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Flow intermittence in river networks: understanding the ecohydrological diversity of aquatic–terrestrial ecosystems

Editorial to the special issue "The ecohydrology of temporary streams"

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With 1 figure and 1 table

Abstract: Temporary streams comprise dynamic mosaics of lotic, lentic and terrestrial habitats and dominate global river networks, occurring across regions with contrasting climate types. Recent advances in our ecohydrological understanding of temporary streams have focused on systems in arid, semi-arid and mediterranean climates. In this special issue, we present new temporary stream research from underrepresented regions, primarily cool, wet temperate climates but also continental central Europe and the mediterranean-climate region of South Africa. We bring together observational case studies, laboratory experiments, and field surveys spanning surface water and groundwater habitats. Papers within the special issue explore ecological responses to flow intermittence; examine biodiversity patterns of rare and endemic species at broad spatial scales; characterize diverse responses to drying events within and among populations; demonstrate the value of long-term observational data in understanding the hydrological drivers that underpin biotic responses; and present opportunities to improve temporary stream monitoring and management. Collectively, these contributions complement dryland research to advance global understanding of temporary stream ecohydrology. However, the terrestrial communities that inhabit dry channels remain a notable research gap, which we address in a review of global literature. As global change causes an increase in their extent across climate regions, we urge researchers and stakeholders to collaborate to implement recommendations that address the challenges associated with the effective management of temporary streams as aquatic–terrestrial ecosystems.

Keywords: flow cessation; non-perennial river; riverbed drying; streambed drying; temperate; temporary river

Introduction

Flow cessation and drying in stream ecosystems create dynamic mosaics of flowing, ponded and dry habitats that support lotic, lentic and terrestrial species (Bogan & Lytle 2007; Larned et al. 2010). Variously described as ephemeral, intermittent, non-perennial and temporary (Uys & O'Keeffe 1997; Datry et al. 2017a), we use the term *temporary* to encompass the diverse range of streams that sometimes cease to flow and/or dry. Temporary streams can dominate networks in arid, semi-arid and mediterranean-climate regions, where their longitudinal extent may encompass entire network branches, especially in headwaters. Flow intermittence is also common in cooler climates with year-round precipitation, including those in Köppen-Geiger classes Cfb (termed *temperate oceanic*; hereafter, *oceanic*) and Dfb (*warm-summer humid continental*;

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hereafter, *continental*; Rohli & Vega 2017). Globally widespread, oceanic regions dominate northwest Europe, and extensive continental regions span central and eastern Europe. In these cooler, wetter climates, the spatial extent of intermittence typically ranges from microhabitat to segment scales (sensu Frissell et al. 1986), creating dynamic patchworks of aquatic and terrestrial habitats. In contrast to drylands, entire streams are rarely temporary, and the temporal extent of intermittence may also be restricted, to either intra-annual periods of weeks to months (e.g. Larned et al. 2011; Straka et al. 2019) or to years with below-average precipitation (e.g. Wood & Armitage 2004; Stubbington et al. 2016; Sarremejane et al. in press).

Leigh et al. (2016a) reviewed the increasing global literature on temporary stream ecology and identified the USA, Australia and Spain, followed by other Mediterranean Basin countries, as the main contributors to research (see Leigh et al. 2016a: fig. S1), with studies in climatically diverse nations focusing on their mediterranean, arid and semi-arid regions. In contrast, the ecohydrology of temporary streams has remained relatively unexplored in other climate zones (Stubbington et al. 2017a). Addressing this research gap, papers in this special issue present recent research advances in temporary stream ecohydrology in less well-known regions, promoting a balanced global understanding of these dynamic ecosystems. Contributions are from relatively cool, wet oceanic and continental climate regions (Fig. 1) with the exception of Chakona et al.'s (2019) contribution from a little-studied mediterranean-climate region of South Africa.

Of six papers in this special issue, three use field data to investigate community (Durkota et al. 2019) and/or population (Chakona et al. 2019; Pařil et al. 2019) responses of aquatic biota to intermittence, and Durkota et al. (2019) report a unique study encompassing both surface water and groundwater habitats. Loskotová et al. (2019) address responses to drying at the scale of the individual organism using laboratory experiments. An applied management context is provided by Sefton et al. (2019), who investigate the hydrological drivers that underpin biotic responses, and England et al. (2019), who present a new index that quantifies aquatic–terrestrial community responses to intermittence. Collectively, the contributions to this special issue emphasize the importance of refuges and thus recolonization pathways in both longitudinal and vertical dimensions; highlight that the refuge role of the subsurface sediments extends from the hyporheic zone into the groundwater; explore biodiversity patterns for rare and endemic species at broad spatial

Fig. 1. Temporary streams included in this special issue. Pařil et al. (2019) studied Gránický stream in continental Czech Republic during **(a)** flowing, **(b)** isolated pool and **(c)** dry phases. The study area explored by both England et al. (2019) and Sefton et al. (2019) includes the River Gade in oceanic England, shown during **(d)** flowing, **(e)** low-flow and **(f)** dry phases.

scales; characterize diverse responses to drying events within and among populations; and present new approaches to improve the monitoring and management of temporary streams.

Here, we set the studies presented in this special issue in a wider context, highlighting how papers build on recent research to advance temporary stream ecohydrology. Reflecting studies conducted to date – including contributions to this special issue – we focus on aquatic invertebrate communities, in particular those present during flowing phases. We also recognize the need to complement these advances with new research that characterizes both aquatic and terrestrial contributions to temporary stream biodiversity. To inform this future research, we review knowledge of the terrestrial invertebrate assemblages that inhabit temporary streams during their dry phases.

Hydrological characterization of intermittence

In all regions, ecohydrological understanding of temporary streams is limited by the availability of hydrological data describing their flow regimes (Ruhi et al. 2018). Temporary streams are poorly represented in gauging station networks, particularly in cool, wet temperate regions in which perennial systems dominate (Snelder et al. 2013). Even where temporary flow regime characterization is temporally continuous, the duration for which data are available may be insufficient to represent long-term patterns, leading to inaccurate classification of sites as perennial and difficulties in recognizing extreme events (Stubbington et al. 2016). Logistic constraints also limit the spatial coverage of monitoring networks, preventing characterization of hydrological conditions in wet-dry habitat mosaics at ecologically relevant spatial scales. Collectively, these limitations prevent description of temporary flow regimes at a spatial and temporal resolution sufficient to fully explain biological responses. In addition, interpretation of biotic responses to hydrological variability is limited by difficulties in using gauging station data to distinguish between two fundamentally different no-flow states: lentic water (in either ponded stretches or isolated pools) and a dry bed (Sefton et al. 2019). Such data therefore require supplementation by field observations (Gallart et al. 2012; Beaufort et al. 2018; White et al. 2018, Beaufort et al. 2019).

In this special issue, Sefton et al. (2019) address this scarcity of hydrological information using a data set of exceptional detail: observations of in-channel conditions made at monthly intervals for 20 years, at 18–32 sites spanning the temporary stretches of each of ten chalk streams (including the River Gade; Fig. 1d–f). The results reveal fine-scale spatial and temporal patterns of cycling between dry, ponded, moderate-flow and high-flow states, and highlight the hydrological character of these groundwater-fed streams, which may remain wet or dry for years, as water levels within the porous chalk aquifer fluctuate in response to precipitation (Sefton et al. 2019; also see Holmes 1999). Such temporal changes contrast with systems which experience predictable, seasonal transitions between wet and dry states, such as some mediterranean stream reaches (Gasith & Resh 1999) and oceanic karst streams (Smith et al. 2003; Hill & Milner 2018), rendering the ‘mean annual’ metrics proposed to describe temporary flow regimes unsuitable for these groundwater-fed streams (Costigan et al. 2017; Leigh & Datry 2017). Instead, Sefton et al. (2019) highlight the need for flexible approaches that reflect the diversity of hydrological regimes occurring within the broad ‘temporary stream’ classification (Reyjol et al. 2014), both among (Costigan et al. 2017) and within climatic regions (Stubbington et al. 2017a).

Recognizing the need to apply insights from their data to ecosystem management, Sefton et al. (2019) present a framework to characterize temporary stream flow regimes using metrics relating to hydrological states. The framework incorporates variability in four states and recognizes spatial and temporal variability in both the composition and configuration of each state, spanning sub-reach to network spatial scales and event to multi-year temporal scales. As such, the framework aligns with strategies seeking to promote effective ecosystem protection by transcending aquatic–terrestrial boundaries (Mainstone et al. 2018) and operating at catchment or landscape scales (Gurnell et al. 2016). Although developed using oceanic-climate chalk-stream data, the framework proposed by Sefton et al. (2019) is sufficiently flexible to warrant evaluating its applicability to other temporary stream types.

Aquatic community and population responses to intermittence

The influence of intermittence on aquatic communities is a focus of temporary stream ecology across climatic regions (Datry et al. 2014; Leigh & Datry 2017; Soria et al. 2017). Variability in the frequency, magnitude, duration and predictability of lotic, lentic and terrestrial states interact to influence the extent and nature of adaptations that evolve in different environments (Lytle & Poff 2004), which may cause biotic responses to differ among regions. Although precipitation restricts the extent of drying in cool, wet climates, aquatic communities in temporary reaches are characterized by lower alpha diversity here as in other regions (Datry et al. 2014; Soria et al. 2017), because drying represents a strong environmental filter that eliminates species without appropriate adaptations (Chase 2007; Datry et al. 2016a). However, as contributions to this special issue highlight, differences in community resilience between temporary and perennial streams may be reduced in temperate regions, due to rapid recolonization from nearby perennial waters (e.g. upstream and downstream reaches; Pařil et al. 2019) and within-reach wet refuges (i.e. the hyporheic zone and pools; Durkota et al. 2019; Pařil et al. 2019). Resistance strategies may also be relatively prevalent in temperate compared to dryland temporary streams, with greater moisture retention in unsaturated interstices promoting persistence of taxa with some degree of desiccation tolerance (Loskotová et al. 2019).

Longitudinal refuges are important recolonist sources

The spatial dimensions with the greatest influence on the resistance and resilience of aquatic communities may vary among climates. In drylands, the greater spatial extent of drying increases the time needed for recolonization from longitudinally connected waters, and distances to upstream and downstream reaches may be farther than some aquatic taxa can migrate within a wet phase (Stanley et al. 1994; Bogan et al. 2013; but see Leigh et al. 2016b). In addition, upstream surface waters may well be absent, eliminating drift as a recolonization pathway and limiting longitudinal recolonists to positively rheotactic taxa. In contrast, the spatial proximity of longitudinally connected perennial waters promotes recolonization of aquatic biota by both downstream drift and upstream migration upon flow resumption in cool, wet regions and other systems with perennial upstream waters (Williams 1977; Sagar 1983; Paltridge et al. 1997;; Stubbington et al. 2016). Contributions to this special issue complement such studies: Pařil et al. (2019) sampled adult gammarid amphipods three weeks after flow resumed in a 2-km stretch of a continental-climate karst stream (Fig. 1a–c), with direct observations documenting upstream migrations, and the presence of upstream perennial reaches making drift a likely second recolonization pathway. Such observations indicate that adults but not juveniles use longitudinal recolonization pathways, enhancing previous understanding of how populations recover after flow resumes (Pařil et al. 2019).

