When the river runs dry: human and ecological values of dry riverbeds

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Temporary rivers and streams that naturally cease to flow and dry up can be found on every continent. Many other water courses that were once perennial now also have temporary flow regimes due to the effects of water extraction for human use or as a result of changes in land use and climate. The dry beds of these temporary rivers are an integral part of river landscapes. We discuss their importance in human culture and their unique diversity of aquatic, amphibious, and terrestrial biota. We also describe their role as seed and egg banks for aquatic biota, as dispersal corridors and temporal ecotones linking wet and dry phases, and as sites for the storage and processing of organic matter and nutrients. In light of these valuable functions, dry riverbeds need to be fully integrated into river management policies and monitoring programs. We also identify key knowledge gaps and suggest research questions concerning the values of dry riverbeds.

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Rivers that intermittently cease to flow and "run dry" have been described as being more representative of the world's river systems than those with perennial flows (Williams 1988). These temporary rivers are a truly global phenomenon (Larned *et al.* 2010), and their spatial and temporal extent is likely to further increase resulting from the combined effects of altered land-use patterns, climate change, and increased water extraction for human uses (Meehl *et al.* 2007; Palmer *et al.* 2008). Dry riverbeds are defined as the channels (the area between river banks) of temporary rivers during the dry (flow cessation) phase that can be exposed during periods of drought. They are habitats in their own right and differ from adjacent riparian and other terrestrial habitats in their substrate composition, topography, microclimate, vegetation cover, inundation frequency, and biota (Kassas and Imam 1954; Coetzee 1969; Steward *et al.* 2011). Often considered to be harsh environments, dry riverbeds are subject to flow disturbances that mobilize, deposit, and scour bed sediments. They can also be exposed to intense solar radiation, wind, and extreme temperatures (Steward *et al.* 2011). Dry riverbeds may be devoid of vegetation; however, in arid regions, they can be where the greatest diversity and density of vegetation is found (Figure 1; Kassas and Imam 1954).

Although often linked with negative connotations, dry riverbeds are associated with a range of important societal and ecological values. Unfortunately, dry riverbeds have been largely ignored by aquatic and terrestrial ecologists, probably because they are perceived to be outside the domain of their respective disciplines. A temporary riverbed can be dry for much of the time and may only be "aquatic" for a brief period after a flood or a period of heavy rainfall. The role of dry riverbeds as habitats is "only beginning to be understood and is an exciting frontier, albeit it is still terra incognita" (Datry *et al.* 2011). This paper aims to advance the traditional view of temporary rivers by (1) recognizing dry riverbeds as important features in the landscape and (2) highlighting their ecological values and their importance to humans.

In a nutshell:

- Most river systems have reaches with temporary flow regimes and riverbeds that can remain dry for days to years at a time
- Dry riverbeds have important human and ecological values that are often overlooked by river and catchment managers
- Conceptual models of riverine landscapes that do not include dry riverbeds are incomplete, and thus lack relevance in many parts of the world

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Dry riverbeds and landscape connectivity

Rivers expand and contract – longitudinally, laterally, and vertically – over time in response to their flow regimes (Stanley *et al.* 1997; Döring *et al.* 2007), and the greatest contraction is seen when the entire riverbed becomes dry. Headwater streams in temperate, subtropical, and tropical zones can cease to flow on a seasonal basis, leaving behind perennial pools in amongst dry sections of riverbed (Figure 2). Water in these systems can continue to flow beneath the riverbed, along subsurface routes. Dry riverbeds are not restricted to headwaters, however, and can also be found in the mid-reaches and lowlands of river networks (Figure 2). Many arid and semi-arid rivers can be dry along most of their length for most of the time, except for the presence of isolated perennial pools (Figure 2). Although common in desert environments, dry riverbeds can be found in a wide range of ecosystems. For example, almost 50% of the network of the 2700-km-long Tagliamento River, an alpine river in northeast Italy, is temporary (Döring *et al.* 2007), whereas streams in Antarctica flow for several months and are dry for the remainder of the year (McKnight *et al.* 1999).

