

SPECIAL ISSUE PAPER

WILEY

Landscape matters: Predicting the biogeochemical effects of permafrost thaw on aquatic networks with a state factor approach

Suzanne E. Tank¹  | Jorien E. Vonk²  | Michelle A. Walvoord³  |
James W. McClelland⁴  | Isabelle Laurion⁵  | Benjamin W. Abbott⁶ 

¹Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada

²Department of Earth Sciences, Vrije Universiteit Amsterdam, The Netherlands

³U.S. Geological Survey, Earth System Processes Division, Denver, CO, USA

⁴Marine Science Institute, University of Texas at Austin, Port Aransas, TX, USA

⁵Centre Eau Terre Environnement, Institut national de la recherche scientifique, Québec, QC Canada

⁶Department of Plant and Wildlife Sciences, Brigham Young University, Provo, UT, USA

Correspondence

Suzanne E. Tank, Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada.
Email: suzanne.tank@ualberta.ca

Funding information

Campus Alberta Innovates Program; BLE LTER program, Grant/Award Number: US NSF grant 1656026

Abstract

Permafrost thaw has been widely observed to alter the biogeochemistry of recipient aquatic ecosystems. However, research from various regions has shown considerable variation in effect. In this paper, we propose a state factor approach to predict the release and transport of materials from permafrost through aquatic networks. Inspired by Hans Jenny's seminal description of soil-forming factors, and based on the growing body of research on the subject, we propose that a series of state factors—including relief, ice content, permafrost extent, and parent material—will constrain and direct the biogeochemical effect of thaw over time. We explore state-factor-driven variation in thaw response using a series of case studies from diverse regions of the permafrost-affected north, and also describe unique scaling considerations related to the mobile and integrative nature of aquatic networks. While our cross-system review found coherent responses to thaw for some biogeochemical constituents, such as nutrients, others, such as dissolved organics and particles, were much more variable in their response. We suggest that targeted, hypothesis-driven investigation of the effects of state factor variation will bolster our ability to predict the biogeochemical effects of thaw across diverse and rapidly changing northern landscapes.

KEYWORDS

aquatic networks, biogeochemistry, permafrost thaw, state factor approach

1 | INTRODUCTION

Permafrost thaw fundamentally alters the flow of materials from land through aquatic networks. Thaw introduces previously sequestered material from frozen soils into active biogeochemical cycles, while also enabling subsurface water to move through deeper flowpaths with potentially longer travel times. These changes are measurable at

scales ranging from the plot to the pan-Arctic,^{1,2} can account for the majority of biogeochemical loss from thaw-affected terrestrial systems,³ and can substantially perturb the ecological functioning of recipient freshwater and nearshore marine systems.^{4,5} As a result, there has been a marked increase in effort to understand the effects of thaw on aquatic systems, with publication output on this topic increasing more than six-fold over the past decade, and more than

25-fold since the year 2000 (Web of Science search, "permafrost and [porewater or stream or river or lake or pond]," 2000, 2008, and 2018).

Although permafrost thaw has been widely observed to alter the biogeochemistry and ecology of affected aquatic systems, work across disparate study sites illustrates that there is considerable regional variation in biogeochemical response. Across organic and inorganic species and particulate and dissolved phases, permafrost thaw has been documented to increase chemical concentrations by orders of magnitude in some recipient aquatic systems,^{6,7} but lead to little response, or even concentration declines, in others.⁸ Thus, there is a growing recognition of the need to quantify how regional, and landscape-specific, factors constrain the biogeochemical response to thaw,⁹ and how this response alters undisturbed rates of organic carbon, inorganic carbon,¹⁰ and nutrient cycling. Indeed, the response of lateral carbon and nutrient flux to permafrost thaw is one of the largest sources of uncertainty in modeling net ecosystem carbon balance of the permafrost zone.¹¹

Here, we build on previous efforts to identify a constrained series of quantifiable factors that shape the biogeochemical response to permafrost thaw within aquatic networks (see also previous reviews by Vonk et al.^{9,12}, Frey and McClelland,¹³ and Lafrenière and Lamoureux¹⁴). Our synthesis is inspired by the seminal work of Hans Jenny,¹⁵ who—by positing that a series of interacting factors control soil development—spurred a systems approach to understanding ecosystem function across multiple, disparate disciplines, and enabled a transition from largely descriptive research towards a framework capable of explaining intersite variability based on factors that could be empirically and theoretically tested.¹⁶ We further acknowledge the important early work of Anders Rapp,¹⁷ who identified variation in biogeochemical processes (in particular, chemical weathering) as one of several key agents of landscape change. Below, we propose a similar approach that seeks to (a) predict the transport of materials from permafrost through aquatic networks, and (b) provide a conceptual framework for hypothesis-driven investigations of controls on the response to thaw across diverse northern regions. We develop this framework alongside a series of case studies that exemplify how variation in key *biogeochemical response factors* shapes the effects of permafrost thaw, and provide a summary of recent progress in the field. We end our review with a discussion of the importance of scale, and a reflection on how the scientific community might move forward with a hypothesis-driven approach to quantifying controls on biogeochemical change.

2 | QUANTIFIABLE FACTORS SHAPE THE BIOGEOCHEMICAL RESPONSE TO THAW

We propose that relief (*r*), ice content (*ic*), permafrost extent (*pe*) and parent material (*pm*) represent primary *state factors* that determine how, over time (*t*), thaw affects the liberation and transport of a given biogeochemical constituent (B_x) within aquatic networks (Eqn 1):

$$B_x = f(r, ic, pe, pm, t...) \quad (1)$$

These factors are similar to Jenny's soil-forming factors of climate, organisms, parent material, and relief, as also modified by time. However, the factors outlined here have all been shown—either via direct study, or indirect comparisons among studies—to shape how permafrost thaw affects the aquatic biogeochemical response. For example, *relief* influences absolute and relative mobilization of particulate and dissolved constituents,¹² water residence and biogeochemical processing time within soils, and waterlogging, anoxia, and organic matter accumulation in soils and aggrading permafrost.¹⁸ *Ice content*, including vertical and lateral dimensions, governs the extent and form of thermokarst¹⁹ and thus the importance of abrupt changes relative to more gradual thaw. *Parent material*, which we define broadly to include how this material was incorporated into permafrost (i.e., syngenetic vs. epigenetic), will affect the degree of biogeochemical processing prior to and during incorporation into permafrost, the composition and permeability of thawed materials, and the depth of permeable and/or mobile materials available for thaw (e.g., contrast the Canadian Shield where active layers can penetrate bedrock with regions where active layers are underlain by deep deposits of frozen till or loess).^{20,21} *Permafrost extent*—which is inextricably linked to climate and ecosystem properties such as vegetation type, distribution, and dynamics²²—influences hydrologic connectivity, including lateral connections and interactions between surface water and groundwater²³. Finally, several *processes that act over time* affect both permafrost composition and how thaw effects progress. Prior to thaw, for example, ongoing activity in frozen pore waters can cause dissolved organics and other reduced species to accumulate in permafrost soils.²⁴ After permafrost thaws, the amount of time unfrozen affects the diagenetic state of material available for transport,²⁵ while ongoing expansion of thermokarst features and active layers exposes previously frozen soil horizons with chemical compositions that may change with depth.^{8,26} In addition, we note that *vegetation*, which we do not review in detail here, can control the movement of biogeochemical constituents through aquatic flowpaths,²⁷ while *hydrologic factors*, particularly precipitation patterns and their intensity, are critical for determining thermokarst event frequency,²⁸ the rapidity with which thawed materials are incorporated into aquatic flowpaths, and the soil depth at which lateral transport occurs.¹⁴ Like Jenny, we use an ellipsis at the end of our conceptual equation to acknowledge additional factors that may be site-, or region-, specific. While we also acknowledge that warming and wetting will additionally affect ongoing biogeochemical cycling in the active layer, we constrain this review to changes specifically associated with permafrost thaw.

Below, we use a case study approach to explore regional variation in the above-outlined state factors, and how this variation directs and constrains the biogeochemical response to thaw. Within this approach, we further highlight how different state factors dominate within distinct landscape types. We focus on five regions with abundant research on these topics (Figure 1), beginning with landscapes that are reasonably homogeneous in their configuration (a–c), and moving towards increasing landscape complexity to describe the

