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Riparian Zone Heterogeneity Influences the Amount and Fate of Biodegradable Dissolved Organic Carbon at the Land-Water Interface

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Key Points:

- Riparian soils are rich potential sources of biodegradable dissolved organic carbon (bDOC)
- Hydrogeomorphology of the riparian zone influences the biogeochemical capacity of soils to generate and process bDOC
- Riparian zones with lower biological capacity to process bDOC in soils, transport larger quantities of bDOC through groundwater flowpaths

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract

The transport of biodegradable dissolved organic carbon (bDOC) across land-water boundaries is central to supporting the ecological and biogeochemical functioning of freshwater ecosystems. Yet, we know little about how the generation and supply of terrestrial bDOC to streams and lakes is regulated by the physical, biological, and hydrological properties of the riparian interface. Here, we assessed how terrestrial, groundwater, and aquatic bDOC differ along flowpaths connecting riparian soils to a headwater boreal stream. We further tested how bDOC generation and supply differs among interfaces with distinct hydrogeomorphologies, as reflected by differences in soil properties, groundwater dynamics, and hydrological connectivity to the stream. We found that bDOC quantity declined sharply from terrestrial sources, to groundwater, to aquatic systems, and that these differences were associated with changes in the optical and chemical properties of the dissolved organic matter pool. However, bDOC generation and potential transport in groundwater varied across site types and reflected local differences in soil organic matter storage, depth to groundwater, and soil microbial community activity. Interface zones with organic-rich soils but weak hydrological connections had a large capacity to produce bDOC, but likely only laterally contributed organic resources during floods. By contrast, sites with stronger lateral hydrological connectivity served as persistent conduits for organic resources generated further upslope, even if the capacity to generate bDOC locally was weak. Overall, our results illustrate how hydrogeomorphic heterogeneity at the land-water interface can add spatial and temporal complexity to the generation and transfer of bDOC from soils to the inland water continuum.

Plain Language Summary

Dissolved organic carbon (DOC) from terrestrial ecosystems is important to the ecological functioning of freshwater ecosystems such as streams and lakes. The extent to which DOC can support ecological processes is dependent on how easily it can be processed (i.e., biodegraded) within these ecosystems. To move into freshwater ecosystems, terrestrial DOC is transported across interfaces between land and water. However, the structure of these interface zones can be variable and we know little about how such variability affects the biodegradability of DOC. Here, we measured biodegradable DOC (bDOC) from riparian soils, groundwater, stream water and lake water in a small boreal catchment to assess how bDOC quantity and degradability varies across landscape components. We found that riparian soils had more bDOC than other landscape components, and that a large fraction of this appears not to be transferred to groundwater and streamwater. Additionally, interface zone variability influenced the amount of bDOC present within riparian soils and groundwater, with groundwater depth and soil properties being influential to the amount of bDOC. Overall, we show that local variability in the structure of riparian interfaces can influence the amount of bDOC that is generated in soils, and ultimately supplied to streams.

1. Introduction

Dissolved organic carbon (DOC) transfer from terrestrial to aquatic ecosystems is an important flux in the carbon (C) cycle (Kothawala et al., 2021; Tank et al., 2018) and is central to the ecological and biogeochemical functioning of streams, rivers, and lakes (Prairie, 2008). DOC plays a wide range of roles in aquatic ecosystems, from directly altering the physical environment (e.g., Karlsson et al., 2009), to serving as a vector for the supply of nutrients and contaminants (Kalbitz et al., 2000), to acting as a major energy source to microbial communities (Tranvik, 1988). Yet, the DOC pool also comprises a highly diverse mix of organic compounds which, depending

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on composition, can determine the nature and magnitude of these various influences within the aquatic environment (Guillemette & del Giorgio, 2011). The amount, character, and reactivity of DOC supplied to aquatic systems, in turn, reflects the diversity of organic matter sources on land (Creed et al., 2015), the types of hydrological flowpaths that drain terrestrial ecosystems (Tank et al., 2018), and the potential for microbial processes to alter DOC along these flowpaths (Freeman et al., 2024). Thus, understanding the controls over terrestrial DOC properties in streams, rivers and lakes requires a landscape perspective that integrates hydrologically-connected patches within and across catchments.

One key property of DOC that determines its role and fate in aquatic ecosystems is the fraction of the pool that can readily be used by microbes (Berggren et al., 2022). The size of the bioavailable pool is important in determining the extent to which terrestrial DOC may fuel aquatic metabolic processes (Findlay & Sinsabaugh, 1999), but also how long DOC persists within the inland water network (Cotner et al., 2022). Biodegradable DOC (bDOC) comprises a diversity of mainly low molecular weight compounds generated in soils through a range of processes, including rhizodeposition (Villarino et al., 2021), leaching from litter (Hensgens et al., 2020), microbial enzyme activity (Sinsabaugh & Follstad Shah, 2011) and fermentation (e.g., acetogenesis) under anoxic conditions (Herndon et al., 2015). However, given susceptibility to rapid mineralization and sorption, the distance traveled and retention times of bDOC in soils is typically short (Qualls et al., 2002). Thus, export of these compounds along hillslopes and across land-water boundaries is often associated with hydrological events and disturbances that overwhelm the high retention efficiency in soils, including flooding (Ågren et al., 2008) and drying-rewetting events (Tiwari et al., 2022). Yet the persistence of even low levels of terrestrially-derived bDOC in small streams during baseflow (e.g., Berggren, Laudon, et al., 2010) suggests at least some inefficiency in degradable DOC retention on land. Further, pronounced variation in stream respiration linked to changes in lateral connectivity (Lupon et al., 2023) highlights important variability in the supply of these resources across the land-water interface.

Variation in bDOC inputs along streams may occur because of differences in the strength of lateral connectivity and/or in the net production of these resources at the land-water interface. As groundwater fluctuates vertically in riparian zones, it effectively "samples" the soil profile, determining what strata have the *opportunity* to contribute dissolved resources laterally to streams (Ledesma et al., 2018). At the same time, such fluctuations in groundwater levels also induce shifts in redox state and/or elicit drying-rewetting dynamics that can elevate the production or consumption of bDOC through effects on microbial activity (Baker et al., 2000; Harms & Grimm, 2008; Peyton-Smith et al., 2017). This *capacity* to generate organic resources is further constrained by whether or not lateral flowpaths intersect soil horizons that are also biogeochemically active. Ultimately, the interplay between hydrological opportunity and biogeochemical capacity is driven by the hydrogeomorphic structure of the land-water interface. For example, the slope and contributing area of hillslopes can determine the vertical position of lateral groundwater flowpaths, and thus what soil strata are likely to intersect the water table (Gift et al., 2010), while also regulating the overall rates of the hydrological flux across the land-water interface (Jensco et al., 2009). Variability in the depth to groundwater can further drive patterns in the composition and production of vegetation along hillslopes, as well as in the edaphic properties of near-stream soils (Elliot et al., 2015). However, despite the clear importance of riparian hydrogeomorphology to land-water interactions (Vidon & Hill, 2004), we know little about how hydrogeomorphic variation affects the generation of bDOC at the land-water interface and its transport to aquatic systems.

Resolving the processes that govern bDOC supply across land-water interfaces is particularly relevant in boreal landscapes, where vast stores of soil organic C support large hydrological fluxes of DOC (Aitkenhead & McDowell, 2000) and where terrestrial bDOC is often crucial to stream and lake food webs given low rates of aquatic primary production (Berggren, Ström, et al., 2010). Additionally, the physical organization of boreal landscapes creates the potential for wide variation in bDOC production and supply across the land-water interface. First, riparian soils are often the dominant source of DOC to boreal streams, primarily due to the long-term accumulation of soil organic matter along stream channel margins (Lidman et al., 2017). Second, for landscapes underlain by glacial till, steep declines in hydraulic conductivity with depth force the bulk of groundwater flow through near-surface, C-rich soils (Bishop et al., 2004). As a consequence, stream chemistry is often determined by a small volume of shallow riparian soil (e.g., 30–50 cm below ground surface) through which most groundwater passes annually (Ledesma et al., 2018). The dominance of near-surface flowpaths also creates strong topographic controls over hydrological routing, leading to conspicuous variability in the hydrogeomorphology of the land-water interface (Figure 1). This includes variability in the vertical position and temporal dynamics of

