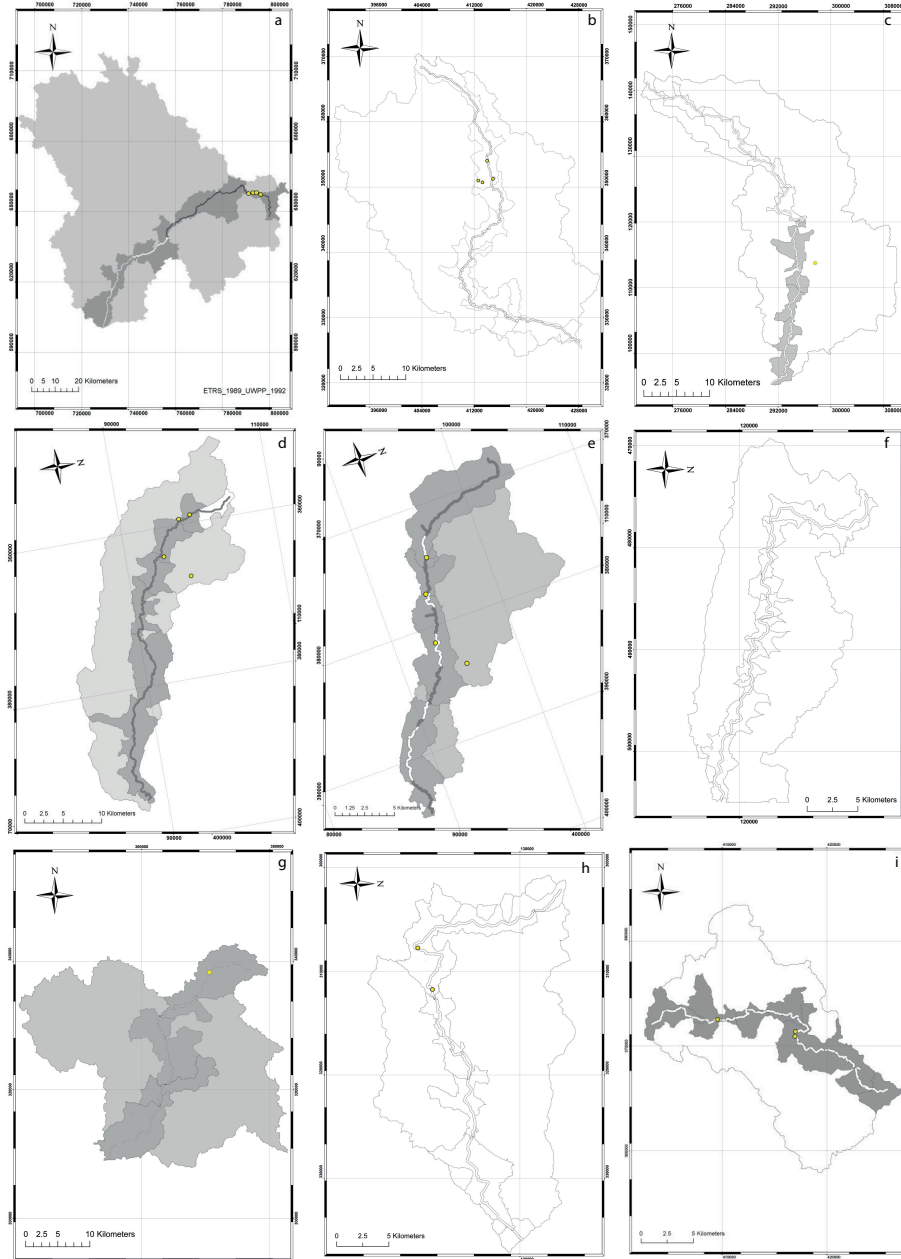


Figure 3.5: Grey-scale coded maps of the case study rivers based on *suitable* “1” (grey scale) and *unsuitable* “0” (white) areas of HEF. a) the Biebrza River, b) the Dove River, c) the Exe River, d) the Frome river, e) the Piddle River, f) the Rother River, g) the Tern River, h) the Tone River, i) the Wye River. Yellow points refer to field data of HEF from Dunscombe (2011); Anibas et al. (2012); Krause et al. (2011a)

3.4 Discussion and Conclusion

The multiscale statistical method was developed and applied to nine rivers across Europe to identify *suitable* and *unsuitable* reaches, segments and catchments for HEF-focused restoration. The results of the classification showed good to moderate agreement (Cohen's Kappa) with expert opinion, indicating reliable categories and semantic interpretations of the clusters. Reasonable agreement is also observed with *in-situ* empirical data from previous studies, given the unavoidable differences in scale between these detailed local research studies (1 m- 1 km) and our broad scale approach. In this section we discuss the results of the classification against field observations of actual HEF, the major predictors of suitable and unsuitable areas (Section 3.4.1) and finally the domain of application of the method (Section 3.4.2).

3.4.1 Linking processes to factors

At each spatial scale, catchment, segment and reach, cluster results show groups of predictors that influence the determination of *suitable* and *unsuitable* areas for HEF-restoration. Hydrological factors (i.e. groundwater level, discharge) influence HEF by changing surface water flow regimes and distributions of hydraulic head. Hydrogeological factors affect water flowing through the river bed by sediment grain size, sediment heterogeneity, and depth, therefore promoting spatially diverse hyporheic exchange (Packman and Salehin, 2003) (Table A.1). Topographic factors, such as catchment gradient, individual bedforms and bedforms sequences, valley confinement, author hydrodynamic and hydrostatic forces that affect the variability of HEF from cm to km scale (Table A.1). Anthropogenic factors, as in-channel structures (i.e. weirs, dams), land management and land use, impact HEF by modifying river stage fluctuations, changing sediment delivery and channel complexity, and by altering vertical hydraulic gradients (Table A. 1). Also vegetation has long been known to exert a strong control on land surface hydrology by moderating streamflow and groundwater recharge (Table A.1). As ecological factor, vegetation feedbacks on the temporal variability of HEF and likely increase the spatial heterogeneity of this ecological hydrological relationship. This

section presents the different factors affecting suitable and unsuitable HEF-restoration areas and compares the HEF predictions at reach scale to *in-situ* empirical data from previous studies.

High percentages of poached banks, emergent in-channel vegetation, improved grassland, and low geomorphological complexity, and low number of pool-and-riffle sequences, were associated with *unsuitable* reaches in the Frome (1 reach) and in the Piddle catchments (15 reaches). Dunscombe (2011), observed weak vertical hydraulic gradients (VHG) at the head and tail of riffles in both the Rivers Frome and Piddle, indicating little to no HEF at this scale. This is a finer scale than the prediction of our model which overall classifies that reach as unsuitable (Figure 3.5e). These neighboring catchments are found in the south of England and are underlain by chalk bedrock. Chalk has a high secondary porosity, and groundwater flows easily through fractures and fissures in the bedrock to these gravel-bed rivers (Waters and Banks, 1997). The combination of a permeable chalk geology and coarse sediment would be expected to strongly support HEF (Hiscock, 2007; Morrice et al., 1997). However, there are several reasons for unsuitable conditions in these rivers: (i) the pronounced groundwater flows create strongly gaining and losing conditions in reaches, which drive contraction (gaining) or expansion (losing) of HZ and shortening of HEF paths (Malzone et al., 2016, 2015; Fox et al., 2014; Wondzell and Gooseff, 2013); ii) the rivers have few instream geomorphic features that would generate advective pore water flow into, through and out of the river bed (Tonina and Buffington, 2009; Elliott and Brooks, 1997); and iii) high fine sediment loads have led to clogging of the coarse gravel bed (Boulton and Hancock, 2006; Pretty et al., 2006). Several studies have shown that chalk rivers in England have elevated fine sediment loads, derived principally from cultivated agricultural land (Grabowski and Gurnell, 2016; Collins and Walling, 2007; Walling and Amos, 1999) and grazing pressure (Bilotta et al., 2010; Bilotta and Brazier, 2008; Trimble and Mendel, 1995). Also, in-channel vegetation appears to be an important factor at this scale of analysis. While vegetation patches have been shown to narrow the active channel, increasing water velocities and mobilizing the gravel bed (e.g. Cotton et al. (2006)), the low flows within patches promote depositions of sediment and organic matter, decreasing bed permeability and reducing or eliminating HEF (Corenblit et al., 2007; Ensign

and Doyle, 2005; Salehin et al., 2004). The result of the statistical method for the Wye River agreed with Dunscombe (2011) observations (weak VHGs), while for the Rivers Tone, Dove, the predictions did not match with collected field data. Our method predicts unsuitable areas for HEF at the reach scale along the Tone and the Dove, while Dunscombe (2011) observed strong patterns of up- and downwelling flows at the head and tail of riffles on both rivers. For the River Tern, all reaches were identified as unsuitable areas by our method, however empirical HEF data at a pool-riffle-pool sequence showed temporal flow patterns occurring around this geomorphic feature at the sub-reach scale (Krause et al., 2011a; Hannah et al., 2009).

Suitable areas for HEF were predicted consistently across all spatial scales for the Rivers Dove and the Tone, but not for the Tern, Wye, Rother, Piddle, Frome, Exe and Biebrza. At catchment scale, the clusters for the Dove and Tone are characterized by well distributed variables: sandstone is mixed with mudstone and siltstone bedrock geology and clay and silt superficial deposits represent more than the 50% of the catchment. Similarly, the hydrogeology is dominated by unconfined but low-producing aquifers. While the sandstone bedrock would normally support surface-subsurface exchange (Hiscock, 2007), the low-conductivity superficial deposits characterizing the clusters (more than 50% of the catchment area) would likely limit or restrict vertical hyporheic flow. Indeed, the role of local sediment deposits in preventing or limiting groundwater flows has been also observed under unconfined alluvial channels (Gurnell et al., 2014). At segment scale, clusters characterized by low slopes, high percentage of in-channel fine sediments, and extensive arable lands around the river channel are depicted in the clusters, possibly suggesting an impact of sediment delivery from the surrounding lands and simplification of landscape complexity (Boano et al., 2014; Gooseff et al., 2007).

At reach scale, suitable conditions for HEF were predicted in some reaches of the Biebrza, Frome and Piddle (Figure 3.5). For the Biebrza River, the reaches identified as suitable (Figure 3.5a) in our classification corresponded in spatial extent to one reach of our analysis which were previously observed to have upwelling and sections of recharge (Anibas et al., 2012). These reaches were characterized mainly by a geology of peat and peat mixed with mud. Our clusters identified peat as an important variable controlling HEF at the reach scale. This reflects the underlying process controls, as the

physical structure and stratigraphy of peat has pronounced influence on the dynamics of water retention, storage and solute transport (Rezanezhad et al., 2016). Anibas et al. (2012) described two main types of peat soils that showed different behaviors in driving HEF flows at the sediment-water interface; soil I has a loose structure, covered in reed vegetation and characterized by high flow fluxes, while soil II is more compact and has lower flow fluxes. In our data for the Biebrza, peat characteristics are heterogeneous across reaches, varying from loose, similar to soil type I (Anibas et al., 2012), to more compact and mud-dominated, similar to soil type II (Anibas et al., 2012). Therefore, the overall assessment and spatial distribution of HEF predictions at reach scale in the Biebrza catchment are supported by the findings of Anibas et al. (2012).

A possible reason of the difference in outputs between the predicted HEF conditions by the multiscale approach and *in-situ* observations is the diverse spatial and temporal resolution. *In-situ* observations are commonly limited to square meters measurements and are often influenced by temporal variations that are not considered in the proposed approach. Moreover, the resolution of geomorphological data used in these case studies is coarser than the detailed, sub-reach-scale observations of HEF. River Habitat Survey (RHS) data was used as point estimates of in-channel conditions. While RHS data is ideal for this type of analyses in many ways (e.g. UK-wide coverage, reach survey scale), it is a visual appraisal of river habitats and geomorphic features, and does not involve topographical or hydrogeological measurements (Raven et al., 1996). Therefore RHS does not able to resolve the sub-reach-scale geomorphological features that were surveyed in the empirical studies. The limitation linked to the spatial resolution can explain differences by scale where *suitable* areas for HEF to occur are predicted only at spatial scales larger than the reach scale (i.e., River Tern and River Rother).

Finally, results in Table 3.6 depicted a scale-dependence effect between catchment and segment. The small increment in the confusion matrix suggests that upper hierarchical levels inform on general conditions at low resolution and exert constraints on the lower level, which informs at higher resolution and provides mechanistic explanation for higher levels.

3.4.2 Application to river restoration planning

This study proposes a multiscale statistical method to identify where HEF potentially occurs at catchment, segment, and reach scale, i.e. a it is *suitable* for HEF-based restoration. The approach and results herein presented use readily available environmental datasets enabling the method to be transferable to other catchments. Restoration practitioners are increasingly considering the HZ in their management plans because of the crucial role it plays in river biogeochemical processing and the transferring of solutes and oxygen between surface waters, groundwater and the HZ (Mendoza-Lera and Datry, 2017; Nogaro et al., 2010; Findlay, 1995). Thus, there is a strong need to provide river managers and restoration practitioners with a tool that can be applied to any catchment, and which is flexible enough to work with the data sources available in different regions and countries. We chose to structure the method around the multiple scales because it allows broader restoration planning that considers catchment-scale solutions (Merill and Tonjes, 2014; Wortley et al., 2013; Hester and Gooseff, 2011).

To assist river restoration practitioners, we propose that this multi-scale statistical process be run as a preliminary assessment step in restoration planning to identify and possibly prioritize restoration actions (i.e. reach locations) across a catchment. Restoration managers can benefit from the classification at any stage of the analysis. First by looking directly at the clusters (Step 2), that describe: i) environmental and hyporheic-drivers on the targeted areas, ii) identify areas with the same hydrological, hydrogeological, topographical and ecological context, and iii) are spatially unique. Second by looking at the final confusion matrices (Step 4), which embed a summary of knowledge across the domains of hydrology, geology, and hyporheic theories and their related environmental data, and provide insights into the spatial variability of HEF in a catchment. Finally, by looking at multi-scale assessment (Step 5), the results at each spatial scale can be used *a posteriori* to define what processes management actions are important for each reaches and then feedback to management actions.

Considering the above information, river managers can choose between a “passive” and an “active” approach. For example, some of the factors depicted in the clusters will be intrinsic (i.e. bedrock geology) and cannot be changed by management measures

while others will be dynamic (i.e. land use, vegetation, channel geomorphology) and therefore might become a target for river management. If *suitable* HEF conditions are predicted, a passive approach will likely be preferred and include measures that do not directly address hyporheic conditions but that take advantage of HEF to preserve and maintain, for example, habitat diversity. The passive approach would include *in-situ* evaluation to verify that the method predictions are representative of local conditions. Conversely, if *unsuitable* HEF conditions are predicted, an active approach can be adopted and local restoration measures applied accordingly to the factors involved.

In our opinion, the identified factors for HEF have intuitive general validity, but we expect that in other applications the method would be tailored to site-specific characteristics and applied to other factors. At reach and sub-reach scales, the classification is generally limited by the resolution and quality of the available data. This is a general issue when using environmental surrogates of hydrological processes, especially due to the coarse resolution of the data (Olden et al., 2012). We qualitatively compared the prediction of the method on available empirical hyporheic evidence that was i) spatially and temporally limited to local scales, ii) collected using multiple methods, and iii) focused on specific geomorphic features, such as bedforms, that likely trigger local advective HEF even when catchment conditions limit larger-scale flows. In the future, we expect this evidence-based problem to be overcome by technology and more complete and uniform metadata associated with hyporheic studies.

Finally, existing scientific literature suggests that knowing how and what to prioritize in restoration actions for aquatic ecosystems are fundamental to effective restoration planning (Wohl et al., 2005). There is an increasing emphasis on addressing hyporheic zones into restoration to allow more comprehensive hydro-ecological understanding of aquatic ecosystems; our model can support restoration as a first-order assessment to target HZ and thus provide the greatest benefits to restoration plans.

Acknowledgements

This work was supported by the Marie Skłodowska-Curie Action, Horizon2020 within the project HypoTRAIN (Grant agreement number 641939); G. Coro was also

supported by the BlueBRIDGE project (Grant agreement number 675680); A.I. Packman was also supported by the U.S. National Science Foundation (Grant agreement number EAR-1344280). We thank the Networked Multimedia Information Systems Laboratory (Ne-MIS), Research Laboratory of ISTI-CNR Italy, for providing full support for the development of this research, the Biebrza National Park for providing the needed data for the development of the River Biebrza case of study (data sources: Preservation of wetland habitats in the upper Biebrza Valley LIFE11/NAT/PL/422 and Restoration of hydrological system in Middle Basin of the Biebrza Valley. Phase I. LIFE project. Thanks to Dr. Christian Anibas for his availability in sharing information on the River Biebrza, the Environment Agency and Dr. Marc Naura who provided the River Habitat Survey data for the U.K. catchments. We also thank the British Geological Survey (BGS), the Centre for Ecology & Hydrology (CEH), the UK Met Office, the European Soil Data Centre, the European Environment Agency and the Polish Geological Institute as data providers.

Chapter 4

Large wood effects on river invertebrates

Abstract

Large wood (LW) is a key element of river channels. Field results have suggested diverse hydrological, physical and ecological effects on river processes and forms. Studies on taxonomy-based descriptors of benthic macroinvertebrate assemblage structure have supported these findings, but evidence of the importance of LW on hyporheic invertebrates remains rare. One of the hypothesised benefits of LW on the hyporheic zone (HZ) is an increase of hyporheic exchange flow (HEF) which drives ecological diversity, although this connection has not been well evidenced in empirical studies.

We examined the effects of active and partial wood jams on the hyporheic and benthic zones. The hypotheses (i) “LW sites would differ in abundance, biomass and taxonomic richness from control sites” and (ii) “these differences are related to environmental variables at wood sites”, were tested on meiofaunal and macrofaunal assemblages. Streamflow, sediment size, water chemistry, wood morphology and invertebrates assemblages were surveyed seasonally in the Hammer stream (UK).

Assemblages responded differently across sites (wood, control). Multivariate analyses revealed a different taxonomic structure in abundance and biomass of hyporheic meiofaunal assemblage in LW, whereas macrofaunal assemblages did not show significant differences between LW and control. Assemblage abundance and biomass were driven by physical and sedimentological predictors revealing the tight coupling between these assemblages of organisms and LW habitat.

Our results suggest that naturally occurring wood plays an important role in the ecological functioning of the hyporheic zone in a lowland river through changing sediment and physical dynamics and despite its limited hydromorphological impact on hyporheic flows. This study has given field-based evidence of the spatial impacts of

LW on the whole river invertebrate community and has provided initial insights on the potential effects of wood-based restoration design on the hyporheic zone.

4.1 Introduction

Large wood (LW) is an essential component of fluvial processes and ecosystems (Wohl and Scott, 2017; Gurnell, 2013). LW is living or dead wood in simple or complex structures, where individual pieces are >1 m length and >10 cm diameter (Wohl et al., 2010; Thevenet et al., 1998). A large body of literature has showed the profound effects of LW on river hydrological, physical and ecological processes, as a result of its interaction with water and sediment (Wohl, 2013; Phillips, 2012; Jeffries et al., 2003; Gregory et al., 2003; Abbe and Montgomery, 2003). In ecology, studies on taxonomy-based structural metrics of benthic macroinvertebrates have supported the role of LW to promote biodiversity and physical habitat complexity, but evidence regarding the hyporheic zone (HZ) remains rare.

LW leads to a mosaic of habitat patches varying in porosity, permeability, and physicochemical conditions that result in the patchy distribution of invertebrates (Pilotto et al., 2014; Lancaster et al., 2009; Loreau et al., 2003; Beisel et al., 2000). In upland and lowland rivers, highly variable distributional patterns have been observed for wood-dwellers and benthic macroinvertebrates on and around wood (Benke and Wallace, 2003; Hoffmann and Hering, 2000; Gerhard and Reich, 2000; Hilderbrand et al., 1997; Wallace et al., 1995). These studies have suggested that assemblage composition differs significantly between wood and no-wood sites, and that the observed higher macrofaunal abundance, diversity or biomass associated with LW are linked to increased mesohabitat heterogeneity of wood sites (Pilotto et al., 2014). Research has also demonstrated that both benthic and hyporheic invertebrate distribution can be attributed to patterns of variation within the river channel imposed by factors such as flow (Wood et al., 2000), temperature regimes (White et al., 2017), sediment grain size (Dunscombe et al., 2018; Jones et al., 2015, 2012), and nutrients (De Castro-Català et al., 2015).

Although LW has been gradually integrated into management strategies as a means

of improving the biodiversity of rivers (Kail et al., 2007; Erskine and Webb, 2003; Larson et al., 2001), very few studies have considered the impacts of LW on hyporheic communities (Wagenhoff and Olsen, 2014; Smock et al., 1992).

Field and experimental studies have demonstrated that LW benefits the hyporheic zone (Orghidan, 1959), the region below the riverbed where surface and ground waters mix. LW affects the bidirectional flow of water occurring in the HZ, known as hyporheic exchange flow (HEF) by driving changes in hydraulic head and imposing high hydraulic resistance (Krause et al., 2014; Hester, 2008; Fanelli and Lautz, 2008; Mutz et al., 2007; Lautz et al., 2006; Mutz and Rohde, 2003; Mutz, 2000). The effects of LW are similar to other in-channel roughness elements that create shallow upwelling and downwelling zones and drive water into the subsurface, where it travels along short hyporheic flow paths (Boano et al., 2007; Lautz et al., 2006). The positive role of wood-driven HEF has been demonstrated for nutrient retention (Gomez-Velez et al., 2015; Krause et al., 2013, 2009; Bernot and Dodds, 2005), sediment deposition (Elosegi et al., 2017), sediment hydraulic conductivity (Hess et al., 1992), oxygen concentration (Krause et al., 2013; Kaller and Kelso, 2007; Naegeli and Uehlinger, 1997) and water temperature (Sawyer and Cardenas, 2012). These studies demonstrated the importance of wood-driven HEF in structuring the physical and the ecological compartments of river systems, although substantial gaps remain in our understanding and ability to quantitatively predict interactions among wood and hyporheic biotic communities. Wood-driven HEF is spatially and temporally dynamic because HEF is defined by the interaction between surface and groundwater and thus both surface and subsurface conditions influence the occurrence of HEF at multiple spatial scales (Boano et al., 2014). Therefore, the magnitude of wood-driven HEF largely depends on short and long-term patterns of land use and geomorphology, valley topographic gradient (i.e. lowland and upland), valley geometry (i.e. wood transport and storage), groundwater dynamics (i.e. gaining and losing), channel morphology (i.e. orientation, stability of the LW and the volume of wood in the channel) and sediment transport (Gregory et al., 2003; Jeffries et al., 2003; Collins et al., 2002).). In lowland rivers for example, where the gradient is low and flow velocity is slow, wood induces less HEF and has less effect on spatial patterns of HEF (Krause et al., 2014), but it still significantly influences total hyporheic residence time

by creating low velocity zones within the channel (Shelley et al., 2017; Stofleth et al., 2008).

In conclusion, wood-driven HEF impacts on nutrient, sediment and oxygen dynamics, processes that have important consequences on both hyporheic and benthic communities. As the HZ plays a key role in the life cycle of many benthic invertebrates (Robertson and Wood, 2010; Marmonier et al., 1993), a better scientific understanding of the role of LW on the HZ is necessary to improve our ability to identify the processes controlling the ecological functioning of the HZ, and emphasizes the need for further research to generate on evidence base for river restoration plans.

The aim of this study is to investigate taxonomy-based descriptors (abundance, biomass, richness, diversity) of hyporheic and benthic invertebrates in LW sites of a UK lowland river, and to link descriptor responses to environmental variables at LW sites. We hypothesize that:

1. taxonomic structure, in terms of (a) taxonomic richness, (b) total abundance and composition, and (c) total biomass, is greater in wood sites compared to sites without wood (no wood control sites) (H1).
2. hydrological (i.e. discharge), physical (i.e. dissolved oxygen) and chemical variables (i.e. ammonia) will be significant predictors of (a) abundance and (b) biomass in wood sites. Sedimentological (i.e. medium grain size, d10) and chemical variables (i.e. nitrate) will be significant predictors of the same invertebrate descriptors in control sites (H2).

4.2 Material and Methods

4.2.1 Study area and experimental design

The study was carried out between October 2016 and August 2017 in the Hammer stream, a major tributary of the River Rother, West Sussex, UK (Figure 4.1). It is a woodland stream characterized by chalk and Cretaceous greensand geology (BGS, 2018; SDNPA, 2015; Evans, 1990) and un-impacted by major abstractions, dams or

diversions (baseflow around $0.16 \text{ m}^3/\text{s}$; (EA, 2018)) Two reaches, with different dominant bed sediment types (gravel and sand) were selected. Four sites with in-channel LW and four control sites (no LW) were selected in each reach. The study sites were selected on relatively straight stretches to avoid confounding effects of channel geomorphology on potential HEF. LW sites were separated by distances $>150 \text{ m}$ ($>20 \times$ the channel width) to avoid spatial dependencies. LW were natural (i.e. not part of any engineered restoration measures), submerged, channel-spanning, stable logs (deflector jams or dam jams) that were not transported downstream or re-oriented throughout the study period. Previous studies reported that hyporheic flow in the sand reach of the Hammer stream was dominated by downwelling surface water and bank flow contribution (Shelley et al., 2017).

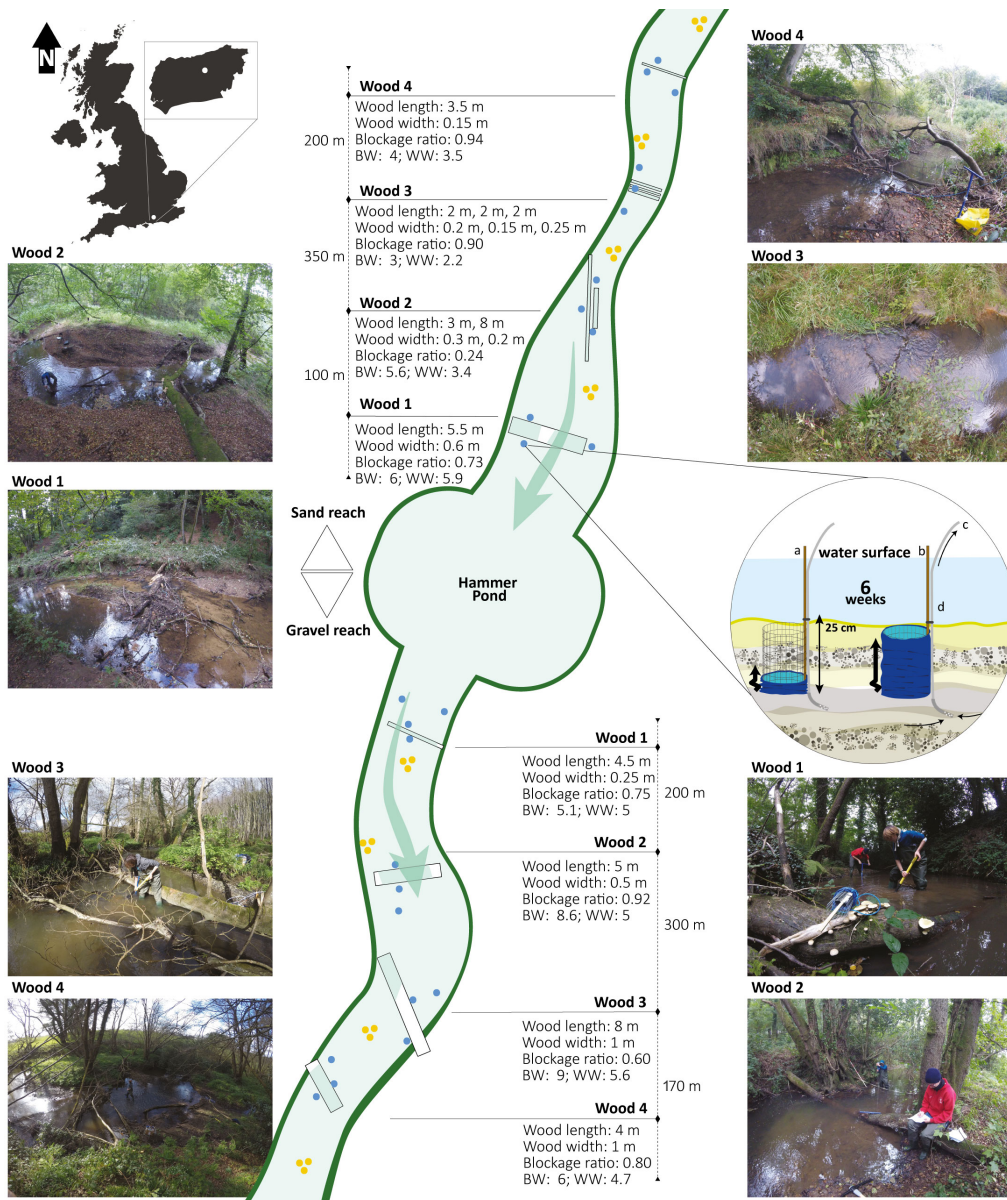


Figure 4.1: Diagrammatic representation of the location of the study area and sampling design. The figure shows the eight sampled LW sites, and the control sites (yellow dots). For each LW information about length, diameter, bankfull width (BW) wetted width (WW) and blockage ratio are displayed. The blockage ratio (B) was estimated as the partial cross-sectional area occupied by each piece of LW and computed as $B = L d/A$, where A is the cross-sectional area, d is the diameter of the LW piece, and L is the projected length of the LW against the flow (Gippel et al., 1996). On the right, an illustration of the colonization pot: a) pot is positioned into the river bed, b) during the extraction, cable is pulled vertically, driving the wire-reinforced tops to the surface and extending the tarpaulin bags, c) minipiezometers for collection of pore water before extraction, d) wood stakes.

4.2.2 Sampling protocol

Hyporheic and benthic invertebrates were sampled three times over the year using colonization pots and a Surber sampler (0.05 m², mesh size = 500 µm), respectively. Three replicates each for wood and control were taken at each sampling site, zone (benthic and hyporheic), for each campaign, and sampling method (144 pots and 144 Surber samples). At LW, invertebrates were sampled upstream, downstream and lateral to the structure (Figure 1). Hyporheic samples were collected using colonization pots (Figure 4.1; 15 cm high, 8 cm diam., mesh size 1 cm²), following a procedure described in Crossman et al. (2013). To minimize the water loss, each colonization pot was equipped with a tarpaulin bag with reinforced top and cable. Holes were excavated by shovel to *ca.* 25 cm deep, and each colonization pot was packed with sediment in stratigraphic order and left *in-situ* for six weeks (Coleman and Hynes, 1970). The colonization pots were also equipped with a minipiezometer for pore water analysis and wooden stakes (Figure 4.1a, c).

