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Ecological roles and threats to aquatic refugia in arid landscapes: dryland river waterholes

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Abstract

Dryland rivers are renowned for their periods of 'boom' related to the episodic floods that extend over vast floodplains and fuel incredible production, and periods of 'bust' where the
15   extensive channel network is restricted to the permanent refugial waterholes. Many of these river systems are unregulated by dams but are under increasing pressure, especially from water abstraction and overland flow interception for agriculture and mining. Although some aquatic organisms with desiccation-resistant life stages can utilize ephemeral floodplain habitats, the larger river waterholes represent the only permanent aquatic habitat during
20   extended periods of low or no flow. These waterholes act as aquatic refugia in an otherwise terrestrial landscape. Variable patterns of connection and disconnection in space and time are a fundamental driver of diversity and function in these dryland river systems, and are vital for dispersal and the maintenance of diverse populations, generate the spatial and temporal variability in assemblage structure for a range of different organisms and fuel the productivity
25   that sustains higher trophic levels. Changes to natural patterns of connection and disconnection of refugial waterholes, owing to water resource development or climate change, will threaten their persistence and diminish their functional capacity to act as aquatic refugia.

07/10/10

30 **Introduction**

Over 50% of the world's land area could be termed "drylands" (Tooth 2000), encompassing hyper-arid, arid, semi-arid and dry-subhumid climatic regions. Although relatively poorly studied, the 'dryland rivers' that flow through these regions are common features (Walker *et al.* 1995; Kingsford and Thompson 2006). In dryland regions, evaporation often exceeds

35 rainfall and many rivers cease to flow for extended periods of time, fragmenting into disconnected waterholes and wetlands. For example, in South Africa, where 60% of the land area is classed as arid to semi-arid, 40% of the 65,000 km of river channels are subject to interruptions of flow (Davies *et al.* 1994). Most of the western flowing rivers of Namibia are ephemeral for much of their length and, for most of the year, the channels contain significant

40 wetlands and waterholes (Breen 1991; Loutit 1991). Dryland rivers, however, are just one sub-group of the broader group of temporary or ephemeral rivers, which are considered to be the most common and hydrologically dynamic of all freshwater ecosystems, occurring across most of the planet, and including rivers in alpine areas as well as temperate zones (Stanley *et al.* 1997; Larned *et al.* 2010).

45 In Australia, 92% of the 3.5 million km of river channels measured at the 1:250,000 scale are lowland rivers (Thoms and Sheldon 2000a), and with 75% of the land area classed as arid to semi-arid, most of these lowland rivers can be characterized as dryland rivers whose hydrographs demonstrate periods of no flow, and are therefore ephemeral rivers. Australian dryland rivers have distinctive ecologies, intimately linked to their highly variable flow

50 regimes (Walker *et al.* 1995; Sheldon and Puckridge 1998; Bunn and Davies 1999; Puckridge *et al*. 2000). Their unique combination of flow variability and geomorphic complexity creates a distinctive *boom and bust* ecology (Walker *et al*. 1995; Kingsford *et al*. 1999; Kingsford 2000a; Bunn *et al.* 2006a), characterized by episodes of intense reproduction and high productivity by opportunistic plants and animals (Puckridge *et al.*

55 2000; Bunn *et al.* 2006b). Jim Puckridge was one of the first to document this in his studies of fish communities in the Coongie Lakes region of the Cooper Creek, Lake Eyre Basin, Australia, describing the exponential increase in diversity, and explosion of abundance and biomass, associated with sequential flooding through this usually dry system (Puckridge 1999).

60 The Lake Eyre Basin (LEB) rivers, along with other dryland rivers, are renowned for their incredible productivity during periods of flooding – the "boom" (Puckridge 1999; Bunn *et al.*

2006b, Balcombe *et al.* 2007; Kingsford, this issue), but fundamental to this ability to respond to flooding is the maintenance of viable habitats during the extended dry periods, the "bust".   For much of the time, Australia's dryland rivers exist as a network of ephemeral

65   channels and turbid waterholes.   The contrasting states of flood and drought mean that dryland rivers fluctuate between being highly 'fragmented' systems where aquatic habitats (pools or waterholes (cf. Knighton and Nanson1994)) exist as disconnected aquatic 'islands' in an otherwise terrestrial landscape, and highly connected, as during floods, when all aquatic habitats are connected via inundation.   Fragmentation is a natural feature of rivers and at

70   small spatial scales has been shown to contribute to a high degree of habitat heterogeneity (Cooper *et al.* 1997).   The demonstrated high flow variability of Australian dryland rivers in both space and time (Walker *et al.* 1995; Puckridge *et al.* 1998; Thoms and Sheldon 2000b) suggests habitat fragmentation, particularly at the reach scale, is likely to be extreme in these systems.   During dry periods, the larger waterbodies, or 'waterholes', represent the only

75   aquatic habitat for biota requiring permanent water to survive (Arthington *et al.* 2005; Bunn *et al.* 2006a).   Although some aquatic organisms with desiccation-resistant life stages may be able to utilize ephemeral aquatic habitats on the floodplain (Boulton and Lloyd 1992; Jenkins and Boulton 2003), permanent and semi-permanent river waterholes are likely to function as *refugia* for a wide variety of aquatic organisms (Morton *et al.* 1995).