Hyporheic sediments are a refuge for benthic and groundwater fauna

The vertical connection to subsurface water in saturated hyporheic and benthic interstices is more likely to be lost in dryland compared to temperate temporary streams (Smock et al. 1994; Boulton & Stanley 1995), restricting interstitial survival to desiccation-tolerant taxa (Stubbington & Datry 2013). In cooler, wetter regions, dry-phase declines in the water table may be of a shorter duration, to a shallower depth, and with greater moisture retention in unsaturated interstices, enabling the hyporheic zone to act as a refuge for primarily benthic taxa (Datry 2012; Vander Vorste et al. 2016). Complementing such previous community-focused studies, contributions to this special issue improve our understanding of the hyporheic zone as a refuge from drying. Specifically, Pařil et al. (2019) present the first study of within-population differences in hyporheic refuge use (but see e.g. Hwan et al. 2017; Rodríguez-Lozano et al. 2019). Very high gammarid densities occurred 0-10 cm into a streambed in which water levels dropped 5 cm below the surface, and compared to larger adults, juveniles were abundant in these shallow subsurface sediments. In addition, only juveniles were recorded in benthic samples 11 days after flow resumed, indicating their survival in local refuges as important for post-drying population recovery (Pařil et al. 2019).

Several studies have examined the hyporheic zone as a dry-phase and low-flow refuge in oceanic (Datry et al. 2007; Wood et al. 2010; Stubbington et al. 2011a; Stubbington et al. 2011b; Datry 2012) and continental climates (Williams 1977), indicating variable refuge use even within such regions. Interactions between species characteristics and environmental variables influence whether an organism migrates into, survives within, and recolonizes from the subsurface sediments (Stubbington 2012; Vadher et al. 2017). For example, hyporheic refuge use differs depending on the direction of hydrological exchange: upwelling groundwater promotes the upwards migration of stygobites whereas downwelling surface water enables the downwards migration of benthic species (Datry et al. 2007; Stubbington et al. 2011b). In this special issue, Durkota et al. (2019) present a unique study extending understanding of invertebrate responses to hydrological variability into the groundwater aquifer. Observations from boreholes, benthic and hyporheic sediments complement previous studies inferring stygobite behaviour from their presence in hyporheic samples (Wood et al. 2010; Stubbington & Wood 2013). Durkota et al. (2019) provide new evidence that the hyporheic zone is a refuge from adverse conditions in both the surface stream and the aquifer: declining groundwater levels trigger upwards migration of stygobitic invertebrates, mirroring downwards migrations by benthic organisms as surface discharge declines.

As climates become drier and characterized by more frequent and severe droughts across global regions (Lehner et al. 2006; Döll & Schmied 2012; Bartholy et al. 2014), the subsurface sediments represent an extensive potential refuge during dry phases. The evidence that these sediments support biotic persistence after surface water is lost, as provided by multiple special issue contributions (Durkota et al. 2019; Loskotová et al. 2019; Pařil et al. 2019) could be applied to improve management and restoration activities by extending typically surface-focused designs into the hyporheic zone (Boulton 2007). Specifically, restoring fine-sediment-impacted substrates could create interstitial pathways that accommodate juvenile migrants to promote recruitment and population recovery (Vadher et al. 2015; Pařil et al. 2019).

Network-scale habitat diversity supports biodiversity

Ecological responses to intermittence are typically studied at the reach scale, and a few temperate-zone studies have investigated stream-scale invertebrate community responses to changes in flow permanence (Datry et al. 2007; Arscott et al. 2010; Datry 2012). Some dryland research has also characterized communities across multiple streams within a catchment (Bogan et al. 2013; Schriever et al. 2015), and many studies span multiple chalk 'winterbournes' in oceanic south England (Holmes 1999; Westwood et al. 2017; White et al. 2018; Sarremejane et al. in press). Recent conceptual advances suggest that explanation of biodiversity patterns also requires recognition that stream networks support catchment-scale metacommunities of organisms linked by dispersal (Larned et al. 2010; Datry et al. 2016b). In this special issue, Chakona et al. (2019) contribute to the field research needed to understand network-scale biotic responses to intermittence by exploring 28 sites across tributaries in a South African catchment. Examining this broad spatial scale enables Chakona et al. (2019) to identify among-stream habitat diversity as supporting persistence of endemic, threatened fish species, and different life stages of each species. In particular, Chakona et al. (2019) note differences in the preferred local habitat characteristics and network position (i.e. headwaters vs. mainstem) of adult and juvenile life stages.

Human alteration can alter connectivity, and where persistence of both connected and isolated aquatic habitats declines, endemic aquatic species can be locally extirpated (Labbe & Fausch 2000; Jaeger et al. 2014; Chakona et al. 2019). Equally, an increase in connectivity can compromise the strongholds in which temporary-stream specialists persist (Armitage & Bass 2013) if controls on the dispersal of both invasive non-native and competitive native species are weakened (Closs & Lake 1996; Maret et al. 2006; Reich et al. 2010). The findings of Chakona et al. (2019) highlight the importance of situating local-scale management activities within catchment-scale strategies that aim to provide the range of habitats needed to support target species at all life stages. By promoting natural hydrological connectivity within such strategies, managers can enable biotic dispersal within integrated networks of perennial and temporary streams.

Population-level studies enable understanding of biotic responses to intermittence

Like network-scale research, temporary stream studies conducted at lower levels of the ecological hierarchy remain rarities. Community-level research is extensive and provides some insight into population responses to intermittence, but population-focused studies remain largely restricted to salmonids in drylands. Here, drying may eliminate whole populations, or survival may be restricted to juveniles in wet refuges including pools and subsurface sediments (e.g. Hwan et al. 2017; Rodríguez-Lozano et al. 2019; also see Kawanishi et al. 2013). In temperate zones, the reduced extent of intermittence may have more complex effects, restructuring populations of desiccation-sensitive species due to differential impacts on within-population cohorts (Lake 2003). For example, extreme low flows eliminated a *Salmo salar* juvenile year class in an oceanic upland stream, severely reducing salmonid recruitment (Cowx et al. 1984). Such studies remain scarce, in particular for biotic groups other than economically important fish, but papers in this special issue explore the population dynamics of an ecologically important macroinvertebrate (Pařil et al. 2019) and endemic, endangered fish (Chakona et al. 2019).

Pařil et al. (2019) examine how short drying events affect *Gammarus fossarum*, a widespread and abundant amphipod with an important role in transferring energy between trophic levels (MacNeil et al. 1997). Characterizing populations in flowing- and dry-phase benthic sediments, pools and subsurface sediments, Pařil et al. (2019) determine the densities and body sizes of adults and juveniles, the relative abundance of males and females, and the reproductive status of females. Despite some persistence in pools and subsurface sediments, and despite drying being limited in both space and time, cohorts of spring-recruited juveniles were largely eliminated by surface water loss. Exacerbating these impacts on recruitment, no reproductive females were recorded post-drying, indicating that true recovery from a dry phase may not begin until the following spring – at which point, it relies on the reproductive viability of an aging population (Pařil et al. 2019). As such, inferring population recovery using total abundance data may overlook structural changes with long-term effects on recruitment and population integrity. In some cases, the suggestion that aquatic biotas recover quickly after flow resumes may simplify and underestimate effects of drying (Bogan et al. 2017; Stubbington et al. 2017b). Management strategies seeking to promote the resistance and resilience of vulnerable within-population cohorts need to be guided by an ecological understanding of the long-term dynamics of populations adapting to changing flow permanence regimes in dynamic river ecosystems.

Loskotová et al. (2019) complement Pařil et al.'s (2019) field study and previous experimental work (McGrath et al. 2007; Poznańska et al. 2013; Vadher et al. 2017) by using mesocosms to identify abiotic drivers of population responses to water loss for four macroinvertebrate taxa including *G. fossarum*. Underpinning biotic responses and demonstrating the hyporheic zone's potential as a drying refuge, Loskotová et al. (2019) identify a gradient of moisture content within the interstices just days after surface drying: sediments retained greater moisture 6-10 cm below the surface. Macroinvertebrate taxa with variable morphologies responded to this greater water availability, but their ability to migrate and thus their survival was influenced by their body size in relation to interstitial volumes. In deeper, wetter sediment layers, *G. fossarum* persisted for longer, highlighting water availability as a fundamental determinant of the potential of any drying refuge (Stubbington & Datry 2013). Such organism-level research is crucial to inform predictions of how populations and communities will respond to changing flow permanence regimes in a context of ongoing climate change.

Tools to support ecological quality assessments in temporary streams

The study of England et al. (2019) builds on research quantifying invertebrate community responses to sequential changes in habitat availability as discharge declines (Boulton 2003; Boulton & Lake 2008). Such a sequence – potentially from a diverse range of flowing to dry habitats – reflects conditions in both near-perennial streams during drought events and in other temporary streams during 'normal' years. Chadd et al. (2017) developed the *Drought Effect of Habitat Loss on Invertebrates* (DEHLI) index to characterize aquatic invertebrate losses in relation to changing habitat availability, and this index can also document responses to flow cessation and drying in temporary streams (Sarremejane et al. in press; White et al. 2019). Here, England et al. (2019) take a further step, by presenting a new index to characterize responses of assemblages encompassing aquatic, semi-aquatic and terrestrial invertebrate taxa to changing instream conditions. Such taxa are all routinely present in regulatory samples collected from drying streambeds, due to their presence in marginal habitats (Fig. 1e). England et al.'s (2019) innovative approach recognizes intermittence as associated with terrestrial taxonomic gains that offset aquatic losses, which enhances the spatial and temporal beta diversity of temporary stream communities (Larned et al. 2010; Corti & Datry 2016; Stubbington et al. 2017a).

Describing the assemblages associated with the changing habitats present as a stream dries implicitly recognizes taxon absences as reflecting sensitivity to intermittence. As such, studies including England et al. (2019), Chadd et al. (2017) and Straka et al. (2019) lay the foundations for future characterization of communities associated with unimpacted temporary streams and how these differ at sites altered by anthropogenic impacts. Further research is also needed to develop classification systems that acknowledge the considerable environmental variability of temporary streams (Skoulikidis et al. 2017; Stubbington et al. 2018a). A long-term goal of such research is to transform the monitoring and management of temporary streams, which are typically underrepresented in or excluded from the routine sampling of regulatory agencies (Stubbington et al. 2018a). Progress towards this goal may be facilitated by recent advances in the Mediterranean Basin (Gallart et al. 2012; Prat et al. 2014; Gallart et al. 2017), where adapted versions of aquatic-invertebrate-based indices have been developed for temporary streams with seasonal, predictable flow regimes (Munné & Prat 2009; Stubbington et al. 2018a). However, aseasonal variability characterizes the flow permanence regimes of some temporary stream types in cooler, wetter regions (Sefton et al. 2019), meaning that regulatory activities cannot always be timed to coincide with peak aquatic alpha diversity (Prat et al. 2014). Instead, regulators need flexible methods that can be applied regardless of in-channel hydrological conditions (England et al. 2019; Stubbington et al. 2019).

Priorities to progress ecohydrological understanding of temporary streams

Recent reviews have outlined ambitious, cross-discipline research priorities to advance temporary stream science and management (Datry et al. 2016a; Leigh et al. 2016a; Datry et al. 2017b; Stubbington et al. 2018a). Instead of replicating these valuable syntheses, we discuss the research priorities identified by contributions to this special issue. Chakona et al. (2019) and Loskotová et al. (2019) highlight the need for autecological studies that identify species-specific physiological tolerances to conditions experienced in temporary stream habitats including isolated pools, and saturated and humid sediments. Generating such knowledge will require controlled laboratory experiments, the findings of which will enable prediction of species-specific vulnerability to flow regime alteration in a context of global change (Chakona et al. 2019). At the next hierarchical level, Pařil et al. (2019) demonstrate the value of field experiments that characterize population-level responses to drying, without which we may fail to recognize the severity of a biotic response. Such research should prioritize species with important roles in ecosystem functioning (Pařil et al. 2019) and those of conservation concern (Chakona et al. 2019). Both Chakona et al. (2019) and Pařil et al. (2019) also emphasize the need to identify the refuges and recolonization pathways that collectively enable different population cohorts to persist during and recover after a drying event.

