Ecohydrological interfaces as hot spots of ecosystem processes

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Abstract The movement of water, matter, organisms, and energy can be altered substantially at ecohydrological interfaces, the dynamic transition zones that often develop within ecotones or boundaries between adjacent ecosystems. Interdisciplinary research over the last two decades has indicated that ecohydrological interfaces are often "hot spots" of ecological, biogeochemical, and hydrological processes and may provide refuge for biota during extreme events. Ecohydrological interfaces can have significant impact on global hydrological and biogeochemical cycles, biodiversity, pollutant removal, and ecosystem resilience to disturbance. The organizational principles (i.e., the drivers and controls) of spatially and temporally variable processes at ecohydrological interfaces are poorly understood and require the integrated analysis of hydrological, biogeochemical, and ecological processes. Our rudimentary understanding of the interactions between different drivers and controls critically limits our ability to predict complex system responses to change. In this paper, we explore similarities and contrasts in the functioning of diverse freshwater ecohydrological interfaces across spatial and temporal scales. We use this comparison to develop an integrated, interdisciplinary framework, including a roadmap for analyzing ecohydrological processes and their interactions in ecosystems. We argue that, in order to fully account for their nonlinear process dynamics, ecohydrological interfaces need to be conceptualized as unique, spatially and temporally dynamic entities, which represents a step change from their current representation as boundary conditions at investigated ecosystems.

Plain Language Summary The movement of water, matter, organisms, and energy can be altered substantially at ecohydrological interfaces that we introduce here as a new concept to support the quantitative analysis of nonlinear system behavior stimulated by the complex and multifacetted interactions of hydrological, biogeochemical, and ecological processes across system boundaries. Ecohydrological interfaces are defined here as the dynamic transition zones that may develop at ecosystem (or subsystem) boundaries and control the movement and transformation of organisms, water, matter, and energy between adjacent systems. In this paper, we explore similarities and contrasts in the functioning of diverse freshwater ecohydrological interfaces across spatial and temporal scales. We use this comparison to develop an integrated, interdisciplinary framework, including a roadmap for analyzing ecohydrological processes and their interactions in ecosystems. We argue that, in order to fully account for their nonlinear process dynamics, ecohydrological interfaces need to be conceptualized as unique, spatially and temporally dynamic entities, which represents a step change from their current representation as boundary conditions at investigated ecosystems.

1. Introduction

The study of system boundaries has been a mainstay in ecological and hydrological research [*Cadenasso et al.*, 2003; *Strayer et al.*, 2003; *Yarrow and Marin*, 2007]. Interdisciplinary research has highlighted the importance of ecosystem boundaries, many of which are "hot spots" of ecological, biogeochemical, or hydrological processes [*McClain et al.*, 2003; *Caraco et al.*, 2006; *Pinay et al.*, 2015; *Peipoch et al.*, 2016].

We introduce *ecohydrological interfaces* as a new concept to support the quantitative analysis of nonlinear system behavior stimulated by the complex and multifacetted interactions of hydrological, biogeochemical, and ecological processes across system boundaries. Ecohydrological interfaces are defined here as the dynamic transition zones that may develop at ecosystem (or subsystem) boundaries and control the movement and transformation of organisms, water, matter, and energy between adjacent systems (referred to by *Hedin et al.* [1998] as "control points"). In contrast to stationary *boundaries* (separators of different ecosystems or subsystems) or *ecotones* (boundaries that have a defined thickness and share characteristics with each of the systems they separate), ecohydrological interfaces are nonstationary, emerging for a limited time and then disappearing, expanding and contracting, or moving around within a boundary or ecotone. Different than boundaries and ecotones, which are delineated primarily based on system properties [*Cadenasso et al.*, 2003; *Strayer et al.*, 2003; *Yarrow and Marin*, 2007], ecohydrological interfaces are defined by their specific functioning (for example, the dynamic extent of surface water mixing in streambed environments forming hyporheic zones as ecohydrological interfaces with distinct redox environments and ecological niche functions and behavior).

Ecohydrological interfaces are manifold, including (1) soil-atmosphere interfaces, (2) capillary fringes as interfaces between phreatic and vadose zones, (3) interfaces between terrestrial upland and lowland aquatic ecosystems, (4) groundwater-surface water interfaces, including those associated with riparian or hyporheic zones, biofilms, and surface water-benthic zone interfaces (Figure 1). Ecohydrological interfaces provide key ecosystem functions and services [*Belnap et al.*, 2003], including water purification, thermal regulation, and maintenance of biodiversity [*Perelo*, 2010; *Krause et al.*, 2011a; *Freitas et al.*, 2015]. They increase ecological resilience by providing refuge for organisms during extreme events or source areas for recolonization after disturbances [*Clinton et al.*, 1996, *Kumar et al.*, 2011; *Crump et al.*, 2012; *Stubbington*, 2012].

In this paper, we aim to uncover the organizational principles—the main drivers and controls, and their interactions and feedbacks—that determine the development and capacity of ecohydrological interfaces to transform the flow of energy, water, and matter between adjacent ecosystems. We therefore do the following:

1. Compare the characteristics of transformation processes at different ecohydrological interfaces in freshwater ecosystems, including groundwater-surface water, groundwater-vadose zone, and benthic-pelagic interfaces (section 2).
2. Determine common or unique features of nonlinear process dynamics in ecohydrological interfaces and outline critical gaps in the understanding of their functioning (section 3).
3. Based on a comparison of the organizational principles of different ecohydrological interfaces, we propose a roadmap for the development of multiscale conceptual models of ecohydrological interface processes and their interactions that can be expanded to other types of ecohydrological interfaces not covered here (section 4).

