



## Towards an improved understanding of biogeochemical processes across surface-groundwater interactions in intermittent rivers and ephemeral streams



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### ABSTRACT

Surface-groundwater interactions in intermittent rivers and ephemeral streams (IRES), waterways which do not flow year-round, are spatially and temporally dynamic because of alternations between flowing, non-flowing and dry hydrological states. Interactions between surface and groundwater often create mixing zones with distinct redox gradients, potentially driving high rates of carbon and nutrient cycling. Yet a complete understanding of how underlying biogeochemical processes across surface-groundwater flowpaths in IRES differ among various hydrological states remains elusive. Here, we present a conceptual framework relating spatial and temporal hydrological variability in surface water-groundwater interactions to biogeochemical processing hotspots in IRES. We combine a review of the IRES biogeochemistry literature with concepts of IRES hydrogeomorphology to: (i) outline common distinctions among hydrological states in IRES; (ii) use these distinctions, together with

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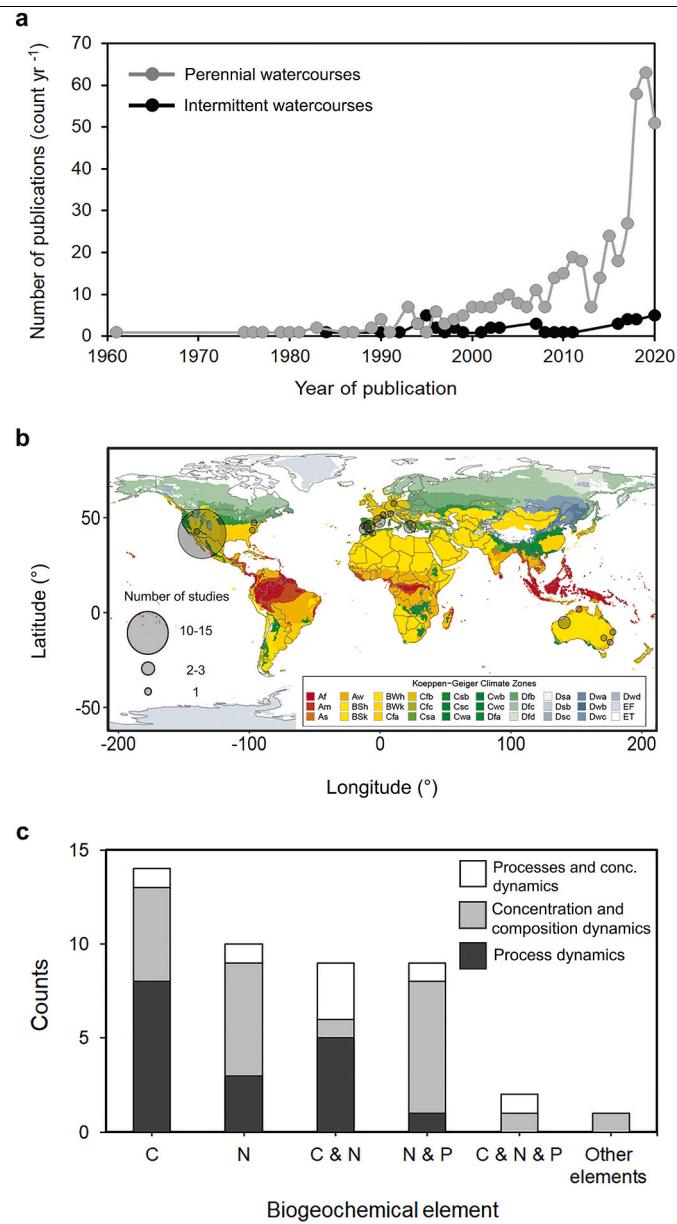
considerations of carbon, nitrogen, and phosphorus cycles within IRES, to predict the relative potential for biogeochemical processing across different reach-scale processing zones (flowing water, fragmented pools, hyporheic zones, groundwater, and emerged sediments); and (iii) explore the potential spatial and temporal variability of carbon and nutrient biogeochemical processing across entire IRES networks. Our approach estimates the greatest reach-scale potential for biogeochemical processing when IRES reaches are fragmented into isolated surface water pools, and highlights the potential of relatively understudied processing zones, such as emerged sediments. Furthermore, biogeochemical processing in fluvial networks dominated by IRES is likely more temporally than spatially variable. We conclude that biogeochemical research in IRES would benefit from focusing on interactions between different nutrient cycles, surface-groundwater interactions in non-flowing states, and consideration of fluvial network architecture. Our conceptual framework outlines opportunities to advance studies and expand understanding of biogeochemistry in IRES.

## 1. Introduction

Flow is the major structuring force in streams and rivers (Poff et al., 1997). Water flows not only longitudinally along the surface of stream channels, but also laterally and vertically through sediment and rock interstices (i.e., from hyporheic, parafluvial, and riparian zones to the stream, and vice versa). These lateral and vertical surface water–groundwater interactions transport key reactants for biogeochemical processes (e.g., organic matter (OM), nutrients and electron acceptors) across redox gradients (Fisher et al., 2004). The temporal and spatial distribution of surface water–groundwater hydrological connections thus strongly influences the rates, types, and location of biogeochemical processes in fluvial networks (Jones and Holmes, 1996).

Intermittent rivers and ephemeral streams (IRES) are waterways that are subject to occasional, periodic or protracted flow cessation and/or drying. IRES cover a substantial area of the global river network (Datry et al., 2014) and their extent is increasing as a result of the combined effects of climate and land use changes (Döll and Schmied, 2012; Pekel et al., 2016; Pumo et al., 2016). The effects of groundwater on surface water biogeochemistry likely increase in importance during flow cessation or drying when compared with flowing periods, as greater surface flows might comparatively “dilute” the influence of groundwater compartments. However, how surface water–groundwater interactions influence biogeochemical processes remains widely unexplored in rivers and streams that experience flow intermittence (Boulton et al., 2017).

A wide literature review of fluvial sciences (Fig. S1 and Table S1 in the Supporting information) shows that since the 1960s an increasing number of studies have reported significant advances and identified complex challenges regarding surface water–groundwater interactions and how they influence biogeochemical processes in rivers and streams (Fig. 1a). This research has yielded over 450 publications, including several review papers (Boano et al., 2014; Boulton et al., 2010; Krause et al., 2010), journal special issues (Lewandowski et al., 2020; Valett et al., 1993; Wondzell, 2015), and a book (Jones and Mulholland, 1999). Yet, only 45 of these publications (11%) contained the word “intermittent stream” (or temporary, or ephemeral, or non-flowing) in the title, abstract, or keyword list (Fig. 1a, Fig. S1 and Table S1 in the Supporting information). This modest attention contrasts with the relatively high interest in the field of temporary stream ecology and biogeochemistry during the late 1980s and early 1990s, motivated by studies conducted at Sycamore Creek (Arizona, United States; Fig. 1b). This pioneering research led to a series of novel studies in the surface, hyporheic, parafluvial and riparian zones of dryland streams, as well as to key biogeochemical models such as “The Telescoping Ecosystem Model” (Fisher et al., 1998). This initial publication growth rate did not persist during the first decade of the 21st century (Fig. 1a), despite continued increases in general biogeochemical research in IRES (Leigh et al., 2016). During the second decade of this century, renewed research into the interactions between hydrology and biogeochemistry in IRES was performed (Fig. 1a), coinciding with an increasing global focus on this topic (e.g., Datry et al., 2018; Shumilova et al., 2019; von Schiller et al., 2019). Nevertheless, research about biogeochemical processing along surface water–groundwater flowpath mosaics within IRES lags far



**Fig. 1.** (a) Number of publications per year including the word “groundwater” AND “surface water” AND “river” AND “biogeochemistry” in the title, abstract, or keywords (from 1960 to 2020). Note that the black line corresponds to papers including the word “intermittent” or synonyms (Methods S1 in the Supporting information). (b) Geographical distribution and density of publications (only for intermittent watercourses). (c) Total number of publications by biogeochemical element (C – carbon, N – nitrogen, P – phosphorus, Fe – Iron, Mn – manganese) and by type of dynamics (only for intermittent watercourses). Data was obtained from Scopus database in August 2020 (Table S1 in the Supporting information for the complete dataset). Singular, plural, and other forms of these terms with the same root were included in the search (see Fig. S1 in the Supporting information for additional details on the search criteria).

behind that of perennial systems (Fig. 1a).

The literature on biogeochemical processes across surface water–groundwater interactions in IRES has also been biased towards carbon (C) and nitrogen (N) cycles (Fig. 1c), and has mostly been conducted in the arid and semi-arid biomes (Fig. 1b) where surface water–groundwater hydrological interactions are highly dynamic compared to temperate biomes (Costigan et al., 2017) due to frequent alternation of dry-wet hydrological conditions or scenarios. Phosphorus (P) dynamics have always been studied together with N (Fig. 1c). Notably absent were studies exploring biogeochemical cycles of other essential elements such as sulfur (S), silica (Si), manganese (Mn) or iron (Fe). Approximately half of the published papers focused on element concentration and composition patterns (“concentration and composition dynamics”; Fig. 1c), while the other half focused on biogeochemical processing rates (“process dynamics”; Fig. 1c), most frequently aerobic respiration and nitrification (Table S1 in the Supporting information). Anaerobic processes such as methanogenesis or denitrification received much less attention. Other processes such as methane oxidation or anaerobic ammonium oxidation have not been studied at all. Publications were also biased towards surface channel environments in headwater reaches (Table S1 in the Supporting information). In contrast, little has been published about processes occurring at the lowland (i.e., deltaic, flood-out) zone. Compared to spatial dynamics, temporal dynamics of biogeochemical processes were represented by more studies. Publications addressed changes occurring over hours, days, seasons, and even years, although biased towards longer time scales (Table S1 in the Supporting information).

Surface water–groundwater hydrological exchange in IRES is characterized by dynamic spatial and temporal variations, such as pulsed rewetting events, fragmented surface flow cessation, and complex upwelling-downwelling patterns (Boulton et al., 2017; Costigan et al., 2017; Rau et al., 2017), which may have large consequences for biogeochemical processing. Following alternation of drying and flowing conditions, IRES can have a pulsed biogeochemical functioning, exporting large amounts of nutrients and OM downstream (Larned et al., 2010). These characteristic hydrological dynamics are currently neglected in most models describing hydrological-biogeochemical interactions, which typically represent permanently flowing systems (Allen et al., 2020; Boano et al., 2014). However, element cycling and transport along fluvial networks may fundamentally differ between IRES and perennial systems. Due to the large heterogeneity in redox potential, resource supply, and hydrological flowpaths, the diversity of biogeochemical processes in IRES may also be greater than in perennial rivers. To better understand these differences in biogeochemical dynamics between perennial and intermittent streams, future research should be oriented on a conceptual framework that integrates the hydrological and biogeochemical processes that occur in IRES.

