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► To cite this version:

T. Datry, A.J. Boulton, N. Bonada, K. Fritz, C. Leigh, et al.. Flow intermittence and ecosystem services in rivers of the Anthropocene. *Journal of Applied Ecology*, 2018, 55 (1), pp.353-364. 10.1111/1365-2664.12941 . hal-01883365

HAL Id: hal-01883365

<https://hal.science/hal-01883365>


Submitted on 28 Sep 2018

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COMMENTARY

Flow intermittence and ecosystem services in rivers of the Anthropocene

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Funding information

CESAB; French Foundation for Research and Biodiversity (FRB); French National Agency for Water and Aquatic Environments

Handling Editor: Steven Vamosi

Abstract

1. Intermittent rivers and ephemeral streams (IRES) are watercourses that cease flow at some point in time and space. Arguably Earth's most widespread type of flowing water, IRES are expanding where Anthropogenic climates grow drier and human demands for water escalate.
2. However, IRES have attracted far less research than perennial rivers and are undervalued by society, jeopardizing their restoration or protection. Provision of ecosystem services by IRES is especially poorly understood, hindering their integration into management plans in most countries.
3. We conceptualize how flow intermittence governs ecosystem service provision and transfers at local and river-basin scales during flowing, non-flowing and dry phases. Even when dry or not flowing, IRES perform multiple ecosystem services that complement those of nearby perennial rivers.
4. *Synthesis and applications.* Conceptualizing how flow intermittence in rivers and streams governs ecosystem services has applied a socio-ecological perspective for validating the ecosystem services of intermittent rivers and ephemeral streams. This can be applied at all flow phases and in assessing impacts of altered flow intermittence on rivers and their ecosystem services in the Anthropocene.

KEYWORDS

Anthropocene, biodiversity, climate change, conservation, ecosystem services, ephemeral streams, flow management, intermittent rivers, management, rivers

1 | INTRODUCTION

Intermittent rivers and ephemeral streams (hereafter IRES) are watercourses that cease flow at some point in time and space. Arguably the world's most widespread type of flowing water (Datry, Bonada, & Boulton, 2017; Larned, Datry, Arscott, & Tockner, 2010), IRES range from ephemeral streams (Figure 1a,b) that flow briefly after rain or snow melt through to intermittent rivers that recede to isolated pools (Figure 1c–e). Flow regimes of IRES span a broad spectrum, varying widely in duration, timing, predictability, volume and spatial extent of flow cessation and drying events, even within the same watercourse. Ecologists assume this vast variability in the different components of the flow regimes promotes species richness in IRES by creating a spatial mosaic of habitats during the wetting-drying cycle (Datry, Larned, & Tockner, 2014). Studies reviewed in Leigh et al. (2016) show that increased flow duration and surface water persistence in IRES correlate with higher biodiversity of aquatic invertebrates and fish. However, the dry phase also promotes local and regional biodiversity, providing habitat and food for semi-aquatic and terrestrial biota (Steward, von Schiller, Tockner, Marshall, & Bunn, 2012).

Far less is known about how flow intermittence governs the provision of ecosystem services such as nutrient cycling, flood mitigation and water purification. Instead, research on ecosystem services

provided by flowing waters has focused on perennial rivers, reflecting the priority placed by society on reliable provision of water (Hill, Kolka, McCormick, & Starry, 2014). IRES are typically undervalued by society, even by people living near IRES (Armstrong, Stedman, Bishop, & Sullivan, 2012) who overlook the more subtle ecosystem services they provide, such as regulation and maintenance services (see later). Ecological functions and service transfers from IRES that translate biophysical structure and ecological processes into benefits that people value (Haines-Young & Potschin, 2010) are extremely poorly understood. This confounds attempts to identify how human impacts on IRES might affect delivery of different ecosystem services at local and regional scales.

Humans alter the flow regimes of IRES by altering runoff patterns in catchments through various land uses and by direct impacts on instream flows from dams and extraction of surface and ground water (Acuña et al., 2014; Palmer et al. 2008). The speed of these changes is unprecedented in this current Anthropocene period (Schimel, Asner, & Moorcroft, 2013), swiftly accelerating spatial and temporal intermittence in many parts of the world, especially where climates are becoming drier. Where human densities are high, flow regimes have been so altered that “novel” ecosystems (*sensu* Hobbs et al., 2014) have resulted, with artificially intermittent (or perennial) flows and, often, novel biota. How this affects



FIGURE 1 Examples of IRES ranging from small headwater streams during wet and dry periods (a. Cèze River, France; b. Río Sacaba, Bolivia) to large rivers during dry periods (c. Río Seco, Bolivia; d. Mortlock River, Western Australia; e. Brachina Creek, Flinders Ranges, South Australia). Photos: B. Launay (a), T. Datry (b–c), A.J. Boulton (d–e). [Colour figure can be viewed at wileyonlinelibrary.com]

the provision of ecosystem services at local and regional scales is completely unknown.

We begin this Commentary with the premise that the global and changing prevalence of IRES is a prime reason why their ecosystem services deserve closer attention and why IRES should be explicitly considered in water management strategies. We review how flow intermittence influences biodiversity and ecological functions in IRES, extending these findings to conceptualize how different hydrological phases might govern provision and transfers of various ecosystem services at local and regional scales. We use our conceptual model to explore the implications of “Anthropogenic intermittence” for ecosystem service provision and transfers by natural and novel IRES, concluding with several questions deserving further investigation.