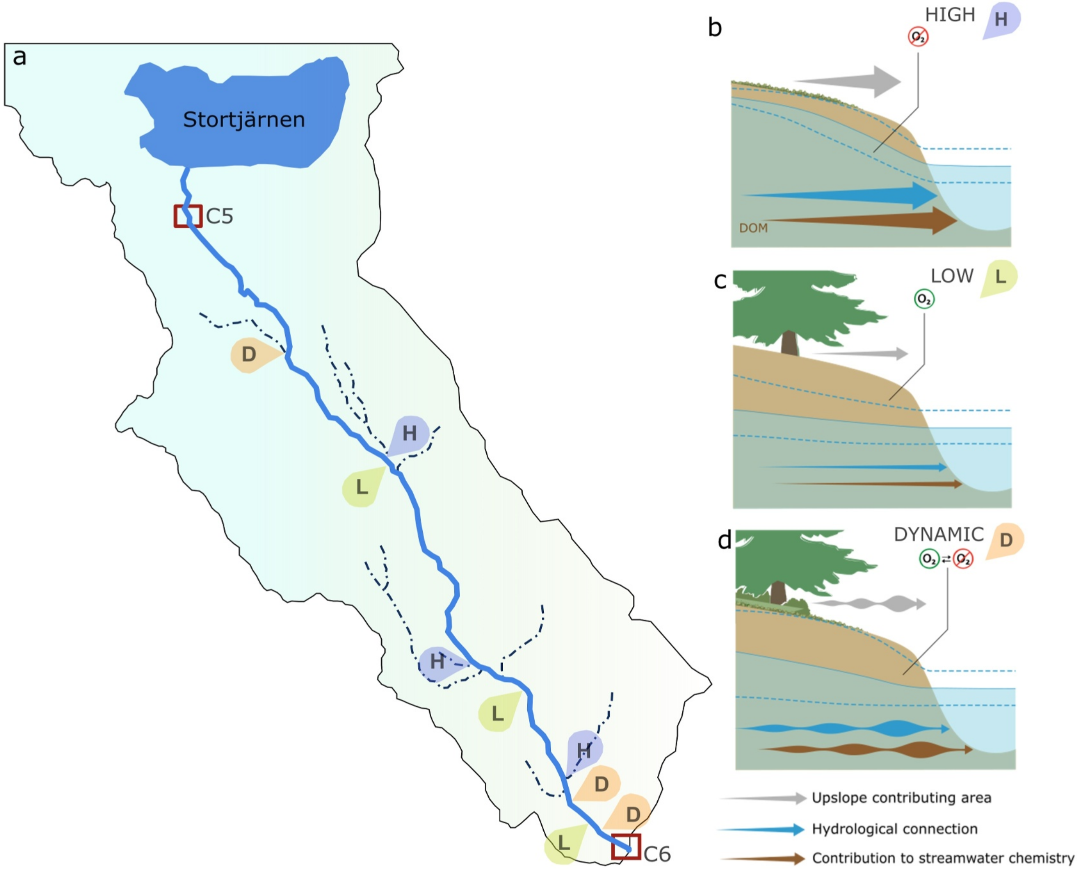

Figure 1. Schematic of the 1.4 km SJB reach between gauging stations C5 and C6, with Stortjärnen Lake. Solid line indicates the main stream channel. Dashed lines that intersect the main stream reach indicate areas that are likely to have lateral subsurface flowpaths connected to upslope areas. Riparian sites for this study are shown with location bubbles along the stream, with letters indicating the riparian site type; "H" for High, "L" for Low and "D" for Dynamic groundwater levels. Conceptual diagrams are included showing the differences between (b) High, (c) Low and (d) Dynamic riparian sites. In each panel, the mean groundwater level during the snow-free period is shown with a blue solid line, with blue dashed sections indicating the average fluctuations of the water table above and below the mean depth. The gray arrow indicates the size of the upslope contributing area and the blue arrow indicates the strength of the hydrological connection between the riparian zone and adjacent stream. The brown arrow indicates the extent to which the riparian zone influences stream chemistry through transporting DOC.

riparian groundwater flowpaths linked to changes in slope (Grabs et al., 2012) as well as differences in the rates and persistence of lateral groundwater flux based on the size of contributing hillslopes (Leach et al., 2017). Indeed, the largest contributing hillslopes support preferential subsurface flowpaths that function as major water and solute sources to streams, while also altering local plant and soil properties (Ploum et al., 2021; Reidy et al., 2025). Collectively, these patterns may generate a high degree of spatial variability in bDOC production and supply along boreal streams, based on differences in soil properties, how frequently a given soil is inundated, and how strongly it is hydrologically connected.

We quantified riparian soil, groundwater and aquatic (stream and lake) bDOC within a boreal headwater catchment to ask: (a) How bDOC varies along a land-water continuum, and (b) to what extent the hydrogeomorphic structure of the riparian zone influences bDOC production and supply. To assess bDOC, we performed 7-, 14- and 28- day incubations using water and soil solutions sampled on eight occasions across four months of the northern growing season. Overall, given rapid turnover of labile dissolved organic matter (DOM; Qualls et al., 2002), we predicted that bDOC concentrations would be greatest in riparian soils, and decline from groundwater to aquatic landscape components. We also hypothesized that variation in bDOC production and supply across hydrogeomorphic settings emerges from interactions between soil properties (e.g., organic content) and groundwater level dynamics. Here, we predicted that bDOC production would be greatest in more organic rich soil strata (Wickland et al., 2007) and would scale with biological variables linked to DOC turnover, including microbial community biomass and soil extracellular enzyme activity. Additionally, we predicted that greater bDOC production would be linked to soils that are subject to more dynamic groundwater levels (Baker et al., 2000). Finally, we predicted that the ability to transfer bDOC from soils to groundwater and aquatic landscape components would be enhanced at sites with greater overall lateral hydrologic connectivity.

2. Materials and Methods

2.1. Study Area

The study was conducted in the 68 km^2 Krycklan catchment in northern Sweden (64°14′N, 19°46′E (see Laudon et al., 2021 for detailed site description) along a 1,400 m first order stream reach (Stortjärnbäcken; SJB) bounded by two hydrometric stations named C5 (upstream) and C6 (downstream). C5 and C6 drain predominantly forested catchment areas of 65 and 110 ha respectively, with C5 located approximately 100 m downstream from Stortjärnen Lake (Figure 1). Hillslope forest till soils are dominated by iron podzols, but riparian zones feature a comparatively thicker surface layer of histosol peat soils (Laudon et al., 2013).

Several riparian sites are instrumented with groundwater well infrastructure along Stortjärnbäcken, all variable in terms of drainage size and groundwater dynamics (Leach et al., 2017; Ploum et al., 2020; Figure 1). Riparian groundwater wells were established within 1–2 m of the stream and made of fully screened PVC 30 mm diameter with a mean depth to ground surface of 91 cm. We selected nine riparian sites in order to capture this variability and grouped these into "riparian site types" based on manual groundwater level measurements ($n = 22$) taken between June to October of 2020. Then, we confirmed the grouping with groundwater level measurements from June to October 2022. From these measurements, we distinguished riparian areas with major, minor and intermediate degrees of hydrological connection to the stream. We included three sites with major connections to the stream, hereafter "High," with relatively large contributing hillslope areas (0.5–5.5 ha) and stable, shallow groundwater levels (average depth: +1 cm above soil surface, max depth: 10 cm below ground surface (b.g.s.), $n = 22$). We also identified three sites with minor connections to the stream, hereafter "Low" sites. Low sites featured smaller contributing hillslope areas (0.0008–0.004 ha) and relatively stable, deep groundwater levels (average depth: 38 cm b.g.s, max depth: 61 cm b.g.s, coefficient of variation (CV) of water depth: 14%–24%, $n = 22$). Finally, we included three sites with intermediate connection to the stream, hereafter "Dynamic" sites, with intermediate-sized contributing areas (0.03–2.6 ha), and shallow yet variable groundwater levels (average depth: 24 cm b.g.s, max depth: 49 cm b.g.s, CV: 29%–59%, $n = 22$). Additionally, for Low sites, the groundwater level was nearly always within lower hydrologic conductivity zones deeper in the soil profile, while groundwater level fluctuations largely occurred within more surficial soils with greater transmissivity in Dynamic sites (Bishop et al., 2004).

2.2. Soil and Water Sampling

To encompass the variability of the northern growing season, we sampled on eight occasions from July to October 2022. This sampling frequency was logistically feasible and allowed us to run multiple incubations in parallel throughout the sampling period. On five occasions, we sampled soils, groundwater and streamwater from one site representative of each riparian typology ($n = 3$), while all riparian sites along the stream reach ($n = 9$) were sampled on three occasions. Soil was sampled with a bucket auger from three depth increments from surface level to 50 cm deep (shallow: 0–15 cm, mid-depth: 15–30 cm, deep: 30–50 cm) and kept in plastic air-tight bags and chilled (4°C) until processing. We sampled riparian groundwater with a peristaltic pump affixed to a drill and groundwater depth was measured manually. Due to deep groundwater levels at some sites, we were unable to take a large enough sample for incubation and analysis on some occasions. Stream samples were collected from the talwag directly adjacent to the riparian well. A sample from Stortjärnen Lake was also taken from a platform extending out onto the lake near the outlet. All water samples were filtered (0.45 μm Filtropur S; Sarstedt AG and Co., Nümbrecht, Germany) and stored at +4°C or −18°C depending on subsequent analysis.

