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Ecology of streams in a biogeographic isolate—the Queensland Wet Tropics, Australia

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Abstract: Global studies of streams are needed to develop general ecosystem and management models. We reviewed research that tested ecological models in streams of the Queensland Wet Tropics bioregion (QWT), which makes up 0.26% of Australia but supports distinctive and high biodiversity, most of which is of Gondwanan or marine origin. QWT streams have seasonal but perennial flow, high insolation, and higher diversity of riparian vegetation, invertebrates, and fish than temperate streams. Consistent physical conditions sustain biological processes through the year, and predictable wet seasons, but unpredictable floods, have shaped a resilient and opportunistic biota. Stream food webs are dominated by predators, and prey turnover is rapid. Small streams are heterotrophic and become autotrophic as canopies open in larger streams. Predation and competition influence assemblage composition most in the dry season, when habitats contract and densities increase. Riparian clearing, weed invasion, and agricultural contamination affect table lands and floodplains. High temperatures exacerbate weed growth and eutrophication, but contaminants may be diluted by high flows from forested catchments. Climate change probably will cause warming and greater hydrological seasonality, threatening endemic species. The biophysical characteristics of QWT streams are found elsewhere in the tropics, but the species pool is not. QWT streams are important because of their insular and remnant nature. Patterns and processes can differ between QWT and comparable temperate systems because of biogeographic and biophysical characteristics and their interactions with anthropogenic effects, exacerbated by the tropical climate. Research in the QWT both affirms and contradicts theories of stream ecology, underpins conservation and management needs of tropical streams, and provides points of reference for comparative studies in stream ecology, conservation, and management.

Key words: tropical stream, invertebrate, fish, diversity, pollution, endemic, conservation, management

Development of ecological theory in fresh waters has generally tracked and sometimes preceded developments in other systems (Hildrew and Townsend 2007). Research on streams has included descriptive studies of populations and communities; tests of theory regarding habitats, competition, disturbance, and trophic dynamics; investigations of landscape processes and human effects; and development of tools for monitoring ecosystem health and conservation planning. Research in the tropics has largely mirrored this progression, but usually with a substantial time lag. The main characteristic of the tropics—consistent insolation (day length, high temperature) through the year—appears to have a major influence on biological processes (e.g., life cycles, productivity) and emergent properties (e.g., diversity) in fresh waters (Boulton et al. 2008). However, the tropical

realm is a vast area with various climates (dry–wet, seasonal–aseasonal), biogeographic and evolutionary histories, landforms and fresh waters, and available information is geographically limited (Jacobsen et al. 2008, Boyero et al. 2009). Studies are needed in regions with differing biogeographic and biophysical characteristics to develop general or comparative ecological models of stream biodiversity, ecosystem functioning, and management guidelines (Minshall 1988, Wantzen et al. 2006). This need provides a rationale for much research on streams of the Queensland Wet Tropics biogeographic region (QWT).

Researchers on the ecology of QWT streams have addressed issues identified above with questions aimed at testing general ecological principles in a tropical setting (Fig. 1). These questions have addressed the biophysical

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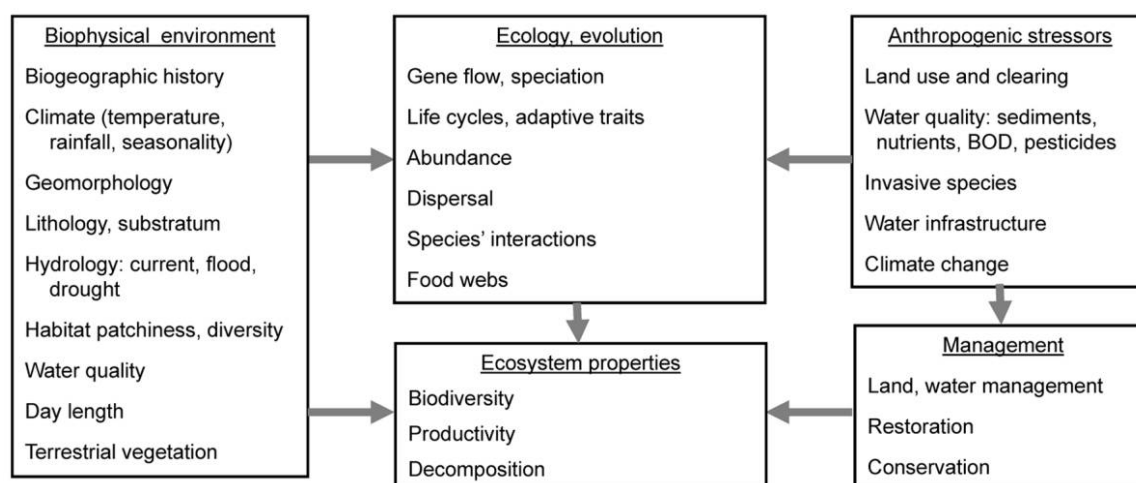


Figure 1. Biophysical factors, ecological/evolutionary patterns and processes, anthropogenic influences, and their interrelationships in Queensland Wet Tropics (QWT) streams. Arrows represent research questions of the type 'How does X affect Y?' linking many items in separate boxes, as discussed in this review. BOD = biochemical O₂ demand.

drivers of ecological patterns, species interactions, ecosystem processes, and anthropogenic disturbance and management. Underlying themes have been to elucidate whether the ecology of these streams is, like the broader QWT, at all remarkable and, if so, how; whether ecological patterns and processes fit accepted paradigms; how any differences are determined by tropical biophysical characteristics; and, therefore, to inform more general models of stream ecology and management.

THE QWT BIOPHYSICAL ENVIRONMENT

Australia is an unusual continent biogeographically, having separated from other Gondwanan continents ~100 million years ago and, unlike South America, Africa, and India, having never reconnected with northern continents (Johnson 2004). The QWT occupies 18,497 km², only 0.26% of the continent. It is a discrete area of humid tropical forest at the edge of the predominantly arid and semi-arid environments (the dry and wet-dry tropics) of northern Australia (Fig. 2). Landforms include weathered 180-million-year-old mountains, table lands, steep escarpments, and coastal floodplains (Nott 2005). The landscape is largely granitic, with some basaltic intrusions. Easterly flowing streams are short, with limited floodplains, but those draining to the west have shallower gradients and join the large Mitchell and Burdekin Rivers, outside the QWT (Fig. 2). Vegetation is mainly rain forest but with woodlands (lowland open forests and coastal mangroves) at the margins (Webb and Tracey 1981). The QWT is remarkable for its ancient rain forests, high biodiversity, and indigenous cultural history, which underpin its listing as a World Heritage Area (WTMA 2013). Most of the table land and lowland forest has been cleared for agriculture over the last ~150 y.

The region has a tropical climate and is the wettest part of Australia. Summer mean daily temperatures are

23–31°C on the coast and 17–28°C in the uplands; winter temperatures are 18–26°C and 9–22°C, respectively; extreme temperatures range from ~0°C on mountains to 40°C in the lowlands; and mean annual rainfall is 1200 mm inland to 8312 mm on Mt Bellenden Ker (annual maximum 12,461 mm) (Australian Bureau of Meteorology data). Over 60% of rainfall occurs in the December–March wet season, and is driven by monsoonal systems and cyclones that dump huge quantities of water on the landscape.

QWT streams are ancient, and probably have remained perennial over millions of years (Nott 2005). The region is drained by 13 mainly small rivers, which flow east to the Great Barrier Reef (GBR) lagoon (Coral Sea) or north to the Gulf of Carpentaria (Fig. 2), and by numerous low-order streams. Substantial connectivity exists between the QWT and GBR aquatic habitats, and many fish and crustacean species use both during their life cycles (WTMA 2013). Stream flow is seasonal and peaks in the late wet season. Base flow contributes a high proportion of total flow, and the annual hydrograph is predictable, although the precise timing of floods is not. Predictability decreases toward the margins of the region (Kennard et al. 2010). Most streams are perennial, with dry-season base flows sustained by aquifers, orographic rainfall, and forest cloud capture (McJannet et al. 2007), but surface flow can cease in the dry season in streams toward the QWT margins, leaving a series of unconnected pools (e.g., Perna and Pearson 2008). Wet-season spates develop rapidly, and floods replenish distributaries and connect wetlands (Karim et al. 2011), but unlike flood-pulse rivers (Junk et al. 1989), do not drain back through the main river channel. Floods scour stream substrata and remove leaf litter and macrophytes, causing shifts in invertebrate and fish assemblages and food webs (Cheshire et al. 2005, Pearson 2005, Rayner et al. 2008, 2010).