80   Rivers in the LEB and northern regions of the Murray-Darling Basin (MDB) of Australia (Figure 1) are typical of dryland rivers.   Many are essentially unregulated but are becoming the focus of major developments that have a high water demand (e.g. intensive irrigated agriculture Kingsford *et al.* 1998; Lemly *et al.* 2000; Kingsford 2000a; Kingsford 2006).   Both water abstraction and interception of overland flows on floodplains are increasing

85   across the region, as are the number and size of on-farm storages (Lutton *et al.* 2010).   For example, from 1993/94 to 1997/98, the number of on-farm water storages in the Condamine-Balonne and Border Rivers basins, northern MDB (Figure 1) increased by 90%, representing an increase of over 50% in diversions of overland flows and water privately diverted from rivers.

90   The Murray-Darling and Lake Eyre basins have several river and wetland habitats that are recognized as being significant for the maintenance of biodiversity, including the Narran Lakes, Bulloo Overflow, Paroo Wetlands and all of the permanent wetland complexes and waterholes within the LEB (Morton *et al.* 1995) (Fig. 1). Key threats to the maintenance of

diversity and ecological processes within these habitats, include land degradation through
95   over-grazing and cropping, alterations to the hydrological regime through water resource
development and invasions by exotic plant and animal weeds (Morton *et al.* 1995). In this
paper, we demonstrate the importance of waterholes as refugia in dryland river catchments,
both for maintaining aquatic biodiversity and biophysical processes during extended dry
periods. Given this, we test the hypothesis that aquatic biodiversity in dryland rivers reflects
100 spatial and temporal patterns of connectivity in the landscape.

Figure 1 here

The Concept of Refugia

105 In the general ecological literature, definitions of *refugia* follow two broad themes. The first
defines a *'refuge'* as a habitat that supports populations not able to live elsewhere in a
landscape (Nekola 1999). The second includes the role of adversity, where refugia are
defined as places (or times) where the negative effects of disturbance are lower than in the
surrounding area (or time) (e.g. Lancaster and Belyea 1997). During adverse conditions,
110 organisms in refugia have a high probability of survival and these organisms are subsequently
available to recruit or recolonise more severely affected areas of the landscape (Lancaster and
Belyea 1997).

The terms 'refugium' or 'refuge' have been used widely in the aquatic literature, in relation to
drought conditions (Wood and Petts 1999), floods and high flows (Winterbottom *et al.* 1997;
115 Rempel *et al.* 1999), thermal stress (Johnson *et al.* 1998; Torgersen *et al.* 1999) and predation
(Dudgeon 1996). Sedell *et al.* (1990) define riverine refugia to include localized
microhabitats and/or zones within the channel, unique reaches, riparian vegetation,
floodplains and groundwater. Riverine refugia are seen to exist as gradients or continua in
both space and time.

120 In ephemeral rivers, including dryland rivers, aquatic habitat expands and contracts
dramatically over both large and small spatial scales under natural flow regimes (Stanley *et
al.* 1997). It is clear that any definition of 'refugia' is essentially taxon-specific and episodic

floods may be favourable (boom times) for some species but represent adverse times to be endured and survived by others before returning to favoured dry periods (see Puckridge 1999;

125 Jenkins and Boulton 2003). Mechanisms of refugium use are diverse and depend on the spatial and temporal attributes of the physical environment and the requirements of the organism (Lancaster and Belyea 1997). In dryland rivers, for example, refugia for aquatic plants may include 'safe sites' for seed storage, germination, establishment and plant reproduction (Capon 2003). For fish and many fully aquatic invertebrates, however, the only

130 refugia during dry periods are likely to be permanent river waterholes (Arthington *et al.* 2005; Marshall *et al.* 2006).

Given the varying refugial requirements of different biota in dryland river systems, we suggest that no single type of waterhole would provide adequate conditions for all aquatic biota. Rather, a spatial and temporal mosaic of refugia providing a range of conditions would

135 more adequately allow different sub-sets of the regional biota to survive dry periods (Bunn *et al.* 2006a). It may not be possible to identify just a few refugia within this mosaic. Whether a particular waterhole constitutes a refugium for any one taxon may vary temporally, as the advent of floods can cause changes in their biophysical attributes. For example, a physically ideal refugium with adequate water quality for many fish species might

140 become intermittently hostile if flooding brings in a few large piscivorous fish, which colonize and persist into the drying phase (Kennard 1995). Temporal variation in waterhole conditions might be necessary for maintenance of diverse assemblages, by providing ideal conditions for a variety of taxa from plants to invertebrates and fish.

145 **Dryland River Waterholes as Aquatic Refugia**

Permanent hydrological features

To serve as refugia for aquatic organisms, waterholes in dryland river networks must be hydrologically permanent or semi-permanent features in the landscape. As a fluvial feature, waterholes are physically diverse (Knighton and Nanson 1994), covering a broad range of
150 shapes and sizes (Davis *et al.* 2002). However, in general, most waterholes in the dryland rivers of the LEB and MDB, Australia, are longer than they are wide and < 2-3 m deep (Davis *et al.* 2002). Despite occurring in a region where annual evapotranspiration typically exceeds 2 m, some waterholes persist for several years in the absence of surface flow or local rainfall (Bunn *et al.* 2006a). Of the 170 named waterholes in the channel country of Cooper
155 Creek, 80 have been estimated to persist for one year without flow or rainfall and only 5 have been estimated to persist beyond two years (Bunn *et al.* 2006b). The degree to which shallow groundwater contributions influence waterhole permanence is likely to vary across different river catchments, however, for the waterholes in the channel country of Cooper Creek, LEB, groundwater inputs were found to be minimal or non-existent (Hamilton *et al.* 2005). This
160 highlights the importance of in-channel flows for maintaining water levels between large flow events in these typically isolated refugia.

