# Causes, responses, and implications of anthropogenic versus natural flow intermittence in river networks

Thibault Datry[1], Amélie Truchy[1], Julian D. Olden[2], Michelle H. Busch[3], Rachel Stubbington[4], Walter K. Dodds[5], Sam Zipper[6], Songyan Yu[7], Mathis L. Messager[1,8], Jonathan Tonkin[9,10,11], Kendra Kaiser[12], John Hammond[13], Eric K. Moody[14], Ryan M. Burrows[15], Romain Sarremejane[1], Amanda DelVecchia[16], Megan L. Fork[17], Chelsea J. Little[18], Richard H. Walker[19], Annika Walters[20], Dan Allen[21]

[1]INRAE, UR RiverLy, Centre Lyon-Grenoble Auvergne-Rhône-Alpes, 5 rue de la Doua CS70077, 69626 Villeurbanne Cedex, France

[2]School of Aquatic and Fishery Sciences, University of Washington, Seattle WA USA 98105

[3]Department of Biology, University of Oklahoma, Norman, OK 73019 USA

[4]School of Science and Technology, Nottingham Trent University, UK

[5]Divison of Biology, Kansas State University, Manhattan, KS 66502, USA

[6]Kansas Geological Survey, University of Kansas, Lawrence, KS, USA

[7]Australian Rivers Institute and School of Environment and Science, Griffith University, Nathan, Queensland, Australia 4111

[8]Department of Geography, McGill University, 805 Sherbrooke St W, Montreal, Quebec H3A 0B9, Canada

[9]School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch 8014, New Zealand

[10]Te Pūnaha Matatini, Centre of Research Excellence in Complex Systems, New Zealand

[11]Bioprotection Aotearoa, Centre of Research Excellence, New Zealand

[12]Department of Geosciences, Boise State University, Boise, ID, USA

[13]Department of Ecosystem Science and Sustainability, Colorado State University, Fort Collins, Colorado, USA

[14]Department of Biology, Middlebury College, Middlebury, VT 05753 USA

[15]School of Ecosystem and Forest Sciences, The University of Melbourne, Burnley Campus, Burnley 3121, Victoria, Australia

[16]Department of Biology, Duke University, Durham, NC 27708, USA

[17]Department of Biology, West Chester University, West Chester, PA 19383, USA

[18]School of Environmental Science, Simon Fraser University, Burnaby, British Columbia, Canada

[19]Department of Biology and Chemistry, Upper Iowa University, Fayette, Iowa, 52142, USA

[20]U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department of Zoology and Physiology and Program in Ecology, University of Wyoming, Larame, WY 82071, USA

[21]Department of Ecosystem Science and Management, The Pennsylvania State University, University Park, PA, 16802, USA

**Corresponding author**: Thibault DATRY, Thibault.datry@inrae.fr

**Keywords:** *global change, drying, freshwaters, biodiversity, ecosystem function, flow management, restoration, conservation*

**Statistics:** Main text: 5419 words, 95 references, 2 tables, 4 figures, 3 appendices

**Abstract:**

Rivers that do not flow year-round are the predominant type of running waters on Earth. Despite a burgeoning literature on *natural* flow intermittence (NFI), knowledge about the hydrological causes and ecological effects of human-induced, *anthropogenic* flow intermittence (AFI) remains limited. NFI and AFI could generate contrasting hydrological and biological responses in rivers due to distinct underlying causes of drying and evolutionary adaptations of their biota. We first review the causes of AFI and show how different anthropogenic drivers alter the timing, frequency and duration of drying, compared to NFI. Second, we evaluate the possible differences in biodiversity responses, ecological functions, and ecosystem services between NFI and AFI. Last, we outline knowledge gaps and management needs related to AFI. Due to the distinct hydrologic characteristics and ecological impacts of AFI, ignoring the distinction between NFI and AFI could undermine management of intermittent rivers and ephemeral streams and exacerbate risks to the ecosystems and societies downstream.

**Introduction**

Rivers and streams that cease to flow (hereafter, IRES; Intermittent Rivers and Ephemeral Streams) dominate global river networks, naturally comprising an estimated 60% of the total river length (Messager et al. 2021). Natural flow intermittence (NFI) is driven by climatic, hydrological, geological, and geomorphological drivers (Larned et al. 2010, Costigan et al. 2016, Hammond et al. 2021). However, humans are altering flow regimes worldwide, as illustrated by the dramatic and widespread changes in flow intermittence duration and timing in the United States, including longer drying durations in many regions, earlier drying in the south, and later drying in the north (Zipper et al. 2021). Such increases in flow intermittence are echoed around the world, with formerly perennial rivers becoming intermittent due to global change across all continents (Larned et al. 2010). In recent decades, six of the largest rivers on Earth have become intermittent in their mainstem, and over 400 rivers in Europe have dried earlier and for longer (Tramblay et al. 2021).

Research on the effects of NFI has accelerated in the past 15 years, reversing years of relative neglect of this topic by the scientific community (Datry et al. 2014, Leigh et al. 2016). Knowledge of these systems now spans many disciplines, including hydrology (e.g., Shanafield et al. 2021), geography (e.g., Messager et al. 2021), toponymy (e.g., Busch et al. 2020), biodiversity (e.g., Soria et al. 2017), biogeochemistry (e.g., Gómez-Gener et al. 2021), socio-economics (e.g., Fovet et al. 2021), ecology (e.g., Allen et al. 2020), and resource management (e.g., Acuña et al. 2020). Drying influences the spatial and temporal distribution of water, nutrients, materials and organisms, thereby controlling ecological functions in river networks (Datry et al. 2014). For example, drying events generally have negative effects on aquatic species, which can be detected weeks, months or years after rewetting (Datry et al. 2014, Gauthier et al. 2021, Sarremejane et al. 2022). Ultimately, the effects of drying events

cascade onto biogeochemical functions and ecosystem services (Datry et al. 2018, Fovet et al. 2021, Kaletova et al. 2021). This growing interest in and understanding of IRES is gradually improving management practices (Mazor et al. 2014, Steward et al. 2018), although national legislation and policy protecting these systems still lags behind that afforded to perennial rivers (Marshall et al. 2018).

Our understanding of the effects of human-induced, anthropogenic flow intermittence (AFI) has not kept pace with the growing research on NFI. The hydrological features and associated ecological impacts of AFI are likely to differ from those of NFI. For example, rivers located downstream of hydropower dams can experience predictable dry periods in response to hydropower use, which often show daily or weekly cycles that contrast with the lower predictability and frequency of NFI (Widén et al. 2021). In various cases, however, human imprints on drying patterns are indistinguishable from natural ones because artificial and natural drivers interact to cause drying events (Snelder et al. 2013). Differences between AFI and NFI rivers may be particularly challenging to parse due to the impacts of climate change, because changing precipitation patterns alter drying patterns in both natural and anthropogenic IRES.

Beyond hydrology, the biological and biogeochemical effects of AFI could differ from those of NFI. In NFI, many organismal responses to cope with drying, whether through resistance or resilience strategies, have emerged from the long-term (> millennia) action of evolution. Such a timescale is orders of magnitude greater than that of the hydrological shift to AFI, which has occurred over decades to centuries. Accordingly, it is reasonable to hypothesize that AFI has stronger effects on biotic communities than NFI, because changes from perennial to intermittent flow regimes could represent tipping points that lead river networks to irreversible, novel states (Zipper et al. 2022). Insufficient knowledge to test such

predictions jeopardizes the effectiveness of current management practices including biomonitoring (Crabot et al. 2021a) and the implementation of environmental flows (Acuña et al. 2020). If physical and biological responses vary between AFI and NFI, so will the responses of ecosystem functions and services.

Here, to the best of our knowledge, we are the first to explore differences between the effects of anthropogenic and natural flow intermittence (AFI and NFI, respectively) on hydrology, biodiversity, ecological functions and ecosystem services in IRES, and review the implications in terms of science, management and policy. First, we discuss sources of AFI and contrast their hydrological signatures with NFI. Second, we investigate why and how the effects of drying differ between AFI and NFI with respect to their biodiversity, ecological functions and ecosystem services. We then identify current knowledge gaps and research priorities, pointing to implications of the differences between AFI and NFI for IRES policy and management.

**What are the drivers of human-induced flow intermittence and their hydrological signatures?**

Multiple human activities can lead to AFI (Zimmer et al., 2020), which we broadly group into four drivers used throughout the paper: 1) water abstraction and diversion, 2) water storage and flow regulation, 3) land-use change, and 4) climate change (**Table 1, Appendix 1 & 2**). While anthropogenic drivers of intermittence can be broadly grouped into these four categories, multiple types of human activities often interact to cause AFI (Doretto et al. 2020). These interactions, specific human activities (e.g., urbanization versus afforestation), and the hydro-climatic and regulatory context of the river can alter streamflow in various ways.

*(1) Water abstraction and diversion* are a ubiquitous cause of AFI (Larned et al. 2010), encompassing various mechanisms, including surface water extraction, groundwater pumping, and surface water diversion (**Table 1**). AFI due to water abstraction and diversion is distinguished from NFI by longer no-flow durations, earlier first no-flow occurrences, and shorter duration of dry-down periods in both Australian and US IRES (**Figure 1a, 1b, Appendix 1**). Longer no-flow durations may be due to increased water use and decreased return flows (i.e., water that returns to the river system after use, including runoff from irrigated fields). Earlier first occurrence of no-flow suggests that anthropogenic water use can trigger earlier seasonal drying than would have occurred naturally, thereby also reducing late-season water availability. Shorter duration of dry-down periods may reflect an acceleration of baseflow recession caused by either surface-water or groundwater abstraction; the former reduces inflows from upstream while the latter reduces storage of groundwater, later release of which sustains flow during dry periods.

*(2) Water storage and flow regulation* by reservoirs for irrigation, flood control, or hydroelectric power generation affects over one-sixth of the total annual river flow globally (**Table 1**; Hanasaki et al. 2006). Dams have extensive impacts on both upstream and downstream ecosystems through flow regime alterations (**Figure 1c, d**; **Appendix 1**; Grill et al. 2019). Flow regulation by reservoirs usually decreases flow variability, shortening or preventing no-flow events, and in extreme cases, causing complete drying of riverbeds for kilometers downstream or preventing natural drying (Allen et al. 2013). However, hydropeaking flow regimes can impart highly unnatural flow variability and create artificially dry banks that fluctuate hourly (Abernethy et al. 2021). The hydrological signature resulting from flow regulation depends on reservoir use (e.g., hydroelectricity, irrigation, flood control), river type (e.g., size, seasonality), and local environmental regulations. For example, environmental flows implemented for downstream river sections may attenuate the effects of

flow regulation and even prevent AFI (Mackie et al. 2013). Additional classification of pre-impoundment hydrological regimes and characterization of dam-induced regime shifts would enable further assessment of how this widespread infrastructure impacts flow intermittence.

*(3) Land-use change,* which we define broadly to include changes in land use, land cover, and land management practices, can impact no-flow characteristics by altering runoff generation and groundwater recharge processes within catchments — how much and how fast precipitation infiltrates, is lost to evapotranspiration, or runs off land surfaces. Different types of land-use change have varying impacts on flow intermittence because of their unique influence on hydrological processes (**Table 1, Figure 1e, 1f, Appendix 1**). For example, urbanization increases the proportion of impervious surfaces, which generally increases high flows, but can also both increase and decrease low-flow events (Bhaskar et al. 2020). While water abstraction is probably the main cause of AFI in agricultural landscapes, conversion of natural ecosystems to crops or pasture, as well as afforestation, can also shift the timing and magnitude of evapotranspiration, runoff, and groundwater recharge (Levy et al. 2018). However, changes to flow intermittence resulting from agricultural expansion depend on the local water balance, management practices, and the water balance of the crop type compared to the natural vegetation that preceded land-use change.

*(4) Climate change* is altering river flows globally (Villarini and Wasko 2021) and is particularly challenging to disentangle from other drivers of AFI. Patterns of change associated with climate-change-driven AFI are distinct from other causes of AFI in that they tend to act at larger spatial and longer temporal scales, but are superimposed upon natural meteorological variability. Natural interannual variability in weather and local geophysical conditions, which in turn create variability in intermittent flow regimes, blur the signal of climate change (Snelder et al. 2013, Hammond et al. 2021). Therefore, identifying climate-

change-driven AFI would require linking climate attribution science, such as tools developed for heatwaves and floods (Zhai et al. 2018), with flow intermittence models to determine the relative proportion of flow intermittence linked to natural climate variability and anthropogenic climate change. In the US and Europe, no-flow events are generally increasing in duration and occurring earlier in regions that have increased in aridity in recent decades (**Table 1,** Zipper et al. 2021, Tramblay et al. 2021). An earlier onset of no-flow compared to historical conditions may thus be a useful signal of climate-driven AFI. However, there is substantial local and regional variability in the impacts of climate change (**Figure 1g, h, Appendix 1**). In the US, for example, climate change may be increasing drying durations in southern, arid areas, whereas in northern streams, flow cessation is driven by stream freezing and climate change may be decreasing no-flow durations and delaying the onset of no-flow conditions in winter (Zipper et al. 2021).

**Do biodiversity responses differ between natural and anthropogenic flow intermittence?**

Shifts among lotic (flowing water), lentic (standing water), and terrestrial (dry riverbed) phases are supposedly associated with pronounced stepwise shifts in biological communities (Boulton 2003). However, empirical evidence of pronounced shifts is rare in NFI. The taxonomic richness of most aquatic taxa decreases linearly as annual flow intermittence increases (Datry et al. 2014, Soria et al. 2017), which may be due to physiological, behavioral, and phenological strategies among the different species that tolerate drying conferring resistance and resilience to biotic communities (Datry et al. 2014; **Appendix 3**). For example, many species tolerate desiccation through dormant life stages, including insects (Bogan 2017), mussels (Lymbery et al. 2021), amphibians (Hillman et al. 2009), crayfish (Kouba et al. 2016), algae and macrophytes (Sabater et al. 2017), riparian plant (Rood et al. 2003, Stella and Battles 2010, Katz et al. 2011) and fish (Eldon 1979). Local decreases in

taxonomic richness can concur alongside regional increases in beta diversity (Katz et al. 2012, Crabot et al. 2020, Gauthier et al. 2020). This contrast stems from the different hydrological phases that coexist at the river network scale, with each phase supporting community successional stages with different compositions (Larned et al. 2010, Katz et al. 2012). Monotonic decreases in functional diversity occur along gradients of increasing flow intermittence (Crabot et al. 2021a), with limited functional redundancy and no evident thresholds of change.

In contrast to the rapidly growing body of ecological literature on NFI, biodiversity responses to AFI remain poorly studied (Aspin et al. 2019, Crabot et al. 2020). AFI often results from pressures (e.g., irrigation) which can cause other concurrent stressors (e.g., poor water quality and altered thermal regimes), that can in turn alter communities (see below "Context-dependence of the effects of AFI"). While communities often return to their pre-drying composition within weeks to months in hydrologically well-connected catchments, irreversible community shifts to alternative stable states are more likely at isolated sites (e.g., Bêche et al. 2009). Shifts from perennial to intermittent flow regimes driven by seasonal pressures may prevent community recovery to pre-disturbance composition: example cases include water abstraction to irrigate agricultural land (Peralta-Maraver et al. 2020) or climate-change-driven decreases in summer rainfall (Bogan and Lytle 2011, Carey et al. 2021). Aquatic communities impacted by AFI may comprise nested subsets of the taxa present before drying occurs in AFI streams and before the increases in the dry period duration for NFI streams (Datry et al. 2014). The remaining taxa typically harbor traits that promote colonization after flow resumes, either from in-situ wet refuges including pools, subsurface sediments, or nearby perennial waters (Vander Vorste et al. 2016b). These colonists may increase in abundance over time to fill the ecological niches left vacant by the elimination of drying-sensitive functional equivalents (Carey et al. 2021). However, the long-term

biological responses to AFI remain poorly documented, limiting our ability to anticipate the effects of global change on riverine biodiversity.