2.3. Soil Extraction

The method for extracting soil water from fresh riparian soils was adapted from Werdin-Pfisterer et al. (2009) and Rousk and Jones (2010). To minimize degradation of the labile soil DOM pool the extraction process was started within 4–6 hr of the samples being taken from the site. 24 g fresh soil and 180 ml Milli-Q water were combined in

250 ml Nalgene® (Nalg Nunc International, Rochester, New York) centrifuge bottles then shaken with orbital shaker at 260 rpm for 10 min then centrifuged for 15 min at 4°C and 14,000 rpm using the Avanti™ J-20 XP centrifuge (Beckman Coulter Inc., Brea, California). Soil extraction solutions were syringe filtered from the bottle (0.45 μm Filtropur S; Sarstedt AG). Samples for DOC and optical property analyses were stored at +4°C and samples for dissolved N were stored at −18°C. Samples for DOC analysis were acidified with 4% HCl prior to chilling.

2.4. Soil Properties and Dissolved Chemistry Analytical Methods

To assess bulk properties of riparian soil, we used a subset of soil samples from the July, September and October sampling dates from all riparian sites and depths. Soil organic matter content was measured as percent loss on ignition (%LOI) after heating at 550°C for 5 hr. Soil mass fractions of carbon (C) and nitrogen (N) were measured on an isotope ratio mass spectrometer (DELTA V, Thermo Fisher Scientific, Waltham, Massachusetts) and elemental analyzer (FLASH 2000; Thermo Fisher Scientific). C:N ratios were calculated as %C/%N.

We used standard methods to analyze the chemistry of soil extractions, groundwater, streamwater and lake water. DOC was measured by combustion (870°C) of acidified water samples (bubbled with O_2), and then analyzed with an infrared gas analyzer attached to the Formacs™ HT-i total organic C/TN analyzer (Skalar, Breda, The Netherlands). Total Nitrogen (TN) was analyzed on an ND25 unit connected to the Fomacs using a chemiluminescent detector (detection to 0.02 mg N/L). Dissolved nutrients were analyzed colorimetrically on a segmented flow analyzer (QuAAtro 39; SEAL Analytical Mequon, Wisconsin). Nitrate (as nitrate + nitrite; NO_3^-) was measured after reagents and samples passed a copperized cadmium reduction coil to form an azo dye [QuAAtro method: MT3B Q-126-12 Rev 1]. Ammonium (NH_4^+) was measured with the salicylate method [QuAAtro method: Q-033-04 Rev. 8] and phosphate (PO_4^-) with the molybdenum blue method [QuAAtro method: MT3A Q-125-12 Rev 1]. Dissolved inorganic nitrogen (DIN) was calculated as the sum of NO_3^- and NH_4^+. Dissolved organic nitrogen (DON) was calculated by subtracting DIN from TN. We also measured DOC optical properties of all soil extractions and water samples from each initial sampling point using an Aqualog ® spectrophotometer (HORIBA Scientific) with 200–600 nm, 1 nm increments in 1 cm quartz cuvettes. All spectra were corrected for blank absorption (Milli-Q). We used absorbance data to calculate $SUVA_{254}$ (specific ultraviolet absorbance at 254 nm, in L mg C^{-1} m^{-1}) and the absorbance ratio of A_{254}:A_{365}. $SUVA_{254}$ is an indicator of the aromaticity of DOC, with lower values indicative of fresher, less aromatic DOC and higher values the opposite (Weishaar et al., 2003). The absorbance ratio of A_{254}:A_{365} is a complementary indicator of DOC quality, with higher values indicative of lower molecular weight DOC (Dahlén et al., 1996). Consistent with this, past research in Krycklan streams have reported positive correlations between the absorbance ratio and bacterial productivity (e.g., Ågren et al., 2008).

2.5. Biodegradable Dissolved Organic Carbon Incubations

To measure biodegradable dissolved organic carbon (bDOC) we used three incubation durations to assess and compare the size of the most labile (fast degradation; 7 days) and semi-labile (slower degradation; 14 and 28 days) bDOC pools. In doing so, we not only compared the size of the bDOC pool across landscape components at any one incubation duration but also evaluated the cumulative size of these pools by testing whether or not bDOC increased as the incubations proceeded.

Soil extracts, groundwater, stream water and lake water were prepared for incubations using adapted methods from Koehler et al. (2012). 100 ml of filtered sample was aliquoted to a 200 ml pre-autoclaved amber glass bottle. To ensure each bottle had a microbial population representative of the local environment, an inoculum of subsamples from all lake, groundwater and streamwater from the day of sampling was collected and filtered through Whatman GF/C filters (1.2 μm pore size) and added to incubation vials at a ratio of 5% of total incubation volume. Four blank incubations of 100 ml of Milli-Q with inoculum added were included in each bioassay. Incubation bottles were kept capped, in the dark and at ambient temperature for 28 days. At intervals of 7, 14 and 28 days after incubation start, 15 ml of water from the incubation bottle was sampled, syringe-filtered (0.45 μm Filtropur S; Sarstedt AG) to remove microbial biomass from subsamples, acidified with 4% HCl at a ratio of 100 μl HCl to 10 ml filtered sample, and stored at +4°C until analysis.

2.6. Biodegradable Dissolved Organic Carbon Calculation and Terminology

We use the term "biodegradable" DOC (bDOC) as our methods measure the reduction in DOC concentration over time, synonymous with other studies (i.e., Vonk et al., 2015). We report bDOC using two measurements. First, for all landscape components, we calculated the percentage loss of the initial DOC pool after a period of time (% bDOC) as

$$\%\text{bDOC} = \frac{\left(\text{DOC}_i - \text{DOC}_f\right)}{\text{DOC}_i} \times 100 \tag{1}$$

where DOC_i and DOC_f are DOC concentrations (in mg/L) in the soil extractions, groundwater, stream water or lake water at the beginning (i) and end (f) of the incubation period, respectively.

Specifically for soils, we also calculated the mass loss of bDOC (mass_bDOC in mg/g soil) as it accounts for the variation in initial dry mass of soils, which may differ between sites due to sample water content. This calculation uses the constant 0.18 to account for the 0.18 L of Milli-Q water added during the extraction process. Using the mass_bDOC term allows us to move beyond a compositional assessment (i.e., %bDOC) and consider the capacity of a given soil to yield a mass of usable DOC.

$$\text{mass\_bDOC} = \left(\frac{\text{DOC}_i \times 0.18}{\text{weight}_i}\right) - \left(\frac{\text{DOC}_f \times 0.18}{\text{weight}_i}\right) \tag{2}$$

where DOC is the concentration of DOC in the soil water extraction (in mg/L) at either the beginning (i) or end (f) of the incubation period and weight is the dry mass of soil (in g) at the beginning (i) of the incubation period.

Prior to statistical analysis, we removed incubation results where, due to unknown factors, all of the incubation timepoints yielded negative results (i.e., indicating DOC production). Such negative values were found in samples that had very low DOC concentrations at the initial timepoint, or in samples that did not change in DOC concentration throughout 28 days. This resulted in a deletion of 9 soil extraction samples, 3 groundwater samples and 2 streamwater samples from the data set with 204 samples remaining. The results from our statistical analyses were not shown to meaningfully change if these negative results were included and set to zero in the data set. In cases that, from an individual sample, negative bDOC values were measured at one incubation duration but not others, the negative value was not included in the statistical test, in part due to the effect of initially low bDOC concentrations in some samples and because we could not specify the sample-specific cause of error. Final n values are shown in each plot that indicate the total amount of samples used in specific analyses.

2.7. Phospholipid Fatty Acid and Extracellular Enzyme Analysis

We analyzed soils sampled from all riparian site types ($n = 9$), depths ($n = 3$) and three sampling dates (July, September, October, $n = 3$), for phospholipid-derived fatty acid (PLFA) composition to quantify microbial biomass and functional group abundance (see Supporting Information S1 and Reidy et al., 2025). We also additionally measured soil extracellular enzyme activity from all riparian sites ($n = 9$), two depths ($n = 2$) and three sampling dates (July, September, October, $n = 3$), as a means to quantify the activity of the microbial community. Extracellular enzyme activity was measured with colorimetric assays for 5 enzymes (β-glucosidase, cellulase, protease, phenol oxidase, peroxidase; in Supporting Information S1). We used both sets of microbial variables as snapshots of community properties from the different riparian interface types and soil depths. These measures were featured in Reidy et al. (2025) to evaluate the influence of riparian interface conditions on soil microbial community structure and activity. Here, we use these measurements only as independent variables in correlations to test whether proxies for microbial biomass and decomposition in different soil environments may be related to the capacity to generate bDOC.

