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# Productivity and Connectivity in Tropical Riverscapes of Northern Australia: Ecological Insights for Management

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## ABSTRACT

Flow regimes are fundamental to sustaining ecological characteristics of rivers worldwide, including their associated floodplains. Recent advances in understanding tropical river–floodplain ecosystems suggest that a small set of basic ecological concepts underpins their biophysical characteristics, especially the high levels of productivity, biodiversity and natural resilience. The concepts relate to (1) river-specific flow patterns, (2) processes ‘fuelled’ by a complex of locally generated carbon and nutrients seasonally mixed with carbon and nutrients from floodplains and catchments, (3) seasonal movements of biota facilitated by flood regimes, (4) food webs and overall productivity sustained by hydrological connectivity, (5) fires in the wet/dry tropical floodplains and riparian zones being major consumers of carbon and a key factor in the subsequent redistribution of nutrients, and (6) river–floodplains having inherent resilience to natural vari-

ability but only limited resilience to artificial modifications. Understanding these concepts is particularly timely in anticipating the effects of impending development that may affect tropical river–floodplains at the global scale. Australia, a region encompassing some of the last relatively undisturbed tropical riverine landscapes in the world, provides a valuable case study for understanding the productivity, diversity and resilience of tropical river–floodplain systems. However, significant knowledge gaps remain. Despite substantial recent advances in understanding, present knowledge of these highly complex tropical rivers is insufficient to predict many ecological responses to either human-generated or climate-related changes. The major research challenges identified herein (for example, those related to food web structure, nutrient transfers, productivity, connectivity and resilience), if accomplished in the next decade, will offer substantial insights toward assessing and managing ecological changes associated with human alterations to rivers and their catchments.

**Key words:** connectivity; floodplains; biogeochemistry; food webs; fluxes; nutrients.

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## INTRODUCTION

The fundamental importance of flow regimes for sustaining ecological processes in rivers and floodplains is well established (Poff and others 1997; Tockner and others 2000; Junk and Wantzen 2004; Hoeinghaus and others 2007; Warfe and others 2011; Winemiller and others 2014). Fluvial processes and hydrological connections are superimposed on landscapes (that is, riverscapes; Fausch and others 2002), and this 'layering' offers the potential to identify general patterns in riverine ecosystem function (Naiman and others 1987; Ward and Tockner 2001; Boulton and others 2008; Warfe and others 2011). Recent studies highlight the importance of flow predictability as a key factor determining whether floods act as a replenishing force, thereby enhancing productivity and heterogeneity, or a disturbing force altering physical templates and establishing new recovery trajectories (Lake and others 2006; Naiman and others 2008; Jardine and others 2015).

The tension between flows acting to replenish production or as a disturbing force is reflected in floodplain and food web characteristics as well as through pathways of spatial and temporal connectivity. It is widely acknowledged that seasonal inundation of floodplains underpins processes that contribute to river productivity (Junk and others 1989; McClain and others 2003; Junk and Wantzen 2004) and resilience (Parsons and others 2006, 2009; Townsend and Douglas 2014). In addition, there is the aquatic transfer from seasonally inundated floodplains of nutrients and organic matter delivered in biogeochemical forms that support food web structure manifested as primary, secondary and tertiary productivities (Tockner and others 2000; Lewis and others 2000; Fisher and others 2004; Lewis 2008). Food webs, representing energy and nutrient exchange pathways among species, are tangible expressions of riverine productivity and physical connectivity among catchments, rivers and floodplains, as well as through time. Food webs convey an integration of ecosystem processes and biological community structure (McCann and Rooney 2009), providing a framework for understanding energy transfer and biogeochemical processes within aquatic systems (Winemiller 1996; Schindler and others 1997; Naiman and others 2012; Thompson and others 2012), and appear to be influenced by flow regime pattern.

Northern Australia represents one of the few relatively undisturbed tropical riverine landscapes in the world, where rivers are characterized by

strong seasonality in flow regimes and high inter-annual variability in flood magnitude, frequency, duration and timing (Kennard and others 2010; Ward and others 2014; Jardine and others 2015; Pearson and others 2015). Rivers in Northern Australia are especially informative because of their relatively intact state (for example, limited flow regulation, low human population densities and little intensive development in the catchments; Stein and others 2002) and their resilience to widely variable environmental fluctuations (Pusey and others 2011). Inter-annual flood variability is largely a consequence of cyclonic events, the El Niño-Southern Oscillation (ENSO), Interdecadal Pacific Oscillation (IPO) and Indian Ocean Dipole (IOD) climatic variation (Hamilton and Gherke 2005; Hamilton 2010; Kennard and others 2010; Warfe and others 2011). The fluvial features of Australian tropical rivers (that is, flooding and disconnection) drive patterns of connectivity and the heterogeneity, diversity, productivity and resilience of biota and biogeochemical processes. In many river systems, floodplains are not inundated across their full extent each year, meaning floodplain waterholes may not be reconnected in some years (Ward and others 2014); aquatic communities become divergent (Leigh and Sheldon 2009; Warfe and others 2013a; Pearson and others 2015), and consumers become highly dependent on locally produced resources (Jardine and others 2012a).

This article synthesizes recent advances in the ecological understanding of river-floodplain characteristics in tropical Australia, articulates six concepts to frame future research and management needs, identifies key knowledge gaps, and identifies similarities and contrasts with rivers from other tropical regions. We explore and discuss the merging of terrestrial and aquatic ecology with biogeochemistry to better understand river functions. Specifically, we examine the extent to which floodplains and associated riparian zones underpin the movement of aquatic biota, food webs and resilience in tropical Australia, and how these processes are driven by flood timing and lateral and longitudinal connectivities. Elsewhere, there have been significant advances in understanding linkages between aquatic biogeochemistry and ecology, particularly those between hydrology, nutrients and organic matter in aquatic food webs (Lewis and others 2001; Vanni 2002; Winemiller 2004; Power and others 2008; Hamilton 2010; Winemiller and others 2014), and those between landscape processes and river function (Rodriguez and Lewis

1997; Allan 2004; Hoeninghaus and others 2007). These and other recent advances provide the foundation for interpreting patterns observed in tropical Northern Australia. This review is particularly timely for Northern Australia, as well as for tropical South America, Africa and southeast Asia, in anticipating the effects of impending development of land and water resources in some of the last relatively undisturbed riverine landscapes in the world (Vörösmarty and others 2010; Finer and Jenkins 2013; Zarfl and others 2015).

## PHYSIOGRAPHIC SETTING FOR TROPICAL AUSTRALIA

The physiography of tropical Australia is largely shaped by the ancient nature of the continent and its proximity to the equator (Latitude 11–19°S, Figure 1; Woinarski and others 2007; Ward and others 2011). The tropical region covers catchment areas that consist of the Timor Sea drainage, Gulf of Carpentaria drainage and the North-East (Coral Sea) drainage Divisions (Figure 1). This area extends across Northern Australia from Broome in the west to Townsville on the east coast, an area of over 1,200,400 km<sup>2</sup> (16% of the Australian land mass and is equivalent to the area of South Africa). The Northern Australian climate is chiefly influenced by an equatorial southern monsoon characterized by sharp seasonal rainfall, seasonally high temperatures (>40°C) and high

evaporation rates (1200–3200 mm year<sup>-1</sup>). Rainfall is primarily generated by local convection storms, tropical cyclones or tropical depressions (monsoons), and is summer-dominated (>90% of rain falls between November and April). The North-East drainage area of the north-eastern coast has a wet tropical climate to the north (Townsville to Cape York), where rainfall is much higher and streams are spatially short and perennial, merging into a wet–dry or dry tropical climate south of Townsville (Figure 1, Pearson and others 2015).

River flows reflect the climate's strong seasonality and high inter-annual variability (Kennard and others 2010). In the dry season, most rivers become disconnected pools (Figure 2) that are maintained to varying degrees by sub-surface and local groundwater flow. Only rivers connected to large groundwater aquifers, such as the Daly and Roper rivers in the Northern Territory, or those that flow east from the high rainfall uplands of NE Queensland, are perennial with sustained base flow throughout the dry season (Kennard and others 2010). The majority of rivers in Northern Australia are naturally flowing, unimpeded by constructed barriers (Stein and others 2002). The Ord River in the Kimberley region of Western Australia and the Burdekin River in north east Queensland are the only large regulated rivers in the region with storage capacities of 35 million and 1.8 million ML, respectively.

