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Expanding towards contraction: the alternation of floods and droughts as a fundamental component in river ecology

S. Bernal · J. L. J. Ledesma · X. Peñarroya · C. Jativa · N. Catalán · E. O. Casamayor · A. Lupon · R. Marcé · E. Martí · X. Triadó-Margarit · G. Rocher-Ros

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Abstract Climate warming is causing more extreme weather conditions, with both larger and more intense precipitation events as well as extended periods of drought in many regions of the world. The consequence is an alteration of the hydrological regime of streams and rivers, with an increase in the probability of extreme hydrological conditions. Mediterranean-climate regions usually experience extreme hydrological events on a seasonal basis and thus, freshwater Mediterranean ecosystems can be used as natural laboratories for better understanding how climate warming will impact ecosystem structure and functioning elsewhere. In this paper, we revisited and contextualized historical and new datasets collected at Fuirosos, a well-studied Mediterranean intermittent stream naturally experiencing extreme hydrological events, to illustrate how the seasonal alternation of floods and droughts influence hydrology, microbial assemblages, water chemistry, and the potential for biogeochemical processing. Moreover, we revised some of the most influential conceptual and quantitative frameworks in river ecology to assess to what extent they incorporate the occurrence of extreme hydrological events. Based on this exercise, we identified knowledge gaps and challenges to guide future research on freshwater ecosystems under intensification of the hydrological cycle. Ultimately, we aimed to share the lessons learned from ecosystems naturally experiencing extreme hydrological events, which can help to better understand warming-induced impacts on hydrological transport and cycling of matter in fluvial ecosystems.

Keywords Hydrological intensification · Extreme hydrological events · Expansion and contraction of fluvial networks · Functioning of Mediterranean rivers

Introduction

Climate change is increasing the frequency of large storms (Wasko et al. 2021) and persistent droughts worldwide (Spinoni et al. 2014; Chiang et al. 2021). The intensification of these extreme weather conditions can influence the hydrological cycle by altering the balance between water storage, evapotranspiration and water transport (Creed et al. 2015; Zipper et al.

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S. Bernal (✉) · X. Peñarroya · C. Jativa · N. Catalán · E. O. Casamayor · A. Lupon · R. Marcé · E. Martí · X. Triadó-Margarit · G. Rocher-Ros
Center of Advanced Studies of Blanes (CEAB), CSIC, Accés Cala St. Francesc 14, 17300 Blanes, Girona, Spain
e-mail: sbernal@ceab.csic.es

J. L. J. Ledesma
Department of Hydrogeology, Helmholtz Centre for Environmental Research–UFZ, Permoserstr. 15, 04318 Leipzig, Germany

G. Rocher-Ros
Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden

2021). In regions with seasonal snowpack, decadal changes in precipitation and temperature are inducing both drier growing seasons and wetter non-vegetative periods (Creed et al. 2015). These long-term changes in climate are accompanied by higher peak flows (Gershunov et al. 2019) and lower overall summer flows in streams and rivers (e.g., Kormos et al. 2016). Stream intermittency is also increasing, with more frequent and longer periods of zero flow, especially in southern regions of the United States (Zipper et al. 2021) and Europe (Gallart et al. 2012). Future projections suggest that the hydrological cycle will continue to intensify with a widespread increase in the alternation of extreme floods and droughts (Ficklin et al. 2022).

Extreme hydrological events impact freshwater ecosystems by changing water resource availability, hydrological connectivity, and the relevance of flood-associated disturbances (sensu Sponseller et al. 2013). Large floods occur over a small period of time and mostly affect the main channel of intermittent fluvial networks (Sponseller et al. 2013). Yet, their advective energy can disproportionately impact stream benthic communities (e.g., Grimm 1987), as well as annual solute budgets (Bernal et al. 2005, 2013). During large floods, solutes and particles are massively pulsed and shunted from terrestrial ecosystems to recipient water bodies, while high water velocity and turbidity hinder stream metabolic activity and biological nutrient uptake (Hensley et al. 2019). In turn, droughts lead to low and zero flows, decreasing water availability. Hydrological contraction is usually accompanied by a decline in water quality and habitat suitability owing to increases in water salinization and temperature, decreases in dissolved oxygen and, potentially, blooms of toxic cyanobacteria (Mosley 2015; van Vliet et al. 2023). As a result, stream biota and associated biogeochemical processes can dramatically change during low flow periods (Gómez et al. 2012; von Schiller et al. 2017). Large increases in algal biomass occur while nutrients are available (Grimm 1987), and anaerobic microbial processes such as denitrification and sulfate reduction can come into play following oxygen declines (Gómez-Gener et al. 2020). In dry streambeds, solutes and particulate organic matter can undergo large biogeochemical processing (Merbt et al. 2016), or else be stored almost passively (Catalán et al. 2023) depending on the type of material and the prevailing environmental conditions. Yet, this topic has traditionally received little attention from the scientific community (Arce et al. 2019; Gómez-Gener et al. 2021).

While reporting and quantifying ecosystem responses to individual extreme hydrological events is important, there is an increasing need to better integrate these episodes and their impacts within the hydrological regime context and foundational frameworks in river ecology (Li et al. 2024). This exercise is crucial to better anticipate climate-induced impacts on fluvial ecosystems, especially under the expected intensification of the hydrological cycle. Floods are already considered in contemporary conceptual frameworks in river ecology. For instance, the Pulse-Shunt Concept (Raymond et al. 2016) quantitatively showed that large storm events, albeit being infrequent, disproportionally account for annual export of dissolved organic carbon. The River Network Saturation Concept (Wollheim et al. 2018), grounded on the nutrient spiraling mathematical framework, considers large floods as extreme cases where supply from terrestrial ecosystems largely overwhelms nutrient demand by stream biota. In contrast, few quantitative models in river ecology explicitly address features typically observed in intermittent streams such as losses of surface water, flow cessation, or stream bed desiccation. Nonetheless, half of the global fluvial network length can experience no-flow conditions during several weeks per year (Messager et al. 2021). Allen et al. (2020) reviewed 18 models in river ecology, and concluded that only three of them provided a valid conceptualization of processes and patterns for intermittent streams: (i) the hyporheic corridor (Stanford and Ward 1993a, b), (ii) the telescoping ecosystem model (Fisher et al. 1998), and (iii) the multiple roles of water (Sponseller et al. 2013). However, we are still far from developing conceptual models explicitly accounting for the intensification of the hydrological cycle (alternation of floods and droughts), and that offer quantitative frameworks comparable to those described for continuously flowing waters.

Previous studies suggest that the alternation of floods and droughts can lead to rapid changes in water flow paths, land-stream connectivity, and biogeochemical reactions in soils and streams (Stanley et al. 1997; Martí et al. 2000; Li et al. 2024). Yet, the effect of alternation of these events on ecosystems properties is still poorly understood, owing to limited historical data and scarcity of conceptual frameworks describing ecological responses to these hydrological regimes. Mediterranean and dryland regions naturally experience floods and droughts on a seasonal basis as a consequence of both irregular distribution of rainfall and high evaporative demand by vegetation (Gallart et al. 2012). Thus, data from rivers in these regions can help us to elucidate the potential impact of hydrological intensification on freshwater ecosystems. With this aim, we use knowledge gained from existing literature and from our own long-term research conducted at the Fuirosos stream. This stream drains a relatively unaltered Mediterranean catchment in northeastern Spain, and has been studied for more than two decades (Vázquez et al. 2013). We revisited the available long-term data sets to illustrate how the alternation of floods and droughts impact key stream ecosystem properties in this intermittent stream. First, we show how intra- and inter-annual climatic variability influence hydrological contraction and expansion patterns. Second, we compare the composition and functional characteristics of stream microbial communities under contrasting hydrological periods. Third, we assess how water chemistry and associated biogeochemical processing change with varying hydrological conditions. Fourth, we analyze the extent to which some of the most influential river foundational concepts consider hydrological contraction–expansion patterns. Finally, we highlight knowledge gaps and discuss the most pressing challenges to be addressed for fostering ecological research in fluvial networks experiencing marked contraction and expansion patterns.

