PERSPECTIVES*

Reconceptualizing the hyporheic zone for nonperennial rivers and streams

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Abstract: Nonperennial streams dominate global river networks and are increasing in occurrence across space and time. When surface flow ceases or the surface water dries, flow or moisture can be retained in the subsurface sediments of the hyporheic zone, supporting aquatic communities and ecosystem processes. However, hydrological and ecological definitions of the hyporheic zone have been developed in perennial rivers and emphasize the mixing of water and organisms from both the surface stream and groundwater. The adaptation of such definitions to include both humid and dry unsaturated conditions could promote characterization of how hydrological and biogeochemical variability shape ecological communities within nonperennial hyporheic zones, advancing our understanding of both ecosystem structure and function in these habitats. To conceptualize hyporheic zones for nonperennial streams, we review how water sources and surface and subsurface structure influence hydrological and physicochemical conditions. We consider the extent of this zone and how biogeochemistry and ecology might

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vary with surface states. We then link these components to the composition of nonperennial stream communities. Next, we examine literature to identify priorities for hydrological and ecological research exploring nonperennial hyporheic zones. Lastly, by integrating hydrology, biogeochemistry, and ecology, we recommend a multidisciplinary conceptualization of the nonperennial hyporheic zone as the porous subsurface streambed sediments that shift between lotic, lentic, humid, and dry conditions in space and time to support aquatic–terrestrial biodiversity. As river drying increases in extent because of global change, we call for holistic, interdisciplinary research across the terrestrial and aquatic sciences to apply this conceptualization to characterize hyporheic zone structure and function across the full spectrum of hydrological states.

Key words: aquatic–terrestrial transition zone, dry rivers, ecotone, hyporheic, intermittent river, intermittent stream, nonperennial stream, ephemeral stream, riverbed sediments, subsurface sediments, temporary river, temporary stream

Nonperennial streams and rivers are dynamic ecosystems in which surface flow ceases and most or all surface water is lost at some point in space and time (Datry et al. 2017; Fig. 1A–C). Nonperennial streams dominate global river networks (Messager et al. 2021), and both their occurrence and extent are increasing because of climate change, land-use change, and human demand for freshwater (Datry et al. 2014, Perkin et al. 2017, Allen et al. 2019). Natural stream drying generates and maintains habitat heterogeneity and extensive aquatic–terrestrial linkages that promote biodiversity and biogeochemical complexity (Datry et al. 2014), providing ecosystem goods and services (Acuña et al. 2014, Datry et al. 2018, Stubbington et al. 2020). Nonperennial stream reaches that are dry at the surface might retain subsurface water as vapor or liquid, the latter sometimes flowing. Thus, the subsurface environment can support abundant and diverse aquatic communities (Williams 1996, Febria et al. 2015) and ecological functions beneath both wet and dry channels (Burrows et al. 2017, Colls et al. 2019).

The hyporheic zone (HZ) allows hydrological and ecological connectivity to exist between surface and subsurface environments. The HZ term originated when Orghidan (1959) examined the fauna within a hole in a streambed, noting that the subsurface sediments provided an ecotone that mixed the physical (temperature, water velocity, light) and chemical (organic content, dissolved oxygen [DO], salinity) conditions of waters originating from both the surface and the groundwater. Importantly, Orghidan (1959) also recognized this zone as a transition from aquatic (saturated) to terrestrial (unsaturated) hydrological conditions. As the number of HZ-focused studies has grown over the past decade (Krause et al. 2011, Ward 2016, Woessner 2017), a range of hydrological and ecological conceptualizations and definitions have been developed for perennial streams (Krause et al. 2009, Cardenas 2015). Hydrological conceptualizations of the HZ typically refer to the mixing of surface water and groundwater and (usually implicitly) assume saturated conditions in the streambed (Gooseff et al. 2003, Runkel et al. 2003, Stonedahl et al. 2010, Boano et al. 2014). Similarly, biological definitions emphasize inhabitation by aquatic communities, including organisms that inhabit the surface stream and groundwater (Stanford et al. 1994, Boulton 2000). However, HZs in nonperennial streams can violate these restrictive conceptualizations because of their variable—and sometimes nonexistent—contributions of surface water and groundwater, resultant range of saturated to

Figure 1. Instream states vary between and within seasons in a winterbourne chalk stream in England, United Kingdom: a winter flowing phase (A), a summer low-flow phase (B), and a summer dry phase (C). Photographs supplied by the United Kingdom Environment Agency under the Open Government License version 3.0.

dry conditions, and corresponding range of resident taxa and biogeochemical conditions. Nonperennial stream HZs, thereby, encompass aquatic and terrestrial conditions, limiting applicability of methods and relevant metrics from either science across the full hydrograph. This cross-disciplinary narrow focus on saturated states and aquatic organisms, as well as independent and potentially divergent discipline-specific definitions of the HZ, fail to represent the structure and function of nonperennial HZs. Thus, interdisciplinary understanding of the biogeochemical, ecological, and hydrological roles of the HZ has been limited.

Here, we compare and synthesize existing HZ definitions and case studies from hydrological, biogeochemical, and ecological research in nonperennial streams to develop a more inclusive conceptualization of the HZ that focuses on its distinct role as dynamic subsurface habitat. First, we investigate how water sources, flowpath directions, and residence times drive the state, extent, and saturation conditions of the HZ (Fig. 2). Second, we synthesize how physicochemical conditions and microbially mediated biogeochemical processes may vary with the degree of saturation, water source, and flowpath length, thereby affecting habitat conditions as well as chemical and biological interactions with the surface stream. Third, we explore the effects of hydrological, physicochemical, and biogeochemical conditions on invertebrate and vertebrate communities and biodiversity in nonperennial HZs. We then conduct a literature review to identify gaps representing priorities for interdisciplinary nonperennial HZ research and propose methods to consistently investigate relationships between hydrology, biogeochemistry, and ecology in these widespread, understudied systems. Integrating insights from across disciplines, we propose a unified definition of the nonperennial HZ that explicitly recognizes these subsurface sediments as dynamic ecotones shifting between flowing, wet, and dry states that support aquatic–terrestrial biodiversity and, thus, ecosystem functioning.