2 | GLOBALLY WIDESPREAD AND INCREASING

We contend that IRES are Earth's most widespread type of flowing waters. They dominate arid, semi-arid, Mediterranean and dry-subhumid regions, which together cover almost half the global land surface. Examples include the semi-arid southwestern US states of Arizona and New Mexico where IRES comprise up to 94% of the total river length (Levick et al., 2008). Analysis of flow records from 2,750 gauging stations across Australia, France, Spain and the conterminous US revealed intermittence at 20% of the stations, with averages of more than five zero-flow days per year ranging from 8% of the stations in France to 65% in Australia (De Vries et al., 2015). Because gauging stations are preferentially installed on perennial rivers, these proportions likely underestimate the true extent of IRES; regional modelling indicates 30%–40% of the river network in France is intermittent (Snelder et al., 2013). Even in temperate and humid areas, IRES are abundant, especially in headwaters that make up over 70% of the channel length of most river networks (Datry et al., 2014).

The present-day Anthropocene is a geological period defined by humanity's massive impact on the planet, with rates of climate change equal to or exceeding the highest rates seen in the recent paleorecord (Loarie et al., 2009). In the Anthropocene, the global extent of IRES is increasing annually. Although some regions are becoming wetter, far more of the land surface is drying (Döll & Schmied, 2012). Reductions and seasonal shifts in precipitation and runoff have increased the duration of zero flows in many IRES while once-perennial rivers are now intermittent. For example, in southwestern Australia, streamflows over the last few decades have declined by more than 50% following a 16% drop in rainfall (Silberstein et al., 2012), causing perennial streams to become intermittent while formerly intermittent streams now seldom flow.

The increase in the frequency and duration of intermittence caused by climatic drying is exacerbated by human activities, such as water abstraction or diversion (Figure 2), many of which have intensified with growing water shortages (e.g. Acuña et al., 2014; Brooks, 2009). Not only is there now less surface water, the quality of what remains often declines when flows become intermittent, largely owing to effects of limited flushing and evapoconcentration of salts during drying (Williams, 2006). Flow regimes and ecological conditions have been so altered during the Anthropocene that IRES now support novel ecosystems characterized by new combinations of species, which have no shared evolutionary history (Arthington, Bernardo, & Ilhéu, 2014). For example, anthropogenic changes to the flow regime of the intermittent Guadiana River, southwestern Iberian Peninsula, coupled with the proliferation of invasive species have created a novel ecosystem characterized by a new fish assemblage comprising 12 invasive species and 14 native species, 9 of which are critically endangered, endangered or vulnerable (Hermoso, Clavero, Blanco-Garrido, & Prenda, 2011). As human pressures and climatic changes intensify, further novel ecosystems will emerge, posing challenges for river restoration and conservation (Moyle, 2014). It is not yet clear how Anthropogenic intermittence and the proliferation of novel ecosystems, including

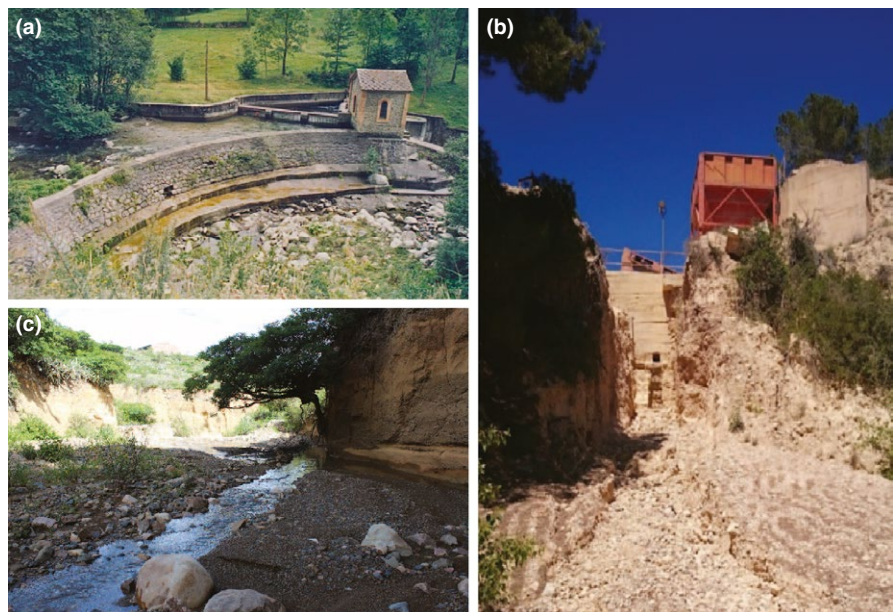


FIGURE 2 Examples of human activities causing intermittence. (a) Flow diversion for hydropower production turning a perennial river intermittent, Riu Freser, Queralbs, Spain; (b) Intermittence caused by a dam in Barranc de l'Estany, Tarragona, Spain; (c) Flow diversion for agriculture, Río Sacaba, Cochabamba, Bolivia. Photos: P Bonada (a), N Cid/TRivers (b), T Datry (c). [Colour figure can be viewed at wileyonlinelibrary.com]

hybrid systems of naturally and artificially intermittent reaches, will influence biodiversity, ecological functioning and ecosystem services in river networks.

