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Organizational Principles of Hyporheic Exchange Flow and Biogeochemical Cycling in River Networks Across Scales

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Key Points:

- The complexity of HZ rivers and controls exceeds the range of conditions considered in previous conceptualizations and model formulations
- Understanding organizational principles of hyporheic exchange flow (HEF) and biogeochemical cycling in landscapes is key for generalizing process knowledge
- Local HEF, metabolism, and biogeochemical cycling are embedded within the larger context of fluvial and terrestrial ecosystem structure

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Abstract Hyporheic zones increase freshwater ecosystem resilience to hydrological extremes and global environmental change. However, current conceptualizations of hyporheic exchange, residence time distributions, and the associated biogeochemical cycling in streambed sediments do not always accurately explain the hydrological and biogeochemical complexity observed in streams and rivers. Specifically, existing conceptual models insufficiently represent the coupled transport and reactivity along groundwater and surface water flow paths, the role of autochthonous organic matter in streambed biogeochemical functioning, and the feedbacks between surface-subsurface ecological processes, both within and across spatial and temporal scales. While simplified approaches to these issues are justifiable and necessary for transferability, the exclusion of important hyporheic processes from our conceptualizations can lead to erroneous conclusions and inadequate understanding and management of interconnected surface water and groundwater environments. This is particularly true at the landscape scale, where the organizational principles of spatio-temporal dynamics of hyporheic exchange flow (HEF) and biogeochemical processes remain largely uncharacterized. This article seeks to identify the most important drivers and controls of HEF and biogeochemical cycling based on a comprehensive synthesis of findings from a wide range of river systems. We use these observations to test current paradigms and conceptual models, discussing the interactions of local-to-regional hydrological, geomorphological, and ecological controls of hyporheic zone functioning. This improved conceptualization of the landscape organizational principles of drivers of HEF and biogeochemical processes from reach to catchment scales will inform future river research directions and watershed management strategies.

1. Introduction—The Need for Identifying Landscape Organizational Principles of Hyporheic Zone Functioning

Over the past three decades, there has been a paradigm shift in groundwater-surface water research from defining rivers and aquifers as discrete entities toward understanding them as an integral part of the stream-catchment continuum (Bencala, 1993, 2000; Bencala et al., 2011; Boulton & Hancock, 2006; Brunke & Gonser, 1997; Fleckenstein et al., 2010; Harvey & Gooseff, 2015; Jencso et al., 2009; Winter, 1998, 1999). This shift started with the early works of hydrobiologists defining the hyporheos, or hyporheic zone as a new habitat (Angelier, 1953; Karaman, 1935; Orghidan, 1959). From an interdisciplinary perspective, the hyporheic zone may be defined as the interface between aquifers and streams where the flow of surface water into streambed sediments and river banks promotes interactions with streambed porewater and potentially groundwater before re-emerging to the stream (Bencala, 2000; Boano et al., 2014; Cardenas, 2015; Gooseff, 2010; Krause, Hannah, Fleckenstein, et al., 2011; Ward, 2016).

Interdisciplinary research focused on the hydrological, biogeochemical, and ecological functioning of hyporheic zones has aimed to understand the extent to which this ecohydrological interface (Krause et al., 2017) influences

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surface water and groundwater flows, water quality, and ecological status of freshwaters (Boano et al., 2014; Boulton, 2007; Boulton et al., 1998, 2010; Brunke & Gonser, 1997; Buffington & Tonina, 2009; Graham et al., 2019; Harvey & Gooseff, 2015). Hyporheic zones both structure and connect surface and subsurface environments, providing key ecosystem services, including stream flow modulation (Costigan et al., 2016; Fleckenstein et al., 2006; Malzone et al., 2016; Villeneuve et al., 2015), moderation of thermal conditions in streams and groundwater (e.g., Arrigoni et al., 2008; Burkholder et al., 2008; Folegot, Hannah, et al., 2018; Hannah et al., 2009; Krause, Hannah, & Blume, 2011), enhanced metabolism and biogeochemical cycling (Bardini et al., 2012; DelVecchia et al., 2016; Fellows et al., 2001; Gomez-Velez et al., 2015; Knapp et al., 2017; Krause et al., 2009, 2013; Pinay et al., 2009; Schmadel, Ward, Kurz, et al., 2016; Trauth et al., 2015; Valett et al., 1997), and contaminant transformation (Freitas et al., 2015; Gandy et al., 2007; Jaeger et al., 2019; Lawrence et al., 2013; Liu et al., 2019; Packman & Brooks, 2001; Posselt et al., 2020; Schaper et al., 2019; Weatherill et al., 2014, 2018). With their distinct physico-chemical conditions, hyporheic zones provide unique habitats that serve as a refugia for a wide range of species (Boulton et al., 2010; Datry et al., 2008; Datry & Larned, 2008; Folegot, Krause, et al., 2018; Hancock et al., 2005; Stanford & Ward, 1988). Clearly, hyporheic zones, and their hydrological interactions with surface water and groundwater, are important for the resilience of freshwater ecosystems to hydrological extremes, landscape development, and global environmental changes including hydrological and climate modifications (Dole-Olivier, 2011; Dole-Olivier et al., 1997; Fisher et al., 1998; Lewandowski et al., 2019; Nelson et al., 2020; Stubbington et al., 2009).

Several landscape-scale conceptualizations of river corridors highlight the relevance of connectivity between groundwater and surface water (Bencala et al., 2011; Buffington & Tonina, 2009; Harvey & Gooseff, 2015; Jencso et al., 2009; Malard et al., 2002; Pinay et al., 2015; Winter, 1998). Evidence from experimental and modeling studies reveals the impact of stream flow velocity and bedform geometry on exchange flow (Cardenas et al., 2004; Cardenas & Wilson, 2007a; Harman et al., 2016; Marzadri et al., 2010; Trauth et al., 2013), residence time distributions (Cardenas et al., 2008; Hester & Doyle, 2008) and biogeochemical cycling (Pinay et al., 2009; Zarnetske et al., 2011a, 2011b) in the hyporheic zone. Previous research has demonstrated the functional significance of hyporheic zone ecosystem services (Boulton et al., 1998; Brunke & Gonser, 1997; Stanford & Ward, 1993) and has explored the drivers and controls of specific hyporheic zone processes and their relevance at multiple scales and in different landscape contexts (Buffington & Tonina, 2009). However, the landscape-wide organizational principles of the drivers and controls of key hyporheic functions in space and time remain elusive (Harvey & Gooseff, 2015; Krause et al., 2014, 2017; Lee-Cullin et al., 2018; Pinay et al., 2015; Stonedahl et al., 2010). The longstanding focus on conceptualizing the principles of hyporheic zone functioning primarily at the local and reach-scale is understandable, given the difficulty investigating this environment. However, this local focus constrains our understanding of the influence of the hyporheic zone on relevant hydrological, biogeochemical, and ecological processes at larger spatial scales, particularly at the catchment scale. Additionally, as studies of temporal dynamics in drivers of hyporheic exchange are now emerging (Hester et al., 2019; Kaufman et al., 2017; Malzone et al., 2016; Singh et al., 2019; Trauth & Fleckenstein, 2017; Wu et al., 2018), we have a new opportunity to describe and predict hyporheic zone functioning through space and time (Boano et al., 2014; Cardenas, 2015; Gooseff, 2010; Harvey & Gooseff, 2015; Krause et al., 2017; Krause, Hannah, Fleckenstein, et al., 2011; Lee-Cullin et al., 2018; Ward, 2016; Ward & Packman, 2019).

We propose that current limitations of upscaling conceptual models of hyporheic zone hydrological and biogeochemical functioning toward a landscape perspective can be overcome by:

1. Better integration and synthesis of complexity from field observations across different scales (and beyond small headwater streams) with systematic modeling and controlled laboratory studies and
2. Rigorous testing of assumptions of drivers and controls of hyporheic process dynamics at their specific scale before extrapolating process knowledge from small-scale studies to the landscape context

Technological advances in sensor and tracer technologies have yielded very detailed data from field investigations, enabling quantifications of hyporheic residence time distributions (Marçais et al., 2018; Rinaldo et al., 2015) and resulting influences on biogeochemical processes under site specific conditions and hydro-geomorphic settings (González-Pinzón et al., 2015; Harvey et al., 2013; Krause et al., 2013, 2014; Zarnetske et al., 2011a). The resulting mechanistic process knowledge helps to understand hyporheic zone functioning under those site-specific conditions. However, the transferability of process understanding to other sites and conditions is still limited because the broader context of the drivers and controls of hyporheic exchange and biogeochemical reactivity are complex and difficult to observe, and the dominant underlying mechanisms that interact in their situation-specific control of hyporheic exchange flow (HEF) processes have not been investigated in sufficient detail to enable cross-site comparisons or upscale projections. Moreover, different field studies reveal that a wide range of site-specific conditions control the relative importance of drivers and controls of hyporheic zone processes at particular locations and scales (Endreny & Lautz, 2012; Jones & Holmes, 1996; Krause, Munz, et al., 2012; Munz et al., 2011; Ward & Packman, 2019). These conditions complicate further generalizations, such as the potential relevance of small-scale low-conductivity structures in streambed sediments for larger scale patterns of hyporheic zone processes (Bardini et al., 2013; Gomez-Velez et al., 2014; Laube et al., 2018; Sawyer, 2015; Sawyer & Cardenas, 2009). We suggest that these limitations can be overcome by accounting for the wider landscape controls of the broad range of encountered site-specific variability in streambed properties. Generalizing and transferring process understanding and concepts across river systems and spatial scales beyond the specific study area is difficult, but the focus to date on local understanding has limited the possibilities for advancing our understanding of hyporheic zone functioning within the wider river network and landscape context.