HOW DO SURFACE WATER AND GROUNDWATER HYDROLOGY AFFECT THE STATE, EXTENT, AND SATURATION CONDITIONS OF THE HZ?

In both perennial and nonperennial streams, water movement into, through, and out of the HZ is controlled by the geomorphic and hydraulic properties of the streambed, its wider corridor (Ward and Packman 2019), and the hydraulic gradient between the stream and underlying groundwater (Winter 1999). Pressure gradients force surface water into and through the subsurface, where flowpaths are controlled by the geomorphic and hydrological characteristics of the stream (Boano et al. 2014, Zimmer and Lautz 2014). Hydrological studies of the HZ often focus on short (0.1–1 m) subsurface flowpaths caused by these pressure-induced interactions (Lewandowski et al. 2019). Depending on research objectives, hydrologists typically define the HZ based on surface water–groundwater interactions (e.g., Woessner 2017), transport of solutes, including nutrients (Triska et al. 1989, Bencala et al. 2011), or solely on surface water circulation (Ward 2016). The recent synthesis of Lewandowski et al. (2019) summarizes the breadth of current

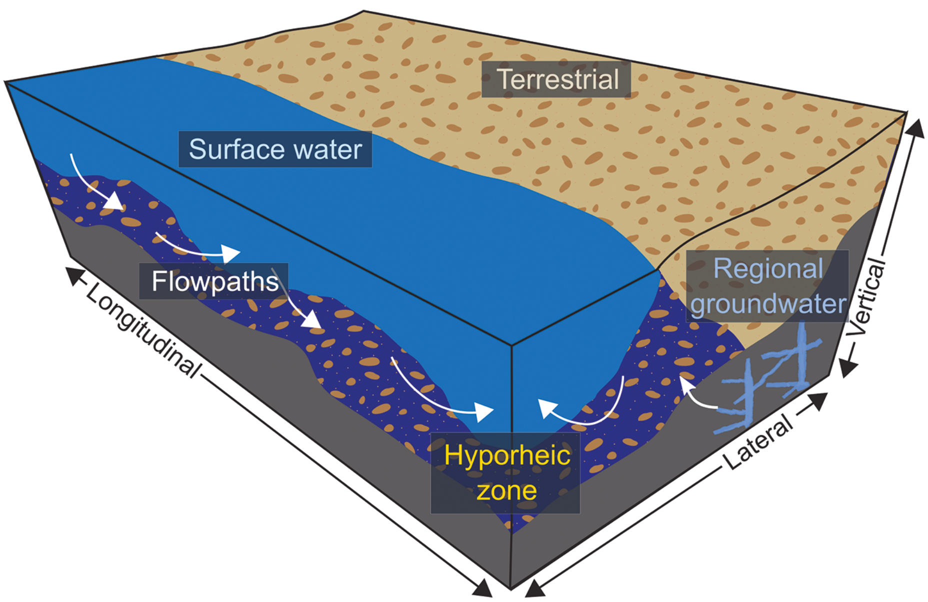

Figure 2. The hyporheic zone, or porous sediments beneath and surrounding the streambed, can contain contributions from various water sources (e.g., surface water, regional groundwater). All flowing water moves along flowpaths. Although depicted in blue, the hyporheic zone is not always saturated.

hydrological definitions by considering the HZ as a zone of saturated, porous streambed sediments in which at least 10% surface water and groundwater interact, or in which flowpaths begin and return to the surface. However, no hydrological definition of the HZ accommodates the dynamic, spatially and temporally discontinuous flow regimes of nonperennial streams.

In contrast to perennial stream HZs, the water content, or 3-dimensional spatial extent of water within interstitial spaces (i.e., saturation), can change profoundly during the hydrological cycle of a nonperennial stream. Nonperennial streams with connection between surface water and groundwater might disconnect seasonally, the HZ potentially comprising a 3-dimensional patchwork of both saturated and unsaturated sediments during dry seasons (Fig. 3E, F) (Fleckenstein et al. 2006). Perched aquifers will likely fill quickly and saturate during periods in which the stream is flowing but slowly desaturate because of infiltration and evapotranspiration when the surface streambed is dry (Villeneuve et al. 2015; Fig. 3C, D). Stream reaches with bypass (or parafluvial) flow, defined as water that circumvents channels via subsurface pathways, would likely have spatially variable saturation due to preferential pathways and surface states (Fig. 3A, B).

The lateral vs vertical extent of the HZ varies considerably, depending on geomorphic landscape characteristics (Stanford and Ward 1993). In gaining reaches (e.g., due to seasonally high groundwater levels or where a perched water table or other geological feature causes persistent inflow), shallow water tables may be more laterally extensive (Fleckenstein et al. 2006). Where floodwaters have overtopped stream banks, return flows to the stream might also occur for relatively long periods (McCallum and Shanafield 2016). Conversely, the HZ is laterally narrow when streambed hydraulic conductivity is high, floodplains are narrow or constricted by bedrock, there is strong groundwater inflow, or a vertically disconnected water table drives a strong losing hydraulic gradient (Wondzell and Swanson 1999, Kiel and Cardenas 2014).

