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REVIEW AND SYNTHESIS

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Ecosystem services of temporary streams differ between wet and dry phases in regions with contrasting climates and economies

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Abstract

1. Temporary streams are dynamic ecosystems in which mosaics of flowing, ponded and dry habitats support high biodiversity of both aquatic and terrestrial species. Species interact within habitats to perform or facilitate processes that vary in response to changing habitat availability. A natural capital approach recognizes that, through such processes, the 'natural assets' of all ecosystems deliver services that benefit people.
2. The ecosystem services of temporary streams remain largely unexplored, in particular those provided during ponded and dry phases. In addition, recent characterizations have focused on dryland systems, and it remains unclear how service provision varies among different climatic regions, or between developed and developing economies.
3. We use evidence from interdisciplinary literature to examine the ecosystem services delivered by temporary streams, including the regulating, provisioning and cultural services provided across the continuum from flowing to dry conditions. We focus on service provision during dry phases and wet–dry transitions, across regions with contrasting climates and economic development.
4. Provision of individual services in temporary streams may be reduced, enhanced or changed by surface water loss. Services enhanced by dry phases include provision of higher-quality subsurface drinking water and unique opportunities for recreation. Shifts between dry and wet phases enable groundwater recharge that mitigates water scarcity, and grant dry-phase access to sediments deposited during flowing phases. However, the accessibility and thus perceived value of these

and other services varies considerably among regions. In addition, accessing provisioning services requires careful management to promote sustainable resource use and avoid ecological degradation.

5. We highlight the need for environmental managers to recognize temporary streams as aquatic–terrestrial ecosystems, and to take actions promoting their diversity within functional socio-ecological systems that deliver unique service bundles characterized by variability and differing availability in space and time.

KEYWORDS

aquatic–terrestrial ecosystem, dry river, dry stream, ecosystem services, intermittent rivers and ephemeral streams, natural capital, non-perennial river, temporary river

1 | INTRODUCTION

A natural capital perspective (Costanza et al., 1997; Maltby et al., 2011) considers physical habitats and biological communities as natural assets (sensu OECD, 2001; Figure 1). Assets interact to facilitate processes that provide regulating, provisioning and cultural ecosystem services (RES, PES and CES), from which people benefit and which thus have value. RES are benefits obtained from the regulation of ecosystem processes, including moderation of climatic extremes and enhancement of water quality. PES provide material products that people use, such as water and food. CES refer to aesthetic, educational, recreational and spiritual services, many of which deliver non-material benefits to people. All ecosystem services (ES) are underpinned by supporting ecosystem services (SES): the biodiversity, habitats and processes which collectively define ecosystems (FAO, 2019; TEEB, 2019). Ecosystems that support high physical and biological diversity can therefore deliver many ES.

Ecosystems that shift in space and time between aquatic and terrestrial phases (hereafter, aquatic–terrestrial ecosystems) create diverse habitat mosaics. Defined by surface flow cessation and encompassing flowing, ponded and dry habitats (Figure 2), temporary streams are archetypal aquatic–terrestrial ecosystems (Leigh et al., 2016). Temporary reaches account for a substantial proportion of the global river length; often dominate arid, semi-arid and mediterranean-climate river networks (Acuña et al., 2014; Raymond et al., 2013); and are also common in cooler, humid climates (Stubbington, England, Wood, & Sefton, 2017). These ecosystems are expanding in space and time as many global regions become characterized by drier conditions (Döll & Schmied, 2012) and greater climatic extremity (Lehner, Döll, Alcamo, Henrichs, & Kaspar, 2006). However, temporary streams generally remain unacknowledged in large-scale assessments of ES delivery by rivers, and in particular, the ES provision of dry and transitional phases is poorly characterized (e.g. Grizzetti et al., 2019; Hanna, Tomscha, Dallaire, & Bennett, 2018; Maltby et al., 2011).

Research exploring biodiversity in temporary streams has focused on aquatic communities during wet phases, and typically reports lower local taxa richness (i.e. α diversity) in temporary compared with perennial streams (e.g. Datry et al., 2014). However, temporal changes between flowing, ponded and dry habitats enable lotic, lentic and terrestrial species to 'time-share' one space (Bogan & Lytle, 2007), and temporary streams may thus have high temporal β diversity (i.e. variation in community composition over time; Tonkin, Bogan, Bonada, Rios-Touma, & Lytle, 2017). Ponding and drying can also enhance habitat diversity, allowing species to co-occur and promoting spatial β diversity (Larned, Datry, Arscott, & Tockner, 2010; Leigh & Datry, 2017). Regional biodiversity can therefore be higher in networks including temporary streams when catchment spatial scales and multi-year temporal scales

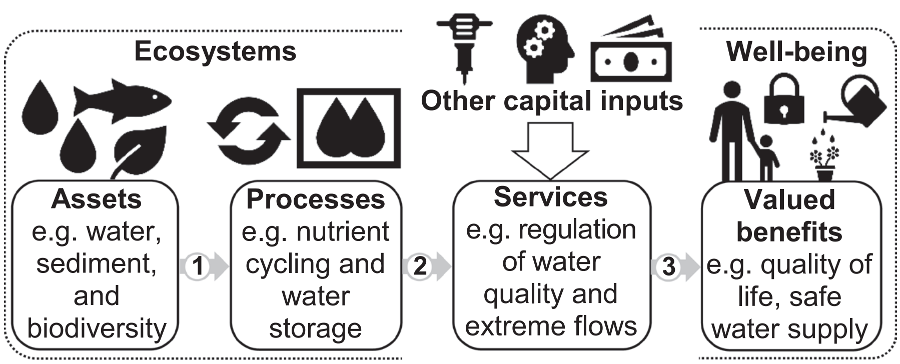

FIGURE 1 The natural capital approach: linking natural assets and ecosystem processes to benefits valued by people (adapted from Haines-Young & Potschin, 2010; Braat & de Groot, 2012; Stubbington, England, et al., 2018). Numbered arrows denote consecutive links described in the text

