SPECIAL REVIEW

Emerging concepts in temporary-river ecology

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SUMMARY

1. Temporary rivers and streams are among the most common and most hydrologically dynamic freshwater ecosystems. The number of temporary rivers and the severity of flow intermittence may be increasing in regions affected by climatic drying trends or water abstraction. Despite their abundance, temporary rivers have been historically neglected by ecologists. A recent increase in temporary-river research needs to be supported by new models that generate hypotheses and stimulate further research. In this article, we present three conceptual models that address spatial and temporal patterns in temporary-river biodiversity and biogeochemistry.

2. Temporary rivers are characterised by the repeated onset and cessation of flow, and by complex hydrological dynamics in the longitudinal dimension. Longitudinal dynamics, such as advancing and retreating wetted fronts, hydrological connections and disconnections, and gradients in flow permanence, influence biotic communities and nutrient and organic matter processing.

3. The first conceptual model concerns connectivity between habitat patches. Variable connectivity suggests that the metacommunity and metapopulation concepts are applicable in temporary rivers. We predict that aggregations of local communities in the isolated water bodies of temporary rivers function as metacommunities. These metacommunities may become longitudinally nested due to interspecific differences in dispersal and mortality. The metapopulation concept applies to some temporary river species, but not all. In stable metapopulations, rates of local extinction are balanced by recolonisation. However, extinction and recolonisation in many temporary-river species are decoupled by frequent disturbances, and populations of these species are usually expanding or contracting.

4. The second conceptual model predicts that large-scale biodiversity varies as a function of aquatic and terrestrial patch dynamics and water-level fluctuations. Habitat mosaics in temporary rivers change in composition and configuration in response to inundation and drying, and these changes elicit a range of biotic responses. In the model, aquatic biodiversity initially increases directly with water level due to increasing abundance of aquatic patches. When most of the channel is inundated and most aquatic patches are connected, further increases in aquatic habitat and connectivity cause aquatic biodiversity to decline due to community homogenisation and reduced habitat diversity. The

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predicted responses of terrestrial biodiversity to changes in water level are the inverse of aquatic biodiversity responses.

5. The third conceptual model represents temporary rivers as longitudinal, punctuated biogeochemical reactors. Advancing fronts carry water, solutes and particulate organic matter downstream; subsequent flow recessions and drying result in deposition of transported material in reserves such as pools and bar tops. Material processing is rapid during inundated periods and slower during dry periods. The efficiency of material processing is predicted to increase with the number of cycles of transport, deposition and processing that occur down the length of a temporary river.

6. We end with a call for conservation and resource management that addresses the unique properties of temporary rivers. Primary objectives for effective temporary river management are preservation or restoration of aquatic-terrestrial habitat mosaics, preservation or restoration of natural flow intermittence, and identification of flow requirements for highly valued species and processes.

Introduction

Rivers that periodically cease to flow comprise a substantial proportion of the total number, length and discharge of the world's rivers (Tooth, 2000). These temporary rivers are not restricted to arid regions; they occur in most terrestrial biomes between 84°N and S latitude (Table 1). Estimates of the total length and discharge of temporary rivers are very rough, but a selection of national and regional estimates indicates the importance of temporary rivers in some areas. There are at least 3 200 000 km of temporary rivers (60% of total river length) in the conterminous United States (Nadeau & Rains, 2007a). At least 43% of Greece is drained by temporary rivers (Tzoraki & Nikolaidis, 2007). Almost 50% of the 2700 km-long Tagliamento River network (NE Italy) is temporary (Doering *et al.*, 2007), as is 70% of the 4670 km-long Chatooga River network (SE USA) (Hansen, 2001). While these examples are limited in spatial extent, they suggest that the proportions of temporary rivers in regions of similar or greater aridity will be substantial.

In the next century, the number and length of temporary rivers may increase in regions that experience drying trends due to climate change and to water abstraction for socio-economic uses. Large-scale changes in intermittence have not been considered in historical trend analyses or forecasts of future river flow patterns. However, negative trends in flow have been detected in many regions (e.g. Zhang *et al.*, 2001; Cigizoglu, Bayazit & Önöz, 2005; Pasquini & Depetris, 2006; Milliman *et al.*, 2008; Tockner, Uehlinger & Robinson, 2009), and linked climate change-runoff models predict future decreases in runoff in some mid-latitude regions (Arnell, 1999; Jones, McMahon & Bowler, 2001; Huntington, 2006; Kundzewicz *et al.*, 2008). If these climate-driven changes eventuate, increases in the occurrence and frequency of intermittence are likely to follow.

Temporary rivers are important links between water stored in soils, aquifers, snowpack, glaciers, vegetation and the atmosphere. For example, ephemeral streams transfer soil water to river networks (Gomi, Sidle & Richardson, 2002; Hunter, Quinn & Hayes, 2005). In arid and semi-arid regions, groundwater recharge is dominated by seepage from temporary river channels (Shentsis & Rosenthal, 2003; Izbicki, 2007); these rivers are also important water vapour sources (Gazal *et al.*, 2006; Costelloe *et al.*, 2007). In alpine, polar and boreal catchments, meltwater from ice and snow moves to perennial rivers and lakes through networks of temporary rivers (McKnight *et al.*, 1999; Malard, Tockne & Ward, 2000; Robinson & Matthaei, 2007). These networks expand during the melt season and contract during freeze-up. Network expansion and contraction also occurs in arid and temperate regions, where expansion phases are driven by rainfall-runoff and rising water tables, rather than icemelt or snowmelt (Stanley,

Table 1 Geographic and geologic classes of temporary rivers, and mechanisms controlling water loss

Class*	Predominant mechanisms of water loss	Example	Reference
Snowmelt and glacial meltwater	Cessation of melting/ablation, freezing of surface and shallow subsurface water	Dry Valley streams, Antarctica; Val Roseg, and Macun catchments, Switzerland	Bronge (1996), McKnight et al. (1999), Tockner & Malard (2003), Conovitz et al. (2006), Robinson & Matthaei (2007)
Perched and semi-perched alluvial	Transmission loss, depletion of bank storage and floodplain aquifer	Selwyn River, New Zealand; Tagliamento River, Italy; Cooper Creek, Australia, Kuiseb River, Namibia; Mohave River, USA; Shashane and Wenlock Rivers, Zimbabwe	Jacobson et al. (2000), Hamilton et al. (2005), Lange (2005), Mansell & Hussey (2005), Konrad (2006), Doering et al. (2007), Izbicki (2007), Larned et al. (2008)
Non-perched, in arid and semi-arid regions	Depletion of surface water and shallow groundwater by direct evaporation and evapotranspiration	Sycamore Creek, USA	Stanley et al. (1997)
Zero-order and headwater streams	Cessation of overland flow, depletion of saturated soil water or hillslope aquifer, macropore recession	Maybeso Creek, USA; Riera de Fuirosos, Spain; Stillman Creek watershed, USA	Butturini et al. (2002), Gomi et al. (2002), Hunter et al. (2005)
Permafrost	Soil freezing, soil water and wetland recession	Granger Creek and Wolf Creek, Canada	Metcalfe & Buttle (2001), Carey & Quinton (2005)
Karstic	Transmission loss, cessation of spring discharge	River Lathkill and River Wye tributaries, UK; Coulazou River and Vene Rivers, France	Wood et al. (2005), Jourde et al. (2007)
Lake outlets	Lake level drops below outlet elevation	Shadow Lake, Canada	Mielko & Woo (2006)

*These classes are not mutually exclusive; for example, alluvial rivers in desert regions are often perched or semi-perched, and water loss is jointly controlled by transmission loss and evaporation (Knighton and Nanson, 1994; Jacobson et al., 2000).

