

Towards an Improved Conceptualization of Riparian Zones in Boreal Forest Headwaters

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ABSTRACT

The boreal ecoregion supports about one-third of the world's forest. Over 90% of boreal forest streams are found in headwaters, where terrestrial–aquatic interfaces are dominated by organic matter (OM)-rich riparian zones (RZs). Because these transition zones are key features controlling catchment biogeochemistry, appropriate RZ conceptualizations are needed to sustainably manage surface water quality in the face of a changing climate and increased demands for forest biomass. Here we present a simple, yet comprehensive, conceptualization of RZ function based on hydrological connectivity, biogeochemical processes, and spatial heterogeneity. We consider four dimensions of hydrological connectivity: (1) laterally along hillslopes, (2) longitudinally along the stream, (3) vertically down the riparian profile, and (4) temporally through event-based and seasonal changes in hydrology. Of particular importance is the vertical dimension, characterized by a 'Dominant Source Layer' that has the highest contribution to solute and water fluxes to

streams. In addition to serving as the primary source of OM to boreal streams, RZs shape water chemistry through two sets of OM-dependent biogeochemical processes: (1) transport and retention of OM-associated material and (2) redox-mediated transformations controlled by RZ water residence time and availability of labile OM. These processes can lead to both retention and release of pollutants. Variations in width, hydrological connectivity, and OM storage drive spatial heterogeneity in RZ biogeochemical function. This conceptualization provides a useful theoretical framework for environmental scientists and ecologically sustainable and economically effective forest management in the boreal region and elsewhere, where forest headwaters are dominated by low-gradient, OM-rich RZs.

Key words: terrestrial–aquatic interface; riparian buffer; soil organic matter; redox; forest management; water quality; catchment biogeochemistry; hydrological connectivity; catchment heterogeneity.

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Author contributions JLLJ proposed the structure of the paper and wrote it in collaboration with MNF, MB, FL, TG, RAS, HJ, KHB, and SJK, who contributed to the writing and conceptualization.

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INTRODUCTION

Surface water quality is to a large degree determined by substances mobilized from the surrounding catchment soils. Thus, the area of interaction between soils and waters is a primary

focus for both research and management. In this context, terrestrial–aquatic interfaces have long been recognized as hot spots for biogeochemical reactions, which may be activated during hot moments connected to hydrological events (McClain and others 2003; Vidon and others 2010).

In boreal forest headwaters, the link between terrestrial and aquatic environments is dominated by organic matter (OM)-rich riparian zones (RZs). The boreal ecozone covers more than ten million square kilometers of the northern circumpolar region including Fennoscandia and large parts of North America and Russia (Apps and others 1993; Magnani and others 2007). RZs along small running waters are an important part of the overall landscape in the boreal ecozone as headwater streams make as much as 90% of the total stream length (Bishop and others 2008). This is a higher proportion than the reported value for other ecozones (Horton 1945; Raymond and others 2013), although headwater stream lengths might have been underestimated in the overall fluvial network in those systems (Benstead and Leigh 2012). Functioning of these sensitive and biogeochemically active interface zones can be altered by natural disturbance (for example, fire) (Adams 2013) or human activity (for example, forest harvesting and resource extraction) (Kreutzweiser and others 2008; Gauthier and others 2015), which occur throughout the boreal ecozone.

The accumulation of high levels of OM at the land–water interface is a distinguishing feature of RZs along many small boreal forest streams, in contrast to RZs in other forest biomes (for example, Mediterranean catchments) (Lupon and others 2016). This OM accrual is the result of paludification following glacial retreat in northern latitudes, that is, the formation of peatlands resulting from the long-term interaction between landscape, climate, biota, and disturbances (Lavoie and others 2005). Topography is the key landscape factor that shaped paludification by controlling the development of drainage structure, hydrological connectivity, and water accumulation (Jencso and others 2009). Climate factors playing a role during paludification include precipitation, which influences groundwater levels and flows and thereby the redox state and potential for OM mobilization, and temperature, which regulates rates of microbial and plant activity which in turn determines the production and decomposition of OM (DeLuca and Boisvenue 2012). Temperature and plant growth also influence rates of evapotranspiration and the overall water balance. Commonly located in low-lying flat areas, boreal RZs usually have shallow

groundwater tables that can cause hypoxic conditions, which together with low temperature for much of the year result in slow decomposition and subsequent accumulation of OM (Luke and others 2007). That is, primary production rates exceed mineralization rates locally, leading to the characteristic OM accumulation, which in turn can increase the soil water holding capacity contributing to more hypoxia. Apart from natural processes, human-related disturbances may significantly alter terrestrial–aquatic connectivity and rates of OM accumulation. For example, ditching was an important disturbance in many headwater streams in Fennoscandia during the early twentieth century (Åström and others 2001). This practice was common to improve drainage and forest productivity.

From both scientific and management perspectives, physical, biogeochemical, hydrological, and ecological aspects of RZ function in the boreal forest and elsewhere are all interrelated. For example, ecologists often focus on the biological communities, which are often more diverse in RZs than in upslope areas (Gregory and others 1991; Jansson and others 2007; Onaindia and others 2013). On the other hand, hydrologists may focus on the relative contribution of riparian and upslope areas to runoff, which is usually disproportionately larger in the RZ that is hydrologically connected to the stream (Rodhe 1989; McGlynn and McDonnell 2003). Ecology and hydrology are related because the high water inputs to the RZ may bring nutrients from upslope areas that are, in part, responsible for high levels of biological diversity (Kuglerová and others 2014b). Hydrology becomes the key factor connecting terrestrial and aquatic environments (Vidon and Hill 2004), which can explain how mobilization of relatively old water during runoff events creates a broad spectrum of flow–concentration relationships across RZs (Bishop and others 2004). From a biogeochemical perspective, the high OM content of soils found in most RZs (Naiman and Décamps 1997), and especially in those located in boreal forests, exerts widespread influences over the processing of substances during their hydrological transport to the aquatic environment. Due to its chemical exchange capacity and potential to support microbial activity, OM interacts and affects biogeochemically almost any chemical element or compound (Schlesinger 1997; Vestin and others 2008; Herndon and others 2015).

