

Geomorphology Imparts Spatial Organization on Hydrological and Biogeochemical Fluxes

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1 Introduction

Watersheds have defined boundaries, which are actual features of the landscape and are useful in the study of fundamental hydrologic, geomorphic, and biogeochemical processes (Bormann and Likens, 1967). Watershed-scale estimates of hydrological and biogeochemical fluxes are commonly made at a wide range of ecosystems and scales worldwide. Current studies provide the basis for cross-site comparisons (Peterson et al., 2001; Ross et al., 2009; Miller et al., 2016), assessment of biophysical controls on flux dynamics (Emanuel et al., 2010; Hale et al., 2015; Raymond, 2017), and insight into short- and long-term ecosystem responses to global environmental change (Shanley et al., 2011; Tetzlaff et al., 2017; Goyette et al., 2018). While reconciling hydrologic and biogeochemical fluxes derived from multiple techniques has proven to be a difficult task, additional complications are introduced by the variability introduced by watershed morphology. This variability is often conceptually assumed but rarely observed experimentally, and quantifying it requires concepts that transcend disciplines. In this article, we present examples that integrate hydrological and biogeochemical processes from the reach to the watershed scale, highlighting the fundamental role of geomorphology in mediating the magnitude and timing of these fluxes. We first describe basic concepts of watershed geomorphology and their significance in imparting spatial organization at the landscape scale. Second, we examine fluvial biogeochemical fluxes at the watershed scale and the role of aquatic transport and in-stream transformation in mediating the magnitude of exported solutes. Finally, we summarize examples of linkages between geomorphology and land-atmosphere exchange of water, carbon, and other elements. Throughout this chapter, we emphasize that understanding hydrologic and biogeochemical processes across different landscape elements requires recognition that the output (loss) from one landscape unit represents the input (gain) to the next. We equally emphasize the importance of reconciling multiple and independent measures (techniques) for flux observation, as well as the role of a dynamic hydrologic cycle across spatial and temporal scales.

2 Watershed geomorphology

A watershed is the area of land that on the basis of topography drains to a particular point (Dingman, 2015). The geomorphic template, or physical structure of a watershed, is the result of various factors including: (1) The underlying bedrock and geologic makeup of the region; (2) The spatial distribution of slope angles (i.e., steep vs. flat areas) of the landscape; (3) The spatial arrangement of convergent and divergent hillslopes; (4) The geometry of the resulting stream network; and (5) The valley width along the river corridor. Combined, these physical characteristics of a watershed impose primary constraints on the movement of water, solutes (ions dissolved in water), and particulate material from the headwaters of each individual stream channel to the watershed outlet. By controlling the distribution and residence times of water, solutes, and particulate material, watershed morphology creates a primary linkage between the physical structure of the landscape and the combined hydrological and biogeochemical response of all landscape elements.

2.1 Spatial distribution of hillslopes

The spatial distribution of hillslopes—or their physical arrangement within the uplands of watersheds—influences upland wetness patterns and the delivery of water, solutes, and particulate material from the uplands to stream networks. This spatial structure forms

the basis for flow routing algorithms in geographical information systems (GIS) and topographically driven hydrologic models. For example, the upslope accumulated area, or area of land draining to a point in the landscape, can be used to derive wetness indices and estimate spatial patterns of wetness within a watershed (Beven and Kirkby, 1979). In landscapes with high relief, the topographically driven redistribution of water is a strong predictor of runoff generation and hydrologic connectivity across the landscape (Jencso et al., 2009; Jencso and McGlynn, 2011). These patterns of wetness and hydrologic connectivity control watershed biogeochemical flux because soil moisture patterns are important drivers of biogeochemical processing occurring in soils (Riveros-Iregui et al., 2007) and saturated connections from hillslopes to stream networks facilitate terrestrial to aquatic transfer (Stieglitz et al., 2003; Lynch et al., 2019).

Hillslopes can be categorized as convergent, divergent, or planar. Convergent hillslopes are concave up and divergent hillslopes are concave down (Fig. 1; Baiaumont and Singh, 2016). This plan curvature is important to watershed hydrology and biogeochemistry (Pacific et al., 2009) because convergent hillslopes concentrate hydrologic flowpaths and consequently tend to have higher soil moisture and soil depths relative to divergent hillslopes given other variables such as climate, slope, and contributing area are equal (Fig. 1; Detty and McGuire, 2010). In addition to influencing patterns of soil moisture and soil depth, the spatial distribution of convergent and divergent hillslopes organizes vegetation patterns as well as the flux of mass from terrestrial to aquatic environments. Within a watershed, large, convergent hillslopes are locations of large inputs to the channel network. Hillslope contributing areas are unevenly distributed across the landscape, leading to spatial and temporal variability in landscape contributions to channel flow. Conversely, divergent hillslopes contribute little to no water to the channel network in most landscapes, especially in dry environments (Jencso and McGlynn, 2011). This arrangement of convergent and divergent hillslopes interacts with land cover and climate to control the delivery of dissolved and particulate material to the channel network. For example, after wildfire convergent hillslopes can contribute large amounts of sediment to the channel network during or after precipitation events (Nyman et al., 2020). Additionally, for most of the year only small portions of the terrestrial landscape are hydrologically connected by saturated subsurface flow to the channel network (Hewlett and Hibbert, 1967). This spatial and temporal variability in landscape hydrologic connectivity is partially responsible for variability in stream chemistry and aquatic biogeochemical flux through the year (Bishop et al., 1993; Hornberger et al., 1994; Boyer et al., 1995; Creed and Band, 1998; Pacific et al., 2010). The relations between watershed structure and temporal variability in streamwater chemistry are purported to control biological and biogeochemical processes, and organize aquatic ecosystem productivity (i.e., how much organic carbon is produced or respired). Understanding these relations provides opportunities to predict and model biogeochemical flux as a function of watershed morphology and ultimately the quality of water delivered downstream. Understanding relations between the physical structure of a watershed, hydrology, and associated biogeochemical function remains an important area of research in watershed science.