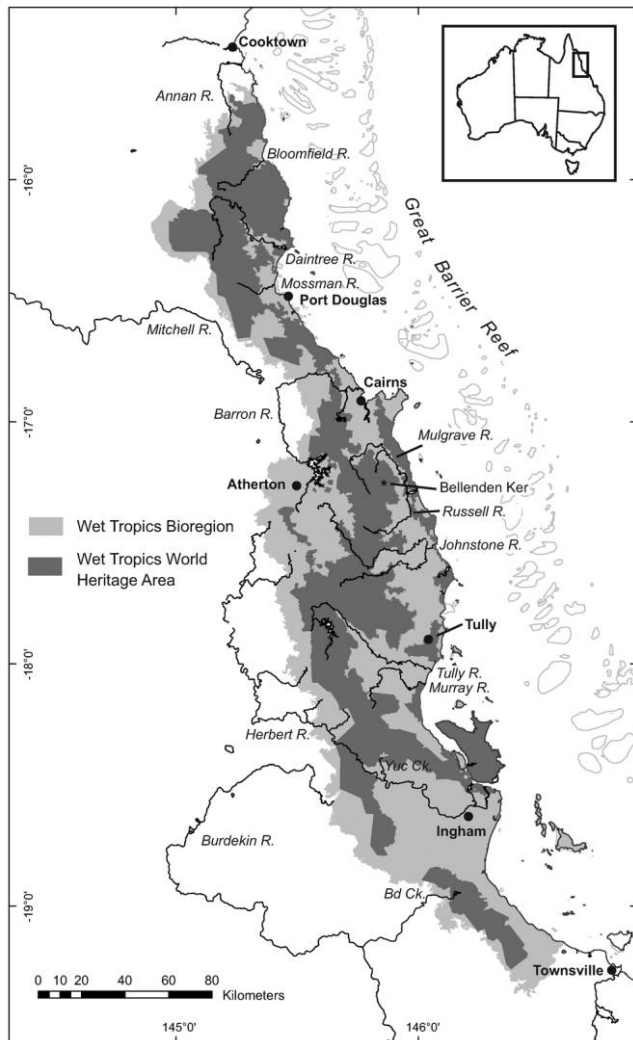


Figure 2. Map of the Australian Wet Tropics biogeographic region showing locations of the Wet Tropics World Heritage Area, major rivers and towns, 2 small streams referred to in the text (Yuccabine Creek [Yuc Ck] and Birthday Creek [Bd Ck]) and Mount Bellenden Ker, site of Australia's maximum annual rainfall.

The mountains are ancient and weathered, so QWT streams typically start with moderate gradients and have sandy substrata. They descend through steep valleys and have rocky substrata before emerging on to the floodplain, where substrata are mainly sandy, with occasional riffles and silty pools (Pearson 2005, Connolly et al. 2007a). Most of stream channel length is in low-order streams (at 1:100,000 scale, orders 1–3: 88%, orders 4–6: 12%; Januchowski-Hartley et al. 2011), like streams elsewhere (e.g., Benda et al. 2004).

Streams are generally warm and have low concentrations of dissolved material: in 75 forest streams across the QWT and across seasons, water temperature was 13–27°C, electrical conductivity 20.0 to 110.9 $\mu\text{S}/\text{cm}$, and pH 5.5

to 8.5, although water temperatures as low as 8°C have been recorded in the uplands (RGP, unpublished data). Lowland streams have greater maxima. For example, in streams on the Herbert River floodplain, conductivity was up to 2000 $\mu\text{S}/\text{cm}$, pH to 8.9, and temperature to 32°C (Pearson et al. 2003). Nutrient concentrations are typically low, except where streams are contaminated by agricultural runoff (Connolly et al. 2007a). Biophysical condition clearly differs between undisturbed upland streams and floodplain streams, particularly those that receive agricultural runoff in deforested landscapes (Connolly and Pearson 2004, Pearson and Stork 2008).

BIODIVERSITY, ECOLOGY, EVOLUTION

Biodiversity of QWT streams

Biodiversity is generally greatest in humid tropical regions, with several possible causes, including climatic stability, high productivity, high rates of speciation, large contiguous area, and overlap between realms (e.g., Willig et al. 2003). Correspondingly, the QWT is Australia's most biodiverse region and supports a high proportion of the continent's plant and animal species, including aquatic plants (Ramsay and Cairns 2004, MacKay et al. 2010), stream invertebrates (Pearson et al. 1986, Lake et al. 1994, Connolly et al. 2008), and freshwater fishes (Pusey et al. 2008). Research on biodiversity has included inventory, taxonomy, phylogenetics, and questions regarding the factors that have created and sustained it (Fig. 1).

Invertebrates Alpha diversity of stream invertebrates is comparable to that of other tropical regions (Vinson and Hawkins 2003), but it varies among taxa, e.g., high for Trichoptera but low for Plecoptera (Pearson and Boyero 2009) (Table 1). For some taxa, especially nonarthropods, it is uncertain because of limited research. Decapod crustaceans are common throughout most stream systems and comprise the Parastacidae (crayfish) of Gondwanan origin and the marine-derived Palaemonidae and Atyidae (shrimps). Insect taxa are largely Gondwanan in origin, with cool-adapted species in the uplands, but also include Oriental elements. Thus, some temperate species of Chironomidae occur in the uplands, whereas cosmopolitan taxa are characteristic of the lowlands (McKie et al. 2005). Genetic studies indicate antiquity of some lineages with restricted dispersal (Krosch et al. 2009), and endemism is high in some taxa. For example, different species of the large crayfish *Euastacus* (Parastacidae) occur on different mountain tops as a result of vicariant speciation (Ponniiah and Hughes 2006). Patterns of diversity vary among taxa. For example, endemic species of Ephemeroptera have restricted distributions (probably because of their short adult lives), limited dispersal abilities, and require cool streams (Christidis 2003, Christidis and Dean 2005), whereas species of Trichoptera and Chironomidae are more widely distributed (McKie et al.

Table 1. Species richness, endemism in the Queensland Wet Tropics (QWT), and biogeographical origins of selected QWT taxa. 'S, global' = regional QWT (γ) richness compared with richness at global scale; 'S, Aus' = regional QWT (γ) richness compared with other Australian regions; and 'S, site' = site-scale (α) richness compared with α richness at global scale. Relative richness and endemism at each scale indicated by x = low, xx = moderate, xxx = high.

Taxon	S, global	S, Aus	S, site	Endemism	Main origin	References
Bryophytes	xx	xxx	xx	xx	Gondwana, Oriental	Ramsay and Cairns 2004
Macrophytes	xx	xxx	xx	x	Cosmopolitan	Mackay et al. 2010
Decapoda	xx	xxx	xx	xxx	Marine	Short and Davie 1993, Connolly et al. 2008
Plecoptera	x	x	x	xx	Gondwana	Sheldon and Theischinger 2009
Ephemeroptera	xx	xxx	xx	xxx	Gondwana	Christidis 2003, Connolly et al. 2008
Odonata	xx	xxx	xxx	xx	Gondwana	Theischinger and Hawking 2006
Trichoptera	xxx	xxx	xxx	xxx	Gondwana	Benson and Pearson 1988, Walker et al. 1995
Chironomidae	xx	xx	xxx	xx	Gondwana, cosmopolitan	McKie et al. 2005, Connolly et al. 2008, Krosch et al. 2009
Osteichthyes	xx	xxx	xx	xxx	Marine	Pusey et al. 2008, Unmack 2013
Anura	xx	xxx	xx	xxx	Gondwana	Hero and Hoskin 2008

2005, Connolly et al. 2008). Gondwanan origins and endemism suggest that the QWT uplands are significant refugia because they were buffered against Pleistocene climate-change effects (McKie 2002, Pearson 2005, Krosch 2006). Taxa that do not follow the common trend of high tropical diversity (e.g., Plecoptera) are most speciose at higher latitudes and altitudes in cool waters, which is where they originated (Pearson and Boyero 2009). Most ecological studies have focused on crustaceans and insects, and other taxa, such as Oligochaeta, are less well known.