Broadly, the RZ can be defined as the zone of direct interaction between terrestrial and aquatic environments (Swanson 1981; Naiman and Décamps 1997). From a management perspective,

boreal RZs have often been conceptualized as a fixed width buffer along a water course (Gundersen and others 2010). Although such an approach is easy to implement and monitor, it fails to adequately capture the spatial and temporal heterogeneity in key functional attributes. Recent work has suggested that there is a need to refine the definition of boreal forest RZ buffer strips (Laudon and others 2016). Specifically, these authors argue that buffer zones should be defined on the basis of landscape hydrology and aimed at identifying and protecting sensitive areas along streams from the potential negative consequences of forestry. Despite this conceptual advance, current forest management approaches still fail to take sufficient account of hydrological connectivity, OM-driven biogeochemical functioning, and spatial heterogeneity. These shortcomings in the conceptualization of RZ functioning increase the likelihood of undesirable outcomes for water quality in the boreal forest due to the interactions of a changing climate and increased demands for forest biomass (Oni and others 2015). Previously, RZ structure and function have been characterized from a longitudinal perspective based on erosional, transitional, and depositional properties (Tabacchi and others 1998). However, such conceptualization lacks a vertical connectivity perspective and may not be appropriate to characterize RZs in low-gradient OM-rich boreal headwaters where gravity-driven erosional processes are often of minor importance.

Here we present a simple, yet comprehensive, conceptualization of boreal RZ hydrological connectivity, OM-driven biogeochemical functions, and spatial heterogeneity as they apply to a wide range of chemical elements and compounds. We focus on RZ control of boreal surface water quality and base our conceptualization on integrating basic biogeochemical and hydrological theory with past and ongoing research in the Swedish boreal forest. Other geographical areas, including elsewhere in the boreal ecoregion and catchments with peat or till soils, are also considered as several RZ features and functions are general and widespread. The spatial scale we focus on includes small to medium size catchments (that is, headwaters from a few hectares to a few square kilometers). At this scale, the RZ influence on stream chemistry is larger than at downstream locations where riparian signals are attenuated by in-stream processes, mixing of upstream waters, or through increased influence of non-riparian sources and processing (for example, deep groundwater or lake) (Hagedorn and others 2000; Bernal and others 2012; Peralta-Tapia and

others 2015). Our conceptualization is timely as it moves beyond the hot spot and hot moment concepts introduced by McClain and others (2003), a need that has been recently highlighted by Bernhardt and others (2017).

We start by defining the RZ in the boreal forest so to establish the context. We then conceptualize RZ hydrological connectivity with special focus on the vertical dimension. We describe the role of the RZ as a main source of OM into streams and the biogeochemical functions of retention and redox-mediated transformation driven by the OM in the RZ. Additionally, we discuss the role of timescales and hydrology in relation to riparian biogeochemical functions. Finally, we characterize RZ spatial heterogeneity and briefly review and suggest methods for mapping hydrological connectivity and RZ areas. The ultimate aim of this paper is to propose a conceptualization that can provide a useful theoretical framework for environmental scientists, land managers, and foresters. Thus, we conclude by discussing potential implications for riparian upscaling and land management.

DEFINING RIPARIAN ZONE IN THE BOREAL FOREST

Our main criterion to define boreal RZs relies on the marked soil transition in boreal catchments from mineral soils in upslope areas (generally podzols) to organic soils in the near-stream zone (generally histosols) (Chesworth 2008). RZs are hence defined as the area between the edge of the stream and the characteristic transition between organic and mineral soils. This definition assigns primary importance to OM content as we assume boreal headwater RZs are typified by organic soils, comparable to small wetlands within forest catchments. This definition based on soil characteristics also has topographical and biological dimensions. The aforementioned soil transition is usually accompanied by an increasing terrain slope and by vegetation changes from mosses (*Sphagnum* spp.), Norway spruce (*Picea abies*), and occasional deciduous trees (*Betula* spp., *Alnus* spp.) present within organic RZs to vaccinium shrubs (*Vaccinium* spp.) and Scots pine (*Pinus sylvestris*) dominating in drier, mineral-soil dominated upslope areas (Grabs and others 2012).

Certainly, soils in the near-stream area can also be inorganic in boreal landscapes, especially in well-drained soils dominated by coarse and deep sediments (Grabs and others 2012). However, our focus is appropriate in the context presented here

as organic RZs dominate in headwaters underlain by till, which is the predominant soil type in the recently glaciated landscape of the boreal region (Chesworth 2008).

Moreover, we primarily focus on RZs that are hydrologically connected to streams and contribute the most to surface water biogeochemistry. Our conceptualization is suitable for RZs adjacent to streams in landscapes that may or may not have been affected by ditching or channel straightening in the past. In summary, the systems we focus on are organic RZs on forest till soils that are hydrologically connected to streams, widespread in boreal regions but also found in other areas worldwide (for example, Dick and others 2015). Hereafter, unless otherwise specified, the RZ acronym will refer to this type of systems.

CONCEPTUALIZING RIPARIAN ZONE HYDROLOGICAL CONNECTIVITY

Hydrological connectivity is a key aspect to consider when assessing RZ biogeochemical functioning and potential impacts on surface water quality (Laudon and others 2011; Blume and van Meerveld 2015). Following Ward (1989), we propose four dimensions of hydrological connectivity: (1) laterally along the hillslope, (2) longitudinally along the stream, (3) vertically down the riparian profile, and (4) temporally through event-based and seasonal changes in hydrology that expand or contract the spatial dimensions (Figure 1A). The longitudinal and lateral dimensions have recently received attention because wet areas which expand and contract synchronously with high and low base flow conditions (Ågren and others 2015) can be mapped using catchment surface topography (Murphy and others 2008; Blume and van Meerveld 2015).

Vertical heterogeneities in RZ down the profile are sometimes acknowledged (Lyon and others 2011), but the current conceptualization of hydrological connectivity between streams and RZs in the vertical dimension remains vague. RZs are often characterized by an exponential increase in field capacity, permeability, and hydraulic conductivity toward the soil surface (Nyberg and others 2001). As a consequence, the lateral movement of water to the stream increases dramatically as groundwater table rises and enters highly conductive layers during episodes (that is, precipitation and snowmelt events). This is a common phenomenon in boreal catchments (Moldan and

Wright 1998; Bishop and others 2011), and in till soils worldwide (McDonnell and others 1998; McGlynn and McDonnell 2003; Seibert and others 2003), which leads to a characteristic relationship between stream flow and groundwater tables in the RZ (Figure 2A). Therefore, the overall lateral flux is a function of both the hydraulic conductivity and the fraction of time that groundwater exceeds a certain depth (Figure 2B). For example, there is only a minor lateral flux from deeper permanently wet sections of the soil profile as the hydraulic conductivity is very low. Similarly, areas of very high hydraulic conductivity very near to the soil surface might not be activated even during extreme high flow events and thus do not contribute to the overall lateral flux. The majority of lateral fluxes to the stream thus originates from a relatively shallow depth and converges to a narrow layer in the riparian profile, as suggested by Schiff and others (1998). We propose to denominate this small region as the 'Dominant Source Layer,' a relatively narrow depth range within the RZ with the highest contribution to solute and water fluxes to the stream (Ledesma and others 2015; Blackburn and others 2017). In other words, the mobilization of solutes to streams is effectively limited to only a small fraction of the total RZ volume (Figure 2B). The Dominant Source Layer thickness was quantified in 11 riparian profiles in till soils within a boreal catchment, spanning from only about 13 cm to about 57 cm, or on average 32 ± 14 cm (Ledesma and others 2015). Narrower Dominant Source Layers were found in RZs with very shallow and relatively stable water table positions that concentrated lateral fluxes to the upper soil layers.