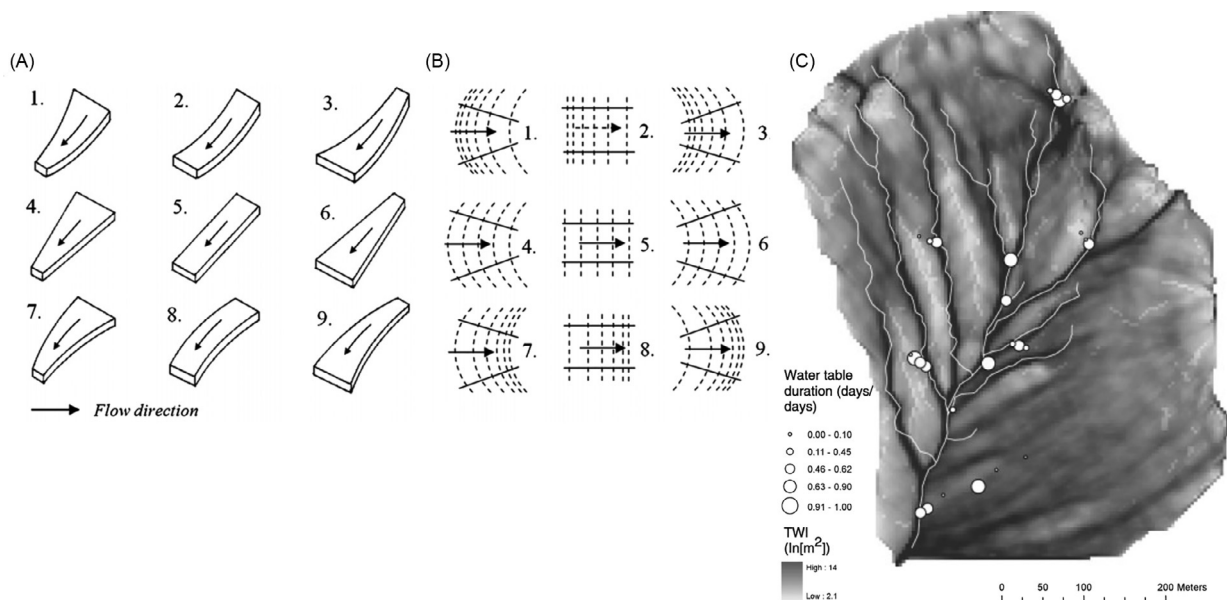


Fig. 1 Three dimensional (A) and plan (B) views of various hillslope shapes. Examples 1, 4, and 7 demonstrate convergent hillslope morphology, and examples 3, 6, and 9 demonstrate divergent hillslope morphology. The dashed lines in panel B represent topographic contours and solid lines indicate hillslope divides. (C) Watershed patterns of topographic wetness index (TWI) and duration of water table observed in ground water wells. Patterns of TWI and water table duration are organized by spatial organization of convergent and divergent hillslopes. Part of the figure also comes from Baiaumont G, and Singh VP (2016) Overland flow times of concentration for hillslopes of complex topography. *Journal of Irrigation and Drainage Engineering* **142**: 04015059. Detty JM, and McGuire KJ (2010) Topographic controls on shallow groundwater dynamics: implications of hydrologic connectivity between hillslopes and riparian zones in a till mantled catchment. *Hydrological Processes* **24**: 2222–2236.

2.2 Network geometry

Channel networks drain the terrestrial landscape of a watershed and come in many different geometries (Fig. 2; Ritter, 2020). Network geometry affects the relationship between channel network length and watershed area, which can be represented by a number of metrics, including drainage density (Eq. 1):

$$\text{Drainage density} \left(\frac{m}{m^2} \right) = \frac{\text{Total channel length (m)}}{\text{Watershed area (m}^2\text{)}} \quad (1)$$

In watersheds with higher drainage densities, there are (on average) shorter distances from any given hillslope to a channel than in a watershed with a lower drainage density. Consequently, watersheds with higher drainage densities facilitate terrestrial-aquatic connectivity because a greater portion of the landscape is proximate to the channel network.

The branching of channel networks has long been used as a basis for stream classification. The Strahler stream order, for example, assigns headwaters that have no tributaries an order of 1 (Fig. 3). When two order 1 streams converge, they form an order 2 stream, and so on. This branching characteristic of channel networks results in small streams (e.g., order 1–2) dominating the total length of any river network (Downing et al., 2012) and draining the majority of land area (Colvin et al., 2019) in any watershed (Fig. 4).

The drainage density provides a useful metric on the relationship between the channel network and watershed area but includes no information about the topology of the network. Another metric used to describe network geometry that does contain information about network topology is the width function. The width function is the probability density function (PDF) of distance from outlet (DFO) to any point in the channel network (Kirkby, 1976) and provides a quantitative representation of network geometry and the distance that water travels through the network to watershed outlet (Fig. 5; Moussa, 2008). Accordingly, the width function is useful for runoff routing and has been used extensively in rainfall-runoff models using the geomorphologic instantaneous unit hydrograph (GIUH) (e.g., Troutman and Karlinger, 1985; Gupta and Mesa, 1988). When combined with a measure of flow velocity, the width function can be used to calculate travel time (i.e., distance/velocity) along the channel network. This framework has most often been used for flood routing and to estimate the timing and magnitude of peak flows but can be modified

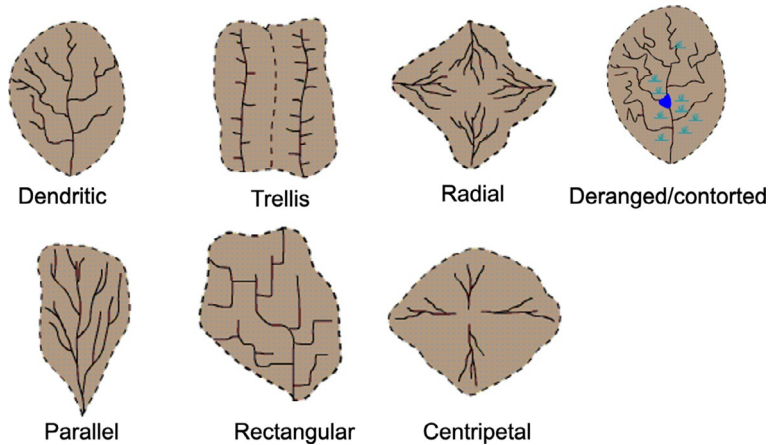


Fig. 2 Examples of river network geometries. Ritter ME (2020) *The Physical Environment: An Introduction to Physical Geography*. Available from https://www.earthonlinemedia.com/ebooks/tpe_3e/title_page.html

Strahler stream order in a 3rd order basin

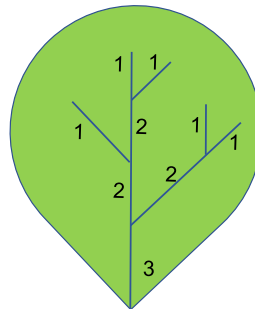


Fig. 3 Example of Strahler stream order classification. Strahler AN (1952) Hypsometric (area-altitude) analysis of erosional topography. *Geological Society of America Bulletin* 63: 1117.