As nonperennial streams shift between 3 surface states: flowing, ponded, and dry (Shanafield et al. 2021), hydrological, biogeochemical, and biological fluxes within the HZ vary depending on stream geology and geomorphology and the direction of hydrological exchange. When surface flow ceases, connected or isolated surface water pools and extensive dry conditions may occur in the surface channel, with concurrent changes in the magnitude, or even occurrence, of subsurface water fluxes. In gaining reaches, the contribution of groundwater can keep the HZ saturated and maintain hyporheic flowpaths during periods without surface flow or water, potentially resulting in persistent isolated pools. In contrast, in a losing stream, the streambed sediments can quickly become unsaturated because of the lack of connection between the stream and groundwater

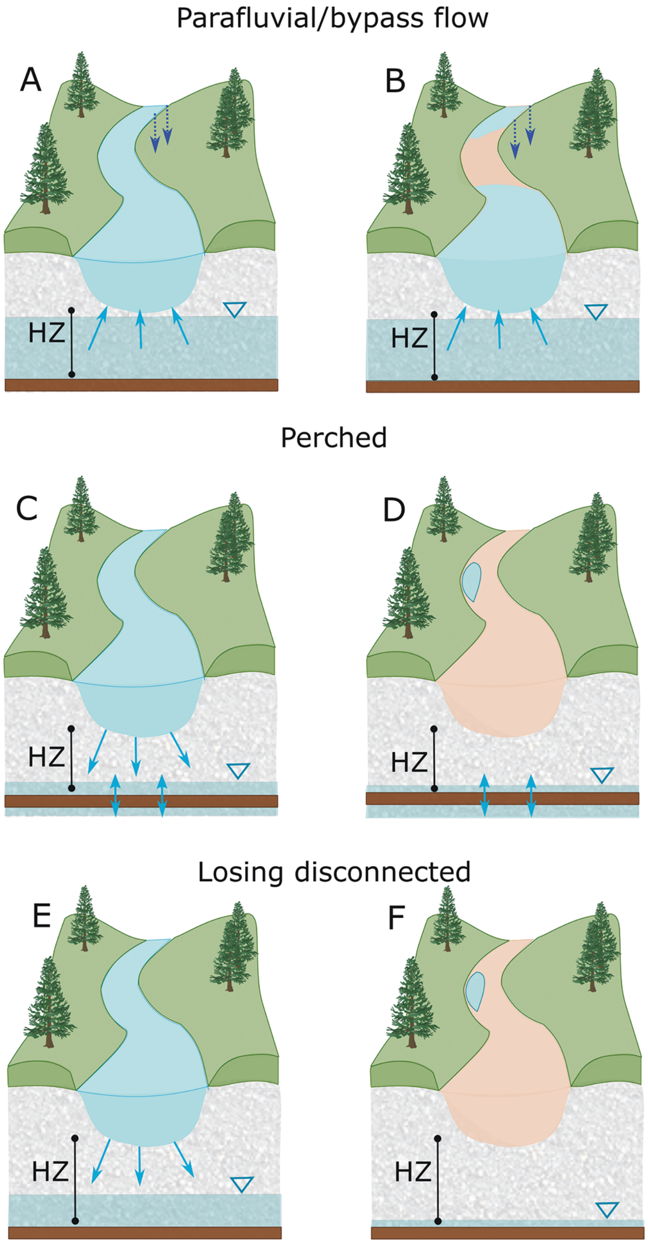

Figure 3. Three exemplary scenarios in which the hyporheic zone (HZ) of nonperennial streams deviates from traditional conceptualizations. In the parafluvial/bypass flow scenario, only a fraction of the HZ might comprise saturated sediments, which may provide refuge for hyporheic communities when the stream ceases to flow (A, B). Where groundwater tables are shallow, the subsurface may remain humid all year. In the perched scenario, surface water inputs to the HZ might be nonexistent after the stream stops flowing or dries, but interstitial water content could be sustained by water retained above the confining layer (represented by brown) (C, D). In the losing disconnected scenario, disconnected pools might be connected by hyporheic exchange (E, F).

(Falke et al. 2011; Fig. 3E, F), although shallow groundwater can influence surface and shallow subsurface flow even when the water table is not hydraulically connected to the stream (Quichimbo et al. 2020; Fig. 3C, D). Where bypass flow occurs, surface water may enter the streambed at an upstream location, exiting and reactivating surface flow at some downstream point, even if the surface sediments in between are dry (Fig. 3A, B) (Costigan et al. 2015, Busch et al. 2020). In each of these situations, water physicochemistry depends on mixing between surface water and groundwater, but literature on hyporheic hydrology rarely defines the term groundwater.

Different groundwater sources to hyporheic sediments have varying impacts on biogeochemical cycling. Regional groundwater that has been in long-term contact with subsurface geology will reflect the characteristic geochemistry of the parent material (Appelo and Postma 2004). In contrast, groundwater flowing through short within-catchment flowpaths (e.g., from subsurface flow during storms or snowmelt) may be compositionally comparable to surface water. For example, springs and seeps drive gaining conditions in some nonperennial stream systems, contributing water that reflects aquifer chemistry (Wroblicky et al. 1998). These differences in the source and age of water entering and exiting nonperennial stream channels influence hyporheic water physicochemistry, including temperature and solutes and, therefore, habitat for biota and potential for nutrient processing within the HZ (Brookfield et al. 2021). Differences in groundwater sources could be especially influential in nonperennial HZs, where surface water contributions could be completely absent at times.

Thus, hydrological conditions in the HZ are particularly dynamic in nonperennial streams, in which drivers of water presence or absence are complex in both time and space (Hammond et al. 2021). However, such variability is at odds with existing definitions of the HZ. If a surface stream is not flowing or is dry (with or without pools), classical hydrological definitions of surface–subsurface exchange flows are not met, but the subsurface sediments may remain hydrologically active. The requirement for the HZ to be saturated, by definition, thus excludes nonperennial HZs that comprise saturated or unsaturated subsurface sediments.

HOW DO SPATIAL AND TEMPORAL LINKAGES BETWEEN SURFACE WATER AND GROUNDWATER AFFECT BIOGEOCHEMISTRY AND MICROBIAL ECOLOGY?

Hydrology affects HZ biogeochemistry by controlling both water sources (surface water, shallow and deep groundwater) and how water travels through the sediment matrix and, thus, interacts with microbial communities. Just as conditions in nonperennial surface streams occur along a continuum encompassing flowing, lentic, and dry states, the HZ ranges between saturated (flowing or lentic), unsaturated, and dry conditions. In saturated flowing conditions, dominant microbial processes change along subsurface flowpaths (Febria et al. 2012, Mach et al. 2015). Transitions between states and source inputs influence sediment moisture, temperature, DO concentrations, redox conditions, specific conductance, and pH (Gómez-Gener et al. 2016). These physicochemical conditions shape and are shaped by microbial communities and associated biogeochemical processes (Sabater et al. 2016), thereby providing a mechanism by which hyporheic hydrology regulates the biogeochemistry of nonperennial streams.