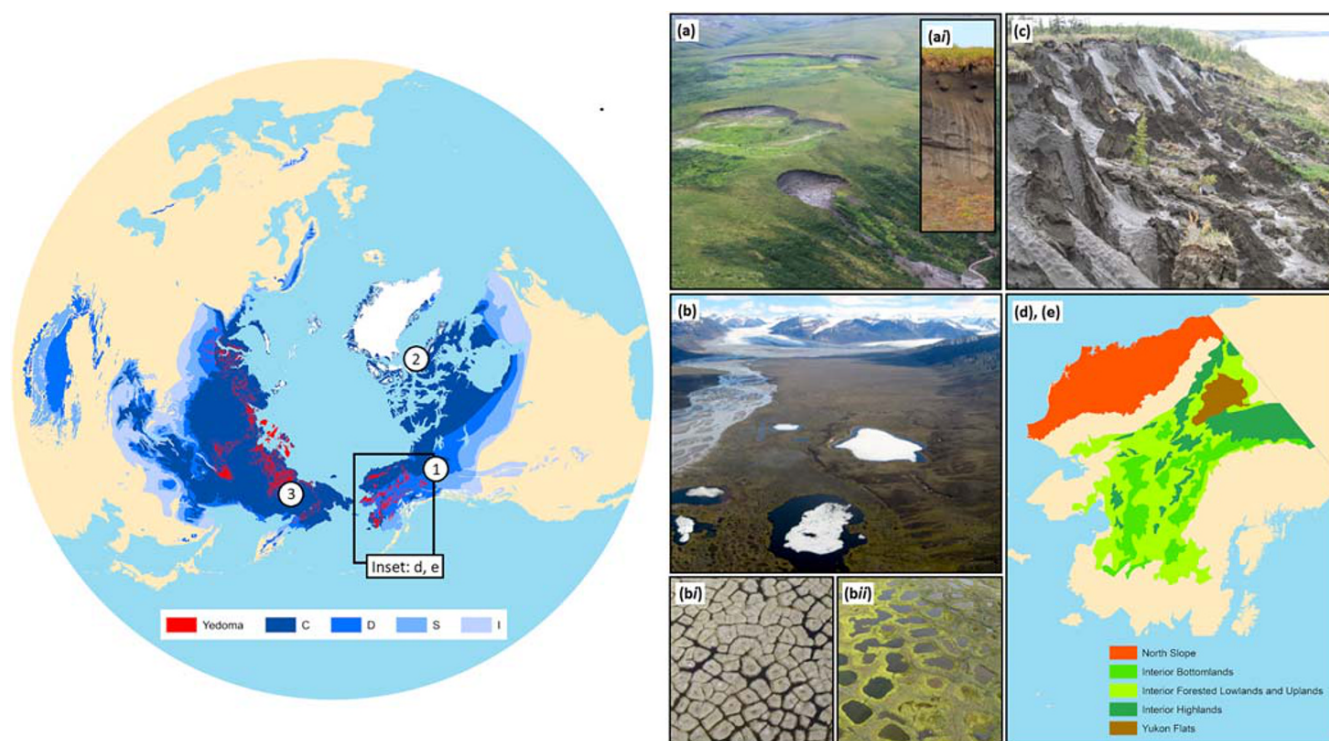


FIGURE 1 Distribution of focal landscapes from this review (left panel), accompanied by site-specific images (right panel). Locations indicated in the left panel include: (1) glacial margin landscapes of the western Canadian Arctic; (2) high Arctic polygonal terrain (Bylot Island); and (3) Yedoma regions. The map legend indicates continuous (C), discontinuous (D), sporadic (S), and isolated (I) permafrost. In the right panel, image (a) portrays a cluster of retrogressive thaw slumps from site (1), with inset (ai) depicting the stratigraphy of a headwall from the Peel Plateau; image (b) shows the Qarlikturvik Valley of Bylot Island (site 2), with sub-images (bi) and (bii) depicting trough ponds and polygonal ponds, respectively; image (c) shows an ice-rich Yedoma exposure on the Kolyma River; and (d) and (e) show the Alaskan North Slope and ecoregions of interior Alaska, respectively. Permafrost extent in left panel is from Brown et al.¹³¹; Yedoma extent is from Strauss et al.⁵⁸ Photo credits: (a, ai) Scott Zolkos; (b, bi, bii) Isabelle Laurion; (c) Guido Grosse [Colour figure can be viewed at wileyonlinelibrary.com]

effect of state factor variation across defined spatial domains (d and e). We conclude with a brief summary of some of the important work on this topic that has occurred elsewhere.

Our review largely focuses on the effects of thaw on carbon, nutrients, and ions, with attention paid to different responses between dissolved and particulate phases. These constituents have been a focus of observation because of their importance for understanding the broader carbon cycle, food web processes, and weathering dynamics, respectively.¹² With respect to organic carbon, the dissolved phase (i.e., as dissolved organic carbon [DOC] or dissolved organic matter [DOM]; operationally defined using a filter pore size of 0.2–0.7 μm) is understood to be more accessible to microorganisms than particulates (i.e., as particulate organic carbon [POC]²⁹), with molecular composition creating variation in bio- and photo-reactivity.^{30,31} With respect to nutrients, we similarly understand that inorganic species (NO_2^- , NO_3^- , NH_4^+ , PO_4^{3-}) are more reactive than their dissolved organic, and particulate, counterparts (where total nutrients are the sum of dissolved inorganic, dissolved organic, and

particulate species). With respect to ions, we understand bicarbonate to be an integral component of the active carbon cycle,¹⁰ while other major ions (e.g., Ca^{2+} , Mg^{2+} , SO_4^{2-}) are indicators of weathering processes that additionally control salinity and the physical structure of water bodies. Thus, variation in the species released by thaw, as well as total release rates, shapes ecological and biogeochemical effect within aquatic and coastal ecosystems.

2.1 | Glacial margin landscapes of the western Canadian Arctic

The western Canadian Arctic is shaped by past action of the Laurentide Ice Sheet, which covered the region briefly (beginning ca. 18 kyr BP on the Peel Plateau³²) during the Last Glacial Maximum, emplacing thick deposits of glacial tills that contain carbonates, sulfides, and silicates³³ that have remained preserved and largely unmodified at depth in permafrost since glacial retreat.³² Permafrost

throughout this region is continuous and contains widespread, Pleistocene-origin ground ice, with ice content ranging from 50% by volume to massive ground ice deposits tens of meters thick.³² The presence of excess ground ice renders the region highly susceptible to thaw-driven slumping (thermokarst),³⁴ which largely manifests as retrogressive thaw slumps¹⁹ that are rapidly increasing in activity and coverage.³⁵ Fluvial incision of the fine-grained glacial sediments that characterize this region has engendered high topographic relief,^{32,35} enabling slump debris to flow downslope and enter valley bottom streams. The largest thaw slump features in the region are tens of hectares in size, with debris tongues that fill valley bottoms to substantial depth.³⁴ Notably, warming during the early Holocene thermal maximum enabled active layers to deepen considerably relative to the present day across the Plateau.³² Today, this evidence of greater thaw depths in the past is preserved in permafrost, and is characterized by higher organic matter content and the loss of massive ground ice that is prevalent in deeper, unmodified tills.³⁶ In contrast, nearby landscapes that did not experience this early Holocene warming (e.g., the Jesse Moraine on Banks Island) are experiencing slump activity that is considerably enhanced relative to sites further south, despite mean annual temperatures that are as much as 5°C lower.³⁵

This mix of thick relict ground ice deposits, incised topography, and variation in past thaw history (Figure 2) has resulted in a biogeochemical response to thaw that is substantial and dominated by processes associated with the particulate and inorganic phase, but also varies among slump features. On the Peel Plateau, suspended sediment increases by orders of magnitude immediately downstream of slump features, with a response that propagates through stream networks and is clearly visible at the 10³-km² watershed scale.²⁸ Concentrations of ions, derived from slump-exposed glacial tills, are similarly

elevated by orders of magnitude immediately below slump features, remain elevated for kilometers downstream, and have been increasing over the past several decades in the downstream Peel River.^{28,33} This substantial inorganic and particle-associated response has broad biogeochemical implications. For example, weathering processes initiated via till exposure have implications for the carbon cycle, with geogenic CO₂ sourced from carbonate minerals spiking substantially in the waters that drain slump features.³³ In contrast, although permafrost-derived DOM appears to be highly biolabile,³⁷ DOC release from slumps is modest, unlike elsewhere. Instead, DOC concentrations typically decline downstream of slumps, apparently via adsorption to mineral surfaces, and dilution at deep slump features that expose substantial ice-rich and organic-poor glacial-origin materials for export.³⁸ Sediment adsorption also appears to play an important role in mercury biogeochemistry, with whole-water mercury concentrations increasing with sediments, but dissolved mercury species declining in slump-affected streams, similar to DOC.³⁹ Finally, as for many other regions, nutrients have been documented to increase substantially as a result of slumping on the Peel Plateau. This effect occurs across inorganic and dissolved organic species but is most pronounced in the particulate phase.⁴⁰

State factor variation can also be used to understand differences in response across glacial margin sites within the western Canadian Arctic, but beyond the Peel Plateau. For example, on the Jesse Moraine, where slump activity is enhanced by the absence of a previously thawed paleo-active layer, third-order streams appear to derive as much as 70% of summertime flows from ground ice.⁴¹ Nearby Herschel Island is similarly an ice-rich glacial margin site, but has parent material derived from the glacial thrust of riverine, marine, and glacial sediments rather than the deposition of unmodified glacial tills.⁴² Like

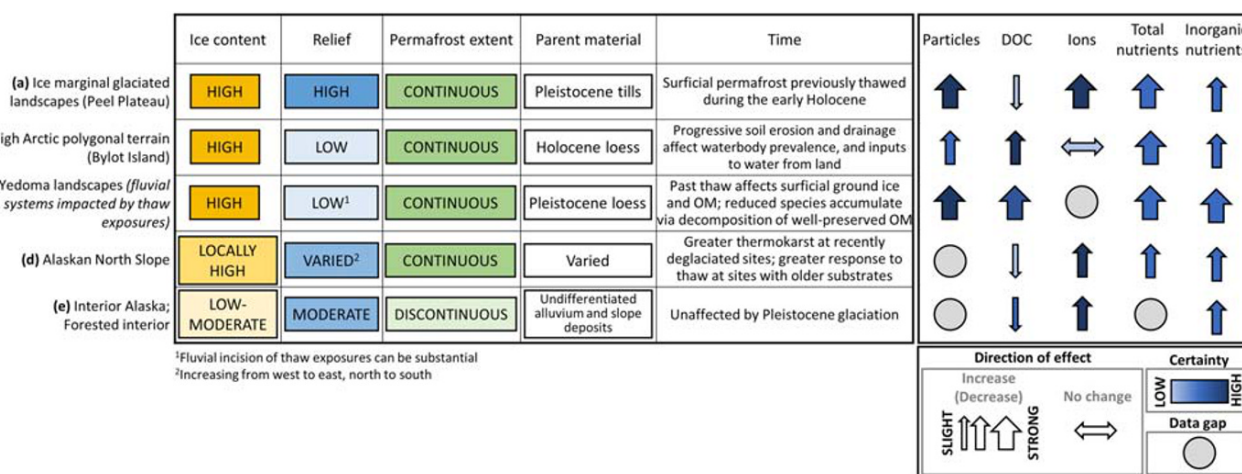


FIGURE 2 A conceptual table illustrating variation in state factors across the focal landscapes of this review (left panel), and the related biogeochemical response within aquatic networks (right panel). In the right panel, the direction of arrows indicates increasing, decreasing, or no response related to thaw. The size of the arrows indicates the magnitude of response, from slight (smallest arrows) to strong (largest arrows). The shading of the arrows indicates the level of certainty of the indicated effect, from low certainty (light blue) to high certainty (dark blue). Gray circles indicate a knowledge gap. Response characterization is focused at the site of thaw, and thus does not include consideration of downstream propagation. DOC, dissolved organic carbon [Colour figure can be viewed at wileyonlinelibrary.com]

the Peel Plateau and Jesse Moraine, permafrost thaw at this site is characterized by widespread retrogressive thaw slumping and the subsequent mobilization of large volumes of sediment, in this case directly to nearshore marine environments.⁴³ However, DOC concentrations in permafrost and slump runoff appear to be higher at this site than on the Peel Plateau.⁴⁴ Although one might predict that thaw will have a less pronounced effect on weathering processes on Herschel Island relative to the Peel Plateau, given the marine and fluvial (i.e., previously reworked) origin of sediments incorporated into permafrost at this site, this prediction is yet to be explored.