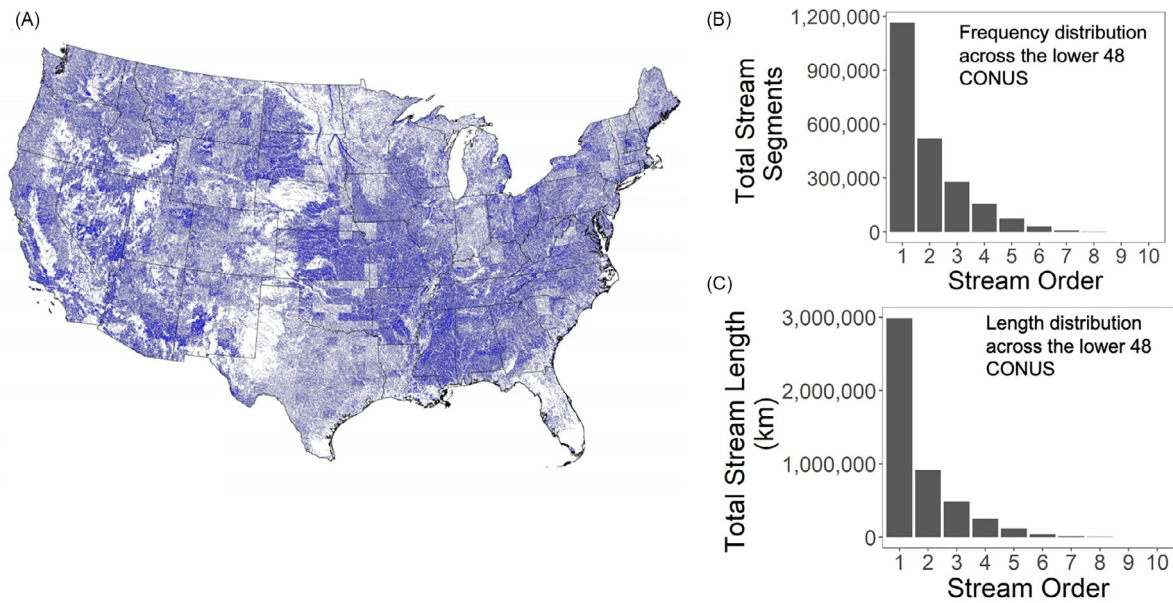


Fig. 4 (A) Map indicating distribution of headwater (1st and 2nd order) streams across the continental US. (B) Frequency distribution and (C) total stream length of streams from order 1–10 across the continental US. Colvin SAR, Sullivan, SMP, Shirey PD et al. (2019) Headwater streams and wetlands are critical for sustaining fish, fisheries, and ecosystem services. *Fisheries* 44: 73–91.

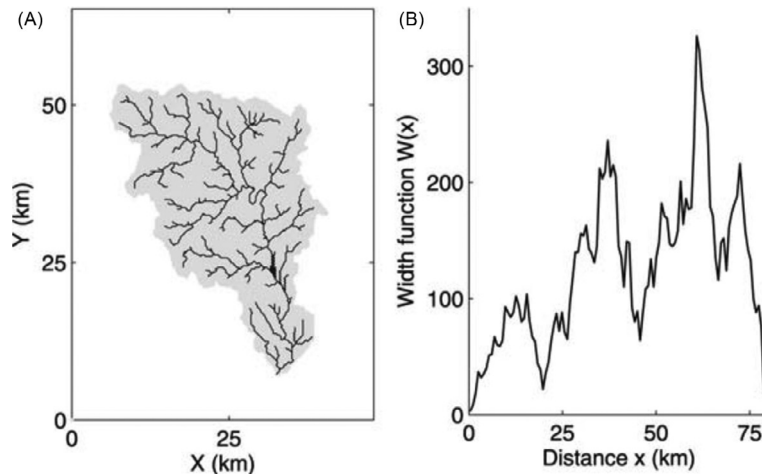


Fig. 5 (A) Map of watershed river network and (B) resulting width function. The width function is a quantitative representation of the distribution of distances to outlet across the river network. Moussa R (2008) What controls the width function shape, and can it be used for channel network comparison and regionalization? *Water Resources Research* 44.

to incorporate solute transit times as well (Bergstrom et al., 2016). The modification for solute transit times is necessary because the velocity of flood waves (i.e., kinematic wave celerity) is faster than the velocity for solutes (Graf, 1995; Luhmann et al., 2012; McDonnell and Beven, 2014). Accordingly, estimating solute transport velocities in a width function framework requires adjusting the velocity from kinematic to solute velocities, which can be accomplished by combining solute velocities from tracer experiments and geomorphic analyses of network geometry to characterize the PDF of solute travel times along a channel network (Bergstrom et al., 2016). This adjustment is important because it is the solute (or particle) velocity that is relevant to biogeochemical processing and not residence times associated with kinematic velocities. The PDF developed from these analyses provides information on the distribution of residence times which is a primary constraint on biogeochemical processing (Eq. 2):

$$\text{BiogeochemicalProcessing} = \text{ResidenceTime} \times \text{ReactionRate} \quad (2)$$

Analysis of fluvial structure has shown that network topology (Bertuzzo et al., 2008; Rinaldo et al., 2011) influences nitrogen and DOC removal, particularly when loading occurs in distal parts of the watershed channel network (Bertuzzo et al., 2017; Helton et al., 2018) and is not simply controlled by drainage density. As such, this framework can be used to estimate the magnitude of processing along the channel network and to evaluate how the opportunity for processing along the fluvial network can influence watershed export at different flow states (e.g., high vs. low flow).

The relationship between transport and reaction rate is also summarized in the Damkohler number (Eq. 3):

$$D_a = \frac{\tau_T}{\tau_R} \quad (3)$$

where, τ_T is the transport or residence timescale and τ_R is the reaction rate or reaction timescale (Lansdown et al., 2015). D_a can be quantified in any system in which there is both transport and reactivity, such as flow in a stream channel or subsurface hydrologic flow through hyporheic or groundwater systems. Accordingly, Damkohler numbers can be assigned to all parts of the watershed through which there is flow. This ratio provides insight to transport vs. reaction dominance over a given process. For example, during high flow periods when residence time is relatively lower, biogeochemical flux will be largely controlled by hydrology. Conversely, as residence time elongates under lower flow conditions biogeochemical flux from whole watersheds or from particular landscape positions or stream reaches will be more strongly controlled by biological processes. Consequently, biogeochemical fluxes are partially the result of interactions between physical hydrologic transport and biologically mediated processing (Cirmo and McDonnell, 1997). These physical and biological processes are organized and strongly mediated by watershed structure. For example, hydrologic residence times tend to be longer in low relief portions of a watershed that function as accumulation zones for fine sediment. Differences in network geometry across watersheds also affects residence times with more dendritic networks having relatively longer travel distances and travel times relative to simpler network geometries. Accordingly, the vast spatial heterogeneity inherent to natural landscapes exhibits “organized heterogeneity” in which physical and biogeochemical processes follow relatively predictable spatial patterns ordered by landscape structure.

2.3 Valley width

Valley width affects floodplain development and the potential for interactions between the stream and the valley floor. Streams that are flanked by wide valley floors have the potential for substantial lateral migration, hyporheic exchange, and hydrologic spreading during flooding (e.g., Stanford and Ward, 1993; Tockner and Stanford, 2002; Hauer et al., 2016). In contrast, each of these processes are laterally constrained in locations where the valley is narrow (Hynes, 1975). In mountainous regions, wide valleys occur infrequently and form the so-called “beads on a string” morphology (Stanford et al., 1996; Wohl et al., 2017). Conversely, in lowland systems valleys are typically wide and lowland rivers are more likely to be confined by human alteration of the river corridor (Kondolf et al., 2006) than by “natural” geomorphic structure.