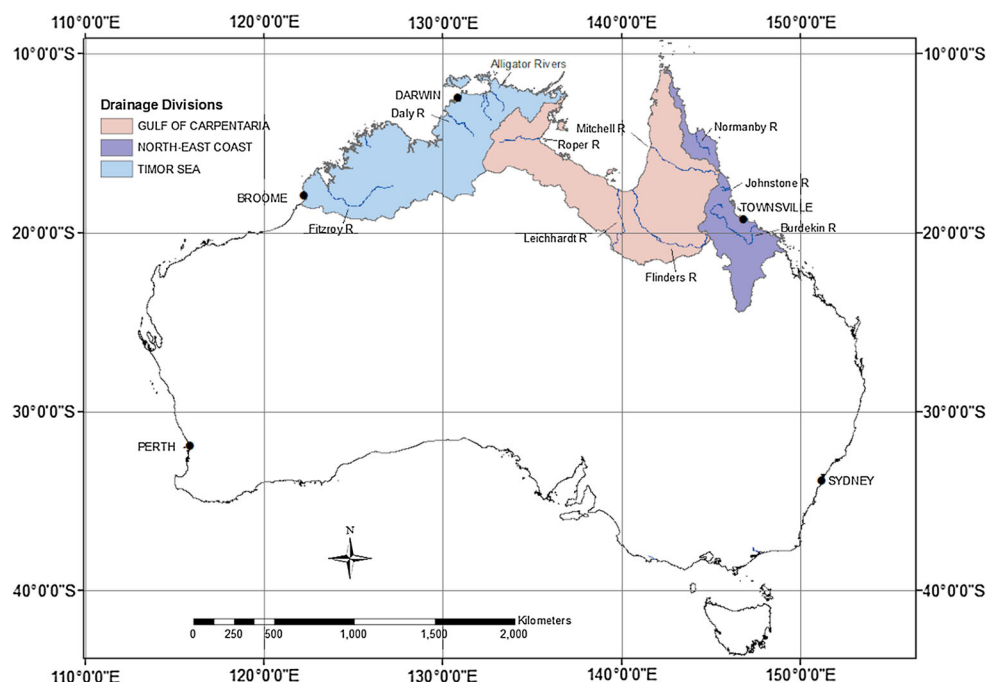
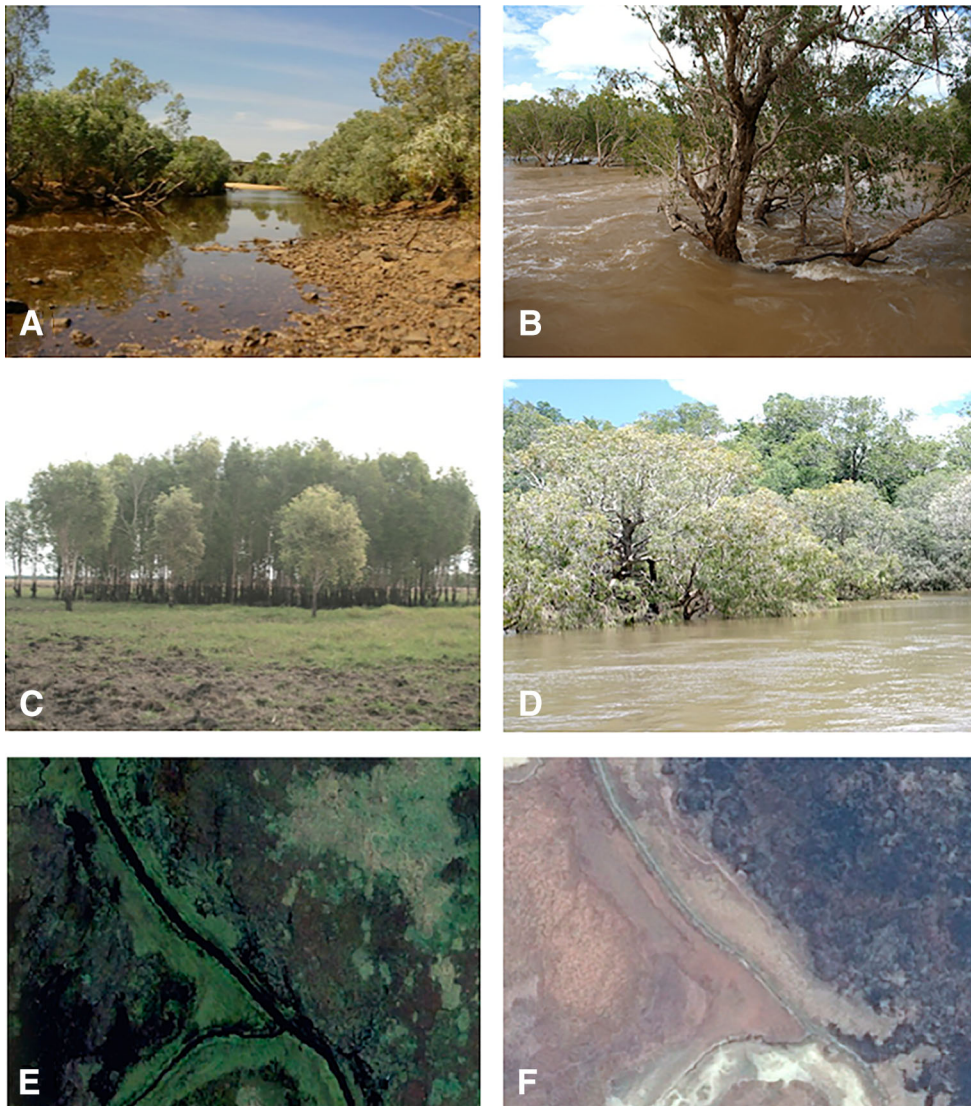


Figure 1. Illustrations of major drainage divisions in the tropical region of Northern Australia and the locations of the main rivers mentioned in the text (map produced by D. P. Ward).





**Figure 2.** Fergusson River in the Northern Territory, Australia **A** dry season disconnected pools; **B** wet season flood flows. **C** South Alligator River floodplain in the dry season and **D** late wet season. Google Earth images of the Magela Creek floodplain **E** flooded at the end of the wet season (April). Note the extent of floodwaters (*dark areas*) and flooded vegetation (*bright green*) and **F** at the end of the dry season (October) with large dry, bare areas of no vegetation and burnt patches in the *top right* third of the photo.

### CORE BIOPHYSICAL CONCEPTS FOR RIVERS IN AUSTRALIA'S TROPICS

Australia's tropical riverscapes represent a model for river–floodplain ecosystem connectivity and how it functions in the absence of hydro-modification. A political focus (ca. 2000) on potential water resource development led to a proposal of five general hypotheses of food webs and ecosystem processes for Northern Australian rivers (Douglas and others 2005) that, if correct, could inform research and management. These related to (1) seasonal hydrology as a strong driver of food web structure and ecosystem processes, (2) hydrological connectivity underpinning food web subsidies, (3) food webs being largely algal-based, (4) a few common macroconsumers having a strong influence on benthic food webs, and (5)

omnivory and short food chains being widespread. The hypotheses, based on minimal data, guided a 10+ year research programme involving multiple institutions that focussed on hydrology, geomorphology, biogeochemistry, biodiversity, productivity, food web structure as well as socio-economic factors such as values, benefits and human dependence on freshwater resources ([www.track.org.au](http://www.track.org.au); [www.nerpnorthern.edu.au](http://www.nerpnorthern.edu.au)). Major discoveries emerging from this research, as well as from concurrent research conducted by others, confirmed that seasonal hydrology and algal carbon are important for consumers (hypotheses 1, 2, 3), and that generalist/opportunistic consumers are common and widespread (hypothesis 5) and, therefore, influential in shaping the structure of aquatic food webs (hypotheses 4, 5). Based on the original hypotheses (Douglas and others 2005) as well as