Dispersal between waterholes

Under low flow or 'disconnected' conditions, dryland river waterholes exist as aquatic
165 islands, or patches, in a terrestrial landscape. In terrestrial systems, increasing habitat fragmentation usually includes a reduction in habitat fragment size, increasing isolation between habitat fragments and loss of habitat (Andren 1996; Gustafsson and Gardner 1996). While waterbirds are known to perceive dryland river environments on large regional scales, and move freely between aquatic "patches" (waterholes) over large distances (Roshier *et al.*
170 2008; Kingsford this issue), organisms that perceive the landscape at fine scales are restricted to local habitat patches and are highly influenced by connection between these patches. Therefore, the long-term persistence and stability of populations within fragmented landscapes, such as dryland rivers, will depend on their rates of dispersal and recolonisation among waterholes (Gustafsson and Gardner 1996).

175

Analysis of the patterns and levels of genetic differentiation among populations of aquatic organisms has been used to infer the mechanisms and extent of dispersal among them (Hughes *et al.* 1995). This approach assumes that if dispersal between patches is high, and thus gene flow is high, little genetic differentiation among populations is expected; however,
180   if dispersal is restricted, genetic differentiation among populations will occur due to natural selection and/or random genetic drift (Slatkin 1985). Analysis of the genetic diversity between populations can, therefore, be used to infer the extent and potential mechanisms of dispersal (e.g. Sweeney *et al.* 1986; Waples 1987; Jackson and Resh 1992). For many aquatic taxa, waterholes during low flow are similar to oceanic islands; they have "hard
185   edges" or low "permeability" (Holmquist 1998). There is likely little to no movement between the waterholes by truly aquatic taxa during these periods, but perhaps higher movement of semi-aquatic taxa such as insects and waterbirds. However, at intermediate and high flow levels there may be strong connections between waterhole "patches", allowing major movements and dispersal by truly aquatic organisms.

190

Data collected from waterholes in the LEB suggest that although dryland rivers appear to be highly fragmented in space and time, this fragmentation may not be evident in the genetic diversity of their inhabitants (Table 1). While many aquatic taxa may not be able to disperse freely between isolated waterholes when flow ceases or is low, for most taxa waterholes will
195   become connected through in-channel flows within their life cycles and real fragmentation is therefore limited. The biota of Australian dryland rivers reflect three hypothetical dispersal 'modes'. For those organisms that are not truly aquatic, connection between waterholes, even under drought conditions, may be high through the riparian network (Lynch *et al*. 2002). These organisms include many of the aquatic insects with terrestrial adults, such as the
200   Hemiptera and Coleoptera; they are the 'movers' or 'mobile-link' organisms (*sensu* Lundberg and Moberg 2003) (Fig. 2). Although the population genetics of highly mobile insects ('mobile links') such as Hemiptera or Coleoptera are yet to be explored in dryland river waterholes, their abundance in both ephemeral and permanent habitats (Sheldon *et al.* 2002; Marshall *et al.* 2006) suggests they move freely throughout the channel network even during
205   periods of low flow.

Another large group of organisms, the 'networker' organisms, may be restricted to refugial waterholes when flows are low, but can rapidly disperse between waterholes in the channel network when waterholes are connected (Fig. 2). In Australian dryland rivers, this

'networker' group includes many of the fish and crustaceans (Table 1). Common population
210   traits of these organisms are low levels of genetic diversity within catchments but high levels
between catchments, suggesting free dispersal between refugia during periods of connectivity
(Table 1). Within this group, however, there is evidence of variation in the ability to disperse
throughout the network during connection. For example, the small glassfish *Ambassis* spp.
displays evidence of within-catchment population structure, based on genetic diversity,
215   suggesting some dispersal but perhaps not over large distances (Huey *et al.* in review). In
comparison, many of the larger fish displayed very little within-catchment population
structure, based on genetic diversity, suggesting extensive dispersal throughout the stream
network (Huey *et al.* 2006; Hughes and Hillyer 2006) (Table 1).

A third group, the 'permanent refugials' are entirely restricted to refugial waterholes,
220   showing very limited dispersal even under flow conditions (Fig. 2). Of the taxa reviewed,
only some of the molluscs show dispersal patterns that can be described as 'permanent
refugial'; both the viviparous gastropod *Notopala sublineata* and the freshwater mussel
Velesunio spp. showed high levels of within-catchment population structure, based on genetic
diversity, suggesting limited dispersal throughout the channel network (Carini *et al.* 2006;
225   Hughes *et al.* 2004; Table 1). The dispersal patterns of the freshwater mussel *Velesunio* spp.
are particularly interesting given that its larvae are parasitic on fish hosts. Gene flow analysis
suggests the fish hosts disperse readily during waterhole connection while, in contrast, the
mussels rarely disperse, with high between-waterhole differences in genetic diversity. We
conclude, therefore, that these mussels spawn only during low or no flow when dispersal
230   between waterholes by fish is limited or impossible.

Table 1 here

Figure 2 here

235   *Spatial and Temporal Patterns of Biodiversity*

In large rivers, the flood pulse is a mediator of disturbance influencing both diversity and
processes by connecting the river with its floodplain (Junk *et al.* 1989, Walker *et al.* 1995),
and likewise, the periods between floods (periods of low or no flow) can be just as important
drivers of riverine function. In dryland rivers, the variability in the magnitude, duration and

240   frequency of flooding over long time scales (20+ years) (cf. Puckridge *et al.* 2000) drives high spatial variability in the connection frequency of different parts of the river network. Ward *et al.* (1999) found α-diversity (local or site scale diversity; within-community diversity) of fish assemblages to decrease with increasing disconnection of waterbodies whereas β-diversity (between site diversity; between-community diversity) increased.