The Fuirosos catchment

The Fuirosos catchment (10 km^2) is a 3rd order stream located in the Montnegre-Corredor Natural Park, NE Spain (41° 42′N, 2°34′, 50–770 m a.s.l.). The climate is typically Mediterranean, with average monthly temperatures ranging from 3°C in January to 24 °C in August. Long-term average annual precipitation is 650 mm, while annual potential evapotranspiration ranges between 975 and 1418 mm per year (Ledesma et al. 2021). The catchment is mainly underlain by granite and covered by perennial forests (*Quercus suber*, *Quercus ilex*, *Pinus pinea* and *Pinus halepensis*). Upslope soils are shallow and poorly developed with a thin organic horizon. The lower parts of the stream channel have a 50 to 130-m wide zone of embedded sandy alluvium with high hydraulic conductivity, flanked by a riparian forest (10–20 m width) composed by *Alnus glutinosa* and *Platanus acerifolia*. The riparian soils are sandy with low organic matter content (3–6% in the first 10 cm) (Bernal et al. 2019). Human activity is minimal due to its location within a natural protected area.

Streamflow in Fuirosos is intermittent, typically ceasing for several weeks during the summer and resuming with the first storms in autumn. The duration of the zero-flow period typically varies between 45 and 121 days per year (Butturini 2019). Notably, Fuirosos has maintained summer flow only three times since 1998, coinciding with exceptionally wet springs (Vázquez et al. 2013). During the contraction phase, stream water can infiltrate into the riparian zone up to 20 m from the stream channel (Butturini et al. 2003). The Fuirosos stream loses water towards the riparian zone until November, after which it tends to gain water from groundwater sources until early summer. Under base flow conditions, average discharge is ca. 7 L s^{-1}. The streambed morphology is well preserved and dominated by sand, rocks, and boulders.

Monitoring of hydrological and chemical data at Fuirosos, including streamflow and riparian groundwater level, was previously conducted in the late 1990s and the 2000s (Vázquez et al. 2013). In 2018, we installed a stream monitoring station that drains an area of 10 km^2. The monitoring station is equipped with sensors recording water level (with a HOBO pressure transducer) and dissolved oxygen (O_2) concentrations (with a MiniDOT) every 10 min. A calibration curve based on "slug" chloride additions ($n=36$) was used to convert stream water level to discharge. Since 2021, we have also measured dissolved carbon dioxide (CO_2) concentrations every 15 min with an Eosense sensor connected to a Campbell data logger (Bernal et al. 2019). Additionally, we have collected biweekly stream water samples for routine chemical constituents (i.e., nutrients and dissolved organic carbon) (Bernal et al. 2019). From 2019 to 2023, we have conducted several surveys to collect stream biofilms for microbial characterization along a 200-m stream reach upstream of the monitoring station (Peñarroya et al. 2023).

In this study, we analyze the hydrological and chemical time series collected at Fuirosos from October 2018 to March 2024. This monitoring period encompasses an exceptionally wet phase (2019–2020) with annual precipitation (1172 mm) exceeding the long-term average (650 mm), followed by a severe drought phase (2020–2023) with annual precipitation falling below 600 mm. The water year 2019–2020 included the impact of the 'extratropical cyclone' *Gloria*, which struck eastern Spain in January 2020. *Gloria* brought extraordinarily heavy rainfall and large flooding, exceeding flows not seen for the previous 30 years. In the Fuirosos catchment, the cyclone resulted in an extraordinary accumulation of 230 mm of rain in just 3 days (stream $Q > 4000$ L s^{-1}), causing infrastructure damage that blocked access to the study site for several weeks (Ledesma et al. 2021).

Hydrological contraction and expansion: essential phases of the hydrological regime

The marked climate seasonality of Mediterranean regions strongly influences the temporal pattern of stream discharge (e.g., Butturini et al. 2002; Godsey and Kirchner 2014) and of the extent of fluvial networks (von Schiller et al. 2011; Bernal et al. 2013). This dynamism in space and time, commonly observed in semiarid and dryland regions, is typically characterized by an expansion phase in fall and a contraction phase in late spring and summer (Fig. 1a). During the expansion phase, hydrological connectivity is high, and streams are well-connected longitudinally within the network, laterally with terrestrial ecosystems, and vertically with the hyporheic zone. This connectivity is maximized during episodic large storms, when streams expand laterally, potentially flooding adjacent riparian zones (Friedman and Lee 2002; Ledesma et al. 2021). In contrast, during the contraction phase, hydrological connectivity diminishes at least in one of the spatial dimensions. For instance, the fluvial network can shrink due to disconnection in the longitudinal dimension (Godsey and Kirchner 2014), or streams can lose water towards terrestrial groundwater due to disconnection in the lateral dimension (Jasechko et al. 2021). Hydrological disconnection can lead to the fragmentation of the fluvial network, and culminate on a dry phase of complete flow cessation (Costigan et al. 2017; von Schiller et al. 2017) (Fig. 1a).

The timing and duration of the expansion, contraction, and dry phases in river networks can vary widely across Mediterranean streams (Cid et al. 2017; Price et al. 2021) and depend on several factors such as climate and associated antecedent moisture conditions, topography, land cover, and anthropogenic disturbances (McDonough et al. 2011; Costigan et al. 2017; Price et al. 2021; Zipper et al. 2021). Some fluvial networks experience smooth contraction phases with gradual reductions in stream flow (Meyer and Meyer 2000; Lupon et al. 2016), whereas others are exposed to abrupt hydrological contraction and flow cessation (Granados et al. 2020). Likewise, climatic variability confers a large inter-annual variability in the expansion–contraction dynamics of Mediterranean intermittent fluvial networks. For instance, intermittent streams may flow during summer if preceded by a wet spring, which highlights the influence of antecedent moisture conditions on the hydrological regime (Vázquez et al. 2013). Hence, most streams can exhibit different drying regimes depending on the climatic characteristics of each water year (Price et al. 2021).

To illustrate the intra- and inter-annual variability of the hydrological regime in Mediterranean intermittent streams, we analyzed the hydrological time series recorded at Fuirosos from October 2018 to March 2024. The hydrologic regime at Fuirosos is highly seasonal and erratic, with discharge varying more than four orders of magnitude during this five-year period (Fig. 2b). The dramatic inter-annual variability in stream discharge has important implications for freshwater habitat availability, as indicated by the high temporal variability of the wet streambed (Fig. 2c). For example, between November 2019 and April 2020, three large storms (including the extratropical cyclone Gloria) hit the region, which rapidly expanded the size of the Fuirosos fluvial network (Ledesma et al. 2021). This is exemplified by the extent of the wet streambed, which covered more than 90% of the bankfull width during 10 days within this period. In the subsequent contraction phase (spring and summer), the wet conditions maintained a stable groundwater table and sustained a discharge of ca. 5–10 L s^{-1} without flow cessation (Fig. 2b). As a result, the wet streambed portion represented more than 60% of the bankfull during summer 2020, an

