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The influence of riparian zone heterogeneity on land-water connections in boreal headwaters

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"By the time it came to the edge of the Forest, the stream had grown up, so that it was almost a river, and, being grown-up, it did not run and jump and sparkle along as it used to do when it was younger, but moved more slowly. For it knew now where it was going, and it said to itself, "There is no hurry. We shall get there some day." But all the little streams higher up in the Forest went this way and that, quickly, eagerly, having so much to find out before it was too late."

A.A. Milne

Table of Contents

List of Papers

I.

Hydrogeomorphology drives biogeochemical patterns in riparian soils along a boreal headwater stream.
Melissa Reidy, Scott Buckley, Sandra Jämtgård, Hjalmar Laudon & Ryan. A. Sponseller (2024)
In revision at Freshwater Science.

II.

Riparian zone heterogeneity influences the production and fate of biodegradable dissolved organic carbon at the land-water interface.
Melissa Reidy, Martin Berggren, Anna Lupon, Hjalmar Laudon, Ryan. A. Sponseller (2024)
Submitted to Journal of Geophysical Research: Biogeosciences.

III.

Biogeochemical responses to drying-wetting in riparian soils influences carbon mobilization.
Martin Škerlep, **Melissa Reidy**, Hjalmar Laudon, Ryan. A. Sponseller (2024)
Manuscript.

IV.

Reconciling modes of lateral connectivity across riparian interfaces in a boreal headwater catchment.
Melissa Reidy, Nícolas Finkler, Jason Leach, Hjalmar Laudon, Ryan Sponseller (2024)
Manuscript.

Author Contributions

I.

The study was designed by MR and RS. Field work was carried out by MR. Laboratory work was carried out by MR with assistance from SB. Specific protocols for assays were designed by SB, MR and SJ. MR performed all statistical analyses. HL provided the infrastructure. SB, SJ and HL provided insights to analysis and interpretation of the data. The manuscript was written by MR and RS, and all authors commented on the manuscript

II.

The study was designed by MR and RS. Field and laboratory work was carried out by MR. Biodegradability incubation protocols were designed by MR with input from AL, MB and RS. HL provided the infrastructure. All authors provided feedback and insights to analysis and interpretation of the data. The manuscript was written by MR and RS and all authors commented on the manuscript.

III.

The study was designed by MŠ, MR and RS. Field work was carried out by MŠ, MR and RS. Laboratory work was carried out by MŠ, with enzyme activity assays performed by MR. MŠ performed data collation and analyses. MR, RS and HL provided insights to data interpretation and analysis. MŠ wrote the manuscript, with contribution from MR and RS and all authors commented on the manuscript.

IV.

The study was designed by MR with assistance by RS. MR performed statistical analyses. NF, JL, HL and RS provided insights to data interpretation, analysis and conceptual direction. MR and RS wrote the manuscript and all authors commented on the manuscript.

MR: Melissa Reidy; **RS**: Ryan Sponseller; **SB**: Scott Buckley; **SJ**: Sandra Jämtgård; **HL**: Hjalmar Laudon; **AL**: Anna Lupon; **MB**: Martin Berggren; **MŠ**: Martin Škerlep; **NF**: Nícolas Finkler; **JL**: Jason Leach.

Abstract

Riparian zones are hydrogeomorphically heterogeneous, which may influence how, when, and where groundwater forms lateral connections between riparian soils and streams. These lateral connections represent important linkages between organic riparian soils and the expansive network of smaller headwater streams that are ubiquitous features of northern boreal landscapes. By way of lateral connections, riparian zones function as a source of organic and inorganic solutes to aquatic ecosystems. Yet, heterogeneity within the riparian interface complicates how we can mechanistically explain the role of the riparian zone as a source.

Here, I explore the influence of hydrogeomorphic heterogeneity on the biogeochemical role of boreal riparian zones. By assessing soil properties, extracellular enzyme activity and microbial community composition I show that the capacity of a riparian site to do important biogeochemical work is directly influenced by the hydrogeomorphic setting. This creates substantial spatial and temporal complexity in the generation and transfer of degradable organic matter from riparian soils to inland water continua. Additionally, we experimentally test how drying and rewetting changes the mobilization of dissolved organic carbon in riparian soils, which may hint to how riparian zones will respond to drought as part of a changing climate. Further, I use relationships between solute concentration and groundwater discharge to show that a range of solute mobilization patterns from riparian sites are linked to the hydrogeomorphic heterogeneity of the riparian interface. Finally, I show that contrasting modes of lateral connectivity can simultaneously influence the stream, but do so via different mechanisms, across different response variables and at different spatial scales.

This thesis shows that hydrogeomorphic heterogeneity influences a boreal riparian zone by determining the capacity of riparian soils to do important biogeochemical work, and the level of hydrological opportunity that riparian zones have to influence the adjacent stream via lateral connectivity. Ultimately, the riparian zone offers us the chance to use interactions between capacity and opportunity to more effectively manage and protect streams and aquatic networks in headwater catchments.

Background

Riparian zones

Riparian zones are the interface between terrestrial and aquatic ecosystems. In a unique landscape position at the border of both land and water, riparian zones can influence the ecological and chemical characteristics of streams, rivers and lakes through multiple above- and belowground mechanisms (Gregory et al. 1991, Wymore et al. 2023). The riparian interface can be relatively small in area compared to other parts of the surrounding landscape, yet may exert an ecological and biogeochemical influence that belies their small size. Because of this, riparian zones have been widely used to buffer streams against influxes of upland solutes (Pinay & Décamps, 1988; Vidon & Hill, 2004), but in some settings, they can also be vital sources of organic resources to adjacent freshwater ecosystems (Hinton et al. 1998; Findlay et al. 2001).

The function of a riparian zone as a 'sink' and/or 'source' is driven by the lateral movement of groundwater through the soil and sediment that sit directly adjacent to the stream. Broadly, groundwater travels from surrounding hillslopes, through riparian soil strata and, eventually, discharges into the stream. As it travels along this pathway, the chemistry of groundwater is altered, as it intersects soils that may generate different solutes in a variety of forms (Li et al. 2020). However, riparian soils are not merely a conduit for groundwater. Riparian soils can support microbial processes under dynamic redox conditions, which consume, transform and release organic matter and nutrients (Hedin et al. 1998; Duncan et al. 2015). Hence, by the time groundwater enters the stream, it has been biogeochemically shaped by the landscape it has travelled through. In some cases, groundwater has lost solutes, which is a key motivation behind the use of riparian zones as nitrate buffers to agricultural streams (Peterjohn & Correll 1984). In other cases, groundwater has gained solutes from the landscape, which can be detected within the stream by changes in chemistry (McDowell & Likens 1988) and posits the riparian zone as a source to stream ecosystems.

Lateral connections across riparian zones

Because riparian zones have the capacity to function as sources and sinks of solutes to streams, they have been well-studied within catchment science and aquatic ecology alike. As such, our understanding of the ways in which groundwater forms the connection between riparian soils and streams has broadened to now encompasses a diversity of lateral connection types (Beven & Kirkby, 1979; Junk et al., 1989; Blume & van Meerveld, 2015) which are not binary classifications, but rather form a gradient of connection strength and frequency.