Fish Compared with other continents, Australia is depauperate in primary freshwater fishes because of its generally dry climate and because its Gondwanan origins precluded occurrence of northern families. None of the Gondwanan Galaxiidae of southern Australia occur in the QWT, and the fauna is of marine origin, with several families showing substantial phylogenetic and ecological diversification (Pusey et al. 2008, Davis et al. 2012b). The QWT supports Australia's highest diversity of freshwater fish (131 native species, including 86 obligate freshwater species, representing most of the non-Gondwanan families) (Unmack 2013). Variable flow predictability can explain variation in fish diversity in QWT streams through effects on habitat and other resources (Pusey et al. 1995, 2000). Major streams of the QWT have been well surveyed (Pusey et al. 2008), so the recent discovery of 13 species of goby (10 new to Australia, 3 undescribed) in short coastal streams was surprising (Thuesen et al. 2011). These species have a marine larval phase and have close relatives across the Pacific, so the fauna of these streams resembles that of Pacific islands rather than larger QWT streams. In addition, cryptic taxa may exist, such as within the Gudgeon *Mogurnda adspersa* with population affinities determined

by past geomorphic events (Hurwood and Hughes 1998, Adams et al. 2013), and Rainbowfish *Cairnsichthys rhombosomoides* with distinct populations minimally separated (~5 km) within streams (Thuesen et al. 2008).

Other vertebrates Freshwater vertebrates in the QWT include 30 frog, 16 reptile, 73 bird, and 3 mammal species (Williams et al. 1996). Sixteen frog species breed in streams (Hero and Hoskin 2008), 8 of which have declined as a result of infection by the fungus *Batrachochytrium dendrobatidis* (McDonald and Alford 1999). Stream reptiles include 6 turtle, several snake and lizard, and 2 crocodile species—*Crocodylus johnstoni* in some upper catchments, and *C. porosus* in the lowlands (WTMA 2013). Larger streams are frequented by many bird species, from kingfishers to cormorants, and many forest birds feed on emerging insects (RGP, unpublished data). The platypus (*Ornithorhynchus anatinus*) occurs in upland streams and has several distinct genetic groups (Kolomyjec et al. 2013). However, little research has been done on the ecology of these vertebrates in the QWT.

Thus, the QWT faunal species pool is mainly of Gondwanan or marine origin, supplemented by Oriental taxa. Two shrimp lineages are of marine origin and are temperate-tropical cosmopolitan, but fish origins and radiation are peculiar to Australia and reach their zenith in the QWT. Within the small QWT region (approximately the size of New Jersey) substantial diversification of invertebrates and fish reflects the stable longevity and isolation of the region, persistence of streams, fluctuating but equable climate, and changes in drainage patterns (Hurwood and Hughes 1998, Nott 2005). Knowledge across taxa, from plants to vertebrates, is variable, and some groups (e.g., Chironomidae) are unusually well documented, but with much remaining

unknown, as indicated by discoveries within 2 of the more obvious stream taxa (mayflies and fishes; see above). Many invertebrate groups are not well described, but even more remains to be discovered for the largely unknown microbial assemblages that drive important ecological processes. Developing environmental DNA technology will greatly facilitate future studies of biodiversity (Thomsen et al. 2012).

Habitats

Stream habitats are defined by flow velocity, substratum particle size, flood/drought disturbance, water physico-chemistry, light regime, in-stream and riparian vegetation, and seasonal variation. Species interact with other species and with habitats via their movements, requirements, and adaptive traits (e.g., McAuliffe 1984, Townsend and Hildrew 1994, Lamouroux et al. 2004). The result is local species composition, which is a sample of the regional species pool (Caley and Schluter 1997). Researchers working in QWT streams have tested hypotheses regarding the importance of habitat and biotic interactions in determining local assemblage composition and structure.

In the QWT, invertebrate α diversity is greatest in upland streams, where benthic habitat diversity and patchiness are greatest (Connolly et al. 2008), and where upland climate refugia appear to have sustained a richer fauna than the lowlands (Pearson 2005). Invertebrate assemblages are more abundant and diverse in riffles than in pools (Cheshire et al. 2005), as elsewhere (Brown and Brussock 1991), although elevated wet-season flows reduce the distinction because riffle species spread to temporarily lotic pools (Benson 1999). Current velocity is the major determinant of microdistribution of some species, especially filter feeders, such as Hydropsychidae, Simuliidae, and the shrimp *Australatya striolata* (Smith 1987, Clayton 1995, Benson 1999). In the QWT, maximum species density per stone occurs with a moderate number of individuals, suggesting that competition for space at greater densities causes local elimination of some species (Pearson 2005). Species density is similar in QWT and temperate Victorian streams, but species accumulation continues over a greater number of stones in the tropics (Lake et al. 1994). Nestedness analysis showed that the species pool was randomly sampled from stones according to relative abundance of the fauna, and that this relationship held across seasons and sites (Pearson 2005). These results concurred with findings elsewhere regarding nestedness and habitat patchiness (Death and Winterbourn 1995, Heino 2005).

Long-term perenniality of streams and diverse terrain explain high regional (γ) diversity of fish in the QWT. The greatest diversity is in centrally located streams, which have the most reliable flows and most diverse fish habitat, and where some species are hydraulic-habitat specialists (Pusey et al. 2008, Donaldson et al. 2013). Intermittency increases

at the periphery of the QWT (Pusey et al. 2008, Kennard et al. 2010, Godfrey 2011) and diversity of fish, which depend on permanent pools as temporal refugia (Erskine et al. 2005, Perna and Pearson 2008), is lower.

Waterfalls are isolated habitats with a diverse specialized invertebrate fauna (Clayton 1995). Patches of high velocity are characterized by species of Simuliidae, moderate velocity by Hydropsychidae and Blephariceridae, and low velocity and splash zones by Pyralidae and beetles. Filter feeders (simuliids and hydropsychids) predominate, and grazers (blepharicerids and pyralids) exploit algal growth enhanced by gaps in the canopy and high flows. Floods overshoot waterfalls and provide connectivity between upstream and downstream via side channels and overland flow for some fish and crustaceans, and so cause less biotic disturbance in waterfalls than elsewhere in the stream (Clayton 1995). Given the small habitat area and disconnected nature of waterfalls, the application of standard stream disturbance/colonization theory may not be appropriate, and special conservation measures may be required.

Epilithic bryophytes, which can provide important habitat for invertebrates (Heino and Korsu 2008), are common in upland QWT streams. In Birthday Creek, they cover ~10% of habitat area and harbor an abundant fauna, especially early developmental stages (e.g., 32 families of invertebrates with total densities >117,000 individuals/m², 40× more than other substrata) (Wulf 1999). Invertebrates in bryophytes are resistant to experimental disturbance, and 30% of the assemblage was able to withstand high flow and abrasion, a percentage that is higher than that for rock-dwelling fauna (Rosser and Pearson 1995). Therefore, bryophytes contribute a small but possibly crucial 'nursery' habitat and flood refugium for invertebrates (Wulf 1999).

Resource partitioning and competition

Partitioning of habitat and food resources can promote diversity and is evident for a range of stream taxa globally (e.g., Townsend and Hildrew 1979, Wheeler and Allen 2003), including the QWT (Table 2). Both spatial and temporal partitioning occur in Chironomidae (Pearson et al. 1986). Habitat partitioning is distinct among many mayflies and odonates, in which overlapping preferences are moderated by differences in body or prey size (Hearnden and Pearson 1991, Charlton 1989). Partitioning of food resources occurs across the food web (Cheshire et al. 2005) and within some taxa. For example, different trichopteran shredders eat leaves in riffles, leaves in pools, or mostly woody material (Boyer et al. 2006). Lowland *Macrobachium* species are distributed according to physical variables but compete for preferred habitat (Kneipp 1979), and tadpole species outcompete each other in their preferred habitats (Trenerry 1988). Differentiation of diets occurs within fish families, such as the Terapontidae across tropical Australia, and ontogenetically within species (Davis et

Table 2. Resource partitioning demonstrated within various Queensland Wet Tropics (QWT) taxa. 'Comp' indicates taxa for which competition has been explicitly demonstrated.