245   Evidence from Australian dryland rivers also suggests that the greatest degree of biotic variance lies at the waterbody scale. In the Goyders Lagoon wetland complex on the Diamantina River, LEB, variation in fish assemblage composition was higher at the waterbody scale than between sites within waterbodies (Puckridge *et al.* 1999), while macroinvertebrate assemblages of the same sites also varied more strongly between

250   waterbodies than between microhabitats within waterbodies (Sheldon and Puckridge 1998). A similar pattern was found for fish in waterbodies of Coongie Lakes (Puckridge 1999) and Cooper Creek (Arthington *et al.* 2005) and for Coongie Lakes invertebrates (Sheldon *et al.* 2002). Looking at wetlands associated with dryland rivers, across a broad range of inundation frequencies, Jenkins and Boulton (2003) found the diversity of microinvertebrates

255   hatching from inundated sediment reflected time since last inundation, with similar patterns found for floodplain plants (Capon 2003)

Site-specific community composition, and hence biodiversity, is the result of an interplay between both local and regional biotic and abiotic factors which act as "filters" (Poff 1997). Dryland rivers can be abiotically very harsh environments with extremes in the range of

260   hydrological and physico-chemical variables (e.g. oxygen, conductivity, pH, temperature), particularly during periods of low or zero flow (Magalhaes *et al.* 2002; McMahon and Finlayson 2003; Sheldon and Fellows this issue). In the channel country of Cooper Creek, the variability in macroinvertebrate composition at one site through hydrological cycles of flooding and drying was far greater than large-scale spatial variability at any one point in

265   time (Marshall *et al.* 2006). A similar pattern was apparent for fish assemblages, with increasing changes in fish assemblage structure with increasing time since the last flood (Arthington *et al.* 2005; Balcombe and Arthington 2009) and for algal assemblages, with high levels of spatial and temporal variability (McGregor *et al.* 2006). This suggests that biodiversity does vary both spatially and temporally, reflecting the heterogeneity of

270   connection in large floodplain rivers (Bornette *et al.* 1998; Tockner *et al.* 1999; Amoros and Bornette 2002).

We suggest that a natural level of connectivity between waterholes is integral in the maintenance of their ecological function. Assemblage dynamics within refugia are likely to change with increasing time since last connection, and biodiversity may be highest in refugia

275   subject to some form of 'intermediate' level of connectivity (Marshall *et al.* 2006). Comparative data from four Australian dryland rivers suggested that during periods of prolonged connection, both environmental and hydrological 'filters' will be homogeneous across a broad range of habitats, and assemblages may show very little dissimilarity (Sheldon and Thoms 2006) (Figure 3). As flood levels recede and connection between waterholes is

280   lost, assemblages in discrete waterholes will diverge in response to a broad range of localised conditions including water quality (Sheldon and Fellows this issue), local waterhole complexity (Arthington *et al.* 2005; Davis *et al.* 2002), waterhole permanence (Hamilton *et al.* 2005), productivity (Burford *et al.* 2008; Fellows *et al.* 2009) and perhaps the presence or absence of predators. If disconnection is maintained, the environment within the

285   waterhole will become increasingly harsh with only tolerant generalists able to survive (Fig. 3).

Figure 3 here

Biophysical Processes that Sustain Refugia

There is increasing interest in the relationship between biodiversity and ecosystem function
for many different ecosystems (see Loreau 2000). To sustain biotic assemblages, refugia
must provide adequate and diverse food resources; a low diversity of food resources may lead
to low trophic diversity in consumers and consequently reduced species richness. To
function as refuges in the long-term, waterholes also need to be sites where organisms can
maintain viable populations while the rest of their habitat is fragmented or dehydrated,
suggesting they have to meet the productivity requirements that sustain higher trophic levels.

Existing ecosystem models of large rivers have emphasized the importance of lateral (Junk
et al. 1989) or longitudinal (Vannote *et al*. 1980) inputs of terrestrial organic matter as a
source of organic carbon for aquatic consumers. In unimpacted large rivers, the main channel
habitats have varying degrees of dependence on their associated floodplain for energy, and
vice versa (Tockner and Stanford 2002). Junk *et al.* (1989) demonstrated the strong
dependence of the Amazon main channel on its floodplain habitats, driven by the very
predictable seasonal flood pulse. At the other end of the hydrological continuum, however,
Walker *et al*. (1995) suggested that the main channels of dryland rivers would not have the
same floodplain dependence given their high variability and the unpredictability of floodplain
inundation.

Despite this, the extensive floodplains and network of anatomising channels and distributaries
in many dryland rivers provide a far greater terrestrial-water interface than would occur with
a single large channel river (Walker *et al.* 1995; Bunn *et al.* 2006a). Many Australian
dryland rivers are often highly turbid and may remain so, even during the long no-flow
periods (Sheldon and Fellows this issue). Given their extensive terrestrial-aquatic interface,
high turbidity and low light penetration, we predict that populations of aquatic consumers
would depend on fluxes of energy and nutrients derived from extensive floodplain exchange
during floods (cf. FPC: Junk *et al.* 1989), even infrequent and unpredictable floods, and by
continual input from fringing vegetation persisting along the vast network of channels during
dry periods (Bunn *et al.* 2003). We also predict that aquatic plant production should be
limited by low light penetration in the turbid water and thus make a minor contribution to
energy flow through the aquatic food web; however, this is not the case (Bunn and Davies
1999; Bunn *et al.* 2003). Despite their high natural turbidity, the permanent river waterholes

of LEB rivers support a highly productive band of filamentous algae restricted to the shallow littoral margins. Stable isotope analysis has revealed that this "bathtub ring" of algae is the major source of energy driving the aquatic food web of Cooper Creek waterholes, supporting large populations of snails, crustaceans and fish (Bunn *et al.* 2003). Periodic phytoplankton
325 blooms and zooplankton may also be important components of the food web under specific flow conditions (see Balcombe *et al.* 2005; Medeiros and Arthington 2008).