**Table 1.** Summary of the Six Concepts that Underpin Ecological Processes, Connectivity, Productivity and Resilience in Australian Tropical Rivers and that Influence Selected Response Variables

Concept	Response variable	Spatio-temporal variability <sup>a</sup>	Knowledge reliability <sup>a</sup>	Evidence—tropical Australia	Evidence—other tropical rivers
1. Flow pattern variability	Primary productivity	Mod-high	High	Finlayson and others (1993), Davies and others (2008), Pettit and others (2011) and Warfe and others (2011)	Winemiller (1990) and Hamilton (2010)
	Biodiversity and habitat connectivity	Mod-high	Moderate	Morton and others (1990), Bishop and others (1995), Leigh and Sheldon (2009), Pusey and others (2011), Warfe and others (2013a) and Jardine and others (2015)	Dudgeon (2000, 2006), Stuart and others (2004), Balian and others (2008) and Vörösmarty and others (2010)
	Nutrient supply to primary producers	Unknown	Low	Finlayson (2005), Pettit and others (2011), Faggotter and others (2013), Jardine and others (2013), Fellman and others (2014) and Townsend and others (2012)	Lewis and others (2000), Hamilton (2010), Saunders and others (2006), Merriam and others (2002) and McClain and others (2003)
2. Biogeochemistry	DOC exchange	Unknown	Low	Townsend and others (2011), Fellman and others (2013, 2014)	McClain and others (1997), Lewis and others (2000), Richey and others (1990) and Aitkenhead and McDowell (2000)
	POM supply	Moderate	Low	Finlayson and others (1993), Bass and others (2013) and Fellman and others (2013, 2014)	Tabacchi and others (2000), Wantzen and others (2008) and Boyero and others (2015)
	Interannual variability	Moderate	Moderate	Townsend and others (1992), Schult and others (2007), Warfe and others (2011) and Novak and others (2015)	Winemiller and Jepsen (1998), McClain and Naiman (2008) and Power and others (2008)
3. Biotic movement	Primary productivity	Moderate	Unknown	Petty and Douglas (2010), Warfe and others (2013a), King and others (2015), Townsend and Pardon (2005)	
	Dependence on local energy	Moderate	Low	Perna and Pearson (2008) and Jardine and others (2011)	
	Trophic resources	Mod-High	Moderate	Leigh and others (2010), Jardine and others (2012a, b), Warfe and others (2013a) and Blanchette and others (2014)	Lewis and others (2001) and Zeug and Winemiller (2008)
4. Food web structure					

Table 1. continued

Concept	Response variable	Spatio-temporal variability <sup>a</sup>	Knowledge reliability <sup>a</sup>	Evidence—tropical Australia	Evidence—other tropical rivers
5. Fire	Dependence on floodplain production	Mod-High	Moderate	Bayliss and Yeomans (1990), Madson and Shine (2000), Douglas and others (2005), Pettit and others (2011) and Jardine and others (2011, 2013)	Winemiller (1996), Rodriguez and Lewis (1997), Hamilton and others (1992), Lewis and others (2000), Jepsen and Winemiller (2002), Thorp and others (2006) and Lewis and others (2001)
	Habitat provision	High	Moderate	Pusey and Arthington (2003) and Pettit and others (2001, 2013)	Arrington and others (2005) and Pettit and Naiman (2005)
	Food web energy exchange	Moderate	Low	Pettit and others (2012b), Leigh and others (2010, 2012), Davis and others (2010)	Sabo and Power (2002) and Baxter and others (2005)
	Biogeochemical linkages	Unknown	Low	Fellman and others (2014)	
	Carbon loss, altered nutrients	Unknown	Low	Gill and others (2000), Pettit and Naiman (2007), Douglas and others (2016), Cook (2003) and Schmidt and Noack (2000)	Winemiller (1996), Pettit and Naiman (2007), Bond and Keeley (2005), Certini (2005) and van Wilgen and others (2003)
6. Resilience	Biodiversity, regeneration	Moderate	Moderate	Jardine and others (2012b), Colloff and Baldwin (2010), Pettit and others (2012a) and Parsons and others (2009)	Parsons and others (2006), Turton (2012), Gunderson and Holling (2002), Scheffer and others (2003) and Naiman and others (2008)

<sup>a</sup>Level of knowledge: (1) High—the uncertainty has been resolved for Northern Australia or elsewhere at least for some focal species and in some geographical areas. (2) Moderate—additional investigation is warranted if results are not yet convincing, or the scale of information collection is not yet sufficient. (3) Low—the uncertainty is high and little information is available. (4) Unknown—no information is available from published studies. Estimates of spatio-temporal variability, knowledge reliability and key references to studies from Australian and other tropical rivers are provided.



our published research and contemporary research advances by others, we identify six ecological concepts (Table 1) that offer an expanded conceptual framework for tropical rivers and suggest ongoing themes for further investigation.

### River Flow Attributes are a Primary Driver of Spatial and Temporal Patterns in Ecological Processes

Whilst flow patterns may be highly predictable for some rivers, predictability is spatially variable across Northern Australia (Kennard and others 2010) and temporally variable within a year as flows alternate between the wet and dry seasons (Figure 2). Flow characteristics are reflected in ecological productivity patterns, in the inherent diversity of organisms and processes, and ultimately in ecosystem resilience (Jardine and others 2015). Some floodplains, for example the floodplains of the Alligator rivers in Kakadu National Park (KNP), can remain inundated for over six months, supporting high levels of aquatic primary production and often large waterbird populations (Bayliss and Yeomans 1990; Pettit and others 2011; Warfe and others 2011). In contrast, many other floodplains are inundated for only weeks or days at a time, and often the inundation is rapid, turbid, and operates as sheet flow over an essentially terrestrial landscape (Ward and others 2013). These systems are characterized by a 'flush' in terrestrial primary production post-flood while aquatic production is short-lived and largely limited to remaining waterholes following flood recession (Pettit and others 2012a). Such spatial and temporal variability leads to highly variable aquatic connectivity with considerable influences on the provision of habitat (Wasson and others 2010; Pettit and others 2013), biotic assemblages (Pettit and others 2001; Leigh and Sheldon 2009; Warfe and others 2013a), population dynamics (Stewart-Koster and others 2011; Ward and others 2014; Jardine and others 2015), biogeochemical processes (Hamilton 2010) and the use of aquatic resources by local Indigenous communities (Jackson and others 2012).