Taxon	Resource	Variables	Comp	References
Chironomidae	Habitat	Current, substratum, seasonal change		Pearson et al. 1986, McKie 2002
Ephemeroptera	Habitat	Current, detritus, substratum		Hearnden and Pearson 1991
Odonata	Habitat	Current, detritus, substratum		Charlton 1989
Trichoptera shredders	Habitat, food	Riffle vs pool, leaf vs wood	✓	Boyero et al. 2006, Boyero and Pearson 2006
<i>Macrobrachium</i> (Decapoda)	Habitat	Temperature, salinity, current, substratum	✓	Kneipp 1979
Anura tadpoles	Habitat	Current, connectivity	✓	Trenerry 1988, Richards 2002, Cashins 2009
Fish	Habitat	Riffle specialists		Pusey et al. 2008, Donaldson et al. 2013
Fish	Food	Trophic guilds		Pusey et al. 1995, Perna 1996
Fish: Terapontidae	Food	Species and ontogenetic differentiation		Davis et al. 2012a, 2013

al. 2012a), and partitioning by fish trophic guilds is evident in sandy lowland streams (Perna 1996) but not in high-velocity forested streams (Pusey et al. 1995).

These relationships indicate that, like elsewhere, physical factors and species' interactions are both important in determining the local distribution of species and assemblage composition among QWT habitats (e.g., Townsend and Hildrew 1994, Thompson and Townsend 2006), and that fine division of niches enhances α diversity. Whether equable temperatures enhance interactions, such as competition, and so promote diversity is unknown. In addition to contemporary variables, phylogenetic history is important because it can determine ecological traits and present-day distributions. Thus, habitat use by QWT mayflies is partly dictated by their history, and partitioning aligns with phylogenetic lineages (e.g., *Koorrnonga* in pools, *Austrophlebioides* on stones) (Christidis 2003). In contrast, trophic radiation of terapontid fishes indicates no such constraints, possibly because of the ecological release afforded by fresh waters (Davis et al. 2012b). It would be useful to know whether species from other speciose taxa (e.g., Chironomidae, Helminthidae) are ecologically constrained by phylogeny.

Predation and disease

Top-down effects of predators can reduce prey abundances and influence behavior (Peckarsky et al. 1993) and, consequently, assemblage structure and dynamics. In the QWT, the number of species and biomass of predatory invertebrates, especially odonates, suggests a major influence on invertebrate assemblages (Cheshire et al. 2005) but, in high-density experimental treatments, their effect was equivocal (Burden 1998). Field experiments demonstrated little influence of the predatory fish *Mogurnda adspersa* on invertebrate prey density (Whitehead 1985). High biomass of predators may be sustained by high prey turnover, such that prey is not a limiting resource (Cheshire et al. 2005,

Jacobsen et al. 2008). Similarly, fish predation had only moderate effects on invertebrate communities in seasonal streams in Zimbabwe (Chakona et al. 2007), whereas in disconnected stream pools at the periphery of the QWT, predatory fish greatly altered the density and composition of communities and acted as keystone species (Smith 1982). Such disparities probably are caused by different fish densities and the open or confined nature of habitats.

Predators can have less direct influences on assemblages. For example, the presence of an ambush predator (Polycentropodidae) reduced adult body and oocyte size of a riffle-inhabiting chironomid but not of a pool-inhabiting species, whereas the presence of the chironomid predator *Australopelopia* had no effect on development of one prey species, but caused another to have a shorter pupal duration and to emerge with smaller oocytes (McKie and Pearson 2006). These results correspond with differences in the threat posed by the predators to the prey species in situ (McKie 2002). The presence of fish predators also had indirect effects via chemical cues on shredder behavior, and reduced activity and slowed leaf litter breakdown (Boyero et al. 2008).

Effects of large predators, such as the eel (*Anguilla reinhardtii*) and platypus in small streams have not been quantified. Small eels feed on insects, then switch to larger prey as they grow (Hortle and Pearson 1990). The effect on assemblages of one or more mid-sized eels in riffles and a large eel (~1.0 m) in each pool can be substantial (Cheshire et al. 2005). Platypus reside in medium-sized upland streams and move among smaller streams in their home range (RGP, unpublished data). They are voracious feeders on invertebrates (Faragher et al. 1979) so their local influence may be important. Kingfishers (*Alcedo* spp.) are sparsely distributed and may have minor effect on stream assemblages (RGP, unpublished data). In larger streams, fish are the most common predators (Rayner et al. 2010). However, freshwater crocodiles (*Crocodylus johnstoni*), which feed on invertebrates, fish, and other small verte-

brates (Webb et al. 1983), occur in some upper reaches of larger rivers, and estuarine crocodiles (*Crocodylus porosus*), which feed on invertebrates, fish, and larger vertebrates (Taylor 1979), occur in the lower reaches of many streams, as do many predatory bird species, with unknown but possibly great effect (cf. Steinmetz et al. 2003).

Parasitism and disease can be important factors affecting biodiversity (Daszak et al. 2000), and great impact can follow novel introductions (Stewart 1991). Stream-dwelling frogs have a depauperate helminth fauna with minor effects (Barton and Richards 1996), but have suffered global population declines following the spread of the fungus *Batrachochytrium dendrobatidis* (McDonald and Alford 1999). Eight low-fecundity, stream-breeding species have been affected in the QWT. Some have disappeared but others are recovering, especially at lower altitudes and at rainforest edges, where they do not develop the disease (Williams and Hero 1998, McDonald and Alford 1999, Woodhams and Alford 2005, Puschendorf et al. 2011). This pattern indicates intolerance of higher temperatures by the fungus, as does survival only at lower altitudes of normally widespread species (McDonald and Alford 1999). The ecosystem effects of loss of frogs and tadpoles in the New World include shifts in ecosystem processes (e.g., Whiles et al. 2013), which highlights the need to understand more about the effects of parasites and disease that influence fresh waters (Strayer 2010).

Therefore, predation and disease can have various levels of control of assemblages. They appear to be influenced by high temperature and productivity, but these interactions have not been quantified. Major competition between predators occurs elsewhere (e.g., Kohler 1992, Elliott 2003), but has not been demonstrated in the QWT, and partitioning of resources appears to be confined to prey size selection (Whitehead 1985, Burden 1998), but further studies of predation are warranted.

Habitat disturbance, movements and migrations

Flow disturbances Flow disturbances (flood, drought) have major structuring influences on stream faunas (e.g., Lake 2000, 2003, Peckarsky et al. 2014). Disturbance effects on QWT stream assemblages were hypothesized to be greater than on, e.g., streams fed by snowmelt because of the unpredictability and intensity of tropical storms (Rosser and Pearson 1995, Boulton et al. 2008). However, floods resulting from tropical storms are perhaps less severe than the daily spates experienced by equatorial streams (Yule and Pearson 1996). The usual hydrological cycle in the QWT includes high flows and frequent floods in the wet season, with lower base flows in the dry (e.g., Karim et al. 2011). Wet-season spates in small streams cause patchy disruption of substrata and litter packs, whereas occasional large floods shift and scour substrata and remove litter. In the dry season, diminishing flows lead to contraction of

habitats and increased litter retention (Pearson 2005). Regular spates reduce invertebrate abundance, but not α diversity because they facilitate coexistence of rarer species (Rosser and Pearson 1995, Rosser 1998). The pool fauna is more resistant than riffle fauna to disturbance, so pools may be important flood refugia. Recovery of invertebrate assemblages after experimental patchy disturbance typically was complete within 24 h, indicating high resilience through rapid redistribution (Rosser 1998). More extensive disturbance led to slower recovery, with recolonization depending on movement from refugia, such as pools and mosses (Wulf 1999), and egg laying by terrestrial adults (Pearson 2005). Artificial turf, used to simulate bryophyte habitats, was colonized rapidly, with richness and abundance of invertebrates achieving natural levels in <2 wk (Wulf 1999).

Faunal resistance to disturbance varies among sites depending on the historical pattern of disturbance, which provides a strong selective force (Rosser 1998). Differences between wet- and dry-season assemblages vary with the magnitude of floods, and variation in assemblage structure among stones is highest in drier years, a result suggesting more intense biotic interactions in the absence of disturbance and with the reduction of habitat area (Rosser 1998). Despite severe wet-season disturbance, persistence was high over several years at Birthday Creek, as reported for temperate streams (Hildrew and Giller 1994), though less so for Yuccabine Creek after long-term habitat changes (Pearson 2005).

