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Biogeochemical and community ecology responses to the wetting of non-perennial streams

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Transitions between dry and wet hydrologic states are the defining characteristic of non-perennial rivers and streams, which constitute the majority of the global river network. Although past work has focused on stream drying characteristics, there has been less focus on how hydrology, ecology and biogeochemistry respond and interact during stream wetting. Wetting mechanisms are highly variable and can range from dramatic floods and debris flows to gradual saturation by upwelling groundwater. This variation in wetting affects ecological and biogeochemical functions, including nutrient processing, sediment transport and the assembly of biotic communities. Here we synthesize evidence describing the hydrological mechanisms underpinning different types of wetting regimes, the associated biogeochemical and organismal responses, and the potential scientific and management implications for downstream ecosystems. This combined multidisciplinary understanding of wetting dynamics in non-perennial streams will be key to predicting and managing for the effects of climate change on non-perennial ecosystems.

Non-perennial rivers and streams are defined by cycles between wet and dry states[1]. Non-perennial streams dominate global river networks[2] and are highly variable in terms of their streamflow generation mechanisms and flow regimes[3]. Each non-perennial stream state (for example, wetting, drying, flowing and dry) is associated with specific biotic communities[4], environmental conditions[5] and ecosystem service provision[6]. Wetting and drying transitions occur across spatial and temporal scales ranging from individual stream reaches[7] to regional drying across entire watersheds[8]. Each state and transition vary in frequency, duration, timing, predictability, magnitude and rate of change[9], highlighting the need to better understand the drivers and implications of transitions between dry and wet states in non-perennial streams[10,11]. Previous contributions have quantified stream drying[12] and the resulting effects on biogeochemistry[5,13], the ecology of stream communities, including microorganisms, invertebrates and fish[14,15], and associated management strategies[16]. However, few studies have focused on the hydrologic state transition from dry to wet in non-perennial streams. Given that all non-perennial rivers and streams transition from dry to wet, there is a critical need to understand the physical and ecological processes that occur during wetting transitions.

Mechanisms of stream wetting vary considerably among streams. Wetting can be rapid and dramatic, in the form of increasing discharge from upstream-sourced debris flows, or near-imperceptibly slow, from saturation as the water table rises into a dry channel[17,18] (Fig. 1). Different wetting mechanisms have important ecological and biogeochemical implications for in-channel material and nutrient processing; for example, sediment loads, organic materials and nutrient concentrations in wetting fronts tend to be much higher than those in reaches that are already wet or flowing[19,20]. In this Perspective our aim is to shed light on the hydrological, biogeochemical and ecological processes associated with diverse stream wetting regimes. We identify research priorities to advance our understanding of wetting regimes in non-perennial streams with the goal of informing actions that support management and policy, and enhance predictive capacity for non-perennial streams.

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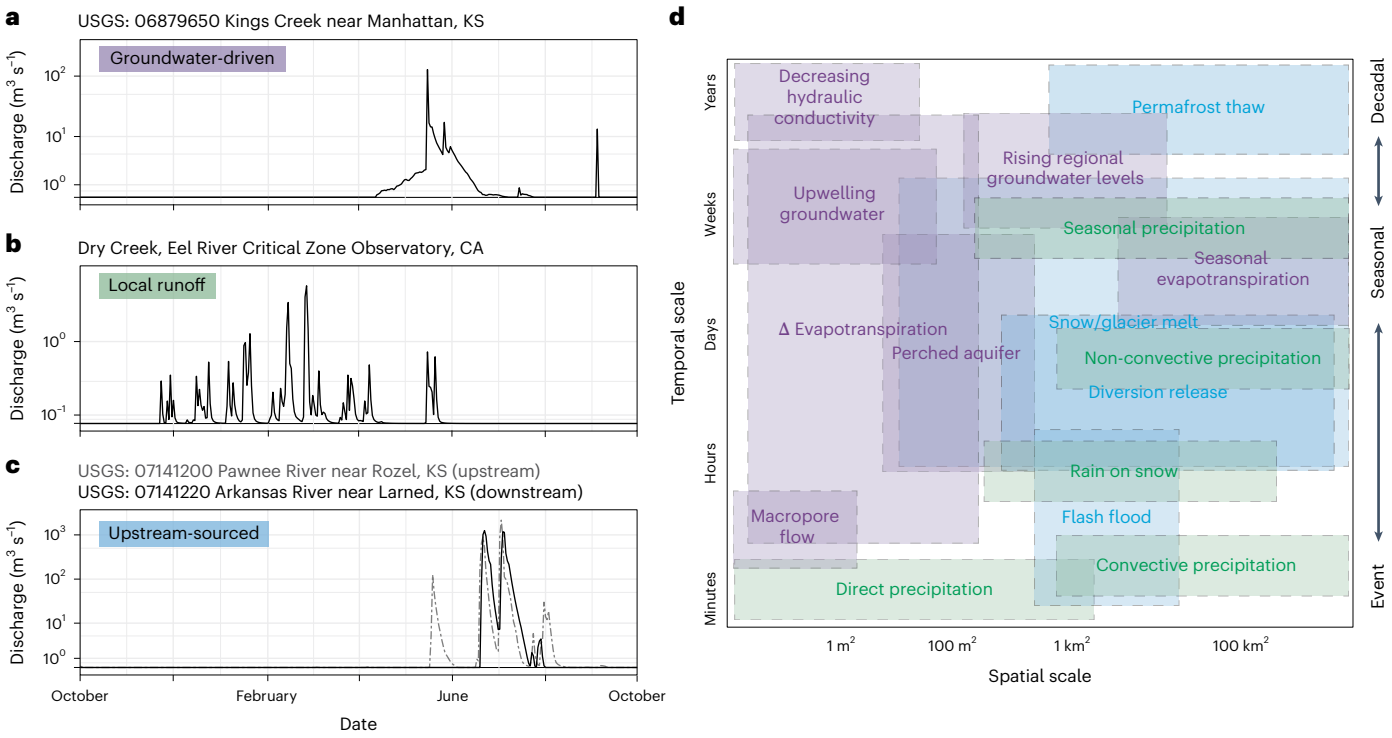

