Opinion

Temporary streams in temperate zones: recognizing, monitoring and restoring transitional aquatic-terrestrial ecosystems

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Temporary streams are defined by periodic flow cessation, and may experience partial or complete loss of surface water. The ecology and hydrology of these transitional aquatic-terrestrial ecosystems have received unprecedented attention in recent years. Research has focussed on the arid, semi-arid, and Mediterranean regions in which temporary systems are the dominant stream type, and those in cooler, wetter temperate regions with an oceanic climate influence are also receiving increasing attention. These oceanic systems take diverse forms, including meandering alluvial plain rivers, 'winterbourne' chalk streams, and peatland gullies. Temporary streams provide ecosystem services and support a diverse biota that includes rare and endemic specialists. We examine this biota and illustrate that temporary stream diversity can be higher than in comparable perennial systems, in particular when differences among sites and times are considered; these diversity patterns can be related to transitions between lotic, lentic, and terrestrial instream conditions. Human impacts on temperate-zone temporary streams are ubiquitous, and result from water-resource and land-use-related stressors, which interact in a changing climate to alter natural flow regimes. These impacts may remain uncharacterized due to inadequate protection of small temporary streams by current legislation, and hydrological and biological monitoring programs therefore require expansion to better represent temporary systems. Novel, temporary-stream-specific biomonitors and multi-metric indices require development, to integrate characterization of ecological quality during lotic, lentic, and terrestrial phases. In addition, projects to restore flow regimes, habitats, and communities may be required to improve the ecological quality of temporary streams.

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INTRODUCTION

Temporary streams (TS) are lotic ecosystems in which water sometimes stops flowing.[1] Defining TS based on *flow* intermittence (i.e., the loss of lotic surface water *movement*) disguises a critical distinction: the presence or absence of surface water,[2] with persistent pools being isolated, extensive, or continuous in some systems, whereas others lose all surface water. A second key distinction between intermittence regimes is predictability: some systems experience predictable flow cessation or drying during

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summer or dry seasons, whereas unpredictable wet-dry cycles characterize other streams. Although TS have been conceptualized as coupled ecosystems that transition between aquatic and terrestrial conditions,[3,4] current definitions remain freshwater-focussed. From a terrestrial perspective, TS can be viewed as linear features that intersect otherwise continuous habitat patches and experience periodic inundation. Equally, their substrates can be conceptualized as permanent habitats that repeatedly fluctuate between aquatic and terrestrial conditions.[5]

TS can be the dominant lotic ecosystem type in arid, semi-arid, and Mediterranean-climate regions, where their hydrology and ecology are relatively well-studied. TS are also common in temperate regions with cooler, wetter climates, their occurrence reflecting interactions between climatic drivers (e.g., precipitation and temperature), physical catchment characteristics (e.g., bedrock and overlying sediments), and human influences (e.g., water abstraction, effluent discharge, and land use). We complement recent global TS research by focusing on systems in temperate regions with an oceanic influence on the climate (Cfb under the Köppen climate classification; hereafter, 'oceanic'). Oceanic climates are characterized by cool, moderate temperatures and year-round precipitation, and occur primarily in north-western Europe and south-eastern Australasia (Figure 1).

We highlight the diverse range of TS that occur in oceanic regions, the high biodiversity that these streams support, and the ecosystem functions that oceanic TS provide. We outline threats to the ecological integrity of TS, and identify opportunities to combat current impacts within a context of international legislation. We identify research priorities, including the work needed to facilitate incorporation of TS into hydrological and biological monitoring programs. Although variable terminology has been used to describe TS, for simplicity, we use: *TS* to refer to ecosystems that lose flowing surface water and often experience complete drying, and *intermittent* to describe such systems; we recognize that these simple definitions reflect our primarily freshwater-related perspective.

A DIVERSE RANGE OF TEMPORARY STREAMS OCCUR IN OCEANIC REGIONS

Although dry streambeds may be perceived as symbolizing human impacts including water abstraction