Figure 1. *In arid regions, dry riverbeds may be where the most diverse and most dense vegetation is found, as shown in this aerial photograph of a dry river channel in the Lake Eyre Basin, Australia.*

Dry riverbeds can be created or inundated by anthropogenic influences (Figure 2). Dams and weirs can intercept flow, drying riverbeds downstream. Alternatively, natural temporary rivers can become perennial as a result of constant flow releases from dams or weirs, or when water is discharged from mining operations or sewage-treatment plants (Hassan and Egozi 2001). Water extraction from rivers and groundwater during droughts can reduce river flows, causing riverbeds to dry (Holmes 1999; Palmer *et al.* 2008). Future climate warming is predicted to increase the frequency of droughts in many regions (Meehl *et al.* 2007), increasing the temporal and spatial extent of dry riverbeds.

The drying of a riverbed represents a loss of longitudinal connectivity for aquatic biota as well as for physical aquatic processes throughout the river network (Figure 2). During a flow event, previously isolated populations can be reconnected through both drift and the active dispersal of aquatic biota. Organic matter and nutrients are transported and processed downstream during this time. Although dry river reaches are barriers to aquatic downstream movement and processing, they are connected laterally to the riparian zone, floodplain, and adjacent terrestrial ecosystems. These surrounding areas provide dry riverbeds with inputs of organic matter and nutrients, and can allow for the movement of terrestrial biota between them. Dry riverbeds are connected to subsurface waters and sediments below; they are also connected to the airspace above and can act as a corridor for aerial biota. A key knowledge gap regarding dry riverbeds in landscape ecology concerns how the spatial configuration and extent of dry riverbeds determine catchment-scale processes, such as the distribution of biota and the transfer of energy through food webs. Further knowledge gaps and research questions are presented in Table 1.

Table 1. Knowledge gaps and questions regarding dry riverbed research

Value	*Knowledge gap/research question*
Value to humans	Which communities of people rely on dry riverbeds? What is the distribution of dry riverbeds at risk of degradation?
Unique biodiversity	During extreme conditions, do dry riverbeds serve as a refuge for upland terrestrial biota? Do dry riverbeds trigger the (rapid) evolution of life-history traits, such as higher dispersal capability and dormancy? Studies are needed to investigate the traits that allow terrestrial invertebrates of dry riverbeds to survive both wet and dry phases.
Refuge for specialized aquatic biota	How long can quiescent stages of aquatic biota remain viable in dry riverbeds, and how will changes in hydrology influence these taxa?
Corridors for terrestrial biota	Is rafting during flood events an important dispersal mode for maintaining the viability of populations of terrestrial invertebrates?
Temporary ecotones linking wet and dry phases	Are there critical thresholds in the duration, spatial extent, and severity of drying in temporary river systems that may lead to fundamental shifts in community structure, ecosystem processes, and services?
Storage and processing of organic matter and nutrients	What is the extent to which ecosystem processes during the wet phase control those during the dry phase, and vice versa?

Values of dry riverbeds

Value to humans

Temporary rivers, streams, and dry riverbeds are widely recognized in human culture and language (Table 2), and feature in stories told by indigenous peoples around the world. In the Dreamtime stories of Australian Aboriginal people, Tiddalik the Frog drank all of the water, leaving the