In lowland streams, floods replenish backwater habitats but disturb substrata and remove macrophytes, thereby causing dietary shifts in fish by influencing habitat structure, food availability, and productivity (Rayner et al. 2008, 2010). In small streams at the edge of the QWT, changes in the fish assemblages were greater following a 1-in-18-y flood than a 1-in-1-y flood. In both cases, assemblage structure recovered, but recovery was more rapid after the smaller event (Perna and Pearson 2008). Thus, stream fish assemblages also show high resilience to flood disturbance, presumably because nonresilient species have been filtered out over time.

Drought Drought has major effects in stream systems (e.g., Bond et al. 2008), but has received less attention than flood in the QWT. Drought expels or excludes obligate lotic species at least temporarily, but provides the stimulus for eventual recovery, driving dynamics of affected systems (Pearson et al. 1986). Peripheral QWT streams that regularly dry to isolated pools have distinct faunas (Smith and Pearson 1987) or subsets of regional faunas (Perna and Pearson 2008).

Movements and migrations Approximately 35% of QWT freshwater fishes are obligate catadromous or opportunistic

marine species, so natural and anthropogenic barriers to movement and distance from the sea strongly influence assemblage composition (Pearson et al. 2010). *Anguilla reinhardtii* is the only fish to traverse whole river systems from the ocean to headwaters because it can negotiate many barriers. Some species are less mobile. For example, genetically distinct populations of *Craterocephalus stercusmuscarum* are separated by waterfalls, reflecting the influence of landscape history on populations (McGlashan and Hughes 2000). Similarly, high levels of genetic differentiation of shrimp (*Caridina zebra*) populations in the Tully catchment indicate that movement is locally limited, whereas less differentiation in the Herbert catchment and similarity of animals between Herbert and adjacent Tully streams suggest past stream capture (Hughes et al. 1996). The crayfish *Cherax cairnsensis* is resident in stream pools (Coughlan 1990), whereas several shrimp species undergo cyclical short or long migrations (Kneipp 1979, Smith 1987). Invertebrate drift is highest in the wet season and accounts for 100% of recolonization. In the dry season, colonization is increasingly effected by upstream migration, with up to 27% compensation for drift (Benson and Pearson 1987). Distances travelled by drifting invertebrates are short, and most riffle animals spend their aquatic stages in their home riffle (Benson and Pearson 1987), as suggested by genetic differentiation among local populations in southern Queensland (Bunn and Hughes 1997). In the QWT, dispersal ability, or lack thereof, clearly continues to play a part in species' distributions, creating assemblages that include endemics, species of limited distribution, and widespread species. Again, these results support the proposition that both neutral and deterministic factors are important influences on assemblage composition (Thompson and Townsend 2006).

Knowledge of the dispersal patterns of taxa and stream connectivity is important in determining the possible effects of environmental change at different scales. For example, dams can impede the crucial breeding migrations of species, or flooding of barriers might facilitate mixing of otherwise distinct populations. Therefore, we need to know more about life cycles of multiple taxa. Nevertheless, we already know that some QWT taxa use a large proportion of the stream profile (e.g., eels and shrimps), demonstrating that streams must be managed in their entirety.

Food webs and ecosystem function Food webs and ecosystem function have been an important focus of global stream research (e.g., Webster and Benfield 1986, Schmid-Araya et al. 2002, Boyero et al. 2012b). Research in the QWT has been done to test whether temperate models of materials inputs, processing, and pathways apply in the tropics, especially given the higher temperatures and litter diversity there (Table 3). As in the temperate zone, in heavily shaded QWT streams, allochthonous detritus is the main

input to the food web (Pearson et al. 1989, Nolen and Pearson 1993, Benson 1999, Cheshire et al. 2005), but in the QWT and elsewhere, both shaded and open streams can have substantial algal production (Bunn et al. 1999, Brito et al. 2006, Davies et al. 2008, Lau et al. 2009), which is consumed by tadpoles, crustaceans, and insects in the QWT (Trenerry 1988, Clayton 1995, Douglas et al. 2005). Many species of invertebrates are dietary generalists, but predators and shredders are prominent in terms of biomass and species richness in small streams (Cheshire et al. 2005). Plant litter entering QWT streams is very diverse compared with temperate streams (e.g., 81 species from one reach; Bastian et al. 2007), reflecting riparian diversity. Leaf fall continues throughout the year but peaks in the late dry season ('spring') (Benson and Pearson 1993, Coughlan et al. 2010).

Litter is consumed by shredders, which can comprise ~20% of the invertebrate α diversity in QWT streams (cf. world average of 11%) (Cheshire et al. 2005, Coughlan et al. 2010) and are important contributors to decomposition (Pearson et al. 1989, Coughlan 1990, Nolen and Pearson 1993). QWT shredder abundance was thought to be unusual because of a reported dearth of shredders in the tropics (e.g., Dudgeon and Wu 1999, Dobson et al. 2002), but it appears that shredder assemblages in tropical streams vary globally (Camacho et al. 2009, Yule et al. 2009, Boyero et al. 2011a, 2012b, 2014). The disparity may be caused by failure to identify shredders, which can include taxa that are not shredders in temperate streams (Boyero et al. 2012b), or by variability among tropical streams, possibly resulting from temporal patchiness caused by spates (Boyero et al. 2015a).

Leaf litter is a patchy resource where competitive interactions are likely to occur, especially in the dry season, when habitats contract and invertebrates congregate on limited resources (Boyero and Pearson 2006, Bastian et al. 2008). Positive interactions also may occur. For example, insect shredders facilitate leaf processing by tadpoles (Iwai et al. 2009). Shredders select more palatable leaf species, e.g., 38 of the 81 species in Birthday Creek (Bastian et al. 2007). Leaves become more palatable with conditioning (Webster and Benfield 1986, Bastian et al. 2007, Boyero et al. 2007), but green leaves also are consumed in the QWT, especially after major storms when most litter and invertebrates are washed away and new litter fall is green (Nolen and Pearson 1993, Coughlan et al. 2010). Shredders vary in their processing capabilities, so species identity is more important than richness in determining breakdown rates (Boyero et al. 2007) as elsewhere (Jonsson et al. 2002). The effect of loss of particular species on ecosystem functioning can be equal to or greater than the direct effect of substantial temperature change (Boyero et al. 2011b, 2014).

Headwater streams are often nutrient limited (Fisher and Likens 1973). In the QWT, nutrient enrichment, especially PO_4^{3-} , enhanced abundance, but not diversity, of the invertebrate assemblage and physiological condition of the

Table 3. Characteristics of litter inputs and shredders in Queensland Wet Tropics (QWT) streams, and contrasts with temperate streams. CPOM = coarse particulate organic matter. FPOM = fine particulate organic matter.

Pattern/process	Characteristics	Contrast	Reference
Litter fall	All year, spring peak	Less seasonal, timing	Benson and Pearson 1993
Litter characteristics	Diverse, varied palatability, often green	Greater diversity	Nolen and Pearson 1993, Bastian et al. 2007
Litter accumulation	Pools, riffles partly; stored as CPOM > 1 mm; removed by floods	Year round, spring peak, summer flush	Pearson et al. 1989, Benson 1999
FPOM	Continuously produced; exported from riffles	Less seasonal	Benson 1999
Shredder characteristics	High diversity and biomass for tropics	More spp. than global mean	Cheshire et al. 2005, Coughlan et al. 2010
Shredder taxa	Decapoda, Leptoceridae, Calamoceratidae, Leptophlebiidae, Chironomidae	No Plecoptera or Amphipoda	Cheshire et al. 2005
Shredder leaf preferences	Strong selection; conditioned leaves; also green leaves	Comparable, except green leaves	Nolen and Pearson 1993, Bastian et al. 2007, Boyero et al. 2007, Coughlan et al. 2010
Shredder abundance	Greatest in dry season (winter–spring)	Not in ‘autumn’	Cheshire et al. 2005
Shredder interactions	Competition, facilitation	Comparable	Boyero and Pearson 2006, Bastian et al. 2008, Iwai et al. 2009
Shredder partitioning	By habitat, diet, and size	? comparable	Boyero et al. 2006, Kobayashi and Kagaya 2004
Nutrient effects	P enhances breakdown and shredder condition via microbial pathway	Comparable	Pearson and Connolly 2000, Connolly and Pearson 2013

shredder *Anisocentropus kirramus* (Pearson and Connolly 2000, Connolly and Pearson 2013). The PO_4^{3-} supplement was transmitted via the microbial pathway, resulting in higher nutritional quality of leaves, enhanced shredder condition, and fine detrital food for other invertebrates.