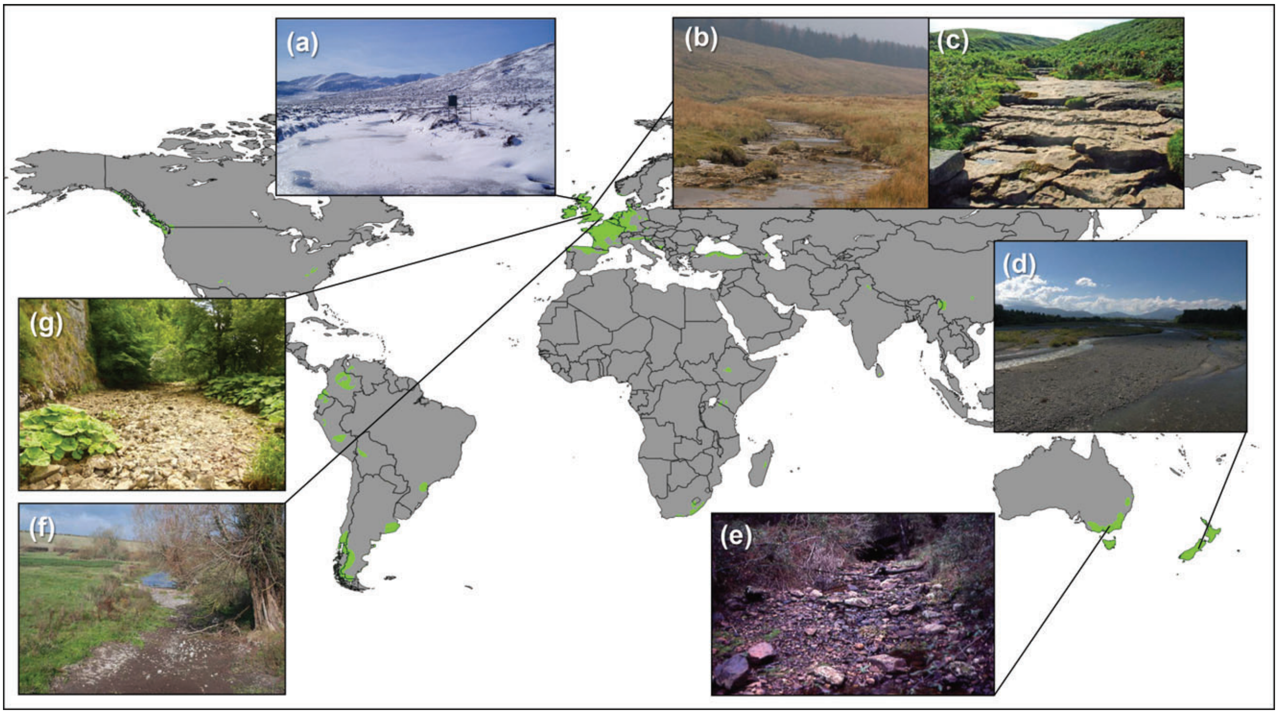

FIGURE 1 | Examples of temporary streams in oceanic (Cfb) environments: (a) a snow-covered mountain stream, Scotland, UK; (b) a ponded peatland tributary of Green Field Beck, England, UK; (c) the bedrock-dominated channel of Deepdale Gill, England, UK; (d) the alluvial plain River Orari, New Zealand; (e) the forested Lerderderg River, Australia; (f) the winterbourne headwaters of the chalk River Till, England, UK; and (g) the karst River Manifold, England, UK. Photo credits: A. Youngson (a); L. Brown (b); J. Clift (c); F. Burdon (d); A. Boulton (e); A. House (f); R. Stubbington (g).

and climate-change-related drought,[6] TS are natural ecosystems in oceanic climates (Figure 1). For example, flow cessation and drying is natural in channels underlain by fissured karst and porous chalk bedrock, and in alluvial plain rivers flowing over permeable deposits (Figure 1). However, TS diversity remains poorly characterized across oceanic regions, and in particular, headwater streams that experience long dry periods have received limited attention,[7] despite comprising a considerable proportion of river networks and making a disproportionate contribution to regional biodiversity.[8]

The spatial arrangement of perennial and intermittent reaches varies between systems. Intermittence may increase gradually with progression upstream due to seasonal water table fluctuations, as in 'winterbourne' chalk streams[9] and systems dissecting upland landscapes.[7] Elsewhere, a mosaic of segments with varying intermittence reflects local changes in geomorphological controls.[10] River regulation and water-resource management can profoundly alter flow intermittence regimes. Overabstraction can cause naturally perennial reaches to dry,[9] water supply diversions and effluent discharges can result in artificial perennialization,[11] and lotic reaches upstream of impoundments may become lentic.

TEMPORARY STREAM COMMUNITIES ARE BIODIVERSE

TS communities are often dominated by generalists[12] (i.e., those also found elsewhere) including resilient taxa that colonize when appropriate habitats become available: lotic taxa when flow resumes, lentic taxa when pools form, and terrestrial taxa when sediments dry. In addition, where the evolutionary driver of intermittence is sufficiently strong[12] and predictable[13] to favor specialization, TS specialists may enhance biodiversity. During flowing phases, some specialist caddisfly larvae inhabit intermittent springs in karst networks,[14] and winterbourne chalk streams support characteristic plant communities[9,15] and specialist stonefly[16] and mayfly[17] nymphs, the latter including nationally rare species in the UK.[18] Other aquatic flora and fauna are headwater specialists,[8,9,15] their isolation increasing endemicity, as reported for a blackfly restricted to few English winterbourne chalk streams.[19] During pool phases, specialists of temporary lentic habitats may colonize; for example, caddisfly larvae largely restricted to floodplain ponds[20] may also inhabit TS pools.[21] In addition, terrestrial invertebrate assemblages include dry-channel specialists in tropical, sub-tropical, and alpine TS, with inundation-tolerant life stages proposed for some taxa.[5,22,23] Such terrestrial specialists are unknown in oceanic dry channels, which may reflect the reduced extent of drying or the limited research conducted.[24] Beetles associated with exposed riverine sediments[25] in perennial rivers experience repeated inundation, and specialists with comparable tolerance of hydrological fluctuations may colonize dry streambeds.

Local-scale Lotic Biodiversity Typically Declines as Intermittence Increases

During flowing phases, site-specific aquatic community diversity (i.e., α-diversity, defined in Box 1 and explored in Box 2) is typically lower at intermittent sites compared to equivalent perennial sites, as demonstrated for invertebrates across climate zones[12] and within oceanic regions.[19,26] Sites with greater intermittence are typically inhabited by a subset of the generalists found at perennial and less intermittent sites.[12] However, where flowing phases are long-lasting and intermittent reaches are short in spatial extent, site-specific lotic diversity may increase over

BOX 1

TEMPORARY STREAM COMMUNITY DIVERSITY: DEFINING DIVERSITY

The taxonomic diversity of an assemblage describes its richness and evenness, i.e., the number of taxa present and the relative contribution each makes to total abundance. Alpha (α) diversity considers the taxa present locally, in an individual sampling unit (Figure 2(a)). Beta (β) diversity describes heterogeneity among sites or times and comprises 'variation' and 'turnover' components. Variation β-diversity refers to differences in assemblages among a set of sampling units (Figure 2(b)) whereas turnover β-diversity describes differences among sampling units positioned along a spatial (S1, S2) or temporal (T1, T2) environmental gradient (Figure 2(c)). Together, α and β components determine gamma (γ), or total regional-scale diversity. Diversity measures can also be applied to nontaxonomic categories, e.g., functional diversity considers the range of traits (characteristics influencing an organism's response to the environment) possessed by taxa in an assemblage.