Given the degree of dependence on littoral primary production and the narrow photic zone (typically < 30 cm), channel morphology clearly plays a major factor in overall productivity at the waterhole scale. We predict that waterholes with shallow sloping banks and bars will
330 be more productive than those with more vertical banks and a restricted photic zone. For example, two waterholes may have similar overall dimensions in terms of length and width, but one with three times the area of shallow habitat is likely to have approximately three times the production (Fellows *et al.* 2009). Across Australia's dryland rivers, there is a great diversity of waterholes, and while predominantly those occurring within the lowland river
335 networks tend to be turbid with low levels of light penetration, there are some, particularly those in the middle and upper reaches of the rivers, and those associated with the vast riverine wetlands (see Leigh *et al.* this issue), where the water is clearer, light penetration is greater and the waterholes can be dominated by macrophytes. The dominance of algal carbon over allochthonous sources, in these waterholes is as yet unexplored. However, given its
340 importance in the highly turbid waterholes, we may expect a similar outcome.

For dryland rivers, waterholes identified as refugia are physically stable over long periods (Knighton and Nanson 1994). The degree of hydrological permanence of these waterholes during dry periods reflects a balance between high rates of evaporation, water use by riparian trees and intermittent surface flows; there is very little evidence of shallow groundwater
345 inputs (Hamilton *et al.* 2005). Variability in hydrological connection combined with high levels of turbidity likely drive variability in ecosystem function among waterholes (Fig. 4) (Fellows *et al.* 2009). Flooding is a distinct phase of the hydrological cycle and although the timing, magnitude and duration of flooding in these dryland rivers is highly variable (Puckridge *et al.* 1998), it always results in the inundation of vast areas of floodplain and
350 incredible productivity (Puckridge *et al.* 2000; Bunn *et al.* 2006b; Balcombe *et al.* 2007).

We suggest that processes occurring within waterholes between large flood events are also important and reflect different hydrological conditions (Fig. 4). In-channel flows, or flow pulses can occur before or after a large flood or occur independently in association with localised rainfall (Bunn *et al.* 2006a). These flows are important for maintaining connection and therefore dispersal between waterholes but do not allow the establishment of either benthic algal communities, as the inundation period is too brief, or substantial pelagic production due to high river flows. Thus during in-channel flow pulses, production in these waterholes is low (Fellows *et al.* 2009) and may not be sufficient to support higher trophic levels (Balcombe *et al.* 2005; Balcombe *et al.* 2007). Once flow ceases, there is a rapid decline in water depth within a waterhole until the height of the outflow sill is reached. During this initial phase of flood recession, there is very little littoral primary production – algal spores in previously dry sediments may become active but not reach high production levels during the short window of inundation. Once a stable sill height is reached, water depth declines primarily as a function of evaporation (Hamilton *et al.* 2005). During this increasingly stable period, there are typically high levels of production associated with a well-established benthic algal community (Fellows *et al.* 2009). This highly productive "bath-tub" ring appears to be able to track the water levels slowly declining through evaporation, fuelling both invertebrate and fish production within isolated waterholes (Bunn *et al.* 2003; Burford *et al.* 2008).

Conclusions and impacts of water resource development on refugia

In this paper, we have suggested that hydrological variability, through variability in waterhole connectivity, is a vital driver of biodiversity and ecosystem function in dryland river waterholes. Patterns of connectivity between waterholes in the channel network influence the dispersal of plants and animals and mediate population structure, and connectivity patterns between waterholes in both space and time drive patterns in assemblage structure. Different phases of the hydrograph, from connected to disconnected, influence in-channel processes and maintain the productivity of refugia, even during extended periods of no flow or groundwater input. This dominant role of connection and disconnection in driving patterns of biodiversity and biophysical processes in Australian dryland rivers concurs with the general concepts of temporary river ecology outlined by Larned *et al.* (2010), where hydrological connectivity controls meta-community and meta-ecosystem dynamics (Concept 1), aquatic-

385   terrestrial habitat mosaics influence biodiversity (Concept 2) and flow pulses trigger biophysical processes (Concept 3). These observations are not new, as similar influences of connection – disconnection, or expansion- contraction, on both biodiversity and biophysical processes were outlined for desert streams by Stanley *et al.* in (1997). However, their general nature, across a broad suite of ephemeral rivers, highlights the importance of not only the

390   flood phase of the hydrological cycle, of which there has been much published (Junk *et al.* 1989; Heiler *et al.* 1995; Tockner *et al.* 2000), but also on the low, or no, flow phase, when there is maximum contraction in ephemeral streams.   Most importantly, however, it highlights the ecological significance of the pattern of hydrological connection – disconnection (expansion and contraction) that the alternate states of flooding and drying

395   provide.

       Throughout the Australian arid region, the position of many homesteads and settlements on the banks of large permanent waterholes is testimony to their relative longevity. However, this physical and hydrological permanence in an arid landscape makes the waterholes targets

400   for land and water resource development (Kingsford 2000a, 2000b).   Water resource development can alter the natural dynamics of connectivity in river systems and could fundamentally impact the refugial role of dryland river waterholes (Kingsford 2000a; Thoms and Sheldon 2000b). Globally, the ecological consequences of fragmentation of permanent river channels by dams or barriers are significant (Ward and Stanford 1995; Dynesius and

405   Nilsson 1994; Bunn and Arthington 2002).   Construction of dams or weirs on the river network causes upstream impoundment and the maintenance of high water levels along much of the channel network, thus constant connection between waterholes and a loss of "refugia function".