A substantial amount of our existing theory and understanding of hyporheic zone processes has been based on systematic studies designed to advance beyond limitations of individual system observations and to analyze the dynamics of hyporheic zone processes across a range of conditions. In particular, systematic modeling (Bardini et al., 2012; Boano, Camporeale, & Revelli, 2010; Boano, Revelli & Ridolfi, 2020; Cardenas et al., 2004; Gomez-Velez et al., 2014) and controlled laboratory studies in flumes (Arnon et al., 2009; Fox et al., 2014, 2016; Salehin et al., 2004; Thibodeaux & Boyle, 1987) have revealed key mechanisms controlling hyporheic exchange fluxes and their associated residence time and ecological function. However, we frequently fail to relate core principles identified in these controlled studies to observations of more complex dynamics and patterns at a river network scale. This failure suggests multiple knowledge gaps that prevent us from effectively linking the design and underlying assumptions of many of our systematic modeling studies to the actual governing mechanisms of those process dynamics and their spatio-temporal variability that can be observed in situ. As an example, current conceptual models propose that hyporheic residence times and the relationship between residence and reaction times (as expressed by the non-dimensional Damköhler number; Marzadri et al., 2012; Pinay et al., 2015; Zarnetske et al., 2012) act as a primary control on the fate of reactive solutes in the hyporheic zone. Longer residence time in the hyporheic zone results in a shift from aerobic to anaerobic metabolic pathways, including denitrification, sulfur reduction, and methanogenesis (Briggs et al., 2014; Pinay et al., 2009; Trauth et al., 2014, 2015; Zarnetske et al., 2011a). However, despite promising advances in representing spatial variability in physical sediment properties (Tonina et al., 2016) and improved in situ measurements (Bray & Dunne, 2017; Ryan & Boufadel, 2007), field observations frequently reveal hyporheic carbon, nitrogen, and oxygen concentration patterns that are inconsistent with the assumption that bulk hyporheic residence time controls biogeochemical reactions and turnover rates. In this sense, considering the spatial variability in sediment biogeochemical reactivity resulting from the structural controls such as the patterns of deposited sediments and autochthonous reagents (e.g., terrestrial organic carbon; Krause et al., 2013) and microbial community structure and activity may help understanding the observed patterns.

There is a similar disconnection between empirical observations and conceptual models for the effects of streambed structural heterogeneity on hyporheic exchange, residence time distributions, and nutrient cycling (Bardini et al., 2012, 2013; Cardenas et al., 2004; Laube et al., 2018; Sawyer & Cardenas, 2009; Tonina et al., 2016). This divergence often occurs due to the significant spatial heterogeneity of hyporheic exchange (Genereux et al., 2008) as well as biogeochemical properties, nutrient concentrations and turnover rates observed in hyporheic zone laboratory and field studies across multiple scales (Hou et al., 2017; Krause et al., 2013; Marion et al., 2008; Packman et al., 2006; Salehin et al., 2004). Consequently, the conceptual boundaries set for many model studies might be based on assumptions which do not necessarily represent the most relevant processes governing the respective real-world context.

We suggest intensifying our efforts on improving the transferability of findings required to overcome fragmentation in process understanding and to increase our capacity to conduct, interpret, and conceptualize field observations across river network and landscape scales. Useful strategies include the development of standardized methodologies for collecting comparable hyporheic zone data and understanding of the drivers of their landscape organizing principles (Barthel & Banzhaf, 2016; González-Pinzón et al., 2015; Krause, Hannah, Fleckenstein, et al., 2011; Lee-Cullin et al., 2018), consistent descriptions of metadata to enable synthesis efforts, and organized synoptic field sampling to assess global patterns in exchange processes and the resultant ecosystem services.

There is a critical need for integrating and advancing existing conceptual approaches to identify landscape organizational principles of HEF and biogeochemical processing in order to better contextualize and understand the role of hyporheic zone functioning in river networks across both spatial and temporal scales. The principal aim of this article is to provide a comprehensive analysis and synthesis of the interactions between important drivers and controls of hyporheic exchange and biogeochemical cycling and how they vary across scales, integrating results from a wide range of case studies that go beyond current conceptual model frameworks. In Section 2, we therefore discuss the interactions of different local-to-regional controls and drivers of hyporheic zone processes, such as hydrodynamic and hydrostatic drivers of hyporheic exchange, sediment hydraulic conductivity, the role of autochthonous organic matter sources, and feedbacks between hydrological exchange and ecological processes in the streambed. We explore the implications of these interactions for biogeochemical cycling in the landscape context. Emerging from this discussion, we identify existing knowledge gaps and mismatches between empirical observations and current concepts and theories. In Section 3, we integrate conceptualizations of organizational principles of hyporheic exchange and biogeochemical cycling from reach to catchment scale. We expect that increasing awareness and embracing the landscape organizing principles of hyporheic zones will advance the future of research at groundwater-surface water interfaces.

2. Drivers and Controls of Hyporheic Exchange Flow: Unraveling Spatio-Temporal Complexity and Their Implications for Biogeochemical Cycling

Mechanistic understanding of hyporheic exchange has advanced significantly in recent years with a large body of field-based, laboratory (flumes), and numerical model investigations. These studies have revealed how hydrostatic and hydrodynamic drivers of hyporheic exchange are controlled by regional flow acting on local head gradients and patterns of stream flow velocity, channel morphology, and flow turbulence (Boano et al., 2006, 2007; Bottacin-Busolin & Marion, 2010; Buffington & Tonina, 2009; Cardenas et al., 2004; Cardenas & Wilson, 2007a; Fox et al., 2014; Hester & Doyle, 2008). Despite this significant progress, the relative importance of different individual drivers and controls of hyporheic exchange, their scale-specific and context-dependent relevance, and the principles that explain their spatial organization in river networks and landscapes are still under debate (Boano et al., 2014; Gomez-Velez et al., 2014; Krause, Klaar, et al., 2014; Stonedahl et al., 2010; Tonina & Buffington, 2011; Ward, 2016). This lack of consensus drives us to unravel the importance of both spatial variability (e.g., sediment hydraulic conductivity and autochthonous organic matter) and temporal dynamics (e.g., in stream flow and stage) as drivers and controls of hyporheic exchange. Moreover, we embrace the idea that this fluvial structural variability strongly influences spatial patterns and temporal dynamics of biogeochemical cycling in hyporheic zones, and ultimately in river networks. In the following sections we discuss—and at times challenge—accepted conceptualizations of drivers and controls of hyporheic exchange and biogeochemical cycling by presenting evidence from field, laboratory, and modeling experiments that do not always fit or may even contradict the application of current concepts and theory.

2.1. Interactive Effects of Hydrodynamic and Hydrostatic Drivers of Hyporheic Exchange Flow

Deconvolution of the combined effects of multiple geomorphic drivers is essential for quantifying scale-dependencies of hyporheic exchange, residence time distributions, and subsequently, biogeochemical transformation rates. Hyporheic exchange and associated hyporheic residence time distributions vary and interact across orders of magnitude in spatial and temporal scales (Figure 1). These exchanges range from relatively short-term (seconds-minutes) and small spatial scale (mm) dynamics to long-term (weeks-years) and large-scale (km) patterns, such as inter-meander flow of several hundreds of meters and beyond (Boano et al., 2014; Krause, Hannah, Fleckenstein, et al., 2011; Stonedahl et al., 2010; Wondzell, 2011).