Wooden stakes of untreated *Pinus pinaster* were used to estimate vertical patterns of interstitial oxygenation following the protocol of Marmonier et al. (2004).

Hyporheic and benthic samples were collected on the same day after the six weeks colonization period. Immediately after collection the samples were preserved in 90% ethanol. Samples were returned to the laboratory (Cranfield University), where they were rinsed and filtered through a set of sieves. For the colonization samples, the 500 µm sieve was used to retain larger individuals, herein considered the hyporheic macrofauna. The rest of the sample was filtered through a 45 µm sieve and the retained invertebrates constituted the hyporheic meiofauna dataset. Meiofaunal samples were preserved in 100% ethanol and stained with Rose Bengal and sorted within a few days following collection. Surber samples were sieved with a 500 µm sieve and the retained individuals formed the benthic macrofauna dataset. Macrofaunal samples were preserved in 80% ethanol.

During identification, individuals were measured to the nearest micrometer using either an Olympus BX50 (Olympus Optical) microscope or a dissecting microscope. Preserved samples were processed and identified at genus or species level under a

stereomicroscope using the following keys: Chironomidae (Cranston, 1982); Crustacea (Gledhill et al., 1982); Gastropoda (Macan, 1994); Trichoptera (Wallace et al., 2003); Ephemeroptera (Elliott and Humpesch, 2003). For meiofauna taxa such as Nematoda, Oligochaeta, Cyclopoida, Acari, Anomopoda, Copepoda, Ctenopoda, Ostracoda were identified at order or class level (Tachet et al., 2002; Dobson et al., 2012). Measurements were converted to dry mass using published body length and biovolume regressions and conversion factors (Table B.1).

4.2.3 Hydrological, physical, sedimentological and chemical data

Three replicates of hydrological, physical, sedimentological and chemical measurements were taken from every sampling site on each sampling occasion (Table 4.1). Velocity measurements were taken before and after LW using a Flow Tracker Acoustic Doppler Velocimeter (SonTek) at each sampling site. Channel width and water depth were also recorded, and discharge was calculated using the velocity-area method. Spot samples at time of placement and removal of colonization pots of temperature (T, °C), pH, dissolved oxygen (DO, %), electric conductivity (EC, $\mu\text{S cm}^{-1}$) were measured with a multiparameter probe (Hannah HI98196). Continuous measurements of T, EC and water levels in the river were collected using CT2X probes (INW) installed at the beginning of every sampling event and for the following 6 weeks to record any possible flooding event. The locations of the LW pieces were surveyed using a total station (TS06 Leica) and georeferential GPS (GS08plus, Leica Viva). Mean channel width, the channel area, and the orientation angle of each LW relative to the channel, the length and diameter of each large wood were calculated using ArcGIS 10.1 (Figure 4.1).

Sediment samples were retrieved using sediment cores (diameter 5 cm, depth 25 cm) and analysed for grain size and loss on ignition analysis (Blott and Pye, 2001; Heiri et al., 2001). Median grain size, sorting coefficient, skewness and cumulative percentile values (i.e. D10, D90) were calculated from the dry weight of the different fractions using the geometric Folk and Ward (1957) method (GRADISTAT program (Blott and Pye, 2001)).

Concentration of nitrate, nitrite, ammonium and phosphate were measured in sediment pore water, following a procedure described in Lewandowski et al. (2011). Sediment pore water was collected using minipiezometers. Pore water samples were extracted before collecting the colonization pots, samples were filtered using syringe filters (28 mm, 0.2 μm) directly into 5 mL sample vials, discarding 1.5-2 times the inner volume of the tube. A new filter was used for each sample. After filtration, the samples were acidified by addition of a few drops of 2 M HCl and pH paper was used to check that the pH was *ca.* 2. The whole procedure of filtration and acidification was conducted within 30 minutes of collection of each sample.

Table 4.1: Mean hydrological, physical, sedimentological and chemical variables ($\pm sd$) recorded at wood and control sites in the Hammer stream between October 2016 and August 2017. Mean Water Depth (MW), Discharge (Q), Conductivity (EC), Dissolved Oxygen (DO), Temperature (T), Median Grain Size (MDGS), Sorting Coefficient (SO), Skewedness (SK), Sediment Organic Matter (OM), Oxygen Depth (OD), Ammonium NH_4^+ , Nitrate NO_3^- , Nitrite NO_2^- , Phosphate (SRP). Detection limit of $0.1 \text{ mg N } L^{-1}$ for Nitrate, $0.01 \text{ mg N } L^{-1}$ for Nitrite, and $0.3 \text{ mg N } L^{-1}$ for Ammonium.

	Wood \pm sd	Control \pm sd
Hydrological Variables		
MW (m)	0.30 \pm 0.11	0.23 \pm 0.12
Q (m^3/s)	0.08 \pm 0.04	0.06 \pm 0.03
Physical variables		
EC ($\mu S \text{ cm}^{-1}$)	233.44 \pm 29.87	243.7 \pm 20.98
DO (%)	94.60 \pm 37.31	90.45 \pm 23.83
pH	6.85 \pm 0.47	7.04 \pm 0.55
T ($^{\circ}C$)	12.14 \pm 3.13	12.67 \pm 3.05
Sedimentological variables		
D10 (μm)	2170.5 \pm 4857.5	475.8 \pm 883.7
D90 (μm)	17148.2 \pm 18043.4	6858.8 \pm 7497.5
MDGS (μm)	7240.4 \pm 9428.7	2237.7 \pm 2621.9
SO (μm)	2.5 \pm 1.1	0.92 \pm 0.5
SK (μm)	-0.1 \pm 0.3	-0.1 \pm 0.2
OM (%)	6.35 \pm 9.04	1.40 \pm 2.44
OD (cm)	5.85 \pm 3.90	5.13 \pm 4.55
Chemical variables		
NH_4^+ ($\text{mg N } L^{-1}$)	0.32 \pm 0.48	1.01 \pm 1.53
NO_3^- ($\text{mg N } L^{-1}$)	3.95 \pm 4.03	3.87 \pm 4.12
NO_2^- ($\text{mg N } L^{-1}$)	0.01 \pm 0.02	0.02 \pm 0.02
SRP ($\text{mg PO}_4 \text{ } L^{-1}$)	0.16 \pm 0.31	0.32 \pm 0.49

4.2.4 Data analysis

4.2.4.1 Ecological data

Hyporheic samples, macrofauna and meiofauna, and benthic macrofauna were analysed separately. Preliminary analysis of faunal abundances showed that there were differences between sampling methods (colonisation pots *vs* Surber samples) and be-

tween ecological zones (benthic vs hyporheic). The resultant data were therefore analysed separately. Organisms were merged by reach x treatment (wood *vs* control) x site (wood 1-4 in Figure 4.1) x sampling campaign (period) (n = 48 samples). Data were log-transformed (x+1) and rare taxa (<5 individuals per sample) were removed. Rare taxa were kept for taxonomic diversity calculations.

First, the Within Reach x Campaign Analysis (Within-Class Analysis- WCA, *wca* function of the R package *ade4*, (Dray et al., 2017)) was performed to assess whether abundance and biomass was identical in wood and control sites. The Within Reach x Campaign Analysis (WCA) was used to perform a particular case of Correspondence Analysis (CA; (Benzécri, 1983)) with respect to the variable of interest (i.e. wood *vs* control in this study). This is a powerful multivariate method that eliminates the effects of confounding variables (i.e. reach and sampling campaign in this study) in the analysed dataset (Dolédec and Chessel, 1987) and allows studying the variability related to between-sites and between-treatment variation.

Second, the Conditional Inference Tree Approach (CIT) (*ctree* function R package *party*, (Hothorn et al., 2017)) was applied to examine groups of sites with similar or significantly different abundances and biomasses. The CIT approach is similar to traditional regression trees and a commonly applied technique to infer quantitative relationships in ecology and predict ecological status (Zeng et al., 2015; Villeneuve et al., 2015; Kwik and Yeo, 2015; Mondy and Usseglio-Polatera, 2014; Johnstone et al., 2014). It is a form of binary recursive partitioning, presenting several advantages in dealing with nonlinear relationships and collinearity of predictors (Jarošik, 2011; Breiman, 2017; De'ath and Fabricius, 2000). The CIT approach splits repeatedly a dataset into binary groups to generate a decision tree, based on the association between the input variables (i.e. wood and control sites) and response variable (i.e. taxon abundances or biomass in this study). CITs stopping criteria are based on adjusted p-values (Hothorn et al., 2006). In our study, CIT was tested using Bonferroni permutation test (9999 permutations, $\alpha = 0.01$).

Based on taxonomic abundances, diversity metrics (i.e. Shannon-Wiener, Taxonomic Richness) were computed using the R package *vegan* (Oksanen et al., 2018) and their significance tested using Mann-Whitney-Wilcoxon Test (n=48).

4.2.4.2 Environmental data

Environmental data was tested for correlation using Pearson's test, and Principal Component Analyses (PCA) was performed on uncorrelated variables (48 samples, 17 parameters, Table 4.1) to check abiotic differences between LW and control sites. A Canonical Correspondence Analysis (CCA, *dudi.coa* function, R Package *ade4* (Dray et al., 2017)) was performed to determine the correlations between environmental variables and invertebrate assemblages. For this analysis, hyporheic macrofauna and meiofauna were considered together. CCAs model significance in wood and control sites and for each assemblage were tested by permutation test (*anova.cca* function R package *vegan*; 1000 permutations, $\alpha = 0.01$ (Oksanen et al., 2018)) and by evaluating canonical coefficients (Ter Braak, 1986).

4.3 Results

4.3.1 Hyporheic and benthic diversity, abundance and biomass

A total of 58, 72 and 69 taxa were identified, respectively for meiofauna and hyporheic and benthic macrofauna (Table B.2). Among these taxa identified, 34 (hyporheic meiofauna), 59 (hyporheic macrofauna) and 46 (benthic macrofauna) taxa were found in both wood and control sites (Table 4.2).

Table 4.2: Number of taxa common and exclusive for hyporheic and benthic invertebrates in wood and control sites

	Hyporheic meiofauna	Hyporheic macrofauna	Benthic macrofauna
wood	24	6	16
control	4	9	7
common	30	57	46
total	58	72	69

The hyporheic meiofaunal assemblage showed significant differences in taxonomic richness and Shannon Wiener Index between wood and control sites (Wilcoxon's test, adjusted p-value <0.001) and values were higher in wood. However, these metrics did not differ significantly between wood and control sites for macrofaunal assemblages, both hyporheic and benthic (Figure 4.2).

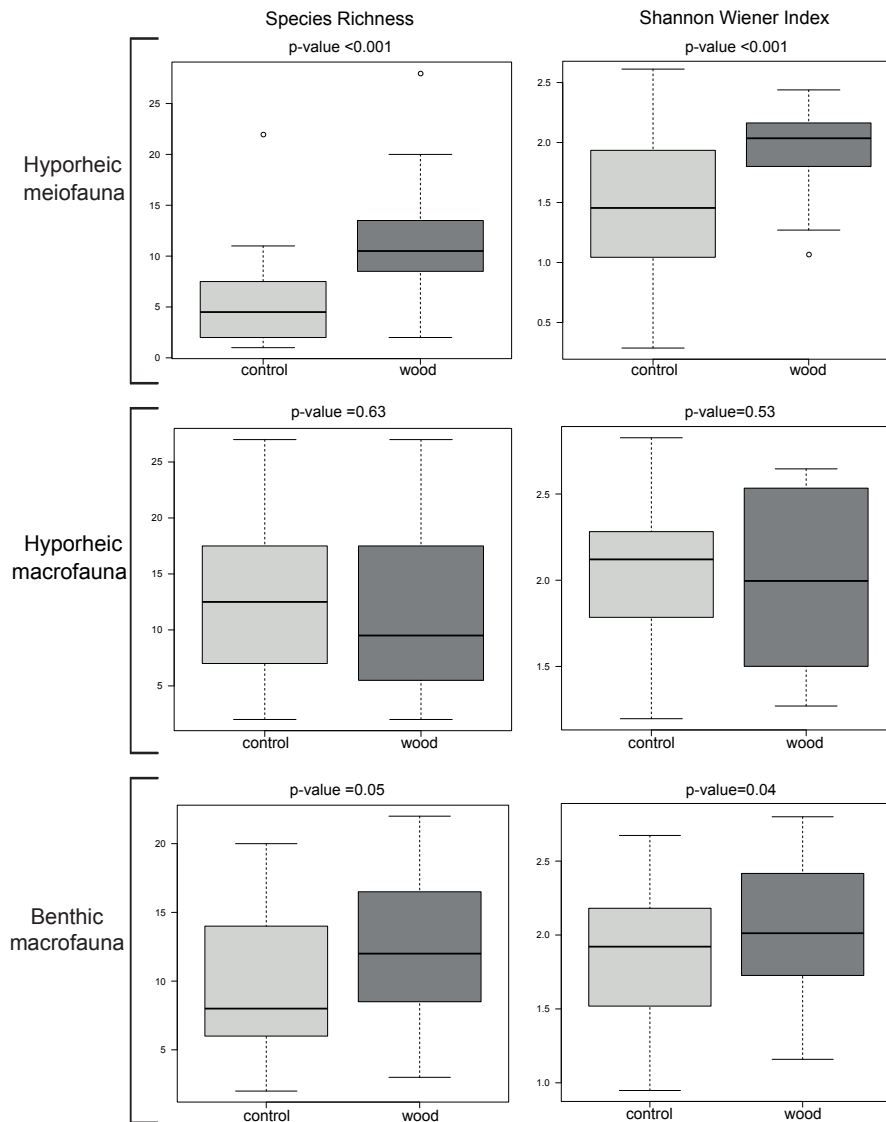


Figure 4.2: Taxa richness and Shannon-Wiener diversity index in control and wood sites for hyporheic and benthic assemblages (Wilcoxon's test adjusted p -value < 0.001).

The total abundance and composition of hyporheic meiofaunal assemblage was different in wood and control sites, and abundances higher in wood. This is confirmed by the Within Reach x Campaign Analysis ($F_1=21.4\%$, $F_2=19.9\%$ of explained vari-

ance, Figure 4.3a) and the Conditional Inference Tree Approach (CIT; Figure 4.3b). The CIT analysis split most of the control and wood sites (coordinates <-0.018 and >-0.018 , respectively) along the second WCA axis ($p = 0.009$, Figure 4.3b), illustrated by the distribution of wood and control samples in each terminal node (Figure 4.3b). Node 2 ($n = 26$, $F2 <-0.018$) gathered about 80% of the control samples whereas node 3 consisted of about 80% of wood samples. In contrast, the taxonomic structure in terms of abundance and composition of the macrofaunal assemblages for both the hyporheic and benthic zones did not differ between sites (Figures B.1 and B.3).

Biomass exhibited similar results; meiofaunal biomass differed between wood and control sites and was higher in wood ($F1 34.6\%$, Figure 4.4), whereas the hyporheic and benthic macrofaunal assemblages were not different in terms of biomass (Figures B.2 and B.4).

Chironomids (i.e. Diamesinae and Tanytarsini), microcrustaceans (i.e. Cyclopoida) and Nematoda accounted for over 60% of the total meiofaunal abundance and biomass in wood sites (Figure 4.5) while “others” (macrofaunal instars) corresponded to about 30% of the total biomass. In contrast, control sites were characterized by the Oligochaeta group which contributed 25% in abundance and more than 60% in biomass. In both wood and control sites, Diptera comprised 30% of hyporheic macrofaunal abundance and Trichoptera comprised 80% of total biomass (Figure B.5). Over 50% of total benthic macrofaunal abundance in wood sites consisted of Diptera (Chironomidae) and Ephemeroptera (Figure B.6). These groups were also abundant in control sites (35%) but here Plecoptera and Trichoptera were numerically dominant (50%). Trichoptera and Diptera comprised about 60% of benthic macrofaunal biomass at wood and control sites (Figure B.6).

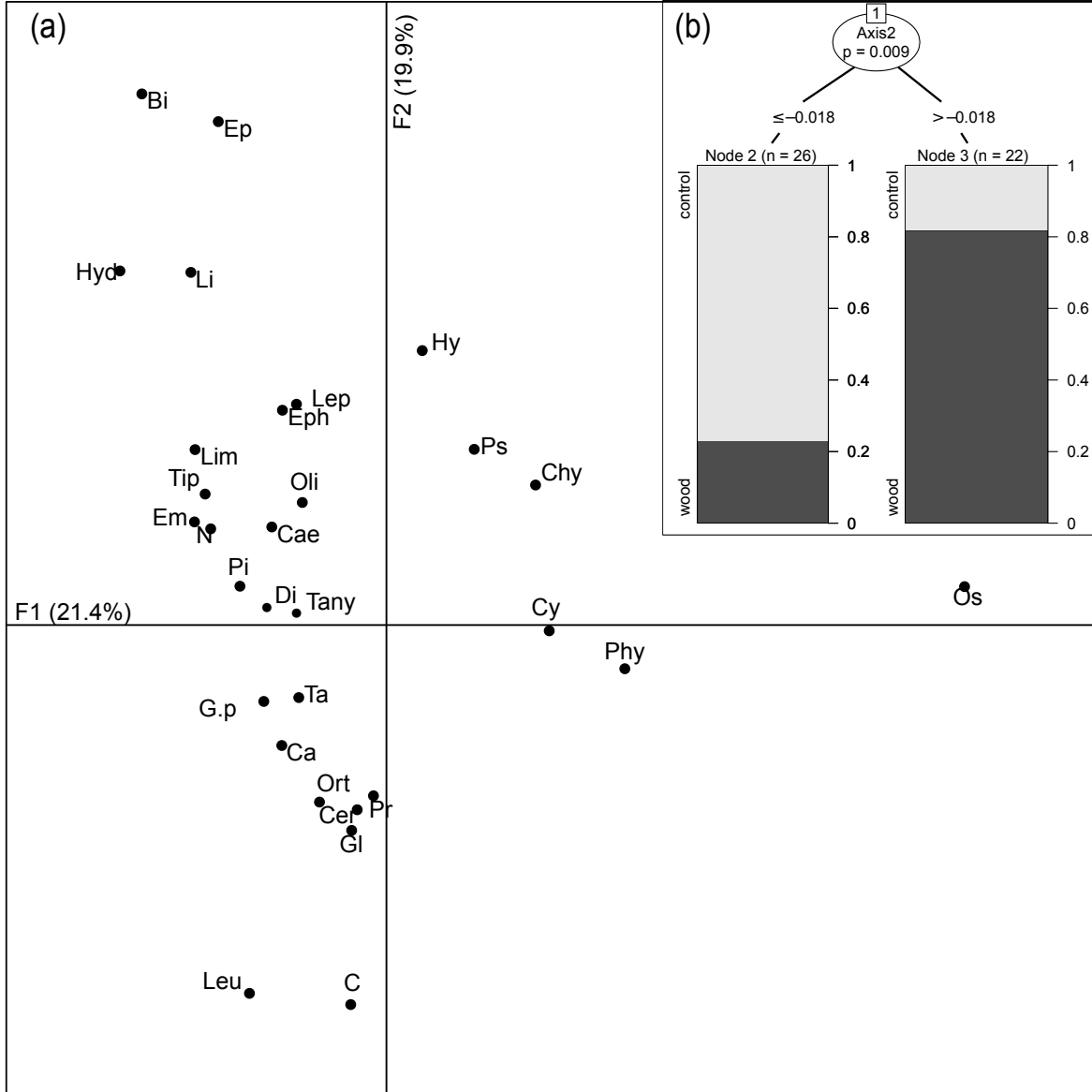


Figure 4.3: Hyporheic meiofauna abundances (log-transformed) per taxon among wood and control sites. (a) First factorial plane of the WCA gives the locations of the meiofaunal taxa (48 samples) in wood and control sites. The percentage of the total variance explained by each axis is indicated. (b) Conditional inference tree (9999 Bonferroni permutations; $\alpha = 0.01$) testing the significance of differences in wood and control sites locations on the second WCA factorial plane (response variables: coordinates of samples along F1 and F2). P-values corresponding to significant wood and control sites differences and the axis coordinates best separating groups of samples (control and wood) indicated at each node of the tree, n = number of samples. See Appendix B for taxa codes.

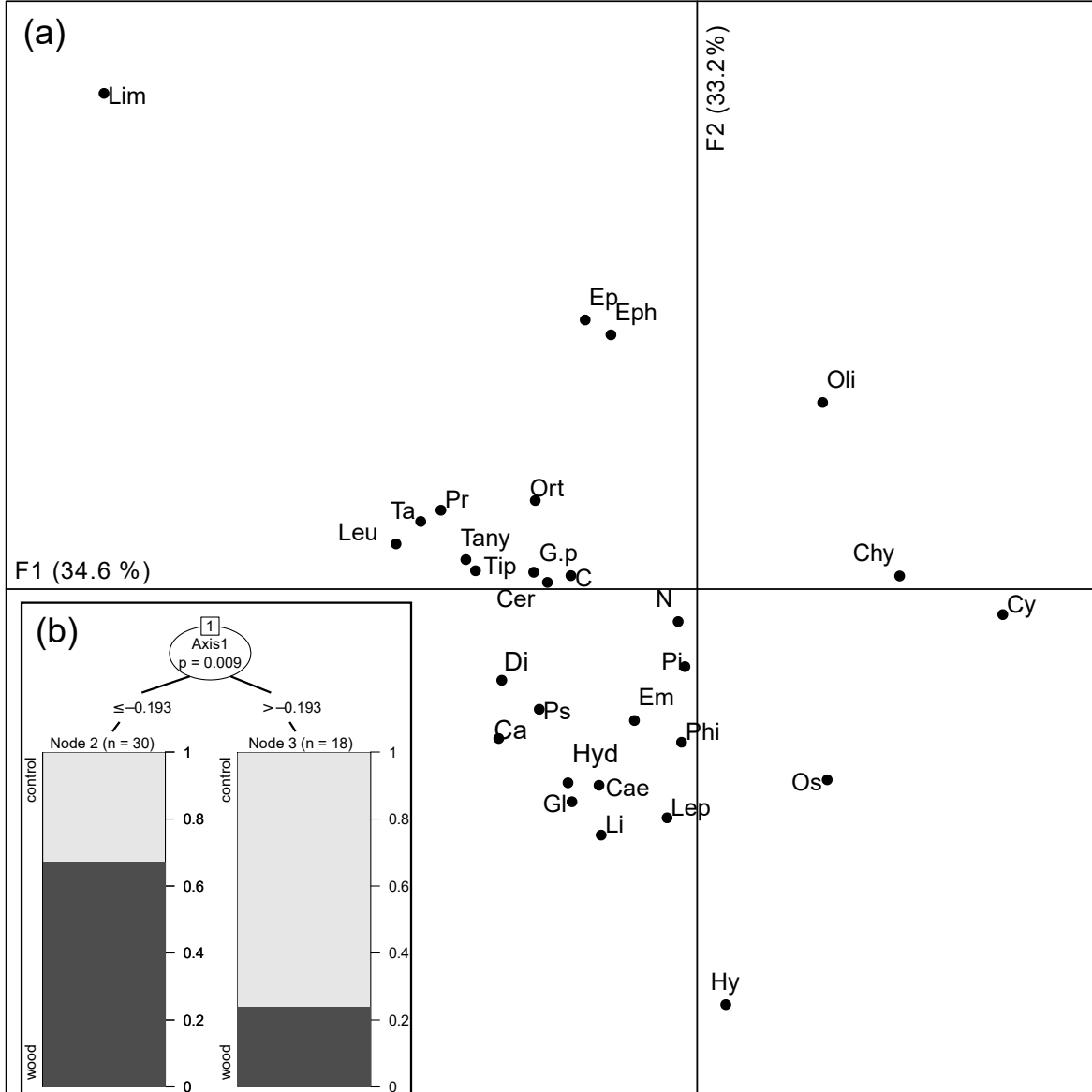


Figure 4.4: Hyporheic meiofauna biomass (log-transformed) among taxa in wood *vs* control sites (48 samples). Locations of meiofaunal taxa in the first factorial plane of the WCA. The percentage of the total variance explained by each axis is indicated. (b) Conditional inference tree (9999 Bonferroni permutations; $\alpha = 0.01$) testing the significance of differences in wood and control sites locations on the first WCA factorial plane (response variables: coordinates of samples along F1 and F2). P-values corresponding to significant wood and control sites differences and the axis coordinates best separating groups of samples (control and wood) indicated at each node of the tree, n = number of samples. See Appendix B for taxa codes

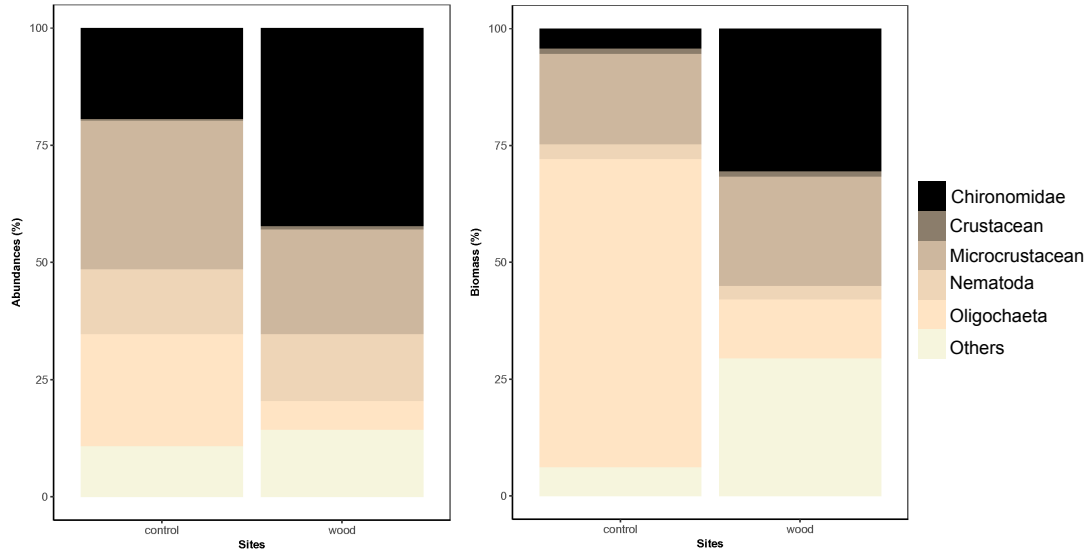


Figure 4.5: The relative contribution in percentage to mean abundance and mean biomass of hyporheic meiofaunal groups found in the Hammer Stream on sampling occasions from October 2016 to August 2017. “Others” includes the taxa Amphipoda, Arhynchobdellida, Coleoptera, Diptera, Ephemeroptera, Plecoptera, Rhynchobdellida, Trichoptera, Tricladida, Trombidiformes, Truncatelloidea, Veneroidea.

4.3.2 Environmental predictors of meiofaunal and macrofaunal assemblages

Environmental parameters varied between reaches (Figure 4.6b), and to a smaller degree between wood and control sites (Figure 4.6d). Differences between reaches were not of primary interest in this study, thus samples were nested in reaches. The PCA revealed that the first axis ($F1 = 29.3\%$; Figure 4.6a) was driven by nutrients (i.e. phosphate, ammonia, nitrate), organic matter and sediment (i.e. median grain size, sediment sorting and skewness), whereas the second axis ($F2 = 11.1\%$) reflected within-site (wood, control) variability (i.e. temperature, dissolved oxygen). Wood sites grouped on the left part of the factorial plane, corresponded to high concentrations of nitrates, median grain size and sediment sorting (Figure 4.6c). In contrast, control sites grouped on the right side of the factorial plane, corresponding with high concentrations of ammonia and phosphate and high percentages of organic matter (Figure 4.6c).

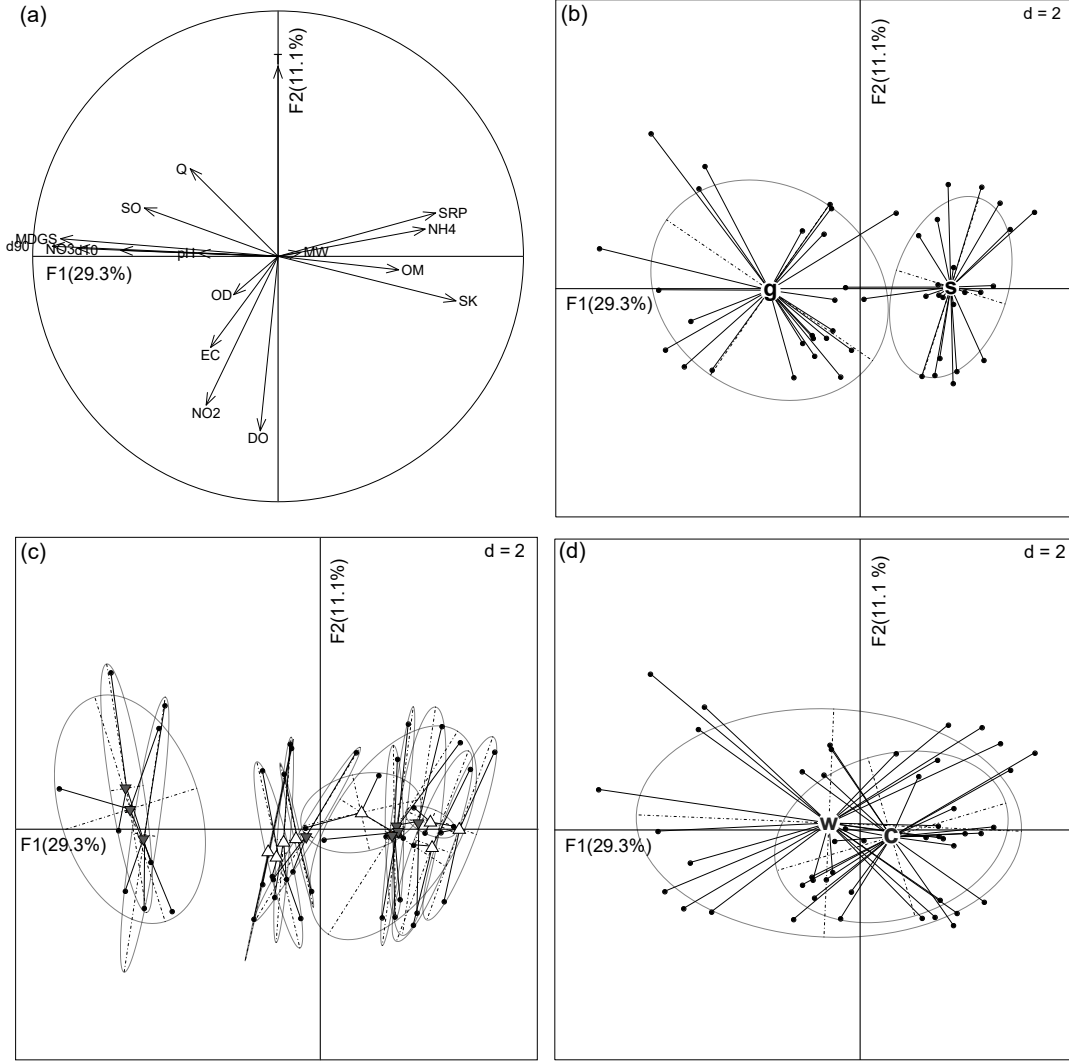


Figure 4.6: Ordination of the environmental samples with principal component analysis (PCA) applied to 48 " sites x date' samples x 17 parameters. (a) Correlation circle giving the correlations of the parameters with the two-first principal components of the PCA; (b) First factorial plane of PCA giving the locations of the 48 samples gathered by reach (sand and gravel). Each reach is located at the weighted average (i.e. the centre of the star) of corresponding samples (solid circles); (c) First factorial plane of PCA giving the locations of the 48 samples gathered by site. Grey triangles refer to wood sites, and white ones to control sites. Each site is located at the weighted average of corresponding samples; (d) First factorial plane of PCA giving the locations of the 48 samples gathered by wood and control. Wood and control are located at the weighted average (i.e. the centre of the star) of corresponding samples (solid circles). Lines link samples to the mean location of their site. The percentage of the total variance explained by each component is indicated. The ellipse of inertia indicates the 95% of confidence interval around the centroids.