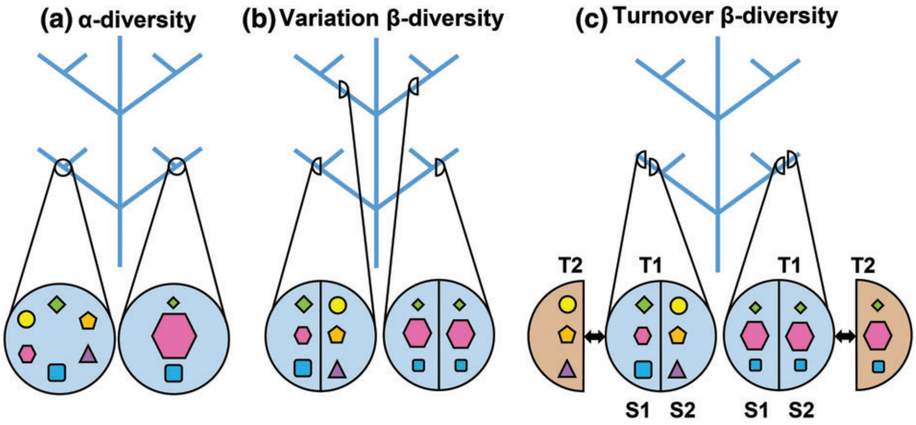

FIGURE 2 | Concepts of diversity illustrated using a theoretical stream network: (a) α-diversity; (b) variation β-diversity; and (c) turnover β-diversity along simplified two-site (S1, S2) and two-time (T1, T2) 'gradients'. Small filled symbols indicate different 'types,' e.g., taxa or traits, their size representing their relative abundance; larger circles and semi-circles indicate sampling units; blue lines represent a plan view of the stream network. In each theoretical case, the left-hand side of the network (as viewed) has higher diversity than the right-hand side; the patterns observed in temporary streams are described in Box 2.

BOX 2

TEMPORARY STREAM COMMUNITY DIVERSITY: ENVIRONMENTAL HETEROGENEITY PROMOTES HIGH FLOWING-PHASE BIODIVERSITY

Figure 3 compares typical patterns of α-, β-, and γ-diversity (defined in Box 1) for communities in temporary and perennial stream networks. A-diversity is typically lower in temporary compared to perennial streams (α^1, Figure 3(a) and (b)), reflecting community nestedness: the taxa at sites with greater intermittence are subsets of those at perennial and less intermittent sites.[12] Over time, lotic diversity may become comparable at intermittent and perennial sites (α^2, Figure 3(a) and (b)) as flowing phases increase in duration, and may even become higher at intermittent sites (α^3, Figure 3 (a) and (b)) characterized by local-scale habitat heterogeneity.

Typical seasonal progression from flowing, to pool, to dry conditions represents a temporal gradient in environmental conditions, and in response, turnover β-diversity is enhanced by shifts between lotic ($tt\beta^1$), lentic ($tt\beta^2$), and terrestrial biota ($tt\beta^3$, Figure 3(a)), as explored in Box 3; equivalent habitat changes and related shifts in community composition are modest in perennial streams ($tt\beta^{1\text{-}3}$, Figure 3(b)). Turnover β-diversity along a spatial, longitudinal gradient may also be higher in TS, due to sequential replacement of taxa adapted to different degrees of intermittence ($st\beta^{1\text{-}2}$, Figure 3(a) and (b)). Equally, variation β-diversity of lotic communities may be higher among intermittent sites sampled during flowing phases ($v\beta^{1\text{-}2}$, Figure 3(a)) compared to perennial sites ($v\beta^{1,2}$, Figure 3(b)), due to spatial variation in environmental conditions.[32] Temporal turnover, spatial turnover, and variation components of β-diversity combine to increase γ-diversity (γ, Figure 3(a) and (b)) in temporary compared to perennial stream networks.

time and become comparable at intermittent and perennial sites[27]; diversity may even be higher at intermittent sites due to greater local habitat heterogeneity.[28]

The typical pattern of local reductions in diversity with increasing intermittence also characterizes TS lentic communities, although in contrast to flowing phases, lentic specialists often replace generalist taxa as wet-phase duration decreases.[20,29] Finally, the dry-phase diversity of terrestrial communities has been little researched in oceanic TS; a rare study by Corti and Datry[24] found that invertebrate assemblages in a dry alluvial plain channel were subsets of those in adjacent riparian zones. This pattern matches that observed for lotic invertebrates,[12] but contrasts with Steward et al.'s finding that 20% of terrestrial invertebrate taxa were unique to dry channels in alpine, tropical, and sub-tropical climates.[22] Further research is required to examine lentic and dry-phase diversity in TS channels across climate

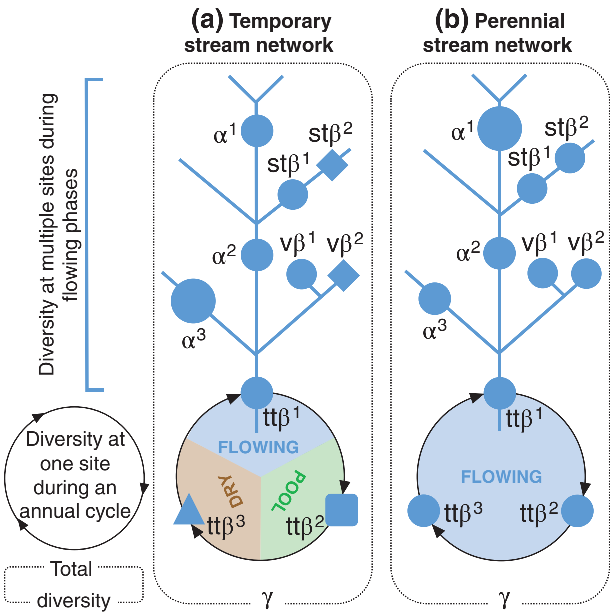

FIGURE 3 | Typical patterns of alpha (α), beta (β), and gamma (γ) diversity of communities in (a) a temporary stream network and (b) a perennial stream network, at multiple sites during flowing phases (blue lines), and at one site during an annual cycle (black circles). The size of blue, filled symbols allows comparison of panes (a) and (b) and is proportional to diversity, i.e., larger symbols indicate higher diversity at temporary or perennial sites; symbol sizes should *not* be compared within a pane. Shapes indicate differences in community composition. Abbreviations: stβ, ttβ and vβ, spatial turnover, temporal turnover, and variation β-diversity, respectively. Superscript letters allow comparison of (a) and (b). Definitions of diversity measures are provided in Box and patterns are described in Box 2.