One way that these lateral connections occur are from groundwater levels rising in response to hydrological events, which links hillslopes to riparian areas (Montgomery et al. 1997; Vidon, 2011). This response will vary across landscapes, dependent on the underlying bedrock and surface topography (Freer et al. 1997; Graham et al. 2010) and the levels of soil moisture already present (Kim et al. 2005). Generally, this type of connection between riparian zone and the surrounding landscape is more episodic, requiring inputs of water that are of a sufficient magnitude to facilitate hydrological connectivity (McGuire & McDonnell, 2010). In contrast, stronger, and more persistent, lateral connections may be formed by large zero-order (i.e., channel-less) basins (Sidle et al. 2018) and concave hillslopes, which can also be associated with groundwater flowpaths that are shallow (i.e., nearer to the surface), higher volume and directly discharge into streams (Briggs & Hare 2018). Overall, riparian zone function, and its relevance to the surrounding terrestrial and aquatic landscape, is inherently tied to the variability of lateral connectivity.

Riparian hydrogeomorphic heterogeneity

Variability in the strength of lateral riparian connections is driven by where, when, and how long it takes for groundwater to move from hillslope to stream, which is a product of the physical structure of the surrounding landscape (Devito et al. 2005; McGuire et al., 2005). Further, riparian zones can be notoriously variable in their local geomorphology, soil properties and the vegetation communities aboveground (Grabs et al. 2012; Elliot et al., 2015), which together can generate considerable hydrogeomorphic heterogeneity at the margin of streams. To contextualize this, if we took our shovels and dug holes in a hydrogeomorphically homogeneous riparian zone, we would find that the properties of the soil we're digging into, how deep we had to dig to find groundwater, and the ways in which groundwater moved through this soil would all be relatively similar along the length of a stream. In reality however, hydrogeomorphically homogenous riparian zones are not what we would encounter in most near-stream areas. Instead, in most riparian areas, we would find that soils, depth to groundwater and flowpaths would differ between the holes that we dug alongside a stream, which reflects the hydrogeomorphic heterogeneity inherent to these interface zones. Importantly, this variability can occur at very local scales, which means that along a single stream, the extent to which the riparian zone shapes groundwater chemistry, and the strength, timing and duration of this groundwater connecting with the stream can be widely different depending on location (Burt & Pinay, 2005).

Riparian zones in boreal catchments

In northern boreal landscapes, extensive networks of small headwater streams (Bishop, 2008) are distributed throughout terrestrial ecosystems that store globally significant amounts of soil organic matter (Gorham 1991). These streams receive, process (Lapierre et al. 2013) and transport (Kothawala et al. 2015) terrestrially-derived organic matter. The extent to which terrestrially-derived organic matter can fuel important metabolic processes in aquatic ecosystems is governed by how readily available it is to microbial communities (Findlay & Sinsabaugh, 1999) and how long it can persist within the inland water network (Cotner et al. 2022). In boreal aquatic ecosystems terrestrially-derived organic matter is a key resource for low-productivity food webs (Berggren et al. 2010; Karlsson et al. 2012). However, there may be substantial variability in the properties, bioavailability and amount of organic matter supplied from terrestrial ecosystems. Yet the extent to which the structure of boreal riparian zones affects this is relatively untested.

The structure of boreal riparian zones is a product of surrounding landscape topography. Riparian soils have accumulated within a landscape underlain by relatively impermeable glacial till, creating steep declines in hydraulic conductivity with depth (Bishop et al., 2004; Grabs et al. 2012). As a consequence, groundwater is forced to flow through near-surface organic matter-rich soils, which have formed from the long-term build-up of organic matter and peat alongside stream margins (Lidman et al. 2017). This is a key reason why shallow riparian soils in boreal landscapes are generally viewed as the major sources of dissolved organic matter, and inorganic solutes, to aquatic systems (reviewed by Ledesma et al. 2018). As in most riparian landscapes however, boreal riparian zones are hydrogeomorphically diverse. This may determine their capacity to locally generate organic and inorganic resources which are ultimately supplied to streams. However, how the local hydrogeomorphic structure of boreal riparian zones affects the belowground microbial processes that underpin organic and inorganic resource cycling, has been relatively unexplored.

Hydrology is a primary control on the function of the riparian zone to a boreal stream. Annually, boreal riparian zones can experience highly variable hydrological conditions. Events such as spring snowmelt and heavy precipitation in autumn raise the catchment water table and elevate groundwater levels into shallower surface soils (Laudon et al. 2004). Not only does this increase overall stream discharge, with an average of 40% of annual discharge attributable to snowmelt within the Krycklan Catchment in northern Sweden (Ågren et al. 2007), rewetting of the wider catchment mobilizes stores of solutes that have accumulated prior to the event. Hence, annual hydrograph events can be peak episodes of resource transfer from terrestrial to aquatic ecosystems which, for dissolved organic carbon, can range between 28% and 65% of total annual exports (Ågren et al. 2007). At other times, catchment connectivity diminishes as water tables drop down deeper, with these baseflow conditions usually occurring during winter or prolonged dry periods in summer (Laudon et al. 2011). Shifts between hydrological conditions can be detected in the concentration of solutes in stream water, relative to increases in stream discharge. Overall, this produces a range of variability in stream water solute abundance within an annual cycle (Mosquera et al. 2023). Yet it is not clear whether these patterns reflect the solute mobilization dynamics occurring in riparian groundwater.

Annual hydrological shifts have been relatively predictable in the boreal landscape, which has meant that we currently have good estimations of how streams may function from year to year. However, as climate change accelerates, boreal landscapes are likely to experience more frequent and severe drought events (Spinoni et al. 2018) and a greater likelihood of intense flooding (Nilsson et al. 2015). Drought has already been shown to impact stream chemistry by altering the inputs of organic and inorganic resources to both non-boreal (Dahm et al. 2003; Lutz et al. 2012) and boreal catchments, such as the Krycklan Catchment (Gómez-Gener et al. 2018; Tiwari et al. 2022). At the same time, the ways in which drought may change redox conditions (Knorr & Blodau, 2009) and carbon cycling (Laiho, 2006) in organic soils (i.e., peat) has been extensively researched in the context of wetlands, but not in riparian zones. Considering that boreal streams are tightly coupled to the resources mobilized from riparian soils, we lack knowledge about how riparian soils will respond to drought and shifts in hydrological regimes.

Diverse lateral connections in boreal catchments

The importance of riparian soils as a source to boreal streams has informed emerging conceptual models that aim to mechanistically explain this function. The Riparian Profile Flow-Concentration Integration Model (RIM) integrates both lateral groundwater flow and the vertical concentration gradients of riparian soil strata (Seibert et al. 2009) within the context of sharp declines in hydraulic conductivity due to the aforementioned underlying till sediments (Bishop et al. 2011). As groundwater flowpaths are pushed towards surface soils in a transmissivity feedback mechanism, groundwater chemistry is shaped by the organic-rich surface soil strata that it moves through, which can be detected by changes of stream water chemistry (Bishop et al. 2004). One consequence of this mechanism is that a relatively shallow and narrow layer of organic soils, or a 'Dominant Source Layer' can be responsible for the bulk of water and solutes moving from soils to streams on an annual basis (Ledesma et al. 2018). Such a conceptual approach is relatively aspatial and idealizes the riparian zone as more homogenous than not, relying on the assumption that groundwater flowpaths generally follow the topography of surrounding hillslopes prior to discharging into the stream.