When previously perennial streams experience unprecedented drying events, or when NFI streams are drying much longer due to artificial causes, ecological tipping points are crossed, leading to dramatic responses in which community composition is pushed to novel and irreversible states (Aspin et al. 2019, Crabot et al. 2020). These shifts occur because perennial stream biota typically lack adaptations to cope with drying, and because dramatic top-down changes to food chains can occur when drying eliminates top predators (e.g., fish, odonates) or increases terrestrial predation, leading to disruption of trophic interactions and partial food web collapse (McHugh et al. 2015, Steward et al. 2022). Over time, however, stream communities exposed to long-term AFI may become increasingly similar to those in comparable NFI streams, with rates of compositional change depending on connectivity with regional NFI metapopulations that represent potential colonists (Sarremejane et al. 2021; **Figure 2**). At the network scale, colonization may be facilitated by both passive drift and active migration if AFI reaches occur close to NFI reaches (e.g., due to irrigation in agricultural lowlands; **Figure 2**). AFI-induced changes in community composition resemble those after single drying events: succession starts as soon as flow resumes, and short-lived, drying-resistant taxa with strong dispersal abilities replace those with longer life cycles and/or desiccation-sensitive life stages. In some cases, this response to a rare drying event can temporarily increase the temporal community turnover (Katz et al. 2012, Aspin et al. 2019, Crabot et al. 2021b; **Figure 2**).

Of the four drivers, the effects of climate change AFI are probably the most similar to the effects of NFI. This is because they occur at large spatial scales and are gradual in time. As such, climate change exerts a continuous ramp disturbance on aquatic communities. Where

drying gradually increases in space and time due to climate change, biodiversity gradually declines, as species-specific desiccation-tolerance thresholds are exceeded during dry phases and as dispersal capacities fall short of distances between refuges and NFI streams (Sarremejane et al. 2021, Bogan et al. 2013). For example, these losses may be particularly pronounced for riparian plants if groundwater levels decrease below the reach of roots (Zhou et al. 2020), or if the refuges in which species could previously persist become ecological traps in which they die due to harsher abiotic conditions (Vander Vorste et al. 2020). In particular, climate-change-induced changes to NFI flow regimes such as earlier dry-phase onset and longer dry-phase duration may extirpate fish species due to lost spawning cues, lack of rearing habitats or increased habitat fragmentation.

Specialist species, which tolerate, or even require, drying to complete their life cycles can sustain the local taxonomic richness in NFI communities, moderating negative biodiversity responses to drying (Bogan et al. 2013). However, these specialists may not occur in AFI streams unless NFI source populations are close enough to supply colonists. Additionally, the flow regimes produced by AFI may differ substantially from the NFI regimes to which these specialists are adapted (**Figure 1**), as seen in the AFI created in the tailwaters of hydropower dams (Abernethy et al. 2021). This lack of specialists in AFI systems suggests that sites along increasing artificial drying gradients will become increasingly depauperate due to nested species losses, whereas moving along NFI gradients may generate distinct communities through species turnover (Rood et al. 2003, Katz et al. 2012, Gutiérrez-Cánovas et al. 2013). Community responses to AFI could thus vary in relation to the occurrence and distribution of specialists and other drying-tolerant species in regional species pools or with the prevalence of NFI in the landscape. Stochastic post-drying trajectories could characterize AFI community recovery where desiccation tolerance is uncommon and where AFI sites are

hydrologically isolated. These conditions could favor priority effects allowing generalists that colonize rapidly to become dominant (Vander Vorste et al. 2016a).

Timing of AFI events could also influence colonization after flow resumes. For example, if a river impacted by AFI has wet and dry phases at different times than natural regional drying events, perennial refuges within the river network could provide a steady supply of species to colonize after rewetting occurs (Sarremejane et al. 2022). Alternatively, if regional NFI and AFI events are concurrent, the capacity of communities to recover decreases, potentially leading to metacommunity collapse due to the absence of colonists in the region. Thus, biological responses to AFI are inherently linked to the landscape context in which they occur.

**Context-dependence of the effects of AFI on biodiversity responses**

The context-dependent effects of AFI are likely to be influenced by the prevalence of NFI in the landscape (see above), the level of river network fragmentation by human-made structures, the severity of other stressors associated with anthropogenic drying, and the occurrence of invasive species. Accumulating evidence indicates that network-scale biological responses to drying are strongly dependent on other fragmentation in the network, especially that caused by dams and other human-made structures (Gauthier et al. 2021). In river networks that are already highly fragmented, AFI might have limited effects on already modified biotic communities, notably on beta diversity patterns, but could alter some pivotal ecological functions (see below). The local, negative effects of AFI might interact with other stressors, most commonly geomorphological and physicochemical stressors associated with urbanization and agriculture. For example, the negative effects of nutrients, microplastics, and pharmaceuticals on aquatic biodiversity are enhanced in the context of water scarcity (Pereira et al. 2017) and AFI could lead to higher pulses of water-transported toxins upon

flow resumption. However, because stressors can directly and indirectly impact biota, and because taxa may be differentially affected by concurrent stressors, stressors may unintuitively interact, in synergistic, neutral, or antagonistic ways. Exploring the interactive effects of drying with other stressors on river biodiversity and ecological integrity represents a promising research avenue (Stubbington et al. 2022).

Shifts from perennial to AFI regimes may also change the outcomes of biological invasions, influencing whether an invasive species establishes and, if so, reaches densities sufficient to have ecological impacts. For example, the invasive mudsnail, *Potamopyrgus antipodarum,* is associated with perennial flow (Arscott et al. 2010) and its spread could thus be limited by shifts to AFI and anthropogenic extensions of dry-phase durations. By contrast, invasive species that thrive in drier conditions include the riparian shrub *Tamarix* sp. (Stromberg et al. 2007), the red swamp crayfish *Procambarus clarkii* (Kouba et al. 2016), and various opportunistic, tolerant fish (Rahel and Olden 2008). These organisms may have greater impacts on rivers prone to AFI, and altered invasion outcomes may have large-scale effects on aquatic communities and ecosystem functions (Moody and Sabo 2013).

**Do the effects of anthropogenic flow intermittence on biodiversity alter ecological functions?**

Most ecological functions are biologically controlled, and biodiversity responses to flow intermittence discussed in the previous section, such as species losses, can alter ecological functions (Truchy et al. 2015). This is particularly true for AFI, because the resultant biodiversity responses are expected to be stronger compared to NFI (**Figure 3**). The cascading effects of AFI on ecological functions will depend on the functional redundancy of a community and the types of organisms involved (Nyström 2006, Acuña et al. 2015).

14

Finally, in locations where AFI causes biodiversity losses and other stressors are present, alterations of ecological functions by AFI could be even more complex. Further research into the extent of functional redundancy in communities exposed to AFI and the mechanisms by which AFI may select for certain combinations of traits will reveal how AFI alters ecosystem function relative to NFI (Aspin et al. 2019; Crabot et al. 2021b).

Both NFI and AFI may reduce the range of functions provided by riverine communities, which highlights the role of functional redundancy in mitigating the effects of taxonomic losses on ecosystem functioning. Indeed, functional traits related to species' life-history strategies that confer resistance and/or resilience to drying are generally selected for in harsh or frequently disturbed environments (Townsend and Hildrew 1994). This selection likely favors taxa with redundant traits linked to mobility, lifespan, body size, timing of maturity, reproduction, and feeding. Shifts in functional trait distribution accompanying drying-induced biodiversity losses in NFI have been well documented (e.g., for invertebrates: Crabot et al. 2021a; diatoms: Falasco et al. 2021; algae and macrophytes: Sabater et al. 2017). These losses may be even more extreme in cases of AFI if the timing and severity of drying is unpredictable and/or different from regional NFI streams (**Figure 3**). For example, AFI reaches of the Salt River in Arizona had lower richness and abundance of riparian birds and plants than restored reaches, which in turn influenced reciprocal flows of energy and nutrients across aquatic-terrestrial boundaries (Bateman et al. 2015). By selecting for taxa that perform well in these novel and unpredictable conditions, AFI can therefore favor invasive species of plants and animals which can lead to drastically different functioning of these systems than naturally intermittent ones (Katz et al. 2012). In contrast to macroorganisms, AFI may negligibly affect microbially mediated processes due to the higher resilience and resistance of microbial populations to short-term drying (i.e., less than a month in duration; Acuña et al.

2015; Truchy et al. 2020). However, if AFI prolongs dry periods, even microbially mediated ecological functions are likely to deviate from those found in NFI streams.

Beyond the loss of functional redundancy, the elimination of certain functional traits from communities could have considerable ecological consequences (**Figure 3**). For example, in reaches prone to flow intermittence, the local elimination of sensitive microbial heterotrophs and invertebrate shredders reduces litter decomposition rates, both in the short and long term (Datry et al. 2011). The functional consequences of drying may depend on the similarity of AFI and NFI flow regimes, but also on connectivity with sources of colonists that maintain key functional traits. However, the specific trait combinations selected by AFI remain essentially unknown, potentially leading to underestimates of the effects of AFI on ecosystem functioning (e.g., Atkinson et al. 2014).

In addition to biodiversity-driven changes in ecosystem functions in AFI streams, alterations of some ecosystem functions are driven by changes in abiotic conditions. For example, higher nutrient concentrations during no-flow conditions can increase gross primary production (Finn et al. 2009). Despite similar underlying mechanisms and physicochemical conditions, the effects of AFI on ecosystem functioning may be greater than the effects of NFI (Mohamad Ibrahim et al. 2019), because AFI is frequently associated with additional human impacts (**Figure 3**). In conclusion, the unique flow regimes and interacting stressors associated with AFI will lead to ecosystem function that differs from NFI, but more empirical work on the specific functional traits favored by AFI and how they interact with other human impacts is needed.

**Does anthropogenic flow intermittence alter delivery of ecosystem services?**

Natural IRES provide a wide range of highly valued ecosystem services during both their wet and dry phases (Datry et al. 2018, Stubbington et al. 2020). However, how the services delivered by AFI and NFI streams differ remains poorly understood. Differences may exist in the provisioning (e.g., food and water), regulating (e.g., erosion control) and cultural (e.g., recreation) services. In each case, changes to physical habitats, biological communities, and ecosystem functions underpin similarities and differences in the services delivered by AFI and NFI streams. In addition, the network-scale extent of intermittence has profound effects on water-based services, and human perceptions of naturalness can profoundly alter cultural services.

*Provisioning services*, in particular the provision of fresh water for domestic use and irrigation of cropland, are highly sensitive to drying (Datry et al. 2018). Anthropogenic increases in drying reduce water availability and thus increase water's social and economic values, particularly in arid regions where water is naturally scarce (**Figure 4a, 4b**, Stubbington et al. 2020). In other cases, drying may promote some ecosystem services. For example, rivers in the Great Plains of the central United States such as the Platte and the Arkansas Rivers historically flooded and had broad sandy floodplains. As they dried due to upstream water uses and groundwater extraction, a more stable riparian forest developed, creating new habitat for forest species in a region where trees are naturally sparse (Strange et al. 1999). However, AFI often reflects diversion of water from streams to provide drinking water, crop irrigation, and industrial water, and AFI may thus reflect increased water provisioning at the expense of other services. In addition to water provisioning, the stranding of fishes as water levels decline is far more frequent in AFI than NFI rivers (Pennock et al.

2022), with consequent mortality potentially impacting subsistence, commercial, and recreational fishing.

The rates at which *regulating services* including sediment erosion control, pollution attenuation (via microbial nutrient processing) and climate regulation (through carbon cycling) are delivered differ profoundly between wet and dry phases, and are thus susceptible to alteration by AFI (Datry et al. 2018, Stubbington et al. 2020). Where AFI increases the spatial extent and/or duration of dry phases, sediment erosion is reduced, which compromises sediment supply to downstream reaches (Gamvroudis et al. 2015). In addition, by reducing microbial activity and eliminating invertebrate shredders, increased drying can limit processing of material, which accumulates along dry riverbeds and can generate pulses of carbon dioxide upon rewetting, thus altering atmospheric composition and climate regulation (Datry et al. 2018). The effects on such ecosystem processes and associated services will depend on the timing, frequency and duration of dry and wet phases, with longer AFI durations potentially delaying and limiting peaks in carbon dioxide release from organic material. Thus, climate change-related extensions of dry periods could increase downstream transport of low-quality organic material (Corti and Datry 2012), with potential repercussions on detrital food webs and associated ecosystem functions and services.

The *cultural services* provided by the wet and dry phases of natural IRES differ markedly, in particular in terms of recreation: wet phases can create opportunities for boating and fishing, whereas dry phases enable in-channel activities including rambling and horse riding (Steward et al. 2012, Datry et al. 2018, Stubbington et al. 2020). AFI thus theoretically changes the nature but not necessarily the extent of recreational service delivery. Yet in practice, use of available services can be altered by human perceptions of the naturalness of an ecosystem (Stålhammar and Pedersen 2017). In areas where NFI is common, AFI could promote greater

valuation of water as perennial sources are lost (**Figure 4b**), whereas in cool, wet regions, streams newly experiencing AFI may be recognized as indicative of anthropogenic degradation (although the presence of perennial reaches may not alter the value of flowing water; **Figure 4c**). Aesthetic values, cultural heritage, and sense of place may also be reduced in AFI during dry phases, due to people's recognition that dry riverbeds symbolize human impacts, even leading to the feelings of 'ecological grief' (Cunsolo and Ellis 2018). This reduced use of cultural services during AFI dry phases limits benefits for human wellbeing, including mental and physical health and social cohesion. Relationships between environmental and socio-hydrological norms are complex and context dependent, and further research exploring the implications of AFI to cultural services is warranted.

In sum, shifts in the frequency, timing, and duration of wet and dry phases caused by AFI, typically including an increase in dry phases, alter the composition of co-occurring provisioning, regulating, and cultural services within ecosystem service bundles (Datry et al. 2018, Stubbington et al. 2018). Understanding trade-offs among different services could mitigate conflicts between users of services delivered by AFI streams – but ultimately, the high social, cultural and economic value of fresh water means that AFI causes marked overall reductions in service delivery. The extent of these reductions is context dependent, being most pronounced in dryland regions in which NFI already restricts delivery of water-based services (**Figure 4a**)**.**

**Research priorities and management recommendations for AFI and NFI**

Major gaps in our understanding of AFI systems have emerged from this study **(Table 2)**. These gaps limit our ability to effectively manage river networks experiencing anthropogenic change, and indicate the need to develop management practices tailored towards the specific

effects of AFI. Although limitations in our capacity to manage NFI streams have been identified (Acuña et al. 2014, Marshall et al. 2018, Stubbington et al. 2018) and are starting to be addressed (Mazor et al. 2014, Steward et al. 2018), distinctions between NFI and AFI are still rarely considered in river management plans (Stubbington et al. 2018, Acuña et al. 2020, Crabot et al. 2021a).

We cannot appreciate all the implications of AFI and NFI without first refining our knowledge of how they differ with respect to temporal and spatial flow regimes. Characterization of drainage network patterns, including hydrological connectivity, is particularly important, as it will allow improved monitoring, evaluation, reporting, restoration, and remediation policies to be developed. The first step towards this goal would be high-resolution mapping of river reaches affected by NFI and AFI (**Table 2**). Managers require detailed spatial and temporal information on the causes and patterns of flow intermittence to embed existing and future knowledge into monitoring, assessment, and reporting mechanisms. Development of quantitative metrics that distinguish NFI from AFI flow regimes would increase the usefulness of this mapping (**Table 2**). These metrics could also include detailed regional- and network-scale information: where streams are located, whether they are prone to NFI and/or AFI, when drying would occur based on seasonal climate patterns, and the likelihood of synchrony between the drying of AFI and NFI. Additionally, quantitatively estimating to what degree flow intermittence is due to anthropogenic stressors (as defined in **Table 1)** would be important. Applying these metrics to mapped patterns could enhance understanding of spatial and temporal variability in network-scale AFI, as well as creating predictive models of flow intermittence (**Table 2**).