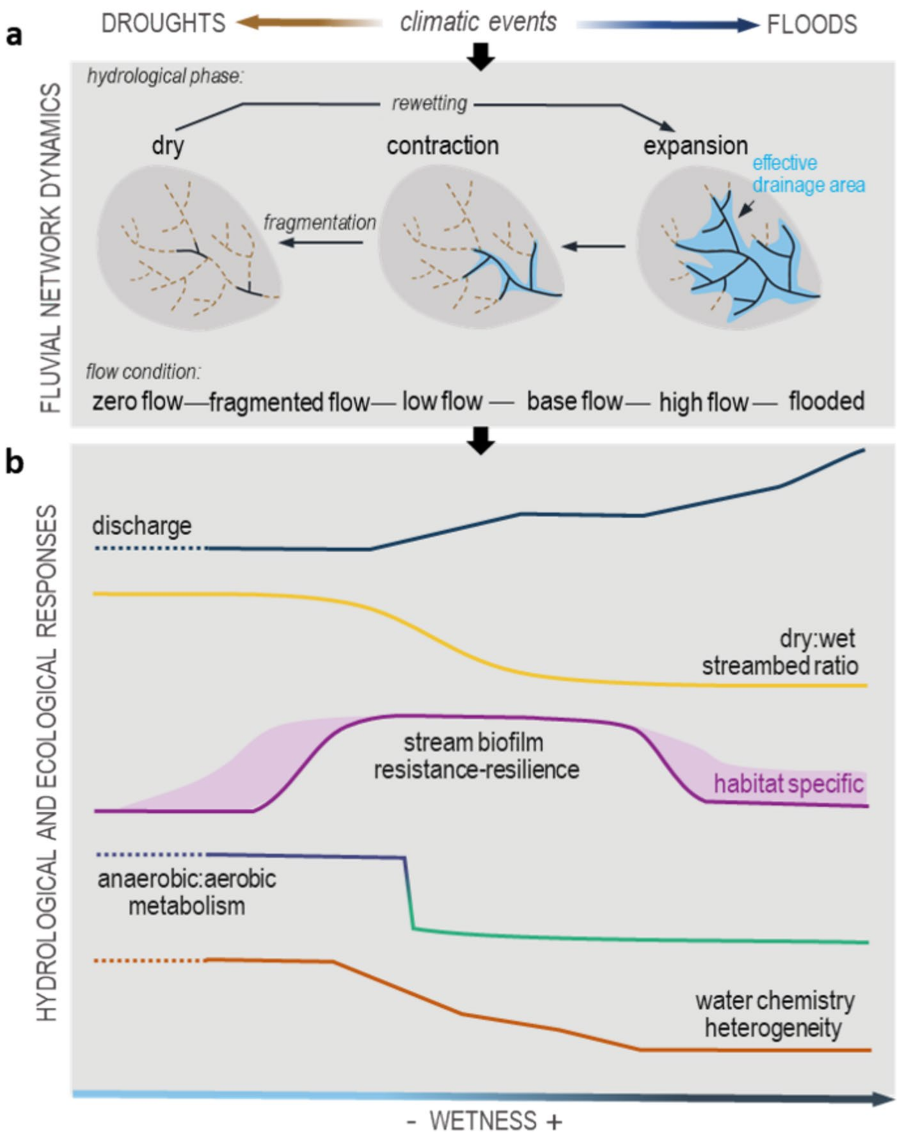

Fig. 1 Schematic representation of **a** fluvial network dynamics, including the three most important hydrological phases (expansion, contraction, dry) and the two specific transitional phases, rewetting and fragmentation along a wetness gradient in response to extreme climatic events (from droughts to floods). This panel also includes the gradation of flow conditions, from zero and fragmented flows (during droughts) to high flows and flooded conditions (during floods). The effective drainage area sourcing solutes and organic compounds to the stream is shown for each hydrological phase (blue areas). Panel **b** shows the hypothetical response of the hydrological and ecological processes of interest. The habitat-specific responses of stream biofilms to extreme hydrological events are represented with a purple shadow

extraordinary situation that ensured habitat availability and dispersion for aquatic species. In contrast, the extreme drought that hit the region during the following three water years (2021–2024) caused an abrupt contraction of the fluvial network in June 2023 and the subsequent drying out of the stream for 203 days. This dry phase included autumn of 2023 and early winter of 2024, seasons that are typically representative of the expansion phase of this intermittent stream (Bernal et al. 2013).

To date, most research in intermittent streams has been focused on understanding changes in longitudinal (Godsey and Kirchner 2014; Costigan et al. 2017) and lateral (Jasechko et al. 2021) hydrological connectivity during the contraction phase. However, there is still little knowledge on how contraction vs expansion phases influence surface-hyporheic exchange of water and solutes. Another major knowledge gap is predicting the timing and duration of the dry phase. Insights from Fuirosos suggest that antecedent moisture conditions, and in particular, the amount of rainfall accumulated during the non-vegetative period (from November to March) can be a good predictor of the duration of the annual dry phase. Note that for the period 2018–2024, this dry phase varied more than two

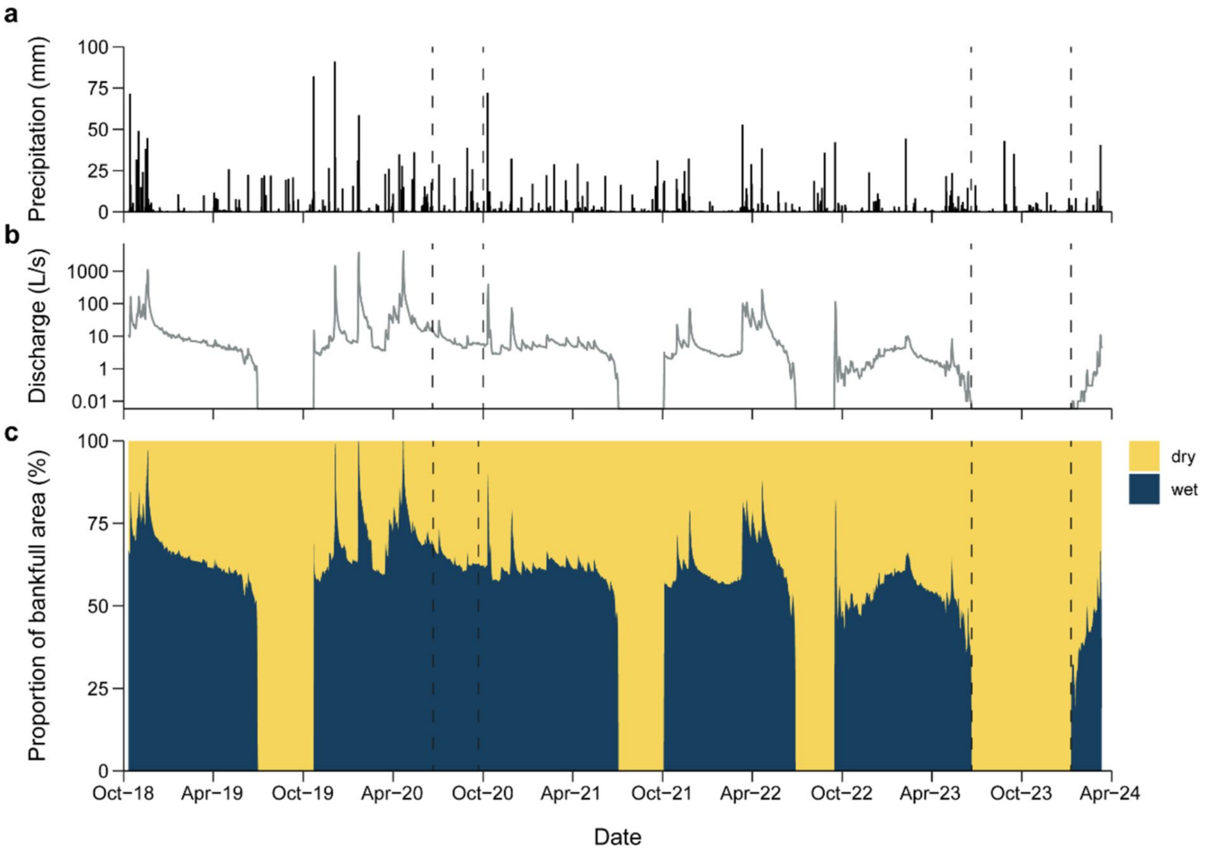

Fig. 2 Time series of **a** daily precipitation (P), **b** mean daily discharge and **c** the proportion of bankfull width covered by water (dark blue) and dry sediment (light orange) in a 150 m reach of the Fuirosos stream during the period October 2018–March 2024. In panel (b), discharge is shown in logarithmic scale. Dashed lines pairs bracket two contrasting situations: [1] the 2020 summer, when the stream did not dry up because of an unusually wet preceding period that included the extra-tropical cyclone Gloria (P during December 2019–April 2020 = 691 mm), and [2] the 2023 summer to 2024 early winter period, when the stream dried up for more than 6 months as a consequence of a severe drought impacting the region (average P during the period 2021–2023 = 456 mm year^{-1})