2. Transformation of Energy, Water, and Matter Fluxes Across Ecohydrological Interfaces

Ecohydrological interfaces developing in aquatic ecosystems (e.g., between groundwater and surface water or groundwater and the vadose zone) extend from the microscale (e.g., interfaces at microbial biofilms) to kilometer scale (e.g., aquifer-river interfaces). Despite their varied dimensions, these interfaces share common properties: (1) abrupt changes in aggregate state (e.g., solid, liquid, or gas phase) and (2) steep gradients in physical and biogeochemical conditions [*Naiman et al.*, 1988; *Naiman and Decamps*, 1997]. The steep physical, chemical, and biological gradients in ecohydrological interfaces often correspond to distinct types and enhanced rates of biogeochemical processes [*Yarrow and Marin*, 2007; *McClain et al.*, 2003] and have significant impacts on ecosystem responses and resilience to environmental change [*Brunke and*
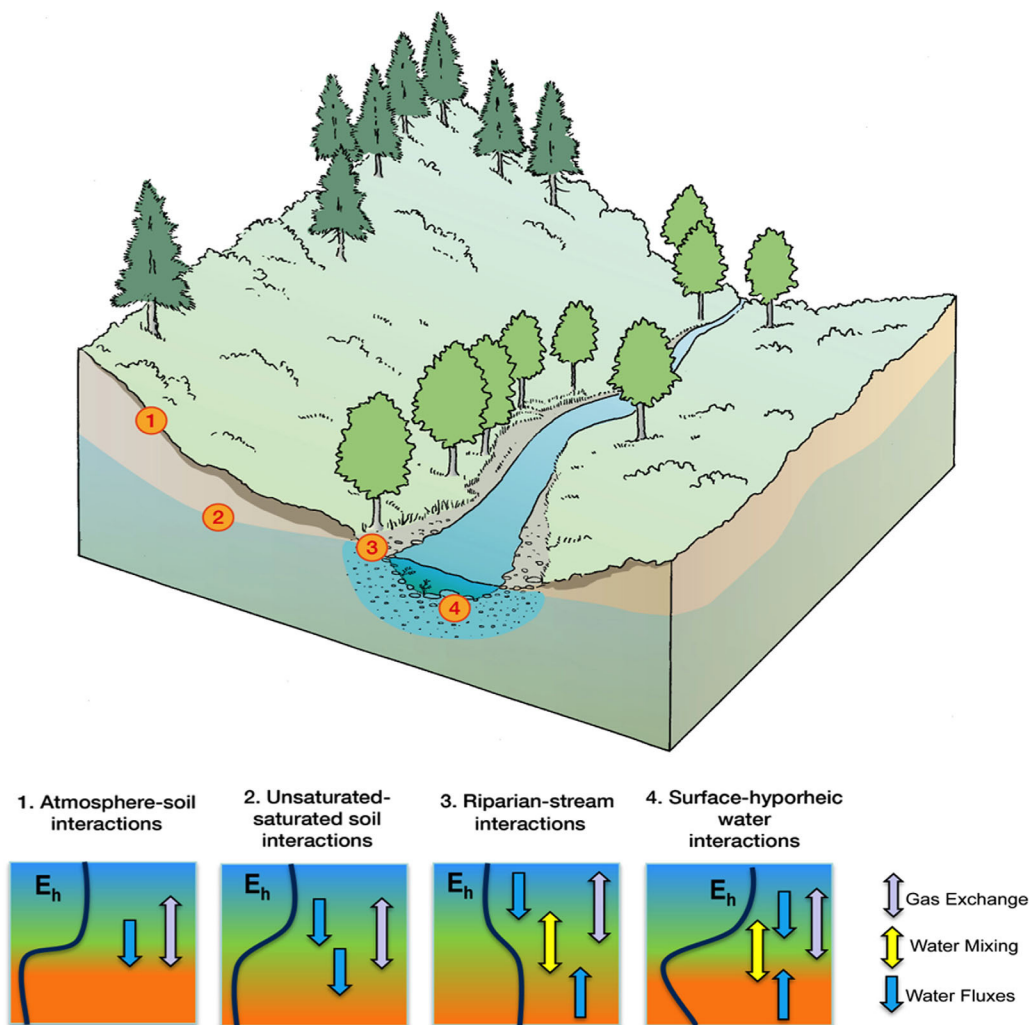
Figure 1. Landscape perspective of different types of ecohydrological interfaces with (1) atmosphere-soil interfaces, (2) unsaturated-saturated soil interfaces, (3) riparian-stream interfaces, and (4) hyporheic zone interfaces and characteristic profiles of water fluxes, mixing, gas exchange, and redox conditions (E_h).

Gonser, 1997]. Examples of specific conditions at ecohydrological interfaces that facilitate transformative processes and/or arise because of their transformative nature include:

1. *Steep redox gradients* across groundwater-surface water interfaces as a result of enhanced biogeochemical activity [*Lewandowski et al.*, 2007; *Lautz and Fanelli*, 2008; *Krause et al.*, 2013; *Trauth et al.*, 2015].
2. *Step changes in microbial metabolic activity* [*Haggerty et al.*, 2009; *Argerich et al.*, 2011] and high concentrations of bioavailable organic carbon, nitrogen, or phosphorus at riparian-wetland interfaces [*Schelker et al.*, 2013], at groundwater-surface water interfaces [*Zarnetske et al.*, 2011a, 2011b], and in biofilms [*Battin et al.*, 2003, 2007, 2016], resulting in microzonation of denitrification [*Briggs et al.*, 2015] and enhanced interface denitrification rates where microbial denitrifiers are concentrated [*Harvey et al.*, 2013].
3. *Coexistence of multiple aggregate states (solid, liquid, gas phase)*, across which energy and matter are transferred, such as between atmosphere and porous soil matrix [*Shahraeeni et al.*, 2012], atmosphere-water interfaces [*Assouline et al.*, 2010], unsaturated and saturated soil compartments [*Li and Jiao*, 2005], and between the soil matrix and soil water or air in soil macropores [*van Schaik et al.*, 2014].
4. *Shifts between physical and biological controls of solute transport* across water-organism interfaces [*Larned et al.*, 2004; *Nishihara and Ackerman*, 2009; *Nishizaki and Carrington*, 2014].

While there have been recent improvements in understanding how ecohydrological interfaces control energy and water fluxes (in particular between groundwater and surface water) [*Krause et al.*, 2011a; *Boano*

et al., 2014; *Cardenas*, 2015], critical knowledge gaps remain with respect to how they affect reactive transport, solute mixing, and biogeochemical cycling across system boundaries [*Puth and Wilson*, 2001; *Krause et al.*, 2011a]. Our understanding of the spatial and temporal organization of driving forces (e.g., hydrostatic pressure distribution, concentration gradients, and turbulence intensity) and controls (e.g., interface transmissivity and roughness) of ecohydrological interface fluxes and reactivity are at an early stage [*Gomez-Velez et al.*, 2012, 2014; *Zhang et al.*, 2015; *González-Pinzón et al.*, 2015].

Many ecohydrological interfaces are spatially heterogeneous and temporally dynamic [*Kennedy et al.*, 2009; *Roskosch et al.*, 2012]. While the physical (structural) boundaries between adjacent and interacting systems (e.g., between groundwater and surface water) are usually clearly defined and stationary, dynamically developing ecohydrological interfaces (e.g., hyporheic zones) are defined by their functioning and may change in time with regard to their spatial extent and activity [*Cardenas and Wilson*, 2006, 2007; *Stubbington*, 2012; *Trauth et al.*, 2015; *Gomez-Velez et al.*, 2014; *Boano et al.*, 2010, 2014]. However, some structural boundaries around which ecohydrological interfaces evolve can themselves be dynamic, such as migrating bed forms and flexible and compressible benthic organisms [*Ren and Packman*, 2004; *Huang et al.*, 2011; *Larned et al.*, 2011; *Harvey et al.*, 2012], further complicating the identification and delineation of ecohydrological interfaces.

Patterns and dynamics of ecohydrological interface activity include the development of hot spots (zones of enhanced activity) [*McClain et al.*, 2003; *Lautz and Fanelli*, 2008; *Frei et al.*, 2012; *Krause et al.*, 2013] and hot moments (periods of increased activity) [*McClain et al.*, 2003; *Battin et al.*, 2003; *Harms and Grimm*, 2008] that disproportionately alter the fluxes of water, energy, and matter. Hot spots or "control points" [*Bernhardt et al.*, 2017] have captured the attention of many researchers, who study how they affect nutrient turnover [*Lewandowski et al.*, 2007; *Moslemi et al.*, 2012], ecosystem productivity [*Poungparn et al.*, 2012], pesticide degradation [*Klaus et al.*, 2014], and the bioavailability of metals, such as mercury, to organisms at higher trophic levels [*Sizmur et al.*, 2013]. Yet when and under what conditions ecohydrological interfaces represent hot spots or control points, or what makes them behave as such, has not always been clearly determined.