In contrast, lateral connections also occur when greater volumes of groundwater move preferentially from the connected upslope area, through riparian soils, discharging into the stream at very localized nodes (Leach et al. 2017). These localized nodes, previously referred to as Discrete Riparian Inflow Points (DRIPs), form a riparian setting with shallow groundwater levels, distinct vegetation communities (Kuglerová et al. 2014) and DOC-enriched groundwater (Ploum et al. 2020). This type of riparian zone hydrogeomorphology also leaves a signature on the stream, through elevated lateral carbon inputs (Lupon et al. 2019) and upregulated rates of stream metabolism directly linked to the node of lateral connection (Lupon et al. 2023). In particular, these riparian settings are generally linked to larger upslope contributing areas (UCA), a linkage that facilitates hydrological connections across the riparian interface (Jencso et al. 2009) and posits these riparian areas as potentially the major hydrological and biogeochemical contributors to the stream. Both modes of lateral connection can co-occur within the riparian zone of a single stream. At the same time, distinct hydrogeomorphic settings also co-exist along the margins of a stream. How lateral connections and hydrogeomorphic heterogeneity collectively influence stream chemistry at the reach scale is not yet resolved.

Knowledge gap and aims

The hydrogeomorphic heterogeneity of riparian landscapes, together with diverse modes of lateral connection across the land-water interface, adds complexity to how we can mechanistically explain the influence of riparian zones on headwater streams.

We have limited knowledge about how the hydrogeomorphic heterogeneity of boreal riparian zones influences the belowground microbial processes that transform and generate organic and inorganic resources. In Chapter **I**, I assess the biological and chemical properties of riparian soils, specifically focusing on microbial community activity and composition within distinct riparian hydrogeomorphic templates.

We know equally little about how the hydrogeomorphic setting of riparian zones affects the biodegradability of organic matter that enters into the inland water continuum. Hence, in Chapter **II**, I test the capacity of different riparian templates to contribute biodegradable dissolved organic carbon to a headwater stream, including the extent to which the supply of organic resources is influenced by riparian hydrogeomorphology.

Further, considering that boreal soils encounter annual variability in hydrological conditions, and that they are part of an ecosystem that is highly sensitive to a changing climate, there is a surprising lack of tests that show how riparian soils will biogeochemically respond to hydrological regime alterations. In Chapter **III** we address this by exposing riparian soils to experimental drought treatments and assessing corresponding changes to carbon mobilization.

In addition, our ability to predict how boreal headwaters are likely to respond to climate change is somewhat limited by not fully incorporating the possible influence of hydrogeomorphic heterogeneity on solute mobilization through riparian groundwater. Therefore, in Chapter **IV**, I apply concentration-discharge relationships to riparian groundwater to establish links between specific riparian hydrogeomorphologies and solute dynamics. Finally, the extent to which the co-occurrence of diverse lateral connections can influence the transport of resources across the land-water interface is as yet unresolved. Hence, in Chapter **IV** I leverage concentration-discharge relationships of key solutes from longer-term data as a first-step towards reconciling the contrasting modes of lateral connection emerging from boreal headwater catchments.

Methods

This thesis comprises two studies that use field measurements and laboratory analyses (**I** and **II**), one experimental study (**III**) and one that combines long-term stream and groundwater monitoring data with conceptual development (**IV**).

Study area and riparian site types

The setting for all work in this thesis was the 68 km^2 Krycklan Catchment in northern Sweden (64°14′N, 19°46′E). The local climate is humid, subarctic with a mean annual precipitation of 623 mm over the last 40 years, of which approximately 30% is snow. Annual mean temperature is 1.8°C with approximately 167 days of persistent snow coverage annually, over 40 years (see Laudon et al. 2021 for detailed site description).

In Chapters **I**, **II** and **IV**, I focused on a 1400 m first-order stream reach (Stortjärnbäcken) bounded by two hydrometric stations. C5 (upstream) and C6 (downstream) drain catchment areas of 65 and 110 ha respectively, with C5 located approximately 100 m downstream from Stortjärnen Lake (Leach et al. 2017; Figure 1). The reach between C5 and C6 drains a catchment area of 45 ha that is mostly covered by forest comprised of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), with some scattered birch (*Betula pubescens)*, and an understory of *Vaccinium* spp and bryophyte moss mats. The upslope forest till soils are dominated by iron podzols, but riparian zones feature deeper histosol soils (Laudon et al. 2013). These organic soils alongside headwater streams in the Krycklan Catchment tend to be acidic, with pH ranging from ca. 4.5 to 5.0 (Kuglerová et al. 2014). Collated monitoring data from 2014 to 2023 from Stortjärnbäcken was used in Chapter **IV**.

Several riparian sites are instrumented with groundwater well infrastructure along Stortjärnbäcken, all variable in terms of drainage size and groundwater dynamics, including sites linked to larger zero-order basins that support persistent subsurface flowpaths, (i.e., discrete riparian input zones or DRIPs) (Leach et al. 2017; Ploum et al. 2020). Previous studies have compared DRIP and non-DRIP zones in terms of groundwater chemistry at these same sites (Ploum et al. 2020) however variation in local riparian conditions along the reach is more continuous than discrete. Hence, in Chapters **I** and **II**, I designed our sampling to capture and test this variability and I distinguished 3 distinct riparian site types with major, minor, and intermediate connections to the stream.

Sites with major connections to the stream were termed 'High', with relatively large sub-basin, or upslope contributing areas (UCA; 0.5–5.5 ha) and stable and high groundwater levels (average depth: +1 cm above soil surface, max depth: -10 cm below ground surface (b.g.s)). Sites with comparatively minor connections to the stream were termed 'Low' sites, with small UCA (0.0008–0.004 ha) and persistently deep and relatively stable groundwater levels (average depth: -38 cm, max: -61 cm b.g.s; %CV of water level height: 14–24%, n = 22 manual observations per site). Finally, sites with intermediate connections to the stream were termed 'Dynamic' sites, with intermediate-sized UCA (0.03–2.6 ha), and variable groundwater levels (average depth: -24 cm, max depth: -49 cm b.g.s; %CV: 29–59%, n = 22). Low and Dynamic sites were further distinguished by where in the soil profile these groundwater fluctuations occur; for Low sites, the groundwater level was nearly always within lower conductance zones deeper in the soil profile, whereas for Dynamic sites, these fluctuations occurred largely within more surficial soil strata with greater transmissivity (Bishop et al. 2004).

In Chapter **III**, we remained within the Krycklan Catchment; however, here we sampled soils from the riparian zone of the Stormyrbäcken reach (Figure 1). At this site we specifically selected a riparian area to collect soil cores that had shallow groundwater levels and high soil organic matter content. This setting allowed us to more easily induce changes in soil water content in a laboratory experiment.

Analytical methods

Riparian soils (Chapters **I** and **II**), groundwater (**I** and **II**), stream and lake water (**II**) were sampled from the Stortjärnbäcken reach between June and October of 2022. The research questions of Chapters **I** and **II** focused on lower molecular weight and fresher, labile, fractions of the soil organic matter pool, which can degrade rapidly within soil and water after sampling. Hence, the sampling and analytical methods were designed to allow for relatively fast processing that also accommodated transportation of soils and water from the field to the lab. I used loss on ignition (%LOI) and mass fractions of soil C and N to assess the organic matter content of riparian soil samples (**I** & **II**). Using methods adapted from Werdin-Pfisterer et al. (2009), and Rousk and Jones (2010), I sampled soil solutions using soil water extractions in Chapters **I** and **II**. Analyses of extractable chemistry from soils and water, including dissolved organic carbon (DOC), organic and inorganic nitrogen (DON and DIN), and phosphate, were performed using standard methods (**I, II, III, IV**). We assessed the quality of the DOC pool using spectrophotometry, specifically $SUVA_{254}$ (specific ultraviolet absorbance at 254 nm) and the absorbance ratio of A_{254}:A_{365} (**II**).