Fig. 1 | Example hydrographs showing distinct wetting mechanisms from four non-perennial streams and potential driving mechanisms for each end-member wetting regime type. a, A slow increase in streamflow over time after a no-flow event, representing a groundwater-driven wetting regime (site characterized in ref. 118). **b**, Streamflow generated by overland flow (site characterized in ref. 119) in short periods is not sustained, representing a local runoff wetting regime. **c**, Wetting from decreased streamflow extraction (site characterized in ref. 8) in an upstream tributary (dashed grey line), representing an upstream-sourced streamflow wetting regime for the downstream reach (solid black line). **d**, Spatial and temporal scales associated with different wetting regimes. Colours of boxes relate to corresponding wetting regimes: groundwater-driven (purple), local runoff (green) and upstream-sourced (blue).

Hydrological, biogeochemical and ecological processes associated with stream wetting

Wetting regimes in non-perennial rivers and streams

Where, when and how quickly water enters a channel defines the hydrological characteristics of stream wetting, the amount and type of nutrients and materials transported, and the conditions that in-stream organisms experience. Many mechanisms contribute to whether or not surface flow occurs at a given location in a watershed, typically expressed as a water balance. The surface flow water balance includes direct precipitation, inflows from upstream, the surrounding land area (that is, overland flow), subsurface (that is, groundwater inputs) and outflows due to infiltration to regional groundwater aquifers, downstream transport, evapotranspiration and human withdrawals and diversions. Although these mechanisms are interrelated (as are their impacts on biogeochemistry and community ecology), for simplicity, we categorize and group wetting mechanisms into three wetting regimes to facilitate the interdisciplinary discussion that follows.

The three wetting regime types are (1) groundwater-driven, (2) local runoff and (3) upstream-sourced wetting. Groundwater-driven wetting is driven by subsurface sources of water, including shallow alluvial or regional groundwater, perched aquifers and sub-channel flow, and characteristically exhibits the slowest rates of wetting of the three regime types. Local runoff wetting is driven by local precipitation events via overland flow or reactivation of shallow subsurface flow paths and is characteristically the flashiest of the three types of wetting regimes. Upstream-sourced wetting is driven by flow generation events (for example, snowmelt and/or monsoonal moisture) or dam releases distal to the dry reach. The definition of these wetting regimes derives from a Eulerian perspective where the dominant mechanism of wetting within the system is relative to the point of interest (for example, where wetting is observed).

Although abundant literature discusses the physical mechanisms of streamflow generation in perennial systems and how landscape structure (for example, topography) influences runoff generation, as well as the characteristics of network connectivity[21,22], we focus here on hydrological mechanisms that result in wetting in non-perennial streams. Grouping these mechanisms into distinct categories of wetting regimes allows us to better connect existing studies on streamflow generation, associated geomorphic controls and wetting of perennial systems to similar streamflow regimes in non-perennial systems. Furthermore, far more studies in the fields of biogeochemistry and ecology focus on the wetting of non-perennial streams than in hydrology. Therefore, leveraging the large body of literature on runoff generation in perennial streams to describe wetting is important to better connect interdisciplinary studies on non-perennial streams. We recognize that these three regimes represent end-members of a continuous distribution of hydrological patterns and that these three regimes can occur even within one stream within one year.

As we state above, these wetting regime descriptions are an idealized representation of the natural world, where multiple mechanisms often combine to induce wetting and the dominance of wetting regimes can vary in space and time[11,23]. Wetting in most rivers and streams falls within a continuum, displaying characteristics of multiple wetting regime types (Fig. 2). In addition, where a system falls within the continuum can be influenced by reach- and watershed-specific geomorphic features (for example, topography, slope, soil texture and channel geometry). However, at certain points in time, systems may display dominant characteristics from an end-member wetting regime. For example, streams in the arid, western United States that experience a high degree of seasonality are dominated by upstream-sourced streamflow wetting regimes during seasonal flow events, whereas those that wet on a diel cycle

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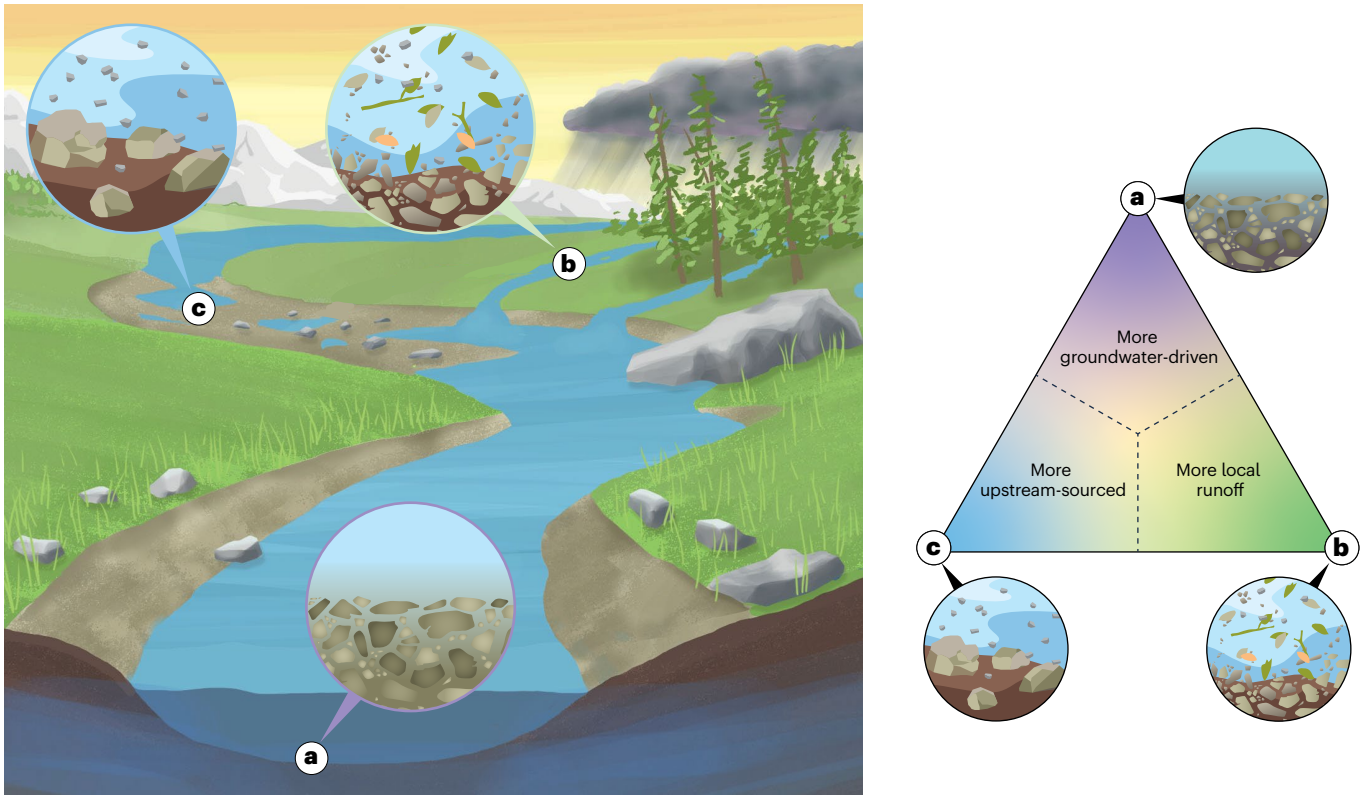