orders of magnitude (from 0 to 203 days per year) (Fig. 3). Riparian phenology, in particular the timing of leaf out, has been related to the onset of the contraction phase in other Mediterranean catchments (Lupon et al. 2016, 2018). More fundamental is the lack of appropriate observational hydrological data, which severely limits our understanding of hydrological processes in this type of stream (Gaume et al. 2009; Marchi et al. 2010). This is partially because of the difficulty to accurately estimate extremely low and high discharges (di Baldassarre and Montanari 2009; Seybold et al. 2023) and the extent of the contraction and expansion of entire fluvial networks. These methodological limitations pose challenges for upscaling and modeling the hydrology of intermittent streams (Shanafield et al. 2021), as well as their contribution to global carbon (C) and nitrogen (N) fluxes.

Response of stream microbial communities to extreme hydrological conditions

The strong seasonality of discharge observed in Mediterranean streams directly impacts freshwater biota, though our understanding on their responses to extreme hydrological events mostly derives from studies focused on macroinvertebrate and fish communities. For instance, as streams turn from contraction to dry phases, macroinvertebrate and fish species

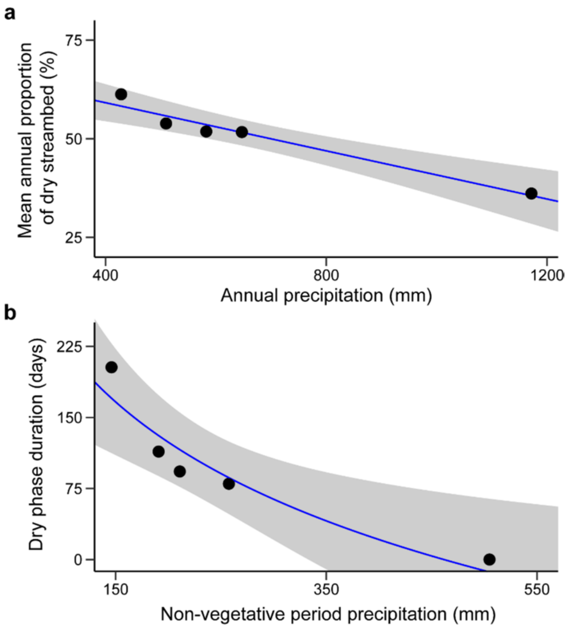

Fig. 3 Relationship between **a** annual precipitation and mean annual proportion of dry streambed from the total bankfull area in a 150 m reach of the Fuirosos stream for the five hydrological years 2018–2023 (linear regression, $R^2 = 0.95$, $p < 0.0001$), and **b** precipitation accumulated during the non-vegetative period (November-March) for the years 2018–2023 and the duration of the subsequent dry phase (logarithmic regression, $R^2 = 0.90$, $p < 0.0001$). The blue lines and gray areas represent the best fit and the 95% confidence intervals, respectively

adapted to aquatic environments are progressively replaced by those more resilient to desiccation (Cid et al. 2017). Prolonged droughts can reduce the size and diversity of fish populations, sometimes ending with local extinctions of the most sensitive species (Matthews and Marsh-Matthews 2003; Bêche et al. 2009). Similarly, large floods often lead to a decline in macroinvertebrate populations, with decline severity increasing with flood magnitude (Argerich et al. 2004). Microbial communities play a pivotal role in most biogeochemical processes and have a large contribution to global C and N fluxes (Falkowski et al. 2008). Thus, gaining knowledge on how microbial communities respond to floods and droughts is essential for elucidating how the acceleration of the hydrological cycle might affect the bioreactivity potential of streams and rivers.

Stream microbial communities show rapid responses, often within a few days, to extreme hydrological events (Merbt et al. 2011). The quite limited number of studies that have investigated microbial composition during or after extreme floods have shown contrasting results. Febria et al. (2012) observed abrupt decreases in microbial diversity following extreme flood events. Conversely, Caillon et al. (2021) found the opposite trend, and suggested that floods act as pulses of bacterial inoculation from terrestrial sources, thereby increasing microbial diversity. These divergences may arise from differences in antecedent moisture conditions, which control hydrological connectivity between groundwater and shallow soils, typically harboring more abundant and diverse microbial communities Caillon et al. (2021).

In Fuirosos, we examined the microbial community four weeks after the extratropical cyclone Gloria (as soon as the study site was accessible). We found significant differences in microbial assemblages after the flood compared to other seasons (purple circles, Fig. 4a), with communities being less diverse and dominated by fewer species (Peñarroya et al. 2023). Although we could not track sequential changes during and right after the Gloria storm, our finding suggests substantial disruption of bacterial communities, highlighting that any potential inoculation pulse induced by the storm Gloria did not persist over time. Remarkably, epipsammic microbial assemblages (i.e., growing in sediments) displayed greater differences from pre-flood conditions than epilithic microbial assemblages (i.e., growing in cobbles), which remained more similar to pre-storm conditions (Fig. 3a). This discrepancy between habitats implies that epipsammic biofilm in Fuirosos was either less resilient or less resistant to this perturbation, likely due to higher erosion, displacement, and disruption of this habitat during the flood. In line with this idea, Marxsen et al. (2010) proposed that microbial community composition following extreme flood events may differ significantly from pre-flood conditions, with only a few opportunistic species championing the recovery process. Likewise, Gionchetta et al. (2020) found that the largest shifts in microbial community composition and structure occurred under sporadic floods and rewetting conditions.

During the transition from contraction to dry phases, changes in microbial composition in Fuirosos were more gradual than during the exceptional conditions of the storm Gloria. Yet, the epilithic biofilm showed relatively higher dispersion in the ordination