The lateral connection between a stream and its valley has substantial implications for river corridor biogeochemical flux. In wide valley segments where the river is able to inundate the floodplain through overbank flow, floodplain soils can retain substantial amounts of biogeochemically relevant materials such as carbon (C) and nitrogen (N) (Tockner et al., 1999). In fact, floodplain soils of wide valley segments have been noted as “hot-spots” of organic carbon (OC) storage and retention within the fluvial network (Wohl et al., 2012). Storage and retention in the wide valley segments of river networks slows or delays the downstream flux of carbon, nutrients and sediment. In so doing the lateral hydrologic connectivity between the river and floodplain impacts downstream longitudinal connectivity (Ward, 1989) and transfer of biogeochemical constituents (Malard et al., 2002). Conversely, in narrow valley segments where floodplain development and lateral hydrologic connections are limited, the downstream transfer of OC is high. The rapid translocation of dissolved organic carbon (DOC) from headwater to lowland portions of the river network represents a common assumption regarding the fate of DOC along the fluvial network; specifically, that DOC derived from headwater locations is rapidly transported downstream to lowland portions of the network where it is subsequently processed (Raymond et al., 2016). Thus, the production and processing of OC are separated in space. However, lateral hydrologic connectivity in wide valley segments may interrupt this process by storing OC in locations more proximal to where it was produced. As such valley width along the river corridor may play an important role in biogeochemical cycling at local and continental scales.

3 Fluvial biogeochemical flux in watersheds

Streams and rivers receive OC and nutrient inputs from lateral, upstream, and internal sources. The River Continuum Concept (RCC) established a set of predictions regarding how inputs to stream ecosystems change moving from headwaters to the coast as a result of interactions between watershed structure, network geometry, and vegetation (Vannote et al., 1980). The RCC predicts that headwater streams receive more lateral input per unit channel length relative to larger order rivers that receive a larger proportion of input from upstream sources. In this way the ratio of lateral-to-upstream sources decreases per unit length downstream as a function of the relationships between Q_{lat} and Q_{long} , where Q_{lat} is lateral flux and Q_{long} is downstream flux. At the channel head the $Q_{lat}:Q_{long}$ ratio is 1 since all input is derived from lateral (i.e., terrestrial) sources (Fig. 6).

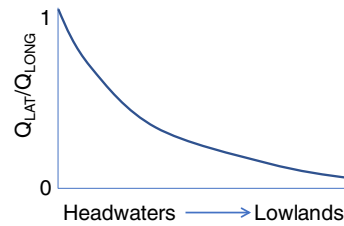


Fig. 6 Conceptual representation of the changing ratio of lateral (Q_{LAT}) and longitudinal (Q_{LONG}) hydrologic flux moving downstream from headwaters to lowland landscapes. Q_{LAT} is the lateral contribution of water and solutes to the channel network from lateral hillslope sources. Q_{LONG} is contributions of water and solutes from upstream sources. At channel heads the Q_{LAT}/Q_{LONG} ratio is 1 because all water and solutes are derived from hillslope inputs. Moving downstream a greater proportion of water and solutes in the river network are sourced from downstream transport from upstream locations.

In headwater locations, streams are strongly connected to their uplands and consequently receive considerable inputs of OC and nutrients (e.g., nitrogen, N and phosphorous, P) from their surrounding watershed. Measurements of the concentration and flux (i.e., discharge X concentration) of various dissolved and particulate constituents at watershed outlets have formed the basis of many watershed biogeochemical studies aimed at understanding the relationship between terrestrial to aquatic transfer and downstream transport. For example, the small watershed approach uses in-stream sampling to evaluate upland processes under the assumption that fluvial export of OC, nutrients, and minerals from small watersheds reflects upland land cover and associated hydro-biogeochemical processes (Bormann and Likens, 1967). However, there have been conflicting results on the ability of headwater streams to transform terrestrial inputs, with some research indicating streams reflect inputs from terrestrial sources and other research suggesting streams react and transform input from their uplands (Bernhardt et al., 2005; Brookshire et al., 2009).

3.1 Biogeochemical processing along the river network

The amount of OC and nutrients that are transported down a river network is the result of combined physical and biological processes and is formalized in the Nutrient Spiraling Concept (Stream Solute Workshop, 1990). In this conceptual model, an element (e.g., C, N, or P) is transported in dissolved form a certain distance downstream, taken up biologically, transported some distance downstream in particulate form, eventually released back to the water column, and transported some distance downstream again. This process repeats itself over and over, and the sequence of transport, uptake, release, and transport creates elemental “spirals” (see Fig. 7).

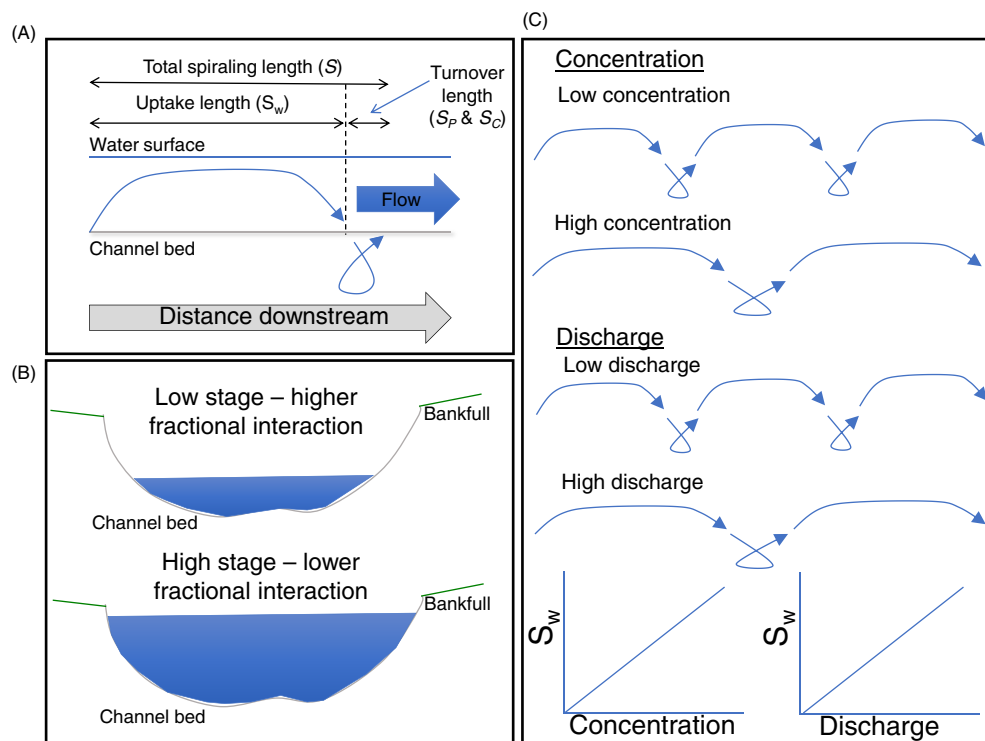


Fig. 7 Fig. 7. (A) Description of nutrient spiraling in streams, where total spiraling length (S) is comprised of uptake length (S_w) and turnover length (S_p and S_c). (B) Stream/river stage controls nutrient processing in channel networks, because the ratio of channel volume to bed area changes from low to high stage conditions. Accordingly, there is higher fractional interaction between streamwater, the channel bed, and the hyporheic zone during low stage vs. high stage conditions. (C) Both flow conditions and in-stream concentrations have strong influence on spiral length, nutrient cycling efficiency, and downstream nutrient transport. Similarly, changes in discharge result in higher downstream loading during higher flow periods. Accordingly, S_w generally increases as a function of both concentration and discharge. Covino T (2017) Hydrologic connectivity as a framework for understanding biogeochemical flux through watersheds and along fluvial networks. *Geomorphology* 277: 133–144.