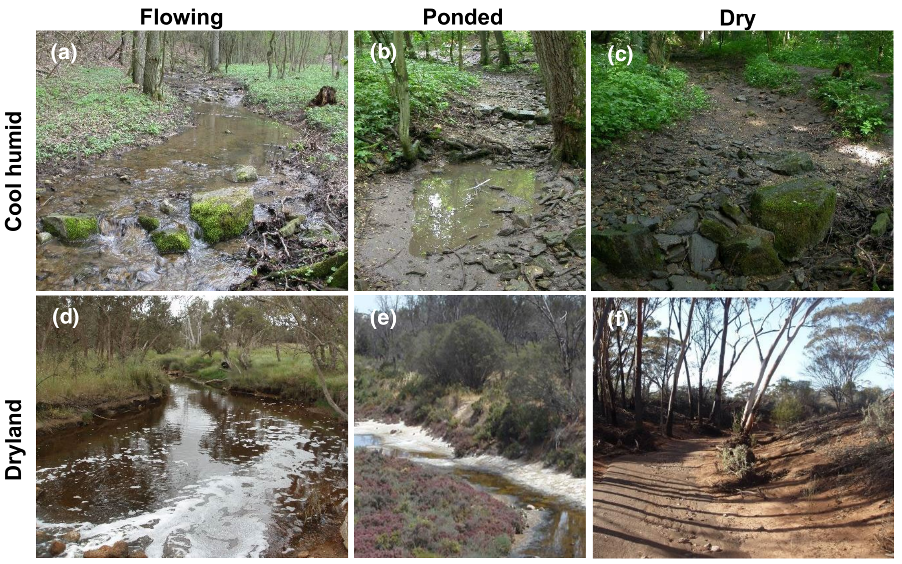

FIGURE 2 Temporary streams in (a, d) flowing, (b, e) ponded and (c, f) dry phases in regions with contrasting climates: (a–c) the cool, humid Czech Republic (Köppen class: continental; Dfb); (d–f) dryland Australia (borderline hot semi-arid/ mediterranean; BSh-Csa). © Petr Pařil (a–c) and Andrew Boulton (d–f)

are considered (Bêche, McElravy, & Resh, 2006; Ruhí, Datry, & Sabo, 2017). Studies characterizing terrestrial biota during dry phases remain limited, but there is evidence that invertebrate communities quickly colonize and can contribute more to local biodiversity than the aquatic communities present during wet phases (e.g. Corti & Datry, 2016; Steward, Langhans, Corti, & Datry, 2017; Stubbington, Milner, & Wood, 2019).

Spatial and temporal variability in habitats and biodiversity cause ES availability and accessibility to vary in temporary streams during wet and dry phases (Thorp et al., 2010). These shifts may result in 'bundles' of ES that co-occur (Raudsepp-Hearne, Peterson, & Bennett, 2010) during flowing, ponded and dry phases. These bundles vary among societies in relation to climate, economic status and culture, and are associated with different trade-offs. The wet and dry phase ES of dryland temporary streams have been highlighted (Steward, von Schiller, Tockner, Marshall, & Bunn, 2012), and Koundouri, Boulton, Datry, and Souliotis (2017) and Datry, Boulton, et al. (2018) provide structured accounts of ES delivery by temporary streams. Koundouri et al. (2017) compare their ES with those provided by wetlands (MEA, 2005), and Datry, Boulton, et al. (2018) consider a full range of aquatic and terrestrial ES (CICES, 2020). Both studies use ES provided during flowing phases as a benchmark against which to compare provision during ponded and dry phases, and suggest ES that are provided by dry channels, including those that are enhanced by or unique to dry phases. However, our understanding of how dry phases and shifts between wet and dry phases contribute to ES delivery in temporary streams remains limited.

To address this research gap, our aim was to bring together evidence identifying the ES of temporary streams, in particular those provided during dry phases and wet–dry transitions, whereas we avoid restating well-known freshwater ES (e.g. Maltby et al., 2011; Postel & Carpenter, 1997). We explore how aquatic and terrestrial species interact with physical assets in temporary streams to mediate ecological processes (1, Figure 1), and how these and physical processes deliver ES (2, Figure 1) from which people benefit (3, Figure 1). We highlight how changes in environments, biotic communities and processes lead to patterns of ES delivery that vary in space and time, and identify unique ES not provided by fully aquatic or terrestrial ecosystems. We compare evidence from streams across regions with contrasting climates and economic statuses, to enable evaluation of how ES provision, access and perceived value differs depending on the climatic, economic and social contexts within which a socio-ecological system operates (Acuña, Hunter, & Ruhí, 2017; Steward et al., 2012). Although we recognize the profound impacts of non-natural drying of perennial streams due to human activities including water resource use (Acuña & Garcia, 2019; Chiu, Leigh, Mazor, Cid, & Resh, 2017; Meybeck, 2003), we focus on ES provision in streams with naturally temporary flow regimes.

2 | METHODOLOGICAL APPROACH

This article originated in workshops convened to develop the report *The Natural Capital of Temporary Rivers* (Stubbington, England, et al., 2018) as part of the UK *Valuing Nature* Programme. Participants in these workshops (i.e. the report authors) consulted resources including CICES (2020), Koundouri et al. (2017) and Datry, Boulton, et al. (2018) to create an extensive list of the ES that temporary streams may provide. We then used ISI Web of Science to gather evidence for each ES using the terms defined in Appendix 1 of Stubbington, England, et al. (2018), but this systematic approach proved too restrictive for our broad, interdisciplinary research topic, and failed to identify many known sources. We therefore extended our search by snowballing (i.e. consulting reference lists) and reverse snowballing (i.e. consulting citing articles) from identified sources using ISI Web of Science and the search engines Google and Google Scholar, the latter enabling access to evidence within non-indexed articles. Most sources are peer-reviewed journal articles, and we also cite other reputable sources. In developing the UK-focused report into the global synthesis presented herein, we (including new international co-authors) continued this broad, synthetic approach, but without geographical limitations.

3 | REGULATING ECOSYSTEM SERVICES

Natural assets facilitate processes that provide RES, including regulation of flow extremes (Section 3.1), sediment dynamics (Section 3.2), climate (Section 3.3) and water quality (Section 3.4). Physical assets enable some processes (and thus ES); for example, water infiltrating the bed can mitigate water scarcity via groundwater recharge (Section 3.1). In other cases, species interact with each other and their habitats to perform ecological processes, for example microbial biofilms coating sediment particles regulate water quality by transforming nutrients (Section 3.4).

3.1 | Mitigation of floods and water scarcity

Many global regions are experiencing greater climatic extremity, including rain events that cause flooding (Blöschl et al., 2019; Trenberth, 2011), and dry periods that culminate in hydrological and socio-economic drought (Prudhomme et al., 2014; Tallaksen & van Lanen, 2004). Precipitation inputs and runoff interact with transmission losses through interception, evapotranspiration and infiltration to determine river discharge. Depending on geomorphological characteristics including sediment size distribution and vertical hydraulic gradient, channels may act as sites for infiltration when dry and following flow resumptions, until the stream and water table reach a saturated hydraulic connection. Losing reaches then continue to recharge groundwater throughout flowing phases (Boulton, Rolls, Jaeger, & Datry, 2017; Reid & Dreiss, 1990). Streams that alternate between wet and dry phases can thus contribute to flow regulation, and potentially to the mitigation of impacts of both floods and water scarcity on society.

