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

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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).

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.

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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 understanding 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	AFI co-occurs with other anthropogenic stressors. Interacting stressors may exacerbate or dampen biologic responses to flow

	competing, interacting and emerging stressors related to human activities.	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.

Figures

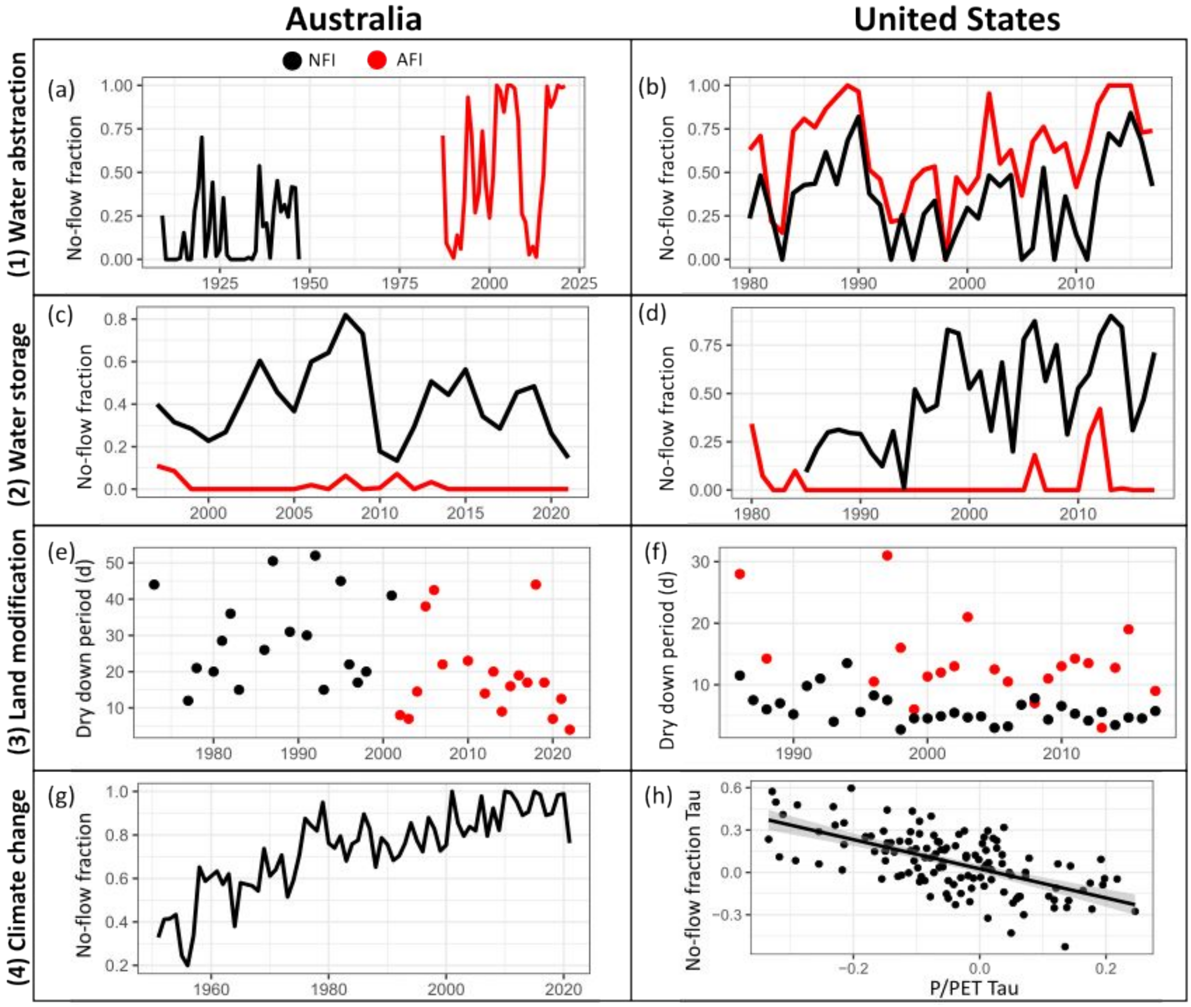


Figure 1. Differences in hydrological signatures between natural (NFI; black) and anthropogenic (AFI; red) flow intermittence for four drivers of AFI in Australia (a,c,e,g) and the United States (b,d,f,h), as summarized in **Appendix 1**. No-flow fraction is the proportion of zero-flow days in a year, 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.