zones, including characterization of temporal changes and the extent to which increasing local-scale terrestrial biodiversity offsets declining aquatic diversity as intermittence increases.

Environmental Controls on Local Biodiversity Extend Beyond Habitat Boundaries

Reach-scale diversity reflects not only timing in a hydrological cycle and local habitat characteristics, but also environmental influences and metacommunity dynamics which extend beyond a local site and interact to influence colonization processes.[30,31] Following flow resumptions, the occurrence of perennial upstream reaches is a notable influence on lotic colonization rates, with drifting organisms promoting rapid community recovery.[10] However, as flowing phase duration increases, differences in peak lotic diversity among intermittent sites with and without perennial upstream reaches may disappear, highlighting downstream perennial reaches and other aquatic and terrestrial refuges as additional colonist sources.[12] Following pool formation, persisting lotic biota are joined by lentic colonists, the latter reflecting interactions between refuge availability and taxon-specific dispersal abilities[31]; implications for pool diversity are described in Box 3. Following

BOX 3

TEMPORARY STREAM COMMUNITY DIVERSITY: TEMPORAL VARIABILITY IN LOTIC, LENTIC, AND TERRESTRIAL COMMUNITY RICHNESS

Figure 4 illustrates how sequential use may allow lotic, lentic, and terrestrial taxa to share an instream space.

When flow resumes, lotic taxa richness increases rapidly as populations from refuges within the intermittent reach proliferate[35] and colonists arrive from elsewhere[36] (Figure 4(a)). Generalists (which also inhabit perennial streams) typically dominate this community, particularly as flowing phase duration increases.[37] A few TS specialists are also present, and lentic generalists may inhabit suitable microhabitats. If inundation-tolerant terrestrial taxa exist[23] and remain within the channel, their wet-phase persistence is probably short-lived.

When flow ceases, extensive and connected, or sparse and isolated pools may form. Richness may initially increase in persistent pools as lentic colonists join lotic refugees, but later decreases due to poor habitat suitability, declining water quality, and intense biotic interactions (Figure 4 (b)).[5] TS pool specialists remain undocumented in temperate regions but may comprise a comparable biota to other temporary lentic waters[20]; limited global evidence suggests such specialists as minor contributors to pool communities.[38]

During dry phases, generalist terrestrial taxa arrive from the riparian zone and catchment, increasing in richness as the dry phase proceeds (Figure 4(c))[39]; dry-channel specialists have not been identified in any temperate TS.[5] Aquatic richness declines as desiccation-sensitive taxa are lost, but the ‘seedbank’ of desiccation-tolerant aquatic life-stages that persists within drying sediments[40] maintains moderate richness.[4,41] Seedbank richness declines with sediment moisture, making oceanic assemblages relatively taxa rich.[40,41]

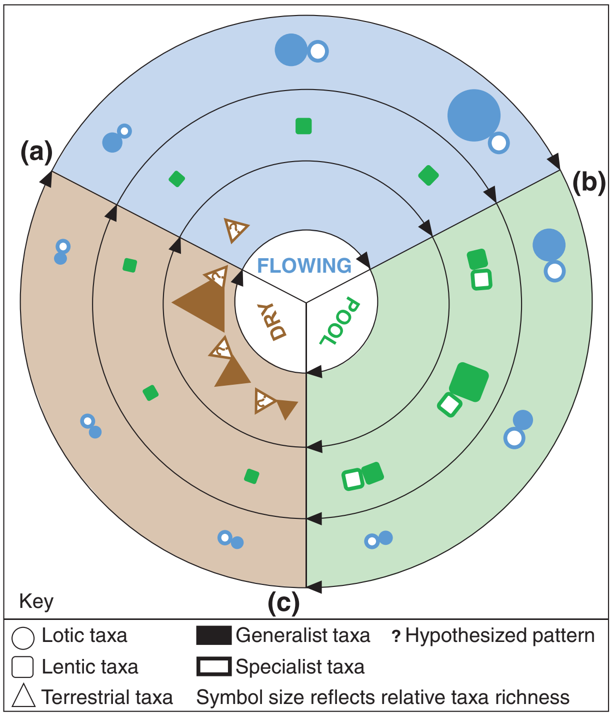

FIGURE 4 | Turnover of lotic, lentic, and terrestrial taxa during (a) flowing, (b) pool, and (c) dry habitat phases in a temporary stream reach. Arrows indicate a typical annual cycle of environmental changes; reversals (e.g., transitions from pool to flowing conditions) and omissions (e.g., flowing-dry-flowing or flowing-pool-flowing transitions) may also occur. Taxonomic patterns are those observed and hypothesized for invertebrate communities, with some plant community data suggesting comparable patterns.

drying, the rate and extent of colonization by terrestrial organisms may reflect the characteristics of marginal habitats, such as riparian vegetation, bank-top height, bank slope, and bank-face materials.[25] Research is needed to examine the environmental controls of dry-phase colonization trajectories, and to identify factors promoting dry-phase community establishment.