The drivers of hyporheic exchange, forcing surface water to down-well into the streambed and reside in the hyporheic zone before re-emerging to the river (Figure 2a), include hydrodynamic and hydrostatic forcings. Hydrodynamic drivers include stream flow turbulence (Boano et al., 2011; Cardenas & Wilson, 2007a; Roche et al., 2018, 2019; Trauth et al., 2013) and advective pumping induced by bedforms, such as ripples, dunes, steps, and pool-riffle sequences (Boano et al., 2007, 2014; Bottacin-Busolin & Marion, 2010; Buffington &

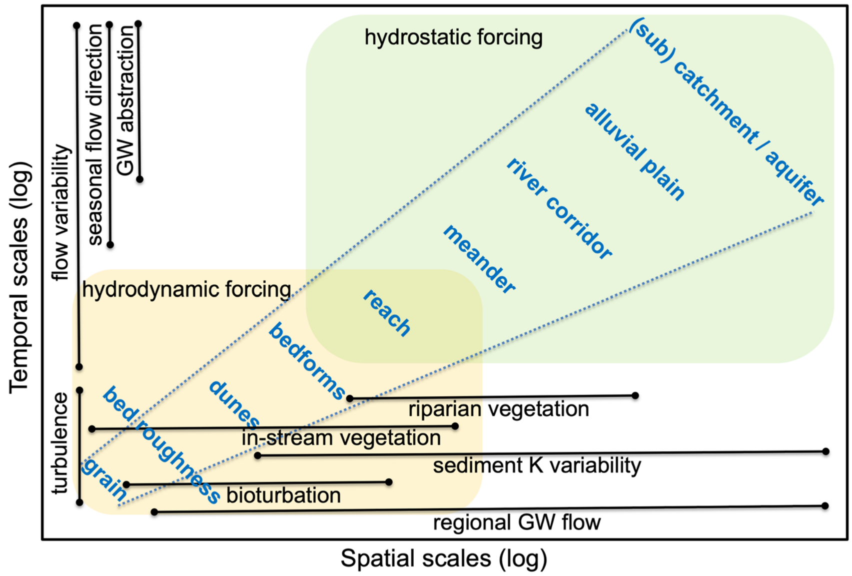

Figure 1. Spatial and temporal scales, overlaps, and interactions of example physical and biological drivers and controls of hyporheic exchange flow and hyporheic residence time distributions (adapted partly from Boano et al., 2014) with consequences for streambed solute mixing and biogeochemical cycling (*Depicted processes are selected to demonstrate scale overlaps and are not claiming to be exhaustive; sediment ksat = sediment hydraulic conductivity*).

Tonina, 2009; Cardenas et al., 2004; Elliott & Brooks, 1997a; Singh et al., 2019; Storey et al., 2003; Trauth et al., 2014) or by flow obstacles such as weirs, boulders, woody debris, and streambed engineering or restoration structures (Briggs et al., 2013; Kasahara & Hill, 2006; Krause, Klaar, et al., 2014; Wondzell, LaNier, & Haggerty, 2009; Zhou & Endreny, 2013). Hydrodynamic drivers usually create small and intermediate scale hyporheic exchange at scales ranging from 0.1 to 100 m (Figure 1). Concurrent hydrostatic forcing is induced by elevation head gradients between surface water and groundwaters or between different surface waters such as river branches or confluences. Hydrostatic gradients are primarily controlled by morphology of individual features or larger river structures (e.g., multi-thread channels) and regional groundwater flows. Hydrostatic drivers cause exchange via mechanisms including bank exchange, inter-meander flow, and large-scale groundwater circulation cells ranging from tens of meters to several kilometres (Boano, Camporeale, & Revelli, 2010; Boano, Demaria, Revelli, & Ridolfi, 2010; Boano et al., 2006; Gooseff et al., 2006; Munz et al., 2011; Pinay et al., 1998; Figure 1).

The majority of hydrological studies on flow in the hyporheic zone have conceptualized hyporheic exchange as a result of either small scale (streambed feature scale) or large scale (catchment-scale) drivers (Figure 1). Few studies have so far attempted to quantify the impact of interactions, either potentially overlapping or counter-acting, between hydrodynamic and hydrostatic forces across spatial and temporal scales (Figure 1). Experimental findings include suppression of local hyporheic exchange by regional groundwater up-welling (Angermann et al., 2012; Krause et al., 2009, 2013; Krause, Hannah, & Blume, 2011), which has been systematically investigated in a range of conceptual models of bedform-induced hyporheic exchange impacted by groundwater up-welling and/or ambient lateral groundwater flow (Boano et al., 2008, 2009; Cardenas & Wilson, 2006, 2007b; Storey et al., 2003; Trauth et al., 2013, 2015; Trauth & Fleckenstein, 2017; Wu et al., 2018; Figure 2b). However, the impact of regionally losing conditions that potentially expand the hyporheic zone and enhance hyporheic exchange and broaden residence time distributions (Figure 2c) has been less examined (De Falco et al., 2016; Fox et al., 2014; Preziosi-Ribero et al., 2020). In particular, the combined influence of hydrodynamic and hydrostatic forcings on hyporheic exchange and biogeochemical cycling under losing conditions still needs to be established in detail (Trauth et al., 2015).

Systematic analyses of hyporheic exchange and hyporheic residence time distributions have predominantly investigated the impact of singular features and successions thereof (Bardini et al., 2013; Boano et al., 2007; Bottacin-Busolin & Marion, 2010; Cardenas et al., 2008; Cardenas & Wilson, 2006; Elliott & Brooks, 1997b; Herzog et al., 2019). Previous research has provided increased evidence of the co-existence of the integrated, and often

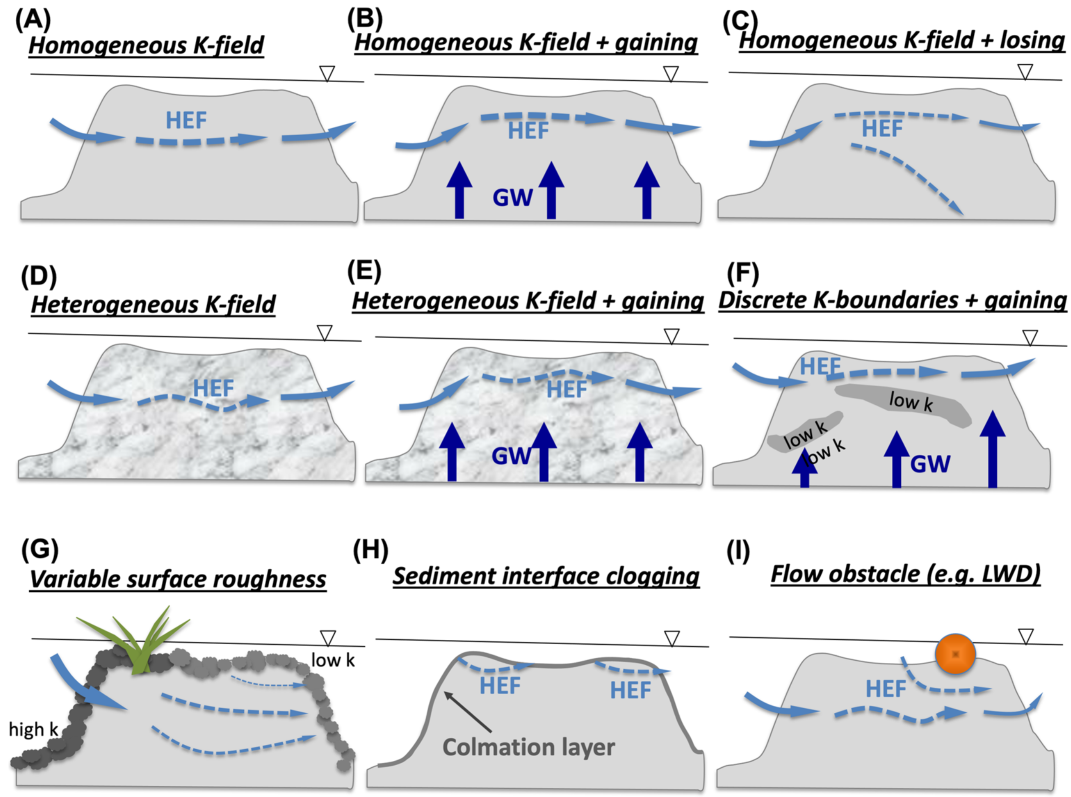

Figure 2. Drivers and controls of hyporheic exchange flow (HEF) through stream bedforms in different landscape contexts with predominantly surface hydrology driven HEF and homogeneous streambed sediments (a), interacting surface water and groundwater (GW) forcings on HEF and homogeneous streambed sediments under gaining (b) and losing (c) conditions, dominant surface water forcing in spatially heterogeneous sediments without (d) and with (e) GW upwelling, under consideration of highly heterogeneous sediment hydraulic conductivities with discrete sediment boundaries (f), under the influence of variable streambed surface roughness through sediment properties and vegetation (g) sediment clogging (h), and stream flow obstacles (i), such as large woody debris (LWD).

nested, impacts of different geomorphic structures on hyporheic exchange, such as the overlapping effects of ripples along pool-riffle structures nested in an inter-meander flow system (Azizian et al., 2017; Kasahara & Wondzell, 2003; Poole et al., 2008; Stonedahl et al., 2010, 2012). The complexity of overlapping geomorphic drivers and controls of hyporheic exchange (Figure 1) requires advanced observation that explicitly focuses on understanding and conceptualization of hierarchical, interacting geomorphological drivers, which are commonly analyzed separately. Such an integrated approach allows systematically exploration of the conditions under which either the impacts of small-scale processes are expressed at larger scales, or the conditions under which the effects of small-scale processes are overwhelmed by larger-scale drivers (Herzog et al., 2019; Krause et al., 2017; Stonedahl et al., 2010).