Fig. 2 | Conceptual figure of the wetting regimes continuum showing end-member behaviours. Left: conceptual framework within an actively wetting stream network, with detailed inset illustrations of the proposed in-stream end-member behaviour. Right: ternary diagram illustrating the wetting regimes continuum with the end-member visuals in detailed insets. **a**, Groundwater-driven wetting regime, such as a rising seasonal water table. **b**, Local runoff wetting regime, representing stream wetting from nearby flow paths, such as riparian overland flow activated by precipitation, which can carry leaves, sticks and other debris. **c**, Upstream-sourced streamflow wetting regime caused by water from upstream sources, such as flash flooding, carrying sediment and debris.

responding to changes in evapotranspiration are dominated by groundwater-driven wetting.

Although each wetting regime type has distinct hydrological characteristics, the resulting functions of these characteristics are important for biogeochemical and community ecological responses in non-perennial systems. Specifically, the source water characteristics (for example, temperature, dissolved oxygen (DO) and others), streamflow velocity and power (for example, scouring versus depositional) and rate of reconnection (for example, rapid versus gradual) facilitated by these wetting regimes define the resulting biogeochemical and community ecological responses.

Groundwater-driven wetting regime. Groundwater-driven wetting occurs when water enters the stream via a subsurface source. These subsurface flow paths are inherently three-dimensional due to variability in possible head gradients in the subsurface (for example, perched aquifer, regional groundwater, sub-channel flow). The location of stream wetting via groundwater is strongly controlled by subsurface properties and structure. Specifically, lithology, hydraulic properties and the geometry of the underlying aquifer and stream channel impact the surface expression of water, its propagation downstream and the duration of its persistence after the initial wetting[21,24,25]. For example, seasonal rise in the water table of an extensive unconfined aquifer may contribute water to streamflow for a longer duration across the entire network[8] than flow from a localized perched aquifer[26]. If the volume of water moving through the subsurface exceeds the ability for a shallow alluvial aquifer to store or transmit water, it is expressed as surface flow in the channel[27–30]. This may result in spatially variable wetting of the stream network as a function of the thickness, slope and hydraulic conductivity of the underlying aquifer layer[21,31].

The timescales of groundwater-driven wetting vary from hourly[21] and daily[23] to seasonal or multi-year[32], but, as proposed here, are generally slower than the other two wetting regimes (Fig. 1a). Regions with strong seasonality or interannual variability in precipitation, evapotranspiration or groundwater use can impart seasonality or annual variability in groundwater dynamics by raising or lowering water tables in hillslope and alluvial aquifers connected to the stream[33]. A seasonal change in overall catchment wetness state is often related to slower, groundwater-driven wetting. For example, groundwater systems can act as subsurface reservoirs buffering short-term hydroclimatic variability[34]; thus, reaches with groundwater contributions may sustain flow for longer periods. In addition, reaches with persistent groundwater contributions (for example, seeps and persistent pools) can help propagate a wetting event along a stream[35]. Groundwater-driven wetting that is caused by rapid fluctuations (for example, daily changes in evapotranspiration or perched groundwater table development during rainfall events) can lead to shorter wetting transitions[36].

Local runoff wetting regime. Local runoff-driven wetting occurs during or following precipitation, when rainfall enters streams via surface runoff or shallow subsurface pathways and immediately contributes to wetting. Direct precipitation on the channel can also fall at a rate that exceeds infiltration capacity or saturates the streambed. This may lead to initial filling of disconnected pools along the streambed and in certain cases can contribute to a considerable proportion of subsequent total streamflow during wetting[24]. Land cover, soil type