As metrics are developed to better characterize the origins and factors leading to AFI, they will also illuminate what characteristics of the landscape and socio-economic circumstances

make a river more prone to AFI. More generally, describing the spatial context of drying in AFI will also help to identify contingencies in responses of biodiversity to drying and help prioritize mitigation and restoration efforts (**Table 2**). Further analyses of such factors could enable managers to identify those management actions which are more likely to conserve or restore the biodiversity of rivers prone to AFI. We are lacking information on 1) drying frequencies, magnitudes, and durations that could push communities or ecosystems to less desirable states, with particular attention to thresholds leading to alternative stable states (i.e., Zipper et al. 2022), 2) how functional redundancy promotes resilience and resistance to AFI, 3) specific functional traits that confer resilience to pool or dry conditions, and whether AFI specifically selects for or against them, 4) cascading effects of AFI on key biogeochemical functions (e.g., carbon and nitrogen cycling), and 5) feedbacks between riparian zones and rivers subject to AFI. As researchers continue to better understand the causes of drying, and biodiversity and ecosystem functioning responses to drying in these dynamic systems, further work can help pinpoint the contexts in which AFI has the greatest relative impacts on ecosystem services (**Table 2**).

Identifying differences between AFI and NFI is critical to managing human impacts on river ecosystems. Such information could lead to policy briefs on critical eco-hydrological thresholds, mechanisms to minimize negative impacts, and eventually the partial or complete mitigation of AFI, which can rapidly lead to improved ecological communities and conditions. Moreover, establishing causal linkages between drying, rewetting, and biodiversity responses to AFI may improve our ability to predict biodiversity under alternative management scenarios. As human impacts continue to alter flow intermittence patterns, understanding the drivers and ecological, biogeochemical, and societal impacts of

AFI as well as how these differ from NFI is essential to inform policies and practices that support the effective management and conservation of river networks globally.

**Conflicts of Interest:** The authors declare no conflicts of interest.

**References**
Abernethy EF, Muehlbauer JD, Kennedy TA, Tonkin JD, Van Driesche R, Lytle DA. 2021. Hydropeaking intensity and dam proximity limit aquatic invertebrate diversity in the Colorado River Basin. Ecosphere 12:e03559.

Acuña V, Casellas M, Corcoll N, Timoner X, Sabater S. 2015. Increasing extent of periods of no flow in intermittent waterways promotes heterotrophy. Freshwater Biology 60:1810-1823.

Acuña V, Datry T, Marshall J, Barceló D, Dahm CN, Ginebreda A, McGregor G, Sabater S, Tockner K, Palmer MA. 2014. Why Should We Care About Temporary Waterways? Science 343: 1080–1081.

Acuña V, Jorda-Capdevila D, Vezza P, De Girolamo AM, McClain ME, Stubbington R, Pastor AV, Lamouroux N, von Schiller D, Munné A, Datry T. 2020. Accounting for flow intermittency in environmental flows design. Journal of Applied Ecology, 57(4), 742-753.

Allen DC, Datry T, Boersma KS, Bogan MT, Boulton AJ, Bruno D, Busch MH, Costigan KH, Dodds WK, Fritz KM, Godsey SE, Jones JB, Kaletova T, Kampf SK, Mims MC, Neeson TM,

Olden JD, Pastor AV, Poff NL, Ruddell BL, Ruhi A, Singer G, Vezza P, Ward AS, Zimmer M. 2020. River ecosystem conceptual models and non-perennial rivers: a critical review. Wiley Interdisciplinary Reviews: Water, 7(5), e1473.

Allen DC, Galbraith HS, Vaughn CC, Spooner DE. 2013. A Tale of Two Rivers: Implications of Water Management Practices for Mussel Biodiversity Outcomes During Droughts. AMBIO 42:881-891.

Arscott DB, Larned S, Scarsbrook MR, Lambert P. 2010. Aquatic invertebrate community structure along an intermittence gradient: Selwyn River, New Zealand. Journal of the North American Benthological Society 29:530-545.

Aspin TWH, Khamis K, Matthews TJ, Milner AM, O'Callaghan MJ, Trimmer M, Woodward G, Ledger ME. 2019. Extreme drought pushes stream invertebrate communities over functional thresholds. Global Change Biology 25:230-244.

Atkinson CL, Julian JP, Vaughn CC. 2014. Species and function lost: Role of drought in structuring stream communities. Biological Conservation 176:30-38.

Bateman HL, Stromberg JC, Banville MJ, Makings E, Scott BD, Suchy A, Wolkis D 2015. Novel water sources restore plant and animal communities along an urban river. Ecohydrology, 8(5), 792-811.

Bêche LA, Connors PG, Resh VH, Merenlender AM. 2009. Resilience of fishes and invertebrates to prolonged drought in two California streams. Ecography 32:778-788.

Benejam L, Angermeier PL, Munné A, García-Berthou E. 2010. Assessing effects of water abstraction on fish assemblages in Mediterranean streams. Freshwater Biology 55:628-642.

Bhaskar AS, Hopkins KG, Smith BK, Stephens TA, Miller AJ. 2020. Hydrologic Signals and Surprises in U.S. Streamflow Records During Urbanization. Water Resources Research 56:e2019WR027039.

Bickerton M, Petts GE, Armitage PD, Castella E. 1993. Assessing the ecological effects of groundwater abstraction on chalk streams: Three examples from Eastern England. Regulated Rivers: Research & Management 8:121-134.

Bogan MT, Boersma KS, Lytle DA. 2013. Flow intermittency alters longitudinal patterns of invertebrate diversity and assemblage composition in an arid-land stream network. Freshwater Biology 58:1016-1028.

Bogan MT, Lytle DA. 2011. Severe drought drives novel community trajectories in desert stream pools. Freshwater Biology 56:2070-2081.

Bogan MT. 2017. Hurry up and wait: life cycle and distribution of an intermittent stream specialist (*Mesocapnia arizonensis*). Freshwater Science, 36(4), 805-815.

Boulton AJ. 2003. Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. Freshwater Biology 48:1173-1185.

Busch MH, et al. 2020. What's in a Name? Patterns, Trends, and Suggestions for Defining Non-Perennial Rivers and Streams. Water 12:1980.

Carey N, Chester ET, Robson BJ. 2021. Flow regime change alters shredder identity but not leaf litter decomposition in headwater streams affected by severe, permanent drying. Freshwater Biology 66:1813-1830.

Corti R, Datry T. 2012. Invertebrates and sestonic matter in an advancing wetted front travelling down a dry river bed (Albarine, France). Freshwater Science, 31(4), 1187-1201.

Costigan KH, Jaeger KL, Goss CW, Fritz KM, Goebel PC. 2016. Understanding controls on flow permanence in intermittent rivers to aid ecological research: integrating meteorology, geology and land cover. Ecohydrology 9:1141-1153.

Crabot J, Heino J, Launay B, Datry T. 2020. Drying determines the temporal dynamics of stream invertebrate structural and functional beta diversity. Ecography 43:620-635.

Crabot J, Dolédec S, Forcellini M, Datry T. 2021a. Efficiency of invertebrate-based bioassessment for evaluating the ecological status of streams along a gradient of flow intermittence. Ecological Indicators 133:108440.

Crabot J, Polášek M, Launay B, Pařil P, Datry T. 2021b. Drying in newly intermittent rivers leads to higher variability of invertebrate communities. Freshwater Biology 66:730-744.

Cunsolo A, Ellis NR. 2018. Ecological grief as a mental health response to climate change-related loss. Nature Climate Change 8:275-281.

Datry T, Corti R, Claret C, Philippe M. 2011. Flow intermittence controls leaf litter breakdown in a French temporary alluvial river: the "drying memory". Aquatic Sciences 73:471-483.

Datry T, Foulquier A, Corti R, Von Schiller D, Tockner K, Mendoza-Lera C, Clément JC, Gessner MO, Moleón M, Stubbington R, Gücker B, Albariño R, Allen DC, Altermatt F, Arce MI, Arnon S, Banas D, Banegas-Medina A, Beller E, Blanchette ML, Blanco-Libreros JF, Blessing JJ, Boëchat IG, Boersma KS, Bogan MT, Bonada N, Bond NR, Brintrup Barría KC, Bruder A, Burrows RM, Cancellario T, Canhoto C, Carlson SM, Cauvy-Fraunié S, Cid N, Danger M, de Freitas Terra B, De Girolamo AM, de La Barra E, del Campo R, Diaz-Villanueva VD, Dyer F, Elosegi A, Faye E, Febria C, Four B, Gafny S, Ghate SD, Gómez R, Gómez-Gener L, Graça MAS, Guareschi S, Hoppeler F, Hwan JL, Jones JI, Kubheka S, Laini A, Langhans SD, Leigh C, Little CJ, Lorenz S, Marshall JC, Martín E, McIntosh AR, Meyer EI, Miliša M, Mlambo MC, Morais M, Moya N, Negus PM, Niyogi DK, Papatheodoulou A, Pardo I, Pařil P, Pauls SU, Pešić V, Polášek M, Robinson CT, Rodríguez-Lozano P, Rolls RJ, Sánchez-Montoya MM, Savić A, Shumilova O, Sridhar KR, Steward AL, Storey R, Taleb A, Uzan A, Vander Vorste R, Waltham NJ, Woelfle-Erskine C, Zak D, Zarfl C, Zoppini A. 2018. A global analysis of terrestrial plant litter dynamics in non-perennial waterways. Nature Geoscience 11:497-503.

Datry T, Larned ST, Fritz KM, Bogan MT, Wood PJ, Meyer EI, Santos AN. 2014. Broad-scale patterns of invertebrate richness and community composition in temporary rivers: effects of flow intermittence. Ecography 37:94-104.

Doretto A, Bona F, Falasco E, Morandini D, Piano E, Fenoglio S. 2020. Stay with the flow: How macroinvertebrate communities recover during the rewetting phase in Alpine streams affected by an exceptional drought. River Research and Applications 36:91-101.

Dudgeon D. 1992. Effects of water transfer on aquatic insects in a stream in Hong Kong. Regulated Rivers: Research & Management 7:369-377.

Eldon GA. 1979. Breeding, growth, and aestivation of the Canterbury mudfish, Neochanna burrowsius (Salmoniformes: Galaxiidae). New Zealand Journal of Marine and Freshwater Research 13:331-346.

Falasco E, Bona F, Risso AM, Piano E. 2021. Hydrological intermittency drives diversity decline and functional homogenization in benthic diatom communities. Science of the Total Environment 762:143090.

Ficklin DL, Abatzoglou JT, Robeson SM, Null SE, Knouft JH. 2018. Natural and managed watersheds show similar responses to recent climate change. Proceedings of the National Academy of Sciences 115:8553-8557.

Finn MA, Boulton AJ, Chessman BC. 2009. Ecological responses to artificial drought in two Australian rivers with differing water extraction. Fundamental and Applied Limnology 175:231.

Fovet O, Belemtougri A, Boithias L, Braud I, Charlier JB, Cottet M, Daudin K, Dramais G, Ducharne A, Folton N, Grippa M, Hector B, Kuppel S, Le Coz J, Legal L, Martin P, Moatar F, Molénat J, Probst A, Riotte J, Vidal JP, Vinatier F, Datry T. 2021. Intermittent rivers and ephemeral streams: Perspectives for critical zone science and research on socio-ecosystems. WIREs Water 8:e1523.

Gamvroudis C, Nikolaidis NP, Tzoraki O, Papadoulakis V, Karalemas N. 2015. Water and sediment transport modeling of a large temporary river basin in Greece. Science of the Total Environment 508:354-365.

Gauthier M, Launay B, Le Goff G, Pella H, Douady CJ, Datry T. 2020. Fragmentation promotes the role of dispersal in determining 10 intermittent headwater stream metacommunities. Freshwater Biology 65:2169-2185.

Gauthier M, Le Goff G, Launay B, Douady CJ, Datry T. 2021. Dispersal limitation by structures is more important than intermittent drying effects for metacommunity dynamics in a highly fragmented river network. Freshwater Science 40:302-315.

Gómez-Gener L, Siebers AR, Arce MI, Arnon S, Bernal S, Bolpagni R, Datry T, Gionchettai G, Grossart HP, Mendoza-Lera C, Pohl V, Risse-Buhl U, Shumilova O, Tzorakir O, von Schiller D, Weigand A, Weigelhofer G, Zak D, Zoppini, A. Towards an improved understanding of biogeochemical processes across surface-groundwater interactions in intermittent rivers and ephemeral streams. Earth-Science Reviews 220:103724.

Grill G, , Lehner B, Thieme M, Geenen B, Tickner D, Antonelli F, Babu S, Borrelli P, Cheng L, Crochetiere H, Ehalt Macedo H, Filgueiras R, Goichot M, Higgins J, Hogan Z, Lip B, McClain ME, Meng J, Mulligan M, Nilsson C, Olden JD, Opperman JJ, Petry P, Reidy Liermann C, Sáenz L, Salinas-Rodríguez S, Schelle P, Schmitt RJP, Snider J, Tan F, Tockner K, Valdujo PH, van Soesbergen A, Zarfl C. 2019. Mapping the world's free-flowing rivers. Nature 569:215-221.

Gutiérrez-Cánovas C, Millán A, Velasco J, Vaughan IP, Ormerod SJ. 2013. Contrasting effects of natural and anthropogenic stressors on beta diversity in river organisms. Global Ecology and Biogeography 22:796-805.

Hammond JC, et al. 2021. Spatial Patterns and Drivers of Nonperennial Flow Regimes in the Contiguous United States. Geophysical Research Letters 48:e2020GL090794.

Hanasaki N, Kanae S, Oki T. 2006. A reservoir operation scheme for global river routing models. Journal of Hydrology 327:22-41.

Hillman SS, Withers P, Drewes RC, Hillyard SD. 2009. Ecological and environmental physiology of amphibians. Oxford University Press.

Kaletova T, Rodriguez-Lozano P, Berger E, Filipe AF, Logar I, Alves MH, Calleja EJ, Jorda-Capdevila D. 2021. Considering temporal flow variability of non-perennial rivers in assessing ecosystem service provision. Ecosystem Services, 52, 101368.

Katz GL, Denslow MW, Stromberg JC. 2012. The Goldilocks effect: intermittent streams sustain more plant species than those with perennial or ephemeral flow. Freshwater Biology, 57(3), 467-480.

Kouba A, Tíkal J, Císař P, Veselý L, Fořt M, Příborský J, Patoka J, Buřič M. 2016. The significance of droughts for hyporheic dwellers: evidence from freshwater crayfish. Scientific Reports 6:26569.

Larned ST, Datry T, Arscott DB, Tockner K. 2010. Emerging concepts in temporary-river ecology. Freshwater Biology 55:717-738.

Leigh C, Boulton AJ, Courtwright JL, Fritz KM, May CL, Walker RH, Datry T. 2016. Ecological research and management of intermittent rivers: an historical review and future directions. Freshwater Biology 61:1181-1199.

Levy MC, Lopes AV, Cohn A, Larsen LG, Thompson SE. 2018. Land Use Change Increases Streamflow Across the Arc of Deforestation in Brazil. Geophysical Research Letters 45:3520-3530.

Lymbery AJ, Ma L, Lymbery SJ, Klunzinger MW, Beatty SJ, Morgan DL. 2021. Burrowing behavior protects a threatened freshwater mussel in drying rivers. Hydrobiologia 848:3141-3152.

Mackie JK, Chester ET, Matthews TG, Robson BJ. 2013. Macroinvertebrate response to environmental flows in headwater streams in western Victoria, Australia. Ecological Engineering 53:100-105.