In this review, we first (i) identify the most important surface water–groundwater interactions that characterize IRES. Next, based on this hydrological template we (ii) develop a conceptual framework for and review the potential rates and diversity of biogeochemical processes in which essential elements (C, N, and P) are involved across contrasting hydrological states. In addition, we (iii) evaluate how biogeochemical processes occurring within stream reaches at specific locations could extrapolate to entire IRES networks. Finally, we (iv) provide a forward-looking perspective to advance the study of IRES biogeochemistry. Through these goals we aim to generate a qualitative, general predictive model which can guide researchers to hot spots or moments (i.e., places and events that exert a disproportionate influence on the processing of elements at the scale of reaches and drainage networks within IRES; sensu McClain et al., 2003) of biogeochemical activity in their study reach or watershed, as well as a starting point from which to develop complementary or alternative hypotheses.

## 2. Mechanisms of surface-groundwater hydrological exchange in IRES

The hydraulic connection between surface water and groundwater occurs in all types of landscapes and climates (Allan and Castillo, 2007). When the groundwater level is higher than in the stream channel, water flows upwards towards the channel surface (gaining conditions). Conversely, when the groundwater level is lower than those in the stream channel water flows downwards towards the groundwater (losing conditions). Losing and gaining flow conditions imply, respectively, a net loss or gain of water, solutes, and particles with respect to surface water. In addition, transfer of solutes can occur between surface water and the streambed due to presence of logs, sequence of alternating topographical highs (riffles) and lows (pools) as well as large-scale geomorphological features such as meanders (Boulton et al., 1998; Brunke and Gonser, 1997; Tonina and Buffington, 2009). In such cases, water infiltrates the subsurface, and returns to the surface after spending some time in the hyporheic zone (i.e., hyporheic exchange; Boano et al., 2014; Harvey and Bencala, 1993; Jones and Mulholland, 1999).

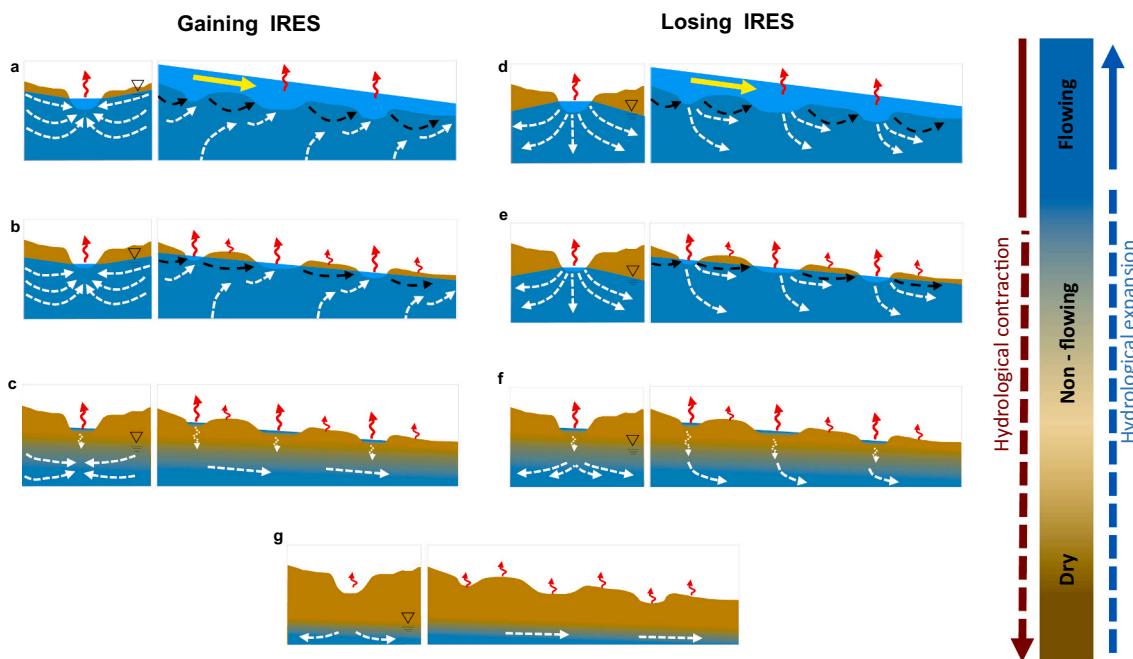
The fluxes and their direction (i.e., gaining vs. losing conditions) of surface water–groundwater interactions may shift dynamically through time in any given reach, particularly in response to surface water velocity or hydraulic head. In IRES, these surface water–groundwater interactions likely shift dramatically as surface flow ceases and channels progressively dry. To elaborate on the relationships between surface water–groundwater interactions and biogeochemical processes in IRES, we first conceptualize the hydrological framework (Fig. 2, Table 1 for the glossary of terms). To do so, we consider a set of simplified situations that illustrate three most characteristic hydrological states of IRES: flowing, non-flowing (pool formation), and dry. We then identify how the directions and magnitude of surface water–groundwater exchange differs within and across each state in response to the highly dynamic flow regimes of IRES.

### 2.1. Flowing state

During the flowing state, mixing of surface water and groundwater is evident in both losing and gaining reaches (Fig. 2a and d). Flowpath patterns during the flowing state in IRES are comparable to those of perennial reaches (Winter et al., 1998). Hyporheic exchange leads to simultaneous mixing of water and solutes, and thus depending on the exchange travel times (Cardenas et al., 2007; Fox et al., 2014) can become critical for the ecological and biogeochemical processes in IRES reaches (Querner et al., 2016; Rau et al., 2017). Hyporheic exchange is additionally induced by various types of geomorphic features such as gravel bars, meander bends, and riffle-pool sequences, which are dominant structures at the scale from tens to hundreds of meters (Harvey and Bencala, 1993; Tonina et al., 2007). Bedform features such as ripples and dunes are common in sandy streambeds and can induce interactions at smaller spatial scales (centimeters to meters), but dominate overall hyporheic exchange fluxes even at the catchment scales (Elliott et al., 1997; Gomez-Velez et al., 2015). Other geomorphic characteristics at smaller spatial scale (e.g., wood logs, boulder clusters, rocks, etc.) promote infiltration into the subsurface and contribute to the overall exchange (Tonina and Buffington, 2009). Consideration of surface water–groundwater flowpaths during the flowing state thus includes both rapid exchange between surface water and groundwater on top of the prevailing, directional template imposed by gaining or losing conditions.

### 2.2. Non-flowing state

The non-flowing state occurs during both hydrological contraction and expansion transitions. However, as long as water appears in the channel, hyporheic exchange may still persist (Fig. 2b, e) (Bonada et al., 2020; Boulton, 2003; Stanley et al., 1997). Surface water fragmentation



**Fig. 2.** Schematic representation of the main SW-GW flowpath interactions occurring in a gaining and a losing IRES reach with homogenous sediments. Cross sections show the vertical (left side of each panel) and longitudinal (right side of each panel) aspects with respect to the direction of water flow in the stream. Following the panels in the vertical direction informs on the water flowpaths and distribution during hydrological contraction (downwards) or expansion (upwards) phases as shown in the right side of the figure (red and blue arrows, respectively). Changes between hydrological states are bidirectional (from hydrological contraction to expansion, and vice versa) and can be partial (dashed line) or complete (continuous line) depending on the intensity of water table fluctuations. Yellow arrows show the advective flow in the stream, white dashed arrows show groundwater flowpaths, white wavy dashed arrows show flow in unsaturated sediments, and black dashed arrows shows hyporheic flowpaths in the sediments (i.e., shallow flowpaths that leave the stream and return after sometime in the streambed). Red arrows show the evaporation pathway. Note that the size of the arrows corresponds to the magnitude of the pathway in each specific context. Colour transparency gradient in panel c and f represents an hypothetical depiction of the dynamic temporal conditions of the non-flowing and dry states (i.e., the fluctuations of sediment water saturation levels in dry sediments over the length of the hydrological state). Case g represents extreme contraction conditons. See Table 1 and text for further details. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

reduces the area of open water, while increasing the area of exposed sediments, overall leading to reduced evaporation (Fig. 2). Water pools that are isolated on the surface may still be hydraulically connected via the subsurface due to vertical and/or longitudinal water exchange (Fellman et al., 2011; Siebers et al., 2016). Directionality of exchange depends on whether the stream reach is losing or gaining, as well as on direction of subsurface flow. Hyporheic exchange is lower as compared to that in the flowing state, driven by substantial reduction of surface flow. Unidirectional surface water-groundwater flowpaths (e.g., groundwater upwelling) should thus increase their relative contribution with respect to hyporheic exchange during the non-flowing state.

### 2.3. Dry state

As hydrological contraction continues, surface water disappears and hyporheic exchange ceases (Fig. 2c, f). During the dry state, groundwater levels retreat downwards from the exposed sediment surface, resulting in downward vertical flow through unsaturated sediments (Datry, 2012). Deep in the groundwater zone, vertical flow continues following the regional water head with directions differing between gaining and losing conditions (see cross sections of Fig. 2c, f). The evaporation rate decreases as it occurs via capillary rise of groundwater in contrast to direct evaporation from surface water (Shanafield and Cook, 2014; Skoulikidis et al., 2017). As hydrological contraction continues, the groundwater table further lowers until surface water-groundwater interactions no longer occur in the emerged sediments, i.e., no evaporation and no flow occurring in the unsaturated zone. This situation, defined here as extreme hydrological contraction (Fig. 2g), is considered the same regardless of whether the stream reach was previously gaining or losing water. The depth where the groundwater table

disconnects depends on climatic conditions, river network architecture, and sediment infiltration/retention characteristics as well as on the hydrological regime, but is likely to be deeper in drier climates (Chen et al., 2013; Quichimbo et al., 2020; Rau et al., 2017; Shanafield et al., 2012).