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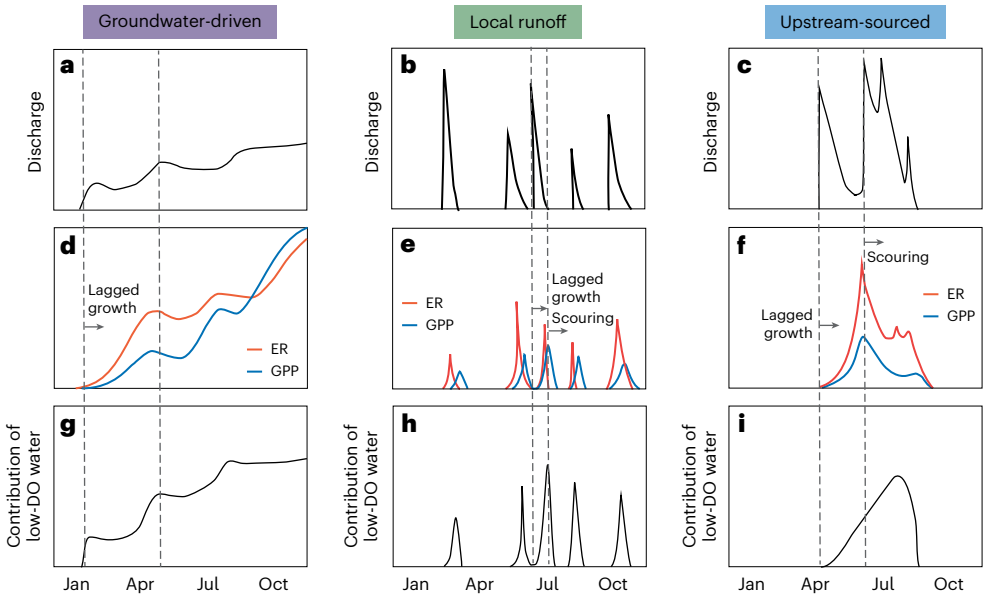

Fig. 3 | Idealized biogeochemical responses for wetting regimes continuum end-members. a–c, Hypothetical time series of discharge indicating resumption of flow for streams where the wetting regime for a stream reach is primarily a groundwater-driven wetting regime (**a**), a local runoff wetting regime (**b**) and an upstream-sourced streamflow wetting regime (**c**). **d–i**, Hypothesized biological activity (**d–f**), hydrologic and relative influence of groundwater and anoxic processes (**g–i**), displayed for each wetting regime. Dashed vertical lines represent lagged growth from the start of a wetting event or scouring of streambeds, suppressing further growth and biological activity. DO, dissolved oxygen; ER, ecosystem respiration; GPP, gross primary production. Months are an indicator of timescale and are not intended to suggest that processes happen at a specific time of year.

and antecedent moisture will impact the amount of local runoff for a given stream reach and precipitation event[37].

Precipitation-driven local runoff generally causes a faster rate of stream wetting than other wetting regimes, because overland or shallow subsurface flow occurs during or soon after precipitation or runoff-generating events[38] (Fig. 1b). Local runoff may lead to shorter wetting durations and unsustained surface flow, known as false starts, which are common in ephemeral streams (that is, non-perennial streams without a groundwater connection[1]).

Upstream-sourced streamflow wetting regime. Streamflow sourced from upstream locations in watersheds can propagate wetting in downstream reaches. Upstream wetting may be caused by diverse mechanisms, including localized rainfall (for example, isolated monsoonal or convective rainfall in the upper part of a catchment), glacier and snowmelt events, distal groundwater discharge or human activities, such as reservoir or irrigation canal operations[8] (Fig. 2c). Streamflow related to these types of mechanisms are vitally important in arid ecoregions, where most precipitation is strongly seasonal, including snowfall and monsoons[39], and can be sources of recharge for local aquifers[40]. Environmental flow releases from dams/diversions can represent a stark endpoint of this type of wetting; water from upstream reaches in a watershed may be held in a reservoir and released suddenly into initially dry downstream areas[41]. Block-flow releases meant to convey stored snowmelt runoff to irrigation diversions can also result in frequent wet and dry cycles[42]. Similarly, diel fluctuations related to snow or glacier melt may yield pulses of runoff to downstream dry channels[43]. Depending on the properties of the upstream flow, channel and subsurface, wetting can either lead to short-term flow (for example, in response to an upstream storm event or short environmental flow release) or sustained flow (for example, in response to snowmelt or sustained reservoir release).

Biogeochemical responses to stream wetting

The biogeochemical characteristics of a stream are set by its hydrological state, such that watersheds exist along a transporter-to-transformer continuum[44]. During periods of high-flow, conditions may favour transport, the longitudinal transfer of materials downstream[45]. During periods of no- to low-flows, networks may be dominated by periods of material transformation, in which conditions promote local biogeochemical reactions[46]. As a stream wets, the streamflow velocity, water source chemistry, and rate and degree of reconnection of the stream network will impact the balance of material transformation versus transportation. The comparison of dimensionless numbers such as Damköhler numbers[47] (that is, the ratio of reaction to transport rates) across surface and subsurface domains may help elucidate the processes leading to post-wetting biogeochemical signatures. Furthermore, there may be opportunities to combine dimensionless numbers with other information (for example, stable isotopes and solute concentrations) to infer the relative contributions of the three wetting regimes.

There are several commonalities across wetting regimes that can result in biogeochemical activated control points during wetting. All three wetting regimes can flush mineralized nutrients, organic matter (OM) and gases accumulated during the dry period out of pore spaces and into surface waters[48]. In turn, stream wetting can alter DO availability in sediments[49], a critical control on redox-associated biogeochemical processes. Wetting also alters the availability and forms of OM[50,51] as microbes decompose plant matter[19]. Microbial decomposition of OM is facilitated when wetting connects microbes and resources previously separated by air-filled gaps during the dry state. Microbial aerobic respiration dominates metabolic use of OM when water and DO are both present. High rates of aerobic respiration can cause anoxia and accelerate anaerobic microbial respiration pathways, which require alternative terminal electron acceptors.

Directly linking wetting regimes to biogeochemical responses is challenging due to the variable results of reach-scale and laboratory measurements of biogeochemical responses to wetting. At the reach scale, gross primary production and ecosystem respiration can recover in less than two weeks following wetting[52]. In the laboratory, one study observed suppression of ecosystem respiration in wetted sediments relative to those maintained in a wet state[53], while another observed

pulses of CO_2 production following wetting[20]. There are insufficient studies to draw general inferences, but at a high level the biogeochemical constituents of the source water driving wetting combined with the degree and speed of flushing and downstream transport will be influential and depend on which wetting regime is dominant.