Species abundance and biomass of both hyporheic (meiofauna and macrofauna) and benthic (macrofauna) assemblages were influenced by river temperature, pH, sediment organic matter, grain size (median, D10, D90) and nitrates (Table 4.3). Assemblages responded differently across sites (wood, control). Physical variables (conductivity, temperature and pH), and sedimentological variables (D90, skewness), had a significant influence on abundance of the hyporheic zone assemblage in wood sites. Organic matter was significant only for HZ abundance in control sites whereas smaller sized sediments (D10) affected significantly both abundance and biomass in control sites. Nitrite was the only chemical variable to correlate with hyporheic community biomass in control sites. Benthic macrofaunal abundances and biomass were not statistically different in control sites for the measured environmental parameters. Conversely, physical variables (conductivity, temperature, pH) were significant for both descriptors in wood sites, and dissolved oxygen was particularly significant for biomass. Sedimentological variables affected benthic macrofaunal abundances in wood sites. They also affected biomass, but to a lesser extent. Organic matter marginally influenced the assemblage descriptors.

Table 4.3: Significant predictors of the relative abundance of benthic and hyporheic invertebrates in the Hammer Stream as found in the CCAs. Codes: “***” = p < 0.001; “**” = p < 0.01; “*” = p < 0.05; “.” = p < 0.1; p = p-value.

	benthic invertebrate				hyporheic invertebrate			
	Abundance		Biomass		Abundance		Biomass	
	wood	control	wood	control	wood	control	wood	control
1st	0.042 *	0.080 .	0.011 *	0.952	0.043 *	0.025 *	0.027 *	0.053 .
2nd axis	0.164	0.457	0.047 *	0.902	0.569	0.087 .	0.705	0.2
1st and 2nd (%)	42.4	29.1	39.3	60	21	23	26.1	43.3
EC	0.020 *	0.275	0.118	0.631	0.034 *	0.108	0.972	0.058 .
DO	0.131	0.067 .	0.001 ***	0.312	0.391	0.29	0.139	0.218
pH	0.024 *	0.473	0.073 .	0.485	0.031 *	0.575	0.75	0.567
T	0.053 .	0.011 *	0.007 **	0.357	0.038 *	0.010 **	0.046 *	0.131
MW	0.765	0.452	0.691	0.466	0.782	0.763	0.596	0.389
Q	0.807	0.239	0.76	0.654	0.437	0.432	0.926	0.448
d10	0.034 *	0.281	0.036 *	0.491	0.138	0.001 ***	0.147	0.033 *
d90	0.068 .	0.728	0.013 *	0.662	0.028 *	0.643	0.117	0.843
MDGS	0.391	0.081 .	0.371	0.873	0.248	0.016 *	0.448	0.030 *
SO	0.493	0.102	0.049 *	0.474	0.222	0.195	0.47	0.347
SK	0.057 .	0.17	0.007 **	0.299	0.036 *	0.072 .	0.14	0.084 .
LOI	0.089 .	0.086 .	0.072 .	0.722	0.339	0.042 *	0.381	0.348
OX	0.207	0.818	0.632	0.98	0.177	0.432	0.906	0.828
NH4	0.554	0.535	0.22	0.877	0.481	0.284	0.942	0.903
NO3	0.857	0.331	0.672	0.327	0.763	0.423	0.844	0.015 *
NO2	0.817	0.215	0.966	0.366	0.96	0.061 .	0.8	0.148
SRP	0.675	0.745	0.165	0.988	0.477	0.736	0.937	0.726

4.4 Discussion and Conclusion

This study assessed abundance, biomass, diversity and richness of both benthic and hyporheic zone invertebrate communities around LW in a lowland river to provide field-based evidence of the spatial impacts of LW on the whole river invertebrate communities. General patterns emerged in terms of the relative contribution of groups to overall abundance and biomass, although the analysed descriptors did not always differ between wood and control sites (e.g. macrofaunal abundances). Several of the environmental parameters that influenced taxa descriptors were common across hyporheic and benthic assemblages. Here we discuss the effects of LW on the hyporheic and benthic zone (Section 4.4.1) and the major environmental predictors of abundance and biomass descriptors (Section 4.4.2).

4.4.1 Effects of LW on hyporheic and benthic zone assemblages

Assemblages responded differently across sites (wood, control). Hyporheic meiofauna was more abundant, taxonomically diverse and with higher biomass in wood sites, whereas macrofaunal assemblages did not show significant differences. Our first hypothesis (H1), that wood and control sites have benthic and hyporheic assemblages with differing taxonomic richness (a), abundance and composition (b), and biomass (c), was partly supported. Hyporheic meiofaunal assemblages in wood had significantly higher taxonomic richness and Shannon Wiener indices than in control sites supporting H1(a). Also multivariate analysis (WCA and CIT) upheld H1(b) for hyporheic meiofaunal assemblages, indicating that abundances and composition in wood sites differed from control sites. To our knowledge, only one other study has investigated hyporheic abundance and richness around LW (Wagenhoff and Olsen, 2014). They observed higher density and lower diversity of hyporheic invertebrates in streams with LW. They also found that the distribution of hyporheic invertebrates in LW was primarily controlled by opposing effects of increased sediment stability and decreasing oxygen concentration, and that native New Zealand taxa benefited from increased percentage of fines in

LW via increased surface area for microbes, and hence food sources. The taxonomic resolution in our study is too coarse to detect species-level preferences for LW. However, the meiofaunal assemblage in wood sites was characterized by detritivore taxa (Tanytarsini, Diamesinae), suggesting an increase of fine particulate food supplies and moderate flow velocities around LW (Collier, 1993; Munn and Brusven, 1991; Armitage, 1987). This assemblage was also characterized by microcrustacean Cyclopoida that inhabit hard substrata covered by a thin layer of silt/clay and detritus in gently flowing waters (Robertson, 2000; Dole-Olivier et al., 2000; Robertson et al., 1995; Shiozawa, 1991).

Taxonomic richness, abundance and biomass did not show significant differences between wood and control sites for macrofaunal assemblages for either hyporheic or benthic zones. Therefore our first hypothesis H1(a, c) was not supported. This contrasts with previous studies on benthic macroinvertebrates in lowland rivers that correlated higher density and diversity at wood sites with changes in organic matter storage (Pilotto et al., 2016; Benke and Wallace, 2003; Smock et al., 1989). In our study, organic matter had only a marginal effect on macrofaunal assemblages, perhaps because it was so abundant in the sediments of the Hammer stream (Shelley et al., 2017). In both hyporheic and benthic zones, macrofaunal assemblages in wood sites were characterized by taxa such as *Gammarus pulex*, Diamesinae, Tanytarsini and Oligochaeta, that are typical of habitats with high detritus content and feeding on settling seston in low flow areas around LW (Cashman et al., 2016; Pilotto et al., 2014; Spänhoff and Meyer, 2004; Collier, 1993). *Ephemera danica* was also present at wood sites. Previous research on fatty-acid analysis at LW sites has observed that this species has a fatty-acid profile with signatures to bryophytes and periphyton suggesting a wood and leaf oriented diet (Cashman et al., 2016). In the benthic zone, control sites were characterized by high abundances of *Hydropsyche* spp and *Limnius* spp taxa. Some species of the Trichoptera family are known to require stable substrates for attaching nets and maximize their food capture (Pilotto et al., 2014; Schröder et al., 2013). Control sites in the hyporheic zone were characterized by Diamesinae and Oligochaeta taxa. Finally, in our study biomass differed between wood and control sites for only the hyporheic meiofauna assemblages, therefore confirming H1(c). Previous studies have shown higher biomasses

in LW than in riverbed sediment habitats (Thompson et al., 2018; Benke and Wallace, 2003; Hoffmann and Hering, 2000; Smock et al., 1992, 1989). However, our study found no significant differences in the biomass of macrofaunal assemblages between hyporheic and benthic zones, or between wood and control sites, perhaps because macrofaunal biomass was mainly linked to the most abundant and common taxa in all sites (e.g. Diptera, Crustacea).

4.4.2 Linkages between environmental variables and assemblages abundance and biomass across sites

Invertebrate responses to LW were mediated by the interaction among physical and sedimentological variables, and to a lesser extent by chemical and hydrological variables. Previous research has shown that grain size is an important driver of invertebrate community structure and that sediment colmation reduces community abundance in both benthic and hyporheic environments (Descloux et al., 2013; Jones et al., 2012; Olsen et al., 2010; Bilotta and Brazier, 2008; Olsen and Townsend, 2003; Strayer et al., 1997; Boulton et al., 1997; Wood and Armitage, 1997). In our study, sediment size is a common predictor of abundance and biomass for benthic assemblages in wood sites and for hyporheic assemblages (macrofauna and meiofauna) in control sites. LW affects sediment distribution by altering local water velocities (Sawyer et al., 2011) and we hypothesised that the effect of wood on the HEF would have increased local sediment hydraulic conductivities and associated hydrological, physical and chemical variables, resulting in a different taxonomic structure (abundances and biomass) for both assemblages. However, in the Hammer stream wood sites were characterized by finer sediments than control sites, and hydrological and physical variables had a low explanatory power for site variation (Figure 4.2).

A recent study on sandy sections of Hammer stream reports that LW in this low-land environment has a limited impact on the hydrodynamic forcing of surface water and results in little hydraulic variation and high deposition of fine grained sediments (Shelley et al., 2017). This might explain why in our study hydrological variables are not significant predictors of benthic and hyporheic descriptors in wood sites whereas

the small size fraction of the substrate is. Most of the physical variables were significant predictors of abundances in wood sites for both assemblages possibly suggesting that LW increased the physical gradient and the spatial variability of river habitats (Pilotto et al., 2016; Collins et al., 2012). Previous empirical research has observed that nutrient dynamics (i.e. denitrification) in riverbed sediments can be affected by wood-driven HEF (Gomez-Velez et al., 2015; Krause et al., 2009; Bernot and Dodds, 2005) but in our study chemical variables were marginal predictors of abundances and biomass descriptors for both macro- fauna and meiofauna in LW. In lowland rivers, little denitrification processes might occur at wood sites as a consequence of the short hyporheic residence time (Shelley et al., 2017). Control sites in our study were characterized by lower oxygen penetration and higher concentration of ammonium whilst nitrite was similar and nitrate was lower than in LW. Also, the higher percentage of fine sediments in control sites compared to LW, particularly in the sandy reach, positively correlate with an increase in anoxic conditions that altered nutrient dynamics in favour of denitrification. This may explain why taxa that are tolerant to hypoxia, such as Oligochaeta, were more abundant in control sites (de Crespin de Billy et al., 2000), whereas taxa with a low tolerance for hypoxia were less abundant (Ding et al., 2016; Saloom and Duncan, 2005). Ecological responses of benthic invertebrates to nutrient levels are also documented (Marmonier et al., 2012; Krause et al., 2011b), but again little is known about the responses of hyporheic meiofauna. Certain groups of invertebrates are good indicators of moderately eutrophic rivers (e.g. caddisflies Philopotamidae and Leptoceridae and Hydropsychidae with higher pollution sensitivity in Philopotamidae) (Pacioglu et al., 2016). In our study Philopotamidae and Leptoceridae were abundant in sites with lower nutrient concentrations, whereas *Hydropsyche* spp was very abundant in control sites. Other taxonomic groups (e.g. chironomids, oligochaetes, nematodes, and amphipods) that were widespread in both wood and control sites in our study showed high tolerance to nutrients in other studies (Pacioglu et al., 2016).

4.4.3 The way forward

The role of large wood in driving HEF, sediment sorting and redistribution, and as a resource for river restoration, is almost certainly enhanced by the valley and the channel planform (Gurnell, 2013; Gurnell et al., 2000; Gurnell and Sweet, 1998). Yet, there is limited understanding of the underlying effects of LW on hyporheic invertebrate assemblage structure despite their importance for the resilience of river systems (Benke and Wallace, 2003).

Our study on a UK lowland river has shown that LW contributes to increased abundance, biomass and diversity of hyporheic assemblage, mainly for meiofauna, through changing sediment and physical dynamics, thus suggesting that LW does impact the HZ. In the Hammer Stream, a typical example of a lowland river, we found that naturally occurring LW played an important role in the ecology of the hyporheic zone despite the limited hydromorphological impact on hyporheic flows (Shelley et al., 2017). These results suggest that LW likely to lead to a higher resilience to disturbance and to an increased ecological connectivity between hyporheic and benthic zones, thus emphasizing the ecological potential of river restorations using large wood. To conclude, our study will help inform the decision-making of restoration practitioners and encourage them to address the HZ by implementing LW solutions in lowland rivers thereby reaping multiple ecological benefits. Although we have examined the effects of habitat structure and complexity on taxonomic-based descriptors, further research needs to be undertaken to understand the impact of LW on functional invertebrate attributes and to disentangle the relative importance of abiotic and biotic interactions to shape spatial patterns of functional trait diversity.

Acknowledgements

This work was supported by the Marie Skłodowska-Curie Action, Horizon2020 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 analysis. Thanks to Dr. Phillip Blaen, Prof. Stefan Krause and Marco

Palma for the technical support and assistance in the field.

Chapter 5

Hyporheic and benthic invertebrates' functional traits reflect large wood-driven hydro - geomorphological processes

Abstract

Trait-research holds promise to disentangle eco-hydrological processes and functions in the hyporheic zone (HZ) although functional approaches have been rarely adopted on hyporheic invertebrates.

In-channel large wood (LW) is a geomorphic structure widely studied in hydrology because driving hydrological (hyporheic exchange flow-HEF) and geomorphological (sediment deposition and sorting) processes, and commonly used in river restoration as promoting biodiversity. LW ensures vertical and lateral hydrological connectivity in rivers but its role in shaping invertebrate multiple functional traits has not been investigated yet in the benthic or in the hyporheic zone.

We selected 17 functional traits and predicted LW sites to be associated with different trait modalities than no-wood sites in relation to wood-driving processes and conditions (i.e. hyporheic exchange flow, oxygen availability, temporal stability, organic matter, hydraulic conductivity). The variation of traits was also studied as function of hydrological, sedimentological, physical and chemical variables, representing important attributes of the LW environment.

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. Significantly different wood-related traits included aquatic active dispersal, aquatic eggs and hard substrate preferences, suggesting an increase of physical-sedimentological constraints at LW sites. In wood

sites, hydrological, physical, sedimentological and chemical variables similarly contributed to meiofaunal-trait variation. Macrofaunal benthic and hyporheic functional traits were only marginally dissimilar between wood and control sites indicating similar functioning of these assemblages at the surface-subsurface interface.

We have highlighted the close relationships between species traits of both benthic and hyporheic assemblages and local LW environmental conditions, providing further understanding on the functional role of LW in rivers. Both hydrological and ecological connectivity promoted by LW are crucial to river functionality and to river management.

5.1 Introduction

Species are continuously subjected to stress in river environment, whether from the swift flow of water, the movement of sediment, or by altered physico-chemical parameters. They migrate or resist to changing environmental conditions. Species adaptations appear in functional traits, a series of morphological, physiological, phenological and behavioural attributes that have an effect on the community fitness (Carmona et al., 2016). How and what species' functions respond to the interplay of abiotic and biotic factors across spatio-temporal scales is one big challenge in ecology.

The study of functional traits is of paramount importance to ecologists because reflecting ecological responses to spatial and temporal environmental gradients and ecosystem changes (Statzner and Beche, 2010; Townsend and Hildrew, 1994). So, trait-based approaches have been advocated as a mechanistic alternative to traditional taxonomic descriptors and have been successfully used to develop environmental river assessment indices and tools potentially linkable to processes (Gagic et al., 2015; Díaz et al., 2007) and pressures (Mondy and Usseglio-Polatera, 2013; Mouillot et al., 2013; Usseglio-Polatera et al., 2001, 2000).

Trait-research holds promise to disentangle eco-hydrological processes and functions in the HZ (Orghidan, 1959), although functional approaches have been rarely adopted on hyporheic invertebrates (Dunscombe et al., 2018; Descloux et al., 2014). The HZ is the area of interaction between surface and ground waters within river beds, characterized by a diverse fauna and by a bidirectional flow of water known as hyporheic

exchange flow (HEF). The HZ is crucial to hydrological and ecological connectivity in rivers (Kondolf et al., 2006; Ward et al., 1999). For example, HEF was observed to play a big role in determining the distribution of hyporheic fauna (Mathers et al., 2017, 2014), in increasing nutrient retention and denitrification processes (Gomez-Velez et al., 2015; Krause et al., 2013, 2009; Bernot and Dodds, 2005), oxygen concentration (Krause et al., 2013; Kaller and Kelso, 2007; Naegeli and Uehlinger, 1997), and mitigating water temperature (Menichino and Hester, 2014; Sawyer et al., 2012). HEF is regulated by potential and kinetic gradients at the stream bed interface (Boano et al., 2014) and therefore enhanced by catchment (i.e. gradient) and streambed topographic variations (i.e. bedforms, large wood). In the last decades, research on geomorphic structures (i.e. riffles and large wood) and HEF has increased broadly and allowed to understand the impact of bedforms on flow and ecology (Mathers et al., 2017; Käser et al., 2009). In particular, studies on large wood (LW; length >1 m; diameter >10 cm; Wohl et al. (2010); Thevenet et al. (1998)) have gained a lot of interest (Wohl and Scott, 2017; Gurnell, 2013), first because LW triggers hydrological, geomorphological, chemical and ecological processes (Wohl and Scott, 2017; Gurnell, 2013) and second for its wide use in river restoration (Cashman, 2015; Kail et al., 2007; Larson et al., 2001). LW drives HEF by creating shallow upwelling and downwelling zones and imposing high hydraulic resistance and changing in hydraulic head (Hester and Doyle, 2008; Fanelli and Lautz, 2008; Mutz et al., 2007; Lautz et al., 2006; Mutz and Rohde, 2003; Mutz, 2000). By enhancing HEF and other processes, LW increases vertical connectivity of river systems (Kondolf et al., 2006) and would likely have an impact on hyporheic communities. However, to date the relationship between LW and hyporheic communities has not been investigated under a taxonomic or functional perspective. The majority of research on wood and species has focused on aspects and changes of macroinvertebrate community structure (i.e. abundance, diversity and biomass) (Thompson et al., 2018; Pilotto et al., 2016; Benke and Wallace, 2003; Hoffmann and Hering, 2000) and very little on functional traits (i.e. mainly feeding groups) in the benthic zone (Flores et al., 2017; Pilotto et al., 2016; Johnson et al., 2003).

Only Wagenhoff and Olsen (2014) has investigate taxonomic metrics of hyporheic communities (i.e. abundance, diversity) and no information is available on species

functional traits as response variables to LW in river systems. Studies on hyporheic functional traits and LW will help unraveling the existing connections between physical and biological systems in the HZ (Boulton et al., 1997). LW and the multiple associated processes would likely trigger stronger variations in invertebrate trait modalities or favor the expression of certain traits. For example, behavioural features encompass traits that would be likely affected by HEF in larger extent and by organic matter and hydraulic conductivity (Table 5.3). Locomotion adaptations and current velocity preferences for example, would likely be constrained by both surface and subsurface water flows (Table 5.3) as wood-driven upwelling and downwelling flows will not occur in absence of wood and if surface velocities and shearing forces are low (Matthaei et al., 1999; Boulton et al., 1998; Statzner and Borchardt, 1994; Lancaster and Hildrew, 1993) (Table 5.3). Therefore, sites where wood is absent, HEF is likely reduced or low, and sediment hydraulic conductivity low, will further promote the presence of crawlers, burrowers, interstitial locomotion and substrate attachment (Descloux et al., 2014; Boulton, 2007) (Table 5.3).

Also, the substrate preferences will likely reflect the presence of organic detritus, litter and roots in LW sites and possibly silt, in bare and compact sites in absence of wood (Table 5.3). Biological features include traits that are affected mainly by temporal stability (i.e. lower variability of environmental parameters) and HEF (Table 5.3). Decreasing temporal stability and increasing HEF at LW sites would promote multivoltine species (i.e. number of cycles/yr >1) and higher species fecundity as species might invest more energy in reproduction (Benke, 1993) (Table 5.3).

Also, larva and small-bodied organisms (i.e. “aquatic stages” and “maximal potential size” traits) would likely characterize LW sites as organisms might invest the available energy more in reproduction than in somatic development in response to decreasing temporal stability and increasing HEF (Thompson, 2014) (Table 5.3). Morphological features cover traits that are likely affected by HEF and hydraulic conductivity (Table 5.3). Cylindrical and spherical body forms have been associated to clogged sediment (Descloux et al., 2014), which could likely occur in reduced HEF conditions (i.e. sites without LW). As for body form and locomotion traits, more highly flexible invertebrate bodies would likely occur in sites where wood is absent to cope with food search and low

hydraulic conductivity sediments (Table 5.3). Lastly, physiological features incorporate also traits that are likely affected by HEF, oxygen and organic matter availability and denitrification processes (Table 5.3). Organic matter availability (CPOM) would likely drive the presence of shredders in LW sites (Pilotto et al., 2016, 2014).

Filter-feeding and dispersal should be more affected by HEF, which will promote passive dispersal in LW as resilient response to flow (movements achieved by use of flow as an external agent) and active dispersal in sites without wood (Bilton et al., 2001). Finally, mainly spiracle and gill respiration could possibly characterize LW sites as higher oxygen availability is locally associated to wood-driven HEF while high proportions of invertebrates with tegumental respiration have been already found in low conductivity sediment (Larsen et al., 2011; Tomanova et al., 2008). Understanding the relationships between LW and trait combinations of invertebrate assemblages in both benthic and hyporheic zones will have particular relevance for determining the fuller ecological and conservation implications of river restoration using large wood to mitigate water quality pressures, support biodiversity and increase ecological resilience. Therefore, the aim of this study is to examine hyporheic and benthic invertebrates functional traits in response to LW-driving processes (Table 5.1). We investigated 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.

Functional traits utilization is expected to differ in LW and control sites (no-wood), taking into account LW-conditions and driving processes: i.e. increasing vertical hyporheic exchange, sediment hydraulic conductivity, oxygen and organic matter availability, and decreasing 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) selected behavioural, biological, morphological and physiological trait-modalities would differ in LW and control sites as in Table 2 for both macrofaunal and meiofaunal assemblages; and (iii) trait variation in LW and control sites would be explained by a set of hydrological, physical, sedimentological and chemical environmental variables responding to LW-driven processes (Table 5.3).

Table 5.1: Processes-based predictions in wood and control sites.

Processes & Conditions	Wood	Control
1. Hyporheic exchange flow	+	-
2. Oxygen Availability	+	-
3. Temporal Stability	-	+
4. Organic Matter	+	-
5. Denitrification	-	+
6. Hydraulic Conductivity	+	-

5.2 Material and Methods

5.2.1 Study area and survey design

The study was conducted in the Hammer stream, in West Sussex, UK (Figure 5.1). Four in-channel LW and four control sites (with no LW) were selected in the gravel and sand reach respectively. LWs were natural and stable structures, active or complete jams, and were not transported downstream or re-oriented during the study period. LW sites were >150 m (>20 x the channel width) apart to avoid spatial dependencies. Control sites were chosen in bare areas of the riverbed without woody material. Both LW and control sites were selected on relatively straight areas of the channel to avoid confounding effects of channel geomorphology on potential hyporheic exchange flow.

5.2.2 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 the LW and ii) in control sites (Figure 5.1).

Hyporheic samples were collected using colonization pots (Crossman et al., 2013) placed between 5 cm and 25 cm deep in the sediment (Figure 5.1), while benthic samples were taken using a Surber sampler (0.05 m², mesh size = 500 µm) from the sediment

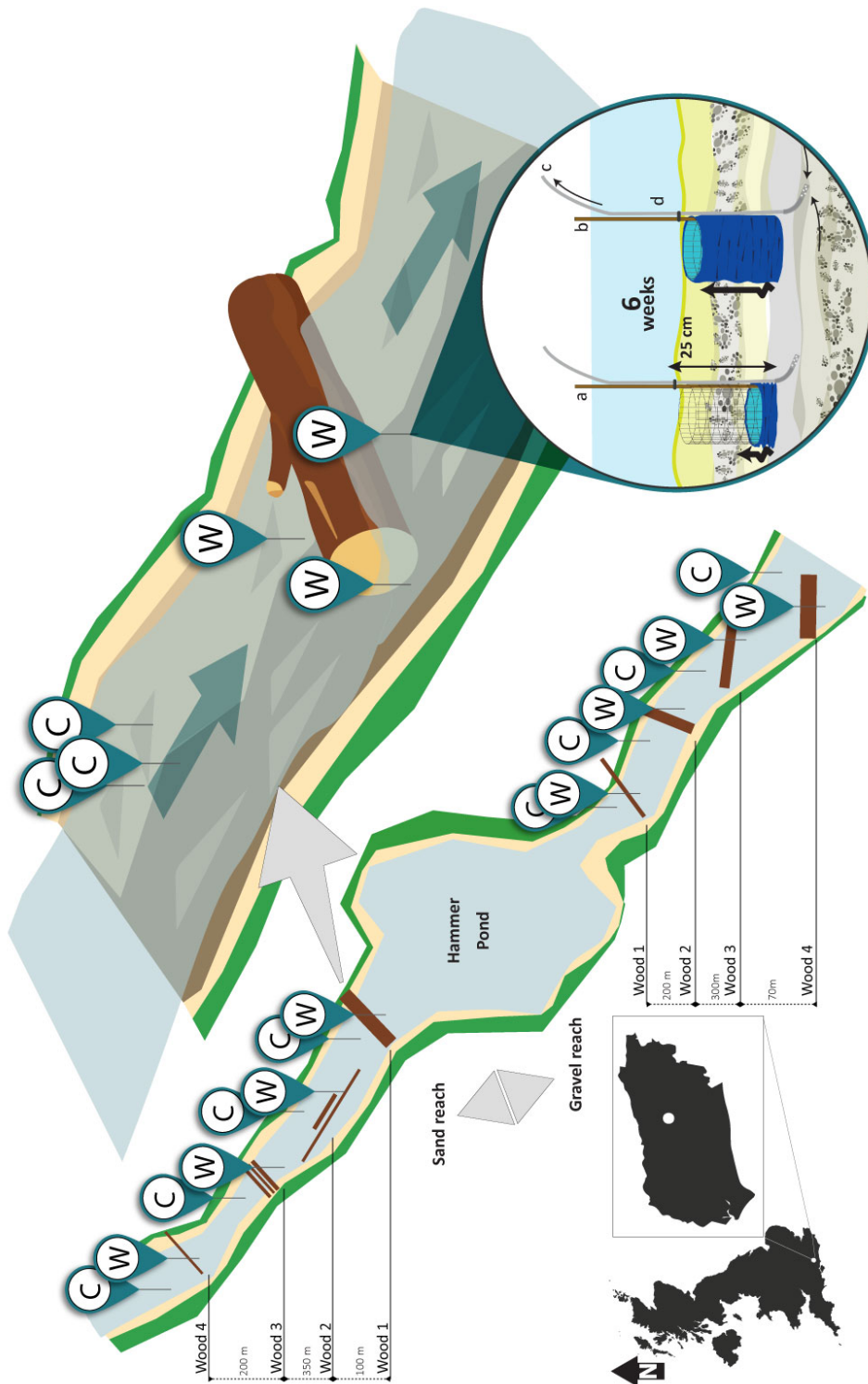


Figure 5.1: Location of the study area and sampling design. The figure shows the eight LW sampled in the gravel and sand reach using the colonization pots and Surber net. The distance between LW sites is displayed. On the right, an illustration of the colonization pot equipped with minipiezometer and wood stakes. The pot is cylindrical steel cages (mesh size 1 cm^2), 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. a) pot is positioned into the river bed. b) during the extraction, cable is pulled vertically, driving the wire-reinforced tops to the surface and extending the tarpaulin bags. c) minipiezometers for collection of pore water before extraction. d) wood stakes.

surface. Pots were left *in-situ* for six weeks to allow invertebrates sufficient time for colonization (Coleman and 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, the 500 μm sieve was used to retain hyporheic macrofaunal individuals; the rest of the sample was filtered through a 45 μm sieve for meiofauna and preserved in 100% ethanol and stained with Rose Bengal. These meiofaunal samples were sorted within five days after collection (Stead et al., 2003).

The Surber samples were sieved with a 500 μm sieve and benthic meiofauna was not sampled given the mesh size of the Surber net. All macrofauna 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 and the following keys: Chironomidae (Cranston, 1982); Crustacea (Gledhill et al., 1982); Gastropoda (Macan, 1994); Trichoptera (Wallace et al., 1990); Ephemeroptera (Elliott and Humpesch, 2003). Due to the quantity of fine sediment which might have damaged hard-bodied organisms, some invertebrates were poorly preserved and thus only identified to family level. Meiofaunal taxa such as Nematoda, Oligochaeta, Cyclopoida, Acari, Anomopoda, Copepoda, Ctenopoda, Ostracoda were identified at order or class level (Dobson et al., 2012; Tachet et al., 2002).

5.2.3 Environmental data

Three measurements of environmental data were taken from every sampling site on each sampling occasion (Table 5.2). Temperature (T; °), pH, dissolved oxygen (DO; %), electric conductivity (EC; $\mu\text{S cm}^{-1}$) 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).