2.2. Potential Influence of Heterogeneous Substrate Hydraulic Conductivity on Hyporheic Exchange Flow

The nested influence of hydrostatic and hydrodynamic forcings of hyporheic exchange is modified by the spatial patterns and temporal dynamics of substrate hydraulic conductivity (Conant, 2004; Genereux et al., 2008; Hester et al., 2017, 2019; Stewardson et al., 2016). Controlled flume experiments (Fox et al., 2014; Salehin et al., 2004) and field studies (Genereux et al., 2008; Krause et al., 2013; Weatherill et al., 2014) confirm that even small-scale spatial variability of sediment hydraulic conductivity can have the potential to substantially impact hyporheic exchange and residence time distributions because of preferential flow through higher-conductivity pathways. Only a limited number of numerical modeling studies consider spatial heterogeneity in streambed properties, such as hydraulic conductivity (Bardini et al., 2013; Cardenas et al., 2004; Gomez-Velez et al., 2014; Irvine et al., 2012; Laube et al., 2018; Poole et al., 2006; Salehin et al., 2004; Sawyer & Cardenas, 2009; Figure 2d). With few exceptions (Bray & Dunne, 2017; Cardenas et al., 2004; Tonina et al., 2016), hydraulic conductivity in numerical modeling studies is conceptualized to be spatially homogeneous, despite abundant field evidence of the importance of river bed heterogeneity in physical properties, such as hydraulic conductivity, particularly in mid-stream or lowland sections of high order streams (Chen, 2004; Genereux et al., 2008; Krause, Blume, & Cassidy, 2012; Krause et al., 2013; Leek et al., 2009; Mendoza-Lera & Datry, 2017; Mendoza-Lera et al., 2019; Sebok et al., 2015; Stewardson et al., 2016; Wondzell, LaNier, Haggerty, Woodsmith, & Edwards, 2009). This common assumption highlights a possible bias in model parameterization toward conditions that have been more frequently observed in low-order headwater streams or in alluvial rivers with moderate to low hydraulic gradients and not constrained vertically or laterally.

Initial modeling studies aimed to quantify streambed heterogeneity impacts on hyporheic exchange, residence time distributions and biogeochemical cycling considered some limited spatial variability of streambed hydraulic conductivity with patterns often characterized by assumed correlation lengths (Bardini et al., 2013; Cardenas et al., 2004; Salehin et al., 2004; Sawyer & Cardenas, 2009). Such studies could be extended toward analysis of how this structural variability affects the interactions of groundwater upwelling and hyporheic exchange (Figure 2e). This variability has been observed and simulated independently, but not included together in integrated multi-scale models. With a few exceptions (Gomez-Velez et al., 2014; Laube et al., 2018; Y. Zhou et al., 2014a), previous conceptual modeling studies do not consider the effects of many-orders of magnitude differences in channel morphology and hydraulic conductivity found in situ (Chen, 2004; Conant, 2004; Fox et al., 2014; Genereux et al., 2008; Krause et al., 2013; Nowinski et al., 2011; Weatherill et al., 2014; Figure 2f). These limitations propagate to conclusions that have suggested only limited impacts of streambed structural heterogeneity on residence time distributions and biogeochemical cycling in the hyporheic zone (Bardini et al., 2013; Laube et al., 2018). In addition, it is crucial to determine how streambed sediment structures and hydraulic conductivity patterns are controlled by ecological drivers, such as interactions between aquatic vegetation and streambed sediments (Baranov et al., 2017; Jones et al., 2008, 2012; Ullah et al., 2014; Figure 2g) causing sediment clogging and by particle deposition and biofilm growth (Brunke, 1999; Nogaro et al., 2010; Rode et al., 2015; Figure 2h), bioengineers causing bioturbation (Baranov et al., 2016; Mendoza-Lera & Mutz, 2013) and the impact of flow obstacles, such as large woody debris (Gippel, 1995; Krause, Klaar, et al., 2014; Sawyer et al., 2012; Shelley et al., 2017; Figure 2i). These processes are critical to engineering streambeds for purposes, such as nutrient removal and river restoration, which involves using spatial heterogeneity to control fluxes and residence times to achieve desired outcomes (Herzog et al., 2018; Vaux, 1968; Ward et al., 2011).

2.3. Multi-Scale Interactions of Lateral and Vertical Drivers of Hyporheic Exchange in the River Corridor

Similar principles to those identified for in-channel controls on hyporheic exchange also apply to interactions between groundwater and surface water across multiple scales in river corridors (Figure 1; Boano, Demaria, Revelli, & Ridolfi, 2010; Revelli et al., 2008; Stonedahl et al., 2010). For instance, stream sinuosity is a dominant control of inter-meander subsurface flow (Figure 3a) in addition to stream flow velocity and sediment hydraulic conductivity (Boano, Camporeale, & Revelli, 2010; Boano et al., 2006; Pescimoro et al., 2019). Regional groundwater up-welling (Figure 3b) and down-welling (Figure 3c) interact with local channel morphology to control patterns of surface-groundwater exchange (Balbarini et al., 2017). Resulting inter-meander flow has been shown to control residence time distributions; and thus, redox zonation and nutrient turnover in sediments (Boano, Demaria, Revelli, & Ridolfi, 2010; Dwivedi et al., 2017). However to date from field studies, we rarely consider the vast spatial heterogeneity of hydraulic and hydrogeological properties of sediments between the river channel, the meanders, and floodplains (Figure 3d; Bersezio et al., 2007; Bridge et al., 1995; Dara et al., 2019), such as preferential flow through sub-surface paleo-channels (Lowell et al., 2009; Stanford & Ward, 1993; Słowik, 2014).

Hyporheic exchange is occurring across a range of scales being controlled by a variety of the processes discussed above (Boano et al., 2014; Harvey & Gooseff, 2015; Krause et al., 2014, 2017; Magliozzi et al., 2018; Poole et al., 2008; Stonedahl et al., 2010). However, increased efforts are required to integrate and compare the respective context specific importance of multi-scale interactions between groundwater and surface water. Recent model-based attempts to quantify the relative importance of bedform-driven versus meander-driven exchange between surface water and groundwater for nitrogen processing in river networks provide a promising path

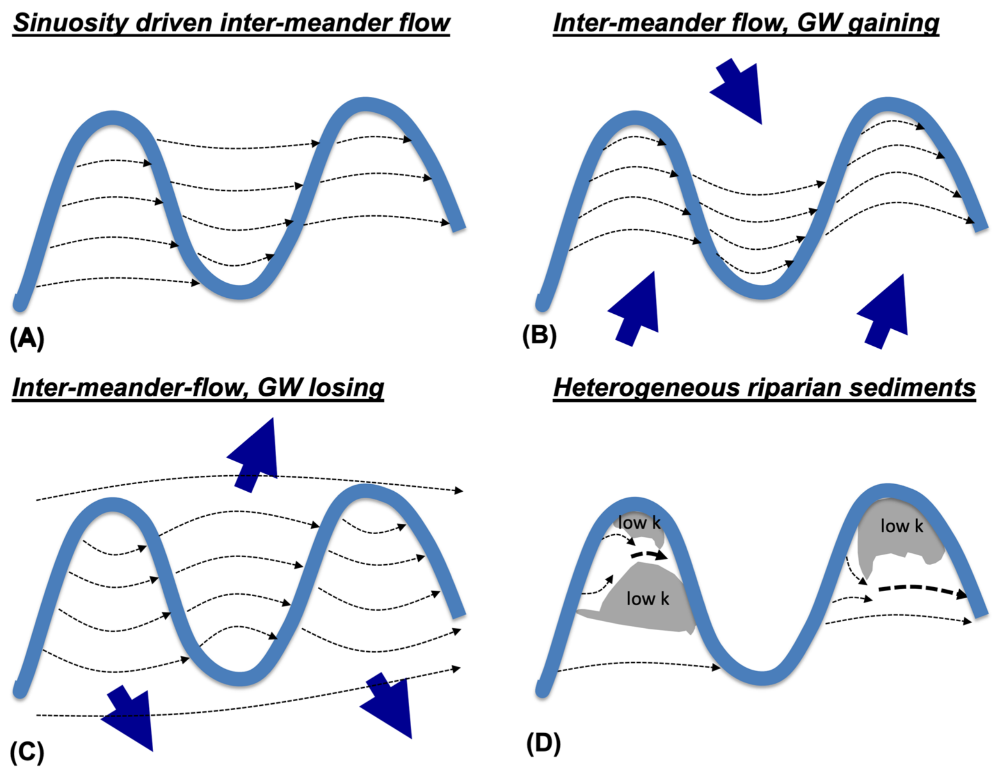

Figure 3. Inter-meander flow of surface water through alluvial sediment driven by stream flow velocity and sinuosity (a), under the influence of regional groundwater (GW) flow with gaining (b) and losing (c) conditions as well as spatial heterogeneity in riparian sediment conditions including paleo-channels as fast conduits and preferential flow paths and stagnation zones caused by spatially variable hydraulic conductivity patterns (d).

forward (Gomez-Velez et al., 2015). However, these results still require field validation and as yet, do not account for spatial heterogeneity in sediment hydraulic conductivity, biogeochemical properties, nor landscape context, known to control both small-scale hyporheic exchange and large-scale groundwater flow.