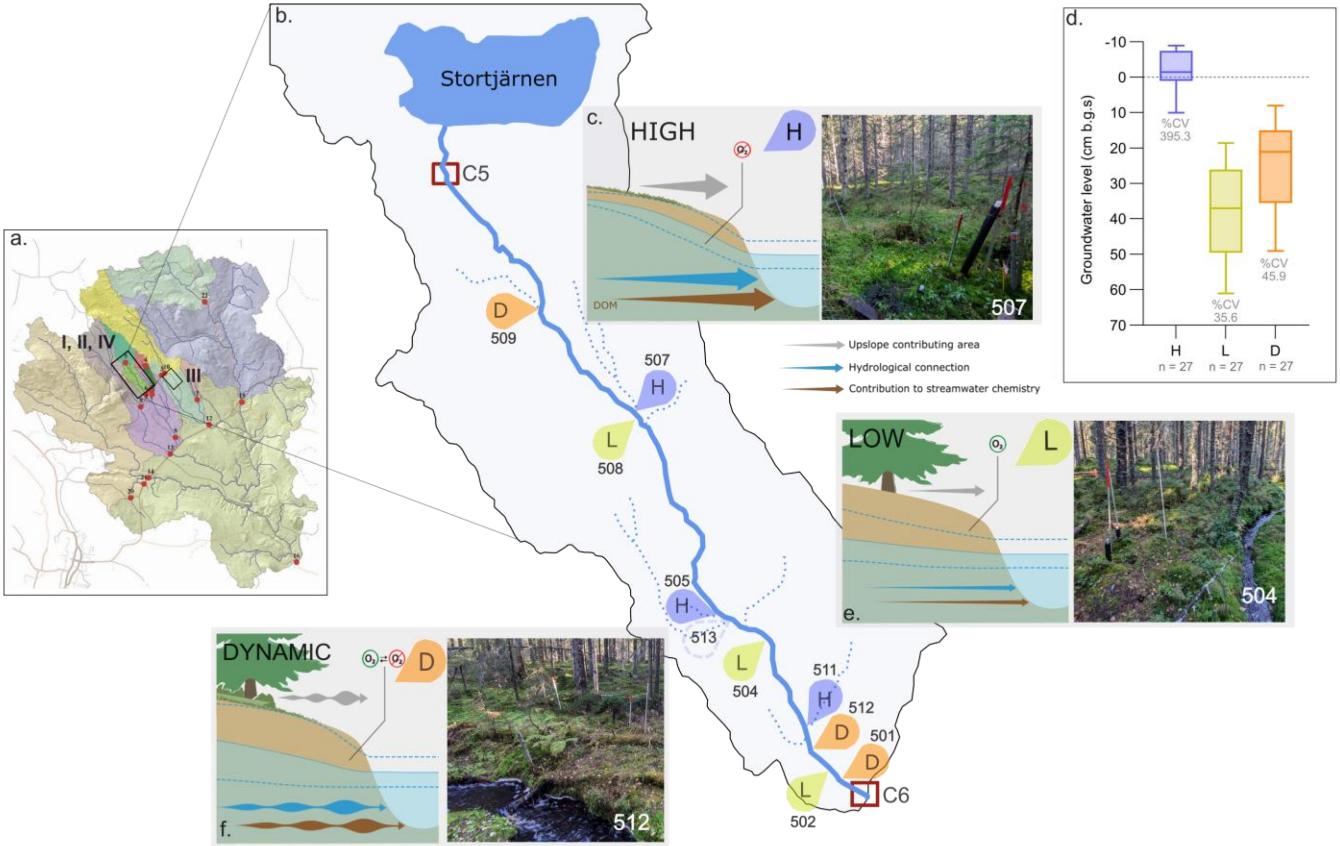

Figure 1. a) Krycklan Catchment map with locations for relevant chapters indicated. b) Schematic of Stortjärnbäcken stream with individual riparian sites numbered and riparian site type indicated with letters. Dashed blue lines show estimated preferential groundwater inputs. c). Conceptual diagram of a High riparian site type (left) with photo from site 507 taken by author. d) Box plot of median groundwater levels below ground surface measured from riparian wells. Whiskers are to maximum and minimum values, with %CV shown. e) Conceptual diagram of a Low riparian site type (left) with photo from site 504 taken by author. f). Conceptual diagram of a Dynamic riparian site type (left) with photo of site 512 taken by author.

To assess microbial community activity specific to decomposition and mineralization processes, I used colorimetric extracellular enzyme assays of riparian soils in Chapters **I** and **II**. Here, I selected extracellular enzymes integral to carbon cycling (β-glucosidase, cellulase), nitrogen acquisition (protease) and oxidative breakdown of organic matter (phenol oxidase and peroxidase). We used oxidative enzyme assays (phenol oxidase and peroxidase) with riparian soil solutions in Chapter **III**. In Chapters **I** and **II**, soils were analysed for Phospholipid Fatty Acids (PLFA) as a proxy for microbial biomass and community composition. In Chapter **II** I used incubations of soil solutions and ground-, stream- and lake water to measure the degradability of the DOC pool, based on adapted methods from Koehler et al. (2012). In Chapter **III**, we measured both CO_2 and CH_4 concentration using the headspace method and gas chromatography from soil solutions collected from intact soil cores.

Statistical analyses

In Chapters **I**, **II** and **IV**, I interpreted and reported significance values using language of evidence, following Muff et al. (2022). By using a gradient of evidentiary strength of difference, rather than a binary p value cut off, I considered $p \leq 0.001$ as very strong evidence of statistical difference, $p \leq 0.01$ as strong evidence of statistical difference, $p \leq 0.05$ as moderate evidence of statistical difference and $p \geq 0.1$ as little to no evidence.

To test for interactions between biological response variables (enzyme activity, microbial biomass) and riparian hydrogeomorphic setting, I used mixed models and two- and three-way ANOVAs (Tukey's post-hoc test) in Chapter **I.** In Chapter **II** I used these same analyses to determine the effects of riparian hydrogeomorphic setting and sample origin (i.e., riparian soil, groundwater, stream water or lake water) on biodegradable dissolved organic carbon concentrations. In Chapter **III**, we used repeated measure ANOVAs to test the effects of drought treatments, time and interactions between.

To explore the strength and direction of relationships between riparian site types and response variables, I used Partial Least Squares regression (PLS-R) in Chapter **I**. In Chapters **II** and **III**, linear regression was used to test the direction and significance of relationships between variables. To further test relationships between key variables, I used Spearman's Rank Correlation (**I**), which we also used in Chapter **III**, and Pearson correlations (**II**). In Chapter **IV**, I used Ordinary Least Squares regression (OLS-R) to test the relationship between solute concentration and discharge. A further explanation about the hydrological data analyses used is in the methods section of Chapter **IV**.

Partial Least Squares (PLS) regression, Spearman's rank correlation (**I**) and Pearson correlations were analyzed with XLSTAT (XLSTAT 2023.2.0). All other statistical tests were done in R (version 4.3.1; R Core Team 2024). For mixed models, I used the *lme4* (version 1.1-34; Bates et al. 2015), *lmerTest* (version 3.1-3; Kuznetsova et al. 2017) and *emmeans* (version 1.8.9; Lenth 2024) packages. All data figures were made in GraphPad Prism version 10.2.2 for Windows.