The physical transport component of the nutrient spiraling model incorporates climate and fluvial morphology. Climate dictates the hydrologic regime (i.e., timing and magnitude of streamflow) that interacts with channel and valley morphology (collectively the stream or river corridor) to control the physics of transport down the stream network. In natural channels, transport downstream is slowed by a variety of processes that collectively constitute “transient storage.” Transient storage can occur by a variety of mechanisms including:

- Surface transient storage within the stream network that occurs as stream water exchanges from main channel flow to in-channel pools and dead zones that have velocities lower than that of the main channel
- Hyporheic transient storage that occurs as surface water exchanges into the subsurface hyporheic zone that has velocities lower than that of the main channel flow
- Overbank flooding that occurs when stream stage is high enough to facilitate stream water inundation of the floodplain

Each of these forms of transient storage can attenuate the downstream transport of C, N, and P and elongate residence times allowing for enhanced biological processing (Battin et al., 2008; Briggs et al., 2010; Zarnetske et al., 2011).

The biological component of the nutrient spiraling concept cannot be fully separated from physical transport, although some spiraling metrics attempt to isolate biological relative to physical influences. Commonly calculated metrics of uptake and transport in the spiraling concept include uptake length (S_w , L), uptake velocity (V_f , $L\ T^{-1}$), and uptake rate (U , $M\ L^{-2}\ T^{-1}$) (Stream Solute Workshop, 1990). S_w is the average distance an element (e.g., N, P, or C) is transported downstream before being taken up biologically; this distance is strongly influenced by stream discharge. Contrastingly, U and V_f account for differences in stream discharge to facilitate comparisons across sites and flow states and attempt to highlight biological over physical processes. Uptake velocity, V_f , is a measure of nutrient uptake relative to nutrient availability (i.e., concentration) and represents uptake efficiency, and the areal uptake rate, U , is a measure of nutrient uptake per area per unit time, representing bulk retention or removal.

3.2 Controls on downstream transport

Downstream transport, and the length of nutrient spirals, are controlled by hydrology and biological demand relative to supply. When flows are higher, spirals elongate and the element of consideration (C, N, or P) is transported further downstream per unit time relative to transport under lower flow conditions. Simultaneously, the strength of biological demand for the element also influences S_w , with longer spirals when or where demand is low and shorter spirals when or where demand is high relative to supply (i.e., concentration, Fig. 7). As such, short spirals represent more efficient nutrient use while inefficient use leads to longer spirals and greater downstream transport (Dodds et al., 2002; Payn et al., 2005).

Downstream transport tends to be highest under high flow conditions. The increase in S_w with greater discharge is generally true within, or across, stream systems. For example, an inter-biome comparison demonstrated clear increases in S_w as stream order and discharge increased (Webster et al., 2003). However, when comparing V_f and U across these same sites, this pattern was less apparent (Peterson et al., 2001; Webster et al., 2003). However, this analysis was somewhat limited with respect to stream size as the largest flows included were around 1000 L/s. This limitation is in part because direct measurement of nutrient uptake in streams typically uses tracer injection of isotopically labeled nutrient (e.g., ^{15}N) and is not feasible in large rivers, although some studies have documented the influence of hydrology on N retention using ^{15}N approaches (Hall et al., 2009; Mulholland et al., 2009). Other approaches that have been used in larger rivers include pulse additions of nutrients (Tank et al., 2008), and mass balance approaches (Alexander et al., 2000; Heffernan and Cohen, 2010; Rode et al., 2016). These analyses have revealed that N retention per unit channel length decrease as a function of water depth (i.e., stage) moving down the channel network (Alexander et al., 2007).

The relationship between depth and N retention has been used to estimate N loading to the Gulf of Mexico from across the Mississippi river basin (Fig. 8). This analysis revealed that source contributions are not simply organized by proximity to the Gulf but by a combination of distance to outlet (i.e., where nutrient enters the river network) and removal rate (Alexander et al., 2000). Network geometry controls the travel distance from initial entry into the river network to arrival at the Gulf, and the magnitude of nutrient loading to the river network is largely a function of land use and land cover. Specifically, areas of intensive agriculture in the mid-west are locations of high N delivery to inland waters. Hence, network geometry (i.e., the width function), land use/landcover, and reaction rate (i.e., RR from Eq. 2) combine to control watershed export. It has also been recognized that nutrients that enter a river network in small streams are much more likely to be retained (i.e., taken up biologically), whereas nutrients that are loaded directly into larger rivers have a higher probability of being exported further downstream (Alexander et al., 2000). This finding highlights the importance of small streams in regulating downstream water quality (Alexander et al., 2007; Dodds and Oakes, 2008). Although small streams (i.e., streams less than 10 m wide) have importance for nutrient flux at large spatial scales (e.g., Mississippi river basin) they are susceptible to degradation and their legal protection remains unclear (Wohl, 2017).

In addition to having high nutrient retention rates, small streams are also important to regional nutrient budgets because they drain the majority of land area in any watershed (Fig. 4). In fact, streams with channel widths less than 10 m constitute up to 85% of network length and accordingly collect most of the water and associated material from adjacent terrestrial landscapes (Horton, 1945; Downing et al., 2012; Colvin et al., 2019). Current estimates derived using the National Hydrography Dataset Plus Version 2 estimate that first and second order streams combine to account for 79% of US streams and drain just over 70% of the land area of the conterminous US (Fig. 4). This geomorphic characteristic of river networks is partially responsible for the importance of

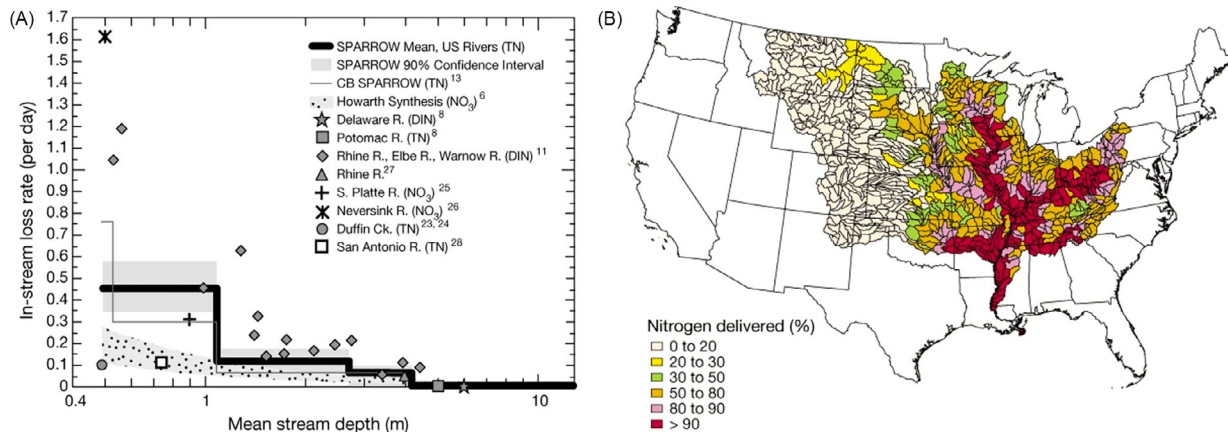


Fig. 8 (A) Relationship between in-stream nutrient loss rate and stream depth, indicating a decrease in loss rate with increasing depth. (B) Map indicating nitrogen (N) contributions to the Gulf of Mexico (GOM) from across the Mississippi River Basin. The amount of N that reaches the GOM is partially a function of location of entry into the river network. N loaded to small streams is more likely to be retained, while N loaded to larger rivers is more likely to be transported to the Gulf. Accordingly, interactions between the locations of N loading, uptake rates, and travel distances to the GOM regulate the fate of N transported across the Mississippi River Basin. Alexander RB, Smith RA, and Schwarz GE (2000) Effect of stream channel size on the delivery of nitrogen to the Gulf of Mexico. *Nature* 403: 758–761.