2.4. Dynamic Hydrological Forcing of Hyporheic Exchange Flow

Recent experimental and modeling based research has started to explore the impacts of transience (non-steady conditions) in hydrostatic and hydrodynamic forcing on hyporheic exchange and residence time distributions (Boano et al., 2007, 2013), with a particular focus on extreme flow conditions during freshets and flood scenarios (Malzone et al., 2016; Schmadel, Ward, Kurz, et al., 2016, Schmadel, Ward, Lowry, & Malzone, 2016; Singh et al., 2019; Trauth & Fleckenstein, 2017; Ward et al., 2018) and temporally variable groundwater flow (Trauth et al., 2014; Wu et al., 2018).

An increasing number of field observations and controlled laboratory experiments provide evidence of the ecological and biogeochemical implications of temporally dynamic hyporheic exchange and hyporheic residence time distributions. However, a systematic analysis of the influence of stream flow dynamics on hyporheic exchange and residence time distributions in different landscape contexts is long overdue (Datry & Larned, 2008; Dole-Olivier et al., 1997; Malcolm et al., 2009; Schmadel, Ward, Kurz, et al., 2016). Recent laboratory and numerical modeling studies have started to more systematically explore the variable importance of different drivers on the temporal dynamics of hyporheic exchange (Kaufman et al., 2017; Singh et al., 2019; Wu et al., 2018). Such studies still need to be extended to explore the impact of episodic high-flow events that mobilize sediments, yielding spatial and temporal erosion, and deposition dynamics and subsequent non-stationary patterns of bed morphology, sediment structure, and hydraulic conductivity as seen in field and flume experiments (Ahmerkamp et al., 2015; Kessler et al., 2015; Packman & Brooks, 2001). Despite small bedforms, such as ripples originating directly from sediment movement and changing in time, most flume studies, conceptual models, and modeling exercises simplify reality and assume stationary bedforms. Some flume studies are now considering bedform migration (Ahmerkamp et al., 2015; Kessler et al., 2015; Wolke et al., 2019) with far-reaching hydrological and biogeochemical implications. Systematic analyses of the wide spectrum of flow transience across different river types, combined with regional groundwater flow interactions, will reveal the degree to which short-term and long-term changes in stream flow alter hyporheic exchange, hyporheic residence time distributions, and related ecological and biogeochemical processes.

2.5. Spatio-Temporal Variability of Hydrological Opportunity and Biogeochemical Reactivity in the Hyporheic Zone

The magnitude and array of hyporheic biogeochemical processes, associated with transitions between aerobic and anaerobic respiration, are a function of the hydrological opportunity for metabolism, defined by the influx and residence time of reactants, nutrients, and metabolic substrates in local environments with specific reactivity. These processes are set by the concentrations of reactants and the frequency of their spatial coincidence (Battin et al., 2008; Marcé et al., 2018; Reeder, Quick, Farrell, Benner, Feris, Marzadri, & Tonina, 2018), microbial community dynamics (e.g., recruitment, growth, and activity) and the hyporheic biogeochemical reactivity (Krause et al., 2017; McClain et al., 2003). The supply and mixing of reactants (including buried autochthonous streambed organic matter), the residence time distributions, and the bulk average reaction rates, are controlled directly by hyporheic exchange, which transports solutes and fine particles from the surface water into and through the streambed sediments, and hence controls both distributions and rates of reactions within porewater.

Most current conceptual models of streambed biogeochemical cycling assume surface water solute concentrations and HEF-driven residence times in streambed sediments to be the primary (and often only) controls of biogeochemical reactions and rates in the hyporheic zone (Bardini et al., 2012; Boano et al., 2014; Hester & Doyle, 2008; Marzadri et al., 2012; Zarnetske et al., 2011a, 2012). In this context, the hyporheic zone is conceptualized as a single, homogeneous chemical reactor that receives reactants (e.g., dissolved organic carbon, nutrients, and dissolved oxygen) exclusively via hyporheic exchange from the surface water (Figure 4a). Biogeochemical reactions and rates are thus dependent on the turnover of solutes in the hyporheic zone (Bardini et al., 2013; Boano et al., 2014; Briggs et al., 2014; Trauth et al., 2014; Zarnetske et al., 2011a). With the exception of recent modeling work that allows for variation in reaction rates with sediment depth (Aubeneau et al., 2015; Caruso et al., 2017; Li et al., 2017) and heterogeneities in the physical pore network structure of hyporheic sediments (Briggs et al., 2015; Sawyer, 2015), biogeochemical reaction rates are typically considered independent from the location of the chemical reaction taking place in the hyporheic zone. Consequently, the efficiency of biogeochemical turnover in the hyporheic zone is often assumed to be limited by the availability of reactants transported by hyporheic exchange from the surface into the streambed (Aubeneau et al., 2015; Bardini et al., 2013; Li et al., 2017; Trauth et al., 2015; Zarnetske et al., 2011b). Such conditions, where types of reactions and rates are solely a function of surface water concentrations of reactants and their HEF-controlled hyporheic residence time, have been observed in the field. For example, carbon respiration in the hyporheic zone of oligotrophic headwater streams has been found to depend on surface water inputs and hyporheic travel time, with respiration shifting from aerobic to anaerobic conditions along hyporheic flow paths (Zarnetske et al., 2011b). As a result, denitrification is reliant on both, sufficient residence time to consume sufficient dissolved oxygen from the infiltrating surface water and bioavailable organic carbon remaining as an electron donor (Holmes et al., 1994; Jones & Holmes, 1996; Ocampo et al., 2006; Zarnetske et al., 2011b). Hyporheic zones support nutrient retention in river corridors, with hyporheic metabolism reducing concentrations of organic carbon, bioavailable inorganic nitrogen, and dissolved oxygen in the hyporheic water before it subsequently returns to the stream (Figure 4a; Gomez-Velez et al., 2015; Krause et al., 2014; Krause, Hannah, Fleckenstein, et al., 2011; Li et al., 2017; Pinay et al., 2009; Poole et al., 2008; Wondzell, 2011).

Such conceptualizations of spatially homogeneous hyporheic reactivity are certainly useful to simplify estimates of solute turnover in hyporheic zone as the ratio of residence time and biogeochemical reaction time, expressed by the dimensionless Damköhler number (Marzadri et al., 2012; Zarnetske et al., 2011a). This approach represents a potentially powerful methodology for spatial upscaling (Pinay et al., 2015; Reeder, Quick, Farrell, Benner, Feris, Marzadri, & Tonina, 2018; Reeder, Quick, Farrell, Benner, Feris, & Tonina, 2018). However, if the goal is to nest biogeochemical function of hyporheic zones at landscape scales, the Damköhler number approach has further potential to be enhanced in its ability to upscale hyporheic biogeochemical function to river network scales

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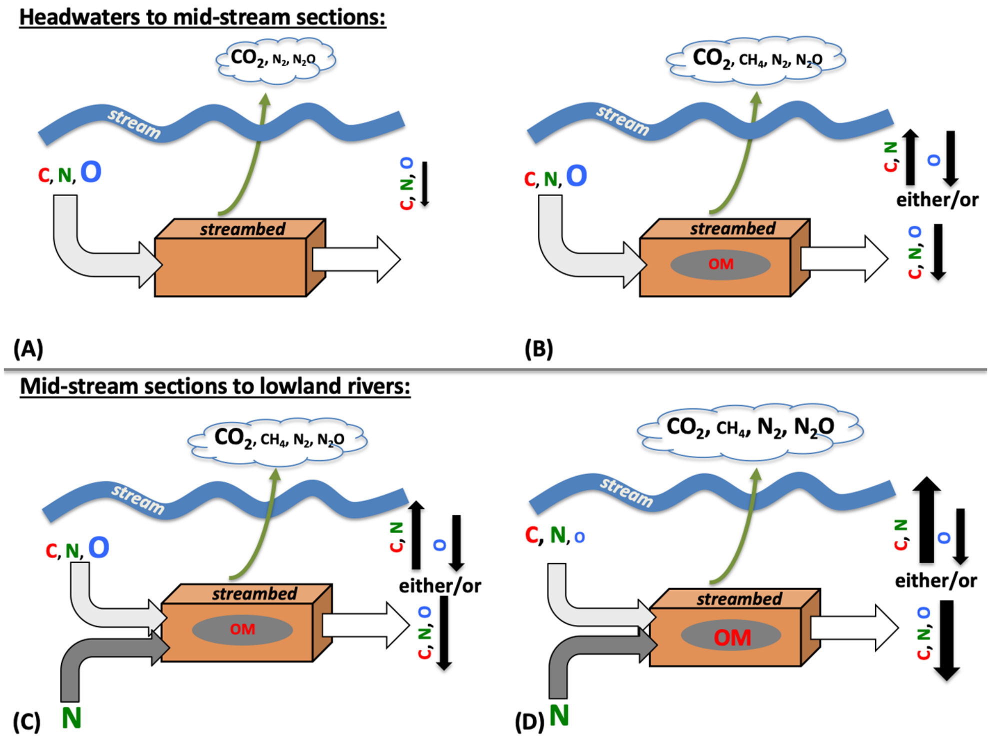

Figure 4. Conceptual models of the hyporheic zone as a biogeochemical reactor: Variability in the mixing of different reactive solute sources [carbon (C) and nitrogen (N) fractions, and free oxygen (O)], impacts on stream(bed) metabolism and down-stream effects of hyporheic processing, for single water source (surface water) dominated systems (a + b) and systems with reactive solute contributions from multiple water sources mixing in the hyporheic zone (c + d), with (b), (c), and (d) and without (a) relevance of autochthonous streambed organic matter (OM). Clouds representing gaseous losses of metabolites and symbol sizes indicating relative proportions of their concentrations with arrow sizes and directions indicating minor or major increases or reductions in downstream concentrations.