Fisher & Grimm, 1997; Tockner, Malard & Ward, 2000).

In addition to their roles in the water cycle, temporary rivers provide a wide range of ecosystem services. Floods in temporary rivers have been used for irrigation for over 3000 years (Nabhan, 1979; Sandor et al., 2007); in some regions, the technology used to capture these floods has remained unchanged for centuries (Bouchair, 2004; Ghebremariam & van Steenbergen, 2007). Temporary rivers also function as flood control systems (Foody, Ghoneim & Arnell, 2004) and drains for agricultural and municipal effluent; in many of these drains, annual effluent flows exceed water flows (Cherifi & Loudiki, 1999; Strange, Fausch & Covich, 1999; Hassan & Egozi, 2001).

After years of near-obscurity, the field of temporary-river ecology is growing rapidly, as indicated by recent dedicated journal issues (e.g. Nadeau & Rains, 2007b). However, the development of conceptual models that contextualise data, generate hypotheses and spur debate and research lags behind the empirical studies. This article is organised around three conceptual models derived from recent research results and existing models from other branches of ecology: (i) hydrological connectivity controls metacommunity and meta-ecosystem dynamics; (ii) aquatic and terrestrial biodiversity patterns reflect the shifting habitat mosaic; and (iii) temporary rivers function as longitudinal biogeochemical reactors. We begin with an overview of the ecohydrology of temporary rivers and end with a comment on potential effects of climate change and water abstraction on temporary-river flow regimes, including a call for management strategies that address the unique properties of temporary rivers.

Ecohydrology of temporary rivers

Flow variability is one of the most important determinants of ecological patterns and processes in rivers (Power et al., 1995; Richter et al., 2003). Flow

intermittence (repeated sequences of river flow, flow cessation and channel drying) is an extreme form of flow variation and one that has pervasive ecological effects. Flow cessation and drying are caused by one or more of the following processes: transmission loss (seepage through porous beds), evapotranspiration, downward shifts in groundwater tables, hillslope runoff recession, and freeze-up (Table 1). In turn, intermittence creates unique longitudinal dynamics in flow regimes. Longitudinal dynamics with significant ecological consequences include advancing and retreating wetted fronts, attenuation of flood and flow pulses, hydrological connection and disconnection of persistent reaches and pools, and gradients in flow permanence.

Advancing and retreating wetted fronts occur along temporary river channels at large and small spatial scales; the former in response to floods, recessions, and changing groundwater levels, and the latter in response to diurnal fluctuations in snowmelt, ablation and evapotranspiration (Fig. 1). Advancing fronts may take the form of meandering rivulets, expanding pools of upwelling groundwater, or steep bores (Dunkerley & Brown, 1999; Cohen & Laronne, 2005; Doering *et al.*, 2007). Retreating fronts are characterised by contraction of flow to deep channels and the formation of chains of pools (Stanley *et al.*, 1997; Boulton, 2003).

Advancing and retreating fronts also occur in river floodplains during overbank floods. Whether moving

Fig. 1 Wetted front moving down a channel braid in the temporary, alluvial Selwyn River, New Zealand. Photograph taken on 12 February 2008, 18 h after the onset of a 51-mm rain event (measured 13 km upstream from the photograph site). Photo: L. Drummond.

longitudinally in channels or laterally across floodplains, advancing fronts carry particulate organic matter (POM), sediment, organisms, and solutes (Fisher & Minckley, 1978; Dunkerley & Brown, 1999; Jenkins & Boulton, 2003; Cohen & Laronne, 2005). Sediment and nutrient concentrations in advancing fronts are often greater than those in perennial reaches, due to dissolution of precipitates and entrainment of particles from dry channel and floodplain surfaces (Obermann *et al.*, 2007). A comparison of an advancing wetted front and a perennial reach in the Tagliamento River, Italy, illustrates the magnitude of those differences; suspended solid, phosphorus, and particulate organic carbon concentrations were 1–3 orders of magnitude higher in the wetted front (Table 2; K. Tockner, unpubl. data).

Advancing and retreating fronts and the material they transport affect the behaviour, development and dispersal of aquatic and terrestrial biota, including refuge-seeking and migration in fish and aquatic and terrestrial invertebrates, emergence in aquatic insects, hydrochory in plants, and feeding by terrestrial predators (Adis & Junk, 2002). Some responses depend on the velocities of advances and retreats. Gradual retreats elicit positive rheotaxis and burrowing in invertebrates and fish (Delucchi, 1989; Cooling & Boulton, 1993; Davey, Kelly & Biggs, 2006; Davey & Kelly, 2007; Lytle, Olden & McMullen, 2008; DiStefano *et al.*, 2009). Rapid retreats lead to stranding and high mortality in aquatic animals (Stanley *et al.*, 1997), while rapid advances entrain aquatic and terrestrial animals and propagules (Chapman & Kramer, 1991; Lytle, 2000).

Advancing and retreating fronts occur in temporary river hyporheic zones, as well as river channels. Flow

Table 2 Concentrations of particulate and dissolved material in an advancing front and a perennial reach upstream of the front, Tagliamento River, Italy. Samples were collected on one date at 30-min intervals

Material	Advancing front (4)	Perennial reach (8)
Total suspended sediment (mg L^{-1})	4053 ± 1193	1.4 ± 1.2
Particulate phosphorus (µg L^{-1})	570 ± 111	5 ± 3
Total dissolved phosphorus (mg L^{-1})	121 ± 209	11 ± 7
Dissolved organic carbon (mg L^{-1})	3.9 ± 1.2	1.2 ± 0.3
Particulate organic carbon (mg L^{-1})	77.7 ± 6.7	0.3 ± 0.1
Nitrate nitrogen (mg L^{-1})	2.1 ± 1.5	0.7 ± 0.1
Dissolved organic nitrogen (mg L^{-1})	0.3 ± 0.2	0.2 ± 0.1

Values are mean ± 1 SD. Sample sizes in parentheses.

pulses and recessions, and fluctuating groundwater tables control these subsurface fronts, and consequently control habitat availability for aquatic organisms (Stanley & Boulton, 1995; Datry & Larned, 2008). Hyporheic zones are often viewed as potential refuges for burrowing organisms following retreating fronts (Del Rosario & Resh, 2000), but supporting evidence is equivocal (Lake, 2003). The coarse, alluvial sediments that dominate many temporary rivers may dry too rapidly to provide refuge between wetted fronts (Boulton & Stanley, 1995).