2.2 | High Arctic polygonal terrain

Our examination of High Arctic polygonal terrains focuses on the Qarlikturvik Valley of Bylot Island (Figure 1), which lies well within the continuous permafrost zone, with active layer depths of about 50 cm. The Qarlikturvik Valley consists of a proglacial river outwash plain bordered by a 3–4-m-high terrace (0.5–0.6° slope). Terrace soils are composed of eolian deposits (fine- to medium-grained poorly sorted loess) layered with poorly decomposed, low-density, fibrous organic matter formed since 3700 yr BP. Continuous sedimentation and a cold climate enabled the growth of syngenetic permafrost during the Holocene throughout this terrace.⁴⁵ These peaty loess deposits contain excess pore ice (on average 110% of dry weight in upper permafrost horizons⁴⁶), with gravimetric organic matter contents reaching more than 50%. Warming in this region has been most pronounced during autumn and winter, leading to shorter snow-covered periods and increased total winter precipitation.⁴⁷

High ice content and flat topography come together to govern the biogeochemical response to thaw at this site. The flat terrace contains abundant and diverse water bodies (~6% cover over its 40-km² area [I. Laurion, unpublished data], including thermokarst lakes, kettle lakes, trough ponds, polygonal ponds, small streams, and gullies^{48,49}). Ice-wedge polygons and associated ponds are abundant (see also other lowland regions in Alaska, Siberia, and the Canadian Archipelago^{50,51}), while thermo-erosional processes are exacerbated by the high porosity and ice content of these soils. Spring snow melt generates underground hydro-thermal erosion, tunneling, and sink holes through permafrost, which serve as preferential flow paths during runoff periods.⁴⁶ These features later develop into gullies with thaw slumping, collapse of active-layer overhangs, slope failure, and mudflows.⁴⁸ While all of the water bodies found on the Qarlikturvik terrace are influenced by permafrost thaw to some extent, trough ponds and gullies are particularly subject to thermokarstic inputs via progressive soil erosion, while polygonal ponds are subject to drainage.

In addition to enabling abundant lakes and ponds, the low relief of the Qarlikturvik terrace creates long residence times and high exposure to sunlight, affecting biogeochemistry. These water bodies are rich in DOM with a clear terrigenous signature, with trough ponds showing the highest concentrations of nutrients (e.g., total P up to 75 µg L⁻¹, total N > 4300 µg L⁻¹) and DOM

(DOC up to 33 mg L⁻¹, with a particular increase in the chromophoric fraction with erosional processes^{52,53}). Total suspended solids are also elevated,⁵⁴ although at concentrations much lower than for thermokarst-affected fluvial systems in glacial margin and Yedoma landscapes. Trough ponds exhibit particularly high concentrations of dissolved methylmercury, with levels directly correlated to DOM and nutrient concentrations.⁵³ If we consider that a trough pond experiences a gradual increase in shoreline erosion, followed by colonization by primary producers (aquatic plants, cyanobacterial mats) and subsequent stabilization during its lifespan, it seems likely that solutes and particles will increase and then decrease over time. However, this trajectory requires a more formal assessment.

Waterbodies on the Qarlikturvik terrace generally emit large amounts of greenhouse gases (GHGs), particularly as CH₄, indicating the bioavailability of carbon at the landscape level. However, only GHGs emitted from thermokarst lakes are from an aged carbon source (CH₄, up to 3400 yr BP) while CH₄ emitted from ponds appears to be modern despite evident erosion of Holocene organic matter into trough ponds.⁴⁹ This suggests that a large fraction of carbon mineralized within this landscape has been recently fixed from the atmosphere. Primary producers are particularly abundant in coalescent ponds (microbial mats; these ponds also act as CO₂ sinks) and stabilized trough ponds (brown mosses and graminoids). However, because all of these water bodies are large CH₄ emitters,⁴⁹ they may be important sites for the production and/or decomposition of labile organic matter, perhaps following the influx of nutrients via thermokarst. Pond DOM is highly photoreactive⁵⁵ and presents clear changes in composition when exposed to microbial decomposition [I. Laurion, unpublished data], but pelagic mineralization of DOC is modest in summer, particularly after dry periods. Therefore, most of the summertime GHG emitted from these systems is apparently produced by the microbial decomposition of organic matter in pond sediments or adjacent soils. This landscape-level processing may be particularly important on flat terrain, allowing more time for organic matter processing in soil pore water before entering water bodies. As permafrost thaw progresses in this low-relief terrain, we can expect that aged pools of carbon will be mobilized to aquatic networks. The mineralization efficiency of this carbon, and its interaction with nutrient mobilization, primary production, and precipitation patterns, remains to be assessed.

2.3 | Pleistocene Yedoma landscapes

Northern Hemisphere Yedoma deposits formed during the Pleistocene in unglaciated regions,^{56,57} and are estimated to cover about 625,000 km² of which ca. 65% is located in Siberia; intact Yedoma underlies about 30% of the Siberian permafrost landscape.^{58,59} Rapid, continuous sedimentation of mostly windblown material (loess) in combination with accretion of the permafrost table formed deposits up to >50 m thick that range in age from >55 to 8 kyr BP.⁶⁰ In contrast to the ice-rich soils from (Canadian) glacial margins described above,

Yedoma deposits are characterized by a relatively high sediment organic carbon (OC) content (3.0 ± 1.6 – 2.2 wt% total OC⁵⁹) as they formed in steppe–tundra ecosystems and hold substantial plant and animal remains.⁵⁶ Ground ice content is high (mean volumetric content 82%⁵⁹), mostly in the form of syngenetic ice wedges. During the Holocene thermal maximum, a large fraction of Siberian and North American Yedoma experienced some degree of thaw, which has led to a heterogeneous landscape where primary and secondary thermokarst features (e.g., thaw lakes, alas deposits) are prevalent.^{57,59} These Holocene-modified deposits hold even higher total OC but are characterized by slightly lower ice contents than unmodified Yedoma.⁵⁹ Yedoma formation was mostly constrained to regions of low topographic relief, and current intact Yedoma deposits are still mostly found in lowlands (< 400 m) underlain by continuous permafrost.^{57,58}

The presence of rapidly frozen, relatively undecomposed organic matter in Yedoma soils,⁵⁶ high ice content at depth, and low topographic relief shapes the response to thaw in Yedoma regions. Within fluvial networks, strong contrasts in age, composition, and degradability of organic matter can be primarily related to the targeted spatial scale (first-order streams vs. river mouths), degree and mode of thaw (abrupt vs. gradual), and mode of transport (DOC vs. POC). Thaw and release of Yedoma OC *only* occurs (a) when active layer deepening reaches the ice-rich subsurface, or (b) when abrupt thaw exposes deeper layers at thermokarst sites, river banks, and coastlines (note that mining exposes deep Yedoma deposits in Yukon,⁶¹ but biogeochemical response in this region is almost entirely unstudied). When gradual thaw has not progressed to this point, mobilized C is overwhelmingly contemporary in age.⁶² In contrast, when deeper Yedoma is exposed via abrupt thaw or erosion, high concentrations of aged OC are released into the aquatic system,^{7,63} with particulate constituents dominating the OC release (e.g., POC:DOC ratios of ca. 40:1 at Duvannyi Yar, even with DOC concentrations as high as 200 mg L^{-1}).⁶³ Numerous studies indicate that thaw exposures—where deep Yedoma material is released—deliver highly degradable, aged, DOC to the aquatic network.^{7,31,63–65} This rapid DOC degradation is mostly attributed to compositional factors (low initial phenolic content, high levels of aliphatics and low-molecular-weight compounds^{7,65}) that may be explained by fast incorporation of organic matter into permafrost upon formation, and, consequently, the lack of pre-processing prior to thaw. Additionally, nutrient concentrations (particularly NH_4^+ and NO_3^-) are elevated in Yedoma thaw waters compared to other local waters not derived from Yedoma.^{7,63} This is supported by studies of intact Yedoma permafrost cores²⁴ that show substantial accumulation of DOC downcore, and an abundance of low-molecular-weight organic acids and other constituents such as NH_4^+ that have formed and been preserved under long-term anoxia.²⁴ Deep thermokarst lakes in Yedoma regions are underlain by unfrozen sediments that can produce CH_4 of Pleistocene age, at concentrations about six times greater than non-Yedoma thaw lakes, and also release substantial CO_2 .⁶⁶