Different water sources can affect physicochemical conditions and biogeochemical processes in the HZ. In some settings, upwelling groundwater can be more NO_3^- rich, P rich, and thermally stable than surface water (Boulton et al. 2010) and can reduce interstitial sedimentation. In contrast, downwelling surface water is often more oxygenated and richer in organic matter than groundwater (Boulton et al. 2010). Interactions between these different water sources can make the HZ an ecotone between oxidizing and reducing conditions (Krause et al. 2011). The characteristics of water from different sources also vary with flow conditions. Downwelling water can carry and deposit fine sediment and biomass that clogs interstices, especially during high-flow conditions, reducing hydraulic conductivity and creating hyporheic conditions favorable to anoxia (Brunke and Gonser 1997). During low surface flows, dense growth of heterotrophic and autotrophic biofilms can cover or infiltrate the HZ, also reducing hydrologic exchange (Stanley et al. 1997, Caruso et al. 2017).

Both the magnitude of hydrologic exchange and conditions in drying surface water can influence conditions in the HZ. As nonperennial streams transition from flowing to lentic, environmental conditions in any persisting surface pools can diverge after hydrological connectivity is lost (Verdonschot et al. 2015, Casas-Ruiz et al. 2016, Fig. 4A, B). High water-residence times in these pools, combined with high temperatures, can fuel gross primary production (GPP) and ecosystem respiration (ER). If light availability is high, GPP : ER ratios can also be high (Casas-Ruiz et al. 2016), and, thus, any water infiltrating the HZ will have higher DO concentrations. In contrast, high dissolved organic C concentrations, such as from leaf leachates and soils (Chafiq et al. 1999, Siebers et al. 2016), light limitation (Casas-Ruiz et al. 2016, Hensley et al. 2019, Hosen et al. 2019), or high decomposer activity (Abril et al. 2016), can cause low GPP : ER ratios in pools as heterotrophic processes (e.g., ammonification; Skoulikidis et al. 2017) dominate and gradually reduce DO concentrations (Stanley et al. 1997, von Schiller et al. 2011).

In both perennial and nonperennial streams, inputs of DO, organic matter, and other terminal electron acceptors (e.g., NO_3^- and SO_4^{2-}) act within the physical structure

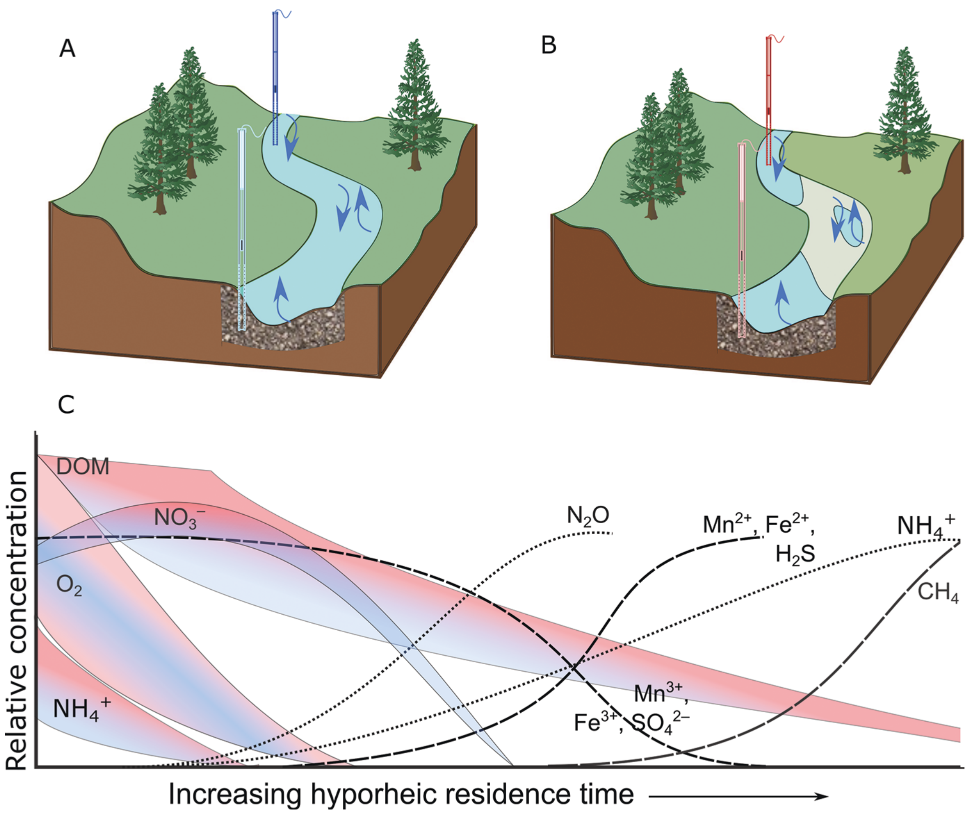

Figure 4. Along flowpaths, the concentrations of various terminal electron acceptors used in respiration are depleted as concentrations of reduced byproducts increase (modified from Kehew 2001 and Schlesinger and Bernhardt 2013), as might occur along a subsurface flowpath from the upstream to downstream piezometers in either connected (A) or disconnected (B) streams. In panel A, surface water is clearly connected, as are subsurface flowpaths. When surface water is disconnected (B), subsurface flowpaths might persist with these concomitant changes in constituents. However, the concentrations of constituents entering the hyporheic zone might differ (blue during the most connected periods, ranging to red as the stream begins to dry; C). Infiltrating water from disconnected pools might have higher NH_4^+ concentrations, more variation in dissolved oxygen concentrations, higher dissolved organic matter, and higher NO_3^-, all of which is depleted at varying rates over time in the hyporheic zone. As the hyporheic zone becomes disconnected from surface water, it is possible that water chemistry will more closely resemble water with a longer residence time.