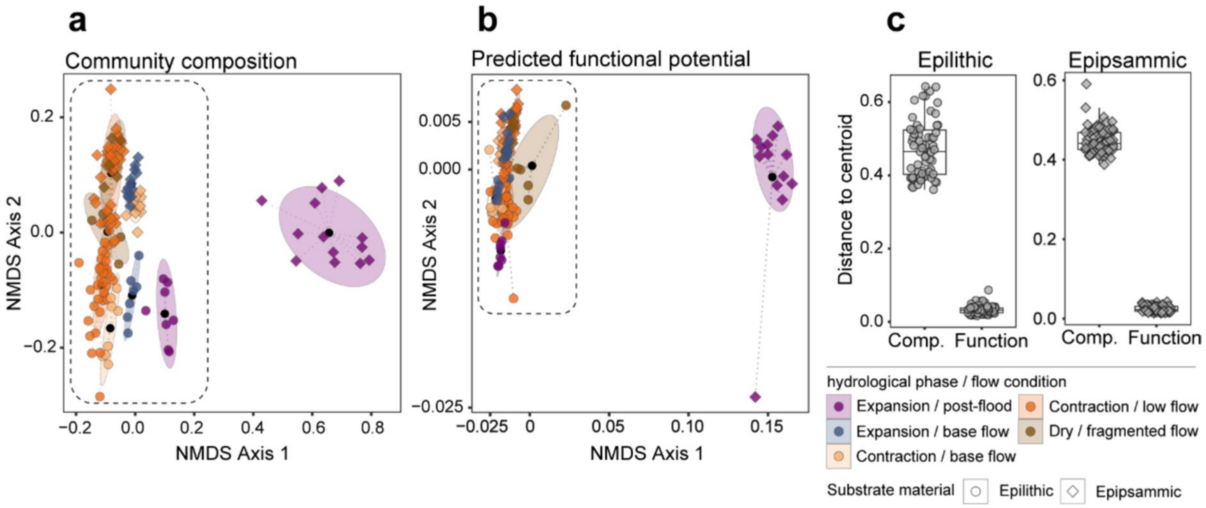

Fig. 4 Non-metric multidimensional scaling ordination analysis (NMDS) based on Bray–Curtis dissimilarities of **a** taxonomic composition of bacterial communities (16S rRNA genes) and **b** predicted whole functional potential (PICRUSt2 analysis) (Douglas et al. 2020) for a survey from 2020 to 2023 encompassing contrasting hydrological conditions in the Fuirosos stream ($n = 150$). Circles and diamonds correspond to epilithic (growing on cobbles) and epipsammic (growing on sediments) biofilms, respectively. Ellipses are drawn at 0.80 probability for the different hydrological conditions. Black circles are the centroid for each subgroup. Note that microbial assemblages from epilithic and epipsammic biofilms responded differentially to the extratropical cyclone Gloria, an extreme flood in 2020, with epipsammic samples being clearly separated from the pool. Panel (c) shows distances to a unique centroid calculated averaging all samples within the dashed lines in panels a and b (post-flood epipsammic samples excluded). Changes at the functional level (Function) were less marked than at the taxonomic level (Comp.) both in epilithic and epipsammic biofilms (hypothesis contrast tests p-value < 0.001). See methodological details in Peñarroya et al. (2023)

axis as contraction proceeded (orange vs brown circles, Fig. 4a), suggesting shifts in community structure as the stream moved from low to fragmented flows. In contrast, the epipsammic communities completely overlapped in the ordination plot during the contraction and dry phases (orange vs brown diamonds, Fig. 4a). This uniformity in community composition and structure suggests that epipsammic biofilm might be more resistant to drought than epilithic biofilm, likely because cobbles are more exposed to desiccation and colonization by terrestrial microbes, while sediments dry out more gradually and hold moisture for longer time periods (Sabater et al. 2016). Our findings underscore the importance of habitat diversification in providing resistance or resilience to environmental extremes and how its role changes depending on the nature of the disturbance (Fig. 1b).

As the dry phase progresses, substantial changes in the structure and composition of microbial communities occur, characterized by marked declines in both microbial community biomass and species richness (Febria et al. 2012; Gionchetta et al. 2020). In Fuirosos, previous studies had shown a reduction in the number of living cells immediately after flow cessation, followed by an increase after several weeks (Timoner et al. 2012). This behavior may result from surviving bacteria either acclimating to dry conditions or gradually being replaced by species adapted to terrestrial environments. Similarly, Gionchetta et al. (2020) reported an increase in the relative abundance of taxa common in arid and soil environments in experimental mesocosms under induced drought.

Overall, previous studies suggest that microbial assemblages in intermittent streams undergo more gradual changes during the transition from contraction to dry phases than after more abrupt perturbations such as rewetting and extreme floods. This difference is likely due to the adaptation to dry conditions of biofilms inhabiting intermittent streams by forming resistant structures such as crusts, mucilages, and cysts (Sabater et al. 2016). In Fuirosos we noticed that differences at the functional level (predicted metagenome functions with PICRUSt2) were less pronounced than at the taxonomic level (16S rRNA gene composition) across all hydrological phases (Fig. 4b and c). Previous studies in Fuirosos also indicate that microbial activity, ranging from enzyme production to C and N uptake, can rapidly return to pre-disturbance levels within a few days (Timoner et al. 2012; Merbt et al. 2016; Peñarroya et al. 2023). Similar results have been observed in other intermittent streams (Austin and Strauss 2011; Gómez et al. 2012). Taken together, these findings suggest high functional redundancy in stream biofilms (Louca et al. 2018), which can be an important strategy for microbial communities to cope with future increases in erratic and unpredictable hydrological conditions.

Shifts in stream water chemistry and biogeochemical processes under contrasting hydrological conditions

Floods and droughts represent end-points in the hydrological connectivity of terrestrial ecosystems with the recipient streams and rivers. Floods are characterized by the rapid movement of particles and solutes through catchments and river networks, often leading to uniform spatial patterns in water chemistry (Dent and Grimm 1999; Thomaz et al. 2007). The decrease in water residence time during large floods typically limits the capacity of streams to process nutrients and organic matter (Marcé et al. 2018), representing periods when terrestrial inputs are mostly pulsed and shunted downstream (sensu Raymond et al. 2016). Moreover, high advection and water velocity during floods increases gas exchange with the atmosphere, facilitating the release of greenhouse gasses such as CO_2 (Raymond et al. 2012).

In contrast, as discharge decreases, stream ecosystems transition from passive pipes to active bioreactors (sensu Casas-Ruíz et al. 2017), a change in behavior that has also been described as streams transitioning from transporters to transformers (Fazekas et al. 2021). First, the increase in water residence time fosters the interaction between solutes and biota, and thus promotes biogeochemical processing (Marcé et al. 2018; Li et al. 2021). Second, the decrease in groundwater inputs accentuates the influence of in-stream biogeochemical processes on stream water chemistry, emphasizing their bioreactivity at the landscape scale (Bernal et al. 2022; Li et al. 2024). Hydrological connectivity decreases as contraction progresses, and local factors become more influential on water chemistry. Consequently, there is often an increase in spatial heterogeneity in water chemistry and associated ecosystem processes, in both surface and hyporheic waters (Dent and Grimm 1999; von Schiller et al. 2017; Gómez-Gener et al. 2021). For example, the coefficient of variation of nutrient concentration can increase from 5- to sevenfold between the contraction and dry phases in intermittent streams (von Schiller et al. 2011). Similar trends have been observed in temperate, tropical, and boreal streams, where the variability of reactive solute concentrations disproportionally increases during low-flow periods (Gómez-Gener et al. 2020; Fazekas et al. 2021). The fragmentation of the river network also leads to more variable metabolic patterns in space. Some reaches may exhibit optimal conditions for primary production, while others may experience anoxic conditions due to high respiration rates (Sabater et al. 2016; Diamond et al. 2021). Thus, while the contraction and dry phases are hot moments of microbial activity and biogeochemical processing, the increase in spatial variability limits our capacity to predict water chemistry and assess the bioreactive capacity of streams (Gómez-Gener et al. 2021; Fazekas et al. 2021).

Likewise, the storage and processing of organic matter and solutes during the dry phase can be highly dependent on local conditions. Catalán et al. (2023) showed that, during the dry phase, particulate organic matter is mostly passively stored in the streambed. Yet, other compounds can be highly processed. Arce et al. (2019) concluded that dry sediments can support high rates of respiration and nitrification, leading to CO_2 emissions even higher than during phases with flowing waters. Upon rewetting, both the leaching of stored materials and pulses of microbial processing typically lead to peaks in solute concentrations (Austin and Strauss 2011; Gómez et al. 2012; Merbt et al. 2016). For instance, ecosystem respiration rates after flow resumption in Fuirosos are among the highest reported in the literature (Acuña et al. 2005). Capturing the rewetting phase is challenging, and the implications of these peaks in solute concentrations and biological activity are not yet fully understood. In some cases, drier conditions can lead to higher annual or seasonal fluxes after the drought. This pattern has been observed for nitrogen in suburban and agricultural catchments (Wollheim et al. 2005; Loecke et al. 2017), as well as for dissolved organic carbon (DOC) in forested headwater catchments (Weng et al. 2020). However, Fazekas et al. (2021) reported similar daily nutrient fluxes regardless of previous climatic conditions for a set of relatively unaltered temperate and tropical catchments. These contrasting results suggest that the impact of droughts on solute processing and export depends not only on drought severity, but also on antecedent climatic conditions and catchment characteristics such as topography and land use.