### 2.4. Variation in surface-groundwater exchange across hydrological states

Our conceptualization of surface water-groundwater interactions is illustrated using selected snapshots in time of the water flowpaths that prevail during hydrological contraction or expansion phases or transitions (Fig. 2). These snapshots do not represent static hydrological conditions, but rather gradually changing hydrological states. The succession and duration of the different hydrological states will depend on a combination of climatic variables (e.g., rainfall seasonality, temperature gradient) as well as water management practices (e.g., direct abstractions from the river, withdrawal from the aquifer, or river recharge). The surface water-groundwater flowpaths which occur in IRES may also be influenced by factors such as sediment type and its heterogeneity (Reid and Dreiss, 1990). Yet we propose that the predominant direction and relative magnitude of surface water-groundwater flowpaths progress through flowing, non-flowing and dry-states, regardless of actual rates. For example, hyporheic exchange will always be less active in the non-flowing than in the flowing states (e.g., Zimmer and McGlynn, 2017). We therefore conclude that the patterns of direction and relative magnitude of flowpaths should provide the template for determining the predominant biogeochemical processes, which we assess in the following section.

**Table 1**  
Glossary of terms and definitions.

Term	Definition
SW-GW flowpath interaction	Most contrasted types of stream water (SW) - groundwater (GW) flowpaths occurring in intermittent rivers and ephemeral streams (IRES). Stream surface water as a reference
Gaining IRES	Type of SW-GW interaction where groundwater flows upwards towards the stream
Losing IRES	Type of SW-GW interaction where stream water flows downwards towards the groundwater
Hydrological state	Most contrasted states occurring in IRES along contraction and expansion hydrological transitions
Flowing (Fl)	State in which surface flow is continuous along the stream. This situation is analogous to the case of a perennial stream
Non-flowing (Nf)	State in which surface water transitions from discontinuous flow along the stream until just before the streambed surface completely dries up (dry state). During the non-flowing state water gradually disappears from the surface and discontinuous surface water sections are formed (i.e., isolated pools)
Dry (Dr)	State in which water is no longer found on the surface stream (i.e., no isolated water pools) but the subsurface environment still holds different degrees of water saturation depending on the severity and duration of the drying period (from water saturated to complete desiccation)
Biogeochemical processing zone	Most contrasted stream reach compartments where biogeochemical processes tend to occur. The volume as well as biogeochemical activity of these stream biogeochemical units varies along hydrological transitions and type of SW-GW flowpath
Surface water (SW)	Continuous water body in the stream channel
Hyporheic zone (HZ)	Transition zone between the SW and GW. In the HZ, water continually enters from and exits to SW and GW and is thus considered separate from either zone
Groundwater (GW)	Subsurface zone in which all the pores are filled with water (i.e., saturated)
Water pool (PO)	Disconnected water body in the stream channel with no or very slow flow
Emerged sediments (ES)	Fraction of the streambed that used to be inundated by SW or PO but has emerged (become air-exposed) during drying

### 3. Linking biogeochemical processes to surface water-groundwater hydrological dynamics in IRES

The various available forms of C, N, and P, as well as terminal electron acceptors (TEAs), are governed by the prevailing redox potential. The redox gradient is strongly correlated with TEA availability, particularly dissolved oxygen (DO), and constitutes a primary determinant of the identity and diversity of biogeochemical processes (Borch et al., 2010). In addition, many biogeochemical process rates are determined by the availability of limiting substrates (e.g. NH<sub>4</sub><sup>+</sup> for nitrification; Findlay and Sobczak, 2000). As described in the previous section, the major drivers of biogeochemical processes along surface water-groundwater flowpaths in IRES might therefore be advective transport and coupled mass transfer, as well as the location and length of surface-subsurface flowpaths (Fig. 2). For example, a predictable series of N cycling processes, driven by changing redox conditions and availability of electron donors, has been documented along hyporheic and parafluvial flowpaths in the intermittent Sycamore Creek (Boulton et al., 2017; Fisher et al., 1998; Malard et al., 2002).

The following sections (3.1, 3.2, and 3.3) explore the diversity and rates of biogeochemical processes within IRES reaches by considering (i) the direction and length of dominant hydrological flowpaths (Fig. 2), and (ii) the co-occurrence of electron donors (e.g., organic substrates) and acceptors (e.g., DO, NO<sub>3</sub><sup>-</sup>, Fe, Mn, SO<sub>4</sub><sup>2-</sup>) (Fig. 3). First, we extensively review the potential activity of seven different biogeochemical processes affecting key elemental cycles (aerobic and anaerobic respiration of C, denitrification, nitrification, ammonification, N<sub>2</sub>-fixation,

and P-mineralization) along the three contrasting hydrological states within IRES. The biogeochemical processes considered are essential for understanding the cycling of compounds such as C, N and P as they are highly coupled and, in all cases, are i) biologically-mediated (i.e., performed by microorganisms or their extracellular enzymes), and ii) follow dissimilatory biogeochemical pathways (i.e., involve the transformation of one compound into another rather than assimilation into biomass). For example, nitrification transforms NH<sub>4</sub><sup>+</sup> into NO<sub>3</sub><sup>-</sup>, and mineralization transforms organic C, N, and P into free inorganic fractions.

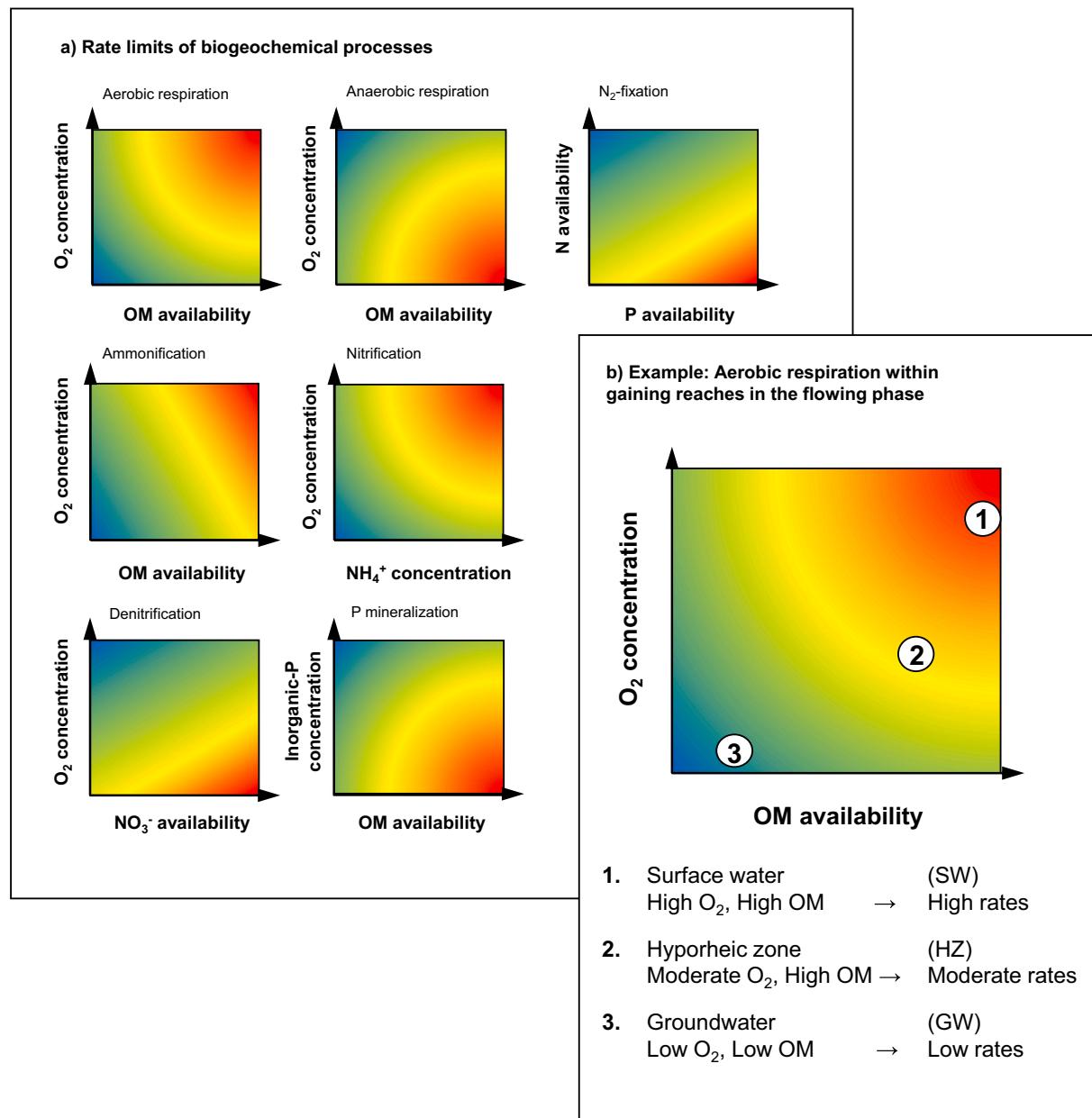
Next, we translate this information into categories of potential activity for each process (i.e., "High", "Moderate", and "Low/Null") and mapped in Fig. 4. While absolute rates will likely differ across climates and geochemical context (von Schiller et al., 2017), rate categories can be compared across differing systems. In addition, considering rate categories for each process avoids the complication of determining the magnitude of difference for contrasting processes which naturally occur at different absolute rates (e.g., N<sub>2</sub>-fixation should generally occur at much lower rates than nitrification). For this exercise, other rate-limiting drivers of biogeochemical processes are therefore considered to be universally equal in relative terms. For example, warming might increase denitrification rates up to an order of magnitude greater than a concurrent increase in N<sub>2</sub>-fixation rates (Grimm and Petrone, 1997; Holmes et al., 1994). Yet, the relative effect of temperature remains the same (i.e., an increase in both processing rates). Predictions are repeated for each of the hydrological scenarios depicted in the previous section (Fig. 2), by considering the following factors:

- i) the two predominant surface water-groundwater flowpath interactions (i.e., gaining and losing reaches)
- ii) the three hydrological states characteristic of IRES during contraction and expansion phases (i.e., flowing, non-flowing and dry).