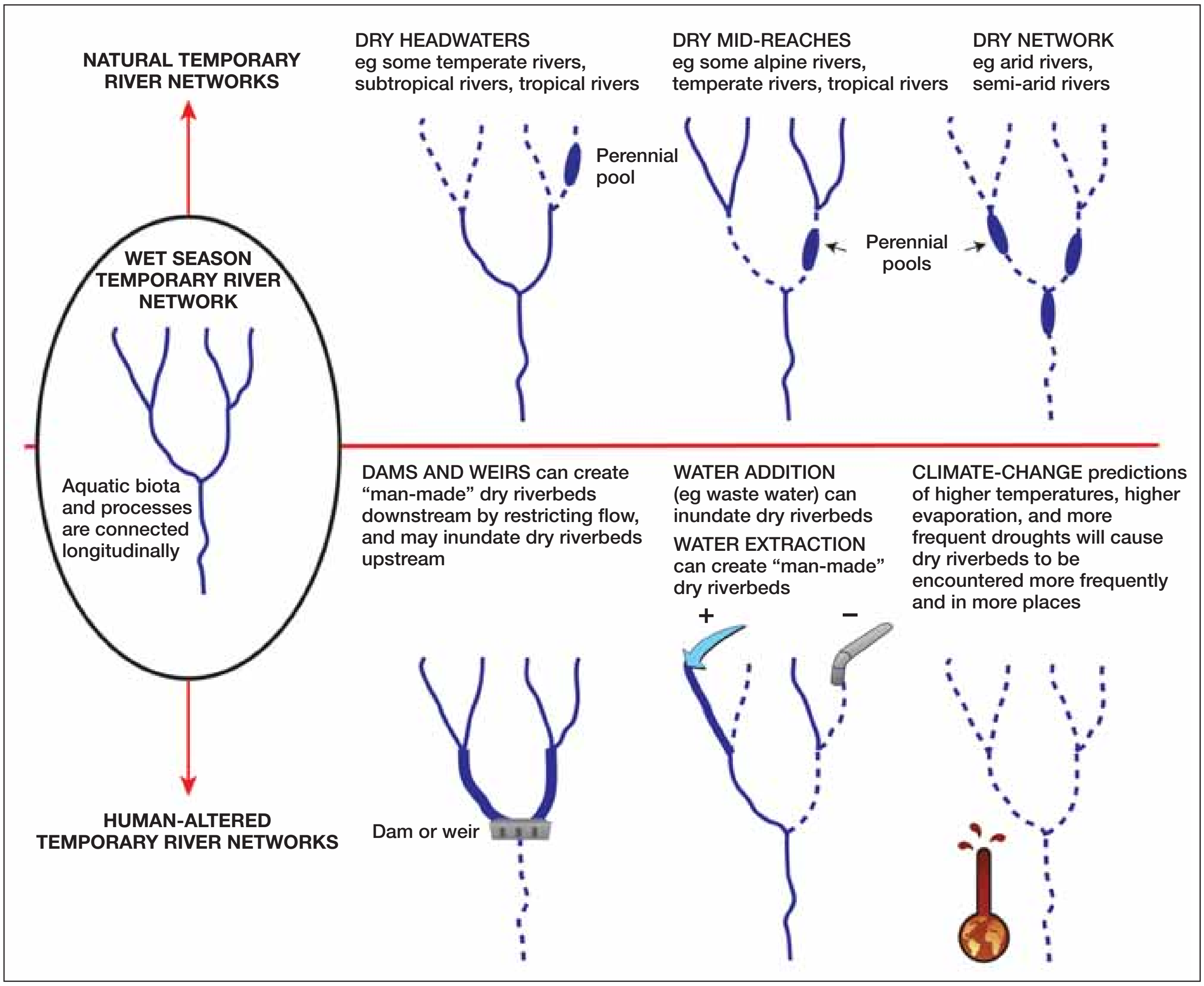

Figure 2. *Dry riverbeds in a landscape context, showing examples of natural and human-altered temporary river networks. Hydrologic connectivity (flowing sections) is represented by solid lines; dashed lines represent disconnected (dry) sections. Perennial pools are indicated by ellipses. Conceptual model symbols are courtesy of the Integration and Application Network (ian.umces.edu/symbols/).*

rivers dry. Dry riverbeds have also been popularized in modern Australian culture; for example, the annual Henley-on-Todd Regatta, which takes place in the arid zone of Australia's Northern Territory, is the world's only dry riverboat race, in which teams of "rowers" race each other along a dry riverbed (Figure 3a).