Field and experimental contributions

Emilia Linder Wiktorsson assisted in field sampling, laboratory preparation and experimental work for Chapters **I** and **II** and without Emilia's work, it would not have been possible to take the frequency and volume of samples that is presented in this thesis. Meredith Blackburn (SLU) assisted with LOI and soil sample preparation for PLFA in Chapters **I** and **II** and her time is much appreciated. Anders Jonsson (UMU), Jenny Ekman (SLU) and Jonas Lundholm (SLU) performed high quality analyses of large numbers of soil and water samples generated in in this thesis. Małgorzata Winkowska (UMU) assisted with soil sampling in Chapter **III**.

Discussion of results

Chapter I: Hydrogeomorphic heterogeneity of the riparian zone shapes belowground microbial processes and communities

The broader catchment influences the upslope contributing area (UCA) size and shape and the distribution of subsurface flowpaths in boreal catchments, creating heterogeneity in the hydrogeomorphology of riparian zones. Results from Chapter I show that this heterogeneity has clear consequences for the vertical patterns of bulk organic resource storage in riparian soils, and produces differences in soil properties across riparian sites. Notably, soils in High riparian sites (shallow, persistent groundwater flowpaths) held markedly lower concentrations of soil organic carbon and nitrogen, and bulk organic matter, compared to riparian sites that had Dynamic or Low (i.e., deeper) groundwater levels. These differences directly influenced patterns in microbial community composition and activity between riparian site types.

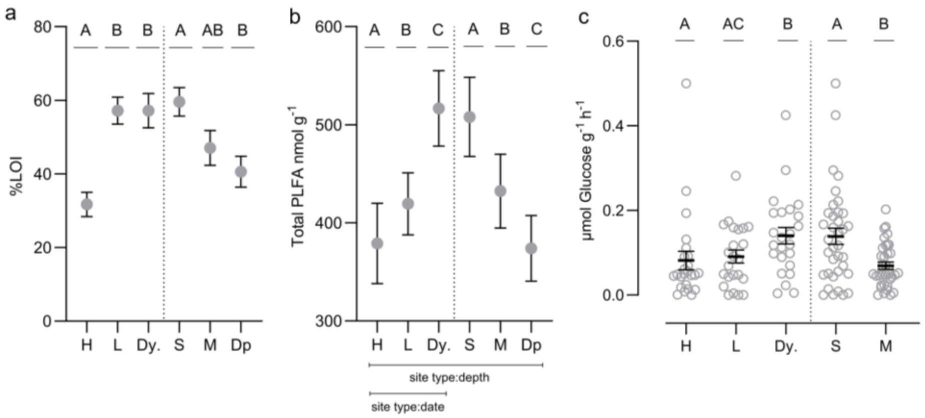

Figure 2. Selected results from Chapter I. On x axis, letters indicating the riparian site type; 'H' for High, 'L' for Low and 'Dy' for Dynamic riparian site types and 'S' for shallow depths, 'M' for mid-depths and 'Dp' for deep depths. All values are means with error bars showing standard error of the mean. Letters indicate statistical differences ($p \leq 0.05$) between site types, and between soil depths. Shared letters indicate statistical similarity. a) Solid soil % mass LOI (n = H: 26, L: 29, Dy.: 26, S: 27, M: 26, Dp: 28). b) Total PLFA marker abundance with y axis starting at 300 (n = H: 80, L: 79, Dy.: 80, S: 80, M: 80, Dp: 79) and interaction between site type and depth, and site type and date. c). Cellulase enzyme activity (n = H: 24, L: 23, Dy.: 24, S: 36, M: 35).

In soils from riparian sites with Dynamic groundwater levels, I also found higher microbial biomass (total PLFA), despite these sites having similar local organic matter concentrations to Low sites (Figure 2). Both Dynamic and Low riparian sites also had elevated rates of extracellular enzyme activity for two enzymes integral to the breakdown of soil organic matter (β-glucosidase and protease). Intriguingly, Dynamic sites were distinct in having higher rates of cellulase enzyme activity, an enzyme linked to the breakdown of larger organic substrates (Baldrian et al. 2011). Across most of the variables measured, High sites had lower microbial biomass and lower rates of extracellular enzyme activity. Although there were correlations between bulk properties of riparian soil and the proxies used to measure microbial biomass and activity, the local groundwater fluctuations influenced several microbial variables (i.e., cellulase enzyme activity and total PLFA), in ways that are not solely predictable from soil organic matter storage.

Overall, the results from Chapter I show that microbial and biogeochemical properties of riparian soils are directly influenced by the hydrogeomorphic heterogeneity of the riparian zone. In particular, this affects the capacity of a riparian site to do important biogeochemical work, such as support microbial communities that can breakdown organic substrates for mobilization to groundwater and streams.

Chapter II: Riparian soils are rich stores of bDOC, but generation and supply to aquatic ecosystems is driven by hydrogeomorphic heterogeneity

Across the broad components of a land-to-water continuum (riparian soils, groundwater, stream water and lake water), the overall quantity of biodegradable dissolved organic carbon (bDOC) was greatest in riparian soils and declined substantially in ground-, stream- and lake water (Figure 3). This was not an overall surprising result, given that boreal soils store large amounts of organic carbon (Aitkenhead & McDowell, 2000) and that labile dissolved organic matter is processed more quickly within soils (Qualls et al. 2002). Yet, it does indicate that despite close proximity with aquatic landscape components, riparian soils are highly efficient at retaining labile organic carbon, despite their documented role as a source of organic matter to streams.

Within riparian soils, the hydrogeomorphic setting appeared to directly influence the quantity of bDOC generated and stored, together with important properties of the soil organic matter pool. This was most obvious when comparing the capacity of High site soils to generate bDOC with that of Low and Dynamic sites. Specifically, soils from High sites generated substantially less bDOC and had soil organic matter properties that indicate this pool is more degraded and processed. Further, despite having different groundwater level dynamics, in both Low and Dynamic sites bDOC generation is likely driven by the overall amount of organic matter available within riparian soils.

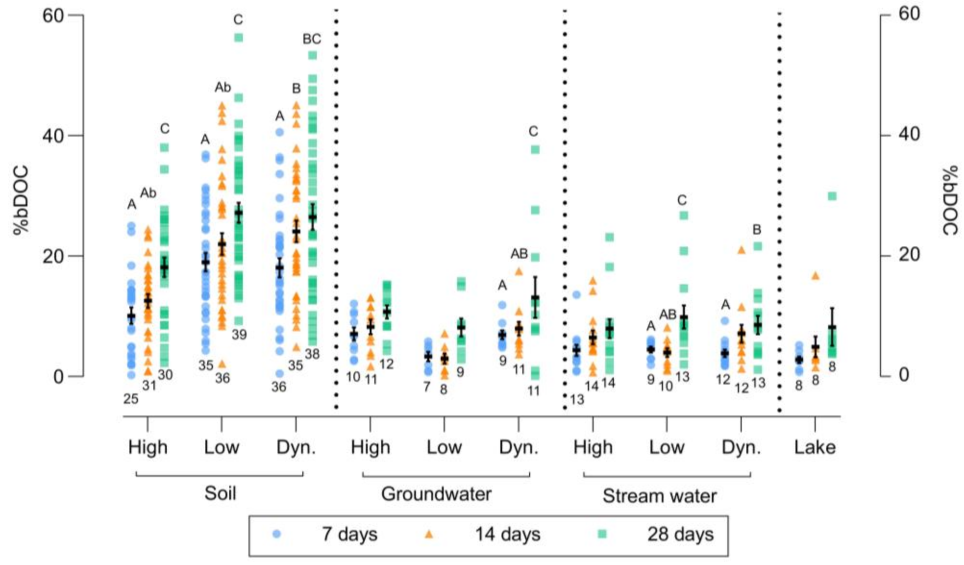

Figure 3. Percent of total bDOC degraded after 7 days (blue circle), 14 days (orange triangle) and 28 days (green square) of incubation for riparian soil extractions, groundwater, stream water and lake water. Riparian site types are indicated by High, Low and Dynamic (Dyn.).Vertical dotted lines denote the separation of each landscape component. Black dots and error bars show mean and standard errors. Upper case letters indicate strong evidence of statistical difference between timepoints (p ≤ 0.001). Lower case letters indicate moderate to low evidence of statistical difference between timepoints (p ≤ 0.1). The number of samples is specified at the base of the data.