Within drainage networks, age and degradation rates of DOC decrease with movement downstream, and Yedoma source-specific signatures disappear from the bulk pool,^{64,65} suggesting that most of

this permafrost carbon is metabolized rapidly. Indeed, the permafrost fraction in Siberian river main stem DOC is low (ca. 5–10%; Lena and Kolyma rivers).⁶⁷ However, contributions of permafrost OC to main stem POC are significantly higher (ca. 59–84%⁶⁷), highlighting the source-specific decoupling in loss rates with transport downstream. Degradation rates of Yedoma-origin POC have yet to be determined, but there are indications of preferential burial of the mineral-bound, aged, fraction.⁶⁸ The release of aged OC also occurs along Yedoma coastlines via erosion of ice-rich permafrost cliffs.^{69,70} Currently, Arctic coasts in the Siberian Yedoma region release more sediments (125 Tg yr^{-1} for Laptev and East Siberian Sea) than regional rivers (54 Tg yr^{-1}) but POC release is comparable between these two sources.^{69,70} Looking forward, reductions in sea ice are expected to increasingly expose these coasts to open water and thus greater wave fetch and storms,⁷¹ suggesting that ice-rich coasts will have an increasingly higher sediment and OC generation potential compared to riverine systems.^{69,71}

2.4 | Alaskan North Slope

Like the three cases discussed above, Alaska's North Slope region (Figure 1) is underlain by continuous permafrost. Unlike the previous cases, however, this region is defined by strong spatial variation in relief, parent material, and ice content (Figure 2) that lead to different permafrost–aquatic linkages across a relatively small domain. This $\sim 254,000\text{-km}^2$ region is bound by the Brooks mountain range to the south and the Beaufort Sea to the north. Distances between the Brooks Range and the coast decrease from west to east, accompanied by a general increase in relief. This variation in physical characteristics creates a strong west–east gradient in river chemistry, including decreases in ratios of dissolved organic to inorganic nutrients in river water.⁷² The west–east gradient is thought to reflect a combination of factors that correlate strongly with increased watershed steepness, including decreased soil organic matter stocks, increased water–mineral interactions, decreased soil water residence times, and more oxygenated soils.⁷² The North Slope was not covered by ice sheets during the Last Glacial Maximum, but there were alpine glaciers that periodically extended from the Brooks Range more than 100 km to the north.⁷³ This created a complex glacial history for the southern half of the North Slope that still structures vegetation, ground ice, water chemistry, and soil properties today.^{6,31} Areas between the northern extent of glaciers and the coastal plain developed rich deposits of Yedoma soils.⁵⁹ Thus, many of the rivers that flow from the Brooks Range to the coast integrate inputs from sub-watersheds that are representative of each of the three previously described cases.

A variety of recent studies have documented changes in permafrost on the North Slope. For example, permafrost borehole temperatures at multiple locations have increased by 0.8 – 1.2°C per decade since the 1970s.⁷⁴ These changes have been linked to increasing mean annual air temperatures, changes in snow depth,

and shifts in vegetation.²² Empirical modeling experiments suggest that temperature increases in shallow lakes over the past 30 years have crossed a critical threshold for talik formation.⁷⁵ Several studies have documented warming-induced increases in thermokarst activity as well. For example, a rapid rise in regional summer air temperatures has been associated with a dramatic increase in thermokarst lake activity in the Prudhoe Bay area between 1990 and 2001, resulting in more ponds, greater microrelief, enhanced lakeshore erosion, and increased landscape heterogeneity.⁷⁶ Likewise, satellite imagery from the western North Slope reveals a strong, nonlinear increase in hillslope thermokarst features since the 1980s, associated with early-season warming and extreme rainfall events.⁷⁷

Increased thermokarst activity on the North Slope is particularly concentrated in locations of high ground ice content and recently deglaciated environments.^{73,77} Studies focused on biogeochemical effects of hillslope thermokarst in this region have shown increases in sediment loading and delivery of organic matter and inorganic N and P to surface water networks.^{6,78} However, some effects of thermokarst are more transient than others, with concentrations of some solutes, including organic N and Cl^- , returning to pre-disturbance levels after thermokarst features stabilize, but others, including DOC, inorganic N, and SO_4^{2-} , remaining elevated for years to decades.⁷⁹ Because thermokarst can displace meters of material rapidly, it can reconnect surface water with surficial geology,¹⁹ meaning that its effect on water chemistry depends on the tied effects of glacial history, local parent material, and ice content.^{31,79} For example, the magnitude of the chemical response to thermokarst differs strongly with time since deglaciation, with larger increases in inorganic N, Cl^- , and SO_4^{2-} at sites that have been deglaciated for more than 50 kyr compared to sites deglaciated in the last 24 kyr.^{31,79} This is likely to be due to older sites having greater differences between active layer and permafrost conditions (e.g., more advanced state of weathering in the seasonally unfrozen active layer). However, one observation that appears to hold across permafrost types (e.g., syngenetic vs. epigenetic) and ages on the North Slope is that degradability of DOM from actively thawing permafrost is elevated compared to undisturbed tundra or stabilized thermokarst features.³¹

In addition to studies focusing on thermokarst effects, several studies have documented long-term changes in fluvial chemistry that appear to be linked to permafrost thaw more generally. One of the earlier examples of broad-scale change comes from the upper Kuparuk River, where an analysis of long-term data revealed a major increase in NO_3^- export between 1991 and 2001.⁸⁰ These changes appear to have continued through to the present, with observations of increasing alkalinity, cations, and NO_3^- , but decreasing total P and DOC over time.⁴ Lengthening flow seasons also appear to be affecting solute transport, with increases in inorganic N and trace metals occurring late in the season when thaw depth is greatest, and plant growth has ceased.^{81,82} This could be due to catchment-scale changes in the active layer, or because of longer persistence of thaw around lakes (taliks) and under streams

and rivers (hyporheic zones).^{83,84} One general finding from studies conducted on the North Slope is that thaw depth acts as a master variable, controlling water flowpath, residence time, and exposure to different physical and biological conditions, including the biological capacity to retain and process DOM and nutrients.⁸⁵

2.5 | Interior Alaska

Like the Alaskan North Slope, Interior Alaska also encompasses substantial diversity in state factors, and thus requires cross-scale investigations to unravel integrated biogeochemical responses. Interior Alaska consists of four main ecoregions: (a) Interior Bottomlands, (b) Interior Highlands, (c) Interior Forested Lowland & Uplands, and (d) Yukon Flats (Figure 1), which are primarily underlain by discontinuous permafrost and have remained unglaciated for several million years.⁸⁶ This case study focuses on the latter two ecoregions, to provide contrasts in state factors with the regions previously discussed. The Interior Forested Lowlands & Uplands are characterized by rolling topography with moderate relief.⁸⁶ Rocky upland soils formed from weathered local rock tend to have higher magnitude and variability in permeability than the less prevalent silty upland soils that are more uniformly low in permeability.⁸⁷ Lowland soils of the Forested Interior consist mainly of silty alluvial material. Parent material in the Yukon Flats, a broad, low-relief sedimentary basin, consists of alluvial sand and gravel with a thin eolian sand sheet deposited during the late Pleistocene.⁸⁸

The discontinuous permafrost of Interior Alaska is characterized by open taliks beneath major rivers and lakes that allow for hydrologic connection and solute exchange between aquatic and sub-permafrost flow systems.^{23,89,90} Permafrost is relatively warm, moderately thick (10–100+ m), and is poised for accelerated thaw that can alter subsurface flowpaths.^{23,90} Ice content ranges from low (<10% by volume) in sandy and colluvial deposits in epigenetic Holocene permafrost, including in the Yukon Flats lowlands and rocky uplands of the Forested Interior, to high (>40% by volume) in patchy deposits of eolian loess in syngenetic Pleistocene permafrost and silty uplands of the Forested Interior.^{88,89} Thermokarst landforms, expressed as thaw slumps and gullies, are present in localized ice-rich areas and are generally not present in the ice-poor Yukon Flats lowlands or rocky uplands.⁸⁸

This mix of warm, discontinuous permafrost, modest relief, and overall moderate to low ice content has resulted in a biogeochemical thaw response that is primarily driven by changing subsurface flow paths and soil-water residence times, with direct mobilization of constituents released from thawing permafrost as a secondary effect that is more prevalent in the silty uplands characterized by higher relief and ice content. Dissolved carbon exports by the Yukon River, which integrates input across all ecoregions of Interior Alaska and includes headwater contributions from the Yukon Territory in Canada, have shifted over several decades towards reduced DOC and increased dissolved inorganic carbon (DIC) export during summer to autumn, when normalized to discharge.⁹¹

Increases in Ca^{2+} , Mg^{2+} , Na^+ , SO_4^{2-} , and P have similarly been observed over decadal scales in this basin.⁹² These shifts have been attributed to deepening flowpaths, increased weathering, and pervasive increases in groundwater input, including from sub-permafrost groundwater sources, resulting from permafrost thaw.^{93,94} Deep sources of groundwater in this region are typically low in DOM and high in inorganic solutes, including dissolved inorganic nitrogen (DIN), compared with near-surface flow, due to longer residence times for decomposition and mineral weathering.^{12,95} Studies conducted on smaller tributaries in the Forested Interior also suggest a decrease in DOC⁹⁶ and increase in DIN export with deepening permafrost tables, enhanced residence time for microbial processing, and increased flow through mineral soils.⁹⁷ The biogeochemical response manifested through enhanced subsurface flow throughout the Forested Interior is primarily dependent on relief and permeability of the parent material, factors that drive groundwater flow.

Evaluation of long-term change in biogeochemical exports from the Yukon Flats is limited by lack of historical data; however, implications for permafrost thaw and corresponding flowpath deepening can be drawn from current studies. For example, comparison of DIC and DOC yields in the Beaver Creek watershed during comparatively high and low water years highlights the importance of flowpath depth for influencing stream biogeochemistry.⁹⁸ Here, DOC export exceeded DIC export during a high flow year when shallow paths through organic-rich soils dominated, while DIC export prevailed during low flow when water tables and corresponding flowpaths were deeper and through mineral soils.