To explore how hydrological extremes can impact water chemistry and associated biogeochemical processes, we used data collected during a 2-year survey period (2021–2023) as a part of the regular monitoring strategy in Fuirosos. We focused on the shifts in two sets of solutes that can be related to reduced and oxidized processes of C and N cycling. The first set comprises the CO_2 vs O_2 ratio calculated from high temporal resolution data sets. This ratio represents the two sides of the coin of stream metabolism. Low CO_2:O_2 ratios indicate prevalent aerobic metabolism and high gas exchange with the atmosphere, typically occurring during expansion phases or floods. Conversely, high CO_2:O_2 ratios can result from either high CO_2 production or high O_2 depletion during respiration, especially during the contraction phase (Bernal et al. 2022). Our data set illustrates the emergence of a clear threshold in CO_2:O_2 ratios, which shifts from below 1 at discharges higher than ~3 L s^{-1} to above 5 at discharges below this threshold (Fig. 5a). The emergence of this inflection point aligns with the idea of an abrupt shift in redox conditions and metabolic flow paths, from aerobic towards anaerobic (Fig. 1b), which is further supported by the fact that high CO_2:O_2 ratios coincide with periods of low O_2 concentration (<5 mg L^{-1}) as the contraction phase advances (Fig. 5a, Bernal et al. 2022). A similar pattern has been reported in boreal streams during extreme summer droughts (Gómez-Gener et al. 2020).

The second set of solutes examined was the NH_4:NO_3 ratio, calculated from regular surveys conducted every two weeks. This ratio represents the balance between the most reduced (ammonium, NH_4^+) and oxidized (nitrate, NO_3^-) forms of dissolved inorganic N; and thus, captures the predominant N processes in the stream. During higher flows ($Q > 10$ L s^{-1}), NH_4:NO_3 ratios were below 0.5, suggesting enhanced nitrification, the microbial process that converts NH_4^+ to NO_3^- under aerobic conditions, either in the stream or in the hydrologically connected soils. In contrast, at lower flows, the NH_4:NO_3 ratio increased to values up to 2, suggesting both limited nitrification and enhancement of microbial processes that decrease NO_3^- concentrations under anaerobic conditions. These processes include dissimilatory NO_3^- reduction to NH_4^+ (DNRA), which would lead to NH_4^+ accumulation, and denitrification, which would transform NO_3^- into N gas (Peñarroya et al. 2024). Similar low ratios (NH_4:$NO_3 > 1$) have been measured in isolated pools as fragmentation progresses in Fuirosos (von Schiller et al. 2011).

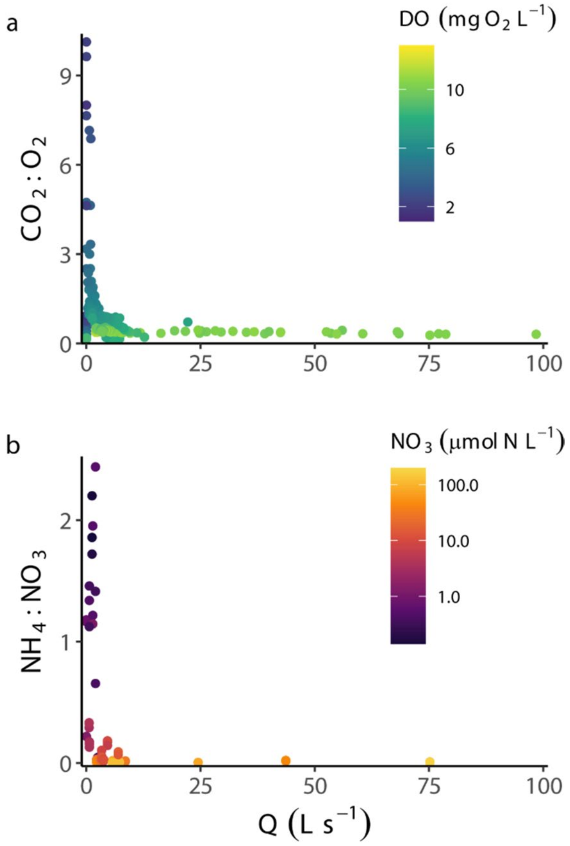

Fig. 5 Changes in **a** CO_2:O_2, and **b** NH_4:NO_3 molar ratios with discharge (Q) in the Fuirosos stream. Color scales show the concentration of the most oxidized solute for each ratio, O_2 and NO_3^-, respectively. Ratios in **a** are daily average values ($n = 339$) for the period from April 2019 to January 2023 obtained from in situ high-frequency monitoring (15-min time intervals). Ratios in **b** are calculated from grab samples taken during the periodic monitoring program from October 2021 to April 2023 ($n = 74$). Methodological details in Bernal et al. (2019; 2022)

The emergence of these thresholds in Fuirosos provides valuable insights into how redox conditions, metabolic pathways, and associated biogeochemical processes may vary between expansion and contraction phases in other streams. For instance, the observed increase in NH_4:NO_3 ratios as contraction proceeds is concordant with previous studies reporting higher concentration of reduced compounds during low flow conditions (Graham et al. 2024). This pattern is often linked to lower water quality and reduced O_2 availability, exacerbated by the decreased solubility of O_2 at higher temperatures. Moreover, this shift towards anaerobic conditions can increase the emissions of greenhouse gasses such as methane (Briée et al. 2007; Gómez-Gener et al. 2021; Zhi et al. 2023).

Hydrological contraction and expansion in river foundational concepts

The publication of the River Continuum Concept (RCC) by Vannote et al. (1980) marked a significant milestone in river ecology and biogeochemistry, providing a general framework on how matter and energy flow along river networks. The RCC has been revisited and refined over time, and physical dimensions not explicitly addressed in the original work have been incorporated, such as the temporal variability in discharge or lateral hydrological connectivity between river and riparian ecosystems (e.g., the Four-dimensional Nature of Lotic Ecosystems, Ward 1989). These previously missing dimensions are crucial for conceptualizing the expansion and contraction of river networks. New versions of the RCC have also incorporated extreme hydrological events, especially droughts, likely driven by the growing awareness of climate warming impacts on freshwater ecosystems. Allen et al. (2020) provided a comprehensive summary of the state of the art of river ecological conceptualizations, examining the extent to which current concepts in river ecology consider the particularities of temporary rivers. Building upon their work, we revisit and update their exercise, focusing on more specific aspects related to how foundational river concepts incorporate hydrological expansion, contraction, and dry phases. In particular, we pay attention to hydrological extreme events (floods and droughts), and assess whether they are captured in both time (e.g., periods of flow cessation) and space (e.g., spots of exposed dry sediments or fragmented pools) domains.

Paramount to the concept of contraction and expansion in river ecosystems is the hydrological connectivity between aquatic and terrestrial ecosystems. This connectivity—encompassing lateral, longitudinal, and vertical dimensions—is a fundamental component of river conceptualizations. Lateral connectivity with terrestrial ecosystems was already the cornerstone of the RCC, but mostly referred to direct inputs of terrestrial particulate organic matter rather than inputs of solutes via lateral flow. Nearly all conceptual models reviewed acknowledge lateral connectivity with surrounding terrestrial ecosystems (Table 1), but only 16 out of 27 explicitly included lateral inflow. In these models, lateral hydrological connectivity is often mediated by floods, leading to floodplain or riparian zone inundation, as exemplified by the Flow Pulse Concept (Tockner et al. 2000). This underscores the importance of floodplains in understanding the impact of large floods on river ecosystem processes, and resonates well with the idea of expansion and contraction of river networks. However, these conceptual models tend to focus on surface water interactions, overlooking the expansion and contraction of the subsurface component. These subsurface dynamics dictate how different catchment portions become connected or disconnected from the fluvial network; and thus, the origin of organic matter and nutrient subsidies. This concept, referred to as the hydrologically effective drainage area, has been already used in some catchment hydrological studies (e.g., Liu et al. 2020), though it still needs to be fully considered in river network models.