3 | FLOW INTERMITTENCE, BIODIVERSITY AND ECOSYSTEM SERVICES

The negative association between flow intermittence and aquatic biodiversity is well known. As annual flow intermittence (proportion of the year without water) increases, there are typically declines in taxonomic richness of aquatic invertebrates, fish and riparian vegetation (Datry et al., 2014). When IRES cease flow, aquatic biodiversity declines, often following a “stepped” trajectory as microhabitats become hydrologically disconnected or dry (Boulton, 2003). When flow resumes, aquatic biodiversity increases again, with the assemblage composition reflecting different degrees of resistance and resilience by the biota to drying (Bogan, Boersma, & Lytle, 2015). However, the complex relationships between aquatic diversity and the interacting components of intermittence such as duration, frequency, timing and antecedent history are still being unravelled (Leigh & Datry, 2017).

When dry, the channels of IRES support diverse assemblages of semi-aquatic and terrestrial fauna, especially invertebrates such as ants and spiders (Steward et al., 2012) whose biodiversity is likely associated with habitat complexity and the duration of the dry phase. Dry channels and the riparian zones of IRES are crucial migration corridors and habitats for numerous terrestrial vertebrate species (Sánchez-Montoya, Moleón, Sánchez-Zapata, & Tockner, 2016), maintaining and enhancing biodiversity at the river network scale. Sometimes, intermittence has a “Goldilocks effect” providing just the right conditions for peak biodiversity; in some American Southwest IRES, riparian vegetation species richness increases as flow changes

from perennial to intermittent before declining to a minimum as flow becomes ephemeral (Katz, Denslow, & Stromberg, 2012).

As well as biodiversity, flow intermittence also governs many ecological functions in IRES. For example, densities of aquatic invertebrate detritivores are sensitive to intermittence, which in turn translates into altered rates of leaf litter decomposition (e.g. Corti, Datry, Drummond, & Larned, 2011) and organic matter processing. Wetting and drying also govern microbially mediated ecosystem functions such as nutrient cycling and dissolved organic matter dynamics (Vázquez, Ejarque, Ylla, Romani, & Butturini, 2015). When IRES dry, ecological functions are facilitated by semi-aquatic and terrestrial organisms although these processes are little studied. For example, vegetation colonizing dry riverbeds likely reduces erosion, promotes genetic diversity locally and helps regulate local climates.

The association of biodiversity, ecological functions and intermittence has major implications for the provision of ecosystem services when IRES are viewed as socio-ecological systems (Figure 3). Ecosystem services are benefits people obtain that are directly attributable to the ecological functioning of ecosystems (De Groot, Wilson, & Boumans, 2002). Applying this perspective to ecosystem management helps practitioners formulate environmental policies, set management priorities and restore or conserve ecosystems (Boulton, Ekeboom, & Gíslason, 2016; Seidl, 2014). The “cascade model” (Haines-Young & Potschin, 2010) shows how biophysical structures and ecological processes support ecosystem functions whose outputs are transferred as services that are defined and valued socio-economically (Figure 3). Factors governing biophysical structure (e.g. channel morphology, substrate composition), rates of ecological processes (e.g. nutrient cycling, organic matter decomposition) and biodiversity are likely to control provision and transfers of ecosystem services. In IRES, the most significant of these factors is intermittence.

Surprisingly, no research has assessed or valued the full suite of ecosystem services potentially provided by IRES or their collective

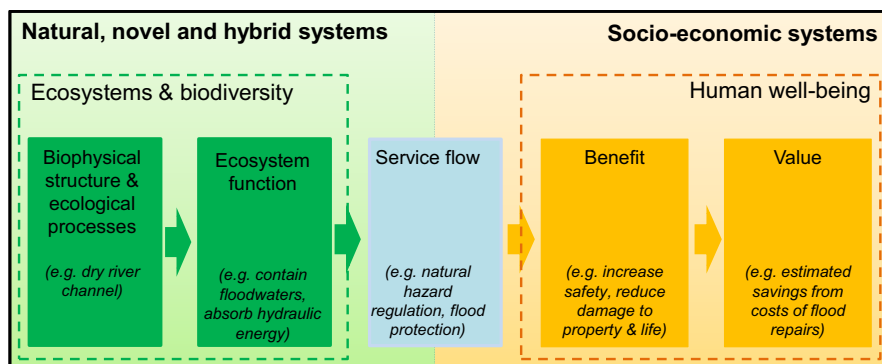


FIGURE 3 The “cascade model” of ecosystem services (modified from Haines-Young & Potschin, 2010), portrayed from a socio-ecological perspective and illustrating an example from intermittent rivers and ephemeral streams (IRES). The sequence of panels from left to right represents how the biophysical structure and ecological processes in a given ecosystem (together with its biodiversity) govern ecosystem functions whose services are transferred to provide benefits that are defined and valued socio-economically. As virtually all aspects of the biophysical structure and ecological processes of IRES are governed by flow intermittence, these effects are inferred to translate into altered ecosystem services and benefits in natural IRES. In novel IRES, human activities and climate change have changed the capacity of ecosystems to provide services, ultimately altering their values to society. [Colour figure can be viewed at wileyonlinelibrary.com]

association with biodiversity or flow intermittence. Although some research has focused on single ecosystem functions as ecosystem services during single hydrological phases (e.g. effects of drying on nitrogen processing in Mediterranean IRES, Arce, del Mar Sánchez-Montoya, Vidal-Abarca, Suárez, & Gómez, 2014), defining values or assessing trade-offs with concurrent ecosystem functions remains wanting. Despite the rich literature describing intermittence in governing virtually every biogeochemical and ecological process in IRES (reviews in Datry et al., 2014; Larned et al., 2010; Leigh et al., 2016) and calls to consider the values of IRES (Boulton, 2014; Steward et al., 2012), no conceptual models exist to predict how intermittence governs ecosystem service provisioning during different hydrological phases in IRES.