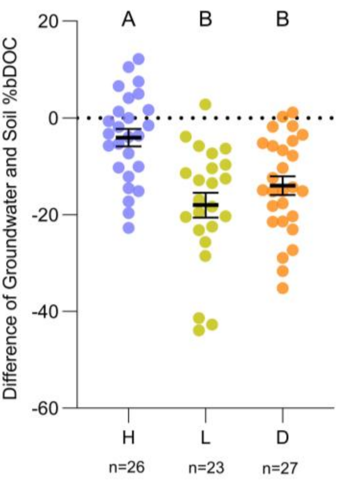

Figure 4. Difference between groundwater and soil %bDOC after 14 days. Negative values show soil %bDOC greater than groundwater.

A key finding from Chapter II was that the capacity of riparian soils to generate bDOC was not closely coupled with the transfer of those same resources into groundwater which is a direct consequence of hydrogeomorphology. The amount of bDOC measured in groundwater from High sites was elevated relative to the amount that could ostensibly be generated locally, given the edaphic properties of High site soils (Figure 4). From this I inferred that the linkage of High sites with larger UCAs allows for the lateral transport of groundwater that is rich in upslope-generated bDOC, through riparian soils that have a diminished capacity to generate, and utilize, this same resource locally. This is in direct contrast to Low, and to some extent Dynamic, sites, that represent a large store of potential bDOC, yet have little hydrological opportunity to transfer these resources laterally into streams. One consequence of this is that High sites represent an important source of bDOC to streams during periods of time where catchment connectivity is lowered (i.e., baseflow) and biological demand in streams is elevated.

Collectively, in Chapter II, I show that the riparian zone as a whole is a rich potential source of bDOC, but that it largely retains much of this resource. Additionally, there is substantial spatial and temporal complexity in how bDOC is generated and transferred from riparian soils into the inland water continuum. This complexity is largely linked to the influence that hydrogeomorphic heterogeneity has on the properties of riparian soils.

Chapter III: Rewetting following drought induces changes in carbon mobilization from riparian soils

Riparian soils within particular hydrogeomorphic settings are likely to have seasonally variable groundwater levels, such as those in Dynamic riparian sites, making them subject to alternating wetting and drying cycles in their standard environment. However, this is not the case for other riparian interfaces, such as High or Low sites which have largely anoxic or oxic conditions by way of relatively stable groundwater levels. Considering that one possible consequence of a changing boreal climate is a higher frequency of drought which would alter groundwater levels (Nilsson et al. 2015), in Chapter III, we experimentally tested how drought may affect the mobilization of carbon from riparian soils.

We induced two drought intensities (semi-dry and dry) which altered the redox conditions of riparian soil cores, and this led to important changes in chemistry after rewetting in both the short and long term. In the short term (up to 9 days after rewetting), we saw increased sulfate (SO_4^{2-}) concentrations in soil solutions, which would have accumulated during the drought period due to readily available oxygen, a preferred terminal electron acceptor. Consistent with other studies that link SO_4^{2-} pulses with DOC suppression (e.g., Clark et al. 2005; Szkokan-Emilson et al. 2013) which is also a driver of surface water browning (Monteith et al. 2007), we saw a decrease in DOC concentrations as a short-term response to rewetting. However, in this experiment, DOC concentrations recovered to pre-drought conditions, and then continued to increase two-fold as a longer-term (57 days after rewetting) response. Intriguingly, we found a correlation between rates of peroxidase enzyme activity and DOC production as a long-term response, indicating that drought events may trigger oxidative enzyme activity that persists into the rewetting phase.

Carbon dioxide (CO_2) concentrations also returned to, but did not surpass, pre-drought levels over the longer-term. In contrast to DOC and SO_4^{2-} , CO_2 production was impacted by drought intensity, with a quicker recovery in soils exposed to milder drought (semi-dry) compared to intense drought (dry). Intriguingly, the changes we observed in CO_2

post-drought were closely correlated with DOC concentrations. Yet, considering that drought-intensity did not appear to affect either DOC or SO_4^{2-}, it is possible that a decrease in microbial respiration and subsequently decreased CO_2 production, is a direct effect of an intense drought event (Stirling et al. 2020). Additionally, our results suggest that the initial pulse of SO_4^{2-} effectively constrained rates of methane (CH_4) production in the short-term. Small boreal streams can support high rates of CH_4 evasion (Rocher-Ros et al. 2023), with near-stream soils responsible for a large fraction of CH_4 production (Lupon et al. 2019). In this experiment, methanogenesis did not appear to commence until 21 days after rewetting, likely due to the accumulation of highly-favorable terminal electron acceptors during drought which were remobilized by rewetting in the shorter-term (Knorr & Blodau, 2009). This suggests that drying and rewetting events that accumulate and mobilize SO_4^{2-} can have important consequences for methanogenesis in riparian soils, but how this may affect in-stream CH_4 evasion is not yet established.

In Chapter III we show that riparian soils can respond to drought events by increasing the production of DOC during the rewetting phase. However, soils may also respond by lowering the production of CO_2 and CH_4 in the short-term. Collectively, these results provide direct evidence and reveal potential mechanisms to support recent observations in this same catchment, which suggest that drying-rewetting may operate as a more important control over DOC production and export if northern landscapes become more prone to drought (Tiwari et al. 2022). In addition, these results also hint at how riparian soils with seasonally dynamic groundwater levels biogeochemically respond to their hydrogeomorphic setting. This affects the capacity of these soils to mobilize DOC, a key resource, but also, depending on the severity of the drying period, affects their role as a source of inorganic C.

Chapter IV: Solute mobilization in groundwater is spatially variable across riparian sites

In Chapter IV I used a novel application of log-concentration (c) log-discharge (Q) relationships, and the ratio between the coefficient of variation (CV) for solute concentration and groundwater discharge (Q_{GW}), methods which are commonly used in streams and rivers (e.g., Godsey et al. 2009; Bieroza et al. 2018) but rarely in groundwater. Across riparian sites, solute mobilization dynamics were linked to differences in the size of the UCA, the average depth to groundwater level during the growing season, and bulk soil organic matter content, which are all characteristics linked to the hydrogeomorphic heterogeneity of this landscape. Overall, applying cQ analyses to groundwater chemistry revealed variability in solute dynamics across the diversity of riparian sites included. Mobilization of DOC in response to higher groundwater discharges was strongly source-limited at two sites with shallow groundwater levels and stronger hydrological connection to the stream (Figure 5). However, DOC was strongly transport-limited at a site with deeper groundwater levels and weaker lateral connection to the stream, more typical of organic solutes being 'flushed' from surface soils as a result of groundwater level rise.