Spatial and Temporal Environmental Variability Increases Biodiversity in TS

Transitions between flowing, pool, and dry phases result in greater temporal variation in environmental conditions in TS compared to perennial streams. In response, shifts between communities dominated by lotic, lentic, and terrestrial taxa mean that intermittent sites can have higher biodiversity than perennial sites when an annual cycle is considered,[33] as explored in Boxes 2 and 3. Bogan and Lytle described this sequential use of one location by lentic and lotic taxa as ‘taxonomic time-sharing’[34], a concept that we suggest be extended to encompass terrestrial taxa (Figure 4, Box 3).

As well as temporal changes, transitions in environmental conditions along spatial, longitudinal gradients may enhance biodiversity (i.e., spatial turnover β-diversity, explored in Box 2) in TS compared to equivalent perennial stream lengths, with sequential taxon replacements reflecting adaptation to different degrees of intermittence. For example, the macrophyte communities of chalk stream headwaters are characterized by longitudinal zonation, with specific assemblages associated with perennial reaches and those with typical annual dry periods of 2–4, 4–6, and >6 months[42] (Figure 5); site-specific community composition also differs between wet and dry years. Similarly, spatial environmental heterogeneity among multiple sites[32] may mean that flowing-phase variation in lotic community composition (i.e., variation β-diversity, explored in Box 2) is higher among intermittent compared to perennial sites, as observed in arid,[32] subtropical,[2] and Mediterranean regions.[28] During dry phases, differences in terrestrial invertebrate assemblage composition increase among-reach diversity,[24] aligning with aquatic patterns.[2,28,32] Further research is required to compare regional patterns, and to examine biota previously combined as “nonaquatic” in freshwater studies.[15,42]

Endemic species including TS and headwater specialists also increase diversity among sites,[8,19] with one study of seven Mediterranean-climate headwater TS describing 13 new aquatic or semi-aquatic insect species.[28] The range of taxa restricted to isolated headwaters may remain underestimated, in particular for small and taxonomically challenging organisms.[43]

Regional-scale aquatic diversity (i.e., γ-diversity, explored in Box 2) may be highest in systems with greater intermittence due to spatial and temporal environmental heterogeneity.[2] In addition, total TS diversity estimates are increased when both aquatic and terrestrial taxa are recognized, as recorded for invertebrate[24] and plant communities.[42] Further collaborations between aquatic and terrestrial ecologists are needed to quantify the total biodiversity of biotic groups across full hydrological cycles.[5,24,44] In addition, whereas macroscopic communities of oceanic TS including chalk streams and alluvial plain rivers are sufficiently well-characterized to warrant description of general patterns, the biodiversity of systems including upland headwater TS requires further research, as do under-represented biotic groups including meiofauna and diatoms.

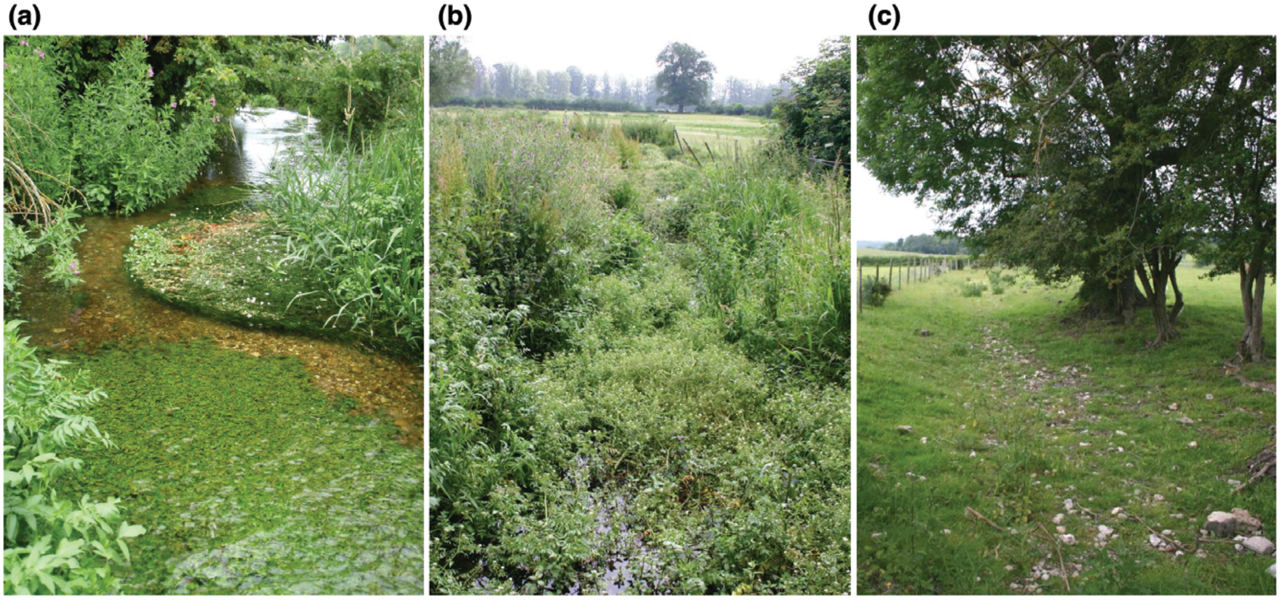

FIGURE 5 | In chalk streams including the River Misbourne (England, UK), macrophyte communities are characterized by longitudinal zonation during the summer months, and differ between sites with (a) perennial flow, (b) shorter (typically 2-4 month) and (c) longer (typically 4-8 month) annual dry periods, as described by Westwood et al..[33] Photo credits: J. England (a); N. Holmes (b-c).