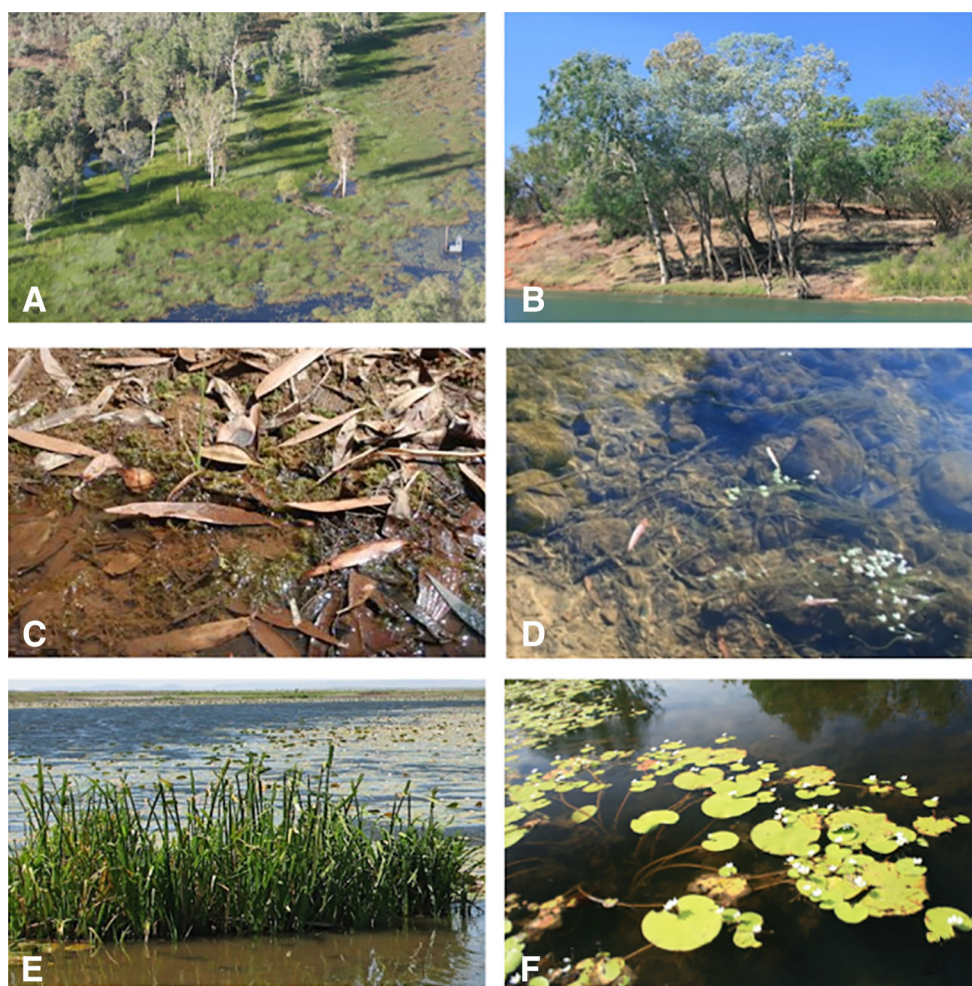
The high variation in timing and predictability of inundation and expression of stream physical characteristics (such as geomorphology and habitat) creates highly complex interactions in biogeochemical processes and fluxes (Ward and others 1999). Flooding exerts selective pressures on river biota while at the same time enhancing productivity and diversity. The consequences of the interaction between these two effects can be

understood through the pattern of timing and magnitude of flood events (rhythm; Winemiller and others 2014; Jardine and others 2015). For instance, flooding is a massive alteration of connectivity pathways (Figure 2), so that not only does an ecosystem expand and reassemble, but organisms need to renegotiate the newly configured physical pathways of connection. Where flow is highly rhythmic, biota are better able to adapt to the cycle of flooding and drought and, as well, biodiversity and annual riparian productivity are higher than for rivers with an unpredictable flood regime (Jardine and others 2015). This suggests that there is more to the relationship between flows and ecology than our original understanding of ecological response as a function of flood events and annual discharge (Junk and others 1989; Loneragan and Bunn 1999).

### Carbon and Nutrient Inputs from the Floodplain and Catchment, Modified by Biogeochemical Processes, May Provide Important Additions to Instream Productivity

The extent to which riparian zones and floodplains supply carbon and nutrients to heterotrophic microbes and primary producers in rivers as well as the dominant sources, remains uncertain. Though aquatic consumers appear to be primarily supported by algal carbon (see Concept 4 below) and the  $^{15}\text{N}$  depleted stable nitrogen isotope values of algae suggest N-fixation in some northern rivers (Davies and others 2008), sediments and terrestrially derived organic matter also contribute nutrients to support aquatic primary production (McIntyre and others 2009; Fellman and others 2013). In general, the majority of nutrients entering these river systems from the floodplain and riparian areas (in particular P) are associated with sediment inputs. In addition, for these low N systems the largest part of the bioavailable N input is likely to come from N-fixation by both algal and fish biomass. However, although terrestrial organic matter (OM) represents a relatively small source of nutrients, we suggest it may be locally important in stimulating algal productivity and thus influencing the metazoan food web, particularly in disconnected pools in intermittent streams (Blanchette and others 2014; Siebers and others 2016). While our understanding of energy sources has improved markedly over the last decade, nutrient sources and sinks represent a considerable knowledge gap (Table 1). Indications are that there may be close river/floodplain biogeochemical connectivity in the





**Figure 3.** Sources of carbon from primary producers found in riparian and floodplain habitats of tropical Australia. **A** The large plant biomass of aquatic macrophytes and *Melaleuca* spp. trees on the flooded Magela Creek floodplain; **B** *Melaleuca argentea*, a common riparian tree of Northern Australia that like most species in the Myrtaceae family produce leaves high in tannins and other volatile compounds that are not readily decomposed **C** conditioned and decomposing *Melaleuca* leaves; **D** benthic algae; **E** floodplain emergent macrophyte, *Actinocarpus grossus*; **F** floating, attached aquatic herb, *Nymphoides indica*.

input of allochthonous dissolved organic carbon (DOC) and available N and P in streams of increasing size in the Kimberley region (Fellman and others 2013). However, whether this is true more generally requires further investigation of other river systems across Northern Australia.

The intermittent flow regimes of most tropical Australian rivers means that rapid transport of carbon is effectively prevented during the dry season. This is when riparian litterfall is likely to be at its greatest. Longitudinal exchange throughout the river network is likely concentrated around transitional flow events between the wet and dry seasons and the peak wet season flows. Both terrestrial and instream organic matter delivered downstream in early season storm-flows occasionally contribute to a short period of poorer water quality (Townsend and others 1992). Such flows can also move large amounts of sediment via channel erosion and gullying (Wasson and others 2010) and has been shown in models of flow-related water quality for the Great Barrier Reef catchments (Davis and others 2016). This movement of sediments will also

provide significant nutrients and carbon to downstream reaches (Garzon-Garcia and others 2015). With increasing time since flooding, controls on stream biogeochemical processes transition from predominantly hydrological to more local scale environmental controls.

Two related factors are especially relevant: sources and fluxes of detritus and nutrient biogeochemistry:

*Sources and fluxes of carbon* Large quantities of carbon as particulate organic matter from seasonal riparian litterfall or overland flow and from channel or gully erosion are carried downstream during the wet season. As stream size increases and modern, terrestrially derived DOC accumulates, bioavailability decreases because of the refractory nature of this latter source (Fellman and others 2014). The input of allochthonous leaf litter may influence instream primary production through indirect priming effects via increased mineralization of recalcitrant OM (Guenet and others 2010). This is generally in the presence of labile carbon inputs, as mediated by microbial action (Siebers



**Figure 4.** Examples of animals that contribute to the lateral, longitudinal and long-distance connectivities of the rivers and floodplains including, **A** barramundi, *Lates calcarifer*; **B** terapontid grunter, spangled perch, *Leiopotherapon unicolor*; **C** palaemonid shrimp, *Macrobrachium spinipes*; **D** estuarine crocodile, *Crocodylus porosus*; **E** Australian pelican, *Pelecanus conspicillatus*; **F** black-necked stork, *Ephippiorhynchus asiaticus*.

and others 2016). In some headwater streams, old bioavailable DOC originating in groundwater is an important source of labile carbon, but due to its labile nature there is rapid uptake by microorganisms (Fellman and others 2014).

The species-specific characteristics of allochthonous material (that is availability, chemical and nutrient composition), as well as the diversity of aquatic microorganisms in receiving environments, play significant roles in the transformation and availability of detritus to consumers (Pettit and others 2012b). The chemical nature of DOC determines its fate; whether it remains stored in the system, undergoes photochemical or physical degradation or is transformed into dissolved inorganic carbon (DIC) via microbial degradation. Many riparian plants common to Northern Australian rivers in the Myrtaceae family, such as *Melaleuca* spp., produce leaves high in tannins and other volatile compounds that are not readily decomposed (Figure 3; Coley and Barone 1996). Decomposition requires high UV light and specialist microorganisms to facilitate breakdown into

chemical forms that are available to stream biota (Fellman and others 2013; Lambert and others 2015).

*Dynamics of nutrient biogeochemistry* Concentrations of stream water N and P are consistently low across northern rivers (Brodie and Mitchell 2005; Townsend and others 2012), with the highest concentrations occurring in waterholes at the end of the dry season (for example Pettit and others 2012a). With the onset of the first wet season flows these nutrients are redistributed across floodplains where concentrations rapidly decline through dilution and uptake (for example Hart and others 1987) or exported to the sea.