We consider five preeminent biogeochemical processing zones: flowing surface water, hyporheic zone, groundwater, isolated surface water pools, and emerged streambed sediments (Table 1). While the biogeochemical processing zones include terms generally used for water bodies alone such as "surface water", we stress that each zone considered here also includes the biogeochemically active sediments in contact with that water body. For instance, by "surface water" processes we refer also to those that will occur at the interface between the streambed and water above. For "emerged sediments", we refer to those sediments exposed to the atmosphere (i.e., "dry" stream channel) but still connected to sub-surface water flowpaths at some point in the vertical profile (i.e., sediments with both water and air content). Emerged sediments are unique biogeochemical processing zones in IRES, and are increasingly recognized as active biogeochemical processing zones (Baldwin and Mitchell, 2000; Gómez-Gener et al., 2016; Marcé et al., 2019).

#### 3.1. Biogeochemical processes affecting the C cycle

The surface water zone has high potential for aerobic respiration in both losing and gaining surface water-groundwater interactions due to the high availability of DO and OM (Fig. 3). Conversely, surface water anaerobic processing rates tend to be low or zero (Fig. 4). Furthermore, the flux of DO and OM from the surface to subsurface under losing conditions supports aerobic respiratory processes (Jones et al., 1995a, 1995b) which tend to rapidly reduce DO availability as surface water down-wells into hyporheic sediment interstices (Holmes et al., 1994; Jones et al., 1995a, 1995b). When DO concentrations are low, OM respiration occurs via anaerobic pathways using alternate TEAs (Baker et al., 1999). Thus, moderate to high anaerobic respiration is expected in these subsurface stream compartments (Holmes et al., 1994; Jones et al., 1995a, 1995b). Less frequently, upwelling of low DO groundwater to the surface (i.e. gaining) can be a source of TEAs and bioavailable OM

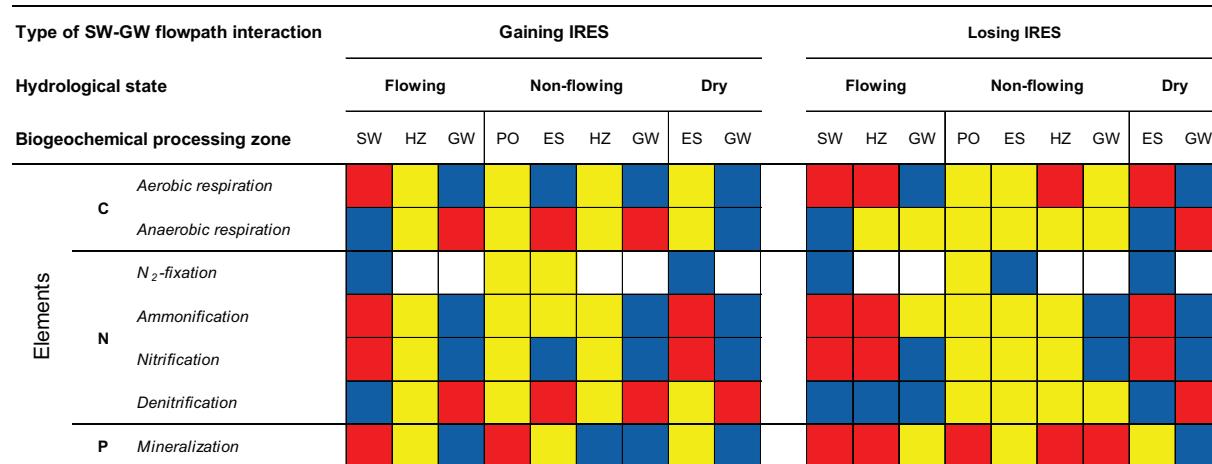


**Fig. 3.** Conceptual framework for prediction of relative biogeochemical process rates across hydrological states in IRES. (a) Prediction of process hotspots across rate-limiting gradients, with axes showing relative concentrations of rate-limiting factors and response surfaces representing relative process rates from Red – high to Blue – low. (b) Example of associating specific biogeochemical processing zones within given hydrological states with predicted process rates, using the case of aerobic respiration in a gaining reach during the flowing state. Open circles with numbers indicate positions along rate-limiting gradients corresponding with specific zones (e.g., at (2.),  $O_2$  concentrations are moderate and OM availability is high, which corresponds to the hyporheic zone). Under these conditions, the prediction for aerobic respiration is thus moderate (yellow square in the heatmap of potential activity shown in Fig. 4). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Valett et al., 1990), thus promoting anaerobic respiratory activity in the hyporheic zone (Fig. 4) if redox gradients are large (Rulifk et al., 2000). Indeed, in gaining streams and flowing conditions, the hyporheic zone has moderate potential for aerobic and anaerobic activity due to moderate concentrations of OM and TEAs (Boulton et al., 2017; von Schiller et al., 2017).

During the non-flowing state, isolated pools (PO in Fig. 4) in gaining streams can receive inputs from upwelling or parafluvial flowpaths with low DO and high TEA concentrations (Boulton et al., 2017; Fellman et al., 2011; Siebers et al., 2016). At the first stages of pool development, DO levels can drop owing to moderate aerobic respiratory processes (Vazquez et al., 2011; von Schiller et al., 2011). At later stages of

pool isolation depleted DO conditions may enhance anaerobic respiratory processes (Gómez-Gener et al., 2015), while the hyporheic zone emerges as an active biogeochemical processing zone for aerobic respiration (Jones et al., 1995a, 1995b; Triska et al., 1990; Valett et al., 1990). Otherwise, groundwater is expected have a high potential for anaerobic respiration and a low potential for aerobic processes (Fig. 4). Similarly, emerged sediments (ES in Fig. 4) can comprise high rates of anaerobic processing and low aerobic respiration since they remain saturated with DO-poor water while also containing labile organic materials derived from microbial cell lysis in the streambed (Gómez-Gener et al., 2016). However, this picture can be complicated if the streambed is unsaturated (i.e., containing not only water but also air). Under this



**Fig. 4.** Heatmap of potential activity (red = high; yellow = moderate; blue = low or null) for a selection of individual biogeochemical processes affecting the carbon (C), nitrogen (N) and phosphorus (P) cycles in preeminent zones across IRES reaches (i.e., surface water = SW, hyporheic zone = HZ, groundwater = GW, isolated water pool = PO, air-exposed or emerged streambed sediment = ES). These processes were evaluated for two contrasted SW-GW flowpath interaction types (i.e., gaining and losing IRES) and three hydrological states typically occurring in IRES along contraction and expansion phases or transitions. See Fig. 2, Table 1 and text for further details. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

circumstance, moderate to low aerobic and anaerobic respiratory activities can be supported given that organic substrates are still available via various sub-surface flowpaths. For example, Gómez-Gener et al. (2015) reported that sediments exposed to the atmosphere transport and emit gaseous CH<sub>4</sub> (likely generated in the hyporheic zone and groundwater) despite low rates of anaerobic activity, equivalent to methanogenesis rates detected in the surface stream (Jones et al., 1995a, 1995b). As drying proceeds, anaerobic processes will gradually give way to aerobic ones as oxygen diffuses into unsaturated sediments (Bolpagni et al., 2019; Bolpagni et al., 2017). Hence, dry streambeds act as aerobic reactors during the dry state, showing high rates of CO<sub>2</sub> emission (Keller et al., 2020; Marcé et al., 2019; von Schiller et al., 2014). However, such moderate to high aerobic respiration rates and associated CO<sub>2</sub> emission in emerged sediments during the dry state will only be maintained until the threshold when microbial activity becomes inhibited by water limitation (Keller et al., 2020; Manzoni et al., 2012). This results in moderate and low respirations mediated by emerged sediments and groundwater, respectively.

In losing streams during the non-flowing state, high flux of surface water into downwelling flowpaths maintains relatively high to moderate DO availability in the sub-surface, likely constraining anaerobic respiratory pathways (Boulton et al., 2017). However, down-welling areas are well-described sinks for nutrients and labile dissolved organic matter (DOM) originating from algal production on the stream surface (Jones and Holmes, 1996). Labile dissolved OM supports moderate aerobic respiration rates and DO depletion (Fig. 4), especially along protracted downwelling or parafluvial flowpaths with extended residence time (Malard et al., 2002), and might activate anaerobic respiratory processes with lower energetic demands (Baker et al., 1999). In such cases, groundwater generally has a low potential for aerobic respiration (Foulquier et al., 2010). Hence, redox conditions in the hyporheic zone or groundwater will likely depend on whether DO or dissolved OM transport predominates. We thus predict moderate rates of aerobic respiration in groundwater during the non-flowing state (Lewis et al., 2007).

In addition, microaerophilic or anaerobic processes due to low DO concentrations should be predominant in the non-flowing state (Acuña et al., 2004, 2007; von Schiller et al., 2011). We therefore predict low to moderate rates of aerobic respiration for water pools (Siebers et al., 2020). During the non-flowing state, water residence time along hydrological flowpaths increases. Consequently, the likelihood for low DO conditions as well as the occurrence of anaerobic processes in the

hyporheic and groundwater zones will increase. Yet, exhaustion of OM or TEAs due to internal processing and/or reduction of downwelling might limit anaerobic respiration rates at the final stages of pool development (Vazquez et al., 2011). However, the hyporheic zone emerges as an active zone for aerobic respiration (Jones et al., 1995a, 1995b; Triska et al., 1990; Valett et al., 1990). At the same time, unsaturated exposed streambeds have moderate and high potential for aerobic respiration during both non-flowing and dry states, respectively (Arce et al., 2015; Gómez et al., 2012; Zoppini et al., 2014). During dry conditions downwelling flowpaths may continue to transport TEAs and OM along subsurface flowpaths, possibly maintaining high anaerobic respiration and low aerobic process rates in groundwater (Fig. 4).

### 3.2. Biogeochemical processes affecting the N cycle

Here, four key N cycling processes are considered: N<sub>2</sub>-fixation, ammonification (i.e., N-mineralization), nitrification (i.e., ammonia oxidation), and denitrification. N<sub>2</sub>-fixation is limited by P availability (Grimm and Petrone, 1997; Howarth et al., 1988) (Fig. 3a). Ammonification is limited mostly by the quality of available OM (Bowden, 1987) (Fig. 3a). In contrast, nitrification rates are limited by oxygen concentrations and supply of ammonium (NH<sub>4</sub><sup>+</sup>) (Strauss and Lamberti, 2000) (Fig. 3a). Finally, denitrification is most likely limited by NO<sub>3</sub><sup>-</sup> supply and is strongly restricted to anaerobic conditions (Groffman et al., 2009; Mitchell and Baldwin, 1999) (Fig. 3a). The N cycling processes in IRES are thus often spatially and temporally variable, dependent upon changing redox conditions as well as the relative rates of other processes that control the forms and availability of OM and inorganic nitrogen (von Schiller et al., 2017).