4 | A CONCEPTUAL MODEL OF ECOSYSTEM SERVICES PROVIDED BY IRES

Our conceptual model focuses on ecosystem services provided during the three hydrological phases in most IRES: flowing, non-flowing (pools) and dry (Figure 4). We adopt the Common International Classification of Ecosystem Services (CICES) because it is widely used (examples in <http://cices.eu/>), standardizes the description of ecosystem services, includes units for the valuation of services, and is more comprehensive than the MEA (Millennium Ecosystem Assessment) (2005) and TEEB (The Economics of Ecosystems and Biodiversity) (2010) classifications. CICES recognizes three broad

categories of services: provisioning, regulating and cultural. The category of “supporting services” originally defined in the MEA (Millennium Ecosystem Assessment) (2005) is considered as part of the underlying structures, processes and functions that characterize ecosystems to avoid “double-counting” ecosystem services (Boulton et al., 2016).

During a typical wetting-drying cycle, IRES pass from a flowing phase (top picture, Figure 4) to a non-flowing pool phase (lower right) and then, often, a dry phase (lower left) when surface water disappears. Transitional periods of varying length, timing and predictability occur between these phases. However, to provide a starting place, our model only explores potential service provision during these three main phases. CICES identifies 16 provisioning services (outputs, Table 1) related to nutrition, materials and energy. When flowing, IRES potentially provide all of these in the same way as perennial rivers, but when flow ceases, water quality issues in dwindling pools may alter the scope of surface water uses (Table 1). Drying removes four provisioning services associated with surface water and alters most of the remaining services (Figure 4).

Of the 19 applicable regulating services (Table 1), all are provided during the flowing phase as in perennial rivers, six are lost when IRES dry and all are altered (usually restricted) during the pool phase (Table 1; Figure 4). Services mediated by biota (e.g. bioremediation, filtration and sequestration) are especially altered by the effects of flow intermittence on biodiversity but there are also abiotic effects where surface waters in IRES play roles such as regulating climate, transporting or diluting materials and maintaining physical, chemical and biological conditions (Table 1). However, much remains to be learned about how intermittence affects provision of most of these services in IRES and the assessments in Table 1 should be treated as hypotheses (see next section). CICES distinguishes 11 cultural services (Table 1). Strikingly, most of these services are provided during all three phases (Figure 4) attesting to the many facets of cultural importance of IRES even when dry (Steward et al., 2012).

We extend the conceptual model from the temporal sequence of flowing, non-flowing and dry phases (Figure 4) to include the spatial components of “service-providing areas” (SPAs), “service-benefiting areas” (SBAs) and “service-connecting areas” (SCAs) (sensu Syrbe & Walz, 2012). This spatial perspective is crucial because these three components are unevenly distributed at the river-basin scale. For example, SPAs of regulating services are more common in headwater streams than downstream where their SBAs occur (Figure 3 in Syrbe & Walz, 2012). At the local scale of the river reach, SBAs are usually close (<1 km) to SPAs, which are typically instream and riparian zones, and SCAs are predicted to be small. However, artificial solutions (e.g. piping water) can mean that people in SBAs can be geographically distant from SPAs and have no need for natural flow, for example, to convey ecosystem goods such as water (Syrbe & Walz, 2012).

Our conceptual model hypothesizes that, under natural conditions, spatial patterns of flow intermittence in IRES are the major driver of the distribution of SPAs, SBAs and SCAs at local and regional scales. For example, because the SPAs of most regulating services predominate in

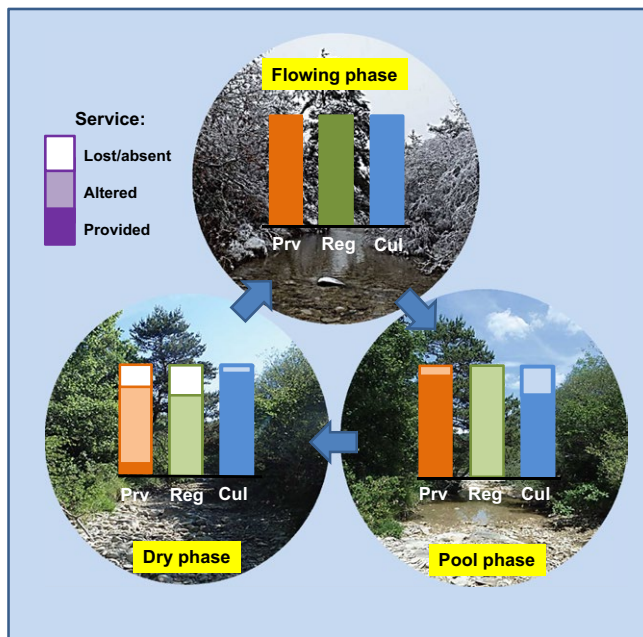


FIGURE 4 Conceptual model of provisioning (Prv), regulating (Reg) and cultural (Cul) ecosystem services hypothesized to be provided (solid bar), altered (light shading) or lost (unshaded) during the three hydrological phases in a typical IRES (photos: B. Launay). Table 1 lists the services (CICES outputs) for each phase. [Colour figure can be viewed at wileyonlinelibrary.com]