We have for instance only begun to understand how biological activity (e.g., earthworm and chironomid burrowing, stream periphyton growth, or riparian plant root growth) can create small-scale ecohydrological interfaces that are hot spots of microbial and biogeochemical activity [*Hölker et al.*, 2015; *Baranov et al.*, 2016]. Furthermore, the concept of hot moments entails long periods of relatively low activity punctuated by pulses of rapid activity. These temporal dynamics suggest that some ecohydrological interfaces can be ephemeral. We now turn to these and other gaps in our understanding of ecohydrological interfaces.

3. Critical Gaps in Understanding Ecohydrological Interfaces

We currently lack an overarching framework that integrates the factors that drive and control transformation processes at ecohydrological interfaces. Perceptions and conceptualizations of boundaries, and with that ecohydrological interfaces, are often scale dependent [*Cadenasso et al.*, 2003; *Strayer et al.*, 2003]. At large scales, some ecohydrological interfaces (e.g., between aquifers and rivers) may be conceptualized as discrete boundaries, causing abrupt transitions with step changes in processes across the boundary (Figure 2a). However, downscaling reveals three-dimensional gradients within interfaces (e.g., in hyporheic zones), and transient or gradual changes of physical or biogeochemical properties (Figure 2b). Acknowledgement of the context and scale-dependent view of ecohydrological interfaces is important because the scale in which ecohydrological interfaces are investigated can preclude the detection and quantification of physical, chemical, and biological activity at other scales [*Atkinson and Vaughn*, 2015]. Further, temporal variation in the shape or spatial extent of interfaces and the steepness of gradients within them suggests that our conceptualizations of interfaces vary over temporal as well as spatial scales—as for instance shown for transient behavior of hyporheic zones in response to hydrological forcing [*Malzone et al.*, 2016].

Clear delineations of the spatial and temporal extent of ecohydrological interfaces are further complicated by discipline-specific perspectives on interface properties, processes, and functions (Figure 2c) [*Yarrow and Marin*, 2007; *Harvey et al.*, 2013]. Based on discipline-specific perceptions, hyporheic zones, for instance, are defined by the spatial extent of groundwater and surface water mixing (hydrology), the extent of steep chemical gradients (biogeochemistry), or the abundance of benthic and hypogean taxa (ecology), resulting
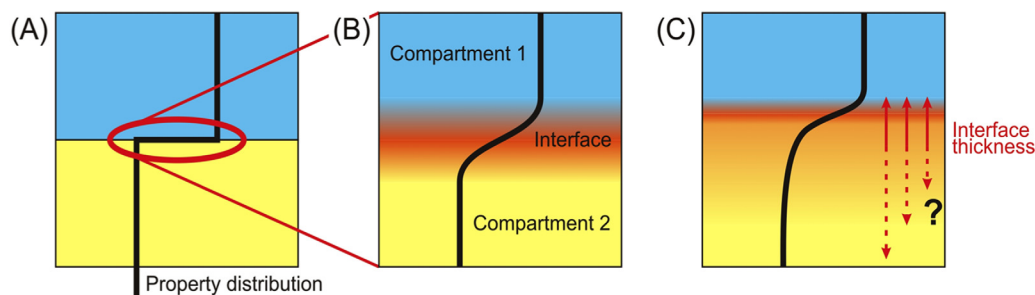
Figure 2. Conceptual model of ecohydrological interfaces connecting two adjacent contrasting environments (Component 1 and Component 2) with scale-dependent representation of gradients of chemical, physical, and biological properties (solid black line). (a) Large scales exhibit step functions in interface properties, where interfaces appear as two-dimensional layers of zero depth; (b) zoomed into smaller scales with steep gradient of chemical, physical, and biological properties and a three-dimensional interface zone with some depth dimension; and (c) difficulties are frequently encountered in determining the upper and lower boundary and depth of the interface zone, especially where property distributions blend into background properties due to their nonlinearity.

in significantly different perceptions of their extent [*Krause et al.*, 2011b, 2014b]. Recent studies of benthic systems have focused on the dynamics and ecological effects of multilayered interfaces (e.g., small-scale diffusive boundary layers nested within larger-scale roughness layers, within larger benthic boundary layers) [*Larned et al.*, 2004; *Nikora*, 2010] and on microzonation of biogeochemical processes, e.g., redox microzones [*Briggs et al.*, 2015]. Views of the capillary boundary at the groundwater-vadose zone interface differ between ecologists focusing on matric potential effects on plant available water and water uptake, (bio)-geochemists interested in redox chemistry differences between pore water and adsorption to mineral surfaces [*Alexander and Scow*, 1989; *Baham and Sposito*, 1994] and groundwater hydrologists and hydrogeological engineers concerned with water table depths. Such discipline-specific perceptions of ecohydrological interfaces can limit the transferability of process understanding and the exchange of data and knowledge across disciplinary boundaries.

Detailed understanding of the drivers and controls of enhanced interface activity is critical for evaluating the functional significance of ecohydrological interfaces. Examples include the shift from aerobic to anaerobic respiration in hyporheic zones, which is controlled by residence time of hyporheic water and nutrients in the streambed [*Zarnetske et al.*, 2011a, 2011b; *Briggs et al.*, 2014], or temperature thresholds triggering bacterial activity [*Bourg and Bertin*, 1994]. Here we pose four critical questions (spanning scales and crossing disciplinary boundaries) that must be answered to understand the role of ecohydrological interfaces in ecosystem functioning:

1. What environmental conditions determine the capacity of ecohydrological interfaces to transform the flow of energy, water, and matter between adjacent ecosystems?
2. How are ecohydrological interfaces organized and how do they evolve in space and time?
3. What mechanisms (drivers and controls) determine the spatiotemporal organization of ecohydrological interfaces?
4. How do the impacts of hot spots and hot moments at ecohydrological interfaces upscale to ecosystem ecohydrological, biogeochemical, and ecological processes?

3.1. What Environmental Conditions Determine the Capacity of Ecohydrological Interfaces to Transform the Flow of Energy, Water, and Matter Between Adjacent Ecosystems?

Ecohydrological interfaces have been described as intensive modifiers of energy, water, and solute fluxes and biogeochemical cycling [*Harvey and Fuller*, 1998], that exhibit hot spot characteristics [*McClain et al.*, 2003; *Lautz and Fanelli*, 2008; *Krause et al.*, 2013] and nonlinear behavior [*Zarnetske et al.*, 2011a, 2011b; *Briggs et al.*, 2014]. To understand why ecohydrological, biogeochemical, and ecological transformation processes in ecohydrological interfaces often differ from their neighboring ecosystems, it is necessary to review the physical, chemical, and ecological interactions that characterize them.