Lowland fish-dominated food webs are complex, with many weak trophic links, but a few strong links that account for most energy transfer from basal sources (Rayner et al. 2010). Foodweb structure is seasonally stable but variable at smaller scales, and wet-season flooding causes dietary shifts in fish by regulating in-stream productivity, habitat structure, and food availability.

Thus, ecological complexities of QWT streams are indicated by the interplay of biophysical factors, microbial function, species diversity and identity across trophic levels, sources of productivity, and species interactions (cf. Silveira and Moulton 2000, Wantzen et al. 2008). Temperate streams differ in seasonality and diversity, but temperate models of materials flow, species redundancy, and nutrient limitation still apply in the QWT. However, models including algal production, top predators, and decapods must be developed. More work is necessary across diverse systems to develop clearer understanding of ecosystem function, including quantification of detrital budgets and productivity through stream networks, their interactions with biophysical processes, including anthropogenic impacts, and with explicit tests of current ecosystem models (Boulton et al. 2008).

Life cycles and community dynamics

In northern temperate streams, life cycles tend to be highly seasonal, whereas southern temperate and tropical species may be seasonal or multivoltine, year-round breeders with short generation times (Campbell 1986, Yule 1993, Boulton et al. 2008, Jacobsen et al. 2008). In the QWT, equable temperatures allow many insect species to breed through the year, although breeding intensity varies seasonally, with greatest emergence in summer (Godwin 1981, Benson and Pearson 1988, Nolen and Pearson 1992), unlike equatorial aseasonal life cycles (Yule 1993, Yule and Pearson 1996). Large mayflies (e.g., *Jappa* spp.) are univoltine, but their mature nymphs are present only in early summer (Godwin 1981). Some odonate species in Birthday Creek require 1 to 2 y to complete larval development, so temporal overlap among these predators is substantial (Charlton 1989).

Most *Macrobrachium* shrimp species undertake short spawning migrations between streams and estuaries (Kneipp 1979), but *A. striolata* shrimp make longer journeys. Adults live in upland streams where, in the wet season, they release zoea larvae, which drift downstream, living on their yolk for up to a month (Smith 1987). They develop in estuaries then return as males to small streams to breed. After 1 or 2 y,

they double in size, change sex, and breed as females, completing the cycle. They occur ≥ 160 km from the sea (Yucabine Creek), but are absent from more distant streams (e.g., Birthday Creek, ~ 500 km from the coast; Fig. 2) (Smith 1987). Therefore, like eels, these shrimp use the entire length of many streams.

Temporal changes in flow, habitat, and food availability may lead to alternating importance of abiotic and biotic factors (Rosser 1998, Pearson 2005). During the variable flows of the wet season, the stone fauna may be dominated by obligate lotic species, such as *Simulium* spp., whereas chironomids predominate when flow declines in the dry season (Rosser 1998). Abiotic processes dominate in the wet season, but in the dry season, contraction of streams and continuing breeding of invertebrates increase densities, and increasing species' interactions have a greater influence on small-scale assemblage structure (Pearson et al. 1986, Pearson 2005). Over a 14-y period (1981–1995) in Yucabine Creek, the most abundant feeding groups shifted from collector–gatherers to filterers (Leptophlebiidae to Hydropsychidae) and from one set of surface scrapers to another (Helicopsychidae and Anura to Psephenidae), accompanied by a decline in some predators (Eustheniidae). Local factors, mainly cyclone-driven canopy loss, were responsible for these changes (Pearson 2014). This temporal patchiness contrasts with the greater consistency of discharge and invertebrate persistence in Birthday Creek and in equatorial streams, in which almost-daily spates maintain constant physical conditions (Yule and Pearson 1996).

Stream-dwelling frogs are seasonal breeders, and spawning takes place throughout the summer. Tadpoles have life-spans up to 12 mo, but most species decline in abundance after the wet season, and development is arrested in winter (Trenerry 1988, Richards and Alford 2005). Fish life cycles are seasonal with variable timing, but some species are opportunists that respond quickly to appropriate conditions and are prevalent in hydrologically variable streams (Olden and Kennard 2010, Godfrey 2011). Gudgeons in small forested streams and some lowland species breed just before the onset of the wet season, whereas others breed in the dry or late wet seasons, depending on their susceptibility to floods or the availability of postflood habitat (Whitehead 1985, Pusey et al. 2002, Godfrey 2011). Some species are diadromous. For example, eels breed near New Caledonia, and the Jungle Perch (*Kuhlia rupestris*) breeds in estuaries before returning to forest streams (Pusey et al. 2004), and the sport fishes, Barramundi *Lates calcarifer* and Mangrove Jack *Lutjanus argentimaculatus*, have marine larvae, as do the Cling Gobies (*Stiphodon* spp., Gobiidae) that inhabit small coastal streams (Thuesen et al. 2011). This behavior restricts these species, apart from the eel, to reaches downstream of hydraulic barriers.

Given the diversity of the QWT biota, the limited number of autecological studies (life cycles, ecophysiological re-

quirements, etc.) is an important gap in our understanding of stream ecology. In particular, the biology of plant species, microbes, and disease organisms are areas needing substantial research effort, as are further comparative studies within invertebrate and vertebrate taxa (e.g., Christidis 2003, Davis 2012b), to facilitate development of more comprehensive ecological models. More attention also should be directed toward the interactions of body size and abundance in descriptive models; e.g., some species may be numerically scarce (e.g., eels, platypus, crayfish, and odonates), but dominant consumers (Cheshire et al. 2005).

ANTHROPOGENIC IMPACTS AND THREATS

Most remaining upland forests have been protected from major direct human impact except selective logging (terminated with World Heritage listing in 1988), but the floodplains and table lands have been cleared for sugar-cane growing, cattle grazing, horticulture, and plantation forestry. The streams draining these areas, including the larger QWT rivers, are not in reserves (Januchowski-Hartley et al. 2011). Land management and waterborne contaminants have received substantial research effort because of their potential effects on the GBR (e.g., Brodie et al. 2009), but research on freshwater ecosystem values and issues have received less attention (WTMA 2013, Pearson et al. 2013). Human impacts on rivers are diverse (Table 4) and may be exacerbated by the tropical climate, including high rain intensities, frequent floods, and high insolation (Pearson et al. 2003, Connolly and Pearson 2004, Karim et al. 2011).

Water quality

Damage from agriculture- and mine-derived sedimentation is a global phenomenon (Wood and Armitage 1997) and is evident in many QWT waterways (e.g., Connolly et al. 2007a). Recolonization and density of an upland invertebrate assemblage were reduced in experimental treatments with high suspended sediments, but a lowland assemblage with a history of exposure to high sediment loads showed some resistance by surviving for 15 d in treatments with high suspended sediments (Connolly and Pearson 2007). However, sediments from mining operations reduced α diversity of fish and invertebrates in the Annan River, suggesting that resistance was not sustained in the longer term (Hortle and Pearson 1990, RGP, unpublished data).

Nutrient concentrations in QWT streams are low (Pearson and Connolly 2000), so even apparently small impacts, such as recreational swimming, can be detected (Butler et al. 1996). Agricultural drainage has substantially raised concentrations of nutrients and suspended solids in streams (Bramley and Roth 2002). NO_3^- concentrations, especially, have increased with the proportion of the catchment under agriculture (Connolly et al. 2007a, Mitchell et al. 2009). Nutrient supplements lead to increased algal growth where

sufficient light and suitable substrate are available and have localized effects on the invertebrate fauna (Connolly et al. 2007a). Enhanced PO_4^{3-} concentrations increase invertebrate productivity and condition, but not diversity, in light-limited forested streams (Pearson and Connolly 2000, Connolly and Pearson 2013). NH_3 in fertilizer runoff is variably toxic to aquatic biota. For example, Barramundi is more sensitive than the small Eastern Rainbowfish (*Melanotaenia splendida*) and has toxicity values comparable to salmonids (Økelsrud and Pearson 2007), results indicating that tropical fish can be at least as sensitive as temperate species (Kwok et al. 2007). Similarly, the atyid shrimp, *Caridina nilotica*, is highly sensitive to NH_3 , as are temperate New Zealand atyid species (Richardson 1997, Økelsrud and Pearson 2007).