Dry riverbeds are a source of food and water. In Botswana, people "fish" for catfish aestivating in dry riverbeds. Water may be found by digging in dry water courses, and wells are often constructed within them (Jacobson *et al.* 1995). In Egypt, they are grazed by cattle and camels, medicinal plants are collected from them, and woody vegetation growing along the edges of the riverbed is harvested for fuel (Kassas and Imam 1954). Dry riverbeds can provide fertile substrates for agriculture. Fruit and vegetables are grown in the dry beds of the Ganges River in India (Hans *et al.* 1999) and in Egypt's Wadi Allaqi (Briggs *et al.* 1993); in Mediterranean Spain, it is common to find citrus orchards and other crops growing within dry riverbeds (Gómez *et al.* 2005). Gravel and sand are often extracted from dry riverbeds for building materials, and they are also places of recreation where people can camp, hunt, hike, ride, and enjoy nature.

Dry riverbeds are used as walking trails and vehicle tracks (Figure 3b), as car parks (Gómez *et al.* 2005), and as animal transportation routes. In Spain, shepherds once used dry riverbeds as migration corridors, and in 1993 it was estimated that more than 100 000 camels were herded along dry riverbeds from Sudan to Egypt to be sold at market (Briggs *et al.* 1993).

Unique biodiversity

Temporary rivers are characterized by frequent and intense disturbances and extreme environmental conditions. These features place strong selective pressure for the evolution of traits for the resistance and resilience of the biota to survive both wet and dry phases (Robson *et al.*

2011). Indeed, the drying of pools in temporary river networks has been postulated to have led to the evolution of traits that first allowed aquatic vertebrates to leave the water and colonize the land (Romer 1958), and may have been the driving force in the evolution of desiccation resistance (Williams 2006). Temporary rivers host a unique combination of aquatic, amphibious, and terrestrial assemblages as a result of their wet and dry phases (Figure 3, c and d). Desiccation-resistant stages of aquatic biota are present in riverbed sediments during the dry phase and, conversely, inundation-resistant stages of terrestrial biota may be present during the wet phase. Amphibious and semi-terrestrial biota may inhabit temporary rivers (Gibbs 1998), and a succession of biota can be observed during the transition from wet to dry phase. An initial "clean-up crew" of amphibious and terrestrial biota may consume any stranded aquatic matter, including dead and dying fish and aquatic invertebrates (Williams 2006). The terrestrial assemblages, such as invertebrates, that follow can be highly diverse, and differ from adjacent riparian and other terrestrial communities (Wishart 2000; Steward *et al.* 2011).