3.1.1. Physical Properties

Contrasts in interface material properties from the adjacent environmental systems (sometimes coinciding with aggregate state boundaries such as between liquid and gas phase, or with changes in transmissivity) affect velocity and direction of exchange fluxes (Figure 3). Impacts of ecohydrological interfaces on
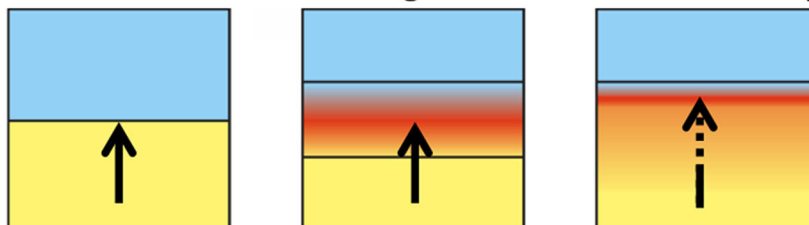
Figure 3. Conceptual model of the scale-dependent complexity of ecohydrological interface exchange-fluxes in systems with interfaces representing thresholds with (left) infinitesimal thickness, (middle) steep gradients with abrupt property changes or (right) variable (transient and abrupt) property changes between interface and adjacent environments, with one-directional flow ceasing at (in) the (a) interface zone or (b) crossing the interface, (c) bidirectional exchange fluxes across the interface, (d) flow reduction across the interface pathway, and (e) the advective mixing of interface exchange fluxes with intracompartmental fluxes.
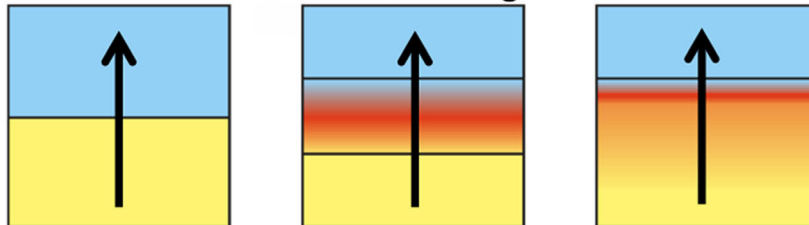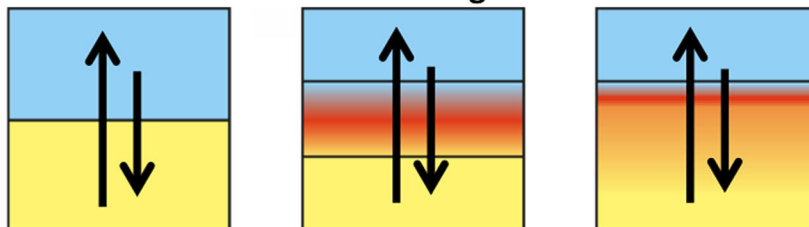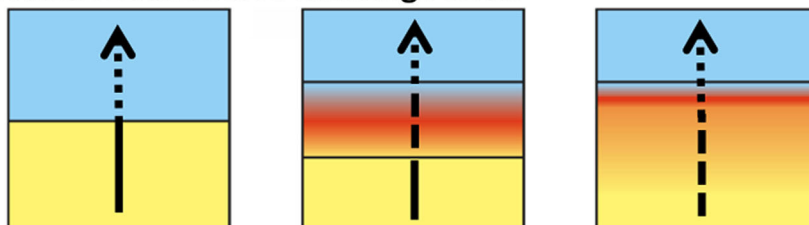
exchange fluxes can vary from complete cessation, if the interface is impermeable (Figure 3a), to unaffected (Figure 3b) or even accelerated exchange. The geometry of property distributions at ecohydrological interfaces (such as hydraulic conductivities at groundwater-surface water interfaces) may cause hysteretic behavior that is dependent on exchange-flow direction (Figure 3c). For example, surface water flow velocities decrease when infiltrating into the streambed, while groundwater upwelling through the streambed

may accelerate toward the interface with surface water. Reduced flow velocities and increased residence times that have been observed at many ecohydrological interfaces (Figure 3d) can substantially enhance biogeochemical processing [*Zarnetske et al.*, 2011b; *Briggs et al.*, 2014]. Quantifying the spatiotemporal variability of biogeochemical processing in heterogeneous interface zones of variable activity will require a shift from the current focus on mean residence times to residence-time distributions that are dynamic [*Botter et al.*, 2011; *Pinay et al.*, 2015].

In many cases, exchange fluxes at ecohydrological interfaces interact with larger flow systems in the adjacent ecosystem (Figure 3e). At aquifer-river interfaces, for instance, exchange fluxes interact across multiple scales. Hyporheic exchange here can be affected by regional groundwater flow, causing complex and nested patterns of exchange fluxes [*Trauth et al.*, 2015; *Gomez-Velez et al.*, 2014] and thus, spatially complex end temporally dynamic ecohydrological interfaces. In this context, we have only begun to understand the impacts of interacting drivers and controls of interfaces exchange. Following the previous example, this includes how streambed transmissivity [*Krause et al.*, 2013] and pressure variations caused by interface topography, such as riparian microtopography [*Frei et al.*, 2012], bed forms [*Cardenas et al.*, 2004] or meanders [*Boano et al.*, 2010], overlap in their impacts on hyporheic exchange fluxes [*Gomez-Velez et al.*, 2014; *Boano et al.*, 2010, 2014] and dynamically evolve in time due to variability in atmospheric and hydrodynamic forcing [*Malzone et al.*, 2016].

3.1.2. Ecological (Including Microbiological) Processes

Ecohydrological interfaces between groundwater, surface water, and vadose zones can have large effects on ecological conditions in the adjacent systems [*Cadenasso et al.*, 2003; *Pinay et al.*, 2015]. Thermodynamically controlled microbial processes drive biogeochemical transformations in these subsurface systems, and in turn, biota respond to the chemical gradients that result from their activity. A classic example is aerobic respiration, which in subsurface zones is largely carried out by microorganisms. As they consume oxygen and organic carbon, microbes create conditions that favor transition to anaerobic metabolism. Although some microorganisms are facultative anaerobes, others are excluded once oxygen concentration drops below a threshold. In fact, a sequence of terminal electron accepting processes, each with their suite of microbial specialists, ensues along redox gradients that characterize anoxic environments [*Morrice et al.*, 2000]. Aquatic macrophytes, benthic biofilms, and riparian vegetation may exude or release organic matter during metabolism or upon death or decomposition, which provides an energy source for microbial metabolism. Community structure and elemental composition of primary producers may influence biogeochemical turnover and location of biogeochemical hot spots at ecohydrological interfaces, as they are likely to release organic matter at different rates and with different chemical composition. Hence, in addition to altering nutrient availability and stoichiometry, aquatic macrophytes, benthic algae, and pelagic phytoplankton colonies may induce hot spots of microbial metabolism [*de Moraes et al.*, 2014].

Aquatic and wetland plants influence the saturated substrate where fine-scale microenvironments develop around their root systems, altering the oxygen concentrations, nutrient uptake, sediment structure, and microbial activity of riparian and hyporheic zones. For example, exudates from the roots of a wetland shrub, *Baccharis* sp., fuel microbial respiration, including denitrification, in streamside sediments and riparian zones [*Schade et al.*, 2001; *Harms and Grimm*, 2008]. The size of the ecohydrological interface zone in which these root exudates drive microbial metabolism tends to be restricted to a few centimeters around the root zone [*Schade et al.*, 2001]. Vascular plants influence not only the interstitial water of the sediment but also the water column, through mutualistic interactions with phytoplankton and bacterial communities [*Brodersen et al.*, 2014], and the atmosphere, by respiration and gas exchange [*Xing et al.*, 2006]. Ecological impacts on ecohydrological interface functioning are not restricted to living organisms. Large woody debris alters streambed topography and enhances groundwater-surface water interactions and supply of organic carbon, thus supporting habitat complexity and biotic activity [*Warren et al.*, 2013; *Krause et al.*, 2014a]. The nutrients and pollutants that had previously been absorbed by biota are now released during decomposition and can stimulate localized hot spots of increased resource availability [*Krause et al.*, 2014a], or invertebrates can induce the development of biogeochemical hot spots through the regeneration of nutrients [*Grimm*, 1988a].

