Causes, Responses, and Implications of Anthropogenic versus Natural Flow Intermittence in River Networks

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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 because of 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 with 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. Because of 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.

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

Intermittent rivers and ephemeral streams (IRES), waterways that cease to flow, dominate global river networks, naturally representing 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 is 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 because of 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), socioeconomics (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

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Table 1. Drivers and examples of anthropogenic flow intermittence.

Driver	Predominant mechanism	Example	Reference
Water abstraction and diversion: Surface water extraction	Reduced stream flow due to removal of surface water	Tordera River, Spain	Benejam and colleagues (2010)
Water abstraction and diversion: Groundwater pumping or removal	Reduced groundwater discharge to stream or induced infiltration from stream into aquifer due to capture by pumping wells	Wissey, Rhee, Pang Rivers, United Kingdom	Bickerton and colleagues (1993)
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)
Water storage and flow regulation	Reduced volume of surface water or altered (unnatural flow dynamics) due to water storage	Tarim River, China	Zhou and colleagues (2020)
Land use or cover change	Changes to land surface affect water balance and catchment hydrology increasing evapotranspiration or flashier runoff, decreasing groundwater recharge or baseflow, and lengthening no-flow periods	Southern and western US rivers	Ficklin and colleagues (2018)
Climate change	Reduced precipitation, drought, increased evapotranspiration, generalized effects of climate change	Po and Pellice Rivers, Italy	Doretto and colleagues (2020)

Note: A single example is provided for each driver. A thorough meta-analysis is available in supplemental material S2.

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 because of 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 (less than 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.

In the present article, to the best of our knowledge, we are the first to explore differences between the effects of AFI and NFI 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 article: water abstraction and diversion, water storage and flow regulation, land-use change, and climate change (table 1, supplemental material S1 and S2). Although 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 hydroclimatic and regulatory context of the river can alter streamflow in various ways.

Water abstraction and diversion are a ubiquitous cause of AFI (Larned et al. 2010), encompassing various mechanisms, including surface water extraction, groundwater