Despite an overall low nutrient environment, instream production rates of  $100\text{--}1230\text{ mg C m}^{-2}\text{ day}^{-1}$  have been recorded in Northern Australian rivers (Davies and others 2008; Townsend and others 2008; Hunt and others 2012; Burford and others 2011). This suggests that, together with N fixation, rapid bacterial degradation of photosynthetically produced DOC releases bound nutrients for primary production (Townsend and others



2011). The ancient and highly weathered geology of the Northern Australian landscape may explain low nutrient concentrations and the adaptations of algae to grow with limited nutrients. Indirect terrestrial-aquatic linkages may be a critical but poorly quantified component of river-floodplain ecosystems, especially during the dry season when hydrologic inputs of N and P are low and at these times, a sizeable fraction of N and P may be in fish biomass (Burford and others 2008). The elemental stoichiometry of many tropical streams is linked to the low availability of P. This likely leads to higher internal recycling of nutrients within biofilms or sediments (Mulholland and others 1995; Kufel and Kufel 2002) but, admittedly, it is not yet clear if this process is broadly expressed in Northern Australia.

The large plant biomass on many riparian and floodplain surfaces (Figure 3; for example, 45–60 t ha<sup>-1</sup>; Magela Creek floodplain; Pettit and others 2011) may also account for nutrient cycling and low nutrient concentrations in floodplain waters and sediments (Finlayson 2005). On the Magela Creek floodplain, the highest total N concentrations are found at the floodplain inlet in the first wet season flows but the spike in N is not detected at the outlet (Hart and others 1987). Although denitrification processes are likely to be the main driver, N sequestration across the floodplain, primarily through the growth of epiphytic algae (Pettit and others 2016) and macrophytes (Finlayson 1991) also may be significant. Recycled plant material also may be an important source of soil nutrients on the floodplain with grass detritus containing substantially higher levels of nutrients (N, P, K) than concentrations in the inputs of water from KNP streams (Northern Territory) to the floodplain (Finlayson 1991). Nutrient sequestration of 4 t total phosphorus, 9 t nitrogen oxides (NO<sub>x</sub>-N) and 14 t ammonium (NH<sub>4</sub>-N) is a significant part of the phosphorus and nitrogen accumulated in soils and aquatic plants growing on the floodplain (Pettit and others 2011). Additional nutrients from sediments are re-cycled through micro-organisms, algae and macrophytes but little is currently known about rates or specific mechanisms. How much of this is then lost to the atmosphere by fire remains an important research question (see Concept 5).

### The Movement of Biota is Facilitated by Hydrological Connectivity

Extensive movement of biota (either seasonal or long-term population exchanges) across riverscapes results in relatively cosmopolitan distributions of some species (Pusey and others 2011) and pre-

dictable assemblages across Northern Australia (Warfe and others 2013a). While these observations may be partly due to insufficient taxonomic and limited genetic knowledge of cryptic fish species (for example, Cook and others 2011) and macroinvertebrates (Garcia and others 2011), they suggest regular hydrological connectivity periodically removes or minimizes dispersal barriers, resulting in population replenishment, generalist feeding strategies (Leigh and others 2010; Pusey and others 2011) and relatively stable food web structures (Warfe and others 2013b).

Considerable lateral exchange of resources and biota occurs between rivers and their floodplains during the wet season. Animals exhibiting lateral movement in response to flooding include waterbirds, crocodiles (*Crocodylus porosus*), fish and crustaceans (Figure 4; Whitehead and Saalfeld 2000; Pettit and others 2011; Warfe and others 2011), and movement occurs even if floodplains are inundated for relatively short periods (Jardine and others 2012b). Highly productive aquatic macrophytes and grasses support recruitment and the fledglings of waterbirds (Bayliss and Yeomans 1990) and crocodiles, even though some crocodile nests risk washout during initial inundation (Webb and others 1977). Reliance of local Indigenous communities on key floodplain biota (for example, long-necked turtle *Chelodina rugosa* and lotus lily *Nelumbo nucifera*) strengthens over the wet season as access to main-stem river resources weaken proportionately (Jackson and others 2012). Small fish and invertebrates graze on periphytic algae living on plants submerged by wet season flooding and the return of these animals to permanent water can support a large fraction of the diet of larger fish and crocodiles in the rivers (Jardine and others 2012b). These movements suggest a substantial energy subsidy from the floodplain to other parts of the river network with a transition from the wet into the dry season, particularly where flow timing and magnitude are relatively predictable (Jardine and others 2015). Thus, the apparent tension between the disturbance and replenishment role of floods (Lake and others 2006) potentially may be seen in the degree of variability among food webs, communities, populations and life histories as regulated by rhythmic connectivity (Jardine and others 2015).

Longitudinal connectivity also provides for the extensive movements of biota. Over a third of fish species in Australia's tropical rivers migrate to the estuary during their life history, about another third are "estuarine vagrants" often found hundreds of kilometres upstream, and many remaining

species (for example, Plotosidae catfish) use periods of hydrological reconnection to move into tributaries and spawn (Pusey and others 2011). Movement patterns are likely to vary spatially, depending on flow regime and the location of refugia (Pusey and others 2011). In small rivers, the upstream movements of plotosid catfish and Terapontidae grunters (Figure 4) peak during the dry-to-wet transition, and downstream movements peak during the wet-to-dry transition, particularly in intermittent streams (Bishop and others 1986; Warfe and Pettit, unpublished data). In contrast, on Magela Creek, plotosids and terapontids generally move downstream (from permanent refugia upstream) during the dry-to-wet transition and then move back upstream to permanent refugia during the wet-to-dry transition (Bishop and others 1986).

Connectivity is paramount in shaping riverine community structure and trophic dynamics as food web links are made and broken across the land-water interface in response to flooding (Naiman and others 2008; Jardine and others 2015). Across Northern Australia, invertebrate assemblages differ according to hydrologic connectivity (Leigh and Sheldon 2009; Warfe and others 2013a) and biomass at many locations is dominated by migratory decapod crustaceans (for example, prawns, *Macrobrachium* sp.; crayfish, *Cherax* sp.; Jardine and others 2013). Fish diversity ranges from less than 10 species in basins with shorter and more irregular flood periods to more than 50 species in larger, more connected basins (Jardine and others 2015), and food web complexity varies accordingly. Some hydrological periods (late dry season) or basins with low connectivity have tight internal ecological links and weak external links (Jardine and others 2012a; Blanchette and others 2014), whereas those with extended connectivity have relatively weak internal links and strong external links.

### Primary and Secondary Productions Rely on Connectivity, and Sustain Food Webs

The source and quality of carbon that support aquatic consumers vary within river and floodplain ecosystems depending on the variability of environmental conditions through space and time. Periphyton are often the dominant carbon source for large consumers (Douglas and others 2005) both in waterholes (Jardine and others 2013) and on floodplains (Jardine and others 2012b; Bunn, unpublished data). Other organic matter sources can make considerable contributions to organisms lower on the food chain; however, spatial and temporal variability is large (Leigh and others 2010;

Hunt and others 2012; Pettit and others 2012b; Fellman and others 2013; Blanchette and others 2014). Leaf litter supplements invertebrate diets, as has been demonstrated for Australian wet tropics headwater streams (Pearson and Connolly 2000) and waterholes in intermittent streams of the Gulf of Carpentaria drainage (Leigh and others 2010), but the low quality of this material is a major dietary constraint and contributions to animals via this pathway likely arise from 'leakage' from the microbial loop rather than from direct consumption (Pettit and others 2012b; Fellman and others 2013). Nevertheless, observations that algae are deemed the dominant food source for metazoans have been reported from a variety of tropical systems (Lewis and others 2001; Brito and others 2006; Lau and others 2009). This is most evident in larger consumers, such as the predatory fish barramundi (*Lates calcarifer*), where isotopic evidence indicates a strong link to algal sources of carbon (Jardine and others 2012b, 2013).