In both gaining and losing reaches of flowing IRES, the surface water zone is predicted to have a high potential for ammonification (Fig. 4) due to high availability of OM from either terrestrial sources or instream production (Pinay et al., 2002) (Fig. 3a). Similarly, we predict high nitrification rates in surface sediments (Fig. 4) due to high DO and NH<sub>4</sub><sup>+</sup> concentrations (Fig. 3a). Given relatively high ammonification and nitrification rates, N<sub>2</sub>-fixation in surface waters may be restricted to low rates (Fig. 4) by high inorganic N availability (Fig. 3a). In addition, because photosynthetic cyanobacteria should largely be responsible for N<sub>2</sub>-fixation (Howarth et al., 1988; Marcarelli et al., 2008), we do not assign N<sub>2</sub>-fixation rates in sub-surface compartments here or in following hydrological states (Fig. 4). Despite high NO<sub>3</sub><sup>-</sup> and OM concentrations, denitrification rates are likely to be low in flowing surface

water (Fig. 4) because of high DO concentrations (Boulton et al., 2017; von Schiller et al., 2017) (Fig. 3a). In the sub-surface, ammonification rates in the hyporheic zone of losing IRES may be relatively high (Fig. 4) because of high DO and OM availability (Boulton et al., 1998) (Fig. 3a), but restricted to moderate rates under gaining conditions by upflows of DO-poor groundwater. Groundwater can be considered as a high active zone for ammonification due to low concentrations of organic C and DO (Fig. 3a) at all considered scenarios (Fig. 4). Similarly, nitrification may proceed at relatively high rates in hyporheic and parafluvial flowpaths of losing systems (Edwardson et al., 2003) Edwardson et al., 2003; Holmes et al., 1994; Jones et al., 1995a, 1995b; Triska et al., 1990) (Fig. 4) because of high influx of DO and  $\text{NH}_4^+$  (Boulton et al., 2017; DeSimone and Howes, 1998) (Fig. 3a). Under gaining conditions, however, nitrification may be restricted to moderate rates in the hyporheic zone (Fig. 4) if upwelling groundwater is DO-poor (Jones et al., 1995a). Nitrification is likely limited to low rates in groundwater (Fig. 4) by low DO availability (DeSimone and Howes, 1998) (Fig. 3a). Finally, denitrification may proceed at moderate rates in the hyporheic zone of gaining systems (Fig. 4), where upwelling of DO-poor flowpaths intersect with relatively high availability of  $\text{NO}_3^-$  and organic C (Groffman et al., 2009; Hill et al., 2000) (Fig. 3a). As the most energy-efficient anaerobic respiration pathway (Dahm et al., 1998), denitrification may thus be coupled with nitrification at oxic-anoxic interfaces in the hyporheic zone (Boulton et al., 2017; Holmes et al., 1996; Malard et al., 2002). However, under losing conditions, high fluxes of DO through hyporheic exchange and along downwelling flowpaths in the hyporheic zone (Boulton et al., 2017; Holmes et al., 1996; Kemp and Dodds, 2002; Malard et al., 2002) likely constrain anoxic zones and thus denitrification to groundwater (Fig. 4).

In both gaining and losing reaches during the non-flowing state, surface pools can accumulate large amounts of allochthonous and autochthonous OM due to the lack of downstream transport (Boulton and Lake, 1992; Romaní et al., 2013), which potentially favors the ammonification process (Gómez et al., 2017). Yet because DO depletes during prolonged pool isolation, ammonification tends to be limited to moderate rates (Arce et al., 2015) and assimilatory N uptake also reduces. The ultimate result is that  $\text{NH}_4^+$  represents the dominant form of dissolved inorganic N in pools (von Schiller et al., 2011), but nitrification is also likely restricted to moderate rates in pools (Fig. 4) by depletion of oxygen (Fig. 3a). Equally, relatively low DO concentrations, stratification, or diurnal anoxia should allow for moderate rates of denitrification (Fig. 3a) in pools (Lillebø et al., 2007; von Schiller et al., 2011) (Fig. 4).  $\text{N}_2$ -fixation may occur at moderate rates due to increased availability of inorganic P (Grimm and Petrone, 1997). Under gaining conditions, unsaturated emerged sediments likely maintain low concentrations of DO, but may also receive nutrient subsidies from upwelling or parafluvial flowpaths (Boulton et al., 2017; Dahm et al., 2003), leading to high potential for denitrification (Fig. 4).  $\text{N}_2$ -fixation may thus also occur at moderate rates (Fig. 4), particularly if cyanobacteria proliferate at the surface. Under losing conditions, higher DO, OM, and  $\text{NH}_4^+$  availability should instead drive moderate ammonification and nitrification rates (Fig. 3a), respectively in unsaturated, emerged sediments (Gómez et al., 2012; Merbt et al., 2016) (Fig. 4), but denitrification may also be moderate at oxic-anoxic interfaces (Revsbech et al., 2005) (Fig. 4). In the hyporheic zone, reduction of exchange between surface and subsurface water relative to the flowing phase likely results in longer residence times and steeper redox gradients in both gaining and losing reaches. Moderate ammonification, nitrification and denitrification rates may all thus be coupled along oxic-anoxic flowpaths (Boulton et al., 2017). Under losing conditions, limitation of nitrification, and thus a source of  $\text{NO}_3^-$ , may constrain denitrification rates in groundwater (Fig. 4), despite the potential for downwelling flowpaths to transport OM and labile C to sub-surface zones.

During the dry state, unsaturated emerged sediments have a high potential for ammonification (Fig. 4) due to an initial supply of OM (e.g. through decaying biofilms and/or UV exposure; Arce et al., 2018;

Reverey et al., 2016) and generally high DO concentrations due to increased air diffusion (Arce et al., 2018) (Fig. 3a). DO diffusion during drying should also enhance nitrification in near-surface sediments (Fig. 4) if the supply of  $\text{NH}_4^+$ , as well as moisture conditions, are non-limiting (Arce et al., 2015; Gómez et al., 2012; Merbt et al., 2016). High  $\text{NO}_3^-$  concentrations (Arce et al., 2018; Arce et al., 2013; Gómez et al., 2012; Merbt et al., 2016) may support denitrification (Fig. 3a) in unsaturated, emerged sediments under gaining conditions (Fig. 4), where intersection of low DO flowpaths with soil OM could promote denitrification activity (Arce et al., 2015). However, higher DO concentrations likely constrain denitrification in emerged sediments under losing conditions (Austin and Strauss, 2011) (Fig. 4). High N availability should also restrict  $\text{N}_2$ -fixation to low rates under both gaining and losing conditions (Fig. 4). In groundwater, low concentrations of DO should constrain both ammonification and nitrification to low rates (Fig. 4). Transport of  $\text{NO}_3^-$  through subsurface flowpaths may continue to promote denitrification in the groundwater.

### 3.3. Biogeochemical processes affecting the P cycle

Publications of P dynamics in IRES are scarce relative to C and N (von Schiller et al., 2017). In IRES, processes and factors controlling the intensity of spatially and temporally distributed P fluxes are tightly linked with C and N cycles through the mineralization of OM. However, P-mineralization rates also decrease with the increasing availability of inorganic P. Inorganic P availability can be substantially influenced by abiotic processes which co-vary with drying cycles e.g., carbonate precipitation. In particular, Fe and aluminum (Al) are P binding elements that strongly contribute to sorption/desorption reactions, precipitation, and mineral formation across the redox gradient, thus greatly affecting the availability of inorganic P (Withers and Jarvie, 2008). Microbial reduction of nitrate and Fe(III)-P compounds can also affect inorganic P availability (Cabezas et al., 2013). Sorption and desorption further depend on the P saturation of the sediment (Hupfer et al., 2007; Lewandowski and Nützmann, 2010; Zak et al., 2006). In contrast to C and N, consideration of abiotic processes using inorganic P availability as an indicator is thus necessary to evaluate P cycling.

Under flowing conditions, the hyporheic zone is well supplied with DO and other TEAs due to advective transport. Consequently, both surface water and the hyporheic zone have a high potential for P-mineralization, particularly in losing systems where groundwater might also receive OM and TEA inputs via downwelling flowpaths. Conversely, in gaining reaches upwellings from reduced sub-surface flowpaths may act as sources of inorganic P and thus reduce mineralization rates in the hyporheic zone (Dent et al., 2001).

In water pools, high retention of particulate OM and a lack of upstream inorganic P inputs likely result in high P-mineralization rates, despite the development of intermittent anoxia which can drive reductive P release (Bernal et al., 2013; von Schiller et al., 2011). Reduced advective transport of available P likely limits mineralization rates in the hyporheic zone in gaining systems. However, transport of labile algal OM from the surface to subsurface might support high P-mineralization rates in the subsurface flowpaths of losing pools.

Under drying conditions, decreased microbial activity and mobility, as well as reduced diffusion rates of soluble substrates, might limit P-mineralization in emerged sediments (Amalfitano et al., 2008). However, extracellular enzymes may still hold part of their ability to hydrolyze organic P under dry conditions (Burns et al., 2013; Sirová et al., 2006; Zoppini et al., 2014). Further, cleavage of OM by abiotic processes like photodegradation can increase the amount of leachable P (Baldwin and Mitchell, 2000; Dieter et al., 2011). Air and UV exposure of unsaturated exposed sediments also increase microbial mortality with a consequent release of intracellular solutes, which can further increase water-extractable P concentrations (Baldwin and Mitchell, 2000; Dieter et al., 2011). Consequently, while emerged sediments might be enriched in organic P, we predict low P-mineralization rates due to readily

available inorganic P. Low OM availability in combination with reducing conditions may enhance desorption of inorganic P in the groundwater (Lewandowski et al., 2020). Hence, the intersection of subsurface flowpaths with emerged sediments may also not result in substantially increased P-mineralization rates.