Sediment cores (diameter 5 cm, depth 25 cm) were collected for sediment grain

size analysis (Blott and Pye, 2001) and organic content estimation by loss of ignition (incinerated at 550°C for 5 h) (Heiri et al., 2001). Median grain size, sorting coefficient, skewness and cumulative percentile values (i.e. D10, D90) were calculated from the dry weight of the different sediment fractions using the geometric (Folk and Ward, 1957) method (GRADISTAT program, (Blott and Pye, 2001)). Wooden stakes of untreated *Pinus pinaster*, were part of colonization pots and used to estimate vertical patterns of interstitial oxygenation (Marmonier et al., 2004).

Finally, sediment pore water was collected from minipiezometers (Lewandowski et al., 2011) for measurements of nitrate, nitrite, ammonium and phosphate, discarding 1.5 to 2 times of the inner volume of the minipiezometer tube before filtering the sample. The samples were filtrated using syringe filters (28 mm, 0.2 μm) into 5 mL sample vials, and 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 et al., 2011) .

Table 5.2: Mean hydrological, physical, sedimentological and chemical variables ($\pm SD$) recorded at wood and control sites in the Hammer stream between October 2016 and August 2017. Mean Water Depth (MW), Discharge (Q), Conductivity (EC), Dissolved Oxygen (DO), Temperature (T), Median Grain Size (MDGS), Sorting Coefficient (SO), Skewedness (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, 0.01 mg N L^{-1} for Nitrite, and 0.3 mg N L^{-1} for Ammonium.

	Control-Gravel	Wood-Gravel	Control-Sand	Wood-Sand
Hydrological				
MW (m)	0.20 \pm 0.14	0.28 \pm 0.09	0.26 \pm 0.09	0.31 \pm 0.11
Q (m^3/s)	0.07 \pm 0.03	0.09 \pm 0.05	0.05 \pm 0.02	0.06 \pm 0.02
Physical				
EC ($\mu S\ cm^{-1}$)	249.71 \pm 19.10	243.29 \pm 19.26	237.68 \pm 19.62	223.58 \pm 30.40
DO (%)	89.50 \pm 19.96	97.66 \pm 34.75	91.40 \pm 28.17	91.54 \pm 40.09
pH	7.23 \pm 0.39	7.02 \pm 0.23	6.85 \pm 0.60	6.67 \pm 0.58
T ($^{\circ}C$)	13.07 \pm 3.43	12.48 \pm 3.11	12.26 \pm 2.68	11.78 \pm 3.11
Sedimentological				
D10 (μm)	906.7 \pm 1107.9	4056.8 \pm 5085.6	44.9 \pm 14.8	158.2 \pm 17.6
D90 (μm)	10677.8 \pm 2126.5	31151.7 \pm 10160.8	3039.8 \pm 8927.4	3144.7 \pm 6296.9
MDGS (μm)	4336.5 \pm 2143.4	14088.7 \pm 7827.6	138.9 \pm 147.9	392.1 \pm 144.7
SO (μm)	1.2 \pm 0.5	3.2 \pm 1.0	0.7 \pm 0.2	2.0 \pm 0.2
SK (μm)	-0.1 \pm 0.1	-0.2 \pm 0.2	-0.1 \pm 0.1	0.1 \pm 0.1
OM (%)	0.00 \pm 0.00	0.00 \pm 0.00	2.81 \pm 2.89	12.70 \pm 7.27
OD (cm)	5.87 \pm 4.68	6.25 \pm 2.77	4.40 \pm 2.71	5.44 \pm 3.13
Chemical				
NH_4^+ (mg N L^{-1})	0.13 \pm 0.12	0.09 \pm 0.06	1.89 \pm 1.28	0.54 \pm 0.41
NO_3^- (mg N L^{-1})	7.04 \pm 3.47	7.24 \pm 3.10	0.69 \pm 0.43	0.67 \pm 0.42
NO_2^- (mg N L^{-1})	0.02 \pm 0.02	0.02 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.01
SRP (mg $PO_4\ L^{-1}$)	0.06 \pm 0.04	0.05 \pm 0.04	0.58 \pm 0.42	0.26 \pm 0.30

5.2.4 Trait description and predictions

The traits used in this study consisted of behavioural, biological, morphological and physiological features identified in literature as reflecting organismal performance and adaptations to environmental pressures (Table C.1) (McGill et al., 2006; Usseglio-Polatera et al., 2001, 2000). Each trait was described by 2 to 9 modalities (Table C.1). 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 (Chevene et al., 1994). Taxa such as Nematoda, Oligochaeta, Cyclopoida, Acari, Anomopoda, Copepoda, Ctenopoda and Ostracoda were described as mean trait profiles of their potential families in the corresponding biogeographic area (Descloux et al., 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.

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Table 5.3: Trait-based predictions in both benthic and hyporheic invertebrate communities according to the processes reported in Table 5.1. The table indicates only the trait modalities expected to be significantly enhanced by the habitat conditions in the corresponding site type (LW or Control). Characters in bold indicate processes that are considered having a stronger influence in driving the predicted trait modality.

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

5.2.5 Data analysis

5.2.5.1 Biological data

Hyporheic macrofauna, hyporheic meiofauna, and benthic macrofauna were analysed separately because preliminary Correspondence Analysis of faunal abundances showed that there were significant differences between sampling methods (colonisation pots *vs* Surbers) and between ecological zones (benthic *vs* hyporheic) and the resultant data were therefore analysed separately.

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 weighing 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.

Then, Within Reach x Campaign Analysis (Within Class Analysis, WCA) (*wca* function of the R package *ade4*, (Dray et al., 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 Within Reach x Campaign Analysis (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 (Dolédec, 1989). WCA was chosen after testing the Fuzzy Correspondence Analysis (FCA, (Chevene et al., 1994)), which did not produce meaningful results due to the between-reach and between-campaign variability of log-transformed trait profiles of faunal assemblages in samples.

Subsequently, the Conditional Inference Tree Approach (CIT) (*ctree* function R package *party*, (Hothorn et al., 2017, 2006)) 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: i) tests the independence between the input variables (i.e. wood and control sites) and the response (i.e. trait profiles), ii) stops if this hypothesis cannot

be rejected or select the variable with the strongest association to the response; iii) applies binary split to the selected input variables; iv) repeats recursively previous steps (Hothorn et al., 2006). 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 non-parametric Wilcoxon Signed-Rank Tests. Bonferroni corrections (p -value < 0.001) were applied for selecting trait modalities with significant differences between LW *vs* control sites.

5.2.5.2 Environmental- traits relationships

The relationship between environmental data and taxon traits was investigated by applying the Partial Least Squares (PLS) Path Modelling (Wold, 1982) using the *pls* function of the R package *pls* (Sanchez et al., 2017).

PLS was applied to link hydrological, physical, sedimentological and chemical variables to the variations of invertebrate trait modalities (Figure C.1). 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 (Grace et al., 2010; Vinzi et al., 2010). In the last few years, this approach has experienced an explosive growth in a wide range of disciplines including econometrics, social sciences and ecology (Villeneuve et al., 2018; Memon et al., 2017; Bizzi et al., 2013; Vinzi et al., 2010).

First, the PLS approach includes the estimation of the latent variables as linear combinations of their respective blocks of manifest variables (Tenenhaus et al., 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 et al., 2005). The calculations are performed on the outer model, which links the manifest variables to the corresponding latent variables (Vinzi et al., 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 et al., 2005). The last step of the PLS analysis involves the computation of the loadings by simple correlations in the

outer model. In this study, hydrological, physical, chemical and sedimentological latent variables were standardized and expressed as formative indicators (manifest variables 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) (Tenenhaus et al., 2005) (Figure C.1). PLS analysis was executed on a sub-set of significant trait modalities (Section 5.2.5.1). 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 et al., 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.

5.3 Results

5.3.1 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 Within Reach x Campaign analysis (F1 = 12.8%, F2 = 10.0% of explained variance; Figure 5.2a) and the Conditional Inference Tree Approach (CIT) (Figure 5.2b).

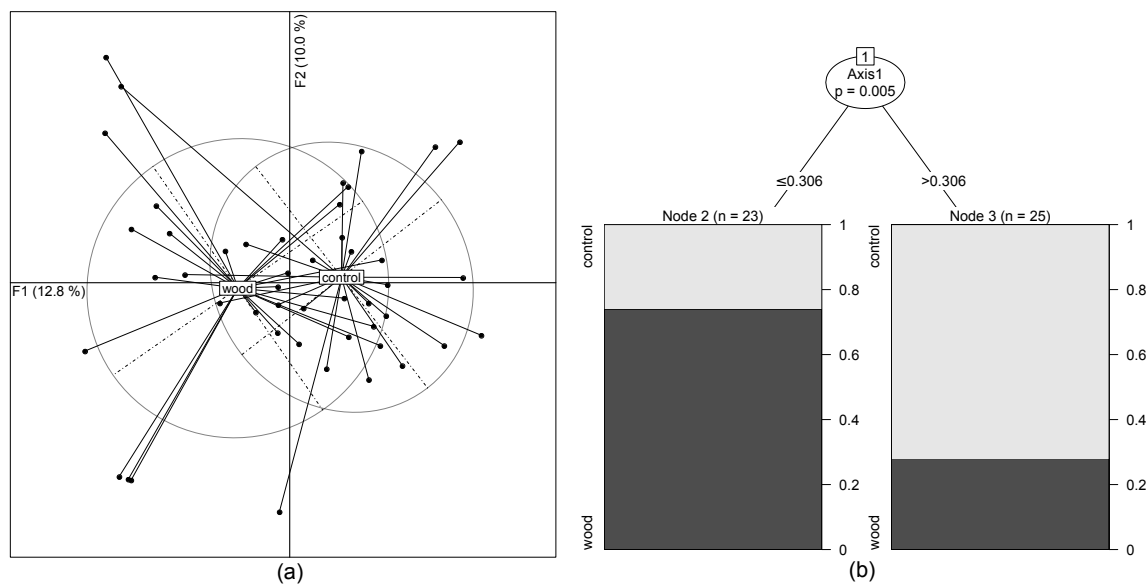


Figure 5.2: Hyporheic meiofauna trait profiles among wood and control sites. First factorial plane of WCA gives the locations of the 48 samples gathered by wood and control. In (a), wood and control are located at the weighted average (i.e. the centre of the star) of corresponding samples (solid circles). Lines link samples to the mean location of treatment category. The percentage of the total variance explained by each axis is indicated. The ellipse of inertia indicates the 95% of confidence interval around the centroid of wood and control sites. (b) Conditional inference tree (9999 Bonferroni permutations; $\alpha = 0.01$) testing the significance of differences in wood and control sites locations on the first WCA factorial plane (response variables: coordinates of samples along F1 and F2). P-values corresponding to significant wood and control sites differences and the axis coordinates best separating groups of samples (control and wood) indicated at each node of the tree, n = number of samples.

The ordination plots of single trait modalities showed that many trait modalities were differently expressed in wood and control sites (Figure 5.3), but these differences were statistically significant for only six of them: aquatic active dispersal, aquatic eggs, aquatic nymphs, and preferences for twigs and roots, sand and hard substrates (Wilcoxon's test, adjusted p-value < 0.001, Figure 5.4, Table C.2). Conversely, 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; Figures C.2, C.3) and no trait modalities exhibited statistically significant differences between control and LW sites (Wilcoxon's test, adjusted p-value < 0.001, Figure C.4, Table C.3).

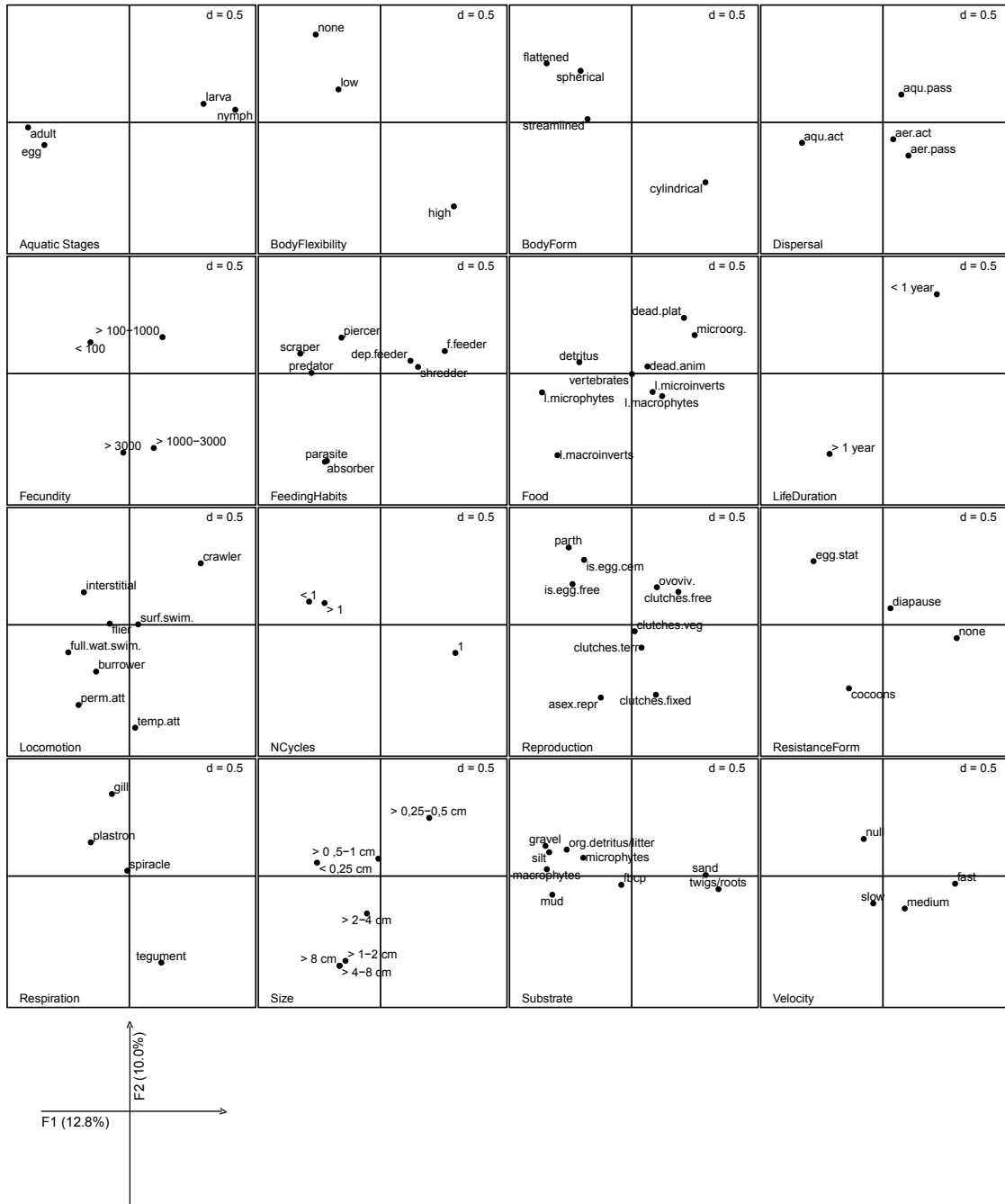


Figure 5.3: Ordination of trait modalities (small black dots) from biological and ecological traits by the Within Reach x Campaign Analysis based on the mean trait profiles of hyporheic meiofauna in LW *vs* control sites. The percentage of the total variance explained by each axis is indicated at the bottom of the figure.

After applying Bonferroni corrections to the Wilcoxon's test results, some other modalities of the corresponding traits (i.e. preferences for mud or macrophytes as substrate, aquatic passive dispersal, adult and larval stages) and of five additional traits (i.e. food and velocity preferences, resistance forms, body form, respiration) were considered as not differently expressed in wood *vs* control (because exhibiting p-values only in the range [0.001 - 0.01]; Table C.2). Wood-related traits included aquatic eggs, aquatic active dispersal and preferences for hard substrates (i.e. flags, boulders, cobbles and pebbles) (Figure 5.4). Control sites were characterized by specific substrate preferences (i.e. twigs and roots and sand) and aquatic stages (i.e. nymph). Finally, macrofaunal assemblages were characterized by trait modalities marginally ($0.01 < p\text{-value} < 0.05$) dissimilar in LW and control sites (Figure C.4).

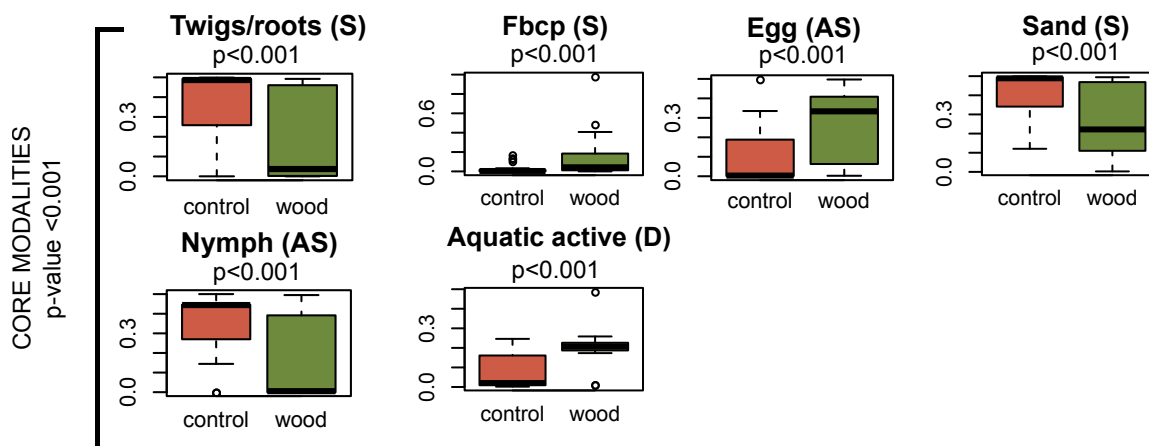


Figure 5.4: Boxplots of the trait modality relative frequency utilization by the hyporheic meiofauna in control *vs* LW sites. Only significant trait modalities exhibiting significant differences (Wilcoxon's test, adjusted p-values < 0.001) between control and LW sites are presented. The corresponding traits are provided into brackets. See Annex D for further details on the full labels of traits and traits modalities.

5.3.2 Links with environment

PLS analysis was applied to the six significant meiofaunal traits and showed that LVs explained 47 % of trait variation in wood sites. The PLS inner model showed moderate prediction capacity of meiofaunal trait modality utilization (R^2 : 47 % in

wood and 55 % in control) (Figure 5.5). Sedimentological and chemical variables were well explained in both control and wood sites ($55\% < R^2$ values $< 61\%$, $40 < R^2$ values $< 62\%$, Figure 5.5). Physical variables were, little and 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%, 22%-43%) despite the response patterns differed between sites (Figure 5.6).

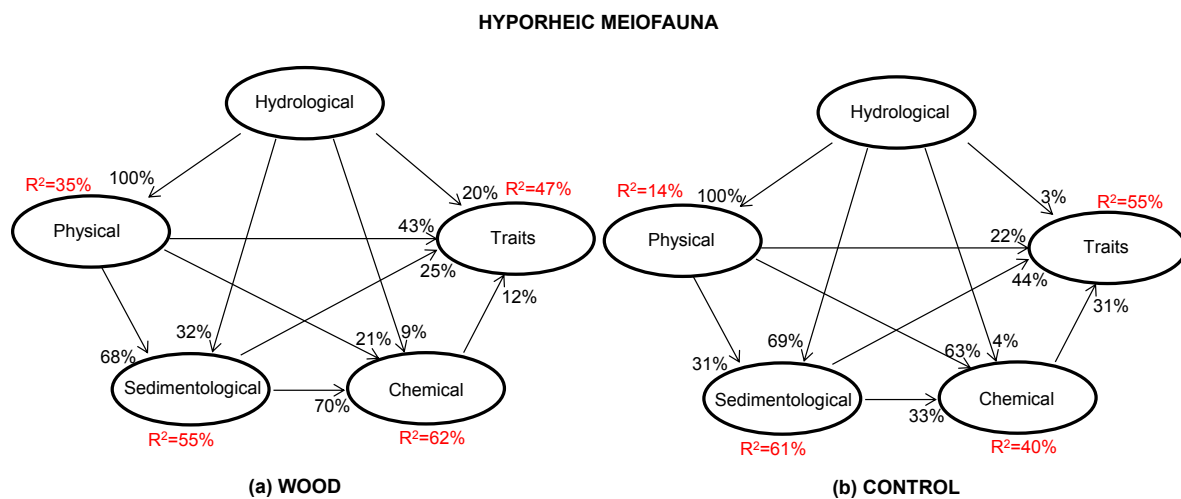


Figure 5.5: Models derived from PLS path modelling for hyporehic meiofauna in wood and control sites. Each latent variable is represented by an ellipse box and each direct effect from this latent variable to another is represented by an arrow. R^2 of each internal model are represented in red. Contributions of latent variables to the variation of trait modalities explained by a model (in percentages of the model R^2) are represented in black.

Wood sites showed a major direct effect of physical variables (43%) and similar effect importance of sedimentological and hydrological LVs (25%, 20%; Figure 5.6). In control sites, sedimentological and chemical LVs explained most of trait variation (44 % and 31%) whereas hydrological variables had only a minor effect (3%).

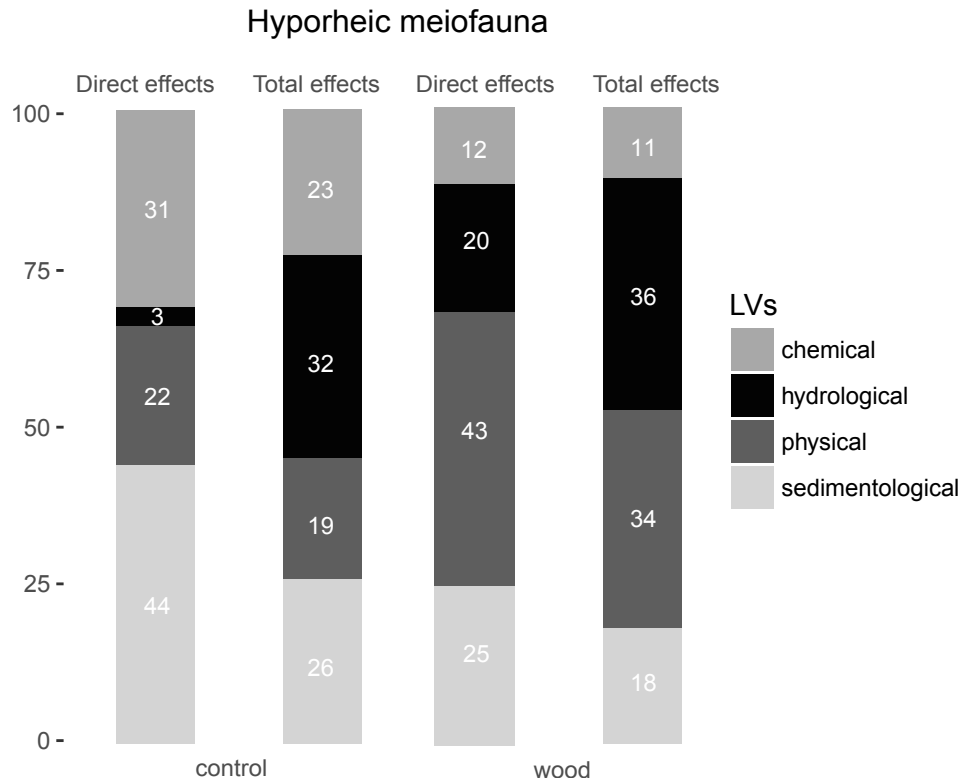


Figure 5.6: Relative contribution (%) of latent variables (LVs) to the variation of core trait modalities (Wilcoxon's test p-value adjusted p-value <0.001) values explained by the model taking into account direct effects only or total effects (direct + indirect effects) for wood and control sites in hyporheic meiofauna.

When looking at total effects, the contribution of LVs to trait variation changed, due to indirect effects (Figure 5.6). A higher effect of hydrology (36%, 32%) and a decrease of sedimentological variables (26%, 18%) are shown in both control and wood sites (Figure 5.6). Finally, sedimentological and physical LVs showed higher impact (50-80%) in control sites on substrate preferences (i.e. sand and twigs/roots) and aquatic stages (i.e. egg, nymph) variation (Figure 5.7). In wood sites, the relative contribution of the LVs to the trait variation is similar among modalities (Figure 5.7).

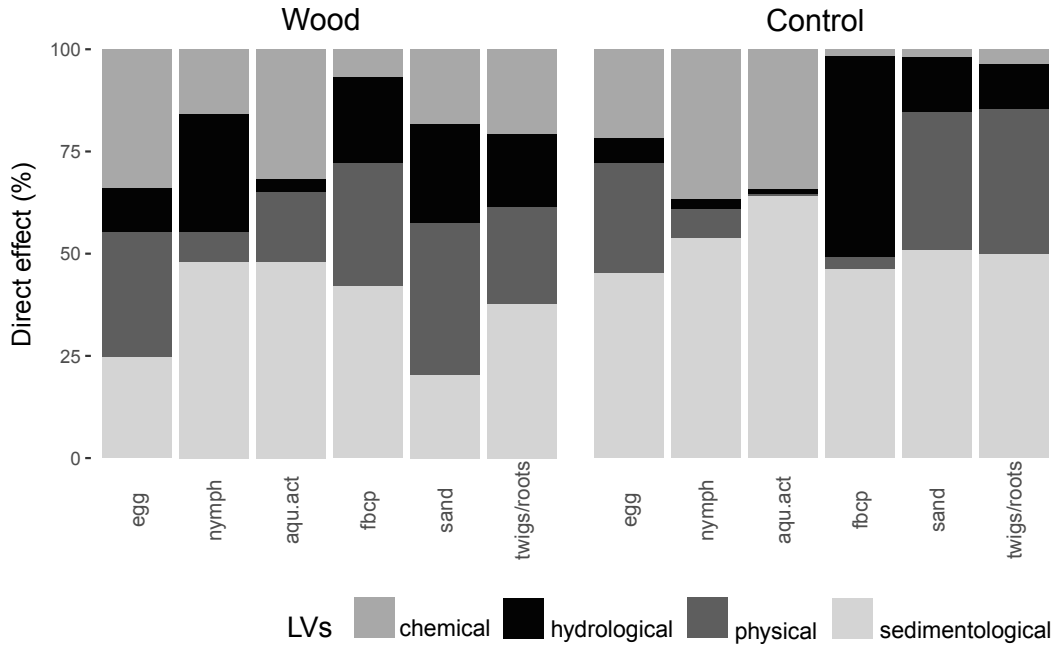


Figure 5.7: Direct effects of LVs on hyporheic meiofauna core trait modalities (Wilcoxon test p-value adjusted p-value <0.001)

5.4 Discussion

This study is, to the authors' knowledge, the first attempt to assess multiple functional traits of meiofaunal and macrofaunal invertebrates around large wood in rivers. Wood and control site assemblages exhibited different profiles of traits and general patterns emerged in terms of responses to wood processes. In this section we discuss wood-related traits in the hyporheic and benthic zone (Section 5.4.1) and the major environmental predictors of trait modality variation (Section 5.4.2).

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

Our study shows that some meiofaunal functional traits differed in wood and control sites, thus upholding our first hypothesis that LW would affect the trait profiles of the hyporheic meiofauna. Significant differences between sites were recorded for single biological, physiological and behavioral meiofaunal modalities, partly supporting our second hypothesis that multiple functional traits would be affected by LW (Table 5.3). Wood-trait significant modalities included aquatic active dispersal, aquatic eggs and hard substrate preferences. These trait modalities relate strongly to temporal instability, flow disturbance and sediment hydraulic conductivity. Counter to our expectations (Table 5.3), active aquatic dispersal was recorded as significant physiological feature 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 5.4.2).

Active aquatic dispersal entails self-generating organism movements often associated to flightless aquatic invertebrates observed to display an active behaviour triggered by changing and unstable environmental conditions (Stubbington et al., 2017; Tonkin et al., 2017; Ponder and Colgan, 2002). Achieving active aquatic dispersal in unstable environment as LW might likely be a sensible strategy, although, generally the cues that trigger aquatic and hyporheic insects to disperse are poorly understood (Tonkin et al., 2017; Bilton et al., 2001). Findings have also indicated that some invertebrates can achieve temporal dispersal in variable habitats by differential egg hatching regimes (Brock et al., 2003; Zwick, 1996), possibly supporting the presence of more organisms with aquatic eggs in LW. Wood meiofaunal assemblages also showed substrate preferences for cobbles and pebbles, possibly due to more heterogeneous habitat conditions and patches of much coarser sediment around LW (Table 5.2) (Pilotto et al., 2014).

Our first and second hypotheses that trait profiles of macrofaunal and meiofaunal assemblages differ between LW and control sites and as in Table 5.3, were not upheld for hyporheic and benthic macrofaunal assemblages as the functional traits did not significantly differ across sites. This result might suggest that the functional traits of

the dominant macrofaunal species (hyporheic and benthic) exhibited similar combination of traits (the mass ratio hypothesis (Grime, 1998)) and as result, at the scale of both benthic and hyporheic zones, similarly driving functional processes. Corresponding assemblages could have rather similar functioning and functional divergence, in the study site (Villéger et al., 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 et al., 2008).

5.4.2 Environmental drivers of hyporheic meiofauna trait variation

Trait variation in LW and control sites was explained by sedimentological and physical variables although their relative contributions changes among sites. Wood-related physical LVs (i.e. pH, conductivity, dissolved oxygen, temperature) were most important in explaining the overall variation of taxon traits, implying that these exhibit strong relationships to local environmental conditions when viewed at reach scale. In agreement with our expectations (Table 5.1), the relative contribution of LVs to wood-trait variation is similar among modalities, underscoring a higher level of temporal instability in LW than control sites (Table 5.1) as contribution of multi-environmental drivers and to similar structuring of abiotic conditions (i.e. abiotic filters) on trait selection in LW assemblages, living in more unstable habitats (Statzner and Beche, 2010; Gurnell et al., 2002).

Control sites exhibited more homogenous responses for sedimentological variables suggesting an increase in temporal stability and a reduction of wood-driven physical constraints (Table 5.1). Sedimentological variables explained more than half of trait variation for all significant modalities, chemical variables and physical LVs explained the remaining 50% in aquatic stages, dispersal and substrate preferences respectively.