(Marzadri et al., 2017, 2021). It currently does not capture the full range of coupling between biogeochemical processes and hyporheic exchange, abiotic and biotic heterogeneities or the scale-dependency resulting from decreasing HEF rates and concentrations of exchanged solutes with depth in the hyporheic zone.

Water residence time may be the main control of hyporheic biogeochemical cycling for many oligotrophic and relatively homogeneous, low-order headwater streams with limited variability in sediment texture (e.g., Pinay et al., 2009; Zarnetske et al., 2011a, 2011b). However, this concept is frequently contradicted by field observations in other small streams (Drummond et al., 2016; Marcé et al., 2018) as well as in more complex lowland rivers, particularly in agricultural areas with enriched nutrient conditions (Abbott, Moatar, et al., 2018; Frei et al., 2020; Krause et al., 2009, 2013; Sawyer, 2015). The assumption of an otherwise "empty" and inert, homogeneous streambed reactor charged by hyporheic exchange driven solute inputs from surface water (Bardini et al., 2012; Boano et al., 2014; Trauth et al., 2014, 2015; Zarnetske et al., 2011a) is not applicable when streambed sediments also contain autochthonous reactants, as both the dissolved form and particulate organic matter (Figures 4b and 4c). In this case, the encountered diversity of turnover rates and reaction types cannot be solely explained by hyporheic exchange controls of reaction times and surface water solute inputs, as these processes are strongly influenced by the concentrations of bioavailable dissolved organic matter and mineralization rates of particulate organic matter in the sediment (Corson-Rikert et al., 2016; Krause et al., 2009, 2013; Reeder, Quick, Farrell, Benner, Feris, Marzadri, & Tonina, 2018; Reeder, Quick, Farrell, Benner, Feris, & Tonina, 2018; Trimmer et al., 2012). Dissolved and particulate organic matter concentrations have significant spatial variability within the sediment (Datry et al., 2017; Drummond et al., 2017, 2018; Krause et al., 2009, 2013; Shelley et al., 2017). The spatial patterns of organic matter distributions in the streambed often coincide with the spatial organization of physical sediment properties that result from the fluvial depositional history of the river (Drummond et al., 2017, 2018; Larsen et al., 2015; Larsen & Harvey, 2017). High organic matter content is generally associated with low hydraulic conductivity strata of organic sediments, while highly permeable mineral sediments are often characterized by low organic matter content (Pinay et al., 1995, 2000). The relationship between physical and biogeochemical sediment controls provide additional and perhaps underutilized predictive capacity to explain observed heterogeneity in hyporheic zone biogeochemical reactivity, as a function of interacting sediment conductivity, residence time, and reactivity patterns. Concordantly, field studies using hydrometabolic tracers have indicated that the entire hyporheic zone is not metabolically active contributing to ecosystem respiration and biogeochemical cycling (Argerich et al., 2011), though the locations and timescales associated with transformation are only beginning to be understood (Ward, Wondzell, et al., 2019). This finding has been corroborated by particle-tracking and pore-network models showing that hyporheic zone biogeochemical turnover can be largely driven by the residence time of water in hyporheic bioactive layers or redox microzones (Briggs et al., 2015; Li et al., 2021).

As a consequence of the heterogenous distributions of residence times (and related hydrological opportunities) and sediment biogeochemical reactivities, reactions of the interlinked carbon and nitrogen cycle are often more complex. For example, contrasting concentrations of dissolved oxygen have resulted in comparable rates of microbial carbon processing due to compensation by the composition of the microbial community (Risse-Buhl et al., 2017). Previous conceptualizations of residence time control of biogeochemical turnover in hyporheic zones also widely ignore other nitrogen transformation processes evidenced in the field, such as dissimilatory nitrate reduction to ammonium (DNRA) and anaerobic oxidation of ammonium (Anammox; Lansdown et al., 2015, 2016; Trimmer et al., 2012, 2015; S. Zhou et al., 2014). Depending on the relative importance of the contribution from buried streambed autochthonous organic matter to hyporheic biogeochemical cycling, hyporheic exchange might result in either a reduction or an increase of in-stream loading of carbon and nitrogen (Figure 4b). Furthermore, hyporheic exchange could decrease in-stream carbon and nitrogen loading due to transport toward the aquifer in the case of losing conditions (Figure 4c).

In many cases, up-welling groundwater may contribute reactive solutes to the streambed (Figure 4d), which is particularly relevant for legacy pollutants, such as nitrate contamination in groundwater, which in many lowland agricultural catchments represent the main nitrogen source (Basu et al., 2010; Bochet et al., 2020; Frei et al., 2020; Withers et al., 2014) and industrial contaminants, such as chlorinated solvents in urban areas (Rivett et al., 2012; Weatherill et al., 2018). The concurrence of spatially variable up-welling of solutes from groundwater and temporally dynamic down-welling of surface water pollutants has frequently been observed to create complex patterns of reactions in the hyporheic zone (Liu et al., 2019; Shelley et al., 2017; Weatherill et al., 2014) that go far beyond the current concepts of hyporheic exchange and residence time controls on streambed biogeochemical cycling. In fact, the observed impacts of groundwater solute contributions and autochthonous sediment organic matter have been shown to produce a hot spot of biogeochemical transformation in the hyporheic zone (Krause et al., 2009, 2013), which does not match current conceptualizations. In particular, the net-effect of hyporheic zone biogeochemical cycling on nitrate removal might be underestimated given that model-based quantifications do not consider the interactions of multiple solute pathways into the streambed sediments which may already contain standing stocks of bioavailable organic matter.

To capture these effects, process conceptualizations currently used in numerical models should be extended to improve identification and representation of the dominant process dynamics across multiple scales, considering solute mixing from different sources, including buried autochthonous streambed organic matter (Figures 4b–4d). This approach will require a dialog to incorporate the frequently observed behaviours that have been identified as being relevant in the field into existing numerical models in parsimonious approaches where parameters remain tractable and identifiable within acceptable confidence bounds. Many of the existing models should have the capability to account for these additional processes if parameterized adequately. However, new numerical frameworks are also needed to better capture multiscale interactions, process interactions, and feedbacks that change system conditions.

2.6. The Missing Link? Ecological Controls on Hyporheic Exchange Flow and Biogeochemical Cycling

Previous interdisciplinary research has mainly focused on the analysis and quantification of hyporheic exchange and biogeochemical cycling impacts on aquatic ecosystem functioning (Figure 5) (Boulton et al., 1998, 2010; Boulton & Hancock, 2006; Hancock et al., 2005). This research highlights that hyporheic exchange and streambed biogeochemical processes create a unique ecological niche (Brunke & Gonser, 1997; Stanford & Ward, 1993; Stubbington et al., 2009) that potentially acts as a refuge during extreme conditions (Folegot, Krause, et al., 2018)

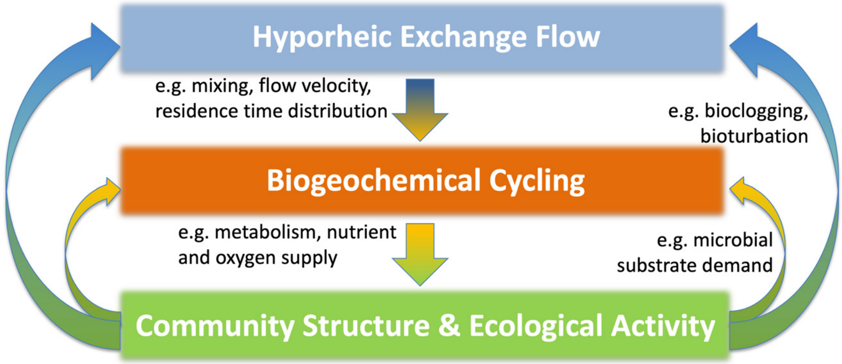

Figure 5. Multi-directional interactions between physical controls of hyporheic exchange flow, streambed biogeochemical cycling, and biological community structure and ecological (metabolic) functioning (red arrows), including ecological feedbacks on streambed biogeochemistry biogeochemistry [e.g., microbial demand for substrate shifting porewater from oxic to anoxic (aerobic to anaerobic metabolic pathways)] as well as hyporheic exchange (e.g., bioturbation, bioclogging, and ecosystem engineering).