This flowpath structure has important biogeochemical implications as stream chemistry will be mostly determined by processes occurring in the Dominant Source Layer. Severe disturbance to forest stands (for example, final felling, windfall via storms, or insect-induced mortality) leading to decreased interception and evapotranspiration will tend to raise groundwater levels. Future climate change with expected increased precipitation will tend to have the same impact, even taking into account the effect of higher temperatures that will increase evapotranspiration (Oni and others 2015). A potential shift of the Dominant Source Layer to upper riparian soil horizons would imply that previously hydrologically disconnected strata within the RZ volume may start reacting with or mobilizing stored substances. These changes could either decrease or increase the capacity of RZs to buffer surface water pollution.

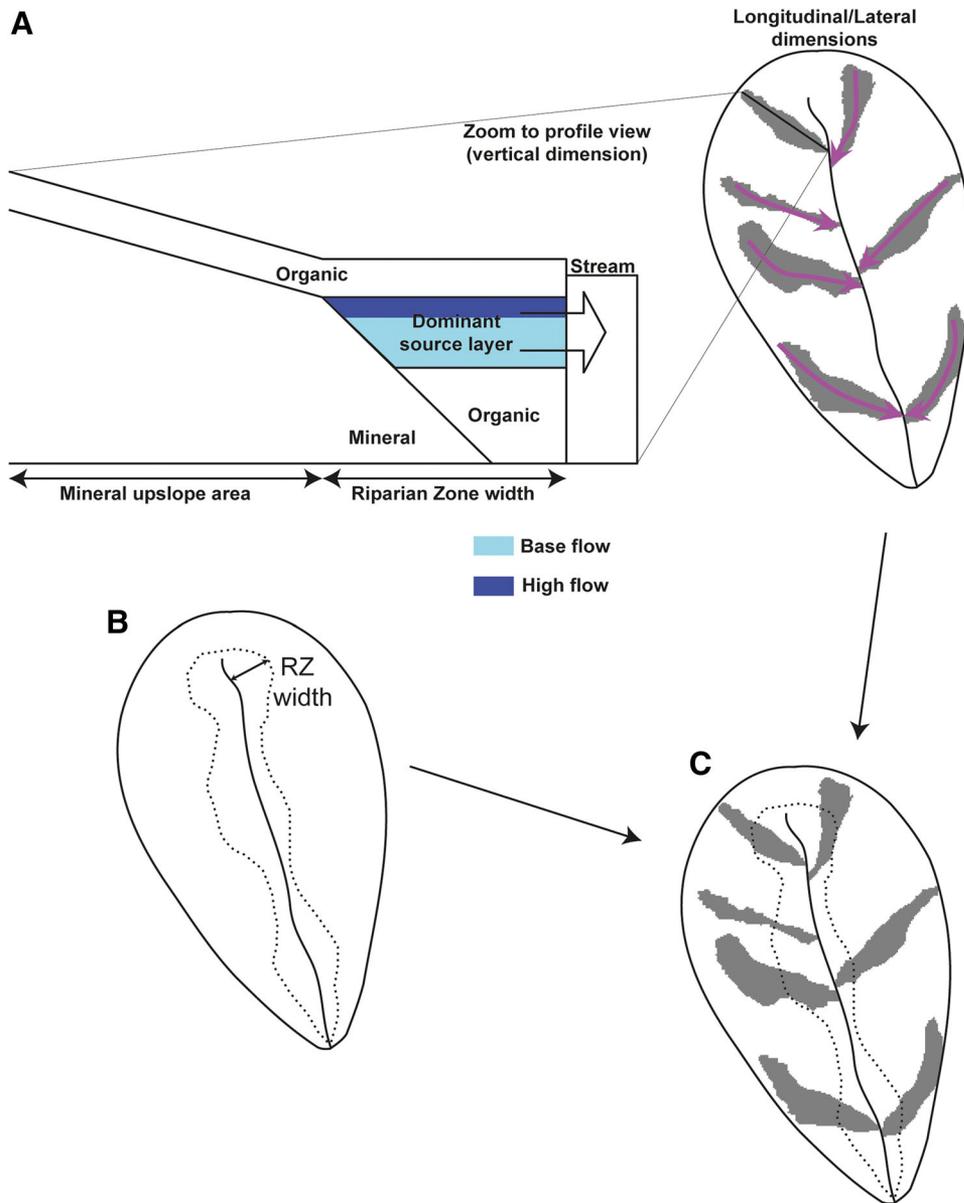


Figure 1. **A** Pattern of hydrological connectivity in a hypothetical headwater catchment including examples of important local drainage areas in the hillslope that represent lateral and longitudinal dimensions that connect to specific reach segments. The vertical dimension down the riparian profile is characterized by a narrow Dominant Source Layer that is responsible of most of the lateral water flux to the stream. **B** Conceptualization of the heterogeneous spatial distribution of riparian zone (RZ) widths along the stream based on the characteristic transition between organic and mineral soils in boreal forest hillslopes. **C** Overlapping between the most important hydrologically connected areas and the RZ widths, which are wider in wetter areas.

CONCEPTUALIZING RIPARIAN ZONE BIOGEOCHEMICAL FUNCTIONS

Chemical elements in soils, including boreal forest soils, originate from four primary sources: (1) biological fixation from atmosphere, (2) atmospheric deposition, (3) weathering from minerals, and (4) point sources from human activities (Table 1). Biological fixation from the atmosphere refers mainly to C (that is, photosynthesis) but can also include nitrogen (N) fixation (for example, riparian alder swamps). Due to the low RZ proportion in relation to the total catchment area (for example, ca. 10%, McGlynn and Seibert 2003), elements

from the atmosphere are deposited mostly in upslope soils, where they can later be leached to the RZ. This implies that most of the water passing through the RZ derives from the upslope areas in the rest of the catchment. Weathering is quantitatively more important in upslope soils as a result of, again, the larger upslope proportion and the mineral-like soils here. Nevertheless, weathering in the RZ can still be quantitatively important, especially if the mineral fraction here has a fine texture that allows for a large mineral surface area and consequent higher rates of element release (Erlandsson and others 2016). Biological nutrients such as C, N, phosphorous (P), and, in general, other elements