The degree of reconnection of the stream network, hydrologic state of the network before wetting, speed of wetting and the flow velocities govern the biogeochemical responses to wetting. For example, a gradually rising water table may result in the development of disconnected pools or conversely, a large rain event may cause rapid reconnection of an entire network with intense scouring of the streambed and transport of particulate matter. The transport of particulate and dissolved constituents is partially dependent on the mechanism by which flow resumes. The duration and scouring potential of wetting also controls the extent to which different components of the microbial and macroscopic communities are able to recover[54]. Substantial scouring of sediments may remove dormant biofilms and resources, thereby decreasing the speed of microbial and biogeochemical recovery to pre-drying conditions (Fig. 3). The signal and influence of in situ processing will be determined by the water residence time, which is influenced by the speed and magnitude of wetting. Networks that do not fully reconnect during a wetting event will be dominated by in situ processing rather than transport. Furthermore, a network that contains isolated pools with high temperatures and low DO will produce a different biogeochemical response than a completely dry network upon wetting. Increased temperatures can stimulate biogeochemical processes, such as respiration, nitrification and methanogenesis[55,56].

Although many overarching mechanisms driving particulate and dissolved constituent movement operate across all wetting regimes, in the subsequent sections we highlight distinctive differences among wetting regimes in solute source, processing and transport, with implications for biogeochemical processes that dominate during wetting (Fig. 3). Biogeochemical responses to runoff generation mechanisms are well studied in perennial systems, but the responses to the timing, magnitude, duration and seasonality of wetting in non-perennial systems are less understood. As a result, the following dynamics are hypothesized responses to wetting and require future study.

Biogeochemical responses to groundwater-driven wetting. Groundwater is often chemically distinct from surface water, which has major implications for biogeochemistry. The longer residence times associated with groundwater generally lead to low DO and reducing environments[5], stable temperatures, more reduced ionic forms (for example, NH_4^+ versus NO_3^-) and a larger range of dissolved organic carbon concentrations and composition[57] compared to surface water. When reduced compounds are transported to the well-oxygenated surface water or to groundwater–surface water mixing zones in the subsurface sediments, they can stimulate productivity, heterotrophy and chemotrophy[20,58]. Surface water derived from groundwater-driven wetting may be either cooler (in summer) or warmer (in winter) than expected under regular flowing conditions[59], which will impact microbially mediated reaction rates such as respiration, nitrification and methanogenesis. Thus, groundwater-driven wetting could enhance or dampen biogeochemical processing rates compared to upstream-sourced or local runoff-driven systems.

Due to these characteristically longer residence times and the locally focused nature of groundwater-driven wetting, local microbially mediated processing can exert a strong influence on the chemistry of stream water[60] (Fig. 3). Slow wetting from groundwater connects microbes to previously isolated resources[61], which results in longer in-channel residence times and greater degrees of biogeochemical processing relative to downstream transport, compared to other wetting regimes. As such, the chemistry of water mobilized and flushed from the system reflects the signature of this internal processing when downstream transport resumes[60] (Fig. 3d). In other cases, groundwater-driven wetting is rapid, which may result in a similar response to other wetting regimes[62].

Biogeochemical responses to local runoff wetting. Compared to groundwater-driven wetting regimes, the water transported during local runoff wetting events may be more closely related to the signature of hillslopes/the adjacent watershed, rather than groundwater or in situ processing. The biogeochemical signature of locally sourced runoff is strongly influenced by factors such as surrounding land cover (for example, agriculture versus forest), soil type (permeable versus impermeable), degree of connection to and flushing of riparian areas, and direct precipitation onto accumulated OM in the channel[19]. We expect substantial cross-system variation in the magnitude and timing of biogeochemical processes following local runoff wetting owing to a complex and interacting suite of physical (for example, scour), biological (for example, microbial dormancy) and chemical (for example, organic sorption) processes (Fig. 3).

Local runoff wetting can result in rapid activation of flow and connection across the stream network. The magnitude and flashiness of local runoff wetting affect whether materials deposited during the dry state will be transported downstream, carried into the riparian zone, buried under sediment, or entrained in sediment pore spaces. High flow events that result in overbank floods/connection to floodplains could contribute to the burial of OM as sediments are mobilized and deposited[63].

Biogeochemical responses to upstream-source streamflow wetting. The nature of the upstream wetting source (for example, dam release, snow and glacier melt) influences the chemical and thermal signatures of wetting events, which are highly variable (for example, due to land use and land cover, geology)[64]. In-stream and subsurface processing are the main drivers of the biogeochemical signature (for example, nutrient concentrations and DO) of the source water as it moves downstream[65,66]. As the source water moves downstream, there are increased losses to the subsurface as a function of channel hydraulic conductivity and gradients, resulting in longitudinal differences in biogeochemical processing rates. As water is lost to the subsurface, it carries particulate and dissolved material into the hyporheic zone and groundwater, likely promoting microbially mediated processing and solute transformation[67] (Fig. 3).

Despite the heterogeneity in water sources and material loads, downstream waters all experience spatially and temporally variable process dynamics driven by the interactions between the surface water and subsurface environment[68]. Spatial and temporal variations in biogeochemical processes are also influenced by the changing physical flow paths themselves, which may vary due to physical clogging or bioclogging by microbial biomass[69]. Excess fine sediments in the hyporheic zone can affect the ability for DO and other constituents to enter into the sediments, as well as future percolation of water[58,70].