Ongoing studies in Interior Alaska promote the use of stream water DOM composition and age to track increases in the mobilization of organic matter released from thawing permafrost.⁹⁵ High DOC and DIN yields coupled with low DOC biodegradability measured in extracts from Holocene-age permafrost cores in the Forested Interior⁹⁹ suggest a high potential for persistence of Holocene-age permafrost DOC upon export to aquatic networks, particularly with the expected expansion of lateral taliks in boreal watersheds.¹⁰⁰ This low biodegradability contrasts with rates for Pleistocene Yedoma permafrost observed here and in other regions.^{31,63,64} Although expected to become increasingly prevalent, at present, detection of aged DOC as a potential indicator of permafrost C in Interior Alaska has been confined to headwater streams, a signal swamped by modern inputs at larger scales.¹⁰¹

2.6 | State factors across regions: A summary of response

Although not reviewed in detail here, other well-studied Arctic regions can also be viewed through a state factor lens. For example, on Melville Island in the Canadian Arctic Archipelago, conditions including ground ice melt and modest relief have enabled a series of active layer detachments that substantially increased the flux of particulate constituents in affected watersheds for several

years following disturbance,¹⁰² but had an effect on DOC flux that was much less pronounced.¹⁰³ On the Tibetan Plateau, thaw depth strongly influences the concentration and reactivity of organic material delivered to aquatic environments, with lower concentration and less reactive DOM when thaw is deeper, as a result of greater in-soil processing and shifts in DOM sources.⁸ In both of these regions, permafrost DOM appears to be biolabile,^{104,105} which contrasts with findings from peat plateau-bog complexes that are common across discontinuous permafrost in western Canada, where DOM sourced from deeper horizons of thawed peat is less labile than that from modern carbon at the surface.¹⁰⁶ Across the biogeochemical constituents that we consider (Figure 2), some have responses to thaw that are controlled by a narrow set of state factors (e.g., the direct effects of relief and ice content on particles; see also Olefeldt et al.¹⁰⁷), while others are influenced by a broader interacting suite (e.g., the influence of relief, parent material, ice content, and permafrost extent on DOC). Still others appear to be reasonably consistent in their response (e.g., nutrients). Below, we describe some unique considerations related to scaling, before closing with thoughts on how a state factor approach may allow us to better enact predictions of change over broad spatial scales.

3 | SCALING RESPONSE WITHIN AND ACROSS LANDSCAPES

Unlike their terrestrial counterparts, aquatic networks are directional systems that integrate over broad (watershed) scales. This imposes unique scaling considerations that nest above state factor effects in our assessment of aquatic network change. Within fluvial networks, for example, differences in reaction rates will control the geographic extent of effect. Some thaw constituents, such as permafrost-origin DOM, are often highly labile⁷ (but see Wickland et al.⁹⁹ and Burd et al.¹⁰⁶), while others, such as readily weathered carbonate minerals, can undergo rapid transformation following thaw.³³ This leads to a biogeochemical effect that—while often substantial—can be highly localized, even when network transport is relatively rapid.¹⁰⁸ In contrast, more conservative species can show a thaw-enabled effect that tracks across broad catchment scales.²⁸ Seasonal variation in reaction rates may also be an important consideration. This is exemplified by recent findings for inorganic nutrients, which appear to show a broad increase with thaw throughout many fluvial networks⁴ that can be particularly pronounced during late summer and autumn, when the seasonally thawed layer is deepest but biological uptake has slowed.¹⁰⁹ Applying realistic reaction, uptake, and sedimentation rates determined elsewhere (e.g., via wide-ranging studies on nutrient spiraling and particle size transport); better constraining these rates for constituents such as organics that present variable, but often permafrost-specific, compositions^{24,65,99}; and quantifying spatiotemporal variability in reaction rates and transport are critical steps for scaling the directional effects of thaw through aquatic networks.

In addition to variable modification during transport, the residence time of, and distribution of thaw sites within, aquatic networks will regulate the location and spatial extent of effect. On the North Slope of Alaska, for example, small drainage areas combined with close proximity to the ocean facilitate relatively short transit times from headwaters to the coast.¹¹⁰ Similarly, thaw immediately adjacent to coastal areas (i.e., via coastal erosion) can have substantial effects on coastal biogeochemistry without transit-associated processing.^{68,111} In contrast, the presence of lakes and ponds within landscapes can increase water residence times substantially, either enabling thaw effects to be geographically constrained to lacustrine environments, or creating biogeochemical filters that modify the composition of water as it transits through broader networks at the landscape scale.^{112,113} Quantifying transit and residence time is thus also critical for modeling the extent and location of effect along an aquatic continuum that ranges from pore-waters to the coast.

Beyond their directionality, the integrative nature of aquatic systems also imparts important scaling considerations. Particularly in discontinuous permafrost regions, movement from headwaters, with localized and typically shallow flow systems,^{6,96} to higher order streams necessitates consideration of the contribution of regional sub-permafrost groundwater,⁹⁴ which has distinct biogeochemical signatures reflecting long residence times.^{83,114} Widespread observations of increased baseflow in major rivers draining discontinuous permafrost basins have been linked to increasing contributions of groundwater resulting from thaw.⁹³ Movement downstream also necessarily integrates a mosaic of landscape patches, where other sources of regional variability can override disturbance signals from thaw,¹¹⁵ or different types of thaw effects (including sediment-dominated thermokarst,^{28,78} solute-dominated active layer deepening,¹¹⁶ and increasing groundwater incorporation^{93,114}) may contribute to the overall biogeochemical response.

4 | MOVING FORWARD WITH A STATE FACTOR APPROACH FOR ASSESSING CHANGE

One clear benefit of a state factor approach is that it provides the scientific community with a scaffold upon which to propose and challenge hypotheses about how the thaw-associated liberation of biogeochemical constituents may vary across permafrost-affected landscapes. This systematic understanding can in turn be targeted towards scaling response across the large and diverse spatial domain of the permafrost zone. While research that considers single, or occasionally, dual, state factors is certainly emerging (see, as examples, Olefeldt et al.¹⁰⁷ and Turetsky et al.¹¹⁷ over broad spatial scales, and Liu et al.¹⁰⁴ O'Donnell et al.¹¹⁸ and Harms et al.¹¹⁹ in more spatially constrained studies), we argue that for many constituents, a specific focus on quantifying change through a state factor lens could enable substantial progress in our discipline, across multiple biogeochemical fronts.

This state factor approach, however, is not without its challenges. First, it requires robust spatial data to quantify state factor variation across the broad circumpolar domain (see also Vonk et al.⁹ for a discussion on this topic), to ensure that fine-scale patchiness does not result in biased extrapolation.^{120,121} While some of these robust datasets exist (relief¹²²; soil organic carbon¹²³) or are available or under development for at least part of our domain (see the work on ice content by O'Neill et al.¹²⁴ and PermafrostNet; www.permafrostnet.ca), information on the chemical composition of what we here term "parent material" (i.e., including sulfide content,^{33,125} which is virtually unknown, and carbonates,¹²⁶ which have been estimated, but with varying levels of constraint) is a clear gap, as is our understanding of permafrost extent and its vertical distribution in discontinuous terrains.

Second, this approach requires our community to work together to set priorities and collect measurements for hypothesis-driven investigations that relate on-the-ground biogeochemical change to state factors across diverse landscapes. While these priorities will be sub-discipline-specific, we suggest several initial priorities: (a) the release and transport of particles relative to relief and ice content³⁴; (b) the release and lability of permafrost DOM relative to permafrost soil composition (driven by relief and parent material), and particle interactions (i.e. sorption^{38,127}; driven by ice content and relief); (c) the relationship between chemical weathering and inorganic carbon cycling rates (driven by parent material composition and past thaw)³³; (d) the ubiquity of nutrient increases across state factors and regions; and (e) efforts to understand how biogeochemical change in discontinuous permafrost regions varies between peatland¹²⁸ and mineral soil⁹³ landscapes. In this process, we must also consider the co-occurring effects of warming and wetting,¹⁴ which will affect organic matter and nutrient accumulation/mineralization in soils,¹²⁹ weathering rates,¹³⁰ and the speed at which land–water transfer occurs.

Finally, and specific to aquatic networks, extrapolation should ideally include the scaling considerations described above. Along these lines, models to constrain residence time based on relief and aquatic network composition (presence of lakes and their connectivity, vs. fluvial systems), coupled with an understanding of reaction rates (see DOM lability, above) and thaw location, are critical to model the downstream freshwater and coastal ocean effects of thaw. Models to elucidate varying groundwater inputs through aquatic networks are also a clear priority (see also Vonk et al.⁹ on this point). Understanding the biogeochemical response to thaw across diverse and rapidly changing northern landscapes necessarily requires extrapolation over space and time. Explicit consideration of key state factors, their distribution, and how they shape biogeochemical response is thus critical in our quest to accurately model northern change.

ACKNOWLEDGEMENTS

Conversations with many co-authors and colleagues over the years, in addition to the excellent biogeochemical research being undertaken in regions not directly highlighted in this review, have shaped the

manuscript. Chris Burn, Bob Hilton, Kim Wickland, Steve Kokelj, and one anonymous reviewer offered comments that substantially improved the manuscript. Joanna Li Yung Lung assisted with the preparation of Figure 1. S.E.T. acknowledges support from the Campus Alberta Innovates Program. J.W.M. acknowledges support from the BLE LTER program (US NSF grant 1656026).