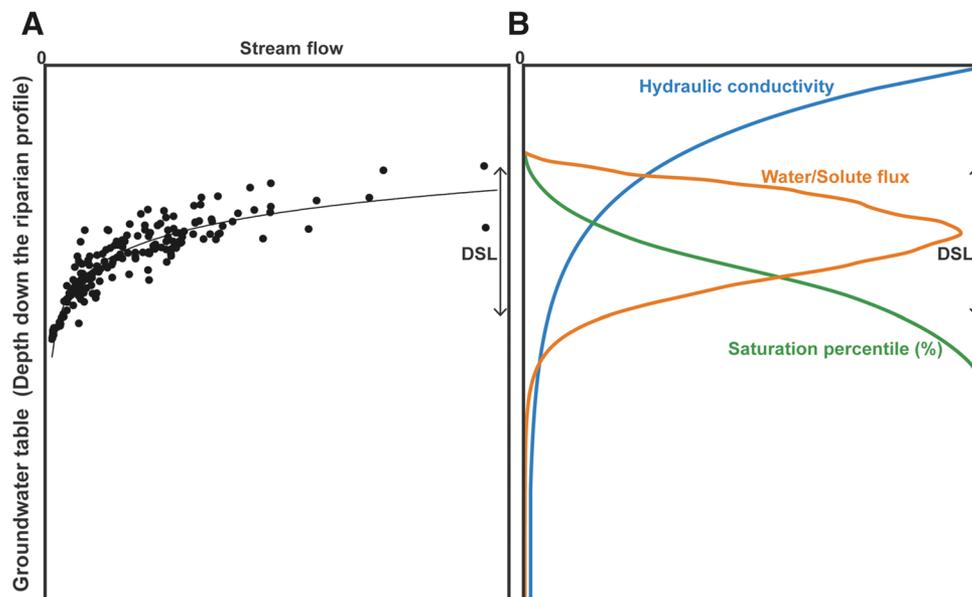


Figure 2. **A** Characteristic relationship between stream flow and groundwater tables in boreal riparian zone soils exemplified with actual daily data from a riparian profile within a Swedish headwater catchment. Following Darcy's law, the amount of water moving laterally through the riparian profile is equivalent to the stream flow. This means that for any given stream discharge, lateral flows at any given soil layer are proportional to the stream discharge-groundwater table *curve* and thus can be calculated and can be used to estimate the Dominant Source Layer (DSL). **B** Conceptualization of the vertical dimension down the riparian profile in hydrological connectivity including the DSL. Saturation percentile refers to the percentage of time that a specific depth is *below* the groundwater table during a hypothetical hydrological year.

that interact with the OM pool, will be subject to important internal cycling, whether they arrive in the RZ via biological fixation, atmospheric deposition, or upslope inputs.

In addition to providing most stream OM (Dosskey and Bertsch 1994), RZs can either retain or transform chemical elements and compounds derived from upslope inputs, in situ deposition, or in situ weathering on their way to the stream (Figure 3). Retention via interaction with OM and transformation via redox reactions are fundamental RZ biogeochemical functions, specific to the particular chemical element or compound. We will now describe these two biogeochemical functions providing specific examples, as well as summarize evidence of the importance of RZs for OM catchment exports. C represents the largest fraction of the OM (Mattsson and others 2009) and will be the primary focus. We will also interpret the role of timescales and hydrology.

Riparian Zones as Sources of Stream Organic Matter

A direct consequence of the RZ potential to accumulate OM is that they act as the main source of

organic compounds to the stream (Figure 3A). For example, RZ width is correlated with lateral organic C fluxes (Ledesma and others 2015) and likely also with the export of other substances interacting with OM. Leaf litter leachate, plant root exudates, and soil microflora degradation products are the secondary sources sustaining the OM pool in the RZ. The quantitative importance of these C fluxes varies over time and is primarily driven by drying/wetting and thawing/freezing cycles (DeLuca and Boisvenue 2012). Direct litterfall to boreal headwater streams is often small relative to temperate zone counterparts (Lidman and others 2017) and likely is less important to the allochthonous OM load than inputs delivered via lateral hydrological transfer through organic-rich RZ soils. At the same time, in-stream processing of bulk organic C is potentially a minor loss term in boreal headwaters, owing to short water residence times (Winterdahl and others 2016), particularly during high flow periods (Raymond and others 2016; but see Rasilo and others 2017).

Multiple lines of evidence support the apparent disconnection between upslope and RZ in the transfer of C to streams (Löfgren and Zetterberg 2011). First, riparian and upslope C differ in both

Table 1. Primary Sources of Chemical Elements and Compounds in Catchments, Retention Capacity of the Riparian Zone via Organic Matter (OM) or Whether the Element can be Part of the OM Itself, and Examples of Main Redox Transformation Processes with Environmental Significance

Chemical	Source in catchments	Retention capacity of the riparian zone	Redox transformations
C	Biological fixation	Part of OM	Methane (CH ₄) formation CO ₂ formation
N	Atmospheric deposition Biological fixation Point sources	Part of OM	Nitrate (NO ₃ ⁻) removal Ammonium (NH ₄ ⁺) formation
P	Weathering Point sources	Part of OM Medium (inorganic)	
S	Atmospheric deposition Weathering	Part of OM Medium (inorganic)	Sulfate (SO ₄ ²⁻) formation
Mg, Ca, Na	Weathering Atmospheric deposition	Low	
K	Weathering Atmospheric deposition	Low interaction with vegetation	
Si	Weathering	Medium via vegetation	
Al	Weathering	Medium	
Fe	Weathering	Medium	Fe ²⁺ (soluble) Dissolution of Fe ³⁺ colloids
Hg	Atmospheric deposition Weathering Point sources	Medium	Net methylation of mercury to methylmercury (MeHg)
Pb	Atmospheric deposition Weathering Point sources	High	
Metals and trace elements	Weathering Point sources	Medium to high	In certain cases: Se, U, V, Mo, As, Sb, Sn, etc.
Persistent organic pollutants (POPs)	Atmospheric deposition Point sources	High	

quantity (Dosskey and Bertsch 1994; Boyer and others 1997; Hinton and others 1998; Köhler and others 2009; Strohmeier and others 2013; Dick and others 2015) and quality (Sanderman and others 2009; Kothawala and others 2015), whereas stream organic C is similar to riparian organic C both quantitatively and qualitatively. Second, estimates of annual net ecosystem production (NEP, Chapin and others 2006) in RZs appear more than sufficient to support annual exports of stream organic C