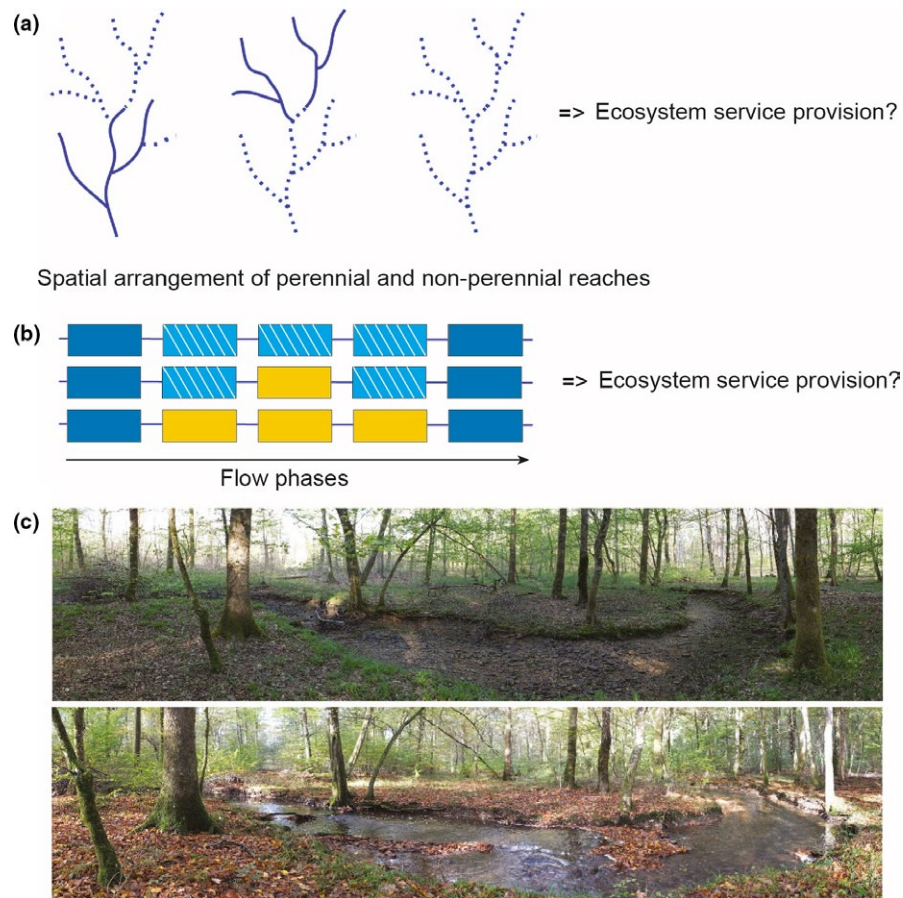


FIGURE 5 (a) IRES networks vary in their spatial arrangements of perennial (solid line) and intermittent (broken line) reaches, ranging from intermittent upper reaches feeding perennial lower reaches (left), perennial (e.g. spring-fed) upper reaches with intermittent lower reaches (middle) through to completely intermittent catchments lacking perennial reaches (right). (b) Different temporal sequences of flow phases (flowing = solid blue, pool = striped blue-and-white, dry = yellow) occur within and among Intermittent rivers and ephemeral streams (IRES). Sequences can include no dry phase (top row), a dry phase preceded and followed by pool phases (middle row) and very brief or no pool phases (bottom row) typical of many ephemeral streams that flow fleetingly after heavy rain. (c). Varying combinations of temporal sequences and spatial arrangements of intermittence are hypothesized to alter ecological functions such as organic matter cycling and its resultant ecosystem services. Organic matter in IRES accumulates during non-flowing phases (upper panel) before being entrained by the first pulse of flow (lower panel), potentially influencing ecological functions and ecosystem services downstream (Photos: B Launay). [Colour figure can be viewed at wileyonlinelibrary.com]

headwaters, river networks with non-perennial headwaters will have a different suite of ecosystem services from networks whose upper reaches are perennial but that dry in their lower reaches (Figure 5a). Similarly, the distribution of SBAs may be determined by water permanence, especially at local scales where people preferentially settle near permanent water. Because intermittence disrupts water flow through in-channel SCAs, the spatial patterns of intermittence in a network will govern the transfers of water-borne ecosystem services from SPAs to SBAs (Figure 5a). We suggest that research into ecosystem services in IRES should explicitly specify SPAs, SBAs and SCAs at multiple spatial scales because their distributions affect valuation, and strategies to optimize management and protection, of ecosystem services in IRES networks.

The applied value of our conceptual model lies in its socio-ecological perspective that human alterations of flow intermittence, and thus the duration, timing and frequency of different hydrological

phases (Figure 5b) are likely to alter the provision of different ecosystem services at different times. Novel systems with highly altered flow regimes may provide similar ecosystem services to natural IRES but to different degrees and with different benefits owing to altered biodiversity and/or ecological functions. Also, the interaction between the spatial arrangements and temporal sequences of hydrological phases (Figure 5) likely governs the diversity and rates of ecosystem services at a single location, complementing the perspective of IRES as “punctuated biogeochemical reactors” (Larned et al., 2010) for ecological functions and ecosystem services such as organic matter cycling and its benefits (Figure 5c). Furthermore, our model implies that intermittence interrupts the transfers of water-borne ecosystem services (Figures 4 and 5) from SPAs to SBAs by disrupting hydrological connectivity along surface channels, laterally across the riparian zone and floodplain and vertically along groundwater flowpaths of IRES. Finally, our conceptual model emphasizes that even when dry or not flowing,