The morphology, physiology, and productivity of benthic autotrophs (e.g., algal and cyanobacterial mats, seagrasses, corals growing on the bottom of streams, lakes, and coastal marine ecosystems) are strongly influenced by the hydrodynamic and chemical conditions in surface water-benthic interfaces. Mass
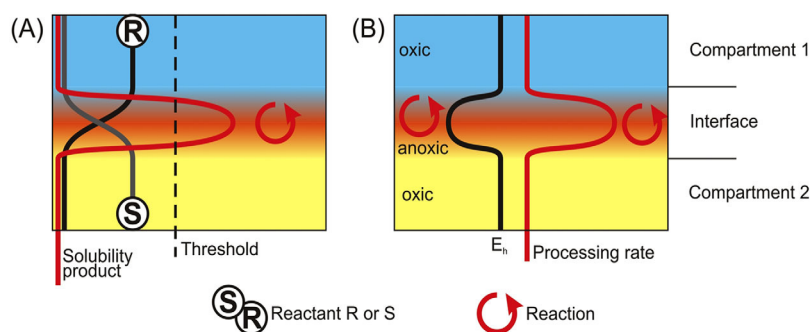
Figure 4. Examples for the development of biogeochemical hot spots at ecohydrological interfaces, hosting distinctly different reaction properties and hence biogeochemical processes than its adjacent environments: (a) enhanced reactivity directly resulting from the interaction of interface exchange fluxes such as the precipitation of a reactant at the ecohydrological interface due to exceeding its solubility product and (b) enhanced reactivity as an intrinsic property of the interface environment, such as anoxic areas in hyporheic or riparian zones.

transport across these interfaces is often the rate-limiting step for nutrient acquisition and gas exchange by the organisms [*Jumars et al.*, 2001; *Larned et al.*, 2004], and hydrodynamic forces imposed by these interfaces affect the organism stature and biomechanical properties [*Statzner et al.*, 2006; *Albayrak et al.*, 2014]. While interface conditions clearly affect benthic autotrophs, the opposite is also true. Benthic autotrophs function as roughness elements that modify flow structure and as biogeochemical reactors that alter water chemistry [*Folkard*, 2005; *Reidenbach et al.*, 2006; *Larned et al.*, 2011]. The picture that is emerging from recent studies of surface water-benthic interfaces is a flow-organism feedback system consisting of responses by organisms to flow conditions, flow modifications induced by the organisms, subsequent responses by the organisms to the modified flow, and so forth [*Nikora*, 2010; *Dijkstra and Uittenbogaard*, 2010; *Larned et al.*, 2011]. Similar feedback systems should apply to the heterotrophic organisms in sedimentary systems, as described below. Such feedbacks are an important source of nonlinearity in process rates at ecohydrological interfaces.

Recently, ecohydrological research has considered biota at higher trophic levels, such as macroinvertebrates and aquatic vertebrates, and their capacity to alter the physical-chemical characteristics that regulate the rate of activity and ecosystem functioning at ecohydrological interfaces [*Coco et al.*, 2006; *Layman et al.*, 2013; *Patrick*, 2014]. *Lewandowski et al.* [2007], *Roskosch et al.* [2012], and *Baranov et al.* [2016], for instance, describe a system of interactions and feedbacks between chironomids and aquifer-lake ecohydrological interfaces. In these studies, chironomid activity had direct impacts on hydrodynamics and biogeochemistry, while physical-chemical conditions, such as temperature, affected chironomid pumping behavior [*Roskosch et al.*, 2012] and hence, subsurface flow pattern and biogeochemical processing rates. Similarly, vertebrates may alter streambed topography, for example through nest-building activities, which lead to changes in connectivity and fluxes across the surface water sediment interface [*Collins et al.*, 2014], through their movement (Hippopotamus) or beaver dam construction [*Naiman et al.*, 1994]. Additionally, fish induce biogeochemical hot spots by excretion [*Grimm*, 1988b; *Vanni*, 2002] and nutrient release following their death and decomposition [*Levi and Tank*, 2013].

3.1.3. Thermodynamics and Biogeochemistry

At stationary boundaries, matter and energy fluxes may be absorbed, transmitted, reflected, transformed, amplified, or unaffected. Boundaries can be highly permeable to some substances, and represent reactive filters for others [*Cadenasso et al.*, 2003; *Strayer et al.*, 2003; *Belnap et al.*, 2003]. We propose that these concepts of flux behavior at boundaries can be extended to nonstationary ecohydrological interfaces, which develop dynamically in space and time. Processing rates at ecohydrological interfaces are controlled by both mass transport and reaction kinetics, with *transport-limited* conditions arising when reaction rates are faster than mass-transport rates [*Sanford and Crawford*, 2000; *Larned et al.*, 2004; *Cornelisen and Thomas*, 2009]. Conversely, process rates tend to be kinetically controlled (*reaction limited*) when mass-transport rates are faster than reaction rates [*Sanford and Crawford*, 2000; *Nishihara and Ackerman*, 2009; *Argerich et al.*, 2011]. Increased biogeochemical activity is often attributed to the spatial and temporal coincidence of reactants in a mixing zone (Figure 4a) [*McClain et al.*, 2003]; however, enhanced turnover may also be controlled by high reactivity in interfaces (Figure 4b), resulting directly from the chemical gradients at the

interface [*Krause et al.*, 2013; *Trauth et al.*, 2015]. It has yet to be established how the mixing of reactants at ecohydrological interfaces influences interface redox conditions and controls residence-time distributions of different reactants, and hence, biogeochemical processing rates. Possible approaches to achieve this involve combinations of residence-time distributions and dimensionless numbers used to describe the transport versus reaction relationships of flow systems, such as the Damköhler number or Peclet number describing diffusion/advection ratios [*Pinay et al.*, 2015]. Furthermore, the reaction significance factor approach (RSF) has been applied for quantifying reaction versus transport limitation in single hyporheic flow paths within basin-scale assessments of the number of river excursions through the hyporheic zone [*Harvey et al.*, 2013; *Gomez-Velez et al.*, 2015]. Despite these advances, predictions of biogeochemical processing at ecohydrological interfaces remain challenging, since not only can biogeochemical turnover be enhanced but also the type of processes and chemical reactions may differ distinctively from adjacent ecosystems [*Naiman et al.*, 1988].

3.2. How Are Ecohydrological Interfaces Organized in Space and Time?

Complex microhabitat structure and biological activity create ecohydrological interface heterogeneity [*Lewandowski et al.*, 2007; *Hanzel et al.*, 2013], with interface processes often varying over a wide range of spatial and temporal scales [*Belnap et al.*, 2003]. Hyporheic exchange flows, for instance, include sinuosity-driven flows in meandering streams [*Boano et al.*, 2010; *Gomez-Velez et al.*, 2012] and bed-form-driven flows caused by streambed features such as riffles and pools [*Thibodeaux and Boyle*, 1987; *Tonina and Buffington*, 2007; *Käser et al.*, 2013], small-scale ripples and dunes [*Cardenas and Wilson*, 2007], and flow obstacles such as dams or wood [*Sawyer et al.*, 2011; *Briggs et al.*, 2012; *Krause et al.*, 2014a].