Papers in this special issue also highlight the improvements to temporary stream monitoring and management that could be achieved by real-world application of research advances. The hydrological metrics developed by Sefton et al. (2019) and the biotic index presented by England et al. (2019) both represent tools with the potential for widespread application in temporary streams across and beyond Europe, subject to testing and appropriate adaptation. However, more field data are first needed: regularly collected observations distinguishing between flowing, ponded and dry instream states (Sefton et al. 2019), and taxon lists detailing the aquatic, semi-aquatic and terrestrial invertebrates present in routine biomonitoring samples (England et al. 2019). In addition, Durkota et al. (2019) emphasize that incorporating both surface water and groundwater ecology can enable effective management of freshwater ecosystems including temporary streams. Academic and stakeholder members of research projects including the EU COST Action CA15113 *Science and Management of Intermittent Rivers and Ephemeral Streams* (Datry et al. 2017c) and the *Dry Rivers Research Coordination Network* (2019) represent networks with the potential to test the tools and implement the recommendations presented herein.

Ongoing research biases are also indicated by papers in this special issue. Macroscopic faunas and in particular macroinvertebrates remain a focus, whereas meiofauna are relatively poorly studied (Robertson et al. 2000); animals are better characterized than any other major taxon. Ecological patterns remain best-known within reaches, whereas other spatial scales from the microhabitat to the network require further study. Similarly, community patterns are better described than those at higher and lower ecological levels including the metacommunity, population (but see Cowx et al. 1984; Pařil et al. 2019) and species (but see Loskotová et al. 2019 and fish studies such as Hwan et al. 2017). Observational field studies dominate, whereas few controlled experiments test hypotheses or disentangle the multiple drivers influencing biotic communities (but see e.g. Vadher et al. 2017; Aspin et al. 2018; Loskotová et al. 2019).

Although described with aquatic communities in mind, the above research biases also relate to terrestrial communities, understanding of which remains notably limited. England et al. (2019) join calls for holistic ecological quality assessments in temporary streams to encompass taxa across the full range of habitat preferences from aquatic organisms that dominate during wet phases to terrestrial assemblages that colonize and establish in dry channels (Stubbington et al. 2018a; Stubbington et al. 2019). First, however, considerable field research is needed to address this major research gap by characterizing terrestrial communities and their ecological requirements across climate zones. As a first step, below, we complement the advances in aquatic macroinvertebrate ecology of spe-

Table 1. Taxonomic richness of dry-phase terrestrial invertebrate assemblages in temporary stream channels in different Köppen-Geiger climate types. Details of each study are provided in Table S1, and climate-type codes are defined in the Table S1 footnote. Alp., alpine; Ctl., continental.

Order / higher taxon (stated)	Family / finest taxonomic resolution	Tropical			Arid and semi-arid						Temperate													Ctl.	Alp.	Total
											Sub-tropical		Oceanic							Mediterranean						
		Am	Aw	Aw	Bsh	Bsk	Bsk	Bsk	Bsk	Bwh	Cfa	Cfa	Cfb	Cfb	Cfb	Cfb	Cfb	Cfb	Cfb	Csa	Csa	CSb	CSb	Dfb	ET	
Acari (subclass)										1		1				1		1				1	1	1		7
	Oribatida																			1						1
Amphipoda														1								1				2
Araneae					1	1	1		1	1					1		1		1	1	1	1	1			12
	Lycosidae							1						1					1		1					4
	Salticidae																		1							1
Archaeognatha																						1				1
Blattodea		1																				1			1	3
Chilopoda (class)															1											1
Coleoptera			1	1					1											1	1	1	1		1	8
	Anthicidae				1																					1
	Carabidae							1			1			1		1	1		1		1			1		8
	Chrysomelidae															1	1									2
	Cicindelidae										1															1
	Dryopidae																1									1
	Dytiscidae									1																1
	Elateridae				1																					1
	Heteroceridae												1													1
	Hydraenidae													1												1
	Hydrophilidae												1													1
	Psephenidae				1																					1
	Scarabaeidae																							1		1
	Staphylinidae				1						1		1		1	1					1			1		7
Collembola (subclass)					1	1	1		1			1			1	1	1	1	1		1		1		1	13
Dermaptera																						1				1
Diptera				1				1												1		1				4
	Anthomyiidae												1													1
	Diopsidae			1				1		1																3
	Cecidomyiidae											1					1									2
	Ceratopogonidae																			1						1
	Chironomidae																1							1		2
	Dolichopodidae												1													1

Table 1. Continued

Order / higher taxon (stated)	Family / finest taxonomic resolution	Tropical			Arid and semi-arid						Temperate													Ctl.	Alp.	Total
											Sub-tropical		Oceanic							Mediterranean						
		Am	Aw	Aw	Bsh	Bsk	Bsk	Bsk	Bsk	Bwh	Cfa	Cfa	Cfb	Cfb	Cfb	Cfb	Cfb	Cfb	Cfb	Csa	Csa	CSb	CSb	Dfb	ET	
	Psychodidae				1															1						2
	Sciaridae											1														1
	Sphaeroceridae												1													1
	Tipulidae												1							1						2
Gastropoda (class)																		1				1				2
	Arionoidea																							1	1	2
	Cochlicopidae																							1		1
Hemiptera						1		1									1				1	1			1	5
	Aphidae														1		1									2
	Gelastocoridae					1		1			1															3
	Lygaeidae				1																					1
	Saldidae										1															1
Hymenoptera	Formicidae		1	1	1	1	1	1	1	1				1	1		1	1			1	1	1	1		17
Isopoda					1																	1				2
	Oniscidae																1	1								2
Lepidoptera					1																	1				2
	Psychidae																1									1
Mallophaga (suborder)																	1									1
Mantodea																						1				1
Myriapoda (class)													1				1									2
Nematoda (phylum)												1														1
Oligochaeta (subclass)													1			1										2
	Enchytraeidae											1												1		2
	Tubificidae																							1		1
Opiliones																			1							1
Orthoptera					1																	1				2
	Acrididae									1																1
	Gryllidae									1	1															2
	Tetrigidae									1	1															2
Protura															1											1
Pseudoscorpiones																	1					1				2
Psocoptera					1											1	1				1		1			5
Solifugae																						1				1
Thysanoptera																	1					1				2

cial issue contributions by examining current knowledge of the terrestrial communities; we also direct readers to Steward et al. (2017). Reflecting research to date, we focus on invertebrates but also outline current knowledge of plant communities. We highlight where our understanding is balanced across regions, where particular regions lag behind or lead ecological advances, and where research gaps are climatically widespread. Addressing these gaps is crucial to inform effective management and protection of the total biodiversity and ecosystem services of temporary streams as aquatic–terrestrial ecosystems (Stubbington et al. 2019).

Recognizing terrestrial contributions to temporary stream biodiversity

Although "terrestrial limnology" (Boulton & Suter 1986: 321) has long been recognized (Allee & Torvik 1927), studies have to date focused on aquatic communities present during flowing phases, and also lentic assemblages, including those in both dryland and temperate ponded reaches and isolated pools (Hill & Milner 2018; Bogan et al. 2019). In contrast, terrestrial communities – which experience temporary streams not as freshwaters that sometimes dry, but as linear terrestrial habitats that are sometimes inundated (Stubbington et al. 2017a) – remain poorly known across climate zones. In addition, very few studies span aquatic and terrestrial environments to characterize the total biodiversity contribution of temporary streams or compare community responses to intermittence (Soininen et al. 2015; Stubbington et al. 2018b; but see Corti & Datry 2016). Variability in the spatial and temporal extent of drying and inundation likely has contrasting effects on aquatic and terrestrial taxa (Leigh et al. 2016b), and biotic responses of terrestrial organisms to wet-dry cycles probably vary among climate types. Across climates, the spatial dimensions of connectivity that influence the resistance and resilience of in-channel assemblages may differ for terrestrial compared to aquatic taxa, with colonization of dry channels by terrestrial invertebrates facilitated primarily by dispersal from laterally connected vegetated riparian zones (Corti & Datry 2016).

Recent research exploring (largely ground-dwelling) terrestrial invertebrate communities joins earlier studies in starting to redress the aquatic–terrestrial balance (Table S1; Steward et al. 2017). These dry-phase studies span tropical (Allee & Torvik 1927; Steward et al. 2011), sub-tropical (Stehr & Branson 1938; Fritz & Feminella 2011; Steward et al. 2011), arid (Blackith & Guillet 1995; Lalley et al. 2006), hot semi-arid (Dell et al. 2014), cold semi-arid (Steward et al. 2011; McCluney & Sabo 2012), continental (Williams & Hynes 1976), mediterranean (Maamri et al. 1997; Wishart 2000; Rosado et al. 2014; Sánchez-Montoya et al. 2016), oceanic (Moon 1956; Boulton & Suter 1986; Larned et al. 2007) and alpine (Steward et al. 2011) regions (Table S1). Of 25 identified study systems, seven are in oceanic regions, a climatic bias which contrasts with the dryland focus of aquatic community research but largely reflects the activity of one research group in the Albarine, France (Corti & Datry 2012; Datry et al. 2012; Corti & Datry 2016) and the Selwyn, New Zealand (Table S1; Larned et al. 2007; Corti et al. 2013). In contrast, single studies represent the continental and polar/alpine Köppen-Geiger climate classes (see Table S1; Steward et al. 2011). Across multiple climate zones, richness estimates indicate the significant contribution of terrestrial taxa to total biodiversity (Table 1). Notably, Corti & Datry (2016) quantified invertebrate biodiversity in the oceanic Albarine, and suggested that terrestrial richness exceeded that of aquatic communities.

Comparing the assemblages recorded in contrasting climate types (Tables 1 and S1) is hampered by inconsistent sampling effort among regions and among studies; the qualitative nature of many data sets; the coarse resolution to which most taxa have been identified; the scarcity of comprehensive taxa lists; and the lack of distinction between adult and juvenile life stages. Nonetheless, 24 studies (but not Lalley et al. 2006; see Table S1) have recorded at least 56 taxa from 27 orders or higher taxa (Table 1). Formicidae (Hymenoptera) are most widespread, occurring in 17 studies from tropical, semi-arid and arid, oceanic, mediterranean and continental climates; followed by Collembola, represented in 13 studies from semi-arid and arid, subtropical, oceanic, mediterranean climates; then Araneae, reported in 12 studies from semi-arid and arid, oceanic and mediterranean regions. Coleoptera are the most diverse order, represented by 13 families, with Carabidae and Staphylinidae occurring in eight and seven studies across arid and semi-arid, subtropical, oceanic, mediterranean and continental climates (Table 1). The Diptera are also diverse (ten families) and widespread, occurring in all climates except alpine. The relatively consistent assemblages described across climate types may reflect the coarse resolution to which taxa have been identified, and across regions, considerable research is needed to characterize terrestrial assemblages at the species level (Soininen et al. 2015; Stubbington et al. 2019).