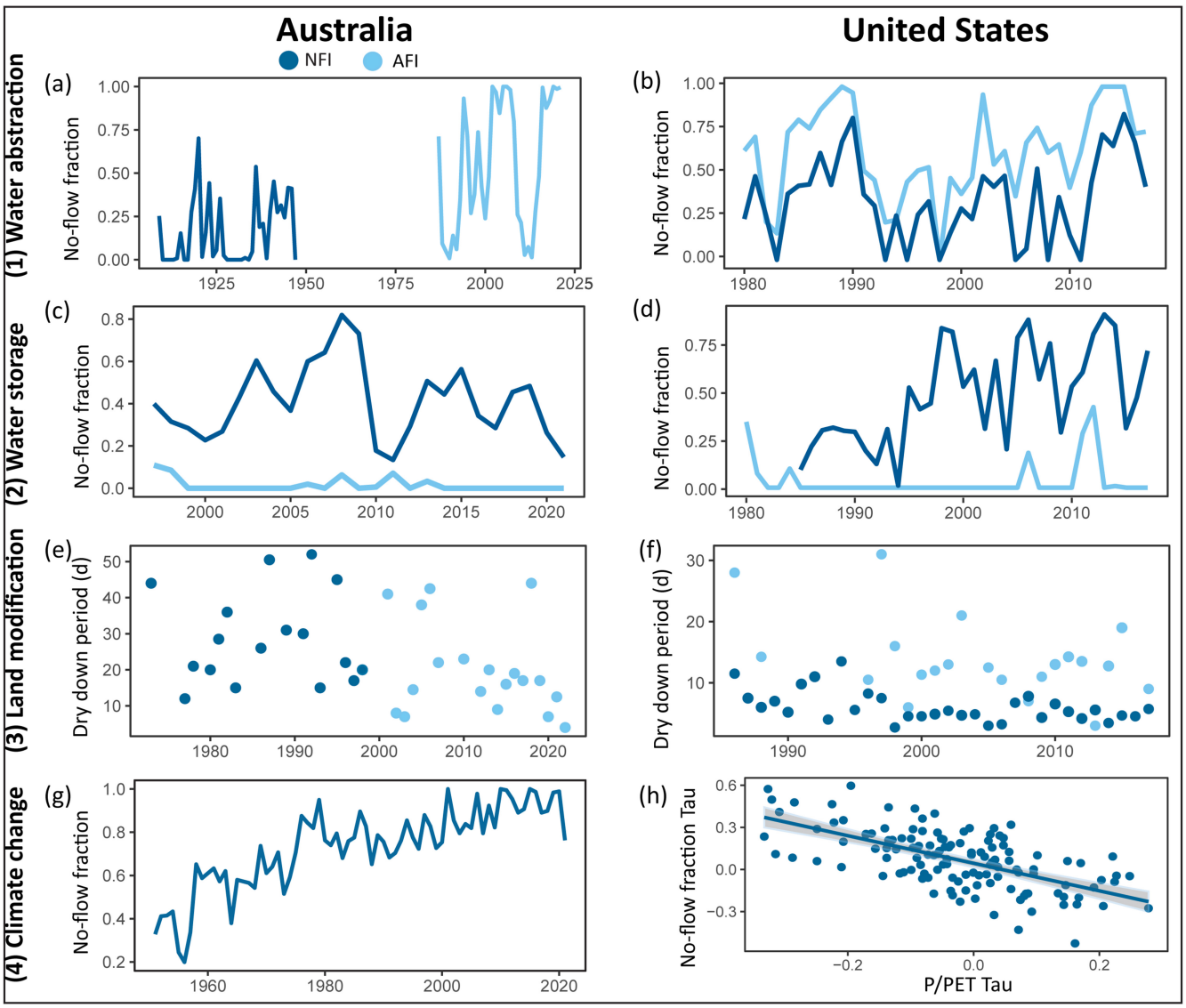

Figure 1. Differences in hydrological signatures between natural (NFI) and anthropogenic (AFI) flow intermittence for four drivers of AFI in Australia (a, c, e, g) and the United States (b, d, f, h), as is summarized in supplemental material S1. No-flow fraction is the proportion of zero-flow days in a year, whereas 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. The results with negative P:PET tau correspond to climate conditions, which have become drier.

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 and 1b, supplemental material S1). 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). An 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. A shorter duration of dry-down periods may reflect an acceleration of baseflow recession caused by either surface- or groundwater abstraction; the former reduces inflows from upstream, whereas the latter reduces storage of groundwater, later release of which sustains flow during dry periods.

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 and 1d; supplemental material S1; 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 preimpoundment hydrological regimes and characterization of dam-induced regime shifts would enable further assessment of how this widespread infrastructure affects flow intermittence.

Land-use change, which we define broadly to include changes in land use, land cover, and land management practices, can affect 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 and 1f, supplemental material S1). For example, urbanization increases the proportion of impervious surfaces, which generally increases high flows, but it can also both increase and decrease low-flow events (Bhaskar et al. 2020). Although 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 with the natural vegetation that preceded land-use change.

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 on 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 United States 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; Tramblay et al. 2021, Zipper et al. 2021). An earlier onset of no-flow compared with historical conditions may therefore be a useful signal of climate-driven AFI. However, there is substantial local and regional variability in the impacts of climate change (figure 1g and 1h, supplemental material S1). In the United States, 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 (supplemental material S3; Datry et al. 2014). 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 plants (Rood et al. 2003, Stella and Battles 2010) 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 the "Context dependence of the effects of AFI on biodiversity responses" below). Although communities often return to their predrying 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 predisturbance composition: The 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 affected by AFI may include 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 for longer because of 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 (figure 2; Sarremejane et al. 2021). 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 or desiccation-sensitive life stages. In some cases, this response to a rare drying event can temporarily increase temporal community turnover (figure 2; Katz et al. 2012, Aspin et al. 2019, Crabot et al. 2021b).