Scale-dependent drivers of the spatial and temporal organization of ecohydrological interface properties are complex. Mixing of chemical reactants in ecohydrological interfaces may involve the transport of multiple reactants from source areas to the interface (Figure 5a) [e.g., *Zarnetske et al.*, 2011a, 2011b] or the mixing of a reactant already present at the interface with another reactant that is transported into it (Figure 5c) [e.g., *Lewandowski et al.*, 2007; *Krause et al.*, 2013]. In many cases, just a fraction of the mass flux crosses the ecohydrological interface. Often mass fluxes return to their original compartments (Figures 5b and 5d); e.g., surface water infiltrates into the hyporheic zone and exfiltrates back into the stream after passage through the bed.

Ecohydrological interfaces are frequently characterized by nonlinear temporal dynamics, including tipping points, caused by rapid changes in thermodynamic or biogeochemical characteristics at the interface, such as the shift from aerobic to anaerobic metabolism [*McClain et al.*, 2003; *Harvey et al.*, 2012; *Zarnetske et al.*,
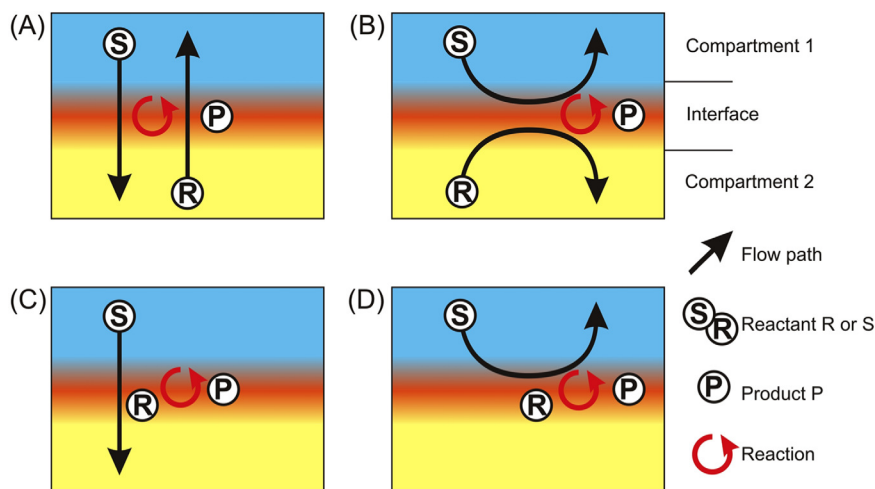
Figure 5. Enhanced ecohydrological interface reactivity as a function of exchange-flow patterns at/in/across the interface with fluxes carrying reactant R and S to meet and mix (a) at the interface with not all but just a fraction of the reactants mixing (b) at the interface due to tangential fluxes and transport of reactant S into the ecohydrological interface already containing autochthonous reactant R, results in (c) processing of S and R to product P (d) with some of the external reactant (S) returning to the compartment it originated from.

2011a, 2011b; *Briggs et al.*, 2014, 2015] or biogeochemical responses to fast changes in soil water content [*Fromin et al.*, 2010]. Also, rainfall pulses in dryland environments can result in rapid and nonlinear increases in microbial respiration at the soil-air interface [*Collins et al.*, 2014] or in the vadose zone-groundwater interface of riparian zones during dry seasons [*Baker et al.*, 2000; *Harms and Grimm*, 2008]. In both of these examples, ecohydrological interfaces come into existence when water is added (i.e., rainfall impinges on the soil surface, or the groundwater table rises into previously dry riparian soil), such that biogeochemical processes are stimulated rapidly. However, the cumulative long-term effects of such hot moments on ecohydrological interfaces, as well as their subsequent contribution to system behavior at a global scale [*Kreyling et al.*, 2014] still need to be investigated in detail.

3.3. What Mechanisms (Drivers and Controls) Determine the Spatiotemporal Organization of Ecohydrological Interfaces?

Spatial patterning in the properties of ecohydrological interface can result directly from interface processes and thus, may partly be explained by the functioning of the ecohydrological interface. Examples include redox patterns in hyporheic zones resulting from oxygen depletion by hyporheic biogeochemical processing [*Zarnetske et al.*, 2011a, 2011b; *Krause et al.*, 2013]. In other cases, the origin of spatial variability is independent of actual interface processes (e.g., spatial variability in hydraulic conductivity can control patterns of exchange fluxes in ecohydrological interfaces). Spatial patterns of solute concentration in ecohydrological interfaces may be controlled partially by the spatial organization of properties in the adjacent ecosystems (Figure 6). For example, spatially homogeneous physical properties in hyporheic zones (Figures 6a–6c)
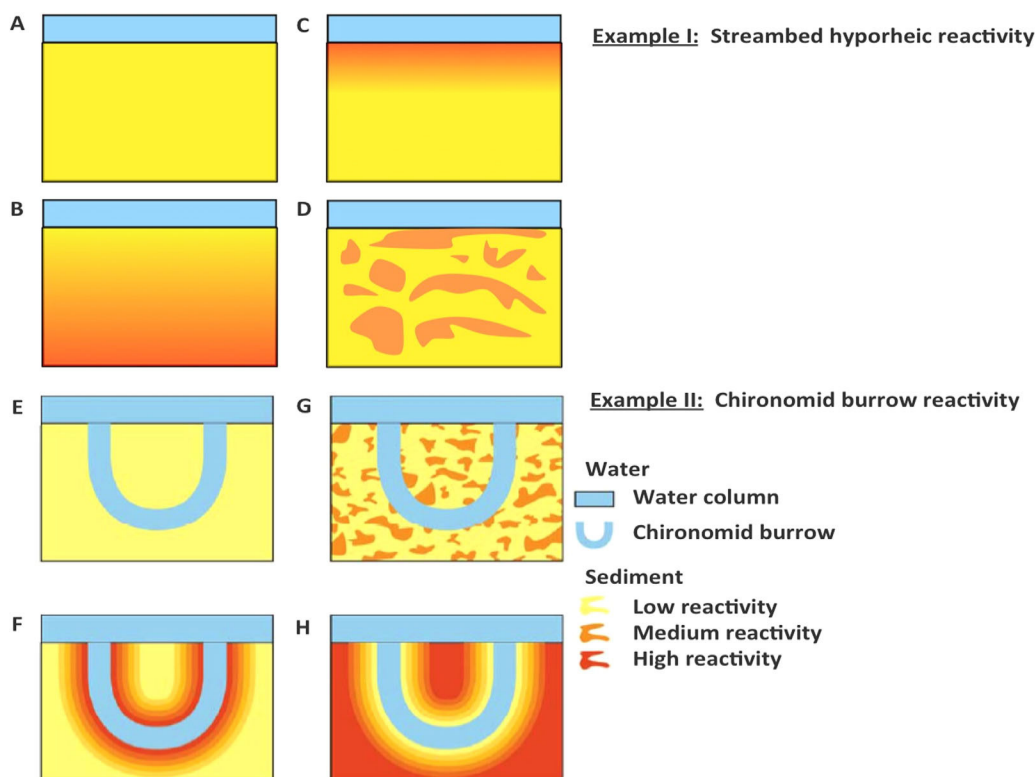
Figure 6. Variable characteristics and heterogeneity of ecohydrological interfaces as result of differences in passive or active organizational mechanisms structuring interface properties, with Example I, passive controls—streambed properties controlling hyporheic zone reactivity: homogeneously low or high ecohydrological interface reactivity (concentrations) at hyporheic zones resulting from (a) continuously low streambed reactivity or (b) depth decreasing or (c) increasing streambed reactivities, in contrast to spatially heterogeneous streambed properties, subsequently causing (d) spatial variability at the interface. Example II, active controls—chironomids as engineers of interface complexity: no effect of chironomids and (e) homogenous and (g) heterogeneous distribution of biological, chemical, and physical properties within the sediment matrix and at the burrow wall interface; chironomid pumping induced gradients of (f) decreasing oxygen concentration from the tube into the adjacent sediment and (h) increasing soluble reactive phosphorus concentration from the tube into the adjacent sediment.