DATA SHARING

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

ORCID

Suzanne E. Tank  <https://orcid.org/0000-0002-5371-6577>

Jorien E. Vonk  <https://orcid.org/0000-0002-1206-5878>

Michelle A. Walvoord  <https://orcid.org/0000-0003-4269-8366>

James W. McClelland  <https://orcid.org/0000-0001-9619-8194>

Isabelle Laurion  <https://orcid.org/0000-0001-8694-3330>

Benjamin W. Abbott  <https://orcid.org/0000-0001-5861-3481>

REFERENCES

- Drake TW, Tank SE, Zhulidov AV, Holmes RM, Gurtovaya T, Spencer RGM. Increasing alkalinity export from large Russian Arctic rivers. *Environ Sci Technol*. 2018;52(15):8302-8308.
- Lafrenière MJ, Louiseize NL, Lamoureux SF. Active layer slope disturbances affect seasonality and composition of dissolved nitrogen export from high Arctic headwater catchments. *Arct Sci*. 2017;3(2):429-450.
- Plaza C, Pegoraro E, Bracho R, et al. Direct observation of permafrost degradation and rapid soil carbon loss in tundra. *Nat Geosci*. 2019;12:627-631.
- Kendrick MR, Huryn AD, Bowden WB, et al. Linking permafrost thaw to shifting biogeochemistry and food web resources in an arctic river. *Glob Chang Biol*. 2018;24(12):5738-5750.
- Harris CM, McTigue ND, McClelland JW, Dunton KH. Do high Arctic coastal food webs rely on a terrestrial carbon subsidy? *Food Webs*. 2018;15:e00081.
- Harms TK, Abbott BW, Jones JB. Thermo-erosion gullies increase nitrogen available for hydrologic export. *Biogeochemistry*. 2014;117(2-3):299-311.
- Mann PJ, Eglinton TI, McIntyre CP, et al. Utilization of ancient permafrost carbon in headwaters of Arctic fluvial networks. *Nat Commun*. 2015;6:7856.
- Mu CC, Abbott BW, Wu XD, et al. Thaw depth determines dissolved organic carbon concentration and biodegradability on the northern Qinghai-Tibetan plateau. *Geophys Res Lett*. 2017;44(18):9389-9399.
- Vonk JE, Tank SE, Walvoord MA. Integrating hydrology and biogeochemistry across frozen landscapes. *Nat Commun*. 2019;10:5377.
- Regnier P, Friedlingstein P, Ciais P, et al. Anthropogenic perturbation of the carbon fluxes from land to ocean. *Nat Geosci*. 2013;6(8):597-607.
- McGuire AD, Lawrence DM, Koven C, et al. Dependence of the evolution of carbon dynamics in the northern permafrost region on the trajectory of climate change. *Proc Natl Acad Sci U S A*. 2018;115(15):3882-3887.
- Vonk JE, Tank SE, Bowden WB, et al. Reviews and syntheses: effects of permafrost thaw on Arctic aquatic ecosystems. *Biogeochemistry*. 2015;12(23):7129-7167.
- Frey KE, McClelland JW. Impacts of permafrost degradation on Arctic river biogeochemistry. *Hydrol Process*. 2009;23(1):169-182.
- Lafrenière MJ, Lamoureux SF. Effects of changing permafrost conditions on hydrological processes and fluvial fluxes. *Earth-Sci Rev*. 2019;191:212-223.
- Jenny H. *Factors of soil formation: a system of quantitative pedology*. New York, NY: McGraw-Hill; 1941.
- Amundson R. Soil Formation. In: Drever JI, ed. *Surface and Ground Water, Weathering, and Soils: Treatise on Geochemistry*. Vol.5 Oxford, UK: Elsevier; 2005:1-35.
- Rapp A. Recent development of mountain slopes in Kärkevagge and surroundings, northern Scandinavia. *Geogr Ann*. 1960;42(2-3):65-200.
- Obu J, Lantuit H, Myers-Smith I, Heim B, Wolter J, Fritz M. Effect of terrain characteristics on soil organic carbon and total nitrogen stocks in soils of Herschel Island, Western Canadian Arctic. *Permafrost Periglac Process*. 2017;28(1):92-107.
- Kokelj SV, Jorgenson MT. Advances in thermokarst research. *Permafrost Periglac Process*. 2013;24(2):108-119.
- Ping CL, Jastrow JD, Jorgenson MT, Michaelson GJ, Shur YL. Permafrost soils and carbon cycling. *Soil*. 2015;1(1):147-171.
- Kuhry P, Bárta J, Blok D, et al. Lability classification of soil organic matter in the northern permafrost region. *Biogeosciences*. 2020;17(2):361-379.
- Lorant MM, Abbott BW, Blok D, et al. Reviews and syntheses: changing ecosystem influences on soil thermal regimes in northern high-latitude permafrost regions. *Biogeosciences*. 2018;15(17):5287-5313.
- Walvoord MA, Kurylyk BL. Hydrologic impacts of thawing permafrost—a review. *Vadose Zone J*. 2016;15(6):1-10.
- Ewing SA, O'Donnell JA, Aiken GR, et al. Long-term anoxia and release of ancient, labile carbon upon thaw of Pleistocene permafrost. *Geophys Res Lett*. 2015;42(24):10,730-10,738.
- O'Donnell JA, Jorgenson MT, Harden JW, McGuire AD, Kanevskiy MZ, Wickland KP. The effects of permafrost thaw on soil hydrologic, thermal, and carbon dynamics in an Alaskan peatland. *Ecosystems*. 2012;15(2):213-229.
- Lacelle D, Fontaine M, Forest AP, Kokelj S. High-resolution stable water isotopes as tracers of thaw unconformities in permafrost: a case study from western Arctic Canada. *Chem Geol*. 2014;368:85-96.
- Carey JC, Abbott BW, Rocha AV. Plant uptake offsets silica release from a large Arctic tundra wildfire. *Earth's Future*. 2019;7(9):1044-1057. <https://doi.org/10.1029/2019EF001149>
- Kokelj SV, Lacelle D, Lantz TC, et al. Thawing of massive ground ice in mega slumps drives increases in stream sediment and solute flux across a range of watershed scales. *J Geophys Res-Earth Surf*. 2013;118(2):681-692.
- Battin TJ, Luyssaert S, Kaplan LA, Aufdenkampe AK, Richter A, Tranvik LJ. The boundless carbon cycle. *Nat Geosci*. 2009;2(9):598-600.
- Mann PJ, Davydova A, Zimov N, et al. Controls on the composition and lability of dissolved organic matter in Siberia's Kolyma River basin. *J Geophys Res-Biogeosci*. 2012;117(G1):G01028.
- Abbott BW, Larouche JR, Jones JB Jr, Bowden WB, Balser AW. Elevated dissolved organic carbon biodegradability from thawing and collapsing permafrost. *J Geophys Res-Biogeosci*. 2014;119(10):2049-2063.
- Kokelj SV, Tunnicliffe JF, Lacelle D. The Peel Plateau of Northwestern Canada: An Ice-Rich Hummocky Moraine Landscape in Transition. In: Slaymaker O, ed. *Landscapes and Landforms of Western Canada*. Cham, Switzerland: Springer International Publishing; 2017.
- Zolkos S, Tank SE, Kokelj SV. Mineral weathering and the permafrost carbon-climate feedback. *Geophys Res Lett*. 2018;45:9623-9632.