In dryland rivers, transmission losses resulting from interception by vegetation and infiltration are the main processes reducing flow after rain, which can attenuate downstream flood magnitudes (Bourke & Pickup, 1999; Camarasa Belmonte & Segura Beltrán, 2001). Such infiltration potential can be exploited by natural flood management schemes that seek to reduce flood risk to lives and livelihoods (Lane, 2017), although such reductions are dependent on channel capacity and may be limited to small flood events (Dadson et al., 2017). Schemes include installation of leaky wood dams in headwater streams (which are often temporary) that promote inundation of land away from human settlements (Burgess-Gamble et al., 2017; Grabowski et al., 2019).

The high infiltration capacity of channels experiencing dry-to-wet shifts can limit evaporative losses and facilitate groundwater recharge (Constantz, Stewart, Niswonger, & Sarma, 2002), with accessible stores of subsurface water potentially able to mitigate water scarcity (Genthon et al., 2015). Short flow pulses can be largely lost to evaporation in arid climates, but 10- to 15-day flow events can recharge aquifers (Batlle-Aguilar & Cook, 2012; Shanafield & Cook, 2014). Temporary streams can also transfer surface water from humid uplands to groundwater stores accessed in more arid lowlands (Tooth, 2000; Weir, 2009). Dry beds may thus be a valued means of securing water resources, in particular where sediment characteristics promote surface water–groundwater interactions. However, surface and groundwater abstractions require careful management to avoid impairing biodiversity, habitats and ecological processes (i.e. SES; Gleeson, Wada, Bierkens, & van Beek, 2012).

3.2 | Sediment dynamics: Supply and erosion control

Geomorphological and hydrological processes underpin fluvial sediment dynamics, which encompass the SES of sediment erosion, transport and deposition to maintain channel form and habitat diversity. Sediment dynamics respond to shifts between flowing, ponded and dry phases, with small, steep headwater temporary streams making notable contributions to downstream sediment transport during flowing phases (Gamvroudis, Nikolaidis, Tzoraki, Papadoulakis, & Karalemas, 2015; Marteau, Batalla, Vericat, & Gibbins, 2017). As flows decline and cease, suspended sediments are deposited, and dry channels may also become sinks that accumulate wind-blown sediments (Good & Bryant, 1985). Colonization by terrestrial vegetation may stabilize such sediments (Arce et al., 2019; Westwood, Teeuw, Wade, Holmes, & Guyard, 2006), and persisting plants may provide comparable RES to aquatic species during wet phases, for example control of sediment erosion through root binding (Gurnell, 2014). Where such binding reduces sediment erosion when flow returns (Corti & Datry, 2012), stabilization of channel form represents a RES that can maintain infrastructure such as bridges (Sousa & Bastos, 2013).

3.3 | Carbon cycling and climate regulation

Carbon cycles in aquatic–terrestrial ecosystems differ from those in water and on land. During dry phases, desiccation-tolerant biofilm species slowly process organic matter (Timoner, Acuña, von Schiller, & Sabater, 2012) with rapid processing by aquatic organisms restricted to pools (von Schiller, Bernal, Dahm, & Martí, 2017). Carbon thus accumulates in dry channels (Acuña & Tockner, 2010), especially if water-stressed riparian plants lose their leaves (Jacobsen & Jacobsen, 2013). A pulse of organic matter then supplies energy downstream when flow resumes (Fritz, Pond, Johnson, & Barton, 2019). This rewetted organic matter is rapidly decomposed first by microbes (Datry, Foulquier, et al., 2018), but 'shredder' invertebrates may become the dominant decomposers if they recolonize (Corti, Datry, Drummond, & Larned, 2011). However, temporary streams can have relatively slow decomposition rates throughout flowing phases if shredder abundance remains low (Datry, Corti, Claret, & Philippe, 2011; Richardson, 1990). Rates can also be slowed when aquatic habitats contract before drying, due to reduced feeding activity by physiologically stressed shredders (Leberfinger, Bohman, & Herrmann, 2010).

Temporary stream reaches thus fluctuate between dry carbon sinks and wet carbon sources, emitting CO_2 pulses that contribute to global carbon cycles (Datry, Foulquier, et al., 2018; Raymond et al., 2013). Where drying reduces photosynthesis but not respiration by microbes (Colls, Timoner, Font, Sabater, & Acuña, 2019), CO_2 emissions could increase, providing a disservice to global climate regulation. Elsewhere, reduced decomposition rates could facilitate climate regulation through carbon sequestration and reduced CO_2 emissions (Berger, Frör, & Schäfer, 2018; Datry, Foulquier, et al., 2018), if organic matter is incorporated into sediments and not transported downstream (Aufdenkampe et al., 2011). Reduced emissions are most likely in streams in which short, unpredictable flowing phases interrupt long dry phases. Such streams are more prevalent in drylands, where aridity may limit microbial communities, leaf litter decomposability and initial processing rates when flow resumes (Datry, Foulquier, et al., 2018), and where the abundance of invertebrate shredders may be low (Bogan, Boersma, & Lytle, 2015). In contrast, temporary streams with long seasonal flowing phases may achieve comparable decomposition rates to perennial systems within an annual cycle (Corti et al., 2011).

Temporary streams can also regulate climates at local scales, from which people obtain multiple benefits. Their channels are topographic lows within corridors of relatively high water availability, supporting the growth of vegetation that delivers PES such as fuelwood and arable crops, as well as other RES. Shading by channel and riparian vegetation protects animals whose thermal preferences are exceeded in the surrounding landscape. Associated livestock herding through dry river channels in arid regions supports both PES and CES by supporting traditional ways of life (Briggs et al., 1993), with livestock viewed as 'physical expressions of … heritage' (Hall, 2019, p. 2). Greater moisture availability also supports plant growth and thus grazing by livestock in and around temporary headwater streams in cooler and more humid regions. Where surface water remains in pools or ponded reaches, and riparian trees mitigate high temperatures, channels can also deliver PES where conditions enable fish to remain below their thermal maxima and CES where humans swim in shaded waterholes.

3.4 | Water quality regulation

During flowing phases, microbial processing of nitrate, phosphate and other inorganic nutrients, sometimes at concentrations indicative of human activity, facilitates regulation of water quality by temporary as well as perennial streams (Berger et al., 2018). Many temporary streams are small headwaters in which high ratios of sediment surface area to water volume promote nutrient processing by biofilm-coated sediments (Alexander, Smith, & Schwarz, 2000). As flow slows then ceases, contact times between these microbes and their nutrient substrates further increase, thus promoting processing, including in saturated subsurface spaces after surface water loss (Harvey, Conklin, & Koelsch, 2003). Ecological processes include denitrification of nitrate to gaseous dinitrogen, which attenuates diffuse inorganic nutrient pollution, particularly in streams that drain agricultural and urban landscapes (Gómez, Hurtado, Suárez, & Vidal-Abarca, 2005).