provided by sediment, affecting interstitial physicochemistry, microbial activity, and biogeochemical processes along hyporheic flowpaths (Gilbert et al. 1990, Vervier et al. 1992, Hancock et al. 2005, Claret and Boulton 2008, Zlatanović et al. 2018, Fig. 4C). Nonperennial streams can have especially variable subsurface flowpath lengths and inputs of organic matter and nutrients. For example, in nonperennial streams with bypass flow, water penetrates further into the subsurface as surface flow increases, creating longer flowpaths (Vázquez et al. 2007). Longer flowpaths in losing reaches can have higher mineralization of dissolved organic matter, leading to more reduced but bioavailable forms of inorganic N (i.e., NH_4^+), or potentially storing infiltrated C and N as microbial biomass and dissolved gases (Newcomer et al. 2018). As demonstrated in gravel-bed floodplains, long flowpaths that contribute to nonperennial spring flow can have extremely low dissolved organic C concentrations, low DO concentrations, chemoautotrophy (e.g., hydrogenotrophic methanogenesis, nitrification), and a tendency toward reducing reactions (e.g., Fe reduction, SO_4^{2-} reduction, and methanogenesis) (Helton et al. 2015, DelVecchia et al. 2016). When these substrates encounter oxidizing conditions caused by surface water, they can enable heterotrophic and chemotrophic processes (Datry and Larned 2008).

As the surface channel dries, photosynthesis and substrate delivery to the HZ diminishes (Colls et al. 2019), altering the quality and quantity of C inputs to underlying HZs. Hyporheic heterotrophs, thus, tend to shift to less labile C sources (Granados et al. 2020). As the HZ itself dries, reduced substrate diffusion and microbial motility can directly inhibit microbial activity (Humphries and Baldwin 2003). However, if subsurface interstices retain moisture, organic matter decomposition and mineralization can continue (Solagaistua et al. 2016, von Schiller et al. 2017) and can even exceed surface rates if conditions are more favorable for biotic processes (Burrows et al. 2017, Arias-Real et al. 2020).

The changes in biogeochemical processes that occur along flowpaths are also mediated by moisture when water is not flowing. For example, N cycling varies depending on whether 1) oxygenated humid conditions facilitate net nitrification, 2) deoxygenated humid conditions limit ammonification and nitrification but favor denitrification, or 3) dry conditions limit each of these processes (Tzoraki et al. 2007, Gómez et al. 2012, Sabater et al. 2016). Drying also has strong but unpredictable effects on sediment affinity for P. P mobility typically increases as redox conditions become more negative (Ann et al. 1999), but the presence of metals, such as Fe and Al, can modulate this process (Peng et al. 2007). As a result, stream drying can either increase or reduce sediment binding (Sabater et al. 2016, von Schiller et al. 2017). Thus, depending on local conditions, drying and rewetting processes can have contrasting outcomes for microbial communities and biogeochemical processes.

When the HZ retains some moisture, it can harbor desiccation-tolerant microbial taxa (Gionchetta et al. 2019). However, drying and rewetting also create strong selective pressures that eliminate some taxa (Zeglin et al. 2011, Febria et al. 2012, Timoner et al. 2014). The duration and severity of dry phases are master variables controlling nonperennial stream microbial communities (Sabater et al. 2016, Colls et al. 2019). If the HZ retains a connection to groundwater during dry periods, hyporheic sediments can remain saturated or humid, enabling the survival of many microbial taxa (Gionchetta et al. 2019). Humidity, redox conditions, and microbial habitat are controlled not only by water sources but by organic matter content and sediment structure, which are, thus, also key determinants of microbial community composition (Zlatanović et al. 2018, Arias-Real et al. 2020).

The hydrological and biogeochemical controls on microbial communities in nonperennial HZs are relatively well established, but the relative importance of different factors and how they interact to control community composition is less clear. Specifically, it remains unclear whether local environmental sorting or dispersal and biotic interactions (e.g., competition) drive community composition. Benthic community composition in nonperennial streams is primarily controlled by redox conditions (Gionchetta et al. 2020), and both the community composition and habitat conditions present before an HZ dries can influence respiration rates that affect dry-phase conditions and communities (Duarte et al. 2017, Newcomer et al. 2018), exemplifying the potential for environmental sorting. Drying alters dispersal patterns by changing the water sources supplying the HZ (Fazi et al. 2013). As a dry phase progresses, surface water inputs decrease, whereas deeper groundwater inputs can remain steady, decrease, or increase, changing the number and taxonomic composition of microbes that passively disperse to hyporheic sediments (Saup et al. 2019). Hydrological conditions likely modulate whether sorting or dispersal mechanisms dominate, with dispersal having more influence during high-flow conditions and environmental sorting and biotic interactions becoming more important as water-residence times increase in drier conditions (Datry et al. 2016).

The biogeochemical transformations that occur during dry phases are likely to affect community recovery following subsequent rewetting. Microbial communities that survive in humid conditions in the HZ can rapidly recover in the surface when streams rewet (Timoner et al. 2020). This recovery can be enhanced by nutrients liberated from microbial cells that lysed during dry phases because of environmental stress (Birch and Friend 1956, Baldwin and Mitchell 2000, Leung et al. 2020). Nutrient mineralization in the HZ can thereby contribute to GPP and ER in the surface sediments of gaining reaches during rewetting events that re-establish vertical hydrological connectivity (Sabater et al. 2016). In addition, both discontinuous flow and long flowpaths create reducing subsurface environments, so flow resumptions that drive hyporheic contributions to the well-oxygenated surface can create potential control points for autotrophic production (Burrows et al. 2020), heterotrophy, chemotrophy, and microbial dispersal (Bernhardt et al. 2017, von Schiller et al. 2019). The contribution of reduced hyporheic substrates to surface water could affect ecological and biogeochemical processes that affect energy sources, contribute to overall ecosystem function, and potentially alter the quality of downstream and laterally connected waters (Brookfield et al. 2021).