Of the four drivers, the effects of climate change on 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 because of climate change, biodiversity gradually declines, because species-specific desiccation-tolerance thresholds are exceeded during dry phases and as dispersal capacities fall short of distances between refuges and NFI streams (Bogan et al. 2013, Sarremejane et al. 2021). 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 because of 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 because of 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. In addition, the flow regimes produced by AFI may differ substantially from the NFI regimes to which these specialists are adapted (figure 1), as is 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 because of 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 therefore 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 postdrying 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).

The timing of AFI events could also influence colonization after flow resumes. For example, if a river affected 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. Therefore, 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

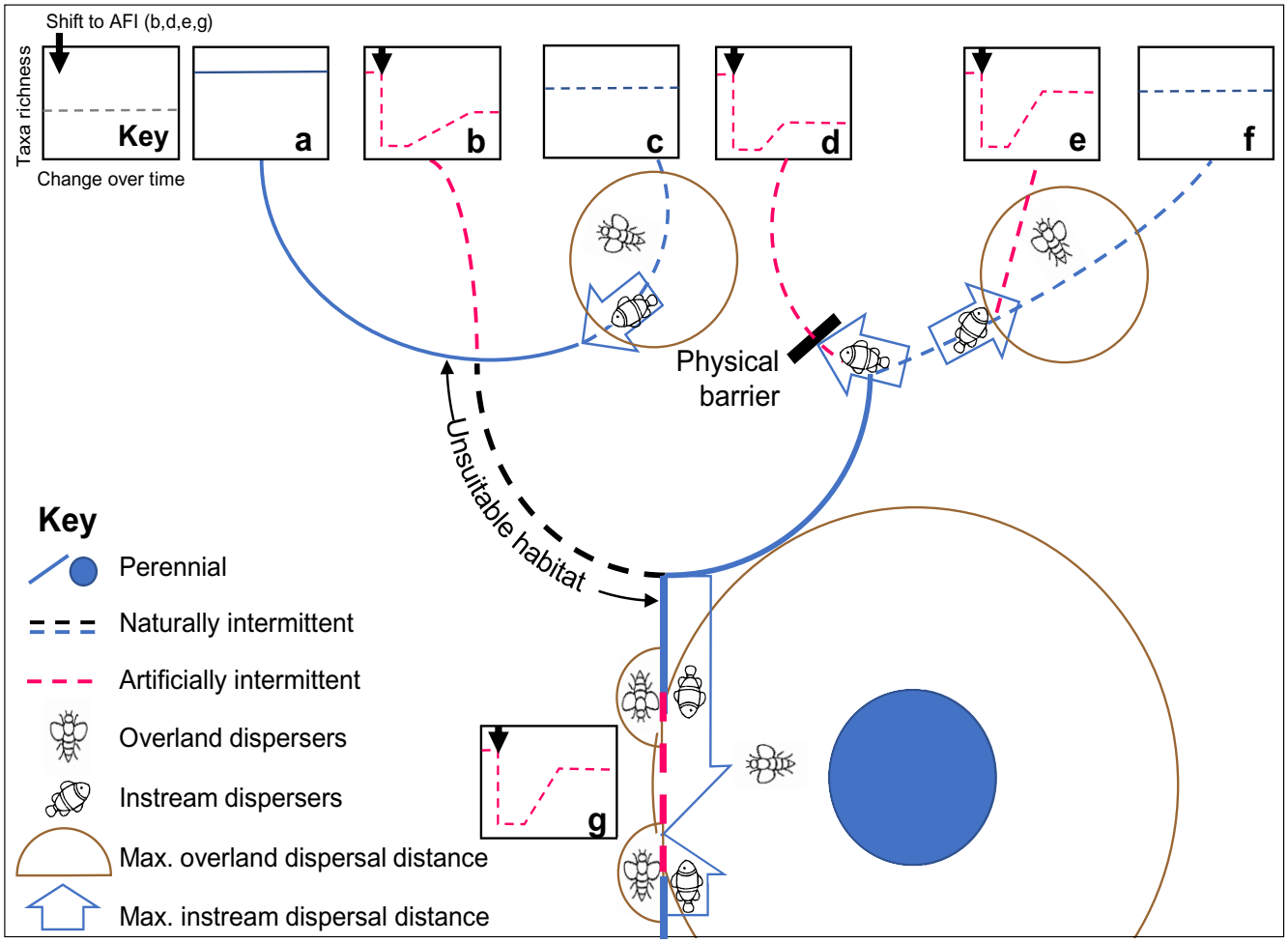

Figure 2. The influence of landscape context on change in biodiversity (as taxa richness) in reaches shifting from perennial flow to artificial flow intermittence (AFI; b, d, e, and g). In headwaters (a–f), intermittence specialist species capable of overland or instream dispersal colonize from reaches 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 or reaches with unsuitable habitat (including perennial reaches) remain taxon poorer (b, d). Barriers or intervening reaches with unsuitable habitat may also prevent intermittence specialists from colonizing downstream AFI sites (g), at which biodiversity instead increases because of colonization by generalists via overland dispersal from nearby aquatic habitats 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 are proportional to stream size.

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 on flow resumption. However, because stressors can directly and indirectly affect 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 therefore 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 with 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 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 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 because of 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.