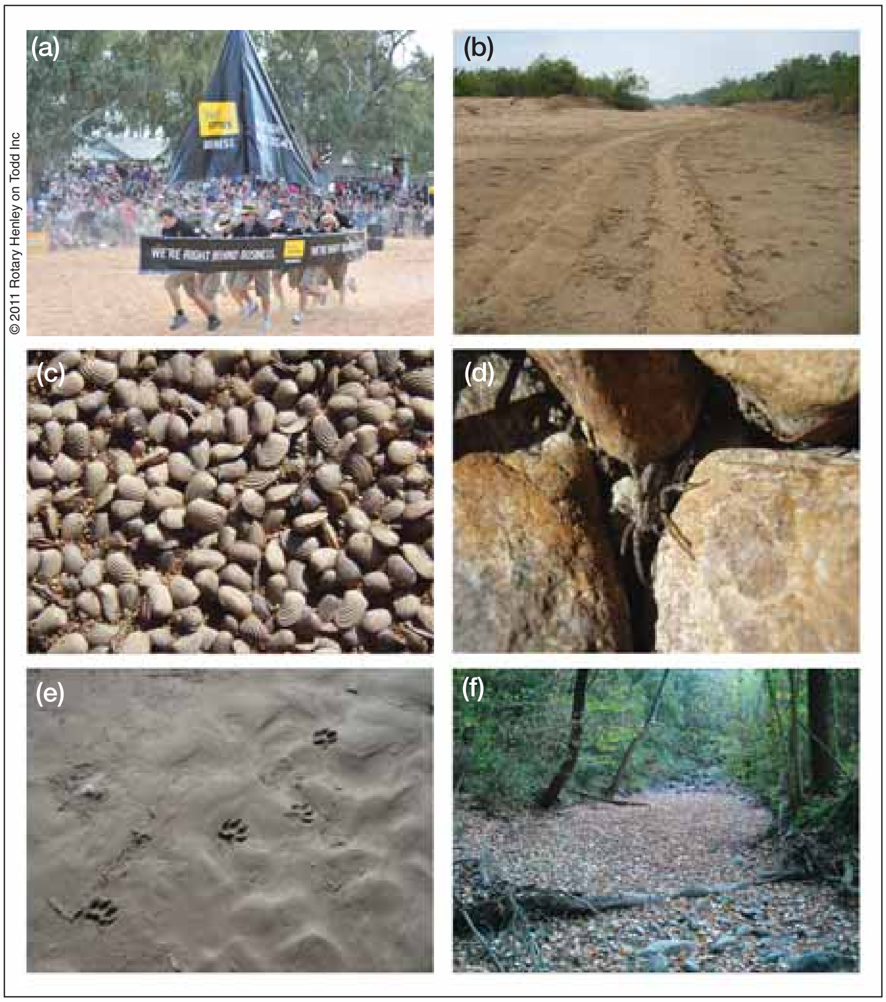

Figure 3. *Values of dry riverbeds: (a) cultural significance – the Henley-on-Todd Regatta (Todd River, Northern Territory, Australia); (b) vehicle transport route (Mitchell River, Queensland, Australia); (c) egg banks for aquatic biota, such as clam shrimp (Branchiopoda: Spinicaudata) (Northern Territory, Australia); (d) habitat for terrestrial biota, such as wolf spiders (Araneae: Lycosidae) (Northern Territory, Australia); (e) wildlife corridors (Tagliamento River, Friuli-Venezia Giulia, Italy); and (f) storage sites for organic matter, such as leaf litter (Riera de Fuirosos, Catalonia, Spain).*

Dry riverbeds have been described as linear oases, containing vegetation that is richer than other types of desert habitat (Figure 1; Kassas and Imam 1954; Fossati *et al.* 1999). They also provide important habitat for vertebrates; for example, riverbeds are the most heavily utilized vertebrate habitat in the southern Kalahari Desert in Africa, with ungulates moving in and out according to food availability (Mills and Retief 1984). Dry riverbeds can also provide abundant prey for mammals (Geffen *et al.* 1992), such that some predatory mammals are now regarded as semi-permanent inhabitants (Coetzee 1969). There is even fossil evidence that they once served as nesting grounds for sauropod dinosaurs (Kim *et al.* 2009).

Refuge for specialized aquatic biota

Dry riverbeds often act as egg banks for aquatic invertebrates and seed banks for aquatic plant, algal, fungal, and bacterial propagules (Williams 2006; Lake 2011). Some aquatic crustaceans live exclusively in temporary waters and require, or benefit from, a desiccation phase in order for their eggs or cysts to hatch (Figure 3c; Brendonck 1996). Other aquatic invertebrates take refuge in moist depressions, under woody debris and leaf litter, or in crevices under rocks, or they burrow into the riverbed itself (Chester and Robson 2011). Some fish species aestivate in dry riverbeds until they are rewetted (Berra and Allen 1989). Such a strategy may provide these fish with a competitive advantage over other fish species that recolonize from upstream, downstream, or lateral refugial pools when flow resumes.