Marshall JC, Acuña V, Allen DC, Bonada N, Boulton AJ, Carlson SM, Dahm CN, Datry T, Leigh C, Negus P, Richardson JS, Sabater S, Stevenson RJ, Steward AL, Stubbington R, Tocknerand K, Vander Vorste R. 2018. Protecting U.S. temporary waterways. Science 361:856-857.

Mazor RD, Stein ED, Ode PR, Schiff K. 2014. Integrating intermittent streams into watershed assessments: applicability of an index of biotic integrity. Freshwater Science 33:459-474.

McHugh PA, Thompson RM, Greig HS, Warburton HJ, McIntosh AR. 2015. Habitat size influences food web structure in drying streams. Ecography 38:700-712.

Messager ML, Lehner B, Cockburn C, Lamouroux N, Pella H, Snelder T, Tockner K, Trautmann T, Watt C, Datry T. 2021. Global prevalence of non-perennial rivers and streams. Nature 594:391-397.

Mohamad Ibrahim IH, Gilfoyle L, Reynolds R, Voulvoulis N. 2019. Integrated catchment management for reducing pesticide levels in water: Engaging with stakeholders in East Anglia to tackle metaldehyde. Science of the Total Environment 656:1436-1447.

Moody EK, Sabo JL. 2013. Crayfish Impact Desert River Ecosystem Function and Litter-Dwelling Invertebrate Communities through Association with Novel Detrital Resources. PLoS One 8:e63274.

Nyström M. 2006. Redundancy and response diversity of functional groups: implications for the resilience of coral reefs. AMBIO 35:30-35.

Pennock CA, Budy P, Macfarlane WW, Breen MJ, Jimenez J, Schmidt JC. 2022. Native Fish Need A Natural Flow Regime. Fisheries n/a.

Peralta-Maraver I, López-Rodríguez MJ, Robertson AL, Tierno de Figueroa JM. 2020. Anthropogenic flow intermittency shapes food-web topology and community delineation in Mediterranean rivers. International Review of Hydrobiology 105:74-84.

Pereira AMPT, Silva LJG, Laranjeiro CSM, Meisel LM, Lino CM, Pena A. 2017. Human pharmaceuticals in Portuguese rivers: The impact of water scarcity in the environmental risk. Science of the Total Environment 609:1182-1191.

Rood, SW, JH Braatne, FMR Hughes. 2003. Ecophysiology of riparian cottonwoods: stream flow dependency, water relations and restoration. Tree Physiology. 23(16): 1113-1124. doi: 10.1093/treephys/23.16.1113

Rahel FJ, Olden JD. 2008. Assessing the effects of climate change on aquatic invasive species. Conserv Biol 22:521-533.

Sabater S, Timoner X, Bornette G, De Wilde M, Stromberg JC, Stella JC. 2017. The biota of intermittent rivers and ephemeral streams: Algae and vascular plants. Pages 189-216 in Datry T, Bonada N, Boulton AJ, eds. Intermittent Rivers and Ephemeral Streams. Academic Press.

Sarremejane R, Stubbington R, England J, Sefton CE, Eastman M, Parry S, Ruhi A. 2021. Drought effects on invertebrate metapopulation dynamics and quasi-extinction risk in an intermittent river network. Global Change Biology, 27(17), 4024-4039.

Sarremejane R, Messager ML, & Datry T. 2022. Drought in intermittent river and ephemeral stream networks. Ecohydrology, e2390. https://doi.org/10.1002/eco.2390

Shanafield M, Bourke SA, Zimmer MA, Costigan KH. 2021. An overview of the hydrology of non-perennial rivers and streams. WIREs Water 8:e1504.

Snelder TH, Datry T, Lamouroux N, Larned ST, Sauquet E, Pella H, Catalogne C. 2013. Regionalization of patterns of flow intermittence from gauging station records. Hydrol. Earth Syst. Sci. 17:2685-2699.

Soria M, Leigh C, Datry T, Bini LM, Bonada N. 2017. Biodiversity in perennial and intermittent rivers: a meta-analysis. Oikos 126:1078-1089.

Stålhammar S, Pedersen E. 2017. Recreational cultural ecosystem services: How do people describe the value? Ecosystem Services 26:1-9.

Stella, J.C. and J.J. Battles. 2010. How do riparian woolly seedlings survive seasonal drought. Oecologia 164: 579-590.

Steward AL, Datry T, Langhans SD. 2022. The terrestrial and semi-aquatic invertebrates of intermittent rivers and ephemeral streams. Biological Reviews.

Steward AL, Negus P, Marshall JC, Clifford SE, Dent CL. 2018. Assessing the ecological health of rivers when they are dry. Ecological Indicators 85:537-547.

Steward AL, von Schiller D, Tockner K, Marshall JC, Bunn SE. 2012. When the river runs dry: human and ecological values of dry riverbeds. Frontiers in Ecology and the Environment 10:202-209.

Strange EM, Fausch KD, Covich AP. 1999. Sustaining ecosystem services in human-dominated watersheds: biohydrology and ecosystem processes in the South Platte River Basin. Environmental management, 24(1), 39-54.

Stromberg JC, Lite SJ, Marler R, Paradzick C, Shafroth PB, Shorrock D, White JM, White MS. 2007. Altered stream-flow regimes and invasive plant species: the Tamarix case. Global Ecology and Biogeography 16:381-393.

Stubbington R, Acreman M, Acuña V, Boon PJ, Boulton AJ, England J, Gilvear D, Sykes T, Wood PJ. 2020. Ecosystem services of temporary streams differ between wet and dry phases in regions with contrasting climates and economies. People and Nature 2:660-677.

Stubbington R, et al. 2018. Biomonitoring of intermittent rivers and ephemeral streams in Europe: Current practice and priorities to enhance ecological status assessments. Science of the Total Environment 618:1096-1113.

Stubbington, R. et al. 2022. Disentangling responses to natural stressor and human impact gradients in river ecosystems across Europe. Journal of Applied Ecology 59: 537-548.

Townsend CR, Hildrew AG. 1994. Species traits in relation to a habitat templet for river systems. Freshwater Biology 31:265-275.

Tramblay Y, Rutkowska A, Sauquet E, Sefton C, Laaha G, Osuch M, Albuquerque T, Alves MH, Banasik K, Beaufort A, Brocca L, Camici S, Csabai Z, Dakhlaoui H, DeGirolamo AM, Dörflinger G, Gallart F, Gauster T, Hanich L, Kohnová S, Mediero L, Ninov Plamen N, Parry S, Quintana-Seguí P, Tzoraki O, Datry T. 2021. Trends in flow intermittence for European rivers. Hydrological Sciences Journal 66:37-49.

Truchy A, Angeler DG, Sponseller RA, Johnson RK, McKie BG. 2015. Chapter Two - Linking biodiversity, ecosystem functioning and services, and ecological resilience: Towards an integrative framework for improved management. Pages 55-96 in Woodward G, Bohan DA, eds. Advances in Ecological Research, vol. Volume 53 Academic Press.

Truchy A, Sarremejane R, Muotka T, Mykrä H, Angeler DG, Lehosmaa K, Huusko A, Johnson RK, Sponseller RA, McKie BG. 2020. Habitat patchiness, ecological connectivity and the uneven recovery of boreal stream ecosystems from an experimental drought. Global Change Biology 26: 3455– 3472.

Vander Vorste R, Corti R, Sagouis A, Datry T. 2016a. Invertebrate communities in gravel-bed, braided rivers are highly resilient to flow intermittence. Freshwater Science 35:164-177.

Vander Vorste R, Malard F, Datry T. 2016b. Is drift the primary process promoting the resilience of river invertebrate communities? A manipulative field experiment in an intermittent alluvial river. Freshwater Biology 61:1276-1292.

Vander Vorste R, Obedzinski M, Nossaman Pierce S, Carlson SM, Grantham TE. 2020. Refuges and ecological traps: Extreme drought threatens persistence of an endangered fish in intermittent streams. Glob Chang Biol 26:3834-3845.

Villarini G, Wasko C. 2021. Humans, climate and streamflow. Nature Climate Change 11:725-726.

Widén Å, Renöfält BM, Degerman E, Wisaeus D, Jansson R. 2021. Let it flow: Modeling ecological benefits and hydropower production impacts of banning zero-flow events in a large regulated river system. Science of the Total Environment 783:147010.

Zhai P, Zhou B, Chen Y. 2018. A review of climate change attribution studies. Journal of meteorological research, 32(5), 671-692.

Zhou H, Chen Y, Zhu C, Li ZW, Fang G, Li YP, Fu A. 2020. Climate change may accelerate the decline of desert riparian forest in the lower Tarim River, Northwestern China: Evidence from tree-rings of Populus euphratica. Ecological Indicators 111:105997.

Zimmer MA et al. 2020. Zero or not? Causes and consequences of zero-flow stream gage readings. WIREs Water 7(3): e1436.

Zipper SC, Hammond JC, Shanafield M, Zimmer M, Datry T, Jones CN, Kaiser KE, Godsey SE, Burrows RM, Blaszczak JR, Busch MH, Price AN, Boersma KS, Ward AS, Costigan K, Allen GH, Krabbenhoft CA, Dodds WK, Mims MC, Olden JD, Kampf SK, Burgin AJ, Allen DC. 2021. Pervasive changes in stream intermittency across the United States. Environmental Research Letters 16:084033.

Zipper SC, Popescu I, Compare K, Zhang C, Seybold EC. 2022. Alternative stable states and hydrological regime shifts in a large intermittent river. *E*nvironmental Research Letters, 17(7), 074005.

**Table 1. Drivers and examples of anthropogenic flow intermittence. A single example is provided for each driver.  A thorough meta-analysis is available on Appendix 2.**

| Driver | Predominant mechanism | Example | Reference |
|---|---|---|---|
| (1) Water Abstraction and Diversion: Surface water extraction | Reduced stream flow due to removal of surface water | Tordera River, Spain | Benejam et al. 2010 |
| (1) Water Abstraction and Diversion: Groundwater pumping/removal | Reduced groundwater discharge to stream and/or induced infiltration from stream into aquifer due to capture by pumping wells | Wissey, Rhee, Pang Rivers, UK | Bickerton et al. 1993 |
| (1) Water Abstraction and Diversion: Stream diversion | Stream rerouted into a new or different channel reducing volume of surface water | Tai Po Kau forest stream, Hong Kong, China | Dudgeon 1992 |
| (2) Water storage and flow regulation | Reduced volume of surface water and/or altered (un-natural flow dynamics) due to water storage | Tarim River, China | Zhou et al. 2020 |
| (3) Land use/cover change | Changes to land surface affect water balance and catchment hydrology increasing evapotranspiration and/or flashier runoff, decreasing groundwater recharge and/or baseflow, and lengthening no-flow periods | Southern and western US rivers | Ficklin et al. 2018 |
| (4) Climate change | Reduced precipitation, drought, increased evapotranspiration, generalized effects of climate change | Po and Pellice Rivers, Italy | Doretto et al. 2020 |

**Table 2. Research gaps related to AFI across river networks**

| Discipline | Gaps | Why it is important |
|---|---|---|
| Geography/Hydrology | Produce maps of river reaches prone to AFI at multiple spatial (from global to local) and temporal (from seasonal to annual) scales. | There are currently no maps that explicitly distinguish reaches prone to AFI from those affected by NFI. These maps are needed at multiple spatial and temporal scales to quantify the prevalence of AFI, upscale the effects of AFI on downstream biodiversity, functions and ecosystem services, manage river flows (e.g., environmental flows implementation), and to inform the design and improvement of monitoring networks. |
| Hydrology | Develop predictive models of flow intermittence that distinguish between AFI and NFI. | Flow intermittence has different drivers but it is challenging to tease out the respective roles of these drivers, whether they are natural or due to human activities. Distinguishing AFI from NFI across river networks in predictive models is pivotal for river managers as conservation and restoration approaches have to be tailored accordingly. |
| Ecology | Quantify long-term biodiversity trajectories upon shifts from perennial to artificially intermittent flow regimes. | Stream biota in perennial rivers and streams can lack adaptations to cope with drying: shifts from perennial to intermittent flow regimes due to human activities could thus have dramatic effects on local and regional biodiversity. In addition, top-down cascades within the food-chain can happen if top predators are removed, disrupting trophic interactions and leading to (partial) foodweb collapse. The magnitude of such responses to AFI, as well as the trajectories of communities recently prone to AFI have to be quantified for biodiversity conservation. |
| | Determine ecological tipping points related to AFI that should not be crossed, along with their generality across climate and biogeographic zones. | Changes in environmental conditions due to AFI may be so drastic that ecosystems are pushed to novel and irreversible states, encompassing completely new (i.e., never encountered before) communities. Identification of such tipping points is needed to predict future biodiversity changes in |

| | | |
|---|---|---|
| | | freshwaters and to guide management and legislations. |
| | Identify mechanistic associations between drying or rewetting events and critical life history events. | Understanding mechanistic linkages will enable a clearer understanding of the differential effects of AFI relative to NFI and enable the construction of mechanistic predictive models to forecast how AFI regimes will affect biodiversity. |
| | Generate a clearer un derstanding of the spatial configuration of drying and how the relative positioning of drying in river networks propagates negative biodiversity effects. | This knowledge will help to deconstruct contingencies in biodiversity responses to drying, and help prioritize mitigation and restoration efforts of underlying causes. For instance, localized vs whole water table drying will have differential effects on the synchrony/stability of metapopulations and metacommunities at network scales. |
| | Identify problematic frequencies of drying and how the effects on biodiversity differ between NFI and AFI. | AFI drying often occurs at unnatural frequencies relative to NFI. Understanding which frequencies (and why) are problematic for various taxa will help prioritize remediation efforts. |
| | Identify differences between traits found in AFI relative to NFI sites. Do NFI regimes select for particular traits that are not present in AFI sites? Are these traits found in AFI sites in networks with NFI? | Identifying the specific traits that are missing in AFI streams relative to NFI will help to deconstruct the differential causal drivers of AFI on biodiversity relative to NFI. |
| Biogeochemistry | Quantify biodiversity and ecosystem functioning (BEF) relationships to predict how biodiversity loss alters ecological functions in drying river networks. | To document how biodiversity loss will alter the functional integrity of river networks undergoing AFI, improved BEF relationships specific to AFI are needed. |
| Biogeochemistry/Ecology | Upscale the effects of AFI on biodiversity and major biogeochemical cycles at the river network scale. | Understanding the effects of AFI on the different "levels" of the ecosystem is needed at multiple scales. How far these effects can be upscaled is critical for global assessments and for tailoring management practices. |