After surface and subsurface drying, desiccation-tolerant biofilm microbes within humid pore spaces continue processing dissolved inorganic nutrients (Febria, Beddoes, Fulthorpe, & Williams, 2012), although processes may be altered (Timoner et al., 2012). For example, drying can enhance nitrification and reduce denitrification, increasing nitrate concentrations in pore water (Merbt et al., 2016; von Schiller et al., 2017), release of which may temporarily reduce water quality as water levels rise, representing an ecosystem disservice (Arce, Sánchez-Montoya, Vidal-Abarca, Suárez, & Gómez, 2014). After flow resumes, denitrification rates may increase rapidly (Arce et al., 2014) or stay low until microbial communities recover (Arce, Gómez, Suárez, & Vidal-Abarca, 2013). In humid regions with year-round rainfall, greater water availability in subsurface spaces may promote dry-phase persistence of microbial communities (Stubbington, Paillex, et al., 2019) and thus facilitate recovery of denitrification rates after water returns.

Terrestrial plants can quickly colonize and establish in dry channels in both humid (Haley, 2009; Holmes, 1999) and dryland regions (Dieterich & Anderson, 1998). Plant roots penetrate sediments and contribute to water quality regulation through uptake of inorganic nutrients and their assimilation into biomass (Hefting et al., 2005). Harvesting the above-ground biomass of such plants could attenuate concentrations of polluting inorganic nutrients (Hefting et al., 2005), but would alter the provision of other ES.

4 | PROVISIONING ECOSYSTEM SERVICES

Natural assets promote PES that produce goods. In temporary streams, physical assets include water, a good that is accessed across regions (Section 4.1); sediment, which is extracted as construction aggregate (Section 4.2); and salt, which is locally harvested from pools in the lower reaches for personal use or trade (Hitchcock & Nangati, 2000). Biological assets provide food products, in particular fish (Section 4.3); wood, which is cut from in-channel plants in dryland regions with developing economies for use as fuel (Kassas & Imam, 1954); and, potentially, biochemical products (Section 4.4).

4.1 | Fresh water

People are most reliant on PES in drylands with developing economies (Suich, Howe, & Mace, 2015), and streams are among the topographic lows in which fresh water remains most accessible. Here, collection of water by local people for drinking and other uses (Hitchcock & Nangati, 2000) is often fundamental to survival and

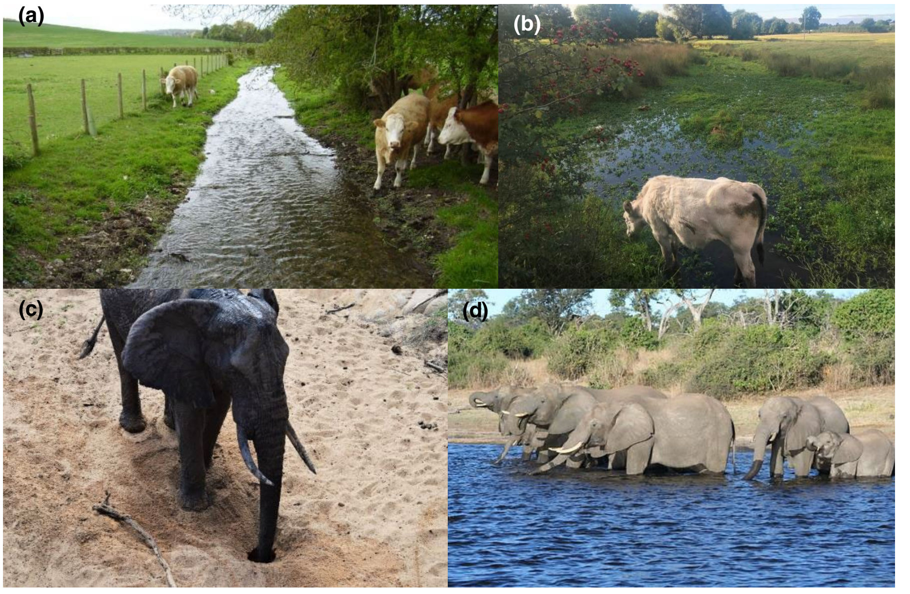

FIGURE 3 Fresh water provided by temporary streams supports well-being across regions with contrasting climates and economies, and is accessed by animals including humans, livestock (a and b) and elephants (c and d) during flowing (a, d), ponded (b) and dry (c) phases. © (a-b) Environment Agency; (c) Gabriella Kiss; (d) Oxfam

thus occurs during all phases (Figure 3). As surface water becomes isolated into pools and is lost, digging into the dry bed can grant safe access to subsurface water of better quality than that in surface pools (McCabe & Ellis, 1987; Steward et al., 2012), and becomes increasingly important to human health as the quality of ponded water declines (Hitchcock & Nangati, 2000). Large mammals including elephants also dig to access higher-quality subsurface drinking water (Figure 3c; Ramey, Ramey, Brown, & Kelly, 2013), and their survival promotes delivery of CES via tourism (Section 5.1).

Across regions and phases, temporary streams also contribute to public water supply (Katz, Catches, Bullen, & Michel, 1998) and irrigation of arable land (Genthon et al., 2015; Kaletová et al., 2019), often via groundwater. Temporary streams can contribute significantly to public water supply; for example, it is estimated that >33% of US citizens are supplied by systems including temporary or headwater streams (US EPA, 2019). However, over-abstraction has environmental consequences, and this ES requires careful management to balance human and ecological needs (Poff et al., 2010; Raudsepp-Hearne et al., 2010).

4.2 | Sediment extraction

Channel sediments such as sand and gravel may be extracted as a good used in construction, with long, predictable dry phases facilitating access in arid (Chiu et al., 2017), mediterranean (Rinaldi, Wyżga, & Surian, 2005) and tropical (Bhattacharya, Dolui, & Chatterjee, 2019) regions. Ease of access during dry phases thus facilitates delivery of sediment goods originating from wet-phase transport and deposition. Localized activities can provide income for individuals in developing economies (Hitchcock & Nangati, 2000). Larger-scale extraction provides construction aggregate and can protect human settlements by reducing flood peaks and constraining channel movement (Piégay, Grant, Nakamura, & Trustrum, 2006). However, such extraction typically has extensive environmental impacts, and even 'sustainable' yields can alter channel geomorphology, lower the water table, and reduce both habitat and biodiversity. Potential consequences include destabilization of instream infrastructure such as bridges, representing an ecosystem disservice (Rinaldi et al., 2005).

4.3 | Food: Fish, crops and livestock

Some temporary streams support fisheries; for example, flowing phases provide habitat for juvenile Coho salmon in coastal temporary streams of the Pacific Northwest (Wigington et al., 2006), which are 'sustainably managed … under U.S. regulations' by recreational and commercial fishermen (Figure 4c; NOAA Fisheries, 2019). In contrast, subsistence fishing spans all phases. Fish densities peak as wet habitats contract during wet–dry shifts (Mmopelwa, Mosepele, Mosepele, Moleele, & Ngwenya, 2009), and dormant fish are dug from sediments during dry phases (Hitchcock & Nangati, 2000; Kassas & Imam, 1954). Invertebrates such as shrimps may also be harvested from temporary streams, especially where populations become trapped in pools. Such exploitation may contribute to localized population declines and extinctions if not sustainably managed (Curtis et al., 1996), altering delivery of other ES.