### 3.4. Predicting biogeochemical potential: a synthesis

This section synthesizes the independent element and process evaluations into conceptual heat maps showing predictions for overall process rates and diversity across different hydrological states, within IRES at the reach scale (Fig. 4). Heatmap visual analysis allows the exploration of complex data sets with, for instance, various processes acting at different spatial and temporal scales, without the need for dimensionality reduction (Bucci et al., 2019). Moreover, they also represent useful tools to identify zones where specific types of processes are more or less likely to occur. Overall, 126 possible combinations of flowpaths, hydrological states, and processing zones were evaluated: 2 flowpaths  $\times$  3 hydrological states  $\times$  5 biogeochemical processing zones  $\times$  7 processes. Note that there was an uneven distribution of processing zones for the different hydrological states (3 for flowing, 4 for non-flowing and 2 for dry states, respectively). We evaluated the potential biogeochemical process activity within each combination, and combined them into the heatmap (Fig. 4). Of the processes evaluated, the most uncertain was anaerobic respiration in the hyporheic zone because of the little information available in previous studies.

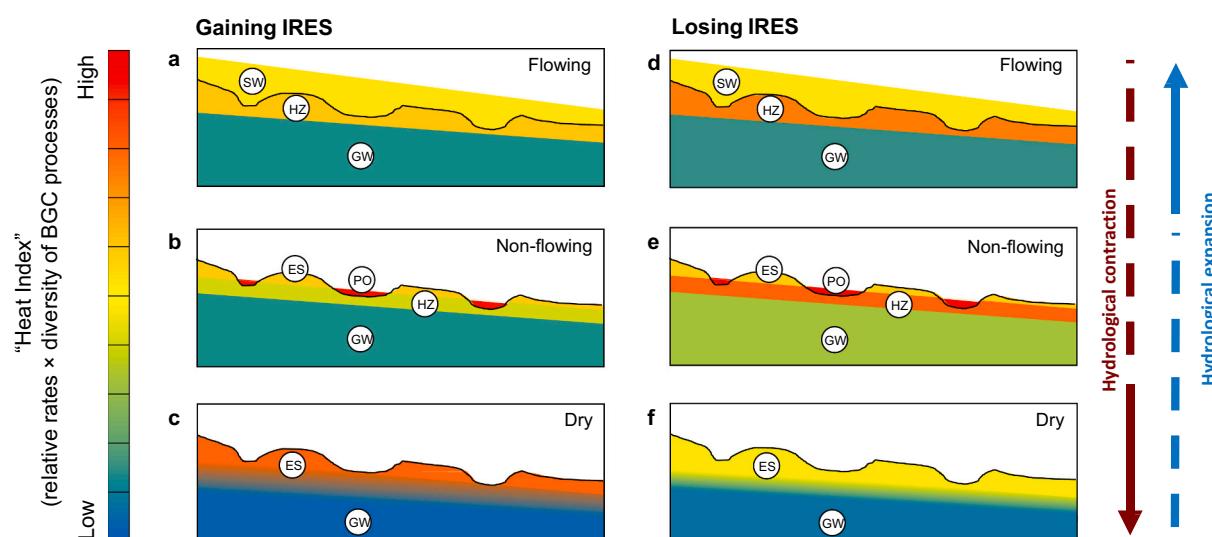
Our heatmap provides a predictive framework to identify the relative potential for biogeochemical processing within IRES at the reach scale. Given the relative paucity of field and experimental studies on surface water–groundwater biogeochemical interactions in IRES (Fig. 1a), provided predictions could then be used to identify hydrological states and biogeochemical processing zones which should prove promising areas of future research. To generate hypothesis for the overall processing rates at the reach scale, we estimated an index of relative “heat” (“Heat Index”; HI) for each biogeochemical processing zone within each hydrological states  $\times$  flowpath category (e.g., water pools in the non-flowing state within gaining reaches). First, we assigned scores to

relative process levels (High = 2, Moderate = 1, Low/Null = 0, Fig. 4). Next, we multiplied the sum of scores by the number of different biogeochemical processes at predicted “High” or “Moderate” levels within each processing zone  $\times$  hydrology category to obtain a final Heat Index value ranging between 0 and 60 (Fig. 5). For each hydrological scenario, this exercise identifies which stream processing zones within a reach might have the greatest potential for overall biogeochemical activity, in terms of both diversity and relative rates of processes.

The Heat Index indicates that, during the flowing state, the hyporheic zone should have a relatively high potential for biogeochemical processing in both gaining (HI = 36) and losing reaches (HI = 45) (Fig. 5). However, our index predicts the highest overall potential during the non-flowing state, for water pools in both gaining (HI = 56) and losing reaches (HI = 56). The hyporheic zone in losing reaches further acts as a hot spot of biogeochemical processes during the non-flowing state (HI = 48). Emerged sediments in gaining reaches are also predicted to be relative hot spots during the dry state (HI = 48). Conversely, groundwater likely represents a relative cold spot for biogeochemical processes in gaining reaches across most states (HI < 10) but may support higher rates and diversity of biogeochemical processes in losing reaches during the non-flowing state (HI = 20).

### 4. Changes in the potential for biogeochemical processes along IRES-dominated fluvial networks

To date, our understanding of how the potential for reach biogeochemical processing changes along fluvial networks is still limited, especially when dealing with intermittency (von Schiller et al., 2017). We propose that the potential for reach biogeochemical processing changes along the fluvial network as a function of the geomorphological characteristics (Pinay et al., 2018). Following classical conceptualizations such as the erosion-transport-deposition concept (Leopold et al., 2020), we defined fluvial networks into three general hydrogeomorphological zones with differing predominant surface water–groundwater interactions: headwaters (which are mainly composed of losing reaches), mid-reaches (mainly gaining reaches) and flood-out and deltaic lowlands (mainly composed of gaining reaches) (see



**Fig. 5.** Synthesis of reach-scale predictions for the “Heat Index” (HI; calculated as the “sum” of relative process rates  $\times$  diversity of processes, see text, Section 3.4) within each biogeochemical processing zone: surface water (SW), hyporheic zone (HZ), fragmented pools (PO), emerged sediments (ES), and groundwater (GW). These processes were evaluated for two contrasted surface-groundwater flowpath interaction types (i.e., gaining and losing streams) and three hydrological states typically occurring in IRES along contraction and expansion phases (i.e., flowing, non-flow and dry). The area representing the different stream biogeochemical zones is based on our conceptual hydrological model (Fig. 2) and thus represents an idealized reach with homogenous sediment and little spatial variation in surface-subsurface flowpath length. Colour gradation in (c) and (f) represents the variability of sediment water saturation levels in dry reach sediments (see Fig. 2). Minimum HI (blue) = 0, maximum HI (red) = 60 (see text, Section 3.4). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Supplementary Methods S1 for further details). The occurrence and duration of each hydrological states (flowing, non-flowing and dry) can also change among these three hydromorphological zones. For instance, Boulton et al. (2017) reported flow during 25% of the year for headwater reaches, while lowland reaches flow for 75% of the year. Based on previous empirical studies of IRES, we estimated the relative duration of each hydrological state (flowing, non-flowing and dry) over the course of a year (Supplementary Methods S1 and Table S2). Note these scenarios represent an archetypal fluvial network, and this pattern may change depending on climate, geology, and river management practices (Costigan et al., 2017).

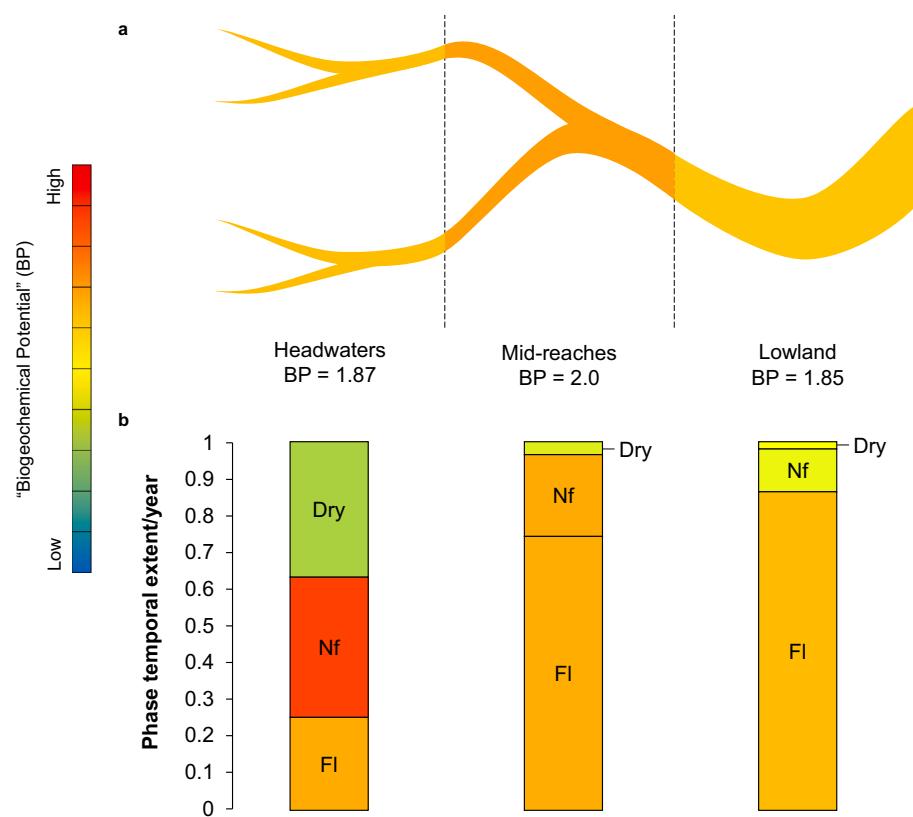
In order to explore changes in reach biogeochemical potential, we combined this simple categorization of the hydrogeomorphological zones with the HI for different biogeochemical processing zones as defined in Section 3.4 (Supplementary Methods S1 and Table S2). Rather than providing a full fluvial network analysis, the aim of this heuristic exercise was to use the information obtained in this review to explore where and when hot spots and hot moments for reach biogeochemical processing occur within IRES networks (*sensu* McClain et al., 2003). The identification of these ecosystem control points (Bernhardt et al., 2017) can help to better frame research questions and future experimental designs, predict longitudinal variation in nutrient concentrations for management, and aid in identifying key parameters that should be included in hydrological and biogeochemical models dealing with stream intermittency at the reach and fluvial network scale.

These back-of-the-envelope calculations suggest that, on average, the magnitude of annual biogeochemical potential is similar among the three hydrogeomorphological zones (Fig. 6a). However, this pattern results from the combination of relative different durations of each hydrological state and biogeochemical potential at each hydrogeomorphological zone. Therefore, both the magnitude of biogeochemical processing and the extent of each hydrological state are important for understanding the biogeochemical potential of a given reach within the fluvial network. Our heuristic exercise suggests that the

most biogeochemically active hydrological state would be non-flowing in headwaters and mid-reaches, but the flowing state in lowland areas (Fig. 6b). Headwaters and mid-reaches are cold biogeochemical spots during the dry state, and the potential for biogeochemical processes drops down in lowlands either in non-flowing or dry states. This information can be useful to better target future biogeochemical studies in IRES-dominated fluvial networks.