34. Kokelj SV, Lantz TC, Tunnicliffe J, Segal R, Lacelle D. Climate-driven thaw of permafrost preserved glacial landscapes, northwestern Canada. *Geology*. 2017;45(4):371-374.
35. Segal RA, Lantz TC, Kokelj SV. Acceleration of thaw slump activity in glaciated landscapes of the Western Canadian Arctic. *Environ Res Lett*. 2016;11(3):034025.
36. Lacelle D, Lauriol B, Zazula G, Ghaleb B, Utting N, Clark ID. Timing of advance and basal condition of the Laurentide ice sheet during the last glacial maximum in the Richardson Mountains, NWT. *Quaternary Res*. 2013;80(2):274-283.
37. Littlefair CA, Tank SE. Biodegradability of thermokarst carbon in a till-associated, glacial margin landscape: the case of the Peel plateau, NWT, Canada. *J Geophys Res-Biogeosci*. 2018;123:3293-3307.
38. Littlefair CA, Tank SE, Kokelj SV. Retrogressive thaw slumps temper dissolved organic carbon delivery to streams of the Peel plateau, NWT, Canada. *Biogeosciences*. 2017;14(23):5487-5505.
39. St. Pierre KA, Zolkos S, Shakil S, Tank SE, St. Louis VL, Kokelj SV. Unprecedented increases in Total and methyl mercury concentrations downstream of retrogressive thaw slumps in the Western Canadian Arctic. *Environ Sci Technol*. 2018;52(24):14099-14109.
40. Chin KS, Lento J, Culp JM, Lacelle D, Kokelj SV. Permafrost thaw and intense thermokarst activity decreases abundance of stream benthic macroinvertebrates. *Glob Chang Biol*. 2016;22(8):2715-2728.
41. Rudy ACA, Lamoureux SF, Kokelj SV, Smith IR, England JH. Accelerating thermokarst transforms ice-cored terrain triggering a downstream cascade to the ocean. *Geophys Res Lett*. 2017;44(21):11080-11087.
42. Lane L, Roots C, Fraser T. *Geology*. In: Burn CR, ed. *Herschel Island Qikiqtaryuk: A natural and cultural history of Yukon's Arctic island*. Calgary, AB, Canada: University of Calgary Press; 2012.
43. Ramage JL, Irrgang AM, Morgenstern A, Lantuit H. Increasing coastal slump activity impacts the release of sediment and organic carbon into the Arctic Ocean. *Biogeosciences*. 2018;15(5):1483-1495.
44. Tanski G, Lantuit H, Ruttner S, et al. Transformation of terrestrial organic matter along thermokarst-affected permafrost coasts in the Arctic. *Sci Total Environ*. 2017;581-582:434-447.
45. Fortier D, Allard M, Pivot F. A late-Holocene record of loess deposition in ice-wedge polygons reflecting wind activity and ground moisture conditions, Bylot Island, eastern Canadian Arctic. *The Holocene*. 2006;16(5):635-646.
46. Fortier D, Allard M, Shur Y. Observation of rapid drainage system development by thermal erosion of ice wedges on Bylot Island, Canadian Arctic archipelago. *Permafrost Periglac*. 2007;18(3):229-243.
47. Bell T, Brown TM. From science to policy in the eastern Canadian Arctic: an integrated regional impact study (IRIS) of climate change and Modernization. Quebec City 2018.
48. Godin E, Fortier D, Coulombe S. Effects of thermo-erosion gully on hydrologic flow networks, discharge and soil loss. *Environ Res Lett*. 2014;9(10):105010.
49. Bouchard F, Laurion I, Prékienis V, Fortier D, Xu X, Whittaker MJ. Modern to millennium-old greenhouse gases emitted from ponds and lakes of the eastern Canadian Arctic (Bylot Island, Nunavut). *Biogeosciences*. 2015;12(23):7279-7298.
50. Lara MJ, McGuire AD, Euskirchen ES, et al. Polygonal tundra geomorphological change in response to warming alters future CO₂ and CH₄ flux on the Barrow peninsula. *Glob Chang Biol*. 2015;21(4):1634-1651.
51. Minke M, Donner N, Karpov NS, de Klerk P, Joosten H. Distribution, diversity, development and dynamics of polygon mires: examples from northeast Yakutia (Siberia). *Peatlands International*. 2007;1:36-40.
52. Wauthy M, Rautio M, Christoffersen KS, et al. Increasing dominance of terrigenous organic matter in circumpolar freshwaters due to permafrost thaw. *Limnol Oceanogr Lett*. 2018;3(3):186-198.
53. MacMillan GA, Girard C, Chételat J, Laurion I, Amyot M. High methylmercury in Arctic and subarctic ponds is related to nutrient levels in the warming eastern Canadian Arctic. *Environ Sci Technol*. 2015;49(13):7743-7753.
54. Laurion I, Vincent WF, MacIntyre S, et al. Variability in greenhouse gas emissions from permafrost thaw ponds. *Limnol Oceanogr*. 2010;55(1):115-133.
55. Laurion I, Mladenov N. Dissolved organic matter photolysis in Canadian arctic thaw ponds. *Environ Res Lett*. 2013;8(3):035026.
56. Zimov SA, Schuur EAG, Chapin FS. Permafrost and the global carbon budget. *Science*. 2006;312(5780):1612-1613.
57. Schirrmeister L, Froese D, Tumskey V, Grosse G, Wetterich S. Permafrost and Periglacial Features|Yedoma: Late Pleistocene Ice-Rich Syngenetic Permafrost of Beringia. In: Elias SA, Mock CJ, eds. *Encyclopedia of Quaternary Science*. Second ed. Amsterdam, the Netherlands: Elsevier; 2013:542-552.
58. Strauss J, Laboor S, Fedorov AN, et al. *Database of Ice-Rich Yedoma Permafrost (IRYP)*. PANGAEA; 2016.
59. Strauss J, Schirrmeister L, Grosse G, et al. The deep permafrost carbon pool of the Yedoma region in Siberia and Alaska. *Geophys Res Lett*. 2013;40(23):6165-6170.
60. Schirrmeister L, Kunitsky V, Grosse G, et al. Sedimentary characteristics and origin of the Late Pleistocene ice complex on north-east Siberian Arctic coastal lowlands and islands – a review. *Quat Int*. 2011;241(1):3-25.
61. Froese DG, Zazula GD, Westgate JA, et al. The Klondike goldfields and Pleistocene environments of Beringia. *GSA Today*. 2009;19(8):4-10.
62. Neff JC, Finlay JC, Zimov SA, et al. Seasonal changes in the age and structure of dissolved organic carbon in Siberian rivers and streams. *Geophys Res Lett*. 2006;33(23):L23401.
63. Vonk JE, Mann PJ, Davydov S, et al. High biolability of ancient permafrost carbon upon thaw. *Geophys Res Lett*. 2013;40(11):2689-2693.
64. Drake TW, Wickland KP, Spencer RGM, McKnight DM, Striegl RG. Ancient low-molecular-weight organic acids in permafrost fuel rapid carbon dioxide production upon thaw. *Proc Natl Acad Sci U S A*. 2015;112(45):13946-13951.
65. Spencer RGM, Mann PJ, Dittmar T, et al. Detecting the signature of permafrost thaw in Arctic rivers. *Geophys Res Lett*. 2015;42(8):2830-2835.
66. Sepulveda-Jauregui A, Walter Anthony KM, Martinez-Cruz K, Greene S, Thalasso F. Methane and carbon dioxide emissions from 40 lakes along a north-south latitudinal transect in Alaska. *Biogeosciences*. 2015;12(11):3197-3223.
67. Wild B, Andersson A, Bröder L, et al. Rivers across the Siberian Arctic unearth the patterns of carbon release from thawing permafrost. *Proc Natl Acad Sci U S A*. 2019;116(21):10280-11285.
68. Vonk JE, Semiletov IP, Dudarev OV, et al. Preferential burial of permafrost-derived organic carbon in Siberian-Arctic shelf waters. *J Geophys Res-Oceans*. 2014;119(12):8410-8421.
69. Wegner C, Bennett K, de Vernal A, et al. Variability in transport of terrigenous material on the shelves and the deep Arctic Ocean during the Holocene. *Polar Res*. 2015;34(1):24964.
70. Vonk JE, Sanchez-Garcia L, van Dongen BE, et al. Activation of old carbon by erosion of coastal and subsea permafrost in Arctic Siberia. *Nature*. 2012;489(7414):137-140.
71. Barnhart KR, Overeem I, Anderson RS. The effect of changing sea ice on the physical vulnerability of Arctic coasts. *The Cryosphere*. 2014;8(5):1777-1799.

72. Connolly CT, Khosh MS, Burkart GA, et al. Watershed slope as a predictor of fluvial dissolved organic matter and nitrate concentrations across geographical space and catchment size in the Arctic. *Environ Res Lett*. 2018;13(10):104015.
73. Hamilton TD. *Surficial Geology of the Dalton Highway (Itkillik-Sagavanirktok Rivers) Area, Southern Arctic Foothills, Alaska*. Fairbanks, AK: Alaska Division of Geological & Geophysical Surveys; 2003.
74. Smith SL, Romanovsky VE, Lewkowicz AG, et al. Thermal state of permafrost in North America: a contribution to the international polar year. *Permafrost Periglac Process*. 2010;21(2):117-135.
75. Arp CD, Jones BM, Grosse G, et al. Threshold sensitivity of shallow Arctic lakes and sublake permafrost to changing winter climate. *Geophys Res Lett*. 2016;43(12):6358-6365.
76. Raynolds MK, Walker DA, Ambrosius KJ, et al. Cumulative geoeological effects of 62 years of infrastructure and climate change in ice-rich permafrost landscapes, Prudhoe Bay oilfield, Alaska. *Glob Chang Biol*. 2014;20(4):1211-1224.
77. Balser AW, Jones JB, Gens R. Timing of retrogressive thaw slump initiation in the Noatak Basin, Northwest Alaska, USA. *J Geophys Res-Earth Surf*. 2014;119(5):1106-1120.
78. Bowden WB, Gooseff MN, Balser A, Green A, Peterson BJ, Bradford J. Sediment and nutrient delivery from thermokarst features in the foothills of the north slope, Alaska: potential impacts on headwater stream ecosystems. *J Geophys Res-Biogeosci*. 2008;113(G2):G02026.
79. Abbott BW, Jones JB, Godsey SE, Larouche JR, Bowden WB. Patterns and persistence of hydrologic carbon and nutrient export from collapsing upland permafrost. *Biogeosciences*. 2015;12(12):3725-3740.
80. McClelland JW, Stieglitz M, Pan F, Holmes RM, Peterson BJ. Recent changes in nitrate and dissolved organic carbon export from the upper Kuparuk River, north slope, Alaska. *J Geophys Res-Biogeosci*. 2007;112(G4):G04S60.
81. Barker AJ, Douglas TA, Jacobson AD, et al. Late season mobilization of trace metals in two small Alaskan arctic watersheds as a proxy for landscape scale permafrost active layer dynamics. *Chem Geol*. 2014; 381:180-193.
82. Treat CC, Wollheim WM, Varner RK, Bowden WB. Longer thaw seasons increase nitrogen availability for leaching during fall in tundra soils. *Environ Res Lett*. 2016;11(6):064013.
83. Zarnetske JP, Gooseff MN, Bowden WB, et al. Influence of morphology and permafrost dynamics on hyporheic exchange in arctic headwater streams under warming climate conditions. *Geophys Res Lett*. 2008;35:L02501.
84. King TV, Neilson BT. Quantifying reach-average effects of hyporheic exchange on Arctic river temperatures in an area of continuous permafrost. *Water Resour Res*. 2019;55(3):1951-1971.
85. Harms TK, Cook CL, Wlostowski AN, Gooseff MN, Godsey SE. Spiraling down hillslopes: nutrient uptake from water tracks in a warming Arctic. *Ecosystems*. 2019;22(7):1546-1560.
86. Gallant AL, Binnian EF, Omernik JM, Shasby MB. Ecoregions of Alaska. In: *Professional Paper 1567*. Reston, VA: U.S. Geological Survey; 1995.
87. Ebel BA, Koch JC, Walvoord MA. Soil physical, hydraulic, and thermal properties in interior Alaska, USA: implications for hydrologic response to thawing permafrost conditions. *Water Resour Res*. 2019; 55(5):4427-4447.
88. Jorgenson MT, Harden J, Kanevskiy M, et al. Reorganization of vegetation, hydrology and soil carbon after permafrost degradation across heterogeneous boreal landscapes. *Environ Res Lett*. 2013;8(3): 035017.
89. Jorgenson MT, Yoshikawa K, Kanveskiy M, et al. Permafrost characteristics of Alaska. In: Kane DL, Hinkel KM, eds. *Ninth International Conference on Permafrost Extended Abstracts*. Fairbanks, AK: University of Alaska; 2008:121-122.
90. Rey DM, Walvoord M, Minsley B, Rover J, Singha K. Investigating lake-area dynamics across a permafrost-thaw spectrum using airborne electromagnetic surveys and remote sensing time-series data in Yukon flats, Alaska. *Environ Res Lett*. 2019;14(2):025001.
91. Striegl RG, Aiken GR, Dornblaser MM, Raymond PA, Wickland KP. A decrease in discharge-normalized DOC export by the Yukon River during summer through autumn. *Geophys Res Lett*. 2005;32(21): L21413.
92. Toohey RC, Herman-Mercer NM, Schuster PF, Mutter EA, Koch JC. Multidecadal increases in the Yukon River basin of chemical fluxes as indicators of changing flowpaths, groundwater, and permafrost. *Geophys Res Lett*. 2016;43(23):12,120-112,130.
93. Walvoord MA, Striegl RG. Increased groundwater to stream discharge from permafrost thawing in the Yukon River basin: potential impacts on lateral export of carbon and nitrogen. *Geophys Res Lett*. 2007;34(12):L12402.
94. Walvoord MA, Voss CI, Wellman TP. Influence of permafrost distribution on groundwater flow in the context of climate-driven permafrost thaw: example from Yukon Flats Basin, Alaska, United States. *Water Resour Res*. 2012;48(7):W07524.
95. O'Donnell JA, Aiken GR, Walvoord MA, et al. Using dissolved organic matter age and composition to detect permafrost thaw in boreal watersheds of interior Alaska. *J Geophys Res-Biogeosci*. 2014; 119(11):2155-2170.
96. Koch JC, Runkel RL, Striegl R, McKnight DM. Hydrologic controls on the transport and cycling of carbon and nitrogen in a boreal catchment underlain by continuous permafrost. *J Geophys Res-Biogeosci*. 2013;118(2):698-712.
97. Harms TK, Jones JB Jr. Thaw depth determines reaction and transport of inorganic nitrogen in valley bottom permafrost soils. *Glob Chang Biol*. 2012;18(9):2958-2968.
98. Dornblaser MM, Striegl RG. Switching predominance of organic versus inorganic carbon exports from an intermediate-size subarctic watershed. *Geophys Res Lett*. 2015;42(2):386-394.
99. Wickland KP, Waldrop MP, Aiken GR, Koch JC, Jorgenson MT, Striegl RG. Dissolved organic carbon and nitrogen release from boreal Holocene permafrost and seasonally frozen soils of Alaska. *Environ Res Lett*. 2018;13(6):065011.
100. Walvoord MA, Voss CI, Ebel BA, Minsley BJ. Development of perennial thaw zones in boreal hillslopes enhances potential mobilization of permafrost carbon. *Environ Res Lett*. 2019;14(1):015003.
101. Aiken GR, Spencer RGM, Striegl RG, Schuster PF, Raymond PA. Influences of glacier melt and permafrost thaw on the age of dissolved organic carbon in the Yukon River basin. *Global Biogeochem Cycles*. 2014;28(5):525-537.
102. Lamoureux SF, Lafrenière MJ. Seasonal fluxes and age of particulate organic carbon exported from Arctic catchments impacted by localized permafrost slope disturbances. *Environ Res Lett*. 2014;9(4): 054002.
103. Lewis T, Lafrenière MJ, Lamoureux SF. Hydrochemical and sedimentary responses of paired high Arctic watersheds to unusual climate and permafrost disturbance, cape bounty, Melville Island, Canada. *Hydrol Process*. 2012;26(13):2003-2018.
104. Liu F, Chen L, Abbott BW, et al. Reduced quantity and quality of SOM along a thaw sequence on the Tibetan plateau. *Environ Res Lett*. 2018;13(10):104017.
105. Fouché J, Lafrenière MJ, Rutherford K, Lamoureux S. Seasonal hydrology and permafrost disturbance impacts on dissolved organic matter composition in high Arctic headwater catchments. *Arct Sci*. 2017;3(2):378-405.
106. Burd K, Estop-Aragonés C, Tank SE, Olefeldt D. Lability of dissolved organic carbon from boreal peatlands: interactions between permafrost thaw, wildfire, and season. *Can J Soil Sci*. 2020.