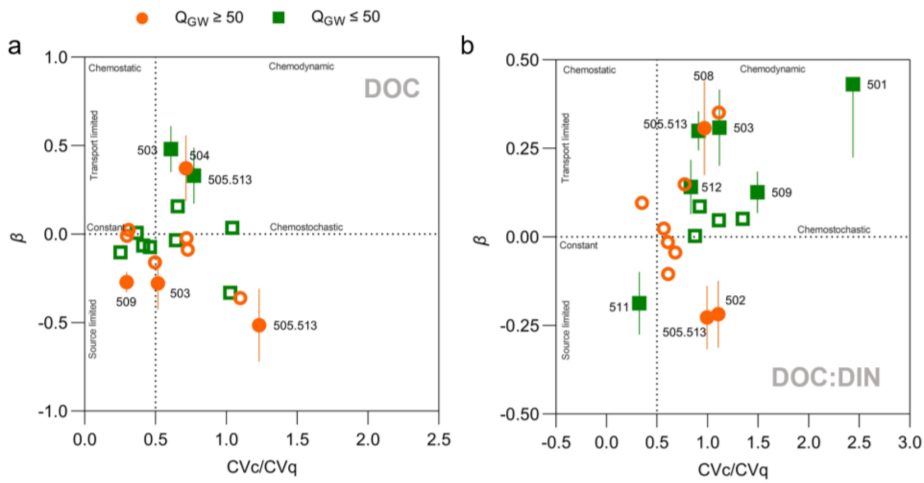

Figure 5. a) Plot showing CV_C/CV_Q with cQ slope (β) for DOC across all riparian sites, separated into $Q_{GW} \geq 50$ (circles) and $Q_{GW} \leq 50$ (squares). Riparian sites with a significant cQ slope have filled-in icons with labels and vertical standard error lines of regression slope. b) Plot showing CV_C/CV_Q with cQ slope (β) for DOC:DIN across all riparian sites.

A significant finding was that the mobilization of DOC in relation to DIN (i.e., DOC:DIN ratios) was strongly transport-limited among five riparian sites across the lower ranges of discharge ($Q_{GW} \leq 50$). The proportion of organic C that is exported to a stream, relative to inorganic N has direct implications for heterotrophic activity and N cycling in the aquatic ecosystem (Bernhardt & Likens, 2002; Lupon et al. 2020), particularly during lower discharges, linked to summer and autumn periods, when headwater streams in this landscape are most heterotrophically active (Burrows et al. 2017). These results suggest that riparian groundwater mobilizes more organic C than inorganic N into streams during lower flow periods, exacerbating, rather than alleviating, in-stream N limitation, which is particularly relevant in light of the ongoing brownification of northern surface waters (de Wit et al. 2016; Kritzberg et al. 2020).

From these analyses in Chapter **IV**, I show that the range of solute mobilization patterns from riparian sites is linked to the hydrogeomorphic heterogeneity of the riparian interface. This also indicated how hydrogeomorphic heterogeneity can potentially govern the timing, and amount, of resources that riparian zones can contribute to streams.

Chapter IV: Contrasting modes of lateral connectivity co-occurring along a stream reach can be simultaneously vital to in-stream function

At the very core of the riparian zone's role as a source to boreal headwater streams, are the changes in stream water conditions that can be linked to lateral connectivity. Because the riparian sites along the Stortjärnbäcken stream are bounded by two hydrometric stations separated by a 1.4 km stream reach, in Chapter IV I estimated the integrated lateral flux of solutes to evaluate the reach-scale dynamics of solute mobilization. Isolating lateral fluxes in this way is typically not possible in the field because few stream reaches have monitoring stations installed in such a way. Hence, the stream reach used in this thesis presented a unique opportunity to essentially remove the chemical and hydrological contributions of the upstream source water, and establish how lateral solute mobilization patterns in the stream are driven by different types of riparian settings.

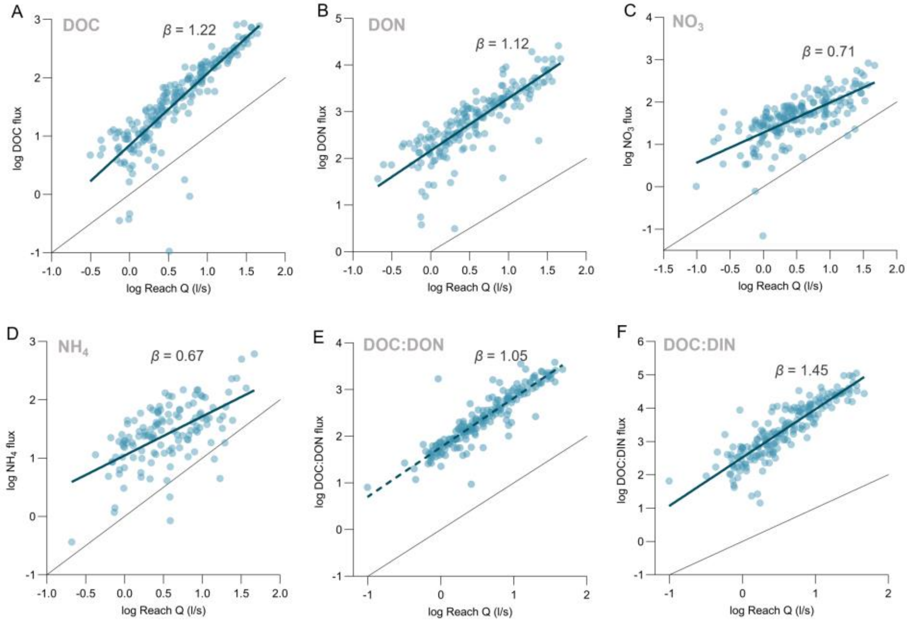

Figure 6. a) log Flux-log discharge plot for DOC for integrated lateral solute contributions, with a 1:1 line plotted and slope of line indicated. b) log Flux-log discharge plot for DON. c) log Flux-log discharge plot for NO_3. d) log Flux-log discharge plot for NH_4. e) log Flux-log discharge plot for DOC:DON with dashed line indicating non-significant slope. f) log Flux-log discharge plot for DOC:DIN.

By using 10 years (2014-2023) of continuous monitoring data, I showed that despite variability in the hydrogeomorphic setting of riparian sites, lateral fluxes at the whole-reach scale were largely consistent with conceptualizations of the boreal riparian zone as a discharge-responsive source (Bishop et al. 2004; Seibert et al. 2009; Figure 6). To evaluate the regime of overall lateral solute supply, we used a modified version of the cQ approach which instead plots log flux vs. log discharge (e.g., Zarnetske et al. 2018). Analysing the data this way requires a different interpretation of the slope, where $\beta > 1$ indicates transport-limitation, $\beta < 1$ indicates source-limitation and $\beta = 1$ indicates constant solute behaviour.

The overall lateral flux patterns of increasing organic solute concentration with increased flows (i.e., transport-limitation) and decreasing inorganic solute concentration with increased flows (i.e., source-limitation) was only observed at a small subset of the riparian sites. These riparian sites are characterized by a relatively small UCA, less persistent lateral connectivity, and greater capacity to generate and accumulate organic resources within surface soils. At the stream-reach scale, riparian interfaces with more persistent lateral connectivity and greater opportunity to hydrologically connect with the stream, appeared to be less influential in shaping solute responses to changes in discharge. However, at very local scales, these types of riparian interfaces have important consequences for spatial patterns of metabolic activity in the stream (Lupon et al. 2023). Likewise, they may also create dynamic thermal regimes along the length of the stream reach (Leach et al. 2021), important functions which are not limited to this single stream, nor the boreal landscape.

Overall, in Chapter IV**,** I show that contrasting modes of lateral connections can simultaneously influence the stream, but do so via different mechanisms, across different response variables and at different spatial scales.