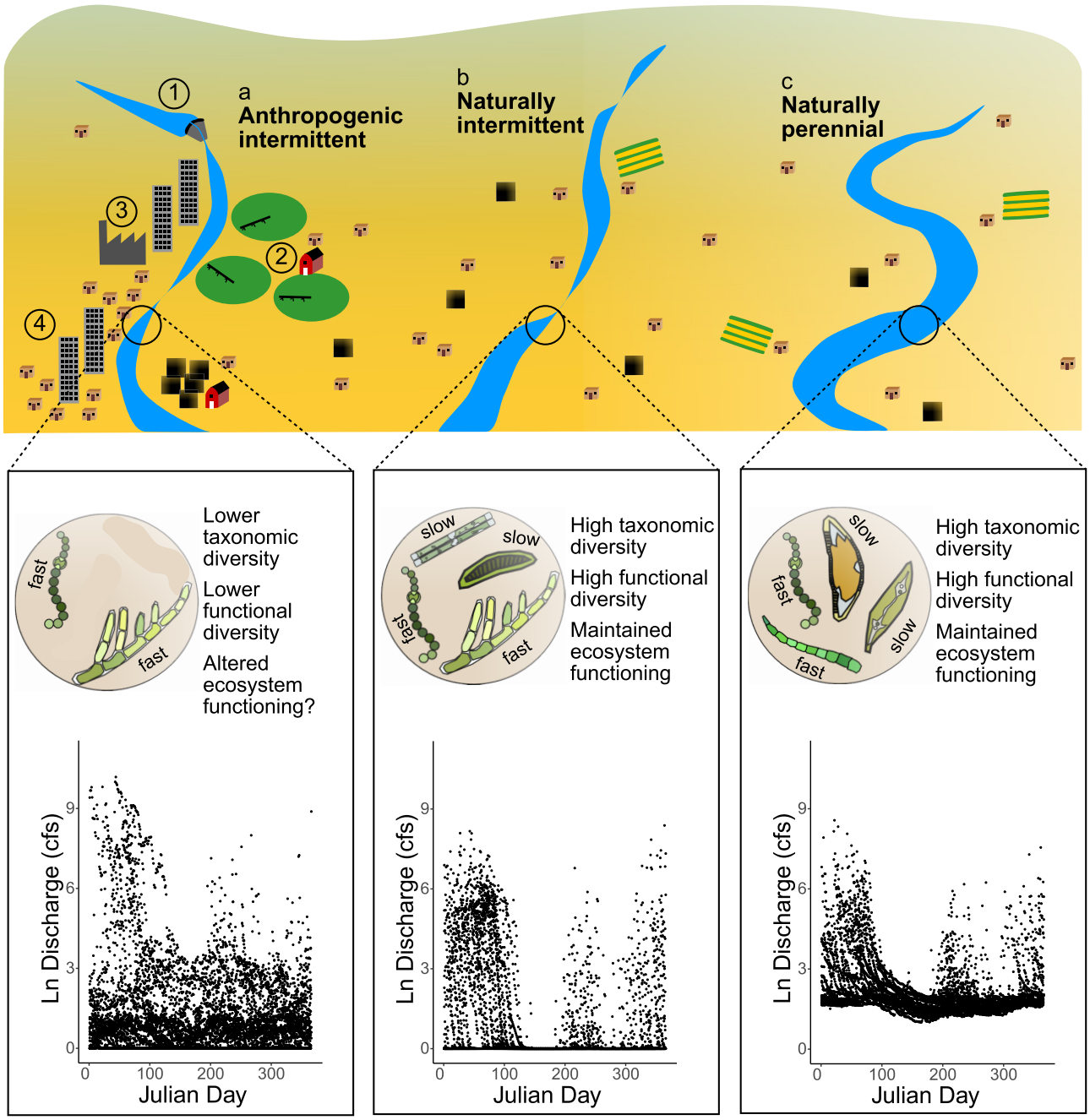

Figure 3. Anthropogenic flow intermittence (AFI) (a) can cause shifts in community composition that alter ecosystem functioning compared with naturally intermittent (NFI) (b) and naturally perennial (NP) (c) reaches. These shifts can result from drivers including (1) water storage and flow reduction below dams; (2) groundwater pumping, shown for center-pivot irrigation; (3) surface water abstraction, 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 with both NP and NFI reaches, as was shown in hydrographs on the basis of 20 years of gauge data from Arizona, in the United States, at AFI (the Salt River), NP (Cherry Creek), and NFI (Dry Beaver Creek) sites. The circles in the insets show hypothetical diatom communities in each reach. The functional trait of cell size is associated with growth rates, with smaller- and larger-cell species having "fast" and "slow" growth, respectively. Only a subset of species in NFI and NP communities are present in the AFI community, because of environmental filtering of taxa with traits conferring resistance to drying. Lower taxonomic diversity is typically associated with lower rates of ecosystem functions, as is 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.