TEMPORARY STREAMS HAVE IMPORTANT ECOSYSTEM FUNCTIONS

TS, including dry channels, have recently been conceptualized as biologically active, biodiverse, and important in ecosystem functioning.[23] However, some wider roles, such as acting as navigation corridors for biotic migrations across landscapes, may be restricted to Mediterranean[45] and arid[46] regions with extensive intermittent networks (Table 1). Other functions may also vary depending on climate.[47] For example, dry streambeds in arid landscapes may be moist microhabitats favored by small mammals[22] whereas those in tropical regions may be hotter and drier than the adjacent riparian zone and so avoided by fauna.[46] In contrast, pools may provide drinking water for livestock and wild animals across climate zones, particularly during droughts.[48] Some ecosystem functions may differ depending on dry phase duration. For example, occasional flow in arid streams provides rare opportunities for aquatic organism dispersal[23]; in contrast, occasional drying of oceanic TS may facilitate dispersal of terrestrial organisms including mammals[49] and turtles[50] across landscapes usually fragmented by water.[51] Other functions may be broadly comparable across climates, including organic matter processing: dry phases allow organic matter to accumulate before release and transformation following rewetting and flow resumptions.[52]

Ecosystem services that benefit people may also differ regionally, with cultural services reflecting the ubiquity of TS (Table 1). Native Australian folklore refers to TS fauna, and recreational events are held in dry channels.[23] In contrast, dry channels are viewed as symptomatic of poor ecosystem health in oceanic systems such as English chalk streams,[6,15] with recreational uses such as fishing and associated perceptions of high value largely restricted to flowing phases. Linked to these contrasting public perceptions of ‘value’, TS provisioning services include food and water in arid landscapes[53] but are minimal in developed temperate regions. In contrast, the regulating service of flood mitigation, common to perennial and intermittent streams, may be greater in densely populated temperate zones.

As well as supporting high biodiversity including rare and endemic taxa, TS provide refuges for specialists outcompeted by generalists in perennial streams. For example, the absence of a dominant grazing snail has been linked to greater diversity of other invertebrate grazers in TS.[8,28] Equally, natives threatened by non-native invasive species may use TS as refuges. For example, a greater decline in non-native than native fish richness with increasing intermittence has been attributed to poor adaptation to habitat contraction in Mediterranean streams.[57]

TS biota perform important ecosystem functions. During wet phases, aquatic invertebrates support food webs that include fish as top aquatic

TABLE 1 | Temporary stream (TS) ecosystem functions provided by (a) dry channels (b) pools and (c) flowing stream habitats. Evidence of each function is provided at a global scale and compared to oceanic zones, with functions hypothesized where data is lacking.

	(a) Dry channels		(b) Pools		(c) Flowing streams	
Ecosystem function	Global evidence	Oceanic zone function	Global evidence	Oceanic zone function	Global evidence	Oceanic zone function
Migration/ navigation corridors for vertebrates	Used by small mammals, reptiles, and birds in deserts[46] and Mediterranean TS[45]	Lower importance due to limited spatial and temporal extent; local movements may be facilitated	None	None	Established (but contested[54]) perennial river function; likely for TS	Lower importance due to limited spatial and temporal extent; may be used by bats.
Inhabited by terrestrial vertebrates	Moist habitat used by hares, mice, and shrews in Namib Desert[46]	Lower importance due to availability of moist riparian habitats	Not known	Not known	Not known	Not known
Habitat for specialist biota	Dry channel invertebrates in tropical and alpine streams[22]	Lower importance due to shorter dry phases; none identified[24]	Not known	Not known	Invertebrate specialists dominate some arid TS[55]	Invertebrate specialists occur in TS and springs[14]
Refuge for lotic taxa	Seedbank established as survival mechanism across climate zones[40]	Enhanced function in oceanic TS due to high sediment moisture content[4,40]	Established, major dry-phase refuge, e.g., in Mediterranean, semi-arid and arid streams[55]	Refuge for many taxa, particularly if habitats are similar to flowing streams, e.g., in regulated / lowland streams[56]	Refuges from competitive taxa including non-native invasive taxa, and from predation by fish in Mediterranean[28,57] and other temperate TS[58]	Greater importance due to widespread river regulation and invasive species in perennial streams
Dispersal	Easier cross-channel dispersal by terrestrial organisms in arid zones due to longer dry phases	Higher importance due to limited spatial and temporal windows in which terrestrial organisms can disperse[51]	May facilitate local dispersal of lentic taxa between pools	May facilitate local dispersal of lentic taxa between pools	Dispersal of aquatic and riparian flora and fauna established across climate zones	Greater dispersal of aquatic and riparian flora and fauna due to long wet phases
Carbon cycling and organic matter processing	CO_2 efflux from dry organic matter quantified in a Mediterranean river and up-scaled to other regions[59]	Not calculated for temperate zones; considered lower than arid zones[59]	Organic matter retained and processed in pools	Organic matter retained and processed in pools[60]	Organic matter processing following flow resumptions established across climate zones	Greater processing in oceanic zones: processing declines as drying increases[61]
Recreation	Events, e.g. a 'dry river race' held in Australia; provide shaded walking routes e.g. in Spain	Limited importance due to extent of larger systems; TS in karst landscapes can act as caving entry points	Waterholes in Australia provide interest along walking routes	Reduced importance due to limited spatial and temporal extent	Established across regions e.g. adjacent walking routes	Lower importance; routes more likely to follow perennial rivers

(*continued overleaf*)