Temporary streams also support agricultural PES across regions. In drylands, dry channels and their riparian corridors are oases that enable livestock and wild animals to graze and drink (Figure 3c,d; Kaletová et al., 2019; Kassas & Imam, 1954; McCabe & Ellis, 1987), with benefits for human quality of life and mortality in developing economies (Godfree et al., 2019). Livestock may also graze and drink in cool, humid channels, reducing farming costs but having little effect on human well-being (Figure 3a,b). Higher water availability also enables in-channel cultivation of crops in dryland streams with long dry phases, including olives and vines in Spanish ramblas (Gómez et al., 2005; Segura-Beltrán & Sanchis-Ibor, 2013);

FIGURE 4 Delivery of regulating, provisioning and cultural services differs between flowing, ponded and dry phases in temporary streams across regions with contrasting climates and economies: (a) high flows in a semi-arid stream in Australia supply sediment to downstream reaches; (b and c) Coho salmon of fisheries in the Pacific Northwest spawn in coastal temporary streams; (d) uptake by semi-aquatic plants during ponded phases attenuates inorganic nutrient pollution in a UK winterbourne stream in an agricultural catchment; (e) cattle access drinking water as flow declines and ceases in a UK winterbourne; (f) elephants congregate at a waterhole on an African safari route; (g) a sand-bed river in semi-arid Australia provides a large surface area for infiltration; (h) people collect subsurface water in Africa; (i) a caver (who has given consent to be identified) accesses a laterally extensive tufa cave in the UK during a period of low water levels. © Andrew Boulton (a, g); Alison Leigh Lilly (b, c); Judy England (d, e); Barnabas Lands (f); Marisol Grandon/Department for International Development, see Baracchini, Leonard, Sherlock, and Estrella (2016) (h); John Gunn (i)

fruit, legume and cereal crops in African wadis (Briggs et al., 1993); and vegetables in Indian rivers (Hans et al., 1999). Such cultivation profoundly alters temporary streams, but ecological impacts have yet to be quantified.

Dry streams also support arable productivity by providing habitat and resources for insect crop pollinators. If terrestrial plants colonize as waters recede (Westwood et al., 2006), vegetated dry channels may become an extensive network of unmanaged and thus relatively biodiverse habitats that cross agricultural landscapes (Öckinger & Smith, 2007; Stubbington, England, et al., 2018). Such land uses dominate much of Europe (Eurostat, 2018) and the United States (Bigelow, 2017). Terrestrial vegetation may also provide habitat for insect crop pollinators such as ground-dwelling bees and the predators of crop pests, which supports arable productivity in humid (Kells & Goulson, 2003; Öckinger & Smith, 2007) and mediterranean regions (Kaletová et al., 2019). For example, Bunting et al. (submitted) recorded aphid predators including carabid beetles, ladybird beetles and rove beetles in the dry channel of 'winterbourne' stream reaches in a UK agricultural catchment.

4.4 | Biochemical products

Across multiple regions, temporary streams are a potential source of biochemical products that could benefit people. Specialist species from across biotic groups—including both desiccation-tolerant aquatic species and inundation-tolerant terrestrial species—represent high-potential targets for applied research in contexts including medicine and agriculture.

Aquatic species with desiccation-tolerant life stages include invertebrates that can survive dehydration and subsequent rehydration. Desiccation tolerance is enabled by trehalose, a disaccharide that stabilizes proteins in the absence of water (Crowe, Crowe, & Chapman, 1984; Kikawada et al., 2007). Characteristics of cellular trehalose transporters from larvae of the non-biting midge *Polypedilum vanderplanki*, which inhabits temporary pools in semi-arid regions, may inform development of preservation techniques that enable the transport and storage of mammalian cells, tissues and organs for medical use (Sakurai et al., 2008) as well as treatment of genetic diseases characterized by aggregation of mutant proteins

(Kikawada et al., 2007). Persistence of *P. vanderplanki* during wet–dry–wet transitions requires a slow dry-phase onset, suggesting that desiccation-tolerant invertebrates warrant further exploration in humid streams characterized by gradual drying. Freshwater meiofauna including rotifers and tardigrades use additional or alternative molecular strategies to protect against dehydration (Eyres et al., 2012; Wełnicz, Grohme, Kaczmarek, Schil, & Frohme, 2011), offering new potential opportunities to isolate and develop biochemical products that benefit human well-being.

For the terrestrial plants that colonize dry channels, inundation deprives roots of oxygen, and submersion can induce production of anaerobic stress proteins that regulate alternative respiratory pathways (Blom & Voesenek, 1994; Kennedy, Rumpho, & Fox, 1992). However, temporary-stream plant specialists are unknown, which may reflect limited research (Stubbington, Paillex, et al., 2019). Elucidating the molecular strategies behind submersion and thus anoxia tolerance has potential to inform engineering of transgenic crops that support sustainable farming (Ronald, 2011) in global regions facing greater climatic extremity and flooding (Schmidhuber & Tubiello, 2007).

5 | CULTURAL ECOSYSTEM SERVICES

The cultural value that people attach to flowing water is well known in ecosystems including temporary streams (Hadwen, Boon, & Arthington, 2012; Leigh, Boersma, Galatowitsch, Milner, & Stubbington, 2019; Teff-Seker & Orenstein, 2019). During flowing phases, their corridors are perceived as 'green spaces of … welfare' in developing drylands (Genthon et al., 2015, p. 1292), with bankside settlements evidencing human reliance on temporary stream ES (Hitchcock & Nangati, 2000). In addition, due to their broad CES provision, flowing temporary streams attract tourists to climatically diverse places including alpine valleys (Uehlinger, Maisch, Rothenbühler, & Zah, 2003), cool, humid dales (Stubbington, England, et al., 2018), semi-arid canyons and African desert wadis (Boulton, 2014). Drying changes the cultural values of temporary streams, and provision of recreational, educational and spiritual CES differs among regions. In contrast to flowing streams, dry channels can be perceived as symbolic of drought and human impacts including over-abstraction, representing a cultural disservice (Stubbington, England, et al., 2018).