Community ecology responses to stream wetting

Flowing surface water promotes the reconnection of previously fragmented habitats, allowing for passive and active dispersal of microbes, invertebrates, amphibians and fish[71]. Drying and wetting events can be spatially patchy and short-lived but frequent; thus, ecological recovery of disturbance-adapted communities following wetting can be relatively rapid[72]. Recovery can also be slower and dependent on the proximity of persistent, high-quality dry-state refuges such as springs, deep pools and the hyporheic zone[72,73] that affect population persistence during dry states and recolonization during and after wetting[11,74]. Rivers with more frequent or severe dry states are more likely to be colonized by a higher proportion of aerial or other overland dispersers[75] regardless of wetting mode, highlighting the importance of antecedent conditions and network-scale refuge availability[74]. Similarly, the history and predictability of drying[76] influences the resistance (the

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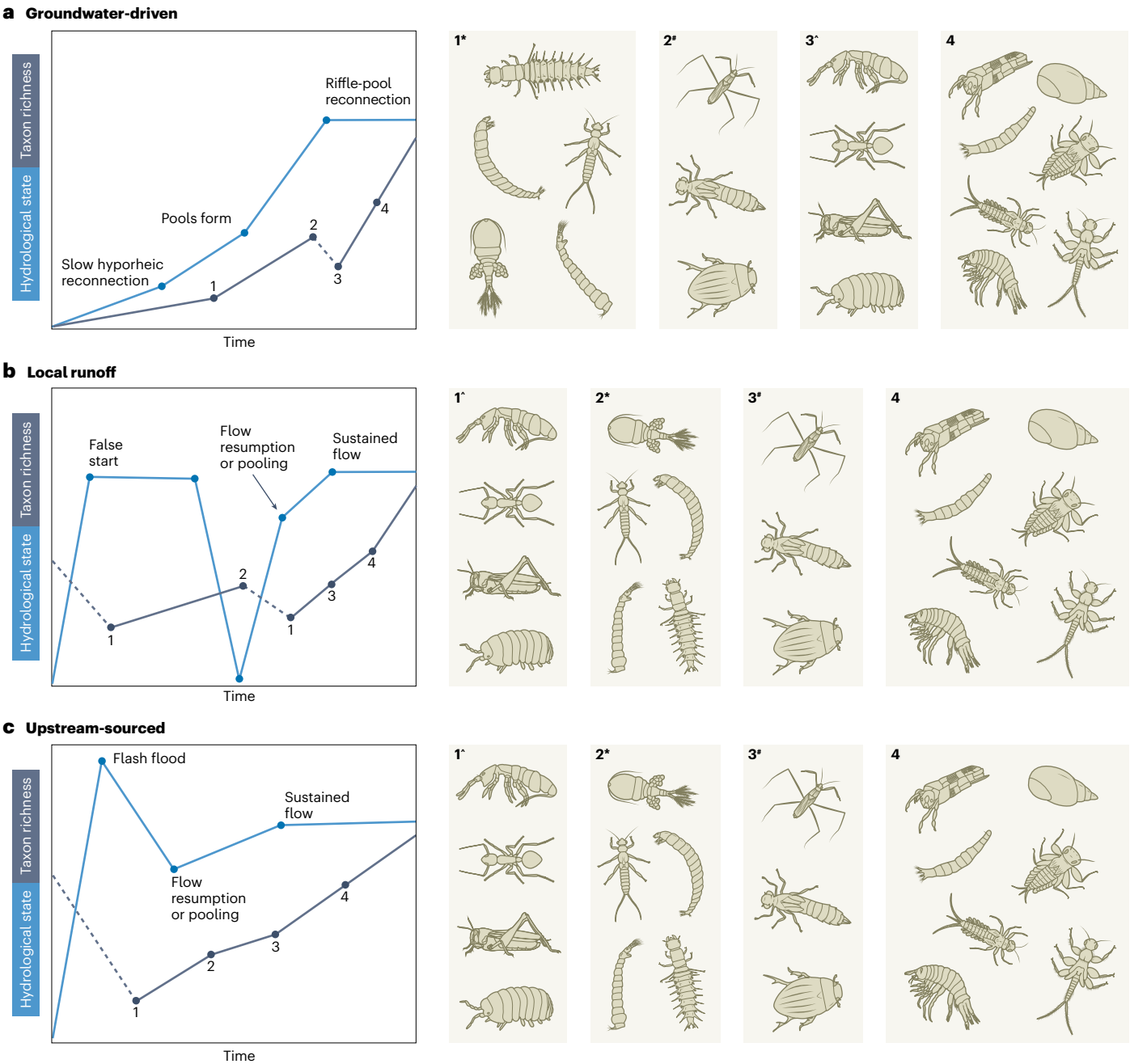

Fig. 4 | Idealized time series of the hydrologic state and invertebrate taxonomic richness for wetting regimes continuum end-members. **a**–**c**, Idealized time series of the hydrologic state and invertebrate taxonomic richness associated with groundwater-driven (**a**), local runoff (**b**) and upstream-sourced (**c**) wetting regimes. Filled blue circles and lines represent surface water, and filled grey circles and grey lines represent invertebrate richness. Numbered panels correspond to the numbered white circles on the time series for each associated wetting regime plot. Groups of taxa include: (1) terrestrial or semi-aquatic taxa (for example, Collembola, Isopoda, Orthoptera and Formicidae; represented by ^), (2) aquatic taxa with drying-resistant traits (for example, dormant life stages: Chironomidae, Simuliidae, Capniidae, Megaloptera and Copepoda; represented by *), (3) aquatic taxa with drying-resilient traits (for example, strong aerial dispersal: Odonata, Coleoptera and Hemiptera; represented by #) and (4) aquatic taxa with fewer drying-resistant and -resilient traits (for example, downstream drift, crawling/swimming ability: Amphipoda, Capniidae, Baetidae, Limnephilidae, Nemouridae and Tipulidae).

capacity to withstand drying) and resilience (the capacity to recover from drying) traits of the organisms that recolonize upon wetting[75]. Over evolutionary timescales, the traits of the organisms themselves may adjust to maximize fitness to these variable environments[77]. Deviation from the typical timing, duration and magnitude of wetting events can elevate the local extinction risk of species adapted to particular wetting regimes[42].

For all wetting modes, ecological responses are modulated by the seasonality and predictability of wetting events and how well they match organismic traits[11,78]. The life histories of some species are timed to coincide with predictable wetting events, such as post-snowmelt fish spawning[79] and the amphibian and insect life histories that predictably track the seasonal wetting of non-perennial habitats[80]. The timing and rate of wetting can also influence the germination and establishment of riparian vegetation via water-mediated dispersal[81] and scouring during wetting[82].