Organic inputs cause hypoxia through enhanced bacterial respiration, with subsequent loss of hypoxia-intolerant fauna (Hynes and Pentelov 1978). Sugar-mill effluents have similar effects in the QWT (Pearson and Penridge 1987), and hypoxia caused by organic runoff from sugar-cane fields is a major problem in some slow-flowing waterways (Pearson et al. 2003). Many taxa tolerate some hypoxia. For example, many invertebrates tolerated all but the lowest dissolved O_2 concentrations ($\leq 10\%$ saturation) in mesocosms for 5 d, but with reduced emergence in treatments of 10–35% saturation (Connolly et al. 2004). Mayflies were sensitive, with lethal effects at 20% saturation for several species, whereas mortality of some Chironomidae occurred only below 8% saturation. Barramundi and Rainbowfish tolerate cycling hypoxia, but respiratory responses commence at moderate concentrations (50% saturation). The most tolerant life-history stages are those that are naturally exposed to hypoxia (Pearson et al. 2003, Flint et al. 2015). However, many animals tolerate short-term hypoxia, probably because of its occasional natural occurrence, but resistance is apparently not long-lasting because chronic contamination (e.g., by organic discharge or run-off) has major negative effects (Pearson and Penridge 1987, Pearson et al. 2003).

Little information is available on the effects of agricultural pesticide residues, which are prevalent in lowland QWT waterways (Pearson et al. 2013), apart from a study in which the authors demonstrated acute toxicity of the herbicide Diquat to *C. nilotica* (Kevan and Pearson 1993). This knowledge gap is worrisome, given the impact of these pesticides on the GBR (Jones et al. 2003).

Invasive species

Alien species cause major problems, including disruptions to geomorphology, habitats, and primary production by invasive plants and to food webs by exotic fish (Strayer 2010). Invasive plants are a significant problem in QWT streams. For example, beds of para grass (*Urochloa mutica*), facilitated by loss of riparian shade in agricultural

Table 4. Anthropogenic effects on Queensland Wet Tropics (QWT) streams. 'Tropical effect' indicates where tropical climate exacerbates the impact; '?' indicates possible effect for which there is little evidence currently.

Stressor	Cause	Ecosystem effect	Biotic response	Tropical effect	Reference
Sedimentation	Agriculture, mining	Habitat loss	Reduced abundance, species loss		Hortle and Pearson 1990, Connolly and Pearson 2007
Nutrients	Agriculture	Plant and microbial productivity enhanced; NH ₃ toxicity; hypoxia	Enhanced secondary productivity; species loss	✓	Pearson and Connolly 2000, Connolly and Pearson 2013, Connolly et al. 2004, Økelsrud and Pearson 2007
Dissolved organic input	Human recreation	Algal growth	? change in species	? ✓	Butler et al. 1996
Invasive plant growth	Agriculture, sugar mills, habitations	Microbial productivity, hypoxia	Species loss	✓	Pearson and Penridge 1987, Connolly et al. 2004
Pesticides	Agriculture	Habitat destruction, hypoxia, barriers	Species loss	✓	Pearson et al. 2003, 2013, Connolly et al. 2004
Change in flow, temperature rise	Water abstraction	?Toxic impacts	? species loss		Kevan and Pearson 1993
Barriers	Infrastructure	Changes in habitat, breeding triggers	? species loss		Arthington et al. 1994, Brizga et al. 2000
Invasive fish	Introductions, translocations	Reduced connectivity	? species loss		Lawson et al. 2010
		? change in assemblages	? native species loss	? ✓	Burrows 2002, 2009, WTMA 2013

landscapes, cause stream narrowing and deepening (Bunn et al. 1998), fill in small streams, and block fish movements (Pearson et al. 2007, Pearson and Stork 2008). Para grass, like sugar cane, is not assimilated into the food web, so the normal inputs of riparian leaf litter are replaced by unpalatable grass (Bunn et al. 1997). Furthermore, nonnative trees, which can invade disturbed riparian zones, also may have unpalatable leaves (Boyero et al. 2012a). Loss of normal allochthonous input can reduce invertebrate α diversity even in streams where algae are productive (Connolly et al. 2007b).

Invasive animals in the QWT include feral pigs, which disturb stream sediments and fauna (Mitchell and Mayer 1997), and exotic fishes, mainly Cichlidae and Poeciliidae (Webb 2003), which may pose a threat to species of high conservation value (WTMA 2013). Most upland QWT streams have few fish species because of natural barriers to movement. This situation has prompted fish introductions to some streams, potentially changing their natural communities (Russell et al. 2003, WTMA 2013). These introductions are one of the few processes currently impinging upon stream integrity in the protected area (WTMA 2013). Cane toads (*Rhinella marina*) were introduced to Australia in 1935 and can breed in QWT streams. They are toxic to many snakes, and are implicated in the decline of some species, but other species (e.g., keelback, *Tropidonophis mairii*) consume toads without dying (Llewelyn et al. 2010). Toxicity of cane toad tadpoles increases ontogenetically, but some crayfish and dytiscid beetles can consume all stages without ill effect (Crossland 1998).

Water infrastructure and abstraction Water infrastructure has huge ecological impacts globally (e.g., Fearnside 2001). In the QWT, water is abstracted from aquifers, streams, and impoundments and supplies irrigation, power generation, aquaculture, tourism, and domestic users, but ecological effects are largely unstudied. Impoundments have caused the loss of terrestrial and stream habitats, but most are in small catchments, so impacts on stream flow, water quality, animal movements, and biodiversity may be minor. However, dams on the Tully and Barron Rivers are managed partly for power generation and whitewater rafting, and deleteriously affect river temperature and fish spawning (Arthington et al. 1994). Smaller structures (culverts, control devices) may be barriers to movement because they are often too shallow or have too strong a current for animals to negotiate. Lawson et al. (2010) identified 5536 potential barriers to fish passage in the QWT in a stream network of 19,764 km, but the number of possible barriers is much higher because only structures >50-m wide were included.

Major interbasin transfers have not occurred, fortunately, given the number of endemic species and genetic separation of many populations. However, drainage works on

floodplains have caused channelization, loss of riparian vegetation, and exposure of acid-sulfate soils, leading to high levels of acidity. All of these effects have reduced biodiversity in some floodplain streams (Powell and Martens 2005, Pearson et al. 2003).

Climate change

Climate models suggest that precipitation in the QWT will become more seasonal, with longer dry seasons, shorter wet seasons, and more intense cyclonic winds and rain (James et al. 2013). Climate change over the last 100,000 y has affected distributions of some stream invertebrates (Pearson 2005), and assemblages vary according to the permanence of streams. Streams in the central QWT are perennial but, at the periphery of the region, surface flow ceases during the dry season. This flow gradient directly influences assemblage composition (Connolly et al. 2008, Perna and Pearson 2008), so increased seasonality and rising temperature, causing loss of cloud capture and up to 70% of dry-season precipitation (McJannet et al. 2007), will reduce the number of perennial streams. Many Australian freshwater fish species are adapted to unpredictable flows, which might possibly confer resistance to climate impacts (Morrongiello et al. 2011), but in the QWT, many species depend on perennial flows (Pusey et al. 2000, 2008). Therefore, climate change threatens the persistence of fish species, especially those with limited ranges or specific habitat requirements, and obligate lotic invertebrates, such as blepharicerid larvae and *Kirrara* nymphs (Ephemeroptera) (Clayton 1995, Christidis 2003). Concurrently, rising sea levels will encroach on already-limited large-river habitat. Rising temperatures will eventually eliminate some core habitats (e.g., mountain-top cool refugia), causing extinctions of associated species (e.g., endemic *Euastacus* crayfish), and will influence key processes, such as litter decomposition, directly and, potentially, through species loss (Boyero et al. 2014).