5.1 | Recreation

Drying prevents flowing-phase recreational activities such as boating and fishing and has been associated with decreased tourism (Castro, Vaughn, Julian, & García-Llorente, 2016), but it also creates unique opportunities. In drylands, extensive dry routes enable channel-based activities such as rambling, horse-riding, quad biking and off-road driving (Gómez et al., 2005; Hadwen et al., 2012), with tour operators noting that 'dry river beds are ideal for faster riding' (In The Saddle, 2019) and isolated pools providing drinking water for horses. However, high-intensity activities require careful management to prevent ecological impacts such as sediment compaction and pollution. In cooler humid regions, their limited extent can make dry channels a source of intrigue and a tourist destination. For example, leaflets describing the River Manifold in England tell visitors to 'watch out for the rivers … as they disappear' (Visit Peak District, 2019). In drylands, pools that provide animals with vital water resources (Sánchez-Montoya, Moleón, Sánchez-Zapata, & Escoriza, 2017) can be hotspots where tourists on safari view large mammals such as elephants (Figure 4f; Hayward & Hayward, 2012).

Organized events are enabled by long, predictable dry phases in drylands. Steward et al. (2012, p. 204) describe 'the world's only dry riverboat race', which attracts international participants and tourists, contributing to the regional economy in Australia's hot, arid Northern Territory (Chalip & Costa, 2005). A dry stream contributes to the unique interest and challenge level of an off-road 'ultramarathon' in Gran Canaria (Spain), attracting participants (Arista Eventos, 2019). In cool, humid climates, their limited spatial extent, duration and predictability may prevent organization of regular dry-phase events. Instead, recreational events are responsive to changing environmental conditions, with droughts creating rare and valued opportunities. For example, low water levels allow access to the subterranean parts of river corridors in karst limestone landscapes, with cavers targeting features including natural caves and sites of historic interest (Figure 4h; Historic England, 2019; Stubbington, England, et al., 2018).

5.2 | Education

Despite ongoing research interest, temporary streams are poorly understood compared with perennial systems (Datry, Bonada, & Boulton, 2017; Datry, Fritz, & Leigh, 2016), and in particular, dry channels remain a terra incognita (Datry, Arscott, & Sabater, 2011; Koundouri et al., 2017; Stubbington, Milner, et al., 2019). These ecosystems thus represent a research gap that creates interdisciplinary opportunities for natural and social scientists to collaborate with stakeholders (Fagerholm, Käyhkö, Ndumbaro, & Khamis, 2012; Milcu, Hanspach, Abson, & Fischer, 2013) including indigenous groups (Darvill & Lindo, 2015) and ecosystem managers (Stubbington, England, et al., 2018). International collaboration is facilitated by major research projects such as the EU *Science and Management of Intermittent Rivers and Ephemeral Streams* network (Datry, Singer, et al., 2017) and the US *Dry Rivers Research Coordination Network* (Dry Rivers RCN, 2019), with related conference sessions and training events used to connect researchers and develop their knowledge and skills (SMIRES, 2019). Involvement of scientific specialists in broader initiatives such as the BlueHealth project (Grellier et al., 2017) could also advance understanding of temporary streams.

Wet and dry temporary streams also provide unique opportunities for formal education from pre-school to post-graduate levels (Creative STAR Learning, 2015; SMIRES, 2019; Williams, 1987), with dry channels allowing detailed study of fluvial landforms and sediments. Wider education of the general public is facilitated by recreational activity, with organizations using webpages and information boards at tourist sites to tell visitors of the natural value of temporary streams (e.g. Chilterns Conservation Board, 2019; Mothersole, 2019). Such education may foster positive attitudes towards these streams (Leigh et al., 2019). In turn, CES delivered by informed attitudes could include an improved sense of place and identification with a distinctive, socially valued landscape (Reese, Oettler, & Katz, 2019), broader enhancements to mental well-being (Brymer, Freeman, & Richardson, 2019) and more pro-environmental behaviour (Schuttler, Sorensen, Jordan, Cooper, & Shwartz, 2018). Public consultation and support also create impetus for policy change (Burstein, 2003), and may influence the success of management activities designed to improve ecological quality and ES provision (Tunstall, Penning-Rowsell, Tapsell, & Eden, 2000).

5.3 | Spiritual benefits

The nature of spiritual benefits differs among global regions. In Western cultures, the psychological (and likely aesthetic) benefits of experiencing and interacting with an ecosystem can promote a connection to a physical environment (i.e. a sense of place; Russell et al., 2013) and are valued (Pritchard, Richardson, Sheffield, & McEwan, 2019). In contrast, the maintenance of traditional, rural lifestyles is typically referred to in countries with developing economies and by indigenous groups (Cooper, Brady, Steen, & Bryce, 2016). In Australian Indigenous culture, stories of how temporary streams formed are of deep spiritual significance (Weir, 2009). Here, artefacts also illustrate the spiritual value of temporary streams; for example, rock art in Sacred Canyon in semi-arid Australia depicts people and waterholes (Bednarik, 2010; Boulton, 2014). Recent amendment of National Park boundaries to protect this site demonstrates its spiritual importance for Aboriginal people and visitors (SA Arid Lands, 2017). Similarly, temporary headwaters of the River Ganges are among those deemed 'sacred and revered', and were granted legal personhood in 2017, although this decision was subsequently overruled (O'Donnell & Talbot-Jones, 2018). Across climate types, specific terms used to refer to temporary stream types in dialects indicate recognition of their character by local people, for example north African *wadis*, Brazilian *corixos*, Japanese *kare-sawa* and English *winterbournes* (Steward et al., 2012), the last contributing to 'landscape character' in designated areas of the UK (Natural England, 2014).

6 | AN INTEGRATED LOOK AT ECOSYSTEM SERVICE PROVISION IN TEMPORARY STREAMS

6.1 | Service provision is enhanced by ecological diversity in temporary streams

Spatial and temporal variability in physical and biological natural assets influence ES provision in temporary streams (Figure 4), which deliver unique ES bundles during dry phases and wet–dry shifts. For example, largely dry channels are uniquely valuable as routes for livestock herding and many recreational activities, due to their combination of navigability, water availability in pools and shaded microclimate. Spatial habitat diversity also allows concurrent delivery of multiple complementary ES by temporary streams, especially during gradual wet-to-dry transitions in which pools remain in otherwise dry channels. For example, people in drylands with developing economies may extract drinking water from beneath dry sediment and fish from pools (Hitchcock & Nangati, 2000). In such regions, the bundle of concurrent ES benefitting herdsmen who graze livestock in a shaded dry channel with isolated pools includes local climate regulation (RES), support for pastoral agriculture (PES) and maintenance of a traditional way of life (CES).

Experiencing repeated shifts between flowing, ponded and dry phases profoundly alters physical and ecological processes in temporary streams, creating unique temporal patterns of ES provision at individual sites. For example, dry-phase sinks that store carbon become wet-phase sources of emitted CO_2. Similarly, flowing water transports nutrient pollution downstream, whereas receding and ponded waters promote nutrient processing. Natural processes and the ES they deliver may also be dissociated in both space and time, such as when infiltration into the bed enables later provision of water in downstream areas of demand, and when water uptake by plant roots during wet phases supports shading vegetation that regulates climates within the stream corridor during dry phases. Complementary processes occurring in wet and dry phases can interact to enable access to available ES. For example, sediments transported downstream during flowing phases can be accessed during subsequent dry phases. Other temporary stream ES are sufficiently crucial to well-being that ingenuity supports their use across phases. For example, people have devised means to access water during both wet and dry conditions, including personal use by local people and industrial extraction by companies.