(Ledesma and others 2015), highlighting the key role of the riparian vegetation for OM accumulation and transport. Furthermore, much of the organic C found in boreal streams is of recent origin, as determined by ¹⁴C measurements (Schiff and others 1998; Ledesma and others 2015). Finally, most of the C stored in boreal forest upslopes is potentially derived from roots and mycorrhizal fungi (Clemmensen and others 2013), but RZs are generally hypoxic and do not support mycorrhizae

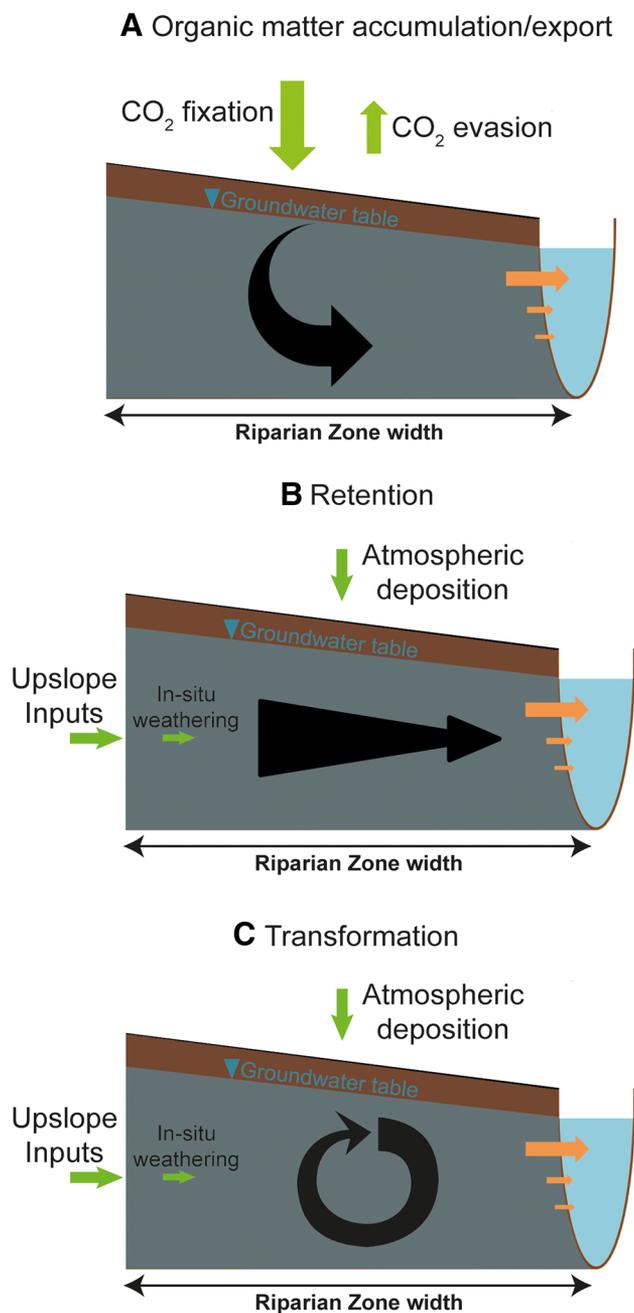


Figure 3. Conceptualization of riparian zone (RZ) biogeochemical functions: **A** organic matter accumulation and export (from leaf litter, plant root exudates, and soil microflora), **B** retention of chemical elements and compounds via interaction with organic matter, and **C** transformation of chemical elements and compounds via redox reactions. *Orange arrows* represent lateral water and solute fluxes from RZs to streams, concentrated in a relatively narrow layer within the riparian profile, the Dominant Source Layer. *Black arrows* represent each of the specified functions (Color figure online).

(Brady and Weil 1999). This provides further evidence for the decoupling of the upslope and riparian C cycles and implies that the terrestrial C exported to streams is regulated in fundamentally different ways than the C stored in the surrounding catchment.

Organic N, organic P, and organic sulfur (S) dynamics are similar to those of organic C, as they are all part of the OM produced in and transported from RZs to streams (Baldwin and Mitchell 2000; Hagedorn and others 2000; Skyllberg and others 2003; Petrone and others 2007). Although there

can be similarities in the behavior of organic forms of, for example, C and N in forest soils (Kothawala and Moore 2009), the two elements do not always display synchronous dynamics (McDowell and others 1998; Michalzik and Matzner 1999). This can be attributed to the relative importance that internal cycling has on the different elements that compose OM as, for example, most N and P mobilized to boreal streams originates from internal cycling (Blackburn and others 2017).

Retention of Chemical Elements and Compounds Via Interactions with Organic Matter in the Riparian Zone

The potential for a soil to store positively charged chemical species is defined by the cation exchange capacity (CEC), an estimate of the total negative charge given by OM and clay minerals. In RZs, the functional groups creating CEC belong mostly to OM. These are hydroxyl ($-OH$) and carboxyl ($-COOH$) groups that interchange their protons with cations in the solution in a pH-dependent process (Skylberg and others 2001). This, in turn, creates the potential for retention of cationic elements in the RZ (Figure 3B). The retention process is complex, especially in acidic soils typical of boreal RZs where aluminum (Al) species play an important, pH-dependent role in the exchange mechanism (Ross and others 2008). Flocculation–precipitation processes mediated by OM can also be responsible for element retention (Selim and Kingery 2003). For the purpose of the conceptualization, we assume a scale of element-specific retention potential, where conduit flow through the RZ would be at the lower end of the scale (no retention) and no transport at all would be at the upper end of the scale (full retention) (Table 1).

It is difficult to find examples of compounds that simply pass through the RZ without alteration as in a conduit system. Some studies suggest that the stream signal of the base cations calcium (Ca), magnesium (Mg), and sodium (Na) is controlled by an upslope mineralogical signal given the small temporal variation in RZ solute concentrations similar to upslope concentrations (Burns and others 1998; Ledesma and others 2013; Lidman and others 2016). The RZ would seem to act as a mere conduit in this case continuously equilibrating to the upslope release of Ca, Mg, and Na. Potassium (K) would also be located at the low side of the retention scale, and it is more strongly influenced by vegetation recirculation than other base cations (Tukey 1970). Silicon (Si) has a low affinity for OM but has been shown to be retained within the RZ

via accumulation by plants (Struyf and Conley 2009; Struyf and others 2009).