headwater streams in controlling nutrient export and water quality at larger spatial scales (Abbott et al., 2017). Additionally, the low water volume to surface area ratios inherent to small streams promote high interactions between stream water, benthic (i.e., stream bed), and hyporheic zones (Thomas et al., 2001) that are thought to be important to stream biogeochemical impacts on watershed export. Hyporheic exchange in headwater streams impacts a larger proportion of channel flow than in larger rivers downstream. Accordingly, there is larger potential for hyporheic uptake, transformation, and/or removal of nutrients in headwater streams. Hyporheic zones have been referred to as the “river’s liver” for their potential to remove nutrients, metals, and other contaminants (Fischer et al., 2005). In addition to small streams, small wetlands (Cheng and Basu, 2017) and ponds (Schmadel et al., 2019) can control biogeochemical flux from local to continental scales, highlighting the importance of headwater systems in terrestrial to aquatic linkages and in controlling retention and transport.

Because headwater streams are strongly connected to the terrestrial landscapes they drain, they are sensitive to changes in watershed land use and land cover (Allan, 2004; Nippgen et al., 2017; Brooks et al., 2019). For example, nutrient exports from headwater burned watersheds can remain elevated for decades post-fire (Rhoades et al., 2018) and past land use can be as, or more, important as current land cover in regulating aquatic ecosystems (Harding et al., 1998). Although small streams can be affected by their surrounding watersheds, they also have the capacity to transform terrestrial inputs thus altering the magnitude and/or form of watershed exports. This is particularly true when there is high in-stream demand for the nutrient (e.g., C, N, or P) being delivered to the stream. As stream size increases moving down the network, more C, N, and P are derived from upstream (longitudinal) relative to lateral hillslope sources (Vannote et al., 1980). In this way, the transport of C, N, and P from headwater to larger systems is a function of upstream inefficiencies in nutrient use. While headwaters can impact downstream water quality, large rivers are responsible for the bulk of mass flux of material and more research into the biogeochemical importance of larger rivers is warranted.

3.3 Scaling and managing biogeochemical transport along the river corridor

There has been considerable attention directed at restoring streams with the goal of enhancing biogeochemical processing to improve water quality. This is in part because large increases in nutrient inputs to freshwaters of North America and Europe associated with agriculture, urbanization, and other forms of land-use/land-cover change have led to degradation of inland and coastal water bodies (Rabalais et al., 2009; Dodds and Smith, 2016). Accordingly, many stream restoration projects have been designed to increase hyporheic exchange, elongate residence time, and enhance nutrient retention. A common approach is to alter the physical structure of the stream in order to enhance stream-hyporheic exchange and increase transient storage (Sparacino et al., 2019). This approach is built on a theoretical underpinning that greater transient storage will result in increased biogeochemical processing. While this is theoretically reasonable, it has proven challenging to document in field settings (Hall et al., 2002).

Research on in-stream processing has been driven, in part, by interest in understanding the potential for streams to attenuate nutrient fluxes and lessen impacts on downstream receiving bodies. For example, land cover and land use change has resulted in major increases in inorganic N loading to inland water bodies (Vitousek et al., 1997). Although inorganic N is often limiting to biological productivity in many natural ecosystems, anthropogenic addition of N has led to N saturation of biological uptake in many streams and rivers draining agricultural and/or urban landscapes (Earl et al., 2006). When a stream reach, or entire network (Wollheim et al., 2018), becomes N saturated, downstream transport is enhanced (Figs. 7 and 8). This transport enhancement occurs because N supply exceeds demand and biological uptake retains a smaller proportion of the total N delivery from the landscape (e.g., Davis et al., 2014). Issues of excess N supply often occur in heavily managed and altered landscapes where streams

are typically straightened and disconnected from their floodplains. This results in compounding affects where physical simplification of the fluvial network and high N concentrations combine to decrease both physical (e.g., river-floodplain hydrologic connectivity) and biological mechanisms of retention and enhance downstream loading (e.g., Loecke et al., 2017).

Many studies have used inter-site comparisons to relate nutrient processing to channel morphology and associated hydraulics. However, in addition to morphology, numerous other environmental factors change between stream reaches including temperature, ambient nutrient concentrations, biomass, and community composition, thus, inter-site comparisons cannot isolate impacts of channel morphology alone. The few studies that have intentionally manipulated residence time within a channel and measured response have demonstrated clear relations between in-channel structure, residence time, and nutrient uptake (Ensign and Doyle, 2005; Hester and Doyle, 2008; Cunha et al., 2018).

Physically based modeling approaches estimate that vertical hydrologic exchange beneath submerged bedforms rather than lateral exchanges that occur at meander bends dominate hyporheic flux and hydrologic turnover along the river corridor (Gomez-Velez et al., 2015). These exchanges have strong influence on transit time and thus influence the amount of time available for biological processing. By increasing transit time, hyporheic exchange can decrease the magnitude of fluvial biogeochemical flux from the watershed. Even in the absence of any biological uptake, hyporheic exchange can delay the timing of watershed nutrient and OC export thus attenuating the downstream flux of inputs from terrestrial sources and leading to dispersion of an initially concentrated, or pulsed, input.

Concentrated input of OC and nutrients occurs regularly during rain and snowmelt events where large amounts of OC and nutrients stored in watershed soils are delivered to streams (Boyer et al., 1996; Creed et al., 1996; Pacific et al., 2010). The delivery of OC and nutrients to streams during precipitation events occurs at times where river corridor (i.e., the stream and surrounding riparian areas sensu Harvey and Gooseff, 2015) biological uptake may be limited and has been hypothesized to lead to network saturation (the Network Saturation Concept sensu Wollheim et al., 2018). The biological processing of nutrients and OC can be limited during precipitation events, either rain or snowmelt, as a consequence of high flow, high velocity, high turbidity, and low temperature. High flow can decrease the amount of channel water interacting with benthic sediments as the water volume to channel bed surface area ratio changes (Alexander et al., 2000). High velocity has the direct effect of reducing transit times. High turbidity decreases the amount of light penetrating through the water column and reaching the channel bottom, thus decreasing autotrophic productivity (Mulholland and Hill, 1997). And low temperature constrains microbial metabolic rates (Demars et al., 2011).