HOW DO HYDROLOGY AND BIOGEOCHEMISTRY AFFECT THE ROLE OF THE HZ IN MAINTAINING BIODIVERSITY IN NONPERENNIAL STREAMS?

Biological definitions of the HZ typically describe the organisms that inhabit it based primarily on our understanding of aquatic invertebrate assemblages. Some such definitions are broad, with Stanford and Ward (1988) considering the HZ as those sediments "penetrated by riverine animals" (p. 64) and Lewandowski et al. (2019) recognizing the subsurface sediments as supporting a "characteristic hyporheic community" (p. 3). Others emphasize the HZ as inhabited by both temporary residents, which mainly live in either the benthic zone or groundwater, and permanent hyporheic specialists (Williams and Hynes 1974, Boulton 2000). All such ecological conceptualizations mirror hydrological definitions in both their ecotonal aspects (i.e., mixing of water or organisms from the surface stream and groundwater; Brunke and Gonser 1999) and their explicit or implicit consideration of only aquatic aspects, here, biota and, specifically, invertebrates. In addition, a separate ecological definition recognizing terrestrial inhabitants has been developed for the alluvial mesovoid shallow substratum beneath dryland nonperennial streams, which flow for a few days each year (Ortuño et al. 2013). Such terrestrial organisms can make significant contributions to biodiversity deep within riverine sediments (Langhans and Tockner 2014). These independent aquatic and terrestrial conceptualizations are in contrast with Orghidan's (1959, 2010) original recognition that hyporheic conditions transition from saturated (aquatic) to unsaturated (terrestrial) states at ecotone boundaries in perennial streams—and in nonperennial systems, spatial and temporal transitions between wet and dry states greatly increase the extent of ecotonal habitats (Stubbington et al. 2017).

During flowing phases in both perennial and nonperennial streams, upwelling and downwelling zones can support distinct aquatic communities (Datry et al. 2007). Where DO concentrations are relatively high and trophic resources (e.g., particulate and dissolved organic matter) are relatively abundant, such as in downwelling water, many organisms are generalists that primarily inhabit the surface stream and its benthic sediments (Williams and Hynes 1974). Predominantly benthic species include some that use the HZ as a nursery that protects juveniles from stressors, including predation and displacement by flowing water (Giberson and Hall 1988, Feral et al. 2005). In contrast, lower availability of oxygen and trophic resources, as typically characterizes upwelling groundwater, can reduce densities of generalist predators and, thus, enable the persistence of communities dominated by hyporheic and groundwater specialists (Datry et al. 2007), including amphipods, isopods, and a diverse meiofauna (Boulton 2000, Hakenkamp and Palmer 2000). Community composition can also change with depth below the sediment surface, with a shift away from the dominance of benthic taxa as the influence of surface water and, thus, habitat suitability for these organisms decreases.

When nonperennial streamflow ceases, the shift from lotic to lentic conditions can cause pronounced changes in benthic communities (Bonada et al. 2006, Hill and Milner 2018, Buffagni 2021). Hydrological changes are subdued in the subsurface, where flowing-phase velocities are typically much lower than in the surface stream, and sediment moisture content may remain at or near saturation (Brunke and Gonser 1997; Fig. 5). Hyporheic communities in nonperennial streams have mainly been characterized during flowing phases (Wood et al. 2010, Datry 2012), and biotic responses to subsurface flow cessation have yet to be characterized. As surface water levels decline, mobile organisms that remain in the stream become concentrated within shrinking submerged habitat areas, triggering vertical migrations into the subsurface by organisms seeking refuge from intensifying biotic interactions and causing increased hyporheic densities of primarily benthic organisms (Stubbington et al. 2011, Pařil et al. 2019). If surface water is lost, hyporheic richness can be further enhanced by an influx of benthic taxa seeking refuge from desiccation (Stanley et al. 1994, Clinton et al. 1996). As interstices transition to unsaturated conditions, such taxonomic gains are offset by the loss of desiccation-sensitive organisms. However, whereas benthic community richness nearly always declines with intermittence (Datry et al. 2014, Soria et al. 2017), the number of taxa present in nonperennial HZs may remain stable

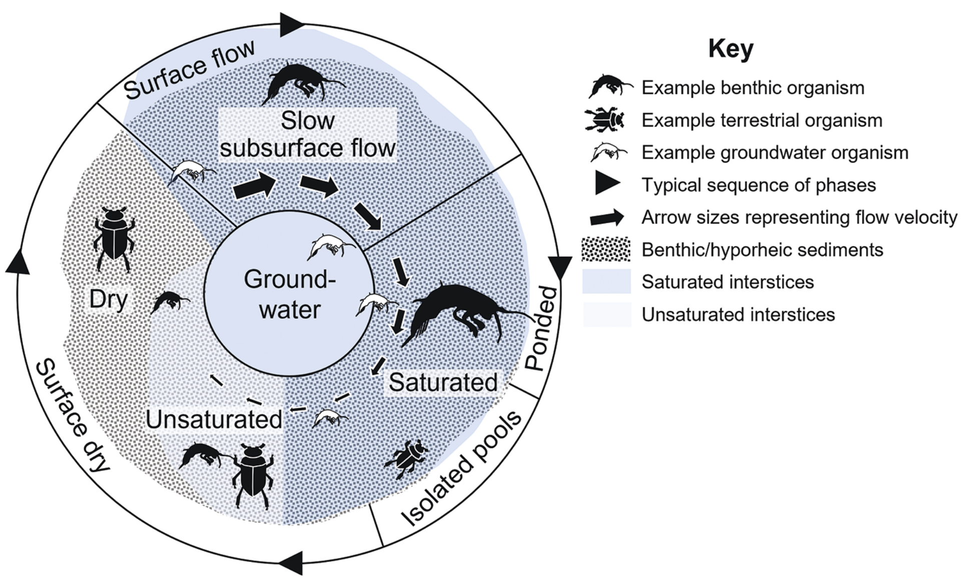

Figure 5. Biotic responses to temporal variability in hydrological conditions in the surface stream and benthic and subsurface sediments of nonperennial streams during a typical annual cycle. In a connected hyporheic zone, sediments can experience flowing phases, remain saturated during surface ponded and dry phases, gradually change from saturated to unsaturated then dry conditions after surface drying, then quickly rewet before surface flow resumes. Variability is less pronounced in the subsurface sediments compared with the surface stream and benthic sediments because flow velocities are slower during flowing phases, and interstices remain more humid after free water is lost. Benthic, groundwater, and terrestrial organisms respond to changing conditions differently. Variation in symbol size is proportional to expected densities of the represented organism.

across a gradient of drying duration (Stubbington et al. 2019).