Plankton appear to be unimportant in waterhole food webs except for small pelagic consumers (Jardine and others 2013). Similarly, planktonic production on floodplains is generally limited in basins with short-duration floods (for example, Mitchell River) where floodplain water column Chlorophyll *a* is less than 2  $\mu\text{g L}^{-1}$  (Jardine, unpublished data). While planktonic production may be substantial in long-duration floods such as those at KNP (Adame and others, unpublished data), there is little evidence that plankton features strongly in the diets of floodplain consumers (Bunn, unpublished data). Given these observations, bottom-up effects are likely to occur via periphyton (Garcia and others 2015a). Many Australian tropical rivers are oligotrophic and either N-limited or N and P co-limited (Faggotter and others 2013; Garcia and others 2015a; Jardine, unpublished data). Light limitation also can be important in lower river reaches (Burford and others 2011) with high turbidity during floods (>2000 NTU; Flinders River, Jardine, unpublished data).

Despite evidence elsewhere for longer maximum food chain lengths in more productive rivers (Takimoto and Post 2013), for Australian tropical rivers it was initially considered that food chain length would be relatively short (Douglas and others 2005). This has been supported to some extent as large predators such as barramundi and crocodile (Hanson and others 2015; Jardine, unpublished data) can feed 'low' in the food chain because of the presence of abundant, large-bodied herbivorous prey such as mullet (*Liza* spp.) and bony bream (*Nematalosa erebi*; compare Layman



and others 2005). Retreat of these predatory species into dry season refuges mixes them with resident biota where there are parallel short food chains terminating at high trophic levels but with relatively small bodied species such as terapontid grunters (Rayner and others 2009; Warfe and others 2013b). As a result of the mixing of itinerant and resident biota, maximum food chain lengths in these systems are similar to those in other tropical freshwater systems outside Australia (Rayner and others 2010; Jardine and others 2011), despite the largest predators feeding low on the food chain (Jardine 2016).

Larger organisms have larger home ranges and consume prey from a wider range of habitats (McCann and others 2005; Hanson and others 2015), making food webs highly scale dependent. For instance, the crocodile food web must include the entire catchment, while small fishes and invertebrates feed at the mesohabitat scale or smaller (Jardine, unpublished data). This mix of spatial scales affects different species as habitat expands and contracts confounding attempts to link food web characteristics to local environmental factors (Warfe and others 2013b). Food web linkages across habitat boundaries and between ecosystems are therefore likely to be important, but these are scale-dependent. Unfortunately, we are only beginning to understand how the habitat-to-habitat food web linkages and biogeochemical connectivity (discussed in the previous sections) are related to aquatic food web assemblages and overall ecological productivity.

### Fire is a Major Consumer of Carbon and a Contributor to Nutrient Dynamics on Floodplains

Unlike wetter African and neotropical systems where senescent primary production left by the recession of floodwaters is consumed by grazers and microbial activity (Winemiller 1996), it appears that a large proportion of the residual production on Australia's wet/dry tropical floodplains is consumed by fire (Pettit and others 2011). Much of this organic matter, therefore, does not find its way the river in a traditional sense. While floodplain and riparian fires in tropical areas have not been extensively investigated (Table 1; but see Douglas and others 2015), fire is likely to have particularly important effects on biogeochemical processing (Pettit and Naiman 2007). On Australian tropical floodplains dry season fires are a significant "consumer" of carbon and nutrients (Pettit and others 2011), with 26% of floodplains within KNP burnt

between 1996 and 2000 (Edwards and others 2003). The estimated fire return interval on the Magela floodplain within KNP (1980–2006) is five years, contrasting with two years for the adjacent savanna woodland (Bayliss and others 2006). Therefore, the more frequent savanna fires can have greater impact as they cause the loss of ground cover and increased surface erosion, which can ultimately result in sediment/turbidity spikes in river–floodplain waters. Most fires, particularly on floodplains, occur late in the dry season and are generally high intensity as fuel is drier, loads are greater and severe fire weather conditions prevail.

The impact of such fires is the production of nutrient-rich ash and loss of the litter layer and grass cover (Cook 1994). Following savanna fires, about 7% of fine fuels remain as charred fragments which contain 40–70% of P, K, Ca and 8% N and S (Cook 2003). However, N loss in a fire ( $1.4\text{--}2\text{ kg ha}^{-1}\text{ y}^{-1}$ ) is the only nutrient to exceed gains from rainfall or dry deposition (Cook 2003). Fixation of N by cyanobacteria in floodplain soils may therefore be particularly important after fire; N-fixing plants and cyanobacteria are crucial for the replacement of soil N (Cook 2003).

Black carbon (that is, charcoal), produced by incomplete combustion of plant material in wild-fires, is found in many soils and floodplain sediments (Goldberg 1985). Charcoal can raise soil pH, improve air circulation and increase the soil's ability to retain water and nutrients. Once added, the benefits of charcoal through adding carbon and nutrients and improving water holding capacity, continue for years. For instance, burning of forest that adds black carbon to infertile soils in the Amazon basin has created small areas of very fertile soils characterized by relatively high levels of organic matter, N and P (Schmidt and Noack 2000). Conversely, burning of biomass has been suggested as another important contributor to potentially refractory organic-N in soils (Cook 2003).

Increased burning of floodplains and associated rainforests and paperbark (*Melaleuca* spp.) forests has been reported for Northern Australia (Russell-Smith and others 1997). For floodplains in KNP, this may be related to the eradication of water buffalo (*Bubalus bubalis*) and the subsequent increase in aboveground grass biomass (McGregor and others 2010), particularly the establishment of invasive Para grass (*Urochloa mutica*) in many floodplain areas. As well, there is evidence of positive feedback between fires and grass invasion in other Northern Australian habitats (Butler and Fairfax 2003; Rossiter and others 2003).

Fire in riparia and floodplains reduce inputs of detritus and increase ash input to aquatic environments (Douglas and others 2015). Fires also affect ecosystem complexity by creating open patches that increase aquatic productivity during the flooded phase. In recent times, there has been a willingness to re-introduce traditional fire management to areas such as the KNP wetlands (MacGregor and others 2010). These traditional patch-burning practices have the potential to enhance biodiversity as well as the cultural importance of these wetlands to local Aboriginal people. Effective burning for natural resource management and for culture requires the cooperation of western science and traditional Aboriginal expert knowledge that has developed over generations (McGregor and others 2010). Intensive fire management for tropical floodplains and rivers is needed to develop fine-scale habitat patchiness so that the multiple objectives of C sequestration, emissions' abatement and biodiversity conservation can be achieved (Richards and others 2011).

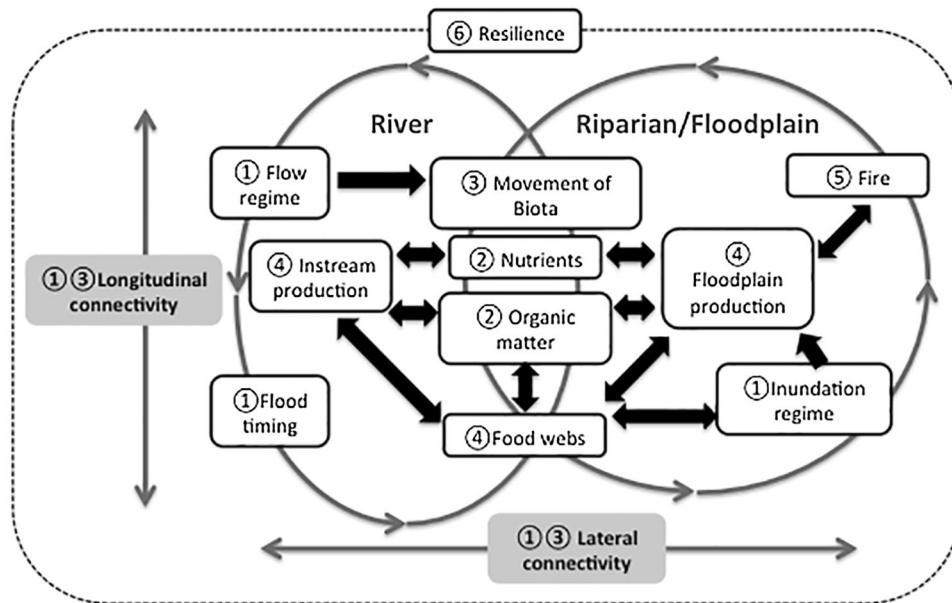
### Through Adaptation to Changing Ecological Conditions, River–Floodplains Have Inherent Resilience to Natural Variability but Only Limited Resilience to Artificial Modifications

Ecological resilience is measured as the magnitude of change that a system can absorb before the system re-assembles into another state, often with different controlling variables and processes (Gunderson and Holling 2002; Gunderson and others 2002; Scheffer and others 2003). The focus of ecological resilience is on maintaining key ecosystem functions (Gunderson and others 2002), such as biogeochemical processes or recruitment events. Properties that confer general resilience include diversity of species, habitats and processes, as well as linkages between these components and the various feedbacks that are at play (Table 1; Dam-bacher and others 2002; Walker and Salt 2006).