| | | |
|---|---|---|
| Biogeochemistry/Ecotoxicology | Understand the individual versus combined effects of AFI in the face of competing, interacting and emerging stressors related to human activities. | AFI co-occurs with other anthropogenic stressors. Interacting stressors may exacerbate or dampen biologic responses to flow changes. Identifying the synergistic and antagonistic effects of stressors will 1) allow to determine whether or not certain types of rivers are more sensitive to AFI than to NFI and 2) assist in the development of multi-criteria tools. |
| Socio-economic | Develop a comprehensive framework of AFI relative to the ecosystem services that rivers provide based on the context in which rivers are embedded. | AFI has profound effects on water-based ecosystem services (e.g., livability, provision of fresh water, habitat creation and maintenance, climate regulation), potentially leading to an increase of its social and economic unit value. Understanding the general context under which AFI has the greatest effects on ecosystem services will 1) help defining useful metrics that quantify relevant water uses (e.g., % water diverted, location in network) and 2) guide management practices as well as policy. |
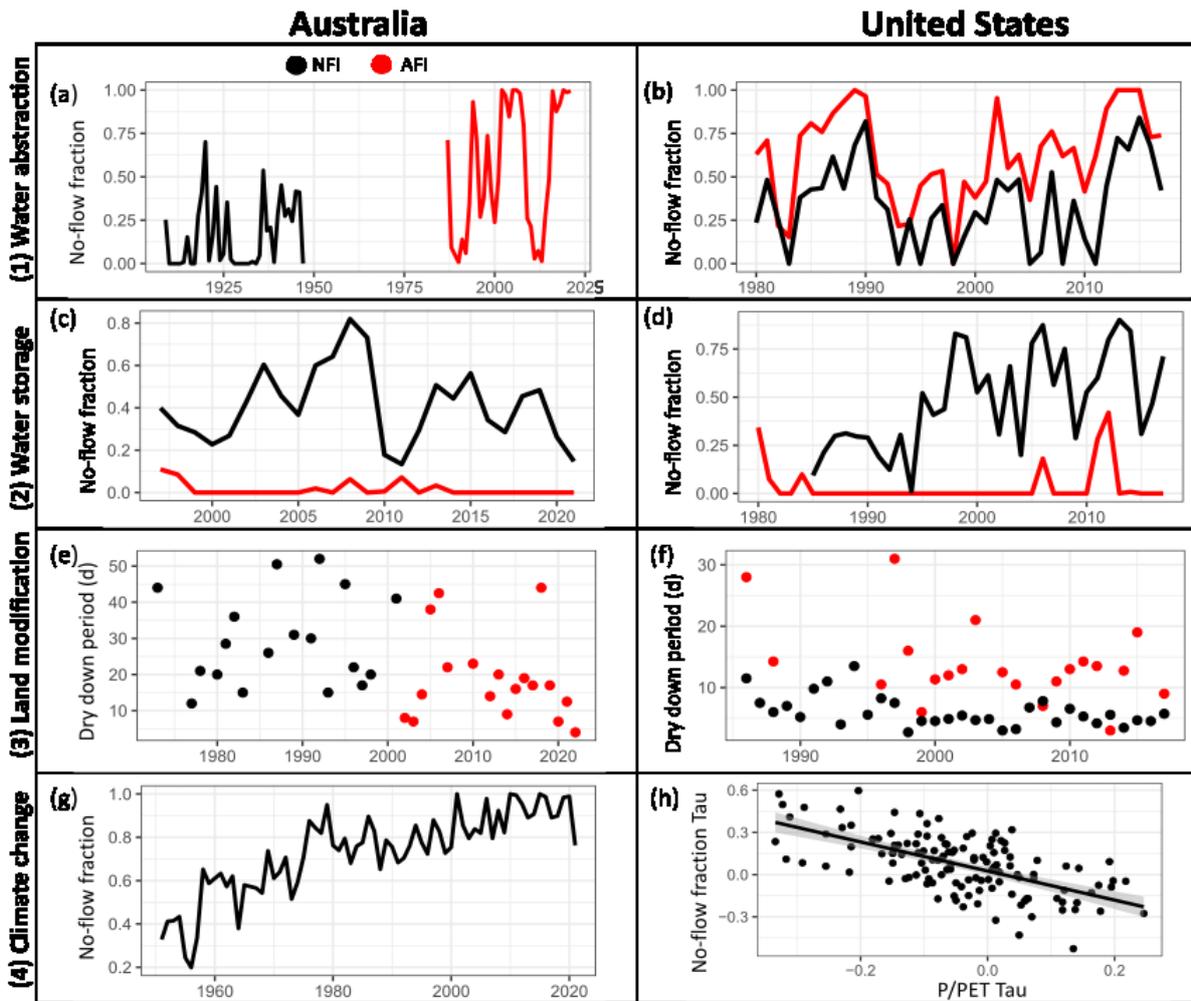
**Figure 1.** Differences in hydrological signatures between natural (NFI; dark blue) and anthropogenic (AFI; light blue) flow intermittence for four drivers of AFI in Australia (a,c,e,g) and the United States (b,d,f,h), as summarized in **Appendix 1**. No-flow fraction is the proportion of zero-flow days in a year, while dry down period is defined as the number of days from peak flow to zero flow. Panel (h) shows the relationship between the strength of the trend (Tau values of Mann-Kendall trend test) in no-flow fraction over time and the strength of the trend in climatic aridity (the ratio of annual precipitation $P$ to potential Evapotranspiration $PET$)) over time in the United States. Results with negative P/PET Tau correspond to climate conditions, which have become drier.
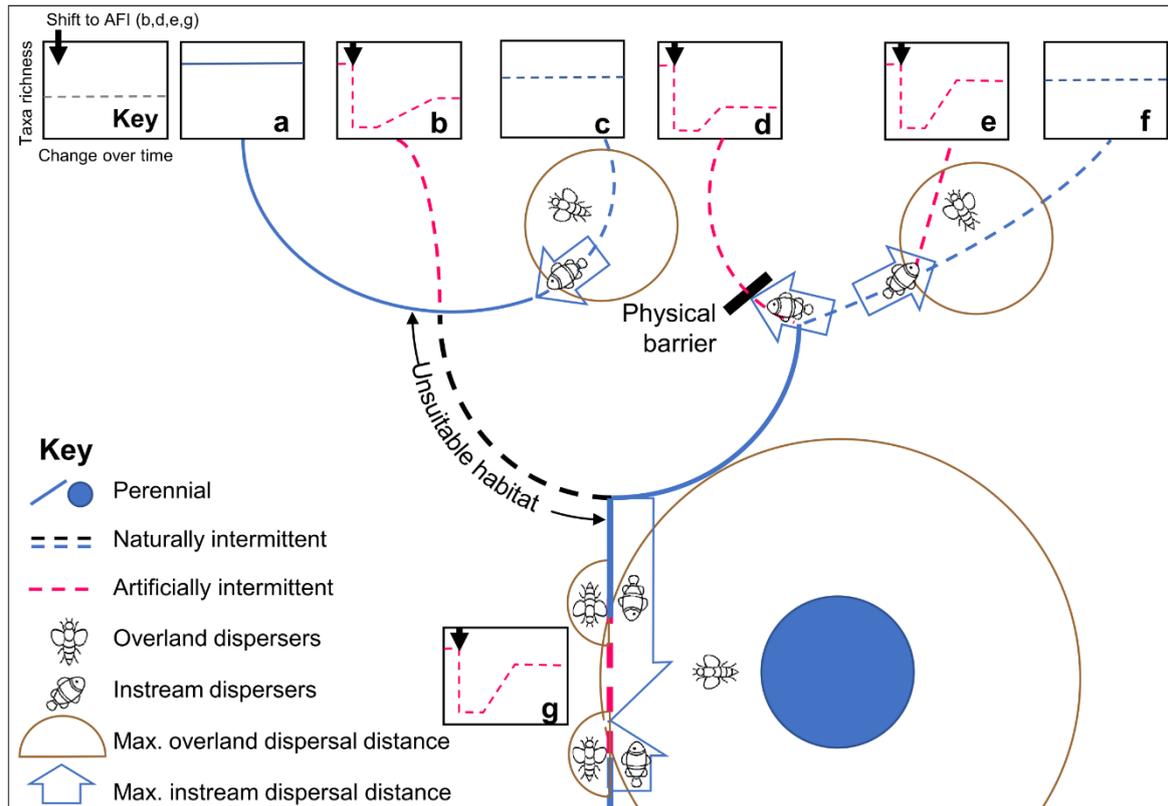
**Figure 2**. The influence of landscape context on change in biodiversity (as taxa richness) in reaches shifting from perennial flow to artificial flow intermittence (AFI; b, d, e and g). In headwaters (a–f), intermittence specialist species capable of overland and/or instream dispersal colonize from reaches with natural flow intermittence (NFI) where their maximum dispersal distances allow, leading biodiversity to increase over time (e) to levels at NFI sites (c, f). In contrast, sites isolated from such colonists by distance, physical barriers and/or reaches with unsuitable habitat (including perennial reaches) remain taxon poorer (b, d). Barriers and/or intervening reaches with unsuitable habitat may also prevent intermittence specialists from colonizing downstream AFI sites (g), at which biodiversity instead increases due to colonization by generalists via overland dispersal from nearby aquatic habitats (blue circle) and instream dispersal from both downstream and upstream sources, the latter instream colonists capable of passively dispersing over greater distances. Line widths represent stream order and proportional to stream size.
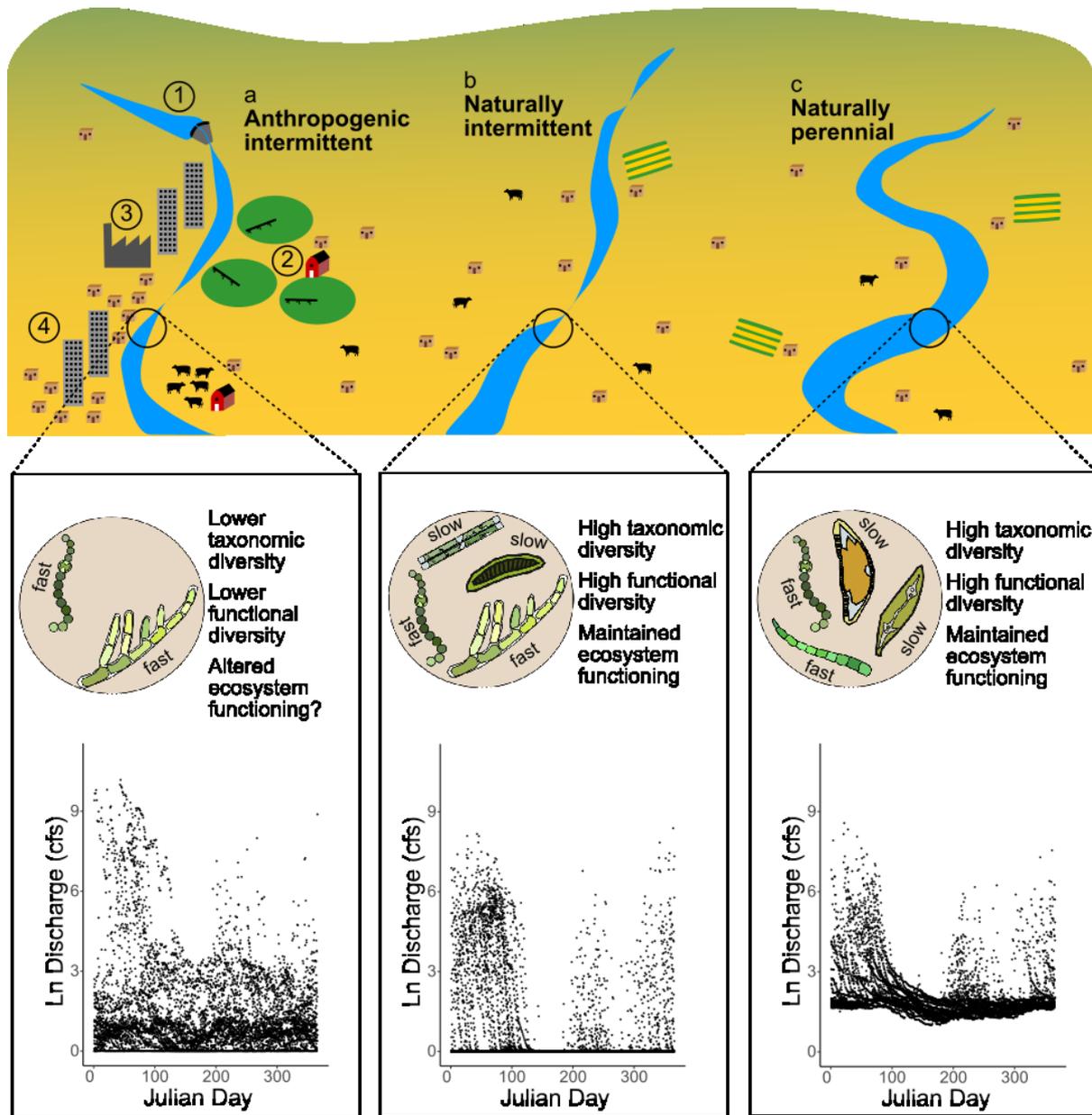
**Figure 3.** Anthropogenic flow intermittence (AFI, A) can cause shifts in community composition that alter ecosystem functioning compared to naturally intermittent (NFI, B) and naturally perennial (NP, C) reaches. These shifts can result from drivers including (1) water storage and flow reduction below dams; (2) groundwater pumping, here shown for center-pivot irrigation; (3) surface water abstraction, here shown for industrial use and public water supply; and (4) land modification, such as an increase in impervious surfaces. In scenario A, these drivers alter hydrological regimes compared to both NP and NFI reaches, as shown in hydrographs based on 20 years of gauge data from Arizona, US, at AFI (Salt River), NP (Cherry Creek), and NFI (Dry Beaver Creek) sites. Circles in insets show

hypothetical diatom communities in each reach. The functional trait of cell size is associated with growth rates, with smaller- and larger-celled species having "fast" and "slow" growth, respectively. Only a subset of species in NFI and NP communities are present in the AFI community, due to environmental filtering of taxa with traits conferring resistance to drying. Lower taxonomic diversity is typically associated with lower rates of ecosystem functions, as illustrated by the more even distribution of small, fast-growing and large, slow-growing species in NP and NFI communities, whereas the AFI community is composed entirely of small, fast-growing pioneer species. This hypothetical shift in traits would alter rates of primary production and temporal variability/stability in algal biomass, leading to altered ecosystem function.
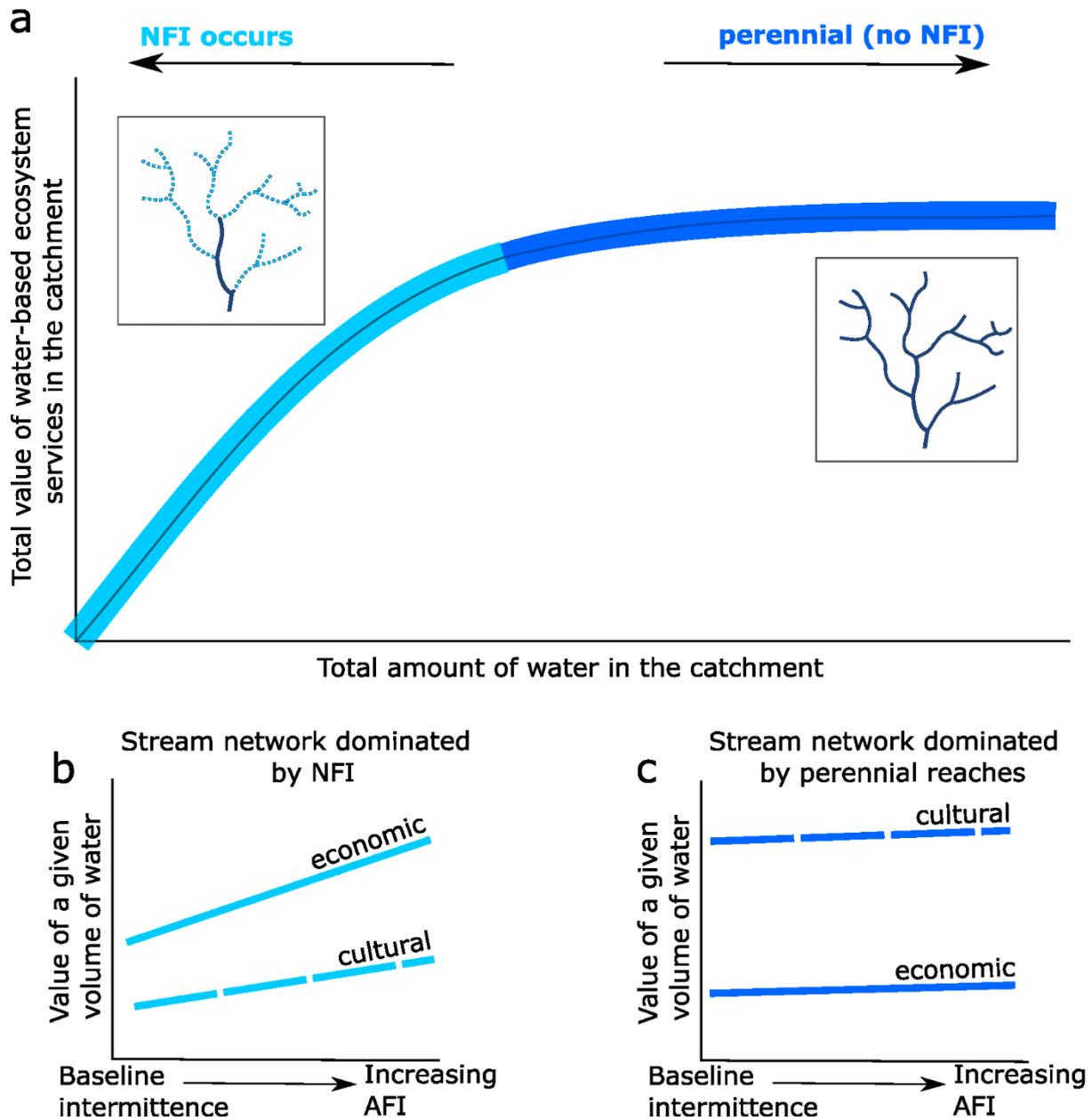
**Figure 4.** Water availability drives differences in the delivery and value of water-based ecosystem services in artificial IRES. (a) The total value of water-based services within catchments is proportional to the perennial network length, with a given increase in water causing a greater increase in value in catchments with low water availability. (b) In networks with extensive NFI, AFI can further raise the already-high economic value of water provision, and a minor increase in already low cultural value. (c) In stream networks dominated by perennial reaches, AFI might have a minimal effect on both the relatively low economic value or the high cultural value of water, though the value of cultural and economic

services for a given volume of water would still increase as AFI within a watershed increases. Note that panels (b) and (c) show the value of services for a given volume (i.e., a unit) of water rather than the total value of water. Accordingly, the total value of water-based ecosystem services would still decrease with increasing AFI, and do so less strongly in networks dominated by intermittent reaches (panel b) than in networks dominated by perennial reaches (panel c) given the higher marginal value of water in the former.