Aquatic plants can have desiccation-resistant fragments – for example, tubers or seeds that persist during the dry phase and then grow or germinate when rewetted (Brock *et al.* 2003). Some algae have physiological attributes that allow them to resist desiccation for years, before reactivating and growing when the waters return. Cyanobacterial and algal taxa can survive within dried microbial biofilms that establish on hard substrates during

Table 2. Examples of words used throughout the world to describe dry riverbeds, temporary rivers, and temporary streams

Region	*Word*	*Region*	*Word*
Australia	Creek Dharrang Koornong Gully "Sand rivers"/ "rivers of sand" Warrego Wundu	Northern Africa and the Middle East	Nahal Oued Ued Ulja Vadi Wadi
		Russia	Balka Ovrag
Brazil	Corixos Vazantes Voçoroca	Somalia	Tug
		South Africa	Donga
Greece	Cheimarros Himaros Xeropotamos	Spain	Barranco Cabuerco Colada Torrente Rambla
India	Nallah Nullah Rau		
Italy	Fiumara Torrente	UK	Bourne Sychnant Winterbourne
Japan	Kare-sawa Kare-nagare	US	Arroyo Gulch Wash
Kenya	Lugga		
Madagascar	Uadi	West Africa	Kouri Marigot

the wet phase (Robson *et al.* 2008), or as freeze-dried mats that naturally form during winter in the frozen riverbeds of Antarctica (McKnight *et al.* 1999).

Corridors for terrestrial biota

Dry riverbeds increase landscape connectivity by acting as migration and navigation corridors for biota (Figure 3e; Coetzee 1969). The channel typically contains few obstructions, such as trees, and the airspace above is clear for use by flying biota. Where isolated waterholes are present within the river network, animals can travel along the dry riverbeds to access water. Dry riverbeds can also aid in the dispersal of biota that inhabit human-altered environments, where surrounding areas are developed and block movement. The beds of shaded rivers may provide a moister microclimate and more herbaceous cover than adjacent open areas, and are therefore more suitable for the movement of organisms that have physiological constraints (Gibbs 1998); for example, in arid landscapes, the adult stages of aquatic insects may disperse along such corridors (Marshall *et al.* 2006).

Large amounts of organic matter may accumulate in dry riverbeds, and this can be colonized by a diverse and abundant array of terrestrial invertebrates. When deposits of organic matter are mobilized during the onset of water flow, this also allows for a mass dispersal of terrestrial biota. Rafting or drifting on floating organic matter is an effective, long-distance dispersal mechanism that increases the likelihood of biota finding suitable habitat (Robson *et al.* 2008). This passive, mass scattering is particularly effective for weak dispersers, such as springtails and spiders, and may therefore be crucial for maintaining biological diversity along temporary river corridors.

Temporary ecotones linking wet and dry phases

A key characteristic of temporary rivers is that they are highly dynamic in space and time. The transition of a riverbed from an aquatic habitat to a terrestrial one represents a critical, but poorly explored, temporal ecotone. Dry riverbeds play an important role in the transfer of energy and materials between aquatic and terrestrial ecosystems. As a river dries, pioneer plants and animals colonize the riverbed, while aquatic species, including fish, insects, and algae, are consumed by terrestrial scavengers (Williams and Hynes 1976; Boulton and Suter 1986). The length of the dry phase influences ecological successions, and biotic communities in riverbeds may become increasingly more terrestrial with time (Lake 2011). It can also determine the distribution of drought refuges for aquatic biota, such as permanent pools, in the landscape (Bunn *et al.* 2006). The rate of responses by aquatic invertebrates and microbes to rewetting, including taxa richness and density, will also be determined by the length of the preceding dry phase (Larned *et al.* 2007). When flow resumes, inundated terrestrial biota and accumulated detritus may provide a highly nutritious food source for newly colonizing aquatic species (Wishart 2000). By providing a temporal ecotone, dry riverbeds maintain the diversity of aquatic and terrestrial assemblages, regulate the transfer and transformation of energy and materials, and define the resilience of the system.