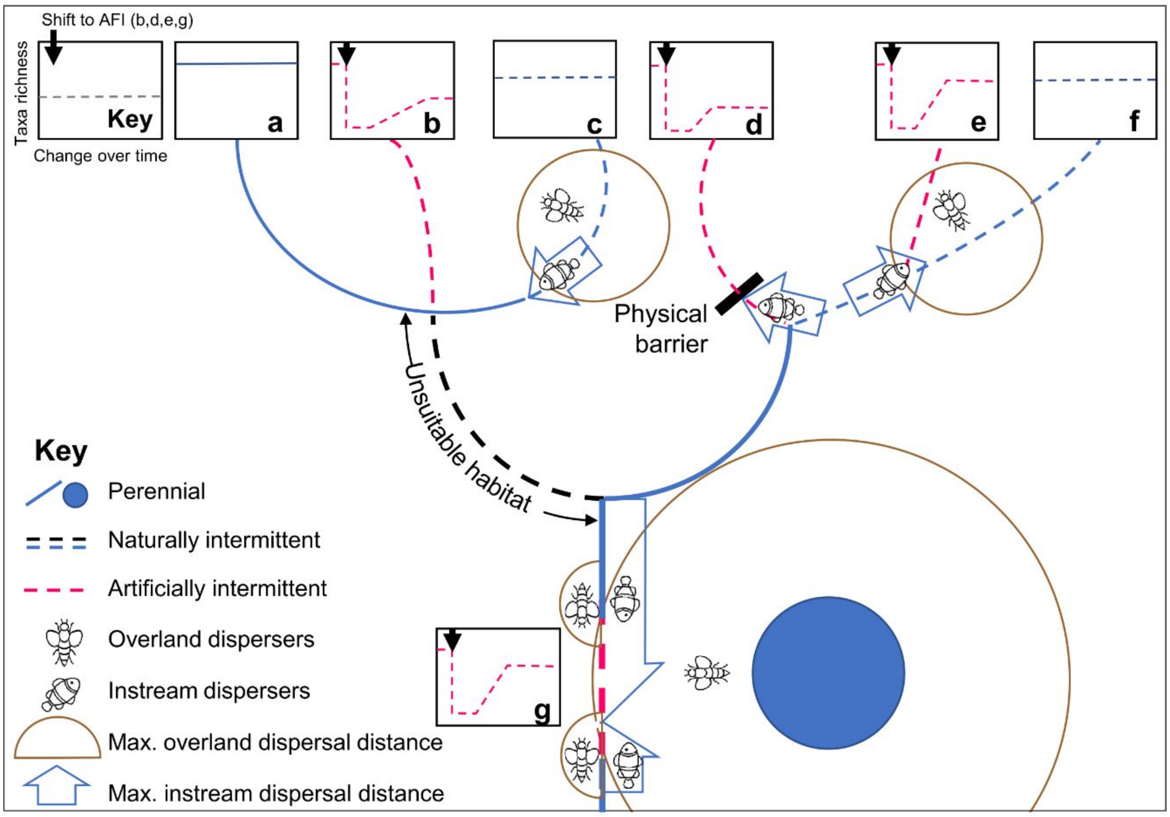


Figure 2. The influence of landscape context on change in biodiversity (as taxa richness) in reaches shifting from perennial flow to artificial flow intermittence (AFI; b, d, e and g). In headwaters (a–f), intermittence specialist species capable of overland and/or instream dispersal colonize from reaches 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.