2.8. Statistical Analysis

We interpreted and reported significance values using language of evidence, based on Muff et al. (2022). We used linear mixed models (LMM) in R, version 4.3.1 (R Core Team., 2025) with *lme4* (version 1.1-34; Bates et al., 2015), *lmerTest* (version 3.1-3; Kuznetsova et al., 2017) and the Tukey's adjustment from the *emmeans*

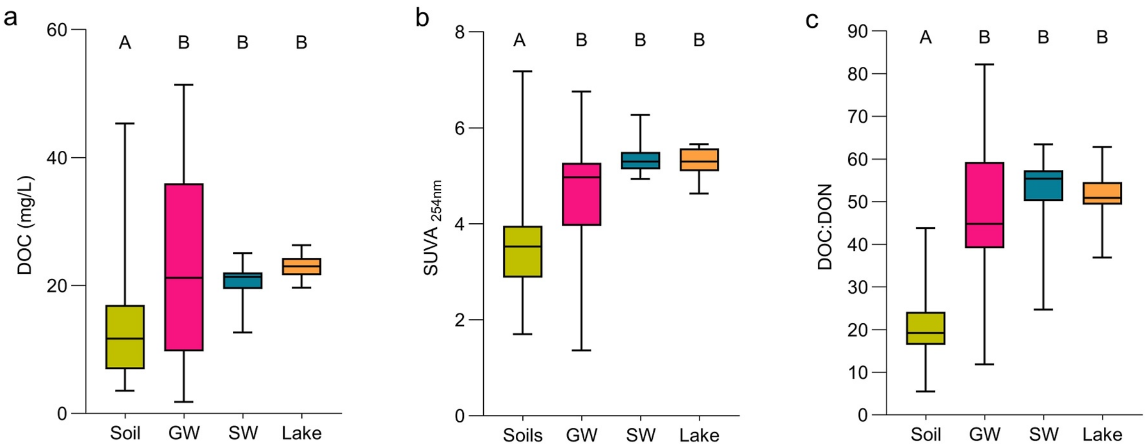

Figure 2. DOM properties in soils (Soil), groundwater (GW), streamwater (SW) and lake water (Lake) measured on the first day of each incubation. Box plots show 25th to 75th percentile with whiskers to minimum and maximum values and horizontal line at median. Compact letter display shows evidence of differences (LMM $p < 0.05$) between each sample type. (a) DOC mg/L, $n = 102, 39, 40, 8$. (b) $SUVA_{254nm}$, from left to right $n = 100, 29, 30, 7$. (c) DOC:DON, $n = 101, 39, 38, 8$.

package (version 1.8.9; Lenth, 2024), to test differences in initial chemical properties ($SUVA_{254}$, DOC mg/L, DOC:DON) and %bDOC between components of the land water continuum. To meet the assumptions of LMM we used Box-Cox transformations, with landscape components as fixed effects, and site type and sample date as random effects. To assess differences in bDOC between incubation durations within each riparian site type (High, Low, Dynamic) and landscape component (i.e., soil, groundwater, stream water, lake water) we used LMMs with incubation length (i.e., 7, 14 or 28 days) as a fixed effect and sample date and site as random effects to account for repeated sampling of sites over time. For this test, data were untransformed as normality assumptions were met within each group.

To determine if there differences in bDOC (both %bDOC and mass_bDOC for soils) and associated variables across riparian site type, soil depth, and for any interactions with sampling date, we used LMM and set site type, depth and sample date as fixed effects, with individual sites as a random effect. Data were Box-Cox transformed to fit normality assumptions. For these mixed models, we focused on differences observed after 14 days of incubation, as patterns in bDOC across riparian site types, and soil depths were statistically similar for all incubation timepoints. To assess relationships between bDOC and predictor variables, we used Pearson correlations with XLSTAT (Lumivero, 2025). Prior to correlations, data were tested for skewedness and kurtosis then a Box-Cox transformation used to fit data to normality assumptions. Finally, to test differences in groundwater and soil extraction %bDOC between riparian site types, we used a one-way ANOVA with Tukey's post-hoc testing on untransformed data that fit normality assumptions. All figures were made in GraphPad Prism version 10.2.2 for Windows.

3. Results

3.1. DOM Properties of the Land to Water Continuum Prior to Incubation

Initial DOC concentrations were lower in soil extractions (13.2 ± 0.7 mg/L; mean ± SE), with higher concentrations in groundwater (22.3 ± 2.4 mg/L), streamwater (20.4 ± 0.5 mg/L) and lake water (22.9 ± 0.7 mg/L; Figure 2a). Concentrations and properties of the DOM pool at the start of each incubation showed that soils were overall distinct from groundwater, streamwater and lake water. For example, $SUVA_{254}$ was lower in soil extractions (3.5 ± 0.1 L mg C^{-1} m^{-1}) compared to groundwater (4.9 ± 0.3 L mg C^{-1} m^{-1}), streamwater (5.2 ± 0.1 L mg C^{-1} m^{-1}) and lake water (5.2 ± 0.1 L mg C^{-1} m^{-1}), indicating lower aromaticity and greater freshness of terrestrial DOM (Figure 2b). Similarly, soil extractions had lower extractable DOC:DON ratios (20.8 ± 0.6) in comparison to other sample types (groundwater: 47.7 ± 2.4; streamwater: 53.1 ± 1.3; lake: 51.1 ± 2.5) (Figure 2c).