Organismal life-history traits (that is, dispersal mode, production of drying-resistant forms, body size, lifespan and reproductive

strategy) affect an organism's ability to respond to different wetting modes[75,83]. Invertebrates with drying-resistant traits can recolonize from damp and dry subsurface sediments[80,84] within days, whereas, depending on the proximity of refuges and wetted reaches, taxa with drying-resilient traits (that is, aerial/overland dispersal, tendency to drift, fast crawling/swimming speed) may take longer (weeks to months) to recolonize[75] (Fig. 4). Wetting regimes can also mediate the dispersal, recolonization and activity of aquatic organisms (for example, fish and amphibians), both within and among species. Additionally, some terrestrial organisms that inhabit dry stream channels (such as ants, beetles and spiders) have strategies to survive inundation and can use wetting events to colonize other (for example, marginal) habitats[17,85]. Differences in wetting regimes may ultimately shape the genetic structure and evolutionary trajectories of populations[86]. Organismal responses to wetting and recolonization strategies likely vary depending on the mode of wetting, which we explore further in the following sections.

Community ecology responses to groundwater-driven wetting. As groundwater levels rise, inundation of the hyporheic zone can trigger the development of dormant organisms[80,84] and transport groundwater fauna into shallower sediments[87]. Successional patterns driven by groundwater wetting may thus be distinguished by a higher proportion of groundwater fauna (for example, crustaceans) in the early stages of wetting[88] compared to other wetting regimes (Fig. 4a). As the flowing state duration continues, organisms including benthic invertebrates, fish and amphibians can recolonize and reproduce, increasing the richness, regardless of the water source[54,89]. In groundwater-fed sites, flow is often sufficiently long-term to support communities with fish and long-lifespan invertebrates, and the organisms therein represent colonists derived from other established habitats[90]. Regular and predictable groundwater-driven wetting may select for species and communities that are specialists, occurring primarily in these habitats[80].

Community ecology responses to local runoff wetting. The rate and duration of wetting strongly influence community assembly[17]. For example, false starts can result in exposure to dry conditions before flow resumes for an extended period, resulting in higher stress, organismal mortality, and related shifts in community composition[91]. However, laboratory experiments show that the cumulative time in a dry state, and not the number of false starts, controls which microbial taxa were active following wetting[53]. Drying duration and false-start frequency may therefore have complex influences across different biological components of river systems. False starts can also increase the persistence of pools in non-perennial streams, which may temporarily support lentic taxa, and can trigger the development and emergence of drying-resistant taxa from resistant eggs within dry substrates, which may die if consistent flow does not develop[4]. Additionally, flow resumption driven by local runoff is generally characterized by water quality that reflects the surrounding environment, which may be a strong control on longer-term ecological patterns by shaping the taxonomic composition of communities[92]. The unpredictable nature of local runoff wetting may favour species with strong dispersal abilities or short generation times and drying-resistant dormant forms[60,93].

Community ecology responses to upstream-sourced streamflow wetting. Sustained upstream-sourced flows and high-magnitude flow events from snowmelt or dam releases reconnect previously wet and disconnected habitats and alter the spatial arrangement and connectivity of habitats within non-perennial systems[94] (Fig. 3c). Upstream-sourced events attributed to dams can disrupt natural wet and dry cycles by storing water upstream and asynchronously (often out of season) releasing water in pulses[95]. Hydropeaking from hydropower dams can disrupt ecological processes, including disrupted reproduction and recruitment, that are synchronized to naturally predictable wetting events, which may have substantial indirect effects on entire riverine and riparian food webs[96]. Severe manifestations of upstream-sourced wetting (for example, a hurricane breaking a dry season, rain on snow events, floods) disturb ecological communities by bed scouring[97]. Additional variations in water quality, such as low DO concentrations, varying sediment loads and differing temperatures of upstream-sourced wetting compared to local conditions, may have immediate ecological consequences including mass mortality events[98]. However, upstream-sourced wetting can also transport aquatic organisms to downstream reaches, facilitating their recovery with rapid recolonization of aquatic organisms and a return to pre-drying abundance and richness after wetting[99]. Floodwaters can connect a channel to its riparian zone and floodplain, increasing the abundance of many microbes, plants, invertebrates, wetland birds, amphibians and fish[81]. The extent of bed scour, channel formation and timing (for example, spring versus autumn) during upstream-sourced wetting can dictate the carbon base of food webs[100] (for example, allochthonous versus autochthonous), as well as the strength and nature of trophic links in aquatic–terrestrial food webs[101].

Scientific community needs and next steps

The wetting regime of a non-perennial stream affects biogeochemical and community ecology responses, but interdisciplinary work that quantifies these relationships remains limited[102]. This hampers our ability to predict responses to wetting regimes across space or time, which is of particular importance as the hydrology of many aquatic systems continues to shift towards increased non-perenniality due to widespread environmental change[103]. For example, wetting events often facilitate a recovery of aquatic ecosystems[72], but high-magnitude, unpredictable wetting events also act as a disturbance[97]. In the following sections we highlight three important research directions that can help advance an interdisciplinary understanding of how flow activation drives the biogeochemical and community ecology responses of non-perennial river systems.

Toward a predictive understanding of wetting regimes

Collaborating across disciplines to co-develop models and frameworks that use common vocabulary and connections will be important to unify and advance predictive understanding of how non-perennial rivers and streams wet. Developing frameworks in collaboration across disciplines[104] can help scientists to rapidly screen potential mechanisms and identify those that are likely important at a given site. Linking these mechanism dynamics to landscape controls (for example, the underlying geologic setting or topography) and climate drivers could facilitate cross-study comparisons and inform macroscale predictions. In addition to identifying mechanisms, a shared set of descriptors to characterize wetting regimes could advance interdisciplinary work. Specifically, we lack consistent definitions of what constitutes the beginning and end of a wetting event (for example, false starts versus sustained flow for multiple days) as well as quantifiable metrics that describe wetting-event characteristics from hydrographs. Leveraging and comparing existing frameworks that describe flow regimes in perennial systems[9] (for example, critical flow components such as timing, duration, magnitude, frequency and rate of change) to the wetting regime framework will be essential in delineating and identifying unique behaviours and drivers of non-perennial systems. Quantitative metrics could then be used as the typological foundation to compare ecological characteristics and biogeochemical processes as well as to detect non-stationarity in wetting regimes and draw ecosystem-wide inferences. For example, previous work on drying-regime categorization, which organized a wide range of river drying events by their hydrological characteristics[12], could provide a quantitative framework to describe ecological and biogeochemical responses to wetting regimes.