Dry-to-wet shifts provide diverse RES, including rapid recharge of groundwater stores and pulsed transport of accumulated sediment (Corti & Datry, 2012). However, we found little evidence of other ES, and concurrent CO_2 emissions represent a disservice to global climate regulation. Flow resumptions end dry-phase delivery of some PES; for example, accessible water resources change from limited high-quality subsurface water to abundant water potentially laden with organic and inorganic matter, and a humid corridor for herding, grazing, crop cultivation and foraging by pollinators is lost. However, many flowing-phase PES and CES comparable with those of perennial streams establish after the initial flow pulse subsides (Datry, Boulton, et al., 2018).

6.2 | Provision and valuation of service bundles varies among regions

We identified parallels and contrasts in dry-phase ES use in regions with dryland and humid climates, and with developing and developed economies. Some of these contrasts reflect technological differences in regional economies, which influence the ability of local people to access available ES and thus their perceptions of ES value. In Figure 5, we interpret evidence in the literature presented above in light of our collective international experience to suggest perceptions of value by local stakeholders. We recognize the subjective nature of these interpretations, in particular our greater understanding of the perceptions of people from countries with developed economies (all authors) and humid climates (seven of nine authors). As such, we present Figure 5 as a tool to stimulate further hypothesis-driven interdisciplinary research that encompasses the natural and social sciences.

Across regions, water is highly valued, but less so in regions with developed economies, where seemingly unlimited resources available to consumers at low monetary cost are taken for granted (Clarke, 2013). In addition, the contribution of temporary streams to public water supply is relatively minor in humid climates (Figure 5; e.g. US EPA, 2019). In contrast, people's livelihoods often depend more directly on ES in countries with developing economies, increasing the perceived value of water and other PES (Martínez-Alier, 2003). Similarly, regulation of flow extremes (i.e. mitigation of floods and water scarcity) is valued everywhere, but more so in developing economies, where both pose a greater risk to life and livelihoods (FitzGerald, Du, Jamal, Clark, & Hou, 2010; Moghim & Garna, 2019).

Aside from these comparable key PES and RES, different ES bundles characterize regions with contrasting climates and economies. In drylands with developing economies, PES are highly valued contributors to bundles of complementary ES, with dry channels that retain isolated pools providing water and fish for human consumption and cool, humid habitats with water and grazing resources for livestock (Figure 5). CES including maintenance of traditional lifestyles and a sense of place (Hausmann, Slotow, Burns, & Minin, 2016) and RES such as local climate regulation are delivered alongside these core PES, whereas delivery of other ES is limited (Figure 5).

In humid regions with developed economies, such as Western Europe, direct access of dry-phase goods is lower. Here, people access PES indirectly via agricultural and water companies, likely reducing their perceived value (Figure 5). In addition, their limited extent may make temporary streams less crucial to people's quality of life, and valuation of CES is thus largely restricted to groups such as cavers (recreation), academic researchers (education) and villagers (sense of place; Natural England, 2014). Other characteristic dry-phase ES bundles may be delivered in drylands with developed economies such as southern Europe. Here, national wealth and the greater extent of dry channels collectively: increase PES delivery compared to humid regions but decrease reliance on them compared to developing regions; increase perceived value of less tangible RES

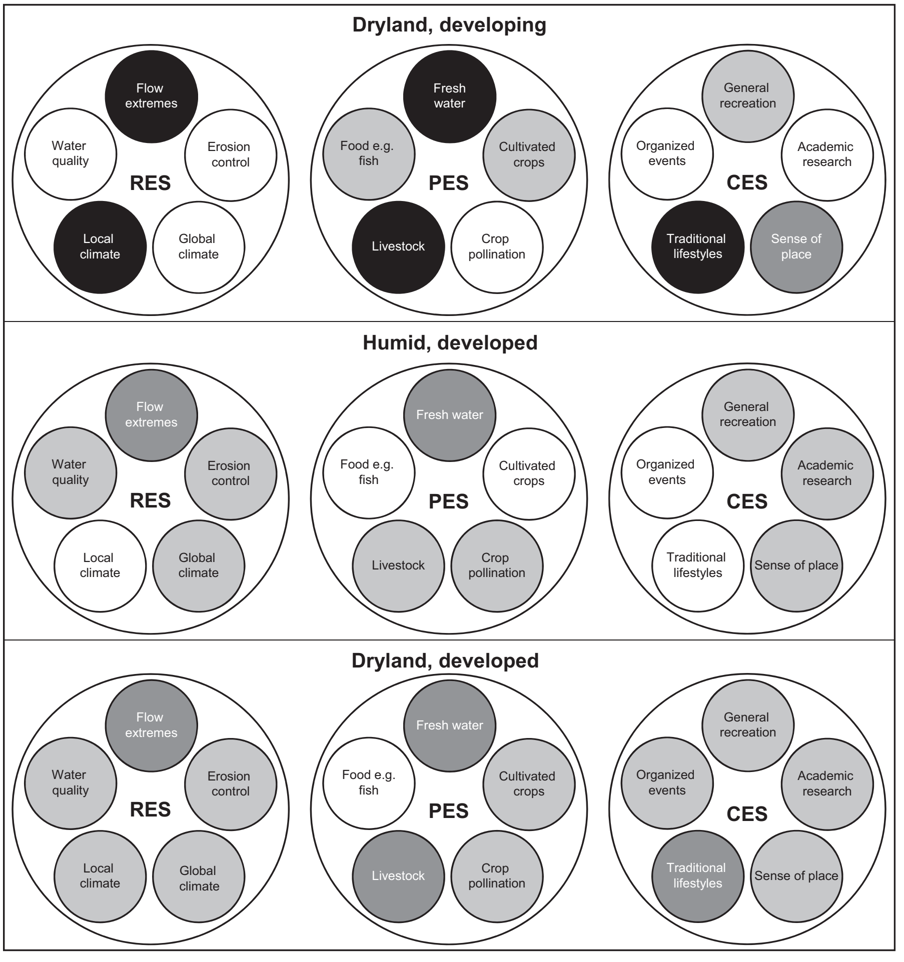

FIGURE 5 Relative valuation of dry-phase ecosystem services (ES) in temporary streams in regions with contrasting climates (dryland, humid) and economies (developed, developing). Shading indicates predicted perceptions of value by local service users, where white = not important; light grey = of minor importance to a small proportion of people; dark grey = important to many people; and black = of considerable importance to most people. Patterns are hypothesized based on evidence interpreted in the text. RES, PES and CES: regulating, provisioning and cultural ES, respectively

compared to developing economies and reduce risks posed by extreme flows and harsh climates; and increase recreational CES compared to humid climates but reduce most people's connection to the landscape compared to developing regions (Figure 5). Across developed economies, education may increase people's valuation of the RES that support environmental quality (Sodhi et al., 2010).