107. Olefeldt D, Goswami S, Grosse G, et al. Circumpolar distribution and carbon storage of thermokarst landscapes. *Nat Commun*. 2016;7(1):13043.
108. Drake TW, Guillemette F, Hemingway JD, et al. The ephemeral signature of permafrost carbon in an Arctic fluvial network. *J Geophys Res-Biogeosci*. 2018;123(5):1475-1485.
109. Khosh MS, McClelland JW, Jacobson AD, Douglas TA, Barker AJ, Lehn GO. Seasonality of dissolved nitrogen from spring melt to fall freezeup in Alaskan Arctic tundra and mountain streams. *J Geophys Res-Biogeosci*. 2017;122(7):1718-1737.
110. McClelland JW, Townsend-Small A, Holmes RM, et al. River export of nutrients and organic matter from the north slope of Alaska to the Beaufort Sea. *Water Resour Res*. 2014;50(2):1823-1839.
111. Tanski G, Couture N, Lantuit H, Eulenburg A, Fritz M. Eroding permafrost coasts release low amounts of dissolved organic carbon (DOC) from ground ice into the nearshore zone of the Arctic Ocean. *Global Biogeochem Cycles*. 2016;30(7):1054-1068.
112. Kling GW, Kipphut GW, Miller MM, O'Brien WJ. Integration of lakes and streams in a landscape perspective: the importance of material processing on spatial patterns and temporal coherence. *Freshwater Biol*. 2000;43(3):477-497.
113. Emmerton CA, Lesack LFW, Vincent WF. Mackenzie River nutrient delivery to the Arctic Ocean and effects of the Mackenzie Delta during open water conditions. *Global Biogeochem Cycles*. 2008;22(1):GB1024.
114. O'Donnell JA, Aiken GR, Walvoord MA, Butler KD. Dissolved organic matter composition of winter flow in the Yukon River basin: Implications of permafrost thaw and increased groundwater discharge. *Global Biogeochem Cycles*. 2012;26:GB0E06.
115. Larouche JR, Abbott BW, Bowden WB, Jones JB. The role of watershed characteristics, permafrost thaw, and wildfire on dissolved organic carbon biodegradability and water chemistry in Arctic headwater streams. *Biogeosciences*. 2015;12(14):4221-4233.
116. Keller K, Blum JD, Kling GW. Stream geochemistry as an indicator of increasing permafrost thaw depth in an arctic watershed. *Chem Geol*. 2010;273(1-2):76-81.
117. Turetsky MR, Abbott BW, Jones MC, et al. Carbon release through abrupt permafrost thaw. *Nat Geosci*. 2020;13(2):138-143.
118. O'Donnell JA, Aiken GR, Swanson DK, Panda S, Butler KD, Baltensperger AP. Dissolved organic matter composition of Arctic rivers: linking permafrost and parent material to riverine carbon. *Global Biogeochem Cycles*. 2016;30(12):1811-1826.
119. Harms TK, Edmonds JW, Genet H, et al. Catchment influence on nitrate and dissolved organic matter in Alaskan streams across a latitudinal gradient. *J Geophys Res-Biogeosci*. 2016;121(2):350-369.
120. Shogren AJ, Zarnetske JP, Abbott BW, et al. Revealing biogeochemical signatures of Arctic landscapes with river chemistry. *Sci Rep*. 2019;9(1):12894.
121. Abbott BW, Gruau G, Zarnetske JP, et al. Unexpected spatial stability of water chemistry in headwater stream networks. *Ecol Lett*. 2018;21(2):296-308.
122. Porter C, Morin P, Howat I, et al. ArcticDEM. *Harvard Dataverse*, V1; 2018. <https://doi.org/10.7910/DVN/OHHUKH>. [Accessed 06 March, 2020].
123. Hugelius G, Bockheim JG, Camill P, et al. A new data set for estimating organic carbon storage to 3 m depth in soils of the northern circumpolar permafrost region. *Earth Syst Sci Data*. 2013;5(2):393-402.
124. O'Neill HB, Wolfe SA, Duchesne C. New ground ice maps for Canada using a paleogeographic modelling approach. *The Cryosphere*. 2019;13(3):753-773.
125. Burke A, Present TM, Paris G, et al. Sulfur isotopes in rivers: insights into global weathering budgets, pyrite oxidation, and the modern sulfur cycle. *Earth Planet Sc Lett*. 2018;496:168-177.
126. Hartmann J, Moosdorf N. The new global lithological map database GLiM: A representation of rock properties at the Earth surface. *Geochim Geophys Geosyst*. 2012;13(12):Q12004.
127. Vonk JE, van Dongen BE, Gustafsson O. Selective preservation of old organic carbon fluvially released from sub-Arctic soils. *Geophys Res Lett*. 2010;37(11):L11605.
128. Connon RF, Quinton WL, Craig JR, Hayashi M. Changing hydrologic connectivity due to permafrost thaw in the lower Liard River valley, NWT, Canada. *Hydrol Process*. 2014;28(14):4163-4178.
129. Tank SE, Fellman JB, Hood E, Kritzberg ES. Beyond respiration: controls on lateral carbon fluxes across the terrestrial-aquatic interface. *Limnol Oceanogr Lett*. 2018;3(3):76-88.
130. Beaulieu E, Godderis Y, Donnadiou Y, Labat D, Roelandt C. High sensitivity of the continental-weathering carbon dioxide sink to future climate change. *Nature Clim Change*. 2012;2(5):346-349.
131. Brown J, Ferrians O, Heginbottom JA, Melnikov E. Circum-Arctic Map of Permafrost and Ground-Ice Conditions, Version 2. *National Snow and Ice Data Center*. Boulder, Colorado USA. 2002.

How to cite this article: Tank SE, Vonk JE, Walvoord MA, McClelland JW, Laurion I, Abbott BW. Landscape matters: Predicting the biogeochemical effects of permafrost thaw on aquatic networks with a state factor approach. *Permafrost and Periglacial Process*. 2020;31:358-370. <https://doi.org/10.1002/ppp.2057>