TABLE 1 Ecosystem services potentially provided by the channels, shallow alluvia and riparian zones of IRES during three hydrological phases (defined as “flowing”, “pool” and “dry”) indicated as provided (✓), lost (✗) or altered compared to the flowing phase (~). The flowing phase is used for reference because the services provided during this phase match those of perennial rivers. Classification of ecosystem services follows CICES (version 4.3). This table was used to generate the histograms in Figure 4

Ecosystem service category	Main output or process	Physical, biological or cultural type or process	Outputs (material, biophysical or cultural) that can be linked back to specific service sources	Provision according to flow phase		
				Flowing	Pool	Dry
Provisioning	Nutrition	Biomass	Cultivated crops	✓	✓	~ (in dry channel)
			Reared animals and their outputs	✓	✓	~ (in dry channel)
			Wild plants, algae and their outputs	✓	✓	~ (in dry channel, not algae)
			Wild animals and their outputs	✓	✓	~ (in dry channel)
			Plants and algae from in situ aquaculture	✓	✓	✗
			Animals from in situ aquaculture	✓	✓	✗
	Materials	Biomass	Surface water for drinking	✓	~ (may be water quality issues)	✗
			Ground water for drinking	✓	✓	✓
			Fibres and other materials from plants, algae and animals for direct use or processing	✓	✓	~ (in dry channel, not algae)
			Materials from plants, algae and animals for agricultural use	✓	✓	~ (in dry channel, not algae)
			Genetic materials from all biota	✓	✓	~ (in dry channel)
			Surface water for non-drinking purposes	✓	~ (may be water quality issues)	✗
	Energy	Biomass-based energy sources	Ground water for non-drinking purposes	✓	✓	✓
			Plant-based resources	✓	✓	~ (in dry channel, not algae)
			Animal-based resources	✓	✓	~ (non-aquatic animals)
			Animal-based energy	✓	✓	~ (non-aquatic animals)
		Mechanical energy				
Regulation and maintenance	Mediation of waste, toxics and other nuisances	Mediation by biota	Bioremediation by micro-organisms, algae, plants and animals	✓	~ (flowing water biota reduced or lost)	~ (aquatic biota lost)
			Filtration/sequestration/storage/accumulation by micro-organisms, algae, plants and animals	✓	~ (loss of surface flow may restrict some biotic activity)	~ (aquatic biota lost)
		Mediation by ecosystems	Filtration/sequestration/storage/accumulation by ecosystems	✓	~ (loss of surface flow alters filtration, transport and storage)	~ (loss of surface water alters filtration, transport and storage)
			Dilution by atmosphere, freshwater and marine ecosystems	✓	~ (loss of surface flow restricts dilution)	✗
			Mediation of smell/noise/visual impacts	✓	~ (loss of surface flow restricts mediation)	~ (loss of surface water restricts mediation)

Continues

Table 1 Continued

Ecosystem service category	Main output or process	Physical, biological or cultural type or process	Outputs (material, biophysical or cultural) that can be linked back to specific service sources	Provision according to flow phase		
				Flowing	Pool	Dry
	Mediation of flows	Mass flows	Mass stabilization and control of erosion rates	✓	~ (wind erosion)	~ (wind erosion)
			Buffering and attenuation of mass flows	✓	~ (nonflowing channel buffers mass flows)	~ (dry channel buffers mass flows)
		Liquid flows	Hydrological cycle and water flow maintenance	✓	~ (loss of surface flow but still seepage through alluvia)	✗
			Flood protection	✓	~ (nonflowing channel buffers flood flows)	~ (dry channel buffers floods flows)
	Maintenance of physical, chemical, biological conditions	Gaseous/air flows	Storm protection	n/a	n/a	n/a
			Ventilation and transpiration	✓ (in riparian zone)	~ (in riparian zone and exposed channel)	~ (in riparian zone and dry channel)
		Life cycle maintenance, habitat and gene pool protection	Pollination and seed dispersal	✓ (including hydrochory)	~ (in riparian zone and exposed channel)	~ (in riparian zone and dry channel)
			Maintaining nursery populations and habitats	✓ (aquatic and riparian biota)	~ (aquatic, semi-aquatic, terrestrial and riparian biota)	~ (semi-aquatic, terrestrial and riparian biota)
		Pest and disease control	Pest control	✓	~	~
			Disease control	✓	~	~
		Soil formation and composition	Weathering processes	✓ (water erosion)	~ (wind erosion)	~ (wind erosion)
			Decomposition and fixing processes	✓	~ (altered rates in pools)	✗ (virtually ceases when channel dry)
		Water conditions	Chemical condition of freshwaters	✓	~ (altered by evapoconcentration)	✗
			Chemical condition of salt waters	✓ (in saline IRES)	~ (altered by evapoconcentration)	✗
		Atmospheric composition and climate regulation	Global climate regulation by reduction of greenhouse gas concentrations	✓	~ (loss of flow may promote methanogenesis)	✗
			Micro and regional climate regulation	✓	~ (evaporation may affect local microclimates)	~ (in riparian zone and dry channel)
Cultural	Physical and intellectual interactions with biota, ecosystems and land-/seascapes (environmental settings)	Physical and experiential interactions	Experiential use of plants, animals and land-/seascapes in different environmental settings	✓	✓	✓
			Physical use of land-/seascapes in different environmental settings	✓	✓	✓
		Intellectual and representative interactions	Scientific	✓	✓	✓
			Educational	✓	✓	✓
			Heritage, cultural	✓	~ (associated with pools)	✓
			Entertainment	✓	~ (associated with pools)	~ (altered uses of dry channel)
			Aesthetic	✓	✓	✓

Continues

Table 1 Continued

Ecosystem service category	Main output or process	Physical, biological or cultural type or process	Outputs (material, biophysical or cultural) that can be linked back to specific service sources	Provision according to flow phase		
				Flowing	Pool	Dry
	Spiritual, symbolic and other interactions with biota, ecosystems and land-/seascapes (environmental settings)	Spiritual and/or emblematic	Symbolic	✓	✓	✓
			Sacred and/or religious	✓	~ (associated with pools)	✓
		Other cultural outputs	Existence	✓	✓	✓
			Bequest	✓	✓	✓

IRES continue to provide multiple diverse ecosystem services and therefore deserve the same protection and conservation as perennial rivers and streams.