       Modelling the impact of water resource development on the hydrology of rivers in Australia's

410   wet-dry tropics, Leigh and Sheldon (2008) suggested that those rivers with a 'dryland' flow signal (high levels of flow variability) were likely to suffer increasing regularity with a reduced frequency of both low flows and high flows under water resource development, namely flow abstraction. This reflects the situation in many regulated rivers in the northern Murray-Darling Basin, Australia, which are either highly regulated and no longer experience

415   periods of 'low-flow', and therefore waterhole disconnection, or are subject to extreme levels of water abstraction for irrigated agriculture and therefore greatly reduced connection both spatially and temporally (Kingsford 2000a; Thoms and Sheldon 2000b). Given the extreme

hydrological variability in dryland rivers and the magnitude, but infrequency, of the large floods, it is the in-channel flows that are most often targeted for abstraction. This is likely to

420 vastly increase the length of time waterholes are disconnected (Bunn *et al.* 2006a) and may constrain or prevent many important processes associated with connection such as replenished water levels, improved water quality (Sheldon and Fellows this issue) and fish survival (Arthington *et al.* this issue).

In summary, waterholes in dryland rivers act as vital refugia in an otherwise arid

425 environment. They maintain riverine diversity and ecosystem function during the extended no-flow periods between the highly variable but infrequent large flood events. In-channel flows, or flow pulses, are important for maintaining connection among waterholes and their physical persistence, facilitating dispersal and mediating water quality. We suggest that hydrological variability, through the connection and disconnection of waterholes, is a

430 fundamental attribute of these dryland river systems; and, given the importance of spatial heterogeneity to assemblage structure (Arthington *et al.* 2005; Marshall *et al.* 2006; McGregor *et al.* 2006), a mosaic of refugia with different connection 'regimes' would be required for the full suite of species to be maintained in a conservation or restoration sense. Landuse patterns and water resource developments that change the connection frequency or

435 permanency of the waterholes will have substantial impacts not only on the functioning of the waterholes themselves, but also on the diversity and resilience of the entire river system and its capacity to respond to the unpredictable flooding when it occurs. Maintaining the natural hydrological variability of dryland rivers is essential from a conservation perspective.

Acknowledgements

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710   Figure Legends

Figure 1. (a) Areas of dryland rivers in Australia covering (i) the western portion of the Murray-Darling Basin and the Lake Eyre Basin; shaded in light grey, and (ii) the south westerly portion of the north-east coastal rivers and, in Western Australia, the rivers of the

715   Gascoyne Basin and Murchison Basin; shaded in dark grey. (b) Murken Waterhole, a typical refugial waterhole on Cooper Creek, Lake Eyre Basin, photo courtesy of Steve Hamilton.

Figure 2: Different dispersal strategies used by organisms in fragmented river landscapes. Waterholes denoted in grey contain water, whereas those in white are dry. Arrows depict

720   movement of organisms within and between waterholes.

Figure 3: Hypothesised shifts in assemblage composition through phases of waterhole connection and disconnection displayed using hypothetical multi-dimensional scaling plots. During waterhole connection (a) there is little dissimilarity between assemblages of different

725   waterholes. After disconnection (b) assemblage composition and structure of distinct waterholes diverges in response to both different abiotic (water quality, habitat) and biotic (competition and predation) factors. After prolonged disconnection (c) environmental attributes of disconnected waterholes become increasingly harsh and the assemblage is dominated by tolerant generalists, reducing assemblage dissimilarity between distant

730   waterholes.

Figure 4. Conceptual models of processes occurring in a dryland river waterhole under different flow conditions. (I) Connection caused by episodic in-channel surface flow events:

735   no littoral primary production due to brief inundation and flowing water; high turbidity limits profundal production; surface flow (curved arrows) provides inputs and mixing of nutrients and conditions for the dispersal of fish and invertebrates. (II) Disconnection of waterholes, connection ceases and waterholes are isolated. (a) Initially rapid drawdown to waterhole sill height (black arrows); low benthic and pelagic algal production; organisms are 'trapped' in

740   the isolated waterholes, abundances are initially high, but overcrowding and low food availability means condition declines. (b) Eventually high evapotranspiration (grey arrows) reduces water levels; algal bathtub ring establishes (thick grey band on waterhole edge); pelagic phytoplankton appears reflecting flow generated nutrient availability; high invertebrate and zooplankton biomass; reduced fish biomass means fish condition improves.

745   (c) Months after flow ceases water levels become more stable; evapotranspiration continues; groundwater inputs are variable and dependent on local conditions (white arrows); increasingly stable water levels fuel high littoral algal production (thick grey band); high benthic invertebrate production; high zooplankton production; trapped fish grow and reproduce.

750

Table 1. Summary of gene flow evidence for different modes of dispersal abilities of dryland river taxa from the Lake Eyre and Murray-Darling basins, Australia.