TABLE 1 | Continued

	(a) Dry channels		(b) Pools		(c) Flowing streams	
Ecosystem function	Global evidence	Oceanic zone function	Global evidence	Oceanic zone function	Global evidence	Oceanic zone function
Provision of food and water for people	Aestivating fish consumed in Botswana; cattle grazed in Egypt; crops grown in India; water found by digging[23]	Not known	Drinking water for deer, humans, and livestock in arid and semi-arid zones[48,62]	Lower importance due to higher water availability in oceanic zones	Drinking water for humans and livestock in arid zones[62]	Groundwater and surface water abstraction for public water supply and agriculture across temperate zones[9]

predators[63] and extend into riparian and terrestrial habitats: adults of insects with aquatic juveniles subsidize terrestrial food webs upon emergence.[64] These pulsed inputs are pronounced in TS if insects emerge *en masse* before drying, and where high aquatic insect abundance is linked to exclusion of predators by intermittence.[65] As drying phases proceed, aquatic invertebrates trapped in contracting pools or stranded on dry streambeds are rich pickings for riparian predators.[66] Equally, riparian and terrestrial organisms that colonize dry channels may be engulfed when flow resumes,[52] and subsidies to terrestrial environments are therefore reciprocated by energy inputs to aquatic webs, supporting early flowing-phase colonists.[58]

INTERACTING STRESSORS COMPROMISE TEMPORARY STREAM HEALTH

Changing rainfall and runoff patterns are altering flow regimes,[67] although patterns are difficult to characterize[68] or to relate to climatic drivers.[69] Global-scale models predict future decreases in summer discharge in the northern hemisphere,[67] and some studies indicate future declines in mean annual runoff in oceanic western Europe,[70] causing summer discharge reductions.[69,71] Hydrological extremes including drought (i.e., significantly below-average water availability over an extended period[72]) may also be increasing in some global[73] and European[74] regions, causing drying of oceanic rivers previously considered perennial.[41] However, the inherent variability of drought disturbances and their interaction with nonclimatic drivers of change make both recent trends and future predictions difficult to confirm.[69,75]

Climatic drivers interact with groundwater and surface water abstractions in temperate regions dominated by urban and agricultural land uses, causing or exacerbating shifts to greater intermittence, including artificial drying events in perennial streams and increased drying in TS. For example, decreased discharge in the intermittent River Selwyn in New Zealand has been linked to abstraction for irrigation[76]; the naturally perennial River Garry in Scotland experienced regular drying due to water diversion for a hydroelectric scheme[77]; and peak water consumption may exacerbate widespread discharge reductions during droughts.[74] However, patterns vary depending on other environmental factors including geology: streams underlain by aquifers with low storage capacity may experience severe discharge declines during droughts, whereas in those supplied by porous aquifers, winter recharge may sustain summer flows.[74] In addition, widespread river regulation in temperate regions may limit natural high- and low-flow extremes, with compensation flows released from impoundments maintaining a minimum discharge that reduces intermittence. Agricultural land use can also reduce hydrological variability and cause artificial perennialization; for example, small agricultural dams release water downstream at a steady rate for irrigation.[78]

The effects of altered hydrology and other human influences on instream communities may be considerable, especially when artificial temporary or perennial streams are created. Increases in intermittence typically reduce aquatic biodiversity, as communities become subsets of taxa associated with perennial flow[12]. Contrary to common perceptions,[79] artificial perennialization also reduces ecological quality, because TS specialists may be lost as biotic interactions with competitors and predators intensify. Where lost taxa played important ecosystem roles, for example as top predators[80] or leaf-litter shredders that release energy for other feeding groups,[61] communities can shift to alternate states.[81] Loss of natural hydrological variability threatens organisms adapted to fluctuating conditions, and equally, where shifts between flow extremes become more common, survival within refuges may be compromised.[41]

REGULATORY MONITORING SHOULD BETTER REPRESENT TEMPORARY STREAMS

The EU Water Framework Directive (WFD) requires EU Member States to attain at least 'good ecological status' in surface water bodies, with status determined by monitoring to compare sites with unimpacted 'reference conditions' for characterized river typologies. Equally, designation as a protected Special Area of Conservation (SAC) under the EU Habitats Directive requires monitoring and reporting of the conservation status of Annex I habitats and Annex II species. SACs include intermittent river reaches, for example, some chalk streams in southern England are designated for their plant communities and for individual invertebrate and fish species. The EU Biodiversity Strategy to 2020 has set specific targets for the attainment of 'favorable' SAC conservation status, determined for habitats by comparison with natural ecosystem 'structure and function'.

In these policy and legislative contexts, recognition and mapping of TS represents a fundamental first step towards their monitoring and protection in and beyond temperate zones.[82] Another key priority is classification of TS into ecologically robust typologies, including discrimination between artificial and natural perennial and intermittent flow.[82–84] Ecologically relevant classification should recognize the flow regime, facilitated by catchment-scale hydrological monitoring that includes intermittent reaches and that differentiates between lentic and dry no-flow states. However, underrepresentation of TS in gauging station networks,[85] limited characterization of longitudinal hydrological variability, and difficulties in distinguishing between different no-flow states make such informative, long-term hydrological data scarce. In addition, the indices used to classify hydrological regimes have been developed for perennial streams[86] and therefore require supplementation in TS by new descriptors of the magnitude, frequency, duration, timing, and rate of change for flow-cessation and drying events.[85,87] Qualitative description of TS typologies based on expert opinion may be a necessary interim measure to facilitate TS monitoring; hydrologically relevant environmental datasets,[88] remote sensing data,[87] and citizen science initiatives[89] may inform such designations. However, regardless of data availability, TS classification is challenging because flow regimes are highly variable within and between systems and years.

Following recognition, mapping, and classification of TS, the communities characterizing unimpacted ecological quality (i.e., WFD 'biological quality elements' indicative of reference conditions[90]; Habitats Directive 'qualifying features' of favorable status) should be established, to facilitate robust future status assessments. However, reference conditions are conceptualized as a single benchmark against which other water bodies can be compared, which may be inadequate to represent TS: ecosystems that, by definition, transition between lotic, lentic, and terrestrial conditions in both space and time. Recent Mediterranean research initiatives[87,91,92] have made recommendations that may inform adaptation of biomonitoring programs in oceanic regions to characterize peak aquatic community diversity despite this variability. Specifically, the use of established perennial-stream metrics may be appropriate in TS flowing-phase assessments, *if* flowing phases are sufficiently long and predictable to allow sampling that coincides with peak diversity[92] and to allow robust status determination based only on lotic assemblages.