5 | CONCEPTUAL CONUNDRUMS AND DESIGNER DILEMMAS

Cogent arguments have been made why we should care about IRES (Acuña et al., 2014). Their global ubiquity makes them an essential part of all landscape-level water resource management. Restoration and conservation of IRES have lagged behind those of perennial rivers, probably because IRES are typically undervalued by society (Armstrong et al., 2012) and their ecosystem services are little recognized (Boulton, 2014). Furthermore, the management of IRES is currently guided by conceptual models and insights gleaned from perennial rivers, and we have yet to ascertain whether these are equally applicable to IRES (Table 2).

We propose our conceptual model as a starting place to provoke hypotheses about the multiple ecosystem services provided by IRES, and how these services might vary at different stages of the wetting-drying cycle and in response to different durations and sequences of each phase. We hypothesize that the spatial arrangement of intermittent and perennial reaches in a river network influence the distribution of SPAs, their ecosystem functions and derivative ecosystem services, especially as varying combinations of hydrological connectivity in SCAs are likely to differentially transport services and benefits to different SBAs. However, the conundrums and associated hypotheses our model pose (Table 2) require testing with empirical data, especially for suites of ecosystem functions and services rather than individual ones (cf. Arce et al., 2014). This includes assessing trade-offs among different ecosystem services when enhanced provision of one service causes declines in one or more different services (Rodríguez et al., 2006). Failure to fully consider trade-offs often leads to exploitation of one service (usually a provisioning service) to the detriment of several others, typically regulating and cultural ones. These problems are probably especially severe in IRES when temporal and spatial patterns of intermittence are altered (Table 2).

6 | CONCLUSIONS

Drying climates and intensifying human demand for fresh water across much of the planet is accelerating artificial flow intermittence. Alterations to flow regimes, water quality and biota are sometimes so severe that restoration back to near-natural conditions is infeasible and may require “designer approaches” (Acreman et al., 2014) to maximize natural capital while supporting economic growth, recreation or cultural needs. Where flow regime alteration is sufficiently severe to generate novel IRES, there may be impairment or even loss of SPAs and SCAs, inducing alteration of ecosystem services as hypothesized in our conceptual model. Our model has applied value in its perspective on strategies for “reconciliation ecology” advocated by Moyle (2014) for restoring severely altered IRES by encouraging biodiversity and, by extension, ecosystem services in human-dominated ecosystems. However, there remain several dilemmas (Table 2) about designer approaches and whether novel systems still provide adequate ecosystem services and have the requisite transfer mechanisms between SPAs and SBAs. Increasing intermittence may cause human demographic shifts where the locations of SBAs change, affecting the values and trade-offs of ecosystem services from IRES. Exciting opportunities await ecologists and managers tackling these challenges in IRES in the Anthropocene, especially where the information can be used to protect or restore the ecosystem services provided during different hydrological phases and at different spatial scales across diverse IRES world-wide.

ACKNOWLEDGEMENTS

The Center for Synthesis and Analysis of Biodiversity (CESAB), funded jointly by the French Foundation for Research and Biodiversity (FRB) and the French National Agency for Water and Aquatic Environments (ONEMA) supported the Intermittent River Biodiversity Analysis and Synthesis (IRBAS, irbas.cesab.org) working group where these ideas were developed. We also thank two anonymous referees for trenchant comments on an earlier draft. The views expressed in this article are those of the authors and do not

TABLE 2 Conundrums, their rationale and some examples of associated questions about ecosystem services in IRES. Most of these emerge from the social-ecological perspective of our conceptual model and seek to better integrate scientific information into improved management, conservation and restoration of natural, hybrid and novel IRES