enhancing biodiversity and ecosystem resilience to environmental change (Kurz et al., 2017). However, our understanding of the impacts in the reverse direction, where ecological processes can influence hyporheic exchange and biogeochemical cycling is in its infancy (Figure 5; Buxton et al., 2015). Initial work on the functioning of microbial biofilms established how dynamic growth of benthic and hyporheic biofilms affects turbulent flow in the stream channel and consequently modifies turbulence-driven hyporheic exchange (Nikora, 2010; Roche et al., 2017). Biofilms also cause bio-clogging of streambed sediments (Caruso et al., 2017; Newcomer et al., 2016; Chowdhury et al., 2020; Figure 2h), where complex biofilm communities on the streambed surface and within sediment pores reduce the effective porosity of the streambed substrate and subsequently hyporheic exchange (Battin & Sengschmitt, 1999; Mendoza-Lera & Mutz, 2013; Newcomer et al., 2016; Roche et al., 2017; Figure 2h). At larger scales, the dynamic growth of submerged macrophytes has been shown to strongly modify turbulent flow patterns in the channel and enhance the trapping of fine sediment (Drummond et al., 2014; Liu et al., 2018; Liu & Nepf, 2016; Sand-jensen, 1998; Figure 2g), directly impacting hyporheic exchange and hyporheic biogeochemical processes (Salehin et al., 2003; Ullah et al., 2014). The presence of macrophytes alters flow paths and residence time distributions, providing additional substrate and input of organic carbon as well as enhancing nutrient uptake during the growth phase (Baranov et al., 2017; Nikolakopoulou et al., 2018; Ribot et al., 2019).

In addition to these microbial- and plant-induced influences on the hyporheic hydrology and biogeochemistry, there is increasing evidence that some invertebrate bioturbator species and ecosystem engineers modify hyporheic hydrological and biogeochemical conditions. These ecosystem engineers alter the conditions of their habitat to augment their ecological needs, with direct and indirect influences on the dynamics of both hyporheic exchange and hyporheic biogeochemical process (Hölker et al., 2015). For example, burrowing chironomid larvae pump significant amounts of surface water through their U-shaped sediment burrows, directly affecting hyporheic exchange by actively transporting greater volumes of water and solute mass to deeper sediments. This process influences sediment metabolism and biogeochemical cycles (Mermillod-Blondin, 2011; Mermillod-Blondin et al., 2004; Nogaro et al., 2009) with potentially significant impacts on greenhouse gas production and sequestration (Baranov et al., 2016). These findings highlight the urgent need to extend analyses toward frequently observed behavior of other species, such as the burrowing of crayfish in streambeds during hydrological extremes or the active movement of *Gammarus pulex* (freshwater shrimp) and other hyporheic invertebrates triggered by thermal and hydrological stress (DiStefano et al., 2009; Statzner et al., 2000; Vander Vorste et al., 2016, 2017). The activities of these invertebrates are likely to alter sediment structure and thus, hydraulic conductivity and hyporheic exchange. Many vertebrates, such as fish or freshwater mammals (Janzen & Westbrook, 2011; Shurin et al., 2020) also directly affect hyporheic exchange and streambed biogeochemical conditions. For instance, when fish select gravel spawning habitat with their preferred hyporheic exchange and biogeochemical conditions, these conditions may be affected also by their spawning activities (Baxter & Hauer, 2000; Buxton et al., 2015; Harrison et al., 2019; Malcolm et al., 2004, 2009; Moir & Pasternack, 2010; Tonina & Buffington, 2009). In Columbia, one of the world's largest mammals, the non-native hippopotamus (*Hippopotamus amphibious*), acts as an ecosystem engineer affecting hyporheic exchange and impacting hydrological habitats (Shurin et al., 2020). This activity is considered valuable to fill an important ecosystem function as megaherbivores amphibious ecosystem engineers became extinct in South America at the end of the Pleistocene (MacPhee & Schouten, 2019).

Given the observed ecological impacts on hyporheic exchange and biogeochemical processes in the hyporheic zone (Figure 5), future research requires in-depth attempts to integrate the advancing knowledge of ecological controls into conceptual and quantitative models of hyporheic hydrological and biogeochemical process dynamics (Hannah et al., 2007; Krause et al., 2017; Krause, Hannah, Fleckenstein, et al., 2011). We are only beginning to understand the magnitude of ecological controls and their impact on non-stationarity and temporal dynamics of hyporheic processes, caused, for instance, by time-variable biological processes. Hence, a fully coupled approach is required that considers ecosystem process response to changes of both hydrological and biogeochemical habitat conditions, as well as the impact of biological activity on physical and chemical properties of the hyporheic zone (Figure 5).

3. A Landscape Perspective of Organizational Principles of Hyporheic Exchange Fluxes and Biogeochemical Cycling Along the Catchment Continuum

Our synthesis of field observations and modeling studies highlights complex interactions among a broad diversity of drivers and controls of hyporheic exchange, biogeochemical cycling, and biological activity. This synthesis furthermore provides evidence that hyporheic exchange, hyporheic biogeochemical cycling, and hyporheic ecosystems are highly organized and spatially structured in fluvial landscapes. Understanding the underlying organizational principles of these systems is key for enabling transferability and generalization of knowledge to predict the landscape-wide significance of hyporheic exchange and hyporheic biogeochemical cycling on water balance, nutrient dynamics, reactive contaminant transport, and ecosystem functioning at catchment scale.

The majority of experimental or modeling studies to date have focused on individual stream reaches and then scaled up observations, with only a few experimental studies attempting to quantify hyporheic exchange along a river continuum using a river network approach (Gootman et al., 2020; Lee-Cullin et al., 2018; Ward, Kurz, et al., 2019; Wondzell, 2011). Here, we build on previous conceptual models of landscape organizational principles (Boulton et al., 1998; Boulton & Hancock, 2006; Buffington & Tonina, 2009; Frissell et al., 1986; Helton et al., 2011; Malard et al., 2002) to synthesize and conceptualize the spatial and temporal organization of different drivers and controls of hyporheic exchange and hyporheic biogeochemical cycling along a river network continuum from first order headwaters to lowland streams (Figure 6a). We propose advances to existing landscape scale conceptualizations of hyporheic exchange that account not only for interactions among different drivers and controls of hyporheic flow, biogeochemical cycling, and ecology, but also their spatially nested co-existence (Figure 1).

Integrating the drivers of hyporheic exchange and hyporheic biogeochemical cycling into a catchment context requires using landscape organizational principles developed in hydrology, geomorphology, and ecology to explain hyporheic exchange patterns (Boano et al., 2014; Magliozzi et al., 2018, 2019). For example, basic principles of sediment transport and storage along river networks indicate a general down-stream reduction in channel slope, lateral channel confinement, sediment grain size, and channel roughness coupled with an increase in streambed organic matter from headwater to lowland streams (Figure 6). This longitudinal change in the characteristics of the streambed sediments results in a downstream shift in hyporheic exchange and often coincides with an increase in groundwater contributions (Figure 3). Decreasing hydraulic gradients cause a downstream reduction in driving forces for vertical hyporheic exchange, coinciding with deeper fluvial and alluvial deposits, leading to longer and deeper hyporheic flow paths and slower hyporheic flow velocities in finer grained sediments with lower permeability, which results in increased hyporheic residence times (Figure 6a). At the same time, river meandering in low-gradient mid-stream sections results in enhanced river corridor connectivity, longer lateral HEF path, and increased hyporheic and riparian residence times and flow permanence (Figure 6b). Depending on the dominant geomorphodynamic processes, these changes and flow path transitions can be highly nonlinear, yielding sharp thresholds at regions of known geomorphic transitions, such as between mountain ranges, foothills, valleys, and lowlands (Marzadri et al., 2017; Wondzell, 2011). Abrupt changes in multiple factors, such as the transition from steep coarse-bedded and constrained mountain rivers into finer-grained and less-constrained