Published rates of wetted front movements range from <1–7 km h^{-1} (advances) to 0.006–5 km h^{-1} (retreats) (Reid, Laronne & Powell, 1998; Dunkerley & Brown, 1999; Jacobson *et al.*, 2000; Doering *et al.*, 2007; Larned, Datry & Robinson, 2007; Lytle *et al.*, 2008). The slowest rates of advance corresponded to the leading edges of floods in gravel streams; these flows are slowed by friction at the channel surface and high sediment loads. Higher advance rates are associated with 'creeping flow' caused by groundwater upwelling (Tockner *et al.*, 2000; Doering *et al.*, 2007). As fronts advance down dry reaches, transmission losses cause progressive reductions in erosive power and competence (Jacobson *et al.*, 2000; Tooth, 2000). As a consequence, and in the absence of large tributary inflows, erosion generally decreases and deposition increases in the downstream direction. In extreme cases, entire channels end abruptly at the downstream extent of flood conveyance (Tooth, 2005).

Flow cessation creates hydrological discontinuities along river corridors and isolates perennial aquatic habitats. These discontinuities take several forms: perennial tributaries joining temporary mainstems (Meyer & Meyer, 2000), temporary tributaries joining perennial mainstems (Storey & Quinn, 2008), and perennial upper and lower reaches separated by temporary mid-reaches (Izbicki, 2007; Larned *et al.*, 2008). Perennial aquatic habitats function as biological refuges during dry periods and as colonisation sources when flow resumes (Magoulick & Kobza, 2003). The floods and flow pulses that inundate dry reaches restore hydrological connections between perennial reaches, and between river channels and parafluvial habitats (Tockner *et al.*, 1999; Jenkins & Boulton, 2003). The effects of hydrological connection and disconnection on biotic dispersal and gene flow are discussed in the following section.

Repeated flow measurements along temporary rivers have revealed complex longitudinal patterns in flow permanence (the proportion of time that water is present) (Stromberg *et al.*, 2005; Doering *et al.*, 2007; Larned *et al.*, 2007). Long-term (>1 year) average flow permanence explains much of the variation observed in invertebrate and fish populations, and annual plant cover and diversity (Stromberg *et al.*, 2005; Datry, Larned & Scarsbrook, 2007; Davey & Kelly, 2007; Arscott *et al.*, in press). These results are intriguing, because mobile and short-lived organisms are expected to respond primarily to short-term hydrological variation, not long-term average conditions. Long-term flow permanence may be a good predictor for temporary-river communities because it integrates correlated hydrological metrics, such as flow frequency and duration (Arscott *et al.*, in press).

Three emerging concepts in temporary river ecology

Concept 1. Hydrological connectivity controls metacommunity and meta-ecosystem dynamics

Hydrological connectivity in temporary rivers refers to the presence or absence of flow paths between persistent patches of aquatic habitat. These flow paths are conduits for solutes and POM and for motile and drifting organisms. Surface disconnection occurs when a channel perimeter dries; channel drying often occurs at numerous points simultaneously, resulting in a series of disconnected reaches (Stanley *et al.*, 1997). Some reaches that are disconnected at the surface remain connected by shallow groundwater flow paths; these also function as conduits (Malard *et al.*, 2001; Datry *et al.*, 2007). Hydrological connections and disconnections occur at multiple spatial scales. At river-corridor scales, entire channels in braided and anabranching rivers become disconnected during low-flow periods and are reconnected by floods (Malard *et al.*, 2006; Sheldon & Thoms, 2006). At river-segment scales, perennial reaches are disconnected when intervening reaches dry, and are reconnected by flow pulses (Doering *et al.*, 2007; Larned *et al.*, 2008). At reach scales, persistent aquatic habitat patches such as scour pools disconnect and reconnect in response to drying and inundation of the surrounding riverbed (Stanley *et al.*, 1997; Labbe & Fausch, 2000).

Frequencies and durations of connections and disconnections between wetted habitats are fundamental hydrological properties of temporary rivers, and may explain much of the between-site variability in temporary-river studies (Lake, 2003). Unfortunately, connectivity is generally treated as a categorical variable (connected versus disconnected; e.g. Taylor, 1997; Bonada *et al.*, 2006), which conveys less information than continuous variables such as frequency and duration of connection (Cottingham, Lennon & Brown, 2005; Larned *et al.*, in press). The latter studies provide a basis from which we can propose more general connectivity–ecology relationships. We use the meta-system approach as a framework for discussing the effects of hydrological connectivity. Meta-systems (metacommunities, metapopulations and meta-ecosystems) are networks of discrete populations, communities and ecosystems that are intermittently connected by gene flow, dispersal, and material and energy flows. The variable spacing, size and connectivity of water bodies in temporary rivers make them ideal for exploring meta-system dynamics. Metapopulation and metacommunity perspectives have been used to analyse population and community dynamics in many ecological networks, though rarely in temporary rivers. The meta-ecosystem is a recent extension of the metacommunity concept (Loreau, Mouquet & Holt, 2003). Temporary rivers appear to function as meta-ecosystems, and we suggest a straight-forward application of this concept below.

Metacommunities. Metacommunities are networks of local biotic communities in which inter-community dispersal and intra-community interactions affect species persistence and turnover (Leibold *et al.*, 2004). Temporary rivers function as metacommunities, as discussed below, with the additional complications of variable hydrological connectivity, and multiple dispersal paths (water, air and dry riverbed). A survey of categorical studies suggests that fish and invertebrate communities are generally depauperate in disconnected pools compared with connected pools, and that disconnected pool communities are often subsets of connected pool communities (Meyerhoff & Lind, 1987; Taylor, 1997; Taylor & Warren, 2001; Bonada *et al.*, 2006). The metacommunity in a chain of disconnected pools may have a longitudinally nested pattern, with progressively smaller sub-
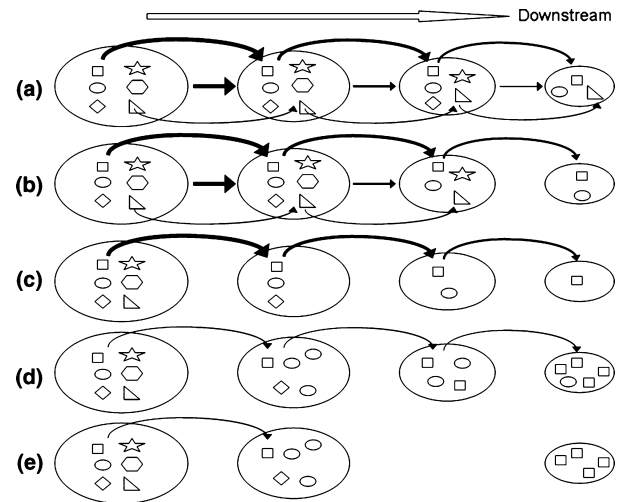

Fig. 2 Hypothetical patterns of metacommunity structure in longitudinal arrays of pools in a temporary-river reach. a: connected pools, b: partially connected pools, c: recently isolated pools, d: long-isolated pools, e: long-isolated pools and complete drying. Straight arrows: aquatic dispersal paths; curved arrows: aerial dispersal paths; line weights correspond to relative dispersal rates. Shapes within pools represent different types of aquatic taxa; squares, ovals and stars represent taxa with an aerial phase; squares and ovals represent taxa that fly along wetted or dry channels, stars taxa that only fly along wetted channels; squares represent the most desiccation-resistant taxa. For clarity, only downstream dispersal is shown.

sets of aquatic species assemblages along the chain (Taylor, 1997) (Fig. 2). Longitudinal nestedness is caused by limited dispersal from source populations, or by local extinction along gradients of competition, predation or physical harshness (McAbendroth *et al.*, 2005). There are exceptions to these patterns, and nested patterns may be undetectable when among-pools variability is high, or when pools are sampled soon after disconnection (Chaves *et al.*, 2008).