Conundrum	Rationale	Examples of associated theoretical and applied questions
How applicable are predictions from current conceptual models of river ecosystems to IRES?	Most freshwater research and associated conceptual models focus on perennial systems	How applicable to IRES is each of the current riverine ecosystem models and what is the influence of flow intermittence on their predictions about, for example, organic matter dynamics or aquatic assemblage composition? To what extent can we use these conceptual models to predict ecological responses to altered flow intermittence in novel and hybrid IRES ecosystems? What modifications might be needed to these models?
What are the links between biodiversity, ecological functions, ecosystem services and service transfers in IRES?	Most freshwater research assumes strong linkages between biodiversity, ecological functions and ecosystem services	Are there different types of quantitative relationships between biodiversity (aquatic, semi-terrestrial, riparian and terrestrial) in IRES and associated ecological functions and ecosystem services? Are nonlinearities in these relationships associated with changes in flow regime (e.g. extended periods of intermittence, altered timing or rate of onset)? Do these relationships influence service transfers across SCAs (e.g. down river channels, across riparian zones)? Do these relationships differ between local (e.g. site) and regional (e.g. river-basin) scales?
What roles are played by semi-aquatic and terrestrial biota in the provision and flow of ecosystem services in IRES?	Most freshwater research overlooks the roles of semi-aquatic and terrestrial biota in river ecosystems	What ecological functions and ecosystem services are mediated or influenced by semi-aquatic and terrestrial biota in IRES? How might these roles be affected by changes in flow regime (e.g. extended periods of intermittence, altered timing or rate of onset)? During the non-flowing or dry phase, can increases in semi-aquatic and/or terrestrial biodiversity compensate for declines in aquatic biodiversity in facilitating particular ecosystem services (e.g. sequestration of materials)? Are the biodiversity-ecosystem service relationships similar during flowing, non-flowing and dry phases?
How does spatial variation in patterns of flow intermittence and hydrological connectivity affect the provision of ecosystem services in IRES?	Many riverine conceptual models emphasize how biodiversity and ecological functions vary along rivers, out onto their floodplains and/or vertically into the hyporheic zone and associated groundwater	Are ecosystem services provided by a given perennial or intermittent section influenced by whether upstream reaches are intermittent? If so, does this apply equally to ecosystem services during different hydrological phases in IRES? How do spatial differences in aquatic biodiversity and ecological processes in IRES influence SPAs and SCAs in adjacent, subsurface and downstream sections of the river network? Are there thresholds of spatial flow intermittence (e.g. the proportion of intermittent river network) beyond which certain ecological processes and/or ecosystem services are lost? Are these consistent over time? How do human activities that influence spatial arrangements of intermittence and hydrological connectivity translate into altered ecosystem services in IRES? How do these activities affect the distribution and transfer capacity of SCAs in IRES?
How do differences in temporal patterns (e.g. sequence, duration, timing) of flowing, non-flowing and dry phases in IRES influence their ecological functions and ecosystem services?	In IRES, biodiversity and many ecological processes are influenced by intermittence, pulsed flow and current and antecedent hydrological conditions	Are ecosystem services provided by IRES influenced by the duration of flow cessation and/or loss of surface water? Are these influences consistent over time or do they vary with seasons or antecedent hydrological conditions? How resilient is the provision of different ecosystem services in IRES to altering the temporal sequence of hydrological phases? Are there threshold durations of intermittence beyond which certain ecological processes or ecosystem services are lost? Is this loss irretrievable? How do human activities that change the sequence or duration of hydrological phases in IRES translate into altered ecosystem services and/or transfers of services provided by each phase? How does this cascade into ecosystem service provision by adjacent perennial, subsurface and downstream waters?

Continues

Table 2 Continued

Conundrum	Rationale	Examples of associated theoretical and applied questions
Do novel or hybrid ecosystem services with artificial intermittence share similar ecological functions and mechanisms of ecosystem service provision with natural IRES?	Novel and artificially intermittent IRES may function very differently from natural IRES because their novel biota (especially invasive species) might alter ecological processes that underpin ecosystem service provision	What ecological processes and ecosystem services are most vulnerable to alteration of flow intermittence (e.g. duration, timing, rate of onset) in novel and hybrid ecosystems? When perennial rivers become artificially intermittent, are ecosystem services provided during flowing, non-flowing and dry phases the same as those provided by nearby natural IRES? If perennial flow is restored, are lost ecosystem services recovered? Are there optimal combinations of ecosystem services and benefits that can be derived from hybrid systems where artificial and natural IRES co-occur in a river network? What potential is there for “designer approaches” that seek to optimize ecosystem services by encouraging biodiversity in human-modified ecosystems (e.g. reconciliation ecology) in IRES? How effectively can trade-offs between ecosystem services be managed in natural, hybrid and novel IRES at local and regional spatial scales by, for example, manipulation of biodiversity or particular ecological processes?
How do changes in the distribution of human populations (SBAs) associated with changes in flow intermittence affect the access to and values of ecosystem services from IRES?	In many parts of the world, climate change and dwindling surface water supplies are causing demographic changes in distribution and water needs of human populations and their activities	Are the changes in the spatial distribution and water needs of human populations and their activities in response to increasing intermittence and surface water shortages affecting the access to and values of ecosystem services provided by IRES? How do regional changes in SBAs affect the capacity of current SCAs to cope with the altered demands? Are some ecosystem services in IRES being overexploited at the cost of others (e.g. use of provisioning services to meet short-term demands for water at the expense of protecting the long-term viability of regulating and cultural services)? Are hybrid or novel ecosystems able to address the needs of changes in SBAs? Might constructed IRES provide adequate ecosystem services in response to changed human needs? How does current and projected spatial and temporal variations in flow intermittence in natural and artificial IRES affect the provision, trade-offs, values and access to their ecosystem services, and how might these variations be effectively incorporated in successful water resource management?

SPAs, service-providing areas; SBAs, service-benefiting areas; SCAs, service-connecting areas.

necessarily represent the views or policies of the U.S. Environmental Protection Agency.

AUTHORS' CONTRIBUTIONS

All authors conceived the ideas and contributed critically to the drafts and gave final approval for publication. All authors initiated the study during IRBAS meetings and contributed to the manuscript.

DATA ACCESSIBILITY

Data have not been archived because this article does not contain data.

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How to cite this article: Datry T, Boulton AJ, Bonada N, et al. Flow intermittence and ecosystem services in rivers of the Anthropocene. *J Appl Ecol*. 2018;55:353–364. <https://doi.org/10.1111/1365-2664.12941>