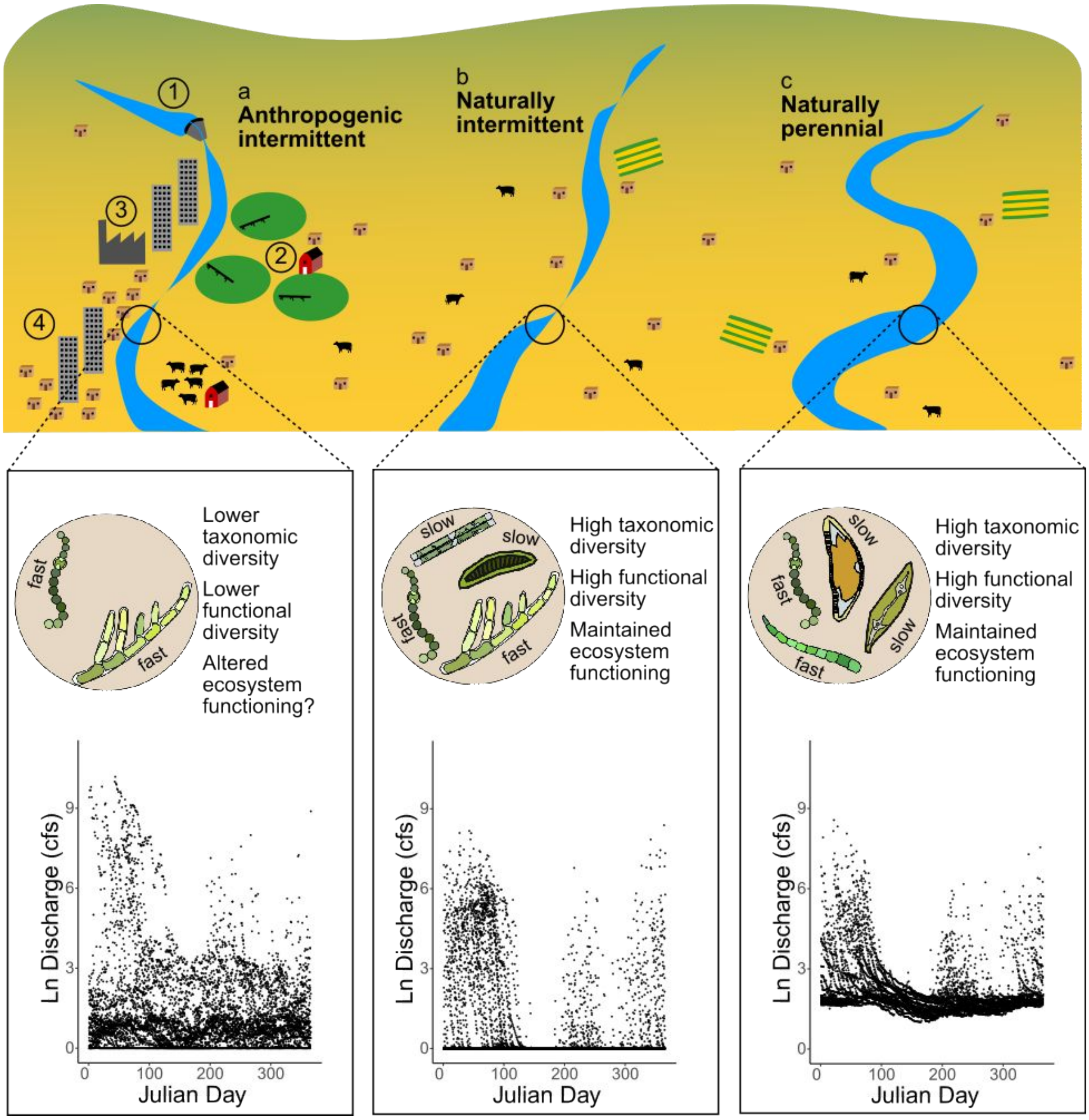
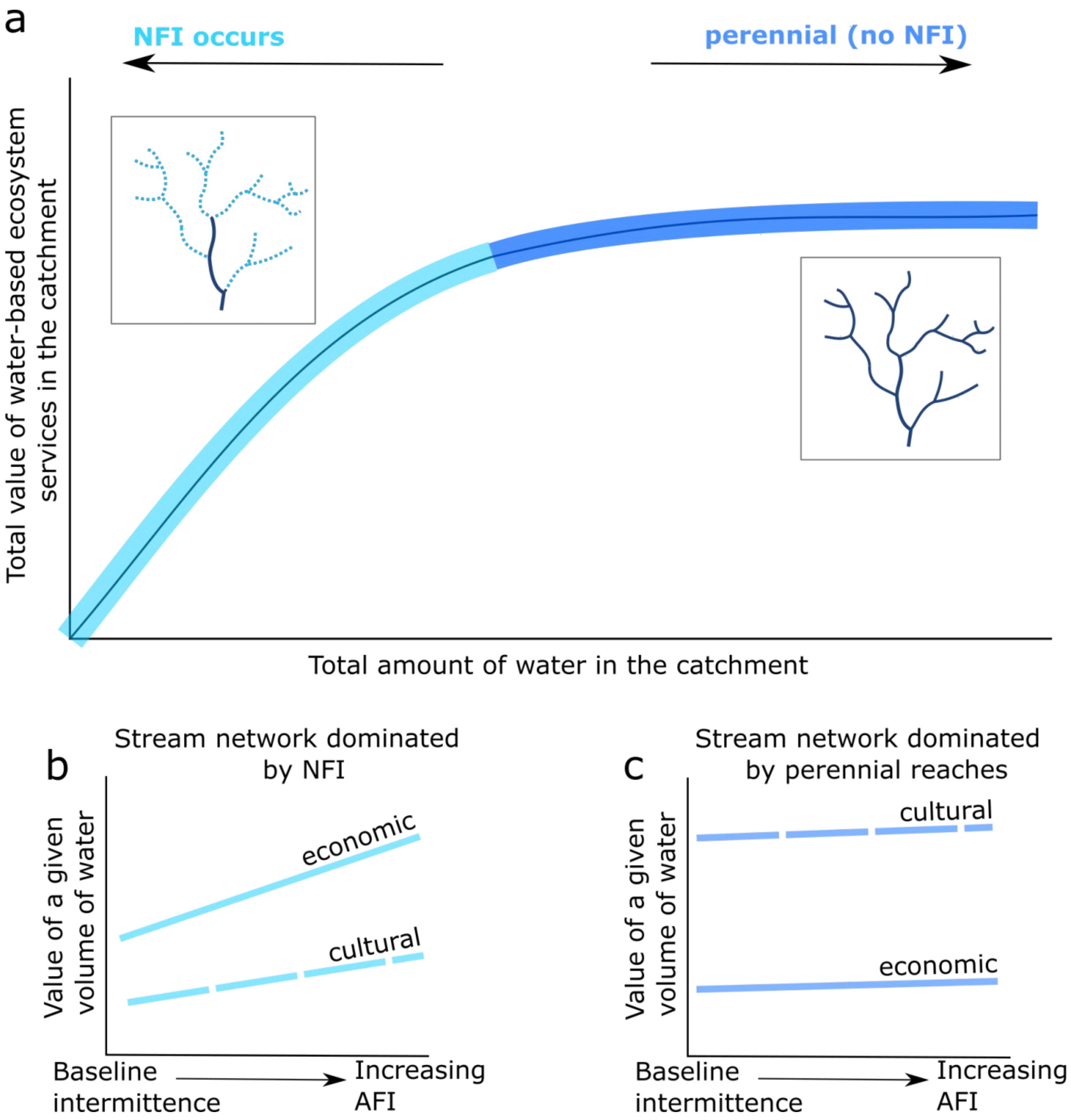


Figure 3. Anthropogenic flow intermittence (AFI, A) can cause shifts in community composition that alter ecosystem functioning compared to naturally intermittent (NFI, B) and naturally perennial (NP, C) reaches. These shifts can result from drivers including (1) water storage and flow reduction below 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.



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898 **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 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**).

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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

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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.

			Environmental associations					
Category	**Adaptation**	**Response**	**Wet phase**	**Dry phase**	**Subsurface habitat**	**Landscape connectivity**	**Example taxa**	**References**
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

		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 Boersma and Lytle 2014
						▨	Fish	Labbe and Fausch 2000 Sheldon et al. 2010 Alexandre et al. 2016
		Vertical migration into hyporheic zone			▨		Insect	Agüero-Pelegrín and Ferreras-Romero 2002 Cover et al. 2015 Vander Vorste et al. 2016b
					▨		Crayfish	DiStefano et al. 2009 Kouba et al. 2016
					▨		Salamander	Feral et al. 2005
					▨		Fish	Secor and Lignot 2010

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