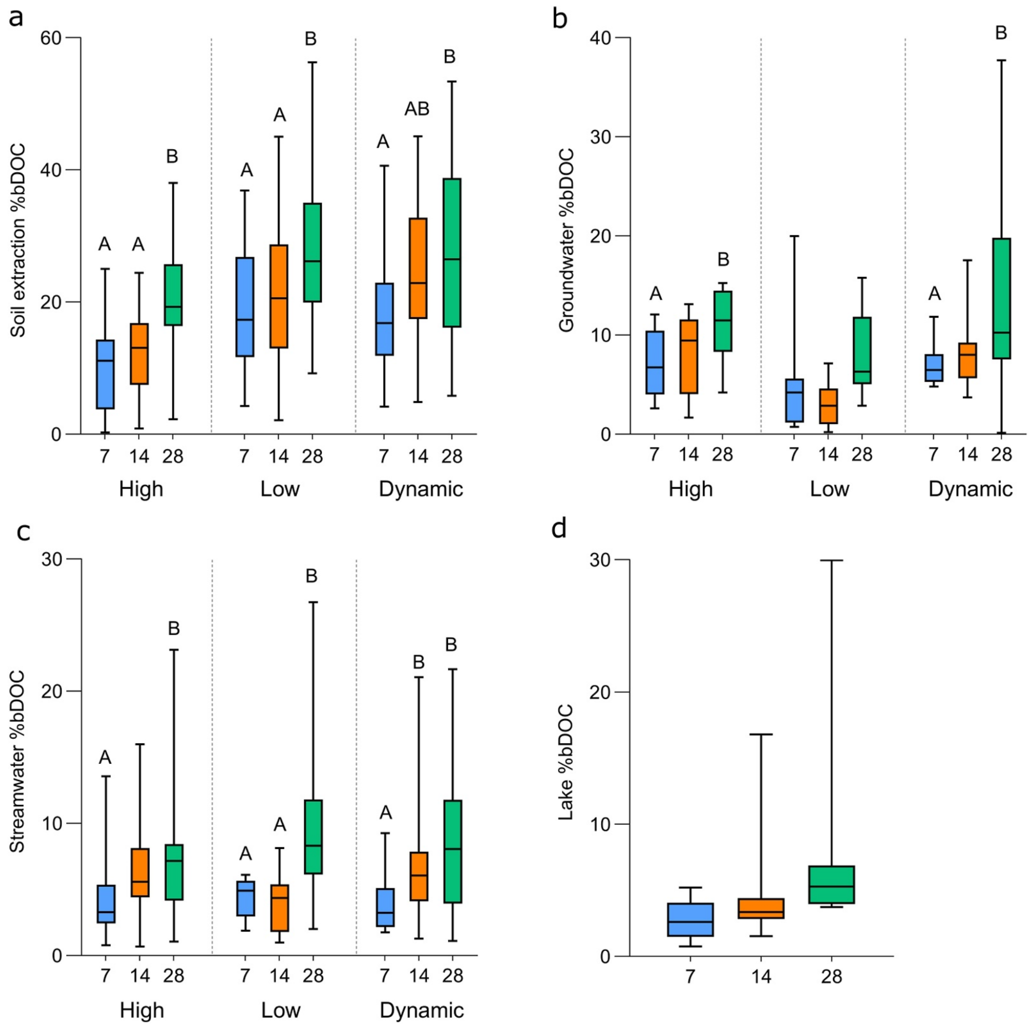

Figure 3. Percent of total biodegradable dissolved organic carbon degraded after 7 days (blue), 14 days (orange) and 28 days (green) of incubation for riparian soil extractions (a), groundwater (b), stream water (c) and lake water (d). Riparian site types in panels (a, b, and c) are indicated below the horizontal axis by High, Low and Dynamic. All boxplots encompass the 25th to 75th percentile and whiskers to minimum and maximum values, with the median shown by horizontal line. Compact letter display shows evidence of differences (LMM, $p < 0.05$) between incubation durations within each riparian site type. (a). From left to right, High $n = 24, 31, 26$; Low, $n = 35, 36, 35$; Dynamic $n = 34, 35, 35$. (b) High $n = 10, 11, 12$; Low $n = 8, 8, 9$; Dynamic $n = 9, 10, 11$. (c) High $n = 13, 14, 14$; Low $n = 9, 10, 13$; Dynamic $n = 12, 12, 13$. (d) Lake $n = 8, 8, 8$.

3.2. bDOC Across Incubation Durations

Across landscape components, the rank-order of %bDOC was always the same, regardless of incubation length, with %bDOC highest in soil extractions (grand mean across incubations: 21.4 ± 0.7%) compared to groundwater (8.0 ± 0.6%), stream water (6.5 ± 0.5%) and lake water (5.3 ± 1.2%) respectively (for all incubation durations: LMM $p < 0.0001$). In general, the cumulative %bDOC increased during the incubation, but this progression was most obvious in soils, where there was always a significant increase in bDOC between 7 and 28 days (Figure 3a). For example, between 7 and 28 days, soil extraction %bDOC increased by 1.8-fold in High sites (LMM $p < 0.001$) and 1.4-fold in Low (LMM $p = 0.02$) and Dynamic sites (LMM $p = <0.001$). By comparison, progressively greater %bDOC across incubation length was not always observed in groundwater, stream water and lake samples, although these tests had comparatively weaker statistical power. Groundwater from High and Dynamic sites increased in %bDOC loss between 7 and 28 day incubations (High, LMM $p = 0.03$; Dynamic, LMM $p = 0.03$), Streamwater from all sites similarly increased between 7 and 28 day incubations; however stream samples from Dynamic sites also increased %bDOC loss between 7 and 14 days (LMM $p = 0.03$). Samples from the lake showed no significant difference in %bDOC based on incubation length (Figure 3d).

Table 1
Pearson Correlation Coefficients Between Biodegradable Dissolved Organic Carbon at 7, 14 and 28 Days of Incubation and Chemical and Optical Properties Measured at Beginning of the Incubations

				Chemical properties				Optical	
Scale	*n*	Days	DOC	DON	DIN	PO4	DOC:DON	$SUVA_{254}$	$A_{254:365}$
Land water continuum (%bDOC)	163	7	−0.01	**0.32**	**0.27**	**0.38**	**−0.34**	**−0.50**	**0.20**
	176	14	−0.05	**0.43**	**0.17**	**0.37**	**−0.50**	**−0.65**	**0.24**
	177	28	−0.09	**0.32**	**0.25**	**0.35**	**−0.44**	**−0.50**	0.16
Soil (%bDOC)	93	7	**0.43**	**0.36**	−0.02	**0.21**	**0.23**	**−0.50**	**0.26**
	102	14	**0.46**	**0.46**	−0.04	**0.22**	0.12	**−0.54**	**0.33**
	102	28	**0.48**	**0.44**	0.10	**0.27**	0.16	**−0.42**	0.15
Soil (mass_bDOC)	93	7	**0.70**	**0.48**	0.14	**0.40**	**0.54**	**−0.41**	**0.27**
	102	14	**0.69**	**0.49**	0.09	**0.39**	**0.48**	**−0.43**	**0.31**
	96	28	**0.70**	**0.48**	0.11	**0.40**	**0.53**	**−0.39**	**0.29**
Riparian groundwater (%bDOC)	27	7	−0.03	0.05	0.19	−0.10	−0.15	−0.06	−0.37
	30	14	**0.59**	**0.68**	**0.72**	**0.75**	0.15	−0.05	**−0.64**
	32	28	−0.31	−0.25	−0.26	−0.34	**−0.39**	−0.24	0.27

Note. Relations are shown at three scales: across the land-water continuum, riparian soils, and riparian groundwater. For riparian soils, data are shown as both %bDOC and mass_bDOC. For riparian groundwater and across the land-water continuum, data are shown only as %bDOC. Values in bold correspond to correlation between variables of $p < 0.05$. 'Days' indicates incubation duration.

3.3. Chemical Properties Correlated With bDOC Along the Land to Water Continuum

At the spatial scale of the land-to-water continuum, %bDOC was negatively correlated with $SUVA_{254}$ and DOC:DON, positively correlated with PO_4^- and DON at all incubation durations, and positively correlated with $A_{254:365,}$ particularly for the 7 and 14 day incubations. At this spatial scale, we observed no significant correlation between %bDOC and initial DOC concentrations (Table 1). However, if we consider only the soil data, %bDOC and mass_bDOC were positively correlated with initial DOC concentrations at all incubation durations, and with DON and PO_4^-. DOC:DON was positively correlated with mass_bDOC; however, it was not correlated with %bDOC in incubations lasting either 14 or 28 days. $SUVA_{254}$ was negatively correlated with both soil extraction bDOC metrics. Focusing only on riparian groundwater, correlations between %bDOC and chemical and optical properties were more variable and dependent on incubation duration. For example, after 7 days of incubation, %bDOC did not correlate with chemical or optical properties, however stronger correlations emerged from the 14 day incubation with PO_4^- ($r = +0.75$), DIN ($r = +0.72$), DON ($r = +0.68$) and DOC ($r = +0.59$). Finally, although %bDOC in stream and lake water was not correlated with DOC:DON after 7 or 14 days, we observed a negative correlation after 28 days.

3.4. Soil DOM Properties and Biodegradability Across Riparian Site Types

To compare soil extraction bDOC between riprian site types, we used %bDOC and mass_bDOC data from the 14 day incubation length, given the similar patterns of %bDOC loss with incubation duration (Figure 3a). Throughout the sampling period, there were notable differences in both %bDOC and mass_bDOC after 14 days of incubation across riparian site types (in both cases: $p \leq 0.0001$). However, there was minimal evidence for an effect of sampling date, or an interaction effect between riparian site type and sampling date for either measurements of degradability ($p > 0.1$). For example, soils from Low and Dynamic sites had respectively 1.7- and 2-times greater %bDOC than High sites (Figure 4a). When measured as mass_bDOC, soils from Low and Dynamic sites had had, on average, 5.7 times more bDOC than soils from High sites (Figure 4b). Further, variation in average mass_bDOC across all locations was positively related to local soil organic content (%LOI; $R^2 = 0.46$) and C:N ($R^2 = 0.35$) (Figures 4c and 4d).