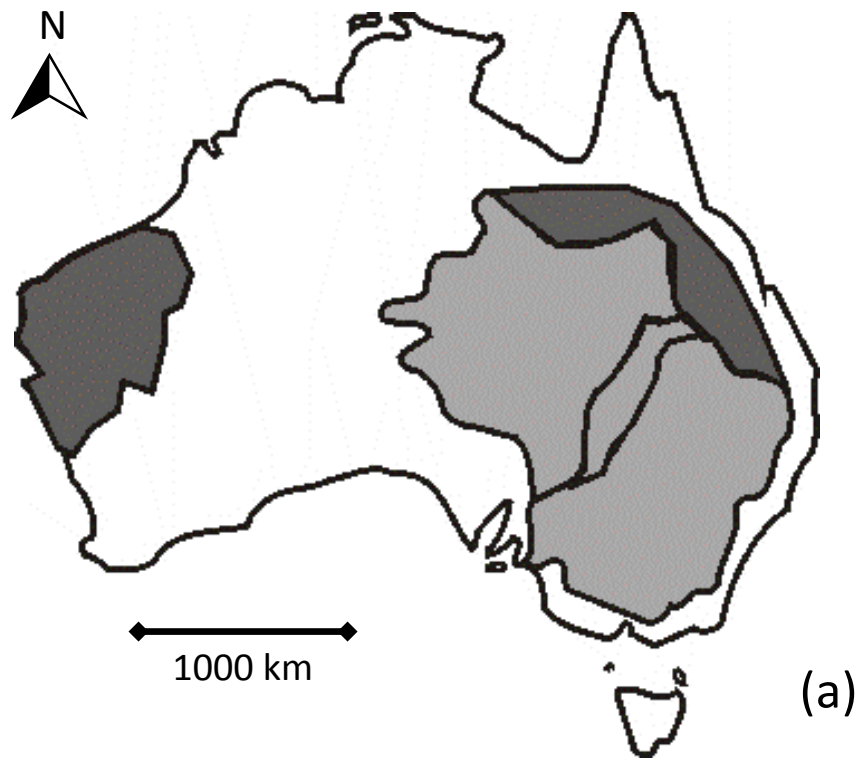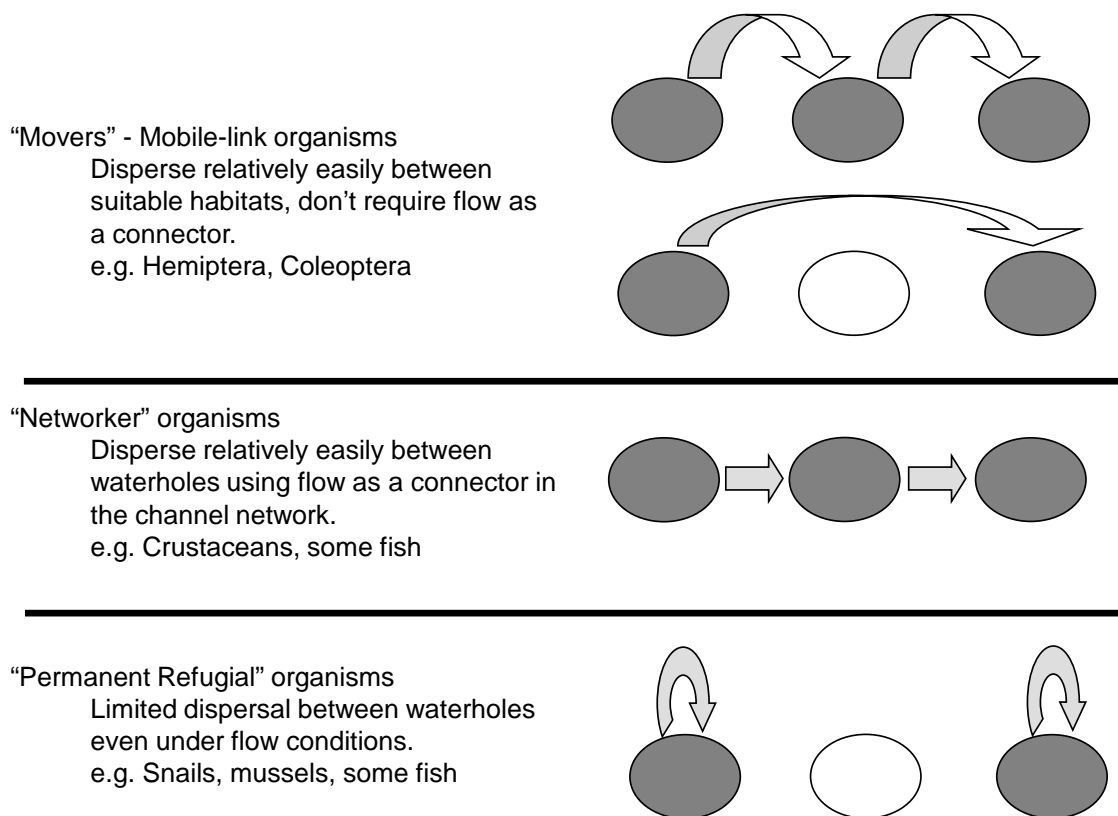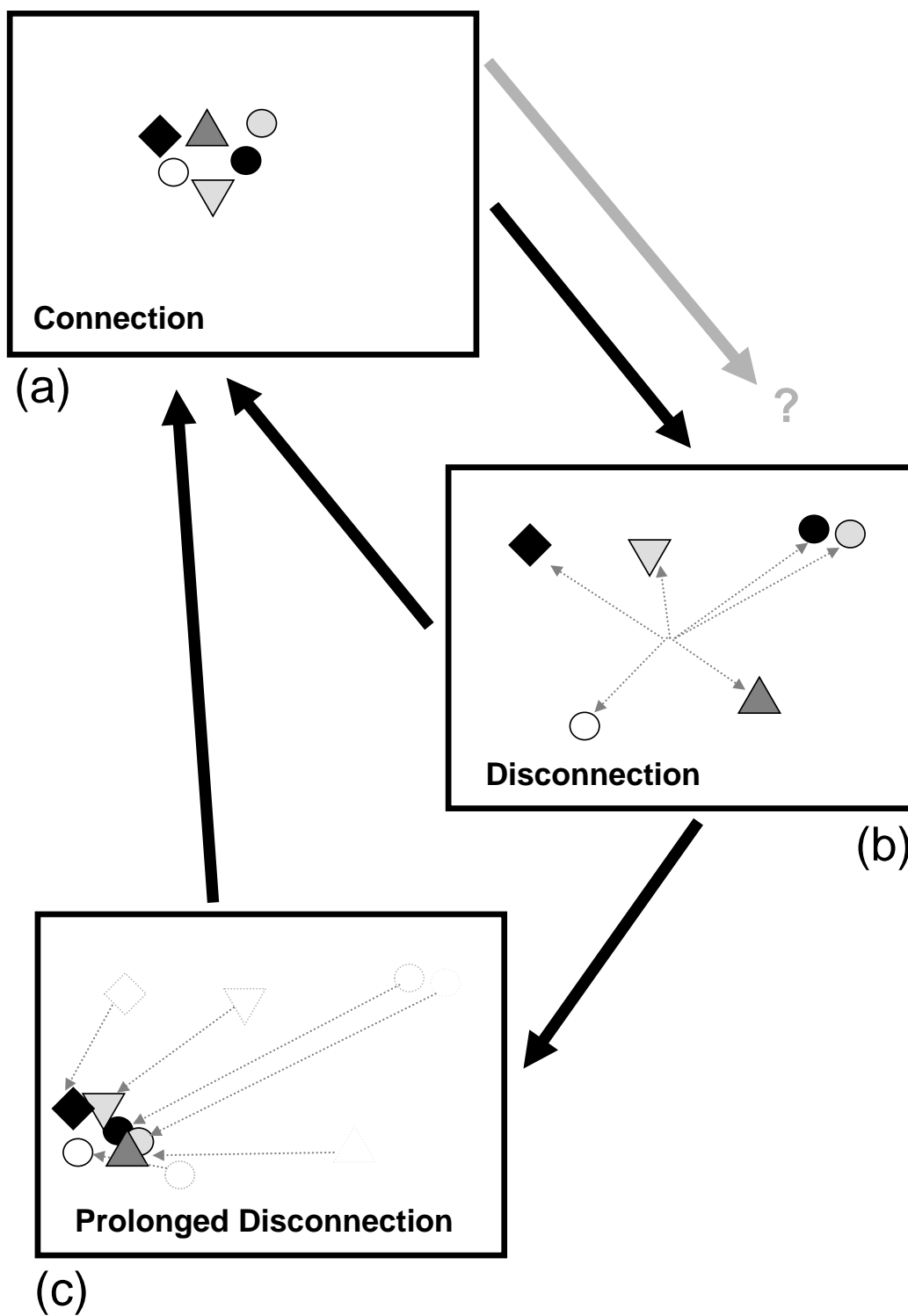| Taxonomic Group	Predicted Dispersal	Gene Flow	Dispersal group	References
Freshwater Molluscs				
Notopala sublineata (Gastropoda: Viviparidae)	Low dispersal ability. Viviparous, produces live young, no planktonic life stage	Restricted gene flow within catchments, thus high levels of genetic structure among populations throughout its distribution in Western Queensland.	Permanent Refugia	Carini & Hughes 2006; Carini et al. 2006
Velesunio spp. (4 undescribed species) (Hyriidae:	Adults sedentary Glochidia larvae parasitic on fish. Dispersal only possible via fish hosts.	Restricted gene flow within catchments. High levels of genetic structure among populations.	Permanent Refugia	Hughes et al. 2004
Freshwater Crustacea				
Macrobrachium australiense (Decapoda: Paelmonidae)	Moderate dispersal ability, pelagic larval stage and possibility of terrestrial dispersal	High levels of connectivity between populations within catchments	Networker	Cook et al. 2002 Carini & Hughes, 2004
Cherax destuctor (Decapoda: Parastacidae)	Terrestrial dispersal	Low levels of genetic subdivision between populations in the same catchment, suggesting high levels of connectivity	Networker	Hughes & Hillyer, 2003
Fish				
Neosilurus hyrtlii (Siluriformes: Plotosidae)	Dispersal through the river network on flooding	Low levels of genetic subdivision between populations in the same catchment, suggesting high levels of connectivity	Networker	Huey et al. 2006