**Causes, responses, and implications of anthropogenic versus natural flow intermittence in river networks**

**Appendix 1:**

We selected stream gauges in Australia and the US to demonstrate differences between NFI and AFI, and to illustrate the potential hydrological signatures of individual anthropogenic drivers. In Australia, pairs of stream gauges were manually selected to compare AFI caused by each of the four drivers to NFI, while minimizing the effects of other drivers. In the US, we compared streamflow time series in which the hydrology primarily reflects prevailing meteorological conditions (Hydro-Climatic Data Network 2009 gauges; Lins 2012) to rivers whose streamflow has been altered by specific anthropogenic activities. Only catchments with similar hydro-environmental characteristics and within the same ecoregion were considered. Catchments were categorized by each driver using hydrological disturbance information in the GAGES2 dataset (Falcone 2011). To compare AFI and NFI, we characterized three hydrological signatures of flow intermittence: 1) The annual no-flow duration (the total number of days without surface water flow); 2) The Julian date of first no flow in a water year (April 1 to March 30); and 3) The duration of the dry-down period (i.e., from a local peak in flow to the first occurrence of no flow), as in Hammond et al. (2021), Zipper et al. (2021), and Price et al. (2021). For both Australia and the US, our analysis was designed to provide only an illustrative depiction of AFI for each driver, since a comprehensive analysis of every variation of a given driver (e.g., land-use change could include urbanization, forest-cover changes, and agricultural intensification, which would all likely have distinct impacts) was beyond the scope of this study.

**Australia analysis**

We manually selected stream gauges in Australia to be representative of NFI and AFI caused by each of the four anthropogenic drivers, while minimizing the effects of other drivers. For the drivers of water abstraction and diversion, and water storage, we selected multiple sites with a subset with clear human influence representing AFI and the other subset with few human impacts characterizing NFI. For the other two drivers, we selected one gauge for each and compared calculated flow metric values before and after the corresponding driver took effect.

*Water abstraction and diversions*

The Lockyer Creek catchment in south-east Queensland, Australia was cleared for intensive agriculture between the 1940s and the 1970s. Since then, water has been often abstracted from the river for irrigation. We selected two adjacent stream gauges in the Lockyer Creek: one (gauge 143201) measured streamflows from 1909 to 1947, and the other (gauge 143210B) from 1988 to 2021. The former was used to calculate NFI metrics while the latter to characterize AFI conditions.

*Water storage*

Three upstream gauges (gauge 406215, 406226, 406235) measuring unregulated inflows to Lake Eppalock in Victoria, Australia were grouped together to represent NFI. The immediate downstream gauge (gauge 406207), which measures regulated dam releases, was used to characterize AFI due to water storage.

*Land use change*

The Mooloolah River catchment in south-east Queensland experienced rapid urbanization from the 1970s to 2000s. We selected a stream gauge (gauge 141006A) that has measured

streamflow since 1972 to explore the impact of land use change from forest to urban area on flow intermittence. We chose the year 2000 as the point to divide the flow record into pre- and post-urbanization periods.

*Climate change*

The Yarragil Brook catchment in Western Australia is pristine with reserve forest as the dominant land use, but has experienced a significant decline in rainfall over the past 60 years. We selected the stream gauge (gauge 614044) to represent the area, and characterized the trend in flow intermittence due to the change in climate from 1953 to 2021.

**United States analysis**

We identified hydro-climatically similar flow regulated (non-Hydro-Climatic Data Network [HDCN] 2009) sites to compare to mostly pristine (HCDN) sites for or AFI-NFI comparison using the variables drainage area, aridity, depth to bedrock, wetland percent of area, forest percent of area, and mean catchment elevation (from GAGES2; Falcone, 2011), that were identified by Zipper et al. (2021) as strong drivers of annual no-flow metrics. We thank Aaron Heldmyer for development of the initial code that was modified for assessing catchment property similarity.

For each HCDN gage used in Hammond et al. (2021) and Zipper at al. (2021), we (1) computed catchment similarity of all non-HCDN sites using the hydro-signatures listed above, (2) identified and listed the 25% most similar non-HCDN sites across the contiguous US, (3) subset this list to consider only non-HCDN sites in the same aggregated Environmental Protection Agency ecoregion as the HCDN gage, and (4) subset this list

46

further to only include sites that have catchment centroids < 500 km of the HCDN gage catchment centroid. This resulted in 59 possible sites to use in the AFI-NFI comparison.

From this list, we then inspected flow regulation and disturbance comments for non-HCDN sites from USGS GAGES-II (Falcone, 2011) to identify four site pairs to use for the AFI-NFI comparison for the four drivers, as listed below: water abstraction and diversions, water storage or hydroelectric use, land use change, and climate change.

*Water abstraction and diversions*

*-HCDN: USGS 11124500 Santa Cruz Creek near Santa Ynez, CA*

*-non-HCDN: USGS 11123000 Santa Ynez River below Gibraltar Dam near Santa Barbara, CA*

*Water storage*

*-HCDN: USGS 08050800 Timber Creek near Collinsville, TX*

*-non-HCDN: USGS 07231000 Little River near Sasakwa, OK*

*Land use change*

*-HCDN: USGS 08050800 Timber Creek near Collinsville, TX*

*-non-HCDN: USGS 08053500 Denton Creek near Justin, TX*

We subset US sites from Zipper et al. (2021) to only those that are a part of the HCDN network from 1980-2018. These gauges demonstrated the concurrent trends in aridity

and no-flow metrics; the changing climate has altered the number of no-flow days and the timing of the first no-flow, but not the duration of the dry-down period.

*Climate change*

*-All HCDN gages in Zipper et al. (2021)*

**AFI versus NFI case studies**

Each AFI driver can have highly variable outcomes on flow intermittence metrics that likely vary depending on watershed characteristics such as climate, land use, physiography, and the specific human activities. These local characteristics can accentuate or lessen the differences between AFI and NFI. The case studies presented here are meant to highlight observed differences between AFI and NFI in some settings.

*Water abstraction and diversions*

South-east Queensland, Australia: Irrigated acreage in the Lockyer Creek catchment rapidly increased from the 1940s to the 1970s. We selected a pair of adjacent stream gauges to respectively characterize flow intermittence hydro-signatures prior to and after the onset of intense water abstraction in this region. After abstraction began, the no-flow fraction increased, no-flow events started earlier, and the median dry-down periods shortened (**Figure 1a**).

Southern California, US: The minimally disturbed Santa Cruz Creek in southern California was compared to the regulated Santa Ynez River below Gibraltar Dam. Between the minimally altered upstream catchment and the regulated downstream site, water is withdrawn

for public water supply, increasing the number of no-flow days and shortening dry-down periods below the abstraction (**Figure 1b**).

*Water storage*

Victoria, Australia: The median annual no-flow fraction was 0.4 upstream of Lake Eppalock, while the downstream gauge rarely measured no-flow events due to regulated constant water release from the dam (**Figure 1c**).

Oklahoma, US: Comparison between two similar watersheds, one which is unregulated and the other below a dam, showed that annual no-flow days increased over time in the unregulated site, while the human-influenced AFI site has consistently had 0 no-flow days due to its management for water supply and recreation (**Figure 1d**).

*Land-use change*

South-east Queensland, Australia: the median dry-down period in the Mooloolah River catchment decreased significantly from 22 days to 14 days after rapid urbanization between the 1970s and the 2000s (**Figure 1e**).

Texas, US: Comparing nearby catchments with natural forest vegetation and widespread irrigated agriculture, dry-down periods is longer in the agricultural catchment irrigation may be sustaining low flows (**Figure 1f**).

*Climate change*

Along the coast of Western Australia: annual rainfall has declined by around 20% over the last 60 years, which cannot be explained solely by natural climate variability (Western Australia Department of Primary Industries and Regional Development, 2020). The decline

in rainfall resulted in an increase in annual fraction of no-flows, earlier occurrence of no flow, and shorter dry-down period in the Yarragil Brook catchment (**Figure 1g**).

Across the contierminous US: As the western US has aridified, the number of no-flow days has increased while in the eastern US, no-flow days have decreased as the region has become wetter. This regional-scale variability highlights the discrepancies in the direction and magnitude of change anthropogenic climate change will have on flow intermittence (**Figure 1h**).

*References*

Falcone JA. 2011. GAGES-II: Geospatial attributes of gages for evaluating streamflow (USGS unnumbered series). Reston, VA: US Geological

Survey. https://doi.org/10.3133/70046617

Hammond JC, et al. 2021. Spatial Patterns and Drivers of Nonperennial Flow Regimes in the Contiguous United States. Geophysical Research Letters 48:e2020GL090794.

Lins HF. 2012. USGS Hydro-Climatic Data Network 2009 (HCDN–2009): US Geological Survey Fact Sheet 2012–3047. US Geological Survey: Reston, VA, USA:4.

Price AN, Jones CN, Hammond JC, Zimmer MA, Zipper SC 2021. The Drying Regimes of Non-Perennial Rivers and Streams. Geophysical Research Letters 48(14): e2021GL093298.

Western Australia Department of Primary Industries and Regional Development. 2020. Climate trends in Western Australia. https://www.agric.wa.gov.au/climate-change/climate-trends-western-australia. Accessed on 2022-02-20

Zipper SC, et al. 2021. Pervasive changes in stream intermittency across the United States. Environmental Research Letters 16:084033.

**Appendix 2. Meta-analysis of the drivers of anthropogenic flow intermittence along with examples. Examples are reference numbers which can be found in the reference list below the table.**

| Climate change | Drying Driver | Examples (Reference numbers) |
|---|---|---|
| Water Abstraction and Diversion | Abstraction | 89, 17, 18, 1, 20, 16, 49, 6, 9, 53, 77, 70, 26, 8, 28, 24, 88, 40, 35, 21, 10, 84, 30, 14, 12, 4, 2, 87, 25, 34, 72, 60, 22, 31, 74, 65, 54, 27 |
| | Experimental drought, abstraction | 73 |
| | Experimental abstraction | 55 |
| | Groundwater pumping | 61, 39, 3, 9, 5, 67, 40, 21, 51, 11, 36, 37 |
| | Irrigation | 16, 76, 32, 49, 44, 9, 29, 8, 33, 28, 40, 35, 23, 30, 15, 4, 69, 60, 22, 31 |
| | Municipal use | 19, 76 |
| | Mining | 61 |
| | Stream diversion | 61, 20, 39, 76, 42, 32, 41, 45, 50, 36, 58, 66, 64, 72 |
| Water storage and flow regulation | Dams / weirs | 1, 20, 7, 42, 46, 44, 49, 47, 48, 52, 33, 43, 88, 56, 41, 85, 23, 84, 38, 45, 50, 81, 2, 36, 25, 66, 64, 72, 82, 86, 22, 27 |
| | Hydropower | 24, 49, 50, 15, 79 |
| | Simulation - dams / diversions | 62 |
| Land use/cover change | Land use / land cover | 33, 45, 14, 78 |
| Climate change | Experimental climate change | 55 |
| | Climate change | 19, 21, 13, 14, 12, 75, 54, 43 |
| | Experimental drought | 71, 80, 83, 57 |
| | Reduced precipitation / drought | 89, 17, 18, 70, 74, 43 |
| | Snowmelt / intense rain | 62, 63 |
| Implied / vague / unclear | | 19, 70, 23, 13, 25, 78, 68 |

*References*

1. Benejam L, Angermeier PL, Munne A, García-Berthou, E. 2010. Assessing effects of water abstraction on fish assemblages in Mediterranean streams. Freshwater Biology, 55(3), 628-642.

2. Bateman HL, Stromberg JC, Banville MJ, Makings E, Scott BD, Suchy, A, Wolkis D. 2015. Novel water sources restore plant and animal communities along an urban river. Ecohydrology, 8(5), 792-811.

3. De Anda V, Zapata-Peñasco I, Blaz J, Poot-Hernández AC, Contreras-Moreira B, Gonzalez-Laffitte, M, Gámez-Tamariz N, Hernández-Rosales M, Eguiarte LE, Souza V. 2018. Understanding the mechanisms behind the response to environmental perturbation in microbial mats: a metagenomic-network based approach. Frontiers in microbiology, 9, 2606.

4. Bobori DC, & Economidis PS. 2006. Freshwater fishes of Greece: Their biodiversity, fisheries and habitats. Aquatic Ecosystem Health & Management, 9(4), 407-418.

5. Perkin JS, Gido KB, Falke JA, Fausch KD, Crockett H, Johnson ER, Sanderson J. 2017. Groundwater declines are linked to changes in Great Plains stream fish assemblages. Proceedings of the National Academy of Sciences, 114(28), 7373-7378.

6. Karaouzas I, Theodoropoulos C, Vardakas L, Kalogianni E, Skoulikidis N. 2018. A review of the effects of pollution and water scarcity on the stream biota of an intermittent Mediterranean basin. River Research and Applications, 34(4), 291-299.

7. Reich P, McMaster D, Bond N, Metzeling L, Lake PS. 2010. Examining the ecological consequences of restoring flow intermittency to artificially perennial lowland streams: patterns and predictions from the Broken—Boosey creek system in Northern Victoria, Australia. River Research and Applications, 26(5), 529-545.

8. Pires AM, Cowx IG, Coelho MM. 1999. Seasonal changes in fish community structure of intermittent streams in the middle reaches of the Guadiana basin, Portugal. Journal of fish Biology, 54(2), 235-249.

9. Skoulikidis NT, Vardakas L, Karaouzas I, Economou AN, Dimitriou E, Zogaris S. 2011. Assessing water stress in Mediterranean lotic systems: insights from an artificially intermittent river in Greece. Aquatic Sciences, 73(4), 581-597.

10. Smith KG, Darwall WR. 2006. The status and distribution of freshwater fish endemic to the Mediterranean Basin (Vol. 1). IUCN.

11. Bickerton M, Petts G, Armitage P, Castella E. 1993. Assessing the ecological effects of groundwater abstraction on chalk streams: three examples from eastern England. Regulated Rivers: Research & Management, 8(1-2), 121-134.