The ongoing focus of dry-phase research on invertebrates may be explained by their mobility and thus rapid arrival after surface water loss. Other biotic communities remain uncharacterized across global regions. Although the effects of intermittence on instream plant communities have been described in oceanic temporary streams, studies have focused on aquatic macrophytes, identifying terrestrial herbs and grasses only as "non-aquatic" (Holmes 1999; Westwood et al. 2006a; Westwood et al. 2006b). Whereas vegetational succession may be limited by short, unpredictable dry phases in some cool, wet regions, ephemeral headwaters and aseasonal groundwater-fed channels may remain dry for years (Sarremejane et al. in press; Sefton et al. 2019). Here, lateral connections to riparian habitats and the prevalence of ruderal plants in frequently disturbed terrestrial habitats may favour resilient dry-channel assemblages dominated by terrestrial generalists. Inundation-tolerant specialists may also occur, including taxa that also inhabit dynamic aquatic–terrestrial habitats such as floodplains (Lytle et al. 2017). However, long-duration flowing phases will eliminate dry-channel inhabitants that lack adaptations to inundation (Adis & Junk 2002), with resistance mechanisms most likely to evolve in systems experiencing long and predictable dry phases; as for aquatic invertebrates, specialists may be the exception (Armitage & Bass 2013), not the norm (Datry et al. 2014). Considerable research is needed to provide evidence that supports, or contradicts, suggested patterns.

Conclusion: towards improved protection of temporary streams in a context of global change

This special issue is dominated by European contributions, partly reflecting recent collaborative research resulting from the EU COST Action CA15113 (Datry et al. 2017c; Pařil et al. 2019) as well as regulatory interest in monitoring and mitigation of interacting drought and water resource pressures (van Lanen et al. 2016; Rey et al. 2017). There is also a bias towards UK temporary chalk streams, where legislative protection (EC 1992) provides an impetus to improve monitoring and management (e.g. Chadd et al. 2017; Westwood et al. 2017; England et al. 2019; Sefton et al. 2019). Although not represented in this special issue, temporary stream research is also gaining momentum in European alpine regions (Piano et al. 2019; Siebers et al. 2019; also see the InterNet project, Eawag 2018), where intermittence may result from drying of snowmelt-fed streams or from loss of free water upon freezing (Prowse et al. 2007; Buttle et al. 2012; Tolonen et al. 2019). As climate change and water resource use interact to increase the extent of intermittence across global regions – including those with alpine, continental and oceanic climates (Beniston 2012; van Vliet et al. 2013; B-Béres et al. 2019) – further research is needed to better characterize community and population responses to natural and human-induced intermittence. Identifying differences in ecological responses among climate zones, including differences in the refuges that act as recolonist sources, may inform effective management interventions that recognize and enhance connectivity along the pathways that support recolonization by aquatic and terrestrial organisms during wet and dry phases, respectively.

In contrast to dryland systems, enhanced visibility during droughts and heatwaves makes dry streams symbols of anthropogenic climate change and unsustainable water resource use in cool, wet regions (Steward et al. 2012; Stubbington et al. 2018b). In some cases, temporary streams are impacted by human activity and negative perceptions of drying are warranted. In many other cases, the considerable 'natural capital' and ecosystem services provided by natural temporary streams are overlooked, including services that are unique to dry phases (Datry et al. 2018; Stubbington et al. 2018b). Despite this, appreciation and legal protection of temporary streams remains restricted to very few types (such as the 'winterbourne' chalk streams in south England; EC 1992), and most ecosystems remain overlooked (Acuña et al. 2017). In particular, small headwater streams are a notable research gap, despite global recognition of their biodiversity value (Finn et al. 2011; Biggs et al. 2017).

The improved scientific understanding resulting from recent advances in temporary stream science – including contributions in this special issue – needs to be shared widely, to enhance societal recognition of the ecological value of natural intermittence, while also acknowledging the profound consequences of human-impacted flow permanence regimes. Improved public attitudes towards temporary streams could ultimately provide political impetus for enhanced ecosystem protection through changes to policy and practice (Leigh et al. 2019). Building on recent progress in Mediterranean regions (Prat et al. 2014; Gallart et al. 2016; Gallart et al. 2017), now is the time to capitalize on recent recognition of natural intermittence by regulatory agencies with responsibility for ecosystem protection in cooler, wetter temperate nations (Mainstone et al. 2018), and to improve temporary stream management within and among regions with contrasting climate types.

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References

Acuña, V., Hunter, M., & Ruhí, A. (2017). Managing temporary streams and rivers as unique rather than second-class ecosystems. *Biological Conservation, 211*, 12–19. https://doi.org/10.1016/j.biocon.2016.12.025

Adis, J. & Junk, W. J. (2002). Terrestrial invertebrates inhabiting lowland river floodplains of Central Amazonia and Central Europe: A review. *Freshwater Biology, 47*(4), 711–731. https://doi.org/10.1046/j.1365-2427.2002.00892.x

Allee, W. & Torvik, M. (1927). Factors affecting animal distribution in a small stream of the Panama rain-forest in the dry season. *Journal of Ecology, 15*(1), 66–71. https://doi.org/10.2307/2256064

Armitage, P. D. & Bass, J. (2013). Long-term resilience and short-term vulnerability of south winterbourne macroinvertebrates. *Proceedings of the Dorset Natural History and Archaeological Society, 134*, 43–55.

Arscott, D. B., Larned, S., Scarsbrook, M. R. & Lambert, P. (2010). Aquatic invertebrate community structure along an intermittence gradient: Selwyn river, New Zealand. *Journal of the North American Benthological Society, 29*(2), 530–545. https://doi.org/10.1899/08-124.1

Aspin, T. W., Matthews, T. J., Khamis, K., Milner, A. M., Wang, Z., O'Callaghan, M. J. & Ledger, M. E. (2018). Drought intensification drives turnover of structure and function in stream invertebrate communities. *Ecography, 41*(12), 1992–2004. https://doi.org/10.1111/ecog.03711

Bartholy, J., Pongracz, J. & Pieczka, I. (2014). How the climate will change in this century? *Hungarian Geographical Bulletin, 63*(1), 55–67. https://doi.org/10.15201/hungeobull.63.1.5

B-Béres, V., Tóthmérész, B., Bácsi, I., Borics, G., Abonyi, A., Tapolczai, K., . . . Török, P. (2019). Autumn drought drives functional diversity of benthic diatom assemblages of continental intermittent streams. *Advances in Water Resources, 126*, 129–136. https://doi.org/10.1016/j.advwatres.2019.02.010

Beaufort, A., Carreau, J. & Sauquet, E. (2019). A classification approach to reconstruct local daily drying dynamics at headwater streams. *Hydrological Processes, 33*, 1896–1912. https://doi.org/10.1002/hyp. 13445

Beaufort, A., Lamouroux, N., Pella, H., Datry, T. & Sauquet, E. (2018). Extrapolating regional probability of drying of headwater streams using discrete observations and gauging networks. *Hydrology and Earth System Sciences, 22*(5), 3033–3051. https://doi.org/10.5194/hess-22-3033-2018

Beniston, M. (2012). Impacts of climatic change on water and associated economic activities in the Swiss Alps. *Journal of Hydrology (Amsterdam), 412–413*, 291–296. https://doi.org/10.1016/j.jhydrol.2010.06.046

Biggs, J., von Fumetti, S. & Kelly-Quinn, M. (2017). The importance of small waterbodies for biodiversity and ecosystem services: Implications for policy makers. *Hydrobiologia, 793*(1), 3–39. https://doi.org/10.1007/s10750-016-3007-0

Blackith, R. & Guillet, A. (1995). The insect fauna of an erratically dry African river bed. *Entomologist's Monthly Magazine, 131*, 65–67.

Bogan, M. T. & Lytle, D. A. (2007). Seasonal flow variation allows 'time-sharing' by disparate aquatic insect communities in montane desert streams. *Freshwater Biology, 52*(2), 290–304. https://doi.org/10.1111/j.1365-2427.2006.01691.x

Bogan, M. T., Boersma, K. S. & Lytle, D. A. (2013). Flow intermittency alters longitudinal patterns of invertebrate diversity and assemblage composition in an arid-land stream network. *Freshwater Biology, 58*(5), 1016–1028. https://doi.org/10.1111/fwb.12105

Bogan, M. T., Chester, E. T., Datry, T., Murphy, A. L., Robson, B. J., Ruhi, A., . . . Whitney, J. E. (2017). Resistance, resilience, and community recovery in intermittent rivers and ephemeral streams. In T. Datry, N. Bonada & A. J. Boulton (Eds.), *Intermittent Rivers and Ephemeral Streams: Ecology and Management* (pp. 349–376). Amsterdam: Elsevier; https://doi.org/10.1016/B978-0-12-803835-2.00013-9

Bogan, M. T., Leidy, R. A., Neuhaus, L., Hernandez, C. J. & Carlson, S. M. (2019). Biodiversity value of remnant pools in an intermittent stream during the great California drought. *Aquatic Conservation, 29*, 976–989. https://doi.org/10.1002/aqc.3109

Boulton, A. J. (2003). Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. *Freshwater Biology, 48*(7), 1173–1185. https://doi.org/10.1046/j.1365-2427.2003.01084.x

Boulton, A. J. (2007). Hyporheic rehabilitation in rivers: Restoring vertical connectivity. *Freshwater Biology, 52*(4), 632–650. https://doi.org/10.1111/j.1365-2427.2006.01710.x

Boulton, A. J. & Lake, P. S. (2008). Effects of drought on stream insects and its ecological consequences. In J. Lancaster & R. A. Briers (Eds.), *Aquatic Insects: Challenges to Populations* (pp. 81–102). Wallingford, UK: CAB International. https://doi.org/10.1079/9781845933968.0081

Boulton, A. J. & Stanley, E. H. (1995). Hyporheic processes during flooding and drying in a Sonoran Desert stream. 2. Faunal dynamics. *Archiv für Hydrobiologie, 134*, 27–52.

Boulton, A. & Suter, P. (1986). Ecology of temporary streams—an Australian perspective. In P. De Deckker & W. D. Williams (Eds.), *Limnology in Australia* (pp. 313–327). Melbourne: CSIRO/Junk. https://doi.org/10.1007/978-94-009-4820-4_19

Buttle, J., Boon, S., Peters, D., Spence, C., van Meerveld, H. J. & Whitfield, P. (2012). An overview of temporary stream hydrology in Canada. *Canadian Water Resources Journal, 37*, 279–310. https://doi.org/10.4296/cwrj2011-903

Chadd, R. P., England, J. A., Constable, D., Dunbar, M. J., Extence, C. A., Leeming, D. J., . . . Wood, P. J. (2017). An index to track the ecological effects of drought development and recovery on riverine invertebrate communities. *Ecological Indicators, 82*, 344–356. https://doi.org/10.1016/j.ecolind.2017.06.058

Chakona, A., Jordaan, M. & Kadye, W. T. (2019). Distribution and summer habitat associations of three narrow-range endemic fishes in an intermittent southern temperate Mediterranean river system. *Fundamental and Applied Limnology, 193*(1). https://doi.org/10.1127/fal/2019/1144

Chase, J. M. (2007). Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences of the United States of America, 104*(44), 17430–17434. Retrieved from https://doi.org/10.1073pnas.0704350104/https://doi.org/10.1073/pnas.0704350104 PMID:17942690

Closs, G. E. & Lake, P. S. (1996). Drought, differential mortality and the coexistence of a native and an introduced fish species in a south east Australian intermittent stream. *Environmental Biology of Fishes, 47*(1), 17–26. https://doi.org/10.1007/BF00002376

Corti, R. & Datry, T. (2012). Invertebrates and sestonic matter in an advancing wetted front travelling down a dry river bed (Albarine, France). *Freshwater Science, 31*(4), 1187–1201. https://doi.org/10.1899/12-017.1

Corti, R. & Datry, T. (2016). Terrestrial and aquatic invertebrates in the riverbed of an intermittent river: Parallels and contrasts in community organisation. *Freshwater Biology, 61*(8), 1308–1320. https://doi.org/10.1111/fwb.12692