In the Australian wet–dry tropics, the dynamics of river and floodplain ecosystems are to a large extent determined by high variability and low predictability in seasonal flooding and drought. The ecological systems change rapidly but then restructure to similar conditions after a major disturbance. Annual floods provide natural change that displaces biota, alters water quality and triggers regrowth of aquatic plants before ultimately returning to a state with characteristics similar to those preceding the flood (Pettit and Froend 2001; Pettit and others 2012a). Variability in flows is

likely to be important in conferring resilience on river systems by enabling a range of biological and physical characteristics to interact with the life history traits of biota (Naiman and others 2008; Davies 2010). This variation in the physical environment, such as shape and depth of waterholes and the type and extent of riparian vegetation, also contributes to resilience in that there is a diversity of biophysical ecosystem functions (Colloff and Baldwin 2010; Pettit and others 2012a). The importance of maintaining flow connectivity between floodplain waterholes and the river, together with sufficient variability in the flow regime (Naiman and others 2008; Opperman and others 2010), allows the seasonal resetting of conditions that maintain resilience. There is evidence from a South African savannah river of floods leaving a heterogeneous imprint on the riparian ecosystem, resulting in multiple trajectories of ecological responses, indicating the longer term resilience of the river to natural floods (Table 1; Pettit and Naiman 2005; Parsons and others 2006). Unfortunately, there is little direct evidence of a similar nature for tropical Northern Australia (see Pettit and others 2012a). Because multiple consumers (for example, Magpie geese, *Anseranas semipalmata*; Bayliss and Yeoman 1990) take advantage of the connectivity provided by inundation and move onto the floodplain, and later switch (at low water) to consuming macrophytes and allochthonous carbon sources, this demonstrates species-scale resilience to flooding through an ability to adapt to changing conditions. Resilience is also seen through the persistence of benthic algal communities in smaller upstream tributary refuges during scouring wet season flows. Algae from these refuges recolonize the main channel when floodwaters recede (Townsend and Douglas 2014).

Like other types of natural ecosystems, Australian tropical river landscapes are characterized by episodic change, patchiness, variability and expression of processes at multiple scales (Warfe and others 2011; Jardine and others 2015). In essence, they can have multiple stable states, some of which have high resilience (Gunderson and Holling 2002). For instance, biophysical heterogeneity and temporal variations in precipitation, flow and flooding operate as selective pressures on biota and result in a broad range of life history traits across tropical Australia as well as within catchments (Bunn and Arthington 2002; Lytle and Poff 2004). This broad range of traits maintains greater functional diversity, allowing a greater range of biota to 'share' the same system and thereby provides a greater scope for sustaining biodiversity and



**Figure 5.** Complexities and connectivities of biogeochemistry and food web components for tropical river floodplain systems summarizing the concepts (numbered) discussed in this article. Flow regime (Concept 1) including flood timing and inundation patterns are the major drivers of biogeochemical processes of nutrients and organic matter (Concept 2), as well biotic movement both laterally and longitudinally (Concept 3), which in turn influences aquatic food webs and productivity (Concept 4). In riparian and floodplain areas in the wet/dry tropics, fire is a major consumer of carbon (Concept 5), as well as an important factor in nutrient redistribution. Natural river/floodplain systems are also likely to have high resilience (Concept 6) to high natural variability in flow regimes.

ecosystem resilience (Poff and Allan 1995; Poff and others 1997; Ward and others 1999; Naiman and others 2008; McCann and Rooney 2009).

There are a number of traits that enable plants to cope with historic riparian and floodplain conditions (Catford and Janson 2014). These include traits that allow tolerating or avoiding anoxia and enabling underwater photosynthesis, traits that confer resistance and resilience to hydraulic disturbance, and attributes that facilitate dispersal, such as floating propagules (Naiman and Décamps 1997). Nevertheless, the vulnerability of riparian and floodplain ecosystems to emerging conditions, such as climate change, is potentially problematic. Their potential exposure, sensitivity, and the adaptive capacity of key biotic components and processes, as well as the potential for invasion by non-native species are all responsive to environmental change (Catford and others 2013). For example, on the floodplains of KNP, the invasive Para grass has the potential to reduce the resilience of the floodplain ecosystem through directly reducing diversity of plants' species and indirectly by altering fire regimes (Douglas and O'Connor 2004). Also, this C4 species is not utilized in the floodplain aquatic food web (Douglas and others 2005), and the dense growth and vertical dimen-

sions of Para grass are likely to also reduce algae production (Pettit and others 2016), a key food source for secondary production on the floodplain.

Physical changes such as trampling and grazing by livestock and other introduced mammals, or widespread hydrological alterations, have the potential to reduce system resilience and cause regime shifts in riparian and floodplain conditions. Feral water buffalos were introduced to the Alligator rivers area in Northern Australia in the early 1800s, and their numbers increased rapidly causing widespread destruction of floodplain habitats and loss of species and ecosystem resilience (Skeat and others 1996; Petty and others 2007). An extensive eradication programme substantially reduced buffalo numbers and, in combination with changed fire regimes, led to large increases in native grass *Hymenachne acutigluma* in wetter areas and exotic Para grass in drier areas, where it replaced native wild rice (*Oryza* spp.), an important food plant for magpie geese (Ferdinands and others 2005). This suggests that the KNP floodplains, for example, were resilient (particularly in the wetter areas) to widespread trampling and grazing by water buffalo. Although the vegetation was denuded across much of the floodplains, within a few years of the buffalo removal, the native plants recolonized and no

species were actually lost (Petty and others 2007). Residual populations of seed banks persisted long enough for recolonization to occur once grazing pressure was removed, suggesting low resistance but high resilience to grazing.

In contrast, projected climate-related sea-level rise is likely to lead to the crossing of a major abiotic threshold for low elevation floodplains as inundation by saltwater and hydrologic alterations following from saltwater intrusion will result in fundamental changes. It is expected that the new saline environment will be recolonized by salt tolerant plants such as mangroves as freshwater vegetation dies out (Catford and others 2013; Bayliss and others 2016). Therefore, although these floodplains may be resilient to other disturbances due to a long history of adaptation to flooding, fire and grazing, it would appear that they would be very unlikely to maintain resilience to rapid sea-level rises.

Australian tropical floodplain rivers operate within a range of natural flow regime variabilities, which can be large and unpredictable (for example, Flinders River) or relatively less variable and more predictable (for example, the Alligator rivers of KNP; Ward and others 2013, 2014). However, if flow variability is extreme (or much reduced) it can have negative effects on biodiversity and productivity (Jardine and others 2015) and ecosystem resilience (Lake and others 2007; Naiman and others 2008). Biophysical alterations, other than the natural flood regime, which cause changes to timing and decreases in magnitude, duration or predictability of flood events, are likely to be detrimental and severely 'test' the resilience of river systems and possibly lead to a change of state. For example, the Ord River in the Kimberley region of Northern Australia was dammed in 1963 and a larger dam constructed 50 km upstream in 1973. River regulation in the ensuing 40 years has produced large ecological changes throughout the downstream river system as the natural highly variable flow regime has been radically changed (Doupé and Pettit 2002). Although there has been some recruitment and increased density of riparian plants in a much narrower riparian zone, restricted to areas close to the river flows, there has been a significant alteration in the age class structure and the spatial distribution of the riparian trees (Doupé and Pettit 2002). This is likely to reduce resilience of the riparian forest to large disturbances such as large floods or fire. As well, the impoundment has had a pronounced impact on the life histories of many fish species and dramatically reduced the

distribution (and the abundance) of barramundi to about one-quarter of its former range in the river (Doupé and Pettit 2002).