Despite these differences across riparian site types, we observed no distinct vertical patterns in %bDOC overall. However, in both Low and High sites, shallow and deep soils were less variable in %bDOC than mid-depth soils,

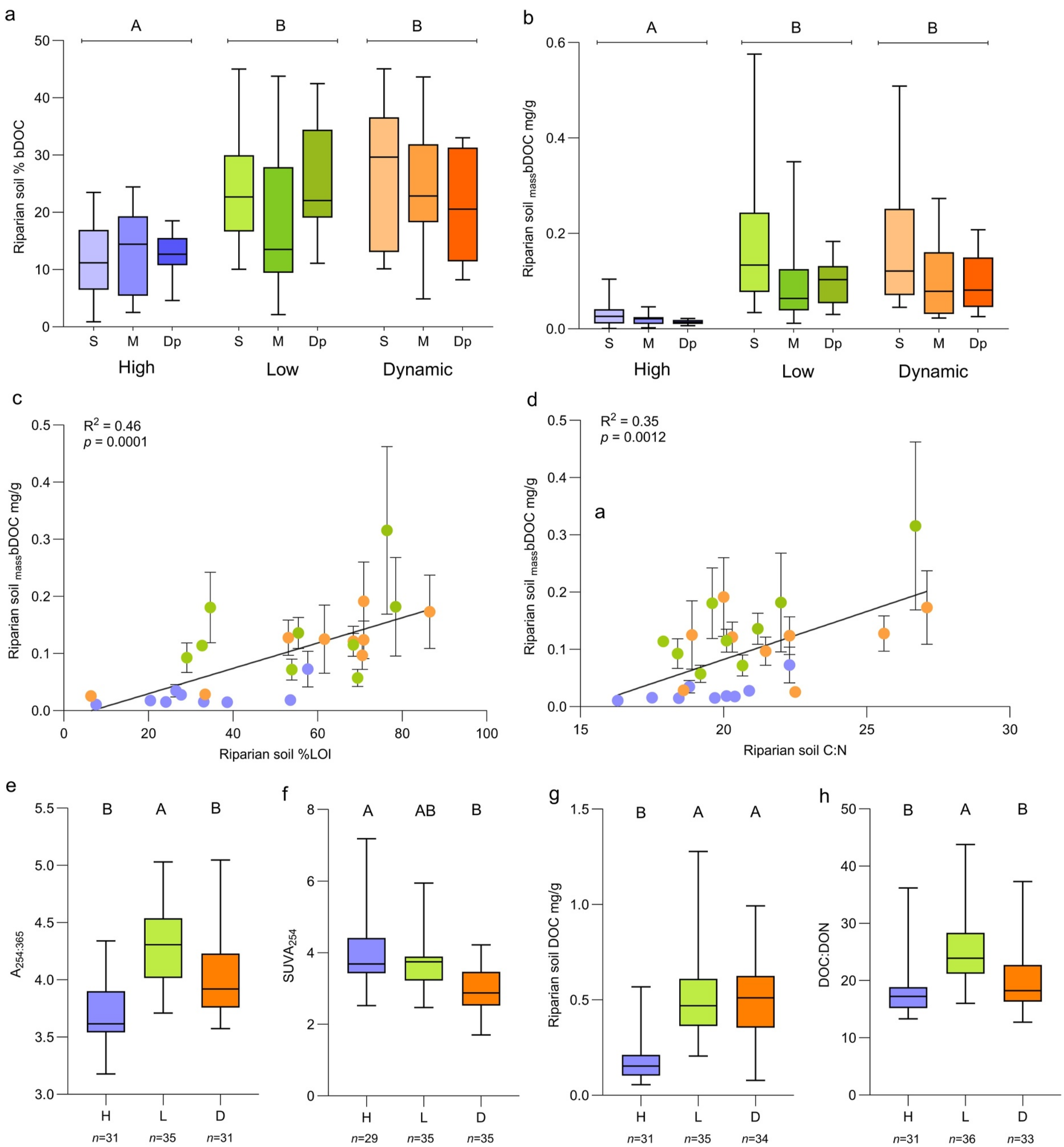

Figure 4. Summarized riparian soil biodegradable dissolved organic carbon (bDOC), correlation with soil physical properties and differences in the soil DOM pool. All box and whisker plots show 25th to 75th percentile with whiskers to minimum and maximum and line at median. Compact letter displays show differences ($p < 0.05$) between riparian site type categories. (a) Percent of total dissolved organic carbon (%bDOC) degraded after 14 days incubation for riparian soils from High (H), Low (L) and Dynamic (D) site types, at Shallow (S), Mid Depth (M) and Deep (Dp) depths. (b). Mass of total bDOC (mg/g) degraded after 14 days for riparian soils. (c). Mean mass of total bDOC (mg/g) after 14 days with standard error for individual site and depths, plotted against riparian soil %LOI with linear regression line. R^2 and p in upper left hand corner. (d). Mean mass of total bDOC (mg/g) after 14 days with standard error for individual site and depths, plotted against riparian soil C:N with linear regression line. R^2 and p in upper left hand corner. (e). Soil extraction $A_{254:365}$ (f) Soil extraction $SUVA_{254}$ (g). Riparian soil DOC (mg/g). (h) Soil extraction DOC:DON ratios.

whereas %bDOC variability was similar across all depths in Dynamic sites (Supporting Information S1). In Low sites, there was low to moderate statistical evidence that shallow soils had greater mass_bDOC than mid-depth and deep soils ($p = 0.04$ and $p = 0.09$ respectively), while there was no evidence of this effect at High and Dynamic sites ($p > 0.1$). Further, variability in mass_bDOC diminished with depth at High and Low sites, while all depths had relatively similar temporal variation in Dynamic sites (Supporting Information S1).

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Table 2
Pearson Correlation Coefficients for Riparian Soils With Microbial Community Indicators and Extracellular Enzyme Activities

Microbial community	mass_bDOC	Enzyme activities	mass_bDOC
GP:GN	0.07	β-glucosidase	0.19
Tot. Bacterial	**0.22**	Cellulase	**0.38**
Tot. Fungal	**0.28**	Protease	**0.42**
Tot. PLFA	**0.24**	Phenol Oxidase	0.03
F:B	**0.26**	Peroxidase	0.19

Note. n = 100 for each microbial community variable, n = 47 for each enzyme activity. Values in bold correspond to correlation between variables of $p < 0.05$.

Soil solution chemistry and indicators of biological activity also varied among riparian site types. For example, $A_{254:365}$ values were lower at High (3.70 ± 0.04) and Dynamic sites (4.00 ± 0.06) compared to Low sites (4.30 ± 0.06) (Figure 4e). In contrast, $SUVA_{254}$ was higher at High sites (4.04 ± 0.2 L mg C^{-1} m^{-1}) compared to Dynamic sites (2.9 ± 0.1 L mg C^{-1} m^{-1}) (Figure 4f) with a significant interaction effect ($p \leq 0.001$ between sample date and site type). Initial soil DOC was lowest in High sites (0.18 ± 0.02 mg/g) compared to both Low (0.52 ± 0.04 mg/g) and Dynamic (0.48 ± 0.04 mg/g) (Figure 4g) and low sites also had 1.3 times higher DOC:DON than High and Dynamic sites (Figure 4h). Extractable PO_4^- concentrations differed among riparian site types being up to one order of magnitude lower at High sites (3.4 μg/L) compared to Low (11.2 μg/L) and Dynamic (23.7 μg/L) sites (data not shown).

Several enzymatic and microbial community variables were also correlated with differences in mass_bDOC (at 14d) across riparan sites and depths (Table 2). For the enzymes, only estimates of cellulase ($r = +0.38$) and protease enzyme activity ($r = +0.42$) were moderately, and positively correlated with mass_bDOC (Table 2). In term of proxies for microbial biomass and composition, mass_bDOC tended to increase with total ($r = +0.24$), fungal ($r = +0.28$), and bacterial ($r = +0.22$) PLFA's, as well as with the fungal to bacterial (F:B) ratios ($r = +0.26$). No significant correlations were observed between mass_bDOC and the activities of β-glucosidase, phenol oxidase, and peroxidase, nor with the ratio of gram positive to gram negative bacteria (GP:GN).

3.5. bDOC Variation in Groundwater, Stream Water, and Lake Water

To compare groundwater and stream water %bDOC between riparian site types, we chose to use data from the 14 day incubation considering similar patterns in %bDOC across all incubation timepoints (Figure 3). After 14 days of incubation, average %bDOC in riparian groundwater was higher in High and Dynamic riparian sites (8.2 ± 1.2% and 7.9 ± 1.1%) compared to Low sites (3 ± 0.8%; Figure 5a). We also observed differences across riparian site types in terms of the similarity in %bDOC loss after 14 days between soil extractions and groundwater (Figure 5b). For example, at High riparian site types, average %bDOC loss was typically more similar between groundwater and