Corti, R., Larned, S. T. & Datry, T. (2013). A comparison of pitfall-trap and quadrat methods for sampling ground-dwelling invertebrates in dry riverbeds. *Hydrobiologia, 717*(1), 13–26. https://doi.org/10.1007/s10750-013-1563-0

Costigan, K. H., Kennard, M. J., Leigh, C., Sauquet, E., Datry, T. & Boulton, A. J. (2017). Flow regimes in intermittent rivers and ephemeral streams. In T. Datry, N. Bonada & A. J. Boulton (Eds.), *Intermittent Rivers and Ephemeral Streams: Ecology and Management* (pp. 51–78). Amsterdam: Elsevier; https://doi.org/10.1016/B978-0-12-803835-2.00003-6

Cowx, I. G., Young, W. O. & Hellawell, J. M. (1984). The influence of drought on the fish and invertebrate populations of an upland stream in Wales. *Freshwater Biology, 14*(2), 165–177. https://doi.org/10.1111/j.1365-2427.1984.tb00030.x

Datry, T. (2012). Benthic and hyporheic invertebrate assemblages along a flow intermittence gradient: Effects of duration of dry events. *Freshwater Biology, 57*(3), 563–574. https://doi.org/10.1111/j.1365-2427.2011.02725.x

Datry, T., Bonada, N. & Boulton, A. J. (2017a). General introduction. In T. Datry, N. Bonada & A. J. Boulton (Eds.), *Intermittent Rivers and Ephemeral Streams: Ecology and Management* (pp. 1–20). Amsterdam: Elsevier; https://doi.org/10.1016/B978-0-12-803835-2.00001-2

Datry, T., Bonada, N. & Boulton, A. J. (2017b). Conclusions: Recent advances and future prospects in the ecology and management of intermittent rivers and ephemeral streams. In T. Datry, N. Bonada & A. J. Boulton (Eds.), *Intermittent Rivers and Ephemeral Streams: Ecology and Management* (pp. 563–584). Amsterdam: Elsevier; https://doi.org/10.1016/B978-0-12-803835-2.00031-0

Datry, T., Bonada, N. & Heino, J. (2016b). Towards understanding the organisation of metacommunities in highly dynamic ecological systems. *Oikos, 125*(2), 149–159. https://doi.org/10.1111/oik.02922

Datry, T., Boulton, A. J., Bonada, N., Fritz, K., Leigh, C., Sauquet, E., . . . Dahm, C. N. (2018). Flow intermittence and ecosystem services in rivers of the Anthropocene. *Journal of Applied Ecology, 55*(1), 353–364. https://doi.org/10.1111/1365-2664.12941 PMID:29681651

Datry, T., Corti, R. & Philippe, M. (2012). Spatial and temporal aquatic-terrestrial transitions in the temporary Albarine River, France: Responses of invertebrates to experimental rewetting. *Freshwater Biology, 57*(4), 716–727. https://doi.org/10.1111/j.1365-2427.2012.02737.x

Datry, T., Fritz, K. & Leigh, C. (2016a). Challenges, developments and perspectives in intermittent river ecology. *Freshwater Biology, 61*(8), 1171–1180. https://doi.org/10.1111/fwb.12789

Datry, T., Larned, S. T., Fritz, K. M., Bogan, M. T., Wood, P. J., Meyer, E. I. & Santos, A. N. (2014). Broad-scale patterns of invertebrate richness and community composition in temporary rivers: Effects of flow intermittence. *Ecography, 37*(1), 94–104. https://doi.org/10.1111/j.1600-0587.2013.00287.x

Datry, T., Larned, S. T. & Scarsbrook, M. R. (2007). Responses of hyporheic invertebrate assemblages to large-scale variation in flow permanence and surface-subsurface exchange. *Freshwater Biology, 52*(8), 1452–1462. https://doi.org/10.1111/j.1365-2427.2007.01775.x

Datry, T., Singer, G., Sauquet, E., Jorda-Capdevila, D., von Schiller, D., Stubbington, R., . . . Zoppini, A. (2017c). Science and management of intermittent rivers and ephemeral streams (SMIRES). *Research Ideas and Outcomes, 3*, e21774. https://doi.org/10.3897/rio.3.e21774

Dell, A. I., Alford, R. A. & Pearson, R. G. (2014). Intermittent pool beds are permanent cyclic habitats with distinct wet, moist and dry phases. *PLoS One, 9*(9), e108203. https://doi.org/10.1371/journal.pone.0108203 PMID:25244550

Döll, P. & Schmied, H. M. (2012). How is the impact of climate change on river flow regimes related to the impact on mean annual runoff? A global-scale analysis. *Environmental Research Letters, 7*(1), 014037. https://doi.org/10.1088/1748-9326/7/1/014037

Dostine, P. L., Humphrey, C. L., Paltridge, R. M. & Boulton, A. J. (1997). Macroinvertebrate recolonization after re-wetting of a tropical seasonally-flowing stream (Magela Creek, Northern Territory, Australia). *Marine and Freshwater Research, 48*(7), 633–645. https://doi.org/10.1071/MF97059

Dry Rivers Research Coordination Network (2019). *Dry Rivers Research Coordination Network*. National Science Foundation award number DEB-1754389. Available at: https://www.dryriversrcn.org/(accessed 7 July 2019).

Durkota, J. M., Wood, P. J., Johns, T., Thompson, J. R. & Flower, R. J. (2019). Distribution of macroinvertebrate communities across surface and groundwater habitats in response to hydrological variability. *Fundamental and Applied Limnology, 193*(1). https://doi.org/10.1127/fal/2019/1156

Eawag (2018). *Biodiversity and Ecosystem Function of Intermittency in an Alpine Fluvial Network: The InterNet Project*. Dübendorf, Switzerland: Eawag Department Aquatic Ecology. Available at https://www.eawag.ch/en/department/eco/projects/alpine-streams-and-flow-intermittency/(accessed 6 July 2018).

EC (European Commission) (1992). *Council Directive 92/43/EEC of 21 May 1992 on the Conservation of Natural Habitats and of Wild Fauna and Flora*. Luxembourg: Office for Official Publications of the European Communities.

England, J., Chadd, R., Dunbar, M. J., Sarremejane, R., Stubbington, R., Westwood, C. G. & Leeming, D. (2019). An invertebrate-based index to characterize ecological responses to flow intermittence in rivers. *Fundamental and Applied Limnology, 193*(1). https://doi.org/10.1127/fal/2019/1206

Finn, D. S., Bonada, N., Múrria, C. & Hughes, J. M. (2011). Small but mighty: Headwaters are vital to stream network biodiversity at two levels of organization. *Journal of the North American Benthological Society, 30*(4), 963–980. https://doi.org/10.1899/11-012.1

Frissell, C. A., Liss, W. J., Warren, C. E. & Hurley, M. D. (1986). A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. *Environmental Management, 10*(2), 199–214. https://doi.org/10.1007/BF01867358

Fritz, K. M. & Feminella, J. W. (2011). Invertebrate colonization of leaves and roots within sediments of intermittent coastal plain streams across hydrologic phases. *Aquatic Sciences, 73*(4), 459–469. https://doi.org/10.1007/s00027-011-0192-9

Gallart, F., Cid, N., Latron, J., Llorens, P., Bonada, N., Jeuffroy, J., . . . Prat, N. (2017). TREHS: An open-access software tool for investigating and evaluating temporary river regimes as a first step for their ecological status assessment. *Science of the Total Environment, 607–608*, 519–540. https://doi.org/10.1016/j.scitotenv.2017.06.209 PMID:28704676

Gallart, F., Llorens, P., Latron, J., Cid, N., Rieradevall, M. & Prat, N. (2016). Validating alternative methodologies to estimate the regime of temporary rivers when flow data are unavailable. *Science of the Total Environment, 565*, 1001–1010. https://doi.org/10.1016/j.scitotenv.2016.05.116 PMID:27251770

Gallart, F., Prat, N., García-Roger, E., Latron, J., Rieradevall, M., Llorens, P., . . . Froebrich, J. (2012). A novel approach to analysing the regimes of temporary streams in relation to their controls on the composition and structure of aquatic biota. *Hydrology and Earth System Sciences, 16*(9), 3165–3182. https://doi.org/10.5194/hess-16-3165-2012

Gasith, A. & Resh, V. H. (1999). Streams in Mediterranean climate regions: Abiotic influences and biotic responses to predictable seasonal events. *Annual Review of Ecology and Systematics, 30*(1), 51–81. https://doi.org/10.1146/annurev.ecolsys.30.1.51

Gurnell, A. M., Rinaldi, M., Belletti, B., Bizzi, S., Blamauer, B., Braca, G., . . . Ziliani, L. (2016). A multi-scale hierarchical framework for developing understanding of river behaviour to support river management. *Aquatic Sciences, 78*(1), 1–16. https://doi.org/10.1007/s00027-015-0424-5

Hill, M. J. & Milner, V. S. (2018). Ponding in intermittent streams: A refuge for lotic taxa and a habitat for newly colonising taxa? *Science of the Total Environment, 628–629*, 1308–1316. https://doi.org/10.1016/j.scitotenv.2018.02.162 PMID:30045552

Holmes, N. T. (1999). Recovery of headwater stream flora following the 1989–1992 groundwater drought. *Hydrological Processes, 13*(3), 341–354. https://doi.org/10.1002/(SICI)1099-1085(19990228)13:33.0.CO;2-L

Hwan, J. L., Fernández-Chacón, A., Buoro, M. & Carlson, S. M. (2017). Dry season survival of juvenile salmonids in an intermittent coastal stream. *Canadian Journal of Fisheries and Aquatic Sciences, 75*(5), 746–758. https://doi.org/10.1139/cjfas-2017-0026

Jaeger, K. L., Olden, J. D. & Pelland, N. A. (2014). Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. *Proceedings of the National Academy of Sciences of the United States of America, 111*(38), 13894–13899. https://doi.org/10.1073/pnas.1320890111 PMID:25136090

Kawanishi, R., Inoue, M., Dohi, R., Fujii, A. & Miyake, Y. (2013). The role of the hyporheic zone for a benthic fish in an intermittent river: A refuge, not a graveyard. *Aquatic Sciences, 75*(3), 425–431. https://doi.org/10.1007/s00027-013-0289-4

Labbe, T. R. & Fausch, K. D. (2000). Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. *Ecological Applications, 10*(6), 1774–1791. https://doi.org/10.1890/1051-0761(2000)010[1774:DOISHR]2.0.CO;2

Lake, P. S. (2003). Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology, 48*(7), 1161–1172. https://doi.org/10.1046/j.1365-2427.2003.01086.x

Lalley, J. S., Viles, H. A., Henschel, J. R. & Lalley, V. (2006). Lichen-dominated soil crusts as arthropod habitat in warm deserts. *Journal of Arid Environments, 67*(4), 579–593. https://doi.org/10.1016/j.jaridenv.2006.03.017

Larned, S. T., Datry, T., Arscott, D. B. & Tockner, K. (2010). Emerging concepts in temporary-river ecology. *Freshwater Biology, 55*(4), 717–738. https://doi.org/10.1111/j.1365-2427.2009.02322.x

Larned, S. T., Datry, T. & Robinson, C. T. (2007). Invertebrate and microbial responses to inundation in an ephemeral river reach in New Zealand: Effects of preceding dry periods. *Aquatic Sciences, 69*(4), 554–567. https://doi.org/10.1007/s00027-007-0930-1