Storage and processing of organic matter and nutrients

Few studies have considered the importance of organic matter and nutrient processing that occurs in dry riverbeds (Larned *et al.* 2010). As with soils, dry riverbeds show little hydrologic transport and tight cycling of materials, and are therefore highly retentive of organic matter and nutrients (Wagener *et al.* 1998). Microbial activity is reduced in dry riverbeds, resulting from the physiological effects, reduced diffusion of soluble substrates, and low microbial mobility associated with low water availability (Amalfitano *et al.* 2008). Consequently, dry riverbeds exhibit low rates of organic matter mineralization and

Panel 1. Case study – dry riverbeds and monitoring and assessment programs

The unpredictability of flows along dry riverbeds has been recognized as a challenge for environmental monitoring (Sheldon 2005). In 2005, Australia's Queensland Ambient Biological Monitoring and Assessment Program was hampered by long-term drought and the scarcity of surface water within Queensland's river network. The Program targeted two regions for assessing river condition: Western Cape and Gulf Freshwater Biogeographic Province and South East Queensland Freshwater Biogeographic Province (Figure 4; Steward 2007). Aquatic macroinvertebrates were used as biological indicators of river health. Each province was divided into 35 cells, and sites were randomly selected for sampling from within each cell. In the Western Cape and Gulf Province, three cells, each measuring approximately 1000 km^2, could not be sampled because of the lack of water within them. Likewise, in the South East Queensland Province, six cells, each measuring approximately 250 km^2, could not be sampled. In each case, many potential sites per cell were visited, but every site was dry. Researchers with the Program could not report on the health of the entire river network but only on the infrequent wet reaches. Thus, results were not representative of the entire network. This can lead to inconsistency, particularly if some sites are sampled at one time but not at another, because they are dry. The size of the wet river network also changes between reporting periods – this is rarely communicated. Robson *et al.* (2011) suggested sampling drought refuges for aquatic invertebrates during the dry phase as a potential solution. Problems remain even with this approach, such as sampling itself depleting the supply of future colonists, variable taxonomic composition in refuges resulting from stochastic founder effects, and strong biotic interactions. Additionally, drought refuges have a variable and patchy distribution at landscape scales. To overcome this problem, we argue that aquatic and terrestrial indicators could be included in the sampling criteria, to make an assessment of the entire river network, thereby representing both wet and dry reaches. Terrestrial indicators are currently being studied for this purpose.

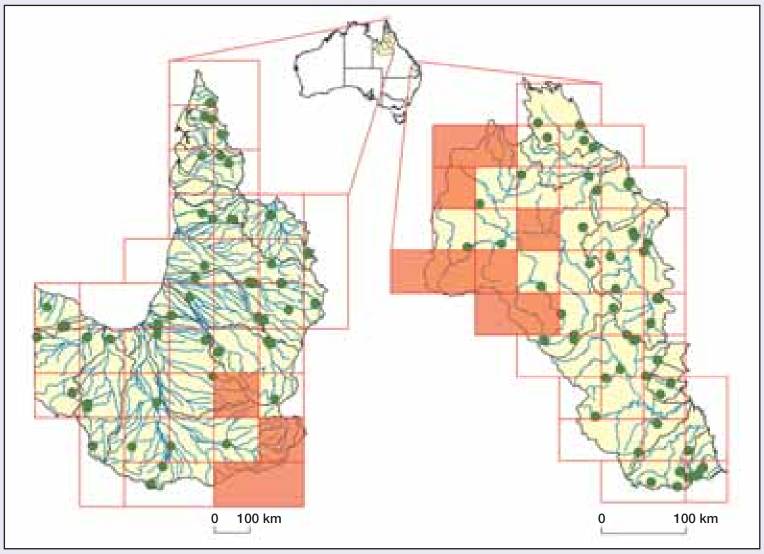

Figure 4. *Riverine monitoring sites (green circles) in (left) the Western Cape and Gulf Freshwater Biogeographic Province and (right) South East Queensland Freshwater Biogeographic Province in Queensland, Australia. Each province was divided into 35 sampling cells. Completely dry sampling cells are identified by red squares.*