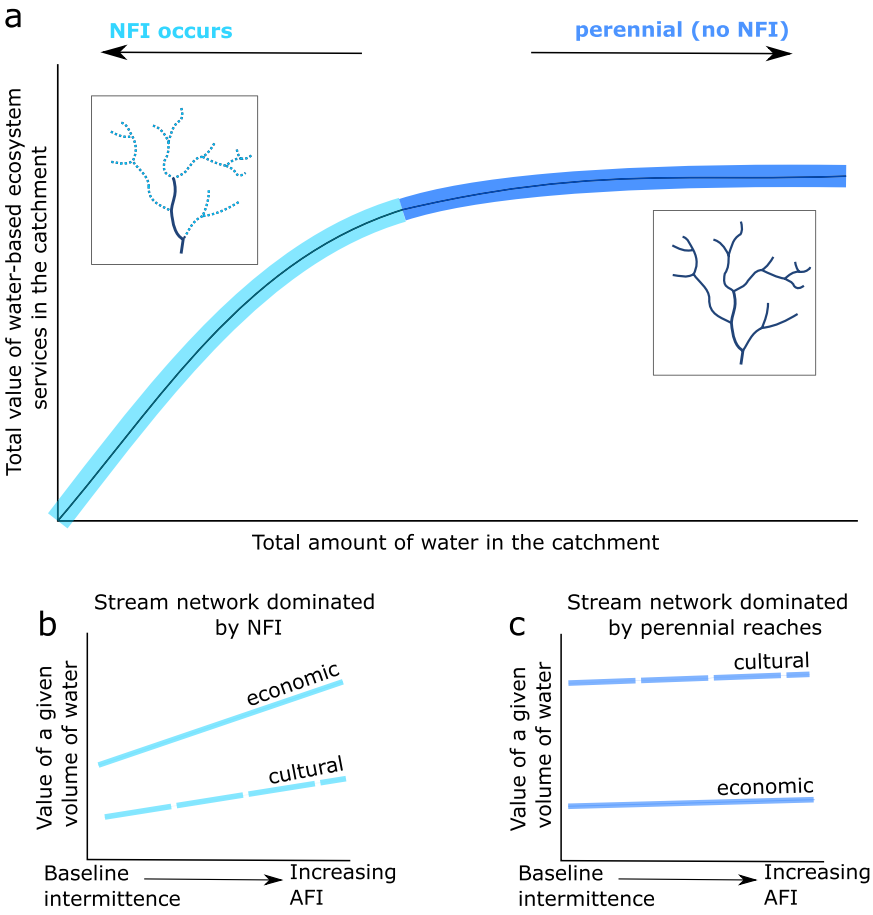

Figure 4. Water availability drives differences in the delivery and value of water-based ecosystem services in artificial IRES. (a) The total value of water-based services within catchments is proportional to the perennial network length, with a given increase in water causing a greater increase in value 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, although 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.

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 therefore increase water's social and economic values, particularly in arid regions where water is naturally scarce (figure 4a and 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 because of 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 therefore 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 affecting 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 therefore susceptible to alteration by AFI (Datry et al. 2018, Stubbington et al. 2020). Where AFI increases the spatial extent 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 on rewetting, 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. Therefore, 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 therefore theoretically changes the nature but not necessarily the extent of recreational service delivery. But 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, because of 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 sociohydrological norms are complex and context dependent, and further research exploring the implications of AFI to cultural services is warranted.

In summary, 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 cooccurring provisioning, regulating, and cultural services within ecosystem service bundles (Datry et al. 2018, Stubbington et al. 2020). 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 toward 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, because it will allow improved monitoring, evaluation, reporting, restoration, and remediation policies to be developed. The first step toward 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 or AFI, when drying would occur on the basis of seasonal climate patterns, and the likelihood of synchrony between the drying of AFI and NFI. In addition, 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 socioeconomic 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 that are more likely to conserve or restore the biodiversity of rivers prone to AFI. We are lacking information on 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); how functional redundancy promotes resilience and resistance to AFI; specific functional traits that confer resilience to pool or dry conditions, and whether AFI specifically selects for or against them; cascading effects of AFI on key biogeochemical functions (e.g., carbon and nitrogen cycling); and feedback loops 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 ecohydrological 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 links 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

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

Discipline	Gaps	Why it is important
Geography or 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 on 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 therefore have dramatic effects on local and regional biodiversity. In addition, top-down cascades within the foodchain 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 links 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 versus 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 or 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 or ecotoxicology	Understand the individual versus combined effects of AFI in the face of competing, interacting and emerging stressors related to human activities.	AFI cooccurs with other anthropogenic stressors. Interacting stressors may exacerbate or dampen biologic responses to flow changes. Identifying the synergistic and antagonistic effects of stressors will allow to determine whether or not certain types of rivers are more sensitive to AFI than to NFI and will assist in the development of multicriteria tools.
Socioeconomics	Develop a comprehensive framework of AFI relative to the ecosystem services that rivers provide on the basis of 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 help defining useful metrics that quantify relevant water uses (e.g., percentage water diverted, location in network) and will guide management practices and policy.

policies and practices that support the effective management and conservation of river networks globally.

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Supplemental material

Supplemental data are available at *BIOSCI* online.

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