Larned, S. T., Schmidt, J., Datry, T., Konrad, C. P., Dumas, J. K. & Diettrich, J. C. (2011). Longitudinal river ecohydrology: Flow variation down the lengths of alluvial rivers. *Ecohydrology, 4*(4), 532–548. https://doi.org/10.1002/eco.126

Lehner, B., Döll, P., Alcamo, J., Henrichs, T. & Kaspar, F. (2006). Estimating the impact of global change on flood and drought risks in Europe: A continental, integrated analysis. *Climatic Change, 75*(3), 273–299. https://doi.org/10.1007/s10584-006-6338-4

Leigh, C. & Datry, T. (2017). Drying as a primary hydrological determinant of biodiversity in river systems: A broad-scale analysis. *Ecography, 40*(4), 487–499. https://doi.org/10.1111/ecog.02230

Leigh, C., Boersma, K. S., Galatowitsch, M. L., Milner, V. S. & Stubbington, R. (2019). Are all rivers equal? The role of education in attitudes towards temporary and perennial rivers. *People and Nature, 1*, 181–190. https://doi.org/10.1002/pan3.22

Leigh, C., Bonada, N., Boulton, A. J., Hugueny, B., Larned, S. T., Vander Vorste, R. & Datry, T. (2016b). Invertebrate assemblage responses and the dual roles of resistance and resilience to drying in intermittent rivers. *Aquatic Sciences, 78*(2), 291–301. https://doi.org/10.1007/s00027-015-0427-2

Leigh, C., Boulton, A. J., Courtwright, J. L., Fritz, K., May, C. L., Walker, R. H. & Datry, T. (2016a). Ecological research and management of intermittent rivers: An historical review and future directions. *Freshwater Biology, 61*(8), 1181–1199. https://doi.org/10.1111/fwb.12646

Loskotová, B., Straka, M. & Pařil, P. (2019). Sediment characteristics influence benthic macroinvertebrate vertical migrations and survival under experimental water loss conditions. *Fundamental and Applied Limnology, 193*(1). https://doi.org/10.1127/fal/2019/1138

Lytle, D. A. & Poff, N. L. (2004). Adaptation to natural flow regimes. *Trends in Ecology & Evolution, 19*(2), 94–100. https://doi.org/10.1016/j.tree.2003.10.002 PMID:16701235

Lytle, D. A., Merritt, D. M., Tonkin, J. D., Olden, J. D. & Reynolds, L. V. (2017). Linking river flow regimes to riparian plant guilds: A community-wide modeling approach. *Ecological Applications, 27*(4), 1338–1350. https://doi.org/10.1002/eap. 1528 PMID:28263426

Maamri, A., Chergui, H. & Pattee, E. (1997). Leaf litter processing in a temporary northeastern Moroccan river. *Archiv für Hydrobiologie, 140*(4), 513–531. https://doi.org/10.1127/archiv-hydrobiol/140/1997/513

MacNeil, C., Dick, J. T. & Elwood, R. W. (1997). The trophic ecology of freshwater *Gammarus* spp. (Crustacea: Amphipoda): problems and perspectives concerning the functional feeding group concept. *Biological Reviews of the Cambridge Philosophical Society, 72*(3), 349–364. https://doi.org/10.1111/j.1469-185X.1997.tb00017.x

Mainstone, C., Jefferson, R., Diack, I., Alonso, I., Crowle, A., Rees, S., . . . Walsh, K. (2018). *Generating more integrated biodiversity objectives – rationale, principles and practice. Natural England Research Reports NERR071, Appendix B – open freshwater habitats* (pp. 1–71). Available at: http://publications.naturalengland.org.uk/publication/5891570502467584(accessed 6 July 2018).

Maret, T. J., Snyder, J. D. & Collins, J. P. (2006). Altered drying regime controls distribution of endangered salamanders and introduced predators. *Biological Conservation, 127*(2), 129–138. https://doi.org/10.1016/j.biocon.2005.08.003

McCluney, K. E. & Sabo, J. L. (2012). River drying lowers the diversity and alters the composition of an assemblage of desert riparian arthropods. *Freshwater Biology, 57*(1), 91–103. https://doi.org/10.1111/j.1365-2427.2011.02698.x

McGrath, K. E., Peeters, E. T., Beijer, J. A. & Scheffer, M. (2007). Habitat-mediated cannibalism and microhabitat restriction in the stream invertebrate *Gammarus pulex. Hydrobiologia, 589*(1), 155–164. https://doi.org/10.1007/s10750-007-0731-5

Moon, H. (1956). Observations on a small portion of a drying chalk stream. *Journal of Zoology, 126*(2), 327–334. https://doi.org/10.1111/j.1096-3642.1956.tb00441.x

Munné, A. & Prat, N. (2009). Use of macroinvertebrate-based multimetric indices for water quality evaluation in Spanish Mediterranean rivers: An intercalibration approach with the IBMWP index. *Hydrobiologia, 628*(1), 203–225. https://doi.org/10.1007/s10750-009-9757-1

Pařil, P., Leigh, C., Polášek, M., Sarremejane, R., Řezníčková, P., Dostálová, A. & Stubbington, R. (2019). Short-term streambed drying events alter amphipod population structure in a central European stream. *Fundamental and Applied Limnology, 193*(1). https://doi.org/10.1127/fal/2019/1164

Piano, E., Doretto, A., Falasco, E., Fenoglio, S., Gruppuso, L., Nizzoli, D., . . . Bona, F. (2019). If Alpine streams run dry: The drought memory of benthic communities. *Aquatic Sciences, 81*(2), 32. https://doi.org/10.1007/s00027-019-0629-0

Poznańska, M., Kakareko, T., Krzyżyński, M. & Kobak, J. (2013). Effect of substratum drying on the survival and migrations of Ponto-Caspian and native gammarids (Crustacea: Amphipoda). *Hydrobiologia, 700*(1), 47–59. https://doi.org/10.1007/s10750-012-1218-6

Prat, N., Gallart, F., von Schiller, D., Polesello, S., García-Roger, E., Latron, J., . . . Froebrich, J. (2014). The MIRAGE toolbox: An integrated assessment tool for temporary streams. *River Research and Applications, 30*(10), 1318–1334. https://doi.org/10.1002/rra.2757

Prowse, T., Bonsal, B., Duguay, C. & Lacroix, M. (2007). River-ice break-up/freeze-up: A review of climatic drivers, historical trends and future predictions. *Annals of Glaciology, 46*, 443–451. https://doi.org/10.3189/172756407782871431

Reich, P., McMaster, D., Bond, N., Metzeling, L. & Lake, P. S. (2010). Examining the ecological consequences of restoring flow intermittency to artificially perennial lowland streams: Patterns and predictions from the Broken—Boosey creek system in Northern Victoria, Australia. *River Research and Applications, 26*, 529–545. https://doi.org/10.1002/rra.1265

Rey, D., Holman, I. P. & Knox, J. W. (2017). Developing drought resilience in irrigated agriculture in the face of increasing water scarcity. *Regional Environmental Change, 17*(5), 1527–1540. https://doi.org/10.1007/s10113-017-1116-6

Reyjol, Y., Argillier, C., Bonne, W., Borja, A., Buijse, A. D., Cardoso, A. C., . . . van de Bund, W. (2014). Assessing the ecological status in the context of the European Water Framework Directive: Where do we go now? *Science of the Total Environment, 497–498*, 332–344. https://doi.org/10.1016/j.scitotenv.2014.07.119 PMID:25146904

Robertson, A. L., Rundle, S. D. & Schmid-Araya, J. M. (2000). Putting the meio- into stream ecology: Current findings and future directions for lotic meiofaunal research. *Freshwater Biology, 44*(1), 177–183. https://doi.org/10.1046/j.1365-2427.2000.00592.x

Rodríguez-Lozano, P., Leidy, R. A. & Carlson, S. M. (2019). Brook lamprey survival in the dry riverbed of an intermittent stream. *Journal of Arid Environments, 166*, 83–85. https://doi.org/10.1016/j.jaridenv.2019.04.016

Rohli, R. V. & Vega, A. J. (2017). *Climatology* (4th ed., pp. 1–425). Burlington, Massachusetts: Jones & Bartlett Learning.

Rosado, J., Morais, M. & Tockner, K. (2015). Mass dispersal of terrestrial organisms during first flush events in a temporary stream. *River Research and Applications, 31*(7), 912–917. https://doi.org/10.1002/rra.2791

Ruhi, A., Messager, M. L. & Olden, J. D. (2018). Tracking the pulse of the Earth's fresh waters. *Nature Sustainability, 1*(4), 198–203. https://doi.org/10.1038/s41893-018-0047-7

Sagar, P. (1983). Invertebrate recolonisation of previously dry channels in the Rakaia River. *New Zealand Journal of Marine and Freshwater Research, 17*(4), 377–386. https://doi.org/10.1080/00288330.1983.9516014

Sánchez-Montoya, M. D. M., von Schiller, D., Ruhí, A., Pechar, G. S., Proia, L., Miñano, J., . . . Tockner, K. (2016). Responses of ground-dwelling arthropods to surface flow drying in channels and adjacent habitats along Mediterranean streams. *Ecohydrology, 9*(7), 1376–1387. https://doi.org/10.1002/eco.1733

Sarremejane, R., Cañedo-Argüelles, M., Prat, N., Mykrä, H., Muotka, T. & Bonada, N. (2017). Do metacommunities vary through time? Intermittent rivers as model systems. *Journal of Biogeography, 44*(12), 2752–2763. https://doi.org/10.1111/jbi.13077

Sarremejane, R., Stubbington, R., Dunbar, M. J., Westwood, C. G. & England, J. (in press). Biological indices to characterize community responses to drying in streams with contrasting flow permanence regimes. *Ecological Indicators*.

Schriever, T. A., Bogan, M. T., Boersma, K. S., Cañedo-Argüelles, M., Jaeger, K. L., Olden, J. D. & Lytle, D. A. (2015). Hydrology shapes taxonomic and functional structure of desert stream invertebrate communities. *Freshwater Science, 34*(2), 399–409. https://doi.org/10.1086/680518

Sefton, C. E. M., Parry, S., England, J. & Angell, G. (2019). Visualising and quantifying the variability of hydrological state in intermittent rivers. *Fundamental and Applied Limnology, 193*(1). https://doi.org/10.1127/fal/2019/1149

Siebers, A. R., Paillex, A. & Robinson, C. T. (2019). Flow intermittency influences the trophic base, but not the overall diversity of alpine stream food webs. *Ecography,* ecog.04597. https://doi.org/10.1111/ecog.04597

Skoulikidis, N. T., Sabater, S., Datry, T., Morais, M. M., Buffagni, A., Dörflinger, G., . . . Tockner, K. (2017). Non-perennial Mediterranean rivers in Europe: Status, pressures, and challenges for research and management. *Science of the Total Environment, 577*, 1–18. https://doi.org/10.1016/j.scitotenv.2016.10.147 PMID:27810301

Smith, H., Wood, P. & Gunn, J. (2003). The influence of habitat structure and flow permanence on invertebrate communities in karst spring systems. *Hydrobiologia, 510*(1–3), 53–66. https://doi.org/10.1023/B:HYDR.0000008501.55798.20

Smock, L. A., Smith, L. C., Jones, J. B., Jr. & Hooper, S. M. (1994). Effects of drought and a hurricane on a coastal headwater stream. *Archiv für Hydrobiologie, 131*, 25–38.