Communities in disconnected habitats within temporary rivers are likely to diverge over time due to differences in founding communities at the time of disconnection, and to interspecific differences in mortality, reproduction, dispersal and colonisation (Capone & Kushlan, 1991; Lake, 2003). Extinctions in isolated pools and persistence in closely spaced pools contribute to divergence and nestedness within the metacommunity (Fig. 2). Conversely, widespread or repeated colonisation by species capable of long-distance dispersal promotes convergence (Loreau & Mouquet, 1999; Jeffries, 2005; McAbendroth *et al.*, 2005). Community convergence may also occur in

long-lived pools through differential extinction, as species with high tolerance to long-term hypoxia and hyperthermia eventually become dominant.

Aquatic insects with aerial stages may be the most common animal migrants to and from disconnected aquatic habitats. Active movement on dry riverbeds is limited to a small number of amphibious taxa, such as dytiscid and hydrophiliid beetles, crayfish and eels (Sayer, 2005; Boulton, Sheldon & Jenkins, 2006). Passive transport by birds and mammals is a third mode of migration between aquatic habitats (Bohonak & Jenkins, 2003; Green & Figuerola, 2005), but its relative importance is unknown. Variation in maximum dispersal distances among species should lead to distinct patterns in the colonisation of disconnected habitats (Fig. 2). This issue is essentially unexplored in temporary river ecology, but data from temporary pond networks support the idea that dispersal abilities and distances between water bodies are primary determinants of community composition (De Meester *et al.*, 2005; McAbendroth *et al.*, 2005).

Metapopulations. Metapopulations are networks of spatially separated populations, some or all of which are prone to extinction, with overall extinction and recolonisation rates in approximate balance. Fish populations in temporary rivers may function as metapopulations, as indicated by source–sink relationships among local populations (Driscoll, 2007). In a study of Arkansas darters (Labbe & Fausch, 2000), permanent pools contained source populations with high survival rates and darters dispersed from these pools during high-flow periods. Intermittent pools functioned as sinks, with far lower survival rates than the permanent pools. As with aquatic species, terrestrial patches in temporary-river habitat mosaics are occupied by spatially fragmented populations of terrestrial species, some of which function as metapopulations (Stetler *et al.*, 1997).

In frequently disturbed environments, fragmented populations may grow (colonisation exceeds extinction) or contract (extinction exceeds colonisation) in response to habitat creation and loss. These extended, non-equilibrium populations are not metapopulations, but they are probably common in temporary rivers where frequent flooding and drying alters habitat over large areas. Results from temporary-river studies have rarely conformed to standard metapopulation models (Gotelli & Taylor, 1999; Magalhaes

et al., 2007), and non-equilibrium populations may be the rule. More important, it is not yet clear how variation in connectivity and dispersal relate to population persistence. The gravel bar grasshopper, *Bryoderma tuberculata* Fabricius, is a case in point (Stetler *et al.*, 1997). This insect requires unvegetated gravel habitat, and establishment of populations on newly devegetated gravel bars requires immigration along terrestrial corridors, so persistence at reach scales is dispersal-limited. Whether metapopulations are common or not, studies of the component processes in metapopulation models (e.g. habitat selection, inter-patch dispersal) will advance understanding of population dynamics and habitat requirements. Such studies have potential value in river management, as levels of connectivity required to prevent local extinction could be used to set instream flow requirements.

Meta-ecosystems. A recent conceptual model of carbon cycling depicts perennial rivers as meta-ecosystems (Battin *et al.*, 2008). In this model, dissolved organic carbon (DOC) derived from headwater vegetation (the 'source') is metabolised as it moves to downstream reaches and floodplains (the 'sinks'). The predominant catabolic pathways for DOC vary down the lengths of rivers in response to changing microbial communities, water residence time, sunlight and channel morphology. Multiple pathways increase the overall efficiency of DOC degradation during transit. The riverine meta-ecosystem concept need not be limited to allochthonous DOC; it is also applicable to longitudinal transformations of POM, dissolved nutrients and autotrophic carbon.

We contend that temporary rivers function as meta-ecosystems, based on the source–sink relationships that exist between intermittently connected aquatic ecosystems (e.g. pools, perennial reaches, backwaters), each of which plays a different role in the meta-ecosystem. In the absence of empirical studies, we consider the following hypothetical example of meta-ecosystem dynamics in temporary rivers. During connected periods, temporary rivers function as in the Battin *et al.* (2008) model, with continual material processing down the length of the river. During disconnected periods, barriers (dry riverbed) separate adjacent aquatic ecosystems. Solutes and POM are transported to these barriers, then deposited in pools and other retention sites as flow ceases. Processing

modes and the rates at which deposited material is processed are likely to differ from those in flowing water. Periodic hypoxia in pools causes microbial metabolism to fluctuate between aerobic and anaerobic pathways (Chan *et al.*, 2005). When pools dry, the POM stored in them also dries, and solutes form evaporites on sediment and POM surfaces (McLaughlin, 2008). At this stage, terrestrial microbial and metazoan communities take over as organic matter consumers, and solar radiation and desiccation enhance degradation (Boulton, 1991; Austin & Vivanco, 2006; Sangiorgio, Fonnesu & Mancinelli, 2007). When flow resumes and pools reconnect, the material in them is transported downstream to the next barrier. In the discussion below (Concept 3), we represent temporary rivers as longitudinal, punctuated biogeochemical reactors, in which diverse abiotic conditions and ecosystem processes enhance material processing.

The meta-system approaches discussed above offer useful tools for testing conceptual models in temporary-river ecology. The fit of temporary-river populations to the standard metapopulation model has been tested in several previous studies. Some of the important population-level questions still facing temporary-river ecologists concern the causes and risks of local and regional extinction, particularly for populations of rare and endangered species. Tools for extinction risk assessment from metapopulation ecology include simulation models and frameworks for viability analysis and for assessing management options (Dreschler *et al.*, 2003). To our knowledge, the predictions associated with metacommunity and meta-ecosystem models have not been tested in temporary rivers. Here we briefly discuss tests of the conceptual model shown in Fig. 2; tests of meta-ecosystem models are discussed below (Concept 3). The main predictions associated with the model in Fig. 2 are that aquatic communities form longitudinally nested subsets as channels dry, and that these communities undergo progressive divergence or convergence following pool isolation. Tests of these predictions are straightforward: nestedness in local communities can be quantified using 'nestedness calculators' (Arscott *et al.*, in press), and divergence or convergence can be assessed with multivariate analyses of community similarity (Legendre & Legendre, 1998). Methods used to test the effects of drying and isolation on aquatic community composition can also be used to test the effects of flooding and isolation on terrestrial communities (Ballinger, Lake & MacNally, 2007).