Sedimentological variables largely explained variation in hyporheic meiofaunal traits in control sites, although significant trait- modalities did not reflect alone a strong sedimentological impact. This finding is supported by other studies that have observed

weaker effects of sediment size on hyporheic trait profiles (Descloux et al., 2014, 2013). Also chemical LVs explained much of the variation of traits for hyporheic assemblages in control sites. Actually, the sandy reach of the Hammer stream was observed to have nitrate-rich riverbed as LW sites are characterized by short hyporheic flow-paths which inhibit local nitrate reduction (Shelley et al., 2017). The responses of benthic invertebrate assemblages to nutrients are well documented whereas those of the hyporheic meiofaunal assemblages are far less known (Marmonier et al., 2012; Krause et al., 2011b). 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 with standing only a low-moderate range of nitrate, ammonium and phosphate concentrations (Pacioglu et al., 2016; Jones et al., 2012; Elliott, 2008; Nijboer, 2004). In our study, Psychomyiidae and *Hydropsyche* spp instars were observed in control sites exhibiting higher concentrations of ammonium and phosphates than LW sites. Besides, other taxonomic groups (e.g. chironomids, oligochaetes, nematodes and amphipods), widespread among wood and control sites, have demonstrated high tolerance to nutrients in previous studies (Pacioglu et al., 2016).

Finally, our findings confirmed the mechanistic impact of LW on hyporheic meiofauna trait-selection as results of a mosaic of LW-driving processes. The effects are more selective on meiofaunal than macrofaunal assemblages highlighting the importance of LW in triggering physical and sedimentological impacts on faunal communities of low-land 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 and Wood, 2010). Our findings give also a glimpse into the mechanisms responsible for local invertebrate assemblage structure in LW, reflecting adaptations to dominant local and regional environmental stresses.

5.4.3 Perspectives

The trait approach has offered a mechanistic alternative to traditional taxonomy-based approach to address the interplay of local biotic and abiotic factors governing

functional relationships of invertebrates to wood-habitat. The hyporheic zone and river connectivity are interrelated structural and functional properties of heterogeneous environments (Ward et al., 1999) and large wood does play a key role promoting vertical hydrological connectivity (Lautz et al., 2006) and, as evidenced in this study, ecological connectivity. Both hydrological and ecological connectivity are crucial to river functionality (“biodiversity maintenance”, (Leibold and Norberg, 2004) and as result to river management (Kondolf et al., 2006; Ward, 1989).

Our results suggest that understanding the effects of LW on the hyporheic and benthic zones depends upon a certain level of disturbance. The decrease of temporal and spatial stability in LW sites, by increasing variability of local abiotic conditions, resulted in species traits alternatively underscoring temporal disturbance and spatial refugia availability (Townsend and Hildrew, 1994). As a result, LW would likely promote species r-strategist sustainability and in turn contribute to maintain the global richness/biodiversity of invertebrate assemblages by facilitating long-term temporal co-existence 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 (Intermediate Disturbance Hypothesis (IDH) theory; (Connell, 1978)).

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 (Kail et al., 2007; Erskine and Webb, 2003; Larson et al., 2001). Yet, such approaches have not always given due attention to the underlying ecological processes supporting river vertical connectivity. 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 possible benefit to river restoration from functional interactions among different ecological niches. Such data is essential within a processdriven and strategic framework to effective restoration planning (Wohl et al., 2005) and has heuristic value for generating further hypotheses about invertebrate functional responses to LW.

Acknowledgements

This work was supported by the Marie Skłodowska-Curie Action, Horizon2020 within the project HypoTRAIN (Grant agreement number 641939). Thanks to the Laboratory of the Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB) for performing the pore water chemical analysis.

Chapter 6

Discussion

6.1 Introduction

Previous chapters have described the importance of hyporheic mixing in river systems, its variability in time and space and the impacts on species structural descriptors and functional traits. HEF plays such a significant role in mediating physical, chemical and ecological processes in rivers that considering the HZ in management plans could bring major benefits to re-establish the processes necessary to support the natural ecosystem within a catchment. But, to develop adequate management strategies, predicting where HEF occurs over multiple scales and its effects on river ecology is required to improve methodological and modelling approaches to HEF and target river management needs.

To this end, spatial and temporal variation of HEF was assessed over three spatial scales (catchment, segment, reach) to uncover the scale-specific factors and interactions that determine its variability (Objective 1), a novel and transferable approach was developed and tested to identify areas with potentially significant HEF (Objective 1), and to investigate the effects of these variations on invertebrate structural descriptors and functional traits assessed for use in restoration priority planning (Objective 2). This last chapter of the thesis will reflect on how process-based hydro-ecological knowledge of HEF can support river restoration through the prioritization of sites and approaches to target the HZ.

6.2 Sites of hyporheic exchange flows and effects on river ecology

HEF is the result of deeply interconnected hierarchical processes and how their influences extend across scales. The consideration of different spatial scales is essential to unravel the underlying factors and process interactions controlling HEF variation, which was illustrated in Chapter 3 when applying a multiscale method to nine contrasting European rivers, and in Chapters 4 and 5 when investigating the effects of large wood, driver of HEF, on structural descriptors and functional traits of invertebrate at reach scale.

In the following sections, the implications of these findings are discussed in terms of: i) the selection of transferable and multiscale spatial planning approaches to predict HEF accounting for interrelated processes and factors, ii) ensuring hydrological connectivity to promote resilience and biodiversity maintenance in rivers, and iii) the valley and reach context to inform the design of LW reintroduction and restoration.

6.2.1 Vertical hydrological connectivity and spatial planning

The multiscale study of HEF presented in Chapter 3 and Chapter 2 demonstrated that individual processes and controls within river corridors (e.g. bedforms) are insufficient to explain the spatial and temporal variation in HEF and do not provide enough insights into the complex, non-linear processes and factors driving HEF. Instead, HEF dynamics require the consideration of hydrological, topographical, hydrogeological, anthropogenic and ecological processes, operating across a spectrum of spatial and temporal scales, to enable multi-scale modelling, assessment of process controls, and identification of common hyporheic predictors. Therefore, the complexity of multiple inter-related processes was used here as a basis, to develop a transferable approach to predict potential areas of hyporheic exchange for river restoration prioritization and planning (Figure 3.2).

Various analytical, probabilistic, and deterministic approaches have been developed to describe HEF with evidence mounting on its importance to ecological processes and community structure and function (Hester et al., 2017; Cardenas, 2015; Boano et al., 2014; Cardenas, 2008; Cardenas and Wilson, 2007; Cardenas et al., 2004; Kasahara and Wondzell, 2003; Storey et al., 2003; Wroblicky et al., 1998; Wondzell and Swanson, 1996; Harvey and Bencala, 1993). Some of these approaches include stream - tracer injection experiments, one- dimensional advection, dispersion, and transient storage models (Gooseff et al., 2003; Runkel et al., 1998). Others measure groundwater flow to estimate quantitatively the fluxes and residence times of water exchanged between the stream and hyporheic zone (Cardenas and Wilson, 2007; Gooseff et al., 2006; Cardenas et al., 2004; Wondzell and Swanson, 1996; Harvey and Bencala, 1993). These different modelling approaches have helped to disentangle the mechanisms driving hyporheic mixing from a theoretical perspective and to quantify HEF at very fine scales, but especially have encouraged drawing from different disciplines (catchment hydrology, fluvial geomorphology and ecology) to discriminate the factors across spatio-temporal scales that influence hyporheic mixing in rivers (Chapter 2).

HEF models usually have intensive data requirement, require definition of several parameters that are difficult to measure in the field (i.e. hydraulic conductivity), are not conducted at larger spatial scales than reach (Wondzell et al., 2010), and finally require sophisticated analysis (Boano et al., 2014). Measurements are typically highly spatially heterogeneous point values collected at sampling sites, restricting the ability to verify model predictions and generalize to other catchments (Woessner, 2017; Wondzell et al., 2010). Spatial limitation and data type are limiting factors to widespread application of management purposes.

Alternatives to these methods are hydrological classification approaches, which have been identified as both organizing frameworks and scientific tools for river research and management (Olden et al., 2012). Deductive approaches in particular (Chapter 3), are common in literature because they are able to integrate factors and principles controlling hydrological processes and the causes of their variations (Olden et al., 2012). By contrast to inductive approaches, they broadly refer to classification methods using environmental attributes assumed to influence a certain parameter. They are often

in hydrology when the objective is to describe or quantify the spatial variation of a parameter across spatial scales but the availability of data is scarce (Olden et al., 2012). They have several advantages: geographically independent and use available high-quality hydrological, geological, topographical and ecological datasets that make deductive reasoning a valid approach to define spatial patterns in hydrological characteristics (Olden et al., 2012). However, deductive approach as require an accurate choice of environmental factors and the underlying process-interactions in order to ensure that the data are representative of the total existing variation (Kennard et al., 2010). Additionally, due to the use of environmental surrogates (i.e. coarse resolution of available data), there are limits when implemented across spatial scales (Chapter 3).

The deductive approach used in Chapter 3 was based on readily available environmental datasets avoiding the need of high resolution hyporheic data, only sparsely available and not easily accessible to river restoration planners. Results showed that the higher the variability of HEF at multiple spatial scales, more processes are likely at play (Chapter 3, Table 6.1). The spatial and temporal variability of HEF at segment and reach scale is driven by dynamic factors such as superficial sediment types, long term land cover changes and topography (Section 3.3.2). This pattern occurs when intrinsic hydrogeological variables at catchment scale indicate hydrological and geological properties affecting the connection with the groundwater (i.e. aquifer type), the heterogeneity of rocks (i.e. porosity) and grain size (i.e. hydraulic conductivities). For example, the case study of the River Wye showed the entire catchment area being predominantly characterized by confined aquifers and poorly sorted deposits (>50 % of the entire catchment area), spatially restricting hyporheic flows to sinuous areas of the river with coarser gravel and sand sediments (Figure 2.5). However, when hydrogeological variables indicate spatial and temporal variations and discontinuity of groundwater flow at the catchment scale, the variability of HEF was higher and more processes are taken in account into a multiscale approach. For example, the River Tern is characterized by potential HEF at catchment and segment scale as a result of productive, unconfined aquifers, topographical sinuosity (Table 3.7). However, the spatial heterogeneity of HEF at reach scale is controlled by local streambed strata (i.e. silt and clay deposits) and the geomorphological context (i.e. channel confinement), that support hyporheic

flow to unconfined areas at reach-channel scale (Chapter 3) and responds to groundwater recharge at bedform scale (Chapter 2, Section 2.4.2). Similarly to the Tern, in the Frome and Piddle rivers, where the combination of permeable chalk geology and coarse sediment would normally strongly support HEF, the spatial variation of HEF at reach scale is instead mainly controlled by pronounced groundwater flows that create strongly gaining and losing conditions, high fine sediment loads supplied by long term land cover changes, and high percentage of in-channel vegetation (Figure 3.3.2). This multiscale approach demonstrated the impact of intrinsic and dynamic factors on HEF, while also showing that upper hierarchical spatial levels inform on general conditions at low resolution and exert constraints on the lower level, which informs at higher resolution and provides mechanistic explanation for higher levels.

Based on this multi- scale and factor approach, the prioritization of sites for restoration can be evaluated in terms of how well hydrological, hydrogeological, topographical and ecological factors describe hyporheic-drivers (Figure 6.1). For example, the case study on the River Rother showed suitable conditions for HEF to occur at the catchment scale (i.e. complex aquifer, gravel to sand deposits), while unsuitable conditions were predicted in segments and reaches (i.e. low channel gradient and sinuosity, clay and fines). An “active” restoration approach would be appropriate to implement local restoration measures for enhancing local hyporheic flows and ecological functioning in this river (Figure 6.1). For example, previous studies on one tributary of the Rother, the Hammer stream, showed that hyporheic flow was dominated by downwelling surface water spatially limited by stream bed substrate rich in fine sand sediments, clay and peat lenses (Shelley et al., 2017). Under these conditions, the active approach in the Hammer stream would include *in-situ* evaluation of the valley (i.e. gradient, confinement) and in-channel topography and planform (i.e. presence of bedforms or ecological factors- Chapter 2 Section 2.6) that impact on HEF. In this thesis, the case study of the Hammer stream provided an *in-situ* evaluation of the HEF effect on hyporheic fauna and local environmental conditions and demonstrated that the multiscale method predictions (Chapter 3) are representative of local conditions and that the use of restoration measures, represented by natural existing large wood, can potentially play a role in controlling dynamic factors affecting HEF and support river ecosystem resilience.

Finally, a scientific understanding of HEF driving factors is needed to predict how these flows generate and support river functioning. This research demonstrated the importance of recognising different spatial scales and factors involved in hyporheic mixing to identify the underlying processes, so that restoration planning can be better adjusted to the larger catchment context. Vertical hydrological connectivity in rivers is a fundamental property of ecological communities and crucial in the context of ecological restoration and thus in next section, the factors driving HEF are thus discussed by focusing on large wood, a hydrostatic driver of HEF, and on its effect on ecological communities.

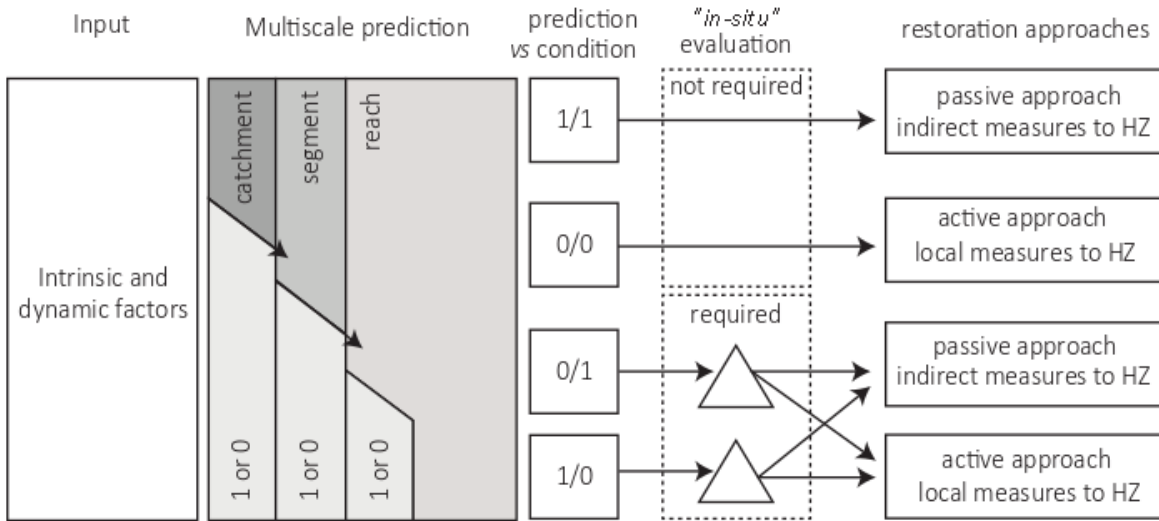


Figure 6.1: Multiscale prediction of hyporheic flows using intrinsic (i.e. aquifer type, bedrock geology) and dynamic factors (i.e. land use, superficial sediment) and potential restoration approaches. “1” refers to likely presence of HEF and “0” to unlikely presence of HEF. The definitions of terms can be found in Chapter 3.

Table 6.1: Suitable (S) and unsuitable (UN) HEF conditions across spatial scales (catchment (C), segment (S), reach (R)) reported in Chapter 3. Major intrinsic and dynamic factors involved in determining suitable areas for hyporheic-restoration.

Suitability	Intrinsic factors	Dynamic factors	Scale
UN	Semi- and confined aquifers	Superficial deposits: sand to silt (>50 % over the catchment)	C
S	Complex aquifers	Sorted sand and gravel, silt and clay (<20 %)	C
UN	Mudstone, sandstone geology	Low channel gradient, >70 % cover arable and grassland, >55 % clay and silt	S
S	Sandstone geology	10-30 % fine sediments, 20-50 % gravel and sand, sinuosity 1.2, low channel gradient 0.002, 10 % pasture lands	S
UN	n/a	Poached river banks, in-channel vegetation and reeds, low percentage of gravel substrates, low number of bedforms low mean velocity	R
S	n/a	Low in-channel vegetation (2-10 %), gravel sediment (>10 %), silt and clay (2-10 %), riffles & pools and wood debris (5-10 %), overgrazed banks (<5 %)	R

6.2.2 Ecological responses to wood-driven HEF

In Chapter 4 and 5, the structural and functional responses of invertebrate communities in the Hammer stream were attributed to variation in wood-driven physico-sedimentological conditions demonstrating that large wood can potentially play a role in controlling dynamic factors affecting HEF and support river ecosystem resilience. Large wood as factor driving HEF, geomorphological changes and in turn affecting the structure and function of hyporheic and benthic communities is generally not accounted for ecological improvements in river restoration.

Much of the focus in documenting the impact of large wood on biodiversity has been on changes in species richness metrics (Dornelas et al., 2014; Lindenmayer et al., 2008), but richness estimates alone in the benthic zone are not enough to understand spatial biodiversity changes (Lindenmayer et al., 2015). Species composition, biomass and traits are more sensitive measures and more likely to reveal community and environmental changes (Hillebrand et al., 2018). This is particularly true for communities dominated by small species, like the hyporheos, that have short generation times and result in rapid turnover of biomass, energy processing, and spatio-temporal changes in population size (Peralta-Maraver et al., 2018; Naegeli and Uehlinger, 1997). Invertebrate biomass is especially important for community structure, ecosystem processes and food web dynamics (Wardhaugh et al., 2014; Ellwood and Foster, 2004; Benke et al., 1999; Basset and Arthington, 1992; Stork, 1988). As evidenced previously by studies in USA and UK streams, considering both meiofauna and macrofauna biomass on a year time would provide better understanding of river secondary production and food webs in LW (Tod and Schmid-Araya, 2009; Stead et al., 2005; Benke and Wallace, 1997; Smock et al., 1992). Production was not accounted in the Hammer stream study due to sampling technique constrictions. However, the evaluation of taxonomic and functional descriptors in conjunction with environmental variables at LW sites, suggested that the decrease of temporal and spatial stability in LW sites, by increased variability of local abiotic conditions, would drive changes in abundance, biomass, diversity and functional traits of hyporheic meiofauna (Chapter 4 and 5). Such heterogeneity of abiotic conditions was summarized by key abiotic parameters (Table 4.1) and reflected on hyporheic

functional and structural descriptors.

Hyporheic meiofauna taxonomic descriptors and functional traits responded significantly to LW-driven environmental change (i.e. physical factors, temporal instability) than macrofauna, exhibiting physiological (i.e. aquatic dispersal) and biological (i.e. aquatic stages) traits alternatively indicating temporal disturbance and spatial refugia (Townsend and Hildrew, 1994). This result suggests that the effects of LW on the hyporheic communities depend upon a certain level of disturbance of hyporheic flow, and that environmental and resource availability at the Hammer Stream were instead within the tolerance of the majority of macrofaunal species. Generally, the taxonomic-based descriptors results for the hyporheic meiofauna and macrofauna agree with previous studies in lowland UK rivers with sand (Tod and Schmid-Araya, 2009; Reiss and Schmid-Araya, 2008) and gravel riverbed sediment (Stead et al., 2003).

Through the sampling period and across reaches, hyporheic meiofauna and benthic macrofauna varied in density and biomass (Figure B.7) and both reaches had quite diverse assemblages proportionally contributing to abundance and biomass (Figure B.8) indicating a strong variability on time and on substrate type. For example, Chironomidae was the dominant hyporheic insect in abundance and biomass in the Hammer and was higher in the HZ's of gravel-cobble reach, and lowest in sand-silt reach at control sites (Figure B.8) as also observed by (Reynolds Jr and Benke, 2012) and Stead et al. (2003). Whereas, changes in macrofaunal assemblage composition were mainly due to seasonal changes in abundance within one generation. Differences in abundance, composition and biomass of hyporheos and benthic invertebrate with geology and sediment type have been confirmed by several studies showing that decreasing sediment size has a negative effect on abundance and taxon richness (Duncombe et al., 2018; Reynolds Jr and Benke, 2012).

At the Hammer Stream, sediment size was a common predictor of abundance, biomass and functional trait variation, but due to the number of samples the relationship “sediment type x wood” was not investigated further. Nevertheless, the high variability between reaches and time suggest that further investigations should explore if the observed hydro-chemical-ecological patterns at wood sites held across a range of lowland setting, sediment type and flow conditions, to compare and calibrate restora-

tion measures at multiple hydrological and geomorphological conditions. To this end, the extent to which LW-driven processes relate to habitat-specific invertebrates' distributions would depend on underlying processes at different spatial scales, which will be discussed in the following section.

6.2.3 Valley and reach context of wood-driven HEF

The relative contribution of single in-channel topographic structures to HEF is altered by complex interactions across the spectrum of topographic scales (Section 2.4.1). Large wood is a hydrostatic driver of HEF, thus the length and residence time of the generated HEF primarily depend on valley-scale conditions inducing changes in the height and slope of the stream water surface (Chapter 2, Section 2.6.2, (Boano et al., 2014)). As result, the impact of LW on hyporheic hydrology (i.e. length and residence time), ecology (i.e. distribution of community) and biogeochemical processes (i.e. denitrification) is likely to be different in low gradient systems, where flow is fairly uniform, and in upland streams, where flow is turbulent and the gradient is high (Figure 6.2).

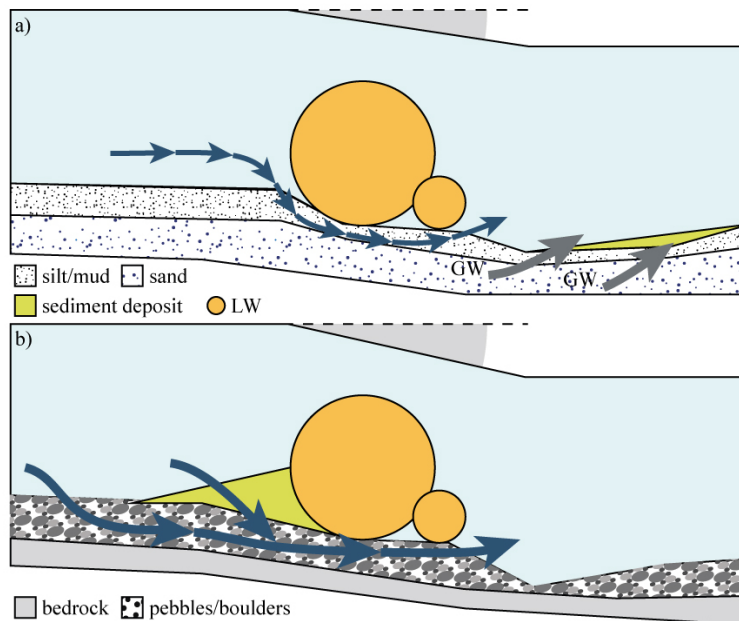


Figure 6.2: Effect of large wood on hyporheic flow in lowland (a) and upland (b) conditions. Blue arrows indicate surface water downwelling and HEF

Lowland rivers situate in unconfined valleys where the active interaction between topography, hydrology and sedimentology allows the development of floodplains (Nanson and Croke, 1992). Generally, under these conditions the spatial variation of water surface topography is less pronounced than in upland systems and HEF is induced by finer pressure variations (e.g. submerged sand ripples and dunes) (Krause et al., 2014). In presence of wood, driving changes in hydraulic head and imposing high hydraulic resistance, geomorphological and hydraulic heterogeneity of lowland rivers with little kinetic energy, can be enhanced (Krause et al., 2014).

For the case study of the Hammer Stream, *in-situ* measurements have shown that LW was characterized by short hyporheic residence times and fast flows, due to slow surface water velocities and dominance of fine sand streambed composition (Shelley et al., 2017). This is a typical lowland river characterized by a longitudinally continuous floodplain and natural wood recruitment. Individual tree falls accumulate and extend across a substantial portion of the channel width (Gurnell et al., 2002; Vannote

et al., 1980; Sedell et al., 1988). The accumulated wood, along with irregularities of the channel-cross sectional area facilitate the formation of active or complete jams characterized by fine bed material (i.e. sand-silt, organic litter) and dammed pool upstream, scour pool with coarser sediment (i.e. coarse sand or gravel) downstream and some scour under parts of the jam (Gregory et al., 1985).

These types of LW structures in small channels such as the Hammer stream become increasingly important to channel morphodynamics and have the potential to drive hyporheic mixing at meter scale by increasing the channel blockage ratio, Froude number and sediment permeability (Sawyer et al., 2012). But, under baseflow conditions, the low energy meandering stream type, the slow surface water velocities, the little variability in height and slope of stream water surface, and the increased fining of the riverbed which decreases hydraulic conductivities, reduce the impact of LW on hydrodynamic forces, resulting in hydrostatically-driven HEF which is usually shallower in length and shorter in residence than in upland systems (Shelley et al., 2017; Krause et al., 2014). The shorter the residence time, the smaller is the impact of LW on nutrient attenuation (i.e. nitrate, (Shelley et al., 2017)) and oxygen availability into the streambed. Still, LW in lowland streams significantly influences total residence time by creating low velocity zones within the channel and allowing biogeochemical transformation to occur (Blaen et al., 2018; Shelley et al., 2017; Stoffleth et al., 2008).

Upland rivers are high energy systems, different from lowland systems in terms of valley gradients (i.e. high gradient), channel flows (i.e. turbulent flows), channel topography (e.g. cascades, steps) and sediment structure (i.e. coarse sediment and supply) (Figure 6.2). Here, the topography (i.e. channel slope, size, spacing of boulders and cascades) increases the variability in surface water slope and in turn the spatial variability of hydrostatic-driven HEF. Under these conditions, LW would typically create steeper head gradients and result in pronounced upwelling and downwelling upstream and downstream the LW (Krause et al., 2014; Crispell and Endreny, 2009), and provide sediment storage sites (Zimmermann and Michael, 2001). Also, as hyporheic flow is proportional to sediment permeability, the coarser riverbed sediment (sand to gravel to boulder) in upland rivers allows deeper and longer hyporheic flows and residence times (Krause et al., 2014; Sawyer et al., 2012).

In these systems, wood-driven HEF is also partially affected by stream discharge (Wondzell, 2006) than in lowland rivers, due to the smaller hydrostatic groundwater contribution (Figure 6.3). Given the topographical variability of upland environments, LW is not the only in-channel structure driving HEF. A study in the steep-mountainous channels of the Oregon Coast Range observed that LW produces greater hyporheic exchange than smaller steps caused by boulders (Wondzell, 2006). Nevertheless, more research is needed to quantify the effects of LW on streambed pressure distributions and hyporheic exchange in upland systems to assess the influences on other in-channel topography, pool spacing, frequency, and sediment sorting (Buffington and Tonina, 2009). With respect to river invertebrates, several studies in upland environment have observed changes in benthic macroinvertebrate community composition in response to sediment deposition at LW sites (Wallace et al., 1995; Gerhard and Reich, 2000) while the effects on hyporheic communities remain unexplored.

Finally, in both lowland and upland river types, LW seems to provide positive ecological responses. However, in lowland rivers, engineered log-jams used in conjunction with other in-channel and floodplain restoration measures, might enhance more efficiently local river hydraulic conditions, naturally limited by geomorphological and topographical characteristics, and favour biogeochemical processing and nutrient turnover by promoting HEF. The impact of different wood jams (e.g. active, complete, partial, high jams) on the HZ and under different environmental settings has yet to be established. Therefore, we need more empirical data on how LW and its context can enhance and facilitate ecological and hydrological connection to strengthen our capacity to not only effectively choose the design of large wood for restoration, but also to select and evaluate its suitability in particular cases.

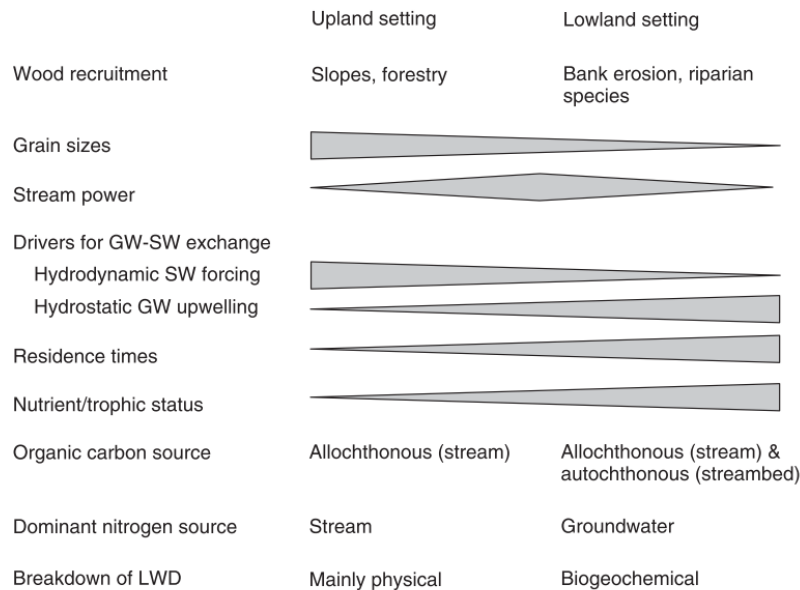


Figure 6.3: Key hydrological, geomorphological, and biogeochemical process driven by LW in upland and lowland rivers . Figure from Krause et al. (2014)

6.3 River management and the HZ

6.3.1 Advantages of considering the HZ in river management

Despite extensive research demonstrating the importance of HZ to river ecosystems, few comprehensive syntheses addressed to HZs and river management exist (Boon et al., 2016; Wood et al., 2012; Hester and Gooseff, 2011; Buss et al., 2009).

Globally, the implementation of restoration approaches responds to multifaceted landscapes strategies linking environment (i.e. natural ecosystems) and development (i.e. urban expansion) to sustainable land management (i.e. The Bonn Challenge (BMUB and IUCN, 2011), the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES, 2012), the United Nations to Combat Desertification (UNCCD, 1994), the Convention on Biological Diversity (CBD, 1993)). However, none of the above legislations specify the HZ. Regionally, regulatory authorities tend to

respond to the EC Water Framework Directive (WFD; (Directive, 2000), the EC Habitats Directive (Directive, 1992) for Special Areas of Conservation and Sites of Special Scientific Interest (SSSIs), but none of these incentivises and regulates HZs protection.

Hyporheic exchange flow provides indication of trophic structure (size and biomass), chemical processes and thermal regimes within a catchment (Boulton and Hancock, 2006). These functions define priority river habitat, species habitat requirements, and drive river restoration to act (Mainstone et al., 2014; Society for Ecological Restoration International Science & Policy Working Group, 2004). Therefore, by predicting and assessing HEF occurrence and the associated processes over different spatial scales, potential HEF-related issues and environmental impacts can be identified that require management intervention (Chapter 3). Also, this a fundamental step to place restoration within and across entire catchments, not individual sites, representing mosaics of interacting hydrological, topographical, geological and anthropogenic pressures. This type of assessment can be used, for example, in conjunction with the “naturalness criteria” now used in restoration to identify priority habitats in Britain (Department for Environment and Affairs, 2013).