As the benthic zone dries, hyporheic sediments that remain saturated can provide a refuge for aquatic invertebrates, including early instar insects, crustaceans and meiofauna (Clinton et al. 1996, Vander Vorste et al. 2016), as explored particularly through testing of the hyporheic refuge hypothesis (Palmer et al. 1992, Stubbington 2012). Vertebrates, including juvenile lamprey (Rodríguez-Lozano et al. 2019), salamanders (Feral et al. 2005), and small adult fish (Stegman and Minckley 1959, Kawanishi et al. 2013), can also persist in saturated interstices. However, when water levels continue to fall, and where the diminishing dimensions of interstitial pathways prevent vertical migrants from accessing deeper, saturated subsurface sediments, organisms become stranded in humid or dry interstices. Here, sediment characteristics, such as organic matter content, and external influences, including shading and rainfall inputs, can maintain interstitial humidity, allowing subsurface interstices to remain a refuge for aquatic invertebrate and vertebrate life stages with some degree of desiccation tolerance. The abundance and richness of these active or dormant forms relates positively to the moisture content within hyporheic interstices (Stubbington et al. 2009, Datry 2012, Stubbington and Datry 2013).

Desiccation-tolerant aquatic inhabitants of humid hyporheic sediments include both resistant generalists and nonperennial stream specialists. For example, amphipods, including specialist stygobites, can persist for weeks in humid interstices (Gilbert et al. 2018). In addition, Jacobi and Cary (1996) recorded dormant juveniles of 10 stonefly species in the unsaturated subsurface sediments of seasonally nonperennial headwater streams, and Bogan (2017) inferred the dry-phase persistence of the specialist stonefly *Mesocapnia arizonensis* in arid streams with flowing phases as short as 3 mo. Among non-insects, some adult crayfish (DiStefano et al. 2009), frogs (Jared et al. 2020), salamanders, and fish (Secor and Lignot 2010) burrow into deeper, more humid sediments during seasonal dry phases, persisting in either active or dormant states (Secor and Lignot 2010). In addition, annual killifish routinely survive dry phases as dormant eggs within the sediments of ephemeral arid-zone waterbodies (Furness 2016).

As species-specific thresholds are surpassed for core abiotic influences on survival (e.g., water, DO, trophic resources, and temperature), drying sediments can change from a refuge to a graveyard for aquatic organisms (Pařil et al. 2019) and, simultaneously, become a new habitat available for colonization by terrestrial biota. However, whereas recent research has recognized the terrestrial invertebrate biodiversity on dry streambeds (Corti and Datry 2016, Stubbington et al. 2019, Bunting et al. 2021) and within occasionally inundated dryland streambeds (Ortuño et al. 2013), very few studies have explored the terrestrial communities that move into subsurface sediments in response to declining water levels. Such studies report aquatic–terrestrial assemblages dominated by taxa ranging from fully aquatic (e.g., mites, fly larvae; Bartoszek 2001), semiaquatic (springtails; Langhans and Tockner 2014), and terrestrial taxa that tolerate inundation (rove beetles; Dieterich 1996).

We also know little about how hyporheic communities respond to flow resumption, with most research considering upward migration of benthic organisms from the subsurface back to the surface stream (Brooks and Boulton 1991, Vander Vorste et al. 2016) rather than characterizing how hyporheic communities colonize and assemble. Assembly may follow similar trajectories to those documented after other disturbances, with faster colonization by benthic compared with groundwater taxa reflecting adaptations that facilitate dispersal in highly dynamic environments (Hancock 2006). In addition, stygobites can colonize quickly where upwelling water passively transports them into groundwater-fed streambeds (Stubbington et al. 2009). Further research is needed to better understand the vertical extent of biodiversity within nonperennial streams, encompassing organisms across the full breadth of environmental preferences from aquatic to terrestrial.

HOW DOES EXISTING NONPERENNIAL STREAM RESEARCH CONSIDER THE HZ?

Above, we present evidence that flowing, ponded, and dry states in nonperennial HZs each have unique, linked hydrological, biogeochemical, and ecological characteristics that interact to contribute to ecosystem processes. This evidence demonstrates that our understanding of these processes—and a broader ecosystem-scale understanding of spatial and temporal variability in HZ structure and function—has been limited by discipline-specific understanding of the HZ, constraining physical and conceptual research. To comprehensively document both disciplinary and cross-discipline biases and limitations, we compiled and examined literature published between 1959 (i.e., the year of Orghidan's seminal paper) and January 2020. We searched for studies of any nonperennial stream (intermittent, ephemeral, temporary) describing sampling of biotic communities in the HZ in any nonperennial stream during a period without surface flow (Table S1). We recorded conditions in which samples were collected and any associated environmental data (e.g., temperature, DO).