4 Land-atmosphere fluxes in watersheds

One of the aspects in which geomorphology can enhance our understanding of co-occurring hydrological and biogeochemical processes is in the study of land-atmosphere exchange of water, C, or N. Historically, land fluxes of C, for example, have been examined by the terrestrial or the atmospheric science communities, whereas aquatic fluxes of C have been studied by the stream or lake science communities, keeping with a long tradition of intellectual separation among landscape elements. Similarly, fluxes of nitrous oxide (N_2O) to the atmosphere are more commonly associated within the context of terrestrial and agricultural landscapes; yet aquatic emissions of N_2O scale with stream order across large regions (Turner et al., 2015) but are rarely evaluated in this

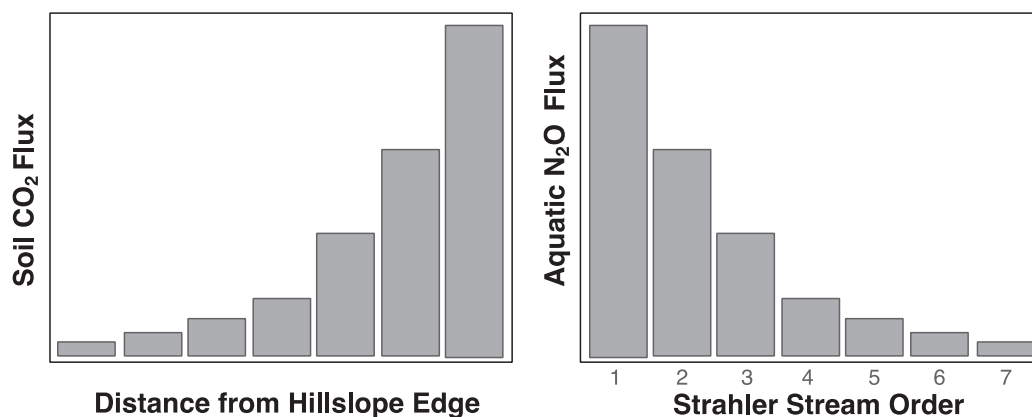


Fig. 9 Conceptual framework for our current understanding on the variability of soil carbon dioxide (CO_2) efflux in dry and semi-dry environments (left) and aquatic nitrous oxide (N_2O) in agricultural regions (right). Left panel is based on Pacific VJ, McGlynn BL, Riveros-Iregui DA, Epstein HE, and Welsch DL (2009) Differential soil respiration responses to changing hydrologic regimes. *Water Resources Research* 45. Riveros-Iregui DA, and McGlynn BL (2009) Landscape structure control on soil CO_2 efflux variability in complex terrain: Scaling from point observations to watershed scale fluxes. *Journal of Geophysical Research-Biogeosciences* 114; Riveros-Iregui DA, McGlynn BL, Emanuel RE, and Epstein HE (2012) Complex terrain leads to bidirectional responses of soil respiration to inter-annual water availability. *Global Change Biology* 18: 749–756. Right panel is modified after Turner PA, Griffis TJ, et al. (2015) Indirect nitrous oxide emissions from streams within the US Corn Belt scale with stream order. *Proceedings of the National Academy of Sciences of the United States of America* 112: 9839–9843.

context. Geomorphology can help us bridge intellectual gaps between hydrology and biogeochemistry, or terrestrial and aquatic sciences, particularly in the study of water, carbon, and other elemental fluxes at the watershed scale (Fig. 9).

Field and modeling observations have both highlighted the role of watershed structure as a primary spatial and temporal driver of the magnitude and timing of fluxes of evapotranspiration (e.g., Mahmood and Vivoni, 2014; Nippgen et al., 2015). Especially evident in dry climates, spatial patterns of shallow subsurface flow are related to volumetric water content and atmospheric vapor pressure deficit at the local scale (Hoylman et al., 2019a). Hillslope topography mediates water availability for plants and vegetation growth, as well as the capacity of plants to withstand drought (Hoylman et al., 2019b). This spatial organization suggests that the superposition of hillslope topography and watershed microclimate affects not only the partitioning of the energy balance at the land surface (e.g., Gu et al., 2006), but also important water fluxes such as soil water evaporation across landscapes of varying vegetation density (Royer et al., 2012). Hillslope topography can thus facilitate the adaptive response of biota to changes in climate, and ultimately the spatial distribution of microclimates (i.e., ~1 m scale) that may be more favorable than others for vegetation growth (e.g., Ivanov et al., 2008; Dobrowski, 2011; McLaughlin et al., 2017).

Evidence suggests that topographic patterns may impose organization of plant productivity from humid to dry environments (Tague et al., 2009; Hwang et al., 2012; Cervantes et al., 2014; Swetnam et al., 2017). This spatial organization is critical to our understanding of aggregate landscape response and useful in multi-method corroborations (e.g., bottom-up vs. top-down; Emanuel et al., 2011; Reyes et al., 2017). One type of analysis in which topographic patterns offer special potential is in the quantification of greenhouse gas fluxes (e.g., CO₂, methane (CH₄), and N₂O) from large regions. In fact, land-atmosphere carbon exchange is among the most uncertain components of the global carbon cycle. Bodmer et al. (2019) highlight that “[c]urrent frameworks [to measure land-atmosphere carbon exchange] do well at representing the different landscape elements that contribute to carbon exchange, yet the frameworks mostly neglect the elements’ interdependence.” The same authors argue that while terrestrial models account for carbon loss in forests and wetlands, current models do not distinguish between direct losses to the atmosphere and losses to the stream network. A different approach is clearly needed to reduce the existing uncertainty in estimates of carbon fluxes from heterogeneous landscapes.

Topography and associated patterns of soil water content drive spatial patterns of soil CO₂ flux (e.g., Webster et al., 2008; Riveros-Iregui and McGlynn, 2009; Pacific et al., 2011), soil N₂O flux (e.g., Poblador et al., 2017), and soil CH₄ flux (e.g., Kaiser et al., 2018) to the atmosphere. Wetter soil conditions enhance CO₂ efflux from uplands but reduce CO₂ flux from the transition zones and lowlands/wetlands where microbial respiration is often oxygen-limited (Riveros-Iregui et al., 2012). In contrast, drier soil conditions offset oxygen limitation and increase CO₂ efflux from lowlands and wetlands but reduce hydrologic connectivity and the transfer of matter and energy downstream (Senar et al., 2018). Concurrently, wetter and flooded conditions may limit CO₂ efflux but favor the generation of CH₄, a more potent greenhouse gas (Huttunen et al., 2003). CH₄ is often released in larger quantities than CO₂ when the water table is at or near the surface (Wieder et al., 2006), and the magnitude of CH₄ flux varies with changes in water table position, particularly in carbon-rich soils (Kellner et al., 2005; Couwenberg and Fritz, 2012).

Reconciling fluxes measured at different scales within a watershed (e.g., point, hillslope, stream reach) has proven a difficult task, and additional complications are introduced by variability of the fluxes controlled by terrain complexity. However, this variability, often assumed and rarely quantified, can be used to our advantage particularly with regards to biologically-mediated elemental exchange between the land and the atmosphere. Fluxes such as CO₂ fluxes from soils (soil CO₂ efflux) or from surface waters (CO₂ evasion) are particularly important because despite the small spatial scale at which these fluxes are measured, there is a relatively high confidence in their measurements. Thus, comprehensive corroborations of C fluxes at the watershed level are feasible and could include two dimensions: (1) a spatial corroboration, including issues of scaling, spatial coincidence, and footprint correction of the measures; and (2) a temporal corroboration, including issues of temporal resolution of each technique, and the feasibility of comparing measurement rates at similar temporal scales among various techniques. Achieving both tasks depends upon data quality, experimental design, and more importantly, the spatial collocation of all techniques.