However, sensitivity to intermittence and to environmental degradation typically covary, meaning that metrics developed to quantify community integrity in perennial streams may underestimate the ecological quality of TS, particularly where flowing phases are short and unpredictable.[93] Equally, perennial metrics may overestimate TS ecological status if applied to samples collected as flow recession forces organisms (whose persistence is threatened by declining water quality) to share a shrinking submerged habitat area. Development of TS-specific indices is therefore required,[92] and balanced, robust ecological status assessments should employ novel multi-metric indices that integrate community-level data encompassing the temporal (i.e., lotic, lentic, and terrestrial phase) and spatial (e.g., longitudinal) variability characteristic of TS, and that use hydrological data to inform interpretation of sampled assemblages. Research priorities include the development of dry-phase biomonitors, with terrestrial invertebrates suggested as one potential indicator of TS dry-phase health.[23] Functional as well as structural (i.e., taxonomic) approaches to community characterization should be investigated,[84] and environmental DNA is a potential game-changer that integrates terrestrial and aquatic biodiversity information.[94]

In association with the development of new TS-specific indices, national regulatory agencies may seek to expand regulatory monitoring networks to improve representation of TS,[95] firstly, to recognize that multiple monitoring sites may be needed to represent variation in environmental conditions and categorized ecological status of water bodies with both perennial and intermittent reaches. Secondly, expansion may be appropriate to better represent headwater streams, which, despite their recognized biodiversity value and ecosystem service provision,[47,96] may be excluded from WFD-related monitoring programs due to their size: the WFD target of good ecological status applies to 'all bodies of surface water,'[97] but streams with catchment areas <10 km^2 are not classified as water bodies unless other criteria are met.[98] Supplementary national monitoring and reporting initiatives that have examined headwaters in[99] and beyond[100] oceanic regions may prove informative.

RESTORATION MAY BE NEEDED TO IMPROVE TEMPORARY STREAM HEALTH

Where TS fail to reach acceptable ecological standards, projects to restore flow regimes, habitats, species, and communities may be implemented, with the European Biodiversity Strategy setting specific targets for the enhancement of ecosystems and their service provision. Globally, ambitious schemes have restored natural intermittence in artificially perennial streams subjected to long-term regulation[101] and, following flow restoration in over-abstracted English chalk streams, characteristic winterbourne macrophyte communities replaced terrestrial grasses[15] and rare aquatic invertebrates recolonized.[35] Such interventions inform abstraction management strategies implemented by national regulatory agencies, and help to characterize the environmental flows (eflows) required to sustain biodiversity and ecosystem services in TS. However, extension of the eflow concept to TS remains very rare globally,[102] and should be further researched, including recognition of the ecological value of lotic, lentic, and terrestrial phases.

Restoration may also involve enhancement of riparian vegetation. During dry phases, reduced evaporation from shaded margins and increased water retention by organic-rich sediments reduce moisture loss from channels with vegetated banks, promoting survival of aquatic biota including desiccation-tolerant invertebrate seedbank inhabitants.[40] However, careful planting is needed to promote diversity across biotic groups, for example dense vegetation that maintains seedbanks may limit instream macrophyte assemblages.[42] Bankside vegetation also provides habitat for a riparian fauna including potential dry-channel colonists, and, as in perennial systems, stabilizes banks and intercepts polluted water. The wider services provided by riparian vegetation mean that planting schemes implemented with nonecological goals (e.g., flood mitigation; climate change adaptation) may have serendipitous effects on TS ecosystem health.

Projects involving physical alteration of the streambed and banks (e.g., sediment manipulation, channel remeandering, bank reprofiling, and bed raising) may be implemented to restore the natural habitat characteristics of TS channels. Such interventions should be informed by new research to identify the bank and riparian features promoting colonization of dry channels by terrestrial organisms. In addition, any restoration activity that disturbs the channel requires careful design informed by the life histories of TS taxa, for example, to avoid the loss of dormant aquatic life stages persisting within dry sediments.[19]

CONCLUSION

Human activity has altered patterns of flow intermittence, including artificial shifts to intermittent or perennial flow as well as physical habitat modification. Altered flow regimes change biological communities and ecosystem functions, with consequences for local species persistence, wider food web complexity, and even global biogeochemical cycling. The biodiversity and ecosystem services of natural TS are gaining recognition by ecological researchers,[103] policy makers[104] and the public,[105] but remain poorly studied compared to perennial rivers, especially outside of Mediterranean and arid regions. Recent advances in these regions may inform wider research efforts to recognize, characterize, monitor, and restore TS at local, regional, national, and international scales, including initiatives in oceanic zones.

Globally, TS research remains freshwater-focussed, with few studies of dry-channel ecology[39] and fewer still that integrate terrestrial and aquatic components.[24] Such integrative research is needed to improve understanding of spatiotemporal variability in community composition as ecosystems transition between lotic, lentic, and terrestrial states.[30,44] In addition, consideration of *all* instream communities should inform the development of holistic ecological health assessments that allow regulatory agencies to determine whether legislative requirements have been met. The accuracy of such assessments may be improved through recognition of taxon-specific co-sensitivity to intermittence and environmental quality,[93] and of broad-scale influences on community composition including metacommunity dynamics and catchment land uses.[31,106] Where interventions to enhance ecological quality are required, these are also most effective (but most challenging) when implemented at broad spatial scales that recognize landscape-level influences. In contrast, headwater catchments with minimal anthropogenic land use may provide opportunities to maximize biodiversity gains.[107] Collaborative, interdisciplinary, international projects that unite academic researchers, policymakers, and regulatory agencies will bring together currently fragmented knowledge and begin to address the research and management challenges that TS present.[107,108]

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