Concept 2. Aquatic-terrestrial habitat mosaics influence biodiversity

Shifting habitat mosaics within active channels are a defining feature of temporary rivers. The patches in these mosaics can be classed as aquatic, terrestrial or transitional, based on the species and biogeochemical pathways present. Transitional patches contain a mixture of aquatic and terrestrial species and pathways that briefly co-exist after inundation or drying. The borders separating adjacent patches function as porous ecotones, through which materials, energy and organisms flow (Sanzone *et al.*, 2003; Reid *et al.*, 2008). The edges of wetted fronts in temporary river channels are large-scale, moving ecotones. Similar ecotones move laterally through aquatic-terrestrial transition zones in river-floodplain systems (Junk, Bayley & Sparks, 1989).

Like river-floodplain systems (Ward, Tockner & Schiemer, 1999), aquatic-terrestrial habitat mosaics in temporary river channels are multiscalar in space and time. Aquatic patches range in size from small scour pools to long reaches with high flow permanence, and terrestrial patches range from boulder tops to long reaches with low flow permanence. The frequencies at which patches shift from dry to inundated and back range from <1 day to >1 year. While inundation and drying can occur very rapidly, transitions between aquatic and terrestrial ecosystems within patches require more time for reactivation of quiescent stages, hatching, emigration and mortality of previous inhabitants, immigration, and establishment of biogeochemical cycles and food webs. These transitions function as temporal ecotones (i.e. relatively short periods of change between persistent, dissimilar states; Larned *et al.*, 2007).

The habitat mosaics and ecotones described above are manifestations of complex expansion and contraction cycles in temporary river channels. These cycles rarely proceed in an orderly way, particularly when flow fluctuations are stochastic, but some distinct stages have been recognised (Stanley *et al.*, 1997; Boulton, 2003). Aquatic habitat contraction begins with flow recession, followed by decreasing flow width and depth, bar and bank emersion, and disconnection of lateral aquatic habitats from active

channels. As recession continues, emersion of riffle crests and other topographic high points causes reaches in active channels to disconnect. The disconnected flow then contracts longitudinally and laterally, and chains of pools form, connected by thin rivulets. When rivulets dry, the remaining isolated pools undergo abrupt thermal and chemical changes. Diurnal temperature fluctuations increase in amplitude due to reduced thermal mass; if algae and macrophytes are abundant, diurnal dissolved oxygen and pH fluctuations may also increase (Williams, 2006). In pools with little primary production, dissolved oxygen may decrease steadily, due to increased respiration and decreased solubility (Chapman & Kramer, 1991). Isolated pools eventually drain or evaporate completely. In the aquatic expansion phase, the preceding stages are reversed, and any stage of the cycle may be reversed by the onset or cessation of flow.

Biotic responses to habitat expansion and contraction in temporary rivers follow four different trajectories (Fig. 3): responses of aquatic organisms to drying (and subsequent terrestrial habitat expansion); responses of terrestrial organisms to drying;

responses of aquatic organisms to inundation (and subsequent aquatic habitat expansion); responses of terrestrial organisms to inundation. Responses by semi-aquatic organisms (e.g. collembolans, heterocerid and staphylinid beetles) during transitional stages comprise a brief, fifth trajectory. There is little information about tolerance to desiccation or inundation in semi-aquatic species, and it is not yet clear whether they generally occur as a distinct group or coexist with aquatic or terrestrial species.

Responses of aquatic organisms to contraction of aquatic habitat are the most intensively studied trajectory, in part because of the insight these responses provide into physiological, behavioural, and life-history adaptations to harsh environments. Physiological responses to drying include aestivation, encystment and anhydrobiosis (Eldon, 1979; Kikawada *et al.*, 2005). Some invertebrates (e.g. nematodes, copepods, ostracods and chironomid flies) persist for years in dry river sediments as cysts, eggs, copepodites, cocoons and dehydrated larvae or adults (Dahms, 1995; Ricci & Pagani, 1997; Williams, 1998). Behavioural responses include rheotaxis and burrowing (Del Rosario & Resh, 2000; Davey *et al.*, 2006; Lytle
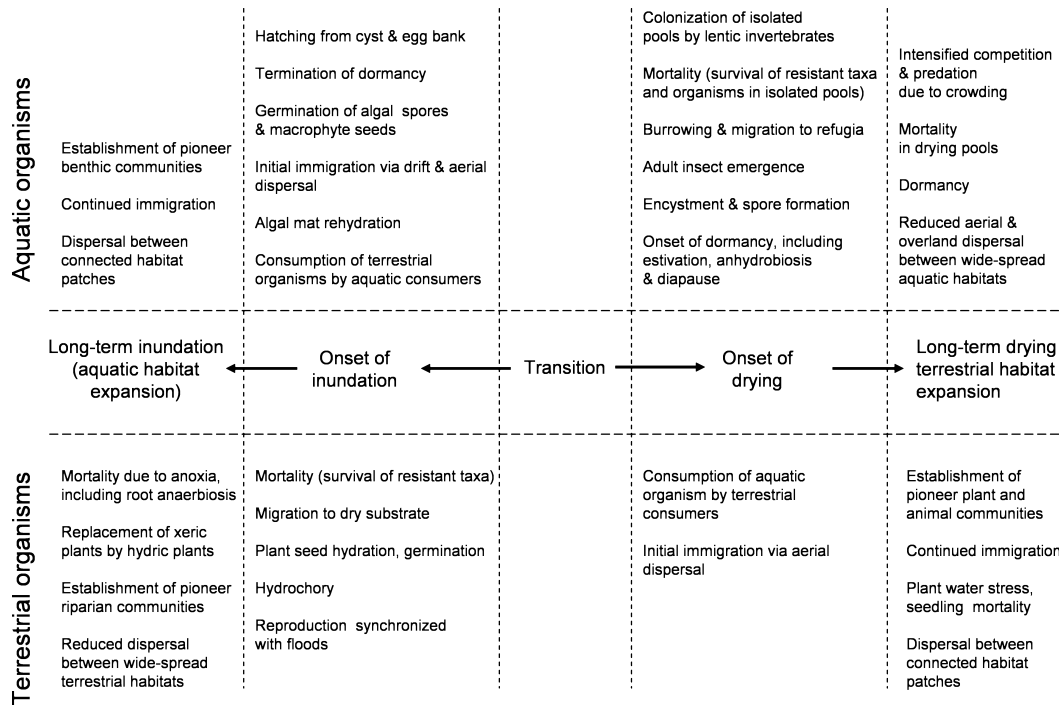

Fig. 3 Examples of responses by aquatic and terrestrial organisms to initial and long-term habitat inundation and drying in temporary rivers. Responses of semi-aquatic organisms are not shown.

et al., 2008). Life-history responses consist primarily of traits that increase reproductive plasticity and reduce time constraints in life-history stages [e.g. rapid development, multivoltinism, asexual reproduction, flexibility in size-at-metamorphosis, facultative dormancy (Nylin & Gotthard, 1998; Williams, 1998)]. Comparisons of aquatic invertebrates and amphibians in temporary and perennial systems suggest that the constellation of traits listed above is more common in temporary systems (Lane & Mahony, 2002; Suhling *et al.*, 2005; Bêche, McElravy & Resh, 2006).