Knowledge of riverine and riparian attributes that confer stability and resilience is critically important in management, particularly in the face of possible combined stressors of invasive animals, weeds, water resource development, and climate change (Pusey and others 2011). Maintaining or restoring natural flow regimes and their natural variability is thus fundamental to the ecology of river systems (Naiman and others 2008; Warfe and others 2011) and therefore is a primary goal of environmental flow regulations designed to maintain ecosystem resilience (Davies and others 2014). In a practical sense, this entails maintaining high biodiversity, natural habitat dynamics and biophysical variability over the long term, which in turn supports ecosystem-scale characteristics underpinning productivity and resilience (McCann and Rooney 2009). Unfortunately, understanding specific ecosystem characteristics and processes conferring resilience remain poorly documented for Australian tropical rivers. In particular, investigations are needed that span many seasons in order to capture the true natural variability and thereby provide insights into understanding and managing specific characteristics and processes imparting resilience to these riverine ecosystems.

## UNDERSTANDING THE ECOLOGICAL INTEGRITY OF NATURAL TROPICAL RIVERS

Many tropical rivers, including those in South America, Africa and Asia, have sustained seasonal flood pulses driven by annual precipitation patterns (for example, Junk and others 1989; Dudgeon 2000; McClain and others 2014; Winemiller and others 2014). These changes in flow alter concentrations of dissolved nutrients, the fates of carbon, aquatic primary production, densities of aquatic organisms, and the strength of top-down effects of animals on basal resources that shift as the annual flood pulse progresses. This emphasizes the predictable and gradual changes in consumer–resource interactions and biogeochemistry associated with the seasonal flood pulse in tropical rivers around the world, which exhibit many similarities to tropical rivers in Australia (Table 1; Figure 5; Jardine and others 2015; Davis and others 2016). These biogeochemical and biotic interactions act within and across scales from micro-surfaces within a pool up to the macro-scale of entire catchments.



The sum of growing knowledge of tropical rivers in Australia and elsewhere aligns well with the recently developed river wave concept (RWC; Humphries and others 2014). In this river ecosystem model, the components of a wave (trough, crest, ascending and descending limbs) correspond to seasonal changes in river flow that have consequent effects on ecological processes. The RWC integrates the three well-established models of riverine function (for example, the river continuum concept—RCC; Vannote and others 1980; the flood pulse concept—FPC; Junk and others 1989; and the riverine productivity model—RPM; Thorp and others 2006) with each model describing processes corresponding to different wave components. This provides an intuitive conceptual overview for river–floodplain ecosystems and how their structure and function are regulated by hydrological connectivity. For example, the disconnection of many river and floodplain aquatic habitats during the dry season correspond to the river wave trough, where local autochthonous production, local allochthonous inputs, decomposition and assimilation predominate, as described by the riverine productivity model (Thorp and others 2006) and as observed in Northern Australia (Pettit and others 2011; Jardine and others 2013; Pettit and others 2012b). On the ascending and descending limbs of the river wave, longitudinal transport of energy and materials are emphasized, as elaborated in the RCC (Vannote and others 1980). In Northern Australian rivers, the transition between the wet and the dry seasons is a key period for material transport (Townsend and others 1992; Schult and others 2007), biotic movement (Jenkins and Forbes 1985; Pusey and others 2011; Warfe and others 2011) and primary production (Pettit and others 2011; Garcia and others 2015b). At this time, large consumers are likely to acquire most of their annual growth from feeding at seasonally available specific locations. The crest of the river wave corresponds to sustained flooding and inundation that facilitates lateral exchanges of energy and materials across the riparian and floodplain zones. This period is well described in the FPC (Junk and others 1989) and is widely observed in Northern Australia (Jardine and others 2012b, 2015).

## RESEARCH CHALLENGES AND MANAGEMENT IMPLICATIONS

The functioning of tropical river systems (and river systems in general) is characterized by an unusual

complexity of ecological processes as well as the importance of river–floodplain/riparian linkages (Table 1; Figure 5). These affect key biogeochemical processes that underpin nutrient availability and primary production as well as how connectivity shapes aquatic food webs and diversity. As noted by Marcarelli and others (2011), our limited understanding of linkages between biogeochemistry and food web processes is a key knowledge gap. To achieve better understanding of how and when these processes operate, cross-disciplinary studies are required to merge terrestrial and aquatic ecology with biogeochemistry and hydrology. For instance, despite a general acknowledgement of the critical role of algae as a basal carbon source in tropical rivers and floodplains, there is little documented knowledge about the dynamics of these primary producers, particularly diversity, production, turnover rates or nutrient dynamics (Townsend and Padovan 2005; Ganf and Rea 2007; Townsend and Douglas 2014). A topic not well understood for tropical rivers is the role of terrestrially derived carbon and nutrients (via subsurface as well as overland flows), especially their role in stimulating instream and floodplain production (Fellman and others 2013; Fellman and others 2014). Documenting the mechanics and dynamics of these linkages is a primary challenge for future research. This includes a fuller understanding of the importance of the variability of flows and connectivity as well as the consequent range of biogeochemical and biotic responses.

Although there are some tropical rivers that still have largely unmodified flow regimes, this is rapidly changing. For example, in Andean tributaries of the Amazon River, 151 new dams over 2 MW are planned over the next 20 years (Finer and Jenkins 2013). This will result in a significant loss in connectivity between headwaters and the lowland reaches of the Amazon which relies on headwater streams for carbon and nutrient supplies (McClain and Naiman 2008). This challenge is also facing Northern Australian rivers, with a strong political interest in development, particularly of water resources (<http://industry.gov.au/ONA/WhitePaper/index.html>). A major consequence of water extraction in Australian systems is likely to be reduced dry season baseflows in perennial rivers. A reduction in baseflow has the potential to reduce the availability of critical flow-sensitive habitats, break vital river/floodplain seasonal re-connectivity, and reduce overall ecosystem complexity (Warfe and others 2011; King and others 2015). Increased flows due to river regulation or dewatering from mining operations are also likely

to have large ecological effects, especially the change from ephemeral to permanent flow regimes (Doupé and Pettit 2002; Fellman and others 2011). Therefore, environmental flow assessment needs to include fundamental ecosystem processes related to the connectivity between the river and the floodplain such as biogeochemical fluxes, rates of primary production and carbon dynamics.

There are few holistic investigations of ecological processes, connectivity, productivity and resilience in tropical regions (for example, Amazon; McClain and Naiman 2008), and limited investigative work in the Australian tropics (Hamilton and Gehrke 2005). In terms of the effects of development on river ecosystem processes, there is an important need to reconcile ecological water requirements with proposed developments and commercial water usage in Northern Australia (Chan and others 2012; Leigh and others 2012; Stoeckl and others 2013). This includes the importance of hydrological connectivity and its role in mediating the transfer of materials to aquatic organisms. It is also imperative to incorporate ecological understanding and management within a social context (Jackson and others 2011; Naiman 2013; Rieman and others 2015) because the riverine resources are often central to regional communities.

Whilst water resource development is clearly a contemporary issue that will certainly alter Australian tropical riverscapes, there are other pervasive issues to consider. These include ongoing climate change, sea-level rise and the proliferation of invasive species, especially fire-prone plants (Pusey and others 2011; Catford and others 2013). Riparian zones and floodplains are considered “hotspots” for climate change adaptation (Capon and others 2013) because they may respond either positively or negatively depending on management actions. Riparia and floodplains in the twenty-first century are likely to play a critical role in determining the vulnerability of natural and human systems to climate change, and in influencing the capacity of systems to adapt. Australia’s tropical riparia and floodplains are particularly vulnerable to the impacts of climate change due to their high levels of exposure and sensitivity to climatic stimuli (for example, flow regimes, importance of seasonal connectivity and fire). It is highly possible that riparia and river–floodplains will maintain resilience to some forms of disturbance such as fire and grazing as a result of their history under substantial levels of climatic and environmental variability. Equally likely, however, is the expectation that they will have low resilience to climate change effects such as rising sea levels.

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