In terms of trophic structure, HEF enhances the growth of periphyton which creates localized hotspots of productivity (Claret and Fontvieille, 1997) and the growth of subsurface invertebrates and microorganisms that i) affect the porosity of the riverbed (i.e. burrowing, palletisation); ii) alter nutrient and river metabolism (i.e. excretion), iii) organic and inorganic matter breakdown, and iv) transfer of material across the hyporheic zone (i.e. migration) (Table 1 in Boulton (2007)). These functions are the base of river ecosystem functioning and are especially relevant in the context of achieving and maintaining “good ecological status” as required by WFD. Benthic macroinvertebrates are regularly used as bio-indicators in river health assessment (Walsh, 2006), whereas possibly because of the difficulties of quantifying and identifying very small invertebrates, restoration attention on hyporheic invertebrates is less advanced. However, previous studies have demonstrated the potential of using hyporheic invertebrates as ecological indicator especially for assessing the health of temporary rivers (EPT metrics, (Leigh et al., 2013)) and ongoing citizen and science initiatives (i.e. Anglers’ Riverfly Monitoring Initiative ARMI) could hopefully open new strategies to promote

restoration awareness on HZ, coordinate sampling approaches and provide benchmark data to complement surface water assessments.

HEF also drives chemical processes (i.e. nutrient attenuation, cycling of oxygen, mineral dissolution and precipitation) by creating T, pH, redox gradients between the surface water and groundwater. Nutrient attenuation together with biodiversity is one of the most critical water quality problem addressed by river restoration to satisfy the requirements of policy drivers (e.g. WFD).

In Chapters 4 and 5, LW was presented as a driver itself of HEF in relation to structural and functional responses of invertebrate communities. But, LW-driven HEF has been especially studied for its impact on biogeochemical cycling, denitrification and therefore on nutrient pollutant attenuation (Blaen et al., 2018; Kail et al., 2016; Craig et al., 2008). Therefore, these studies in conjunction with ecological ones (Thompson et al., 2018; Pilotto et al., 2014) (Chapters 4 and 5) suggest that instream LW can be used in river restoration to improve water quality and ecology of upland and lowland rivers. If the observed hydro-chemical-ecological patterns at LW sites would be true across a range of lowland setting and flow conditions, then there is a potential in river restoration to implement catchment-field approaches including design and placement of wood considering the HZ. More studies are however required that use restored-LW, ecology and nutrient dynamics to improve the scientific understanding on how changes in HEF relate to hydrological processes and vertical connectivity in rivers.

In terms of thermal regimes, the HEF regulates river temperature through buffering, lagging, or cooling (Arrigoni et al., 2008). Temperature regulates microbial-mediated reactions such as denitrification (Zarnetske et al., 2011) and is essential for fish larvae refuge (Baxter and Hauer, 2000; Geist, 2000); a critical topic to restoration given the decline in salmon numbers in more recent years (EA, 2014 accessed May 10, 2018).

Finally, restoration would be an opportunity for hyporheic research to access information - rich data being collected by government and private consultant at large geographical scale. Restoration projects, whose design is informed by scientific understanding of ecological and hydrological processes within a catchment context, can provide to science a wide range of fine-resolution data with more intensive sampling at a local scale (e.g. river type, spatial extent and frequency, data type) to evaluate

physical, ecological and chemical factors drivers of HZ processes. Also the information obtained from broad-scale restoration can be used to create baseline data to test and use hyporheic flow and fauna in river surveys and assessment.

6.3.2 Project management plans

The HZ physical and biological processes are the result of multiple interacting factors, thus efforts to address its functioning in river management require a multifaceted response. The trade-off between the beneficial and detrimental effects on hyporheic organisms and habitat, need to be understood within the context of multiple effects provided by them in specific environments (Chapter 3).

Therefore, a starting point for HZ and HEF to be targeted by river restoration is considering the prioritization of sites with a catchment-specific approach. By focusing on strengthening the resilience of river ecosystems at catchment scale, river restoration can optimise its goods and services as societal needs change or new environmental challenges arise (Society for Ecological Restoration International Science & Policy Working Group, 2004). This means including specific hydrogeological, topographical and anthropogenic characteristics driving and affecting HEF (Chapter 2), and so achieving a more inclusive understanding of the short, medium and long-term implications of HZ-functioning to river restoration (Figure 6.1). The catchment-scale approach to the HZ requires adopting holistic policy-responses that go beyond narrowly-defined policy agendas and put in place the enabling conditions necessary for long-term change (i.e. IPBES Assessments, (IPBES, 2012; CBD, 1993)). To this end, dynamic and multifunctional approaches to restoration practices are good examples and already adopted globally in the Bonn Challenges within the Forest Landscape Restoration project (BMUB and IUCN, 2011) to re-establish ecological functionality of deforested landscapes, and in the strategic framework of the International Conventions to Combat Desertification (UNCCD, 1994).

At regional scale, the HZ can be included into the current river restoration plans on SSSI rivers in Britain (Wheeldon, 2013). The plan includes seven action stages, from geomorphological and ecological appraisal to site monitoring (Wheeldon, 2013).

As starting point, HEF can be considered in the prioritisation of actions (Stage 1 and Stage 2, Figure 6.4) and in the selection of restoration measures (Stage 3) of the SSSI plans. While ecological assessment can be carried out at Stage 6 and 7 of the physical restoration strategy (Figure 6.4). This first assessment can, for example, include targeting areas already identified in the priority maps as “poor” status (WFD) and discussing what is the problem and how this issue affects the functions and ecosystem services of the hyporheic zone (i.e. Section 6.3.1, trophic structure, chemical processes and stream temperature). Alternatively, WFD ecological and hydrological metrics can be evaluated under the hyporheic perspective and assessed, in case of failure, to underscore where the HZ can play a role to achieve “good ecological status”. When *in-situ* measurement is needed (Figure 6.1), excellent guidance encompassing a variety of levels of complexity exist to develop field methods in the river channel, reach and floodplain (i.e. piezometers, seepage meters, stream flow measurements, Table 8.1 in (Buss et al., 2009)) and distinguish the hyporheic flows. The most common and easy-to-use methods are mini-piezometers, stream stage data and groundwater monitoring wells. For example, mini-piezometers or wells are used to measure the elevation of water levels in the saturated riverbed sediments (e.g. Figure 5.1)(Rivett et al., 2008).

For the ecological assessment, hyporheic fauna could be collected in conjunction with Surber sampler, by portable standpipe (i.e. Bou Rouch Pump) and ETP metrics applied to evaluate river water quality (Leigh et al., 2013). In this context, community involvement could take many different forms (i.e. recent started Riverfly Partnership Anglers - Monitoring Initiative (AMI)), promote awareness and actions across broad geographical scales. Especially at this stage that interdisciplinary collaboration with academic institution would be beneficial to understand the extent to which restoration strategies promote specific hyporheic functions.

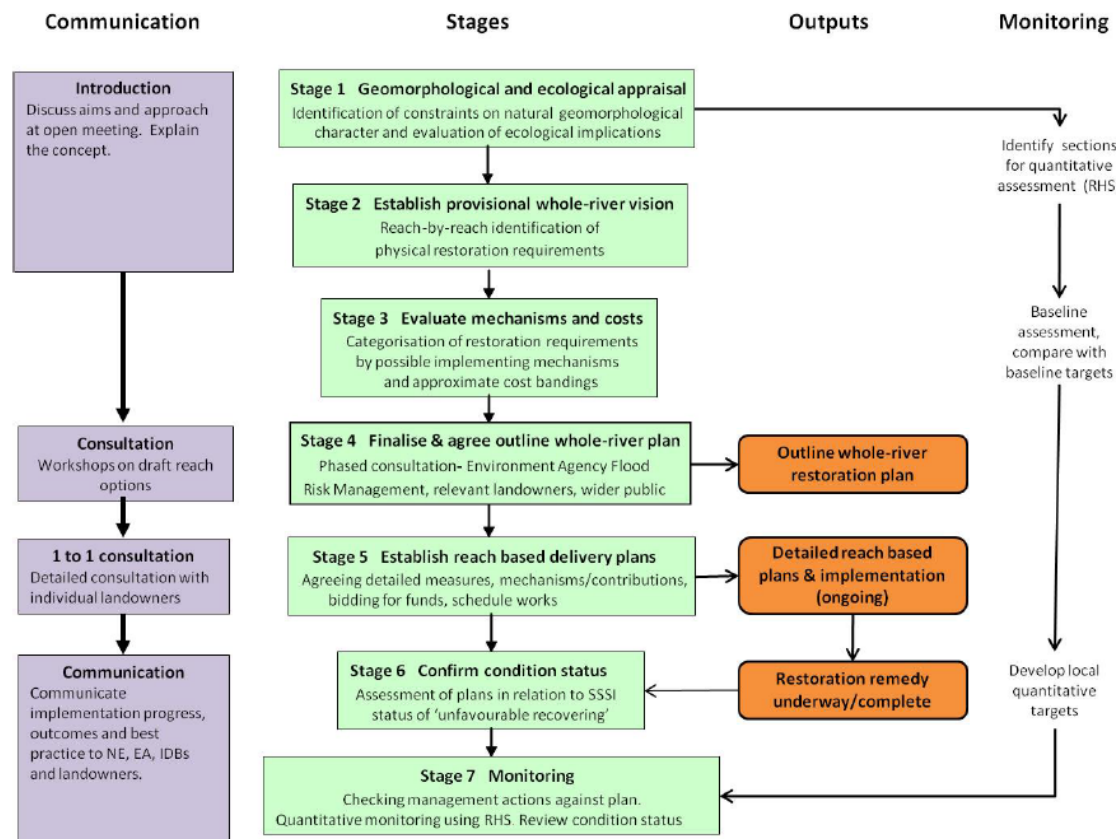


Figure 6.4: Main steps for developing a SSSI physical restoration strategy. Green colour refers to the strategy, purple to communication aspects and orange to main outputs. Figure from Wheeldon (2013)

6.4 Implication for future research

It is important to acknowledge that the results of this research and the interpretation of processes are constrained by methodological limitations. Therefore, recommendations for further research are formulated here in terms of (i) hyporheic exchange measurements and data availability; and (ii) ecological information about HEF and LW.

6.4.1 Hyporheic exchange flow and data availability

In this study, the use of direct measures of HEF in most field studies was limited by the spatial coverage of published hyporheic studies within the river network, and by the variable quality and quantity of data at each site (Chapter 3). Therefore literature published data of HEF were used to qualitatively assess the results of the clusters and only few *in situ* study sites could be used to compare model predictions and in a qualitative way. More spatially distributed hyporheic data is required to systematically test, compare and calibrate predictive models at multiple spatial and temporal scales. Research should explore alternative possibilities to increase the temporal and spatial resolution of HEF monitoring by sharing and promoting collaborative experimentation of scientific findings.

Quantifying HEF in the field is challenging because both hydrologically complex and relatively difficult to manipulate under undisturbed conditions (Palmer, 1993).

First, there are a variety of terms associated with mixing and boundary conditions and therefore vastly field and modelling expectations (Hester et al., 2017). Consequently, there are not conventional indicators of HEF. Second, being the HZ at the interface between surface and subsurface waters, it can extend from considerable meters to few centimetres, implying that the selection of measuring methods depend on a sound understanding of the local environmental conditions. Also, the direct connection with groundwater means that the HZ may change significantly during field experiment which is a possible reason of limited experimental manipulation. Thirdly, the volume of water that is involved in the HEF is small compared to stream flow (Bencala and Kimball, 2011) and therefore several measurement methods are used in conjunction (i.e. vertical hydraulic gradients, water temperature). These challenges partly explain the reliance of HEF quantification on small-scale sampling. Finally, while technological advancements have made it easier to collect large amounts and high resolution data, access and processing of this information are often constrained.

Data processing platforms and open-source computational systems could be a valid solution to meet science requirements of reproducibility, repeatability and re-usability, and to promote the use of collaborative approaches among restoration managers and

scientists. Data platform systems enable to share computational information with other colleagues, to execute processes provided by communities of practice and reduce calculation effort at the same time. If more and high quality HEF data was available at the time of this research, alternative modelling approaches like ANNs would have been likely used. ANNs are methods promising to capture the dynamics of highly nonlinear chaotic system (Parasuraman and Elshorbagy, 2007) and can be used in conjunction with numerical and analytical groundwater models (Daliakopoulos and Tsanis, 2005). These approaches could have offered the possibility of teasing out multiple processes without the need of defining “a priori” physical constraints and therefore helping a more accurate identification of patterns and clusters of hyporheic data at larger spatial scales.

To this end, the success of including the HZ into restoration plans lies in the ability of providing tools for easy hyporheic measure and predictions, suitable to the scale of assessment, and responding to catchment impacts in an interpretable way.

6.4.2 Ecological information on large wood

More studies are required that target hyporheic communities at LW sites to improve scientific understanding on how LW-driving processes and valley setting relate to ecological processes. Information on the impacts of LW on HEF is needed to better relate species structure and functions to environmental responses.

As discussed in the previous section, data on HEF are limited, so our field study was constrained by available hyporheic data at LW sites, and therefore focused on only one river. But, consideration of environmental factors will help to discern anthropogenic-induced changes in hyporheic fauna. Furthermore, Chapter 4 and 5 suggested that LW variability (i.e. upstream, downstream and lateral to wood) might be important to explain benthic invertebrate distribution at LW sites. Due to time constraints, it was not possible to study the ecological responses to LW variability (downstream, upstream, lateral LW) which might provide, in the future, additional information on the distribution of invertebrates as a function of vertical and horizontal subsurface flows, like those shown in riffle studies (Mathers and Wood, 2016). Additionally, in lowland rivers

groundwater discharge is very pronounced and during stream gaining conditions the hydrodynamic forcing of LW on HEF is reduced (Krause et al., 2014). Changes on HEF and HZ extent might potentially be followed by changes in invertebrates composition, distribution and diversity (Dole-Olivier et al., 1997) and therefore future studies might want to determine whether the environmental instability of groundwater-fed stream influence invertebrate community distribution in LW sites.

Despite univariate diversity metrics remaining the principal tool for biodiversity assessment and monitoring (Hillebrand et al., 2018), multivariate species trait and temporal data on biomass can reveal trends of community changes (i.e. species specialization decline and homogenization) likely to be important to conservation and ecosystem function (Boulton and Hancock, 2006; Larsen et al., 2018).

Finally, restoration programmes incorporating hyporheic invertebrate in their planning will benefit of a conceptual understanding of how river flow variation and groundwater mediates changes of HEF (Chapter 2) and in turn physical, sedimentological, nutrient parameters. Pilot studies and analytical methods will then help supporting on-ground restoration.

6.5 Conclusion

This research aimed to improve our understanding of the multi-scale drivers for spatial and temporal variation of HEF, and the effects on hyporheic and benthic biodiversity from structure-induced HEF for river restoration planning. By using a multi-scale perspective on HEF, this research provides a comprehensive hydro-ecological understanding of aquatic ecosystems and can support river restoration prioritizing sites and approaches to target the HZ.

First, the multi-scale method based on environmental information at different scales demonstrated the importance of identifying underlying processes and factors in order to predict HEF. In the study catchments, suitable areas for HEF-focused restoration embed a summary of environmental information across the domains of hydrology, geology, and ecology (Section 3.4.1) forming the basis to capture the attention for effective and problem-oriented river management (Section 3.4.2). The results of the study confirm

the need of co-ordinated approaches to pooling hyporheic data and creating uniform and long-term datasets, the lack of which limit the capacity to quantitatively assess model predictions (Section 6.2.3).

Second, by examining the effect of large wood on hyporheic and benthic communities and linking to multiple environmental data, the role of LW as structure-induced HEF to maintain river ecological connectivity could be assessed (Chapters 4 and 5). The findings confirmed hypotheses made in previous research about the role in LW in lowland rivers and provided new information about the tight association between abiotic and biotic interactions to shape spatial patterns of functional trait diversity. However, it is essential to establish further knowledge on how large wood effects on HZ vary in different valleys and river types and over multiple spatial and temporal scales, so that wood-based restoration design can account for heterogeneity of riverscapes and specific processes (Sections 6.2.2, 6.2.3).

In conclusion, through new methodological approaches and empirical evidence, this research highlights that unravelling the process interactions underlying HEF is essential to improved prediction of HEF and help management to target HZ. Future research will aid better-resolved scientific understanding of the hyporheic ecosystem and further encourage river management to commit to hyporheic restoration.

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Appendix A

The multiscale geostatistical method

Table A.1: Effects of hydrological, hydrogeological, topographical, anthropogenic and ecological factors on HEF at catchment (C), segment (S) and reach (R) scale. This table relies on empirical evidences and theories from hydrology, geology and hyporheic fields.

Functional variables	Scale	Processes	Major effects on HEF	References
GW discharge	C	changes in hydraulic gradients	High GW upwelling velocities, reduce depth and intensity of HEF and prevent bedform-induced HEF at reach scale. Gaining conditions: limit HZ extent with depth and HEF. Losing conditions: minor contribution of GW to HEF which will depend on channel topography and superficial geology	(Caruso et al., 2016) (Schmadel et al., 2016, 2017)
stream discharge	S, R	changes in hydraulic gradients	HEF increases with stream velocity and stage. Flood events: the extent of HZ with depth increases and hyporheic residence time too.	(Cardenas, 2009b) (Fox et al., 2014, 2016)
precipitation	C	changes in stream level and GW flows	High precipitation areas are more subjected to change in HEF than areas with average low precipitation. Steep headwater catchment: quick catchment response to rainfall, especially in transmissive soils, because small storage capacity and HZ and HEF will contracts and decreases in response to GW flows. Lowland catchment: slow catchment responses to rainfall, HEF responses depend on topography.	(Ward et al., 2013) (Bhaskar et al., 2012) (Malcolm et al., 2004) (Malzone et al., 2016)
elevation	C	GW head distribution and upwelling	Lowland and upland areas indicate spatial distribution of GW recharge and discharge areas. Therefore, where surface water contributes to subsurface flow. (Greater variation in water stage contribute on average to greater hyporheic fluxes. HEF upwelling and downwelling decrease with decreasing water surface concavity and increasing catchment area.	(Gomi et al., 2002) (Penna et al., 2016) (Woods et al., 1995)
area	C, R	changes in hydrostatic head		(Caruso et al., 2016) (Laudon et al., 2007)
				(Harvey and Wagner, 2000) (Anderson et al., 2005) (Bergstrom et al., 2016)

Table A.1 – continued from previous page

Functional variables	Scale	Processes	Major effects on HEF	References
C	S	adjustment river to planform and changes in hydraulic gradients	Confined valleys: limited HEF, depends on bedrock fractures and aquifer connectivity. Unconfined valleys: HEF is driven by hydrodynamic forces generated by the presence of mesoforms and sediment heterogeneity. Low gradient: HEF is induced by hydrodynamic heads of reach-scale bedforms. High gradient: HEF is induced by changes in the cross-sectional area, and by reach scale bedforms. In steep and constraint channel sections, the HEF is limited by the underlying bedrock. Lateral HEF increases with the growth of the meander length and decrease with reduction of river sinuosity. No strong reduction of HZ under losing and gaining condition	(Kasahara and Wondzell, 2003) (Buffington and Tonina, 2009) (Ibrahim et al., 2010)
gradient	S, R	changes in hydrostatic heads		(Stonedahl et al., 2013) (Tonina and Buffington, 2011)
sinuosity	R	changes in hydraulic gradients		(Cardenas, 2009a) (Boano et al., 2006) (Stonedahl et al., 2013)
bedform sequences		changes in hydraulic gradients	HEF is maximised when one single bedform dominates. Step-pool: depth of HZ increases with channel slope, higher the slope and deeper the HEF. Riffle-pool: generally driving HEF downwelling and upwelling but also depending on local GW recharge. dune & ripples: HEF depends on hydrodynamic pressures and less on spatial changes in water surface elevation. Riffle: HEF is possible with high permeability sediment and considering the GW discharge to the river. Gravel bars: behaves as riffles. When partially submerged, HEF decrease with increasing stream discharge.	(Tonina and Buffington, 2011) (Gariglio et al., 2013) (Stonedahl et al., 2013)
single bedform	R	changes in hydraulic gradients		(Packman et al., 2004) (Buffington and Tonina, 2009) (Trauth et al., 2014) (Trauth et al. (2015)

Table A.1 – continued from previous page

Functional variables	Scale	Processes	Major effects on HEF	References
bedrock	C, S	GW head distribution and upwelling	Carbonatic: efficient for GW recharge and fracture type flow. Wide range of base flow with different impact on HEF. Siliceous: efficient for GW recharge presenting intergranular porosity and fractures. Igneous and metamorphic: shallow fracture systems, possibly shorter GW flow paths and residence times. Gneiss basins have high hydraulic conductivities. Outcrops limit HEF to superficial deposits of the riverbed when steep positive vertical hydraulic gradients results from discontinuities of superficial deposits permeability and shallow bedford. When irregularities of bedrock favour change in alluvium volume, than HEF is present. Braided rivers: strong spatial and temporal variability of lateral HEF depending on grain size material (see HG-superficial-reach) and cross-valley head gradient. Sinuous rivers: See T-sinuosity. HEF will be restricted where low-permeability units and unconsolidated deposits. Straight/low sinuosity rivers: HEF restricted to shallow sediment above low conductivity strata.	(Sear et al., 1999) (Morrice et al. (1997) (Kawahara and Wondzell, 2003) (Pretty et al., 2006) (Hiscock, 2007) (Ibrahim et al., 2010) (Allen et al., 2010) (Wondzell (2011)
superficial	S	spatial changes in hydraulic conductivities	Greater the connectivity within sediment strata and higher HEF. HEF is higher in coarse sediment where high velocity gradient and turbulence increase diffusion processes that induce exchange even in low gradient conditions. In the case of peat soils, HEF is enhanced when mud and silt content are very low in % (less than 5%).	(Brunke and Gonser, 1997) (Malard et al. (2002) (Gurnell et al., 2016) (Angermann et al., 2012) (Krause et al., 2012) (Stonedahl et al., 2012)
superficial	R	changes in turbulence, diffusion processes, hydraulic conductivities		(Salehin et al., 2004) (Packman et al., 2004) (Marion et al., 2008) (Pryshlak et al., 2015)

Table A.1 – continued from previous page

Functional variables	Scale	Processes	Major effects on HEF	References
aquifer	C	GW upwelling	<p>Aquifer confinement can prevent or limit GW leading to low or high potential of HEF (see H-groundwater, HG-bedrock). Confined aquifers: limit or prevent GW. If the confinement is due to near-surface bedrock, the lack of alluvium will limit HEF. Unconfined aquifers: GW flow is not prevented. effect on HEF as in (see H-groundwater, HG-bedrock, HG-superficial).</p> <p>Increase of sediment loads as consequence of land erosion, decrease of in-channel hydraulic conductivity which lead to decrease in channel storage and HEF. Irrigation systems often include pumping of stream surface and GW, causing changes in water tables. Lower water tables generally reduce vertical extent of HZ by increasing water losses and reducing hydraulic gradients. Reduction of HEF length due to lower geomorphological complexity that likely cause flow dead zones</p>	<p>(Winter, 1998) (Kasahara and Wondzell, 2003) (Buffington and Tonina, 2009) (Gurnell et al., 2016)</p>
land use	C, S	changes in sediment delivery, geomorphological complexity, water levels	<p>Effects on HEF are linked to channel flow variations. Usually reduce turbulent HEF and reduce advective HEF by increasing the channel cross sectional area and reducing flow velocity. For dam structures, highest HEF occur downstream of dam while it is limited in upstream pools where fine sediment deposits yield low hydraulic conductivities.</p>	<p>(Gooseff et al., 2007) (Hancock, 2002) (Kasahara and Hill, 2006) (Ryan et al., 2010) (Maalim et al., 2013)</p>
spanning structures (i.e. dams)	S, R	river-stage fluctuations, sediment delivery, changes in vertical hydraulic gradient	<p>Effects on HEF are linked to channel flow variations. Usually reduce turbulent HEF and reduce advective HEF by increasing the channel cross sectional area and reducing flow velocity. For dam structures, highest HEF occur downstream of dam while it is limited in upstream pools where fine sediment deposits yield low hydraulic conductivities.</p>	<p>(Blois et al., 2014) (Boano et al., 2010) (Packman and Brooks, 2001) (Schmadel et al., 2016) (Rana et al., 2017)</p>

Table A.1 – continued from previous page

Functional variables	Scale	Processes	Major effects on HEF	References
riparian vegetation	S	evapotranspiration	The ET from riparian vegetation can increase hyporheic fluxes by 1-2 orders of magnitude at time scales of weeks to months. This is especially significant in low energy environments, where ET drives mixing comparable to that of molecular diffusion. Conversely in high-energy environments where turbulent mixing and bedform-induced pumping are very rapid the effect of ET will be lower.	(Larsen et al., 2014) (Duke et al., 2007)
in-channel vegetation	R	changes in flow resistance, streambed permeability	Generally inverse relationship between streamflow and vegetation where for increase of vegetation cover, streamflow decreases. HEF increases due to bed roughness and by variation in hydraulic gradients but decrease with in presence of extensive in-channel vegetation where flows are channelled and slow.	(Harvey et al., 2003) (Corenblit et al., 2007) (Jones et al., 2008) (Kjellin et al., 2007) (Heppell et al., 2009) (Sun et al., 2011)
wood	R, sub-reach	changes in hydraulic gradient	Generally, in-channel wood induces deeper HEF.	(Mutz, 2000) (Mutz et al., 2007) (Lautz and Fanelli, 2008)

Environmental data derived from the original datasets and used in the UK and Polish case studies

Table A.2: Environmental data used in the UK case studies derived from the datasets listed in Table 2 in the main manuscript

Parameters	Spatial scale	Derived information	Data type
DTM	Catchment	Catchment size (km ²)	Spatial, quantitative, continuous
	Catchment Segment Reach	Elevation (m) : min,max, mean, std	Spatial, quantitative, continuous
	Segment Reach	Gradient and Sinuosity (Stream and Gradient Sinuosity Toolbox (ArcGIS 10.2) Roughness (ArcGIS 10.2)	Spatial, quantitative, continuous
	Segment	Stream Order (ArcGIS 10.2)	
Precipitation	Catchment	Rainfall (mm): mean daily per season (autumn, winter, spring, summer). From 1981 to 2010. Min, max, mean, std.	Temporal, quantitative
Air Temperature	Catchment	Temperature (degC): mean daily per seasons (autumn, winter, spring, summer). From 1981 to 2010. Min, max, mean, std.	Temporal, quantitative
Bedrock geology (1:625,000)	Catchment	Bedrock classes: classes expressed on the overall area in the range between 0 and 1.	Spatial, fuzzy
Superficial geology (1:50,000)	Segment	Superficial geology: classes expressed on the overall area in the range between 0 and 1	Spatial, fuzzy
Soils; <i>Aquifers</i>	Catchment	Soils and aquifer classes expressed on the overall area in the range between 0 and 1	Spatial, fuzzy
	Catchment	Hydrogeology: expressed on the overall area in the range between 0 and 1	Spatial, fuzzy

Table A.2 – continued from previous page

Parameters	Spatial scale	Derived information	Data type
	Catchment	Permeability: Range, max, min. Assigned categories accordingly to very high, high, moderate, low, very low permeability	Spatial, fuzzy
Land Cover	Catchment Segment Reach	Riparian vegetation and land use classes expressed on the overall area in the range between 0 and 1	Spatial, quantitative, categorical
Vegetation	Reach	Riparian vegetation at 5 and 50 m from the river bank. Expressed on the overall area in the range between 0 and 1. In-channel vegetation expressed between 0 and 1.	Spatial, fuzzy
River Flows	Reach	Mean flow velocities	Temporal, quantitative
Bank and in-channel geology	Reach	Superficial and bedrock geology classes expressed in the 0 and 1 range.	Quantitative
	Reach	Presence of riffles, pools expressed on the overall area in the range between 0 and 1	Quantitative

Table A.3: Environmental data used in the Polish case studies derived from the datasets listed in Table 3 in the main manuscript

Parameters	Spatial scale	Derived information	Data type
DTM	Catchment	Catchment size (km ²)	Spatial, quantitative, continuous
	Catchment Segment Reach	Elevation (m): min, max, mean, std.	Spatial, quantitative, continuous

Table A.3 – continued from previous page

Parameters	Spatial scale	Derived information	Data type
	Segment, reach	Gradient and Sinuosity (ArcGIS 10.2)	Spatial, quantitative, continuous
Precipitation (5 km)	Catchment	Rainfall (mm): mean monthly per seasons from 1950 to 2013 (autumn, winter, spring, summer). Min, max, mean, std	Temporal, quantitative
Precipitation (interpolated)	Reach	Rainfall (mm): mean monthly per seasons from 1994 to 2013 (autumn, winter, spring, summer). Interpolated (IDW-ArcGIS 10.2) Min, max, mean, std	Temporal, quantitative
Air Temperature	Catchment	Temperature (degC): monthly average per seasons from 2000 to 2013 (autumn, winter, spring, summer). Min, max, mean, std	Temporal, quantitative
Bedrock Superficial Geology (1:250,000)	Catchment Segment Reach	Bedrock classes expressed on the overall area in the range between 0 and 1. Superficial geology: classes expressed on the overall area in the range between 0 and 1.	Spatial, fuzzy

Table A.3 – continued from previous page

Parameters	Spatial scale	Derived information	Data type
Soils	Segment, reach	Soils classes expressed on the overall area in the range between 0 and 1. Peat depth at reach scale was obtained by interpolation (IDW method ArcGIS 10.2) Min, max, mean, std	Spatial, fuzzy
Aquifers (1:50,000)	Catchment	Aquifer classes expressed on the overall area in the range between 0 and 1.	Spatial, fuzzy
River Flows	Reach	Average discharge from 1971 to 1995. Spatial interpolation with IDW (ArcGIS 10.2).	Spatial, quantitative, continuous
Groundwater flows	Reach	Average per years from 1998 to 2013 per season (autumn, winter, spring, summer). Spatial interpolation with IDW ArcGIS 10.2. Min, max, mean, std	Spatial, quantitative, continuous
Land Cover	Catchment Segment Reach	Riparian vegetation and land use classes expressed on the overall area in the range between 0 and 1	Spatial, quantitative and categorical

Results of the Large scale merging (Step 5) for the UK and Polish case study

Table A.4: Summary table of the Absolute Percentage of Agreement obtained by the confusion matrices and the Large scale merging for the UK and Polish case study

Scales	UK	Polish
catchment	88%	75%
segment	75%	78%
reach	74%	82%

Large Scale Merging		
Segment-Catchment	76%	78%
Reach-Segment	64%	82%

Table A.5: UK case study Step 5: reach agreement with enrichment of the 20% using the information of the segment

Clustering Reach-Segment			
Expert	Classifier 1	Classifier 0	Total
Classifier 1	25	13	38
Classifier 0	36	61	97
Total	61	74	135
Agreement	25	61	86
By Chance	17.17	53.17	70.34
		Fleiss	Landis-Koch
Kappa	0.24	<i>Poor</i>	<i>Fair</i>
Absolute % of agreement	64%		

Appendix B

Large wood and invertebrates' taxonomic-based metrics

Table B.1: Taxon-specific regression equations and parameters used to calculate biomass of invertebrates. Taxa are ordered alphabetically. DW= weight (mg), WW= wet weight (mg), V= volume (mL, nL), L= body length (mm), SL= shell length (mm), W=body width (mm), H= body height (mm), HW = head-capsule width (mm).