Aquatic-terrestrial habitat mosaics and aquatic and terrestrial communities at different successional stages should be easily observed in temporary-river channels. However, patch dynamics in temporary rivers and their effects on biodiversity are not well studied. The conceptual model described below represents biodiversity as a function of patch composition and flow fluctuations. While the model is an over-simplification (e.g. it presumes that water levels change without altering the patch mosaic through sediment movement) and is strictly heuristic, it should help organise thinking at this early stage of development in temporary-river ecology. In the model description, we follow the terminology of Amoros & Bornette (2002): alpha diversity is species richness in individual habitat patches, beta diversity is between-patch biodiversity (i.e. spatial species turn-over), and gamma diversity is species richness across habitat mosaics.

In studies of river-floodplain patch mosaics, water level fluctuations have been shown to influence the abundance and proportions of aquatic and terrestrial habitat patches, and inter-patch connectivity (van der Nat *et al.*, 2002; Sommer *et al.*, 2004). The abundance of aquatic patches initially increases with increasing water level, then decreases as adjacent patches connect and coalesce. Connectivity among aquatic patches initially increases with water level, then approaches an asymptote when most patches have connected; further increases in water level simply increase the depths of connected patches. The same processes work in reverse for terrestrial habitat patches: patch numbers and connectivity increase with decreasing water level, then approach an asymptote at a minimum water level. Another relevant observation from river-floodplain studies is that high water levels and high connectivity can lead to homogenisation of aquatic communities due to migra-

tion between connected patches and decreased environmental heterogeneity (Amoros & Bornette, 2002; Thomaz, Bini & Bozelli, 2007). Thus, inundation can have opposing effects on aquatic gamma biodiversity by increasing alpha diversity (through the creation of aquatic habitat patches), and decreasing beta diversity (through homogenisation). Recent studies of terrestrial invertebrates in floodplains suggest some parallels with aquatic communities; inundation and drying create a mosaic of terrestrial habitat patches, and differences among communities in disconnected patches can lead to high beta diversity (Ballinger, Mac Nally & Lake, 2005; Ballinger *et al.*, 2007).

While the homogenisation process described above is not widely-tested, and terrestrial homogenisation has not been reported, it is a useful concept for assessing biodiversity patterns in aquatic-terrestrial habitat mosaics. A simple model that applies homogenisation to temporary rivers is shown in Fig. 4. The model suggests that river-wide aquatic biodiversity (gamma diversity) increases with water level and the proportion of aquatic habitat, due to increasing numbers of aquatic patches and consequent increases in both alpha and beta diversity. At some water level, the effect of additional aquatic patches is balanced by the homogenising effect of patch connection and coalescence; beta diversity is maximal at this point. Further increases in water level cause further increases in connectivity, and beta diversity begins to
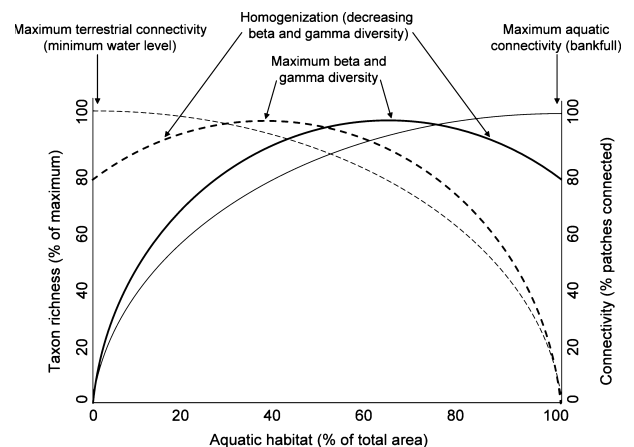

Fig. 4 Predicted relationships between habitat-patch connectivity & biodiversity (as taxon richness) versus % aquatic habitat (or % of bankfull area inundated). Solid lines indicate aquatic connectivity and taxon richness; dashed lines indicate terrestrial connectivity and taxon richness. Heavy lines indicate taxon richness; light lines indicate connectivity.

decrease. The combination of decreasing beta diversity and decreasing habitat diversity causes gamma diversity to decline as aquatic habitat approaches 100% (bank-full). In our simple model, the response of terrestrial biodiversity to changes in water level is the approximate inverse of the aquatic response. The actual shapes and inflection points of the curves in Fig. 4 are not known for any river.

Tests of the predictions listed above and plotted in Fig. 4 may take the form of controlled experiments or mensurative studies. Mensurative studies can be used to identify biodiversity patterns in the habitat mosaics of temporary rivers, and to relate those patterns to levels of patch connectivity. Comparable studies have already been carried out in floodplains (reviewed in Amoros & Bornette, 2002; Robinson, Tockner & Ward, 2002). Connectivity is shown in Fig. 4 as a simple proportion of connected habitat patches, but there are many connectivity metrics (Kindlmann & Burel, 2008). Mensurative studies cannot be used to establish causal relationships between dispersal, homogenisation, patch structure, and biodiversity; controlled experiments are needed. No large-scale experimental manipulations of temporary river habitat mosaics have been attempted. However, landscape ecologists frequently manipulate terrestrial habitat mosaics, and their methods can be adapted to temporary rivers. In terrestrial experiments, connectivity is altered by creating or eliminating dispersal corridors, and patch structure is altered by subdividing, removing, enlarging and fusing patches (McGarigal & Cushman, 2002). In temporary rivers, connectivity can be altered by artificially connecting or disconnecting pools, and aquatic and terrestrial patches can be manipulated through sediment excavation and deposition (Sawyer *et al.*, 2009).

Concept 3. Flow pulses trigger biogeochemical and physiological processes in temporary rivers, which function as longitudinal biogeochemical reactors

Dry river reaches are biogeochemically and physiologically quiescent compared with flowing reaches. In the absence of river flow or sustained rainfall, the moisture content of river sediments is typically <5%, and microbial activity is very low (Larned *et al.*, 2007; McIntyre *et al.*, 2009). Organic material may accumulate on dry riverbeds, but decomposition, mineralisation and ingestion of this material is slow in the

absence of water. Flow pulses in dry channels trigger the onset or rapid acceleration of biogeochemical processes by rehydrating and activating microbes, plants and metazoans, dissolving nutrients and organic matter, transporting chemical reactants to reaction sites, and catalysing enzyme-controlled reactions (Scherer *et al.*, 1984; Larned *et al.*, 2007; McIntyre *et al.*, 2009).

Aridland soils have been model systems for exploring ecological, biogeochemical and physiological responses to water pulses (Austin *et al.*, 2004; Belnap *et al.*, 2005). A primary aim of these studies is to identify relationships between water pulse size (i.e. rainfall duration and magnitude), and response magnitude, duration and diversity. These pulse–response relationships comprise a nested hierarchy, in which the number of responses increases with pulse size (Schwinning & Sala, 2004). Short pulses generate few responses, most of which are limited to microbial activity in surface soils. Longer pulses generate the same responses, and additional responses that require longer hydrated periods or deeper water penetration. Very long pulses elicit an inclusive set of responses, including the slowest (e.g. community succession).