increased relative importance of abiotic mineralization processes, such as photodegradation (Dieter *et al.* 2011) or the disruption of soil aggregates and the rupture of cell walls through drying (Borken and Matzner 2009).

The oxygenated environment within dry riverbeds favors aerobic over anaerobic nitrogen and phosphorus transformation processes (Baldwin and Mitchell 2000). Despite low microbial activity, nitrification is enhanced and denitrification is restricted to anaerobic areas, leading to the accumulation of mineral nitrogen (Austin and Strauss 2011). Extended sediment exposure leads to phosphorus release through mineral aging (Baldwin and Mitchell 2000). Microbial mortality during sediment drying releases large amounts of nitrogen and phosphorus (Amalfitano *et al.* 2008). Nutrients may be further stored as precipitated solutes through evaporation (McLaughlin 2008). Moreover, temporary rivers that run through forested areas receive a substantial input of leaf litter from riparian vegetation as a result of water stress during the dry phase (Figure 3f; Acuña *et al.* 2007). As a consequence, large amounts of organic matter and nutrients accumulate in the riverbed, ready to fuel river metabolism at the biogeochemically important moment of flow resumption (McClain *et al.* 2003).

Conclusions

Dry riverbeds have numerous ecological values and play important roles among humans. Research on the dry phase of temporary rivers is a novel concept (Datry *et al.* 2011), despite the prevalence of dry riverbeds throughout the world and the unique biotic assemblages that they contain. Researchers have only just begun to examine these important habitats, and yet many more perennial rivers are being turned into temporary ones as a result of water abstraction or changes in land use and climate. There is much we do not know about the likely effects of these changes – for instance, will "anthropogenic" dry riverbeds have the same values as natural ones? Do changing flow regimes increase the susceptibility of temporary rivers to invasions by exotic species?

Temporary river systems are under threat because their societal and ecological values are poorly recognized. Livestock trampling, overgrazing, weed infestation, and human uses, such as their use as roadways, can impact and damage dry riverbeds. Temporary rivers in some urban settings have been covered altogether by roads and now represent some of the most important avenues of these cities (eg the famous "Ramblas" in Barcelona, Spain).

Other dry riverbeds have been inundated as a result of construction of dams or weirs (eg Wadi Allaqi in Egypt; Briggs *et al.* 1993), or by wastewater discharged from mining operations (eg coal seam gas effluent) or sewage-treatment plants (Hassan and Egozi 2001). One major reason that dry riverbeds and temporary rivers are at risk of degradation is because they are not recognized in most river management policies; as a result, they are rarely considered in river health monitoring and assessment programs (see Panel 1). For example, draft guidelines developed for the US Environmental Protection Agency Clean Water Act will fail to protect small temporary rivers, including dry riverbeds that do not meet certain criteria (US EPA 2011). Dry riverbeds are also ignored in European water legislation (eg European Union Water Framework Directive; European Commission 2000).

In order to safeguard the many valuable aspects we have identified here, the protection of dry riverbed habitats should be incorporated into biodiversity and conservation planning. Furthermore, the health of these ecotones should be monitored and assessed through the use of appropriate indicators, in the same way that indicators are currently used to monitor and assess the health of aquatic ecosystems. Dry- and wet-phase river assessment could then be combined when reporting on the health of the entire river network. Most importantly, dry riverbeds must be incorporated into government policy and legislation. We need to recognize dry riverbeds as important elements of temporary rivers – that is, as habitats in their own right.

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