In general, the affinity of heavy metal cations for OM binding is larger than that of alkali and alkaline cations and tends to increase with oxidation state (Förstner and Wittmann 2012). These organophilic properties would situate these elements in the medium to high range within the RZ retention scale (Table 1). Both Al and iron (Fe), quantitatively important metals in boreal catchments (Löfgren and others 2010; Temnerud and others 2014), have been shown to be retained in RZs (Mulder and others 1991; Pellerin and others 2002; Knorr 2013; Riedel and others 2013). Mercury (Hg) also tends to bind to OM (Lee and others 2000; Ravichandran 2004) and can be retained in organic soils (Johansson and others 2001; Skylberg and others 2006). Lead (Pb) can be highly retained in RZs (Klaminder and others 2006) and would appear in the upper end of the retention scale. Depending on pH and redox behavior, other organophilic metals including toxic metals, trace elements, and heavy metals in general can be expected to be moderately to highly retained in RZs (Neubauer and others 2013; Köhler and others 2014; Lidman and others 2014, 2016). Persistent organic pollutants (POPs) such as polychlorinated biphenyls (PCBs) and legacy pesticides have high affinity to bind to OM via hydrophobic interactions and are usually highly retained in RZs (Bergknut and others 2011).

Many of the chemical elements and compounds discussed above are environmental pollutants that in many cases are toxic to biota. Therefore, the retention function makes RZs extraordinary buffers of surface water pollution. However, the high affinity for OM also allows for co-transport when OM is solubilized and mobilized to the streams, for example, in the case of Al (Cory and others 2007), trace elements (Köhler and others 2014), and potentially POPs. The combination of long-term pollutant accumulation, disturbances such as ditching, and future climate with predicted increase in precipitation and OM leaching could have far-reaching and unknown consequences for surface water quality in boreal regions unless a conceptual framework suitable for organizing information and making predictions is provided.

Transformation of Chemical Elements and Compounds Via Redox Reactions in the Riparian Zone

Microbial oxygen consumption in riparian soils is positively correlated with OM content (Gurwick

and others 2008), with especially high rates of biochemical processing in highly organic soils. Thus, OM is the essential substrate for microbes in reduction–oxidation processes. Although RZs are dominated by hypoxia due to shallow water levels and microbial activity, transient oxic–hypoxic conditions can occur as a consequence of groundwater table fluctuations. This process is especially important in the Dominant Source Layer (Figures 1A, 2B). Oxygen (O_2) is energetically the most preferable electron acceptor for reduction reactions under the frequently occurring hypoxic conditions, but inorganic forms of N, S, or Fe (among others) can act as alternative electron acceptors driving important elemental transformations (Hedin and others 1998). Different OM compounds at different reduction states act as electron donors during both hypoxic and oxic conditions. As in the case of cation exchange ascribed to the retention function, pH plays an important role in reduction–oxidation processes because many redox reactions involve the transfer of one or more protons, which makes these reactions pH-dependent (Becking and others 1960).

Reducing conditions in the RZ can lead to the formation of methane (CH_4), a potent greenhouse gas which could be either transferred laterally to the stream or released to the atmosphere (Hope and others 2001; Sun and others 2013), but also reoxidized to carbon dioxide (CO_2) before leaving the system. CO_2 is the main product of OM oxidation and a subproduct of most other redox reactions. The lateral transfer of inorganic C including CO_2 from the terrestrial to the aquatic system is quantitatively important in regional and global C budgets (Wallin and others 2013), and it appears that most of it could originate in the RZ (Leith and others 2015).

Inorganic N, largely in the form of nitrate (NO_3^-), has been widely studied in riparian systems (for example, Cirimo and McDonnell 1997). RZs effectively remove NO_3^- through uptake and denitrification (Vought and others 1994), a process driven by the local occurrence of hypoxic zones in conjunction with labile organic C (McClain and others 2003). Denitrification results in the production of inert molecular N gas (N_2), although nitrous oxide (N_2O), a powerful greenhouse gas, can also be produced (Lashof and Ahuja 1990; Hedin and others 1998). NO_3^- removal is important for reducing the impact of N export in agricultural systems (for example, Ocampo and others 2006; Duval and Hill 2007; Pinay and others 2015), but the process has also been shown in RZs in natural temperate and boreal catchments (for

example, Simmons and others 1992; Fölster 2000; Ranalli and Macalady 2010). Given the potential importance of RZs for the breakdown of OM to CO_2 , there is also the possibility for these environments to generate ammonium (NH_4^+) via OM mineralization and elevated levels of NH_4^+ have been observed in riparian wells under hypoxic conditions (Mulholland 1992). In boreal headwaters, NH_4^+ production in hydrologically active layers of the RZ may serve as the dominant source of inorganic N to streams (Blackburn and others 2017). Nonetheless, NH_4^+ production and accumulation has also been reported in RZs from different biomes (for example, tropical rain forest catchments) (McDowell and others 1992; McClain and others 1994), supporting the universality of many of the processes presented here.

Hypoxic conditions in RZs can also lead to a reduction in the oxidation state of metals, which can have far-reaching consequences for their mobility and biogeochemistry. For example, the mobility of Fe is enhanced under such conditions because of the reduction to the more soluble Fe^{2+} form. Manganese (Mn) can also be expected to be generally more mobile under more reducing conditions (Björkvald and others 2008).

Episodic oxic conditions can lead to the oxidation of reduced organic S compounds and the formation of sulfate (SO_4^{2-}) (Devito and Hill 1997; Ledesma and others 2016), which controls the solubility of OM and the acidification status of soils and waters (Clark and others 2006; Futter and others 2014). Similarly, episodic changes in the redox conditions of the RZ have profound effects on the oxidation state and, consequently, the mobility of selenium (Se), both an essential and potentially toxic element to biota (Lidman and others 2011).

RZs do not always play the role of buffering water bodies. On the contrary, they can potentially contribute to stream pollution and toxicity, depending on the degree of hydrological connectivity and availability of OM to support microbial activity. One of the most important examples relates to Hg. Fluctuating oxic–hypoxic conditions in RZs and the presence of OM, which acts as an energy source and co-transport Hg, are ideal for the net methylation of mercury (Bishop and others 1995; Eklöf and others 2015). Methylmercury (MeHg) is a highly toxic species of Hg with high potential for bioaccumulation. Methylation is carried out by microbes such as sulfate-reducing bacteria and therefore coupled to the availability of OM substrate (the electron donor) and electron acceptors such as SO_4^{2-} . In boreal catchments, where atmospheric deposition of both Hg and

Table 2. Driving Factors and Dominant Processes in the Riparian Zone and Their Effects on the Dominant Source Layer (DSL) Over a Range of Timescales

Timescale	Driving factors	Dominant riparian zone processes	Effect on DSL
Millennia	Topography Geology	Restricted water flows and development of areas of poor drainage	
Centuries	Climate Vegetation	Accumulation of organic matter in areas of restricted flow Development of reducing environments	Gradual rise
Decades	Disturbances (fire, ditching, forest harvesting)	Changes in oxygenation Changes in organic matter mineralization Alteration in hydrological connectivity	Abrupt and long-lasting changes both up and down
Annual	Seasonality of temperature and runoff	Retention of elements and compounds Reduction–oxidation processes	Predictable seasonal cycle based on dominant hydrograph
Event (hours–days)	Storm and snowmelt events	Mobilization and transport	Activation of more conductive strata

There is a super-position of effects as processes occurring at a longer timescale (for example, organic matter accumulation over centuries) influence the behavior of the DSL at shorter timescales (for example, long-lasting shifts due to ditching or other disturbance).