or around chironomid burrows (Figure 6e) will facilitate ecohydrological interface activity that is controlled primarily by interface exchange fluxes and mean residence times [e.g., *Zarnetske et al.*, 2011a, 2011b]. In contrast, a heterogeneous matrix in surrounding ecosystems (Figures 6d and 6g) will add further complexity, making it important to quantify not only exchange fluxes and residence times but also their distributions [*Gomez-Velez et al.*, 2014]. In addition to spatial heterogeneity, patterns may evolve with time as interface processes progress. For instance, chironomid pumping can affect property distributions at the sediment/burrow wall interface (Figures 6f and 6h), where they have been shown to induce gradients of decreasing oxygen concentration with increasing distance from the tube (Figure 6f) or increasing concentration of soluble reactive phosphorus with increasing distance from the tube walls into the adjacent sediment (Figure 6h) [*Lewandowski et al.*, 2007; *Baranov et al.*, 2016].

Disentangling the impacts of different drivers and controls on processes in ecohydrological interfaces remains a challenge, partly due to combined effects and feedbacks between hydrological, biogeochemical, and biological processes that may be additive, synergistic, antagonistic, or undetectable. To use freshwater microbial biofilms as an example, biogeochemical turnover in biofilms is related to their biomass [*Singer et al.*, 2010; *Haggerty et al.*, 2014]. Hence, biofilm growth causes biogeochemical turnover rates to increase. At the same time, increased biofilm thickness changes its permeability and has the potential to cause significant clogging, increasing contact area and residence and reaction times at the biofilm surface, which in some cases has been shown to accelerate biogeochemical turnover [*Battin et al.*, 2007] or even change the type of chemical reactions, inducing shifts from aerobic to anaerobic conditions or limiting biogeochemical processing at the interface [*Treese et al.*, 2009].

Improving the understanding of the functioning of ecohydrological interfaces across spatial and temporal scales will require to start acknowledging that traditional hierarchical classification schemes where physical boundary conditions and hydrological behavior control thermodynamic processes and biogeochemistry, which then define the biological template or ecological niche are not suitable to adequately describe the complex interactions between biological, biogeochemical and hydrological processes at ecohydrological interfaces. As discussed above, biological activity can be a major driver of the spatial and temporal organization of ecohydrological interface functions and often actually shape the physicochemical template. It is essential to fully acknowledge this complexity of multidirectional interactions also in experimental and conceptual model designs as oversimplification of cause-impact relationships will not yield the required understanding of what drives organizational principles of ecohydrological interface functions.

3.4. How Do the Impacts of Hot Spots and Hot Moments at Ecohydrological Interfaces Upscale to Ecosystem Ecohydrological, Biogeochemical, and Ecological Processes?

Our capacity to quantify and predict the large-scale and long-term importance of hot spots and hot moments at ecohydrological interfaces is hampered by our limited understanding of how mechanisms structuring ecohydrological interfaces and their processes scale in space and time [*Krause et al.*, 2011b; *Pinay et al.*, 2015]. The effects of interface hot spot activity have been observed at scales ranging from microscales such as biofilms to intermediate scales of stream reaches [*Lautz and Fanelli*, 2008; *Trauth et al.*, 2015], and conceptual frameworks have been developed to explain interface process dynamics [*Fisher et al.*, 1998; *McClain et al.*, 2003; *Harms and Grimm*, 2008; *Pinay et al.*, 2015]. For example, there is evidence that hyporheic zone processes can have implications for the whole stream network [*Kiel and Cardenas*, 2014; *Harvey and Gooseff*, 2015; *Gomez-Velez et al.*, 2015; *Zarnetske et al.*, 2015], with hyporheic nitrification and denitrification in headwater streams altering the nitrogen load in rivers [*Alexander et al.*, 2007]. Although hot spot activity has been shown to be at least temporarily significant at small local scales, its larger-scale importance for energy transfer or biogeochemical turnover in entire river networks or catchments is still widely debated. This partly results from the fact that processes specific to ecohydrological interfaces have often been studied by coupling conceptual models of different ecosystem types (e.g., coupling groundwater and surface water models) [*Markstrom et al.*, 2008; *Yuan et al.*, 2011] or land-surface schemes and atmospheric models with hydrological models [e.g., *Maxwell and Miller*, 2005]. In both cases, ecohydrological interface conditions are at least partly defined as boundary conditions instead of integrating ecohydrological interface conditions and behavior implicitly, a practice that restricts the way dynamic interface processes can be analyzed across scales.

4. A Vision for Integrated Research at Ecohydrological Interfaces

The pressing challenges of global environmental change, such as increasing frequencies and magnitude of extreme events [*Hall et al.*, 2014; *Blöschl et al.*, 2015], call for improved understanding of their impacts from plot to regional scales, across ecosystem types, and beyond disciplinary boundaries. This will require advanced methods for multiscale monitoring of highly dynamic ecosystem behavior [*Blaen et al.*, 2016; *Abbott et al.*, 2016] in order to enhance the current understanding of quantitative implications and dynamic behavior of ecohydrological interface processes for coupled water, matter, and energy fluxes and biogeochemical turnover. The most critical knowledge gaps outlined in this review include the following:

1. Inadequate conceptual frameworks for understanding how processes occurring at ecohydrological interfaces vary with scale and how and whether small-scale interface processes are manifested at large scales across complex landscapes.
2. Failure to transfer and integrate scale-dependent methods and knowledge of mechanisms controlling ecohydrological interface processes across disciplinary and ecosystem boundaries [*Hannah et al.*, 2007; *Krause et al.*, 2011b, 2014b; *Abbott et al.*, 2016].

Interdisciplinary research strategies will need to move the research of ecohydrological interfaces from a descriptive to a mechanistic and predictive stage, extending the scope to a wider range of ecohydrological interfaces than explored in this paper. Ecohydrological interfaces not only connect different environmental domains but also represent a research topic that requires and fosters novel linkage between traditionally distinct disciplines. The development of multiscale conceptual models of ecohydrological interface functioning requires interdisciplinary thinking and integration of discipline-specific methods. Following this rationale, we propose the following "roadmap" to catalyze research advances.