The longitudinal aspect of fluvial networks is explicitly recognized in most river conceptualizations considered (21 out of 27 models). However, only the conceptual models that include intermittent streams consider the contraction and expansion of river networks (e.g., Boulton et al. 2017), which is essential for understanding how droughts can impact habitat availability and biogeochemical fluxes. The vertical connectivity is represented in only 8 out of 27 models, despite the critical role that groundwater-surface water interactions play in providing refugia for biota, influencing water quality and biogeochemical processing, especially during fragmented flows in the contraction phase (Gómez-Gener et al. 2021). The

Table 1 Summary table of the 27 river ecosystem conceptualizations reviewed

Model	Aquatic terrestrial connectivity	Spatial dimension				Discharge		Biota				Stream functioning			Mention to IRES	Active vs Passive transport	Processing in dry portion	Quantitative framework
		Longitudinal	Lateral	Vertical	Across regions	Discrete	Continuous	Habitat diversity	Bio diversity	Life cycles	Food webs	Metabolism	Organic Matter	Nutrients				
River continuum concept[1]	●	●	●									●	●					
Nutrient spiralling concept[2]		●				●								●		●		●
4-dimensions of streams[3]	●	●	●	●					●				●	●			●	
Flood pulse concept[4]	●		●	●			●	●	●				●	●	○	●		
Serial discontinuity concept[5]		●							●			●	●	●				
Hyporheic corridor concept[6]	●	●		●						●			●	●		●		
Riverine productivity model[7]	●	●	●								●		●			●		
Natural flow regime[8]	●	●	●				●	●	●		●				○			
Telescoping ecosystem model[9]	●	●	●	●			●							●	●	○	○	●
Process domains[10]	●	●						●										
Flow pulse concept[11]	●		●				●							●	○			
Fluvial landscape ecology[12]	●	●	●	●					●				●	●				●

Table 1 (continued)

Model	Aquatic terrestrial connectivity	Spatial dimension				Discharge		Biota				Stream functioning			Mention to IRES	Active vs Passive transport	Processing in dry portion	Quantitative framework
		Longitudinal	Lateral	Vertical	Across regions	Discrete	Continuous	Habitat diversity	Bio diversity	Life cycles	Food webs	Metabolism	Organic Matter	Nutrients				
Network dynamics hypothesis[13]	●				●			●										
Riverine ecosystem synthesis[14]	●				●	●			●				●	●		•		
Multiple roles of water[15]	●	●				●			●	●					●			
River wave concept[16]	●	●	●				●						●	●		●		
Natural sediment regime[17]	●	●	●				●											
Pulse shunt concept[18]	●	●				●							●			●		●
Hydrological connectivity in IRES[19]	●	●	●	●		●							●	●	●	○	●	
Biogeochemical heartbeat[20]	●	●	●	●		●							●	●	●	●	●	
River network saturation concept[21]	●	●					●						●	●	○	●		●
Stream biome gradient concept[22]	●				●				●			●			○			
Bending DOM concept[23]	●	●	●			●							●			●		
Drivers of leaf litter decomposition[24]	●						●						●		●			

Table 1 (continued)

Model	Aquatic terrestrial connectivity	Spatial dimension				Discharge		Biota				Stream functioning			Mention to IRES	Active vs Passive transport	Processing in dry portion	Quantitative framework
		Longitudinal	Lateral	Vertical	Across regions	Discrete	Continuous	Habitat diversity	Bio diversity	Life cycles	Food webs	Metabolism	Organic Matter	Nutrients				
Grandi & Bertuzzo[25]	●	●	●			●							●		○			●
Pulse-shunt-storage concept[26]	●	●	●			●							●		●	●	●	●
Multi-dimensional river corridor[27]	●	●	●	●		●	●	●	●				●	●	○			●
Total	25	21	16	8	3	9	9	5	9	2	2		18	14	●6/○7	●11/○2	●4/○1	7

The models were classified into categories by their focus on: the connectivity with terrestrial ecosystems (longitudinal, lateral, vertical) and across regions, the temporal dynamics of discharge, either as a discrete or continuous variable, and ecosystem processes related to either stream biota or stream functioning. We highlight when models mention directly (●) or indirectly (○): the existence of intermittent and ephemeral streams (IRES); active vs passive transport in wet stream portions; and biogeochemical processing in the dry portion. The final column indicates whether the conceptual model is directly associated with a quantitative framework. Active vs passive refers to the dual capacity of streams to act either as conservative conduits or storages (low biogeochemical processing) or as bioreactors (high biogeochemical processing). Models listed in chronological order

[1]Vannote et al. (1980), [2]Newbold et al. (1981), [3]Ward (1989), [4]Junk et al. (1989), [5]Stanford and Ward (1993a), [6]Standford and Ward (1993b), [7]Thorp and Delong (1994), [8]Poff et al. (1997), [9]Fisher et al. (1998),[10]Montgomery (1999), [11]Tockner et al. (2000), [12]Poole (2002), [13]Benda et al. (2004), [14]Thorp et al. (2008), [15]Sponseller et al. (2013), [16]Humphries et al. (2014), [17]Wohl et al. (2015), [18]Raymond et al. (2016), [19]Boulton et al. (2017), [20]von Schiller et al. (2017), [21]Wollheim et al. (2018), [22]Dodds et al. (2019), [23]Casas-Ruíz et al. (2020), [24]Follstad Shah et al. (2021), [25]Grandi and Bertuzzo (2022), [26]Catalán et al. (2023), [27]Wymore et al. (2023)

temporal variability of river discharge is considered in most model conceptualizations (18 out of 27), either as a discrete set of hydrological conditions (baseflow, floods, droughts) (e.g., the Pulse-Shunt Concept, Raymond et al. 2016) or as a continuous variable (e.g., the Bending DOM Concept, Casas-Ruíz et al. 2020). This widespread incorporation of discharge dynamics highlights that temporal patterns of expansion and contraction are well-rooted in our perception of river ecology and functioning. However, few models explicitly mention the existence of zero-flow conditions, prevalent in intermittent rivers (only 6 out of 27) (Table 1). Overall, 23 of the 27 conceptual models reviewed lacked at least one physical dimension related to hydrological connectivity, a limitation previously highlighted by Wymore et al. (2023) after reviewing 38 river corridor conceptual frameworks. They argue that only a multi-dimensional perspective, similar to that used in critical zone science, can adequately capture hydrological expansion and contraction patterns and their implications for ecosystem functioning in fluvial networks.