12. Doretto A, Bona F, Falasco E, Morandini D, Piano E, Fenoglio S. 2020. Stay with the flow: How macroinvertebrate communities recover during the rewetting phase in Alpine streams affected by an exceptional drought. River Research and Applications, 36(1), 91-101.

13. Crabot J, Polášek M, Launay B, Pařil P, Datry T. 2021. Drying in newly intermittent rivers leads to higher variability of invertebrate communities. Freshwater Biology, 66(4), 730-744.

14. Falasco E, Piano E, Doretto A, Fenoglio S, Bona F. 2018. Lentification in Alpine rivers: patterns of diatom assemblages and functional traits. Aquatic sciences, 80(4), 1-11.

15. Fenoglio S, Bo T, Cucco, M, Malacarne G. 2007. Response of benthic invertebrate assemblages to varying drought conditions in the Po river (NW Italy). Italian Journal of Zoology, 74(2), 191-201.

16. López-Rodríguez MJ, Márquez Muñoz C, Ripoll-Martín E, Tierno de Figueroa JM. 2019. Effect of shifts in habitats and flow regime associated to water diversion for agriculture on the macroinvertebrate community of a small watershed. Aquatic Ecology, 53(3), 483-495.

17. Piano E, Doretto A, Falasco E, Fenoglio S, Gruppuso L, Nizzoli D, Viaroli P, Bona F. 2019. If Alpine streams run dry: the drought memory of benthic communities. Aquatic Sciences, 81(2), 1-14.

18. Piano E, Doretto A, Falasco E, Gruppuso L, Fenoglio S, Bona F. 2019. The role of recurrent dewatering events in shaping ecological niches of scrapers in intermittent Alpine streams. Hydrobiologia, 841(1), 177-189.

19. Pinna M, Marini G, Cristiano G, Mazzotta L, Vignini P, Cicolani B, Di Sabatino A. 2016. Influence of aperiodic summer droughts on leaf litter breakdown and macroinvertebrate assemblages: testing the drying memory in a Central Apennines River (Aterno River, Italy). Hydrobiologia, 782(1), 111-126.

20. Belmar O, Bruno D, Guareschi S, Mellado-Díaz A, Millán A, Velasco J. 2019. Functional responses of aquatic macroinvertebrates to flow regulation are shaped by natural flow intermittence in Mediterranean streams. Freshwater Biology, 64(5), 1064-1077.

21. Jaeger KL, Olden JD, Pelland NA. 2014. Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. Proceedings of the National Academy of Sciences, 111(38), 13894-13899.

22. Chessman BC, Jones HA, Searle NK, Growns IO, Pearson MR. 2010. Assessing effects of flow alteration on macroinvertebrate assemblages in Australian dryland rivers. Freshwater Biology, 55(8), 1780-1800.

23. Arthington AH. 1996. The effects of agricultural land use and cotton production on tributaries of the Darling River, Australia. GeoJournal, 40(1), 115-125.

24. Petts GE, Bickerton MA. 1994. Influence of water abstraction on the macroinvertebrate community gradient within a glacial stream system: La Borgne d'Arolla, Valais, Switzerland. Freshwater Biology, 32(2), 375-386.

25. Belmar O, Bruno D, Martinez-Capel F, Barquín J, Velasco J. 2013. Effects of flow regime alteration on fluvial habitats and riparian quality in a semiarid Mediterranean basin. Ecological Indicators, 30, 52-64.

26. Mukherjee A, Bhanja SN, Wada Y. 2018. Groundwater depletion causing reduction of baseflow triggering Ganges river summer drying. Scientific reports, 8(1), 1-9.

27. Jiang B, Wong CP, Lu F, Ouyang Z, Wang Y. 2014. Drivers of drying on the Yongding River in Beijing. Journal of hydrology, 519, 69-79.

28. Elisa M, Kihwele E, Wolanski E, Birkett C. 2021. Managing wetlands to solve the water crisis in the Katuma River ecosystem, Tanzania. Ecohydrology & Hydrobiology, 21(2), 211-222.

29. Kihwele E, Muse E, Magomba E, Mnaya B, Nassoro A, Banga P, Murashani E, Irmamasita D, Kiwango H, Birkett C, Wolanski E. 2018. Restoring the perennial Great Ruaha River using ecohydrology, engineering and governance methods in Tanzania. Ecohydrology & Hydrobiology, 18(2), 120-129.

30. Ngigi SN, Savenije HH, Gichuki FN. 2008. Hydrological impacts of flood storage and management on irrigation water abstraction in upper Ewaso Ng'iro river basin, Kenya. Water resources management, 22(12), 1859-1879.

31. Gichuki FN. 2004. Managing the externalities of declining dry season river flow: A case study from the Ewaso Ngiro North River Basin, Kenya. Water resources research, 40(8).

32. Pereira LS, Gonçalves JM, Dong B, Mao Z, Fang SX. 2007. Assessing basin irrigation and scheduling strategies for saving irrigation water and controlling salinity in the upper Yellow River Basin, China. Agricultural Water Management, 93(3), 109-122.

33. Leduc C, Ammar SB, Favreau G, Beji R, Virrion R, Lacombe G, Tarhouni J, Aouadi C, Zenati Chelli B, Jebnoun N, Oi M, Michelot JL, Zouari, K. 2007. Impacts of hydrological changes in the Mediterranean zone: environmental modifications and rural development in the Merguellil catchment, central Tunisia/Un exemple d'évolution hydrologique en Méditerranée: impacts des modifications environnementales et du développement agricole dans le bassin-versant du Merguellil (Tunisie centrale). Hydrological Sciences Journal/Journal des Sciences Hydrologiques, 52(6), 1162-1178.

34. Martín-Rosales W, Pulido-Bosch A, Vallejos Á, Gisbert J, Andreu JM, Sánchez-Martos F. 2007. Hydrological implications of desertification in southeastern Spain/Implications hydrologiques de la désertification dans le sud-est de l'Espagne. Hydrological Sciences Journal/Journal des Sciences Hydrologiques, 52(6), 1146-1161.

35. Humphries P, Lake PS. 2000. Fish larvae and the management of regulated rivers. Regulated Rivers: Research & Management: An International Journal Devoted to River Research and Management, 16(5), 421-432.

36. Stromberg JC, Beauchamp VB, Dixon MD, Lite SJ, Paradzick C. 2007. Importance of low-flow and high-flow characteristics to restoration of riparian vegetation along rivers in arid south-western United States. Freshwater Biology, 52(4), 651-679.

37. Stromberg JC, Lite SJ, Rychener TJ, Levick LR, Dixon MD, Watts JM. 2006. Status of the riparian ecosystem in the upper San Pedro River, Arizona: application of an assessment model. Environmental Monitoring and Assessment, 115(1), 145-173.

38. Gehrke PC, Harris JH. 2001. Regional-scale effects of flow regulation on lowland riverine fish communities in New South Wales, Australia. Regulated Rivers: Research & Management: An International Journal Devoted to River Research and Management, 17(4-5), 369-391.

39. Compare K, Zipper SC, Zhang C, Seybold E. 2021. Characterizing streamflow intermittency and subsurface heterogeneity in the middle Arkansas river basin. Kansas Geological Survey Open-File Report 2021, 1.

40. Fuchs EH, King JP, Carroll KC. 2019. Quantifying disconnection of groundwater from managed-ephemeral surface water during drought and conjunctive agricultural use. Water Resources Research, 55(7), 5871-5890.

41. Marchetti MP, Moyle PB. 2001. Effects of flow regime on fish assemblages in a regulated California stream. Ecological applications, 11(2), 530-539.

42. Humphries P, Serafini LG, King AJ. 2002. River regulation and fish larvae: variation through space and time. Freshwater Biology, 47(7), 1307-1331.

43. Griswold BL, Edwards CJ, Woods III LC. 1982. Recolonization of macroinvertebrates and fish in a channelized stream after a drought.

44. McMahon TA, Finlayson BL. 2003. Droughts and anti-droughts: The low flow hydrology of Australian rivers. Freshwater biology, 48(7), 1147-1160.

45. Ficklin DL, Abatzoglou JT, Robeson SM, Null SE, Knouft JH. 2018. Natural and managed watersheds show similar responses to recent climate change. Proceedings of the National Academy of Sciences, 115(34), 8553-8557.

46. Ponsatí L, Acuña V, Aristi I, Arroita M, García-Berthou E, Von Schiller D, Elosegi A, Sabater S. 2015. Biofilm responses to flow regulation by dams in Mediterranean rivers. River Research and Applications, 31(8), 1003-1016.

47. Abril M, Muñoz I, Casas-Ruiz JP, Gómez-Gener L, Barceló M, Oliva F, Menéndez M. 2015. Effects of water flow regulation on ecosystem functioning in a Mediterranean river network assessed by wood decomposition. Science of the Total Environment, 517, 57-65.

48. Abril M, Muñoz I, Menéndez M. 2016. Heterogeneity in leaf litter decomposition in a temporary Mediterranean stream during flow fragmentation. Science of the Total Environment, 553, 330-339.

49. Aristi I, Arroita M, Larrañaga A, Ponsatí L, Sabater S, von Schiller D, Elosegi A, Acuña V. 2014. Flow regulation by dams affects ecosystem metabolism in Mediterranean rivers. Freshwater biology, 59(9), 1816-1829.

50. Arroita M, Aristi I, Díez J, Martinez M, Oyarzun G, Elosegi A. 2015. Impact of water abstraction on storage and breakdown of coarse organic matter in mountain streams. Science of the Total Environment, 503, 233-240.

51. Chessman BC, Royal MJ, Muschal M. 2011. The challenge of monitoring impacts of water abstraction on macroinvertebrate assemblages in unregulated streams. River Research and Applications, 27(1), 76-86.

52. Mackie, J. K., Chester, E. T., Matthews, T. G., & Robson, B. J. (2013). Macroinvertebrate response to environmental flows in headwater streams in western Victoria, Australia. Ecological Engineering, 53, 100-105.

53. Finn MA, Boulton AJ, Chessman BC. 2009. Ecological responses to artificial drought in two Australian rivers with differing water extraction. Fundamental and applied limnology, 175(3), 231.

54. Sun T, Feng ML. 2013. Multistage analysis of hydrologic alterations in the Yellow River, China. River research and applications, 29(8), 991-1003.

55. Palmia B, Bartoli M, Laini A, Bolpagni R, Ferrari C, Viaroli P. 2019. Effects of drying and re-wetting on litter decomposition and nutrient recycling: a manipulative experiment. Water, 11(4), 708.

56. Walker KF, Thoms MC. 1993. Environmental effects of flow regulation on the lower River Murray, Australia. Regulated Rivers: Research & Management, 8(1-2), 103-119.

57. Proia L, Vilches C, Boninneau C, Kantiani L, Farré M, Romaní AM, Sabater S, Guasch H. 2013. Drought episode modulates the response of river biofilms to triclosan. Aquatic toxicology, 127, 36-45.

58. Hax CL, Golladay SW. 1998. Flow disturbance of macroinvertebrates inhabiting sediments and woody debris in a prairie stream. The American midland naturalist, 139(2), 210-223.

59. Verdonschot RC, van Oosten-Siedlecka AM, ter Braak CJ, Verdonschot PF. 2015. Macroinvertebrate survival during cessation of flow and streambed drying in a lowland stream. Freshwater Biology, 60(2), 282-296.

60. Merciai R, Molons-Sierra C, Sabater S, García-Berthou E. 2017. Water abstraction affects abundance, size-structure and growth of two threatened cyprinid fishes. PLoS One, 12(4), e0175932.

61. Stromberg JC, Lite SJ, Marler R, Paradzick C, Shafroth PB, Shorrock D, White JM, White MS. 2007. Altered stream-flow regimes and invasive plant species: the Tamarix case. Global Ecology and Biogeography, 16(3), 381-393.

62. Henszey RJ, Skinner QD, Wesche TA. 1991. Response of montane meadow vegetation after two years of streamflow augmentation. Regulated Rivers: Research & Management, 6(1), 29-38.

63. Wolff SW, Wesche TA, Hubert WA. 1989. Stream channel and habitat changes due to flow augmentation. Regulated Rivers: Research & Management, 4(3), 225-233.

64. Dudgeon D. 1992. Effects of water transfer on aquatic insects in a stream in Hong Kong. Regulated Rivers: Research & Management, 7(4), 369-377.

65. Extence CA, Balbi DM, Chadd RP. 1999. River flow indexing using British benthic macroinvertebrates: a framework for setting hydroecological objectives. Regulated Rivers:

Research & Management: An International Journal Devoted to River Research and Management, 15(6), 545-574.

66. Rader RB, Belish TA. 1999. Influence of mild to severe flow alterations on invertebrates in three mountain streams. Regulated Rivers: Research & Management: An International Journal Devoted to River Research and Management, 15(4), 353-363.

67. Wright JF, Berrie AD. 1987. Ecological effects of groundwater pumping and a natural drought on the upper reaches of a chalk stream. Regulated Rivers: Research & Management, 1(2), 145-160.

68. Contreras-B S, Lozano-V ML. 1994. Water, endangered fishes, and development perspectives in arid lands of Mexico. Conservation Biology, 8(2), 379-387.

69. Crippen JR, Waananen AO. 1969. Hydrologic effects of suburban development near Palo Alto, California (No. 69-63).

70. Bogan MT, Lytle DA. 2011. Severe drought drives novel community trajectories in desert stream pools. Freshwater Biology, 56(10), 2070-2081.

71. Zlatanović S, Fabian J, Premke K, Mutz M. 2018. Shading and sediment structure effects on stream metabolism resistance and resilience to infrequent droughts. Science of the total environment, 621, 1233-1242.

72. Zhou H, Chen Y, Zhu C, Li Z, Fang G, Li Y, Fu A. 2020. Climate change may accelerate the decline of desert riparian forest in the lower Tarim River, Northwestern China: Evidence from tree-rings of Populus euphratica. Ecological Indicators, 111, 105997.

73. Ledger ME, Brown LE, Edwards FK, Milner AM, Woodward G. 2013. Drought alters the structure and functioning of complex food webs. Nature Climate Change, 3(3), 223-227.

74. Bruno MC, Doretto A, Boano F, Ridolfi L, Fenoglio S. 2020. Role of the hyporheic zone in increasing the resilience of mountain streams facing intermittency. Water, 12(7), 2034.

75. Pařil P, Polášek M, Loskotová B, Straka M, Crabot J, Datry T. 2019. An unexpected source of invertebrate community recovery in intermittent streams from a humid continental climate. Freshwater Biology, 64(11), 1971-1983.

76. Bond N, McMaster D, Reich P, Thomson JR, Lake PS. 2010. Modelling the impacts of flow regulation on fish distributions in naturally intermittent lowland streams: an approach for predicting restoration responses. Freshwater Biology, 55(9), 1997-2010.

77. Boddy NC, Fraley KM, Warburton HJ, Jellyman PG, Booker DJ, Kelly D, McIntosh AR. 2020. Big impacts from small abstractions: The effects of surface water abstraction on freshwater fish assemblages. Aquatic Conservation: Marine and Freshwater Ecosystems, 30(1), 159-172.

78. Shivoga WA. 2001. The influence of hydrology on the structure of invertebrate communities in two streams flowing into Lake Nakuru, Kenya. Hydrobiologia, 458(1), 121-130.

79. Anderson EP, Freeman MC, Pringle CM. 2006. Ecological consequences of hydropower development in Central America: impacts of small dams and water diversion on neotropical stream fish assemblages. River research and applications, 22(4), 397-411.

80. Davey AJH, Kelly DJ, Biggs BJF. 2006. Refuge-use strategies of stream fishes in response to extreme low flows. Journal of Fish Biology, 69(4), 1047-1059.

81. Scruton DA, Anderson TC, King LW. 1998. Pamehac Brook: a case study of the restoration of a Newfoundland, Canada, river impacted by flow diversion for pulpwood transportation. Aquatic Conservation: Marine and Freshwater Ecosystems, 8(1), 145-157.