Assessing the role of climate change and human alterations on non-perennial stream wetting regimes

Changing climate (for example, precipitation timing and intensity) coupled with widespread human alterations to land use and water extraction are causing some river systems to get wetter and some to get drier[103]. These changes will influence drying and wetting characteristics and may complicate the implementation of water resource management actions and broader strategies (that is, adaptive plans based on latest data[105]) designed to prevent negative or undesired ecological, biogeochemical and social impacts of altered flow regimes[106].

Additional long-term research would improve our understanding of how changes in wetting regimes due to climate change and human pressures shape biological communities and the ecological and biogeochemical functions they provide. Precipitation events in some regions have been forecasted to become less frequent and more intense[107], which will affect dominant wetting and drying regimes. The dry duration between wetting events is important for predicting future streamflow activation responses, and also shapes resident microbial communities, material accumulation and the resulting biogeochemical processes in stream systems[5,102]. Climate-induced changes in stream wetting patterns can also decouple OM and nutrient fluxes from the life histories of resident taxa. Time lags in ecosystem responses could complicate timely assessment of these relationships. A particular focus would be moving beyond broad-scale climate-influenced flow predictions (for example, mean annual flow) to metrics describing ecologically meaningful aspects of flow regimes such as the length and frequency of no-flow periods. Long-term studies with permanent instrumentation and repeat sampling of cross-disciplinary processes will be central to assessing time lags and long-term change. Linking these responses in biogeochemistry and community ecology can further inform our understanding of wetting regimes and important mechanisms across terrestrial and aquatic ecosystems.

Expanding from traditional point-scale measurements to network-scale understanding

Wetting mechanisms are traditionally studied at the point scale (for example, gauges and site observations) or reach scale (for example, site survey). Although point- or reach-scale measurements inherently integrate upstream behaviour, they do not provide information regarding specific wetting dynamics throughout stream networks[108]. Characterizing wetting dynamics across stream networks requires multi-gauge or multi-reach studies, which is time-consuming and costly[109]. Lagrangian approaches or network-scale spatiotemporal analysis of wetting dynamics can reveal mechanisms of stream wetting through examination of stream connectivity[110]. Alternative approaches to monitoring the presence or absence of water across stream networks include using cameras[111], community science[112] or using satellite data to study larger river networks[113]. These emerging remote sensing technologies are promising, particularly with the advent of global high-resolution daily datasets[114], but are limited in their ability to determine wetting mechanisms. Therefore, they are most useful when combined with other sources of data including multiple remote sensing products, in situ observations, or models. Although community science initiatives can provide effective monitoring of river drying at regular intervals[112], more frequent observations are often needed to capture the rapid initiation of some wetting events. Finally, given the global prevalence of non-perennial river systems, quantifying the implications of wetting regimes also requires moving beyond single watersheds and networks to regional and global scales. Although globally continuous observations of drying–wetting patterns are not attainable, statistical models could be further developed[27] to identify environmental proxies of wetting regimes, which, combined with global hydrological models, could predict the global distribution of wetting regimes.

From an ecological perspective, river science and management are shifting from local to network-scale approaches with the rise of meta-system theory[115]. Current research is exploring how drying shapes biogeochemical functions and biotic communities across local and river-network scales[78]. However, the influence of spatiotemporal patterns of wetting at the river-network scale is largely unknown, and the meta-system implications of different types of wetting events remain unexplored, particularly for the dispersal of both aquatic[75] and terrestrial[85] organisms. For example, the spatiotemporal variability of wetting regimes may promote substantial variations in community composition within and across river networks, but no study exists to test this hypothesis. Due to the technical challenges and effort associated with standard sampling for understanding community dynamics at large scales, the development of molecular tools (for example, metabarcoding) is likely to promote further understanding and research[116]. Finally, continued coordinated experiments across climates and biogeographical settings[117] will provide powerful ways to advance our understanding of the impacts of wetting and drying mechanisms on biogeochemical functions and biotic communities at network and among-network scales.

Conclusions

In this Perspective, we have presented a hydrological continuum that describes three end-member wetting regimes based on different causal hydrological mechanisms. We define these three end-member wetting regimes as groundwater-driven, local runoff and upstream-sourced streamflow by typical hydrological characteristics (timing, magnitude, frequency, duration and rate), water sources and water-quality signatures. Each wetting regime distinctly impacts the community ecology and biogeochemistry of non-perennial systems. Wetting regimes control the transport, processing and retention of materials, as well as the recolonization of organisms and their trait distributions. A better quantification and definition of wetting regimes offers a unique and interdisciplinary opportunity for standardized studies that assess climate change and anthropogenic impacts on wetting and its associated mechanisms and advance our understanding of river networks. Producing such information requires coordinated collaborative efforts that generate interoperable datasets integrating ecology, biogeochemistry and hydrology. Standardized terminology, data and metrics will advance cross-disciplinary non-perennial stream science, thereby allowing the scientific community to address the research frontiers articulated herein. Such studies will promote the development of novel process-based modelling frameworks that integrate all dimensions of wetting regimes, including key factors such as residence times tied to hydrologic conductivity, source water chemistry and organismal traits linked to function. Such modelling frameworks are essential for predicting the future hydrological, biogeochemical and organismal state of non-perennial streams. Exploring and monitoring the wetting regimes of non-perennial systems alongside their drying regimes will enable holistic conceptual model development and inform management actions and policy development to protect these dynamic ecosystems.

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Author contributions

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The authors declare no competing interests.

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