Regarding aquatic fluxes of CO₂, studies suggest that they are regulated by biological processes at multiple scales, leading some stream reaches to act as net sources of CO₂ even in environments such as the arctic (Rocher-Ros et al., 2020). However, geomorphology determines spatial patterns of stream CO₂ evasion and the overall spatial variability of the drivers of CO₂ evasion to the atmosphere (Rocher-Ros et al., 2019; Schneider et al., 2020). Additionally, localized groundwater inputs along the stream channel can drive sharp increases (or decreases) in stream CO₂ evasion and generate hotspots of aquatic CO₂ flux along streams (Duvert et al., 2018). Mountain streams in particular have been highlighted as important sources of aquatic CO₂ fluxes despite their low areal coverage (Horgby et al., 2019), and this potential may be enhanced further if streams are hydrologically connected to carbon-rich environments such as wetlands (Aho and Raymond, 2019). Nonetheless, channel topography and related physical properties can introduce uncertainty in the estimation of gas exchange rates in mountain streams (Zappa et al., 2007; Ulseth et al., 2019).

The effects of both channel geomorphology and stream-wetland connections have been recently addressed in high-altitude tropical peatlands that are seasonally connected to streams (Schneider et al., 2020). These researchers found that regardless of discharge level, portions of the channel immediately downstream of a peatland exhibited greater CO₂ evasion, whereas portions of the channel farther from the peatland exhibited lower CO₂ evasion (Fig. 10). Additionally, when evaluated on a cumulative basis (Fig. 10), CO₂ evasion differs widely along the stream channel and geomorphic features such as waterfalls play an important role in determining the magnitude of CO₂ evasion and the baseline of dissolved CO₂ concentrations. Fig. 10 shows that stream CO₂ evasion downstream of a waterfall can be up to an order of magnitude lower than stream CO₂ evasion upstream of the waterfall, due to the enhanced gas exchange that is induced by the waterfall. Furthermore, the rates of the CO₂ evasion reported

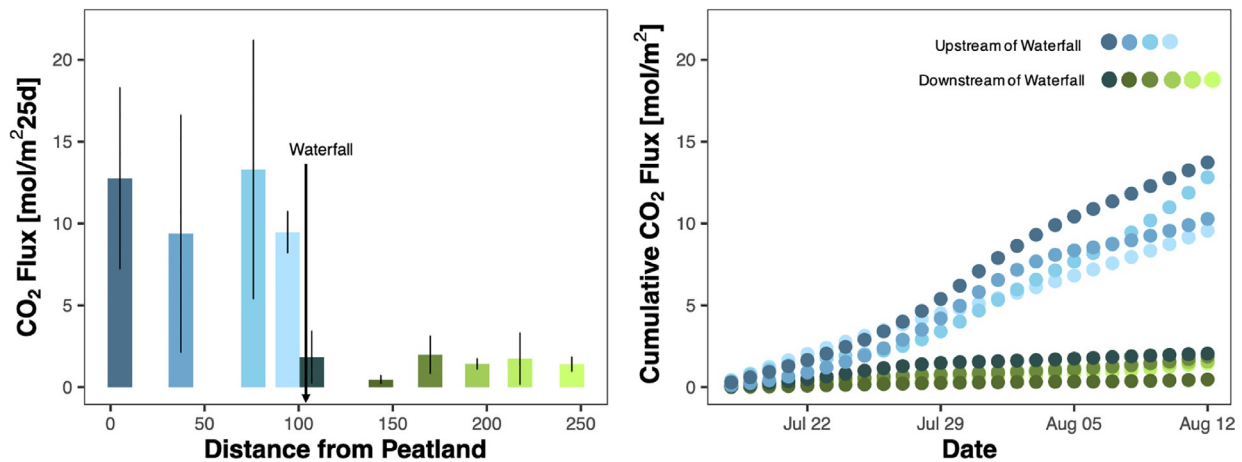


Fig. 10 (Left) Total CO₂ flux collected over 25 days from 10 sites along a 250-m stream reach draining a tropical peatland in the Andes Mountains of Ecuador (modified after Schneider et al., 2020). Aquatic CO₂ flux was measured using a forced diffusion flux system (EosFD, Eosense Inc., Dartmouth, Nova Scotia) every 5–7 days and averaged and scaled over the 25-day period. (Right) Same as left, but shown cumulatively over the same period. Blue shades represent site locations upstream of a 4-m waterfall (which was 107 m downstream of the peatland outlet). Green shades represent site locations downstream of the waterfall. These data suggest that geomorphology (namely the waterfall) plays a major role in mediating the magnitude of CO₂ evasion from the stream surface, highlighting the role of watershed structure in influencing the dynamics and spatial patterns of CO₂ evasion in headwater streams. (Left) Modified after Schneider CL, Herrera M, Raisle ML, Murray AR, Whitmore KM, Encalada AC, Suárez E and Riveros-Iregui DA (2020) Carbon dioxide (CO₂) fluxes from terrestrial and aquatic environments in a high-altitude tropical catchment. *Journal of Geophysical Research – Biogeosciences* 125: e2020JG005844. <https://doi.org/10.1029/2020JG005844>.

from these stream-wetland connections in high-altitude tropical peatlands are far greater than the reported rates from low-elevation tropical wetlands elsewhere (Sjogersten et al., 2014). Tropical wetlands are considered a missing link in the global carbon cycle (Page et al., 2011; IPCC, 2013) and thus these results suggest that high-altitude wetlands—which remain understudied compared to their low-elevation counterparts—may be important sources of atmospheric CO₂, at least during the times of the year when they remain hydrologically connected to the stream network. Precipitation regimes and wet and dry seasons determine the magnitude and timing of these CO₂ fluxes to the atmosphere and likely the concurrent emissions of other forms of C such as CH₄. Additional research is needed to evaluate large-scale effects of geomorphology in mediating the transport potential of streams and the transformation potential of high-altitude peatlands and other tropical wetlands located in areas of complex topography.

5 Conclusions

Geomorphology mediates hydrological and biogeochemical fluxes from the reach to the watershed scale. Some of these fluxes are among the most uncertain in global elemental cycles and thus implementing geomorphological understanding in the spatiotemporal analysis of these fluxes may help reduce errors in large-scale estimates. We argue that geomorphology offers an intellectual framework of reference for understanding and predicting how watershed morphology organizes hydrologic and biogeochemical patterns. Relating watershed form (geomorphology) to function (hydrologic and biogeochemical response) provides an opportunity to leverage the “organized heterogeneity” that exist in complex watershed systems. Integrating hydrologic and biogeochemical process in a geomorphic framework offers a path toward stronger integration across disciplines, coupling process from upland, river corridor, and in-stream settings, and for scaling hydrologic and biogeochemical processes across space and time.

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