Taxa	Formula	Source
Acroloxidae	$DW = -3.3319 + 3.1403 * SL$	Meyer (1989)
<i>Agabus</i> spp	$DW = -4.4518 + 2.4724 * L$	Meyer (1989)
Asellidae	$DW = 0.0054 * L^{2.948}$	Benke et al. (1999)
<i>Atherix</i> spp	$DW = 0.0038 * L^{2.586}$	Benke et al. (1999)
<i>Baetis</i> spp	$DW = 0.0033 * L^{3.196}$	Benke et al. (1999)
Beraeidae	$DW = 0.0034 * L^{3.212}$	Benke et al. (1999)
Bosminidae (Cladocera)	$V \text{ (mL)} = (LW^2 * \pi)/6$	Reiss and Schmid-Araya (2008)
Bithyniidae	$DW = -4.54 + 3.66 * SL$	Baumgärtner and Rothhaupt (2003)
<i>Caenis</i> spp	$DW = 0.0069 * L^{2.61}$	Benke et al. (1999)
Calopterygidae	$DW = 0.005 * L^{2.742}$	Benke et al. (1999)
<i>Capnia</i> spp (Capniidae)	$DW = 0.0049 * L^{2.562}$	Benke et al. (1999)
Ceratopogonidae	$DW = 0.0020 * L^{2.438}$	Poepperl (1998)
Chironomini	$DW = 0.059 * L^{2.099}$	Benke et al. (1999)
Chloroperlidae	$DW = 0.0065 * L^{2.724}$	Benke et al. (1999)
Chrysomelidae	$DW = 0.039 * L^{3.111}$	Benke et al. (1999)
Chydoridae (Cladocera)	$V \text{ (mL)} = (LW^2 * \pi)/6$	Reiss and Schmid-Araya (2008)
<i>Corbicula</i> spp	$DW = 0.0078 * L^{3.12}$	Benke et al. (1999)
<i>Cordulegaster boltonii</i> (Cordulegastridae)	$DW = 0.0067 * L^{2.782}$	Benke et al. (1999)
Crangonyctidae	$DW = 0.0058 * L^{2.798}$	Benke et al. (1999)
Cyclopoida (Copepoda)	$V \text{ (nL)} = L * W^2 * 560$	Reiss and Schmid-Araya (2008)

Continued on next page

Appendix B. Large wood and invertebrates' taxonomic-based metrics 227

Table B.1 – Continued from previous page

Taxa	Formula	Source
Cylindrotomidae (Tipulidae)	$DW = 0.0064 * L^{2.443}$	Benke et al. (1999)
Daphniidae (Cladocera)	$V \text{ (mL)} = (LW^2 * \pi) / 6$	Reiss and Schmid-Araya (2008)
Dasyheleinae (Ceratopogonidae)	$DW = 0.0020 * L^{2.438}$	Benke et al. (1999)
Diamesinae	$DW = 0.0020 * L^{2.602}$	Benke et al. (1999)
Ecnomidae	not calculated	
Empididae	$DW = 0.0054 * L^{2.546}$	Benke et al. (1999)
<i>Ephemera danica</i>	$DW = 0.0021 * L^{2.737}$	Benke et al. (1999)
<i>Ephemera vulgata</i>	$DW = 0.0021 * L^{2.737}$	Benke et al. (1999)
Ephemerellidae	$DW = 0.0103 * L^{2.676}$	Benke et al. (1999)
Ephydriidae	$DW = -5.17 + 1.8 * L$	Steingrímsson and Gíslason (2002)
<i>Erpobdella</i> spp	$DW = 0.0058 * L^{2.225}$	Poepperl (1998)
<i>Gammarus pulex</i>	$DW = 0.0019 * L^{2.964}$	Poepperl (1998)
<i>Glossiphonia</i> spp	$DW = 0.0198 * L^{2.212}$	Poepperl (1998)
Glossosomatidae	$DW = 0.0082 * L^{2.958}$	Benke et al. (1999)
<i>Goera pilosa</i>	$DW = 0.0016 * L^{4.244}$	Meyer (1989)
Haliplidae	$DW = 0.0271 * L^{2.744}$	Benke et al. (1999)
Hebridae (Hemiptera)	$DW = 0.0108 * L^{2.734}$	Benke et al. (1999)
Heptageniidae	$DW = 0.0108 * L^{2.754}$	Benke et al. (1999)
Hydrachnidia	$V \text{ (nL)} = L * W^2 * 399$	Reiss and Schmid-Araya (2008)
Hydrobiidae	not calculated	
<i>Hydropsyche</i> spp	$DW = 0.0019 * L^{2.89}$	Burgherr and Meyer (1997)
<i>Hydroptila</i> spp	$DW = 1.30 + 3.62 * L$	Baumgärtner and Rothhaupt (2003)
Hygrobiidae	not calculated	
Lepidostomatidae	$DW = 0.0079 * L^{2.649}$	Benke et al. (1999)
Leptoceridae	$DW = 0.0034 * L^{3.212}$	Benke et al. (1999)
Leptophlebiidae	$DW = 0.0047 * L^{2.686}$	Benke et al. (1999)
<i>Leuctra</i> spp	$DW = 0.0022 * L^{2.66}$	Burgherr and Meyer (1997)
Limnephilidae	$DW = 0.0054 * L^{2.966}$	Meyer (1989)
<i>Limnius</i> spp (Elmidae)	$DW = 0.0074 * L^{2.879}$	Benke et al. (1999)
Limoniidae	$DW = 0.0039 * L^{2.44}$	Poepperl (1998)
<i>Molanna</i> spp	$DW = 0.0034 * L^{3.212}$	Benke et al. (1999)
Muscidae	$DW = -7.8392 + 3.1059 * L$	Meyer (1989)

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Appendix B. Large wood and invertebrates' taxonomic-based metrics 228

Table B.1 – Continued from previous page

Taxa	Formula	Source
Nematoda	$WW (\mu g) = L \mu m^*$ $W \mu m^2 / 16 * 10^5$	Andrassy (1956)
Niphargidae (Amphipoda)	$DW = 0.0058 * L^{3.015}$	Benke et al. (1999)
<i>Notidobia ciliaris</i> (Sericostomatidae)	$DW = 0.0074 * L^{2.741}$	Benke et al. (1999)
Oligochaeta	$V (nL) = L * W^2 * 530$	Feller (1988)
Orthoclaadiinae	$DW = 0.0020 * L^{2.254}$	Benke et al. (1999)
Ostracoda	$V (nL) = L * W^2 * 450$	Reiss and Schmid-Araya (2008)
Pediciidae	$DW = -7.8392 + 3.1059 * L$	Meyer (1989)
Perlodidae	$DW = 0.0196 * L^{2.742}$	Benke et al. (1999)
Philopotamidae	$DW = 0.0050 * L^{2.511}$	Benke et al. (1999)
Phryganeidae	$DW = 0.0054 * L^{2.811}$	Benke et al. (1999)
Physidae	not calculated	
Piscicolidae	$DW = 0.0198 * L^{2.212}$	Benke et al. (1999)
<i>Pisidium</i> spp	$DW = 0.0163 * L^{2.477}$	Benke et al. (1999)
Planariidae	$DW = 0.0082 * L^{2.168}$	Benke et al. (1999)
Planorbidae	not calculated	
Podonominae	$DW = 0.0059 * L^{2.099}$	Benke et al. (1999)
Polycentropodidae	$DW = 0.0047 * L^{2.705}$	Benke et al. (1999)
Potamanthidae (Ephemeroptera)	$DW = 0.0071 * L^{2.832}$	Benke et al. (1999)
<i>Procloeon pennulatum</i> (Baetidae)	$DW = 0.0053 * L^{2.875}$	Benke et al. (1999)
Prodiamesinae	$DW = 0.0020 * L^{2.602}$	Benke et al. (1999)
Prosimuliini	$DW = 0.0012 * L^{3.190}$	Benke et al. (1999)
Psychodidae	$DW = 0.0025 * L^{2.692}$	Benke et al. (1999)
Psychomyiidae	$DW = 0.0018 * L^{3.129}$	Meyer (1989)
<i>Radix</i> spp	$DW = -4.76 + 3.19 * S * L$	Baumgärtner and Rothhaupt (2003)
<i>Rhithrogena</i> spp	$DW = -2.29 + 3.52 * HW$	Burgherr and Meyer (1997)
Rhyacophilidae	$DW = 0.0016 * L^{3.123}$	Meyer (1989)
<i>Scarodytes</i> spp (Coleoptera)	$DW = 0.0077 * L^{2.910}$	Benke et al. (1999)
<i>Sericostoma</i> spp	$DW = 0.0114 * L^{2.649}$	Meyer (1989)
<i>Serratella ignita</i>	$DW = 0.0054 * L^{3.057}$	Meyer (1989)
Sialidae	$DW = 0.0037 * L^{2.753}$	Benke et al. (1999)
Sididae (Cladocera)	$V (mL) = (LW^2 * \pi) / 6$	Reiss and Schmid-Araya (2008)

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Appendix B. Large wood and invertebrates' taxonomic-based metrics 229

Table B.1 – *Continued from previous page*

Taxa	Formula	Source
<i>Silo</i> spp	$DW = 0.0016 * L^{4.244}$	Meyer (1989)
Simuliidae	$DW = 0.0029 * L^{2.67}$	Benke et al. (1999)
Siphonuridae	$DW = 0.0027 * L^{3.446}$	Benke et al. (1999)
<i>Sphaerium</i> spp (Sphaeriidae)	$DW = 0.0163 * L^{2.477}$	Benke et al. (1999)
Tabanidae	$DW = 0.0050 * L^{2.591}$	Benke et al. (1999)
Talitridae (Amphipoda)	$DW = 0.0058 * L^{3.015}$	Benke et al. (1999)
Tanypodinae	$DW = 0.0026 * L^{2.503}$	Benke et al. (1999)
Tanytarsini	$DW = 0.0012 * L^{2.294}$	Benke et al. (1999)
Thaumaleidae (Diptera)	$DW = 0.0025 * L^{2.692}$	Benke et al. (1999)
Tipulidae	$DW = 0.0064 * L^{2.443}$	Benke et al. (1999)

Table B.2: Taxa list for the Hammer Stream found during the study period from October 2016 to August 2017

Hyporheic meiofauna	Hyporheic macrofauna	Benthic macrofauna
Asellidae	Acroloxidae	Asellidae
Beraeidae	<i>Agabus</i> spp	<i>Atherix</i> spp
Bithyniidae (Bi)	Asellidae	<i>Baetis</i> spp
Bosminidae	<i>Atherix</i> spp	Bithyniidae
Caenidae (Cae)	<i>Baetis</i> spp	<i>Caenis</i> spp
<i>Capnia</i> spp (Ca)	Beraeidae	Calopterygidae
Ceratopogonidae (Cer)	Bithyniidae	<i>Capnia</i> spp
Chironomini (C)	<i>Caenis</i> spp	Ceratopogonidae
Chydoridae (Chy)	<i>Capnia</i> spp	Chironomini
Cyclopoida (Cy)	Ceratopogonidae	Chloroperlidae
Cylindrotomidae	Chironomini	Chrysomelidae
Daphniidae	Chydoridae	<i>Cordulegaster boltonii</i>
Diamesinae (Di)	<i>Corbicula</i> spp	Crangonyctidae
Dytiscidae	<i>Cordulegaster boltonii</i>	Dasyheleinae
Empididae (Em)	Crangonyctidae	Diamesinae
<i>Ephemera danica</i> (Eph)	Cyclopoida	Ecnomidae

Continued on next page

Table B.2 – Continued from previous page

Hyporheic meiofauna	Hyporheic macrofauna	Benthic macrofauna
Ephemerellidae (Ep)	Cylindrotomidae	Empididae
Erpobdellidae (Er)	Dasyheleinae	Ephemera
<i>Gammarus pulex</i> (G.p)	Diamesinae	Ephemerellidae
<i>Glossiphonia</i> (Gl)	Empididae	<i>Ephydridae</i>
Glossiphoniidae	<i>Ephemera danica</i>	<i>Erpobdella</i>
Heptageniidae	<i>Ephemera vulgata</i>	<i>Gammarus pulex</i>
Hydrachnidia (Hy)	Ephemerellidae	<i>Glossiphonia</i>
<i>Hydropsyche</i> (Hyd)	<i>Erpobdella</i> spp	Glossosomatidae
Leptoceridae (Lep)	<i>Gammarus pulex</i>	<i>Goera pilosa</i>
Leptophlebiidae	<i>Glossiphonia</i> spp	Haliplidae
Leuctridae (Leu)	Glossosomatidae	Hebridae
<i>Limnius</i> spp (Li)	<i>Goera pilosa</i>	Heptageniidae
Limoniidae (Lim)	Hebridae	Hydrachnidia
Molannidae	Heptageniidae	Hydrobiidae
Nematoda (N)	Hydrachnidia	<i>Hydropsyche</i> spp
Niphargidae	<i>Hydropsyche</i> spp	<i>Hydroptila</i> spp
Oligochaeta (Oli)	<i>Hydroptila</i> spp	Lepidostomatidae
Orthoclaadiinae (Ort)	Hygrobidae	Leptoceridae
Ostracoda (Os)	Leptoceridae	Leptophlebiidae
Pediciidae	<i>Leuctra</i> spp	Leuctridae
Philopotamidae	Limnephilidae	Limnephilidae
Physidae	<i>Limnius</i> spp	<i>Limnius</i> spp
Piscicolidae	Limoniidae	Limoniidae
<i>Pisidium</i> spp (Pi)	<i>Molanna</i> spp	<i>Molanna</i> spp
Planariidae	Nematoda	Muscidae
Polycentropodidae	Niphargidae	Oligochaeta
Prodiamesinae	<i>Notidobia ciliaris</i>	Orthoclaadiinae
Prosimuliini (Pr)	Oligochaeta	Pediciidae
Psychodidae	Orthoclaadiinae	Ostracoda
Psychomyiidae (Ps)	Ostracoda	Perlodidae
Sericostomatidae	Pediciidae	Philopotamidae
Sialidae	Philopotamidae	Phryganeidae
Sididae	Phryganeidae	Planorbidae
Simuliidae	Physidae	Podonominae
Siphonuridae	Piscicolidae	Polycentropodidae
Sphaeriidae	<i>Pisidium</i>	Potamantidae

Continued on next page

Table B.2 – *Continued from previous page*

Hyporheic meiofauna	Hyporheic macrofauna	Benthic macrofauna
Tabanidae	Planorbidae	<i>Procloeon pennulatum</i>
Talitridae	Podonominae	Psychodidae
Tanypodinae (Ta)	Polycentropodidae	Psychomyiidae
Tanytarsini (Tany)	Prodiamesinae	<i>Radix</i> spp
Thaumaleidae	Prosimuliini	Rhithrogena spp
Tipulidae (Tip)	Psychodidae	Rhyacophilidae
	Psychomyiidae	<i>Scarodytes</i> spp
	<i>Radix</i> spp	<i>Sericostoma</i> spp
	<i>Sericostoma</i> spp	<i>Serratella ignita</i>
	<i>Serratella ignita</i>	<i>Silo</i> spp
	Sialidae	Siphonuridae
	Sididae	<i>Sphaerium</i> spp
	Simuliidae	Tabanidae
	Siphonuridae	Talitridae
	<i>Sphaerium</i> spp	Tanypodinae
	Tabanidae	Tanytarsini
	Talitridae	Tipulidae
	Tanypodinae	
	Tanytarsini	
	Thaumaleidae	
	Tipulidae	

Within Reach x Campaign Analysis and Conditional Inference Tree of hyporheic macrofauna

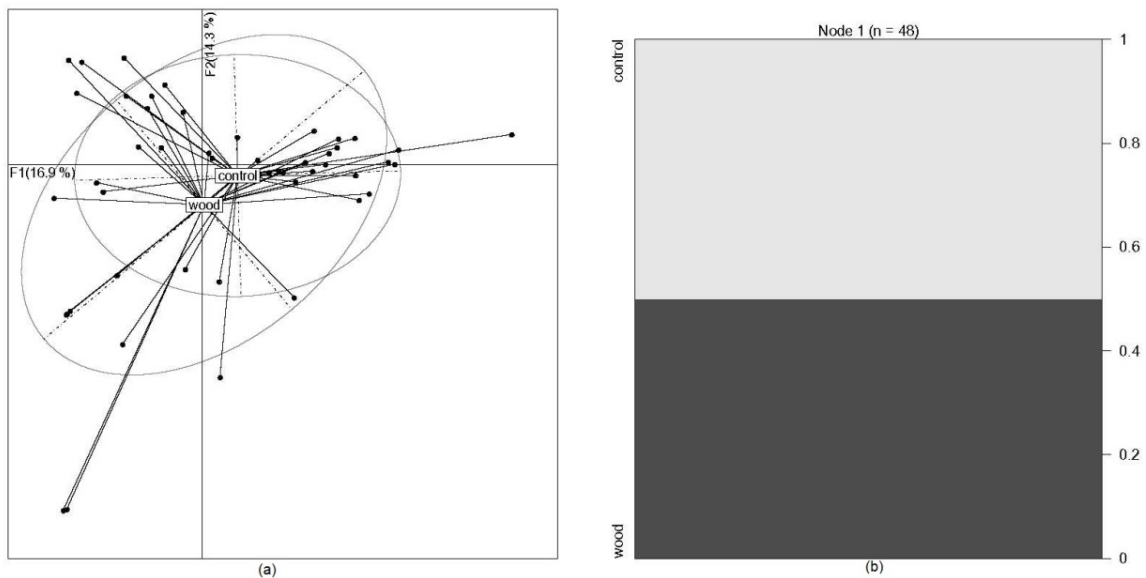


Figure B.1: Comparison of hyporheic macrofauna abundance (log-transformed) among wood and control sites. Within Reach x Campaign Analysis gives the locations of the 48 samples grouped by wood and control. Wood and control are located at the weighted average (i.e. the centre of the star) of corresponding samples (solid circles). Lines link samples to the mean location of their site. The ellipse of inertia indicates the 95% of confidence interval around the centroids. (b) Conditional inference tree (9999 Bonferroni permutations; $\alpha = 0.01$) testing the significance of differences in wood and control sites locations on the first WCA factorial plane (response variables: coordinates of samples along F1 and F2), the CIT analysis does not identify significant differences

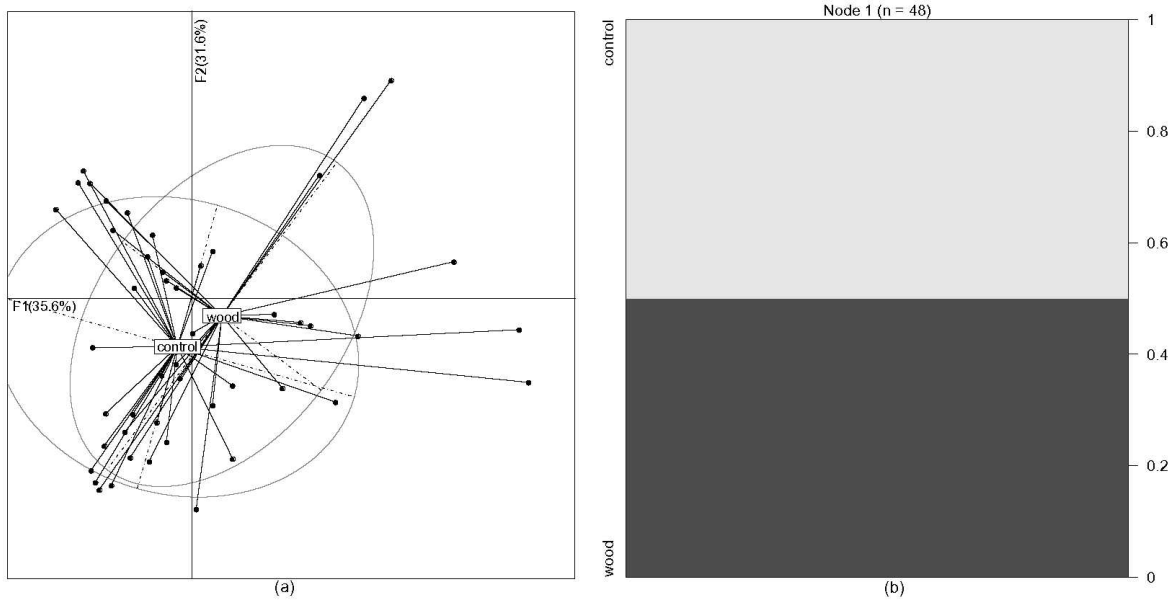


Figure B.2: Comparison of hyporheic macrofauna biomass (log-transformed) among wood and control sites. Within Reach x Campaign Analysis gives the locations of the 48 samples grouped by wood and control. Wood and control are located at the weighted average (i.e. the centre of the star) of corresponding samples (solid circles). Lines link samples to the mean location of their site. The ellipse of inertia indicates the 95% of confidence interval around the centroids. (b) Conditional inference tree (9999 Bonferroni permutations; $\alpha = 0.01$) testing the significance of differences in wood and control sites locations on the first WCA factorial plane (response variables: coordinates of samples along F1 and F2), the CIT analysis does not identify significant differences.

Within Reach x Campaign Analysis and Conditional Inference Tree of benthic macrofauna

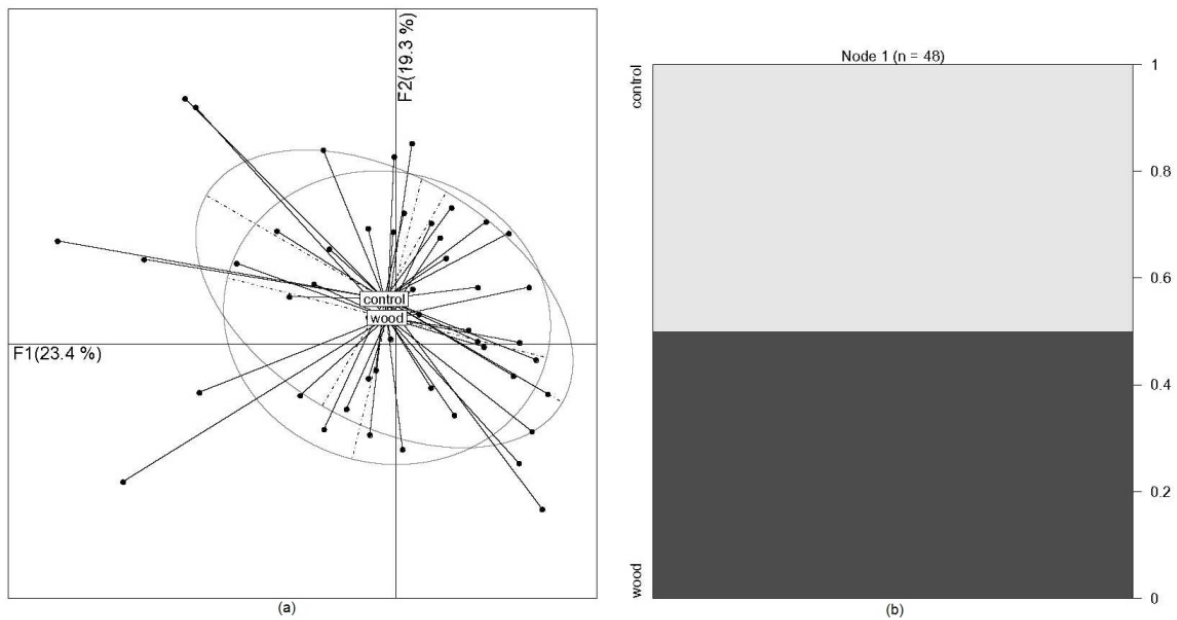


Figure B.3: Comparison of benthic macrofauna abundance (log-transformed) among wood and control sites. Within Reach x Campaign Analysis gives the locations of the 48 samples grouped by wood and control. Wood and control are located at the weighted average (i.e. the centre of the star) of corresponding samples (solid circles). Lines link samples to the mean location of their site. The ellipse of inertia indicates 95% of confidence interval around the centroids. (b) Conditional inference tree (9999 Bonferroni permutations; $\alpha = 0.01$) testing the significance of differences in wood and control sites locations on the first WCA factorial plane (response variables: coordinates of samples along F1 and F2), the CIT analysis does not identify significant differences.

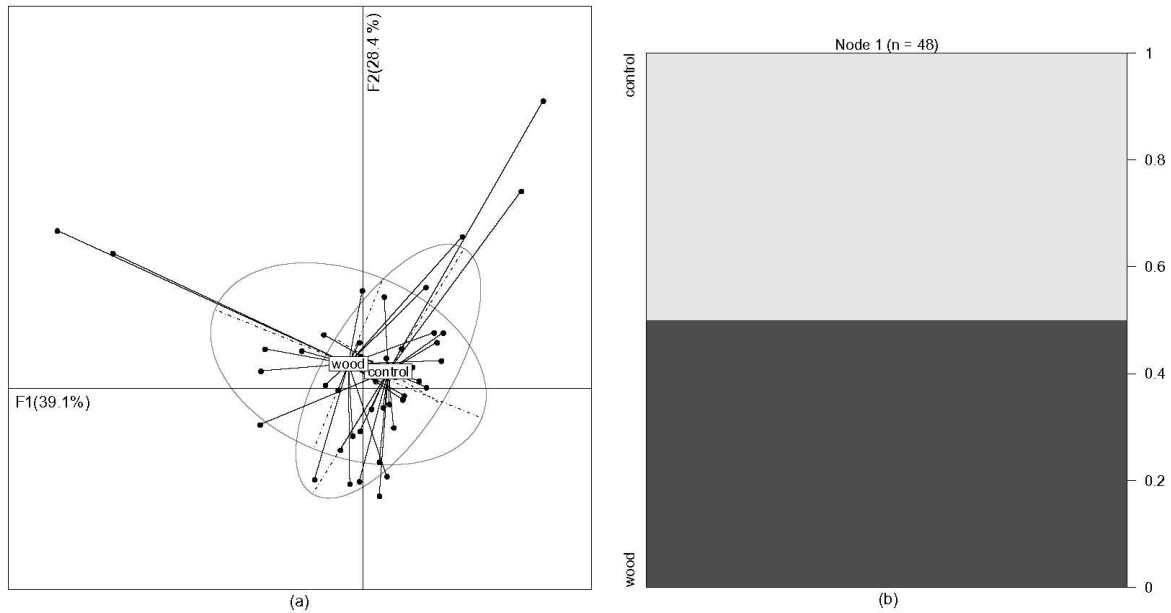


Figure B.4: Comparison of benthic macrofauna biomass (log-transformed) among wood and control sites. Within Reach x Date Campaign gives the locations of the 48 samples grouped by wood and control. Wood and control are located at the weighted average (i.e. the centre of the star) of corresponding samples (solid circles). Lines link samples to the mean location of their site. The ellipse of inertia indicates 95% of confidence interval around the centroids. (b) Conditional inference tree (9999 Bonferroni permutations; $\alpha = 0.01$) testing the significance of differences in wood and control sites locations on the first WCA factorial plane (response variables: coordinates of samples along F1 and F2), the CIT analysis does not identify significant differences

Relative contribution of meiofauna and macrofauna groups to abundance and biomass.

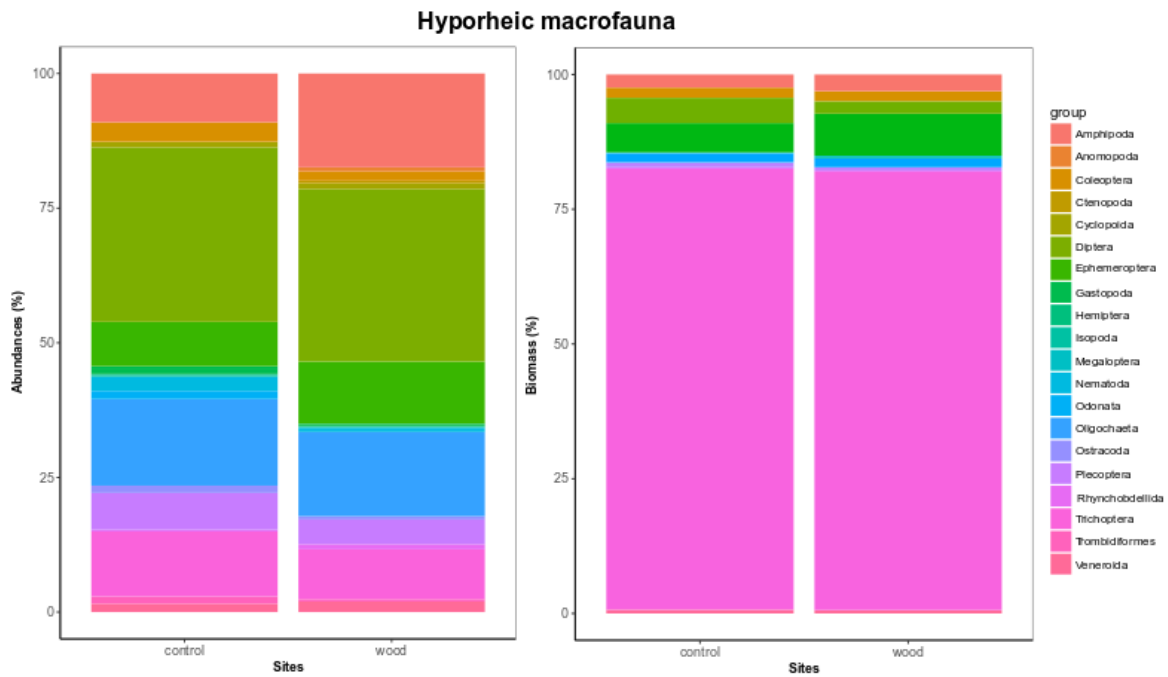


Figure B.5: The relative contribution in percentage to mean abundance and mean biomass of hyporheic macrofaunal groups found in the Hammer Stream on sampling occasions from October 2016 to August 2017.