Experimental datasets and conceptual models that explain the roles of water pulses in temporary rivers lag far behind those for aridland soils. However, it appears that the biogeochemistry of dry riverbeds and of aridland soils are broadly similar, and a comparable hierarchy of responses to water pulses exists in both systems (Table 3). In temporary rivers, as in soils, water pulses trigger biogeochemical responses (McClain *et al.*, 2003). Complete saturation of river sediments and soils inhibits aerobic microbes and slows some aerobic mineralisation pathways (McIntyre *et al.*, 2009). Both systems shift from a predominance of anaerobic to aerobic microbial processes during drying phases (Baldwin & Mitchell, 2000; Holden & Fierer, 2005). Response times of biogeochemical and physiological processes to water pulses in aridland soils range from seconds to weeks (Schwinning & Sala, 2004). A survey of measurements made after rewetting dry riverbeds reveals a comparable range of response times (Table 3). These observations suggest that conceptual models used in aridland soil ecology will also be useful for temporary-river ecology.

The temporary-river meta-ecosystem and pulse-response concepts discussed earlier can be combined in a conceptual model analogous to the trigger-transfer-

Table 3 Minimum duration of inundation required to trigger biogeochemical and ecological processes in temporary rivers and their riparian zones

Process	Pulse duration	Reference
Rehydration of anhydrobiotic cyanobacteria	<1 min	Scherer *et al.* (1984)
Activation of nitrifying and denitrifying bacteria	minutes	Austin *et al.* (2004)
Release of carbon dioxide from bacterial carbon mineralisation	minutes	Sponseller (2007)
Respiration in anhydrobiotic cyanobacteria	<20 min	Scherer *et al.* (1984)
Photosynthesis in cyanobacterial mats	20 min	Scherer *et al.* (1984), Vincent & Howard-Williams (1986)
Ectoenzyme activity in cyanobacterial stromatolites	<1 h	Romani & Sabater (1997)
Flush of inorganic solutes from streambed sediments	<1 h	Meixner & Fenn (2004)
Dissolved inorganic nutrient uptake in cyanobacterial mats	<1	Vincent & Howard-Williams (1986), Scherer *et al.* (1984)
Rehydration of anhydrobiotic chironomid larvae	1 h	Kikawada *et al.* (2005)
Photosynthesis in cyanobacterial stromatolites	1 h	Romani & Sabater (1997)
Phosphorus desporption from calcareous algal crusts	1 h	Thomas *et al.* (2006)
Nitrogen fixation in anhydrobiotic cyanobacteria	2–3 h	Scherer *et al.* (1984)
Microbial biomass accrual	<1 day	McIntyre *et al.* (2009)
Attachment and germination of fungal conidia on leaf litter	<1 day	Dang *et al.* (2007)
DOM release from dried leaf litter	<1 day	Taylor & Barlocher (1996)
Cyst and egg hatching in protozoa, nematodes, and rotifers	1–3 days	Boulton *et al.* (2006)
Biomass loss in *Eucalyptus* leaf litter	3 days	Boulton (1991)
Hatching of dormant crustacean eggs	<1 week	Frisch & Threlkeld (2005)
Algal biomass accrual	7 days	Robson & Matthews (2004)
Algal oospore germination	10–20 days	Casanova & Brock (1996)
Emergence of adult chironomids	14 days	Tronstad *et al.* (2005)

reserve-pulse (TTRP) concept developed for aridland soils (Belnap *et al.*, 2005). The TTRP concept predicts the following sequence of events: rainfall triggers water and nutrient transfers in the soil profile or downslope by subsurface or overland flow. Soil interspaces, rills and plant islands are reserves, or sites of temporary retention. The arrival of water and reactants in a reserve stimulates a biogeochemical pulse, followed by nutrient losses through leakage and gains from de novo synthesis. Subsequent rains transfer mobile nutrients to other reserves downslope, where further pulses occur. The core predictions of the TTRP are (i) mosaics of microbial activity are produced when water pulses interact with a patchwork of reserves; (ii) there is positive feedback between microbial processes, and water and nutrient retention; and (iii) nutrient retention efficiency increases with reserve density.

In the analogous temporary-river model, the trigger may be direct rainfall, or inundation by downstream flow or upwelling groundwater. Advancing fronts transfer dissolved and particulate organic matter to reserves downstream. These reserves may be pools, bar tops, or other sites where material is retained during flow recessions. Within reserves, the temporary presence of water sustains biogeochemical and

ecological processes such as exoenzyme activity and invertebrate shredding and scraping. Eventual drying in reserves causes the cessation of many water-dependent processes, and the onset or intensification of processes such as photodegradation, dehydration, and comminution by terrestrial invertebrates (Austin & Vivanco, 2006; Collins *et al.*, 2008). Subsequent flow pulses transfer partially processed material from one reserve to others downstream, where water-dependent processing begins again. Through repeated cycles of material and water transfer, retention, processing, and displacement to downstream reserves, temporary rivers function as longitudinal biogeochemical reactors, as described by Battin *et al.* (2008). However, unlike the model described by Battin *et al.*, material processing in temporary rivers is likely to be highly punctuated, with transfers confined to high-flow periods, fast processing during inundated periods, and slower processing during dry periods. The core predictions of the 'punctuated longitudinal reactor' concept are: (i) longitudinal gradients develop in organic matter processing rates and modes in temporary rivers, in response to repeated cycles of transport, retention, and processing; (ii) rates of most biogeochemical processes are higher during

inundated periods than dry periods; and (iii) processing efficiency (e.g. the proportion of allochthonous organic matter mineralised or converted to consumer biomass) increases with the number of transport, retention, and processing cycles.

The first prediction, that longitudinal gradients develop in processing rates and modes, is not exclusive to temporary rivers; it is a basic prediction of the River Continuum Concept and related longitudinal models (Vannote *et al.*, 1980; Webster, 2007). Longitudinal changes in chemical substrates, biotic communities, and abiotic conditions all contribute to gradients in organic matter processing. In temporary rivers, periodic flow cessation modifies these gradients through the addition of terrestrial processing modes. The second prediction, that processing rates are higher during inundated periods than dry periods, is based on changes in river sediment microbial activity and biomass in response to drying and re-inundation (Tzoraki *et al.*, 2007; Amalfitano *et al.*, 2008; McIntyre *et al.*, 2009), and comparisons of POM decomposition under inundated and dry conditions (Herbst & Reice, 1982). The third prediction, that processing efficiency increases with the number of transport, retention, and processing cycles, is based in part on the lotic spiralling concept (Webster, 2007). Processing efficiency in perennial rivers generally increases with retention or spiral frequency and with the number of biotic and abiotic processing modes (Battin *et al.*, 2008). In temporary rivers, retention is further enhanced by repeated flow recessions, and the number of processing modes is increased by the addition of terrestrial modes.