Snelder, T. H., Datry, T., Lamouroux, N., Larned, S. T., Sauquet, E., Pella, H. & Catalogne, C. (2013). Regionalization of patterns of flow intermittence from gauging station records. *Hydrology and Earth System Sciences, 17*(7), 2685–2699. https://doi.org/10.5194/hess-17-2685-2013

Soininen, J., Bartels, P., Heino, J., Luoto, M. & Hillebrand, H. (2015). Toward more integrated ecosystem research in aquatic and terrestrial environments. *BioScience, 65*(2), 174–182. https://doi.org/10.1093/biosci/biu216

Soria, M., Leigh, C., Datry, T., Bini, L. M. & Bonada, N. (2017). Biodiversity in perennial and intermittent rivers: A meta-analysis. *Oikos, 126*(8), 1078–1089. https://doi.org/10.1111/oik.04118

Stanley, E. H., Buschman, D. L., Boulton, A. J., Grimm, N. B. & Fisher, S. (1994). Invertebrate resistance and resilience to intermittency in a desert stream. *American Midland Naturalist, 131*(2), 288–300. https://doi.org/10.2307/2426255

Stehr, W. C. & Branson, J. W. (1938). An ecological study of an intermittent stream. *Ecology, 19*(2), 294–310. https://doi.org/10.2307/1929643

Steward, A. L., Langhans, S. D., Corti, R. & Datry, T. (2017). The biota of intermittent rivers and ephemeral streams: terrestrial and semiaquatic invertebrates. In T. Datry, N. Bonada & A. J. Boulton (Eds.), *Intermittent Rivers and Ephemeral Streams: Ecology and Management* (pp. 245–271). Amsterdam: Elsevier; https://doi.org/10.1016/B978-0-12-803835-2.00008-5

Steward, A. L., Marshall, J. C., Sheldon, F., Harch, B., Choy, S., Bunn, S. E. & Tockner, K. (2011). Terrestrial invertebrates of dry river beds are not simply subsets of riparian assemblages. *Aquatic Sciences, 73*(4), 551–566. https://doi.org/10.1007/s00027-011-0217-4

Steward, A. L., von Schiller, D., Tockner, K., Marshall, J. C. & Bunn, S. E. (2012). When the river runs dry: Human and ecological values of dry riverbeds. *Frontiers in Ecology and the Environment, 10*(4), 202–209. https://doi.org/10.1890/110136

Straka, M., Polášek, M., Syrovátka, V., Stubbington, R., Zahrádková, S., Němejcová, D., . . . Pařil, P. (2019). Recognition of stream drying based on benthic macroinvertebrates: A new tool in Central Europe. *Ecological Indicators, 106*, 105486. https://doi.org/10.1016/j.ecolind.2019.105486

Stubbington, R. (2012). The hyporheic zone as an invertebrate refuge: A review of variability in space, time, taxa and behaviour. *Marine and Freshwater Research, 63*(4), 293–311. https://doi.org/10.1071/MF11196

Stubbington, R. & Datry, T. (2013). The macroinvertebrate seedbank promotes community persistence in temporary rivers across climate zones. *Freshwater Biology, 58*(6), 1202–1220. https://doi.org/10.1111/fwb.12121

Stubbington, R. & Wood, P. J. (2013). Benthic and interstitial habitats of a lentic spring as invertebrate refuges during supra-seasonal drought. *Fundamental and Applied Limnology, 182*(1), 61–73. https://doi.org/10.1127/1863-9135/2013/0409

Stubbington, R., Bogan, M. T., Bonada, N., Boulton, A. J., Datry, T., Leigh, C. & Vander Vorste, R. (2017b). The biota of intermittent rivers and ephemeral streams: Aquatic invertebrates. In T. Datry, N. Bonada & A. J. Boulton (Eds.), *Intermittent Rivers and Ephemeral Streams: Ecology and Management* (pp. 217–243). Amsterdam: Elsevier; https://doi.org/10.1016/B978-0-12-803835-2.00007-3

Stubbington, R., Chadd, R., Cid, N., Csabai, Z., Miliša, M., Morais, M., . . . Datry, T. (2018a). Biomonitoring of intermittent rivers and ephemeral streams in Europe: Current practice and priorities to enhance ecological status assessments. *Science of the Total Environment, 618*, 1096–1113. https://doi.org/10.1016/j.scitotenv.2017.09.137 PMID:29074240

Stubbington, R., England, J., Acreman, M., Wood, P. J., Westwood, C., Boon, P., Mainstone, C., Macadam, C., Bates, A., House, A. & Jorda-Capdevila, D. (2018b). *The natural capital of temporary rivers: characterising the value of dynamic aquatic-terrestrial habitats* (pp. 1–52). Natural Capital Synthesis Report VNP12. http://valuing-nature.net/TemporaryRiverNC(accessed 1 July 2018).

Stubbington, R., England, J., Wood, P. J. & Sefton, C. E. M. (2017a). Temporary streams in temperate zones: Recognizing, monitoring and restoring transitional aquatic-terrestrial ecosystems. *WIRES Water, 4*(4), e1223. https://doi.org/10.1002/wat2.1223

Stubbington, R., Gunn, J., Little, S., Worrall, T. P. & Wood, P. J. (2016). Macroinvertebrate seedbank composition in relation to antecedent duration of drying and multiple wet-dry cycles in a temporary stream. *Freshwater Biology, 61*(8), 1293–1307. https://doi.org/10.1111/fwb.12770

Stubbington, R., Paillex, A., England, J., Barthès, A., Bouchez, A., Rimet, F., . . . Datry, T. (2019). A comparison of biotic groups as dry-phase indicators of ecological quality in intermittent rivers and ephemeral streams. *Ecological Indicators, 97*, 165–174. https://doi.org/10.1016/j.ecolind.2018.09.061

Stubbington, R., Wood, P. J. & Reid, I. (2011b). Spatial variability in the hyporheic zone refugium of temporary streams. *Aquatic Sciences, 73*(4), 499–511. https://doi.org/10.1007/s00027-011-0203-x

Stubbington, R., Wood, P. J., Reid, I. & Gunn, J. (2011a). Benthic and hyporheic invertebrate community responses to seasonal flow recession in a groundwater-dominated stream. *Ecohydrology, 4*(4), 500–511. https://doi.org/10.1002/eco.168

Tolonen, K. S., Picazo, F., Vilmi, A., Datry, T., Stubbington, R., Pařil, P., . . . Heino, J. (2019). Parallels and contrasts between intermittently freezing and drying streams: From individual adaptations to biodiversity variation. *Freshwater Biology,* fwb.13373. https://doi.org/10.1111/fwb.13373

Uys, M. C. & O'Keeffe, J. H. (1997). Simple words and fuzzy zones: Early directions for temporary river research in South Africa. *Environmental Management, 21*(4), 517–531. https://doi.org/10.1007/s002679900047 PMID:9175541

Vadher, A. N., Leigh, C., Millett, J., Stubbington, R. & Wood, P. J. (2017). Vertical movements through subsurface stream sediments by benthic macroinvertebrates during experimental drying are influenced by sediment characteristics and species traits. *Freshwater Biology, 62*(10), 1730–1740. https://doi.org/10.1111/fwb.12983

Vadher, A. N., Stubbington, R. & Wood, P. J. (2015). Fine sediment reduces vertical migrations of *Gammarus pulex* (Crustacea: Amphipoda) in response to surface water loss. *Hydrobiologia, 753*(1), 61–71. https://doi.org/10.1007/s10750-015-2193-5

Vander Vorste, R., Malard, F. & Datry, T. (2016). Is drift the primary process promoting the resilience of river invertebrate communities? A manipulative field experiment in an intermittent alluvial river. *Freshwater Biology, 61*(8), 1276–1292. https://doi.org/10.1111/fwb.12658

Van Lanen, H. A., Laaha, G., Kingston, D. G., Gauster, T., Ionita, M., Vidal, J. P., . . . Van Loon, A. F. (2016). Hydrology needed to manage droughts: The 2015 European case. *Hydrological Processes, 30*(17), 3097–3104. https://doi.org/10.1002/hyp. 10838

van Vliet, M. T., Franssen, W. H., Yearsley, J. R., Ludwig, F., Haddeland, I., Lettenmaier, D. P. & Kabat, P. (2013). Global river discharge and water temperature under climate change. *Global Environmental Change, 23*(2), 450–464. https://doi.org/10.1016/j.gloenvcha.2012.11.002

Westwood, C. G., England, J., Dunbar, M. J., Holmes, N. T., Leeming, D. J. & Hammond, D. (2017). An approach to setting ecological flow thresholds for southern English chalk streams. *Water and Environment Journal, 31*(4), 528–536. https://doi.org/10.1111/wej.12275

Westwood, C., Teeuw, R., Wade, P. & Holmes, N. (2006a). Prediction of macrophyte communities in drought-affected groundwater-fed headwater streams. *Hydrological Processes, 20*(1), 127–145. https://doi.org/10.1002/hyp. 5907

Westwood, C., Teeuw, R., Wade, P., Holmes, N. & Guyard, P. (2006b). Influences of environmental conditions on macrophyte communities in drought-affected headwater streams. *River Research and Applications, 22*(6), 703–726. https://doi.org/10.1002/rra.934

White, J. C., Armitage, P. D., Bass, J. A. B., Chadd, R. P., Hill, M. J., Mathers, K. L., . . . Wood, P. J. (2019). How freshwater biomonitoring tools vary sub-seasonally reflects temporary river flow regimes. *River Research and Applications, 35.* https://doi.org/10.1002/rra.3501

White, J. C., House, A., Punchard, N., Hannah, D. M., Wilding, N. A. & Wood, P. J. (2018). Macroinvertebrate community responses to hydrological controls and groundwater abstraction effects across intermittent and perennial headwater streams. *Science of the Total Environment, 610–611*, 1514–1526. https://doi.org/10.1016/j.scitotenv.2017.06.081 PMID:28687118

Williams, D. (1977). Movements of benthos during the recolonization of temporary streams. *Oikos, 29*(2), 306–312. https://doi.org/10.2307/3543619

Williams, D. D. & Hynes, H. B. N. (1976). The ecology of temporary streams I. The faunas of two Canadian streams. *International Review of Hydrobiology, 61*(6), 761–787. https://doi.org/10.1002/iroh.19760610604

Wishart, M. (2000). The terrestrial invertebrate fauna of a temporary stream in southern Africa. *African Zoology, 35*(2), 193–200. https://doi.org/10.1080/15627020.2000.11657090

Wood, P. J. & Armitage, P. D. (2004). The response of the macroinvertebrate community to low-flow variability and supra-seasonal drought within a groundwater dominated stream. *Archiv für Hydrobiologie, 161*(1), 1–20. https://doi.org/10.1127/0003-9136/2004/0161-0001

Wood, P. J., Boulton, A. J., Little, S. & Stubbington, R. (2010). Is the hyporheic zone a refugium for aquatic macroinvertebrates during severe low flow conditions? *Fundamental and Applied Limnology, 176*(4), 377–390. https://doi.org/10.1127/1863-9135/2010/0176-0377

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Supplementary material

Table S1. Studies examining the dry-phase terrestrial invertebrates of temporary stream channels, indicating climate type. Studies are ordered chronologically within climate groups. Temporary habitats associated with perennial rivers are not included; for a broader consideration, see Steward et al. (2017).