Note that the biogeochemical potential as described in here does not distinguish among specific processes, but highlights when processing rates might increase in relative terms. Yet, it should be emphasised that different biogeochemical processes might show a different level of significance in each state. Specific biogeochemical processes such as N<sub>2</sub>-fixation or denitrification might be of minor relevance for overall reach biogeochemistry during the flowing state, while they could become important during the non-flowing state when DO concentrations decrease. Therefore, the net result of all the biogeochemical processes occurring in a particular stream reach during a given hydrological state should be carefully examined in future studies. Depending on the biogeochemical process targeted, research should be oriented towards the respective key state, hydrogeomorphological zone, and biogeochemical processing compartment.

We acknowledge that our approach is a simplification of the “real” complex mosaic of surface water–groundwater interactions and associated biogeochemical processes that occur over time along the fluvial system, especially in IRES which are highly dynamic systems. Moreover, for the sake of simplicity, some aspects have been intentionally excluded from our approach. For instance, channel width, density and size of pools, and canopy cover. In fact, these scenarios are representative of an archetypal fluvial network, and this spatial variation may strongly change depending on climate, geology, and river management practices (Costigan et al., 2017). Additionally, information on drying duration is scarce and difficult to obtain (Zimmer et al., 2020). Yet, these are important aspects that should be considered if we are to model water and nutrient fluxes along IRES fluvial networks, for example expanding



**Fig. 6.** Predicted “Biogeochemical Potential” index (BP; determined as the product of the Heat Index and the relative area occupied by each compartment (see Supplementary information for details) averaged to different hydrogeomorphological zones within a simple, hypothetical IRES network. (a) Spatial variability along different hydrogeomorphological zones, with BP values representing differences in the yearly sum of process potential between zones. (b) Temporal variability in hydrological state, and BP of different hydrological states, within different hydrogeomorphological zones. Bar size indicates proportion of year spent within each hydrological state (flowing – Fl, non-flowing – Nf, Dry – Dr) within each hydrogeomorphological zone. BP values indicate differences in the sum of process potential between hydrological states, within each hydrogeomorphological zone. Minimum BP = 0, maximum BP = 3 (see text, Section 4 for details).

the work of Allen et al. (2020). Our approach integrates several hydrological states and spatial scales (within reach: biogeochemical processing zones, and within network: hydrogeomorphological zones), and thus implicitly acknowledges the scale dependence of hot spots and hot moments. (McClain et al., 2003).

## 5. Concluding remarks and future directions

### 5.1. Our conceptual framework shows potential for application across scales

Our conceptual framework predicts a wide range in potential for biogeochemical activity across hydrological states at the reach scale. Spatially, this variation tends to even out when viewed across different river network units (e.g., headwaters, mid-reaches, lowland) suggesting that the longitudinal continuum of geomorphological changes along an archetypical IRES network may be able to predict patterns in biogeochemical process rates (Vannote et al., 1980) Yet, our extension of the conceptual framework to a simple fluvial network showed much more variation across temporal than spatial scales. These patterns suggest that reaches within an IRES network likely act as individual processing zones (Thorp et al., 2006), although with the additional complexity of the extreme variability in hydrological connectivity of IRES. In this respect, our model also does not fully integrate the changing spatial scales at which biogeochemical processes occur as drying progresses, as the “telescope” of surface-groundwater flowpaths (*sensu* Fisher et al., 1998) contract and processes integrate into ever-more condensed spaces. These differing patterns illustrate the utility, and associated challenges, of our approach for predicting activity of biogeochemical processes in IRES, reflecting the difficulty of integrating IRES into river ecosystem conceptual models more generally (Allen et al., 2020). One notable limitation of the framework presented here is a balanced consideration of bi-directional hydrological change, i.e., both expansion and contraction dynamics, particularly in the context of rewetting events. Rewetting events may represent the highest potential for biogeochemical activity within IRES (i.e., a key “hot moment”) (Datry et al., 2018; Larned et al., 2010; von Schiller et al., 2019). However, biogeochemical responses to rewetting events might be much more variable in time than space (Boulton et al., 2017), and the magnitude of biogeochemical responses to rewetting events depends on the timing, intensity, and duration of previous conditions (e.g. non-flowing vs. dry) as well as intensity and duration of rainfall events (Arce et al., 2019; Arce et al., 2018; Datry et al., 2018; Gionchetta et al., 2020). Incorporating rewetting or network hydrological expansion dynamics (i.e., processes occurring from dry to flowing hydrological transitions) into our framework will likely present a fuller, although much more complex, approximation of biogeochemical potential across IRES.

On the other hand, our conceptual framework can serve to expand current fluvial network biogeochemical models such as INCA for Nitrogen and Carbon (Futter et al., 2007; Wade et al., 2002). The incorporation of intermittent dynamics into fluvial network or catchment models often remains difficult (von Schiller et al., 2017). These models incorporate terrestrial inputs into stream biogeochemistry, yet the implication of, for instance, network contraction or expansion transitions on dissolved C and N is not considered: no flow is considered as a static rather than dynamic hydrological phase. However, as widely recognised, this phase is far from inert. Flow resumption can have significant implications in the DOC and DIN dynamics of downstream reaches. Our conceptual framework can assist in the parametrization of the biogeochemistry during the non-flowing and dry phases, as well as in the duration of each phase at different points in the fluvial network. Since quantitative models parametrize terrestrial inputs of DOC and DIN by, for example, runoff considering different descriptors of storage, similar approaches could be used to incorporate upstream inputs upon flow resumption considering surface water–groundwater interactions as well as more local descriptors such as sediment properties.

### 5.2. Many climatic zones, regions, elements, and scales remain understudied

Several broad knowledge gaps in IRES biogeochemistry across surface water–groundwater flowpaths became apparent from our literature review. As defined in the Introduction, there are three major imbalances in the literature.

Firstly, publications are dominated by studies from arid and semi-arid regions. Furthermore, publications representing these regions were largely conducted in the USA, Mediterranean countries, or Australia. More than 80% of the world's land area remains unstudied (Leigh et al., 2016). Clearly, considerable opportunities to enhance research across climates and regions exist. An excellent place to begin is likely with identification of gaps along temperature and precipitation gradients which can drive freshwater ecological patterns more generally (Dodds et al., 2019); while warm drylands are well represented in the literature, exploring biogeochemical processes in the IRES of colder biomes such as arctic, alpine or boreal regions (Paillex et al., 2020; Tolonen et al., 2019), or in wetter regions such as the sub-tropics or tropics that nevertheless still contain many IRES (Sharma and Dutta, 2020; Warfe et al., 2011).

Secondly, most publications dealt with C and/or N cycling exclusively (although this may also be regarded as a general limitation of freshwater biogeochemistry). Even if C and N represent key elemental cycles, P dynamics are understudied, as are the dynamics of other key elements (e.g., S, Fe, Mn or Si). Questions also remain about the influence of regional or climatic or regional biases on our predictions of C and N process activity. For example, the role of downwelling in transporting labile dissolved OM to subsurface flowpaths may be greater in dryland than mesic, forested catchments due to the potential for high algal productivity in hot climates (Mulholland et al., 2001). Anaerobic process dynamics might instead dominate in organic-rich low-productivity forest streams, where humic substances could also act as fully regenerable TEAs (Lau et al., 2017). Similarly, sparse riparian vegetation (Bunn et al., 1999) and a predominance of above-ground vs. subsurface pathways (Martí et al., 2000) might generally restrict denitrification in dryland streams through a lack of soil OM and transport of nutrients. Most publications focusing on nutrient cycling in IRES also concentrate on ‘major’ processes such as nitrification and denitrification while neglecting those which occur at lower rates, e.g., ammonification and anaerobic ammonium oxidation (Pereira et al., 2017; van Niftrik and Jetten, 2012). While the more frequently measured processes do usually dominate fluxes overall, less frequently measured processes might characterize the finer-scale changes in redox potential and nutrient availability or stoichiometry that should characterize non-flowing and dry phases in IRES. Furthermore, the influence of surface-subsurface connectivity on micronutrients represents a large knowledge gap with many potentially important, unanswered questions. For example, whether essential algal micronutrients (e.g., S, Fe, Mn or Si) constrain the in-stream production of OM such that certain C or N processes are promoted over others (e.g., N<sub>2</sub>-fixation over ammonification).

Our predictions of N cycling processes are particularly affected by the underlying model assumptions. For example, anthropogenic sources can result in high concentrations of NO<sub>3</sub><sup>-</sup> in groundwater (Melita et al., 2019), which could then drive high denitrification rates in any zone connected to low-DO upwelling flowpaths (e.g. surface pools in the non-flowing phase). Our predictions also rely on NH<sub>4</sub><sup>+</sup> production via ammonification as a predictor of nitrification rates, but NH<sub>4</sub><sup>+</sup> can also be produced via other processes (e.g. leaching, desorption from sediments). Dissimilatory NO<sub>3</sub><sup>-</sup> reduction to NH<sub>4</sub><sup>+</sup> (DNRA) can be an additional source of NH<sub>4</sub><sup>+</sup> in pools with low redox potentials (Arce et al., 2015). Increasing sediment pore water content in emerged sediments can also drive decreased aerobic mineralization rates (Arce et al., 2018) and thus NH<sub>4</sub><sup>+</sup> supply, which potentially flows on to high variation in the effects of drying on sediment nitrification rates (Arce et al., 2018; Austin and