6.3 | Trade-offs between services and conflicts between service users

Delivery of multiple ES within regional bundles is associated with trade-offs, in which accessing one set of ES reduces or prevents delivery of others. Over-extraction of PES such as water and fish often impairs physical and ecological processes and related CES, RES and SES (Raudsepp-Herne et al., 2010; Rodríguez et al., 2006). For example, livestock activity in dry channels has negative impacts on SES including plant and animal biodiversity (Robertson & Rowling, 2000; Steward, Negus, Marshall, Clifford, & Dent, 2018). Grazing and herding can also compact sediments (Mulholland & Fullen, 1991), limiting infiltration and reducing mitigation of flow extremes. Livestock also disturb bank and bed sediments, compromising erosion control during flowing phases (Trimble, 1994). Plant removal by grazing animals may reduce food resources for insect crop pollinators, as well as nutrient uptake by roots and thus water quality regulation. Nutrient release from faeces deposited in channel may reduce water quality after flow resumes, with pathogens representing a particular risk to human health during gradual dry–wet transitions (Chase, Hunting, Staley, & Harwood, 2012).

Limited water availability can also create conflict between users of different ES. In drylands with developing economies, tensions arise between herdsmen and fishermen over valued pool resources: livestock access reduces habitat quality for fish while fishing disturbs sediment, thus impairing drinking water quality for livestock (Hitchcock & Nangati, 2000). Limited water resources also ignite debate in developed regions, due to the impacts of abstraction for public water supply on SES (O'Neill & Hughes, 2014). Here, its lesser benefits and indirect delivery reduce valuation of water by local people, and some sections of society place greater value on SES that underpin ecosystem quality (Poff et al., 2003). Trade-offs between SES and other ES underpin the optimized delivery of ES bundles that reflect the values of people (i.e. service users) within socio-ecological systems (Gilvear, Spray, & Cases-Mulet, 2013; Raudsepp-Hearne et al., 2010).

7 | PROTECTING ECOSYSTEM SERVICE PROVISION WITHIN SOCIO-ECOLOGICAL SYSTEMS

Conservation and restoration activities that seek to enhance the resilience of ecosystems adapting to global change can be driven largely by ecological goals (Lebel et al., 2006). In addition, recognizing human dependence on ES is now motivating management strategies that position ecosystems within wider socio-ecological systems to which people contribute, and from which people benefit (Berkes, Colding, & Folke, 2008). However, access to some benefits requires advanced technologies, resulting in contrasting use of available ES among regions with different economic statuses, even where climates are comparable.

Protection of ES within integrated strategies that balance ecological and societal needs must thus recognize the climatic, economic and social context in which a socio-ecological system operates (Boulton, Ekebom, & Gíslason, 2016; Ormerod, 2014). Despite concerns that socio-ecological integration may compromise the effectiveness of biodiversity protection (Boon, 2012; Dudgeon, 2014), ES provision can relate positively to ecological quality (Grizzetti et al., 2019), with concepts of biocultural diversity identifying positive feedbacks between biodiversity and CES (Bridgewater & Rotherham, 2019). Management strategies can therefore legitimately seek to maximize delivery of ES bundles without compromising ecosystem quality (Bennett, Peterson, & Gordon, 2009; Gilvear et al., 2013), aligning with the ‘wise use of wetlands’ philosophy proposed by the Ramsar Convention.

Ecological engineering can be used to design conservation and restoration projects that achieve both societal and environmental benefits (Palmer, Filoso, & Fanelli, 2014). Within this broad approach, environmental flows seek to deliver the water needed to support river ecosystems and the ES they provide, with ‘designer’ regimes used to support aquatic ecology and ES outcomes in human-modified rivers (Acreman et al., 2014). The integration of cultural demands into environmental flows (Anderson et al., 2019; Arthington et al., 2018) and recognition of these cultural flows (Magdaleno, 2018) advances this approach. Delivering environmental flows within an adaptive management framework is appropriate in temporary streams, although the effectiveness of proposed interventions is often uncertain due to limited experience (Conallin, Wilson, & Campbell, 2018). Collaboration with stakeholders to establish their priorities and expectations in light of guidance regarding the ES of temporary streams can enable delivery of designer flow regimes that balance ecological and societal needs (Anderson et al., 2019; Conallin et al., 2018).

Despite recognition of their value and discussion by the EU Water Framework Directive Working Group on ecological status (Martínez et al., 2018), omission of temporary streams from legislation and policy (Stubbington, Chadd, et al., 2018) jeopardizes their ES (Acuña et al., 2017). For example, under the EU Habitats Directive (Council Directive 92/43/EEC), only Member States in six Mediterranean Basin countries must designate Special Areas of Conservation that represent a temporary stream type, *intermittently flowing Mediterranean rivers* (Fritz, Cid, & Autrey, 2017). In the United States, the *Navigable Waters Protection Rule* came into effect in 2020, removing the legal protection of many temporary streams and thus risking reductions in their delivery of ES including water supply (Marshall et al., 2018; US EPA, 2020). Without legal protection, the ES provision of temporary streams may be lower than at designated sites (Keele, Gilvear, Large, Tree, & Boon, 2019). By advancing our understanding of the ES provided by temporary streams, in particular during dry phases and wet–dry shifts, we support calls to enhance their protection using mechanisms from local restoration to international legislation.

We have focused on ES in natural temporary streams, although difficulties in distinguishing between natural and artificial drivers of flow cessation and drying can complicate ES assessments in these ecosystems. Such difficulties contribute to negative attitudes towards dry streams, especially in cool humid regions (Leigh et al., 2019; Stubbington, England, et al., 2018). Where human activities such as abstraction of surface water or groundwater cause or extend drying, such attitudes are justified, and dry-phase ES may well be lower than and/or different to those outlined here. Identifying such artificial temporary streams and restoring their natural perennial flow is crucial to create networks of resilient riverine ecosystems that sustain robust ES provision despite global change. Equally, by highlighting the diverse ES provided by natural temporary streams during wet and dry phases, we hope to enhance awareness of and appreciation for their contribution to wider socio-ecological systems across regions with contrasting climates and economies. As changing climates cause temporary streams to expand in both space and time in many global regions, societal recognition that these ecosystems can provide people with diverse, complementary, and sometimes unique benefits across wet and dry phases is essential to motivate their protection and thus robust ES delivery.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHORS' CONTRIBUTIONS

R.S., A.J.B., J.E., P.J.B. and P.J.W. conceived the original ideas, which were developed by all authors; R.S. and A.J.B. led development of the manuscript structure. All authors contributed to collation and interpretation of literature, contributed critically to drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

This paper does not include any data.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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