82. Brown LR, Ford T. 2002. Effects of flow on the fish communities of a regulated California river: implications for managing native fishes. River Research and Applications, 18(4), 331-342.

83. Siebers AR, Paillex A, Misteli B, Robinson CT. 2020. Effects of an experimental increase in flow intermittency on an alpine stream. Hydrobiologia, 847(16), 3453-3470.

84. Boix D, García-Berthou E, Gascón S, Benejam L, Tornés E, Sala J, Benito J, Munne A, Sola C, Sabater S. 2010. Response of community structure to sustained drought in Mediterranean rivers. Journal of Hydrology, 383(1-2), 135-146.

85. Balcombe SR, Arthington AH, Thoms MC, Wilson GG. 2011. Fish assemblage patterns across a gradient of flow regulation in an Australian dryland river system. River Research and Applications, 27(2), 168-183.

86. Andersson E, Nilsson C, Johansson ME. 2000. Effects of river fragmentation on plant dispersal and riparian flora. Regulated Rivers: Research & Management: An International Journal Devoted to River Research and Management, 16(1), 83-89.

87. Peralta-Maraver I, López-Rodríguez MJ, Robertson AL, Tierno de Figueroa JM. 2020. Anthropogenic flow intermittency shapes food-web topology and community delineation in Mediterranean rivers. International Review of Hydrobiology, 105(3-4), 74-84.

88. Rubio-Garcia F, Almeida D, Bonet B, Casals F, Espinosa C, Flecker AS, García-Berthoua E, Martí E, Tuulaikhuu BA, Vila-Gispert A, Zamora L, Guasch H. 2017. Combined effects of hydrologic alteration and cyprinid fish in mediating biogeochemical processes in a Mediterranean stream. Science of the Total Environment, 601, 1217-1225.

89. Piano E, Doretto A, Mammola S, Falasco E, Fenoglio S, Bona F. 2020. Taxonomic and functional homogenisation of macroinvertebrate communities in recently intermittent Alpine watercourses. Freshwater Biology, 65(12), 2096-2107.

**Appendix 3. Examples of adaptations, accompanying trait responses, associated environmental conditions, and taxonomic groups known to respond to increased flow intermittence. Grey blocks within the environmental associations section indicate conditions where each trait is favoured or represented.**

| Category | Adaptation | Response | Environmental associations | | | | Example taxa | References |
|---|---|---|---|---|---|---|---|---|
| | | | Wet phase | Dry phase | Subsurface habitat | Landscape connectivity | | |
| Life history | Duration of aquatic stage | Plasticity in emergence timing | ▓ | | | | Insect | Cover et al. 2015 |
| | | | ▓ | | | | Amphibian | Richter-Boix et al. 2006 |
| | Developmental | Rapid development/growth | ▓ | | | | Insect | Delucchi and Peckarsky 1989 |
| Phenology | | Asynchronous/delayed egg hatching with flow resumption | | ▓ | | | Insect | Sandberg and Stewart 2004 Ruiz-García and Ferreras-Romero 2007 |
| Physiological | Desiccation | Aestivation | | ▓ | ▓ | | Non-arthropod | Pennak 1989 Ricci and Pagani 1997 |
| | | | | ▓ | ▓ | | Insect | Hinton 1960 Bogan et al. 2015 |
| | | | | ▓ | ▓ | | Mussel | Lymbery et al. 2021 |
| | | | | ▓ | ▓ | | Amphibian | Navas et al. 2004 Hillman et al. 2009 Jared et al. 2020 |
| | | | | ▓ | ▓ | | Fish | Eldon 1979 Fishman et al. 1986 |

| | | | | | | | Taxa | Reference |
|---|---|---|---|---|---|---|---|---|
| | | Drought resistant eggs | | ■ | | | Insect | Delucchi and Peckarsky 1989 |
| | | Dormancy | | ■ | | | Non-arthropods | Watanabe 2006 |
| | | | | ■ | | | Insect | Cover et al. 2015 |
| | | | | ■ | | | Biofilms | Holzinger and Karsten 2013, Sabater et al. 2016 |
| | | Water use efficiency | | ■ | | | Riparian vegetation | Rood et al. 2003, Stella and Battles 2010 |
| | Respiration | Air breathing | ■ | ■ | | | Insect | Lake 2011 Bogan and Boersma 2012 |
| | | | ■ | ■ | | | Fish | van der Waal 1997 |
| | | Tolerate low DO | ■ | | | | Micro-crustacean | Storey and Quinn 2008 |
| Morphological | Body armoring | Building mobile cases | ■ | | | ■ | Insect | Ruiz-García and Ferreras-Romero 2007 |
| | Body size | Reduced leaf area/ Branch sacrifice | ■ | | | ■ | Riparian vegetation | Rood et al. 2000, Stella and Battles 2010 |
| Behavioral | Dispersal | Adult flight | | | | ■ | Insect | Wickson et al. 2014 Chester et al. 2015 |
| | | High mobility/ Colonization after rewetting | | | | ■ | Insect | Vander Vorste et al. 2016a, Vander Vorste et al. 2016b |
| | | | | | | ■ | Fish | Balcombe et al. 2007 Kerezsy et al. 2013 Walker et al. 2013 Pires et al. 2014 |
| | | High seed/vegetative fragment dispersal | | | | ■ | Riparian vegetation | Karrenberg et al. 2002 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Seeks surface refuges during drying | | | | ▨ | Insect | Bogan and Boersma 2012<br>Boersma and Lytle 2014 |
| | | | | | | ▨ | Fish | Labbe and Fausch 2000<br>Sheldon et al. 2010<br>Alexandre et al. 2016 |
| | | Vertical migration into hyporheic zone | | | ▨ | | Insect | Agüero-Pelegrín and Ferreras-Romero 2002<br>Cover et al. 2015<br>Vander Vorste et al. 2016b |
| | | | | | ▨ | | Crayfish | DiStefano et al. 2009<br>Kouba et al. 2016 |
| | | | | | ▨ | | Salamander | Feral et al. 2005 |
| | | | | | ▨ | | Fish | Secor and Lignot 2010 |

1  *References*

2  Agüero-Pelegrín M, Ferreras-Romero M. 2002. The life Cycle of *Guadalgenus franzi* (Aubert,

3  1963) (Plecoptera: Perlodidae) in the Sierra Morena Mountains (Southern Spain):

4  Semivoltinism in Seasonal Streams of the Mediterranean Basin. Aquatic Insects 24:237-245.

5  Alexandre CM, Almeida PR, Neves T, Mateus CS, Costa JL, Quintella BR. 2016. Effects of

6  flow regulation on the movement patterns and habitat use of a potamodromous cyprinid

7  species. Ecohydrology 9:326-340.

8  Balcombe SR, Bunn SE, Arthington AH, Fawcett JH, McKenzie-Smith FJ, Wright A. 2007.

9  Fish larvae, growth and biomass relationships in an Australian arid zone river: links between

10  floodplains and waterholes. Freshwater Biology 52:2385-2398.

11  Boersma KS, Lytle DA. 2014. Overland dispersal and drought-escape behavior in a flightless

12  aquatic insect, *Abedus herberti* (Hemiptera: Belostomatidae). The Southwestern Naturalist

13  59:301-302.

14  Bogan MT, Boersma KS. 2012. Aerial dispersal of aquatic invertebrates along and away from

15  arid-land streams. Freshwater Science 31:1131-1144.

16  Bogan MT, Boersma KS, Lytle DA. 2015. Resistance and resilience of invertebrate

17  communities to seasonal and supraseasonal drought in arid-land headwater streams. Freshwater

18  Biology 60:2547-2558.

19  Chester ET, Miller AD, Valenzuela I, Wickson SJ, Robson BJ. 2015. Drought survival

20  strategies, dispersal potential and persistence of invertebrate species in an intermittent stream

21  landscape. Freshwater Biology 60:2066-2083.

22  Cover MR, Seo JH, Resh VH. 2015. Life History, Burrowing Behavior, and Distribution of

23  *Neohermes filicornis* (Megaloptera: Corydalidae), a Long-Lived Aquatic Insect in Intermittent

24  Streams. Western North American Naturalist 75:474-490.

25

26    Delucchi CM, Peckarsky BL. 1989. Life History Patterns of Insects in an Intermittent and a

27    Permanent Stream. Journal of the North American Benthological Society 8:308-321.

28    DiStefano RJ, Magoulick DD, Imhoff EM, Larson ER. 2009. Imperiled crayfishes use

29    hyporheic zone during seasonal drying of an intermittent stream. Journal of the North American

30    Benthological Society 28:142-152.

31    Eldon GA. 1979. Breeding, growth, and aestivation of the Canterbury mudfish, Neochanna

32    burrowsius (Salmoniformes: Galaxiidae). New Zealand Journal of Marine and Freshwater

33    Research 13:331-346.

34    Feral D, Camann MA, Welsh J, Hartwell H. 2005. Dicamptodon tenebrosus larvae within

35    hyporheic zones of intermittent streams in California. . Herpetological Review 36:26-27.

36    Fishman AP, Pack AI, Delaney RG, Galante RJ. 1986. Estivation in Protopterus. Journal of

37    Morphology 190:237-248.

38    Hillman SS, Withers P, Drewes RC, Hillyard SD. 2009. Ecological and environmental

39    physiology of amphibians. Oxford University Press.

40    Hinton HE. 1960. Cryptobiosis in the larva of Polypedilum vanderplanki Hint.

41    (Chironomidae). Journal of Insect Physiology 5:286-300.

42    Holzinger, A. And U. Karsten. 2013. Desiccation stress and tolerance in green algae:

43    consequences for ultrastructure, physiological and molecular mechanisms. Frontiers in Plant

44    Sciences 4: 327. 10.3389/fpls.2013.00327

45    Jared C, Mailho-Fontana PL, Mendelson J, Antoniazzi MM. 2020. Life history of frogs of the

46    Brazilian semi-arid (Caatinga), with emphasis in aestivation. Acta Zoologica 101:302-310.

47    Kaletova T, Rodriguez-Lozano P, Berger E, Filipa Filipe A, Logar I, Helena Alves M, Calleja

48    EJ, Jorda-Capdevila D. 2021. Considering temporal flow variability of non-perennial rivers in

49    assessing ecosystem service provision. Ecosystem Services 52:101368.

50 Karrenburg S, Edwards PJ, Kollman J. The life history of Salicaceae living in the active zone

51 of floodplains. Freshwater Biology 47(4): 733-748.

52 Kerezsy A, Balcombe SR, Tischler M, Arthington AH. 2013. Fish movement strategies in an

53 ephemeral river in the Simpson Desert, Australia. Austral Ecology 38:798-808.

54 Kouba A, Tíkal J, Císař P, Veselý L, Fořt M, Příborský J, Patoka J, Buřič M. 2016. The

55 significance of droughts for hyporheic dwellers: evidence from freshwater crayfish. Scientific

56 Reports 6:26569.

57 Labbe TR, Fausch KD. 2000. Dynamics of intermittent stream habitat regulate persistence of

58 a threatened fish at multiple scales. Ecological Applications 10:1774-1791.

59 Lake PS. 2011. Drought and aquatic ecosystems: effects and responses. John Wiley &

60 Sons.Lymbery AJ, Ma L, Lymbery SJ, Klunzinger MW, Beatty SJ, Morgan DL. 2021.

61 Burrowing behavior protects a threatened freshwater mussel in drying rivers. Hydrobiologia

62 848:3141-3152.

63 Navas CA, Antoniazzi MM, Jared C. 2004. A preliminary assessment of anuran physiological

64 and morphological adaptation to the Caatinga, a Brazilian semi-arid environment. International

65 Congress Series 1275:298-305.

66 Pennak RW. 1989. Fresh-water invertebrates of the United States. John Wiley and Sons.

67 Pires DF, Beja P, Magalhães MF. 2014. Out of pools: Movement patterns of Mediterranean

68 stream fish in relation to dry season refugia. River Research and Applications 30:1269-1280.

69 Ricci C, Pagani M. 1997. Desiccation of Panagrolaimus rigidus (Nematoda): survival,

70 reproduction and the influence on the internal clock. Hydrobiologia 347:1-13.

71 Richter-Boix A, Llorente GA, Montori A. 2006. Effects of phenotypic plasticity on post-

72 metamorphic traits during pre-metamorphic stages in the anuran Pelodytes punctatus.

73 Evolutionary Ecology Research 8:309-320.

74  Rood SB, Patino S, Coombs K, Tyree MT. 2000 Branch sacrifice: cavitation-associated

75  drought adaptation of riparian cottonwoods. Trees Struct Funct 14:248–257

76

77  Rood SW, Braatne JH, Hughes FMR. 2003. Ecophysiology of riparian cottonwoods: stream

78  flow dependency, water relations and restoration. Tree Physiology. 23(16): 1113-1124.

79  Ruiz-García A, Ferreras-Romero M. 2007. The larva and life history of Stenophylax crossotus

80  McLachlan, 1884 (Trichoptera: Limnephilidae) in an intermittent stream from the southwest

81  of the Iberian Peninsula. Aquatic Insects 29:9-16.

82  Sabater, S., X. Timoner, C. Borrego, and V. Acuna. 2016. Stream biofilm response to flow

83  intermittency: from cells to ecosystems. Frontiers in Environmental Sciences 4, 14-23.

84  Sandberg JB, Stewart KW. 2004. Capacity for Extended Egg Diapause in Six Isogenoides

85  Klapálek Species (Plecoptera: Perlodidae). Transactions of the American Entomological

86  Society (1890-) 130:411-423.

87  Secor SM, Lignot J-H. 2010. Morphological Plasticity of Vertebrate Aestivation. Pages 183-

88  208 in Arturo Navas C, Carvalho JE, eds. Aestivation: Molecular and Physiological Aspects.

89  Berlin, Heidelberg: Springer Berlin Heidelberg.

90  Sheldon F, Bunn SE, Hughes JM, Arthington AH, Balcombe SR, Fellows CS. 2010. Ecological

91  roles and threats to aquatic refugia in arid landscapes: dryland river waterholes. Marine and

92  Freshwater Research 61:885-895.

93  Stella JC, Battles JJ. 2010. How do riparian woolly seedlings survive seasonal drought.

94  Oecologia 164: 579-590.

95  Storey RG, Quinn JM. 2008. Composition and temporal changes in macroinvertebrate

96  communities of intermittent streams in Hawke's Bay, New Zealand. New Zealand Journal of

97  Marine and Freshwater Research 42:109-125.

98    Vander Vorste R, Corti R, Sagouis A, Datry T. 2016a. Invertebrate communities in gravel-bed,

99    braided rivers are highly resilient to flow intermittence. Freshwater Science 35:164-177.

100   Vander Vorste R, Malard F, Datry T. 2016b. Is drift the primary process promoting the

101   resilience of river invertebrate communities? A manipulative field experiment in an

102   intermittent alluvial river. Freshwater Biology 61:1276-1292.

103   van der Waal BCW. 1997. Some observations on the fish life in a seasonal sand river. Southern

104   African Journal of Aquatic Sciences 23:95-102.

105   Walker RH, Adams GL, Reid Adams S. 2013. Movement patterns of southern redbelly dace,

106   Chrosomus erythrogaster, in a headwater reach of an Ozark stream. Ecology of Freshwater Fish

107   22:216-227.

108   Watanabe M. 2006. Anhydrobiosis in invertebrates. Applied Entomology and Zoology 41:15-

109   31.

110   Wickson SJ, Chester ET, Valenzuela I, Halliday B, Lester RE, Matthews TG, Miller AD. 2014.

111   Population genetic structure of the Australian caddisfly *Lectrides varians* Mosely (Trichoptera:

112   Leptoceridae) and the identification of cryptic species in south-eastern Australia. Journal of

113   Insect Conservation 18:1037-1046

114