SO₄²⁻ has been relatively high during the industrial period (Mylona 1996; Johansson and others 2001), the formation of MeHg in RZs is a present and a future threat for aquatic ecosystems.

The role of Timescales and Hydrology in Relation to Riparian Biogeochemical Functions

As proposed by Burt (2005), the RZ acts, paradoxically, as both a conduit and a barrier between the terrestrial and the aquatic environments. We also highlight the importance of transformations within the RZ and argue that the proposed paradox is ultimately regulated by hydrology; specifically, the time water takes to transit the landscape and the degree of connectivity between terrestrial and aquatic environments (Table 2).

Over the long term (centuries to millennia), RZ function is controlled by the manner in which climate, vegetation, and topography mediate hydrology. When there is sufficient precipitation, OM and atmospherically deposited pollutants can build up in areas of poor drainage. OM buildup is facilitated by slow drainage, which limits oxygen availability, thereby promoting reducing conditions and slowing decomposition rates (DeLuca and Boisvenue 2012). Because OM increases the water holding capacity of the soil, there is a feedback process that can further increase OM buildup.

Over decades to centuries, previously retained or accumulated compounds can be slowly detached from the riparian OM matrix due to changes in physicochemical equilibria and leached to the stream in the same or different chemical form. Depending on the strength of the association between the particular element or compound and the riparian OM, this process can be delayed for a few years, decades, or even centuries, as suggested for Pb (Klaminder and others 2006). Over a similar time period, disturbances including fire, ditching, or upslope and riparian forest harvesting can alter the hydrological connectivity between zones of OM buildup and the stream. For example, widespread ditching could have had two important consequences: (1) a change in the hydrological connectivity and transit times between soils and streams and (2) a shift in the soil redox status toward more extensive and frequent oxic conditions. As reduction–oxidation processes are key to functioning of terrestrial–aquatic transition zones (Hedin and others 1998), changes in redox state have likely had important implications for material cycling and water quality in the region (for example, Lidman and others 2014).

Over an annual timescale, the manner in which weather and precipitation patterns control flows through the RZ are the primary control on stream chemistry. During relatively long periods of low flow or summer dryness, transport and oxygen

availability are both limited and there is often time to transform (or remove as a particular case of transformation) specific compounds (for example, NO_3^- , MeHg).

In the short term (hours–days), hydrological events (rain storms and spring floods) mobilize compounds stored in the RZ. These events are typically too rapid to significantly alter the redox environment in the RZ. Events can, for example, export accumulated elements or compounds that would otherwise be degraded or transformed if there was enough time, turning the RZ function from retention or transformation to conduit (as a particular case in the retention scale). Thus, the biogeochemically processed substances in the RZ are mostly mobilized to the stream during relatively short periods of the year (Boyer and others 1997; Köhler and others 2008).

Bearing in mind the role of hydrology and how connectivity and transit times influence retention, transformation, and mobilization of solutes can help in understanding how RZs can act as both conduits and barriers, and so also as both sinks and sources of pollutants (for example, Cory and others 2007). Hydrological processes governed by longer timescales can both amplify or diminish hydrological effects observed at shorter timescales. For example, future climate in the boreal region will tend to increase the frequency of snowmelt episodes but these will be of less intensity (Oni and others 2015).

CONCEPTUALIZING RIPARIAN ZONE SPATIAL HETEROGENEITY

The rate and spatial pattern of soil OM accumulation is typically heterogeneous within catchments (Zimmer and others 2013; Herndon and others 2015). The RZ extent is therefore heterogeneously distributed along streams (Figure 1B) as driven by local hydromorphological characteristics. For example, wider RZs are related to shallower groundwater tables and a larger topographic wetness index (TWI), a surrogate for shallow groundwater table positions (Grabs and others 2012; Ledesma and others 2015). These relationships are not surprising, but their implications are often ignored.

To explore the consequences of spatial heterogeneity in the RZ, the lateral extent of organic soils from the stream edge to the transition to mineral podzols following the local topographical slope was measured in ten forest hillslopes located in the boreal catchment from which our conceptualization was developed. Because of the large hetero-

geneity in hydromorphological and topographical characteristics of the hillslopes, the extent of the RZ width varied widely, between only about 2 m to as much as 40 m, or on average 19 ± 15 m (Ledesma and others 2015). At the same time, the actual OM content of those organic riparian soils, defined by their C content, was somewhat variable and in general correlated positively with the extent of the RZ. Typically, the C content of the Dominant Source Layer of relatively flat and wet RZs was not below 30% and it could reach more than 50% (Ledesma and others 2015). This contrasts strongly with the corresponding upslope podzols, for which C content below the narrow organic topsoil horizon is typically below 3% (unpublished data from the same catchment). These simple measurements provide a clear picture of RZ spatial heterogeneity and importance for biogeochemical processing and surface water chemistry in relation to the rest of the catchment.

As OM is the key in the riparian biogeochemical control, the potential magnitude of the RZ functions is larger in wider RZs. In other words, the wider the RZ (which serves as a proxy to OM content), the longer the transit distance of the water in organic-rich layers and the larger the potential for retention or transformation of elements and chemical compounds. Hence, the heterogeneous distribution of RZs in space translates into a heterogeneous intensity of the RZ biogeochemical functions. These functions are important for soil water chemistry and also influence surface water quality in wet areas hydrologically connected to streams (Figure 1C), particularly if they occur within the Dominant Source Layer, a concept that explicitly recognize the importance of the vertical dimension for hydrological connectivity.

Bernhardt and others (2017) recently criticized the tendency of researchers to only consider the spatial or temporal component of biogeochemical variation, referring to the hot spot and hot moment concepts introduced by McClain and others (2003). Our conceptualization of the Dominant Source Layer integrates both process and transport phenomena. Thus, it addresses the recommendation from Bernhardt and others (2017) to incorporate both spatial and temporal components, as well as the interplay between resource pools and hydrological pattern, and in this way illustrates how important ‘ecosystem control points’ can emerge in low-gradient boreal landscapes. So as to specifically characterize the RZ structures and processes that will allow identifying ‘ecosystem control points’ such as the Dominant Source Layer, we briefly

review and suggest methods for mapping hydrological connectivity and RZ areas below.