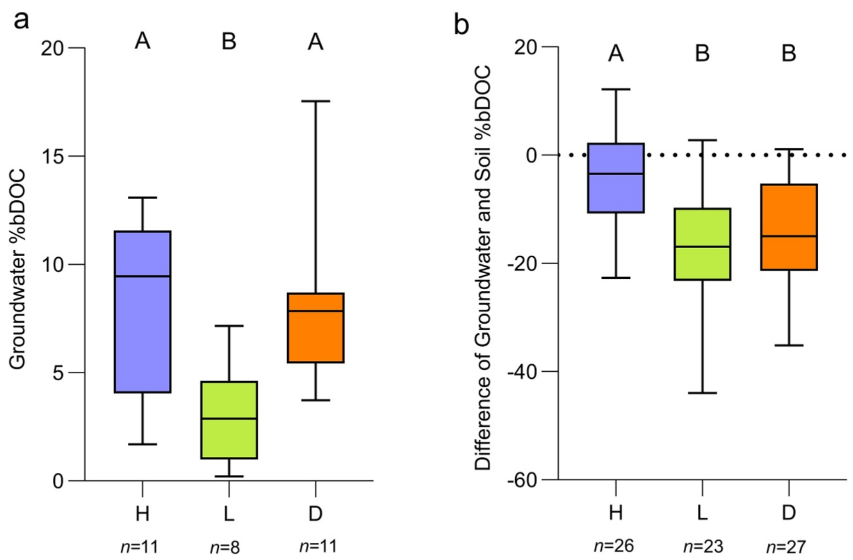

Figure 5. (a). Percentage of biodegradable dissolved organic carbon (%bDOC) degraded after 14 days of incubation for groundwater samples from High (H), Low (L) and Dynamic (D) riparian site types. (b) Difference between groundwater and soil extraction %bDOC after 14 days for each riparian site type from all dates and depths. Negative values indicate soil %bDOC greater than groundwater %bDOC loss after 14 days, and positive values indicate groundwater %bDOC is greater than soil %bDOC loss after 14 days. All box plots show 25th to 75th percentile with whiskers to minimum and maximum and line at median. Compact letter display shows differences ($p < 0.05$) between riparian site types.

soil extractions, measured as the difference between groundwater %bDOC and soil extraction %bDOC ($-4.09 \pm 1.80\%$). By comparison, groundwater from Low and Dynamic site types had considerably lower %bDOC when compared to local soil extractions (Low = $-18.02 \pm 2.60\%$; Dynamic = $-14.02 \pm 1.90\%$). Note that these patterns were also similar for comparisons between groundwater and soil %bDOC after 7, and 28 days of incubation (Supporting Information S1). Further, considering all sites and sampling dates together, the difference between groundwater and soil %bDOC increased with sample depth relative to groundwater level ($r = +0.34$, $p = 0.003$), meaning that as soils became more vertically removed from the extant groundwater level, they tended to accumulate bDOC relative to that observed in local groundwater. Finally, %bDOC in stream water after 14 days was similar across each riparian site type (High = $6.5 \pm 1.1\%$, Low = $3.8 \pm 0.8\%$, Dynamic = $7.1 \pm 1.5\%$), and %bDOC in lake water not statistically different to streamwater ($4.9 \pm 1.7\%$).

4. Discussion and Conclusions

Terrestrial inputs of organic resources to inland waters are important drivers of aquatic ecosystem processes (Karlsson et al., 2012). Yet, this supply is determined by the potential for soils to generate degradable DOC and the likelihood that these materials can move across the riparian interface. In boreal headwaters, the edaphic and hydrological properties of these interfaces vary dramatically based on the topographic structure of the landscape and how this orchestrates differences in hillslope size and in the lateral subsurface flowpaths that ultimately feed streams. Our results highlight how this landscape template creates differences in the local production of bDOC in soils and the potential supply of bDOC across land-water boundaries.

4.1. bDOC Across the Land-Water Continuum

As predicted, we observed clear differences in the degradability and chemical properties of DOC across the components of the land-water continuum. Specifically, at the broadest scale, bDOC declined from riparian soils to groundwater to stream and lake water, which is consistent with other studies exploring these patterns at similar scales (e.g., Fellman et al., 2009; Hutchins et al., 2017; Vonk et al., 2015). Comparisons across the 7-, 14-, and 28-day incubations further suggest that riparian soils store a broader array of labile and semi-labile DOC when compared to connected groundwater and aquatic systems. Direct comparison with other bDOC estimates is complicated by the lack of standardized methods (McDowell & Likens, 1988) and a paucity of studies from headwater streams during baseflow periods. Despite this, our results are well within the ranges of bDOC reported for other boreal ecosystems (ca. 4%–15% Wickland et al., 2007; 17% Speetjens et al., 2022). Similarly, groundwater, stream, and lake water samples throughout the study period had generally low bDOC (6.8%, 6.6% and 4.9% respectively after 14 days), consistent with previous observations from Krycklan streams (e.g., Rulli et al., 2022). Overall, while riparian soils in northern landscapes are well documented as sources of bulk DOC to streams (e.g., Ledesma et al., 2018), our results suggest that, at least during baseflow, riparian soils are generally efficient at retaining the most labile components of this pool.

The differences in bDOC across the landscape scaled with simple proxies of DOM properties, with higher % bDOC corresponding to declining aromaticity ($SUVA_{254}$) moving from soils, to ground- and stream water. Negative correlations between aromaticity indices and bDOC are common for soils and freshwater from other northern landscapes (e.g., Abbott et al., 2014; Fellman et al., 2008). Further, bDOC increased with DON concentrations and declined with DOC:DON ratios, suggesting that labile DON may be preferentially retained within the soil environment (e.g., Lutz et al., 2011). Such retention is consistent with the significance of N as a limiting nutrient in boreal landscapes and the high likelihood for efficient DON cycling in these soils (Sponseller et al., 2016). However, other studies from northern landscapes have documented a large pool of bioavailable DON that remains adsorbed, or otherwise spatially inaccessible in soils (e.g., protected from biotic uptake within soil aggregates or via microsites with low matric potential) and thus fails to enter the mobile soil solution (Darrouzet-Nardi & Weintraub, 2014). Regardless of whether the patterns observed here emerge via biological or physical mechanisms, our findings indicate that decreases in bDOC across the land-water interface correspond to strongly non-linear changes in the characteristics of DOM that is transferred from soils to groundwater.

4.2. Variation in bDOC Production Among Riparian Soils

In addition to patterns across components of the land-water continuum, there was notable variation in the capacity of riparian soils to generate bDOC, based on local hydrogeomorphology. Here, the overall range of bDOC in soils was large, from undetectable to 44.2% bDOC, and up to 0.57 mg/g when measured as mass_bDOC. Despite this variability, both bDOC indices were significantly lower in soils from sites with persistently high groundwater levels (High sites), when compared to Low and Dynamic sites (Figures 4a and 4b). Soils from High sites also had notably lower concentrations of soil organic matter and lower C:N ratios, and, as predicted, both of these variables were positively related to mass_bDOC production across sites and depths (Figures 4c and 4d). However, despite vertical gradients in several soil properties (e.g., %LOI, C:N, extractable DOC), we did not see clear evidence for vertical patterns in bDOC production, which has been observed in other studies (e.g., Scott & Rothstein, 2014). Similarly, %bDOC was not as closely correlated with soil properties as was mass_bDOC. In both cases, the lack of clear patterns may be because our bioassays did not distinguish between different potential sources of bDOC that may contribute to this pool at different soil depths, including rhizodeposition nearer the surface (Schade et al., 2001), leaching from surface litter (Hensgens et al., 2020) and fermentation in deeper layers (Herndon et al., 2015). In fact, acetate is among the most abundant low molecular weight DOM forms in Krycklan streams (Berggren, Laudon, et al., 2010), suggesting that bDOC production at depth, and under anoxic conditions, is likely an important process within these interface zones. Thus, the overall diversity of potential sources may be why the capacity to produce bDOC was highly variable regardless of site type or soil depth.

As observed across the land-water continuum, patterns of bDOC amongst soils were also linked to DOM properties, but the specific predictors were not identical at this more targeted scale (Table 1). Most notably, variation in soil bDOC amounts among sites and depths consistently increased with DOC concentrations and DOC:DON ratios, particularly when considering mass_bDOC. When assessed across the full land-water continuum, these two predictors were either unimportant (e.g., DOC) or inversely related (e.g., DOC:DON) to bDOC. Such shifting relationships with scale suggest that, while bDOC patterns across the land-water boundary appear shaped by differences in the labile DON pool, the variation amongst riparian sites and depths reflects differences in the degree to which soils have been processed over the longer term (e.g., Freeman et al., 2024). Further, along the SJB stream reach, variation in capacity to generate bDOC seems strongly influenced by the hydrogeomorphic template and extent to which different soil strata are inundated and hydrologically flushed. Specifically, the relatively high DOC concentrations and DOC:DON ratios at Low and some Dynamic sites are consistent with soils that, due in part to deeper local groundwater levels, are less microbially processed (e.g., have higher C:N; Rumpel & Kögel-Knabner, 2010), subject to less frequent hydrological flushing (Scott & Rothstein, 2014), and thus have retained a greater capacity to generate and accumulate bDOC. By comparison, lower DOC concentrations and DOC:DON observed in soil solutions from High sites are consistent with a more highly processed organic matter pool (i.e., lower C:N) that is also more persistently flushed, which has consequences for the DOM it yields (Michel & Matzner, 2002; Yates et al., 2019) including its potential to support bacterial growth. Most importantly, the shifts in the correlates of bDOC that we observed across scales underscore the importance of interpreting the drivers of DOC degradability with caution, as attributes of this pool and the environmental contexts that influence its degradation may change along the flowpaths that connect soils to aquatic systems (Berggren et al., 2022).