Conclusions

Riparian opportunity and capacity

An emerging theme from this thesis is that hydrogeomorphic heterogeneity influences boreal riparian zones by determining the *capacity* of local soils to do important biogeochemical work, and the level of hydrological *opportunity* that riparian soils and groundwater have to influence the adjacent stream. Here, I assessed capacity by examining how organic resources are stored within riparian soils (I), measuring the properties and degradability of dissolved organic matter (II), quantifying the activity and composition of the microbial communities that these soils support (I, II) and evaluating the extent to which riparian soils will respond to extreme events such as drought (III). Likewise, I evaluated opportunity by characterizing the groundwater level dynamics at the riparian interface (I), assessing the relative abundance of organic solutes in riparian groundwater (II) and interpreting the influence of lateral riparian connectivity at both local and whole-stream scales (IV).

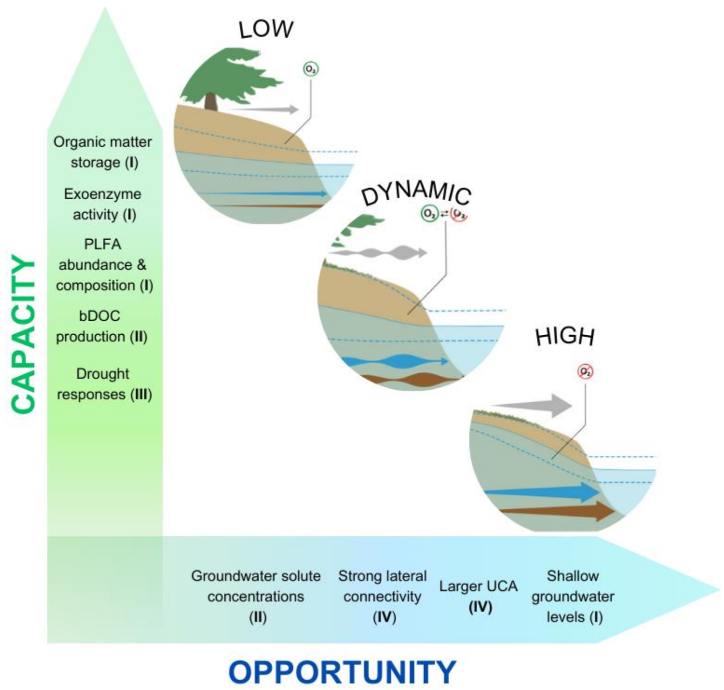

Figure 7. Conceptualization of how riparian site types organize along the axis of opportunity and capacity.

Collectively, my results show that along streams there is a gradient of interaction between capacity and opportunity. The interaction of these two properties ultimately governs how a given riparian interface will impact the stream, and at what scale these impacts are relevant. My research highlights that a diversity of interface types may collectively influence streams at different spatial and temporal scales, across different response variables and via different mechanisms.

Spatial and temporal relevance of opportunity and capacity

Rather than passive, unreactive pipes, streams and aquatic networks are biogeochemically dynamic (Cole et al. 2007) and spatial variability of the riparian influence is key to supporting this dynamism. Riparian settings akin to the High sites presented in this thesis can form distinct habitat patches and refuges for temperature-sensitive aquatic species (Ebersole et al. 2015; Briggs & Hare, 2018), and modulate rates of leaf litter breakdown, potentially altering in-stream resource availability (Hare et al. 2024). Specific to the Krycklan Catchment, interface types that have higher opportunity but limited capacity, create spatial patterns of metabolic activity in the stream (Lupon et al. 2023) and drive dynamic thermal regimes along the length of the reach (Leach et al. 2021). Ultimately, these interface types enhance the stream environment by making it patchier and more locally heterogenous which, following Poole et al. (2002) clearly builds a more dynamic lotic ecosystem.

Similarly, temporal variability of the riparian influence is highly relevant to boreal headwaters, especially in light of annual hydrological dynamics and the increasing likelihood of extreme events, such as drought. Riparian interfaces with high capacity, but lower opportunity (i.e., Low sites), likely represent a large fraction of the near-stream zone of boreal headwaters (e.g., Kuglerová et al. 2014). My results indicate that not only are these sites responsible for driving lateral flux patterns at the reach scale, but their enhanced capacity to generate labile organic matter and nutrients is most relevant in their response to hydrological events. During snowmelt or flood periods, these sites export resources that have accumulated in riparian soils, boosting in-stream productivity (Berggren et al. 2009) which would likely not be possible if these sites had higher hydrological opportunity (i.e., shallower groundwater levels and potentially shorter water residence times). Importantly, these riparian soils with lower hydrological opportunity (i.e., deeper groundwater levels) are likely to lack sufficient antecedent wetness to buffer against shorter-term drying events.

By contrast, it is the higher opportunity and lower capacity of sites with preferential groundwater flowpaths and strong lateral connections (i.e., High sites) that posit these interfaces as important support systems for streams during baseflow. These interfaces contribute water and a range of solutes to streams even when catchment connectivity is low (Ploum et al. 2020). This is achieved by way of their connections with potentially organic-rich hillslopes (Jutebring Sterte et al. 2022) and the lower capacity of riparian soils to utilize solutes that transit into and through them. Additionally, in response to shorter-term drought events, these sites likely benefit from high antecedent wetness which lowers their sensitivity to intensely dry periods. What is clear from my thesis is that near-stream zones with different levels of opportunity and capacity are equally important to headwater streams but that this varies both temporally and spatially.

Future perspectives

Moving forward, the riparian zone offers us the chance to use interactions between capacity and opportunity to evolve how stream ecosystems are protected and managed. Considering that riparian zones will more often than not be hydrogeomorphically heterogeneous, it is vital that we incorporate the range of effects that a diversity of riparian interface types can have on streams. Our ability to investigate the effects of this heterogeneity on both riparian and stream functioning is largely limited to candidate systems where we are able to conduct experimental work and deploy monitoring infrastructure. Such systems are relatively rare and it is therefore simply not possible to assess the full range of hydrogeomorphic heterogeneity that exists across the many forms of riparian zones, and similarly impossible to speculate as to how riparian zones will affect streams universally. Yet, the mechanistic understanding of riparian zone functioning that comes from research based on candidate systems, such as from this thesis, is highly valuable and can be applied within a variety of contexts.

While interfaces with higher opportunity can have benefits to stream ecosystems, if not managed effectively riparian zones with strong hydrological linkages present ample opportunity for contaminant transfer from terrestrial to aquatic systems (Laudon et al. 2016; Hester & Fox, 2020). Not only are these types of interfaces likely to have shorter water residence times (Jutebring Sterte et al. 2022) which may reduce the likelihood of contaminant retention in riparian soils, their connection to hillslopes means they have greater opportunity to hydrologically encounter and mobilize non-riparian contaminant sources (Ocampo et al. 2006). Indeed, these types of riparian interfaces already inform recommendations for Hydrologically Adapted Buffers (Kuglerová et al. 2017) but equal importance should be placed on sites with lower opportunity and higher capacity.

We know that hydrological regimes in boreal landscapes are likely to shift in response to climate change (Nilsson et al. 2015). Furthermore, we know that catchment connectivity can be altered in response to dry periods (Tiwari et al. 2022) and forms of land-use (Schelker et al. 2013) and that riparian soils with high capacity are biogeochemically influenced by drought conditions (Chapter III). With this in mind, alterations in hydrological opportunity at Low and Dynamic sites, whether opportunity increases or further decreases, may have important consequences for the capacity of these riparian soils to function as sources to streams.

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