Methods for Mapping Hydrological Connectivity and Riparian Zone Areas

Heterogeneity in hydrological connectivity between the RZ and aquatic environment must be recognized in any assessment of RZ function. Blume and van Meerveld (2015) reviewed different methods that have been used to study subsurface hydrological connectivity, including trenches, distributed groundwater table measurements, tracer experiments, and stream chemistry measurements. These methods have difficulties handling the large variability in hillslope responses. Recent advances in remote sensing techniques provide new opportunities to map hydrological connectivity. In particular, high-resolution Digital Elevation Models (DEMs) based on Light Detection and Ranging (LiDAR) data can be used to identify subsurface flow direction and accumulation (Ali and Roy 2010). This information can, in turn, be used to delineate wet areas (Ågren and others 2014; Pinay and others 2015), as well as to estimate longitudinal/lateral connectivity (Jencso and others 2009) and depth to groundwater (Grabs and others 2012). Estimating groundwater levels is essential to identify the vertical position and extent of the Dominant Source Layer. Monitoring of groundwater levels is an alternative to establish the relationship between stream flow and groundwater tables of individual riparian sites that will allow estimating Dominant Source Layers empirically (Figure 2A). We argue that identifying the spatial structure of vertical connectivity to the stream within the riparian profile is at least as important as mapping wet areas in the catchment surface and should be considered in any assessment of headwater hydrological connectivity.

Linking hydrological transport to RZ width and OM properties, however, is still challenging. Precise RZ width estimates are usually based on field observations in a number of selected transects within a catchment (McGlynn and Seibert 2003; Ledesma and others 2015). This method is time-consuming and does not produce a complete RZ delineation. Terrain attributes like the recently developed depth-to-water (DTW) index, which represents the elevation difference between the soil surface and the nearest open water body, appear to be more effective than the traditional TWI in determining soil types (Murphy and others 2011; Ågren and others 2015) and could be a promising tool to map RZs.

IMPLICATIONS FOR RIPARIAN UPSCALING AND LAND MANAGEMENT

RZs have been traditionally conceptualized as linear features buffering lotic water bodies. These lumped conceptualizations of the RZ from single representative riparian profiles or single RZ widths have often been used to investigate the links between riparian and stream chemistry and hydrology (Boyer and others 1996; Smart and others 2001; Sanderman and others 2009; Seibert and others 2009; Gundersen and others 2010). However, given the large spatial heterogeneity in RZ distribution and function, this lumped approach leads to oversimplifications when upscaling results to catchments and landscapes (Blume and van Meerveld 2015). As such, spatially explicit and distributed representations of RZ structures and functions are needed to accurately upscale the integrated riparian signal to the catchment level. More efforts should be made using indexes based on remote sensing techniques to map wet areas and water flowpaths and to try to differentiate histosols from mineral soils, the typical soil configuration in boreal forest catchments, and thereby RZs. This would help characterizing hydrological connectivity and the landscape ordination of RZ heterogeneity along the stream continuum, facilitating riparian upscaling. Once hydrological connectivity and RZ ordination are delineated, hypotheses based on the conceptual model presented here can be tested empirically. The idea of a Dominant Source Layer is one under-explored concept which could explain differences in stream chemistry observed between wet and dry years (for example, Köhler and others 2008) or following forest clear-cutting (for example, Schelker and others 2012). Combining estimates of lateral water fluxes and solute concentration measurements, in both RZs and upslope soils, will allow for evaluating mass balances and potential biogeochemical processes occurring in relevant areas of the landscape. From a surface water quality perspective, measurement efforts should then be made only on those specific areas of the landscape that contribute the most to water and solute fluxes to the stream.

Forestry, an important economic activity and the most common type of management in boreal forests (Gauthier and others 2015; Futter and others 2016) can amplify Hg mobilization (Eklöf and others 2012) or increase NO_3^- leaching (Keller and others 2006; Futter and others 2010). The mobilization of Hg is associated with both a higher methylation potential and an increase in co-transportation with C following the corresponding rise

in groundwater tables after harvesting. Leaching of NO_3^- is favored by the decrease in plant uptake and increased hydrological transport. So-called riparian buffer strips are an important management practice in forestry to avoid adverse impacts of forest harvesting on aquatic environments (Kreutzweiser and others 2008; Gundersen and others 2010). For biodiversity and aquatic protection purposes, it has been suggested that unharvested buffers should be between 30 and 200 m wide (Castelle and others 1994). Although different buffer widths might be recommended based on local variations in features such as slope (Hazlett and others 2008), fixed width buffers are often applied without consideration of the spatial heterogeneity of the RZ (Richardson and others 2012; Kuglerová and others 2014a). Fixed width buffers have been used as they are easily implemented, but new conceptual understanding of riparian functioning, together with computational techniques and digital maps, provide the tools needed to optimize buffer designs that move beyond fixed width approaches (Kuglerová and others 2014a). Indeed, recent studies suggest that riparian buffers closely resembling their natural regimes should vary in width, tree-age structure, and species composition across relatively small spatial scales to optimize protection (Kreutzweiser and others 2012). In light of the hydrological, biogeochemical, and spatial heterogeneity of RZs presented here for locally adapted management, improved water quality protection can be achieved more efficiently. By including more mechanistic insights related to local RZ characteristics concerning hydrological connectivity, storage and transformation of elements and compounds, and susceptibility to perturbation, forest management can take action to minimize impacts on stream water quality (Laudon and others 2016).

Conceptualizations of forest biogeochemical processes can be an important tool for communicating the consequences of anthropogenic activities including forestry on water quality (Futter and others 2016). The conceptualization presented here, which has been mainly, but not only, exemplified by boreal forest headwaters, should also be useful for other similar areas (for example, low-gradient, peat-rich RZs in temperate and tropical forests) and other land-use types within the boreal biome (agricultural systems and lakes). In essence, hydrological connectivity and biogeochemical functions of OM-rich areas such as the RZs presented here are universal, extending the applicability of these concepts to a broad scale. However, it would still be necessary to verify our

conceptualization in similar areas, but also most interesting to assess its utility in environments in which RZs are not defined by OM content, there is no relationship between groundwater tables and stream flow, runoff generation is dominated by overland or subsurface unsaturated flow, or climate is warm and dry. Particularly, it would be most valuable to test whether the Dominant Source Layer concept is applicable in such environments. A refined picture of RZs in terms of hydrological connectivity, biogeochemical functioning, and spatial heterogeneity is an essential prerequisite for ecologically sustainable and economically effective land management that preserves surface water quality. This includes the specific recognition and identification of the Dominant Source Layer, a deeper understanding of the processes of retention and transformation and, foremost, an adaptive consideration of RZ spatial distribution.

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