Climate[1]	Bed characteristics	Dry phase	Sampling strategy	Assemblage description, including observations of behaviour	Source and river[2]
Am	Not described	Seasonal, duration not stated	Assemblage in a dry (“moist”) rainforest streambed	Termitoidae (Blattodea) stated as among the “numerous land animals” present.	Allee & Torvik 1927
Aw	Sand-dominated, some gravel and pebbles	Seasonal, duration not stated	Assemblage in 36 pitfall traps installed for 24 h at 6 sites; comparison with riparian assemblages	48 morphospecies, of which 36 shared with riparian zones and 12 unique. Formicidae (Hymenoptera) and Coleoptera dominated.	Steward et al. 2011, Mitchell
	Silt, clay, sand; gravel, sand; gravel, cobble	Seasonal, duration not stated	Assemblage in 36 pitfall traps installed for 24 h at 6 sites; comparison with riparian assemblages	66 morphospecies of which 48 shared with riparian zones and 18 unique. Formicidae dominated; Coleoptera and Diptera noted.	Steward et al. 2011, Flinders
BSh	Bedrock + sand, pebbles, boulders	Seasonal flow for “several weeks” i.e. long dry durations	Assemblages in wet, drying and dry leaf packs placed at pool margins at six sites.	35 taxa from 13 orders/higher taxa. Isopoda, Collembola, Orthoptera, Psocoptera, Hemiptera (Lygaeidae), Coleoptera (Anthicidae, Elateridae, Psephenidae, Staphylinidae), Diptera (Psychodidae), Lepidoptera larvae, Formicidae and Araneae noted.	Dell et al. 2014
BSk	Gravel, cobble; silt, clay, sand	Unpredictable, can dry for months	Assemblages in 20 pitfall traps installed for 24 h at 4 sites; comparison with riparian assemblages	87 morphospecies of which 60 shared with riparian zones and 27 unique. Formicidae, Hemiptera, Collembola, Araneae dominated.	Steward et al. 2011, Brisbane
	Silt, clay	Unpredictable, can dry for months	Assemblages in 12 pitfall traps installed for 24 h at 2 sites; comparison with riparian assemblages	39 morphospecies of which 32 shared with riparian zones and 7 unique taxa. Formicidae, Collembola, Araneae dominated.	Steward et al. 2011, Moonie
	Varying % of sand to boulder-sized clasts	Seasonal	Assemblages of arthropod families including carabid genera, collected in pitfall traps at 62 sites along 6 km of drying and dry active channel	30 families in 8 orders. Araneae (6 families); Coleoptera (6); Hemiptera (5); Diptera (4); Hymenoptera (4) most diverse. Carabidae (Coleoptera) most abundant (55 % of all individuals) then Formicidae (Hymenoptera, 24 %), Lycosidae (Araneae, 9 %). 10 carabid genera: *Syntomus* most abundant (70 % of all carabids) and *Brachinus* also common.	McCluney & Sabo 2012
	%: 66 silt/clay, 24 sand, 14 gravel, 6 pebble	Dry Jun-Jul to Nov-Dec	Samples collected 2, 4, 10, 15 and 29 d after complete drying, along 3 transects of 5 pitfall traps installed for 48 h.	31 % Formicidae; 26 % Araneae; 1 % Collembola; 4 % Coleoptera; no other taxa indicated.	Sánchez-Montoya et al. 2016, Rogativa
BWh	“superficial silt layer”; otherwise undescribed	“Erratically dry”	Insect assemblages in “intermittently dry beds”	4 spp. and 1 genus: 1 Dytiscidae (Coleoptera); 1 Gryllidae and 1 Acrididae (Orthoptera); 2 Diptera including Diopsidae, which were most abundant.	Blackith & Guillet 1995
	Dwarf shrubs / grass; loose sand	“Ephemeral”	Arthropod assemblages in 5 pitfall traps from 1 ephemeral streambed site	23 taxa. Formicidae, Araneae and Acari. (Note: study not included in Table 1 due to insufficient taxonomic information.) Behaviour: web-building (Araneae) and burrowing (Insecta, Araneae).	Lalley et al. 2006
Cfa	Four substrate types: rocky riffles, sandy riffles, rock-bottomed pools, sandy pools	Regular flow from autumn to spring; persistent isolated pools	Description of “shore” assemblages in a dry small stream channel. 38 visits in a 1-year period, with population counts made in 1 m^2 at multiple sites in each substrate type.	25 taxa. Tetrigidae and Gryllidae (Orthoptera); Saldidae and Gelastocoridae (Hemiptera); Carabidae, Cicindelidae and Staphylinidae (Coleoptera). Behaviour: seasonal migration into channel; scavenging of aquatic biota by Carabidae and Staphylinidae; hibernation at low temperatures.	Stehr & Branson 1938
	Coarse-fine sand over hardpan clay	Ephemeral flow Jun-Sept; discontinuous flow Oct-May	Assemblages (including meiofauna) in litter bags placed in tree roots for 18-366 d. 3 streams with 45 bags stream^{-1}	Enchytraeidae (Oligochaeta), Collembola, Sciaridae and Cecidomyiidae (Diptera) were the dominant macroinvertebrates. Oribatida and Nematoda (*Hemicyclophora* and *Xiphenema*) dominated the meiofauna.	Fritz & Feminella 2011

Table S1. Continued

Cfb	Algal masses on wet mud and marginal gravel	Predictable summer dry phase; sampled in late summer	Assemblage in the drying, moist bed of a chalk stream; collection methods not described	Heteroceridae (1 sp.), Hydrophilidae (3 spp.) and Staphylinidae (1 genus, 2 spp.) (Coleoptera); Myriapoda (1 sp.); Anthomyidae (1 sp.), Borboridae (1 sp.), Dolichopodidae (2 spp.) and Tipulidae (2 spp.) (Diptera); Oligochaeta (3 spp.). Behaviour: feeding by Coleoptera and Oligochaeta; feeding and searching for prey by carnivorous adult flies. Staphylinidae tolerated 2 h inundation.	Moon 1956
	Not described; various	Predictable (implied)	A review of assemblages in 2 rivers	Taxa common to both rivers included Amphipoda, Carabidae and Hydraenidae, Lycosidae, and Formicidae.	Boulton & Suter 1986
	Cobble and pebble dominated	Predictable longitudinal gradient	Assemblages in 54 × 2.5 L rewetted sediment samples collected from 10 sites which dried 1-592 d prior to sampling	8 taxa: Araneida (Arachnida), Chilopoda, Collembola, Coleoptera including Staphylinidae, Aphidae (Hemiptera), Formicidae, Protura. Inundation tolerance noted for Collembola and Staphylinidae	Larned et al. 2007
	NA	Predictable longitudinal gradient from < 1-142 d dry	Assemblages in advancing wetted fronts at 12 sites collected using 3 replicate 5-min drift net samples site^{-1}	71 taxa. Collembola (78 % of individuals), Psocoptera (4 %), and Chrysomelidae (Coleoptera, 2 %) most abundant. Chrysomelidae (32 % of individuals), Staphylinidae (16 %), and Carabidae (14 %) were the most abundant living taxa. Oligochaeta and Acarina also noted.	Corti & Datry 2012
	Equivalent to sediments on gravel bars		Assemblages in experimentally rehydrated dry sediments. 2-3 samples collected from 13 sites that dried 0.1-142 d before sampling	18 taxa. Heteroptera including Aphidoidea the most abundant. Also Araneae and Pseudoscorpiones (Arachnida); Collembola; Carabidae, Chrysomelidae, Dryopidae and Staphylinidae (Coleoptera); Cecidomyiidae and Chironomidae; Formicidae; Oniscidae (Isopoda); Psychidae (Lepidoptera); Mallophaga; Myriapoda; Psocoptera; Thysanoptera.	Datry et al. 2012
	Gravel and sand bars		Description of community in 7 pitfall traps set for 7 d at each of 4 sites in 3 months (Aug, Oct, Feb)	113 taxa. Dominated by Collembola (57 %), Oniscidea (Isopoda, 6 %), Acarina (6 %), Gastropoda (4 %) and *Lasius fuliginosus* (Formicidae, 3 %).	Corti & Datry 2016
	"coarse sediment" plus fine layer of fine sediment	Predictable longitudinal gradient	6 sites across 2 rivers. Sites dried 1 week to > 1 month pre-sampling. 5-36 pitfall traps and 10-20 quadrat samples site^{-1}. Quadrat sampling on 2 dates.	51 taxa, including 45 taxa in pitfalls and 26 in quadrats. The most abundant taxa in pitfall traps were Carabidae, Lycosidae and other Araneae, and Opiliones. The most abundant taxa in quadrat samples were Carabidae and Staphylinidae, Salticidae (Araneae) and Opiliones.	Corti et al. 2013
Csa	Boulders, cobbles, gravel and occasionally sand	< 5 months, with unquantified inundation	Assemblages in experimental leaf packs (3 replicates for each of 2 leaf species) placed at 2 sites for 12 (4 dry, then 7 wet, then 1 dry) months.	Few organisms; mainly predatory Araneae, plus Oribatida, adult Coleoptera, and Diptera including Tipulidae, Ceratopogonidae and Psychodidae.	Maamri et al. 1997
	Not described	Seasonal, approx. 2-4-month dry phase	Arthropod assemblages in coarse particulate organic matter deposits. 8 samples collected in 25 × 25 cm quadrats at 1 site in each of 3 years.	Coleoptera (mainly Staphylinidae and Carabidae) and Araneae (mainly Lycosidae) dominated; Psocoptera, Collembola and Hymenoptera (mainly Formicidae) also common; Hemiptera noted.	Rosado et al. 2014
Csb	Sand	Seasonal, approx. 70 d dry phase	Assemblages from 8 pitfall traps installed for 28 d at each of 3 sites	9850 individuals in 327 taxa/morphotaxa: Coleoptera (57 %), Araneae (15 %), Formicidae (13 %), and Diptera (7 %) dominated. Also Acari, Pseudoscorpiones, Solifugae (Arachnida); Amphipoda; Isopoda; Gastropoda; Dermaptera, Hemiptera, Orthoptera and 6 other insect orders. Behaviour: most (78 % of taxa / 68 % of individuals) capable of flight.	Wishart 2000
	%: 13 silt/clay, 22 sand, 16 gravel, 22 pebble, 25 cobble, 3 bedrock	Dry from Jun-Jul to Nov-Dec	Samples collected 2, 4, 10, 15 and 29 d after complete drying, along 3 transects of 5 pitfall traps installed for 48 h.	13 % Formicidae; 26 % Araneae; 6 % Collembola; 6 % Coleoptera, 1 % Acari, 1 % Psocoptera; no other taxa indicated.	Sánchez-Montoya et al. 2016, Fuirosos
Dfb	Soil, tangled mass of grass roots	< 4 months	Assemblages in two streams sampled with dipnet (? – no terrestrial sampling methods stated).	Common taxa: Enchytraeidae and *Tubifex tubifex* (Oligochaeta); Arionoidea and Cochlicopidae (Gastropoda); Carabidae, Scarabaeidae and Staphylinidae (Coleoptera); Chironomidae; Formicidae; Acari.	Williams & Hynes 1976
ET	Gravel, pebbles, cobbles	Unpredictable	Assemblage in 24 pitfall traps installed for 24 h at 4 sites; comparison with riparian assemblages	48 morphospecies, of which 34 shared with riparian zones and 14 unique taxa. Formicidae, Collembola, Coleoptera, Arionoidea (Gastropoda) dominated.	Steward et al. 2011, Tagliamento

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[1] Köppen-Geiger climate classes: Am, tropical monsoon; Aw, tropical wet / dry; BSh, Steppe (semi-arid) hot; BSk, Steppe (semi-arid) cold; BWh, Desert (arid) hot; Cfa, humid subtropical; Cfb, oceanic; Csa, mediterranean / hot dry summer; Csb, mediterranean / warm dry summer; Dfb, humid continental, warm; ET, alpine/polar – tundra (in this case, the Italian Alps).

[2] River names are provided for studies considering more than one river; full details of cited sources are provided in the main manuscript.