Each of the three predictions stated above can be tested with field experiments. The first prediction, concerning longitudinal gradients in organic matter processing, has been partially tested in a temporary river using sediment microbial activity (Larned *et al.*, 2007). Many other organic substrates and processing modes remain to be measured along these rivers, and surveys of microbial functional diversity are needed to assess longitudinal gradients in catabolic pathways. Such surveys have been made along soil moisture gradients (Zak *et al.*, 1994), but not river intermittence gradients. The second prediction, that nutrient and organic matter processing rates vary between inundated and dry periods, has also been partially tested. However, the relative importance of many processing pathways (e.g. leaching, enzymatic degradation),

substrate parameters (e.g. POM stoichiometry) and environmental variables (e.g. temperature, humidity, pH) are unknown. The third prediction, that the efficiency of organic matter processing increases with the frequency of inundation and drying, has been tested in floodplain studies (Langhans & Tockner, 2006), and similar methods can be used in temporary-river studies. The temporary-river experiments should also address the different stages of drying described in Concept 2 (e.g. flow recession, isolated pool formation, complete drying), as these stages are associated with distinct thermal and chemical conditions and microbial assemblages.

Intermittence, climate change and human appropriation of river flow

Most ecological studies of temporary rivers are conducted at sites where flow intermittence is a natural phenomenon. However, anthropogenic flow intermittence is a looming environmental problem, and the need to reduce or mitigate its effects is urgent. Anthropogenic intermittence may lead to fishery declines, loss of migratory pathways, altered nutrient cycles, and reductions or losses of other ecosystem services (Jackson *et al.*, 2001; Xenopoulos *et al.*, 2005; Larson *et al.*, 2009).

Anthropogenic intermittence is caused directly by surface water and groundwater abstraction, and indirectly by climate change. Cases of direct anthropogenic intermittence are common and increasing in frequency (e.g. Fu *et al.*, 2004; Bernard & Moetapele, 2005; Qi & Luo, 2005; Hao *et al.*, 2008). These cases are characterised by relatively abrupt changes from perennial to intermittent flow regimes. Flow intermittence caused by climate change is likely to occur more gradually, in phase with regional drying trends. Documented trends in the magnitude or frequency of intermittence are very rare (Rupp *et al.*, 2008), as are robust predictions of future changes in intermittence. However, circumstantial evidence suggests that climate-driven flow intermittence has increased in some regions in the last century, and that these changes will continue in the near future. Runoff has declined for several decades in regions of Africa, Europe, North and South America, and Australia (Milly, Dunne & Vecchia, 2005; Xenopoulos *et al.*, 2005). Linked climate-runoff models indicate that areas with declining runoff will expand, and that initial positive

trends in runoff in other areas will reverse by mid-century (Hughes, 2003; Christensen *et al.*, 2004; Milly *et al.*, 2005). A global-scaled runoff analysis has corroborated these regional predictions (Arnell, 2003). The global-scaled predictions include a decrease in annual average flows in 25–45% of all river catchments by 2050, and a 2–3 fold increase in the frequency of severe low flows in southern Africa, Europe, the Amazon and western North America. Model uncertainty precludes extrapolating these predicted trends to zero (i.e. to intermittence). However, given the large regions that will be affected, it is likely that some perennial rivers will become temporary.

The prediction of future increases in anthropogenic flow intermittence is reinforced by projected increases in surface and groundwater abstraction to meet agricultural, urban and industrial demands (Vörösmarty & Sahagian, 2000). Rates of runoff and groundwater abstracted relative to availability are greatest in arid and semi-arid regions, where climate-driven reductions in runoff are also forecast. Synergistic effects of climate change and abstraction will reduce flows in accessible rivers of arid and semi-arid regions relatively rapidly, and may hasten the onset of intermittence.

Unique management needs for temporary rivers

In view of their roles as source of biodiversity and providers of ecosystem services, the generally negligent management of temporary rivers is concerning. The European Union Water Framework Directive requires rivers to be classified in order to apply appropriate management plans, but temporary rivers are not recognised in Water Framework classifications (Logan & Furse, 2002). In the United States, litigants have sought to exclude temporary rivers from the protection afforded by the Clean Water Act (Nadeau & Rains, 2007a). Efforts to 'improve' temporary rivers are indicative of the poor state of knowledge about them. For example, flow augmentation has been used to improve intermittent rivers by creating perennial flow (Wolff, Wesche & Hubert, 1989; Henszey, Skinner & Wesche, 1991; Cluett, 2005). Unintended consequences of flow augmentation includes invasions of non-native species (Howell & Benson, 2000), loss of native species, and loss of predator refugia (Labbe & Fausch, 2000; Reich *et al.*, 2009).

River managers generally apply perennial river-management principles to temporary rivers when making decisions about water allocation, river engineering, effluent discharge and restoration. In this section, we make a case for managing temporary rivers as a distinct class of ecosystems, rather than as hydrologically challenged perennial rivers. The emerging ecological concepts described earlier may provide some insight for management. These concepts can be translated into three broad management objectives: preservation or restoration of aquatic-terrestrial habitat mosaics, preservation or restoration of natural flow regimes, and identification of flow requirements for highly valued species and ecological properties.

The first objective concerns aquatic-terrestrial habitat mosaics. Conservation and restoration work on temporary rivers, and the underpinning science have focussed on aquatic or terrestrial habitat exclusively (e.g. Mouw & Alaback, 2003; Stromberg, Hazelton & White, 2009; Arscott *et al.*, in press). However, management decisions affect both aquatic and terrestrial biota and habitats, and the aquatic/terrestrial distinction is artificial. Restoration of habitat mosaics in degraded temporary-river channels may require excavation and construction of geomorphic structures (e.g. pools, bars, islands), sediment augmentation, and/or the provision of large floods (Kondolf & Wilcock, 1996; Sawyer *et al.*, 2009). These geomorphic structures interact with shifting water levels to produce shifting aquatic-terrestrial habitat mosaics.

The second management objective is the preservation or restoration of natural flow regimes, where possible (Hughes, 2005). This seemingly straight-forward requirement is often problematic. Current management strategies for temporary rivers favour reliability of water supply, effluent conveyance, and flood control over natural flows. While managers have little incentive to restore natural flow regimes in hydrologically altered temporary rivers, partial restoration can be beneficial. For example, losses of riparian vegetation caused by flow diversions from temporary rivers have been reversed by partial flow restoration (Rood, Braatne & Hughes, 2003; Nagler *et al.*, 2005).

The third management objective is the identification of flow requirements for highly valued species and ecological properties. In cases where restoration of entirely natural flow regimes is impractical, an alternative is to provide the flow components required to

sustain the greatest values. This approach requires managers to identify and prioritise values, which may be rare species, high gamma diversity, or the absence of invasive non-native species. The next steps are to determine and prescribe the flow components that high-priority values require. These components may include floods, low-flows, and zero-flow periods. Ecological flow requirements for perennial rivers have been studied and refined for decades, but comparable studies of temporary rivers are at an early developmental stage (Hughes, 2005; Larned *et al.*, in press).

The current shortage of information about temporary rivers is an impediment to effective management (Hughes, 2005). The recent acceleration of temporary-river research is promising, and represents an opportunity for rapid advances through collaborations between aquatic and terrestrial ecologists and hydrologists. These collaborations could make temporary rivers model systems for testing concepts in the emerging research areas of ecohydrology and aquatic-terrestrial transitions.

Acknowledgments

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