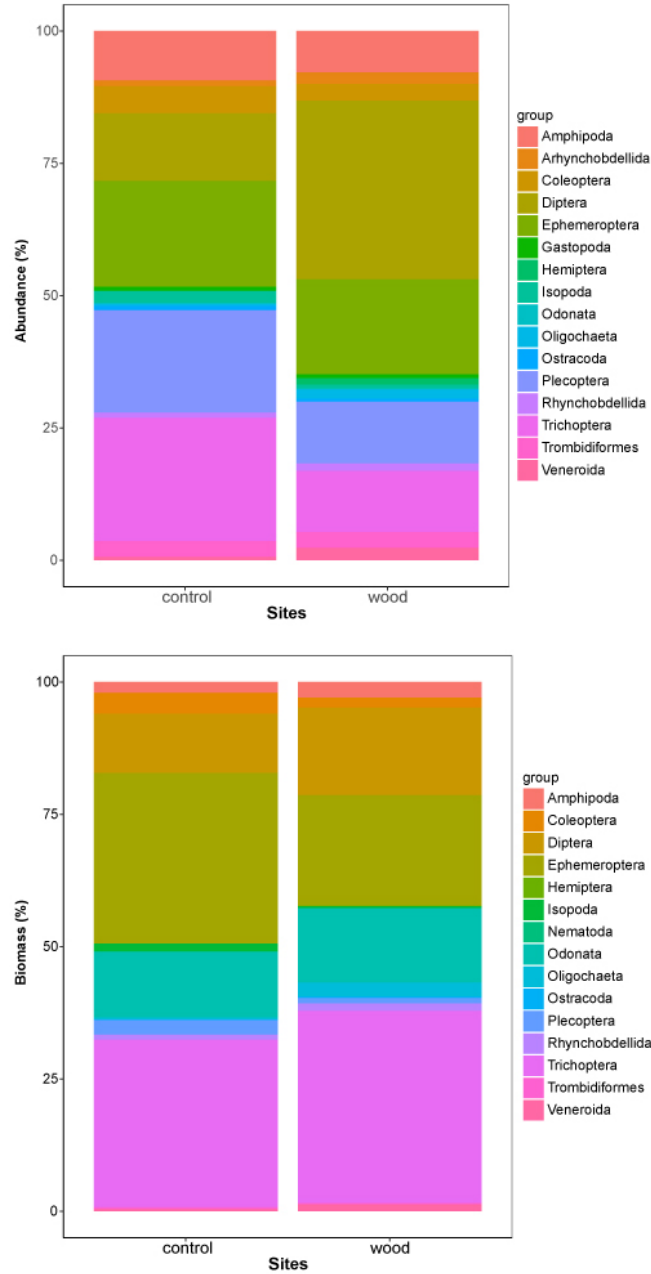


Figure B.6: The relative contribution in percentage to mean abundance and mean biomass of benthic macrofaunal groups found in the Hammer Stream on sampling occasions from October 2016 to August 2017.

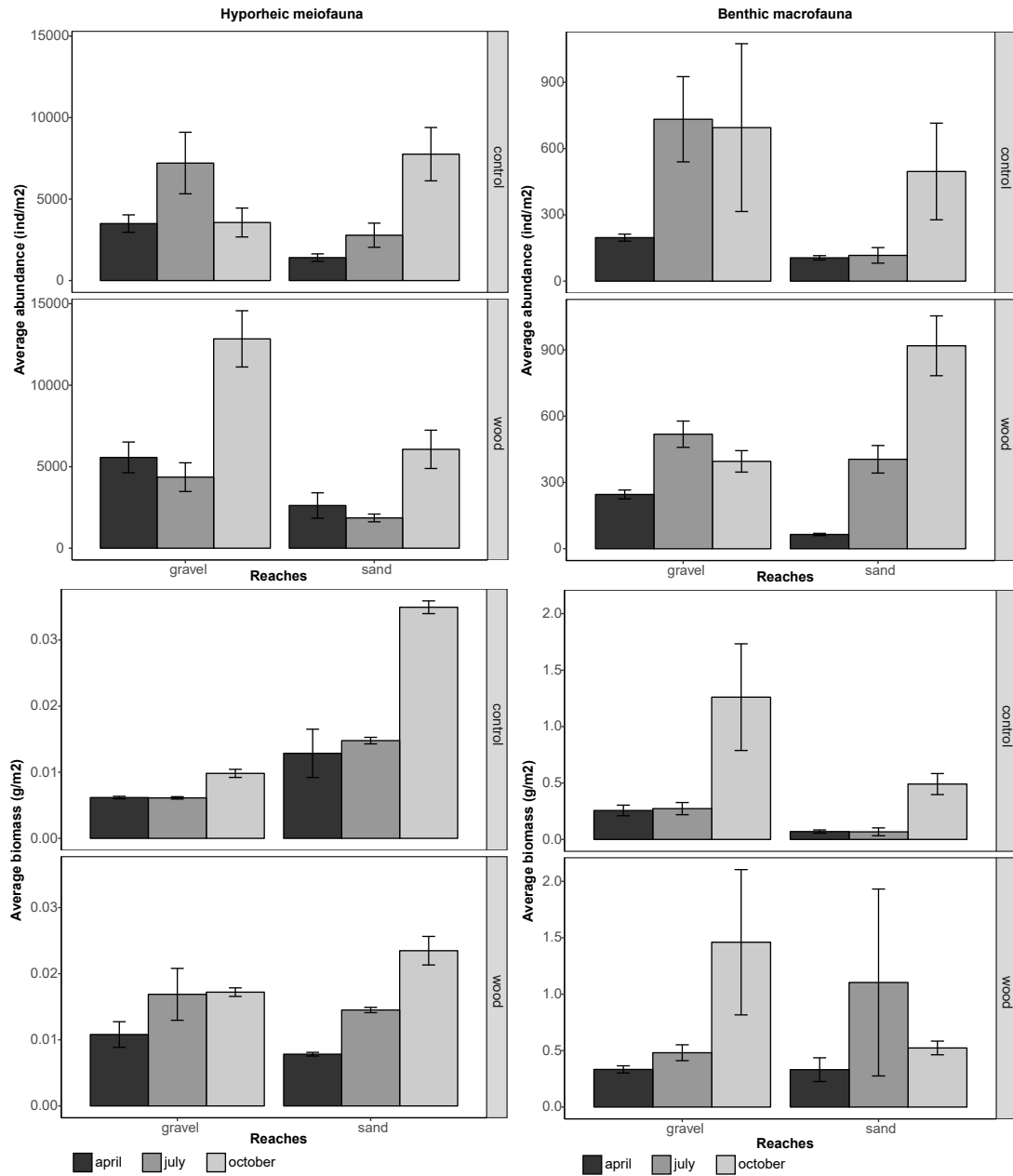


Figure B.7: Average abundance and biomass($\pm SD$) of hyporheic meiofauna and benthic macrofauna across reaches and sampling campaign.

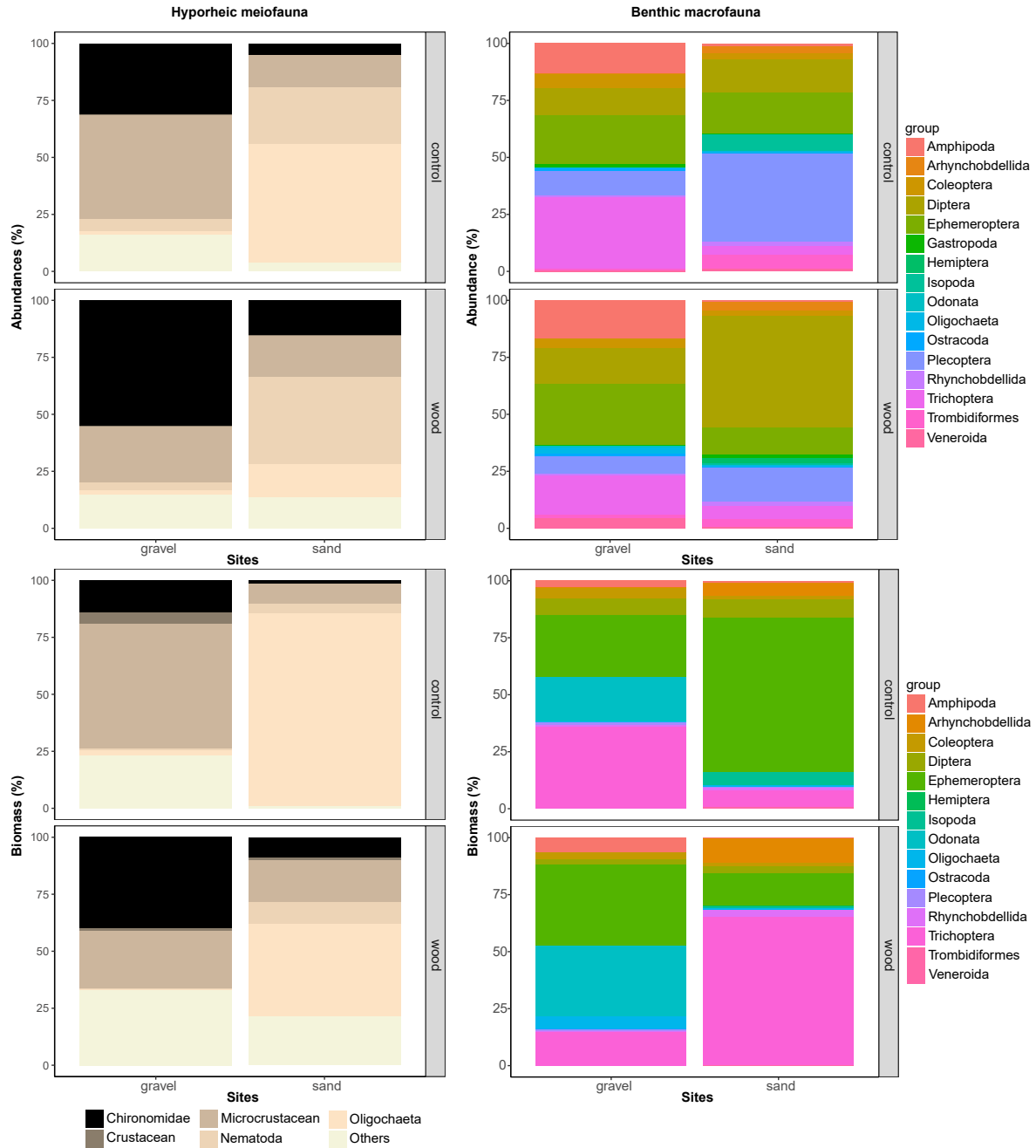


Figure B.8: Relative contribution in percentage of hyporheic meiofauna and benthic macrofauna to abundance and biomass.

Appendix C

Large wood and invertebrates' functional traits

List of traits and modalities used in this study

Table C.1: Biological and ecological traits and modalities of freshwater invertebrates used in this study.

Trait	Modalities	Abbreviations
Maximal potential size (MPS)	≤ 0.25 cm	
	$>0.25-0.5$ cm	
	$>0.5-1$ cm	
	$>1-2$ cm	
	$>2-4$ cm	
	$>4-8$ cm	
	>8 cm	
Life cycle duration (LCD)	≤ 1 year	
	>1 year	
Potential number of cycles per year (PNC)	<1	
	1	
	>1	
Fecundity (F)	≤ 100	
	$>100-1000$	
	$>1000-3000$	
	>3000	
Body Flexibility (BF)	none ($<10^\circ$)	none
	low ($>10-45^\circ$)	low
	high ($>45^\circ$)	high
Body Form (BFo)	streamlined	
	flattened	
	cylindrical	
	spherical	
Aquatic Stages (AS)	egg	
	larva	

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Table C.1 – *Continued from previous page*

Trait	Modalities	Abbreviations
	nymph	
	adult	
Reproduction (R)	ovoviviparity	ovoviv.
	isolated eggs, free	iso.egg.free
	isolated eggs, cemented	iso.egg.cem
	clutches, cemented or fixed	clutches.fixed
	clutches, free	clutches.free
	clutches, in vegetation	clutches.veg
	clutches, terrestrial	clutches.terr
	asexual reproduction	asex.repr
	parthenogenesis	parth
Dispersal (D)	aquatic passive	aqu.pass
	aquatic active	aqu.act
	aerial passive	aer.pass
	aerial active	aer.act
Resistance Forms (RS)	eggs, statoblasts	
	cocoons	
	housings against desiccation	house.diss
	diapause or dormancy	diapause
	none	
Respiration(Re)	tegument	
	gill	
	plastron	
	spiracle	
Locomotion and substrate relation (L)	flier	
	surface swimmer	surf.swim
	full water swimmer	full.wat.swim
	crawler	
	burrower	
	interstitial	
	temporarily attached	temp.att
	permanently attached	perm.att
Food (Fo)	microorganisms	microorg
	detritus <1 mm	
	dead plant ≥ 1 mm	
	living microphytes	l.microphytes
	living macrophytes	l.macrophytes

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Table C.1 – *Continued from previous page*

Trait	Modalities	Abbreviations
	dead animal ≥ 1 mm	dead.animal
	living microinvertebrates	l.microinverts
	living macroinvertebrates	l.macroinverts
	vertebrates	
Feeding Habits (FH)	absorber	
	deposit feeder	dep.feeder
	shredder	
	scraper	
	filter-feeder	f.feeder
	piercer	
	predator	
	parasite	
Substrate preferences (S)	flags/boulders/cobbles/pebbles	fbcp
	gravel	
	sand	
	silt	
	macrophytes	
	microphytes	
	twigs/roots	
	organic detritus/litter	org.detritus/litter
	mud	
Current velocity (V)	null	
	slow	
	medium	
	fast	
Temperature (T)	psychrophilic	
	thermophilic	
	eurythermic	

Path diagram of the PLS modelling approach

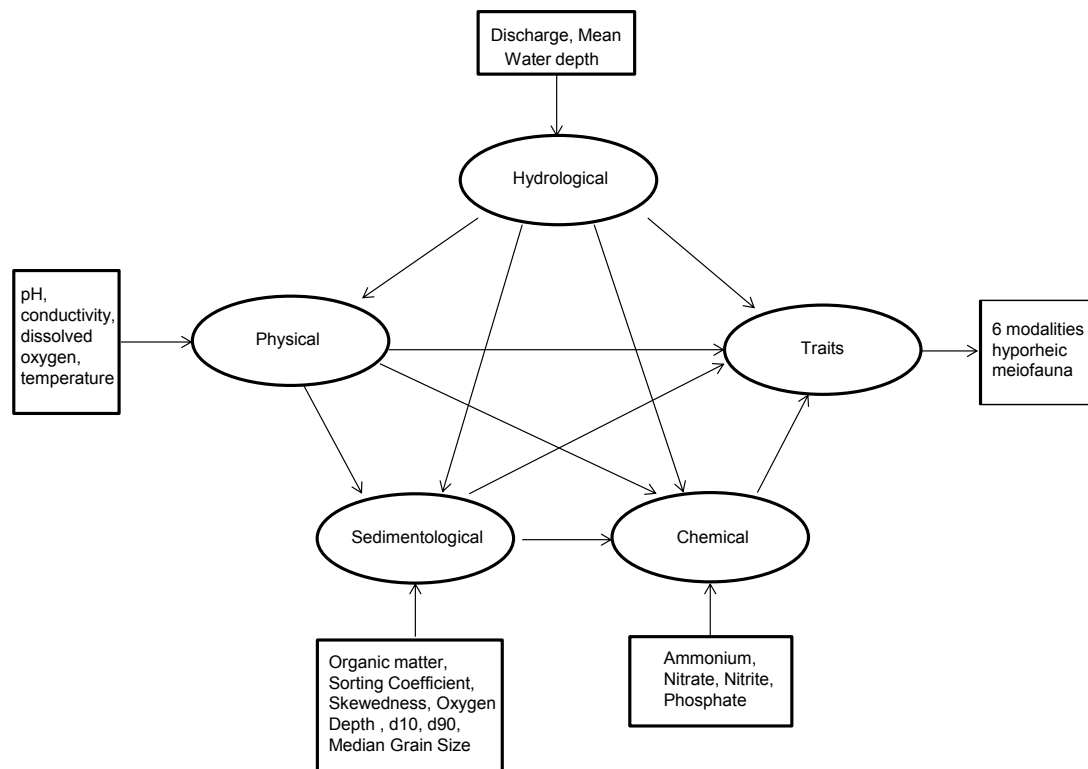


Figure C.1: Path diagram depicting the outer and inner model of the PLS approach used for both benthic and hyporheic invertebrates in wood and control sites. Latent variables are represented by an ellipse box and each direct effect from this latent variable to another is represented by an arrow. Manifest variables are displayed in *reflective* or *formative* mode.

Supporting results Within Reach x Campaign Analyses

Hyporheic zone: hyporheic macrofauna

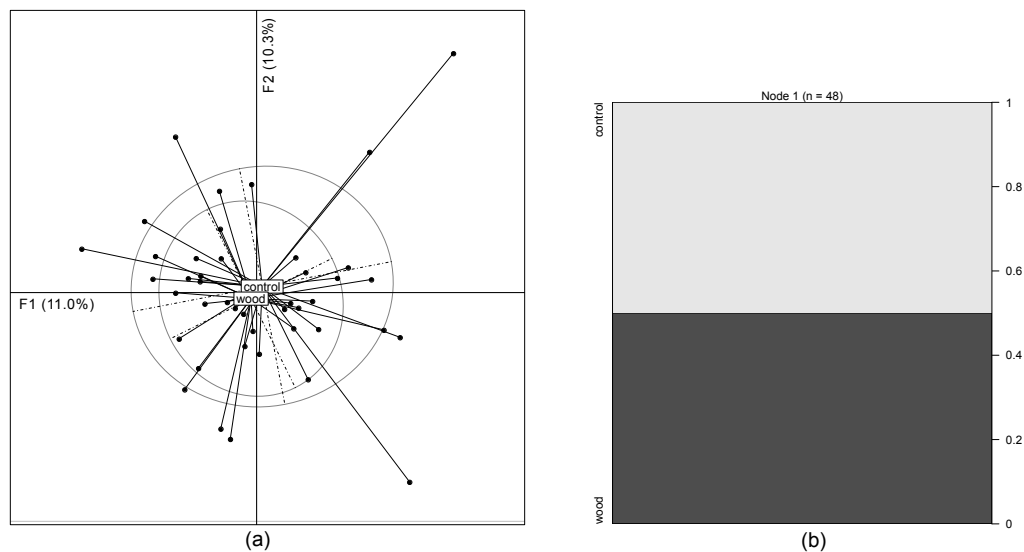


Figure C.2: Hyporheic macrofauna trait profiles among wood and control sites. First factorial plane of WCA gives the locations of the 48 samples gathered by wood and control. In (a), wood and control are located at the weighted average (i.e. the centre of the star) of corresponding samples (solid circles). Lines link samples to the mean location of treatment category. The percentage of the total variance explained by each axis is indicated. The ellipse of inertia indicates the 95% of confidence interval around the centroid of wood and control sites. (b) Conditional inference tree (9999 Bonferroni permutations; $\alpha = 0.01$) testing the significance of differences in wood and control site on the first WCA factorial plane (response variables: coordinates of samples along F1 and F2); the CIT analysis does not identify significant differences.

Benthic zone: benthic macrofauna

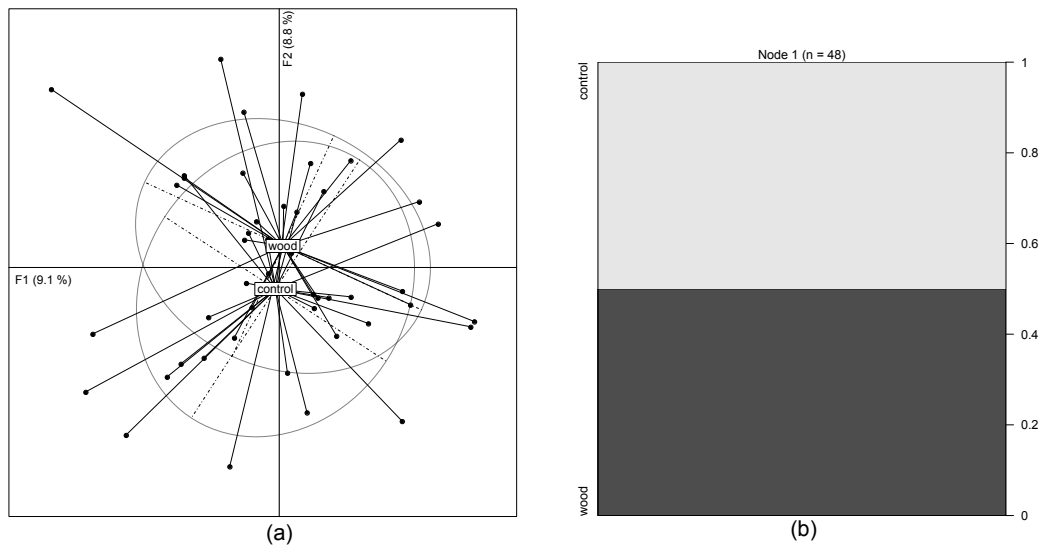


Figure C.3: Benthic macrofauna trait profiles among wood and control sites. First factorial plane of WCA gives the locations of the 48 samples gathered by wood and control. In (a), wood and control are located at the weighted average (i.e. the centre of the star) of corresponding samples (solid circles). Lines link samples to the mean location of treatment category. The percentage of the total variance explained by each axis is indicated. The ellipse of inertia indicates the 95% of confidence interval around the centroid of wood and control sites. (b) Conditional inference tree (9999 Bonferroni permutations; $\alpha = 0.01$) testing the significance of differences in wood and control site on the first WCA factorial plane (response variables: coordinates of samples along F1 and F2); the CIT analysis does not identify significant differences.

Supporting results Wilcoxon Signed-Rank Test Hyporheic meiofauna

Table C.2: Results of Wilcoxon Signed-Rank Test on hyporheic meiofauna trait profiles among wood and control sites.

Modalities	p-value	Modalities	p-value	Modalities	p-value
aqu.act	<0.001	>8 cm	0.067	diapause	0.439
twigs/roots	<0.001	aer.act	0.069	1	0.456
sand	<0.001	<1	0.076	medium	0.456
egg	<0.001	<0,25 cm	0.079	scraper	0.473
nymph	<0.001	>4-8 cm	0.08	perm.att	0.507
fbcp	<0.001	low	0.097	tegument	0.509
none (RF)	0.004	vertebrates	0.100	l.macroinverts	0.527
shredder	0.004	null	0.121	absorber	0.587
macrophytes	0.004	temp.att	0.143	>3000	0.602
mud	0.005	>1-2 cm	0.178	crawler	0.603
slow	0.005	detritus	0.178	microphytes	0.643
flattened	0.005	dep.feeder	0.188	none	0.649
cylindrical	0.005	>2-4 cm	0.208	l.microphytes	0.663
spiracle	0.006	>100-1000	0.208	parth	0.702
aqu.pass	0.010	high	0.218	plastron	0.722
adult	0.010	clutches.fixed	0.241	gill	0.726
dead.anim	0.010	is.egg.free	0.252	microorg.	0.726
larva	0.010	egg.stat	0.267	>1	0.747
org.detritus/litter	0.021	cocoons	0.267	ovoviv.	0.749
l.macrophytes	0.029	predator	0.317	asex.repr	0.763
gravel	0.029	streamlined	0.339	burrower	0.768
l.microinverts	0.037	<100	0.345	clutches.veg	0.789
surf.swim.	0.038	aer.pass	0.360	flier	0.834
spherical	0.041	>0 ,5-1 cm	0.390	piercer	0.834
>0,25-0,5 cm	0.046	<1 year	0.390	is.egg.cem	0.855
clutches.free	0.046	>1 year	0.390	>1000-3000	0.891
interstitial	0.053	parasite	0.390	full.wat.swim.	0.989
silt	0.056	dead.plat	0.406	f.feeder	1.000
fast	0.056	clutches.terr	0.408		

Benthic and hyporheic macrofauna

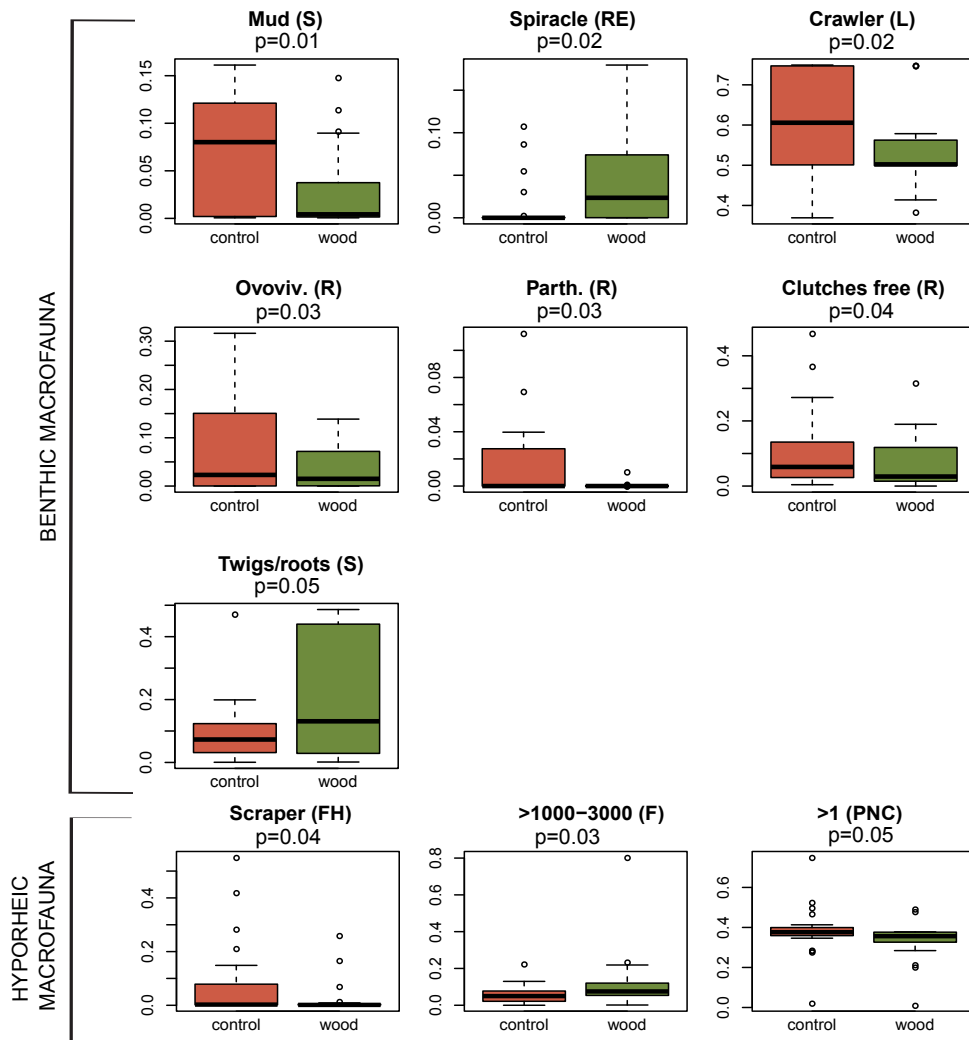


Figure C.4: Boxplot of trait modalities marginally different between LW and control sites (Wilcoxon test $0.01 < p\text{-value} < 0.05$) of benthic and hyporheic macrofauna. In brackets the corresponding trait category.

Table C.3: Results of Wilcoxon Signed-Rank Test on benthic (SM) and hyporheic macrofauna (HM) trait profiles among wood and control sites.

Modalities	p-value SM	p-value HM	Modalities	p-value SM	p-value HM
1	0.20	0.17	gill	0.88	0.12
<0,25 cm	0.90	0.35	gravel	0.22	0.94
<1	0.21	0.43	high	0.25	0.81
<1 year	0.35	0.95	house.diss	0.68	1.00
<100	0.83	0.55	interstitial	0.07	0.40
>0,5-1 cm	0.71	0.63	is.egg.cem	0.14	0.34
>0,25-0,5 cm	0.75	0.67	is.egg.free	0.66	0.15
>1	0.81	0.05	l.macroinverts	0.30	0.58
>1 year	0.35	0.95	l.macrophytes	0.09	0.10
>1000-3000	0.66	0.03	l.microinverts	0.20	0.34
>100-1000	0.32	0.89	l.microphytes	0.79	0.66
>1-2 cm	0.55	0.62	larva	0.53	0.80
>2-4 cm	0.97	0.42	low	0.29	0.78
>3000	0.53	0.40	macrophytes	0.07	0.30
>4-8 cm	0.14	0.58	medium	0.46	0.41
>8 cm	0.94	0.60	microorg.	0.28	0.39
absorber	0.53	0.50	microphytes	0.35	0.26
adult	0.80	0.20	mud	0.01	0.66
aer.act	0.12	0.59	none	0.78	0.64
aer.pass	0.57	0.50	none.1	0.06	0.68
aqu.act	0.38	0.44	null	0.44	0.80
aqu.pass	0.30	0.86	nymph	0.33	0.96
asex.repr	0.44	0.77	org.detritus/litter	0.10	0.96
burrower	0.12	0.33	ovoviv.	0.03	0.44
clutches.fixed	0.11	0.51	parasite	0.07	0.49
clutches.free	0.04	0.64	parth	0.03	0.44
clutches.terr	0.15	0.43	perm.att	0.37	0.94
clutches.veg	0.55	0.75	piercer	0.13	0.61
cocoons	0.18	0.75	plastron	0.81	0.53
crawler	0.02	0.41	predator	0.55	0.83
cylindrical	0.36	0.23	psychrophilic	0.57	0.71
dead.anim	0.90	0.84	sand	0.21	0.40
dead.plat	0.73	0.29	scraper	0.49	0.04
dep.feeder	0.81	0.66	shredder	0.90	0.99
detritus	0.12	0.71	silt	0.13	0.75
diapause	0.06	0.66	slow	0.30	0.10

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Table C.3 – *Continued from previous page*

Modalities	p-value SM	p-value HM	Modalities	p-value SM	p-value HM
egg	0.66	0.89	spherical	0.34	0.17
egg.stat	0.11	0.41	spiracle	0.02	0.87
eurythermic	0.53	0.83	streamlined	0.41	0.91
f.feeder	0.58	0.46	surf.swim.	0.09	0.63
fast	0.86	0.46	tegument	0.36	0.38
fbcp	0.75	0.41	temp.att	0.12	0.21
flattened	0.58	0.60	thermophilic	0.86	0.84
flier	0.60	0.38	twigs/roots	0.05	0.62
full.wat.swim.	0.16	0.48	vertebrates	0.66	0.63