Porochilus argenteus (Siluriformes: Plotosidae)	Dispersal through the river network on flooding	Low levels of genetic subdivision between populations in the same catchment, suggesting high levels of connectivity	Networker	Huey et al. 2006
Nematolosa erebi Clupeidae	Dispersal through the river network on flooding	Some genetic subdivision between populations in the same catchment, suggesting high levels of connectivity	Networker	Hughes & Hillyer, 2006
Retropinna semoni Retropinnidae	Dispersal through the river network on flooding	Low levels of genetic subdivision between populations in the same catchment, suggesting high levels of connectivity	Networker	Hughes & Hillyer, 2006
Ambassis sp. Ambassidae	Dispersal through the river network on flooding	Moderate levels of genetic subdivision within catchments	Networker / Permanent Refugial	Huey et al. in review

Figure 1

(a)

1000 km

(b)

Figure 2

"Movers" - Mobile-link organisms
  Disperse relatively easily between
  suitable habitats, don't require flow as
  a connector.
  e.g. Hemiptera, Coleoptera

"Networker" organisms
  Disperse relatively easily between
  waterholes using flow as a connector in
  the channel network.
  e.g. Crustaceans, some fish

"Permanent Refugial" organisms
  Limited dispersal between waterholes
  even under flow conditions.
  e.g. Snails, mussels, some fish

Figure 3

Figure 4