There is a suite of ecological processes included in river ecosystem conceptualizations, from community composition and structure (habitats and species diversity, life cycles, food webs) to stream metabolic activity and the processing of organic matter and nutrients, N in particular (Table 1). These ecosystem processes have been examined individually (e.g., particulate organic matter in the Pulse-Shunt-Storage Concept, Catalán et al. 2023), or in combination. For instance, some conceptualizations have linked organic matter processing with species diversity (e.g., Stanford and Ward 1993a, b), while others have jointly considered biogeochemical processing of organic matter and nutrients (e.g., Humphries et al. 2014). As the idea of rivers as landscape bioreactors consolidates, particularly in terms of their relevance for global C cycling (Cole et al. 2007), conceptual models have started to focus more on specific C pools such as DOC. This has led to the development of conceptual models that combine biogeochemical and hydrological processes (e.g., Raymond et al. 2016; Catalán et al. 2023; Grandi and Bertuzzo 2022; Casas-Ruíz et al. 2020). The majority of the conceptual models reviewed only consider biogeochemical processes in wet channels, disregarding potential processes occurring in exposed dry river beds. Yet, empirical studies clearly show that dry sediments can substantially contribute to both nutrient cycling (Gómez et al. 2012) and greenhouse gas emissions (von Schiller et al. 2014). Biogeochemical processing in the dry portion of the river bed is considered only in four conceptual models (Table 1), while other ecological aspects, such as the influence of dry sediments on stream biodiversity, are considered in only one model (Ward 1989).

River ecosystem conceptualizations are valuable tools for improving our mechanistic understanding of running waters and for generating new hypotheses to be tested through experimental designs and mathematical frameworks. However, extraordinarily useful concepts in river ecology often do not find an obvious translation into numerically tractable equations. This translation process becomes easier when the conceptualization already includes a quantitative framework that facilitates field measurements and predictions. Yet, the development of a mathematical framework requires a clear definition of the spatial and temporal scale of the processes at play, which is not straightforward. Indeed, only 7 out of the 27 models reviewed were accompanied by a well-developed quantitative framework, such as the Nutrient Spiraling Concept (Newbold et al. 1981) or the Pulse Shunt Concept (Raymond et al. 2016). These models share some common characteristics: they focus on biogeochemical cycling; they quantify transport and processing of different compounds during different flow conditions (at least to some extent); and they can be applied to additional compounds whenever processing coefficients can be defined. However, none of them readily incorporate biogeochemical processing within dry streambeds. An exception is the Pulse-Shunt-Storage concept (Catalán et al. 2023), a model conceptualization inspired by the Pulse-Shunt concept (Raymond et al. 2016), and specifically designed to quantify storage, processing, and transport of particulate organic matter in the dry portion of the streambed. Overall, the scarcity of quantitative frameworks highlights the challenge of translating rich and complex concepts and ideas about ecological processes into simple, somewhat reductionist, mathematical frameworks. This challenge becomes even more apparent when considering the spatiotemporal variability characteristic of the contraction and dry phases in intermittent streams.

Final remarks and future challenges

The expected intensification of the hydrological cycle, with more frequent and intense floods and droughts, poses important technological, methodological, and conceptual challenges for assessing hydrological and ecological processes in freshwater ecosystems. In this evolving context, fluvial networks cannot be treated as static features, but as highly dynamic ecosystems that expand and contract over time and space (Stanley et al. 1997). The Fuirosos stream, with its natural intra- and inter-annual variability in wet width, served as an example of such high hydrological variability. There are still significant methodological constraints in accurately estimating key hydrological variables. For instance, measuring extremely low and high discharges remains a challenge, particularly in ungauged catchments (di Baldassarre and Montanari 2009; Seybold et al. 2023). Wet width and fluvial network length, essential variables for assessing aquatic habitats and riverine transport, become especially intractable during contraction and dry phases as fluvial networks retract and surface flow fragments. Previous attempts to document the expansion and contraction of fluvial networks have involved exhaustive fieldwork under different flow conditions. In California, for instance, the length of headwater fluvial networks can decrease by a factor of two or three during the contraction phase (Godsey and Kirchner 2014). While these case studies, including those in Fuirosos, are insightful, their conclusions are site-specific, making extrapolation to other catchments or environmental contexts difficult. Simple approaches based on topography (e.g., Prancevic and Kirchner 2019), are promising for estimating the effective size of the fluvial network at large scales. However, these methods still need testing in water-scarce regions with more erratic hydrological regimes. Changes in the effective catchment drainage area and groundwater-surface water connections between expansion and contraction phases remains one of the most difficult issues in stream hydrology (Gómez-Gener et al. 2021). Yet, vertical connectivity is essential for quantifying refugia for stream biota and identifying drivers of spatial heterogeneity of microbially-mediated biogeochemical processes during fragmented and no-flow conditions.

Regarding stream microbial communities, there is still a lack of studies focused on extreme floods and their post-flood impacts, primarily because these events are unpredictable and extremely difficult to capture. Future research should focus on better understanding the underlying mechanisms driving changes in microbial communities during these extreme events. Factors such as antecedent soil moisture conditions, flood characteristics, and microbial community traits may all play critical roles in shaping microbial responses to floods. Conversely, the contraction, dry, and rewetting phases have been well-documented in the literature (e.g., Sabater et al. 2016). Many of these studies have been conducted in Fuirosos and nearby streams, motivated by the substantial amount of research conducted in this Mediterranean catchment over the last two decades (Vázquez et al. 2013). While further research in other regions and climatic contexts are necessary, available results suggest that microbial assemblages are generally more resistant to droughts than to extreme floods. Yet, this response varies depending on the type of habitat. In Fuirosos, for instance, epilithic biofilm (growing on cobbles) seem to be more resistant to floods than epipsammic biofilm (growing on sediments), while the latter is typically more resistant to desiccation. This difference underscores the importance of promoting habitat heterogeneity in stream ecosystems to provide refugia for microbial communities, thus contributing to the resilience and fast recovery after large hydrological perturbations. We found that functional redundancy likely helps minimize the impact of extreme hydrological events on microbial communities. Both functional redundancy and resilience are two promising avenues for future research on microbial communities in streams experiencing hydrological extremes, and our results encourage further exploration by combining massive functional metagenomic approaches, high-performance bioinformatics processing and experimental testing.

Hydrological expansion and contraction have a clear impact on riverine biogeochemical processing, as evidenced by the abrupt shifts in solute ratios observed in Fuirosos. However, the extent to which the intensification of the hydrological cycle affects the role of streams as passive conduits or active bioreactors remains elusive. Extreme floods increase the rapid transport of solutes and particulate organic matter downstream, limiting the opportunity for onsite biogeochemical processing, while the stream bioreactive capacity may intensify during low and fragmented flows. Yet, the latter may not necessarily translate to increased nutrient or organic matter retention; and thus, to better water quality (Casas-Ruíz et al 2017). In fact, extremely low and fragmented flows clearly decrease the quality of water resources (Mosley 2015). High-temporal resolution sensors offer potential to capture rapid changes in water chemistry, especially during floods and rewetting phases, which can then be associated with shifts in stream dynamics along the transporter-to-transformer continuum (e.g., Fazekas et al. 2021). Moreover, they can also help us to integrate the spatial variability of biogeochemical processes during the transition from contraction to dry phases.

Field experiments and surveys need to be carefully designed to accurately resolve mass balances in fluvial networks with marked expansion and contraction phases, and both dry and wet portions of the streambed need to be considered to better understand how alternating droughts and floods impact the transport, storage, and biogeochemical processing of nutrients and organic matter. Addressing this complexity requires an integrated view on how discharge fluctuations drive shifts in water chemistry, greenhouse gas emissions, and biogeochemical processes. Our empirical, conceptual and quantitative frameworks need to embrace this complexity, and expand to better integrate contraction and dry phases.

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Author contributions SB contributed to the study conception and structure with inputs from all the other coauthors. Data analysis and first draft of each section was developed by: SB for the introduction and final remarks section; JLL and AL for the hydrological section, XP, XT, and EOC for the microbial section, GRR and CJ for the water chemistry section, RM and NC for the river conceptualization section. All sections were edited by SB with input and feedback from the rest of coauthors. GRR standardized and revised data analysis and R codes. All authors read and approved the final manuscript.

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Data availability The data sets analyzed during the current study is available in available http://www.hydroshare.org/resource/b7f9d294de0941a485d5daba466d0fce.

Declarations

Competing interest The authors have no relevant financial or non-financial interests to disclose.

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