We identified 43 primary journal articles published between 1966 and 2020 (Table S1), with most covering a localized spatial scale and with 49 and 33% conducted in North America and Europe, respectively (Fig. S1C). Most studies were conducted in a cool, wet temperate climatic zone (46%), followed by Mediterranean (24%) and arid zones (24%). Two research gaps in particular reflected the disconnect between discipline-specific conceptualizations of the HZ: 1) few studies explicitly included sampling during the unsaturated, dry, or rewetting phases of the HZ; and 2) only 40% examined how physicochemistry (which, as discussed, varies with hydrology) affects biota during saturated and unsaturated phases. Only a single study (Boulton et al. 1992) characterized the complete range of hydrological conditions within the HZ (high to low infiltration, humid to dry sediments), and only 23% sampled throughout the period in which the surface stream was inundated until dry (Fig. S1D, E). For example, 19% of studies sampled only while water was infiltrating into the HZ, whereas 15% sampled while the HZ had low moisture (Fig. S1E). Only 14% of studies reported sediment moisture content, and most samples were small water volumes collected at a depth of 20 to 50 cm (Fig. S1A, B), regardless of the total extent of the HZ, which was rarely reported. Water characteristics and biota were concurrently measured in 40% of studies, limiting inference of how physicochemical changes, influenced by hydrology, drive biotic patterns. These research gaps reflect both difficulties in sampling the biotic and abiotic conditions within the HZ—especially during unsaturated and dry conditions—and, potentially, a lack of consensus on the relevant parameters to address different ecological research questions in nonperennial streams. It is precisely these gaps regarding connections between the hydrology, biogeochemistry, and biology of the full spatial and temporal extent of the HZ that require further study.

DEFINING AND STANDARDIZING INTERDISCIPLINARY NONPERENNIAL HZ RESEARCH

As nonperennial HZs increase in both spatial and temporal extent because of global change, we call for a return to ideas at the heart of the original conceptualization of the HZ (Orghidan 1959), namely its inclusion of conditions from wet to dry and its consequent support of organisms from aquatic to terrestrial. From its 1st use (Orghidan 1959) and throughout the intervening decades, HZ research has been broad enough to pave the way for its formal extension to include the full range of hydrological, ecological, and biogeochemical conditions experienced in nonperennial systems. Accordingly, we propose a more inclusive definition of nonperennial HZs as the porous subsurface sediments of nonperennial streams, which sometimes directly exchange water, energy, and organisms with adjacent ecosystem components, including the surface channel. This broad definition reflects HZ fluctuations between saturated (lotic or lentic) and unsaturated (humid to dry) interstitial conditions that support organisms with aquatic to terrestrial habitat preferences. Our definition does not constrain the HZ within precise upper or lower boundaries. Instead, during dry phases a gradual decrease in interstitial humidity typically characterizes the vertical transition from benthic to hyporheic sediments. We call for interdisciplinary research spanning the breadth of hydrological conditions experienced within nonperennial HZs, encompassing how biogeochemical processes and ecological communities vary within and between saturated, unsaturated, and dry states.

To promote interdisciplinarity, measurement of a few crucial variables could be standardized across nonperennial HZ research to enable inference of how hydrology influences biogeochemical conditions and ecological communities. Fundamentally, interstitial water requires characterization, ideally including quantification of water movement during saturated conditions and of sediment moisture content during unsaturated states. Although hyporheic water sources and flow directions are difficult to measure, La Montagne et al. (2014) suggest measuring the water level in the stream, adjacent bank, and streambed to determine if the stream is connected to groundwater and to estimate hydraulic gradients that indicate the direction of flow. Simple temperature measurements can be used to trace water movement through the streambed (Constantz 2008), although this method is more complicated when considering lateral fluxes (Shanafield et al. 2010, Xie and Batlle-Aguilar 2017). Automated seepage meters (Solomon et al. 2020) and 3-dimensional sensors (Banks et al. 2018) can also enable rapid capture of hyporheic fluxes at multiple locations within a streambed. During periods in which the stream is not flowing, sediment profiles can be collected (or tensiometers installed in an unsaturated streambed) and analyzed in the laboratory to estimate actual moisture content within the streambed. Geophysical methods, such as electrical resistance tomography, in which low frequency currents are transferred between electrodes and compared, can indicate sediment moisture content, clay content, temperature, and salinity (Ulrich et al. 2015). These methods can be used to characterize whether a stream is connected, disconnected, or in transition and can thereby document both spatial and temporal variation. Lastly, modeling approaches facilitate prediction of the effects of varying hydraulic gradient on physicochemical and biological properties of the HZ (Brunner et al. 2017).

Across hydrological states, DO concentrations and temperature represent key determinants of community composition and, thus, priorities for measurement, ideally by logging data from pre-installed in-situ probes at regular spatial and temporal intervals (e.g., Evans and Petts 1997). Where unsaturated conditions prevent the use of standard meters for in-situ DO measurement, pumping hyporheic water from appropriate depths during both lotic and lentic saturated phases could facilitate collection of sufficiently accurate data to enable comparison among sites and times (Stubbington et al. 2016). Furthermore, sampling campaigns documenting these core abiotic variables should aim to represent the spatial and temporal heterogeneity driven by interactions between sediment types and water sources by sampling across and within areas with contrasting sediment types and directions/strengths of hydrological exchange. Global-scale studies implemented by interdisciplinary research groups using common standardized protocols have recently generated sufficient data to significantly advance understanding of ecosystem functioning in nonperennial surface streams (e.g., von Schiller et al. 2019), and comparable initiatives could extend into the subsurface.

We also suggest that measurements consider the full spatial and temporal extent of the HZ in its hydrogeological context. The HZ includes the sediments directly beneath the stream and can also extend laterally and stretch to confining layers (Fig. 1A–C). The HZ can also be several meters deep, and if only the shallow HZ is sampled, organisms migrating downward to remain in the wettest available conditions could be missed. Furthermore, physicochemical and biogeochemical conditions that vary, for example, with depth, sediment heterogeneity, and position along a flowpath, could go uncharacterized.

Nonperennial streams may dominate global river networks and are increasing in extent in both space and time. Understanding the linkages between their hydrology, biogeochemistry, and biology is, thus, crucial to inform management strategies that support the structure, function, and integrity of these dynamic ecosystems, including their extensive but often overlooked subsurface components. Our relatively advanced understanding of nonperennial HZs during their saturated and, in particular, their flowing phases covers a subset of their total function. Dry HZs are ecologically active ecosystem components that require greater recognition within nonperennial stream research. We call for research that applies the holistic, interdisciplinary conceptualization of nonperennial HZs developed herein to advance our understanding of these sometimes extensive hidden components of dynamic stream ecosystems as they adapt to global change.

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