Patterns of bDOC generation from riparian soils were also related to differences in biological indicators associated with the riparian hydrogeomorphic settings. For example, extracellular enzyme production by soil microbes drives biogeochemical transformations of organic resources (Freeman et al., 2024), in particular carbon, which may then be mobilized elsewhere in the landscape. Consistent with this, we found positive correlations between mass_bDOC and two hydrolytic enzymes integral to soil organic matter breakdown: cellulase, which targets the abundant plant polymer cellulose and is important in C cycling (Baldrian et al., 2011), and protease, which targets peptide chains and is important in both C and N cycling (Vranova et al., 2013). The activity of both enzymes differed among riparian site types, as did the overall microbial biomass as represented by total PLFA (Reidy et al., 2025). Interestingly, some soil biological variables (e.g., cellulase activity) along this stream are enhanced at Dynamic sites beyond what would be expected based solely on soil properties, consistent with an added effect of drying-rewetting dynamics on microbial activity (Reidy et al., 2025). Yet, contrary to our expectations, we did not observe a similar influence of groundwater fluctuations on bDOC generation (i.e., Low and Dynamic sites were similar), potentially because our bioassays were not sensitive enough to resolve such influences. Nevertheless, our results show that variation in the structure of headwater riparian zones not only influences the physical and hydrological attributes of the land-water interface, but also sets a template for the microbial communities and processes that underpin bDOC production in soils.

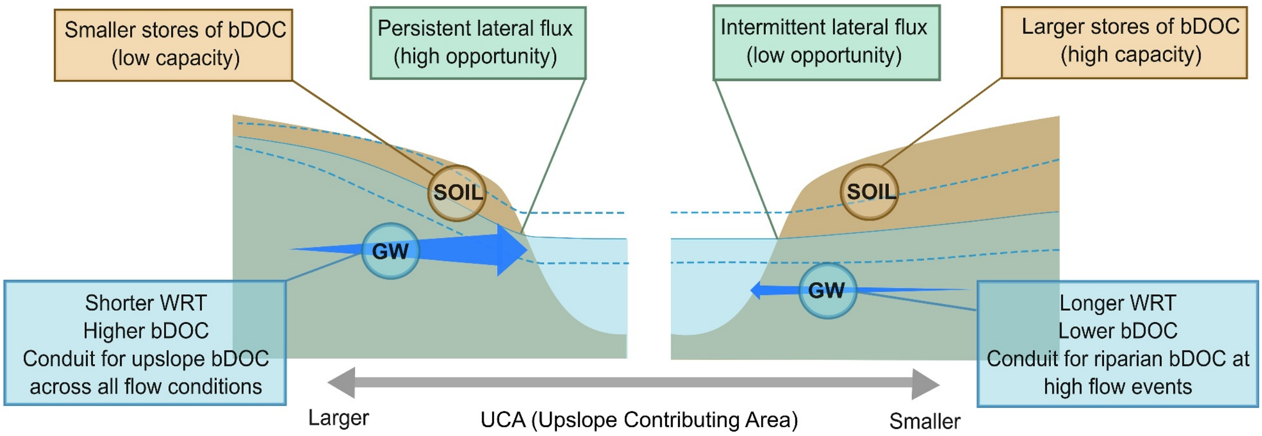

Figure 6. Conceptual representation of how variation in riparian hydrogeomorphology influences biodegradable dissolved organic carbon (bDOC) supply from soils to streams based on differences in local biogeochemical capacity and hydrological opportunity. Based on our findings, interface soils linked to larger upslope contributing areas (UCA, *left*) have a weaker capacity to produce or process bDOC locally, but are drained by surficial lateral flowpaths (blue arrow), with shorter water residence times (WRT), which act as persistent conduits for bDOC generated and stored in upslope areas. Conversely, interface soils linked to smaller UCAs (*right*) have a greater capacity to produce bDOC, but have limited opportunity for lateral transfer which only occurs during high flow events that activate surficial soils. In this way, interfaces linked to larger UCAs are crucial bDOC sources to streams during baseflow, but interfaces linked to smaller UCAs are likely major sources of bDOC to the river network during high flow and flood events.

4.3. Transport of bDOC From Soils to Groundwater and Streams

In addition to the capacity of riparian soils to generate bDOC, our results suggest important spatial and temporal variability in the potential transfer of bDOC from soils to groundwater across riparian site types (Figure 6). This transfer seems mainly regulated by the degree of contact between soils and lateral subsurface flowpaths and the water residence time (WRT) of those flowpaths, which varies across the different interface zones studied here (Jutebring Sterte et al., 2022). For example, at Low and to some extent Dynamic sites, there is a large volume of riparian soil that has a strong capacity to generate bDOC, but very little opportunity to transfer these resources laterally. Here, surficial soil strata with the strongest potential to yield bDOC are rarely in contact with lateral subsurface flowpaths. Further, for bDOC supplied to these flowpaths, the relatively long WRT during baseflow (Jutebring Sterte et al., 2022) likely promotes extensive degradation, such that very little of this material reaches the stream (e.g., McLaughlin & Kaplan, 2013; Shen et al., 2015). Only during hydrological events, such as snowmelt, or large rain events, would there be sufficient hydrological opportunity to mobilize the substantial amounts of accumulated bDOC from these sites to the aquatic environment (Berggren et al., 2009). While such events are clearly important for DOC mobilization from soils to aquatic systems, the associated high transport rates during floods also means that these resources are likely to be processed further downstream in the drainage network, and thus, are of less ecological relevance to the adjacent aquatic ecosystem (Raymond et al., 2016).

By contrast, soils within High sites have a relatively weaker biogeochemical capacity, but form a riparian interface with near-constant opportunity to deliver resources laterally to streams. A surprising feature of these sites is that bulk DOC and bDOC in groundwater is notably elevated relative to what might be expected given the capacity of local soils to generate either of these resources (Figure 5). Indeed, while lateral flowpaths within High sites are in close contact with the whole soil profile, soils here store less organic matter, and have lower microbial biomass (i.e., total PLFA) and rates of enzyme activity compared to other riparian site types, indicating a diminished ability to either locally generate, or process bDOC moving through this interface (Reidy et al., 2025). However, these interfaces are also connected to large contributing hillslopes, and the DOC moving through them appears to be produced much further upslope when compared to other site types (Jutebring Sterte et al., 2022; Ploum et al., 2021). That groundwater in these sites moves through soil strata with an overall poorer capacity to utilize organic resources likely further increases the chance that any reactive solutes in transit (including bDOC) may be delivered to the stream. In this way, the combination of diminished biological capacity, but strong lateral connectivity, appears to give rise to riparian interfaces that serve as important conduits for bDOC that is generated further away from the stream.

Finally, while there has been much focus on DOC (and bDOC) mobilization during floods (e.g., Baker et al., 2000; Berggren et al., 2009), the transport of bDOC across interface zones that have preferential flowpaths may be particularly important to streams during baseflow. As an example, Leach et al. (2017) suggest that up to 75% of stream water during baseflow at this same reach can be derived from a small number of sites with preferential subsurface flowpaths, inclusive of High, and one of the Dynamic, sites used in this study. If we apply modeled values for groundwater discharge through each riparian site (see Leach et al., 2017) to estimate total lateral bDOC flux during summer baseflow, we find that High sites contribute, on average, 2 and 70 times more bDOC to the stream when compared to Dynamic and Low sites, respectively. While these estimates are coarse, such elevated inputs of bDOC from High sites are energetically important to small boreal streams, which otherwise can support very low rates of primary productivity (Lupon et al., 2019). In fact, while we did not detect elevated stream bDOC adjacent to High and Dynamic sites, Lupon et al. (2023) showed that rates of stream respiration along this same reach were enhanced in areas where discrete subsurface flowpaths meet the stream. In this way, interface environments that have the weakest local capacity to produce bDOC are potentially most important to the stream at times when aquatic biota are in greatest need, that is, baseflow. More broadly, our findings suggest that boreal headwaters are comprised of a continuum of interface environments that differ in capacity to generate bDOC in soils, and in opportunity to mobilize and convey bDOC laterally, creating variability in terms of when and where these inputs may be most important to aquatic ecosystems within the broader stream network.

Data Availability Statement

The data set "Biodegradable dissolved organic carbon (BDOC) and associated physical and chemical measurements from a boreal first-order stream reach" by Reidy, M. (2025), which supports the findings of this study is openly available at the Swedish National Data Service (https://researchdata.se/en) via URL https://researchdata.se/en/catalogue/dataset/2024-636/1 with CC BY 4.0 licensing.

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