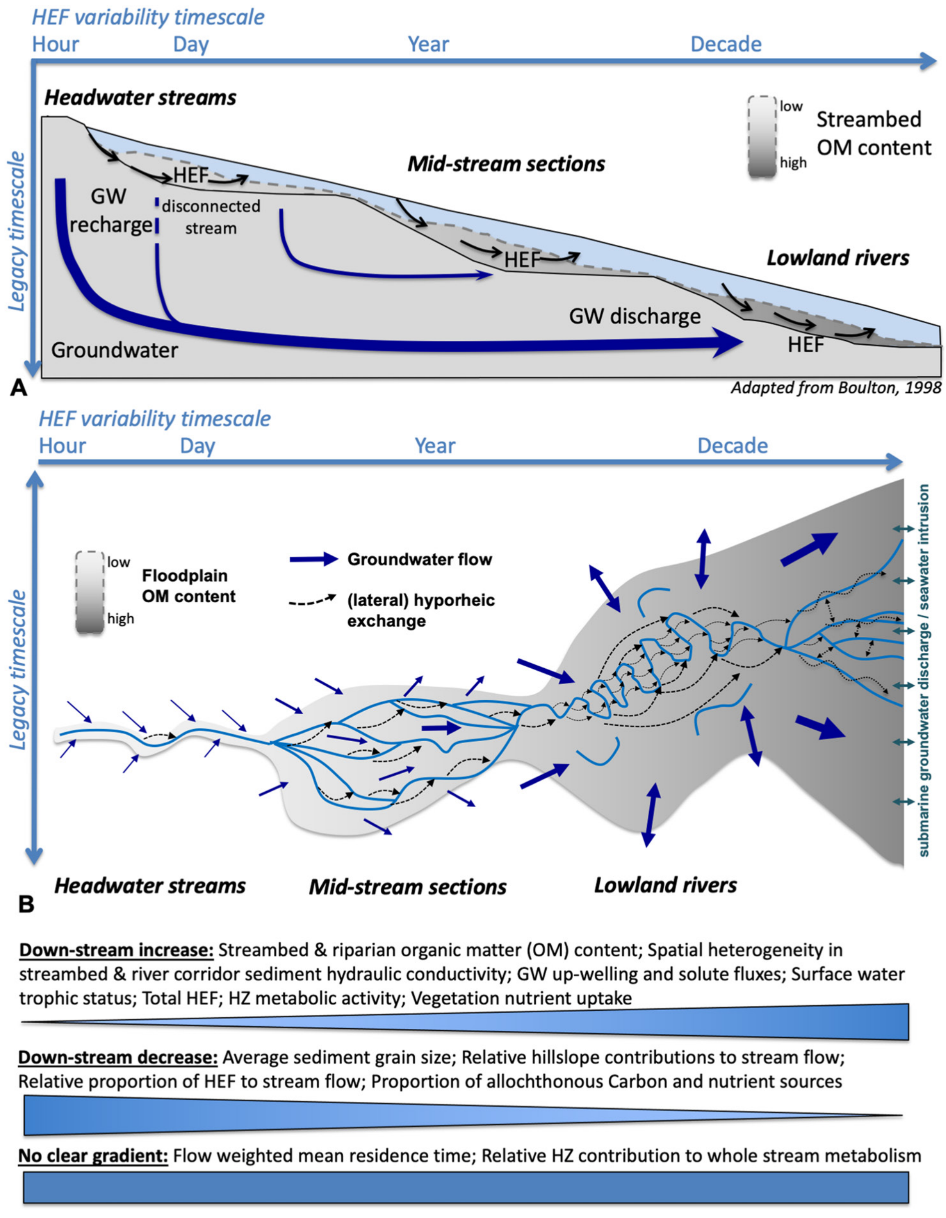

Figure 6. Landscape scale organizational principles of vertical hyporheic exchange flow (HEF) from headwater streams to lowland rivers (a—vertical profile) and of lateral inter-meander and parafluvial flow (b—plane view) as a function of surface hydrological drivers and multi-scale groundwater flow controls, and distribution of physical and chemical sediment properties, such as spatial variability in sediment hydraulic conductivity, hyporheic residence time (RT), or streambed organic matter (OM) content as drivers of biogeochemical processing (*visualization of downstream tendencies are indicating general trends only and do not imply linear changes*).

lowland rivers is expected to yield sharp transitions in hyporheic exchange (Figures 6a and 6b), but these patterns have not been systematically investigated for a range of fluvial system conditions.

The wider application of fluvial sedimentology principles (Dara et al., 2019) and understanding of alluvial depositional history (Słowik, 2014) provides further and perhaps underutilized predictive capacity for the spatial distributions of sediment properties in river valleys and their impact on hydrologic connectivity between streams and groundwaters, including, hyporheic exchange, residence time distributions, and biogeochemical reactivity in river channel and riparian sediments (Figure 6b). The potential for combining model-based information of fluvial sediment transport to predict river valley and streambed sediment stratigraphy as controls of hyporheic exchange and hyporheic biogeochemical processes is currently untapped, leaving a great underutilized potential for achieving step changes in understanding of hyporheic zone processes across large catchments.

This landscape perspective emphasizes that local hyporheic exchange dynamics are strongly modulated by larger-scale patterns of topography, biogeography, and groundwater circulation (Figure 6). In this context, hyporheic interactions can be considered a local, near-surface manifestation of larger spatial scale and longer temporal scale surface-groundwater circulation patterns. Similarly, landscape patterns of terrestrial ecosystems, primary production, and organic matter inputs both drive and condition hyporheic microbial activity and biogeochemistry. Looking forward, the accumulated advances in knowledge of surface-groundwater systems outlined above, together with new capability in sensing, simulation, and data science, provide the potential to unify understanding of local drivers of ecological processes and their interactions with larger aquatic and terrestrial ecosystems.

The intensity and distribution of groundwater upwelling and the associated delivery of legacy pollutants, such as nitrate or chlorinated solvents, into hyporheic zones are likely to increase from headwaters (often with less agriculture and urbanization) to more intensively managed and impacted downstream lowland ecosystems (Figure 6). Similarly, the flow permanence of river channels increases in downstream direction, with many headwater streams being prone to drying and flow cessation (Benstead & Leigh, 2012; Boulton et al., 2017) and largely unknown impacts of dry phases on hyporheic zone functioning (Boulton et al., 2017; Datry et al., 2017; Datry & Larned, 2008). An overall downstream increase is assumed in the complexity of interactions of different hydrodynamic, sedimentological, and biogeochemical drivers, including distributions of sediment structure and properties, groundwater upwelling, and solute contributions as well as patterns of autochthonous organic matter content in streambed sediments. On the other hand, spatial variability in stream chemistry, including pollutants, typically decreases moving downstream in river networks, suggesting a homogenization arising from averaging of different signals and attenuation of discrete sources (Abbott, Gruau, et al., 2018; Creed et al., 2015; Dupas et al., 2019).

We advocate for hyporheic research to embrace a wider landscape perspective when interpreting local observations, and to avoid applying principles derived predominantly from small headwater streams throughout the river network continuum. Furthermore, the current fragmentary approaches can lead to inaccuracies in system-level understanding and management of the hyporheic zone at catchment scale. Therefore, studies considering a greater diversity in the ecological conditions of hyporheic zone are needed. Arid and semi-arid systems have fundamentally different hydrology and biogeochemistry (Fisher et al., 1998; Harms & Grimm, 2008). Still, many of the conceptualizations considered in this article predominantly reflect patterns under hydrologically gaining conditions with net groundwater to surface water flux, typical of temperate regions.

Acknowledging interactions between different drivers and controls of hyporheic exchange and hyporheic biogeochemical cycling in a landscape context provides a pathway toward more accurate representations of governing processes in conceptual hyporheic zone models. This does not necessarily need to lead to an increase in complexity for site specific models but supports the development of parsimonious approaches where the selection of representative processes is justified by understanding the most important hyporheic exchange controls at each location in a wider landscape context. We emphasize here that the general patterns illustrated in Figure 6 represent an overall expectation based on current understanding of watershed structure, both geophysical and ecological. Hyporheic hydrology and biogeochemistry at any site in the landscape can vary substantially from the general expectation, necessitating careful consideration of both local- and landscape-scale drivers. New observational approaches are needed that are capable of capturing a wider range of environmental conditions in hyporheic zones across river networks (Krause, Hannah, Fleckenstein, et al., 2011; Lee-Cullin et al., 2018; Ward & Packman, 2019). To ensure the contribution of hyporheic zone research to efficiently manage the interface between aquifers and rivers (Krause et al., 2014, 2017; Lewandowski et al., 2019), future research will need to test how those landscape principles either hold or need to be adapted across catchments, including heavily anthropogenically modified and polluted urban streams that are currently underrepresented in hyporheic investigations (Lawrence et al., 2013; Schaper et al., 2018, 2019).

The proposed advancements of process conceptualizations across scales also highlight the need for intensifying efforts to improve mechanistic process understanding through interdisciplinary research and knowledge exchange in emerging areas of hyporheic research. This includes providing evidence of the biological, physical, and biogeochemical process interactions (i.e., how the physical environment controls habitat functioning), and also of how biological behavior is a feedback to hyporheic physical and biogeochemical conditions. Therefore, it will be critical to establish landscape organizational principles of the abundance and activity of hyporheic and benthic fauna, including bioturbators, along the river continuum and as a consequence of changes in the type of sediments and accumulation of organic matter in streambeds.

To improve promising recent attempts into predictions of larger scale implications of hyporheic exchange and hyporheic biogeochemical processing, as well as to quantify the resilience of hyporheic functioning to global environmental change, future research also needs to specifically address the flow-dependent mobility of streambed sediments, and its impact on hyporheic zone processes and ecological functioning. With climate change projections suggesting that many rivers are likely to experience an increase in extreme hydrological events, it will be important to advance the understanding of hyporheic processes in particular under conditions of increased flow intermittence and sediment mobilizing flow events. The key for success in both hyporheic science and river ecosystem management lies in understanding the interactions of physical, biogeochemical, and ecological processes and how they vary across scales, as well as integrating knowledge between (field and lab) experimental and modeling approaches. We hope that the framework we propose here will stimulate discussions and open opportunities for further integrating existing and new process knowledge across scales within the landscape context.

Data Availability Statement

Data were not used nor created for this research.

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