5. Roadmap for Ecohydrological Interface Research

5.1. Enhance Capacities for Multiscale Monitoring and Modeling

Developing multiscale conceptual models of ecohydrological interfaces will require advances in physical, microbial, biogeochemical, and ecological monitoring using innovative sensing and tracing technologies [*Gonzales-Pinzon et al.*, 2014; *Abbott et al.*, 2016; *Blaen et al.*, 2016]. In turn, the application of these technologies will require new methods for managing big data sets, and advanced tools for spatial and time-series analysis. Recent advances in distributed sensor networks such as Fibre-optic Distributed Temperature Sensing [*Selker et al.*, 2006], thermal IR imagery [*Pfister et al.*, 2010], and high-frequency in situ sensors, analyzers and imagers [*Jordan et al.*, 2007; *Reidenbach et al.*, 2010; *Neal et al.*, 2012] provide capacity for improved resolution and frequency in monitoring exchange fluxes across ecohydrological interfaces in real time [*Grant and Marusic*, 2011; *Krause et al.*, 2015; *Blaen et al.*, 2016]. Technology exchange among disciplines has the potential to advance process monitoring beyond current observations of average, compartmental system behavior, including identification and quantification of hot moments and hot spots. Using terrestrial diatoms to detect the rapid onset and cessation of flow path connectivity in the hillslope-riparian zone-stream continuum [*Pfister et al.*, 2009; *Martínez-Carreras et al.*, 2015 is a promising example of such a cross-disciplinary approach.

5.2. Improve Conceptual Understanding of Interface Processes and Their Interactions

In addition to improving monitoring capacity, resulting discipline and system specific knowledge needs to be integrated to improve understanding of the scale-dependent processes and mechanisms that lead to the development of bioreactive hot spots and hot moments [*Soulsby et al.*, 2008]. For instance, the application of process understanding gained in groundwater-vadose zone or groundwater-surface water interfaces to other ecohydrological interfaces, ecosystem types, and disciplines will support the development of an integrated conceptual framework for ecohydrological interfaces. Promising examples include the following:

1. The linking of spatial patterns and behavior of anecic earthworm populations to the generation of preferential flow pathways through macropores, which in turn affects pesticide infiltration [*Palm et al.*, 2013; *van Schaik et al.*, 2014].
2. Investigations of biogeochemical hot spots developing around chironomid burrow walls with fluxes of pore water infiltrating from the adjacent sediment and active ventilation of water from the tube into the surrounding sediment [*Roskosch et al.*, 2012; *Baranov et al.*, 2016].

3. The extension of boundary layer research from atmosphere-forest and atmosphere-soil interfaces [*Finnegan*, 2000] to a variety of surface water-benthic interfaces [e.g., *Nikora*, 2010; *Larned et al.*, 2011; *Nepf*, 2012].

4. Novel approaches for analyzing process dynamics at plant-soil interfaces including plant root endosphere and rhizosphere [*Vandenkoornhuyse et al.*, 2015].

5.3. Quantify the Impact of Interface Hot Spots and Hot Moments at Regional Scales

To improve the prediction and quantification of landscape-scale water, matter, and energy fluxes and biogeochemical cycling, quantitative model frameworks need to incorporate improved mechanistic understanding of the space-time organization of ecohydrological interface activity. This may be achieved by advancing conceptual modeling frameworks that integrate traditionally separate model domains. In addition, there is great potential for enhanced interdisciplinary knowledge exchange by transferring subject-specific theory across disciplinary boundaries and testing its validity at ecohydrological interfaces [*Abbott et al.*, 2016]. For instance, concepts linking the spatial organization and hydrological functioning of intermediate-scale catchments [*Zehe et al.*, 2014] provide potential for being applied to advance the process understanding of the functioning of ecohydrological interfaces. In this catchment-scale example, a hierarchy of functional units (i.e., coevolving elementary functional units) has been shown to control catchment functioning, ultimately resulting in spatially organized landscapes [*Zehe et al.*, 2014]. In other applications, the blurring of system boundaries and adopting of flow path approaches has been advocated to more realistically scale up to larger landscapes [*Fisher et al.*, 1998, 2004; *Kolbe et al.*, 2016]. Adaptations of such concepts may have great potential to improve large-scale quantification of ecohydrological interface activity.

5.4. Manage Ecohydrological Interfaces to Enhance Ecosystems Services and Increase Resilience to Environmental Change

Ecosystem services provided by ecohydrological interfaces need to be restored and their resilience to future environmental perturbations improved, in order to better manage the adjacent ecosystems [*Kasahara and Hill*, 2008; *Hester and Gooseff*, 2011; *Harvey and Gooseff*, 2015]. For example, multiple restoration measures have been trialed with the goal of enhancing hyporheic exchange fluxes across groundwater-surface water interfaces (e.g., constructed channel structures [*Crispell and Endreny*, 2009] and bed forms [*Kasahara and Hill*, 2006], altered streambed hydraulic conductivity [*Ward et al.*, 2011], planting [*Gurnell*, 2014], and woody debris installation [*Krause et al.*, 2014a]). A key challenge remains to identify drivers that can be manipulated or managed at relevant scales. New high-frequency and high-resolution data obtained from novel distributed sensor networks can help to improve the understanding of dominant controls of ecohydrological interface reactivity [*Krause et al.*, 2015; *Blaen et al.*, 2016]. Such an understanding is required to design potential engineering and management measures to restore, maintain, or enhance processes of ecohydrological interfaces. Explicit consideration of the dynamics of processes at ecohydrological interfaces also has the potential to improve management and risk assessment frameworks. Specifically, managing ecohydrological interfaces may permit their efficient use and promote their moderating impact and remediation potential, for example, by enhancing nutrient retention or removal at hyporheic or riparian interfaces.

6. Conclusions

This paper has elaborated our view that to better understand the functioning of ecosystems, their component subsystems, and their interactions, it is important to explicitly account for the dynamics of processes occurring at ecohydrological interfaces. This implies consideration and analysis of ecohydrological interfaces in their own right, as entities with unique functioning and inherent, often complex, spatial patterns and temporal dynamics of physical, biogeochemical, and ecohydrological properties. Ecohydrological interfaces often occur at boundaries and ecotones, but they are not boundaries per se. They may appear and disappear, having a large or a small role in determining larger-scale processes that vary over space and time. An improved understanding of the wider landscape interactions between connected ecosystems will only be possible if current ecosystem and landscape concepts incorporate the processes that occur at ecohydrological interfaces.

The analysis of the actual causes of dynamic ecohydrological interface reactivity, including reasons for nonlinear behavior such as hot spots and hot moments, requires intensification of interdisciplinary research and enhanced capacity for high-frequency/resolution monitoring to adequately capture nonlinear process

dynamics as they occur. Combining technological and conceptual advancement from different disciplines can help us to understand nonlinear ecohydrological interfaces behavior. This will advance our understanding and conceptual frameworks of ecosystem processes, from their current, often disciplinary, descriptions of patterns and dynamics of ecosystems as segregated entities to dynamic systems with interconnected processes and interferences that are substantially controlled by the conditions at system and subsystem interfaces.

We recognize that we have provided insight into the importance of processes at a subset of the universe of ecohydrological interfaces, with a bias toward examples of ecohydrological interfaces involving freshwater ecosystems such as groundwater-surface water and benthic-pelagic interfaces. Further interdisciplinary research is needed to develop new strategies for extending and integrating this process understanding to other types of ecohydrological interfaces in more terrestrial ecosystems, such as plant-atmosphere, soil-plant, or microbe-plant interfaces.

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