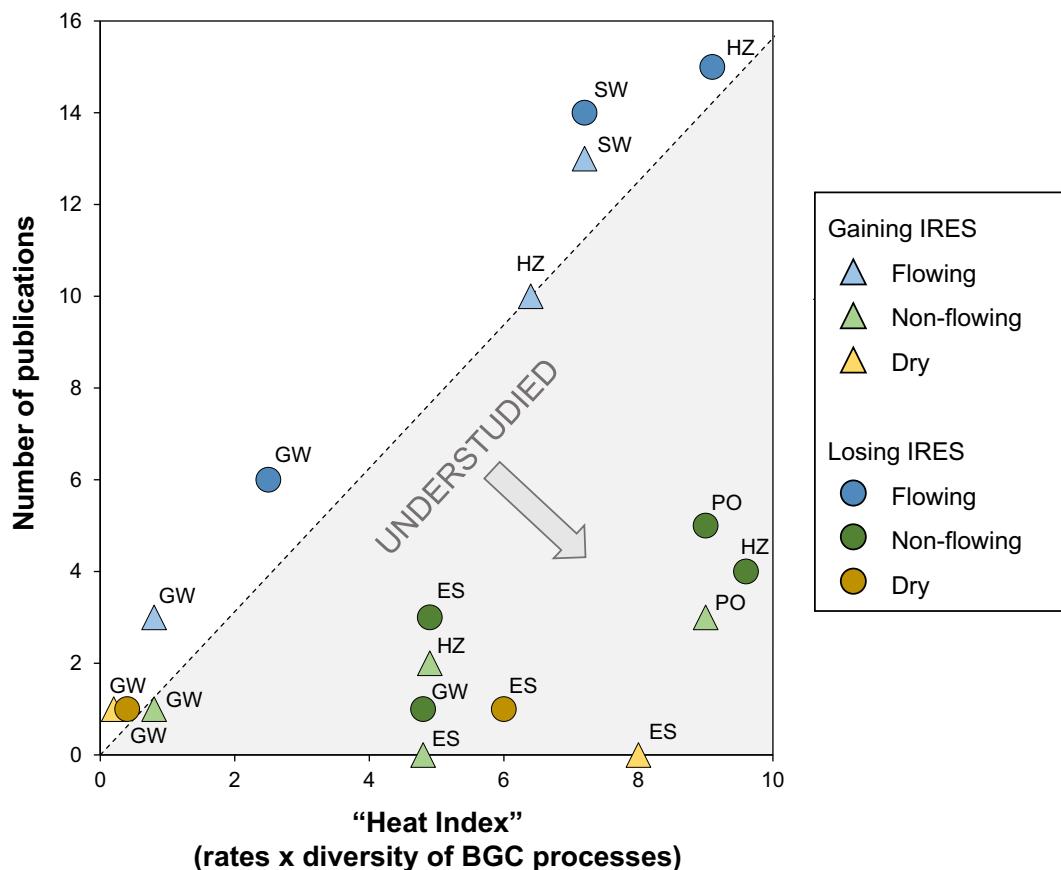
Strauss, 2011; Mitchell and Baldwin, 1999). We also assume that DO and substrate availability are the major limiting factors on N processing rates, but additional environmental limits on N processing and microbial community composition (e.g., pH; Sun et al., 2019) might both covary with DO or diverge due to local geochemical processes (e.g., carbonate weathering). Nitrogen processing can also be indirectly limited, for example when increased C availability promotes  $\text{NH}_4^+$  assimilation by heterotrophic bacteria which can outcompete nitrifiers (Starry et al., 2005). Presence of vegetation within the streambed can further modify ammonification within the exposed sediments of IRES, whereas our model assumes channels are unvegetated. On the one hand, dead plant biomass is mineralized slowly on dry channels (Datry et al., 2018). Alternatively, ammonification can locally increase via a combination of living and dead vegetation, as living plants create favorable conditions for ammonification due to active input of DO via their aerenchyma (Reverey et al., 2016). In this context, we recommend a focus on N processing rates during non-flowing and dry states as the first tests of our predictions and the effects of additional environmental gradients (e.g. land use, riparian or streambed vegetation cover) on potential deviations from them.

Thirdly, almost all studies were conducted at the reach scale. As with many other issues in river and stream ecology, a landscape perspective which explicitly considers the configuration of fluvial networks will likely inform and expand the predictions we are able to make (Benda et al., 2004; Datry et al., 2016). We expand on this point further below (Section 5.4).

### *5.3. Potential hotspots at the reach scale remain understudied*

Our model predicts zones within reaches where process rates should be higher relative to the surrounding matrix. Consequently, we can also identify several areas in which research might be intensified. To do so, we calculated the number of instances where studies in our initial literature review measured processes in each of our defined stream biogeochemical zones. In cases where gaining and losing conditions were not identified or mesocosm experiments were performed, we made approximations based on site and experiment descriptions. Only empirical and modelling studies were counted (i.e., review papers were not included). Subsequently, we compared the predicted “Heat Index” with the number of published studies for each stream biogeochemical processing zone in order to assess whether research efforts are focused on those stream compartments and hydrological states that may have the highest biogeochemical potential in IRES (Fig. 7).

Stream biogeochemical zones during the flowing state of IRES have been studied to the same relative extent as we have predicted the potential for specific processes (Fig. 7). These results reflect the initial, seminal work on surface water-groundwater exchanges in IRES conducted within Sycamore Creek, USA (Fisher et al., 2004). The Sycamore Creek studies represent a long-term ecological monitoring effort by multiple researchers that allowed identification of, and then particular focus on, biogeochemical hotspots during the flowing state (Fisher et al., 1998). In contrast, fewer studies have focused on the non-flowing state (Fig. 7). Further, non-flowing, gaining reaches (6 studies) have been studied less than losing non-flowing reaches (13 studies) (Fig. 7). This



**Fig. 7.** Comparison of predicted hotspots for biogeochemical processes within IRES reaches based on our conceptual model (“Heat Index” = “sum” of relative process rates  $\times$  diversity of processes, see text, Section 3.4) with the number of publications included in our literature review identified as focusing on particular hydrological states and stream biogeochemical processing zones: surface water (SW), hyporheic zone (HZ), fragmented pools (PO), emerged sediments (ES), and groundwater (GW). The dotted line connects the minimum (0,0) and maximum (9.6,15) values of the Heat Index (here, standardized by maximum to a range from 1-10) and publications, respectively. Points falling below the line (shaded area) therefore indicate potentially understudied state and zone combinations (i.e., comparatively fewer studies than other state/zone combinations with similar potential for biogeochemical activity).

likely reflects the rarity of gaining, non-flowing reaches, given that most IRES should be losing during non-flowing and dry states (Boulton et al., 2017). The dry state of IRES is the least well studied of all the hydrological stages with respect to surface-subsurface exchanges (Fig. 7), likely because surface water-groundwater interactions are difficult to identify when surface reaches are dry (see Section 3).

We can thus confidently recommend several areas at the reach scale in which future research could confirm, further inform, or build on our predictions. Non-flowing and dry states generally require more studies focusing on emerged sediments due to the effect of upwelling or parafloodplain flowpaths (Fig. 7). In the non-flowing state attention should focus on the hyporheic zone in losing reaches and pools in gaining reaches. All these areas should support abundant OM and TEAs as well as high redox gradients across fine spatial scales. Redox potentials might also vary dynamically with diurnal stratification and/or periods of intermittent anoxia. Consequently, all these biogeochemical zones should support similarly high rates and diversity of biogeochemical processes in IRES. For example, coupled methanogenesis and methane oxidation, or the complete range of N cycling processes, might occur across very fine spatial and temporal scales within these processing zones, rather than being segregated across longer flowpaths.

#### 5.4. The configuration of fluvial networks may alter biogeochemical potential within reaches

Biogeochemical processes depend on the products or by-products, i.e., the configuration of upstream reaches influences the rates and diversity of processes downstream. To fully upscale our predictions to networks, integration of other concepts such as patch dynamics or their IRES-specific extension, shifting habitat mosaics (Datry et al., 2016), is likely necessary. The network morphology is strongly linked to hydrological exchange, surface water-groundwater interactions and dissolved and particulate transport, for example by controlling the density and relative size of confluences (Ibisate et al., 2011). Yet our heuristic exercise shows that marked variation can be expected in nature. Our predictions strongly consider vertical connectivity, yet floodplain and terrestrial processes and linkages can dominate biogeochemical fluxes (Valett et al., 2005). Consideration of lateral expansion and contraction dynamics may improve our model similarly to, for example, how the River Continuum Concept was expanded by consideration of flood pulses (i.e., Flood Pulse Concept) (Junk et al., 1989). In IRES, these dynamics may be encapsulated by incorporation of temporally-explicit conceptual models such as the Wave Concept (Humphries et al., 2014) or the Pulse-Shunt concept (Raymond et al., 2016). In addition, anthropogenic impacts on fluvial networks (e.g., dams, eutrophication) markedly affect the spatial and temporal patterns of both surface water-groundwater interactions and water quality (Ward and Stanford, 1995). Overall, incorporating the spatial and temporal configuration of fluvial networks into our predictions is a logical next step.

#### 5.5. Final statement

Here we reviewed a large body of existing literature and key concepts to evaluate the potential activity and diversity of biogeochemical processes across surface water-groundwater hydrological states in IRES. We started from an evaluation of individual processes affecting key biogeochemical element cycles, then synthesized them into a predictive framework which identifies hot spots of process activity and diversity at the reach scale. We then used river network hydrogeomorphological theory to explore how the potential for biogeochemical processing could change among stream reaches when located in different zones of a river network, driven by different surface water-groundwater regimes. Finally, we compared the results derived from our conceptual predictive framework at the reach scale with previous research efforts, identified in our initial literature review, to provide an agenda of research priorities in the field. This review paper thus represents an attempt to unify

research and provides a path for future research on surface water-groundwater interactions and biogeochemical processes in IRES. We acknowledge that some of the steps we have chosen for our evaluations might represent a simplification of the “true” mosaic complexity of natural surface water-groundwater interactions and associated biogeochemical processes that occur through time and along IRES fluvial networks. However, the variation in our predictions over both space and time illustrates both the challenges and applicability of our exercise. This multiscale predictive and conceptual framework therefore establishes a solid base to guide further research questions and hypothesis testing in the field of IRES biogeochemistry.

#### Data availability

We show all data used in this manuscript in text, figures and tables.

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#### Author contributions

(following <https://dev.biologists.org/content/author-contributions>)

L.G. and A.S.: leading working group, conceptualization; methodology; data curation; formal analysis; validation; visualization; writing original draft; writing, review, and editing.

S.A., T.D., A.Z., V.P., R.B., HP.G., C.M.L.: leading working group, conceptualization; methodology; formal analysis; visualization; writing original draft; writing, review, and editing.

R.T., G.G., A.W., G.W., D.Z., M.A., D.vS., O.S., U.R., S.B.: conceptualization; writing, review, and editing.

#### Declaration of Competing Interest

The authors have no competing interests to declare.

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.earscirev.2021.103724>.

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