CONSERVATION STATUS AND MANAGEMENT

The QWT has had substantial protection relative to much of Australia, and most upland streams and some coastal freshwater wetlands are protected in World Heritage areas and national parks. However, larger streams are short, provide limited large-river habitat, are affected by agriculture, and are unprotected (Pearson and Stork 2008, Januchowski-Hartley et al. 2011). The major challenge for conservation of the QWT is to maintain both production and conservation values of off-reserve lands (Pearson and Stork 2008). Management activities to alleviate impacts have included environmental flow guidelines (Brizga et al. 2000), best-practice farming (stock access to streams, harvesting protocols, and fertilizer application), improved effluent discharges (e.g., Greenaway 2005), stream-bank stabilization (Kapitzke et al. 1998), and riparian tree plant-

ing (Tucker and Murphy 1997), mostly with a view to reducing contaminant input to the GBR (Brodie et al. 2009), but streams are still contaminated by organic material and nutrients (Pearson et al. 2003, Connolly et al. 2007a). Changes in the climate and associated agriculture may bring new problems. Restoration of riparian vegetation would improve stream ecosystem health (Pusey et al. 2008), but even intact riparian zones do not protect QWT waterways (Connolly et al. 2007a). Little can be done regionally to avert the effects of climate change, but other issues, such as habitat damage, pollution, and invasive species could be addressed to improve the long-term resilience of ecosystems (Pearson and Stork 2008).

Management of fresh waters in their own right has been limited and somewhat piecemeal, but some initiatives, such as the creation of catchment groups, Natural Resource Management bodies, and Water Quality Improvement Plans, have had positive outcomes (Terrain 2013). Many lowland systems are still in poor condition because of weed invasions and agricultural runoff, whereas others are partly protected by strong flows and dilution (Pearson and Stork 2008, Rayner et al. 2008, Pearson et al. 2013). A huge challenge is for researchers and managers to find cost-effective ways to reduce agricultural contaminants, invasive species, and complex interactions (e.g., riparian loss plus fertilizer promotes weed growth, requiring herbicide treatment).

CONCLUSION

The value of regional studies, including our research on QWT streams, is their contribution to broader comparative studies and their usefulness for testing prevailing theory via their detailed examination of ecological patterns and processes. Such studies have demonstrated that paradigms developed in temperate regions may or may not be applicable in the tropics. Moreover, just as no single temperate stream type exists, tropical streams exist in great variety (Boulton et al. 2008, Boyero et al. 2009). Even in apparently well studied regions, such as the QWT, major gaps in basic ecological knowledge and its application provide a possible agenda for future research (Table 5). Addressing some of these gaps may be facilitated by new technology, such as analysis of environmental DNA applied to research on biodiversity, community ecology, and human impacts on aquatic ecosystems (Thomsen et al. 2012).

The ecology of QWT streams is influenced by their physical longevity and biogeographic isolation, seasonal but perennial flows, consistent solar radiation that sustains biological processes through the year, high diversity of riparian vegetation and stream biota, complex food webs dominated by predators, and multiple anthropogenic disturbances. Many of these characteristics apply elsewhere in the tropics, and although biological processes may not differ qualitatively among regions, they may differ quantitatively under these varying influences (Boulton et al. 2008). For example, for the QWT Ephemeroptera, ancient biogeographic his-

tory has provided a mainly Gondwanan fauna, but subsequent biogeographic and evolutionary processes have resulted in speciation (Christidis 2003, Connolly et al. 2008); phylogeny, adaptation, and competitive mechanisms have determined habitat use (Christidis 2003, Hearnden and Pearson 1991); equable temperatures and year-round organic production have facilitated continuous reproduction (Godwin 1981, Benson 1999); a resilient fauna has resulted from flood disturbance (Rosser and Pearson 1995, Rosser 1998); and anthropogenic impacts have impinged on mayfly occurrence (Pearson and Penridge 1987, Connolly et al. 2004). Thus, for mayflies, differences between the QWT and elsewhere are consequences of biogeography, flow regime, and latitude (insolation). The same applies to stream fish (Pusey et al. 2008), and probably to other taxa.

We asked whether streams of the QWT are, like their terrestrial environment, remarkable. The biophysical characteristics of QWT ecosystems occur elsewhere in the tropics, but their interactions with the current species pool do not. The insular nature of the QWT is noteworthy—it is a humid forested island surrounded by dry lands and the sea on the driest inhabited continent that also has been long separated from other continents. Its remnant ‘ark’ nature is remarkable because it is the last bastion of what were once widespread humid tropical forests in Australia. These features have contributed to extinctions (Williams and Pearson 1997) and to speciation (e.g., Christidis 2003, Ponniah and Hughes 2006, Pusey et al. 2008). Thus, the QWT can be regarded as something of an evolutionary and ecological experiment, which, not surprisingly, has produced regional differences. The invertebrates have unique diversity at the species level, but higher taxa are essentially Gondwanan or cosmopolitan; the fish are unusual in being dominated by marine-derived families (as in most of Australia), with greatest diversity in the QWT and with radiation paralleling freshwater fish elsewhere (e.g., Davis et al. 2012b). Ecological patterns and processes mirror those of comparable systems elsewhere. Although the QWT appeared unusual in its abundance of shredders (Cheshire et al. 2005), other work has shown that shredders also are abundant in other tropical streams (Boyero et al. 2012b). However, the QWT might be unusual in its prevalence of predators (Cheshire et al. 2005). No doubt a case could be made for the distinctiveness of streams in other regions, particularly those isolated biogeographically over a long period.

Our review supports the view that comparisons of tropical and temperate models may be more an issue of ensuring suitable biophysical comparability than of latitude, as is the case within bioregions (Boulton et al. 2008). It also suggests that variation within the tropics must be better understood before we can explain apparent inconsistencies among tropical stream ecosystems (Boyero et al. 2009, 2015b). Regional tropical systems have their own identities, and their ecology is characterized by complex interactions and variability that are unlikely to be captured adequately by simple generalizations, especially because we have insuf-

Table 5. Examples of research gaps and needs for understanding and management of Queensland Wet Tropics (QWT) stream ecosystems.

Research area	Questions regarding . . .	Examples
Biogeography, evolution Biophysical environment	Species descriptions, cryptic species More explicit interactions with biota and processes Typology of streams and habitats	Microbes to vertebrates Climate, lithology and autecology, synecology; climate refugia, resilience, adaptation Evolution, ecosystem function, dispersal Ecological models of whole streams vis à vis stream and habitat types
Autecology	Life cycles, ecological requirements: plants, microbes, invertebrates; vertebrate (top predator) ecology	Key taxa, redundancy; phylogenetic constraints; role of rare species; role of animal size; ontogenetic variability; biophysical requirements, flexibility, resilience; drivers of diversity in aquatic vs terrestrial stages
Communities	Biodiversity	Predator–prey interactions, predator diversity effects; top-predator influence; diversity within and across trophic levels; diversity and efficiency of food webs; habitat, diversity-explicit models for whole streams; influence of decapod crustaceans; influence of disease
Ecosystems	Ecosystem function	Biomass vs productivity; productivity, decomposition through stream network; ecosystem model development/testing
Anthropogenic stressors	Responses to interactions between stressors	Temperature, contaminants, disease; nutrients, light, productivity; shade, nutrients, weeds, herbicides, toxicity; hypoxia and herbicides
	Invasive species effects Ecosystem effects of loss of species Water abstraction	Plants: habitat, food webs; fish: predation, competition, disturbance Vulnerable species, e.g., frogs, crayfish; species' functional redundancy Loss/change of habitat and species; loss of connectivity/reliability
Management, policy	Conservation actions and priorities Stressor mitigation Management effects Improving research uptake	Stream types; targets and surrogates; climate refugia, mitigation, species transfers 'Best-practice' outcomes and improvements; control of invasive species Cost-effective weed, nutrient, pesticide control; species, assemblage, process thresholds Land and water: policy, management

ficient information to assess whether the variability is systematic (e.g., by region, realm, or stream type). Stream ecosystems in the QWT are characterized by their biogeographic and climatic templates; i.e., their biodiversity and their 'tropicalness'. Further comparative regional studies are needed to enhance general understanding, if not general models, of ecosystem patterns and processes in the tropics and globally, and are vital to informed, effective management in perpetuity.

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